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NEW INSIGHTS INTO *ANUROGNATHUS* AND ANUROGNATHIDS

The Anurognathidae is an enigmatic family of short-skulled and short-tailed rhamphorhynchoid pterosaurs, which until the last few years was known from only two specimens. The first was Döderlein's fragmentary holotype of *Anurognathus ammoni* from the Upper Jurassic (Tithonian) Solnhofen Limestone of southern Germany. Although its skull was difficult to interpret, the specimen was described as having a short tail that was pygostyle-like, a short metacarpus, a very long antebrachium and first wing phalanx that suggested that the wing was very long relative to the trunk, and a long pedal digit V with four phalanges; a combination of characters unlike any other pterosaur. The second specimen was the even more fragmentary holotype of *Batrachognathus volans* from the Upper Jurassic (Oxfordian/ Kimmeridgian) Karatau deposits of Kazakhstan, and thus roughly contemporaneous with *Anurognathus*. The skull of the holotype of *Batrachognathus* is better preserved than that of *Anurognathus* and demonstrates that the anurognathid skull was short and very broad, with a T-shaped premaxilla and broadly curving mandibular rami, quite unlike those of other pterosaurs. Unfortunately, the specimen is incomplete and adds little else to our understanding of anurognathids.

In the past few years, two new anurognathids, *Dendrorhynchoides curvidentatus* and *Jeholopterus ningchengensis*, have been described from relatively complete single specimens from the Lower Cretaceous (middle Barremian) Yixian Formation of China. The skulls of *Dendrorhynchoides* and *Jeholopterus*, though badly crushed and inadequately described, are clearly short and broad, and like *Anurognathus* the specimens exhibit a short metacarpus, elongate antebrachium and first wing phalanx, elongate pedal digit V, and a short tail.

The four specimens do not provide much information about the skull, and given our present knowledge of anurognathids, the discovery of a complete specimen of *Anurognathus ammoni* from the Solnhofen Limestone with an excellently preserved skull is a welcome addition to the anurognathid record. The new specimen has permitted the first detailed reconstruction of the skull, and leads to a new interpretation of *Anurognathus* and new insights into the ecology of the Anurognathidae.

The specimen is fully articulated and preserved in dorsal view, wings folded alongside the body and the hindlimbs folded as well. It is 67 mm long from snout to the tip of the tail, and has an overall length of 85 mm. The skull is well preserved, though it was crushed flat and in the process the skull roof was translated forward relative to the palate, and the vertical elements of the skull (i.e., the median process of the premaxilla, the postorbital, and the quadrate) were rotated forward about their ventral ends. Much of the skull consists of slender bones separating large openings, though the posterior skull roof consists of large triangular frontals followed by a large rectangular parietals. The premaxilla is T-shaped and the maxilla is robust and strongly curved as in

Batrachognathus. The jugal overlaps the maxilla for most of its length and sends an ascending process up in front of the orbit. The process passes upward and medially and then is continued anteriorly by the lacrymal and nasal, which contact the frontal near the midline. A very slender ascending process of the maxilla passes up to contact the nasal-jugal process and separates the naris from the antorbital fenestra. Behind the jugal, the orbit is enormous and contains a very large sclerotic ring. Behind the orbit is a triradiate postorbital, which with the squamosal separates the upper and lower temporal fenestrae. The quadrate is a robust straight bone directed up and in to contact the squamosal. The mandible is broadly curving and its retroarticular process is directed posterolaterally such that it would not limit depression of the mandible by contacting the quadrate. The teeth are sharply pointed, slightly curved, peg-like, and widely spaced such that there are 3 premaxillary teeth, 6 maxillary teeth, and 8 mandibular teeth.

Reconstruction of the skull shows that it was broader than long and quite tall. However, the most striking feature is the great size of the eye. The eyes were directed anterolaterally at about 45° and would have permitted binocular vision.

The tail consists of about 10 caudal vertebrae posterior to the ilia. The anterior ones are simple flattened disks, while the more distal ones are rather poorly preserved. The tail is short, but there is no evidence of fusion into a pygostyle-like structure, and the morphology is quite different from the short tail of pterodactyloids, and thus a convergence rather than a synapomorphy. The tails of *Jeholopterus* and *Dendrorhynchoides* are also short, and it is likely that a short tail is characteristic of anurognathids.

The wingfinger, unlike that of almost all pterosaurs, is reduced to three phalanges. In addition, the three phalanges decrease in length progressively (100:77:43) so that the wing is relatively shorter than that of other pterosaurs even though the antebrachium and first wing phalanx are very long. The interphalangeal joints of both wings are preserved at about 140°, thus flexed much more than is typical of pterosaurs. The articular surfaces of adjacent phalanges are preserved are marked angles from one another, showing that the interphalangeal joints could be flexed and extended, which is unlike the condition in other pterosaurs. The combination of the short wingfinger and the long hindlimb suggests that the patagium, which presumably attached near the ankle, had a large area and a low aspect ratio. The wing of *Jeholopterus* clearly has four wing phalanges, but the fourth phalanx is very short because of the progressive reduction in phalangeal length from proximal to distal. Its wings are also preserved with the phalanges strongly flexed as in *Anurognathus*, suggesting that its interphalangeal joints could also be flexed and extended, and moveable interphalangeal joints probably were characteristics of anurognathits.

It has been suggested that anurognathids were insectivorous, and the skull is well suited to insectivory. The very large eyes would enable locating and tracking of flying insects in low light conditions, and their forward placement might have permitted binocular vision to aid in catching insects. The widely spaced, sharp teeth would be perfect for catching and holding insects, and the broad, widely opening mouth would form an excellent insect trap.

The structure of the wing and tail of *Anurognathus* suggest that it was adapted for a slow, highly maneuverable flight. The wing, with its large area and low aspect ratio,

is similar in planform to those of many microchiropterans, which exhibit a highly maneuverable flight well suited to aerial insectivory. The reduction of the tail in anurognathids would have removed its stabilizing effect, its mass, and reduced its moment of inertia, all of which would contribute to increased maneuverability. Thus, *Anurognathus* would have been well suited to hunting insects in low light conditions like extant microchiropterans and caprimulgid birds.

The new specimen of *Anurognathus* and other anurognathid specimens are preserved dorsoventrally in a distinctive posture with the wings folded compactly along the sides, a posture rather uncommon in the sample of Solnhofen pterosaurs. It is possible that the posture represents a typical resting posture of anurognathids, one that would be well suited to resting in trees and among rocks when not flying and feeding.

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