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# The neuroanatomy of *Zulmasuchus querejzus* (Crocodylomorpha, Sebecidae) and its implications for the paleoecology of sebecosuchians

Yohan Pochat-cottilloux, Jeremy E Martin, Stéphane Jouve, Gwendal Perrichon, Jérôme Adrien, Céline Salaviale, Christian de Muizon, Ricardo Céspedes, Romain Amiot

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**The neuroanatomy of *Zulmasuchus querejazus*  
(Crocodylomorpha, Sebecidae) and its implications for the  
paleoecology of sebecosuchians**

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## Abstract

The internal endocranial structures of the sebecid crocodylomorph *Zulmasuchus querejazus* (MHNC 6672) from the Lower Paleocene of Bolivia are described. Using Computed Tomography scanning, the endocast, associated nerves and arteries, endosseous labyrinth and cranial pneumatization are reconstructed and compared with those of extant and fossil crocodylomorphs, representative of different ecological adaptations. *Zulmasuchus querejazus* exhibits an unusual curvature of the brain, pericerebral spines, thin semi-circular canals, as well as over-developed intertympanic diverticula and pharyngotympanic sinuses. The ecological significance of these structures is explored and allows to infer the alert head posture and hearing capabilities of *Zulmasuchus*. Functional comparisons are proposed between this purportedly terrestrial taxon, semi-aquatic (extant crocodylians) and aquatic forms (thalattosuchians and dyrosaurids): the morphology of the endosseous labyrinth and the dorsal pneumatization of the skull are discussed within ecological and phylogenetic frameworks. Our results highlight the need to gather new data, especially from altirostral forms in order to further our understanding of the evolution of endocranial structures in crocodylomorphs with different specializations.

**Keywords:** paleoneuroanatomy, Sebecidae, *Zulmasuchus*, Crocodylomorpha, Bolivia, Paleocene.

## Introduction

Sebecidae is an extinct family of crocodylomorphs, known from the Paleocene to the Miocene (Langston, 1965; Paolillo & Linares, 2007; Pol & Powell, 2011). It is considered as the latest survivor of the highly diversified notosuchians, a group of terrestrial crocodylomorphs. Most of the phylogenetic analyses retrieve the sebecids as closely related to the baurusuchids, another group of large Cretaceous terrestrial predators, forming the sebecosuchians (Turner & Sertich, 2010; Pol et al., 2014; Leardi et al., 2015, 2018; Fiorelli et al., 2016; Godoy et al., 2016; Martinelli et al., 2018) but this monophyly has been extensively discussed and both groups have been sometimes considered as distantly related (Larsson & Sues, 2007; de Andrade et al., 2011; Young et al., 2017).

Sebecids were diverse and widely distributed in South America and were one of the major groups of terrestrial predators during the Early Cenozoic (Pol et al., 2012). This family has been intensively studied (Colbert et al., 1946; Langston, 1965; Gasparini, 1984; Busbey, 1986; Buffetaut & Marshall, 1992; Gasparini et al., 1993; Paolillo & Linares, 2007; Molnar, 2010, 2012; Pol & Powell, 2011; Pol et al., 2012; Kellner et al., 2014; Jouve et al., in prep.) and is inferred to be terrestrial based on the similarity between the skulls of sebecids and those of other terrestrial reptilian carnivores (Busbey, 1986; Molnar, 2013) as well as their post-cranial anatomy (Pol et al., 2012). Apart from an endocranial cast of *Sebecus icaeorhinus* (Colbert et al., 1946), no data are available on the neuroanatomy of this group, although this is not the case of other sister taxa.

Indeed, numerous Computed Tomography (CT) data have been published in the last years on the crocodylomorphs (apart from the pioneering study of Colbert, 1946). Based on extant crocodylians for comparison (Witmer et al., 2008; George & Holliday, 2013; Dufeu & Witmer, 2015; Bona et al., 2017), the paleoneuroanatomy of extinct crocodylomorphs has received a lot of attention. These works have mostly been focused on eusuchians (Holliday & Gardner, 2012; Bona & Carabajal, 2013, Bona et al., 2013, 2017; Blanco et al., 2015; Serrano-Martinez et al., 2019) and thalattosuchians (Wharton, 2000; Fernandez et al., 2011; Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018; Schwab et al., 2021). Descriptions of other groups remain scarce (Leardi et al., 2020; Erb & Turner, 2021). There are a few studies on notosuchians (Serenio & Larsson, 2009; Kley et al., 2010; Sertich & O'Connor, 2014) and recently the neuroanatomy of two baurusuchids, *Baurusuchus* sp. and *Campinasuchus dinizi* was published

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3 (Dumont et al., 2020; Fonseca et al., 2020). On the other hand, Sebecidae, its sister taxon, has  
4 not received any attention yet.  
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7 We describe here the internal anatomy of a skull of *Zulmasuchus querejazus* (MHNC 6672)  
8 from the Lower Paleocene of Bolivia, originally described as a Sebecidae indet. by Buffetaut,  
9 1992.  
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13 *Zulmasuchus querejazus* was originally described by Buffetaut & Marshall, 1992 as a more  
14 primitive ziphodont form than *Sebecus*, another genus of the same family first reported by  
15 Simpson, 1937. The holotype (MHNC-P 3701) is an incomplete but well-preserved skull,  
16 lacking the premaxillae and the posterior portion. The skull studied here is from another  
17 specimen and consists mostly of the posterior part of the skull (up to the frontal dorsally and  
18 the pterygoids ventrally). Another complete juvenile specimen is known and is currently under  
19 description (MHNC-P 2706; Jouve et al., in prep.), which allows to link these two previous  
20 specimens as belonging to *Z. querejazus*.  
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28 All these specimens were found in the Santa Lucia Formation, in the Tiupampa locality, near  
29 the Vila Vila village, about 90 km southeast of Cochabamba in the Mizque Province  
30 (southcentral Bolivia). The sediments are dated as early Paleocene (Buffetaut & Marshall, 1992;  
31 Gayet et al., 1992; Marshall et al., 1997; Muizon et al., 1998; Muizon & Cifelli, 2000; Muizon  
32 et al., 2015; Jouve et al., 2020) In a recent review of the age of the Tiupampa beds, Muizon &  
33 Ladevèze, 2020 (Fig.4) have confirmed the early Paleocene age of the fauna, which is referred  
34 to the early Danian and corresponds to the paleomagnetic Chron 28r (ca. 65 Ma). The Tiupampa  
35 locality has provided a diverse fauna including diapsids (Muizon et al., 1983; Buffetaut &  
36 Marshall, 1992; Rage, 1991a; Jouve et al., 2020; Jouve et al., in prep.), fishes (Gayet, 1988,  
37 1990; Gayet & Meunier, 1992), amphibians (Rage, 1991b), turtles (Broin, 1991) and mammals,  
38 which constitute a large part of the relative abundance of the fossils remains (Marshall et al.,  
39 1983; Muizon, 1992, 1994, 1998; Muizon & Cifelli, 2000 ; Muizon et al., 1998, 2015, 2018;  
40 Muizon & Ladevèze, 2020).  
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51 Using Computed Tomography, we have reconstructed and analysed the cranial endocast and  
52 associated nerves and arteries, endosseous labyrinth and braincase pneumaticity of *Z.*  
53 *querejazus*. This enabled us to discuss these structures in terms of alert head posture, hearing  
54 and other ecological traits, and put it into perspective with what is already known of  
55 baurusuchids, their probable closest relative, as well as thalattosuchians, dyrosaurids and extant  
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3 crocodylians (the last three living in a more aquatic environment), to further assess their  
4 paleobiology.  
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## 10 11 12 **Material and methods** 13

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15 A nicely preserved, uncrushed and undeformed braincase of *Zulmasuchus querejazus*  
16 (Buffetaut & Marshall, 1992; MHNC 6672) was investigated to reveal its internal anatomy. The  
17 Computed Tomography (CT) scan was performed in November 2020 at the Laboratoire Mateis  
18 (INSA, Lyon) with a Vtomex laboratory X-ray computed tomograph (GE Phoenix X-Ray  
19 GmbH). Scanning parameters were set to 150 kV tube voltage and 80  $\mu$ A current; we also used  
20 a 0.5 mm copper filter at the source exit. Two acquisitions were made, with a voxel size of 75  
21  $\mu$ m and 30  $\mu$ m, respectively. The exposure time was one second for each projection and there  
22 was a total of 1200 of them for the global acquisition and 1500 projections for the zoomed  
23 acquisition that served for the reconstruction of the endosseous labyrinth. Volume rendering  
24 and processing of scans of the endosseous labyrinth, sinuses and cranial endocasts were  
25 obtained using the software Avizo Lite (version 9.5.0), MeshLab (version 2020.02) and Blender  
26 (version 2.91). Processed volume files are available in MorphoMuseum (Pochat-Cottilloux et  
27 al., 2021). It is worth noting that the inner ear of this specimen has already been briefly  
28 illustrated in David, 2010, although it was only identified as Sebecidae indet. at the time and  
29 remains unpublished.  
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41 Because the brain of nonavian reptiles does not entirely fill the endocranial cavity, the resulting  
42 endocast should be considered a cast of the dural envelope (including venous sinuses) rather  
43 than the brain itself (Witmer et al., 2008). We refer to these bone-bounded spaces that house  
44 soft-tissue structures as if they were the structures themselves. Furthermore, recent studies on  
45 extant taxa showed that the shape of the endocast and the brain of reptiles and birds is strongly  
46 correlated (Watanabe et al., 2019; Early et al., 2020), which further validates this procedure.  
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52 The best mean hearing and hearing range of *Z. querejazus* were calculated following the  
53 correlation between these parameters and the length of the cochlear duct (normalized to  
54 basicranial length), as described in Walsh et al., 2009. The best hearing frequency range is equal  
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to  $6104.3x + 6975.2$ , where  $x = \log \frac{\text{length of the cochlear duct}}{\text{length of the basicranium}}$ . The best mean hearing frequency is equal to  $3311.3x + 4000.8$ , where  $x = \log \frac{\text{length of the cochlear duct}}{\text{length of the basicranium}}$ .

### Comparative material

Descriptive data on extinct and extant crocodylomorph taxa used for comparison are summarized in Table 1 to avoid over-repetitions of references in the description. We follow the anatomical nomenclature published by Colbert et al., 1946; Kley et al., 2010; Sertich & O'Connor, 2014; Brusatte et al., 2016; Bona et al., 2017; Pierce et al., 2017; Herrera et al., 2018; Serrano-Martinez et al., 2019; Fonseca et al., 2020; Dumont et al., 2020, Erb & Turner, 2021 & Schwab et al., 2021) concerning the endocranial structures (and references therein).

### Institutional abbreviations:

AMNH: American Museum of Natural History

BRLSI: Bath Royal Literary and Scientific Institute (Bath, England)

BSPG: Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany)

CPPLIP: Centro de Pesquisas Paleontológicas « Llewellyn Ivor Price » (Uberaba, Brazil)

CNRST: Centre National de la Recherche Scientifique et Technologique, Mali

FEF-PV: Fernandopolis Educational Foundation (Sao Paulo, Brazil)

FUP: University of Brasilia, campus Planaltina (Brasilia, Brazil)

IFSP-VTP: Federal Institute of Education, Science and Technology of Sao Paulo (Sao Paulo, Brazil)

MHNC: Museo de Historia Natural “Alcide d’Orbigny” (Cochabamba, Bolivia)

MLP: Museo de La Plata (Buenos Aires, Argentina)

NHMUK: Natural History Museum UK (London, England)

OUVC: Ohio University Vertebrate Collections (Ohio, United States)

RRBP: Rukwa Rift Basin Project (Ohio, United States)

STUS: Sala de las Tortugas ‘Emiliano Jiménez’ de la Universidad de Salamanca (Salamanca, Spain)



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3 TMM: Texas Memorial Museum (Texas, United States)  
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5 UA: Université d'Antananarivo (Antananarivo, Madagascar)  
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## 15 Results

### 16 Cranial endocast and associated nerves and arteries (fig. 1, 2 and 3):

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20 The specimen lacks the anterior part of the frontal; therefore, the anterior part of the forebrain  
21 (i.e., optic region and olfactory tracts) is not reconstructed. The endocast shows a very well-  
22 marked angle between the mid-brain and the hindbrain (sigmoid shape in lateral view; fig. 3D).  
23 When compared with *Crocodylus porosus*, the dorsal margin of the endocast shows a much  
24 longer hindbrain in *Zulmasuchus querejazus*. The angle between the hindbrain and the mid-  
25 brain is much higher than in the extant species as well as in the baurusuchids and in the  
26 notosuchian *Simosuchus clarki*, even more than in thalattosuchians and dyrosaurids (see Table  
27 2 for comparative measurements). This condition is only observed to a lesser degree in  
28 *Rukwasuchus yajabalijekundu* and *Sebecus icaeorhinus*, which would make it a unique trait of  
29 *Zulmasuchus* among crocodylomorphs so far (although it does not differ statistically from the  
30 sample). At this level, the dorsal part of the midbrain appears compressed mediolaterally where  
31 it accommodates for the labyrinths, as in other crocodylomorphs but to a lesser degree than the  
32 extreme conformation seen in *Rhabdognathus aslerensis* (fig. 3E). The cerebral hemispheres  
33 are not developed and do not show the typical round shape of extant and of some extinct  
34 crocodylians; they are more closely similar in shape to those of baurusuchids and to the  
35 thalattosuchians belonging to the genus *Steneosaurus* (Table 2). They are symmetrically  
36 developed along the midline in dorsal view.  
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49 The dorsal longitudinal venous sinus is well developed anteroposteriorly, bearing a depression  
50 fully surrounded by pericerebral spines just anteriorly to the curvature between the hindbrain  
51 and the forebrain (fig. 3E). *Rukwasuchus* and *Campinasuchus* are the only taxa where such a  
52 structure has been reported (only with lateral ridges in *Rukwasuchus* and a posterior one for  
53 *Campinasuchus*). Recently, it has also been reported in *Rhabdognathus*, linked with the caudal  
54 middle cerebral vein, but it differs from the specimen described here because it does not show  
55 a depression there. *Zulmasuchus* is thus unique among crocodylomorphs in possessing these  
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3 structures on all the sides of this characteristic depression, accommodating for the internal face  
4 of the parietal.  
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6 The hindbrain is well preserved. The medulla oblongata is longer but narrower anteriorly  
7 compared to that in *C. porosus*. Laterally, it bears two reliefs on each side: the posterior most  
8 one is the starting point of the cranial nerve XII (which has a small perimeter and is directed  
9 posterolaterally); the anteriormost one could either be a second passage for the hypoglossal  
10 nerve (cranial nerve XII; as in *G. gangeticus*) or the starting point of the cranial nerve IX-XI,  
11 but it is difficult to identify because they could not be segmented in their entirety (fig. 3D). On  
12 the ventral side, the medulla oblongata bears a venous sinus that is clearly visible and well  
13 developed, especially anteriorly: it is the ventral longitudinal venous sinus (fig. 3F). In  
14 *Zulmasuchus*, it is ridge-shaped, whereas it is much more rounded and shallower in extant  
15 crocodylians and dyrosaurids.  
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17 The passage for the cranial nerve V (fig. 1B) is the largest in the neurocranium (as in other  
18 crocodylomorphs). It is laterally projected from the endocast and is located just anteriorly to  
19 the endosseous labyrinth (fig. 3D). It was not possible to determine with certainty the position  
20 of the emerging nerves V<sub>1</sub>, V<sub>2</sub> and V<sub>3</sub>. The facial nerve (cranial nerve VII) is not visible.  
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22 The cranial nerve VI is clearly visible and developed anteroposteriorly, between the pituitary  
23 fossa ventrally and the ventral edge of the endocast dorsally. Posteriorly it originates from the  
24 endocast, at the level of the anterior edge of the cranial nerve V (fig. 3F).  
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26 In the basicranium, the pituitary fossa is well developed dorsoventrally when compared with  
27 that of *C. porosus*, but not as much as in gavialoids. It is also directed posteroventrally, in an  
28 intermediate manner between extant crocodylians and '*Metriorhynchus*' *brachyrhynchus*  
29 (where it is directed fully posteriorly) and baurusuchids and *Steneosaurus* (where it is directed  
30 almost ventrally). Moreover, this condition is also seen in *Pelagosaurus*, *Cricosaurus*,  
31 *Rhabdognathus* and *Sebecus*. In *Zulmasuchus*, the pituitary fossa bears a ventral crest, and its  
32 posterior part reaches the level of the anterior margin of the trigeminal fossa (fig. 2D and 3D).  
33 The internal carotid arteries enter the posterior end of the pituitary fossa separately at the level  
34 of the midline (fig. 3F; as in other crocodylomorphs; Witmer et al., 2008). The canals for these  
35 arteries are large and the segmentation is missing a section at the ventral level of the endosseous  
36 labyrinth where they are not enclosed by bone (fig. 3D). The posterior section of the carotid  
37 artery runs anterodorsally from the foramen for the internal carotid artery to below the  
38 endosseous labyrinth. On this section, the departure of the stapedia artery can be seen (fig. 3).  
39 The anterior section runs anteroposteriorly and is curved medially entering the pituitary fossa  
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3 (the limit between the internal carotid arteries and the pituitary fossa was established where the  
4 arteries are no longer separated and merge into a single structure).  
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### 8 **Endosseous labyrinth (fig. 3, 4 and 5):**

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10 The endosseous labyrinth of *Z. querejazus* is well preserved, including the cochlea and the  
11 vestibular system. The left labyrinth is better preserved than the right one, the latter lacking the  
12 distal part of the lateral semi-circular canal. The ampullae are not clearly distinguishable from  
13 the canals, their shape is continuous with those of the semi-circular canals. Both the anterior  
14 and posterior semi-circular canals are circular in cross section (fig. 4) and are extremely thin  
15 compared to those of extant crocodylians, and they all have the same maximum diameter, which  
16 is not the case in gavialoids for example (fig. 5). The common crus has a rather thin diameter.  
17 The semi-circular canals being thinner than those of extant crocodylians, the space between  
18 them is therefore much larger. The lateral semi-circular canal is even thinner than the anterior  
19 and posterior ones (but this could be due to a preservation bias, as it appears to be filled and  
20 therefore difficult to distinguish from the bone during the segmentation process) and is curved  
21 ventrodorsally in lateral view, which is a peculiar characteristic regarding the comparison  
22 material. In dorsal view, it is somewhat extended laterally (fig. 4E). The anterior and posterior  
23 semi-circular canals have a pyramidal shape rather than the typical ovoid shape exhibited by  
24 extant crocodylians: this shape is the result of the canals rising higher from the common crus  
25 and therefore also having to turn ventrally more sharply and run in a straighter, more direct  
26 course toward the anterior (or posterior) end. This morphology is consistent with what is found  
27 in other extinct crocodylomorphs. Therefore, the angle between the anterior and the lateral  
28 semi-circular canals, for example, is higher than in extant crocodylians ( $70^\circ$  for *Zulmasuchus*  
29 vs  $50^\circ$  to  $60^\circ$  in modern crocodylians). The angle formed between the anterior and the posterior  
30 semi-circular canals is approximately  $90^\circ$ , as it is in derived eusuchians (Bona & Paulina-  
31 Carabajal, 2013). The anterior canal is slightly more expanded dorsally than the posterior one,  
32 as it is in modern crocodylians (Witmer et al., 2008). As a result, the anterior gap is slightly  
33 larger than the posterior one. On the other hand, both canals are similarly expanded  
34 anteroposteriorly. This condition is seen in thalattosuchians and *S. clarki* but not in extant  
35 crocodylians and *R. aslerensis* (fig. 5). The lagenar section is quite developed and appears to  
36 be directed anteriorly, although this could be due to incomplete segmentation because this area  
37 is not enclosed by bone. This part also bears a process directed laterally below the lateral semi-  
38 circular canal, which could be one of the connexions with the vestibulocochlearis nerve (cranial  
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3 nerve VIII), as in extant crocodylians or the contact with the columella (the auditory bone that  
4 connects the eardrum to the lateral part of the cochlea). It is difficult to assess because this part  
5 has never been described in other fossil crocodyliforms (apart from *Pelagosaurus*, where it is  
6 only briefly mentioned in Pierce et al., 2017, Fig. 4), and therefore comparisons are very scarce.  
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### 10 **Braincase pneumaticity (fig. 2):**

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13 The pharyngotympanic system and the middle pharyngeal system are part of the paratympanic  
14 sinus system, which serves to enhance acoustic capabilities of the middle ear (Dufeu &  
15 Witmer, 2015). They are described here following the nomenclature proposed by the same  
16 authors.  
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21 The intertympanic diverticula are developed dorsal to the cranial endocast, contacting with the  
22 parietal and the supraoccipital internally (fig. 2A, 2B, 2C, 2D and 2E). Laterally, they are  
23 continuous with the pharyngotympanic sinus. They are located just dorsal to the endosseous  
24 labyrinth level. They can be separated in three parts: a central core and two lateral expansions  
25 (as in extant crocodyloids and gavialoids). In dorsal view, the connection between the two large  
26 lateral parts is situated more anteriorly than the lateral expansions and shows a hole at the  
27 midline, which has not been reported in other crocodylomorphs (fig. 2E). In *C. porosus*, the  
28 intertympanic diverticula is much more developed posteriorly, reaching the level of the  
29 posterior part of the medulla oblongata but it is less developed anteriorly. In fact, the condition  
30 of *Zulmasuchus* looks more like that of *Caiman* (fig. 6). These structures are not observed in  
31 thalattosuchians.  
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41 The pharyngotympanic sinus is developed laterally to the inner ear region and merges dorsally  
42 with the intertympanic diverticula (at the level of the supraoccipital-occipital suture; fig. 2E;  
43 Dufeu & Witmer, 2015). It extends ventrally and laterally to the level of the endosseous  
44 labyrinth, surrounding the posterior part of the anterior section and the anterior part of the  
45 posterior section of the internal carotid artery (fig. 2D and 2F). The starting point of the large  
46 left cranioquadrate passage is segmented (fig. 1D and 2D) ventrally to the opening of the middle  
47 ear, but not the rest of it nor the siphonium. This is different from what is seen in *Cricosaurus*  
48 and others metriorhynchids where it is completely separated from the sinus by a thin bony  
49 lamina, but similar to what is known in extant crocodylians. The lateral expansions are  
50 extremely developed and rounded, which is another peculiar characteristic of *Zulmasuchus*  
51 among other crocodylomorphs so far. The pharyngotympanic tubes, connected to the pharynx,  
52 are large, expanded lateromedially and ventrally directed. Ventrally, the pharyngotympanic  
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3 sinuses merge posteriorly at the level of the basisphenoid diverticula, bordering the hindbrain  
4 (fig. 2F).

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7 Ventrally to this structure is the median pharyngeal sinus (fig. 2A, 2B, 2C, 2D and 2F). It is  
8 directed anteroventrally, joins the ventral edge of the basisphenoid diverticulum and exits  
9 through the median pharyngeal foramen. The ventral most part could not be segmented (fig.  
10 1F). It does not connect with the pharyngotympanic tubes directly, the latter being linked  
11 through the pharyngotympanic sinus. Dorsally, the median pharyngeal sinus bifurcates into two  
12 branches: anterodorsally it joins a cavernous sinus located between the posterior part of the  
13 pituitary fossa and the ventral edge of the forebrain (fig. 2D); posterodorsally, it meets with the  
14 pharyngotympanic sinus. This splitting suggests that the specimen is not a juvenile but rather a  
15 subadult, as this canal would then have been more horizontal (fig. 2E; Serrano-Martinez et al.,  
16 2019). The basisphenoid diverticulum is located between the anterior parts of the anterior  
17 section of the internal carotid arteries (where they meet at the midline, fig. 2E and 3F). It is  
18 connected to the median pharyngeal sinus ventrally and extends posteriorly to meet with the  
19 pharyngotympanic sinuses.  
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## 30 Discussion

### 31 Comparison of the endocranial cavities of altirostral crocodylomorph taxa

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33 *Zulmasuchus* exhibits several characteristics that are also observed in other altirostral taxa such  
34 as baurusuchids or peirosaurids. The endocast shows a very well-marked angle between the  
35 mid-brain and the hindbrain, that is also seen to a lesser degree in *Sebecus icaeorhinus* (Colbert  
36 et al., 1946) and *Rukwasuchus yajabaliyekundu* (Sertich & O'Connor, 2014), as well as in  
37 baurusuchids (Dumont et al., 2020; Fonseca et al., 2020). The dorsal part of the midbrain is  
38 compressed mediolaterally where it accommodates for the endosseous labyrinths, as in other  
39 altirostral taxa (and to various degrees in other crocodylomorphs). The cerebral hemispheres  
40 are not developed, as in baurusuchids (but also as in *Steneosaurus*; Brusatte et al., 2016; Herrera  
41 et al., 2018).  
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51 Another peculiar characteristic of *Zulmasuchus* is the presence of a pair of pericerebral spines  
52 on the dorsal surface of the longitudinal sinus (fig. 3), which have also been reported, but to a  
53 lesser degree in *Rukwasuchus* (Sertich & O'Connor, 2014, Fig. 6). *Sebecus* and *Zulmasuchus*  
54 share the posteroventral orientation of the pituitary fossa (but it is also the case of some  
55 thalattosuchians; *Steneosaurus*, Brusatte et al., 2016; Herrera et al., 2018).  
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3 On the other hand, *Zulmasuchus* seems to bear its own characteristics, such as a ventral crest  
4 on the pituitary fossa (fig. 3), thin semi-circular canals with a lateral one curved both laterally  
5 and ventrally (fig. 4), as well as an overdeveloped cranial pneumaticity (fig.2). However, those  
6  
7 last two are subject to caution because those parts are not well documented yet in altirostral  
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9 taxa.

### 11 12 **Head posture**

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14 The orientation of the lateral semi-circular canal is used in most studies as a proxy for the alert  
15 head posture where it is thought to be roughly horizontal in reptiles and birds (Erichsen et al.,  
16 1989; Witmer et al., 2003, 2008; Hullar, 2006; Sampson & Witmer, 2007; Sereno et al., 2007;  
17  
18 Witmer & Ridgely, 2008). This method has been contested by some other studies mainly  
19  
20 focused on dinosaurs (Taylor et al., 2009; Marugan-Lobon et al., 2013) due to interspecific  
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22 variation in orientations. Other proxies involve the alignment of either the maxillary tooth row  
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24 (Marugan-Lobon et al., 2013) or the endocranial surface of the parietal (Kley et al., 2010; von  
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26 Backo et al., 2018) with the horizontal plane.

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29 Depending on the structure selected to align with the horizontal plane, we obtained a very  
30  
31 different result on the head posture of *Zulmasuchus*. Considering a horizontal alignment of the  
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33 lateral semi-circular canal, the longitudinal axis of the skull makes an angle of 35° with the  
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35 horizontal plane (fig. 7A), whereas it is “only” of 10° if one relies on the orientation of the  
36  
37 endocranial surface of the parietal (without considering the pericerebral spines; fig. 7B). This  
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39 difference could be explained because the lateral semi-circular canal in MHNC 6672 has such  
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41 a peculiar morphology (curved anteroposteriorly as well as mediolaterally), and consequently  
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43 its orientation is more difficult to determine with precision. Although we do not have access to  
44  
45 the maxillary tooth row of the specimen studied here, this data could be extrapolated by  
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47 combining the holotype (MHNC-P 3701) and the specimen studied here (MHNC 6672), as they  
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49 represent two parts of the skull that almost overlap. This can be seen in figure 8, this schematic  
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51 allows to extrapolate the head posture of *Zulmasuchus*, but in no way it does represent an  
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53 attempt to reconstruct the skull, as it is understood that these two specimens are distinct from  
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55 each other. The value given by this proxy is approximately 7°, which is quite close to the  
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57 alignment with the endocranial surface of the parietal. To avoid any morphological bias or  
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59 individual variation, we have chosen to rely on the latter for our reconstruction (fig. 9). It is also  
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61 consistent with what is found in other notosuchians (Kley et al., 2010; Dumont et al., 2020;  
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63 Fonseca et al., 2020).



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3 The head of *Zulmasuchus* would thus have been more inclined towards the ground than that of  
4 extant crocodylians (which are considered to have their longitudinal axis almost parallel to the  
5 horizontal plane; Witmer et al., 2008; Bona et al., 2017; Serrano-Martinez et al., 2019, fig. 9),  
6 thus allowing us to infer its ecology. This posture would have indeed allowed the nostrils to be  
7 closer to the ground and would have provided a better binocular vision over its high and narrow  
8 snout. These constitute further arguments in favour of terrestrial habits. Furthermore, this would  
9 also imply lower energy costs compared to keeping the head on the horizontal plane. It probably  
10 had effects on the musculature of the neck of *Zulmasuchus* although it is difficult to assess  
11 because post cranial elements have not been described yet. Such data would also enable studies  
12 on functional morphology linked to ecology, as it has already been done on theropods (Snively  
13 & Russell, 2007a, b). This skull morphology is particularly evident in baurusuchids as well (da  
14 Silva Marinho et al., 2013; Dumont et al., 2020; Fonseca et al., 2020) and, to a lesser degree,  
15 in some theropods (Stevens, 2006; Schade et al., 2020), and suggests a similar ecology and  
16 predatory habits for *Zulmasuchus*. On the other hand, the body of modern crocodylians often  
17 floats completely submerged, just leaving their cranial sensory organs above the water line,  
18 which implies to keep the head in the horizontal plane (fig. 9), which does not appear to be the  
19 case in *Zulmasuchus*. This would also imply a lower energy cost because the head is partially  
20 held horizontal by its buoyancy.  
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35 The anterior semi-circular canal appears slightly more expanded, which is in line with what is  
36 known from most other crocodylomorphs and is correlated with a moderate sensitivity to  
37 pitching (given its position, the endolymphatic liquid inside the canal moves when the head  
38 goes up and down, giving the information to the hair cells and allowing the brain to control the  
39 amount of acceleration of the head in one direction; Hudspeth, 1983; Rabbitt et al., 2004).  
40 Furthermore, although it has a very thin cross-sectional diameter (David, 2010), the lateral  
41 semi-circular canal is quite curved and expanded, which is a sign of increased sensitivity to  
42 yawing (again, the endolymphatic liquid inside this canal is subject to the movement of the head  
43 from side to side).  
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51 This suggests that *Zulmasuchus* needed to move its head to the full extent of its capabilities in  
52 the three axes in relation to its body, which further supports a terrestrial lifestyle. In fact, its  
53 inferred hunting strategies and adaptation to its living environment required it to have a highly  
54 mobile head. On the other hand, aquatic crocodiles such as thalattosuchians, dyrosaurids or  
55 extant crocodylians have less expanded canals (Schwab et al., 2020), meaning a decreased  
56 sensitivity to pitching and yawing (as well as their head being more in line with their body  
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3 movement; Schwab et al., 2020) which could confirm this hypothesis. In addition, although the  
4 semi-circular canals of thalattosuchians and dyrosaurids appear more expanded than those of  
5 extant crocodylians, linked to enhanced agility and aerobatic ability (Witmer et al., 2003; Sipla,  
6 2007; Pierce et al., 2017), those of *Zulmasuchus* are even thinner and more expanded. Thus, it  
7 must have had a very agile and fast locomotion, which again makes sense if we consider a  
8 terrestrial ecology. This is also confirmed with what is observed in other large predatory  
9 reptiles: theropods have a strikingly close morphology of the endosseous labyrinth compared  
10 with *Z. querejazus* (Sanders & Smith, 2005; Witmer & Ridgely, 2009; Paulina-Carabajal &  
11 Succar, 2014; Xing et al., 2014; Paulina-Carabajal & Filippi, 2018; Cerroni & Paulina-  
12 Carabajal, 2019; Paulina-Carabajal & Nieto, 2019), whereas marine reptiles such as mosasaurs  
13 and plesiosaurs have a more rounded and less expanded morphology (Evans, 1999; Yi & Norell,  
14 2019); see also figure 5.

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17 Finally, the expanded anterior semi-circular canal of *Z. querejazus* also means that it had an  
18 important head mass (Georgi et al., 2013): this taxon showing this characteristic high-snouted  
19 condition (Buffetaut & Marshall, 1992; Jouve et al., in prep.), a heavier head mass can indeed  
20 be inferred and would have also probably relied on developed neck musculature to hold this  
21 mass, in turn making the head movements mentioned above easier.

## 22 23 24 **Hearing**

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27 Hearing in extant crocodylians is challenging to understand, because these organisms interact  
28 with sound waves travelling in both the aquatic and in the aerial environment. Although their  
29 ear morphology and structures are very similar to those of birds (Gleich & Manley, 2000), and  
30 would therefore seem to be adapted to aerial hearing, crocodylians spend a lot of time  
31 submerged, more or less completely. It has been shown that they can hear in similar frequency  
32 ranges in both environments (Higgs et al., 2002). While they retain the classic scheme of  
33 hearing an airborne sound as in other reptiles, the way they can hear under water remains  
34 hypothetical and difficult to assess. The most logical explanation is that sound information  
35 underwater is conducted to the inner ear via the cranial bones, rather than through the tympanic  
36 membrane (Higgs et al., 2002). In terms of frequency, modern crocodylians globally emit and  
37 receive in the low to middle range (Wever, 1971). The sounds they emit are mostly used for  
38 inter-individual communication and social interactions (i.e. reproduction, parental care and  
39 protection of juveniles; Beach, 1944; Herzog & Burghardt, 1977; Vliet, 1989; Wang et al.,  
40 2007; Vergne et al., 2012 and references therein). Recent studies also showed that the middle  
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3 ear cavities are connected in Crocodylia, further enhancing their auditory capability (Bierman  
4 et al., 2014 and references therein).  
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7 The hearing range of *Z. querejzus* can be inferred because it is strongly correlated with  
8 cochlear duct measurements (derived from extant taxa; Walsh et al., 2009). This equation has  
9 already been applied on thalattosuchians (Brusatte et al., 2016) and baurusuchids (Dumont et  
10 al., 2020). Here, we complete this sampling with the addition of the presently described  
11 specimen of *Zulmasuchus* and other crocodylomorphs from which the data is available but has  
12 not been added yet (i.e., *P. typus*, Pierce et al., 2017; *S. bollensis* and *C. araucanensis*, Herrera  
13 et al., 2018; *R. aslerensis*, Erb & Turner, 2021; '*M.*' *brachyrhynchus*, Schwab et al., 2021; see  
14 fig. 10).  
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21 *Zulmasuchus* displays a hearing range similar to the terrestrial baurusuchids with a best mean  
22 hearing frequency of 841 Hz and a hearing range of 1150 Hz. As mentioned by Dumont et al.,  
23 (2020), the juvenile specimen of *Baurusuchus* has lower values probably because the  
24 endosseous labyrinth was not segmented as precisely as that of the adult, therefore the  
25 calculation is not the most accurate. However, obtained values for these specimens are in the  
26 range of the hearing capabilities of extant crocodylians (Walsh et al., 2009) and, more  
27 importantly, are lower than the ones of the aquatic crocodylomorphs (mean of best hearing  
28 ranges: 2149.4 Hz and mean of best mean hearing frequency: 1393.8 Hz; fig. 10). This is with  
29 the notable exception of the aquatic thalattosuchian *Cricosaurus araucanensis*, probably  
30 because the data on which its cochlear duct is reconstructed (Herrera et al., 2018) do not allow  
31 for a complete reconstruction of this part.  
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41 It also means that *Zulmasuchus* probably had vocalization frequencies in the same range as its  
42 hearing faculties, as it is the case in extant crocodylians (Vergne et al., 2009). As a result,  
43 terrestrial sebecosuchians would have been able to hear and vocalize in mid to low frequencies  
44 (< 2000 Hz; Dumont et al., 2020), which is towards the known lower range of extant  
45 crocodylians.  
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50 Although not statistically significant (p-value = 0.8 for mean best hearing frequency and best  
51 mean hearing range), this result differs from sampled aquatic crocodylomorphs which have a  
52 much larger hearing range and a higher mean hearing frequency, linked to a longer cochlear  
53 duct (Brusatte et al., 2016, Pierce et al., 2017, Herrera et al., 2018; Erb & Turner, 2021).  
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57 This difference could be explained by different needs in terms of communication. Lower  
58 frequencies travel further than higher frequencies, so organisms using those lower frequencies  
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3 (such as *Zulmasuchus*) would have had the need to communicate in long ranges, as is the case  
4 nowadays with elephants (Garstang, 2004) or cetaceans (Tyack & Clark, 2000 and references  
5 therein).  
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9 However, it remains difficult to assess the living environment of an organism based on its  
10 auditory capacities, as extant birds globally show high frequencies and aquatic turtles exhibit  
11 the lower values, whereas the aquatic thalattosuchians have higher values than the terrestrial  
12 sebecosuchians, so a specific trend does not emerge there. Furthermore, the segmentation of  
13 the cochlear duct can also be difficult, as the distinction between the sinus system and the  
14 anterior part of this duct is not clearly delimited by bone (fig. 11), so caution needs to be  
15 exercised when interpreting those values.  
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### 21 **Cranial pneumaticity**

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23 *Zulmasuchus* exhibits very developed intertympanic diverticula and pharyngotympanic sinuses  
24 (as in *Campinasuchus*; Fonseca et al., 2020), whereas these structures are less developed in  
25 extant crocodylians (Witmer et al., 2008; Bona et al., 2017; Serrano-Martinez et al., 2019) and  
26 the intertympanic diverticula are absent in thalattosuchians (Brusatte et al., 2016; Pierce et al.,  
27 2017; Herrera et al., 2018, Schwab et al., 2021). It is difficult to assess the ancestral state of this  
28 trait, but it would seem to be related to the living environment (aquatic vs terrestrial; Brusatte  
29 et al., 2016). An enlargement of these structures allows improved resonance and sound pickup  
30 in aerial environments (Dufeu & Witmer, 2015). The selection of such structures then appears  
31 logical considering a terrestrial ecology for *Zulmasuchus* as the sound is more difficult to  
32 capture in the air than in the water (this is also the case of *C. dinizi*; Fonseca et al., 2020). On  
33 the other hand, thalattosuchians and dyrosaurids, and to a lesser degree extant crocodylians,  
34 would not necessarily rely on such developed structures, because the sound they capture does  
35 not come exclusively from the aerial environment but also from the aquatic one, where it travels  
36 more easily. Another hypothesis, which could be coupled with the first one, is the impact of  
37 such structures on the buoyancy and the density of the skull of aquatic forms (Brusatte et al.,  
38 2016). Finally, Dufeu & Witmer, 2015 proposed a link between the extension of these  
39 structures and the shape of the rostrum: long-snouted specimens with a specialized diet  
40 (gharials, dyrosaurids or thalattosuchians for example, Brusatte et al., 2016; Erb & Turner,  
41 2021) exhibit smaller structures than feeding generalists with smaller snouts such as  
42 *Hamadasuchus* (Dufeu, 2011). This last hypothesis appears controversial because on one hand  
43 it is reinforced by what is found in *Zulmasuchus*, which shows a combination of a snout of  
44 moderate length, with terrestrial habits (so probably a more generalist diet than aquatic forms)  
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3 but on the other hand, if we compare the cranial pneumaticity between *Gavialis gangeticus*  
4 (longirostre taxon with specialized diet) and *Caiman crocodylus* (brevirostre taxon with  
5 generalist diet), they do not differ much when compared with other forms such as  
6 thalattosuchians or sebecosuchians (fig. 6). Further studies are thus needed to assess whether  
7 cranial pneumaticity is linked with rostrum morphology and thus diet. As longirostrine taxa  
8 seem to be mostly aquatic, a possible explanation could also be linked in the difference in the  
9 point of equilibrium of the skull between floating in the water and holding thanks to the neck  
10 musculature in an aerial environment. As the constraints exercised on a submerged skull are  
11 less important than on a non-submerged one, the development of “extreme” morphologies  
12 would then be facilitated.  
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22 The median pharyngeal sinus and the pharyngotympanic sinus are interconnected in extant  
23 crocodylians (Colbert, 1946; Witmer et al.; 2008, Bona et al., 2017; Serrano-Martinez et al.,  
24 2019), thalattosuchians (Brusatte et al., 2016; Pierce et al., 2017; Herrera et al., 2018; Schwab  
25 et al., 2021) and dyrosaurids (Erb & Turner, 2021), to allow pressure equalization between the  
26 middle ear, the pharynx and the external environment (Colbert, 1946; Dufeu & Witmer, 2015).  
27 In *Alligator mississippiensis*, this phenomenon has been reported to be controlled by the median  
28 pharyngeal valve, which opens and closes regularly (Young & Bierman, 2018). This  
29 mechanism has only been observed in this taxon for now, so further studies are needed to assess  
30 if it is the rule inside Crocodylia, or even Crocodylomorpha. The only difference found so far  
31 in all sampled crocodylomorphs comes from *Pelagosaurus typus*, which does not possess a  
32 verticalized pharyngeal sinus, because of the ventral displacement of the basicranium (Pierce  
33 et al., 2017). *Zulmasuchus* and other sebecosuchians (Colbert et al., 1946; Fonseca et al., 2020),  
34 although having a different ecology, do not differ from the general organisation of other  
35 crocodylomorphs, thus these structures seem to be of low interest when looking at behavioural  
36 or phylogenetic inferences. Caution must be exercised though, because it is difficult to  
37 reconstruct these structures in fossils, so the access to exquisitely preserved specimens or more  
38 precise work might contradict these observations in the future.  
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## 51 **Perspectives**

52 The endocranial cavities of crocodylomorphs are understudied and a lot of data are still missing  
53 to get a more complete view of the diversity and peculiarities of the group. This could prove  
54 important to better understand both their phylogenetic relationships and paleoecological  
55 characteristics.  
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3 First, the endocranial structures surely bear phylogenetic information and would benefit from  
4 being incorporated into future phylogenetic studies. New characters would of course need to be  
5 diagnosed, and their relevance tested, but it could bring new information in untangling the  
6 systematics of Crocodylomorpha, provided that new data are published concerning those  
7 structures in yet unsampled taxa. For example, it is difficult to tease apart whether the observed  
8 short cochlear ducts in sebecosuchians is characteristic of the group (i.e., a synapomorphy) or  
9 if it is the ancestral condition of a larger taxonomic group that contains Sebecosuchia (for  
10 example, the middle Triassic suchian *Parringtonia gracilis* also has a rather short cochlear duct;  
11 Nesbitt et al., 2018). However, this does not seem to be the ancestral condition of the diapsids,  
12 as *Youngina capensis*, a Permian basal diapsid reptile shows an elongated cochlear duct  
13 (Gardner et al., 2010). Other peculiar characteristics of *Z. querejazus* are the high curvature  
14 observed between the hindbrain and the forebrain, as well as the pericerebral spines associated  
15 with a depression described on the surface of the dorsal longitudinal venous sinus. Could these  
16 be considered synapomorphies of this taxon? It is of course too early to determine but these  
17 characteristics will need to be described with great consideration in future studies on other  
18 specimens.

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21 The endocranial structures, by the very nature of the systems they house, are equally important  
22 when taking into consideration the paleoecology of these taxa. For example, the cochlear duct  
23 can be used as a proxy to the hearing capabilities of extant taxa (see above), which can already  
24 be of great use if we aim to know more about the behavior of such taxa. Other structures which  
25 are of particular interest are the pharyngotympanic sinus and the intertympanic diverticula: as  
26 mentioned above, their development could also be linked with living environment, behavior  
27 and diet. These assumptions again require more data to be collected on other terrestrial taxa,  
28 and if used in combination with the endosseous labyrinth data, could prove very useful to assess  
29 the living environment of a fossil taxon for which the data is available (as a supporting argument  
30 to more traditional inferences). This has allowed to better understand and strengthen the  
31 terrestrial habits of several sebecosuchians (Dumont et al., 2020; Fonseca et al., 2020; this  
32 study), and this approach needs to be generalized to other taxa in this group, some of which are  
33 nicely preserved and would surely represent a source of high-definition reconstructions in future  
34 studies.

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37 Finally, these features must be analysed with caution, to separate properly the ecological and  
38 phylogenetic signals, so as not to confuse them and thus reach erroneous conclusions (Losos,  
39 2008). For example, if a given characteristic is thought to be the proof of a specific ecological

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3 trait, it could also be linked to a taxonomic sampling bias: that it could be a synapomorphy of  
4 this taxonomic group, rather than an ecological trait as a rule (one should note that it could very  
5 much be both as well). The same reasoning is valid the other way around (phylogenetic vs  
6 ecological information).  
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## 10 **Conclusion**

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13 The endocranial cavities of *Zulmasuchus querejazus* are described. This taxon exhibits a highly  
14 curved endocast between the forebrain and the hindbrain, as well as pericerebral spines, the  
15 combination of both features being observed for the first time inside Crocodylomorpha. The  
16 endosseous labyrinth of MHNC 6672 is quite expanded but the semi-circular canals are very  
17 thin in cross section. Finally, the intertympanic diverticula and the pharyngotympanic sinuses  
18 are well developed compared to those of thalattosuchians, whereas the ventral part of the  
19 braincase shows no real difference from what is already known in other extinct and extant taxa.  
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26 The alert head posture of this specimen is inferred to be slightly inclined towards the ground  
27 ( $\sim 10^\circ$ ), based on the alignment of the endocranial surface of the parietal with the horizontal  
28 plane. This value is higher than that of extant crocodylians (which have a posture parallel to the  
29 horizontal plane for ecological reasons) and is coherent with what has been inferred in other  
30 notosuchians. This posture allowed *Zulmasuchus* to benefit from a binocular vision over his  
31 altirostral snout, a feature that can be associated with predatory and terrestrial habits.  
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37 Furthermore, the morphology of its endosseous labyrinth further supports a terrestrial lifestyle  
38 because its expanded canals allow for more mobility of the head, an essential trait in these  
39 hunting and motion methods. The length of the cochlear duct is linked with the hearing  
40 capabilities (which range among low frequencies in *Zulmasuchus*), inducing the need to  
41 communicate at long distances between individuals. Caution still needs to be exercised because  
42 of segmentation biases.  
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48 Finally, the overly developed intertympanic diverticula and pharyngotympanic sinus of this  
49 specimen, compared with thalattosuchians, allow to link these structures with the living  
50 environment of the organism they belong to. Aquatic forms (such as thalattosuchians) do not  
51 need the enhanced aerial perception given by the enlargement of these structures, hence they  
52 are more likely associated with terrestrial taxa. Other hypotheses are about the effect of the  
53 pneumatization on buoyancy or on the morphology of the snout (linked with diet). While it is  
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3 difficult to favour one of those hypotheses for now, the differences observed are clearly linked  
4 to the living environment of the specimens.  
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7 All these observations could be introduced as phylogenetic characters in future studies, to  
8 further understand the systematics of this highly diverse group of archosaurs, but caution will  
9 need to be exercised regarding the conflict between ecological and phylogenetic signal in these  
10 structures. Further studies in the field of the neuroanatomy of Crocodylomorpha should help  
11 clarify those issues.  
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3 **Figure captions:**  
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5 **Figure 1:** Three-dimensional reconstruction of the segmented part of the skull of *Z. querejazus*  
6 (MHNC 6672) in anterior (A), anterior  $\frac{3}{4}$  (B), posterior (C), lateral (D), dorsal (E) and ventral  
7 (F) views. Blue: endocast, green: paratympanic sinus, red: internal carotid artery, yellow:  
8 cranial nerve, purple: pituitary fossa. V: cranial nerve V, XII: cranial nerve XII, cq: cranio  
9 quadrate passage, eo: exoccipital, fb: forebrain, ic: internal carotid artery, ls: laterosphenoid,  
10 mef: medial eustachian foramen, mps: median pharyngeal sinus, oc: occipital condyle, p: palate,  
11 pf: pituitary fossa, ps: pharyngotympanic sinus, q: quadrate, sf: supratemporal fossa, so:  
12 supraoccipital, sq: squamosal.  
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20 **Figure 2:** Three-dimensional reconstruction of the pneumatic cavities within the braincase of  
21 *Z. querejazus* (MHNC 6672) in anterior (A), anterior  $\frac{3}{4}$  (B), posterior (C), lateral (D) dorsal  
22 (E) and ventral (F) views. Blue: endocast, light green: pharyngotympanic sinus and eustachian  
23 system, dark green: intertympanic diverticula, red: internal carotid artery, yellow: cranial  
24 nerve, purple: pituitary fossa. V: cranial nerve V, XI: cranial nerve XI, XII: cranial nerve XII,  
25 bd: basisphenoid diverticulum, cq: cranio quadrate passage fb: forebrain, hb: hindbrain, ic:  
26 internal carotid artery, id: intertympanic diverticula, mps: median pharyngeal sinus, pf:  
27 pituitary fossa, ps: pharyngotympanic sinus, pt: pharyngotympanic tube, sa: stapedial artery,  
28 vlvs: ventral longitudinal venous sinus.  
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36 **Figure 3:** Three-dimensional reconstruction of the endocranial cavities of *Z. querejazus*  
37 (MHNC 6672) in anterior (A), anterior  $\frac{3}{4}$  (B), posterior (C), lateral (D) dorsal (E) and ventral  
38 (F) views. Blue: endocast, red: internal carotid artery, yellow: cranial nerve, purple: pituitary  
39 fossa, V: cranial nerve V, VI: cranial nerve VI, XII: cranial nerve XII, fb: forebrain, hb:  
40 hindbrain, ic: internal carotid artery, ie: internal ear, pf: pituitary fossa, ps: pericerebral spines,  
41 vlvs: ventral longitudinal venous sinus.  
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47 **Figure 4:** Three-dimensional reconstruction of the left endosseous labyrinth of *Z. querejazus*  
48 (MHNC 6672) in posterior (A), anterior (B), lateral (C and D), dorsal (E) and ventral (F) views.  
49 asc: anterior semi-circular canal, cc: common crus, lsc: lateral semi-circular canal, psc:  
50 posterior semi-circular canal.  
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54 **Figure 5:** Three-dimensional reconstructions of the endosseous labyrinths of extant and extinct  
55 crocodylomorphs in lateral view: A: *Zulmasuchus querejazus* (left, MHNC 6672); B:  
56 *Crocodylus porosus* (left, OUVC-10899); C: *Gavialis gangeticus* (left, uf herp 118998); D:  
57 *Viavenator exxoni* (left, MAU-Pv-Li-530 from Paulina-Carabajal & Filippi, 2018); E:  
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3 *Baurusuchus* sp. (right, FUP-Pv 000021 from Dumont et al., 2020, Figure 9b); F: *Pelagosaurus*  
4 *typus* (left, BRLSI M1413 from Pierce et al., 2017, Figure 6b); G: *Simosuchus clarki* (right, UA  
5 8679 from Kley et al., 2010, Figure 32c); H: *Platecarpus tympaniticus* (left, AMNH FRAB1645  
6 from Yi & Norell, 2019). All structures are oriented with the lateral semi-circular canal oriented  
7 horizontally.  
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12 **Figure 6:** Three-dimensional reconstructions of the cranial pneumaticity of numerous  
13 crocodylomorphs in posterior view: A: *Zulmasuchus querejazu* (MHNC 6672); B:  
14 *Steneosaurus bollensis* (BSPG 1984 I258, from Herrera et al., 2018, Fig. 3G); C: *Caiman*  
15 *crocodilus* (UMMZ HERPS 128024); D: *Gavialis gangeticus* (UF HERP 118998).  
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20 **Figure 7:** Inferred alert head posture aligning the lateral semi-circular canal (A, B and C) and  
21 the endocranial surface of the parietal (D, E and F) with the horizontal plane of *Z. querejazu*  
22 (MHNC 6672). Drawings are taken from Figure 9.  
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26 **Figure 8:** Attempted extrapolation of the head posture of *Zulmasuchus*, combining the holotype  
27 MHNC-P 3701 (left part) and MHNC 6672 (right part) and aligning with the maxillary tooth  
28 row, left lateral view.  
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32 **Figure 9:** Interpretative drawings of the posture of *Zulmasuchus querejazu* (A; inspired by the  
33 work of Marco Auditore) and *Caiman crocodilus* (B; drawing by Mohamed Hassan).  
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36 **Figure 10:** Mean hearing range (A, blue trend line:  $y = 6104.3x + 6975.2; \pm 1483$  Hz) and best  
37 hearing frequency (B, blue trend line:  $y = 3311.3x + 4000.8; \pm 764$  Hz) for *Z. querejazu* and  
38 other crocodylomorphs, using the methods of Walsh et al., 2009. Yellow crosses: Aves, purple  
39 crosses: Squamata; green circles: Testudines; grey circle: Rhynchocephalia, red circles: extant  
40 crocodylians; blue circles: aquatic crocodylomorphs; black circles: terrestrial crocodylomorphs  
41 (see Supplementary File 1 for more information). 1: Juvenile *Baurusuchus* sp., 2: *Cricosaurus*  
42 *araucanensis*, 3: *Crocodylus acutus*, 4: *Zulmasuchus querejazu*, 5: Adult *Baurusuchus* sp., 6:  
43 *Pelagosaurus typus*, 7: 'Metriorhynchus' *brachyrhynchus*, 8: *Steneosaurus gracilirostris*, 9:  
44 *Alligator mississippiensis*, 10: *Rhabdognathus aslerensis*, 11: *Steneosaurus bollensis*, 12:  
45 *Caiman crocodilus*.  
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54 **Figure 11:** Illustration of one of the problem of segmentation: the limit between the cochlear  
55 duct and the pharyngotympanic sinus. A: posterior transverse slice where the limit is clear, B:  
56 anterior transverse slice where the limit is not clear.  
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3 **Table captions:**  
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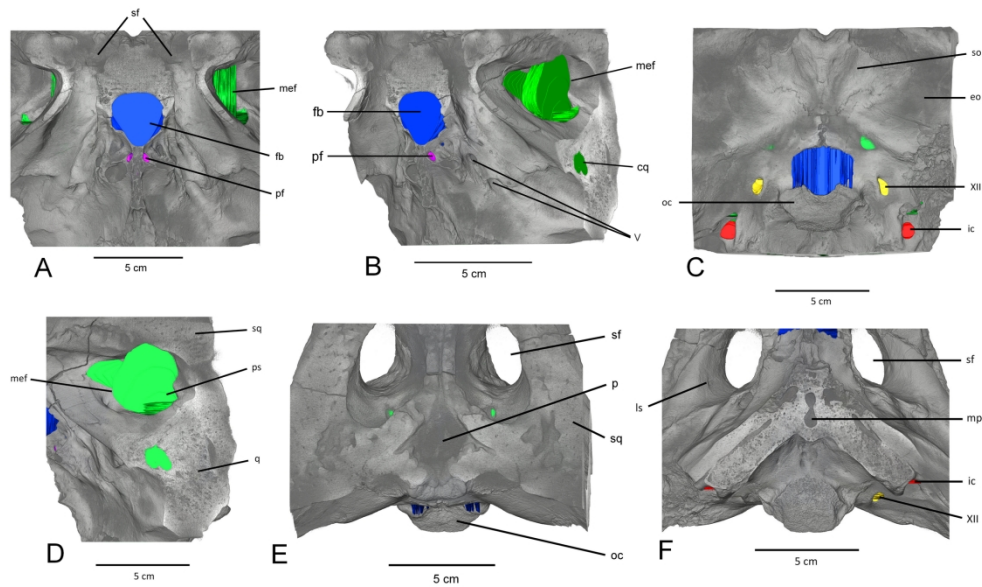
5 **Table 1:** Comparative material used in this study is reported along with the published references  
6 of their associated studies.  
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9 **Table 2:** Raw morphometric data of *Zulmasuchus* (MHNC 6672) and comparative material.  
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For Peer Review

Taxon	Specimen	Publication or database
<i>Crocodylus porosus</i>	OUVC 10899	Morphosource
<i>Gavialis gangeticus</i>	MLP 602, UF HERP 118998	Bona et al., 2017, Pierce et al., 2017, Morphosource
<i>Caiman crocodilus</i>	UMMZ HERPS 128024	Morphosource
<i>Diplocynodon tormis</i>	STUS-344	Serrano-Martinez et al., 2019
<i>Pelagosaurus typus</i>	BRLSI-M1413	Pierce et al., 2017
<i>Steneosaurus</i> cf. <i>gracilirostris</i>	NHMUK PV OR 33095	Brusatte et al., 2016
<i>Steneosaurus bollensis</i>	BSPG 1984 1258	Herrera et al., 2018
<i>Cricosaurus araucanensis</i>	MLP 72-IV-7-1	Herrera et al., 2018
' <i>Metriorhynchus</i> ' <i>brachyrhynchus</i>	NHMUK PV O 32617	Schwab et al., 2021
<i>Rhabdognathus aslerensis</i>	AMNH FARB 33354 formerly CNRST- SUNY 190	Erb & Turner, 2021 Brochu et al., 2002
<i>Rukwasuchus yajabalijekundu</i>	RRBP 08630	Sertich & O'Connor, 2014
<i>Simosuchus clarki</i>	UA 8679	Kley et al., 2010
<i>Campinasuchus dinizi</i>	CPPLIP 1319 and 1360	Fonseca et al., 2020
<i>Baurusuchus</i> sp.	IFSP-VTP/PALEO- 0002 and 0003, FEF- PV-R-1/9 and FUP-Pv 000020 and 000021	Dumont et al., 2020
<i>Sebecus icaeorhinus</i>	AMNH 3160	Colbert et al., 1946

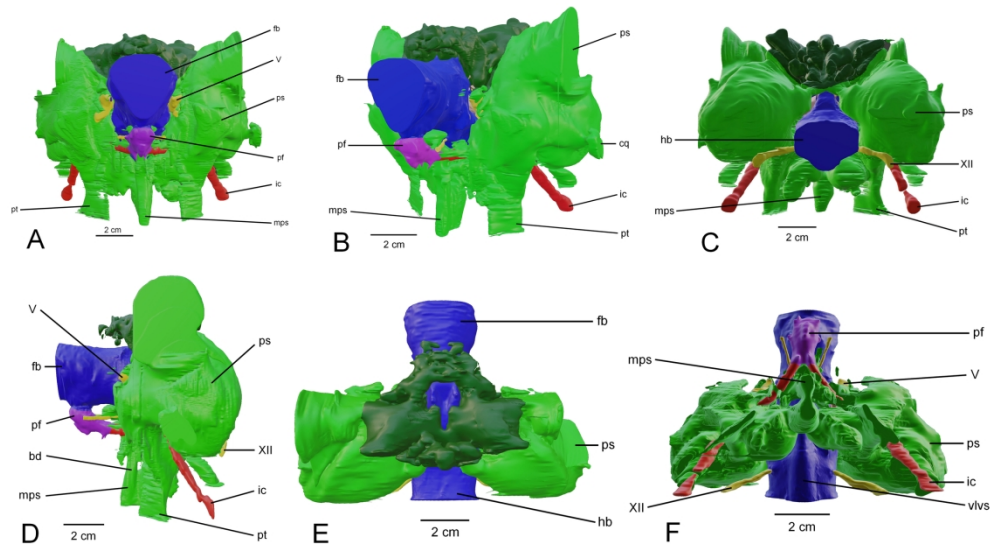
(Rounded to nearest mm)	<i>Pelagosaurus typus</i>	<i>Steneosaurus</i> cf. <i>gracilirostris</i>	<i>Steneosaurus bollensis</i>	<i>Cricosaurus araucanensi</i>	' <i>Metriorhynchus</i> ' <i>brachyrhynchus</i>	<i>Rhabdognathus aslerensis</i>	<i>Gavialis gangeticus</i>	<i>Alligator mississippiensis</i>	<i>Crocodylus porosus</i>	<i>Diplocynodon tormis</i>	<i>Simosuchus clarki</i>	<i>Rukwasuchus yajabaljekundu</i>	<i>Campinasuchus dinizi</i>	<i>Baurusuchus</i> sp.	<i>Sebecus icaeorhinus</i>	<i>Zulmasuchus querejazus</i>
Skull width at cerebrum (SW)	52	?	33	40	74	89	168	73	39	25	58	37	32	?	147	42
Cephalic flexure angle (CF)	160	175	?	135	155	158	150	135	125	140	142	145	155	165	150	130
Pontine flexure angle (PF)	160	170	165	170	165	152	154	145	170	160	165	145	150	165	160	130
Endocast length (EL)	57	?	?	140	?	171	146	98	40	82	79	100	85	70	120	?
Olfactory tract length (+ bulbs) (OL)	21	?	?	69	?	49	55	48	18	36	25	45	39	32	46	?
Cerebrum width (CW)	15	28	19	25	40	26	32	21	18	23	25	28	13	14	30	35
Pituitary width (PW)	6	14	4	11	16	5	6	5	4	2	5	7	4	?	?	14
Pituitary height (PH)	7	12	8	9	12	10	9	8	3	6	9	10	4	?	9	17
Pituitary length (PL)	10	17	24	14	30	14	11	10	13	4	10	5	4	?	8	27
Labyrinth height (LH)	14	26	22	19	20	25	21	18	9	?	?	?	?	12	?	22
Labyrinth width (LW)	11	26	18	18	21	26	21	14	9	?	?	?	?	13	?	14
Endosseous Cochlear duct length (ECL)	8	13	12	7	9	12	9	8	3	?	?	?	?	6	?	7
Anterior semi-circular canal area (AA)	9	38	2	?	?	19	36	35	11	?	?	?	?	2	?	7
Posterior semi-circular canal area (PA)	6	19	1	?	?	4	15	12	3	?	?	?	?	4	?	7
Lateral semi-circular canal area (LA)	4	14	3	?	?	8	22	13	3	?	?	?	?	1	?	6
Source	Pierce et al., 2017	Brusatte et al., 2016	Herrera et al., 2018	Herrera et al., 2018	Schwab et al., 2021	Erb & Truner, 2021	Pierce et al., 2017	Witmer & Ridgely, 2008	This study	Serrano-Martinez et al., 2019	Kley et al., 2010	Sertich & O'Connor, 2014	Fonseca et al., 2020	Dumont et al., 2020	Colbert et al., 1946	This study



Three-dimensional reconstruction of the segmented part of the skull of *Z. querejazus* (MHNC 6672) in anterior (A), anterior  $\frac{3}{4}$  (B), posterior (C), lateral (D), dorsal (E) and ventral (F) views. Blue: endocast, green: paratympanic sinus, red: internal carotid artery, yellow: cranial nerve, purple: pituitary fossa. V: cranial nerve V, XII: cranial nerve XII, cq: cranio quadrate passage, eo: exoccipital, fb: forebrain, ic: internal carotid artery, ls: laterosphenoid, mef: medial eustachian foramen, mps: median pharyngeal sinus, oc: occipital condyle, p: palate, pf: pituitary fossa, ps: pharyngotympanic sinus, q: quadrate, sf: supratemporal fossa, so: supraoccipital, sq: squamosal.

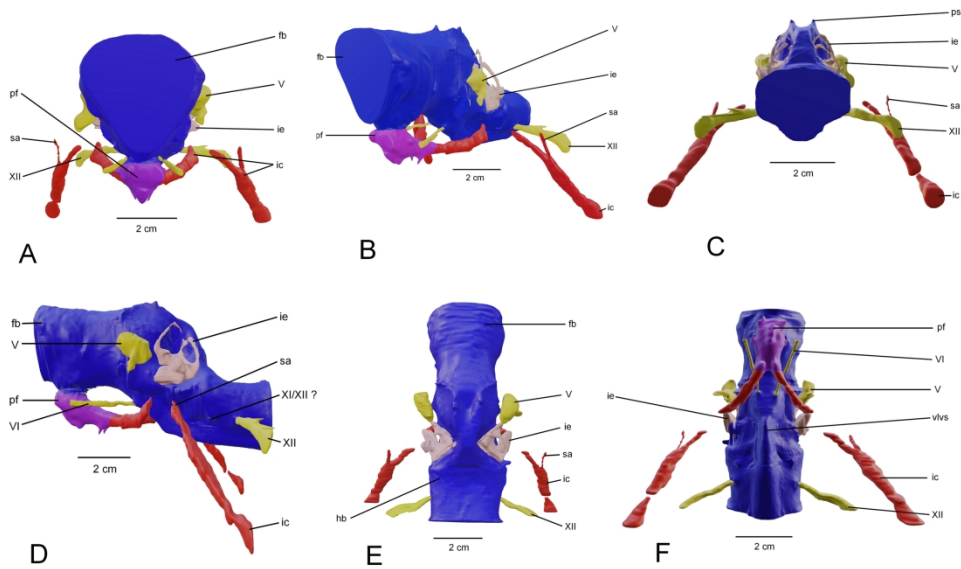
209x127mm (300 x 300 DPI)





Three-dimensional reconstruction of the pneumatic cavities within the braincase of *Z. querejazus* (MHNC 6672) in anterior (A), anterior 3/4 (B), posterior (C), lateral (D) dorsal (E) and ventral (F) views. Blue: endocast, light green: pharyngotympanic sinus and eustachian system, dark green: intertympanic diverticula, red: internal carotid artery, yellow: cranial nerve, purple: pituitary fossa. V: cranial nerve V, XI: cranial nerve XI, XII: cranial nerve XII, bd: basisphenoid diverticulum, cq: cranio quadrate passage fb: forebrain, hb: hindbrain, ic: internal carotid artery, id: intertympanic diverticula, mps: median pharyngeal sinus, pf: pituitary fossa, ps: pharyngotympanic sinus, pt: pharyngotympanic tube, sa: stapedial artery, vlvs: ventral longitudinal venous sinus.

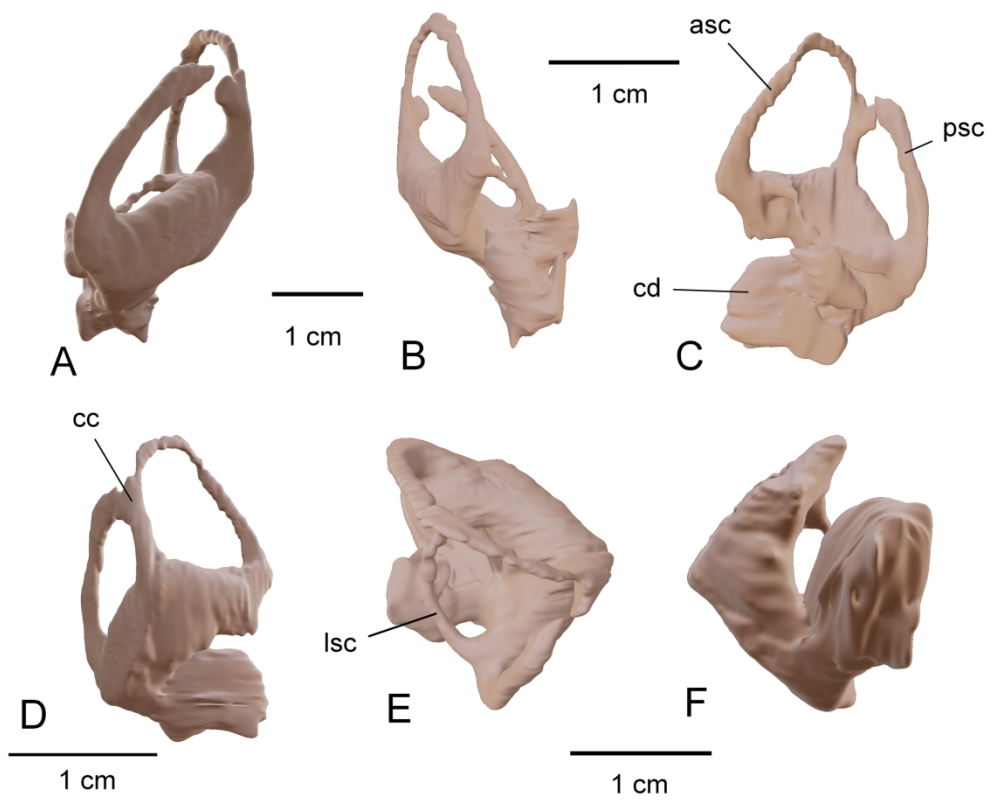
209x127mm (300 x 300 DPI)



Three-dimensional reconstruction of the endocranial cavities of *Z. querejazus* (MHNC 6672) in anterior (A), anterior 3/4 (B), posterior (C), lateral (D) dorsal (E) and ventral (F) views. Blue: endocast, red: internal carotid artery, yellow: cranial nerve, purple: pituitary fossa, V: cranial nerve V, VI: cranial nerve VI, XII: cranial nerve XII, fb: forebrain, hb: hindbrain, ic: internal carotid artery, ie: internal ear, pf: pituitary fossa, ps: pericerebral spines, vlv: ventral longitudinal venous sinus.

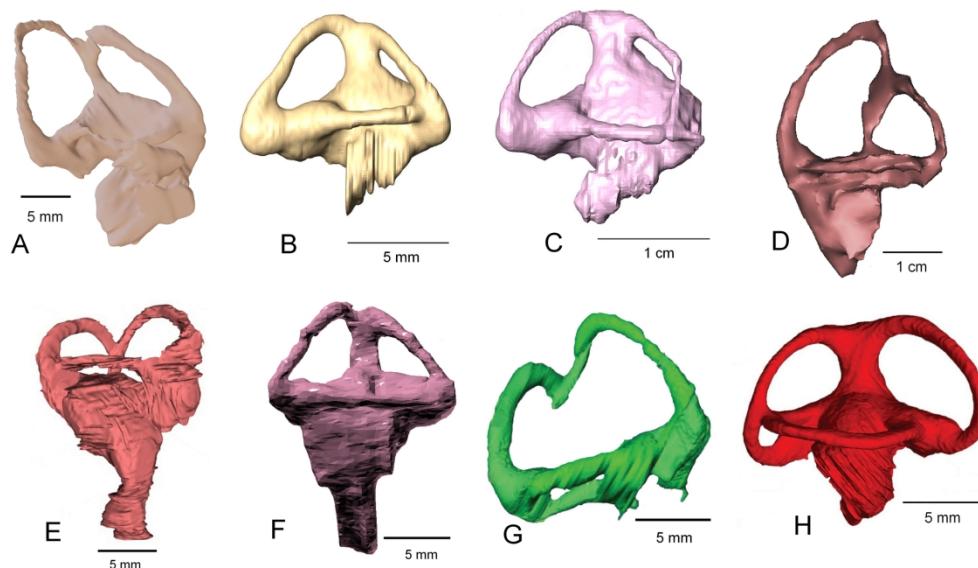
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Three-dimensional reconstruction of the left endosseous labyrinth of *Z. querejazus* (MHNC 6672) in posterior (A), anterior (B), lateral (C and D), dorsal (E) and ventral (F) views. asc: anterior semi-circular canal, cc: common crus, lsc: lateral semi-circular canal, psc: posterior semi-circular canal.

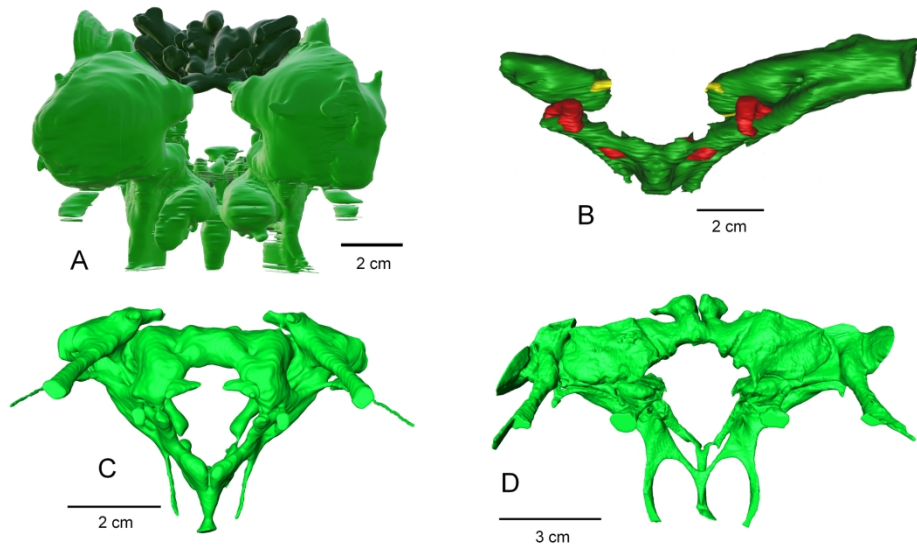
209x175mm (300 x 300 DPI)



Three-dimensional reconstructions of the endosseous labyrinths of extant and extinct crocodylomorphs in lateral view: A: *Zulmasuchus querejazus* (left, MHNC 6672); B: *Crocodylus porosus* (left, OUV-10899); C: *Gavialis gangeticus* (left, uf herp 118998); D: *Viavenator exxoni* (left, MAU-Pv-Li-530 from Paulina-Carabajal & Filippi, 2018); E: *Baurusuchus* sp. (right, FUP-Pv 000021 from Dumont et al., 2020, Figure 9b); F: *Pelagosaurus typus* (left, BRLSI M1413 from Pierce et al., 2017, Figure 6b); G: *Simosuchus clarki* (right, UA 8679 from Kley et al., 2010, Figure 32c); H: *Platecarpus tympaniticus* (left, AMNH FRAB1645 from Yi & Norell, 2019). All structures are oriented with the lateral semi-circular canal oriented horizontally.

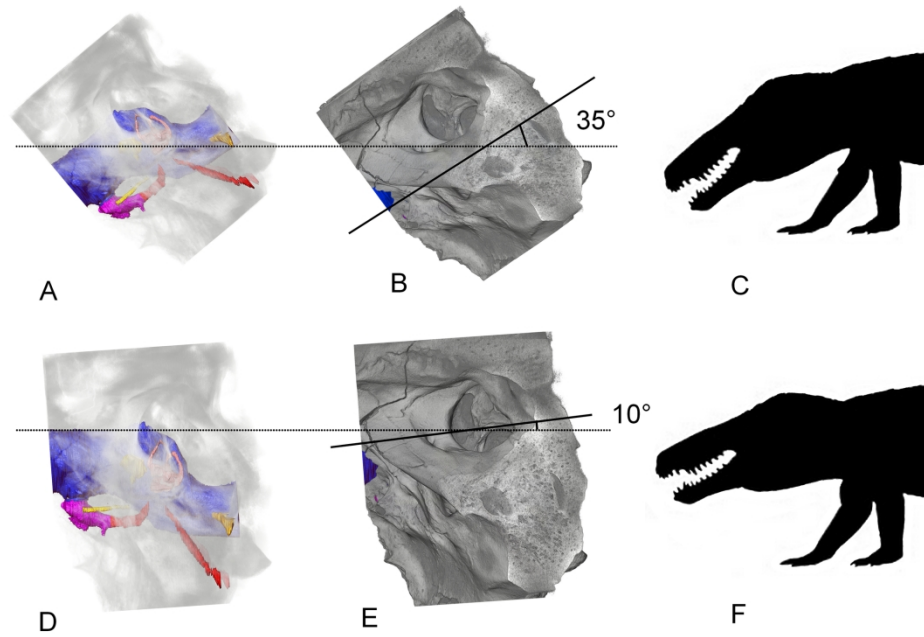
211x126mm (300 x 300 DPI)

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Three-dimensional reconstructions of the cranial pneumaticity of numerous crocodylomorphs in posterior view: A: *Zulmasuchus querejazus* (MHNC 6672); B: *Steneosaurus bollensis* (BSPG 1984 I258, from Herrera et al., 2018, Fig. 3G); C: *Caiman crocodilus* (UMMZ HERPS 128024); D: *Gavialis gangeticus* (UF HERP 118998).

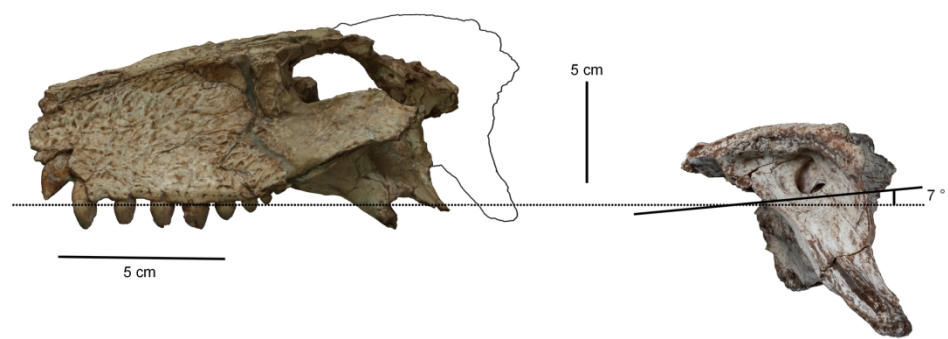
209x129mm (300 x 300 DPI)



Inferred alert head posture aligning the lateral semi-circular canal (A, B and C) and the endocranial surface of the parietal (D, E and F) with the horizontal plane of *Z. querejazus* (MHNC 6672). Drawings are taken from Figure 9.

209x141mm (300 x 300 DPI)

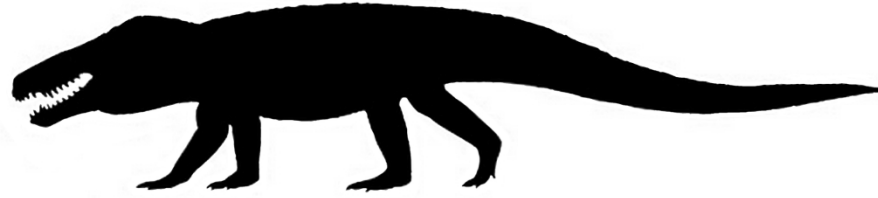
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Attempted extrapolation of the head posture of *Zulmasuchus*, combining the holotype MHNC-P 3701 (left part) and MHNC 6672 (right part) and aligning with the maxillary tooth row, left lateral view.

180x64mm (300 x 300 DPI)





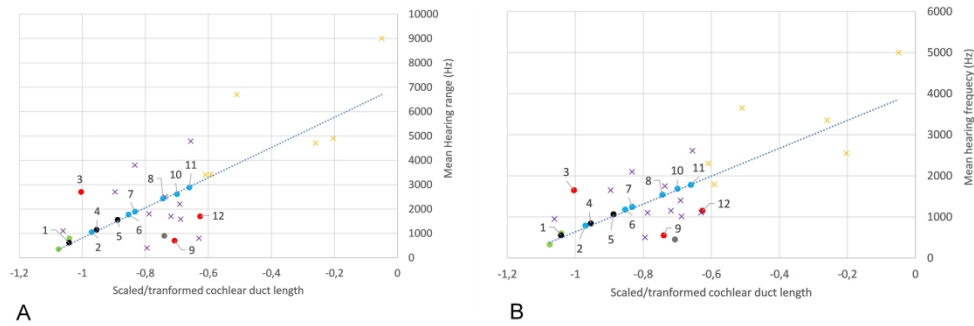
A  
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30 cm

Interpretative drawings of the posture of *Zulmasuchus querejazus* (A; inspired by the work of Marco Auditore) and *Caiman crocodilus* (B; drawing by Mohamed Hassan).

209x160mm (300 x 300 DPI)



Mean hearing range (A, blue trend line:  $y = 6104.3x + 6975.2; \pm 1483$  Hz) and best hearing frequency (B, blue trend line:  $y = 3311.3x + 4000.8; \pm 764$  Hz) for *Z. querejazus* and other crocodylomorphs, using the methods of Walsh et al., 2009. Yellow crosses: Aves, purple crosses: Squamata; green circles: Testudines; grey circle: Rhynchocephalia, red circles: extant crocodylians; blue circles: aquatic crocodylomorphs; black circles: terrestrial crocodylomorphs (see Supplementary File 1 for more information). 1: Juvenile *Baurusuchus* sp., 2: *Cricosaurus araucanensis*, 3: *Crocodylus acutus*, 4: *Zulmasuchus querejazus*, 5: Adult *Baurusuchus* sp., 6: *Pelagosaurus typus*, 7: '*Metriorhynchus*' *brachyrhynchus*, 8: *Steneosaurus gracilirostris*, 9: *Alligator mississippiensis*, 10: *Rhabdognathus aslerensis*, 11: *Steneosaurus bollensis*, 12: *Caiman crocodilus*.

258x87mm (300 x 300 DPI)

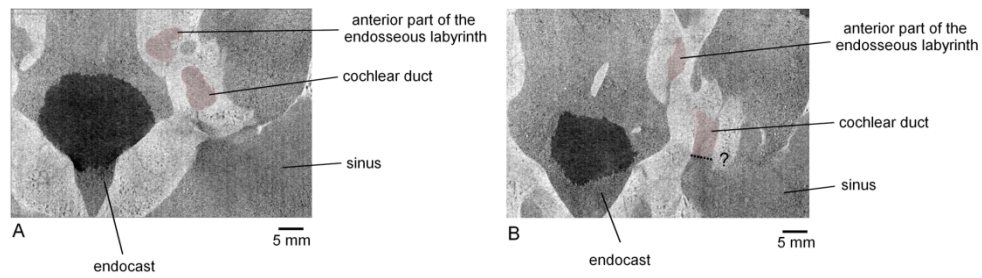


Illustration of one of the problem of segmentation: the limit between the cochlear duct and the pharyngotympanic sinus. A: posterior transverse slice where the limit is clear, B: anterior transverse slice where the limit is not clear.

180x53mm (300 x 300 DPI)

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<b>Order</b>	<b>Family</b>	<b>Genus</b>	<b>Species</b>
Crocodylomorpha	Crocodylidae	<i>Crocodylus</i>	<i>acutus</i>
Crocodylomorpha	Alligatoridae	<i>Alligator</i>	<i>mississippiensis</i>
Crocodylomorpha	Alligatoridae	<i>Caiman</i>	<i>crocodylus</i>
Crocodylomorpha	Sebecidae	<i>Zulmasuchus</i>	<i>querejazus</i>
Crocodylomorpha	Dyrosauridae	<i>Rhabdognathus</i>	<i>aslerensis</i>
Crocodylomorpha	Metriorhynchidae	<i>Pelagosaurus</i>	<i>typus</i>
Crocodylomorpha	Metriorhynchidae	<i>Cricosaurus</i>	<i>araucanensis</i>
Crocodylomorpha	Metriorhynchidae	' <i>Metriorhynchus</i> '	<i>brachyrhynchus</i>
Crocodylomorpha	Teleosauridae	<i>Steneosaurus</i>	<i>bollensis</i>
Crocodylomorpha	Teleosauridae	<i>Steneosaurus</i>	<i>gracilirostris</i>
Crocodylomorpha	Baurusuchidae	<i>Baurusuchus</i>	sp.
Crocodylomorpha	Baurusuchidae	<i>Baurusuchus</i>	sp.
Testudines	Cheloniidae	<i>Chelonia</i>	<i>mydas</i>
Testudines	Chelydridae	<i>Chelydra</i>	<i>serpentina</i>
Rhynchocephalia	Sphenodontidae	<i>Sphenodon</i>	<i>punctatus</i>
Squamata	Gekkonidae	<i>Gekko</i>	<i>gecko</i>
Squamata	Gekkonidae	<i>Ptyodactylus</i>	<i>hasselquistii</i>
Squamata	Gekkonidae	<i>Hemitheconyx</i>	<i>caudicinctus</i>
Squamata	Lacertidae	<i>Podarcis</i>	<i>scicula</i>
Squamata	Scincidae	<i>Tiliqua</i>	<i>rugosa</i>
Squamata	Scincidae	<i>Chalcides</i>	<i>occelatus</i>
Squamata	Varanidae	<i>Varanus</i>	<i>niloticus</i>
Squamata	Crotaphytidae	<i>Gambelia (Crotaphytus)</i>	<i>wislizenii</i>
Squamata	Polycrotidae	<i>Anollis</i>	<i>sagrei</i>
Squamata	Agamidae	<i>Uromastyx</i>	<i>hardwickii</i>
Squamata	Trogonophiidae	<i>Diplometopon</i>	<i>zarudnyi</i>
Strigiformes	Tytonidae	<i>Tyto</i>	<i>alba</i>
Psittaciformes	Psittacidae	<i>Melopsittacus</i>	<i>undulatus</i>
Struthioniformes	Casuariidae	<i>Dromaius</i>	<i>novaeollandiae</i>
Sphenisciformes	Spheniscidae	<i>Spheniscus</i>	<i>demersus</i>
Passeriformes	Corvidae	<i>Corvus</i>	sp.
Passeriformes	Estrildidae	<i>Taeniopygia</i>	<i>guttata</i>

	Range (Hz) ≤ 30dB	Overall range (Hz)	Mean (Hz)	Log Length	Comments
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4		300-3000	2700	1650	-1.0034883
5		100-1000	900	550	-0.73969005
6		300-2000	1700	1150	-0.62598526
7		266-1416	1150	841	-0.954242509
8		382-2990	2608	1686	-0.698970004
9		292-2062	1770	1177	-0.852784869
10		264-1314	1054	789	-0.970036777
11		297-2191	1894	1244	-0.832508913
12		339-3219	2880	1779	-0.66
13		320-2755	2435	1538	-0.743782349
14		243-861	618	552	-1.041524477 Juvenile
15		283-1841	1558	1062	-0.887506417 Adult
16		150-500	350	325	-1.075204
17		200-1000	800	600	-1.0409586
18		100-800	700	450	-0.70685852
19		220-5000	4780	2610	-0.65560773
20		300-2500	2200	1400	-0.69036983
21		220-1800	1580	1010	-0.68739956
22		500-3000	2500	1750	-0.73660067
23		200-4000	3800	2100	-0.8329782
24		300-2000	1700	1150	-0.71851211
25		400-1500	1100	950	-1.0609802
26		300-700	400	500	-0.79452496
27		200-2000	1800	1100	-0.78754604
28		300-3000	2700	1650	-0.89585445
29		700-1500	800	1100	-0.62967199
30		500-9500	9000	5000	-0.049197177
31		300-7000	6700	3650	-0.50947969
32		80-3500	3420	1790	-0.59125139
33		600-4000	3400	2300	-0.60853559
34		100-5000	4900	2550	-0.20300961
35		1000-5700	4700	3350	-0.25932157
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