# Is *Oculudentavis* a bird or even archosaur?

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Recent finding of a fossil, *Oculudentavis khaungraae* Xing et al. 2020, entombed in a Late Cretaceous amber was claimed to represent a humming bird-sized dinosaur [1]. Regardless the intriguing evolutional hypotheses about the bauplan of Mesozoic dinosaurs (including birds) posited therein, this enigmatic animal, however, demonstrates various lizard-like morphologies, which challenge the fundamental morphological gap between Lepidosauria and Archosauria. Here we reanalyze the original computed tomography scan data of *Oculudentavis*. A suit of squamate synapomorphies, including pleurodont marginal teeth and an open lower temporal fenestra, overwhelmingly support its squamate affinity, and that the avian or dinosaurian assignment of *Oculudentavis* is conclusively rejected.

## Introduction

Birds and their close dinosaurian relatives have gained a large spectrum in body size from tens of milliliters to meters. The smallest bird, Bee hummingbird, measures only about 60 mm in length, which is one fifth the size of the smallest known non-avian theropod. A recent work reported a new "bird", *Oculudentavis* from a 99 million-year-old Burmese amber, which was claimed to be the smallest bird ever known and represent a previously unknown bauplan and novel ecology in Archosaur [1].

Here we re-analyze the original computed tomography (CT) scan data and challenge the primary results — bird or bird-like dinosaur affinity of *Oculudentavis* [1]. Morphological evidences demonstrated here highly contradicted the avian or even archosaurian phylogenetic placement of *Oculudentavis*, and revealed multiple synapomorphies of the Squamata for this taxon (Figures 1 and 2).

## Results and discussions

Instead of demonstrating synapomorphies of the Aves, *Oculudentavis* show multiple "new" characters that has never been found in any previously known birds or non-avian dinosaurs. One of the most bizarre characters is the absence of an antorbital fenestra. Xing et al. [1] argued the antorbital fenestra fused with the orbit, but they reported the lacrimal is present at the anterior margin of the orbit [1]. This contradicts the definition of the lacrimal in birds, where the lacrimal is the bone between the orbit and antorbital fenestra [2]. In addition, a separate antorbital fenestra is a stable character among archosaurs including non-avian dinosaurs and birds [3-5], and all the known Cretaceous birds do have a separate antorbital fenestra [6-8].

Another highly questionable feature in *Oculudentavis* is the maxilla extending caudally to the level of mid-orbit and forming half of the ventral margin of the orbit, which is extremely unusual in Aves. In most crown birds, the maxilla terminates anterior to the orbit. The ventral margin of the orbit is formed by the jugal [2, 9]. This is also the condition among Mesozoic birds, including *Archaeopteryx* [5, 10, 11], *Sapeornis* [12], enantiornithines [6, 8] and ornithuromorphs [8]. In *Ichthyornis*, maxilla is elongate and extends further caudally beneath the jugal [13], which means the ventral margin of the orbit is still mostly composed by the jugal, different from *Oculudentavis*. In addition, we need to note that the skull of *Jeholornis* was incorrectly reconstructed with a maxilla extending most of the orbit, and a shortened jugal [1], which certainly lead to a strong similarity between the skull of *Oculudentavis* and *Jeholornis*. However, the maxilla of *Jeholornis* is short and most of the ventral margin of the orbit is formed by the elongate jugal followed by the quadratojugal [8], in stark contrast with *Oculudentavis*.

In *Oculudentavis*, the maxillary tooth row extends as far caudally as the rostral half of the antorbital fenestra. Among most Mesozoic birds, maxillary tooth row ends well cranially to the cranial margin of the orbit [5, 6, 8]. In contrast, at least four teeth are located beneath the ventral margin of the orbital, and the last one even ends below the rostral third point of the orbit in *Oculudentavis*.

Although Xing et al. mentioned that the scleral ring and dentition of *Oculudentavis* resemble lizards [1], they failed to recognize that pleurodont dentition is diagnostic for squamates [14]. The maxillary and dentary teeth are ankylosed to the jaw with their labial side (Figure 1E), and replacement teeth develop posterolingual to the functional teeth. The authors also stated that the tooth implantation appears to be acrodont to pleurodont. However, there is no evidence for acrodonty based on our reexamination of the original CT data.

In comparison, dinosaurs have thecodont teeth that develop in tooth sockets, with replacement teeth developing beneath the functional teeth. Although the Late Cretaceous ornithuromorph bird *Hesperornis* retain teeth in a groove (tooth sockets fused together) [15], it is clearly distinguishable from the pleurodont dentition in *Oculudentavis*. Non-archosaurian dentition of *Oculudentavis* has also been interpreted as the result of miniaturization [1]. To our best knowledge, there is no concrete evidence suggesting such a drastically change of dentition in miniaturized archosaurs. Pleurodont dentition falsifies the dinosaurian or even archosaurian affinity of *Oculudentavis* — instead it supports the squamate affinity of this new species.

Another unambiguous squamate synapomorphy in *Oculudentavis* is the loss of the lower temporal bar. In the original publication, a complete orbit was illustrated on the left side of the skull with an unnamed piece of bone between the jugal and postorbitofrontal [1]. In addition, the anterior margin of the quadrate articulates with an unlabeled bone. The misleading illustration suggests that the quadratojugal might be present in *Oculudentavis*. On the basis of the original CT scan data, we demonstrate that the orbit on the left side of the skull is crushed. The left jugal is not preserved. The right side of the skull preserves a complete orbital region, which shows the jugal has a smooth posterior margin, lacking contact with the quadrate. The quadratojugal is absent (Figure 1A and B), which means the lower temporal fenestra is open in *Oculudentavis* – a condition shared with all squamates but not dinosaurs or birds [14, 16, 17].

Additional morphologies of *Oculudentavis* that contradict its avian affinity include the presence of the parietal foramen (Figure 1G), the separate ventral down growths of frontal (Figure 1H), as well as palatal teeth present on palatine and pterygoid (Figures 1D and 2)

## Conclusion

*Oculudentavis* means "eye-tooth bird", yet neither the eyes (scleral ring) nor the teeth suggest this new species was a bird. Xing et al assigned this enigmatic animal to Aves based on superficial appearances, such as the exterior contour of the dome-shaped cranium [1]. Therefore, all the extended discussions, including the morphological changes related to miniaturization and the ocular morphology, lost their foundation with a problematic phylogenetic placement of this animal. In addition, multiple unambiguous characters support the squamate affinity of *Oculudentavis*, including the loss of quadratojugal, pleurodont marginal teeth, and presence of palatal teeth (Figure 3). The phylogenetic analysis in Xing et al suffers from biased taxonomic sampling [1]. Our new morphological discoveries suggest that lepidosaurs should be included in the phylogenetic analysis of *Oculudentavis.*

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## Figure legends

**Figure 1.** Re-analysis of cranial anatomy of *Oculudentavis khaungraae* Xing et al. 2020 (holotype, HPG-15-3) based on original computed tomography scan data [1]. A-C, Scale bar, 2 mm; D-H, Not to scale.

(A) Right lateral view.

(B) Line drawing of right lateral view, showing the absence of quadratojugal in *Oculudentavis*, and the arrangement of the orbital bones has been reinterpreted.

(C) Anterolateral view. (D) Tomographs through palatine, showing palatine teeth

(E) Tomographs through dentary, showing the typical pleurodont tooth

(F) Dorsal view

(G) Tomographs through pineal foramen

(H) The top half part of the skull has been removed, showing the narrowed frontals

**Figure 2.** Simplified reptile family tree, illustrative drawings showing the comparison of the skull in *Oculudentavis*, squamates (green lizard *Lacerta bilineata*, modified from [18]) and birds (Cretaceous bird *Sapeornis*, modified from [19]).

**Figure 3.** Detailed anatomical characters supporting squamate affinity of *Oculudentavis* revealed by CT.

(A) Pterygoid tooth shown in three-dimensional reconstruction of the skull

(B) Pterygoid tooth shown in coronal section of the skull

## Methods and Data availability

The original CT scan data was obtained upon request from the authors of original paper [1]. Two 3D format files (9.5G in total) were combined into one and re-rendered in Drishti 2.6.5 (https://github.com/nci/drishti/releases). Scan data were analyzed in Avizo (www.thermofisher.com) and imaged in Adobe photoshop (www.adobe.com). For more scanning, 3D reconstruction and data information see [1].

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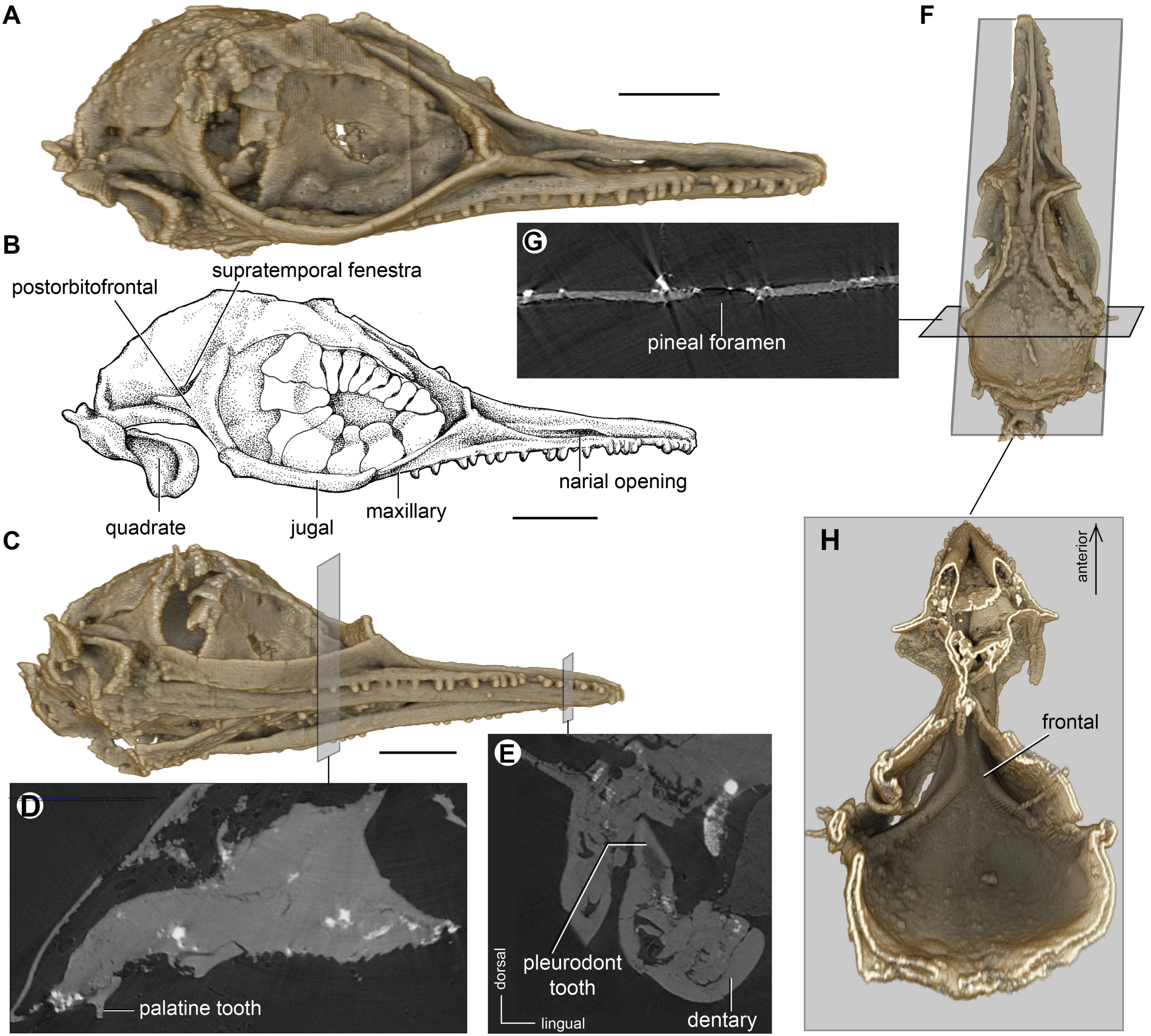
## Author Contributions

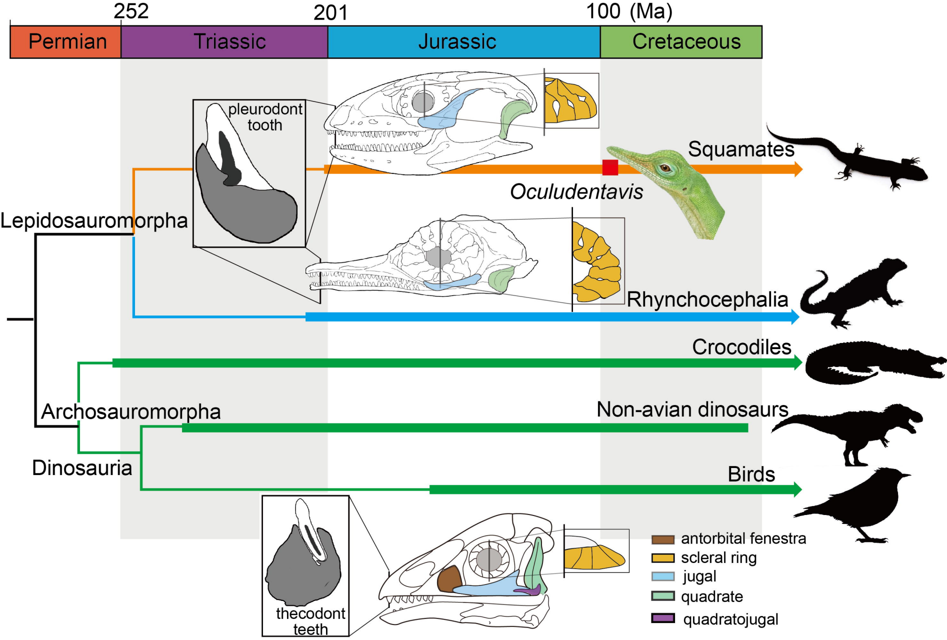
All authors designed the project, analyzed and discussed the data, and wrote the manuscript. All authors contributed equally.

## Conflict of Interests

No


A
B
supratemporal fenestra
postorbitofrontal
quadrate
jugal
maxillary
narial opening
C
D
palatine tooth
E
pleurodont tooth
dorsal
lingual
dentary
F
G
pineal foramen
H
anterior
frontal


A
B
lower jaw
pterygoid tooth



252
201
100 (Ma)
Permian
Triassic
Jurassic
Cretaceous
pleurodont tooth
Squamates
*Oculudentavis*
Lepidosauromorpha
Rhynchocephalia
Crocodiles
Archosauromorpha
Non-avian dinosaurs
Dinosauria
Birds
thecodont teeth
antorbital fenestra
scleral ring
jugal
quadrate
quadratojugal