Preface: advances in cichlid research III: behavior, ecology, and evolutionary biology

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The hyperdiverse freshwater fish family Cichlidae accounts for approximately 10% of today's teleost diversity. For decades, researchers have been thrilled by their enormous diversity in morphology, behavior, and ecology, and by the stunning speciation rates in their adaptive radiations (e.g., Boulenger, 1898; Kosswig, 1947; Fryer, 1960). Today, cichlids are undisputedly among the prime model systems in evolutionary biology research (e.g., Salzburger, 2018).

The current special issue is the third in a series of special issues published in *Hydrobiologia* exclusively devoted to cichlid research and presents a collection of 22 papers that focus on various aspects of cichlid behavior, ecology, conservation, evolutionary biology, and genomics. Together, they advance our knowledge of the mechanisms generating and maintaining the tremendous diversity within this freshwater fish family. Below, the papers are briefly summarized in the order in which they appear in this special issue.

Guest editors: S. Koblmüller, R. C. Albertson, M. J. Genner, K. M. Sefc & T. Takahashi / Advances in Cichlid Research III: Behavior, Ecology and Evolutionary Biology

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Time scale of cichlid diversification

The timescale of cichlid evolution has proven difficult to determine, as molecular phylogenies calibrated by biogeographic and fossil calibrations have often generated strongly contrasting results. Did American and African cichlid fishes diverge when the continents separated 100 million years ago, or did cichlid fishes disperse across the Atlantic at a later date? Matschiner (2019) reviewed the datasets and phylogenetic approaches that have been used to investigate this issue, and conducted re-analyses using more contemporary approaches. Matschiner concludes that the most likely timescale of divergence between American and African cichlids would be 75–60 million years ago and therefore that one or more marine dispersal events must have taken place.

Generally, one major problem that hampers robust divergence time inference in cichlids is the sparsity of fossils that can be used to calibrate time-trees. Any new reliably identified and dated fossils are more than welcome by cichlid researchers in their struggle to put cichlid diversification in a temporal context. By describing the thus-far oldest reliably identified haplotilapiine cichlid, †*Rebeccachromis* gen. nov. (tentatively placed in the tribe Etiini), from the middle-to-late Miocene (c. 11 MYA) from the Central Kenya Rift, Kevrekidis et al. (2019) provides a robust minimum constraint for the age of haplotilapiine cichlids. In addition, Kevrekidis et al. discuss how extensive volcanic activity in the region might have facilitated the evolution of haplotilapiine cichlids.

East African Great Lakes

The East African Great Lakes are known for their extremely species-rich and largely endemic cichlid species assemblages. Lake Tanganyika is the deepest and oldest of these lakes and harbors the genetically, eco-morphologically and behaviorally most diverse cichlid species assemblage, even though the number of recognized species for Lake Tanganyika is considerably lower than for Lakes Malawi and Victoria (Turner et al., 2001; Koblmüller et al., 2008). Among the many eco-morphological convergences across lakes (Kocher et al., 1993; Santos & Salzburger, 2012), feeding on scales of other fish is certainly among the most peculiar ones. Even though scale-eating species are also found in other lakes (Fryer & Iles, 1972), their diversity is the highest in Lake Tanganyika. There, they show varying degrees of dependence on scales for food (Takahashi et al., 2007), with *Perissodus micolepis* being the most specialized scale eater, exclusively feeding on scales. This highly specialized feeding behavior goes along with a clear left–right head asymmetry that has become a textbook example of balanced polymorphism. Raffini & Meyer (2019) provide a comprehensive review of the genetics, development, and adaptive significance of head asymmetries in *P. micolepis*. This review is timely, as the publication of partially contradictory results over the past 10 + years has complicated our understanding of this system. The authors reviewed this body of literature, which includes evidence for both genetic and nongenetic sources of skull/jaw asymmetries, and

provides a roadmap for future studies in this fascinating yet complex system. Scale eaters were also studied empirically for this special issue. Based on morphological assessment and partial sequences of the mitochondrial ND2 gene of ingested scales, Kovac et al. (2019) investigated the prey spectrum of *P. micolepis* in southern Lake Tanganyika. They found that larger fish take larger scales and that *P. micolepis* feeds on a wide prey range that reflects the typical cichlid communities in the lake's rocky littoral zone, indicating that *P. micolepis* is an opportunistic feeder.

Another niche that is occupied by cichlids in all East African Great Lakes is that of pelagic piscivores (Witte & van Oijen, 1990; Coulter, 1991; Turner et al., 2002). Little is known about their population genetic and phylogeographic structure. Previous work on large (benthopelagic) piscivores from Lakes Malawi and Tanganyika revealed a lack of phylogeographic structure on lakewide scales (Genner et al., 2008; Koblmüller et al., 2015), leading to the expectation that this might be true for all highly mobile large eupelagic and benthopelagic predators in these lakes. Koblmüller et al. (2019) tested this hypothesis in four deepwater species of the tribe Bathibatini from Lake Tanganyika. They found that only eupelagic species show panmixis on a lakewide scale, whereas a clear phylogeographic structure was detected in benthopelagic species, and they propose that different predatory niches (i.e., preferred prey species) are responsible for differences in patterns of genetic diversity between eupelagic and benthopelagic species.

Paedophagous cichlids *sensu stricto*, i.e., species that exploit the buccal phase of mouthbrooding by ramming the heads of mouthbrooding females and feeding on the then-released eggs or larvae, are only found among the haplochromine cichlids from Lake Malawi and the Lake Victoria region, but are absent from Lake Tanganyika. Thus far, only very few species have been reported to show this peculiar behavior. Vranken et al. (2019) focused on the paedophagous cichlids from Lake Edward, a thus-far understudied Great Lake of the Upper Nile region. In general, the taxonomy of cichlid fish endemic to the Lake Edward system is still immature, but even if the total number of cichlid species in this lake is still unknown, it is clearly smaller than in the larger and more intensively studied Lakes Tanganyika, Malawi, and Victoria (Turner et al., 2001). In their study,

Vranken et al. (2019) provide evidence for five paedophagous cichlids in Lake Edward, three of which are new to science and formally described.

In all East African Great Lakes, the diversity of cichlid species is the highest in the rocky littoral zone, which is not surprising as many of the species are highly stenotopic rock-dwellers for which already very minor stretches of unfavorable habitat might pose significant barriers to gene flow (Rico & Turner, 2002; Sefc et al., 2017a), facilitating allopatric diversification. Whether allopatrically distributed populations are subject to diversifying selection has been rarely explicitly tested in cichlid populations (Mattersdorfer et al., 2012). Recently, hybridization facilitated by rearrangements of dispersal barriers, for instance, in the wake of lake-level fluctuations, has been suggested to constitute a selection-free pathway to phenotypic diversification (Sefc et al., 2017b). To determine whether population-level differences in phenotype were more likely due to active selection or neutral drift, Husemann et al. (2019) compared patterns of genetic and phenotypic divergences across populations of the Lake Malawi species *Maylandia zebra*. They focused on traits that are subject to both natural and sexual selection. They found that general levels of phenotypic divergence exceeded those of neutral genetic divergence, which is consistent with diversifying selection as a driver of population-level differences.

Why do some lineages evolve more rapidly or extensively than others? In their article, Albertson & Pauers (2019) tested a series of hypotheses related to this question using geometric morphometric data in three genera of Lake Malawi rock-dwelling cichlids. They found that levels of morphological disparity, a measure of realized evolutionary potential, did not differ between ecologically diverse and constrained lineages. Rather, disparity was found to be three times higher in species with lakewide versus more limited distributions. This work underscores the complex interplay between ecology and phylogeny in shaping patterns and levels of morphological variation.

Parasites are increasingly recognized as an important factor for shaping patterns of diversification of their hosts (Morand, 2015; Betts et al., 2018). However, to what extent parasites have shaped cichlid adaptive radiations is still largely unknown. Meyer et al. (2019) explored the potential role of parasites for the cichlid radiation in Lake Tanganyika. In a

phylogenetically controlled analysis, they compared metazoan parasite infection levels, genetic diversity at the major histocompatibility complex (MHC; important in vertebrate immunity), trophic ecology, and morphology among tribes. Indeed, significant proportions of the variation in parasite abundance and MHC variation are explained by morphology and trophic ecology, respectively. These findings imply that parasites and immunogenetic adaptation might be more important for cichlid diversification than previously assumed.

In addition to highly complex social behaviors and diverse morphologies, cichlid fishes exhibit a striking variation in body coloration. A large amount of previous work have identified numerous selective forces involved in origin and divergence of cichlid body coloration, but we are still far from understanding the genomic, transcriptomic, and physiological bases of color diversity in cichlids (Maan & Sefc, 2013). Border et al. (2019) investigated the physiological mechanisms regulating body color change from blue to yellow in males of *Astatotilapia burtoni*, a species distributed in the lower reaches of tributaries to Lake Tanganyika and in the lake proper close to river mouths. In their study, evidence for a role of the melanocortin system comes from the observation that administration of α -melanocyte-stimulating hormone increased yellowness of the body due to pigment dispersion of the xanthophores. In contrast, social stress did not influence the expression of color phenotype. Intraspecific color variation was also the focus of the study by Takahashi (2019), who examined the ultimate causes for pale and dark coloration of the shell-breeding *Telmatochromis temporalis*. Based on data about habitat use, the visual anti-predator adaptation of the dark individuals was attributed to pattern matching, i.e., mingling of dark fish with the shadows of shells, rather than crypsis in the darkness within shells, while pale fish tend to prefer sandy bottoms.

Competition among siblings for limited resources, particularly food provided by parents, is usually nonviolent, but aggression between siblings does occur in some species (Mock & Parker, 1997; Roulin & Dreiss, 2012). So far, no studies are available that target the effect of food availability on sibling aggression in species without parental provisioning. Satoh et al. (2019) used field observations and experiments to monitor the dynamics of aggression among siblings in broods of *Neolamprologus furcifer*,

a substrate-breeding Lake Tanganyika cichlid species, in relation to age-dependent food type, hunger level, and food availability. Although the study is the first to address sibling aggression in species without parental provisioning, even human parents may gain hope from the distinct effect of increased food supplies on domestic peace.

East African rivers and crater lakes

For decades, much of the research on African cichlid fishes has focused on the species-rich assemblages in the Great Lakes, and only recently the cichlid faunas of rivers and smaller lakes have received increasing attention (e.g., Stelkens & Seehausen, 2009; Hermann et al., 2011; Egger et al., 2015; Malinsky et al., 2015; Decru et al., 2017; Moser et al., 2018). It emerges that the cichlid diversity and degrees of endemism in these water bodies are much higher than previously assumed (e.g., Koblmüller et al., 2012; Genner et al., 2015; Schedel et al., 2018).

A growing concern for freshwater ecologists and evolutionary biologists is the threat to river and small lake biodiversity from invasive species. Native oreochromine cichlids in particular are vulnerable to hybridization with invasive tilapia (Deines et al., 2014; Shechonge et al., 2018) as they are distributed around Africa for aquaculture and attempt to improve fisheries yields. In this issue, Shechonge et al. (2019) report unexpectedly broad distributions of the invasive Nile tilapia (*Oreochromis niloticus*) and blue-spotted tilapia (*Oreochromis leucostictus*) in Tanzania and clarify the distributions of native species. To quantify the extent of hybridization among invasive and indigenous oreochromines, Bradbeer et al. (2019) studied *Oreochromis* communities in the Lake Victoria and Pangani catchments of northern Tanzania using microsatellites and geometric morphometrics. They found that hybrids were relatively rare at their study sites, compared to purebreds, implying that assortative mating dominates in these habitats. This contrasts with other results showing the formation of *Oreochromis* hybrid swarms at other locations in Tanzania where invasive oreochromines have been introduced (Shechonge et al. 2018), suggesting that the outcome of introduction is not necessarily straightforward to predict. One of the more geographically restricted cichlids in East Africa is *Oreochromis*

hunteri. This species is endemic to Lake Chala—a crater lake that straddles the border between Tanzania and Kenya. This issue features two papers that describe parallel research on the diversity of *Oreochromis* species in the lake. Both papers show the morphological and molecular (mtDNA) distinction between the *O. hunteri* and a more recently introduced species, referred to as “Bandia” in Dieleman et al. (2019) and *O. sp.* “blue head” in Moser et al. (2019). Both papers use mtDNA to demonstrate that while *O. hunteri* is closely related to species in the neighboring Pangani catchment (e.g., *Oreochromis jipe*), the more recently introduced species is closely related to *O. urolepis* which is naturally distributed in coastal rivers far southeast of Lake Chala. Collectively, the evidence is suggestive of *O. urolepis* being introduced into Lake Chala. Moser et al. (2019) are concerned that this introduced species, which is now the numerically dominant *Oreochromis* in the lake, will outcompete the Critically Endangered *O. hunteri* for shared resources and precipitate its extinction.

Crater lake cichlid assemblages are particularly useful for studying evolutionary diversification because of the strong likelihood that diversification of sister taxa has taken place within the lake itself. Lemoine et al. (2019) studied an apparent case of early-stage speciation between two haplochromine cichlids in Lake Saka, a relatively shallow small crater lake in Uganda. Here, male fish have either yellow or blue breeding color, and the two color morphs show subtle levels of genetic differentiation at neutral microsatellite markers, as well as different microhabitat preferences. The authors conclude that speciation may be driven by divergent selection acting on male color in the different habitats.

South America

Unlike in Africa, where most of the cichlid diversity is found in lakes, South American cichlids mainly diversified in riverine environments, with several examples of adaptive radiations (e.g., Burress et al., 2018a, b). More than half of the South American cichlid species occur in the Amazon Basin (Kullander, 2003), and many of these species are popular aquarium fish. Yet, their taxonomy is complex and poorly resolved, and identifying these fish to species level is often impossible for nonexperts. To overcome this

issue, DNA barcoding (Hebert et al., 2003) might be a rapid and effective approach to identify Amazonian cichlids to species level. Carvalho et al. (2019) generated DNA barcode reference data for 56 Amazonian cichlid morpho-species. They found that the species/lineage diversity is geographically structured and that the current species diversity in the Amazon basin is drastically underestimated. They further show that for some genera, DNA barcoding is not suitable for reliable species identification because of recent divergence and/or hybridization.

The Paraná and Uruguay rivers constitute the second largest drainage in South America, harboring a tremendous diversity of fishes. Three contributions to this Special Issue target the species diversity of two cichlid genera in this system (Piálek et al., 2019a, b; Říčan et al., 2019). Using phylogeographic and traditional morphological approaches, Říčan et al. (2019) found that the Middle Paraná harbors a higher diversity of endemic *Gymnogeophagus* species than previously thought. Waterfalls and rapids appear to act as main barriers to dispersal and thus have driven and drive diversification of *Gymnogeophagus* in this region, a pattern consistent with that found in other cichlid lineages of this region. Piálek et al. (2019a) used a phylogenomic approach combined with mitochondrial data to infer the phylogeny and phylogeography of pike cichlids of the genus *Crenicichla* in the Middle Paraná system. They found single tributary endemism, parallel evolution of ecomorphs, and strong signatures of (past) introgression among various species. A thus-far undescribed pelagic piscivorous *Crenicichla* species from the Middle Paraná was shown to be of hybrid origin and described as a new species in Piálek et al. (2019b).

Cichlid sex chromosomes

How and why sex chromosomes evolve, remain undifferentiated in some taxa and degenerate in others, is a hot topic in evolutionary biology research. Fishes are known for their great variety of different sex-determining systems. This is particularly true for African cichlid fishes, for which a stunning diversity of sex chromosomes and potential environmental sex determination have been documented (Gammerdinger & Kocher, 2018; Böhne et al. 2019). Using whole genome data, Gammerdinger et al. (2019)

characterized and compared young sex chromosomes across three species of basal haplotilapiine tribes. Their approach confirmed previously reported sex-determining systems, and identified novel systems. Overall, this work illustrates the utility of the cichlid system for studying the evolution of genetic sex determination and provides a road map for future investigations on the topic.

Taken together, the diverse array of papers presented here furthers our knowledge about the organism-specific and environmental factors, as well as evolutionary processes that have contributed to the outstanding diversity among cichlid fishes. However, this information is not only relevant to this exceptional family of vertebrates. Rather, the messages established by this research have considerable relevance for our general understanding of the evolution of biological diversity. We hope you enjoy reading the contributions.

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