

Avian Hybrids

An Overview of Hybridization in Birds

Where did all these fish come from?! A genomic perspective on the explosive diversification of cichlids

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Cichlids provide important insights into the drivers of explosive speciation.

There are more than 1700 species of cichlid fishes, 90% of which can be found in the Great Lakes of East Africa. Since the 19th century, biologists have been visiting the Lakes Victoria, Malawi and Tanganyika to explore the diversity of cichlid species. In 1931, Woltereck introduced the term ‘Artexplosion’ (now known as explosive speciation) to describe the situation. In a [recent review paper](#) (<https://www.nature.com/articles/s41576-018-0043-9>), Walter Salzburger (University of Basel) puts the cichlid explosion into perspective:

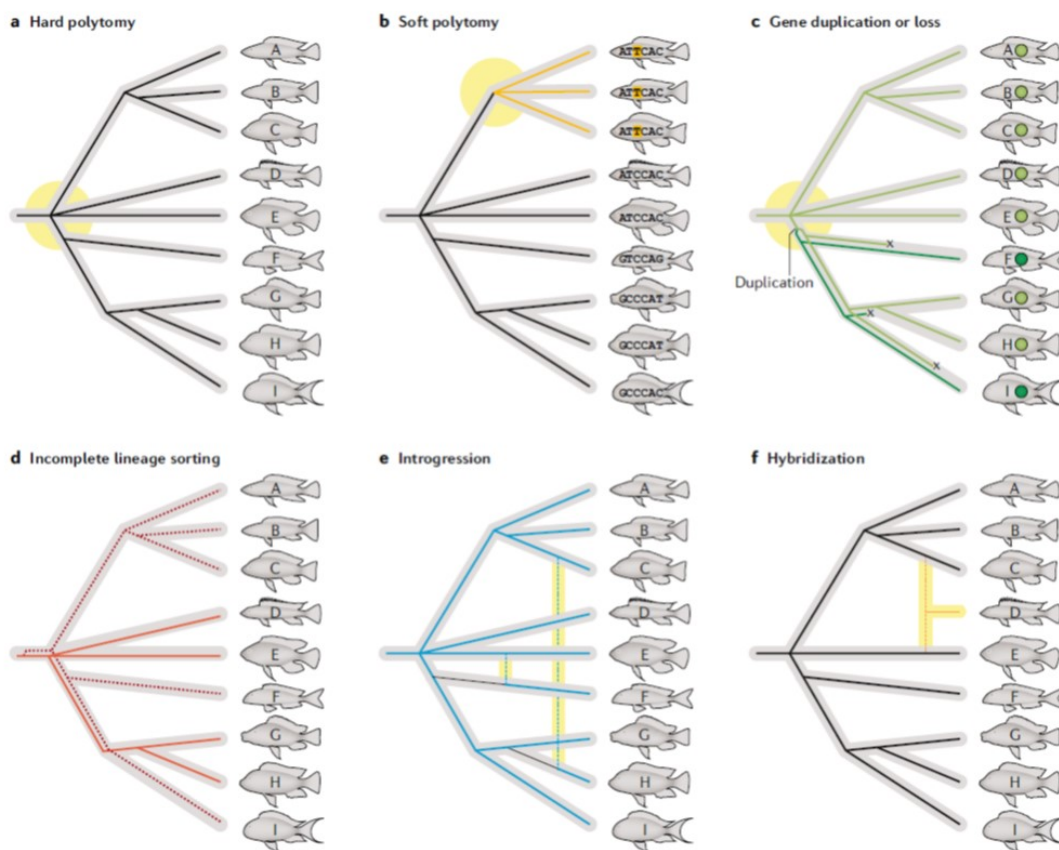
To put cichlid radiations into a temporal context, during the evolutionary time span of our own species, starting with the split between chimpanzees and humans some 5–7 million years ago, approximately 2,000 species of cichlid fish evolved in East Africa, the geographic region where the chimpanzee–human split initially occurred. Within the time span that it took for 14 species of Darwin’s finches to evolve on the Galapagos archipelago, about 1,000 cichlid species evolved in Lake Malawi alone. In addition, since the last ice age, which is when sticklebacks began to diverge into replicate species pairs in the Northern hemisphere, hundreds of cichlid species evolved in Lake Victoria.

It’s complicated

To sum up the introductory paragraph of this blog post: that is a lot of fish in a short amount of time. Reconstructing the evolutionary history of such rapidly diversifying species groups is challenging. There are multiple biological processes that hamper the construction of phylogenetic trees. Figure 3 in Salzburger’s review paper provides a nice overview of these processes (honestly, one of the best pictures I have come across). The most important ones to keep in mind are incomplete lineage sorting (d) and introgression (e). Incomplete lineage sorting occurs when lineages fail to coalesce in the ancestral population (I have explained this process in more detail [previously](#)).

(<https://avianhybrids.wordpress.com/2018/04/15/dont-forget-the-hybrids-antbird-study-shows-that->

not-taking-into-account-hybridization-leads-to-the-wrong-species-tree/)), while introgression refers to the exchange of genetic material by means of hybridization and backcrossing (see practically all posts on this website...).

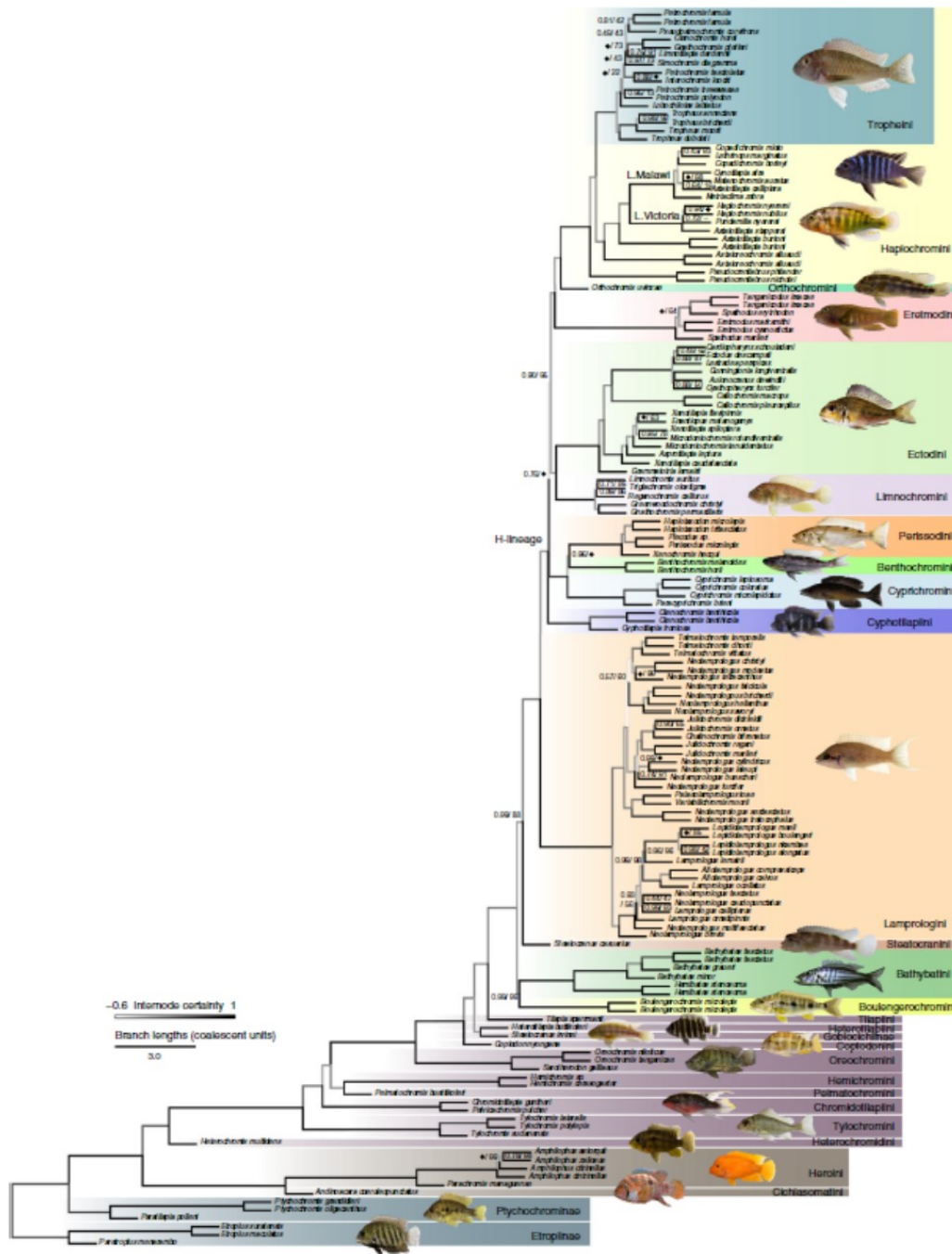


Several biological processes that can complicate the estimation of phylogenetic trees (from: Salzburger 2018 Nature Reviews Genetics)

Untangling Tanganyika

Because of these processes, it has been difficult to produce a completely resolved phylogenetic tree of cichlid fish. However, Iker Isarri, Pooja Singh and colleagues (<https://www.nature.com/articles/s41467-018-05479-9>) managed to disentangle the relationships between all cichlid species of Lake Tanganyika. In addition, they uncovered introgression that the base of this explosive radiation, suggesting that 'hybridization might have facilitated these speciation bursts.'

This suggestion was supported by further analyses, revealing that several genes related to key innovations in cichlids, such as dietary adaptations and color vision, showed signs of positive selection and introgression. This is nicely illustrated by the opsin-genes (<https://en.wikipedia.org/wiki/Opsin>), which shape the visual system of these fish. In cichlids that feed on plankton the UV-sensitive opsin *sws1* shows faster evolution, facilitating foraging because plankton is more visible under UV-light. Fish that graze on green algae, on the other hand, show faster evolution in the green-sensitive opsin *rh2α-α*.



The resolved cichlid phylogeny. Check out the original paper for a higher quality image: [Irisarri et al. \(2018\) Nature Communications \(https://www.nature.com/articles/s41467-018-05479-9\)](https://www.nature.com/articles/s41467-018-05479-9).

Multiple Opportunities

So, does that answer our question? Did we get all these fish because of introgressive hybridization? It is definitely one of the factors that has fueled cichlid speciation, but other factors also need to be taken into account, such as ecological opportunity: the African Great Lakes are conducive for diversification by providing a plenitude of ecological niches to fill. [Genomic analyses \(https://www.nature.com/articles/nature13726\)](https://www.nature.com/articles/nature13726) of several cichlids also revealed that the genomes of these fish have certain features that could potentially facilitate explosive speciation (I cannot go into great detail here, but I have provided links to relevant literature for interested readers):

1. Accumulation of standing genetic variation (https://en.wikipedia.org/wiki/Genetic_variation) before the radiation (partly supplied by introgressive hybridization)
2. Increased rate of gene duplications which speeds up the process of genes acquiring new functions (i.e. neo-functionalization (<https://en.wikipedia.org/wiki/Neofunctionalization>))
3. Greater dynamics in gene regulatory processes compared to other fish species (check out this review (<https://www.sciencedirect.com/science/article/pii/S0168952516301500>) if you want to know more about gene regulation and speciation).
4. Elevated levels of coding sequence evolution (see examples of opsin-genes above)
5. Three waves of transposable element (https://en.wikipedia.org/wiki/Transposable_element) expansion that might have sped up cichlid evolution (see these recent reviews the role of transposable elements in speciation (<http://www.mdpi.com/2073-4425/9/5/254>) and adaptation (<http://doi.wiley.com/10.1111/mec.14794>))

Clearly, the explosive diversification of cichlids is a complex interplay of several factors. Disentangling these processes – and possibly discovering new ones – will likely fuel the research community for some time.

References

- Irisarri, I., Singh, P., Kolbmüller, S., Torres-Dowdall, J., Henning, F., Franchini, P., Fischer, C., Lemmon, A.R., Lemmon, E.M., Thalinger, G.G., Sturmbauer, C. & Meyer, A. (2018) Phylogenomics uncovers early hybridization and adaptive loci shaping the radiation of Lake Tanganyika cichlid fishes. *Nature Communications* **9**, 3159.
- Salzburger, W. (2018) Understanding explosive diversification through cichlid fish genomics. *Nature Reviews Genetics*,

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