

LIVEBEARERS



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JUST ASK A SCIENTIST!

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Question: What fishes have livebearing poeciliids evolved from, and what are they most closely related to?

This is an excellent question to which – it turns out – there is no simple answer, because our understanding of the evolutionary relationships of poeciliids with other fishes is continuously evolving. The live-bearing poeciliids belong to the order Cyprinodontiformes, a diverse group of fishes with a wide distribution spanning the Americas, Africa, Europe, and Asia. Cyprinodontiformes includes a variety of fish families that are primarily egg-laying, including a variety of killifishes that are popular in the hobby, as well as pupfishes and topminnows that live in many streams that flow through our neighborhoods. In addition, there are three primary lineages that reproduce through live-bearing: the poeciliids, the goodeids (splitfins), and the anablepids (four-eyed fishes and one-sided livebearers).

The famous ichthyologist Dr. Carl Hubbs was among the first scientists to rigorously investigate the live-bearing cyprinodontiforms and their egg-laying brethren. In the 1920s, he combined all the egg-laying species together into a single family (Cyprinodontidae) and differentiated four livebearing families based on differences in their modified anal fins (e.g., the andropodium in goodeids and the gonopodium on poeciliids).

In 1981, Dr. Lynne Parenti (now a curator at the Smithsonian National Museum of Natural History) shook up the evolutionary tree of cyprinodontiform fishes in a seminal paper. Comparing morphological traits in a diversity of egg-laying and live-bearing species, she hypothesized that the live-bearing poeciliids

are closely related to egg-laying killifish such as the African lamp-eyes (e.g., *Aplocheilichthys*) and some South American killifish (e.g., *Fluviphylax*). As a consequence, she redefined the family Poeciliidae to include egg-laying species (in the subfamilies *Aplocheilichthyinae* and *Fluviphylacinae*), relegating the live-bearing poeciliids into a subfamily (the *Poeciliinae*).

Over the following decades, there were several modifications of Parenti's classification that largely focused on improving the evolutionary relationships of the many egg-laying species but leaving the livebearers in their subfamily. The conclusion of these works was that our favorite poeciliid livebearers may in fact be more closely related to egg-laying species in Africa and South America than to other

livebearing fishes within the order Cyprinodontiformes. This perspective of evolutionary history implies that the ability for internal fertilization using the gonopodium and for internal gestation with live birth evolved specifically in the shared common ancestor of all poeciliids.

Fast forwarding into the age of gene sequencing, we are now witnessing another paradigm shift in our understanding of the cyprinodontiform evolutionary tree, which sheds new light into the origins and relatedness of poeciliids. Most importantly, new analyses that have leveraged genetic data for the estimation of evolutionary trees have cast doubt on Parenti's classification, finding that live-bearing poeciliids are most closely related to fishes in the family *Anablepidae*. Together, these two families are closely related to *Fluviphylax*, thus forming group of egg-laying and live-bearing species exclusively distributed in the Americas. In contrast, live-bearing poeciliids do not appear to be closely related to some of the African lineages of killifish, as previously hypothesized. These new results indicate that the morphological similarities between some killifish and poeciliids documented by Parenti were ultimately a product of convergent evolution (i.e., the independent evolution of similar traits in



unrelated lineages), which clouded the accurate estimation of evolutionary relationships based on morphological analyses alone.

These new findings have prompted a group of authors around Dr. Wilson Costa from the Federal University of Rio de Janeiro in Brazil to once again revise the classification of the Cyprinodontiformes just earlier this year. Most importantly for the discussion here, they have restricted the family Poeciliidae to the livebearers, removing the egg-laying species added by Parenti in 1981. Now, such continuous changes to the classification may seem tiring, but it reflects our ever-improving understanding of how the evolution of these interesting species has unfolded.

The close relationship between the Anablepidae and the Poeciliidae prompts the question of whether livebearing in this group has evolved once (in the shared common ancestor that gave rise to both families) or twice (independently in each family). Considering that the Anablepidae also includes an egg-laying species, the white-eye (*Oxyzygonectes dovii*), there are two possible scenarios: (1) Livebearing may have evolved once in the shared common ancestor of the Anablepidae and Poeciliidae. If this was the case, the ability to bear live young must subsequently have been lost in the lineage that gave rise to the white-eye. It is unclear how plausible this evolutionary scenario is, because of losing complex traits associated with internal fertilization and livebearing may be difficult. (2) Livebearing in the Anablepidae and the Poeciliidae may have evolved independently, once in the ancestor that gave rise to all poeciliids, and once in the ancestor that gave rise to the livebearing anablepids (*Anableps* & *Jenynsia*).

While it remains unclear how many times exactly live-bearing has evolved in the Cyprinodontiformes, we know that the shift from egg-laying to live-bearing has had important consequences for the evolutionary diversification of these groups. Researchers around Dr. Vincent Savolainen from Imperial College in London have recently documented that live-bearing lineages (especially the Poeciliidae and the Goodeidae) have substantially higher rates of diversification compared to other lineages within the Cyprinodontiformes. The interesting aspects of the reproductive biology of these fishes therefore seem to be tightly linked to the incredible diversity of species that we all appreciate.

*“Just Ask a Scientist!” will hopefully be a regular component of Livebearers Journal. However, **this requires your input.** Have you ever wondered about the meaning of observations you made in your fish tank? Do you have questions about the behavior, reproduction, ecology, or evolution of livebearers? Submit your questions directly to Michi (tobler@ksu.edu). He will do his best to answer your question or find somebody that can!*