Preface: Advances in cichlid research: behavior, ecology, and evolutionary biology

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With about 1,300 validly described species, but at least 2,200 species known, cichlid fishes (Cichlidae) represent the second most species-rich family of freshwater fish after the Cyprinidae (2,700 described species), and account for about 13% of extant freshwater fish diversity. They are naturally distributed from Central and South America, across Africa to Madagascar, and southern India. Throughout this distributional range, they have repeatedly demonstrated their capacity of forming adaptive radiations—explosive speciation with niche partitioning—generating an outstanding

variation of body shapes, color patterns, behavior, and ecomorphological specializations (e.g., Schlieven et al., 1994; Danley & Kocher, 2001; Joyce et al., 2005; Barluenga et al., 2006; Muschick et al., 2012; López-Fernández et al., 2013). This extraordinary diversity and an often stunning pace of speciation makes cichlid fishes particularly well suited for studying the factors and mechanisms underlying population differentiation, diversification, and speciation. They are now well established among the prime model systems in evolutionary biology research (Kocher, 2004; Seehausen, 2006). With the development of an increasing number of genetic and genomic resources, including the recent sequencing of several cichlid genomes (Brawand et al. 2014), cichlids will receive even greater attention in future evolutionary and ecological research.

This special issue comprises sixteen studies with a particular focus on behavior, ecology, and/or evolutionary biology of cichlid fishes. Together, they advance our knowledge of the mechanisms generating and maintaining the tremendous diversity of this freshwater fish family.

Over the last few decades, a multitude of studies have employed various approaches to shed light on the factors responsible for the stunning diversity within this family. An elaborate reproductive behavior and a highly developed pharyngeal jaw have long been recognized as important key factors for the cichlids' evolutionary success (Liem, 1973; Keenleyside,

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K. M. Sefc & T. Takahashi / *Advances in Cichlid Research:*
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1991). However, the picture is not simple as additional intrinsic factors like mouth morphology, body shape and size, coloration, color perception, sound and smell, and phenotypic plasticity, combined with ecological opportunity, appear equally important for driving diversification of cichlids (Salzburger, 2009; Takahashi & Koblmüller, 2011; Wagner et al., 2012; Maan & Sefc, 2013; Salzburger et al. 2014). In the current special issue, Burress (2015) reviews major ecological patterns associated with the evolutionary history of cichlids and discusses factors promoting ecological diversification as well as the consequences of ecological diversification by comparing and contrasting Neotropical and Afrotropical lineages.

The empirical studies included in this special issue focus on African cichlids, with a particular emphasis on the cichlids from Lakes Tanganyika and Malawi and riverine taxa, as well as on Central and North American representatives of the family.

East African Great Lakes

East Africa represents a particular hotspot of cichlid diversity and the extremely species-rich flocks endemic to the East African Great Lakes Tanganyika, Malawi and Victoria certainly represent the most spectacular vertebrate adaptive radiations (Turner et al., 2001; Koblmüller et al., 2008; Salzburger et al. 2014). Since the publication of the first reports on the East African fish faunas at the end of the nineteenth century (Boulenger, 1898, 1899a, b), the exceptional diversity of East African lacustrine cichlid fishes has attracted the attention of ichthyologists and evolutionary biologists. Ten papers included in this special issue target behavior, ecology, and population genetics in cichlids of the East African Great Lakes.

The population genetic structure of a species depends on both environmental factors and species-specific characteristics. Thus, habitat structure as well as differences in the degree of stenotopy and mobility bear on dispersal capacity and hence population connectivity in lacustrine cichlid species. This special issue includes two examples from Lake Tanganyika with opposing phylogeographic patterns. Koblmüller et al. (2015) studied the phylogeography of the world's largest cichlid species, *Boulengerochromis microlepis*, an endemic to Lake Tanganyika. They found that this highly mobile predator showed no

phylogeographic structure in a lake wide sample and that patterns of genetic diversity are indicative of recent population growth and/or potentially large variance in reproductive success in this extremely fecund species. Van Steenberge et al. (2015) studied *Tropheus duboisi*, a highly stenotopic rock-dweller with a patchy distribution in northern Lake Tanganyika, and found that this species, as predicted by its biology, exhibits pronounced levels of population genetic structure and considerable geographic variation in morphology.

Three studies addressed sexual and competitive interactions in Lake Tanganyika cichlids. Hermann et al. (2015) examined the effect of male body coloration and male territory characteristics on the mate preferences of female *Tropheus moorii* in the context of sexual selection within and reproductive isolation between populations. Pisanski et al. (2015) report a lack of sound production during competitive and sexual interactions of the cooperatively breeding *Neolamprologus pulcher*, which contrasts with evidence for acoustic communication in other cichlids and demonstrates that the evolution of complex social behavior in cichlids does not rely on acoustic signaling. The costs and benefits of cooperative breeding were the focus of the study by Garvy et al. (2015), which investigated contributions to territorial defense by dominant and subordinate members of social groups of *Neolamprologus savoryi*.

Lake Tanganyika's spectacular cichlid species flock likely hosts an even more diverse parasite community. The monogenean genus *Cichlidogyrus* appears to be particularly species rich, and previous studies have demonstrated extremely high levels of host specificity in the megadiverse littoral cichlid communities (Gillardin et al., 2011; Vanhove et al., unpublished). Here, Pariselle et al. (2015) describe a new *Cichlidogyrus* species and show that this species parasitizes a range of distantly related host species within the benthopelagic deepwater cichlid genus *Bathybates*, suggesting that reduced host specificity may represent an adaptation to low host availability in deep water habitat.

Four contributions focus on Lake Malawi's cichlid species flock, two of which highlight the importance of ecological opportunity and habitat discontinuities for the evolution of exceptional species richness in this lake's littoral habitats. Genner and Turner (2015) reconstructed past changes in effective population size

in several species and populations. They found that pelagic species were not significantly affected by late Pleistocene megadraughts ~100,000 years ago, whereas shallow-water and benthic taxa experienced rapid population expansion after the megadrought period. Given the extreme micro-endemism observed among shallow-water Lake Malawi cichlids, these findings suggest that many taxa have originated only since the last major lake level rise. Ding et al. (2015) examined the roles that various environmental variables have played for generating and maintaining the high diversity of Lake Malawi's rock-dwelling cichlid communities. They found that cichlid species diversity and functional diversity can be readily predicted by habitat complexity; whereas community similarity is strongly dependent on the geographical distance between communities. Many rock-dwelling cichlid lineages predominantly feed on epilithic algae. Maruyama et al. (2015) show that there is considerable microhabitat-level spatial variation in epilithic periphyton in the littoral zone of Lake Malawi potentially facilitating niche differentiation among rock-dwelling cichlid species. Habitat characteristics not only impact community structure but also intra-specific variation in body shape as evidenced by the study of Pauers and McMillan (2015), who conducted geometric morphometric analyses of body shapes in numerous populations of two *Labeotropheus* species. They found large variation in body shape among populations, hampering accurate species identification, and implying that estimates of species richness in the genus should be revisited.

African riverine cichlids

Although cichlids are found throughout Africa, riverine cichlids have traditionally been less enthusiastically studied by ichthyologists and evolutionary biologists because of low levels of diversity present in rivers and small lakes as compared to the spectacular lacustrine species flocks of the East African Great Lakes. This low species richness has been explained by reduced opportunities for niche differentiation in the comparatively unstable riverine environments (e.g., Joyce et al., 2005). Only recently, riverine cichlids have received increased attention as the source of lacustrine radiations and as ideal taxon for reconstructing African paleohydrology. This

special issue contains two studies on African riverine cichlids. Schwarzer et al. (2015) inferred the phylogeny and phylogeography of the Chromidotilapiini, a thus far largely understudied ancient cichlid tribe from West and Central Africa. They provide evidence for a thus far unknown link between West Africa and the Congo basin, implying a large ancient hydrogeographic corridor across half of the African continent. In general, diversification of this cichlid lineage appears to have been shaped mainly by paleogeographic patterns with ecological factors being less important. Egger et al. (2015) address the phylogeography and phenotypic variation of the basal haplochromine cichlid *Pseudocrenilabrus philander* from northern Zambia, including a population from the small and shallow Lake Chila. The study revealed quite complex phylogeographic patterns with evidence for past faunal exchange between currently separated river systems and admixture of divergent mtDNA lineages in Lake Chila, producing a hybrid swarm with large phenotypic variability. Such an increased phenotypic variation in a hybrid swarm has been proposed, and in part also shown to be an important pre-condition for rapidly generating species-rich cichlid radiations (Seehausen 2004; Joyce et al. 2011), and thus Egger et al.'s (2015) study has direct relevance also for research on the large lacustrine species flocks.

Central American cichlids

In the Americas, cichlids are distributed from Argentina in the south to the southern US in the north, with the genus *Herichthys* being the northernmost cichlid genus, occurring from Mexico north to Texas. This special issue includes two contributions about the genus *Herichthys*. De la Maza-Benignos et al. (2015) describes the genus *Nosferatu*, which they separate from the genus *Herichthys*, as well as a new *Herichthys* species. By integrating phylogeographic analyses with information about paleogeology and paleoclimatology, the authors put forward biogeographic hypotheses for both genera. Oldfield et al. (2015) provide an in-depth account of the parental care behavior of *Herichthys minckleyi*, which, unlike its monogamous close relatives is polygynous and exhibits pronounced sexually dichromatic reproductive coloration. By combining phylogenetic and behavioral

analyses, this study infers how and why the unique body coloration, mating system, and parental care behavior in *H. mickleyi* evolved. Also addressing the evolution of brood care, Wisenden et al. (2015) correlate parental brood defense with larval anti-predator competence in the convict cichlid *Amatitlania siquia*. They suggest trait co-evolution driven by interactions between parental care behavior, swimming performance of young, and habitat-specific predation pressure.

Taken together, the selection of papers presented here furthers our knowledge about the environmental factors and evolutionary processes that have contributed to the outstanding behavioral, morphological, ecological, and genetic diversity among cichlid fishes. However, this information is not only relevant to this exceptional family of vertebrates. The messages established by the research have considerable wider relevance for our understanding of evolution of biological diversity in general.

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