



Koblmüller, S., Albertson, R. C., Genner, M. J., Takahashi, T., & Sefc, K. M. (2023). Preface: Advances in Cichlid Research V: Behavior, Ecology, and Evolutionary Biology. *Hydrobiologia*, 850(10-11), 2139–2147. <https://doi.org/10.1007/s10750-023-05240-4>

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## Preface: Advances in Cichlid Research V: Behavior, Ecology, and Evolutionary Biology

Stephan Koblmüller<sup>1</sup>, R. Craig Albertson<sup>2</sup>, Martin J. Genner<sup>3</sup>, Tetsumi Takahashi<sup>4</sup> & Kristina M. Sefc<sup>1</sup>

<sup>1</sup>, Institute of Biology, University of Graz, Universitätsplatz 2, 8010 Graz, Austria

<sup>2</sup>, Department of Biology, University of Massachusetts, Amherst MA 01003. USA.

<sup>3</sup>, School of Biological Sciences, University of Bristol, Bristol, BS81TQ. UK.

<sup>4</sup>, Institute of Natural and Environmental Sciences, University of Hyogo, Sanda, 669-1546, Japan.

Correspondence to: [stephan.koblmueeller@uni-graz.at](mailto:stephan.koblmueeller@uni-graz.at) (SK)

The current special issue is the fifth in a series of special issues published in *Hydrobiologia* exclusively devoted to cichlid fish research. The freshwater fish family Cichlidae accounts for approximately 10% of today's teleost diversity and is naturally distributed from southern North America to southern South America, across most of Africa, to Madagascar and India. Their tremendous diversity in morphology, behaviour, and ecology, as well as their astounding speciation rates and numerous species-rich adaptive radiations have enthralled biologists for decades (e.g., Boulenger, 1898; Kosswig, 1947; Fryer, 1960), such that cichlids are now among the prime model systems in evolutionary biology research (e.g., Salzburger 2018). We are pleased to present a collection of 19 papers that investigate questions of taxonomy, biogeography, morphology, behavior, physiology and parasitology. Many of the key ingredients of cichlid diversification are addressed by these studies, including mating, brood care and social interactions, color pattern and body shape, as well as adaptations of the visual system and the trophic apparatus. Papers are summarized below in the order in which they appear in this special issue. We hope you enjoy reading the contributions.

### *The beginnings of diversity: How to spark a radiation*

Genome analyses have identified hybridization as a potential trigger of the explosive cichlid fish radiations in the African Great Lakes (Irisarri et al., 2018; Malinsky et al., 2018; Meier et al., 2017; Svardal et al., 2020). The fates of early-generation hybrids and any phenotypic and performance differences between reciprocal hybrids are crucial factors shaping the onset of hybrid swarm radiations, but seldom studied. To fill this gap, Pauers et al. (2023) performed morphological, chromosomal and behavioral analyses of reciprocal hybrids between the sympatric *Labeotropheus fuelleborni* Ahl, 1926 and *Labeotropheus trewavasae* Fryer, 1956 from Lake Malawi. The reciprocal hybrids differed in several phenotypic traits; while one direction of the cross produced intermediate males, the males from the reciprocal cross displayed transgressive phenotypes. Mate choice experiments indicated selection against transgressive hybrids, which might in part explain the low prevalence of actual hybrids in Lake Malawi cichlids in the wild, even though many species readily hybridize in the aquarium.

### *Who are they, and where?*

The taxonomic status of populations, morphs or closely related cichlid species is still often unclear. One particular case involves a pair of very similar zooplanktivorous cichlid species from Lake Malawi, *Copadichromis mloto* (Iles, 1960) and *Copadichromis virginalis* (Iles, 1960). The former species - *C. mloto* – has been described based on reproductively inactive individuals, and no breeding individuals have ever been positively identified. In this issue, Turner et al. (2023) used genomic data and geometric morphometric analyses, including type specimens and recently collected material, to reveal that one of the traditionally recognized forms of *C. virginalis* (the Kajose form) actually represents sexually active or maturing individuals of *C. mloto*.

Another taxonomically difficult case is presented by the Hemichromini, a primarily West African tribe containing over a dozen species in two genera. Traditionally, two morphologically distinct groups within the genus *Hemichromis* Peters, 1857 have been recognized: the reddish, so-called jewel cichlids and the larger five-spotted *Hemichromis* (e.g., Loiselle, 1979; Greenwood, 1985). The taxonomy and the phylogenetic relationships of the members of the tribe have been unclear, and the study by Lamboj & Koblmüller (2023) is the first to provide a comprehensive phylogeny of the tribe. DNA sequences date the divergence between jewel cichlids and five-spotted *Hemichromis* to 6-12 MYA. Morphological data and body coloration support this deep split, thus justifying the erection of a new genus, *Rubricatochromis*, for the jewel cichlids. In addition, the study confirms the validity of *H. angolensis* Steindachner, 1865 and the synonymy of *H. frempongi* Loiselle, 1979 with *H. fasciatus* Peters, 1857. Together with a recent study by Bitja-Nyom et al. (2021), the findings of Lamboj & Koblmüller (2023) now build a comprehensive picture of the phylogenetic relationships and the taxonomy of *Hemichromis* (sensu novo) across large parts of their distribution range. The systematics and taxonomy within the new genus *Rubricatochromis*, however, remains unclear as several currently recognized species show little if any morphological and genetic differences.

On the other side of the Atlantic Ocean, the rivers in the vast Amazon basin host megadiverse freshwater fish communities, including numerous cichlid species. In general, riverine faunal evolution is tightly linked to geological processes, in particular to the paleo-dynamics of river systems (e.g., BurrIDGE et al., 2008; Goodier et al., 2011; Van Steenberge et al., 2020). In their contribution, Řičan et al. (2023) studied the cichlid genus *Bujurquina* Kullander, 1986, which is predominantly found in rivers of the western Amazon, with high diversity in Ecuador and Peru. A dated phylogeny based on mitochondrial DNA provided evidence for multiple undescribed, locally endemic species that differ in head and dorsal fin pigmentation. Based on the phylogenetic and biogeographic data of the Ecuadorian *Bujurquina*, Řičan et al. (2023) reconstructed reconfigurations of Western Amazon river networks and discuss their findings in the framework of a detailed account of Ecuadorian paleogeography.

#### *What differs? On jaws, fins and color patterns*

Cichlids have two functionally decoupled sets of jaws, the oral jaws and the pharyngeal jaws. Whereas the pharyngeal jaws have long been regarded as a key innovation for the evolutionary success of cichlid fishes (Liem, 1973; Galis & Metz, 1998), the importance of oral jaws for niche and species diversification has only recently received increased attention. Indeed, variation in cichlid jaw protrusion predicts foraging niche and is now thought to facilitate trophic diversification (e.g., Cochran-Biederman & Winemiller, 2010; Hulsey et al., 2010; Albertson et al., 2012; Ronco et al., 2021). Here, Hulsey & Gorman (2023) used a combination of phylogenetic comparative methods, morphometrics, and field measurements to assess the relationship between premaxillary shape and overall jaw protrusion among Lake Malawi cichlids. They documented a significant correlation between the length of the ascending arm of the premaxilla and maximum protrusion distance, but

not between ascending arm length and protrusion angle. They conclude that evolved differences in premaxillary shape, especially the length of the ascending arm, likely facilitated functional divergence in jaw protrusion among species.

Also in this issue, Gilbert et al. (2023) explored the capacity of *Satanoperca daemon* (Heckel, 1840), a cichlid in the tribe Geophagini, to mount a plastic response to different foraging challenges. *Satanoperca daemon* employs a specialized mode of foraging – winnowing - which involves taking mouthfuls of substrate, separating out the prey and ejecting sediments through the gills. The authors exposed experimental groups of *S. daemon* to three different substrate types, two of which encouraged winnowing behaviors on either fine or coarse substrate and a third that prevented winnowing entirely, and used geometric morphometrics to quantify craniofacial morphology. The experimental groups differed in the shape of hard and soft tissue as well as in shape disparity, i.e. in the amount of variation within groups. The work has implications for understanding how species may respond to rapid human-induced environmental change, as well as the functional morphology of winnowing foraging behavior.

Cichlids are characterized by large fins of diverse shape, including filamentous elongations and fork- and spade shaped caudal fins. Fin shape is determined by differential growth of fin rays and connecting soft tissue, and genes expressed during regeneration of damaged fin tissue inform on the genetic basis of fin shape. Based on a previously identified gene regulatory network involved in fin growth (Ahi & Sefc, 2018), Ahi et al. (2023) examined conservation of the molecular mechanism of fin shape across distantly related cichlids. Expression patterns of several candidate genes were consistently associated with fin shape across species, while the expression of other candidate genes varied in species-specific manners. Congruent with the observed differentiation in the molecular mechanisms behind fin shape, the investigated species also differed in the anatomical basis of fin ray elongation, growing either longer or more segments in the longer fin rays.

Many cichlid species display conspicuous body coloration and color patterns. Within species, body coloration may be sexually dimorphic, show ontogenetic and geographic variation as well as vary with social status (Maan & Sefc, 2013). In this issue, Wang and colleagues (2023) investigated the mechanisms that underlie the amelanistic variant of the oscar, *Astronotus ocellatus* (Agassiz, 1831), a cichlid from the Amazon basin. Using a combination of ultrastructure, metabolome, and transcriptome profiles, they compared the skin from normal and amelanistic individuals. While normal skin contained stellate-shaped melanophores with mature melanosomes, amelanistic skin was characterized by oval shaped melanophores and immature melanosomes with lower melanin content than normal skin. The study also documented differences in the metabolomes and transcriptomes of normal and amelanistic fish. Furthermore, a number of well-studied melanin-related genes contained non-synonymous SNPs in functional domains. With this integrative approach, the study provides new insights into the genes, metabolites and pathways responsible for loss of pigmentation.

#### *The molecular basis of visual adaptation, and when it's adaptive to not see too well*

African cichlids exhibit a great diversity in their visual system, reflecting the wide range of light environments that they inhabit (Sugawara et al., 2005; Carleton, 2009). This variability in visual sensitivities, ranging from UV to red color, is likely key to divergence in foraging niche, mate recognition, and speciation. Moreover, environmental and developmental plasticity allows cichlids to fine-tune their visual system to shifting light conditions (Carleton et al., 2016). In this issue, Wilwert et al. (2023) investigated the roles for opsins and Vitamin A, the precursor of the opsin-carrying chromophore, in mediating visual plasticity in three Lake Victorian cichlid species adapted to

different visual habitats. They found species-specific differences in the expression patterns of opsin genes, as well as *cyp27c1*, which codes for an enzyme that converts Vitamin A<sub>1</sub> into A<sub>2</sub>. Exposing each species to different visual spectra resulted in changes in opsin expression in all three species, and shifts in *cyp27c1* in one species. Notably, the study shows large magnitudes of variation in *cyp27c1* within species, and no correlation between opsin and *cyp27c1* expression levels. The authors conclude that plasticity in the visual system can be differentially mediated by opsin and *cyp27c1* expression.

Also focusing on visual plasticity, the study by Schreiner et al. (2023) investigated the mechanisms that regulate cone opsin sensitivity in Burton's mouthbrooder, *Astatotilapia burtoni* (Günther, 1894), specifically the effects of thyroid hormone levels and UV light treatment. In *A. burtoni*, the single cones shift from UV to blue sensitivity during development, whereas the long-wavelength sensitive double cones maintain similar sensitivities throughout life. Both the light environment and thyroid hormone levels affected the opsin expression in the single cones, whereas double cones appear to have lost this plasticity.

Nandamuri et al. (2023) examined the regulation of short wavelength sensitivity and investigated a previously identified quantitative trait loci responsible for differential expression of the short wavelength sensitive opsin gene, *SWS2A*. Fine mapping, DNA sequence and gene expression analysis in Lake Malawi cichlids implicated *MITFA* and *BHE40* as candidate genes and suggested *MITFA* as a causative factor regulating differential *SWS2A* expression. The authors then generated a CRISPR/Cas9 *MITFA* knockout in *A. burtoni*, to test the effect of *MITFA* loss on *SWS2A* expression in a closely related cichlid model. They showed that the mutation altered *SWS2A* expression; however, its effect was in the opposite of the expected direction, with *MITFA*<sup>d10/d10</sup> mutants expressing higher levels of *SWS2A*. The authors conclude that while their study provides support for a role for *MITFA* in regulating opsin gene expression, more work is needed to understand the mechanism by which this occurs. Collectively, the studies by Wilwert et al., Schreiner et al. and Nandamuri et al. expand existing knowledge of the factors and processes underlying visual adaptation in East African cichlid fishes.

There are also circumstances, under which the inability to visually discriminate between stimuli may turn out beneficial. The anal fins of haplochromine cichlids are adorned by circular yellow, orange or red spots surrounded by translucent rings. When first described, these spots were likened to cichlid eggs and proposed to increase fertilization success (Wickler, 1962). This is because haplochromine cichlids are mouthbrooders, and the egg dummies on the males' fins supposedly trick females into pecking at the males' fins and take up the males' sperm into their buccal cavity, where fertilization occurs. However, egg mimicry has subsequently been debated on the basis of color mismatches between the spots and the actual eggs. The debate has suffered from the flaw that color match or mismatch was gauged by human vision. Now, Gonzalez et al. (2023) measured the color of eggs and fin spots of two haplochromines, *Metriaclima benetos* (Stauffer, Bowers, Kellogg & McKaye, 1997) and *A. burtoni*, and they also modelled the visual systems of these species. They discovered that in the light conditions of the natural habitat, these fish would be unlikely to be able to distinguish the colors of eggs and fin spots, thus supporting Wickler's proposal that fin spots function as "egg spots" - made in the pages of *Nature* over 60 years ago.

#### *Well-bred: How cichlids raise their young and stand their ground (or not)*

Cichlid fishes show elaborate mate choice and brood care behavior, and the effort invested in securing mates and rearing offspring also invites the expression of alternative tactics (Sefc, 2011). This includes cuckoldry, i.e. sneak fertilizations by extra-pair males which intrude into the territory

while the resident pair is spawning. Cuckoldry reduces the reproductive success of paired males, counters mate choice decisions of females, and therefore modifies the sexual selection regime in the population. Depending on environmental conditions, the prevalence of cuckoldry in a population may vary over time. Taking advantage of time series dataset of brood parentage collected from the biparental breeder *Variabilichromis moori* (Boulenger, 1898), Zimmermann et al. (2023) demonstrate seasonal fluctuations in cuckoldry rates. Paternity shares of paired males ranged from 0 – 100% and were consistently higher in broods that were spawned in the dry season compared to broods spawned in the rainy season, perhaps because seasonal fluctuations in environmental conditions such as water turbidity affect cuckold success.

Many cichlid species are mouthbrooders, i.e., they incubate their eggs and fry in the buccal cavity of one or both parents. While this strategy has some clear advantages as compared to substrate breeding, it also incurs costs (reviewed in Sefc, 2011). Protection of eggs and fry against predators and environmental stressors is a clear benefit of mouthbrooding (Corrie et al., 2008). However, how effective this strategy is, i.e. how much of the brood is lost during buccal incubation, is still largely unknown. Takahashi (2023) collected a large number of mouth-brooding females of two species of *Cyprichromis* Scheuermann, 1977 from Lake Tanganyika and compared the brood size and developmental stages of the offspring, taking into account the size of the mothers' mouth. He found that despite a significant reduction of brood size between egg and larval phase, and a significant larval mortality in one of the two species investigated, the general survival rate of offspring seems to be high, demonstrating the effectiveness of this breeding mode.

While it is generally assumed that inbreeding is costly and inbreeding depression not uncommon (Hedrick & Kalinowski, 2000; Charlesworth & Willis, 2009), there are a few species that do show active kin mating preferences (e.g., Schjørring & Jäger, 2007; Loyau et al., 2012). One of them is the West African river cichlid *Pelvicachromis taeniatus* (Boulenger, 1901) (Thünken et al., 2007). Juveniles of this species also prefer to shoal with related individuals, which ensues benefits of enhanced cooperation among kin. In the present study, Vitt et al. (2023) compared the shoaling behavior of inbred and outbred full sib groups to weigh the benefits of elevated relatedness in the inbred groups against potential negative effects of inbreeding depression. Using automated tracking, they revealed shorter travel distances and faster recovery from disturbance in the inbred shoals. These differences may be fitness relevant, as they indicate lower stress levels and reduced predation risk in fish shoaling with inbred siblings, and may furthermore affect foraging success.

Cichlid communities are structured by social dominance hierarchies which determine access to resources such as territories and reproductive opportunities (Dijkstra et al., 2009; Riebli et al., 2012). Individual fish hardly ever maintain the same social rank throughout their life, but ascend and descend in rank according to their physiological condition and the opportunities and constraints provided by their social and abiotic environment. In their contribution to this special issue, Dijkstra et al. (2023) used social network analysis to meticulously investigate the behavioral changes accompanying rank transitions in males of *A. burtoni*. In contrast to previous studies focusing on dyadic or small-group interactions, they used large groups of several males and females to study aggressive interactions in a more complex group setting. Dominant males were highly aggressive, chased a large number of subordinate community members and engaged in reciprocal display interactions with other dominant males. Social instability was triggered by removals of dominant and subordinate males from the experimental groups. Social descent was marked by territory loss and the reduction of aggressive behavior towards group members. When a subordinate ascended in rank, this involved the acquisition of a territory and was accompanied by elevated aggression towards group members. Surprisingly, ascending males started to become more aggressive already

several days before they actually acquired their new territory, in contrast to abrupt changes in the behavior of males that experienced social descent.

### *Tilapia: Feeding the world with a stress-resistant fish*

Fish and other aquatic organisms are an important food source for billions of people. Over the last decades, aquaculture has gained increasing economic relevance, and will influence human wellbeing and environmental health also in the future (Gephart et al. 2020; Fiorella et al. 2021). Tilapia are now key species in global aquaculture, with the Nile tilapia, *Oreochromis niloticus* Linnaeus, 1758, now being one of the most cultured fish in the world (FAO, 2020). The species has a natural distribution range covering much of the Nile river system and across West Africa, but the species has now been widely introduced to non-native habitats across much of tropical and subtropical Africa, Asia and the Neotropics via aquaculture and attempts to improve inland capture fisheries (El Sayed & Fitzsimmons, 2023). In their review, Geletu & Zhao (2023) discuss the increasing importance of Nile tilapia for food production globally, and they outline the value of the native genetic resources of tilapia species for future enhancement and resilience of tilapia-based aquaculture. Geletu & Zhao (2023) also review the threat to native tilapia from hybridization with invasive species, and describe the need for conservation of native species given the likely expansion of tilapia aquaculture to support a growing human population.

Because of its high tolerance to carbonate alkalinity (Zhao et al., 2020), Nile tilapia is also a useful model for studying the adaptation to alkali-saline waters in freshwater fish. In their study, Zhao et al. (2023) investigate how *O. niloticus* manages to cope with the stress induced by carbonate alkalinity. Specifically, they show that during early stages of stress, the plasma bicarbonate concentration decreases, thereby helping to return the plasma pH to normal. They further show that two carbonic anhydrases (CA<sub>Hz</sub> and CA<sub>IV</sub>) as well as HCO<sub>3</sub><sup>-</sup> transporters are involved in the regulation of homeostasis through HCO<sub>3</sub><sup>-</sup> metabolism and transport in tilapia during carbonate alkalinity stress.

### *Diversity on the edge (of the gill and the continent)*

Parasites have been proposed as important agents of natural selection in cichlid fishes (Raeymaekers et al., 2013). Vice versa, because of their intimate relationship, cichlid fishes also greatly impact the patterns of diversification of their parasites. Among the many taxa that parasitize cichlids, the monogenean flatworm genus *Cichlidogyrus* Paperna, 1960 is the most species-rich. Their direct life cycle and amenability to experimental work makes this flatworm-fish system an ideal model system for studying host-parasite interactions on a macroevolutionary scale (Cruz-Laufer et al., 2021). Recent work suggests that both the phylogeny and the ecology of the cichlid hosts determine the diversity and phylogenetic relationships among the monogenean parasites (Cruz-Laufer et al., 2022a; Rahmouni et al., 2022). However, still only a minor fraction of the entire *Cichlidogyrus* diversity is known (Cruz-Laufer et al., 2022b), constraining conclusions regarding generalities and idiosyncrasies in particular host-parasite interactions in this model system. Louizi et al. (2023) explored the *Cichlidogyrus* communities on cichlids in Morocco, the northwestern limit of their natural distribution range in Africa. They found a low parasite diversity and load on the three autochthonous cichlid species, *Coptodon guineensis* (Günther, 1862), *C. zillii* (Gervais, 1848) and *Oreochromis aureus* (Steindachner, 1864), with evidence for host-switching between different cichlid genera and potential synxenic diversification in one of the *Cichlidogyrus* species.

## Acknowledgements

We want to thank all the authors for their excellent contributions and all the reviewers for participating in the work on this special issue. We are particularly grateful to the journal's editor-in-chief Koen Martens and the associate editor-in-chief Sidinei M. Thomaz, who kindly gave us the opportunity to publish this fifth special issue devoted to cichlid research in *Hydrobiologia*.

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