PALEONTOLOGY

Enigmatic amphibians in mid-Cretaceous amber were chameleon-like ballistic feeders

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Albanerpetontids are tiny, enigmatic fossil amphibians with a distinctive suite of characteristics, including scales and specialized jaw and neck joints. Here we describe a new genus and species of albanerpetontid, represented by fully articulated and three-dimensional specimens preserved in amber. These specimens preserve skeletal and soft tissues, including an elongated median hyoid element, the tip of which remains embedded in a distal tongue pad. This arrangement is very similar to the long, rapidly projecting tongue of chameleons. Our results thus suggest that albanerpetontids were sit-and-wait ballistic tongue feeders, extending the record of this specialized feeding mode by around 100 million years.

The extinct amphibian clade Albanerpetontidae is currently represented by five genera spanning a period of more than 165 million years, from the Middle Jurassic (*1*) to the Early Pleistocene (*2*), and a geographical range from North America (*3*, *4*) through Europe (*5*) and central Asia (*6*) to Japan (*7*). To date, the only records from a southern (Gondwanan) continental mass, albeit marginal, are from Morocco (*8*, *9*). Most of albanerpetontid records comprise jaws and sculptured frontal bones (*5*), although Cretaceous localities [in Spain and Italy (*1*, *10*, *11*) and Japan (*7*)] have yielded more substantive material, some with associated soft tissue showing the presence of dermal scales (*10*). Originally classified as salamanders (*11*, *12*), albanerpetontids are now considered a distinct lineage (*10*, *13*). Nonetheless, many questions remain as to the anatomy, lifestyle, and relationships of these unusual amphibians.

Here we describe a new genus and species of albanerpetontid from the amber deposits of Myanmar. The material includes a complete three-dimensional adult skull, a tiny juvenile skeleton originally identified as a putative stem-chameleon (*14*), and a partial adult postcranium. The exquisite preservation of both skeletal remains and soft tissues reveals important clues about the morphological and ecological character of these enigmatic amphibians.

Systematics

Amphibia Linnaeus 1758. Albanerpetontidae Fox & Naylor 1982. *Yaksha perettii* gen. et sp. nov. lSID urn:lsid:zoobank.org:pub:0C8EC7C5-66D4-4144-917D-5BFA3704EFA4. **Etymology:** The generic name is derived from Yaksha, a type of mythical spirit in Eastern belief systems, guardian of natural treasures hidden in the earth or tree roots. The specific epithet recognizes Adolf Peretti, director of the Peretti Museum Foundation and GemResearch Swisslab (GRS), who discovered the fossil and has conducted fieldwork and humanitarian projects in Myanmar for the past 10 years. **Holotype:** Peretti Museum Foundation, Switzerland, GRS-Ref-060829 (*15*), a complete articulated skull (Figs. 1, A and G to N; 2, A and B; and 3). **Paratype:** JZC Bu154 (*16*) [Fig. 1, B to F; figs. S2 and S3; and figure 2K in Daza *et al.* (*14*)], James Zigras Collection, juvenile specimen, housed at the American Museum of Natural History, New York, USA. **Referred material:** Peretti Museum Foundation, Switzerland, GRS-Ref-27746 (*17*), partial postcranial skeleton (fig. S5). **Locality and horizon:** GRS-Ref-060829 (holotype) and GRS-Ref-27746 (referred material) were ethically sourced from the Hukaung Valley, near Tanaing Township, Myitkyina District, Kachin Province, Myanmar, and legally exported (materials and methods section S1.1 in the supplementary materials). The juvenile paratype, JZC Bu154, is recorded as being from ~100 km west of the Myitkyina District. Amber from these mines has been dated as early Cenomanian, ~99 million years ago (Ma), using U-Pb isotopes (*18*). **Diagnosis for genus and species:** A genus and species of albanerpetontid distinguished by the following combination of character states: paired robust premaxillae with a dorsal boss, wide lateral lingual buttress, and elongate vertical suprapalatal pits (Fig. 3, A to C); posteriorly bifurcate parietals bounding cranial fenestrations anteriorly and medially (Fig. 3, D and E); triangular frontal with long broad-based internasal process, frontal anteroposterior length equal to maximum anteroposterior length of parietal (Fig. 3, F to H), prefrontal facets extending posterior to midlength of frontal, weakly developed midventral crest, and ventrolateral crests that meet in ventral midline; medium-length parietal postorbital processes sculptured in their proximal half; separate prefrontal and lacrimal bones; nasal excluded from narial margin; trifurcate unpaired vomer; dentition showing size heterodonty anteriorly, resulting in sinuous occlusal surface; and small body size (supplementary text section S2.1, "Differential diagnosis").

Description

The holotype (GRS-Ref-060829) is the first fully articulated three-dimensional skull of an albanerpetontid (Fig. 1, A and G to N, and supplementary text S2.2). It is 12.18 mm in overall length (snout tip to occiput), giving an estimated snout-to-pelvis length (SPL) of 52 mm [based on the proportions of *Celtedens ibericus* (*10*)]. The newly discovered Myanmar skull reveals the presence of epipterygoids [misinterpreted in the Japanese *Shirerpeton* (*7*)] that form an integral part of the jaw suspension; a complete braincase with ossification of the pila antotica; a palate with a large, open pyriform fossa undivided by a median parasphenoid rostrum; a trifurcated unpaired vomer, with paired palatines and pterygoids, all lacking teeth; and a long median hyoid "entoglossal" process (not homologous with that of lizards). There are no ossified ceratobranchial elements. GRS-Ref-060829 also preserves remnants of the original soft tissues, notably the anterior tongue pad, into which the tip of the entoglossal process is embedded, and parts of the eyelids, palatal fascia, and jaw musculature.

The juvenile specimen, JZC Bu154 (Fig. 1, B to F, and supplementary text S2.3), establishes the presence of a four-digit manus, uncertain in other articulated specimens (*1*, *10*), and curved ungual phalanges covered by claw sheaths. GRS-Ref-27746 (fig. S5 and supplementary text S2.4) demonstrates that the tripartite pelvis (pubis, ischium, and vertical ilium) was supported by two sacral ribs (unlike the single sacral rib typically found in lissamphibians). Moreover, the vertical iliac blade, like that of chameleons, suggests a deep pelvis that may have allowed the legs to be angled ventrally for climbing.

Phylogenetic position

Most albanerpetontid species are represented by isolated bones, and data matrices for the group rely mainly on frontal and jaw character states. We ran an analysis using the most comprehensive recent data matrix (*7*, *19*). In their possession of dorsal cranial fenestrae, *Yaksha*

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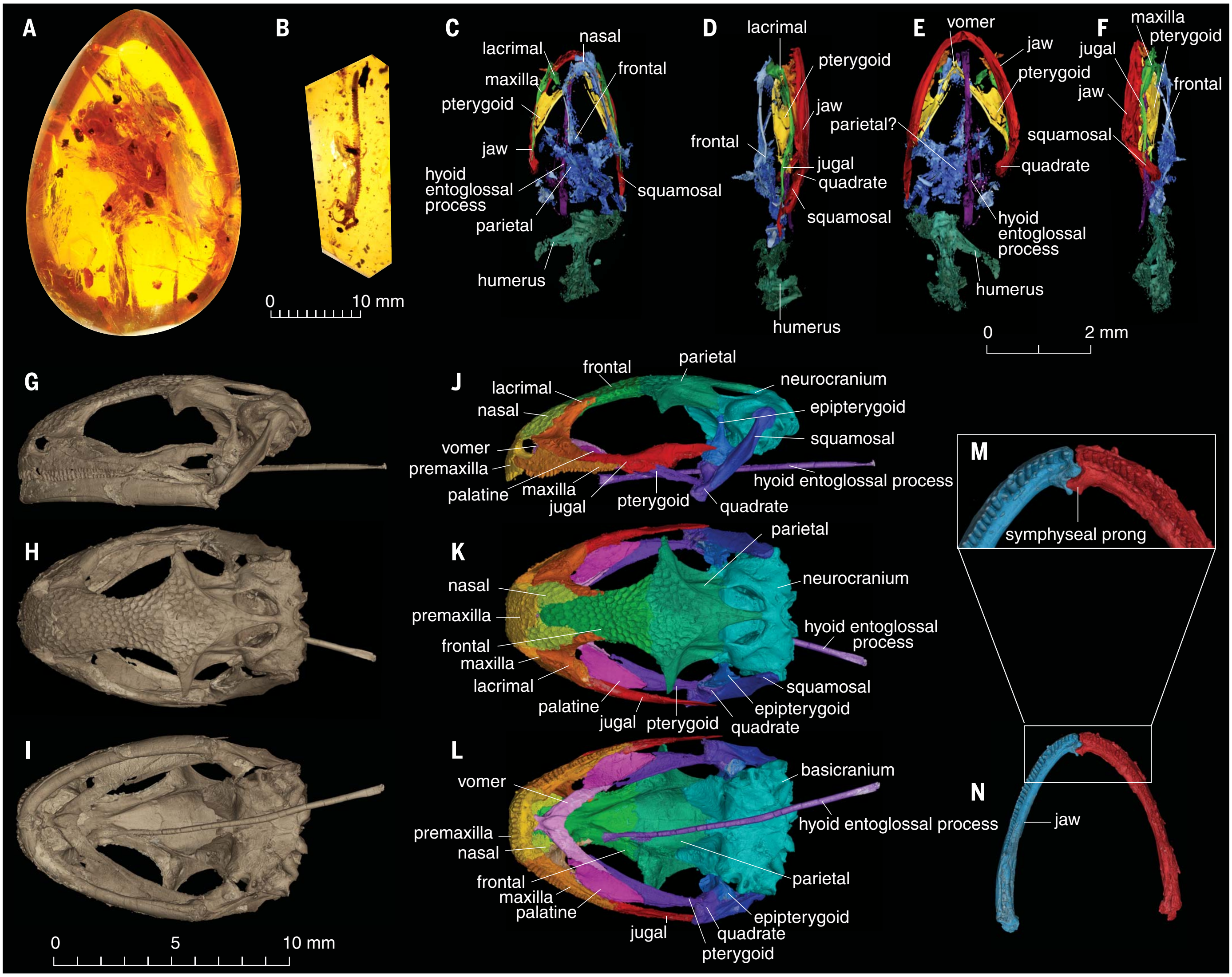


Fig. 1. Holotype and paratype of *Y. perettii*. Holotype GRS-Ref-060829 (**A** and **G** to **I**) and paratype JZC Bu154 (**B** to **F**). High-resolution computed tomography (HRCT) of the paratype with segmented bones [(C) to (F)]; the holotype with jaw articulated [(G) to (I)]; the holotype with all bones segmented and jaw removed (**J** to **L**); and the jaw of the holotype, with close-up of the mandibular symphysis (**M** and **N**). Lateral [(D), (F), (G), and (J)], dorsal [(C), (H), (K), (M), and (N)], and ventral [(E), (I), and (L)] views.

most closely resembles the older (120 Ma) Japanese *Shirerpeton* (7), but the phylogenetic analysis placed *Yaksha* as the sister taxon to *Shirerpeton* and either a clade of derived *Albanerpeton* species (Fig. 4A) or *Albanerpeton nexuosum*. Both *Yaksha* and *Shirerpeton* are thus nested within *Albanerpeton* as currently defined. However, we support the view that the single genus *Albanerpeton*, extending from the mid-Cretaceous of North America [~100 Ma (*3*)] to the Early Pleistocene of Italy [~2 Ma (*2*)], requires revision and subdivision (*7*), with the name *Albanerpeton* restricted to the type species, *A. inexpectatum*, and those Cenozoic species that consistently group closely with it (Fig. 4, supplementary text S3.1, and figs. S6 to S11).

As the relationships of albanerpetontids to extant amphibians (Lissamphibia), and the wider relationships of lissamphibians to fossil amphibians, are currently debated, we updated the coding for albanerpetontids, based on *Yaksha*, into four recent data matrices (*20*–*23*). Depending on the matrix used, albanerpetontids were placed (i) as sister to Batrachia (frogs and salamanders) within lepospondyls (*20*), (ii) as stem-Lissamphibia (*22*), (iii) nested within Lissamphibia (*21*), or (iv) nested in a clade comprising derived lepospondyls and lissamphibians (*23*). Nevertheless, all analyses placed albanerpetontids either as stem- or crown-group Lissamphibia (Fig. 4, C to F). Frustratingly, the new data provided no resolution to the lepospondyl versus temnospondyl origin hypotheses (*23*, *24*) (supplementary text S3.2 and figs. S13 to S16).

Biological implications

The paratype of *Yaksha* (JZC Bu154) was previously identified as a stem-chameleon (*14*), mainly on the basis of the long entoglossal hyoid process. In chameleons, this hyoid element is embedded in the base of the tongue, surrounded by collagenous sheaths (*25*) and a circular accelerator muscle (*26*). Contraction of the muscle, enhanced by an elastic storage-and-release effect from the wrapping sheaths (*25*, *27*), propels the tongue and entoglossal process out of the mouth, extending the tongue at speeds of up to 500 m/s and to a distance of at least a body length (*25*). An analogous mechanism exists in some plethodontid salamanders: as the tongue extends, the entire hyoid apparatus is folded into a bundle of cartilaginous rods that is projected out of the mouth again by circular protractor muscles (*27*, *28*). The entoglossal process of *Yaksha* [and other albanerpetontids (*1*)] is embedded into the remnant of the tongue pad (Fig. 2B), which suggests that albanerpetontids also had a ballistic feeding strategy (fig. S1), plausibly using a

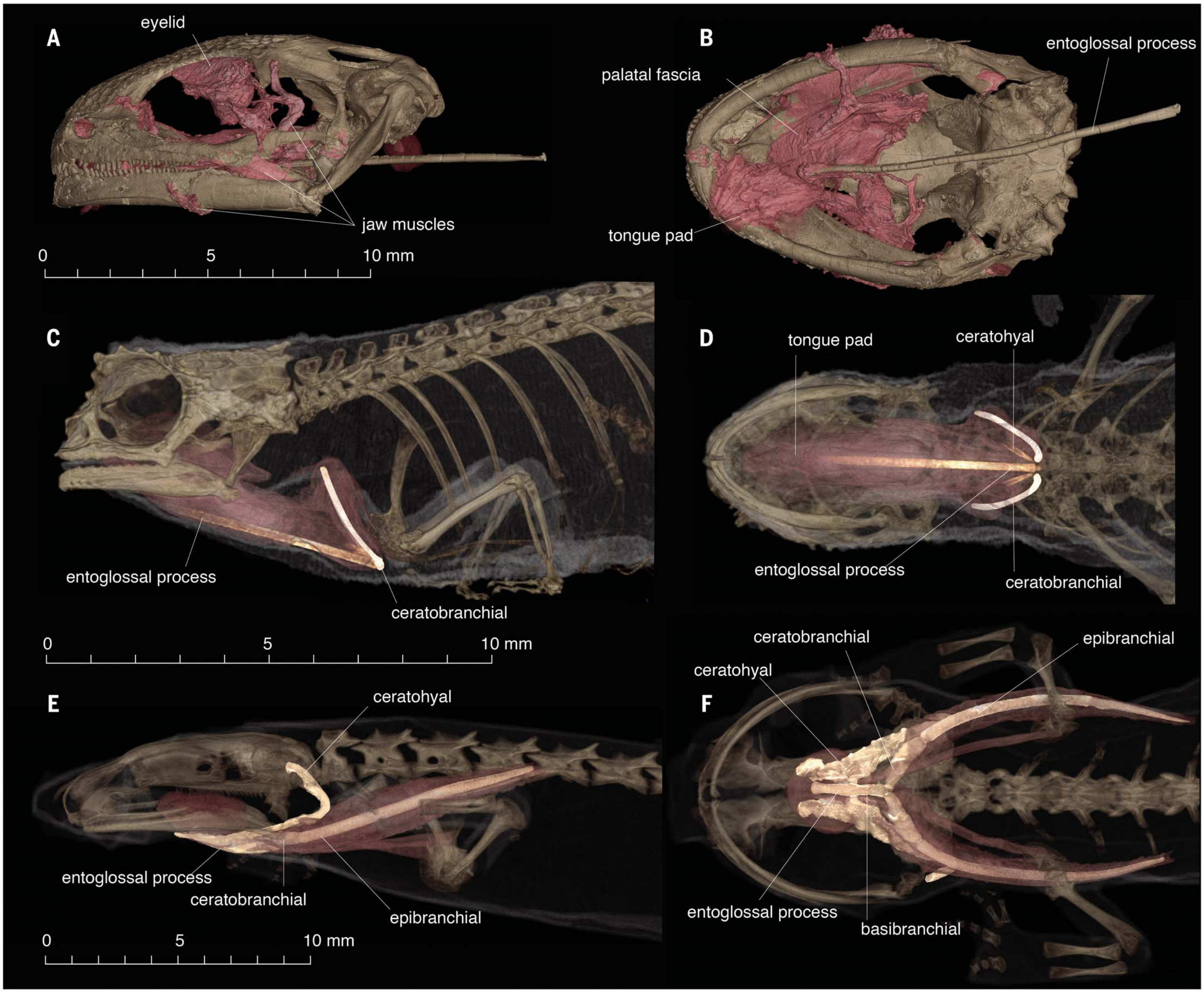


Fig. 2. Comparison of skeletal components in three tetrapods with ballistic tongues. Holotype of *Y. perettii* (GRS-Ref-060829) showing the preserved soft tissue (pink), including the tongue in lateral (**A**) and ventral (**B**) views. Diffusible iodine-based contrast-enhanced computer tomographies (DiceCT) of a leaf litter chameleon [*Brookesia* sp. UADBA:herps:15550 (*34*)] in lateral (**C**) and ventral (**D**) views. DiceCT of lungless salamander [*Bolitoglossa porrasorum* UF156522 (*35*)] in lateral (**E**) and ventral (**F**) views.

similar combination of circular muscles and wrapping collagen. This interpretation of *Yaksha* as a chameleon analog may help to explain some of the specialized features of albanerpetontids, including the complex neck and jaw joints, the long curved unguals covered in claw sheaths (fig. S3), and the large forward-looking orbits. We therefore interpret *Yaksha* (and all albanerpetontids) as a sit-and-wait predator, living on or around trees, and using a ballistic tongue to catch small invertebrates. In external appearance, albanerpetontids probably resembled tiny lizards more than salamanders.

There is a corollary to this interpretation of albanerpetontids as ballistic feeders. Most lissamphibians use a combination of lung breathing and cutaneous respiration. Lacking rib-mediated ventilation, these amphibians inflate their lungs by buccal pumping, using the hyoid apparatus to raise and depress the floor of the mouth (*12*). Plethodontid salamanders are lungless and rely on cutaneous gas exchange; this freed the hyoid apparatus from its constraints (*29*), permitting modification for specialized tongue feeding. By analogy, this respiratory mode must also apply to albanerpetontids, given their derived hyoid anatomy. Although the possession of scales might seem contradictory, studies on scaled caecilians have revealed some capacity for cutaneous gas exchange (*30*). For miniaturized amphibians such as albanerpetontids, it may have been sufficient.

The paratype of *Yaksha* (JZC Bu154) has a skull one-fourth the size of that of the miniaturized adult specimen of *Yaksha*. In amphibians, miniaturization is frequently coupled with direct development (*31*). The diminutive paratype of *Yaksha* may therefore indicate that albanerpetontids lacked a free-living larva.

Yaksha provides considerable new morphological, functional, and phylogenetic data for this enigmatic Jurassic-Pleistocene clade. Albanerpetontids are revealed as specialized, sit-and-wait terrestrial predators, combining lifestyle features of miniaturized chameleons and plethodontid salamanders and extending the history of ballistic tongue feeding by ~100 Ma, given molecular divergence estimates dating the origins of crown chameleons (*32*) and plethodontids (*33*) to the Late Cretaceous or Paleocene.

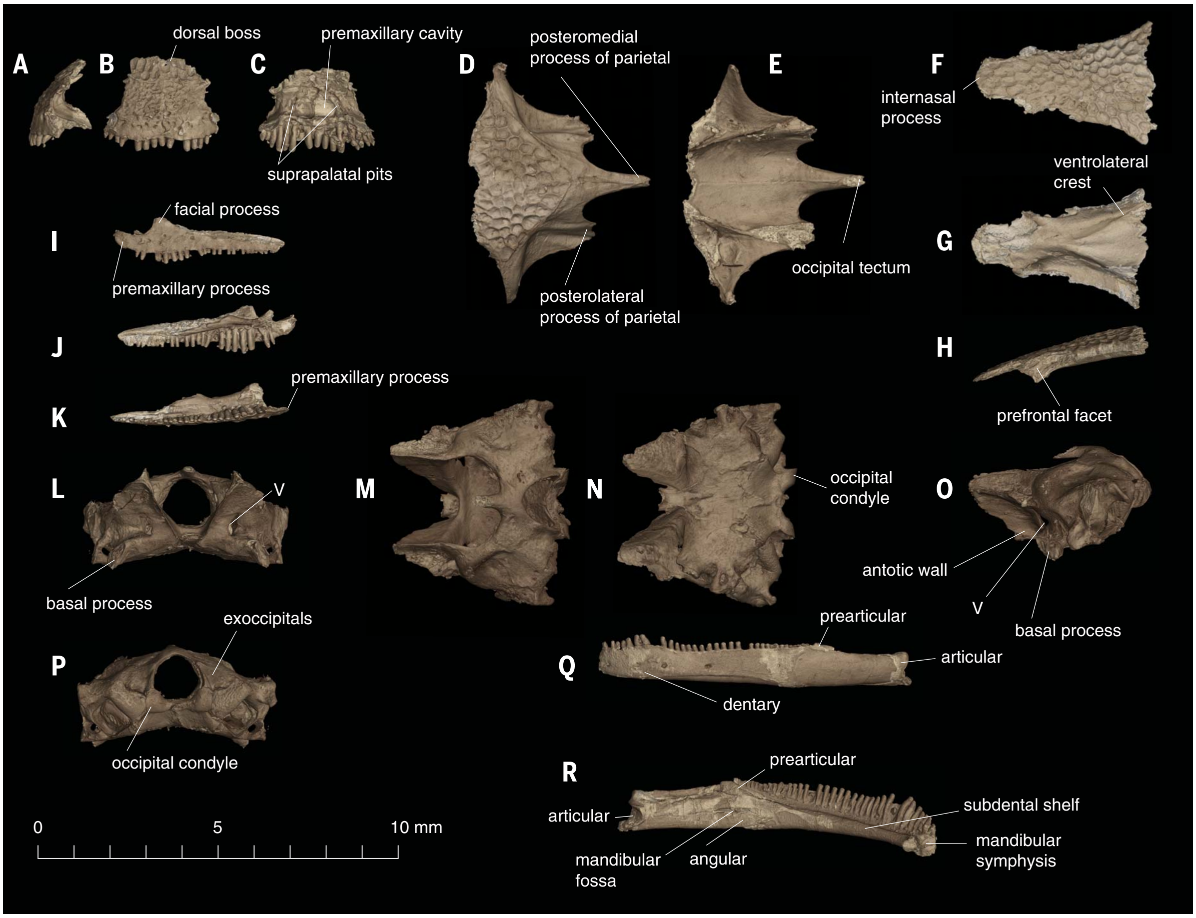
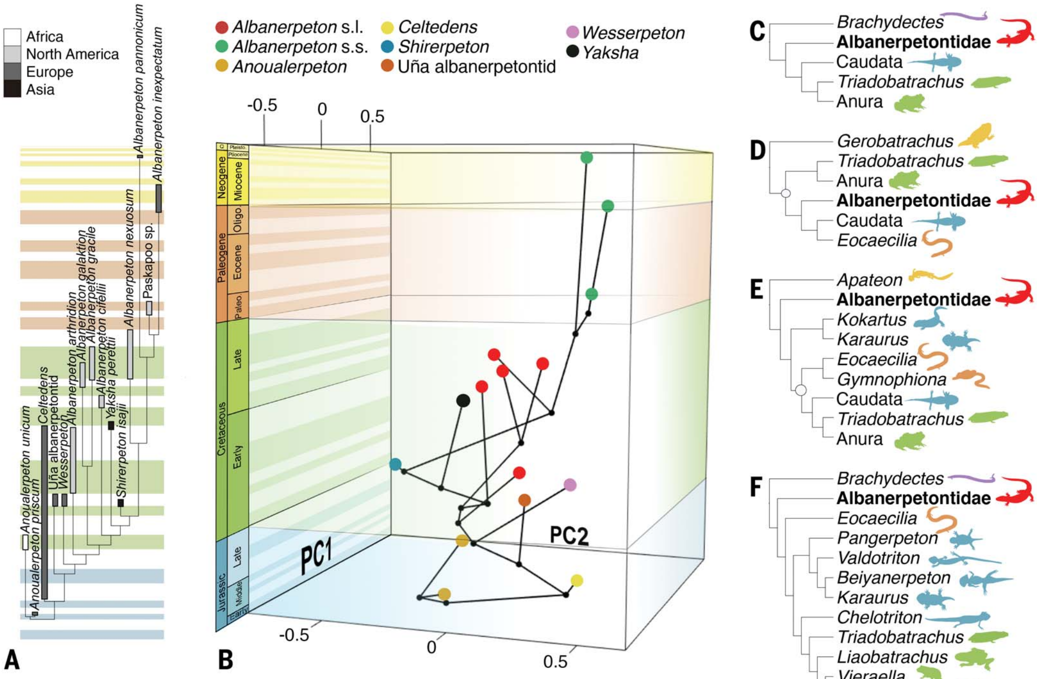


Fig. 3. Isolated elements of the holotype skull of *Y. perettii* (GRS-Ref-060829). Fused (or tightly paired) premaxillae (**A** to **C**), parietal (**D** and **E**), frontal (**F** to **H**), left maxilla (**I** to **K**), neurocranium (**L** to **P**), and left mandible (**Q** and **R**). Lateral [(A), (H), (I), (O), and (Q)], medial [(J) and (R)], anterior [(B) and (L)], posterior [(C) and (P)], dorsal [(D), (F), and (M)], and ventral [(E), (G), (K), and (N)] views.

Fig. 4. Phylogenetic relationships of albanerpetontids calibrated against age and chronophylomorphospace using the dataset for albanerpetontids. (**A**) Phylogenetic relationships of albanerpetontids with geographical distribution plotted against time. (**B**) First and second principal components (PC1 and PC2) explain 35.5 and 23.8% of the total variance, respectively. Note the position of purported members of the genus *Albanerpeton* in separate clades and regions of the morphospace. The tree was dated using the "equal" method, but an alternative tree dated under the "mbl" method is also provided in the supplementary materials. s.l., sensu lato; s.s., sensu stricto. (**C** to **F**) Alternative positions recovered for Albanerpetontidae in relation to lissamphibians using different data matrices: (C) (*25*), (D) (*26*), (E) (*27*), and (F) (*28*).



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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Figs. S1 to S15
References (*36*–*74*)

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Enigmatic amphibians in mid-Cretaceous amber were chameleon-like ballistic feeders

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Ancient amphibians preserved in amber

Extant amphibians are represented by three fairly simple morphologies: the mostly hopping frogs and toads, the low-crawling salamanders, and the limbless caecilians. Until the early Pleistocene––and for more than 165 million years––there was another group, the albanerpetontids. We know little about this group because amphibian fossils are poorly preserved, and previous specimens from this group are both rare and mostly badly damaged. Daza *et al.* describe a set of fossils preserved in amber showing that this group was unusual both in their habitat use (they may been climbers) and their feeding mode, which appears to have been convergent with the ballistic feeding now seen in chameleons (see the Perspective by Wake).

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