INSIGHTS

PERSPECTIVES

Ballistic tongue representation of *Yaksha perettii* is shown. The albanerpetontid is dwelling in the understory of the forest, and is illustrated an instant before being trapped by tree resin.

PALEONTOLOGY

A surprising fossil vertebrate

An ancient amphibian converged on a chameleon-like way of feeding

By **David B. Wake**

The invasion of land by vertebrates initiated an explosion of new kinds of organisms—amphibians—whose diversity ballooned until the extinction event that ended the Paleozoic Era 252 million years ago (Ma) nearly wiped them out. Several early amphibians became specialized in morphology and life history, even including forms that lost limbs. Many had bizarre shapes, and they also varied greatly in size. Among them were the ancestors of the still-living salamanders, frogs, and caecilians, collectively known as lissamphibians. By the dawn of the Mesozoic Era, which followed the Paleozoic, only lissamphibians and one other group (trematosaurs) survived. The last trematosaurs disappeared in the late Mesozoic, 120 Ma. But paleontologists had overlooked one clade. On page 687 of this issue, Daza *et al.* (*1*) introduce an unusual fossil of the obscure and apparently extinct albanerpetontids.

First detected in Late Cretaceous (100 to 66 Ma) formations and recorded as salamanders, albanerpetontids gradually became recognized by paleontologists as a fourth kind of lissamphibian, albanerpeton-

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ILLUSTRATION: STEPHANIE ABRAMOWICZ

tids (Order Allocaudata). With the discovery of several new taxa, albanerpetontids (named for the Albian, a mid-Cretaceous age and stage, 100 to 113 Ma) became better known. They were salamander-like, or maybe lizard-like, biologically, and persisted for a very long time, first appearing in the Triassic (252 to 201 Ma) and only disappearing "yesterday" (they were living in Italy with other still-surviving amphibians until the Early Pleistocene, about 2 Ma). With luck we might still have them somewhere (hopefully, one will turn up in what remains of biological wilderness on this planet—but time is running out). There is now a much better idea of the kind of organism we seek, thanks to the report by Daza *et al.* of their spectacular discovery of a new albanerpetontid, *Yaksha perettii*, encased in Myanmar amber (*1*).

The Myanmar amber, in this case about 99 million years old, preserves some spectacular fossils. In 2016, Daza's team (*2*) reported amazingly well-preserved vertebrates, including one thought to be the earliest chameleon. The basis for that identification was a long skeletal element in the head and throat, an entoglossal, found only in chameleons and the key component in its intricate ballistic tongue. The very elongated entoglossal plays a special role in tongue firing in chameleons. It is enveloped by specialized accelerator muscles, which wrap around it. At the anterior end is the massive fleshy tongue pad. The entoglossal of chameleons slightly tapers toward the front, so when the accelerators squeeze down on it the tongue pad is swiftly advanced and slips forward off its end, literally flung into space (*3*). No other taxon was thought to have such an extreme entoglossal. Hence, the initial identification seemed to make sense. Logical—but spectacularly wrong. Daza *et al.* now show that not only are the bearers of the specialized tongue not chameleons, or even squamates; they instead are members of the mysterious albanerpetontids. What strange lissamphibians these albanerpetontids are: They have claws, scales, and armored skulls—and at least one had a tongue like a modern chameleon.

How the lissamphibians are related to each other and to Paleozoic forms is closely studied and contentious, but salamanders and frogs are likely sister taxa (Batrachia), caecilians are mysterious but might be derived from stereospondyls, and albanerpetontids seem likely to be basal derivatives.

Although many salamanders are almost prototypical tetrapods, with four limbs of roughly equivalent length, a generally long tail, and roughly proportional head and body, there are also some bizarre exceptions. Sirens lack hind limbs and are very elongate, permanently aquatic forms with gills and a keratinous beak. Aggressively predaceous amphiumas are large, very elongate aquatic forms lacking gills. They have ludicrously small limbs and reduced digits—down to one in one species. Asian giant salamanders reach 180 cm in length and weigh over 50 kg. By contrast, frogs, the most numerous (88% of lissamphibians) and widespread living amphibians, are tailless, short-bodied, usually large-headed, and have limbs of often very unequal length. Caecilians are virtually blind, limbless, nearly tailless but very long-bodied burrowers, except for a bizarre clade of aquatic species in South American rivers and swamps.

Now, enter the albanerpetontids. Superficially salamander-like in their prototypical tetrapod habitus, albanerpetontids had features that seemed to suggest a burrowing way of life, with a strange, strengthened lower jaw with an interlocking articulation, a strengthened skull with solid bones covered with stout scales and elaborate bony sculpturing suggesting co-ossification of bone and skin, and with limbs bearing claws on their digits (four front, five hind). But what about the tongue? And how could these animals have been captured in amber sap? Were they arboreal (see the figure)? The closest analogs may be the strange tropical plethodontid salamanders of the genus *Oedipina*, a group of highly specialized burrowers, which—such as *O. alleni*—occasionally become arboreal. Their exquisitely specialized ballistic tongue is as if designed in reverse to that of chameleons—the homolog of the entoglossal (the basibranchial) is itself, together with the tongue pad, projected completely out of the mouth (*4*).

The elongated entoglossal is a vivid example of evolutionary convergence, which justifiably continues to receive intense scientific scrutiny (*5, 6*), because it is common and profoundly important. The expanded lissamphibians display different levels of convergence, including what might be termed complete convergence between *Yaksha* and chameleons, which entails both structural and functional components, and incomplete convergence between *Yaksha* and plethodontids like *Oedipina*, a convergence that is functional but only partially structural. ■

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EVOLUTIONARY BIOLOGY

The genetic law of the minimum

The genetic code evolved to reduce the impact of nutrient limitations

By **Martin F. Polz**[1] and **Otto X. Cordero**[2]

How organisms are optimized in the face of environmental challenges remains one of the key unanswered questions in biology. The optimization of enzymes for changing nutrient concentrations in an organism's environment is well known (*1*). However, intricate genomics studies have revealed that optimization might affect the architecture of the entire genome (*2*). On page 683 of this issue, Shenhav and Zeevi (*3*) illuminate how selection driven by resource scarcity can affect the evolution of nucleotide and protein sequences in marine microbes.

In extremely nutrient-scarce regions of the ocean, microbial genomes are often small and streamlined, containing only the most essential genetic information (*4*). However, the essential selective factor often is not the absolute concentration of a single nutrient but rather its ratio with other required nutrients (*5*). For example, the sunlit ocean surface is typically limited in nitrogen but not organic carbon, because photosynthetic organisms require much of the former but produce copious amounts of the latter. When biomass from this surface layer dies and sinks, it is degraded by heterotrophic bacteria, which, because of the stoichiometry of elements in their food versus their cells, shift the balance toward carbon limitation (*6*, *7*).

Recent work has shown that this transition from nitrogen to carbon limitation provides an explanation for an abrupt shift in the guanine-cytosine (GC) content in the genomes of marine microbes at the ocean surface versus those in the deep ocean (*8*, *9*). Organisms living under consistent nitrogen limitation have a low GC content in their genomes, leading to a lower nitrogen demand for DNA synthesis. These orga-

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