

Adaptive, pre-adaptive and non-adaptive components of radiations in ancient lakes: a review

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Abstract

Ancient lakes are ideal model systems for evolutionary studies, as they hold hundreds of endemic species. The vast majority of these still occur in the cradle of their origin. We distinguish three different modes of speciation (allo-, para- and sympatric) which have occurred in these habitats. Although radiations from ancient lakes are generally assumed to be adaptive, we cannot fully support this point of view, because non-adaptive radiations also appear to be common, for example through chromosomal changes, hybridization or sexual selection. Even in supposedly adaptive cladogenesis, e.g. as concerns the presumed trophic adaptations of cichlid (Pisces) mouth and tooth shapes, both adaptive and non-adaptive components are acting. Distribution patterns of non-marine ostracods (Crustacea) within and outside of ancient lakes indicate that sexual reproduction might be an additional requirement for successful radiations in ancient lakes, at least in certain groups. This can best be understood by invoking ecology-based hypotheses on the evolutionary superiority of sexual reproduction such as Fisher–Muller accelerated evolution and the Tangled Bank.

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Introduction

Lakes are intrinsically suicidal, as their basins tend to fill up by sediment influx. Consequently, most of the hundreds of thousands of inland water bodies on our planet are of Holocene (<18,000 years) age. A few dozen or so lakes in the world, however, are much older, by up to three orders of magnitude (Martens 1997; Rossiter and Kawanabe 2000; Martens et al. 1994). These ancient lakes have survived for millions of years, for example Lake Tanganyika (East Africa) is thought to be 9–12 million years (myr) old (Cohen et al. 1993), while the origins of Lake Baikal (Siberia) may lie as far

in the past as pre-Miocene times (approximately 30 myr; Sherbakov 1999). These two are the oldest extant ancient lakes, others are considerably younger (see Table 1 for details). Lake Malawi (East Africa) is an estimated 4.5–8.6 myr (Owen et al. 1990), Lakes Titicaca (South America; Dejoux 1994), Ohrid (Balcans; Salemaa 1994) and Biwa (Japan; Yokohama 1984; Nishino and Watanabe 2000) are 2–4 myr, while the largest (in surface area) of all extant ancient lakes, the Caspian Sea, is 3–5 myr old (Dumont 2000). Research on other putatively ancient lakes has just begun so that no reliable age estimations for their basins exist as yet (e.g. the Malili lakes in Sulawesi, with the exception of Lake Matano for which an age of 2 myr has been proposed — Haffner et al. 2001 — and Lake Lanao in the Philippines).

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Table 1. Some features of selected ancient lakes; modified from Martens (1997)

Lake	Age (myr)	Max. depth (m)	Species number	Endemism (%)
Baikal	25–30	1700	1825	54
Tanganyika	9–12	1470	1119	56
Malawi/Nyasa	4.5–8.6	785	800 ^a /65 ^b	99 ^a /100 ^b
Caspian Sea	2–3	1025	1495	27
Victoria	0.75 or less ^c	70	500 ^a	99 ^a
Biwa	4	104	517	10

^a Cichlids (Snoeks 2000).

^b Ostracods (Martens 2003).

^c Johnson et al. (1996) and Seehausen (2002).

Most ancient lakes, like Tanganyika and Baikal, are situated in tectonically active rifts. Because these rift valleys are becoming progressively wider and deeper, the depth of these lakes increases faster than the infilling by sedimentation. Sediment influx nevertheless occurs constantly, and Lake Tanganyika (with a maximum water depth of about 1.4 km) and Baikal (approximately 1.7 km) both have accumulated sediment layers 5–7 km in depth. Should tectonic activity cease, then these lakes, too, would in time disappear. A number of such long-lived lakes have indeed become extinct. Examples are the Miocene, crater-formed Steinheim Basin in Germany (Gorthner and Meier-Brook 1985), Shanwang Lake in China (Chen 2000), the Mio-Pliocene lake Pannon (Geary et al. 2000) and the continent-wide, Jurassic Newark Basin in North America (Geary 1990).

Most long-lived lakes are characterized by a highly diverse and largely endemic fauna and, to a lesser degree, flora. Such lacustrine radiations have been reported in a wide variety of animal groups, both vertebrate and invertebrate (see Table 1 for an overview of some selected lakes). The best-known ancient lake species flocks (definition see below) are doubtlessly those of the East African cichlid fishes, with hundreds of species occurring in Lakes Tanganyika, Malawi and, surprisingly, also in the much younger Lake Victoria. More than 300 species of gammaroid amphipods have so far been described from Lake Baikal (Kamaltynov 1999), which would amount to around 30% of the gammaroid species known worldwide. But it is presently assumed that the Baikal flock might even consist of more than 1000 species (Väänölä and Kamaltynov 1999). Ostracoda, small bivalved crustaceans, occur in significant flocks in all non-acid ancient lakes. Gastropod molluscs, Turbellaria, Oligochaeta and several other invertebrate groups all have significant radiations in such lakes, and most species in these flocks are confined to the single respective lake only (Table 1). This high degree of endemism has led researchers to believe that these taxa are neo-endemics, i.e. that they are presently living in the cradle in which they originated. This phenomenon, if genuine, makes ancient lakes objects of

special interest to evolutionary studies, because the combinations of extant taxic diversity patterns can be linked to past processes through analyses of a variety of palaeoecological proxies contained in the lake's sediments. Aspects of the speciation history are known for one in roughly every 300,000 metazoans (Bush 1993), but the ratio is already much higher in ancient lakes and could potentially increase further (Martens et al. 1994).

The extant species flocks of ancient lakes are, more often than not, said to constitute examples for adaptive radiation, which could, for instance, explain the numerous examples for convergent evolution in both invertebrates (Martens and Schön 1999) and fish (Fig. 1). The present paper reviews whether or not species flocks from ancient lakes in general can be seen as radiations and, more specifically, to what degree they can be considered as genuinely adaptive. As there appears to be considerable confusion with regard to the exact content and meaning of these (and related) concepts, we first provide some definitions. After this general appraisal of extant theoretical approaches, several case studies illustrate instances of adaptive and non-adaptive speciation. Special attention is devoted to a powerful driver of speciation in ancient lakes: the prevalence of sexual reproduction in these habitats.

Setting the stage

Species, species flocks, radiations

To date, about 25 species concepts have been recognized (Mayden 1997). These either use reproductive criteria, refer to phylogenetic history, or assess the degree of phenotypic or genotypic similarity. Because of the nature of the ancient lakes' animals and plants, which are nearly exclusively sexually reproducing, we mostly use the Biological Species Concepts here, notably Mayr's isolation species concept (ISC) and Paterson's (1993) recognition species concept (RSC). The first requires a high degree of reproductive isolation between

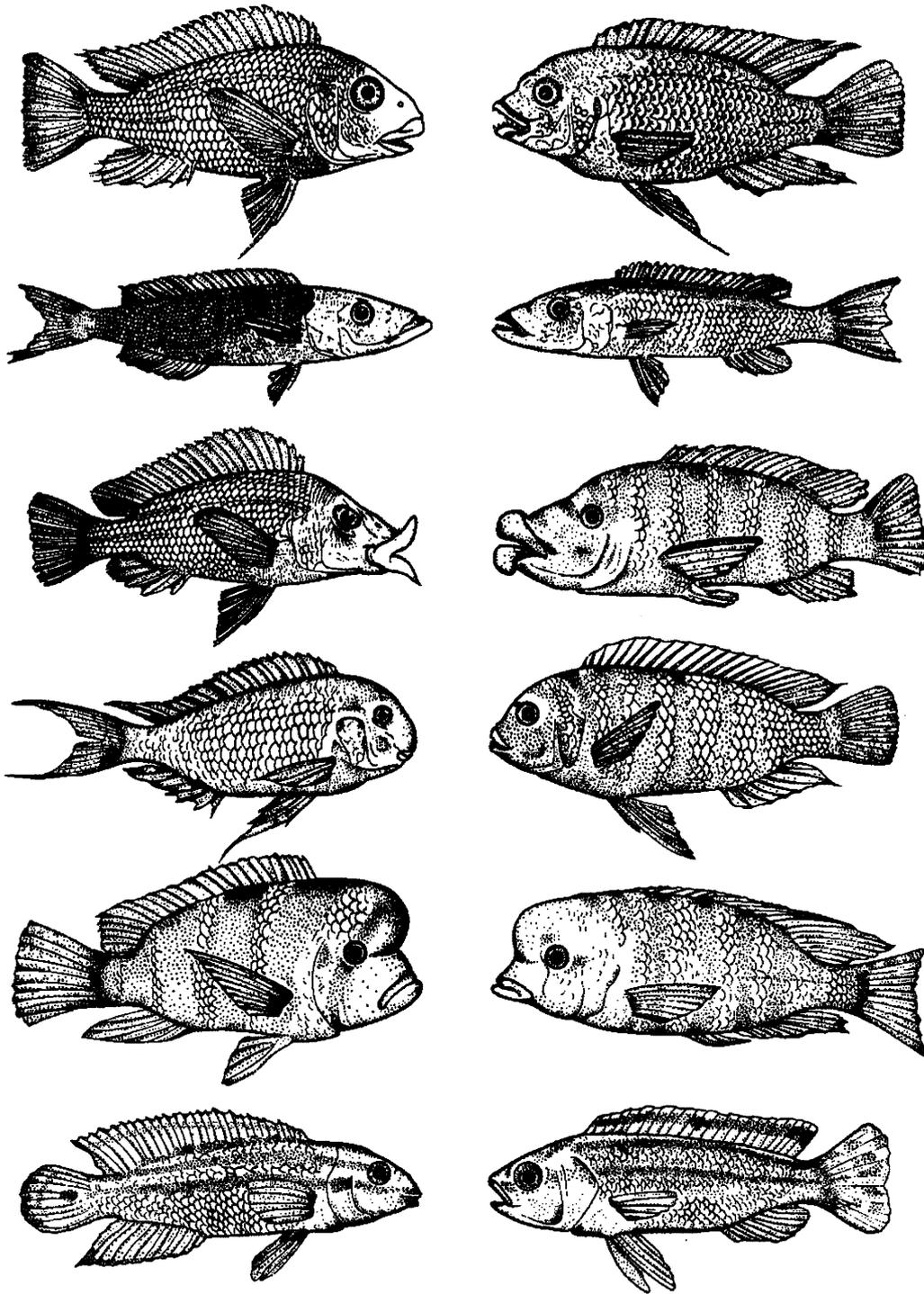


Fig. 1. Convergent evolution of body and mouth shapes from Tanganyikan (left column) and Malawi (right column) cichlids. Redrawn after Kocher et al. (1993).

individuals of different species, the latter requires that members of either sex belonging to the same species will recognize each other as such. Both concepts can be seen as two sides of the same coin. Their differences are related less to patterns (species identity) than to processes (speciation mechanisms). In the present discussion, a significant degree of reproductive isolation

is required for two clades to be considered different species. This reproductive isolation can be either pre- or post-zygotic but does not have to include both, as instances of hybridization are manifold in ancient lakes.

Species flocks is a term often used in discussions on ancient lake biodiversity. It was defined well by Greenwood (1984), who identified three requirements for a

group of species to be considered as a flock: speciosity, monophyly and endemcity. In the meantime, some modifications to these criteria have been proposed. Species groups consisting of no more than 3–4 taxa have been called flocks, and the species ancestral to the flock is no longer required to be endemic to the lake. In addition, the criterion of endemcity is becoming more and more difficult to apply, since it has been found that some species that are nested within an ancient lake flock can be non-lacustrine, i.e. they do not (any longer?) occur in the lake. For example, some cichlid species phylogenetically belonging to the Lake Victoria species flock occur in adjacent rivers and lakes (Verheyen et al. 2003), whereas Park et al. (2002) have found evidence for the fact that several non-Tanganyikan species of the ostracod genus *Gomphocythere* cluster together with Tanganyikan taxa. Likewise, the African gastropod *Cleopatra ferruginea* clusters with endemic Tanganyikan taxa (West and Michel 2000). An increasing number of similar examples has been cited from Lake Baikal. For examples, a common Holarctic *Gammarus* species clusters within the Baikal flock (Sherbakov et al. 1998), the North American asellid genus *Caecidotea* is sister taxon to the (endemic) *Baicalasellus* (Hidding et al. 2003), and the Holarctic ostracod species *Cytherissa lacustris* appears to be one of the more recent branches of the Baikalian *Cytherissa*-clade (Schön et al. 2000). *Cottus bairdi*, a cottoid fish from the North American Great Lakes also clustered within a Baikalian clade in a study by Kirilchik and Slobodyanyuk (1997), although recent, more extensive sequence data from the mitochondrial genome provide evidence to the contrary (Kontula et al. 2003).

In such cases, the term ‘superflock’ can be used (Verheyen et al. 2003), although this could lead to confusion with Greenwood’s concept of a superflock, which was much wider (including, for example, Lakes Victoria, Tanganyika and Malawi). The latter also assumed supra-lacustrine relationships between similar fish types. For example, it was postulated that members of a certain trophic type (e.g. piscivores) in the three lakes would be more closely related among each other than to members of other trophic types (e.g. molluscivores, algal grazers) in the respective same lake. Subsequent molecular phylogenies have shown that this is not the case (see e.g. Rüber et al. 1999), and that all three lakes have intra-lacustrine flocks of cichlids, albeit with a striking degree of parallelism.

Radiations, then, is a vaguely defined but popular term in evolutionary biology. The use of the epithet ‘adaptive’ suggests that not all radiations are of necessity ‘adaptive’, i.e. that there can also be non-adaptive radiations. Otherwise, the term ‘adaptive radiation’ becomes tautological (Gittenberger 1991). If a radiation is defined purely taxonomically, then it becomes a relatively large, monophyletic group of taxa

(Gittenberger 1991), which at the species level is synonymous to a species flock without the criterion of endemcity. Since, as we have seen above, increasing difficulties exist with the endemcity-criterion in the use of ‘species flock’, the term radiation is used below as defined by Gittenberger (1991).

An aspect often missing from discussions on radiations in ancient lakes is the rate at which the taxa are formed. Is the radiation the result of rapid speciation or simply of an accumulation of taxa which evolved gradually over a long period of time? While at least one lineage of haplochromid cichlids is an example for the first case (Seehausen 2002), thalassoid gastropods from Lake Tanganyika lack an increased rate of speciation (Wilson et al. 2004). Note also that the rate of speciation is not necessarily related to the age of the lineages. Old lineages could have evolved rapidly, after which an extended period of stasis might have occurred. A recent study on the Baikalian gastropods reveals that the first, ancestral lineages might be up to 200 myr old, even predating Lake Baikal itself, whereas the family Baicaliidae is much younger but still predates the Pleiocene–Pleistocene border (Hausdorf et al. 2003).

A term frequently encountered in the literature on ancient lake speciation is ‘explosive radiation’ or ‘explosive speciation’ (Fryer et al. 1983; Fryer 1991; Seehausen 2000; Sturmbauer et al. 2003), with the ‘explosive’ referring to a very high rate of speciation. The major gammaroid lineages are believed to have arisen in an explosive manner (Sherbakov et al. 1998), as have the Baikalian cottoid fishes (Kontula et al. 2003), a single lineage of haplochromid cichlids from Lake Victoria (Seehausen 2002), and the Tropheini from Lake Tanganyika (Sturmbauer et al. 2003). Just like in the case of ‘adaptive’ radiation, we should theoretically accept that ‘explosive’ is not automatically included in the term ‘radiation’, so that radiations can in theory originate in both gradual and punctuated ways. Nevertheless, radiations are most likely the result of higher speciation rates than in non-radiative cases (Schluter 1998, 2000).

Adaptations

An adaptation is a character or trait that causes niche diversification and that has evolved through natural selection. Not all adaptations are ideally linked to a certain aspect of niche exploitation. This is so because there are trade-offs (between different adaptations, or between natural and sexual selection pressures), developmental and historical impediments, time factors (number of generations since the process of adaptation started), etc. Also, several characters that appear to be

adaptations are instead related to other mechanisms. Firstly, some characters are pre-adaptations. Pre-adaptation is a confusing term that includes concepts such as exaptations (an old structure obtaining a new function) or spandrels (non-functional side effects of adaptations acquiring their own function). Secondly, some seemingly adaptive traits are phenotypic only. A third problem relates to phenotypic traits having evolved through sexual selection. For instance, bright colours in male cichlids could decrease fitness, as measured in terms of survival, because of the higher probability that predators are attracted. These colours have therefore not evolved as adaptations through natural selection. But if sexual selection is seen as part of natural selection, then these colours increase fitness for reproduction through a special kind of natural selection, and as such are adaptive. In the present essay, traits evolved solely through sexual selection, i.e. that have either neutral or negative effects in terms of survival, are not seen as adaptations, but see [Seehausen \(2000\)](#) for a more extensive discussion on the topic of sexual selection and adaptive radiation of cichlid fishes.

Degree of isolation

Most literature on speciation makes a distinction only between allopatric and sympatric speciation. However, we feel that these two terms allow for insufficient discrimination. Applied to ancient lakes, three different circumstances and categories can be discerned using the degree of isolation as a criterion ([Martens et al. 1994](#)).

‘Allopatric’ speciation occurs under strict geographical isolation, for example in isolated sub-basins during low lake stands, with (almost) zero gene flow. When water levels rise again, the separated sub-basins are re-incorporated in the original lake basin. Intra-lacustrine migrations may then obscure the previous geographical segregation. Other examples include water bodies associated to the main lakes, such as wetlands and riverine deltas in the East African lakes, or lagoons in Lake Baikal (called ‘sors’), or a string of separate lakes on the same plateau (Titicaca) or in the same rift valley (Baikal).

‘Parapatric’ speciation allows for some gene flow that is nevertheless either geographically or ecologically impeded. Along a geographical cline, speciation occurs at the extremes of the cline, e.g. the North or South ends of the elongate rift lakes, with limited gene flow in between, after which disruptive selection pressures can eliminate the intermediate hybrids. Through ecological segregation, the clinal preference occurs along an ecological gradient (bathymetry, oxygen and temperature; see [Takhteev 2000](#) for Baikalian amphipods). This can create so-called ‘dumb-bell’ population structures, with limited gene flow in intermediate environments.

Again, directional selection will eliminate intermediate phenotypes. Mosaic patterns of distribution, which are especially common in the fragmented littoral of ancient lakes, constitute a third possible example, and in lakes, where many organisms have a very patchy distribution, this may very well be the most important of the three modes for parapatric speciation.

‘Sympatric’ speciation occurs in one and the same habitat, without initial geographical or ecological segregation. This non-allopatric mode of speciation was controversial for a long time, but now appears as accepted ([Mallet 2001](#); [Via 2001](#)). Note that several mechanisms may be active, in sequence, in one speciation event (for cichlids see [Baric et al. 2003](#); [Danley and Kocher 2001](#)). For example, after initial (incomplete) allopatric speciation, the process may continue along a geographical cline.

The use of the term parapatric is not purely semantic ([Gavrilets et al. 2000](#)) and is useful to avoid confusion. For example, it is assumed that demes of rock-dwelling cichlids are isolated from each other by sandy stretches. According to some authors, a sandy stretch of 50 m is sufficient to cause an allopatric distribution ([Van Oppen et al. 1997](#)); even 35 m combined with a cold water influx can apparently be enough ([Rico and Turner 2002](#)). [Schilthuisen \(2001\)](#) would call this sympatric speciation. [Kornfield \(1978\)](#) constructed artificial rocky outcrops in the middle of a sandy stretch between two rocky shores and found that some rock-dwelling species colonized these habitats very quickly. At least some rock-dwelling cichlids are not completely blocked in their movements by such submerged barriers, and gene flow is thus not fully impeded. It is useful to distinguish between such instances of impeded gene flow and the two other, extreme scenarios. [Table 2](#) summarizes our interpretation for the mode of speciation in cichlids from East African lakes, by far the best-studied group of animals from ancient lakes. The data are controversial, and even within the same lineage different modes of speciation are inferred. How do isolation and adaptation interact, if at all? [Rice and Hostert \(1993\)](#) regarded the relationship between gene flow and diverging selection as a circularly regulating system, in which both gene flow and diverging selection will cease when populations have acquired the necessary adaptations and, consequently, competition is reduced. This is then followed by another round of diversification, when selection can start to act again because of reduced gene flow. Such subsequent episodes of diversification have been suggested for the evolution of the cichlid flock in Lake Malawi ([Danley and Kocher 2001](#)), but this hypothesis still requires further investigations. [Schilthuisen \(2001\)](#), in his most entertaining science ‘thriller’ on speciation, postulates that the two forces are inversely interactive: in cases with major gene-flow impediments (allopatry), only little niche diversification is needed to lead to speciation; in

Table 2. Examples for modes of speciation in cichlid fishes from East-African, ancient lakes

Lake	Cichlid lineage ^a	Allopatric ^b	Parapatric ^b	Sympatric ^b	Reference
Tanganyika	Eretmodini	+	—	—	Rüber et al. (1999)
	Eretmodini	+?	+?	—	Rüber et al. (2001)
	<i>Tropheus</i>	+	—	+	Baric et al. (2003)
	<i>Tropheus</i>	—	+	—	Sturmbauer et al. (2001)
Victoria	Mbunas	—	—	+	Sturmbauer et al. (2001)
Malawi	<i>Ophthalmotilapia</i>	+	—	—	Sturmbauer et al. (2001)
	<i>Diplotaxadon</i>	—	—	+	Shaw et al. (2000)
	<i>Pseudotropheus callainos</i>	+	—	—	Rico and Turner (2002)
	<i>Metriaclima</i>	—	+	—	Danley et al. (2000)
	<i>Capadichromis</i>	—	+	—	Taylor and Verheyen (2001)
	<i>Eretmodius cyanostictus</i>	—	+	—	Taylor et al. (2001)

^aOwing to problems with taxonomic research in this group (Snoeks 2000), no proper scientific names can be provided for some lineages or tribes.

^bOur categories for modes of speciation.

cases of putatively large gene flow (called sympatry, although most of his examples would here be considered parapatric) strong niche diversification is required. Evidence for such balanced interactions is not strong in ancient lake biota (see below).

Adaptive or non-adaptive radiations

What drives speciation in general and radiative speciation in particular remains, almost literally, a puzzle. “Simpson (1953) went so far as to claim that adaptive radiation could explain all of life’s diversity.” (Schluter 2000, p. 7) Even if this is wrong, at least an adaptive component might be involved, requiring the interaction of both intrinsic and extrinsic factors. The jury is still out regarding the relative relevance of the various interacting factors. Moreover, the main ‘chicken or egg’ problem remains: does species formation first cause reproductive isolation, followed by differential adaptation, or is it the other way around? Or are both scenarios possible? Or do both processes act simultaneously?

Schluter (1998, 2000), following Mayr (1963) and others, defined (adaptive) radiations as “lineages experiencing a burst of speciation and rapid phenotypic evolution under conditions of high ecological opportunity, such as colonization of resource-rich environments free of competitors and predators...” (Schluter 1998, p. 115), thus focusing on how ecology drives speciation. Such an approach, concentrating on the ecological causes of speciation and radiation, appears to single out adaptive speciation (and radiation) as the most important speciation mode.

How does one test whether a radiation is adaptive or non-adaptive? If one accepts the Popperian rule that

hypotheses (or their predictions) cannot be proven but only rejected, then the null hypothesis (NH) needs of necessity always be that radiations are non-adaptive. Indeed, one can falsify this hypothesis by demonstrating niche diversification along a single one of the innumerable axes, but one can never demonstrate to satisfaction that no diversification has occurred in any of the niche dimensions. It is of prime importance, however, that singular tests of trophic, bathymetric, osmotic, or other diversification be reported in the literature, even (perhaps especially) when the results are negative, that is when no diversification is found. Schluter (2000) has pointed out that mere utilization of different environments, not leading to increased fitness, should also be considered non-adaptive as the term ‘adaptive’ should only be used in cases where ecological diversification is accompanied by traits that increase the efficiency to exploit these resources. Larval (or juvenile) ecological diversification should not be ignored.

Schluter (2000, p. 242) listed some “entirely possible” mechanisms of non-adaptive speciation. He considered non-adaptive radiations (rapid proliferation of species accompanied by negligible or infrequent ecological differentiation, see Gittenberger 1991) to be those in which differences between species are limited to (secondary) sexual traits, and their evolution is not driven by the environment. In a number of cases it can be argued that sexual selection and niche diversification can be linked processes (see below). In other cases (genetic) mechanisms such as hybridization leading to polyploidy (Rieseberg et al. 1999), a variety of chromosomal architectural changes (King 1993; Rieseberg 2001), and gene or even genome duplication (Meyer and Schartl 1999) could have led to fully non-adaptive speciation and even radiation. There is mounting evidence that hybridization might also have

contributed to cichlid speciation (see below), but this is highly controversial.

Extrinsic drivers of ancient lake radiations

The causes for higher speciation rates in radiations can be extrinsic (environmental or ecological; Schluter 2000) or intrinsic (Martens et al. 1994; Martens 1997) or, more likely, a combination of both. Several putative drivers of speciation in ancient lakes have been cited in the literature, summarized in Brooks (1950), Martens et al. (1994) and Martens (1997).

The most obvious factor in ancient lakes is their long and continuous history. Indeed, speciation can take its time in those groups that are expected to evolve slowly (e.g. Martens 1994 for ostracods). Of prime importance here is the fact that the lakes must have been continuously extant as a stable biotic environment. Some lakes are geologically ancient as they have existed for millions of years, but they nevertheless have no species flocks. Such lakes have experienced catastrophes during their histories. For example, Lake Kivu has experienced intra-lacustrine volcanic eruptions (Degens et al. 1973), while Lake Turkana (both East Africa) suffered several so-called salinity crises and at times even dried out completely (Kolding 1992). The best-documented extrinsic factors further fuelling speciation in ancient lakes are lake-level fluctuations, for example in the East African lakes (Coulter 1994). Minor fluctuations, which occur frequently, create dynamic conditions in seemingly stable littoral communities; major fluctuations can cause a lake to be divided in several isolated basins for extended periods of time. Lake Tanganyika has experienced a series of dramatic lake-level fluctuations which split the lake into two (<300 m) or three (<600 m) basins for a period of time (Scholz and Rosendahl 1988; Coulter 1991; Tiercelin and Mondéguer 1991). The southern basin of Lake Malawi has been completely dry less than 200 years ago (Owen et al. 1990). Such dramatic events, leading to fully divided populations, have been cited as evidence for the relevance of allopatric speciation, for which cichlids are the most prominent example. Several studies of genetic data on the inter- and intraspecific level have been published, which show segregation patterns mirroring the previous formation of the three Tanganyika sub-basins (Snoeks et al. 1994; Verheyen et al. 1996; Sturmbauer et al. 2001, 2003; Baric et al. 2003).

Speciation during low lake-level stands can happen through the ‘founder-flush’ model (Geary 1990). In this model, populations first pass through genetic bottlenecks (the founder phase)—e.g. due to low water levels and the resulting salinity crises, as has happened at least in Tanganyika—most likely causing massive extinctions. This is followed by a period of abundant

proliferation (the flush phase) during the re-flooding of the lake, in a predator-free environment rife with empty niches. Geary (1990) provided evidence for this model with data from the Jurassic Newark Basin, a continent-wide ancient lake bed in North America. In fossil series of the gastropod *Melanopsis* Geary observed that morphological stasis prevailed in the period of allopatry caused by low lake stands, while punctuated morphological diversification abounded during re-flooding. These results are congruent with Schluter’s ‘ecological speciation’ models, but again reveal nothing about the relative timing of the origin of reproductive isolation and of adaptation. If reproductive isolation occurs during the period of allopatry, then this does not necessarily leave phenotypically identifiable traces in the fossil record, whereas the morphological changes due to adaptation in the flush phase might leave clear fingerprints. Another external factor is the fragmentation of the littoral (Fryer 1996), which might be of special importance for small and poorly dispersing groups. The formation of the cold, oxygenated abyss of Lake Baikal (Sherbakov 1999) relatively recently in the lake’s history (2–3 myr ago) presents another example of an extrinsic factor which has greatly influenced speciation. The beginnings of several species flocks, e.g. the *Cytherissa* flock (Schön et al. 2000) and the flock of cottoid fish (Kirilchik and Slobodyanyuk 1997; Kontula et al. 2003) coincide with this climatic change. Different substrate types can be (more or less efficient) barriers for littoral molluscs and cichlid fishes (see above).

Intrinsic drivers of ancient lake radiations

Various intrinsic factors, most of which are thought to limit intra-lacustrine dispersal, have been cited as promoting speciation. These factors are deduced from extant species flocks, the results of speciation processes. It is assumed that these same factors were present in the ancestral taxa. Reproductive modes mostly cited are: (1) mouth brooding and philopatry, as well as homing and home-site fidelity in cichlids, all of which considerably affect the genetic population structure (Taylor et al. 2001); (2) brooding in general, e.g. in the carapace of ostracods (Martens 1994), the marsupium of gammaroids (Yampolsky et al. 1994) or the shells of molluscs (Michel 1994); (3) ovoviviparous and viviparous reproduction in molluscs (Michel 1994); (4) gonochoristic reproduction as common in Tanganyikan thiarids (Michel 1994), this will be elaborated on below, as will the effects of sexual reproduction. Ecological segregation can provoke parapatric speciation in so-called dumb-bell structures. Bathymetric segregation will be most important in Lake Baikal, where the entire water column is oxygenated. Cottoid fish there are found to have high body lipid concentrations while lacking swim

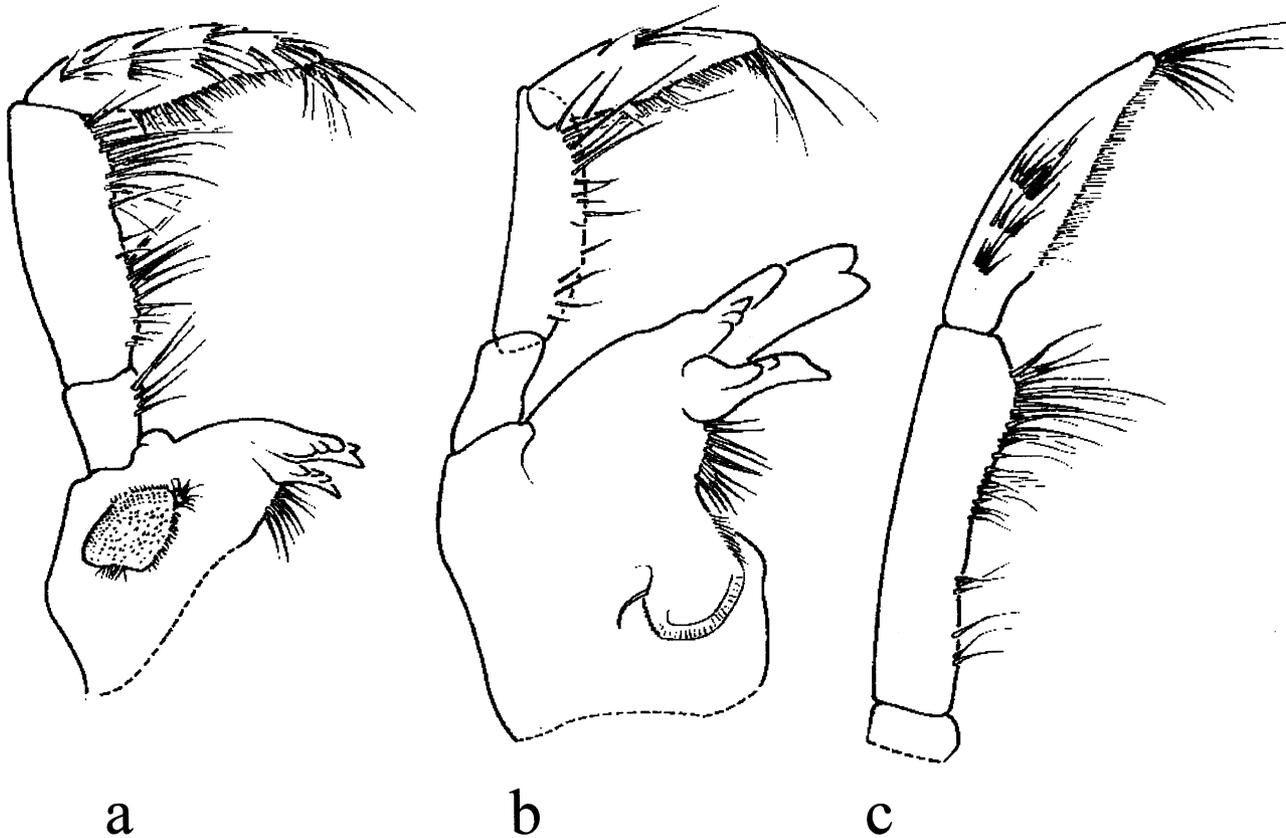


Fig. 2. Three types of mandible morphology in *Eulimnogammarus* from Lake Baikal. Type a occurs in 18 *Eulimnogammarus* species, types b and c are exclusive to *E. violaceus* and *Corophiomorphus kietlinskii*, respectively. Redrawn after Morino et al. (2000).

bladders, both features conducive to full exploitation of this habitat. This is a case in point of a pre-adaptation allowing speciation in abyssal environments (Sideleva 1994). Owing to the lack of swim bladders (the intrinsic factor), the fish can more easily invade the abyss in which free niches provoke adaptive speciation. Likewise, certain deep-water amphipod species from Lake Baikal show specific physiological adaptations, such as highly concentrated hemolymph, which their relatives from shallow habitats are lacking (Zerbst-Boroffka et al. 2000). Also the shifts in the spectral sensitivity of visual pigments in cichlid (Terai et al. 2002) and cottoid (Cowing et al. 2002) fishes can be considered (pre-) adaptations to a life at great depths. Different oxygen requirements can cause vertical distribution in the sediment, following different sediment oxygen penetration (SOP) depth profiles, and this can be important for the benthic infauna (Martin et al. 1993).

Trophic specialization is considered important in a variety of ancient lake (and other) radiations, such as East African cichlid speciation, but trophic traits do not necessarily produce dietary specialization. Comparing the data from two crustacean groups, endemic copepods and *Eulimnogammarus* amphipods in Lake Baikal, reveals that trophic specialization is apparent through

different morphologies of the maxillae in the former group (Boxshall and Evstigneeva 1994). On the other hand, the 18 (of the 20) Baikalian *Eulimnogammarus* species share the same mandible morphology and furthermore show considerable overlap in their diets (Morino et al. 2000; Fig. 2).

Other phenotypic traits putatively identified as drivers of radiations, such as the special structure of the cichlid jaw, remain to be conclusively tested (see below). For example, the relevance of brooding is recognized in several Tanganyikan biota: all species of the ostracod *Cyprideis* flock are brooders, as are species of *Gomphocythere*, whereas the cypridoid lineages in the same lake most likely are not, nor are any of the 50+ species of the *Cytherissa* radiation in Lake Baikal (Martens 1994).

Adaptive aspects in ancient lake radiations

Species flocks of ancient lakes are commonly referred to as examples of adaptive radiations. The two best-documented radiations are the inevitable cichlid fish in the East African lakes (Sturmbauer 1998) and the gammaroid amphipods of Lake Baikal (Kamaltynov 1992, 1999). A range of adaptive features have been

identified in both groups, e.g. bathymetric, trophic, substrate-related ones, etc. Both groups, one vertebrate and one invertebrate, have invaded a wide variety of niches through processes which have doubtlessly been driven by (rapid) ecological speciation.

The cichlid fishes in Lakes Tanganyika, Malawi and Victoria all have formed monophyletic flocks in which a variety of trophic guilds have originated. Algal grazers, scavengers, molluscivores and piscivores are the common types, but highly specialized guilds such as scale-biters (with left- and right-skewed races, see below) have also evolved (Fig. 3). In addition, flocks of cichlids have adapted to different substrate types, with sand-dwellers and rocky-shore species as the extremes. Supra- and infra-littoral taxa and demersal flocks show that bathymetric segregation has occurred. But even a combination of three factors, substrate, depth and trophic fails to fully separate all species from the major tribes of Tanganyikan cichlid fishes ecologically (Salzburger et al. 2002b). Each of the three East African lakes harbours several hundreds of endemic cichlid species, which is all the more surprising as this high diversity has to survive in the upper layers of the lakes. Tanganyika has a water depth of approximately 1400 m, but only the upper 100 m (in the north) to 150 m (in the south) are oxygenated, the entire abyssal being fully anoxic. Lake Malawi is about 800 m deep,

but only the top 200–250 m is oxygenated. Lake Victoria is a shallow basin on the whole (the maximum measured depth is 82 m), but there, too, oxygen availability decreases rapidly with depth, even more so during the past decades because of increasing eutrophication (Seehausen et al. 1997). Having summarized the most recent literature we interpret it as evidence for both adaptive and non-adaptive radiation in cichlids (Table 3).

Baikalian gammaroids have explosively invaded (nearly) all possible habitats of Lake Baikal. Although the roots of the flock may reach as far back in time as the origin of the lake itself, or even beyond, the present diversity for the larger part appears to be a relatively recent phenomenon (2.5–3 myr; Sherbakov 1999). Hundreds of species have been formally recognized, and these occupy a variety of adaptive spaces along ranges of bathymetry, trophic, lifestyle from mutualism to parasitism, body size from dwarves to giants, etc. (Kozhova and Izmet'eva 1998; Takhteev 2000). One of the most striking examples is *Macrohectopus branickii* (Dybowski, 1874), a pelagic predator with bizarre morphological adaptations (Martens and Schön 1999). Amphipods are generally benthic or free-swimming, and this Baikalian taxon is the only known pelagic amphipod (Martens and Schön 1999). In spite of the seemingly drastic morphological alterations in this lineage, the

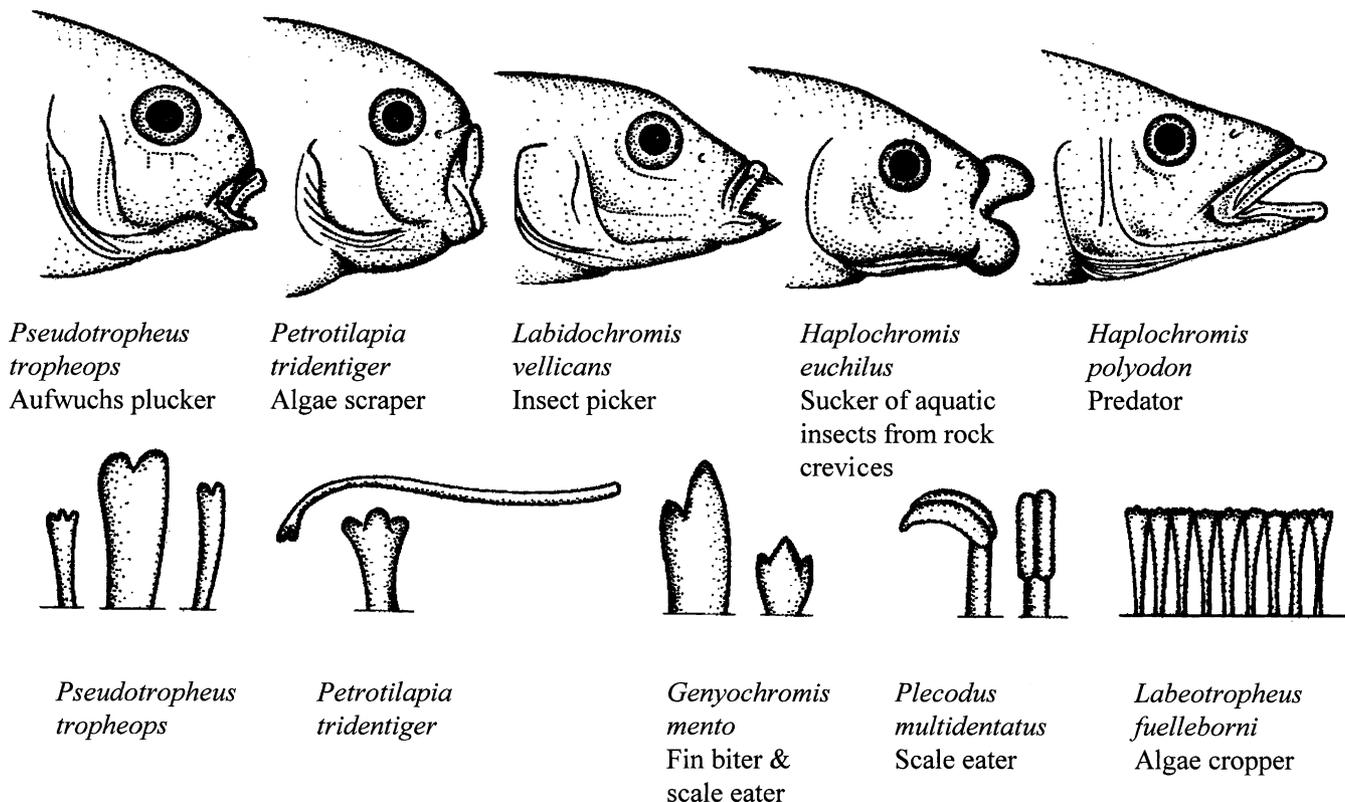


Fig. 3. Trophic specialization and associated head, mouth and tooth shapes in cichlids. Redrawn after Fryer and Iles (1972) in Futuyma (1986).

Table 3. Our interpretation of evidence for adaptive and non-adaptive speciation in cichlids from East-African, ancient lakes

Lake	Cichlid lineage ^a	Adaptive	Non-adaptive	Reference
Tanganyika	Eretmodini	+		Rüber et al. (2001)
	Eretmodini		+	Rüber et al. (2001)
	<i>Eretmodus cyanostictus</i>	+ ?		Wautier et al. (2002)
	<i>Tropheus</i>	+	+	Baric et al. (2003)
	<i>Lamprologus</i>	+		Salzburger et al. (2002b)
	<i>Neolamprologus</i>		+	Salzburger et al. (2002a)
	Tropheini 12 tribes	+ +	 +	Sturmbauer et al. (2003) Takahashi et al. (2001b)
Victoria	<i>Neochromis</i>	+ ?		Bouton et al. (2002)
	Haplochromines	+		Terai et al. (2002)
Malawi	<i>Diplotaxadon</i>		+	Shaw et al. (2000)
	<i>Pseudotropheus callainos</i>		+	Rico and Turner (2002)
	<i>Pseudotropheus</i>		+	Smith and Kornfield (2002)
	<i>Pseudotropheus</i>		+	Knight and Turner (1999)
	<i>Metriaclima</i>	+ ?		Danley et al. (2000)
	<i>Metriaclima zebra</i> ,	+		Albertson et al. (2003)
	<i>Labeotropheus fuelleborni</i>	+		
	<i>Eretmodius cyanostictus</i>		+	Taylor et al. (2001)
	<i>Metriaclima zebra</i>		+	Carleton and Kocher (2001)
	<i>Dimidiochromis compressiceps</i>		+	
	<i>Labotropheus fuelleborni</i>		+	
	<i>Oreochromis niloticus</i>		+	
	Mbunas	+	+	Danley and Kocher (2001)
<i>Oreochromis korangae</i>		+	Harvey et al. (2002)	
Mbunas and non-mbunas		+	Takahashi et al. (2001a)	

^aOwing to problems with taxonomic research in this group (Snoeks 2000), no proper scientific names can be provided for some lineages or tribes.

clade appears to be of relatively recent origin (Sherbakov et al. 1998).

Some further unusual features, such as spinosity, have evolved in the Baikalian amphipods. Parallel evolution has occurred in Tanganyikan thiarid molluscs and cytherideid ostracods, where the heavy calcification of the valves and the high incidence of spinosity were previously linked to a supposedly marine origin of these lineages (Moore 1898; Brooks 1950). It has since been conclusively demonstrated that Tanganyikan biota (in fact all ancient lake biota, except for some Caspian taxa) all have freshwater ancestors. The thalassoid aspects of these biota are now assumed to be the result of predator–prey arms races, for example in the case of gastropods with predation by freshwater crabs (West and Cohen 1994). Since such features enhance fitness related to survival they should also be deemed adaptive, although it remains unknown to which extent these biotic interactions have contributed to the origin of new species. By their very nature arms races operate in a gradual way, so that a rapid origin of taxa through such forces is almost certainly excluded.

There can be little doubt that ancient lake radiations, such as the East African cichlids and the Baikalian amphipods, have originated under the influence of adaptive forces. Nevertheless, few studies have rigorously tested if these presumed adaptive features are in fact true adaptations. Moreover, there is growing, although so far largely circumstantial, evidence that not all branches of the radiations have originated purely adaptively or even under the influence of any adaptation at all.

Non-adaptive (parts of) radiations in ancient lakes

Circumstantial evidence

Väinölä and Kamaltynov (1999) showed significant genetic structuring between, but also within, amphipod populations. A large part of this hidden reproductive isolation is (thus far) not recognized morphologically, and not (yet) linked to any niche diversification.

According to Väinölä and Kamal'tynov (1999), the number of Baikalian amphipod species might be three times higher than presently assumed. The greater share of these species appear to show no niche diversification (Morino et al. 2000, see above).

Mazepova (1990) reported on the occurrence of almost 20 ostracod species on 1 m² of sand in Lake Baikal, a biotope with minimal microhabitat structuring. Cohen (1995) found a continuous diversity of about 30 ostracod species in 1 m cores from Lake Tanganyika. Some degree of microscale segregation (for example by vertical distribution of living specimens in the sediment) may be assumed, but that can still not explain such high levels of standing diversity. Trophic specialization is not known in Tanganyikan benthic ostracods, which are all of similar size and are mostly continuously crawling on and into the top millimetres of the sediment. Except when some hidden form of biochemical diversification occurs, for example different enzymatic exploitation of the same food resources, which has never been reported in this group, the high specific diversities occurring sympatrically cannot be explained by niche diversification alone. An estimated 200 species of ostracods occur in both Baikal and Tanganyika (Martens 1994), and it is difficult to imagine an equal number of different niches occupied by these species. Furthermore, preliminary results on genetic diversity in the Baikalian ostracod genus *Cytherissa* show the occurrence of reproductive isolation amongst putatively cryptic species without obvious adaptive divergences (Schön et al. 2000), similar to the above case with Baikalian amphipods. Several other clades in ancient lake groups apparently lack adaptation as a driving force in their evolutionary history (see e.g. thiarid molluscs, Wilson et al. 2004).

None of these cases, with the exception of the thalassoid Tanganyikan gastropods (Wilson et al. 2004), even comes close to being conclusive, but they nevertheless suggest that (1) even within adaptive events a non-adaptive component might have operated, and amongst the major adaptive events (2) some non-adaptive background speciation has been ongoing. Examples supporting both notions are discussed in the following sections.

Non-adaptive components in adaptive speciation and radiation — the example of cichlid jaws

It has long been postulated that the jaw morphology of cichlids is one of the key factors promoting the impressive diversity of this group (Table 1). Very recently, evidence was provided for trophic adaptations of oral jaws in two cichlid species from Lake Malawi (Albertson et al. 2003). From combined morphological and quantitative genetic analyses, Albertson et al. concluded that positive selection has acted on quanti-

tative traits of jaw morphology, and that the gene for bone morphogenetic protein 4 might play a role in coordinating shape differences in cichlid oral jaws. Albertson et al. (2003) also observed genetic linkage between several loci responsible for morphological features of the jaw, and this could have facilitated the explosive radiation of cichlids. Future research will show to which extent selection has also acted on other traits related to jaw or head morphology and whether the same pattern can be found in other cichlid species.

In order to test general relevance of jaw evolution for the cichlid radiations in the East African lakes, two different NHs can be formulated, each with some predictions. The first NH says that the cichlid jaw is not the (main) driver of the radiations, and comes with two predictions: (a) some fish clades without this jaw can have radiations; (b) some fish clades with this jaw have no radiations. The second NH says that the jaw is the main driver of these radiations, and predicts that (a) no fish clade without the jaw can have radiations, and (b) fish clades with these jaws do have radiations.

The very wide morphological variation and diversification in cichlid jaws have been linked to trophic adaptations, to mouth brooding or to the production of mating sounds in males (Rice and Lobel 2002). Such morphological plasticity is only possible through restructuring of the pharyngeal jaw apparatus (Liem 1974), namely the decoupling of the upper jaw elements and the independent manipulation of premaxilla and maxilla (Liem 1980). These morphological prerequisites occur in all labroid fish (Danley and Kocher 2001), but only the cichlid lineages have undergone such tremendous radiation. Thus, the second NH is clearly rejected. Furthermore, non-cichlid fish as well have undergone considerable radiations in ancient lakes (e.g. De Vos and Snoeks 1994; Snoeks 2000; Agnese and Teugels 2001).

Jaw morphology can therefore not be the sole factor causing the extensive cichlid radiations in the East African lakes. Presumably the different jaw, lip and tooth shapes are the result of trophic adaptations and specialization. However, there is evidence that the supposed trophic specialists do not behave as such at all. Reinthal (1990) reported on non-adaptive diets in a number of cichlids, i.e. that putative mollusc crushers and algal scrapers will both also eat benthic invertebrates or scavenge on dead fish. Only the guild feeding on the prey with the highest energy content, the piscivores, will stray little, if at all, from their trophic specialization. The common explanation for these non-adaptive diets holds that fish specialize during times when food is scarce, whereas they become more generalistic during times when there is plenty of food. But there is no evidence that periods of scarce and abundant food sources oscillate. Most likely there are always algae, molluscs or other fish in relatively equal measures, even during periods of low lake stands, as

subsequent extinction will hit all groups. An alternative explanation for Reinthal's results is presented in the final text section of this paper.

Between the seemingly identical teeth of two Eretmodini lineages which are separated in molecular phylogenies (Rüber et al. 1999), small but significant differences in morphology were found after extensive statistical analyses (Wautier et al. 2002). It remains unclear, however, to which extent these differences are relevant in natural habitats and if they do not simply reflect standing, morphological diversities or reaction norms. The outcome of model-tests on the oscillation of left and right asymmetry in scale eaters illustrates that morphological differences can be phenotypic instead of genetic (Takahashi and Hori 1998). Moreover, the phenotypic plasticity of at least two morphological jaw features in a Lake Victoria cichlid species, which was observed by Bouton et al. (2002) after a dietary shift, can only lead to further adaptive speciation when these differences become genetically fixed.

Non-adaptive speciation and radiation

Genetic structuring through non-adaptive processes (such as gene and genome duplications; Eichler 2001) can lead to polyploidy and chromosomal arrangements. Genome duplication has been suggested for ray-finned fish (Actinopterygia) in the Devonian (Meyer and Schartl 1999), and evidence for it has been found in numerous duplicate genes from zebra fish, guppies and puffer fish (Taylor et al. 2001, 2003; Van de Peer et al. 2001, 2002). Genome duplication is considered one of the key mechanisms to acquire functional innovations (Meyer and Schartl 1999). Furthermore, duplication of a gene for the eye cone opsin has been reported from cichlids (Carleton and Kocher 2001).

Evidence for chromosomal speciation has been presented for amphipods from Lake Ohrid (Salemaa and Kamaltynov 1994) and asellid isopods from Lake Baikal (Hidding et al. 2003). Harvey et al. (2002) have found chromosomal fusion in a Malawian *Tilapia* species, which does not (yet) inhibit the species from hybridizing with its sister species. In Lake Victoria, where eutrophication has increased turbidity, cichlids which had been reproductively isolated through different colour patterns have started to hybridize in recent years, because visual mate recognition becomes blurred in waters with reduced transparency (Seehausen et al. 1997). Under these circumstances, two extant species may coalesce into one hybrid species, in which case biodiversity decreases. Genetic evidence for hybridization in cichlid species from various East African lakes has been provided (Nagl et al. 2000; Rüber et al. 2001; Takahashi et al. 2001a, b; Smith and Kornfield 2002; Salzburger et al. 2002b; Baric et al. 2003; Seehausen et al.

2003). Some hybridization events have even produced novel jaw morphologies in Malawian cichlids (McElroy and Kornfield 1993).

Transposable elements have repeatedly been cited as factors promoting rapid speciation or macromutations (Schön and Martens 2002), and the activity of such selfish genetic elements can only be considered as non-adaptive. SINEs, one class of transposable elements, are present in cichlids and have been used for phylogenetic reconstructions in this group (Takahashi et al. 2001a, b). Likewise, the retrotransposon *Rex3* has been found in high copy numbers in two cichlid species from the Old and New World, respectively (Volf et al. 2001).

Researchers have wondered for a long time why there are no extensive amphipod radiations in the East African lakes, whereas all temperate ancient lakes have them, either in Gammaroidea (e.g. Lake Baikal) or in Orchestidae (e.g. Lake Titicaca). It is possible that fast speciation in amphipods, for example in Lake Baikal, is at least partly transposon-driven. It is known that transposon activity can be temperature-mediated. For example, in yeast cultures a temperature drop from 25°C to 15°C leads to an increase in activity of the Insertion Sequence Element by a factor of 100 (Chen and Fonzi 1992). Maybe, the 'speciation transposons' in amphipods are only active at lower temperatures. Once the responsible elements have been identified, it would be relatively straightforward to test this hypothesis.

Differences in regulatory genes could provoke morphological changes, which might or might not be adaptive. There is no evidence for this from ancient lakes yet, but the example of Hawaiian silversword plants shows that genetic changes in regulatory genes can indeed cause rapid morphological changes (Barrier et al. 2001).

As stated above, we do not consider the male cichlid colours in East African lakes, probably an essential element of sexual selection (Seehausen et al. 1997, 1999; Seehausen 2000; Van Oppen et al. 2000), as adaptive speciation. Schilthuisen (2001) argued that the differential colour preferences lead to a degree of habitat shift, because the blue form will be better visible in the upper littoral, whereas the red form can still be seen at greater depths. However, following Schluter's (2000) definition of adaptive radiations, such a case of mere habitat shift, not accompanied by superior exploitation of this habitat, is also non-adaptive. Some of these shifts could also be caused by a mere change in the level of gene expression, as has been demonstrated by Carleton and Kocher (2001) for four species of Lake Malawi cichlids. In such cases, the observed differences are not necessarily heritable, and thus cannot cause adaptation through natural selection.

If, as proposed by Seehausen (2000), disruptive sexual selection goes hand in hand with subsequent ecological differentiation, sexual selection could become a

powerful engine causing and accelerating adaptive radiations. But even in this point of view sexual selection alone will not be able to cause adaptive radiation.

Pre-adaptive components in ancient lake radiations: sex in ancient lakes

The paradox of sex

Why sex is the dominant reproductive mode throughout the living world is still a largely unresolved enigma (Maynard Smith 1998). The need for males requires twice as much energy to produce offspring (the two-fold cost of sex), meiosis breaks up as many favourable combinations as it produces new ones (Hurst and Peck 1996), and dispersal is more difficult in sexuals, as both genders need to locate each other in spatially and temporally diluted environments. However, more than 20 different hypotheses attempt to explain why sexual reproduction will be more successful over longer evolutionary time frames (West et al. 1999). The most important ones are Müller's ratchet, Mutation load, Fisher–Muller accelerated evolution, Red Queen effect, Fluctuating Selection, DNA repair, Sib-competition, and the Tangled Bank (Butlin et al. 1998). Most of these theories deal with intrinsic biological features of the organisms and can be considered as 'variation and selection' models. Others are habitat-related, ecological models.

In spite of these theoretical considerations, some groups do show a disturbingly high incidence of asexual reproduction. A few taxa even manage to persist without any sexual reproduction for long periods of time, defying any ruling evolutionary theories. Because of this, they have been called 'ancient asexual scandals' (Judson and Normark 1996). In the animal kingdom, only three putative examples of such ancient asexuals are known, bdelloid rotifers (Mark Welch and Meselson 2000), oribatid mites (Maraun et al. 2003) and the darwinulid ostracods (Schön et al. 1998). The fossil record shows that the latter have reproduced exclusively asexually for at least 200 myr (Martens et al. 2003). Non-marine ostracods are excellent model groups to study the evolutionary effects of asexual reproduction. This is so because their extensive fossil record allows the calibration of evolutionary models within real-time frames. Furthermore, they show a broad variety of reproductive modes, ranging from fully asexual lineages (Darwinulidae) through taxa with mixed reproduction (Cyprididae) to fully sexual lineages (some lineages in Candonidae and Cytheroidea). In the following, we mainly use the presence or absence of different ostracod groups in ancient lakes to test the putative relevance of sexual reproduction in these habitats.

Sexual reproduction in ancient lake biota, with special reference to Ostracoda

Martens and Schön (2000) provided evidence that sexual reproduction in ostracods is even more common in ancient lakes than in shorter-lived water bodies. Endemic species of ancient lakes indeed nearly invariably occur in bisexual populations, although the sex ratio can show significant deviations from equilibrium.

Michel (1994) has indicated that in gastropods sexual reproduction is often coupled with the potential for speciation. Pulmonates, for instance, have relatively low endemicity compared to prosobranchs and are often hermaphrodites with self-fertilization. Within the prosobranchs, thiarid gonochoristic brooders form endemic radiations (e.g. *Lavigeria* in Lake Tanganyika) while parthenogenetic brooders are cosmopolitan (Michel 1994). Future research will have to reveal whether the patterns are as clear-cut as in ostracods (see below), or whether other reproductive strategies such as brooding are more important for gastropod radiations in ancient lakes. An example of parthenogenetic gastropods with polyploidy is the Baikalian *Benedictia*, which probably form a group of independent species (Kozhova and Izmest'eva 1998) and require further investigation.

Other taxonomic groups as well reveal a prevalence of sex in ancient lake biota. For example, in Lake Baikal there are more than 67 endemic species of Turbellaria, but none of these belongs in the Planariidae (Timoshkin, pers. comm.), a group with high incidence of parthenogenesis. The same is true for free-living Nematoda, where 39 of the 47 known species are endemic, none of which are Heteroderidae (Kozhova and Izmest'eva 1998), again a lineage with a high incidence of asexual reproduction. In all, 198 species of Rotifera are known from the lake, but only two of these are cosmopolitan bdelloids, which are fully asexual (Kozhova and Izmest'eva 1998). Baikalian Porifera do not produce gemmules (Kozhova and Izmest'eva 1998), the asexual form of reproduction. Although members of ancient lake biota, for example ostracods, themselves reproduce sexually, their closest, extra-lacustrine relatives can be exclusively parthenogenetic. *C. lacustris* constitutes a recent branch of the extensive (50+ species) Baikalian *Cytherissa* flock (Schön et al. 2000). Outside of the Baikalian province, throughout the Holarctic, it reproduces exclusively parthenogenetically, whereas in Baikal only sexual populations can be found. This means that the ability to reproduce asexually has survived genetically throughout the 3 myr evolution of Baikalian *Cytherissa*, but that it can only be expressed outside of that lake, namely in lakes of Holocene age.

This pattern is also compatible with higher taxonomic levels within the Ostracoda. The ancient,

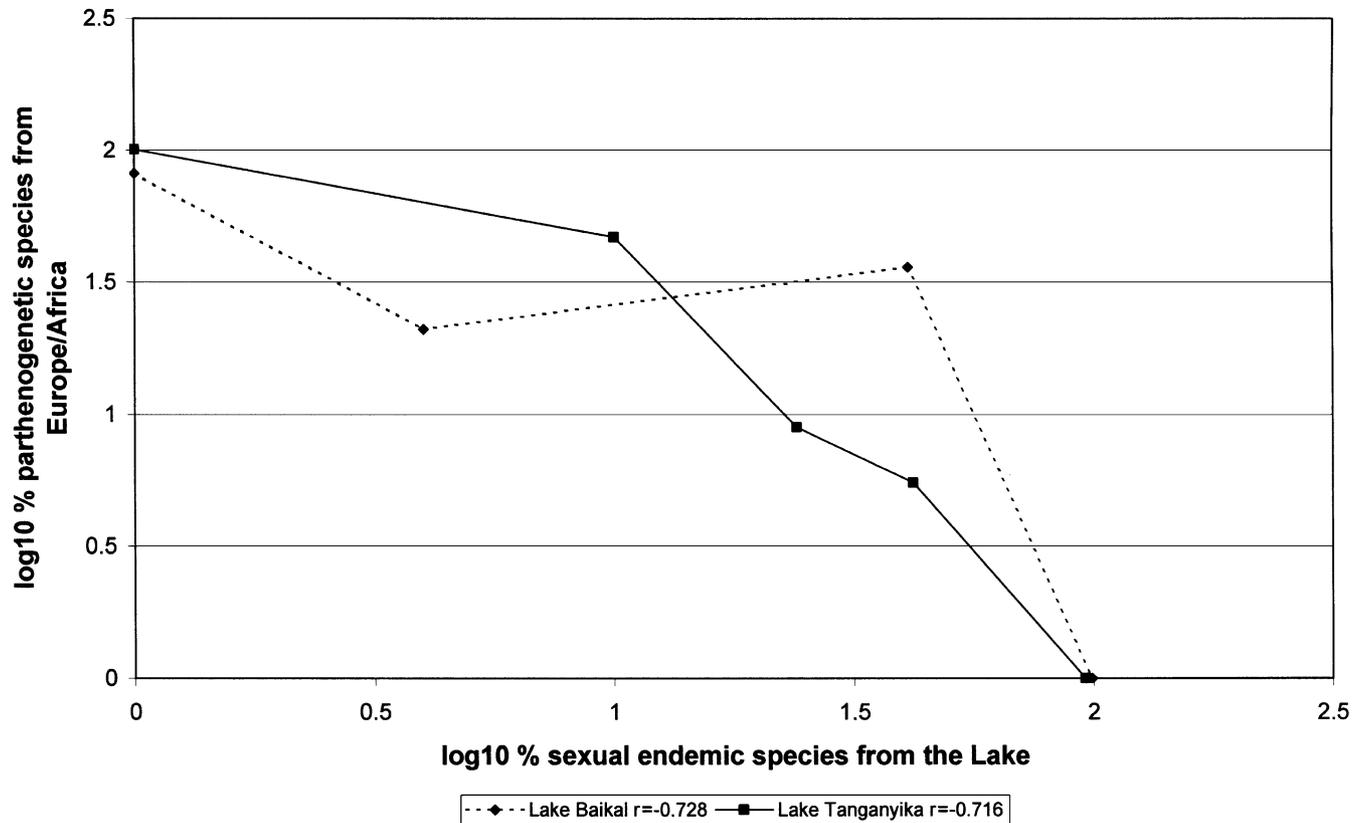


Fig. 4. The negative correlation (r) between the log 10 of the percentage of parthenogenetic species from Europe and Africa and the percentage of sexual, endemic species from Lake Baikal and Tanganyika, respectively, for the ostracod families Darwinulidae, Cyprididae, Limnocytheridae, Candonidae and Cytheridae.

asexual Darwinulidae hardly occur in ancient lakes, and certainly have no endemic species flocks there. The family Cyprididae, which has mixed reproduction but with a dominance of asexual lineages, are nearly completely absent in spite of the fact that they constitute up to 80% of the specific diversity of non-marine ostracods in short-lived habitats (Martens 1998). Cytheroidea and Candonidae represent the most extensive ostracod radiations in ancient lakes, two groups in which sex is the most dominant reproductive mode (Martens 1994).

A correlation between general incidence of parthenogenesis in several ostracod lineages and the extent of their (endemic) species flocks in Lake Baikal and Lake Tanganyika is given in Fig. 4.

In conclusion, sexual reproduction is more common in the ancient lake lineages in a variety of animal groups, while lineages with high incidence of parthenogenesis either do not have endemic radiations in ancient lakes, or have been far less successful in establishing such lineages. The importance of the reproductive mode has so far been mainly ignored in discussions on ancient lake speciation.

Sex as a pre-adaptation for persistence in ancient lakes

Schluter (1998) has convincingly argued that there are two main ecological causes of speciation. The first, ecological speciation, reiterates that reproductive isolation evolves from the same forces that cause phenotypic differentiation. This view harkens back to the early days of the Modern Synthesis, summarized by Huxley (1942). The second hypothesis, termed ecological persistence, holds that ecological processes affect speciation mainly through their influence on the viability of populations undergoing speciation. This was first proposed by Mayr (1963), subsequent literature also states that short-term ecological changes in environments mainly influence the persistence of geographically isolated populations, which then acquire the time necessary to evolve reproductive isolation. Schluter (1998) argues that data to illustrate the relevance of this hypothesis are badly needed. The relevance of sexual reproduction in ancient lake radiations is a case in point.

One of the many hypotheses attempting to explain the prevalence of sex in the animal and plant kingdoms (see above) is Fisher–Muller accelerated evolution (Fisher

1930; Muller 1932), which says that sexual reproduction allows faster formation of beneficial gene combinations, necessary to adapt to changing environments. Whereas the Red Queen hypothesis (Van Valen 1973) uses this concept to explain the need for sex in biotic interactions (e.g. host-parasite co-evolution), the Fluctuating Selection hypothesis (Maynard Smith 1980; Roughgarden 1991) does the same for adaptation to abiotic changes (especially climatic fluctuations). Although ancient lakes are geologically stable basins, they are still susceptible to significant ecological change as a consequence of climatic cycles, e.g. through water-level fluctuations in the East African lakes or glaciation in the Baikal region. Moreover, the high standing diversity in all ancient lakes provokes biotic interactions of an order of magnitude higher than in shorter-lived water bodies. Both Red Queen and Fluctuating Selection thus predict that environments like ancient lakes indeed would pose a higher need for sexual reproduction, in order for biota to persist in these highly competitive, ecologically fluctuating environments.

Regarding the survival of ancient lake taxa, sexual reproduction is thus either an adaptation or a pre-adaptation. Since it is already prevalent in most (all?) lineages forming endemic species flocks in ancient lakes, the latter alternative most likely applies. If Red Queen and Fluctuating Selection will eventually turn out to be the main explanations for the existence of sexual reproduction in general, one could argue that sex is an adaptation. If, however, research on the paradox of sex will reveal that sex originated for other reasons—e.g. for resetting epigenetic markers (Jablonka and Lamb 1999), or to counter the accumulation of deleterious mutations (Kondrashov 1988) or the loss of mutation-low genotypes (Muller's ratchet; Muller 1964) or mutational meltdown (Gabriel et al. 1993)—then the high incidence of sexual reproduction in ancient lake biota constitutes an exaptation.

Consequences of the prevalence of sexual reproduction in ancient lake biota

Sexual reproduction seems to be a necessary, or at least beneficial, trait for the long-term persistence of clades in ancient lakes, whereas in short-lived water bodies the advantages of asexuality (Maynard Smith 1998) might be more important. One could argue that this has important consequences for the speciation rates of these lineages. Firstly, the Fisher–Muller accelerated evolution hypothesis (see above) predicts faster evolution, which may lead to accelerated speciation rates compared to asexual lineages. Secondly, the presence of sexual reproduction entails the need for mate recognition and mate choice, two processes invoking the possibility of non-adaptive speciation through sexual

selection. Sexual reproduction, initially (pre-)adaptive for reasons of persistence, thus turns into a driver of rapid evolution and leads to accelerated speciation rates. This is in line with an old argument by Fisher (cited in Leigh 1999) that recombination furnishes evolvability because of “honest meiosis”, the spread of only those alleles which contribute to the fitness of their bearers and which are most crucial for adaptive evolution.

In addition, the Tangled Bank hypothesis (Ghiselin 1974; Bell 1982), another sex-related hypothesis, relies on economic analogy and argues that it is more profitable to concentrate on the production of a single product in an unsaturated market, but to diversify when the market becomes saturated. This has interesting consequences for adaptive radiations. Initial speciation events during phases where many empty niches exist (e.g. during re-flooding of lakes after low stands) would lead to rapid specialization in sexual organisms. However, in an environment in which niche space is tightly packed with interacting organisms, frequency-dependent selection will favour novel or rare genotypes, which utilize different resource combinations. This is the missing link needed to explain the results of Reintal (1990) cited above: the various morphological trophic adaptations in cichlids evolved during the re-flooding of lakes, but as the bank became more tangled, the species were forced to revert to more generalistic feeding behaviour. Sexual selection, in this case stabilizing, caused the sub-optimal jaw and tooth structures to persist.

However, speculation aside, theoretical reasons and comparative evidence both indicate that sexual reproduction is (pre-)adaptive to the persistence of ancient lake biota, and that its presence could be a driver to elevated speciation rates in ancient lakes, leading to species radiations, be they adaptive or non-adaptive.

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