# Study of fish fossil shows that 'head-first' diversity drives vertebrate evolution

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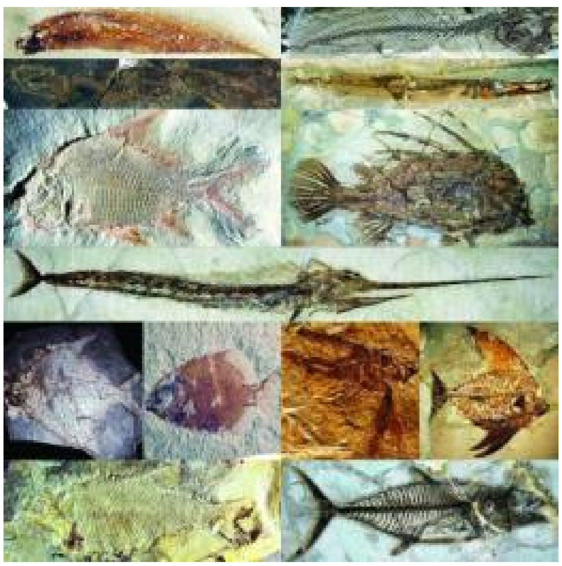

Two radiations of ray-finned fishes (Actinopterygii), Carboniferous forms (facing left) and acanthomorph teleosts (facing right) underwent distinct cranial (feeding) and later postcranial (habitat) stages in trait diversification. Credit: (Photographs by Lauren Sallan and Matt Friedman).

The history of evolution is periodically marked by explosions in biodiversity, as groups of species try out a wide range of shapes and sizes. With a new analysis of two such adaptive radiations in the fossil record, researchers have discovered that these diversifications proceeded head-first.

By analyzing the physical features of fossil fish that diversified around the time of two separate extinction events, scientists from the University of Chicago and the University of Oxford found that head features diversified before body shapes and types. The discovery disputes previous models of adaptive radiations and suggests that feeding-related evolutionary pressures are the initial drivers of diversification.

"It seems like resources, feeding and diet are the most important factors at the initial stage," said lead author Lauren Sallan, graduate student in the Department of Organismal Biology and Anatomy at the University of Chicago. "Strange heads show up first – crushing jaws, animals with big teeth, with long jaws – but they're all pretty much attached to the same body."

Adaptive radiations underlie the evolution of dominant and diverse groups. After a major disruption, such as an extinction event, surviving species diversify into a myriad variety of forms. Modern examples of this diversity are the fish family of cichlids, with more than 1,000 documented species, or "Darwin's finches" of the Galapagos Islands, which exhibit many different beak types.

Evolutionary biologists have used these living species to propose at least two models of how adaptive radiations work. One model proposes a single "burst" of divergence followed by a long period of relative stability. Another, sometimes known as the "general vertebrate model," introduced the idea of staged divergences, with habitat-driven changes in body type preceding diversification of head types.

However, these models had not yet been tested with the rich data sets available in the fossil record.

"There hadn't been any tests of these things using fossils," said Sallan, a graduate student in the laboratory of University of Chicago Professor Michael Coates. "You have all these analyses of diversification, yet not one of them goes back to the fossil record and says what's happening at this time period, and the next time period, and the one after that."

Sallan and co-author Matt Friedman, PhD, lecturer in paleobiology at the University of Oxford and a former member of Coates' laboratory, looked at two different adaptive radiations in the fossil record. The first was the explosion of ray-finned fishes after the Hangenberg extinction, an event 360 million years ago that decimated ocean life on Earth. The second group was the acanthomorphs, a group of fish that exhibited a burst in diversity around the time of the end-Cretaceous extinction that ended the age of dinosaurs.

In both datasets, the researchers used a method called geometric morphometrics to quantify differences in features such as body depth, fin position and jaw shape between species. Crucially, Sallan and Friedman separated head features from body features in their analysis, to better detect the timing of when each compartment showed a burst of diversity in the record.

The results of the two analyses were in agreement: Diversification in cranial features preceded diversification in body types. Unusual head features such as jaws lined with sharp teeth or blunt teeth for crushing appeared before diverse body shapes on a spectrum from slender and eel-like to broad and disc-shaped.

"We have these two entirely separate radiations, and in both of them the pattern is heads first. So feeding might be more important to diversification than habitat use," Sallan said. "It's against both the adaptive radiation model and the proposed stage model."

The pattern detected with the new analyses suggests that the appearance of new sources of food drives a burst of diversity before species begin to change to adapt to new habitats.

"Ecological limits are taken away," Sallan said. "There's more opportunity out there, more available resources, and they're taking advantage of that. Later, they're taking advantage of specializing to new habitats. So it's not something within the animals themselves; it's more opportunity that matters."

While the new study offers two distinct examples of head-first diversification separated by hundreds of millions of years, the universality of the model remains to be conclusively proven.

"Evolution is really complex, and it's not really clear that there should be only one model," Sallan said. "It might be that this model might apply to fishes in certain time periods, or might apply to vertebrates, but a lot more investigation is needed to see whether that is actually true."

**More information:** The paper, "Heads or Tails: Staged Diversification in Vertebrate Evolutionary Radiations," was published online Dec. 21 by the journal *Proceedings of the Royal Society B.*

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