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Is *Oculudentavis* a bird or even archosaur?

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Zhiheng Li¹, Wei Wang², Han Hu³, Min Wang^{1,*}, Hongyu Yi^{1,*}, Jing Lu^{1,*}

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1 Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of

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Sciences, Beijing, China.

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2 Institute of Geology and Geophysics, Chinese Academy of Sciences, Beijing, China.

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3 University of New England, Armidale, Australia

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Recent finding of a fossil, *Oculudentavis khaungrae* Xing et al. 2020, entombed in a

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Late Cretaceous amber was claimed to represent a humming bird-sized dinosaur [1].

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Regardless the intriguing evolutionary hypotheses about the bauplan of Mesozoic

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dinosaurs (including birds) posited therein, this enigmatic animal, however, demonstrates

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various lizard-like morphologies, which challenge the fundamental morphological gap

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between Lepidosauria and Archosauria. Here we reanalyze the original computed

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tomography scan data of *Oculudentavis*. A suit of squamate synapomorphies, including

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pleurodont marginal teeth and an open lower temporal fenestra, overwhelmingly support

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its squamate affinity, and that the avian or dinosaurian assignment of *Oculudentavis* is

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conclusively rejected.

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Introduction

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Birds and their close dinosaurian relatives have gained a large spectrum in body size

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from tens of milliliters to meters. The smallest bird, Bee hummingbird, measures only

24 about 60 mm in length, which is one fifth the size of the smallest known non-avian
25 theropod. A recent work reported a new “bird”, *Oculudentavis* from a 99 million-year-old
26 Burmese amber, which was claimed to be the smallest bird ever known and represent a
27 previously unknown bauplan and novel ecology in Archosaur [1].

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

33

34 **Results and discussions**

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

44 Another highly questionable feature in *Oculudentavis* is the maxilla extending
45 caudally to the level of mid-orbit and forming half of the ventral margin of the orbit,
46 which is extremely unusual in Aves. In most crown birds, the maxilla terminates anterior

47 to the orbit. The ventral margin of the orbit is formed by the jugal [2, 9]. This is also the
48 condition among Mesozoic birds, including *Archaeopteryx* [5, 10, 11], *Sapeornis* [12],
49 enantiornithines [6, 8] and ornithuromorphs [8]. In *Ichthyornis*, maxilla is elongate and
50 extends further caudally beneath the jugal [13], which means the ventral margin of the
51 orbit is still mostly composed by the jugal, different from *Oculudentavis*. In addition, we
52 need to note that the skull of *Jeholornis* was incorrectly reconstructed with a maxilla
53 extending most of the orbit, and a shortened jugal [1], which certainly lead to a strong
54 similarity between the skull of *Oculudentavis* and *Jeholornis*. However, the maxilla of
55 *Jeholornis* is short and most of the ventral margin of the orbit is formed by the elongate
56 jugal followed by the quadratojugal [8], in stark contrast with *Oculudentavis*.

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

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

69 In comparison, dinosaurs have thecodont teeth that develop in tooth sockets, with

70 replacement teeth developing beneath the functional teeth. Although the Late Cretaceous
71 ornithuromorph bird *Hesperornis* retain teeth in a groove (tooth sockets fused together)
72 [15], it is clearly distinguishable from the pleurodont dentition in *Oculudentavis*. Non-
73 archosaurian dentition of *Oculudentavis* has also been interpreted as the result of
74 miniaturization [1]. To our best knowledge, there is no concrete evidence suggesting such
75 a drastically change of dentition in miniaturized archosaurs. Pleurodont dentition falsifies
76 the dinosaurian or even archosaurian affinity of *Oculudentavis* — instead it supports the
77 squamate affinity of this new species.

78 Another unambiguous squamate synapomorphy in *Oculudentavis* is the loss of the
79 lower temporal bar. In the original publication, a complete orbit was illustrated on the left
80 side of the skull with an unnamed piece of bone between the jugal and postorbitofrontal
81 [1]. In addition, the anterior margin of the quadrate articulates with an unlabeled bone.
82 The misleading illustration suggests that the quadratojugal might be present in
83 *Oculudentavis*. On the basis of the original CT scan data, we demonstrate that the orbit
84 on the left side of the skull is crushed. The left jugal is not preserved. The right side of the
85 skull preserves a complete orbital region, which shows the jugal has a smooth posterior
86 margin, lacking contact with the quadrate. The quadratojugal is absent (Figure 1A and B),
87 which means the lower temporal fenestra is open in *Oculudentavis* – a condition shared
88 with all squamates but not dinosaurs or birds [14, 16, 17].

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

93

94 **Conclusion**

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

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164 **Figure legends**

165 **Figure 1.** Re-analysis of cranial anatomy of *Oculudentavis khaungraae* Xing et al. 2020

166 (holotype, HPG-15-3) based on original computed tomography scan data [1]. A-C, Scale

167 bar, 2 mm; D-H, Not to scale.

168 (A) Right lateral view.

169 (B) Line drawing of right lateral view, showing the absence of quadratojugal in

170 *Oculudentavis*, and the arrangement of the orbital bones has been reinterpreted.

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

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

173 (F) Dorsal view

174 (G) Tomographs through pineal foramen

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

176

177 **Figure 2.** Simplified reptile family tree, illustrative drawings showing the comparison of

178 the skull in *Oculudentavis*, squamates (green lizard *Lacerta bilineata*, modified from [18])

179 and birds (Cretaceous bird *Sapeornis*, modified from [19]).

180

181 **Figure 3.** Detailed anatomical characters supporting squamate affinity of *Oculudentavis*

182 revealed by CT.

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

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

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186

187 **Methods and Data availability**

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

193

194 **Acknowledgement**

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198 and writing the manuscript.

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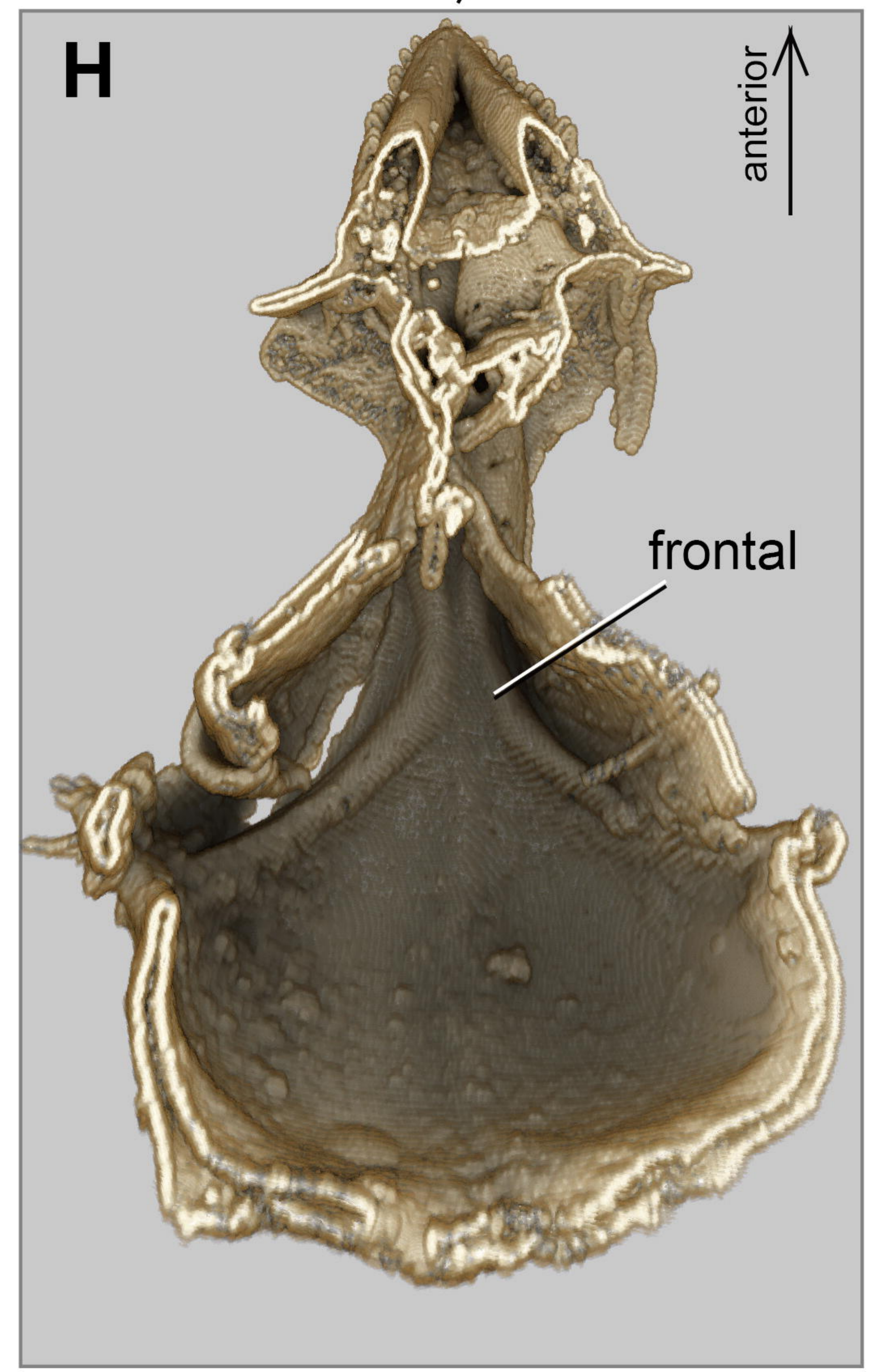
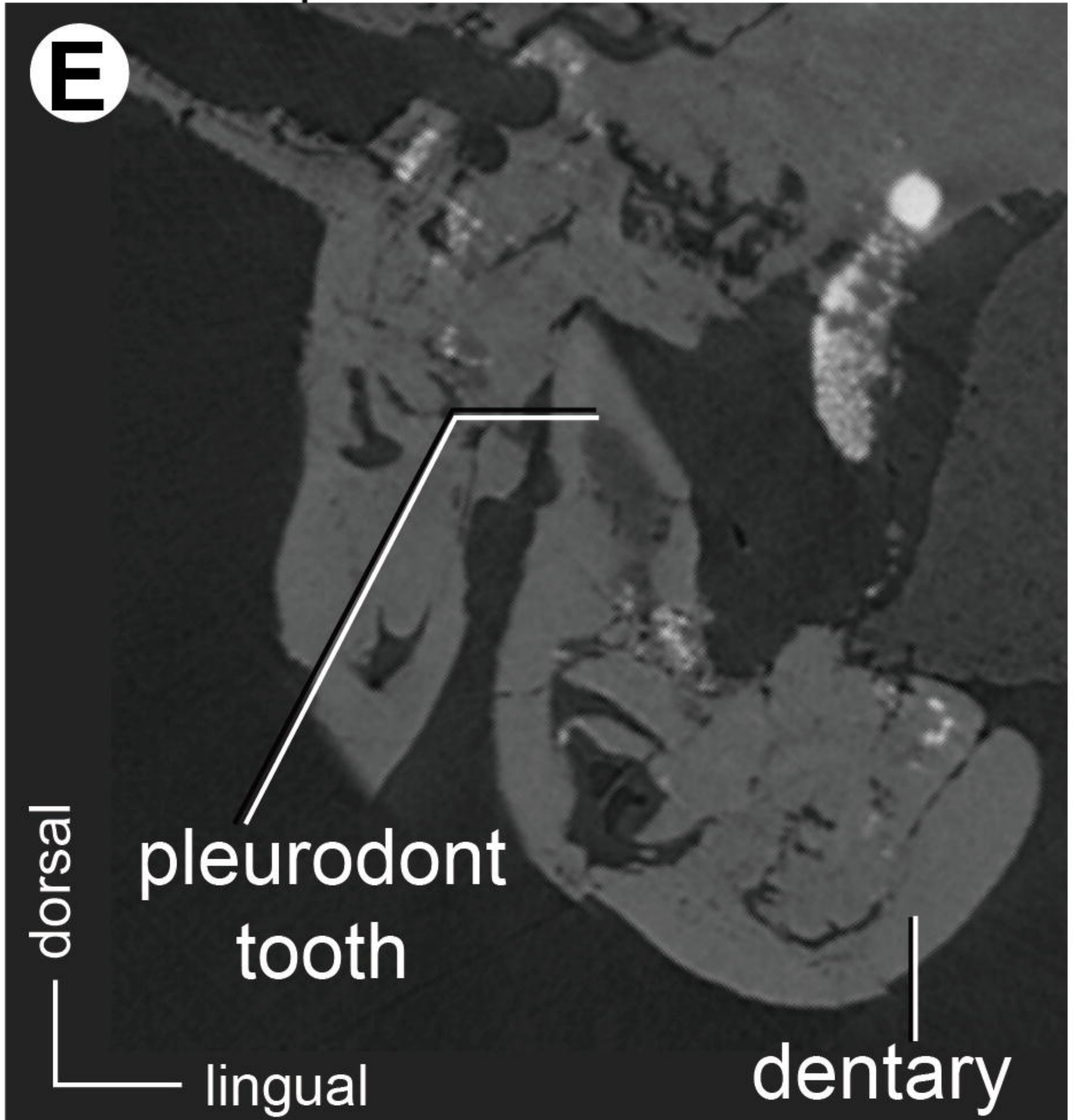
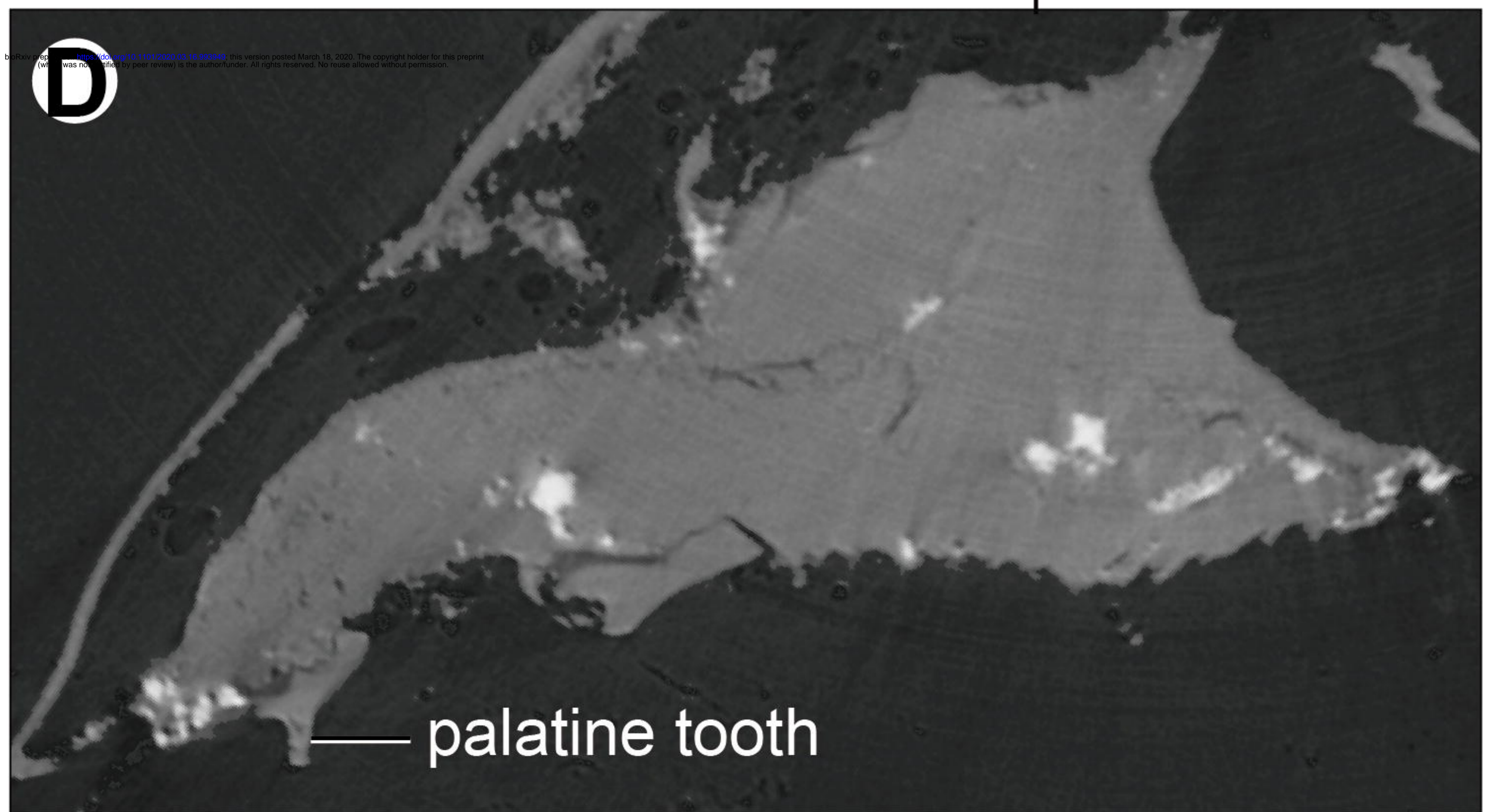
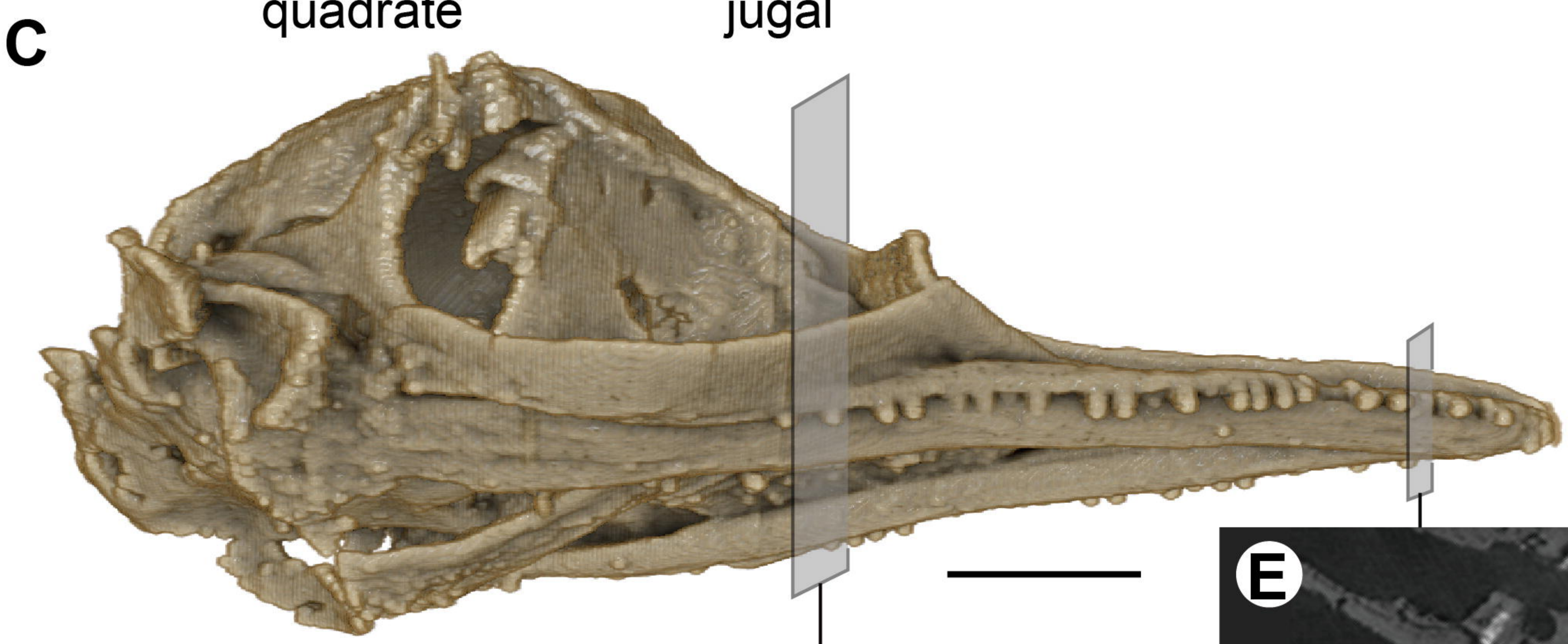
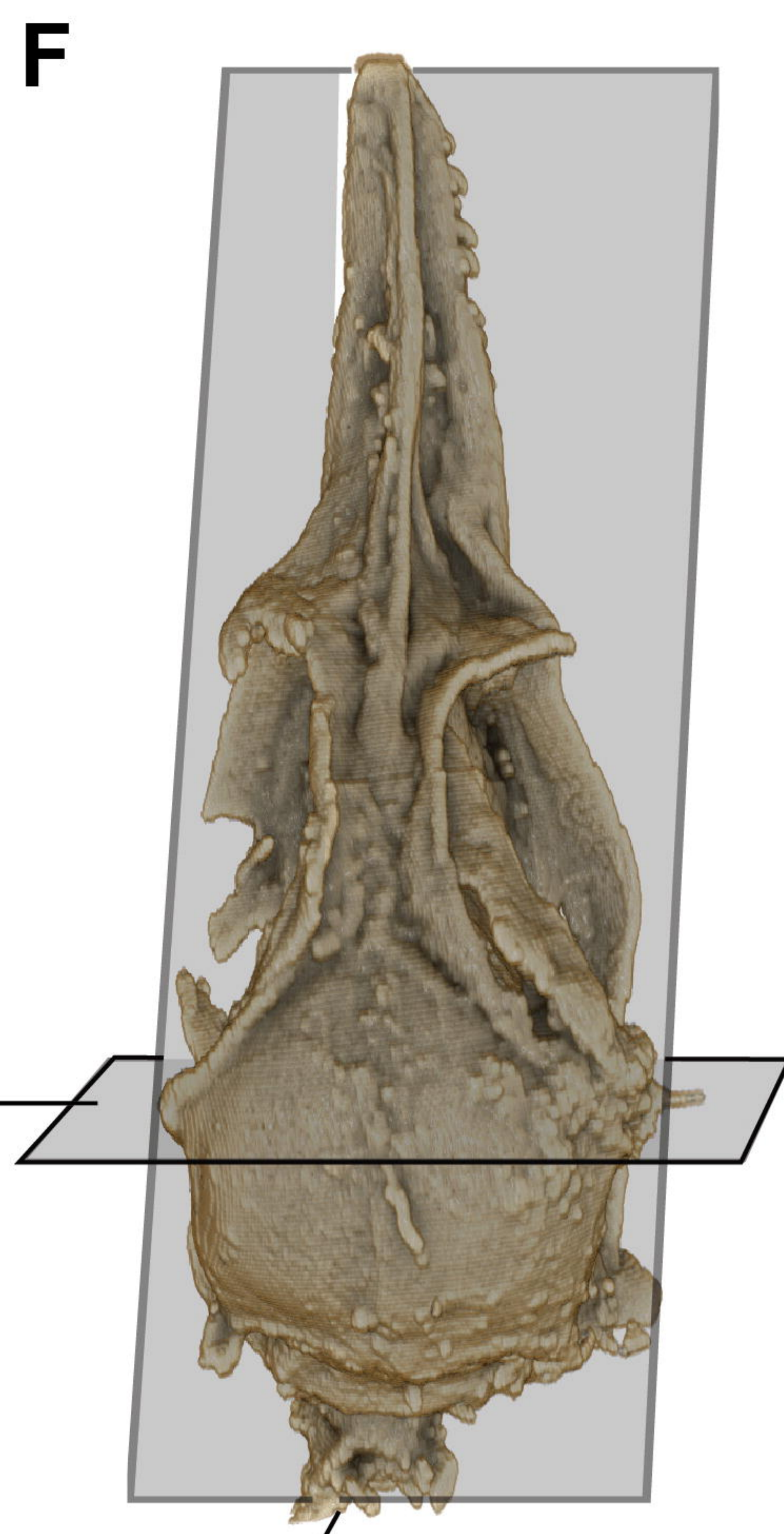
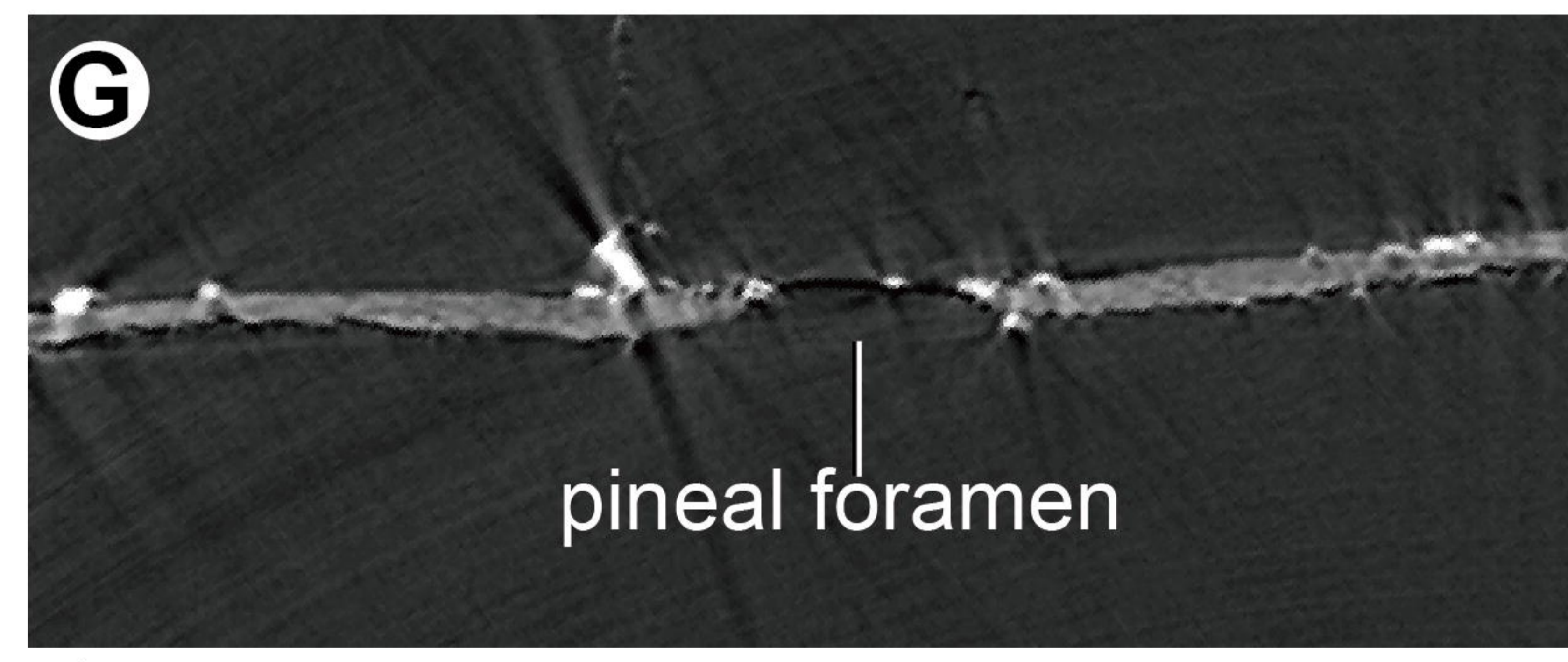
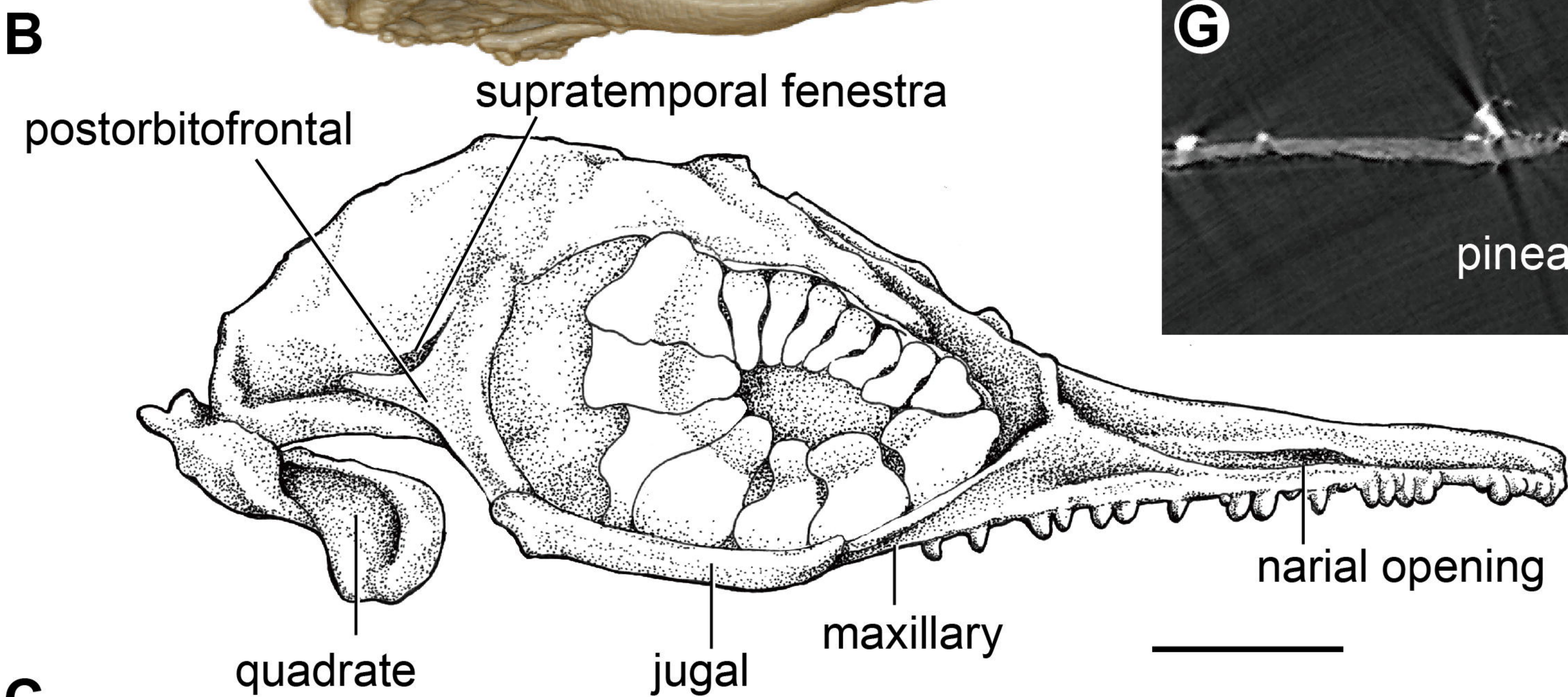
200 **Author Contributions**

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

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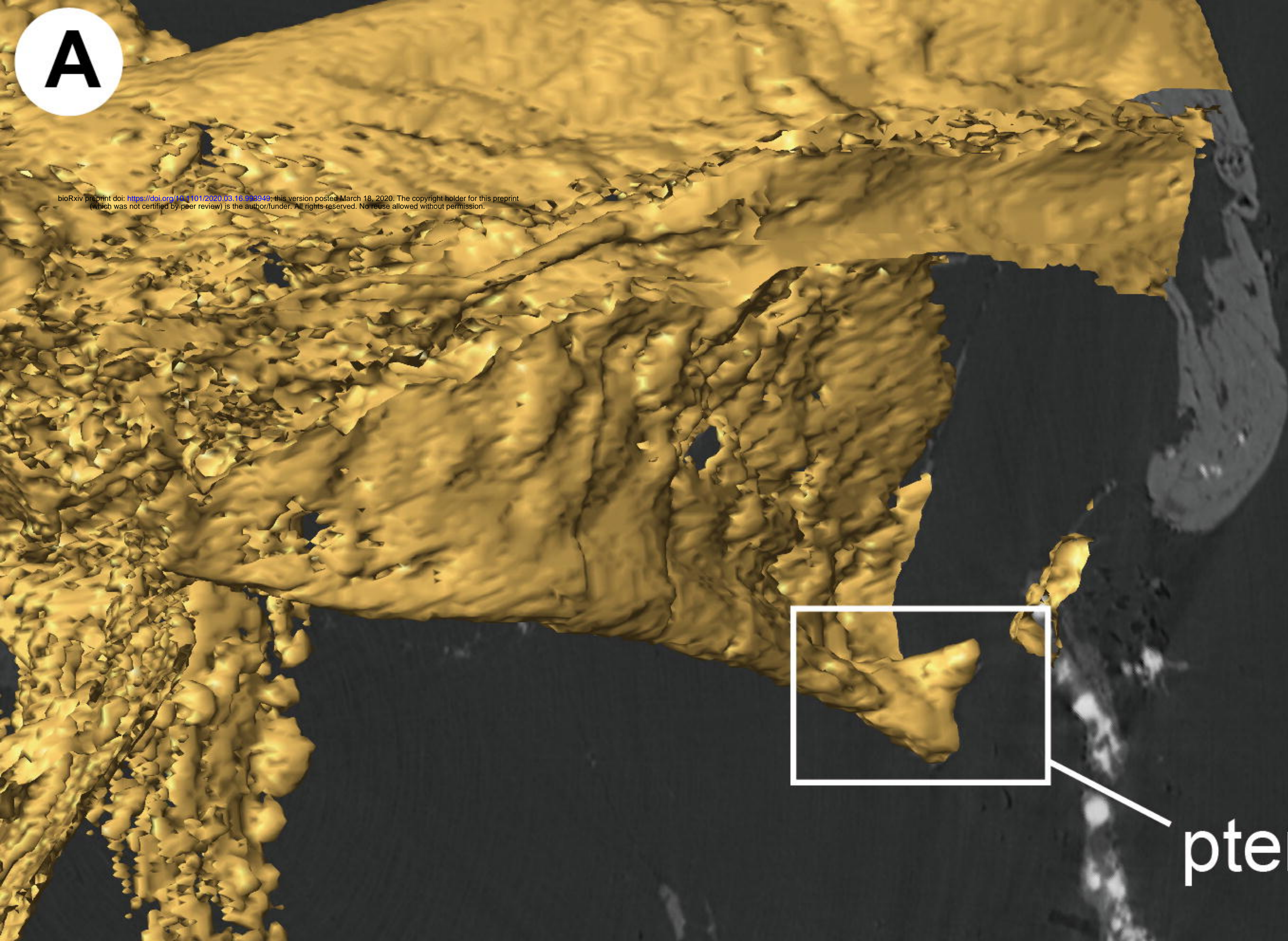
204 **Conflict of Interests**

205 No



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**B**

lower jaw —

pterygoid tooth

