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

Stephan Koblmüller · R. Craig Albertson · Martin J. Genner · Kristina M. Sefc · Tetsumi Takahashi

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With currently 1703 valid species, 195 of which have been described only in the last ten years (Eschmeyer & Fong, 2017), and several hundreds more that still await formal description, cichlid fishes are among the most species-rich families of freshwater fish. They are naturally distributed from southern North America to southern South America (570 species), across most of Africa (1100 species), in southern Iran (1 species), Madagascar (29 species), and the Indian sub-continent (3 species) (Eschmeyer & Fong, 2017). They are famous for their extraordinary diversity and rapid speciation, and are well established as a prime model system in evolutionary biology research (e.g., Turner, 2007; Santos & Salzburger, 2012; Brawand et al., 2014; Henning & Meyer, 2014). A multitude of publications on cichlid fish has furthered not only our understanding of the factors and processes that underlie the diversification of this exceptional fish family, but also our knowledge of the evolution of biological diversity in general. Considering the importance of cichlids, a special issue was devoted to behavioral, ecological, and evolutionary biological research on cichlid fish in 2011 (Koblmüller et al., 2011). We were overwhelmed by the enthusiastic response to our call for contributions and the positive feedback by the readers of this first special issue on cichlid research. Since then, we have continued a series of special issues on cichlid fishes, which was hosted by *Hydrobiologia* since 2015 (Koblmüller et al., 2015). The importance of these volumes is underscored by recent reminders of the anthropogenic threats to cichlid-dominated habitats (e.g., Seehausen et al., 1997; Tweddle et al., 2015; Abila et al., 2016; Cohen et al., 2016). The prospect of oil drilling in the Great Lakes of East Africa in particular (Abila et al., 2016) is a chilling reminder of the sensitivity of these fishes and their ecosystems, and motivates us to inform the scientific and general public about the importance of these fascinating and unique species.

The current special issue presents a collection of seventeen papers that tackle various aspects of cichlid

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S. Koblmüller (✉) · K. M. Sefc
Institute of Zoology, University of Graz, Universitätsplatz 2, 8010 Graz, Austria
e-mail: stephan.koblmueller@uni-graz.at

R. C. Albertson
Department of Biology, University of Massachusetts, Amherst, MA, USA

M. J. Genner
School of Biological Sciences, Life Sciences Building, 24 Tyndall Avenue, Bristol BS8 1TQ, UK

T. Takahashi
Institute of Natural and Environmental Sciences, University of Hyogo, Yayoigaoka 6, Sanda, Hyogo 669-1546, Japan

behavior, ecology, evolutionary biology and genomics. Together, they advance our knowledge of the mechanisms generating and maintaining the tremendous diversity within this freshwater fish family. Naturally, the studies included in this special issue do not fully represent all fields of research that have contributed to what we know about cichlids and their evolution. Nonetheless, they do represent rich and diverse knowledge, which we are happy to share with the readers of *Hydrobiologia*. Below, the papers are briefly summarized in the order in which they appear in this special issue.

East African Great Lakes

The East African Great Lakes' biodiversity has awed scientists since the beginning of its exploration (e.g., Boulenger, 1899; Worthington, 1937). These lakes are renowned biodiversity hotspots, hosting a remarkable set of radiations of both invertebrates and fishes, of which the largely endemic cichlid species flocks, counting several hundred species each, are the most famous and species rich (Turner et al., 2001; Koblmüller et al., 2008; Salzburger et al., 2014). Twelve papers included in this special issue target various aspects of evolution, ecology, and behavior in cichlids of the East African Great Lakes. Takahashi-Kariyazono et al. (2017) investigated the evolution of c-type lysozyme, an enzyme involved in the innate immune system, during the adaptive radiation of East African cichlid fish. Based on Southern blot and sequence-based analyses, they found that while all Lake Tanganyika cichlid species investigated have only one copy of the c-type lysozyme gene, haplochromine cichlids from Lake Victoria and Lake Malawi have two and four copies, respectively. Furthermore, many of the inferred amino acid substitutions were found to change the charge of amino acid residues, changing the optimum pH for enzymatic activity. These findings are suggestive for an important role of lysozyme gene duplications and amino acid replacements in defense mechanisms against bacteria in environments with different salt concentrations, pH, or temperature, and a particular role of these genes in the radiation of the extremely species-rich tribe Haplochromini.

An important issue in studies of population differentiation and speciation relates to the timing of divergence events, and how these relate to past environmental changes. Four studies on Lake Tanganyika cichlid fish address the role of habitat fragmentation and changing lake levels on patterns of population genetic differentiation, divergence, and hybridization. Winkelmann et al. (2017) asked if divergence of rock-living and shell-living "ecomorphs" of *Telmatochromis temporalis* could have been driven by the availability of new habitat that followed the last major rise in lake level that took place approximately 100 kya. Using information within mitochondrial DNA sequences, they were able to determine that local ecomorph divergence and local population expansions most likely post-date the lake-level rise. Thus, the results are consistent with divergent evolution into ecomorphs taking place in response to the availability of new habitat, consistent with theory of "ecological opportunity" as a promoter of adaptive radiation. Koblmüller et al. (2017) investigated the phylogeographic structure in two closely related species of the genus *Altolamprologus*. Using mitochondrial and nuclear DNA sequences, they found (a) that divergence between these two species was fairly recent (approximately 100 kya) and proceeded with little if any gene flow, (b) that a geographically restricted divergent haplogroup originated from ancient introgression, and (c) that habitat-induced population fragmentation contrasts with weak phylogeographic structure, a pattern consistent with low levels of periodic gene flow mediating genetic connectivity across large geographic distances. The studies by Sturmbauer et al. (2017) and Sefc et al. (2017) focus on cichlids of the genus *Tropheus*, highly stenotopic rock-dwellers of the shallow littoral zone from the north and south of the lake, respectively. Both studies found, based on a combination of mitochondrial and nuclear markers, that the present population genetic structure is highly complex and shaped primarily by past and current habitat fragmentation and recurrent Pleistocene lake-level fluctuations. In Sefc et al. (2017), the observed pattern of unidirectional introgression across a large habitat barrier in the south of the lake is best explained by habitat change-driven population extinctions that truncated a previously symmetric admixture zone. At the opposite (northern) end of the $\sim$700-km-long lake, Sturmbauer et al. (2017) related repeated introgression between genetic lineages and lake-level fluctuations.

Another study on Lake Tanganyika cichlids targets the relationships between feeding behavior and tropic morphology. Tada et al. (2017) studied trophic morphological traits in the predominantly herbivorous tribe Tropheini. They found differences both within and among ecomorphs, namely grazers and browsers. While morphological and phylogenetic distances are significantly correlated in grazers, no such correlation was observed in browsers. These differences in trophic morphological traits among species likely facilitate niche partitioning by utilizing slightly different microhabitats, which enables the coexistence of several closely related species along the same rocky shore. Despite ecological differentiation, this coexistence is of course accompanied by interspecific competition. In this issue, Ochi et al. (2017) address the interaction between the zoobenthivorous *Neolamprologus mustax* and the algivorous *Variabilichromis moorii*. Consistent inter-individual variation in the behavior of *V. moorii* towards *N. mustax* as well as the selective use of particular *V. moorii* territories by *N. mustax* suggests that the structure of their interactions is shaped by personality and recognition of individuals and/or territories.

Communication among fishes employs a variety of modalities, including sound. In their study on sound production in the cooperatively breeding *Neolamprologus pulcher*, Spinks et al. (2017) discovered the emission of unusually high-pitched sound. Interestingly, the species remains silent in the low frequencies which are typical for the acoustic signals known of fish, including many cichlids.

One study focuses on Lake Malawi cichlids. In African cichlid fishes, the mating behaviors and reproductive strategies have been studied relatively well, but the diversity in genital morphology has been little studied. Moore & Roberts (2017) compared genital morphology among two riverine and eleven Lake Malawi cichlid species. They found that sexual differences in genital morphology of Lake Malawi cichlids are greater than those of the riverine species, which may reflect a difference in their evolutionary histories. This study also proposes the possibility that the sexual dimorphism of genital morphology may be used for reliably sexing individuals without killing them and extracting the gonads from the fish.

Three studies included in this special issue target the radiation of Lake Victoria cichlids. This species flock is renowned for very rapid speciation and characterized by rapid diversification in both ecologically relevant morphology and ecological niche space. Theory predicts that such early-stage divergence should be constrained along phenotypic "lines of least resistance," characterized by tight associations between measurable traits. Lucek et al. (2017) tested this idea, and found that most divergence events were indeed along such lines of least resistance. Notably, they also discovered intriguing evidence that interspecific hybridization can relax these constraints, potentially speeding up adaptive divergent evolution. Thus, these results provide further alternative support for a creative role of hybridization in adaptive radiations, as suggested by studies of transgressive segregation. There are increasing concerns about the effect of human activities on the fish communities of the African Great Lakes. One of the largest changes over the history of Lake Victoria took place during the 1980s when there was major loss of cichlid fish biodiversity driven largely by predation from invasive Nile perch. This was accompanied by extensive eutrophication of the system linked to deforestation and expansion of agriculture within the lake catchment. Kishe-Machumu et al. (2017) ask if it is possible to compare the diet of Lake Victoria haplochromines before (1977–1982) and after (2005–2007) these major changes, using stable isotope as dietary tracers in formalin-preserved fish. The results demonstrated that species in the historic ecosystem exhibited greater levels of niche partitioning than today, suggestive of environmental change broadening diets, either from shifts in resource availability or choosiness. Similarly, van Rijssel et al. (2017) asked how isotopic signatures varied over time (1978–2011). Their results were also consistent with temporally changing diets in Lake Victoria cichlids, and in this case the data indicated that the diet shifts potentially reflected changes to primary productivity. Clearly, there is still a lot to learn about how Lake Victoria has changed, and with this in mind it is valuable to know that historic samples can provide insight into past ecological process as well as changes to species richness.

Riverine cichlids from Africa and the Middle East

While the cichlid species flocks of the East African Great Lakes are famous both among scientists and aquarists, the cichlid fauna of African (and Middle Eastern) rivers and small lakes is much less known, even though their species richness is, although admittedly less diverse than that of the Great Lakes, high and dramatically underestimated, with numerous recent phylogenetic and phylogeographic studies reporting a large number of hitherto undescribed species (e.g., Schwarzer et al., 2011; Koblmüller et al., 2012; Egger et al., 2015; Genner et al., 2015). Two contributions to this special issue target riverine cichlids in Africa and the Middle East.

The genus *Iranocichla* from southern Iran is the easternmost representative of the African cichlid clade and was thus far considered to be monotypic. Schwarzer et al. (2017) surveyed populations of *Iranocichla* for phenotypic variation and inferred phylogeographic patterns based on mitochondrial DNA data. They found conspicuous differences in male nuptial coloration that coincided with considerable genetic distances among populations from distinct river systems, which the authors interpreted as evidence for the existence of at least two allopatric species in this genus. Diversification within *Iranocichla* was found to have started in the middle to late Pleistocene, with the late Quaternary sea-level fluctuations shaping present-day distribution of haplotypes, analogous to the role of lake-level fluctuations in the East African Great Lakes.

Introductions of alien species might pose a considerable threat to an ecosystem, and are considered one of the most important causes of extinctions worldwide (Canonico et al., 2005). In Africa, numerous cichlid species have been translocated intentionally or accidentally, and established viable populations in non-native habitat. Decru et al. (2017) report on the occurrence of an Eastern African haplochromine cichlid in the Ituri River, a northeastern tributary to the Congo River. Based on morphological characteristics, the Ituri River individuals were assigned to a species known from the Lake Edward/George system, which probably has accidentally been introduced into the Ituri River together with tilapias used in aquaculture. Small, but significant, morphological differences especially in head morphology between the Ituri River and the native populations suggest rapid morphological adaptation to a riverine habitat in this originally more lacustrine cichlid species, once again highlighting the adaptive potential of cichlids.

American cichlids

In the Americas, cichlids are found from the southern US in the north to Argentina in the south. With 570 valid species (Eschmeyer & Fong, 2017), cichlids constitute an important part of the American ichthyofauna and numerous studies aimed at identifying the factors and processes underlying the diversity of American cichlids (e.g., Hulsey et al., 2010; López-Fernández et al., 2012, 2013). As there are no large lakes harboring species-rich cichlid radiations, the vast majority of American cichlids are found in the numerous, often large, rivers. Usually, spatial turnover in fish assemblages is attributed to the presence of dispersal barriers, whereas other factors such as environmental properties and biotic interactions are assumed to be of less importance. By analyzing cichlid fish assemblages along a large river without significant hydrogeological barriers—the upper Río Madera in Bolivia, Brazil, and Perú—Hablützel & Pantel (2017) were able to show that, at least in this drainage system, spatial turnover in cichlid assemblages has been determined by climate and ecological gradients, and possibly also habitat structure and biotic interactions. Hence, physical dispersal barriers are not necessarily required for structuring fish assemblages along a river's course.

Elaborate parental care is considered to be a promotor of the evolutionary success of cichlid fishes. Biparental care—rare in fishes in general but common in cichlids—raises opportunities for the division of labor and possibilities for sexual conflict. By staging intruder experiments and quantifying male and female defense efforts in *Amphilophus labiatus*, Sowersby et al. (2017) identified sexual differences in defense behavior, which changed over the course of the breeding cycle, and emphasize that both the sex of the parent and the developmental stage of the brood influence parental behavior.

Novel genomic resources

The publication of the first cichlid genomes (Brawand et al., 2014) launched a new era in cichlid research. DNA methylation is the process by which methyl groups are added to DNA, which in turn modifies the structure and function of the DNA molecule. This "epigenetic" modification of DNA has been shown to play important roles in regulating gene expression, and thus is essential for organismic development. Cytosine is the predominant nucleotide to be methylated in vertebrates, but patterns and rates of cytosine methylation (e.g., the methylome) can differ significantly between species. Thus, it has been suggested that divergence in DNA methylation might be associated with species divergence. In the paper by Chen et al. (2017), the authors report the first detailed methylome for the Nile tilapia. Using a combination of methylated DNA immunoprecipitation and high-throughput sequencing, they identified several hundred methylation peaks in both tilapia ovaries and testes. Approximately 60 genes showed differential methylation rates between ovaries and testes. Results were verified using qPCR and bisulfite sequencing. All the results provide both a robust methylation map for tilapia as well as a list of candidate genes for sex differentiation and/or maintenance in this species.

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