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INVITED REVIEW

The interaction of sexually and naturally selected traits in the adaptive radiations of cichlid fishes

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Abstract

The question of how genetic variation translates into organismal diversity has puzzled biologists for decades. Despite recent advances in evolutionary and developmental genetics, the mechanisms that underlie adaptation, diversification and evolutionary innovation remain largely unknown. The exceptionally diverse species flocks of cichlid fishes are textbook examples of adaptive radiation and explosive speciation and emerge as powerful model systems to study the genetic basis of animal diversification. East Africa's hundreds of endemic cichlid species are akin to a natural mutagenesis screen and differ greatly not only in ecologically relevant (hence naturally selected) characters such as mouth morphology and body shape, but also in sexually selected traits such as coloration. One of the most fascinating aspects of cichlid evolution is the frequent occurrence of evolutionary parallelisms, which has led to the question whether selection alone is sufficient to produce these parallel morphologies, or whether a developmental or genetic bias has influenced the direction of diversification. Here, I review fitness-relevant traits that could be responsible for the cichlids' evolutionary success and assess whether these were shaped by sexual or natural selection. I then focus on the interaction and the relative importance of sexual vs. natural selection in cichlid evolution. Finally, I discuss what is currently known about the genes underlying the morphogenesis of adaptively relevant traits and highlight the importance of the forthcoming cichlid genomes in the quest of the genetic basis of diversification in this group.

Keywords: adaptive evolution, evo-devo, evolutionary genomics, explosive speciation, organismal diversification, parallel evolution

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> 'I've never met an animal, or a plant for that matter, that wasn't interesting, but some stand out as special. Cichlid fishes are right up there.'
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> George W. Barlow (2000) The Cichlid Fishes

As many as 150 years after the publication of Charles R. Darwin's *The Origin of Species*, the identification of the processes governing the emergence of novel species remains a fundamental question to biology (Coyne & Orr 2004; Carroll *et al*. 2005; Brakefield 2006). Why is it that some groups have diversified in a seemingly explosive manner, while other lineages have remained virtually unvaried over millions of years? What are the external factors and environmental conditions that promote diversification? And what is the molecular basis of adaptation, evolutionary innovation and diversification? A key to these and related questions is the comparative study of exceptionally diverse yet relatively young species assemblages that have radiated in geographically well-defined areas. This strategy is anything but novel and dates back to the dawn of evolutionary research, with the fringillid finches of the Galapagos archipelago being the primary and most prominent case. These 14 songbird species — commonly referred to as Darwin's finches in honour of their discoverer — make up the classic example of adaptive radiation, i.e. the rapid proliferation of an ecologically and morphologically differentiated species assemblage from a single ancestor as a consequence of adaptation to divergent environments (Simpson 1953; Schluter 2000). Other textbook examples of adaptive radiations are the Caribbean *Anolis* lizards, the

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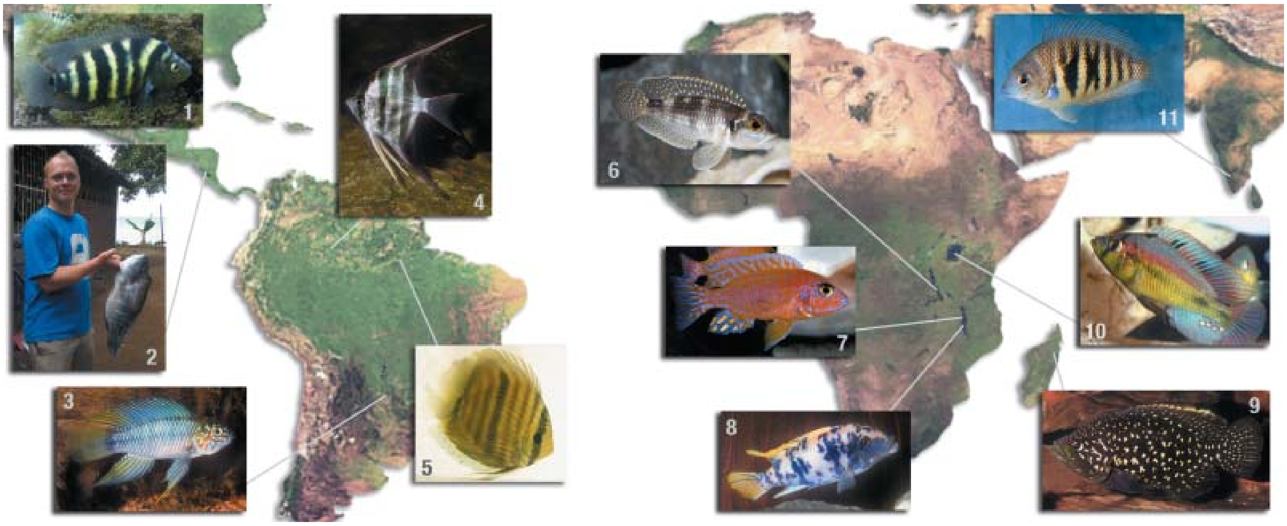

Fig. 1 The diversity of cichlid fishes. The Cichlidae (Perciformes) are distributed in India, Sri Lanka, Madagascar, South and Central America, Africa, and the Middle East, and show a great diversity of body morphologies, body sizes, and colour patterns. Some representatives are shown here: (1) *Amphilophus xiloaensis*, (2) *Parachromis managuensis* (and the author), (3) *Apistogramma borelli*, (4) *Pterophyllum altum*, (5) *Symphysodon discus*, (6) *Lamprologus meleagris*, (7) *Aulonocara* sp., (8) *Maylandia fainzilberi*, (9) *Paratilapia bleekeri*, (10) *Haplochromis aenicolor*, (11) *Etroplus canarensis*.Images by M. Barluenga (*P. managuensis* and the author), T. Lehtonen (*A. xiloaensis*) and E. Schraml (the rest).

Hawaiian silverswords, and the species flocks of cichlid fishes in East Africa, which are the focus of this review article.

The adaptive radiations of cichlid fishes ...

The species flocks of cichlid fishes in the East African Great Lakes undoubtedly constitute the most diverse extant vertebrate adaptive radiations (Seehausen 2006). Like all other famous cases, these radiations have occurred in habitats with island-like properties: large freshwater lakes that, from the fishes' point of view, are what an island is for terrestrial animals (Salzburger 2008). Lakes Tanganyika, Malawi, and Victoria are each teeming with a unique set of hundreds of endemic cichlid species, which are likely to have evolved — together with plenty of species in rivers and smaller lakes — in the last few millions to several thousands of years only (Seehausen 2002; Verheyen *et al*. 2003; Kocher 2004; Joyce *et al*. 2005; Salzburger *et al*. 2005; but see Genner *et al*. 2007b). The East African cichlid species flocks exhibit an exceptionally high proportion of endemism nearing 100%. Most notably, not a single cichlid species is shared between the three Great Lakes (Fryer & Iles 1972; Salzburger & Meyer 2004) and nonendemic species are those that have left a lake habitat to occupy connected rivers or those that have colonized a lake secondarily.

The actual number of cichlid species in East Africa's Great Lakes is undetermined and, at least in the cases of Victoria and Malawi, a matter of debate. About 250 cichlid species are known to occur in Lake Tanganyika. Higher estimates for Lake Malawi range around 700–800 species (Snoeks 2001; Turner *et al*. 2001), making its fauna the most species-rich species flock known. The situation is less clear for the cichlid assemblage of Lake Victoria for two reasons. First, the cichlid fauna of this lake is not precisely independent but forms, together with cichlids from neighbouring lakes (e.g. Kivu, Edward, George, Kyoga) and rivers, a 'superflock' of closely related species (Nagl *et al*. 2000; Verheyen *et al*. 2003). Second, this cichlid assemblage has suffered from severe ecological changes along with the population explosion of the introduced Nile perch (Witte *et al*. 1992) and eutrophication (Seehausen *et al*. 1997a) leading to the extinction of a substantial part of its original fauna (Seehausen *et al*. 1997b; Witte *et al*. 2000). It is estimated that the cichlid assemblage in pristine Lake Victoria consisted of 500 (Snoeks 2001) to 700 (Turner *et al*. 2001) species.

Cichlid adaptive radiations are, however, not confined to the Great Lakes in East Africa. In a recent evaluation, Seehausen (2006) identified 24 additional lacustrine cichlid radiations in Africa. And cichlid radiations are also known from outside the African continent. As an initially Gondwanian group that was split with the fragmentation of this supercontinent, cichlids are now distributed in India, Sri Lanka, Madagascar, South and Central America, Africa, and the Middle East (Fig. 1). About one-third of the cichlid species known worldwide occur outside of Africa (Turner 2007). Truly lacustrine non-African cichlid radiations are less frequent however, which can be explained by the lack of similarly substantial bodies of freshwater within the cichlids' tropical distribution. Yet, when permitted by the ecological settings, such as in the area of the Great Lakes and some smaller crater lakes in Nicaragua (Barlow 1976; Barluenga & Meyer 2004; Barluenga *et al*. 2006), cichlid radiations have occurred outside of Africa, too.

... as model systems for evolutionary genomic and evo-devo research

In the last few years, the cichlid adaptive radiations have been advanced as excellent model systems for evolutionary genomic and evolutionary–developmental research (Kocher 2004; Brakefield 2006; Abzhanov *et al*. 2008). There are indeed many advantages that the cichlid system provides. First, the hundreds of closely related — yet ecologically and morphologically distinct — species in East Africa's cichlid assemblages are akin to a 'mutagenic screen' (Kocher 2004; Albertson & Kocher 2006), with the peculiarity that hundreds of 'mutant lines' (i.e. natural populations) have passed through selection, thereby unfolding admissible combinations of alleles under natural conditions and real ecological set-ups. Second, most of these 'mutant lines' can be transferred to the laboratory and are, as the cichlids' popularity among aquarists shows, unproblematic to rear. Third, many of the species can be crossed under laboratory conditions allowing genetic experiments (see e.g. Albertson *et al*. 2003a, 2005; Streelman *et al*. 2003a; Haesler & Seehausen 2005). Since generation times are relatively short,[1] crossing experiments are accomplishable in a reasonable amount of time. Fourth, the close relatedness of the species leads to technical advantages and the wide applicability of genetic and genomic resources. Furthermore, cichlid adaptive radiations have occurred in plenty of replicates — from small crater lakes in Central America and West Africa through small and middle-sized lakes throughout their distributional range to very large lakes in East Africa — permitting the unique possibility of studying adaptive radiation and explosive speciation in radiations of different ages and of different scales but in the same group of organisms. Finally, it is the multitude of parallel morphologies (Box 1) that make the cichlid adaptive radiations most useful for evolutionary genomic and evo-devo research (Brakefield 2006).

The cichlid community has established a variety of genetic and genomic resources, which not only facilitate research in this group, but also consolidate the cichlids' role as comprehensive model system in various fields of research. Among these are genetic maps (Albertson *et al*. 2003a; Lee *et al*. 2005), bacterial artificial chromosome (BAC) libraries (Katagiri *et al*. 2001; Watanabe *et al*. 2003; Lang *et al*. 2006), and cDNA microarrays (Renn *et al*. 2004; Kijimoto *et al*. 2005; Kobayashi *et al*. 2006); more than 45 000 expressed sequence tags (ESTs) are already available in public databases (Watanabe *et al*. 2004; Salzburger *et al*. 2008); and low survey sequencing of five Lake Malawi cichlids revealed thousands of cross-species SNPs (Loh *et al*. 2008). Most importantly, high-coverage sequencing of the cichlid genome is currently under way. For a detailed description, see the homepage of the Cichlid Genome Consortium at www.cichlidgenome.org.

Adaptive radiations and the genetic basis of animal diversification

The question of how variation on the level of DNA is interrelated with organismal diversity has fascinated biologists for decades (reviewed in Carroll *et al*. 2005; Brakefield 2006; Abzhanov *et al*. 2008). In spite of recent advances in evolutionary and developmental biology, in genetics and genomics, the molecular mechanisms that underlie diversification and adaptation remain largely unknown. For example, the relative importance of *cis*-regulatory evolution vs. changes in coding regions of genes in morphological adaptation and, hence, in the generation of biological diversity, is undetermined and a matter of debate (Carroll *et al*. 2005; Hoekstra & Coyne 2007; Ellegren & Sheldon 2008). Similarly, the contribution of epigenetic factors to adaptation and, possibly, to diversification is as yet unknown (Bossdorf *et al*. 2008). So far, only very few genes causing reproductive isolation between closely related species (so-called 'speciation genes') have been identified and little is known about how discrete groups of organisms can emerge that subsequently are able to co-exist as separate lineages in nature (Coyne & Orr 2004). One of the main hopes that ecologists and evolutionary biologists have in the field of genomics is to be able to identify the genetic and developmental basis of adaptively relevant traits in natural populations (Kocher 2004; Brakefield 2006; Ellegren & Sheldon 2008).

Organismal diversity is generated through the interplay of adaptation and speciation (see e.g. Hoekstra & Coyne 2007). Since adaptive radiations are characterized by the action of the exact same two processes, adaptation to novel habitats and rapid speciation from a common ancestor (Schluter 2000), they emerge as ideal set-ups to explore biological diversification in general and the relative importance of natural selection in species formation in particular (Greenwood 1984; Brakefield 2006). The great number of eco-morphologically distinct species in the various cichlid adaptive radiations, their anchorage at different stages of a radiation, and the multiple occurrences of evolutionary

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[1] For example, our laboratory strains of the East African riverine haplochromine *Astatotilapia burtoni* have a generation time of about 4 months.

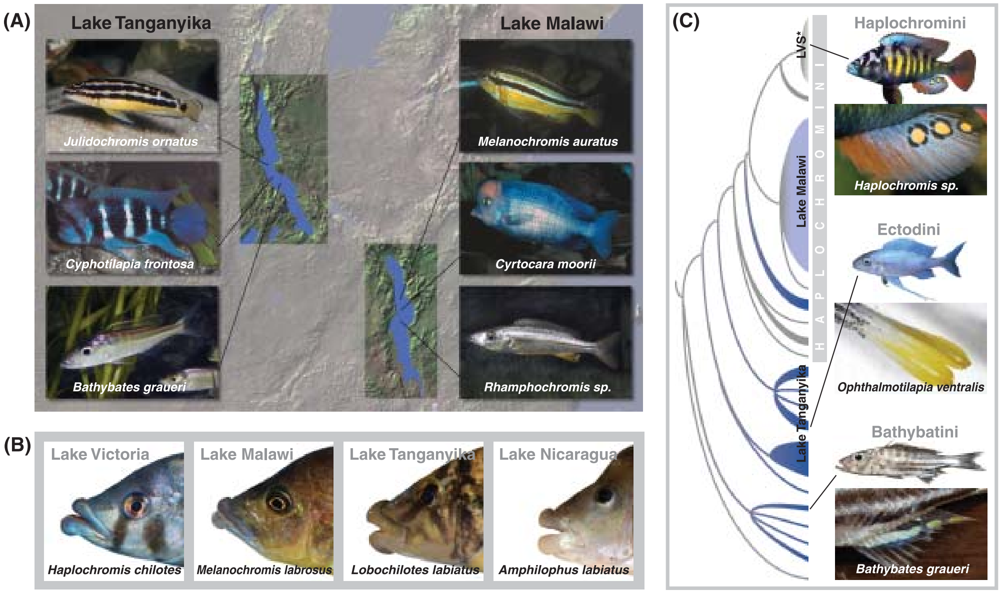
Box 1 Evolutionary parallelisms in cichlids

The repeated occurrence of evolutionary parallelism is certainly among the most fascinating aspects of cichlid evolution. Evolutionary parallelisms have been reported with respect to overall body morphology (Kocher *et al*. 1993; Clabaut *et al*. 2007), the morphology of the trophic apparatus (Rüber *et al*. 1999; Hulsey *et al*. 2008), coloration and pigmentation (Kocher *et al*. 1993; Seehausen *et al*. 1999; Allender *et al*. 2003; Duftner *et al*. 2007; Salzburger *et al*. 2007), and brood-care behaviour (Goodwin *et al*. 1998). Parallelisms at the molecular level have been observed, too. For example, the same mutation in *rhodopsin 1*, causing a blue-shift in the adsorption spectrum of this colour perception gene, has occurred in deep-water species from lakes Tanganyika and Malawi, most likely as an adaptation to the deep-water photic environment (Sugawara *et al*. 2005). In another case, it has been shown that the same gene (*csf1ra*) is expressed in the yellow pigment cells in the anal fin egg-dummies in haplochromines and in the egg-dummies at the tips of the elongated paired pelvic fins of some Tanganyikan ectodines (Salzburger *et al*. 2007).

Evolutionary parallelism provides good evidence for comparable, yet independent, responses to similar selective conditions. Parallel evolution in coloration may also be due to similar female preferences. Alternatively, parallel colour patterns may also emerge as a consequence of genetic or developmental constraints (Brakefield 2006; Arendt & Reznick 2008). For example, parallel ecotypes in cichlid species flocks often show strikingly similar colour patterns (Kocher *et al*. 1993), which could indicate that body and/or mouth morphology and coloration are interlinked through such a constraint. The identification of the genetic and developmental basis of parallel morphologies is clearly one of the major challenges.

A few examples of evolutionary parallelisms in cichlids are illustrated below. (a) Morphologically similar species ('ecomorphs') have evolved independently in different lakes in East Africa (Kocher *et al*. 1993); three such species pairs from Lakes Tanganyika and Malawi are shown. (b) Thick-lipped phenotypes have evolved repeatedly in independent cichlid species flocks, e.g. in each of the three East African Great Lakes as well as in the Nicaraguan Great Lakes. The exact function of the fleshy lips is currently unknown. (c) Egg-dummies, which mimic real eggs and play an important role in the breeding cycle of some mouth-brooding cichlid lineages, have evolved at least three times in East African cichlids. Yellow to reddish anal fin egg-dummies are found in males of the exclusively Tanganyikan tribe Bathybatini and in the East African Haplochromini. In some Ectodini from Lake Tanganyika male individuals have evolved yellow egg-dummies on the elongated ventral fins (see Salzburger *et al*. 2007 for further details). The phylogeny shown is based on (Salzburger *et al*. 2002b, 2005), Lake Tanganyikan tribes are depicted in dark blue, the Lake Malawi radiation is shown in light blue, riverine lineages are indicated in grey.

*LVS refers to the Lake Victoria region superflock that also includes the assemblages of neighbouring lakes and rivers (Verheyen *et al*. 2003).



Images are courtesy of E. Schraml (except for *L. labiatus*, *A. labiatus*, Bathybatini and Ectodini egg-dummies, which have been taken by the author) parallelisms make the cichlid system highly suitable for the study of traits under selection and in the quest for the genetic pathways underlying these traits.

The evolutionary success of the cichlids

The cichlids' evolutionary success has been attributed to the interaction of different types of biological factors in combination with the environment in which cichlid evolution has taken place. There is little doubt that the multitude of suitable habitats existing in the Great Lakes of East Africa is conducive to cichlid diversification (Kornfield & Smith 2000; Kocher 2004; Salzburger & Meyer 2004; Seehausen 2006). This is consistent with the view that ecological opportunity in the form of 'still-to-be-filled' niches plays — together with the readiness of the participating species to compete for those — a key role in triggering adaptive radiation (Schluter 2000). What might be even more important for rapid speciation in cichlids of the East African Great Lakes is the combination of habitat discontinuities (as observed along the lakes' shores) and the philopatric and stenotopic behaviour of many of the lakes' cichlid species. A number of studies on different species from Lake Malawi (and, more recently, also Lake Tanganyika) revealed high levels of population structure, providing strong evidence for the importance of 'micro-allopatric' processes in cichlid diversification (van Oppen *et al*. 1997; Arnegard *et al*. 1999; Markert *et al*. 1999; Rico & Turner 2002; Rico *et al*. 2003; Pereyra *et al*. 2004; Duftner *et al*. 2006; Sefc *et al*. 2007). In large lakes, the ample opportunities for local adaptation together with barriers to gene flow might additionally facilitate allopatric (or parapatric) speciation (Fryer 1959; Mayr 1984; Rico & Turner 2002; Salzburger & Meyer 2004), just as smaller satellites lakes might do (Greenwood 1965; Genner *et al*. 2007a). On the other hand, the relatively fine-scaled geographic structuring found in some rock-dwelling cichlids does not seem to be a general feature as at least some pelagic species show panmixis (Shaw *et al*. 2000) or limited geographic population structure (Taylor & Verheyen 2001).

Another external factor that appears to have influenced cichlid evolution — again in older and larger lakes — is fluctuation of the water level (both climatologically and/or geologically induced), which has repeatedly occurred in the history of East Africa's Great Lakes (Kornfield & Smith 2000; Sturmbauer *et al*. 2001). Lake Tanganyika, for example, was split into three to five smaller sub-basins several times during its history, when it was more than 500 m below its present level (note that today this lake is 1450 m deep) (Cohen *et al*. 1997). The level of Lake Malawi underwent similar fluctuations (Delvaux 1995), and for Lake Victoria, it is still debated whether or not the entire lake fell dry completely as little as 18 000 to 14 000 years ago and what effect such an event might have had on its endemic species assemblage (Johnson *et al*. 1996; Seehausen 2002; Fryer 2004; Stager & Johnson 2008). Clearly, the fauna of these lakes must have been heavily affected by such severe changes in the water level. A lake-level drop is likely to cause large-scale extinction and/or the collapse of species through secondary admixis of allopatric forms. On the other hand, secondary contact of formerly isolated populations could be seen as an ideal set-up for reinforcement to act. Hybridization itself may promote speciation and adaptive radiation via the intermediate step of novel 'transgressive' phenotypes (Salzburger *et al*. 2002a; Seehausen 2004; Parnell *et al*. 2008). The opposite scenario, a rise in the lake level, would open access to new habitats and lead to the splitting up of populations into geographically separated units, thus positioning small founder populations in allopatry. It is due to this combination of events that cyclic lake-level fluctuations are regarded as '*species pumps*' promoting speciation rather than as '*species dumps*' preventing it (Rossiter 1995; Kornfield & Smith 2000; Sturmbauer *et al*. 2001).

Diversification in cichlid adaptive radiations is presumably influenced by abiotic factors such as those mentioned above, as well as by chance and historical contingency in the form of, for example, seeding events or the presence of other species in the same habitat (Seehausen 2007). There is enough evidence, however, that the cichlids' unparalleled propensity for diversification is something inherent to the group, and not purely a consequence of ecological opportunity, chance, the vastness of the lake habitats in East Africa or fluctuation of the water level. Probably the best argument in favour of the exceptional position of cichlids is that about 20 other families of freshwater fishes are also present in the East African Great Lakes, but these have not diversified in a noteworthy manner (Fryer & Iles 1972; Greenwood 1984; Coulter 1991; Koblmüller *et al*. 2006). This is reinforced by the observation that among these other families, there are two catfish families and the Cyprinidae, which are otherwise species-rich and diverse. Still, none of these groups have radiated in a way similar to cichlids. The situation is not very different in water-bodies other than the three Great Lakes and outside of (East) Africa. In most of the lake systems, in which cichlids have undergone adaptive radiation, they dominate in terms of species number and eco-morphological diversity (see e.g. Barlow 1976; Greenwood 1984; Snoeks 2001). Finally, that speciation rates in cichlids are among the fastest known (McCune & Lovejoy 1998; Seehausen 2002; Coyne & Orr 2004), once more illustrates the distinctiveness of this group. Perhaps, it is the unique synergistic interaction of external factors (ecological opportunity, habitat structure in large tropical lakes) *and* intrinsic characteristics of the cichlids (life-history traits, evolutionary key innovations) that accounts for their evolutionary success.

Sex, jaws and rocky shores: naturally and sexually selected traits in adaptive radiations of cichlid fishes

So what are the intrinsic (biological) factors that underlie the cichlids' propensity for explosive speciation?

A promising approach to address this question is to identify traits that are relevant to the cichlids' evolutionary success by affecting fitness in natural populations, and to then focus on the genetic and developmental basis thereof. Fortunately, the quest for such traits is greatly facilitated by the replicative nature of cichlid adaptive radiations: characters that are persistently modulated in the same way in independent cichlid adaptive radiations (and features that emerged multiple times in the course of those radiations) are primary candidates for adaptively relevant traits. Such traits may have been shaped by natural and/or sexual selection. A distinction of whether *natural* or *sexual selection* was the primary force that drove the evolution of reproductive isolation also allows the grouping of the responsible underlying factors into *ecological* and *non-ecological* ones (Coyne & Orr 2004). In the following, I will discuss naturally and sexually selected traits that appear to be important in the adaptive radiations of cichlid fishes, and I will review what is known about their molecular basis.

Mouth morphology and trophic apparatus

A main ecological hypothesis to explain the cichlids' unique diversity refers to their highly adaptable mouth morphology (see e.g. Fryer & Iles 1972; Albertson & Kocher 2006; Streelman & Albertson 2006). Cichlid species differ greatly in their feeding apparatus and in the structure and dentition of their jaws (Fryer & Iles 1972; Rüber *et al*. 1999; Streelman *et al*. 2003b; Barluenga *et al*. 2006), suggesting that the jaw apparatus is a key element in niche adaptation in this group. The cichlids' trophic apparatus is a complex structure that consists of two independent functional units, the oral jaws primarily responsible for ingestion, and the pharyngeal jaws utilized for processing edible matter. Only a few families of fishes show jaw-like structures in the pharynx, and none of them surpasses the diversity of pharyngeal jaws seen in cichlids (see Fig. 2). Hence, it has been suggested that the particular architecture of the cichlids' pharyngeal jaw apparatus acted as an evolutionary key innovation (Liem 1973; Hulsey 2006).

Several recent studies have addressed the question of the genetic basis of adaptive differences in the cichlids' oral jaws and dentition. Albertson *et al*. (2003b, 2005) applied quantitative trait loci (QTL) mapping on the basis of crosses between Lake Malawi cichlids with different mouth morphologies. They provided evidence for strong selection on a few loci encoding oral jaw traits, and showed that the *bone morphogenetic protein 4* (*bmp4*) is one of the genes involved in mandibular morphology. This gene is also expressed in early tooth formation (Streelman & Albertson 2006), and it has been demonstrated that the pro-domain of *bmp4* shows an accelerated rate of protein evolution in East African cichlids (Terai *et al*. 2002c; Box 2). Interestingly, Darwin's finches also exhibit a strong correlation between *bmp4* expression and beak morphology (Abzhanov *et al*. 2004, 2006), making this growth factor a prime candidate for a universal modulator of trophic diversity. Other candidate genes for craniofacial bone development that emerged from cDNA microarray experiments with closely related Lake Victoria cichlids are *cimp1* (Kijimoto *et al*. 2005) and *magp4* (Kobayashi *et al*. 2006). Many more candidate genes for craniofacial development are available from zebrafish mutation screens (see e.g. Neuhauss *et al*. 1996).

Body shape and size

Cichlids show a great diversity in body shapes and sizes (Fryer & Iles 1972; Barlow 2000). Body shape in cichlids is primarily determined by the feeding strategy of a species and its preferred habitat (Clabaut *et al*. 2007). Thus, body shape is not really independent from the morphology of the trophic apparatus (Rüber & Adams 2001). Evolutionary parallelisms in body shape are quite frequent in independent cichlid assemblages (Kocher *et al*. 1993), which is yet another argument that body shape is an ecologically highly relevant trait that is primarily influenced by the action of natural selection (Clabaut *et al*. 2007). Whether body morphology and/or body size could also play a role in mate recognition in cichlids (see McKinnon *et al*. 2004 and Bolnick *et al*. 2006 for examples in other fish taxa) still needs to be investigated.

Although differentiation in body shape, such as the occurrence of benthic and limnetic morphs, is a common first step in ecological speciation in fishes (Schluter & McPhail 1992; Gíslason *et al*. 1999; Barluenga *et al*. 2006), little is known about the genetic mechanisms that underlie the morphological modifications involved. The exceptions are candidate (gene) loci obtained through QTL studies in stickleback (Shapiro *et al*. 2004; Albert *et al*. 2008) and lake whitefish (Rogers & Bernatchez 2007).

Coloration

It has long been noted that in some adaptive radiations — and in those of the cichlids in particular — the descendant species differ not only in ecologically relevant and, hence, naturally selected characters such as the mouth apparatus, but also in sexually selected traits such as coloration (Dominey 1984; Schluter 2000; Seehausen 2000). The

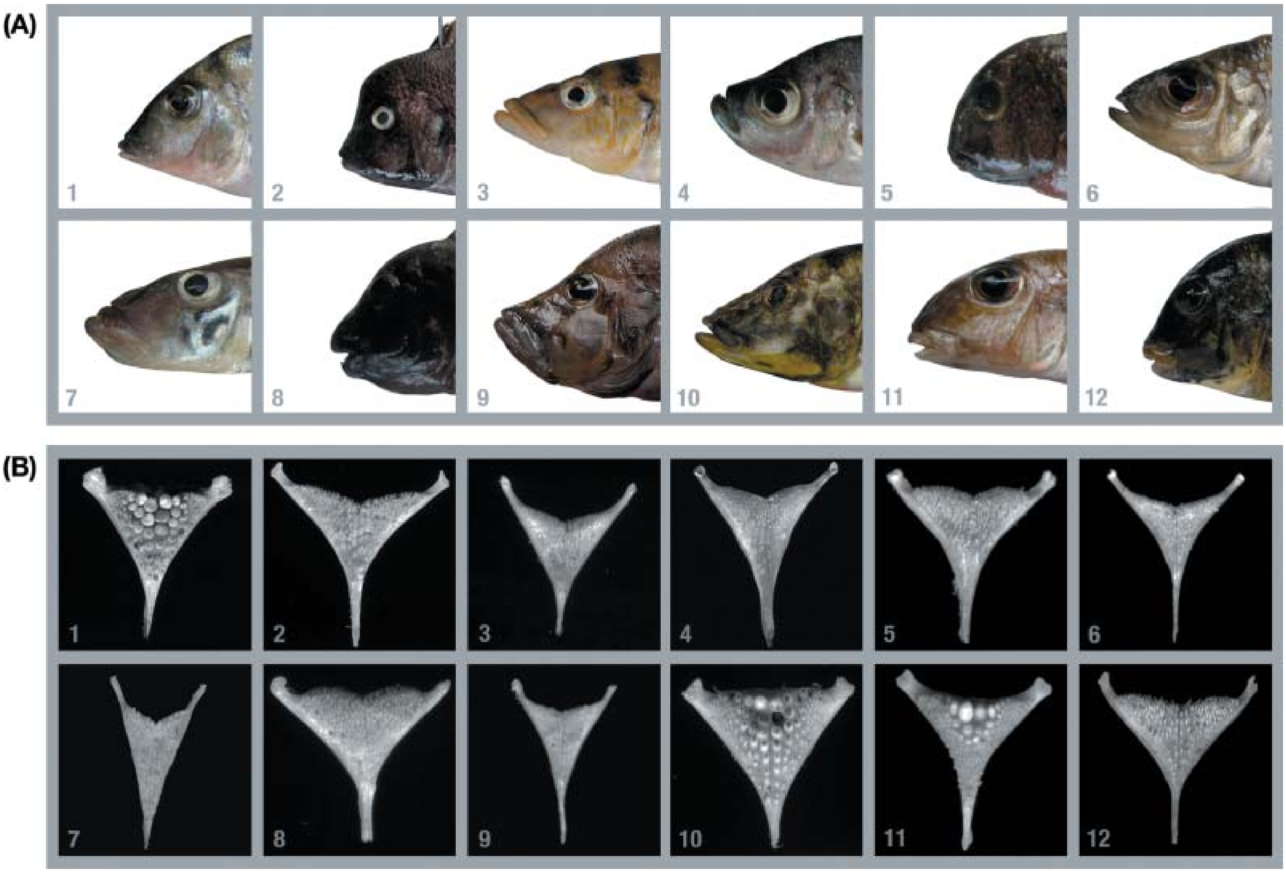


Fig. 2 Trophic diversity in cichlid fishes from Lake Tanganyika. (A) The different mouth morphologies and head shapes reflect the feeding strategies of the species. (B) Lower pharyngeal-jaw-bones of the same species. Pharyngeal jaws are a formation of the branchial skeleton and consist of an upper jaw located beneath the pharyngeal apophysis and a more mobile lower jaw representing the fusion of the fifth ceratobranchial bones. Just as the oral jaws, pharyngeal jaws are tooth-bearing. (1) *Tylochromis polylepis*, (2) *Cyphotilapia frontosa*, (3) *Lamprologus fasciatus*, (4) *Haplotaxodon microlepis*, (5) *Tropheus moorii*, (6) *Aulonocranus dewindtii*, (7) *Bathybates graueri*, (8) *Eretmodus cyanostictus*, (9) *Altolamprologus compressiceps*, (10) *Ctenochromis horei*, (11) *Xenotilapia boulengeri*, (12) *Simochromis diagramma*. Pharyngeal jaw scans were performed by M. Muschick. Note that the images have been adjusted in size to fit the boxes.

spectacular colour diversity and the sexual dimorphism prevalent in cichlid species flocks have led many authors to suggest that sexual selection via female choice of male (nuptial) coloration has played an important role in cichlid evolution (Turner & Burrows 1995; Seehausen & van Alphen 1999; Maan *et al*. 2006; Seehausen *et al*. 2008). Speciation by disruptive sexual selection has been proposed on the basis of field studies (van Oppen *et al*. 1998; Salzburger *et al*. 2006), laboratory experiments (Knight *et al*. 1998; Stelkens *et al*. 2008; van der Sluijs *et al*. 2008), and the observable breakdown of visual reproductive barriers under monochromatic light conditions or turbid waters (Seehausen *et al*. 1997a). Coloration is, furthermore, involved in inter- and intraspecific social interactions and in mimicry (Baerends & Baerends-Van Roon 1950; Wickler 1962; Fryer & Iles 1972; Salzburger *et al*. 2006). For example, the egg-dummies of males of the most species-rich group of cichlids, the haplochromines, mimic real eggs and play an important role in the breeding cycle of these maternal mouth-brooding fish (Wickler 1962; Hert 1989; Goldschmidt 1991; Salzburger *et al*. 2007). Like many other colour patterns, egg-dummies have also evolved repeatedly in cichlids (Salzburger *et al*. 2007; Box 1). Intrasexual selection through competition among males appears as another important component of colour evolution in cichlids (Seehausen & Schluter 2004). The evolution of nuptial coloration seems to be primarily driven by sexual selection. However, since coloration is also important in camouflage (at least in some species), and since some pigmentation patterns appear to be correlated to certain habitats (Seehausen *et al*. 1999), a naturally selected component in the evolution of cichlid coloration cannot be dismissed.

The inheritance of colour patterns has long been studied in fishes on the basis of crossing experiments (reviewed in Braasch *et al*. in press). Genes involved in colour and pigment pattern determination have mostly been investigated in

Box 2 Adaptive sequence evolution in cichlid fishes

Mutations in protein-coding DNA sequences can either lead to a change in the amino-acid sequence (which is termed a 'nonsynonymous substitution') or leave the amino-acid sequence unchanged ('synonymous substitution'). The rate of nonsynonymous substitutions (*d*N) over synonymous ones (*d*S) in a sequence alignment can then serve as indicator for the form of sequence evolution. Under purifying selection, much fewer nonsynonymous substitutions will be observed compared to synonymous ones (the latter are assumed not to be exposed to selection and, hence, to reflect the rate of neutral evolution). Under neutrality, the rate of nonsynonymous substitutions approaches the rate of neutral evolution so that *d*N is not significantly different from *d*S. Whenever there is strong selection favouring change, *d*N will become significantly greater than *d*S. This is called positive selection or adaptive sequence evolution.

Several genes have so far been found to show the signature of adaptive sequence evolution in cichlids (or subgroups thereof). Applying a large-scale database screen in cichlids, Gerrard & Meyer (2007) found high *d*N/*d*S ratios in several genes such as two MHC class IIB loci (as previously reported by Blais *et al.* 2007), in an *aromatase* P450 and in a gene called SPP120, which encodes for a protein with sperm-binding affinity. When comparing cichlid ESTs to those of other fish taxa, we recently identified four genes that are likely to have evolved under positive selection: the neuroendocrine *convertase subtilisin/kexin type 1*, *claudin 3*, *glutathione peroxidase 3*, and *ménage a trois 1* (Salzburger *et al.* 2008). In the East African haplochromine cichlids, the by far most species-rich group of cichlids (Box 1; Salzburger *et al.* 2005), adaptive sequence evolution has been found in *bmp4* that is involved in jaw formation (Terai *et al.* 2002c), in the egg-dummy related colour gene *csf1ra* (Salzburger *et al.* 2007), in the colour gene *hagoromo* (Terai *et al.* 2002b), and in several colour perception genes (Terai *et al.* 2002a; Spady *et al.* 2005). This once more corroborates the view that both the jaw apparatus and the mating system play an eminent role in cichlid diversification.

zebrafish and medaka, but recently also in other taxa (Parichy *et al.* 1999, 2000; Fukamachi *et al.* 2001; Quigley *et al.* 2005; Streelman *et al.* 2007; Braasch *et al.* in press). Thus, a series of candidate genes for colour determination exists from fish model systems that have been (or can now be) applied to cichlids (see for example Sugie *et al.* 2004). Terai *et al.* (2003) identified the F-box/WD40 repeat gene *hagoromo* (*hag*) as being involved in colour determination in cichlids and detected a greater complexity of alternatively spliced mRNA variants in this gene in the haplochromines. The same authors found accelerated protein evolution in a domain of *hag* in cichlids (Terai *et al.* 2002b; Box 2). Streelman *et al.* (2003a) mapped a specific colour morph found in several cichlid radiations, the orange blotch (OB) phenotype, and showed that OB is tightly linked to the *ski proto-oncogene* (*c-ski1*). Another transcription factor, the *colony-stimulating factor 1 receptor a* (*csf1ra*), was shown to be expressed in the yellow pigment cells (xanthophores) in the cichlids' egg-dummies in haplochromines *and* in ectodines (Braasch *et al.* 2006; Salzburger *et al.* 2007). In addition, *csf1ra* shows the signature of adaptive sequence evolution in the egg-dummy bearing haplochromine lineage (Box 2).

Colour perception

Colour vision in cichlids is essential in foraging behaviour, in adaptation to habitats with different light regimes (e.g. turbid waters or deep-water zones), as well as in intra- and interspecific communication (Terai *et al.* 2002a, 2006; Carleton *et al.* 2005; Spady *et al.* 2005). In vertebrates, colour perception is mediated through retinal photoreceptor cells containing visual pigments with different spectral sensitivities. These visual pigments consist of chromophores derived from vitamin A and different types of opsins (Yokoyama 2000). In cichlids, up to eight *opsin* genes have been identified, of which those that absorb the extreme ends of the light spectrum are the most variable (Spady *et al.* 2005; Terai *et al.* 2006). The association of the absorption spectra of visual pigments to the photic environment in which different species live — such as a blue-shift in *opsin* genes of deep-water species in clear lakes (Sugawara *et al.* 2002, 2005) — suggests that natural selection has played an important role in the evolution of colour perception genes. Yet, since colour vision is likely to influence female mating preference (Maan *et al.* 2006; Seehausen *et al.* 2008), these genes appear to also be involved in sexual selection.[2] This view is further substantiated by the recent discovery of incipient ecological by-product speciation as a consequence of divergent natural selection on visual pigments, which in turn may affect mate choice (Terai *et al.* 2006), and by the finding of speciation through sensory drive in cichlids from Lake Victoria (Seehausen *et al.* 2008).

In terms of its molecular basis, colour perception belongs to be the best-studied traits in cichlid evolution. Not only has the majority of genes been identified and characterized in a variety of cichlid species (Sugawara *et al.* 2002, 2005;

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[2] Note that this does not mean that the genes evolved under sexual selection themselves.

Terai *et al*. 2002a; Carleton *et al*. 2005, 2008; Spady *et al*. 2005), but these genes have also been studied in natural populations (Terai *et al*. 2006). Visual pigment complements also belong to those characteristics that have evolved in parallel in different cichlid assemblages. Deep-water cichlids in both lakes Malawi and Tanganyika, for example, have accumulated the same amino acid change in *rhodopsin 1* (*rh1*) (Sugawara *et al*. 2005). Several *opsin* genes have evolved under positive selection in cichlids (Terai *et al*. 2002a, 2006; Spady *et al*. 2005; Box 2).

Sound and smell

Apart from coloration, acoustic and olfactory cues may play a role in mate recognition in cichlids. Male cichlids are known to produce sound during courtship, and these sounds can differ between species (Amorim *et al*. 2004). Interestingly, it has been suggested that male cichlids deploy the pharyngeal jaw apparatus to produce their courtship sounds (Rice & Lobel 2002; Rice & Lobel 2003). Thus, the ecologically important pharyngeal jaw apparatus might have an accessory function in mate choice. That enzyme activity differs in the pharyngeal jaw musculature between the sound-producing males and silent females could be taken as argument that specializations in the muscle apparatus are involved in species-specific male acoustic cues (Rice & Lobel 2002, 2003).

Recent behavioural experiments also suggested that olfactory cues contribute to assortative mating in Lake Malawi cichlids (Plenderleith *et al*. 2005). Although little is known about the nature of odour-mediated communication in cichlids, it has been proposed that — just like in other groups of organisms — major histocompatibility complex (MHC) genotypes influence mate choice. Blais *et al*. (2007) detected adaptive sequence evolution in MHC class II in Lake Malawi cichlids, and suggested that MHC alleles, which play a central role in immune defence, evolve under local host–parasite co-evolutionary dynamics in this group. At the same time, the naturally selected MHC alleles may trigger by-product speciation by mediating mate choice (Blais *et al*. 2007).

Behaviour

Many authors have suggested behaviour as a key factor in cichlid evolution — in particular territorial behaviour, mating behaviour, and parental care (see e.g. Keenleyside 1991; McKaye 1991; Turner & Burrows 1995; Barlow 2000; Grosenick *et al*. 2007). These features set the cichlids apart from most other fish families in that they reach high levels of complexity: cichlids show various kinds of mating systems ranging from monogamy to different strategies of polygamy (often including territoriality of males); some species form harems or leks; others breed in empty snail shells and/or have evolved sneaker strategies; males often display conspicuous nuptial coloration (including facial stripe patterns or egg dummies; see above), perform courtship sequences, or build sand bowers to which females respond to (reviewed in Barlow 2000). Almost all cichlid species are engaged in long periods of parental care (Keenleyside 1991), either as substrate brooders guarding the brood close to the substrate from spawning, or as mouth-brooders carrying their offspring in the mouth. In some species, such as in the *Neolamprologus brichardi/pulcher* species complex of Lake Tanganyika, cooperative breeding has evolved in which juveniles of previous broods are recruited to aid in brood care (Taborsky 1984; Bergmüller *et al*. 2005). Since behaviour is involved in foraging, habitat choice, territoriality, social interactions, mating and breeding, etc., it can be regarded as both naturally and sexually selected. There is indeed strong evidence that the morphology of certain parts of the cichlid brain is correlated with environmental complexity while the morphology of other parts reflects the social system (Pollen *et al*. 2007). Comparatively little is known about the genetic basis of behavioural traits in cichlids. So far, most studies have concentrated on the analysis of differences in hormone levels between individuals showing distinct behaviour or social status (Burmeister *et al*. 2005; Bender *et al*. 2006; Hofmann 2006; Trainor & Hofmann 2006; Trainor & Hofmann 2007). Recently, also cDNA microarrays have been used to study gene expression in cichlid brains (Aubin-Horth *et al*. 2007).

Phenotypic plasticity

Phenotypic plasticity, i.e. the capability of an individual genotype to produce different environmentally induced phenotypes, is quite frequently observed in cichlids, which has led to speculations about its contribution to cichlid diversification (West-Eberhart 2003; Stauffer & Gray 2004). The most common examples of plasticity in cichlids relate to behavioural plasticity in response to social rank (Hofmann 2003; Aubin-Horth *et al*. 2007; Burmeister 2007) and to plasticity in the jaw apparatus (Sage & Selander 1975; Meyer 1987; Huysseune 1995; Stauffer & Gray 2004). Especially, the pharyngeal jaw apparatus shows a plastic response to different types of diet (in some species). The East African cichlid species *Astatoreochromis alluaudi*, for example, shows massive pharyngeal jaws when primarily feeding on snails (which it crushes with its pharyngeal jaws) but comparably thinner jaws when feeding on other types of food (Fryer & Iles 1972; Huysseune 1995).

Although the relative importance of phenotypic plasticity in evolution is unclear, there are some conditions under which phenotypic plasticity is plausible to result in directional selection, for example when it is costly (Price *et al*. 2003). A popular scenario suggests that alterations in behaviour may drive morphological and physiological evolution, assigning to the brain a key role in phenotypic plasticity (Price *et al*. 2003; West-Eberhart 2003; Burmeister 2007). Here is where cichlids have served as model for quite some time, so that some aspects of the molecular mechanisms underlying behavioural plasticity are known (Burmeister *et al*. 2005; Hofmann 2006; Aubin-Horth *et al*. 2007; Burmeister 2007).

An eminent role for the neural crest in cichlid evolution?

What many of the above-mentioned sexually and naturally selected traits in cichlids (such as coloration and pigmentation, the jaw and mouth apparatus, the midbrain, sensory neurons and parts of the body morphology) have in common is that they are, from a developmental perspective, derived from the neural crest (Kocher 2004; Albertson & Kocher 2006; Braasch *et al*. 2006; Streelman *et al*. 2007). The neural crest, an evolutionary innovation of the vertebrates (Shimeld & Holland 2000), is an embryonic cell population that originates early in development, at the neural plate border. Neural crest cells become migratory and give rise to pigment cells, neurons and glia of the peripheral nervous system, smooth muscle, craniofacial cartilage and bone (LaBonne & Bronner-Fraser 1999), as well as fin mesenchyme in fishes (Kelsh & Eisen 2000). A series of transcription factors, including *bmp4*, *fgf8*, *msx1* and *pax3*, are involved in the induction of the neural crest and the specification and migration of its cells (see e.g. LaBonne & Bronner-Fraser 1999; Albertson & Kocher 2006; Streelman *et al*. 2007). Neural crest-derived cell lineages, and, in particular, the genetic and developmental mechanisms that modulate their fates are thus of outstanding interest for the study of cichlid evolution.

The interaction and the relative importance of naturally vs. sexually selected traits in the adaptive radiations of cichlid fishes

Ecological and non-ecological factors have been suggested to act at different stages of cichlid adaptive radiations. Danley & Kocher (2001) proposed a three-stage model for the adaptive radiation of cichlids in Lake Malawi, in which disruptive sexual selection based upon nuptial coloration (their stage III) becomes the dominant mode of speciation only after an initial diversification into macrohabitats (stage I) and the adaptive radiation on the basis of divergent trophic morphologies (stage II) driven by disruptive natural selection. This model is based on the observation that the deepest split in the phylogeny of the Lake Malawi *mbuna* cichlids separates sand- from rock-dwellers, while — within these two groups — the different genera (defined by intermediate nodes in the phylogeny) have distinct mouth morphologies. Coloration (and possibly other cues) is then what distinguishes the many species within genera, suggesting that the third stage of diversification is mainly mediated through sexual selection (see also Streelman & Danley 2003). While it is less evident from this verbal model which factors were responsible for speciation events early in the radiation, it may be concluded that ecological factors are less important in the young splits.

A similar succession of events can be outlined for at least some of the lineages in Lake Tanganyika. This oldest of the East African lakes is home to a polyphyletic assemblage of cichlids, meaning that the lake has been colonized by several cichlid lineages independently (Salzburger *et al*. 2002b). Today, it constitutes an evolutionary reservoir of ancient East African cichlid lineages that are to be found nowhere else in the world (Nishida 1991; Salzburger *et al*. 2002b). At the same time, Lake Tanganyika appears to be the cradle for some younger lineages, possibly including the most species-rich group of cichlids, the haplochromines (Salzburger *et al*. 2002b, 2005; but see Genner *et al*. 2007b, who suggest that many of the Tanganyikan lineages predate the lake itself). On the basis of distinct genetic, morphological and ecological characteristics, the Tanganyikan cichlid assemblage has been divided in up to 16 main lineages — so-called tribes (Takahashi 2003).[3] These tribes sort according to macrohabitats, with some of them being confined to the shallow rocky habitat (Tropheini, Eretmodini), others to the deep rocky zones (Baileychromini, Cyphotilapiini), the open water above rocks (Benthochromini, Cyprichromini, Perissodini), deeper water habitats (Bathybatini, Limnochromini, Trematocarini) or intermediate (sandy) habitats (Boulengerochromini, Ectodini). The most species-rich Tanganyikan tribe, the substrate spawning Lamprologini, form their own radiation, are ecologically more diverse (Salzburger *et al*. 2002b; Salzburger & Meyer 2004), and have colonized different macrohabitats in the lake, ranging from shallow to deep rocky zones and intermediate habitats. Within the tribes, a diversification via ecological specialization is likely, since the different species primarily differ in mouth morphology, while the overall body shape remains relatively similar within tribes (Sturmbauer *et al*. 2003; Clabaut *et al*. 2007). Just as in Lake Malawi, an amazing diversity of colour-morphs exists within some of the Tanganyikan genera, e.g. within *Cyprichromis* (Brandstätter *et al*. 2005) and *Neolamprologus* (Konings 1998; Duftner *et al*. 2007), suggesting that here, too, sexual selection may have played a role in triggering the young splits.

For Africa's largest lake, Lake Victoria, it is difficult to infer the succession and the relative contribution of natural and sexual selection, which is primarily due to the lack of

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[3] Note that the species flocks of lakes Malawi and Victoria are made up of only one of these tribes, the Haplochromini, which also include the Tanganyikan Tropheini (Salzburger *et al*. 2005).

a phylogenetic hypothesis for the cichlid assemblage in this lake. More precisely, it is unknown whether the deepest splits in the assemblage are those separating major ecological guilds. With the Nicaraguan Midas cichlid species complex, there is, however, another comprehensively studied cichlid assemblage supporting the '*habitat-first rule*', i.e. that the initial steps of a cichlid radiation involve the splitting into ecologically distinct units. There, the evolution of new species in small but deep crater-lakes appears to be connected to the existence of a novel macrohabitat in the form of the open-water column above greater depths, which is absent in the larger ancestral lakes (Barluenga *et al*. 2006). Similar eco-morphological differences have also been observed in crater-lake cichlids in Cameroon (Schliewen *et al*. 2001). Yet, since these fishes differ in breeding coloration, too, it is unclear whether ecological specialization or mate choice was the initiating driving force of diversification.

That just like in other fishes (see e.g. McKinnon *et al*. 2004) ecological factors seem to govern early phases of diversification in cichlids does not answer a central question: *Is speciation in cichlids* overall *dominated by either ecological or non-ecological factors or do these interact equivalently to generate the cichlids' unparalleled diversity?* In terms of the underlying fitness-relevant traits, the question would then be whether it is a particular class of traits (and the genetic basis thereof) or whether it is the combination of several naturally *and* sexually selected traits that, together, are responsible for the cichlid's propensity for speciation. Cases of ecological by-product speciation (Terai *et al*. 2006), the great diversity of trophic morphologies, and the high frequency of parallel evolution are suggestive for a key role of natural selection in speciation in cichlids. Yet, because of the extent of similarity in these 'ecomorphs', it has also been questioned whether selection alone is sufficient to produce such parallelisms, or whether a developmental or genetic bias has influenced the direction of diversification in cichlids (Brakefield 2006; Box 1). It has also been argued that behavioural alterations may drive diversification in cichlids, e.g. through disruptive selection via female preferences for distinct male characteristics (see e.g. Turner & Burrows 1995). Similarly, preferences for different habitats and, hence, food types could — via plastic responses — immediately result in distinct phenotypes (Price *et al*. 2003) upon which sexual and/or natural selection may act. For a combination of ecological and non-ecological factors speaks that many traits are under the influence of both sexual and natural selection. Pharyngeal jaws, for example, are — as central components of the trophic apparatus — evidently ecologically relevant. At the same time, male cichlids seem to use them to produce courtship sounds.[4]

In summary, the question of the interaction and of the relative importance of natural and sexual selection in the adaptive radiations of cichlid fishes remains unanswered. It has often been argued that life history is the one factor that separates cichlids from other groups (see e.g. Dominey 1984; Barlow 2000). Life history would indeed provide a framework in which natural and sexual selection interact on small (geographic) scales. Not much is known, however, about the genetic basis of life-history differences in cichlids, making this question a prime target for future research — together with ecological and behavioural experiments (e.g. in the cichlids natural environments) aiming to understand the adaptive value of sexually and naturally selected traits.

The 'cichlidomics' era

With the currently ongoing sequencing of the Nile tilapia genome and of additional haplochromine genomes thereafter, the cichlids have entered the '-omics' era. This suffix, which tags holistic approaches towards the analysis of complex biological systems, virtually gains an additional meaning here: the hundreds of closely related cichlid species in East Africa themselves form such a complex system that is characterized by various levels of (ecological) interrelationships between the different species. Thus, with the cichlid genome in hand, it will not only be possible to study the totality of genes and their interactions in a single model organism, but it will also be possible to analyse and to compare the genomes, the transcriptomes, the proteomes, and the phenomes of hundreds of closely related, yet ecologically, morphologically and behaviourally distinct species. The following topic groups demonstrate that 'cichlidomics' (the application of evolutionary genomics to the cichlid system) has the potential to reach beyond the 'sequence first, ask questions later' strategy and to answer important questions in evolutionary biology and ecology.

Some 'basic' questions. There clearly is a question one cannot help asking when considering the unparalleled diversity of cichlid fishes. Is there something special in the genome of cichlids that allows them to radiate and, if so, are there genomic hotspots that are responsible for the cichlids' ability to adapt and to diversify? The cichlid genome sequences will, moreover, make it possible to address the questions whether, compared to other organisms, (i) the rate of molecular evolution is accelerated in cichlids; (ii) there is a larger number of evolutionarily relevant genes, e.g. transcription factors, in the cichlid lineage; (iii) there are more gene duplicates in cichlids and/or high level of copy number variation among cichlid species; (iv) there are unusual frequencies of active genomic features such as mobile genetic elements; and (v) the

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[4] Interestingly, pharyngeal jaws also appear to show, at least in some species, an adaptive plastic response to the preferred type of food (Meyer 1987; Huysseune 1995).

genes underlying fitness-relevant traits are physically linked.[5]

Finding the genes underlying naturally and sexually selected traits. The availability of several genomes will greatly facilitate the quest for genes underlying adaptively relevant characters in cichlids. For example, candidate genes from other (fish) model systems will become easily accessible for large-scale genetic, genomic and developmental experiments. Then, it will be possible to design microarrays covering the entire transcriptome to be used in gene expression assays. Also, by the integration of existing and future genetic maps, QTL can immediately be associated with candidate genes.

The behaviour of genomes in natural populations. Population genomic approaches appear highly suitable to study the cichlid system. On the one hand, genome-wide marker sets, such as SNPs, emerging from the cichlid genome project should be ideal for large-scale screens of natural cichlid populations, for association mapping, for F_{ST}–Q_{ST} tests, and for the determination of linkage disequilibrium. On the other hand, complete cichlid genomes should be conducive to the subsequent acquisition of massive sequence data for many more cichlids via high-throughput next-generation sequencing, as it should be possible to align the relatively short pieces of DNA emerging from these techniques to the reference genomes. Such sequences should be of great use in demographic analyses and in the study of genome evolution in natural systems.

cis-regulatory evolution vs. changes in the coding region. Heritable natural variation, which is the raw material for evolutionary processes such as adaptation and diversification, can be accomplished by mutations in coding or in the regulatory regions of genes. The relative importance of either mechanism for generating morphological diversity is currently under debate (see e.g. Carroll *et al*. 2005; Hoekstra & Coyne 2007). The closely related species in the cichlid adaptive radiations could aid in solving this dispute. Proponents of a dominant role of regulatory evolution often argue that this mechanism would more readily lead to adaptation and diversification compared to changes in protein-coding sequences (Carroll *et al*. 2005; Liang *et al*. 2008). Hence, explosively evolving lineages, such as the cichlids in East Africa, should predominantly rely on this mechanism. This is a testable prediction.

The molecular basis of parallel evolution. Finally, cichlid adaptive radiations are ideal to study parallel evolution and, hence, the relative importance of natural (and/or sexual) selection and of genetic and developmental constraints as determinants of organismal diversification (Brakefield 2006). Arendt & Reznick (2008) suggest five methods that are qualified to determine the genetic basis of parallel morphologies: hybrid complementation tests, QTL mapping, gene expression assays, gene sequence analyses and transgenic experiments. With the exception of the latter, these strategies are currently feasible or will become feasible with the completion of the cichlid genomes.

Conclusion

The species flocks of cichlid fishes are the most species-rich, extant animal adaptive radiations and powerful model systems to study the genetic basis of adaptation and diversification. The cichlid's evolutionary success has been attributed to the interaction of extrinsic factors such as ecological opportunity, habitat diversity, lake-level fluctuations, chance and historical contingency, as well as intrinsic factors in the form of adaptively relevant traits. Depending on whether these traits are predominantly under natural or sexual selection, they can be considered ecological and non-ecological. Naturally selected traits in cichlids are the *morphology of the trophic apparatus*, *body size and shape* and the adsorption spectra of *visual pigments*, while *coloration*, *courtship sound* and *smell* appear to be primarily sexually selected. The classification into sexually and naturally selected traits is, however, not always that clear-cut in cichlid adaptive radiations, as is illustrated by the recent discovery of ecological by-product speciation as a consequence of divergent natural selection on *visual pigments*, which also affects mate choice. Similarly, MHC alleles seem to evolve in response to local co-evolutionary dynamics, but might — at the same time — influence odour-based mate choice. Different aspects of *behaviour* also appear to be influenced by sexual and natural selection. Finally, it has been suggested that *phenotypic plasticity* could be important in cichlid evolution. All these traits and their underlying genetic and developmental pathways are promising candidates for the cichlid's unparalleled propensity for explosive speciation and adaptive radiation. The forthcoming cichlid genomes will greatly facilitate the quest for the genetic basis of diversification in this fascinating group of organisms.

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[5] A strong argument in favour of this hypothesis comes from theoretical work demonstrating that speciation is more likely and rapid if the loci controlling ecologically relevant traits and mating and habitat preferences become linked (Gavrilets 2004; Gavrilets *et al*. 2007). Here, sex chromosomes or sex determining loci with reduced levels of recombination could act as ideal genomic neighbourhoods for the evolution of physical linkage between genes underlying adaptively relevant traits (reviewed in Streelman *et al*. 2007).

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