

NEWS AND VIEWS

Perspective

Visual adaptation could aid sympatric speciation in a deep crater lake

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Allopatric speciation was originally suggested to be the primary mechanism of animal speciation (Mayr, 1942; Figure 1). During allopatric speciation, populations diverge when gene flow is reduced across significant biogeographic barriers. Sympatric speciation, where species diverge while inhabiting the same location, was thought to be essentially impossible. However, the advent of theoretical models followed by new experimental evidence made sympatric speciation more plausible (Via, 2001). The cichlid fishes of Barombi Mbo, a small crater lake in western Cameroon, became one of the most widely accepted examples of sympatric speciation (Schliewen, Tautz, & Paabo, 1994). Although the phylogenetic history of this clade is not quite as simple as originally thought, it remains one of the best examples of sympatric speciation (Richards, Poelstra, & Martin, 2018). However, little is known about the molecular mechanisms contributing to the splitting of these species in situ. In a From the Cover article in this issue of *Molecular Ecology*, Musilova et al. (2019) focus on the diversity of visual systems among these fishes. They identify genetic changes associated with several aspects of visual adaptation that may have contributed to the ecological specialization and sympatric speciation of cichlids in this lake.

KEYWORDS

adaptation, fish, speciation, vision

Barombi Mbo is a relatively small lake, only 2.5 km wide. It is more than 110 m deep, but the water becomes anoxic below about 25 m. Eleven endemic cichlid species have been described from the lake (Trewavas, Green, & Corbet, 1972). Each species has a particular depth preference, with nine species living in the shallows, and two preferring deep waters close to the anoxic zone. Both mitochondrial DNA (Schliewen et al., 1994) and nuclear DNA (amplified fragment length polymorphisms; Schliewen & Klee, 2004) suggest these 11 species are monophyletic relative to species in the surrounding rivers, and that they diverged during the past 1 MY. Because of the geographic isolation of this crater lake from nearby rivers, this system was one of the first accepted examples of sympatric speciation.

The sympatric hypothesis was challenged by double digest restriction associated DNA data that suggested secondary introgression from riverine species (Martin et al., 2015). However, more thorough whole genome sequencing found that

introgression affected an extremely small part of the genome (0.24%) without any obvious candidate genes that might be associated with differentiation (Richards et al., 2018). These authors also identified alternative fixation of ancestral alleles suggesting that a hybrid swarm might have predated diversification of the species flock. Thus, the Barombi Mbo system seems to have retained its celebrated status as a prime example of sympatric speciation.

In this issue, Musilova et al. (2019) have taken a candidate gene approach to understand the diversification of sensory systems in the Barombi Mbo flock. They used quantitative PCR, retinal transcriptomes, and in situ hybridization to study the expression of the opsin genes that determine visual sensitivity. Cichlids use rod cells for low light vision and cone cells for bright light vision. The cones are arranged in a retinal mosaic in which each single cone is surrounded by four pairs of double cones (Fernald, 1981; Figure 1).

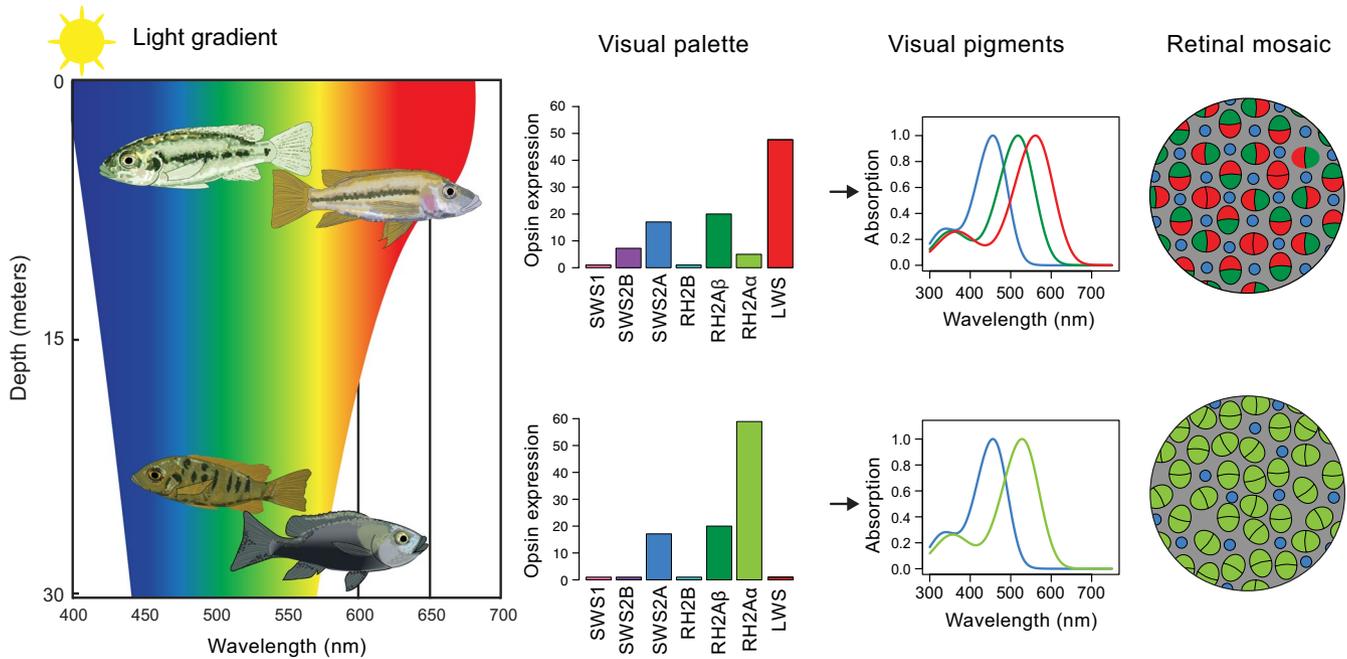


FIGURE 1 The visual system of cichlids from Cameroon crater lake Barombi Mbo have adapted to deep versus shallow habitats within the lake with changes in opsin gene expression producing different visual pigments and retinal mosaics. This adaptation may contribute to sympatric speciation

The light sensitivity of these photoreceptors is conferred by opsin proteins that combine with 11-cis retinal to form light-absorbing visual pigments. The cichlid genome encodes one rod opsin and seven different cone opsins, though individual species typically express only a subset of these genes in their retina. Of the seven cone opsin genes, three produce short wavelength sensitive visual pigments (*SWS1*, *SWS2B* and *SWS2A*) in single cones, and four produce medium (*RH2B*, *RH2Aβ*, *RH2Aα*) to long wavelength sensitive (*LWS*) visual pigments in double cones (Carleton, Dalton, Escobar-Camacho, & Nandamuri, 2016).

The available light spectrum varies dramatically with water depth. Both ultraviolet and red wavelengths are absorbed as the light travels through the water. Because the various Barombi Mbo species prefer to live at different depths, the authors looked for evidence of visual adaptation by comparing the two species that live in deep water with the nine species that live in shallow water. Retinal transcriptomes, as well as direct sequencing of the opsin genes, revealed that all of the species have the expected set of eight opsin genes. Furthermore, they found little variation in opsin sequence among species for either the rod or cone opsin genes. However, they did find significant differences in cone opsin expression, particularly between the shallow and deep dwelling species. The deep species express the *SWS2A* gene, which produces a blue-sensitive opsin in single cones. In contrast, the shallow species likely coexpress *SWS1* and *SWS2B* together with *SWS2A*, which shifts the sensitivity of the single cones to shorter wavelengths (Figure 1).

Double cone expression in the deep species is dominated by *RH2Aα*, with some *RH2Aβ*, but no *LWS* opsin expression. This makes

the double cones of the deep species sensitive to somewhat shorter wavelengths than the shallow species that have high *LWS* expression. On the whole, the range of visual sensitivity in the deep species is compressed to better match the available light spectrum at depth (Figure 1). The authors performed in situ hybridization to show that the deep species express *SWS2A* in single cones and either *RH2Aβ* or *RH2Aα* in the double cones. They were not able to distinguish the *RH2A* genes but this matters little since the two *RH2A* genes have minimal sequence difference and therefore similar sensitivities. These results suggest that the deep species have adapted to the light environment of their habitat, and would effectively be dichromats with a lower ability to discriminate colours compared to the shallow water species. How this might impact evolution of mating colours remains to be seen.

In addition to the opsin genes, the authors examined retinal transcriptomes for two shallow and two deep living species. They identified 26 upregulated genes and 20 downregulated genes that are shared among all four shallow/deep comparisons. These included some interesting candidates known to be involved in retinal development, regulation of circadian rhythm, and response to hypoxia. They further used transcriptome sequences to examine the phylogenetic relationships of the species. Their tree suggests that the deep species adapted to depth separately, such that the visual adaptations are convergent. This offers further support to the idea that cichlid visual systems readily adapt to different light environments through differential gene expression in both the African rift lakes as well as Central American crater lakes (O'Quin, Hofmann, Hofmann, & Carleton, 2010; Torres-Dowdall et al., 2017).

This work has finally identified candidate phenotypes contributing to the rapid sympatric diversification of cichlids in this crater lake system. In addition, the authors have suggested an important role for several interesting candidate genes. While further studies are needed to better understand the evolution of these candidate genes, that work is not currently possible. Political strife in this region of Cameroon precludes the field work needed to study this unique system. Hopefully, peace will return for the people of Cameroon, and allow scientists access to further work on this classic model of sympatric speciation.

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