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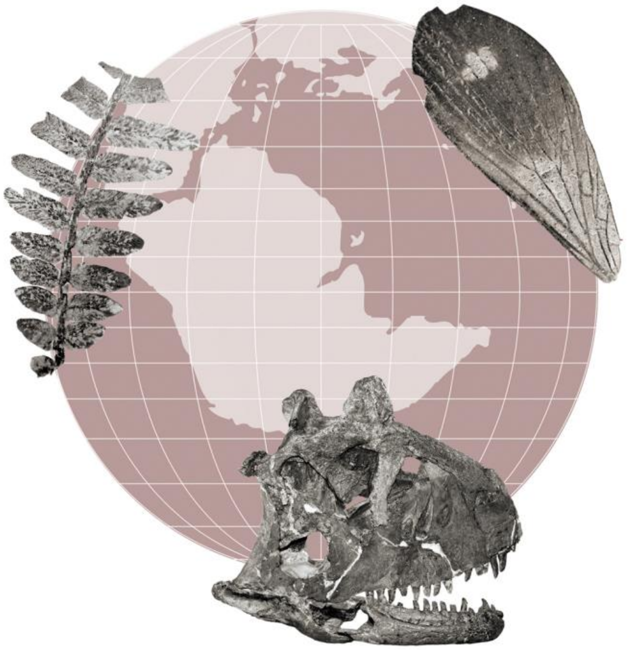

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NOVEL INFORMATION ON THE BRAINCASE OF *MEGARAPTOR NAMUNHUAIQUII* (DINOSAURIA: THEROPODA) USING X-RAY TOMOGRAPHY: PNEUMATICITY, PALEONEUROLOGY AND THEIR PALEOBIOLOGICAL IMPLICATIONS

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32 Pag; 5 figures

Running Header: Paulina-Carabajal and Porfiri: NEUROANATOMY OF MEGARAPTOR

Short Description: The braincase anatomy of *Megaraptor* was explored using CT scans. The braincase and endocranial anatomies exhibit intermediate and derived features that support the inclusion of this taxon among basal coelurosaurs. The reconstructed neuroanatomy suggests this theropod was an agile bipedal predator with hearing and balance capabilities matching the range of coeval hunting coelurosaurs.

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Abstract. X-ray computed microtomography was used to segment and re-describe the braincase of the juvenile specimen of *Megaraptor namunhuaiquii* providing novel anatomical endocranial information. The reconstructed soft tissues include brain, cranial nerves, blood vessels, inner ear and pneumatic sinuses. Some structures of the braincase anatomy were re-interpreted, and the endocranial anatomy was compared with that of *Murusraptor barrosaensis* (the only other megaraptoran with studied endocranial anatomy), and more derived theropods. The braincase and the brain exhibit a mosaic of primitive and derived characters that support the previously proposed close relation of *Megaraptor* with basal coelurosaurian theropods (including basal Tyrannosauroidea). A high degree of braincase pneumaticity, a high mean range of hearing, and a relatively large floccular lobe of the cerebellum are features that suggest that *Megaraptor* was an agile bipedal predator compared to non-coelurosaur coeval theropods, such as abelisaurids. Its cognitive and sensorial abilities may have allowed *Megaraptor* to compete with coelurosaurs (unenlagines?) or at least reach many of their hunting capabilities.

Key Words. Megaraptoridae. Neuroanatomy. Sense Biology. Hearing. Cretaceous. Hunting habits.

Resumen. NUEVA INFORMACIÓN SOBRE EL NEUROCRÁNEO DE MEGARAPTOR NAMUNHUAIQUII (DINOSAURIA: THEROPODA) USANDO TOMOGRAFÍA COMPUTADA POR RAYOS X: NEUMATICIDAD, PALEONEUROLOGÍA Y SUS IMPLICANCIAS PALEOBIOLÓGICAS. Se utilizó microtomografía computarizada por rayos X para segmentar y redescribir el neurocráneo del ejemplar juvenil de *Megaraptor namunhuaiquii*, proporcionando información anatómica endocraneal novedosa. Los tejidos blandos reconstruidos incluyen encéfalo, nervios craneales, vasos sanguíneos, oído interno y senos neumáticos. Se reinterpretaron algunas estructuras de la anatomía de la caja craneana y se comparó la anatomía endocraneal con la de *Murusraptor barrosaensis* (el único otro megaraptórido cuya cavidad endocraneana ha sido estudiada) y otros terópodos más derivados. Tanto el neurocráneo como el encéfalo exhiben un mosaico de caracteres primitivos y derivados que respaldan la estrecha relación previamente propuesta de *Megaraptor* con terópodos celurosaurios basales. Un alto grado de neumaticidad del neurocráneo, un alto rango medio de frecuencia auditiva y un lóbulo flocular relativamente grande del cerebelo sugieren que *Megaraptor* era un depredador bípedo ágil en comparación con los terópodos coetáneos no-celurosaurios, como los abelisaurios. Sus capacidades cognitivas y sensoriales podrían haber permitido a *Megaraptor* competir con los celurosaurios (¿unenlaginos?) o al menos alcanzar muchas de sus capacidades de caza.

Palabras Clave. Megaraptoridae. Neuroanatomía. Biología Sensorial. Audición. Cretácico. Hábitos cazadores.

MEGARAPTORANS are a group of tetanuran theropods –recorded in Late Cretaceous rocks of Australia, Asia, probably Europe, Africa and particularly South America– characterized by elongate skulls, pneumatized bones and hypertrophied unguals on the first and second manual digits (*e.g.*, Novas 1998; Azuma & Currie, 2000; Calvo *et al.*, 2004; Novas *et al.*, 2013; Porfiri et al., 2014; Aranciaga-Rolando *et al.*, 2022). Since the first record of a representative of this clade, there have been an increasing number of discoveries –particularly in Gondwanan lands– indicating than megaraptorans constituted a relatively diverse and abundant clade of predatory dinosaurs during the Late Cretaceous (*e.g.*, Coria & Currie, 2006; Benson *et al.*, 2010; Méndez *et al.*, 2012; Novas *et al.*, 2013; Porfiri *et al.*, 2014; Lamanna *et al.*, 2020; Aranciaga-Rolando *et al.*, 2022; Ibiricu *et al*., 2025; Morrison et al 2025). However, the skeletally incomplete nature of most of the studied megaraptoran species translates into controversial relationships within Theropoda, whether as allosauroids or basal coelurosaurs (*e.g*., Novas, 1998, Calvo *et al*., 2004; Smith *et al*., 2008; Benson *et al*., 2010; Carrano *et al*., 2012; Novas *et al*., 2013see; Apesteguía *et al*., 2016; Aranciaga-Rolando *et al*., 2022; Ibiricu *et al*., 2025; Morrison *et al*., 2025). The later are the hypotheses most accepted recently, with phylogenetic analyses that found Megaraptora nested within Coelurosauria (e.g., Ibiricu *et al*., 2025).

Here, we re-describe the braincase of *Megaraptor namunhuaiquii* Novas 1998 including novel information on the endocranial morphology and non-preserved soft tissues (brain, inner ear and cranial pneumatic sinuses) using X-ray CT scans. This species lived in South America between Mid-to Late Cretaceous, during the Turonian–Coniacian (about 80 million years ago). The study of the skull of a juvenile specimen suggested that this taxon is a primitive tyrannosauroid (Porfiri *et al*., 2014) or a basal member of the Coelurosauria (Aranciaga Rolando *et al*., 2019). However, these relationships were not analyzed under the light of the neurocranial data before. In the present study, we compared important soft tissue anatomical features of the *Megaraptor* skull with those of *Murusraptor roseae* Coria & Currie 2006 (the only other megaraptoran with known neuroanatomy), and with other coelurosaurian and non-coelurosaurian theropods. On the one hand, we evaluate whether these new soft tissue anatomical data support any of the phylogenetic hypotheses previously proposed for *Megaraptor* and Megaraptoridae. On the other hand, the new anatomical data was used to interpret sensorial capabilities and predict behavior in *Megaraptor*. Extinct species had complex behaviors but the fossil record generally reveal little of these details (Hanson *et al*., 2021). Therefore, the study of structures that directly or indirectly relate to behavior, such as many of the neural soft tissues, provides a new approach to better understand the lifestyle and the trophic ecology of these extinct life forms. In this context, the prediction of hunting prey ability in theropods relay on the neuroanatomy and interpretation of the senses, including the size of the flocculus of cerebellum, field of binocular vision, hearing range, and also skeletal morphology, among others (King *et al*., 2020 and references therein). A high degree of braincase pneumaticity, a high mean range of hearing, and a relatively large floccular lobe of the cerebellum, are features that suggest that *Megaraptor* was an agile bipedal predator.

Institutional abbreviations. **MUC**, Museo de Ciencias Naturales de la Universidad Nacional del Comahue, Neuquén, Argentina; **MCF**, Museo Carmen Funes, Neuquén, Argentina.

MATERIAL AND METHODS

Material

The braincase of *Megaraptor* (MUCPv 595) is partially preserved, missing the anterior part of the lateral walls (laterosphenoids and orbitosphenoids), distal ends of the paroccipital processes, the occipital condyle, the basipterygoid processes, and the cultriform process. Besides the lack of these elements, the preservation of the remaining braincase bones is exceptionally good (Fig. 1). The left frontal is the only preserved element of the skull roof. Osteological correlates of the forebrain (olfactory tracts and anterior region of the cerebrum) are partially preserved on the ventral surface of the frontal, allowing an interpretation of the dorsal anatomy of the olfactory apparatus of *Megaraptor*.

Since the general braincase anatomy was described elsewhere (Porfiri *et al*., 2014), we will mention here only those features described by first time –such as the endocranial cavity- or those anatomical features that were re-interpreted after the original description.

Comparisons. Comparisons were made with the braincase and endocranial cast of *Murusraptor* (MCF-PVPH 411) and the isolate frontal MCF-PVPH 320 (Paulina-Carabajal and Coria, 2015; Paulina-Carabajal and Currie, 2017). The braincase of the recently described megaraptorid *Joaquinrapto*r (Ibiricu *et al* 2025) has not been described or illustrated in detail to allow comparison at this point.

Methods

CT-scanning and segmentation. The small size of the specimen prevents the use of medical tomographers -the most accessible non-invasive technique in Argentina- for endocranial studies. This situation led us in 2016 to use an odontological tomographer -for the first time in our country- to study the fossil (Paulina-Carabajal *et al*., 2018). The CT scanning was performed at the Clínica Kranex (Neuquén city, Argentina), using a Planmeca ProMax, and applying an energy of 90 Kv and 14 mA, resulting in 534 slices, with a slice increment of 0.15 mm (Slice thickness= 0.15 mm; pixel size = 0.15 mm).

Renderings of the bones, brain, inner ear, and pneumatic sinuses were made using the software Materialise Mimics (16.0). 3D models are available in the format of 3D PDFs as Supplementary Information and at MorphoMuseum: link to the site here.

The volume of the preserved endocranial cavity (midbrain and hindbrain) is 21.8 cm^3, including the roots of the cranial nerves.

Hearing calculations. The mean hearing frequency and the high hearing frequency of *Megaraptor* was calculated using the method of Walsh *et al*. (2009) and following King *et al*. (2020) on the measurements of the basisphenoid instead of the basicranium to allow comparison with *Velociraptor*.

Olfactory Ratio. It was calculated as the ratio between the greatest diameter of the olfactory bulb (measured from the impression on the ventral side of the frontal) and the longest diameter of the cerebral hemisphere (measured from the incomplete impression on the ventral side of the frontal), and multiplied by 100 (see Zelenitsky et al., 2009). Olfactory ratios can be used to interpret the olfactory acuity in extinct animals (see Zelenitsky et al., 2009). However, in the absence of data on brain volume and body mass of the juvenile *Megaraptor*, we use the olfactory ratio only as an element of comparison of the relative development of the olfactory bulb among megaraptorans.

Abbreviations. Regarding the labelling of pneumatic features in figures, to avoid confusion, abbreviations in lower case indicate pneumatic recesses and abbreviations in upper case indicate the 3D modelling of the pneumatic sinuses. For example, “caudal tympanic recess”: ctr indicates the osteological correlate, whereas CTR indicates the segmentation of the sinus.

DESCRIPTIONS

Braincase external anatomy

The preserved braincase of *Megaraptor* (Fig. 1) is a small and complex structure, measuring 46 mm anteroposteriorly (the complete skull of this individual would have been approximately 30 cm long; see Porfiri *et al*., 2014). Sutures are still visible between several bones, particularly the basioccipital-basisphenoid suture, and the contact between the basioccipital and the exoccipital-opisthotic complex. The lack of the laterosphenoids and orbitosphenoids in front of the prootics (symmetrically, in both sides) may correlate with a non-ossified juvenile or subadult condition of the specimen.

The prootic forms the dorsal, posterior and ventral margins of the maxillo-mandibular (CN $V_{2,3}$) branch of the trigeminal nerve foramen, which is relatively large (8 mm diameter) and circular (Fig. 1.1, 1.2). The laterosphenoid is not preserved, but formed probably the anterior margin of this foramen. Evidence of a separate ophthalmic branch of the trigeminal nerve (CN V_1) is preserved on the right side, as a groove within the prootic running anteriorly from the anteroventral margin of the CN $V_{2,3}$ foramen (Fig. 2.1). The exit foramen of the ophthalmic branch was bounded possibly only by the laterosphenoid, as in *Murusraptor* (Paulina-Carabajal & Currie, 2017).

Just posterior to CN $V_{2,3}$ opens a foramen markedly smaller (3.5 mm diameter) for the facial nerve (CN VII). This foramen was misinterpreted in the original description as the anterior (=rostral or lateral) tympanic recess. The CT scans allowed the identification of this nerve, and also the identification of a pneumatic recess located posteroventrally to CN VII (Fig. 1.1, 1.2). This pneumatic foramen is a small subcircular opening –near the basisphenoid but probably enclosed by the prootic only– identified here as the prootic recess (PROR), following Tahara and Larsson (2011). Internally, the prootic recess represents the dorsal extension of the anterior tympanic diverticulum (see below) (Fig. 1.1).

The prootic contacts the opisthotic posteriorly at the base of the paroccipital process delimiting the otic recess anteriorly and contacts the supraoccipital posterodorsally as observed endocranially (Fig. 1.1, 1.3). On the lateral side of the braincase, the otic recess represents the middle ear, which is often not clearly delimited in most non-coelurosaur dinosaurs. In *Megaraptor*, it is large and deep. Because there are fractures, the middle ear region is a virtual window into the endocranial cavity, preventing the delimitation of the actual margins of the fenestra ovalis. The fractures made impossible to determine the exact margins of the external opening of the caudal tympanic recess, located at the base of the paroccipital process and delimited between the prootic and the opisthotic. The caudal tympanic recess (CTR) excavates the base of the paroccipital process internally (see below), and is widely exposed dorsally by fractures (Fig. 1.6).

The opisthotic is fused to the exoccipital forming the exoccipital-opisthotic complex or otoccipital, and there are no visible sutures between these bones, as in most adult dinosaurs (Currie, 1997). The opisthotic forms most of the body of the paroccipital process, which is better preserved on the left side. The ventral process of the opisthotics forms a well-developed crista tuberalis that projects ventrally almost reaching the distal end of the basal tuber on each side (Fig. 1.5). The crista tuberalis is deep and concave posteriorly bounding laterally a complex (subdivided) pneumatic recess on each side of the neck of the occipital condyle (Figs. 1.5, 3). This paracondylar recess (PCR) separates into a ventral larger depression and a dorsal smaller one respectively. The ventral paracondylar recess is a deep oval depression delimited by the basal tuber medially and the crista tuberalis laterally. The clear basioccipital-opisthotic suture runs across this recess. On the right side, there is a small foramen that communicates internally with the posterior projection of the basisphenoid recess (BSR). The smaller dorsal paracondylar recess is oval and locates at the base of the paroccipital process, dorsal to the metotic foramen. Within this recess opens a small foramen that communicates internally with the endocranial cavity. The dorsal position of this passage regarding the posterior cranial nerves suggests that it belongs to a blood sinus or an endolymphatic duct (Fig. 3).

Lateral to the neck of the condyle, there are three cranial foramina (Figs. 1.5, 3). The larger and dorsal opening corresponds to the metotic formen (exit foramen for CNs IX-XI and internal jugular vein), which opens within a depression (and seems continuous with the paracondylar recess at the base of the paroccipital process). The two smaller foramina are closer to the neck of the occipital condyle and correspond to branches of CN XII (Figs. 1.3, 3). These openings face posterolaterally and are not clearly visible in posterior view.

The exoccipital forms the lateral margins of the foramen magnum. Sutures with the supraoccipital dorsally and the basioccipital ventrally indicate that exoccipitals are not excluded from the dorsal and ventral margins of the foramen magnum, respectively. The foramen magnum is oval and relatively large, as is commonly seen in small sized theropods, but not as large as seen in troodontids or the basal dromaeosaurid *Mahakala* (Turner *et al*., 2007). Since the occipital condyle is not preserved it is not possible to determinate the degree of participation of the exoccipitals on the body of the condyle.

The supraoccipital is tall and wide, and markedly anteroventrally inclined. Therefore, it is completely observed in dorsal view of the braincase, as in *Murusraptor*, the possible megaraptoran *Fukuivenator* (Azuma *et al*., 2016), and in other theropod clades including carcharodontosaurids, some abelisaurids (*e.g*., Méndez *et al*., 2022), the therizinosauroid *Falcarius utahensis* (Kirkland *et al*., 2005), and the dromaeosaurid *Velociraptor* (Barsbold & Osmólska, 1999; Norell *et al*., 2004). The supraoccipital knob in *Megaraptor* is a weak protuberance, but is yet well-developed occupying more than 50% of the length of the supraoccipital. Laterally, the supraoccipital delimits the foramina for the caudal middle cerebral veins on each side, which are widely separated from the midline (Fig. 1.1). The supraoccipital contributes broadly on the dorsal margin of the foramen magnum, a feature shared with derived coelurosaurs, including tyrannosaurids and dromaeosaurids (Currie, 1995), but not with *Murusraptor*.

The basioccipital is almost complete, missing the portion involved in the occipital condyle, which is lost by fracture. Below the neck of the occipital condyle, the basal tubera are short finger-shaped structures ventrally and slightly anteriorly projected (Fig. 1). The basituberal web -a lamina of bone connecting transversely both basal tubera-is eroded distally. It forms the anterior wall of the subcondylar recess (=median subcondylar recess, SCR), a large and wide triangular depression limited laterally by the basal tubera. The distal end of each basal tuber is triangular in ventral view. The left basal tuber has a fracture that shows an internal pneumatic cavity invading the process, also confirmed by the CT scans. On the ventral aspect of the basicranium, the basituberal web delimits posteriorly a well-developed basisphenoid recess.

The basisphenoid is badly preserved anteriorly. It is missing the dorsum sellae on the floor of the endocranial cavity, and the cultriform process anteriorly. The basisphenoid is deeply excavated ventrally by the basisphenoid recess whose external opening (the preserved section) is quadrangular in shape (Fig. 1.4). Deep inside the recess, the dorsal wall of bone bears two large oval cavities separated by a median longitudinal septum leading into deeper paired pneumatic cavities that largely excavate the basisphenoid posterodorsally (see below).

Endocranial anatomy

The endocranial cavity was virtually emptied after digital removal of sediment (Figs. 1, 2). The floor of the endocranial cavity is smooth and there is no medullar eminence (a median ridge formed by the basioccipital or basisphenoid) (Fig. 1.3). The floor of the endocranial cavity is deeply concave, as in the dromaeosaurid *Itemirus* (Sues &

Averianov, 2014) and *Velociraptor* (Norell *et al*., 2014), and the tyrannosauroid *Timurlengia* (Brusatte *et al*., 2016). Posteroventral to the trigeminal opening there is an oval depression, the acoustic fossa, bearing three foramina for CNs VII and VIII (Fig. 2). A similar configuration of these nerves exiting within the acoustic fossa has been reported in *Velociraptor* and *Dromaeosaurus* (Currie, 1995; Norell *et al*., 2004), and seems to be a derived feature among theropods. The vestibular eminence is a convex protuberance protruding little into the endocranial cavity. Its anterior surface bears a relatively large and oval floccular recess, more reminiscent of that observed in derived coelurosaur theropods (*e.g*., troodontids, Paulina-Carabajal, 2015; dromaeosaurids, Sues & Averianov, 2014) rather than those of in non-coelurosaur theropods, such as abelisaurids and carcharodontosaurids, which have slit-like floccular recesses (*e.g*., Paulina-Carabajal *et al*., 2021) (Fig. 1.3). There is a shallow vertical groove connecting the dorsal margin of the floccular recess with the ventral margin of the internal foramen of the caudal middle cerebral vein, indicating the presence of a venous sinus, a drainage pathway, in this region of the cranial endocast (Fig. 2). A large internal metotic foramen is posterior to the floccular recess, transmitting CNs IX-XI and the internal jugular vein. There are two foramina for CN XII. Near the foramen magnum and dorsal to the foramina for CN XII, there is a large foramen identified here as a venous sinus or an endolymphatic duct. A similar foramen is present in the endocranial cavities of *Itemirus* (Sues & Averianov, 2014) and *Murusraptor*, although in the latter the passage is obliterated and there is no external exit foramen.

Braincase pneumaticity

The braincase of *Megaraptor* is highly pneumatized if compared with other Cretaceous non-coelurosaur south American theropods, such as abelisaurids, carcharodontosaurids, and even the closely related *Murusraptor,* all of them taxa that in general develop pneumaticity only within the basicranium. The degree of pneumatization of *Megaraptor*, however, is not comparable to the highly pneumatized braincases in tyrannosaurids, which have paratympanic pneumatic sinuses surrounding the cranial endocast ventrally, laterally and dorsally (*e.g.*, Witmer *et al*., 2008; Witmer & Ridgely, 2009; Bever *et al*., 2011; Paulina-Carabajal *et al*., 2021). In *Megaraptor*, particularly interesting is the presence of large pneumatic cavities affecting the basicranium, including the basisphenoid recess (BR), the anterior tympanic recess (ATR), and a large subcondylar recess (SCR). There is also a relatively large caudal tympanic recess (CTR) that greatly invades the base and mid-length of the paroccipital process. The complex cranial sinuses which originate these osteological correlates correspond to the paratympanic sinuses (which originate from the middle ear), the median pharyngeal system (affecting the ventral side of the basicranium) and the cervical air sacs (affecting the posterior side of the basicranium), more recently grouped under the term “pharyngotympanic sinuses” (Witmer, 1997; Witmer *et al*., 2008; Dufeau, 2011).

Paracondylar and subcondylar recesses (= lateral and median recesses). Here we differentiate between subcondylar recess (SCR, single depression below the occipital condyle) and paracondylar recesses (PCR, paired lateral depressions). Below the neck of the occipital condyle of *Megaraptor* there is a large but shallow median SCR, clearly observed in posterior view (Fig. 1.5). Laterally to the SCR there is a deep PCR on each side, better observed in posterolateral view (Figs. 1.5, 3). Each PCR is an oval depression subdivided in a dorsal (smaller) and a ventral (larger) sub-recesses. Dorsal to the PCR, there is an oval depressed area that houses CNs IX-XII, and a smaller oval depression with well-marked margins on the posterior side of the paroccipital process (dorsal to the metotic foramen) (Fig. 3). A small foramen within this oval depression leads into a passage that connects with the lateral side of the medulla oblongata (Fig. 3).

This passage has been recorded also in *Itemirus* (Sues & Averianov, 2014: fig.4A), and in *Murusraptor* (although its obliterated). Its function is unclear, and can be related to an endolymphatic duct or a venous sinus.

The subdivisions of the PCR in *Megaraptor* are extensive and deep, reaching dorsally the base of the paroccipital process, surpassing the level of the occipital condyle. The SCR and the PCR are present in the braincases of many theropod groups. A large and deep PCR, with two or more well-marked subdivisions is observed in the basicranium of the therizinosauroid *Falcarius* ("subcondylar recess" in Kirkland *et al*., 2005: fig. 1A).

Anterior (=rostral, lateral) tympanic recess. In theropod braincases, the external opening of the ATR opens on the lateral wall of the basisphenoid and can be overhanged, if present, by an alar preotic pendant. The development of the ATR strongly varies from wide depressions on the lateral side of the basisphenoid to small openings, but is always related to the path of the cerebral branch of the internal carotid artery (Paulina-Carabajal, 2015). In *Megaraptor* the ventral portion of the basisphenoid is missing, and therefore the external openings of both, right and left ATR are not preserved. Posteroventrally to the foramen for CN VII, there is a small pneumatic opening, which leads internally to a tubular cavity that projects posteroventrally inside the basisphenoid (Fig. 1.1). A markedly similar recess was identified in onithomimosauroids as the "prootic recess" by Tahara and Larsson (2011). These authors defined the prootic recess (PROR) in *Ornithomimus* as a dorsal extension of the anterior (=lateral) tympanic recess, an osteological correlate of the anterior tympanic diverticulum that excavates the ventral portion of the prootic beneath the maxillomandibular (CN $V_{2,3}$) foramen (and this is a feature partially observed in *Megaraptor*). A large ascending diverticulum of the ATR within the prootic has been mentioned for tyrannosaurids, such as *Alioramus, Daspletosaurus, Gorgosaurus* and *Tyrannosaurus* (Bever *et al*., 2011; Witmer & Ridgely, 2009; Paulina-Carabajal *et al*., 2021). Moreover, in *Alioramus*, the prootic diverticulum connects with the exterior through a narrow slit between the prootic and the basisphenoid (Bever *et al*., 2011). Interestingly, a subcircular external opening for the ascending diverticulum, named here "prootic recess" (PROR) is observed in the lateral wall of the braincase ventral to the foramen for CN VII in *Velociraptor* (Norell *et al*., 2014), and in *Megaraptor* (Fig. 4). In *Alioramus* the ATR affects more extensively the body of the prootic, surrounding the trigeminal and facial canals, and communicating with the lateral surface of the braincase through a small fossa. In *Megaraptor,* the PROR excavates the prootic and the basisphenoid, but its ventral extension remains unknown because of fractures (Fig. 4.1). Internally, this pneumatic cavity reaches the ventral margin of the foramen for CN VII but does not affects the surroundings of the trigeminal foramen, unlike the case in tyrannosaurids. Despite being a small recess compared to that observed in tyrannosaurids, the degree of pneumaticity of *Megaraptor* braincase has not been recorded in non-coelurosaurs, in which, if present, the ATR affects only the basicranium. In *Megaraptor*, the presence of a PROR indicates the presence of a well-developed ATR in this taxon. In turn, the moderate development of the PROR as a dorsal expansion of the ATR could represent an intermediate stage between non-coelurosaur (apneumatic laterosphenoid and prootic) and coelurosaurian (pneumatic lateral wall of the braincase with extensive PROR) taxa. The PROR, however, is absent in *Murusraptor* and probably in *Joaquinraptor*, suggesting that could be a unique feature of *Megaraptor* within Megaraptoridae.

Basisphenoid recess. The BSR is large and deep. The margins of the external opening are not preserved, but the preserved cavity faces ventrally and has a rectangular outline

(Fig. 1.5). Internally, the dorsal wall of the BSR bears two elongate foramina that communicate with large pneumatic cavities extended posterodorsally reaching the neck of the occipital condyle. Each of these recesses has an inverted L-shaped morphology (Fig. 4.1). Within the basioccipital, right and left cavities remain separated, but they are connected to the BSR anterodorsally. Paired cavities or projections of the BSR within the neck of the occipital condyle are also present in *Murusraptor* (Paulina-Carabajal & Currie, 2017), other theropods, such abelisaurids and tyrannosauroids (*Alioramus*, *Daspletosaurus*, *Timurlengia*, *Tyrannosaurus*), and some dromaeosaurs (*e.g.*, *Velociraptor*, *Dromaeosaurus*, Norell *et al*., 2004). Posteroventrally, the BSR projects within each basal tuber, making this structure hollow (Fig. 4.1). The BSR communicates with each PCR via a pneumatopore (Fig. 3), whereas *Murusraptor* exhibits an obliterated single pneumatopore. The connection of the BSR with the external surface of the braincase is observed in the basicranium of the tyrannosaurid *Daspletosaurus* (Paulina-Carabajal *et al*., 2021: fig. 1G

Caudal (=posterior) tympanic recess. The CTR excavates the prootic and the opisthotic at the base of the paroccipital process, as shown by fractures and the tomograms (Figs. 1.6, 4.1). The external opening of the CTR (for the entry of the posterior tympanic diverticulum) is not clearly preserved as the surface of the bone is eroded or fractured in both sides. However, it seems possible that there was an external opening of the CTR caudolateral to the columellar recess and below the otosphenoidal crest. In tyrannosaurids the CTR pneumatizes almost the complete length of the paroccipital process, and projects dorsally affecting also the supraoccipital (Witmer *et al*., 2008; Witmer & Ridgely, 2009; Bever *et al*., 2011; Paulina-Carabajal *et al*., 2021). The CTR was thought to be absent in non-coelurosaurian theropods. However, a small pneumatic recess has been recently identified in the abelisaurid *Llukalkan* (Gianechini *et al*., 2021), and in the allosauroids *Sinraptor* (Paulina-Carabajal & Currie, 2012), *Sinosaurus* (Xing *et al*., 2014), and probably *Acrocanthosaurus* (Dufeau, 2011). Among them, only *Sinraptor* has an external opening for the CTR leading into a relatively small internal cavity at the base of the paroccipital process. In the other mentioned taxa, the external opening leads into a shallow recess and the pneumatic sinus does not affects internally the body of the paroccipital process. In *Murusraptor* the CTR is absent and the paroccipital processes are massive, as shown by the CT scans (Paulina-Carabajal & Currie, 2017). In *Megaraptor*, the CTR projects posterolaterally affecting largely the base of the paroccipital process, dorsal to the middle ear region. While the proximal section of the paroccipital process is inflated and hollow (internal development of the CTR) it narrows distally. The tips of the paroccipital processes are missing, preventing to know if they are massive or not. In this regard, the development of the CTR resembles that of some tyrannosauroids, such as *Timurlengia* (Brusatte *et al*., 2016: fig. 2A,G), but without affecting the complete length of the paroccipital process nor the supraoccipital, as do occurs in derived tyrannosaurids (*e.g*., Witmer & Ridgely, 2009; Bever *et al*., 2011; Paulina-Carabajal *et al*., 2021).

Cranial endocast and inner ear

The complete cranial endocast information of *Megaraptor* comes from two sources, the CT scans of the braincase (Fig. 5) and the osteological correlates of the forebrain preserved on the left frontal of *Megaraptor*. On the ventral side of the frontal, the osteological correlates of the olfactory apparatus (olfactory tracts and olfactory bulbs) are preserved together with most of the cerebral hemisphere. The impressions are poorly marked but allowed an interpretation of the outline of the dorsal shape of the forebrain (Fig. 6.1).

The general morphology of the complete cranial endocast (hindbrain and midbrain reconstructed three-dimensionally, and the forebrain outlined shape) has an overall tubular shape, sharing with *Murusraptor* the reduction of the flexure of the midbrain in lateral view. The long axis of the cerebrum is probably oriented horizontally, but the lack of parietal prevents the natural contact between the forebrain and midbrain regions. When complete the cranial endocast would have had at least 10 cm length from the foramen magnum to the tip of the olfactory bulbs, with the widest part (approximately 49 mm) across the cerebral hemispheres.

The cast of the olfactory tracts is anteroposteriorly short and wide, as in *Murusraptor* (Fig. 6.2) and the megaraptorid MCF-PV 320 (Paulina-Carabajal and Coria, 2015; Fig. 6.3). The olfactory bulbs are relatively small, lateromedially compressed, and divergent from the midline (Fig. 6). The olfactory bulbs are markedly divergent in *Megaraptor* (Fig. 6.1) and MCF-PVPH 320 (Fig. 6.3) and are more parallel in *Murusraptor* (Fig. 6.2). The anterior margin of the cerebral hemisphere of *Megaraptor* is distinguishable from the olfactory tract in dorsal and ventral views, but the transition is not abrupt, as in tyrannosaurids and abelisaurids (Voris *et al*., 2025). On the contrary, the lateral margin of the cerebral hemisphere gradually tapers into the olfactory tract, as in *Murusraptor* and in MCF-PVPH 320 (the latter having a more conspicuous constriction). This condition occurs in derived maniraptorans, such as troodontinds and dromaeosaurids (Voris *et al*., 2025).

The ventral margin of the medulla oblongata is markedly convex in lateral view, a trait also observed in *Murusraptor, Itemirus*, and *Velociraptor* (Sues & Averinov, 2014; Paulina-Carabajal & Currie, 2017; King *et al*., 2020). Whereas, the dorsal margin of the endocast projects anterodorsally from the top of the foramen magnum forming a slight sigmoid contour. As in other non-maniraptoran theropods, the only recognizable region of cerebellum in the endocast corresponds to the floccular process of the cerebellum that is a relatively large finger-shaped projection (oval in section). This projection is long enough to invade the space between the anterior and posterior semicircular canals of the inner ear. In dorsal view of the endocast the distal end of the flocculus reaches the level of the posterior semicircular canal, as in *Velociraptor* (King *et al*., 2020) and many South American abelisaurids which have slender but long flocculi (Paulina-Carabajal & Filippi, 2018). The flocculi of *Megaraptor* are markedly oriented posteriorly (less than 90°), more or less as in *Murusraptor* and tyrannosaurids (Witmer & Ridgely, 2009: fig. 3) but markedly less than in the dromaeosaurid *Velociraptor,* whose flocculi diverge at 120° (King *et al*., 2020).

The medulla oblongata of *Megaraptor* is anteroposteriorly short and tall, oval at the level of the foramen magnum, and is narrower than the rest of the hindbrain, as in maniraptorans (King *et al*., 2020). Just dorsal to the floccular process of the cerebellum is the caudal middle cerebral vein, a small passage oriented posterodorsally. Each of these passages is markedly small in diameter and short (Fig. 5.1–3). The hindbrain lacks a prominent dorsal expansion (or dural peak) overlying the cerebellum. The absence of a large dural peak is consistent with *Murusraptor* and some dromaeosaurs and basal tyrannosauroids (King *et al*., 2020). Contrarily, a prominent flexure is a distinctive feature in the tyrannosaurid brain (*e.g*., Bever *et al*., 2011; Witmer & Ridgely, 2009; Brusatte *et al*., 2016; Paulina-Carabajal et al., 2021).

Cranial nerves. The root for CN V has a large diameter and runs laterally from the endocast (Fig. 5.2). All the branches of the trigeminal nerve leave the endocranial cavity through a single foramen. Within the bone, the ophthalmic branch (CN V_1) separates and runs anteriorly leaving a short osteological correlate on the prootic as observed by fractures (Fig. 2.1). The branching of the CN V_1 within the wall of the braincase (across the prootic and often exiting through the laterosphenoid) is also present in *Murusraptor*, and in abelisaurids. Contrarily, tyrannosaurids have separate roots for CN V_1 and CN $V_{2,3}$ in the endocast. The latter is a derived feature shared with avialans (Bever *et al*., 2011).

The paired roots of CN VI project anteroventrally from the medulla oblongata (Fig. 5.4). They are small in diameter and slightly divergent from the midline. The pituitary region is not preserved preventing to know if these nerves entered the pituitary fossa or not. The divergent angle between the right and left CNs VI suggests that these nerves run laterally to the pituitary to exit through the foramina on the lateral side of the basisphenoid, as in *Murusraptor*.

Posterior to CN $V_{2,3}$ there is an oval protuberance on the endocast (representing the cast of the acoustic fossa) that bears three passages of small diameter, corresponding to CNs VII and VIII (Fig. 5.3). The most posterior passage projects posterolaterally entering the otic capsula and reaching the vestibular region of the inner ear medially (Fig. 5.2). This branch corresponds to the vestibulo-ocular nerve (CN VIII). The most anterior branch is the larger and runs laterally exiting the endocranial cavity through the CN VII foramen (facial nerve). Whereas, the middle branch runs posterodorsally, and enters the otic capsula reaching the vestibule of the inner ear laterally. It is not possible to determinate if this nerve innervates the inner ear or runs laterally through the middle ear region. In the latter case, the close relation between this root and the facial nerve suggests that may correspond to a second branch for the CN VII, or to the chorda tympany. The chorda tympani is a branch of the facial nerve, rarely recorded in fossils, that passes through the tympanic cavity on its way to the lingual side of the lower jaw and its path is remarkably consistent among living tetrapods (Hotton, 1960). However, a second branch for the acoustic nerve (CN VIII) cannot be discarded, as two foramina for this nerve were figured in other theropods, such as *Itemirus* (Sues & Averianov, 2014, fig. 4B), and *Velociraptor* (Norell *et al*., 2004: fig. 5.2B). The close proximity of these two nerves (VII and VIII) in reptiles is common (Jacobs, 1979) and further analyses using micro-CT scans of *Megaraptor* are needed before clearly understand their pathways. The bulge on the endocast shared by the three roots may indicate an intracranial ganglion, although not the geniculate ganglion. This ganglion seems to be extracranial in *Megaraptor*, as in *Murusraptor* and most theropods, including the more derived tyrannosaurids except *Alioramus* (Bever *et al*., 2011). In *Murusraptor* the exit foramen for CN VII is eight-shaped, clearly exhibiting the paths of the hyomandibular (CN VIIh) and palatine (CN VIIp) branches, which also leave grooves on the lateral surface of the prootic (Paulina-Carabajal & Currie, 2017). These osteological correlates are not observed in *Megaraptor*.

The metotic passage, for CNs IX-XI and internal jugular vein, has a large diameter and oval section. This passage is posteriorly oriented, with the exit foramen located within a shallow recess lateral to the neck of the condyle. The wider proximal end probably represents a ganglion and/or a ventrolateral venous sinus draining through the same canal. Posteroventral to the metotic passage there are two smaller passages for branches of CN XII. Dorsal to them, near the foramen magnum, there is an elongate passage that projects posterolaterally to exit within the pneumatic paracondylar recess on the posterior side of the paroccipital process (Figs. 2, 3). This passage does not correspond to a nerve, and probably correspond to a vascular element or an endolymphatic duct. As mentioned, similar passages are present in the same endocranial region in *Murusraptor* (obliterated; Paulina-Carabajal & Currie, 2017), and *Itemirus* (Sues & Averianov, 2014). Whereas, an endolymphatic duct was identified between the metotic foramen and the floccular recess in *Velociraptor* (Norell *et al*., 2004).

Inner ear. The inner ear has triangular shape in lateral view, as in other non-avian theropods (*e.g.*, Balanoff *et al*., 2009; Witmer & Ridgely, 2009; Lautenschlager *et al*., 2012), where the anterior semicircular canal (ASC) is larger and taller than the posterior semicircular canal (PSC), and the lateral semicircular canal (LSC) is smaller than the other two. The semicircular canals are slender, and there are no marked swollen anterior and posterior ampullae associate to the ASC and the PSC. In *Velociraptor* there is a large anterior ampulla where the ASC meets the vestibule (King *et al*., 2020). This is a derived condition not observed in *Megaraptor*.

The ASC is circular, whereas PSC and LSC are more elliptical. Anterior and posterior semicircular canals are tall and project over the level of the crus commune. These two semicircular canals form an angle of approximately 90° in dorsal view (Fig. 5.1). The vestibular anatomy is not well defined and the margins of the oval window are not clear. The lagena is robust, simple and conical and not particularly different from most studied theropods. The distal end of the lagena projects slightly below the medulla oblongata, as in *Murusraptor* (Paulina-Carabajal & Currie, 2017) and *Alioramus* (Bever *et al*., 2011). Whereas in *Timurlengia* (Brusatte *et al*., 2016), and *Velociraptor* (King *et al*., 2020) the distal end is more ventrally projected. *Megaraptor* exhibits some ventromedial inclination of the lagena, as observed in derived coelurosaurs.

APROACH TO SENSORAL HABILITIES

Degree of braincase pneumaticity

The braincase of *Megaraptor* is highly pneumatized when compared to non-coelurosaur theropods, such as abelisaurids, carcharodontosaurids and allosauroids. This is true particularly because of the development of an extension of the ATR (the PROR) and the presence of a large CTR. While in most non-coelurosaur theropods the paratympanic pneumaticity affects only the basicranium, in *Megaraptor* the lateral walls of the braincase are pneumatized as well, as in tyrannosaurids (e.g., Witmer & Ridgely, 2009). In *Megaraptor*, the PROR, a dorsal projection of the ATR, reaches the level of the foramen of CN VII (but not CN V, as it does in tyrannosaurids, Fig. 7.1), and a large CTR hollows out great part of the paroccipital process (Fig. 7.3). These are features particularly interesting because differentiates *Megaraptor* from *Murusraptor* (which has no CTR, Fig. 7.5), and from any other non-coelurosaur with smaller CTR (i.e. *Acrocanthosaurus*, *Sinraptor*, *Sinosaurus*). Furthermore, only coelurosaurs possess extensive CTR affecting internally large regions of the posterior braincase (*e.g.*, Bever *et al*., 2011; Tahara & Larsson, 2011; Brusatte *et al*., 2016) (Fig. 7.1). In theropods, the presence of braincase pneumaticity –particularly enlarged tympanic chambers acting– associates with enhanced hearing, particularly sensitivity for low-frequency sounds, as seen in tyrannosaurids (Witmer & Ridgely, 2009). The relative extensive tympanic pneumaticity in *Megaraptor* may have amplified certain range of hearing frequencies (see below), marking a different hearing capability with *Murusraptor,* and with other coeval groups, such as abelisaurids (e.g. Paulina-Carabajal & Filippi, 2028). This supports a predatory lifestyle for *Megaraptor* involving hunting prey.

Paracondylar recesses (=subcondylar recesses for some authors, Kirkland *et al*., 2005) lateral to the occipital condyle, are not unusual in non-coelurosaur theropods. However, *Megaraptor* shows complex subdivisions of the PCR in chambers affecting the basicranium and the ventral section of the paroccipital process above the occipital condyle, a feature observed in *Falcarius* (Kirkland *et al*., 2005). The PCR is shallow in basal tyrannosauroids but is deeply excavated in tyrannosaurids (*e.g*., Bever *et al*., 2011), ornithomimids (*Ornithomimus edmontonicus*, Tahara & Larsson, 2011), basal therizinosaurians (Kirkland *et al*., 2005) and oviraptorosaurs. There are relatively smaller PCRs in *Itemirus* (Sues & Averianov, 2014) and *Velociraptor* (King *et al*., 2020, supplementary 3D information), and reduction or even absence of PCR seems to be common among dromaeosaurids and other derived coelurosaurs (Brusatte *et al*., 2016). The implications of this feature for *Megaraptor* lifestyle remains unclear. Still, the relatively large development of the PCRs appears similar to that of basal coelurosaurs. Studies of the pneumaticity of the whole skull of tyrannosauroids showed that basal taxa possess extensive pneumaticity, but large bodied tyrannosauroids do not (Gold et al., 2013), suggesting a probable size-related feature.

Enlarged floccular process of cerebellum

In extinct forms, the size of the flocculi has been linked to agility and balance (Witmer & Ridgely, 2009), although its reliability as a proxy of behavior and ecology is controversial (Walsh et al., 2013; Ferreira-Cardozo et al., 2017). Within vertebrates, the floccular processes or lobes of the cerebellum relate to the stabilization of the head and eyes (gaze stabilization) during the movements of the animal (e.g., Voogd et al., 2004). Since good balance is a necessary quality for stable bipedal movement, among theropods, larger flocculi have been associated to the ability to track moving objects, as proposed for *Velociraptor* (King *et al*., 2020).

The flocculus in *Megaraptor* is a large finger-shaped projection that surpass the level of the anterior semicircular canal of the inner ear reaching the posterior semicircular canal. This feature is reminiscent of more derived coelurosaurs, whereas in non-coelurosaurs and basal tyrannosauroids the flocculus of the cerebellum is in general wing-shaped and barely projects into the area delimited by the anterior semicircular canal. Although the size of the cranial endocast in most theropods may not be representative of the volume of the non-preserved soft brain tissues (Walsh *et al*., 2013; Ferreira Cardoso *et al*., 2017), a relatively large floccular recess in the endocranial cavity likely correlates with a large flocculus of the cerebellum (King *et al*., 2020). In *Megaraptor* the volume occupied by the flocculus within the area delimited by the three semicircular canals is relatively large for a non-coelurosaur theropod, but yet small for a derived coelurosaur. The flocculi together account for approximately 3.12 % of the total hindbrain volume, whereas this value is 7% in *Velociraptor* (King *et al*., 2020). This suggests that even the apparent large development of the flocculus does not represent a derived coelurosaur condition, but an intermediate stage that may support *Megaraptor* as a basal coelurosaur or even a basal tyrannosauroid. As the enlargement of the flocculus has been used as indicative of strong vestibuleocular and vestibulocollic reflexes (Witmer & Ridgely, 2009), this suggests that the predator habit of *Megaraptor* relied on quick movements and stable gaze. There was a high diversity of predator theropods during the middle Turonian-late Coniacian of north Patagonia (e.g., Meso *et al*., 2024). *Megaraptor* was probably good pursuing prey more easily than other coeval mid-to-large sized theropods such as *Murusraptor* and abelisaurids, competing directly with small sized coelurosaurs such as *Neuquenraptor* Novas and Pol, 2005, *Patagonykus* Novas, 1993, *Unenlagia* Novas and Puerta, 1997, and *Pamparaptor* Porfiri *et al*., 2011.

Olfactory apparatus

The most complete anatomical information on the olfactory apparatus in megaraptorids is that provided by the osteological correlates of the olfactory tracts and olfactory bulbs on the ventral side of the frontals, and the grooves left by the olfactory nerve (CN I) on the isolated ethmoidal elements of *Murusraptor* (Paulina-Carabajal & Currie, 2017).

Moreover, the preserved ethmoidal elements allowed a partial reconstruction of the volume of the cavities that housed the olfactory bulbs. Based on this information, the olfactory bulbs of *Megaraptor* and MCF-PVPH 320 seem to share the same size proportions (Fig. 6). The megaraptorid olfactory apparatus represents half or less than the complete length of the forebrain, whereas this proportion is larger in tyrannosaurids (*e.g.*, Voris *et al*., 2025). The Olfactory Ratio (Zelenitzky *et al*., 2009) of *Megaraptor* is estimated in a range of approximately 45–50%, as in *Murusraptor* and MCF-PVPH 320 (Paulina-Carabajal & Currie, 2017, tab.1). This value lies within the range of allosauroids, but is smaller than that observed in carcharodontosaurids and tyrannosaurids, suggesting megaraptorids were less reliant on olfaction for survival compared to certain groups of theropods. The lack of information regarding the complete length of the cerebral hemisphere in *Megaraptor*, prevents further analysis of the olfactory acuity in this taxon.

Hearing range

The endosseous cochlear duct or lagena is intimately linked to hearing performance (*e.g.*, sensitivity and frequency range) because it houses the basilar papilla. The mean hearing range (2317 Hz) and high frequency limit (3868 Hz) of *Megaraptor* were calculated measuring and logarithmically transforming the escalated ratio between the length of the basisphenoid (38.5 mm) and the lagenar length taken from the vestibulum (12 mm). These results are highly similar to those calculated for *Velociraptor* (2368 and 3965 Hz, respectively) by King *et al*. (2020), and overlap with the values calculated for *Falkarius* (1630 Hz and 4000 Hz). These authors compared these hearing capabilities with those present in some living birds. We acknowledge here the limitations of using lagenar length (Walsh *et al*., 2009) or basilar papilla length (Gleich *et al*., 2005) to predict hearing in extinct animals, but understand these methods as tentative approaches to hearing and particularly comparison among non-avian theropods.

As mentioned above, closely related to the enhancing of the hearing capabilities is the development of tympanic pneumaticity (Witmer & Ridgely, 2009). In therizinosaurids, the expansion of the basicranial pneumatic system is limited to the paratympanic system, enhancing low frequency sound sensitivity (Smith *et al*., 2018). In this group of theropods the presence of tympanic sinuses suggests a much lower frequency range than predicted by the lagenar length, and this is probably the case for *Megaraptor* as well.

CONCLUSIONS

Using micro-CT scans, we re-described the braincase morphology and described for the first time the pneumaticity, endocranial cavity, brain and inner ear of *Megaraptor*, discussing possible implications for the sensory biology of this taxon. Remarkable features are a high pneumatization that exceeds the basicranium affecting the walls of the braincase and the paroccipital processes, a relatively large flocculus of the cerebellum, and a hearing range matching that calculated for the dromaeosaurid *Velociraptor*. Particularly interesting for *Megaraptor* is the presence of a relatively high degree of braincase pneumaticity, expressed as several pneumatic recesses including a well-developed CTR, being the later a feature that supports the close relationship of this taxon with Coelurosauria.

Megaraptor and other studied megaraptorids share a morphology of the forebrain characterized by poorly expanded cerebral hemispheres (the lateral margins are leveled to the lateral margins of the olfactory bulbs), absence of visible interhemispheric fissure, short and wide cast of the olfactory tracts and relatively small and oval olfactory bulbs. In a wide perspective, the braincase and the neural anatomies exhibit a mosaic of derived characters (among non-coelurosaurs) and primitive characters (among coelurosaurian theropods) within Theropoda. This coincides with the evolutionary complexity and morphological plasticity at the base of Coelurosauria stated by Bever *et al*. (2011) after finding primitive and derived character states within Tyrannosauroidea, and supports the close relation of *Megaraptor* with non-tyrannosaurid basal coelurosaurs.

The paleoneurology and interpreted sensorial biology points out *Megaraptor* as an agile bipedal predator with abilities that allow it to compete with coeval coelurosaurs, or at least mimic many of their hunting capabilities.

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Figure captions

Figure 1. Renderings of the braincase of ***Megaraptor namunhuaiquii*** (**MUCPv**-595) in **1**, right lateral; **2**, left lateral; **3**, right medial; **4**, ventral; **5**, posterior; and **6**, dorsal views. Abbreviations: **bo**, basioccipital; **bo-op.s**, basioccipital-opisthotic suture; **bs**, basisphenoid; **bsr**, basisphenoidal recess; **bt**, basal tubera; **chty**?, chorda tympany (or branch for CN VIII); **ct**, crista tuberalis; **ctr**, caudal tympanic recess; **eo-op**, exoccipital-opisthotic; **floc.r**, floccular recess; **fm**, foramen magnum; **mea**, middle ear area; **met**, metotic foramen for CNs IX-XI and internal jugular vein; **op**, opisthotic; **pcr.d**, paracondylar recess, dorsal section; **pcr.v**, paracondylar recess, ventral section; **pnf**, pneumatic foramen for the prootic recess; **pop**, paraoccipital process; **pro**, prootic; **scr**, subcondylar recess; **so**, supraoccipital; **sok**, supraoccipital knob; **V-XII**, Cranial Nerves (CNs) foramina. Scale bar equals 10 mm.

Figure 2. Half sagittal section of the endocranial cavity of ***Megaraptor namunhuaiquii*** (**MUCPv**-595) in right medial view. **1**, detail of cranial foramina, and **2**, reconstruction of the trigeminal, facial, and acoustic nerves (B). Abbreviations: **chty**, chorda tympany; **cmcv.i**, caudal middle cerebral vein, internal foramen; **floc.r**, floccular recess; **fm**, foramen magnum; **met**, metotic foramen, internal opening; **eld**, endolymphatic duct?; **V-XII**, cranial nerves. Scale bar equals 10 mm.

Figure 3. Detail of right posterior cranial foramina and paracondylar recesses in ***Megaraptor namunhuaiquii*** (**MUCPv**-595) in posteroventral view. Abbreviations: **bt**, basal tuber; **ct**, crista tuberalis; **eld**, endolymphatic duct, exit opening; **fm**, foramen magnum; **met**, metotic foramen for CNs IX-XI and internal jugular vein; **XII**, hypoglossal nerve. Scale bar equals 10 mm.

Figure 4. Braincase of ***Megaraptor namunhuaiquii*** (**MUCPv**-595) in 1, right lateral; and 2, dorsal views showing the internal pneumatic recesses. The bone is rendered semitransparent to allow the observation of internal structures. Abbreviations: **CTR**,

caudal tympanic recess; **ie**, inner ear; **PROR**, prootic recess, dorsal part of the anterior (=lateral) tympanic recess; **BSR**, basisphenoidal recess; **$V_{2,3}$**, maxillomandibular branches of trigeminal nerve; **VII**, facial nerve. Not to scale.

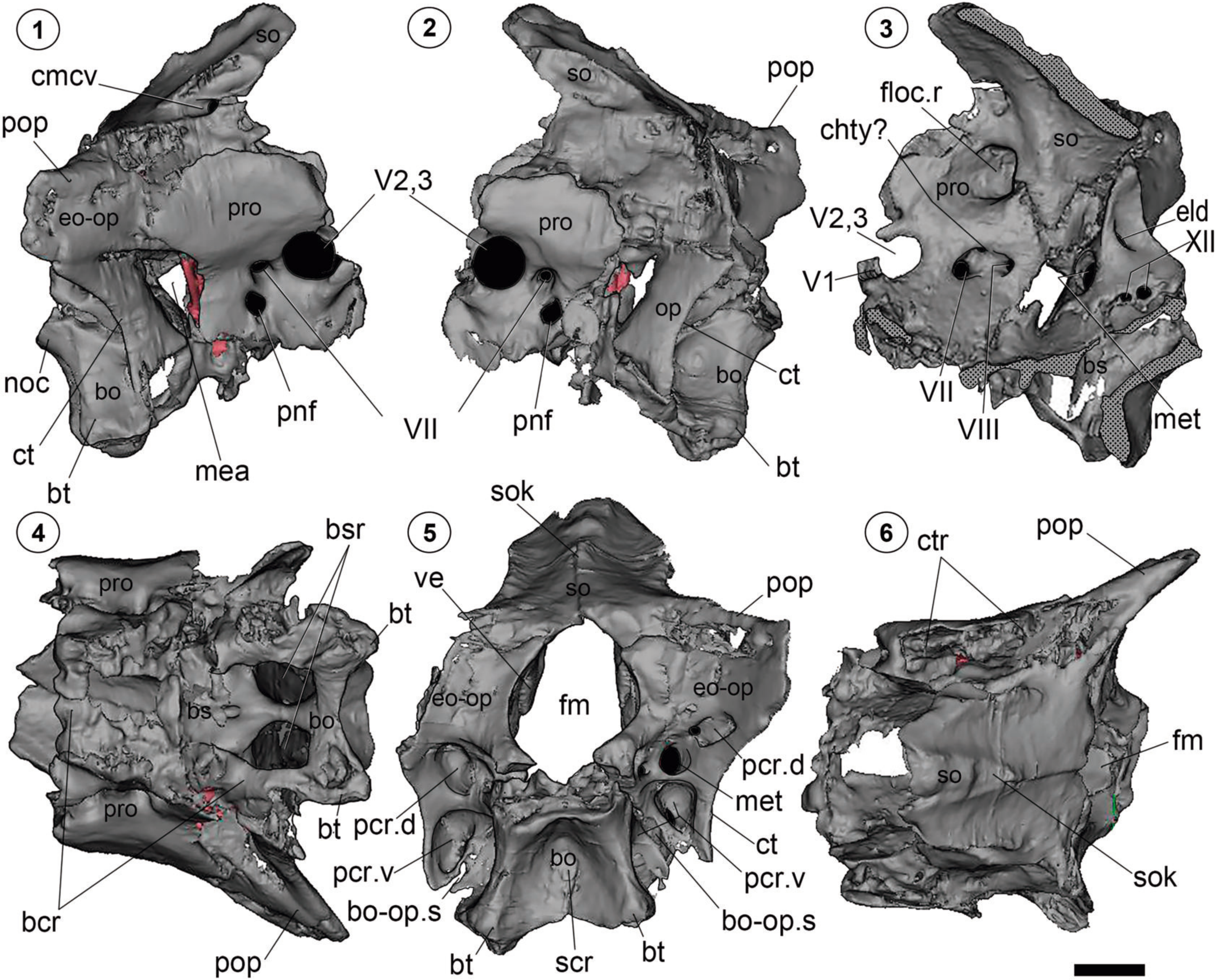
Figure 5. Renderings of cranial endocast and inner ear of ***Megaraptor namunhuaiquii*** (**MUCPv**-595) in 1, dorsal; 2, right lateral; 3, right lateral without inner ear; 4, ventral; 5, left lateral; and 6, posterior views. Abbreviations: **asc**, anterior semicircular canal; **chty**, chorda tympany (or second branch of CN VIII)?; **cmcv**, caudal middle cerebral vein; **eld**, endolymphatic duct; **floc**, flocculus of cerebellum; **ie**, inner ear; **lag**, lagena; **lsc**, lateral semicircular canal; **med**, medulla oblongata; **met**, metotic passage; **psc**, posterior semicircular canal; **V_1, $V_{2,3}$, VI, VII, VIII, IX-XI, XII**, cranial nerves.

Figure 6. Line drawings of the osteological correlates of the forebrain (cerebral hemispheres, olfactory tracts and olfactory bulbs) on the ventral side of the frontals of **1**, ***Megaraptor namunhuaiquii*** (**MUCPv**-595). Right frontal shape mirrored from the left frontal; **2**, ***Murusraptor barrosaensis*** (MCF-PVPH-411; segmentation of the skull roof, after Paulina-Carabajal & Currie, 2017); and **3**, the megaraptorid **MCF-PVPH 320** (after Paulina-Carabajal & Coria, 2015). Not to scale.

Figure 7. Braincase pneumaticity in **1**, ***Daspletosaurus*** sp.; **2**, ***Megaraptor namunhuaiquii*** (MUCPv-595); and **3**, ***Murusraptor barrosaensis*** (MCF-PVPH-411). Renderings of braincase, cranial endocast, inner ear and pneumatic sinuses in right lateral view. The bone is rendered semitransparent to allow the observation of the internal features. Abbreviations: **ATR**, anterior (=lateral) tympanic recess; **ATR.f**, external foramen for the ATR; **BSR**, basisphenoid recess; **bt**, basal tuber; **btp**, basipterygoid process; **BTR**, basipterygoid recess; **CTR**, caudal tympanic recess; **CTR.f**, external foramen for CTR; **endo**, cranial endocast; **fm**, foramen magnum; **ie**, inner ear; **n.oc**, neck of occipital condyle; **pop**, paroccipital process; **PROR**, prootic

recess (ascending projection of the ATR); **PROR.f**, external foramen for PROR. **$\mathbf{V}_{\mathbf{2,3}}$**, maxillomandibular foramen. Not to scale.

Supplementary Information. 3D PDF of braincase, pneumaticity, cranial endocast and inner ear.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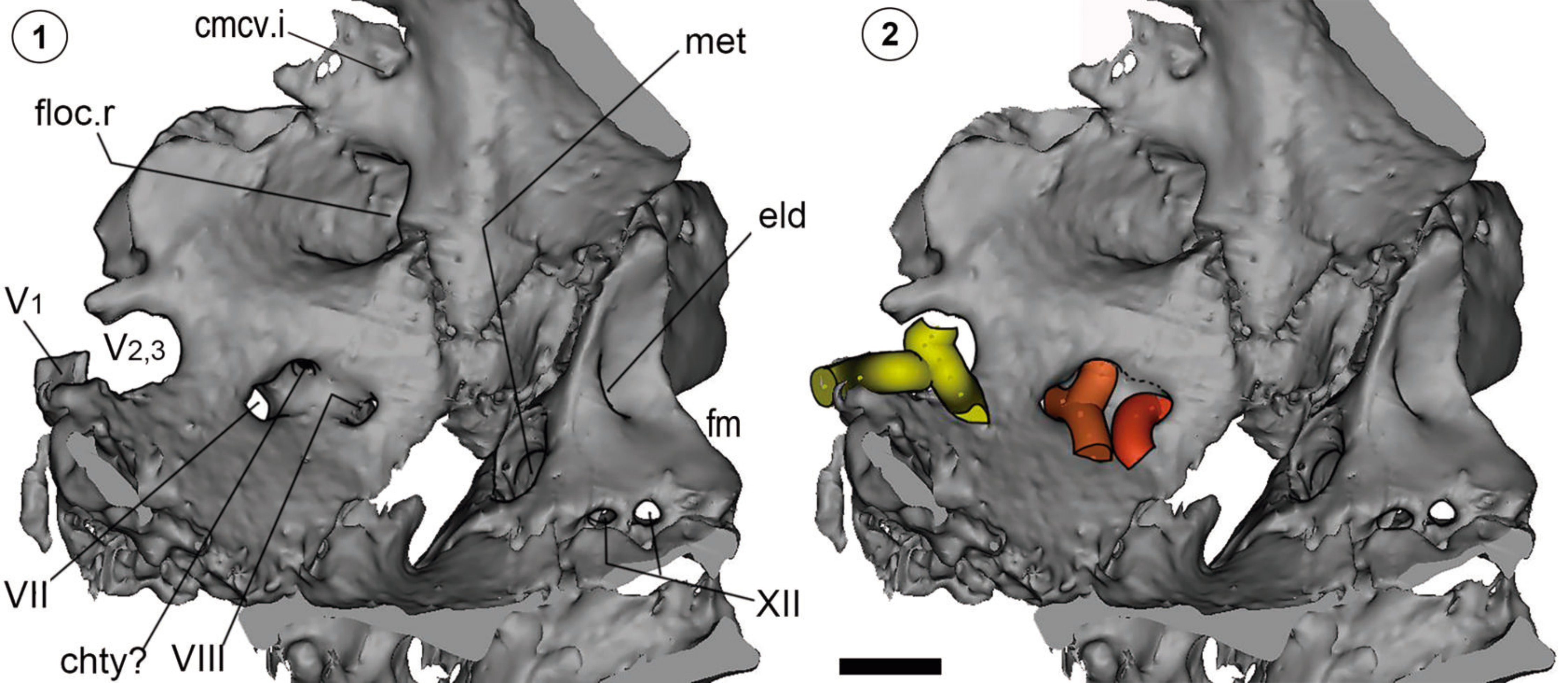
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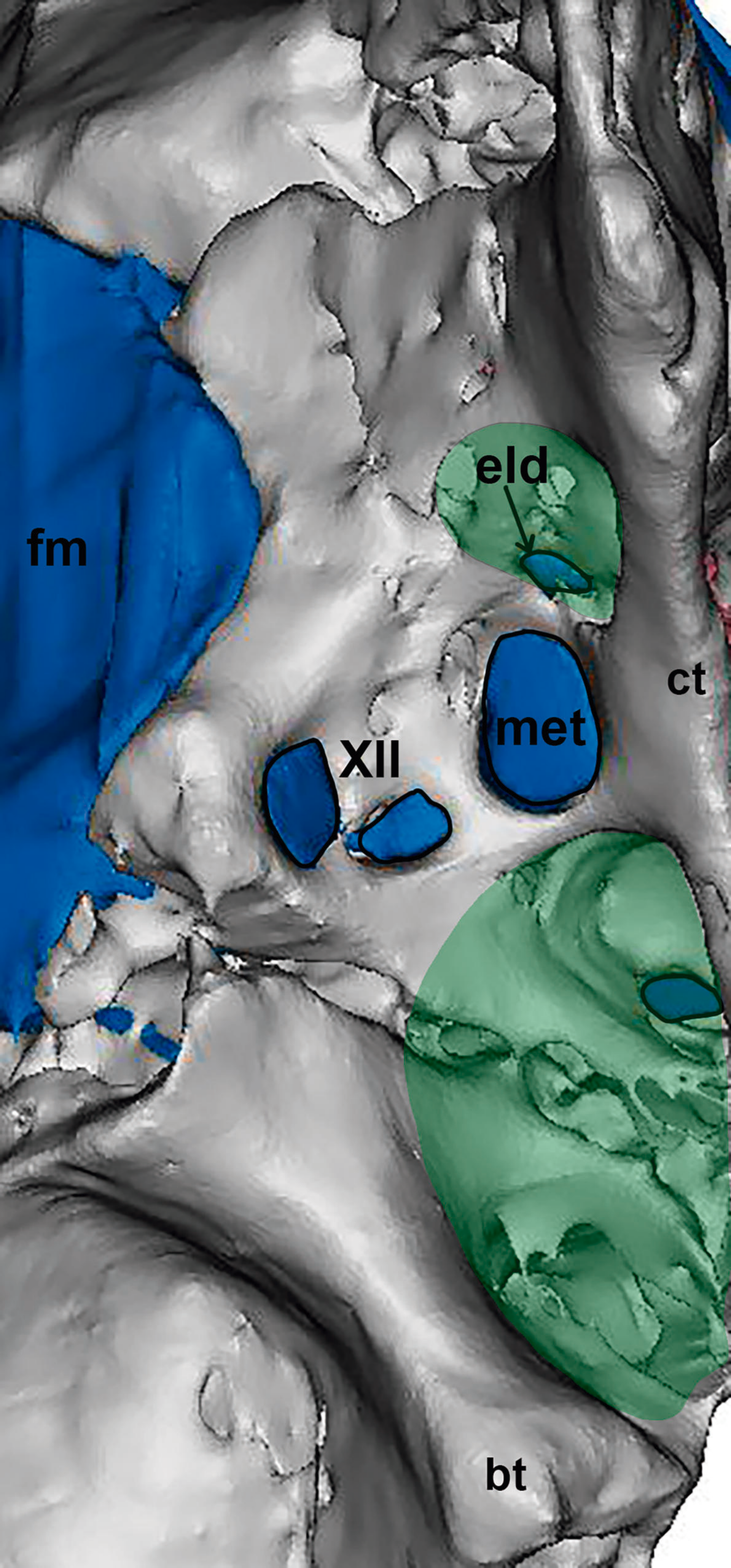
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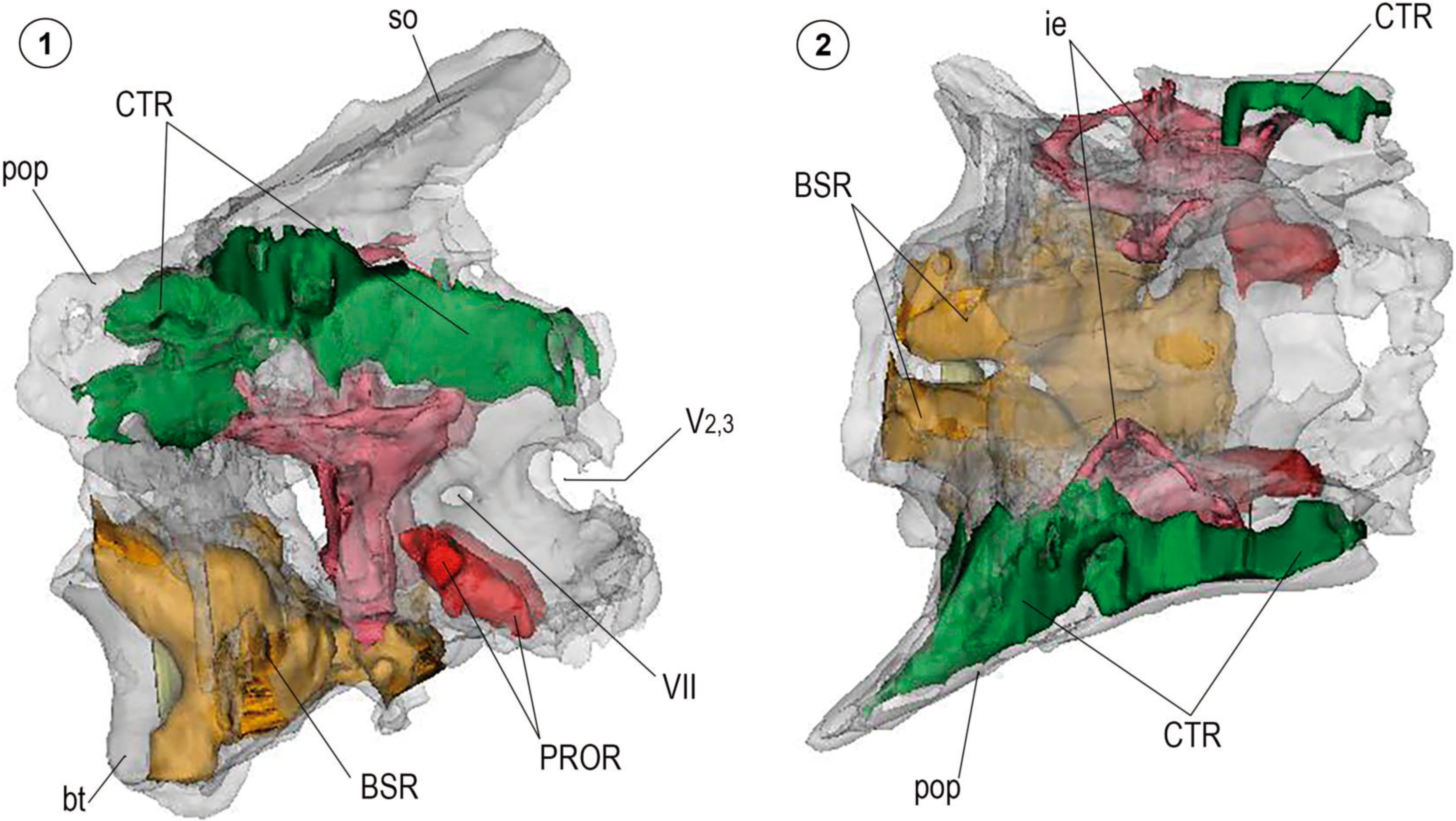
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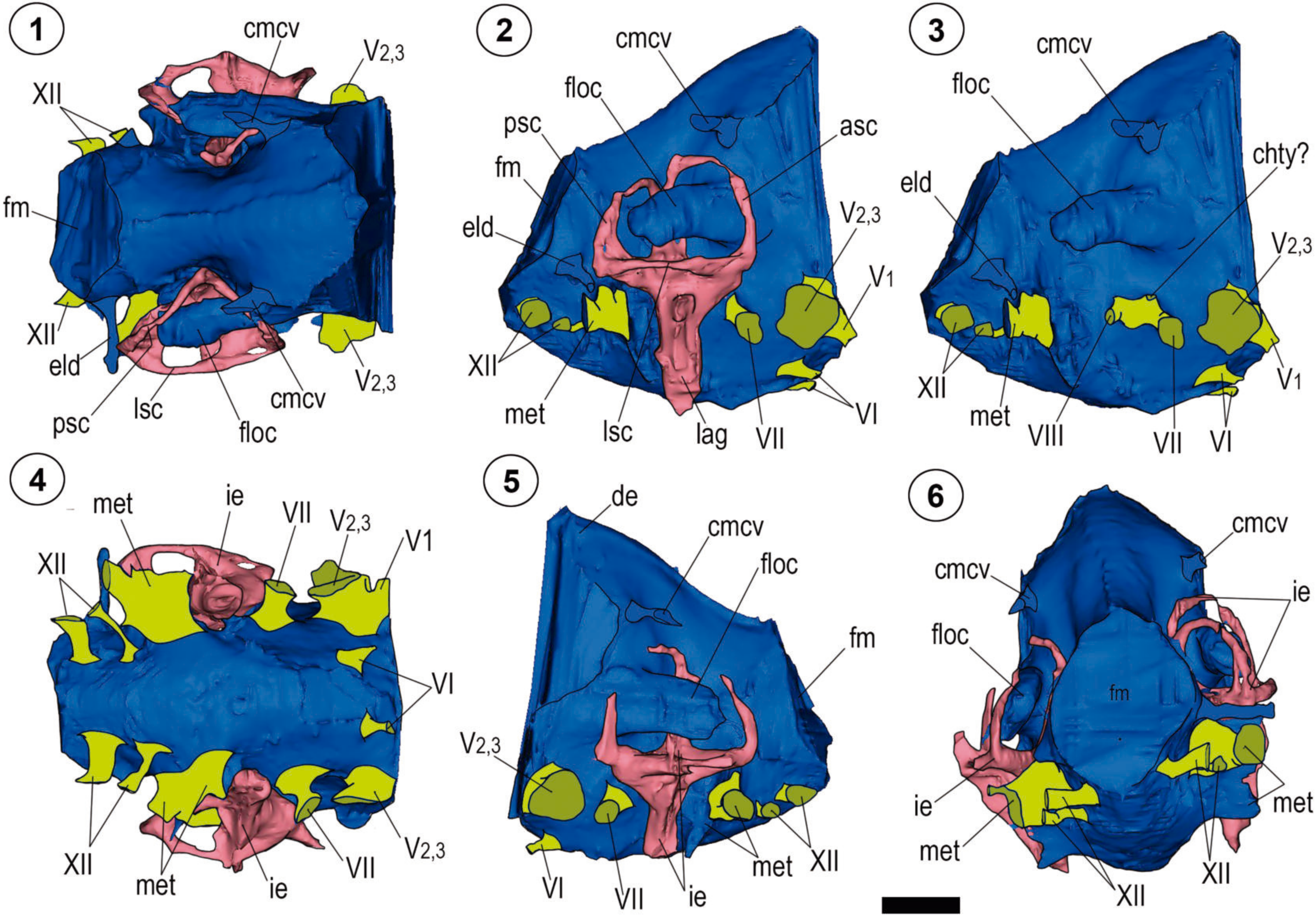
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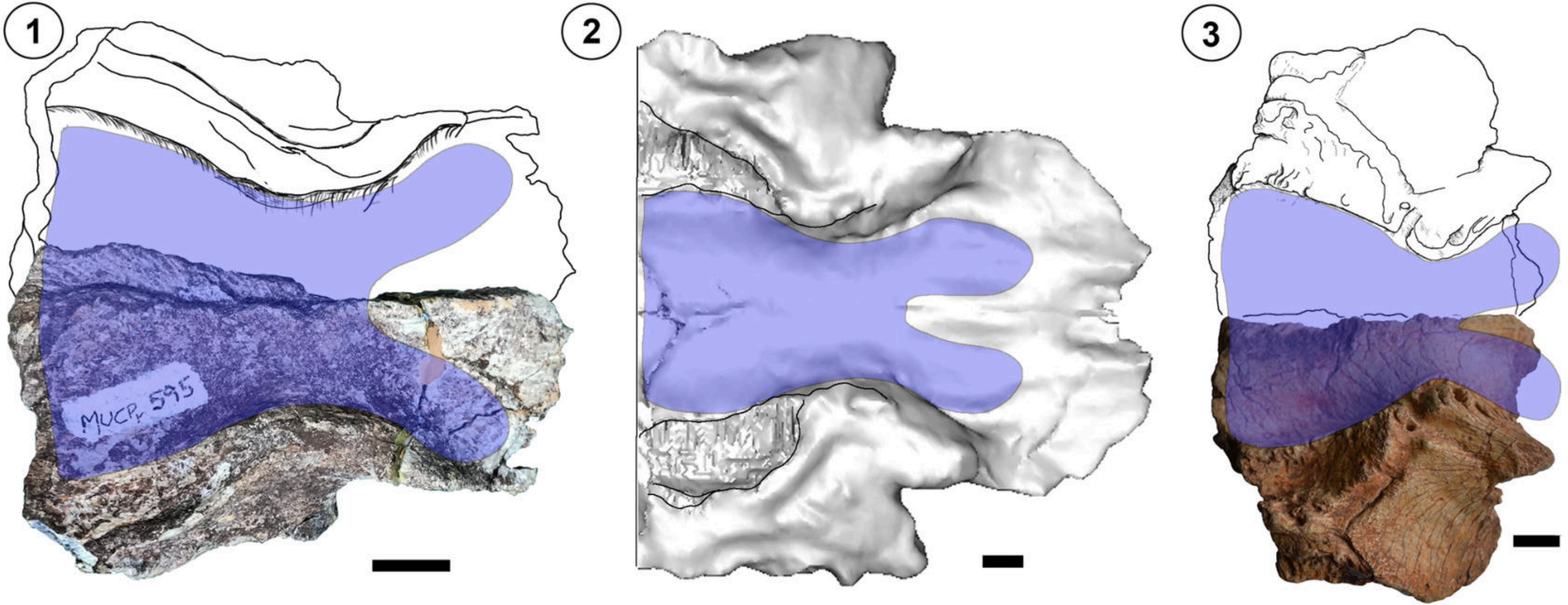
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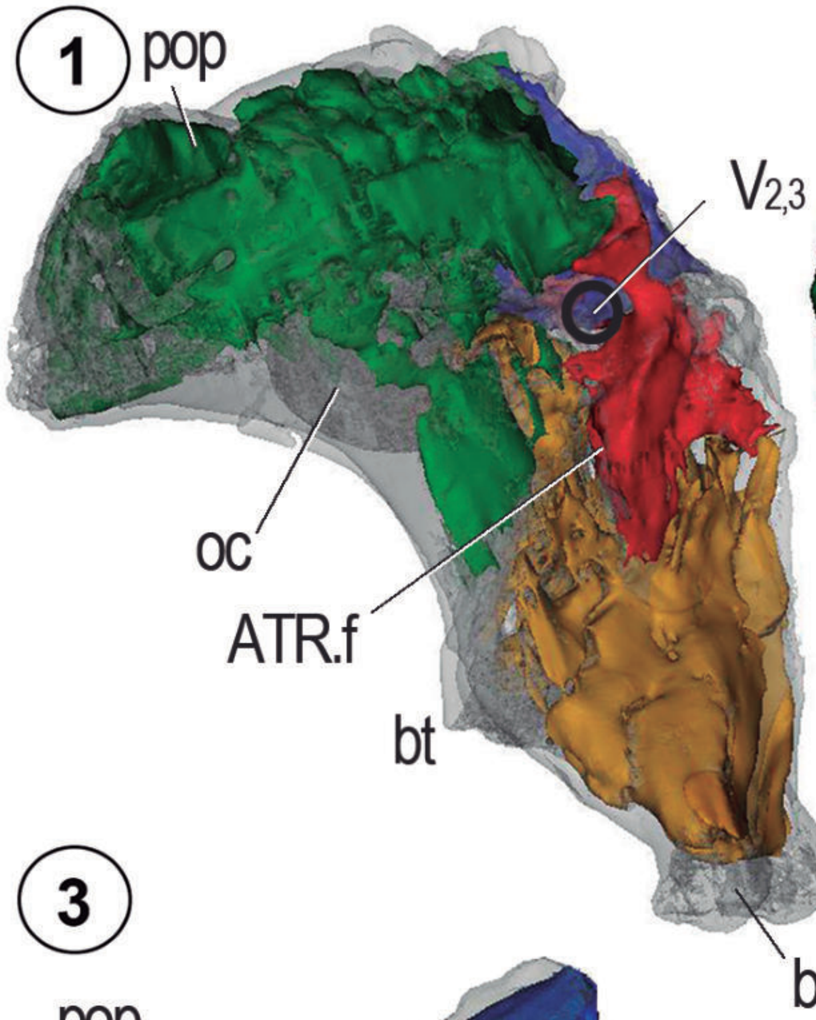
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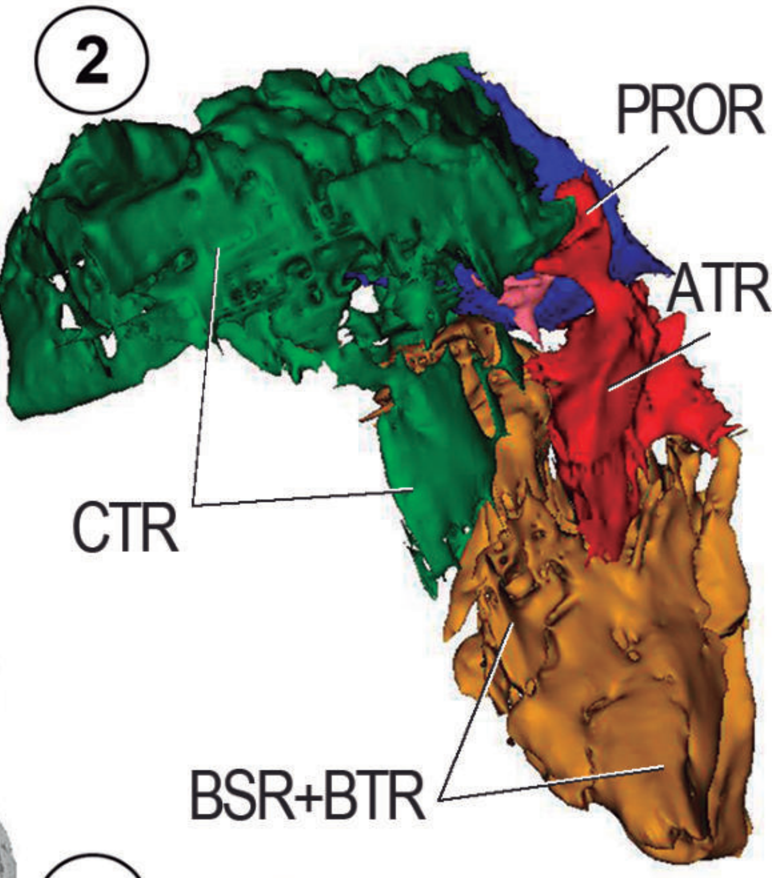
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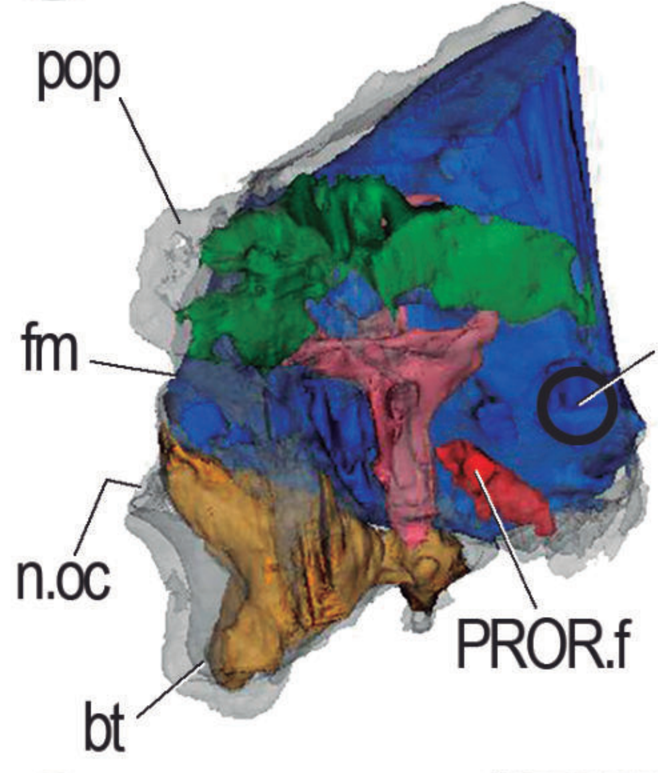
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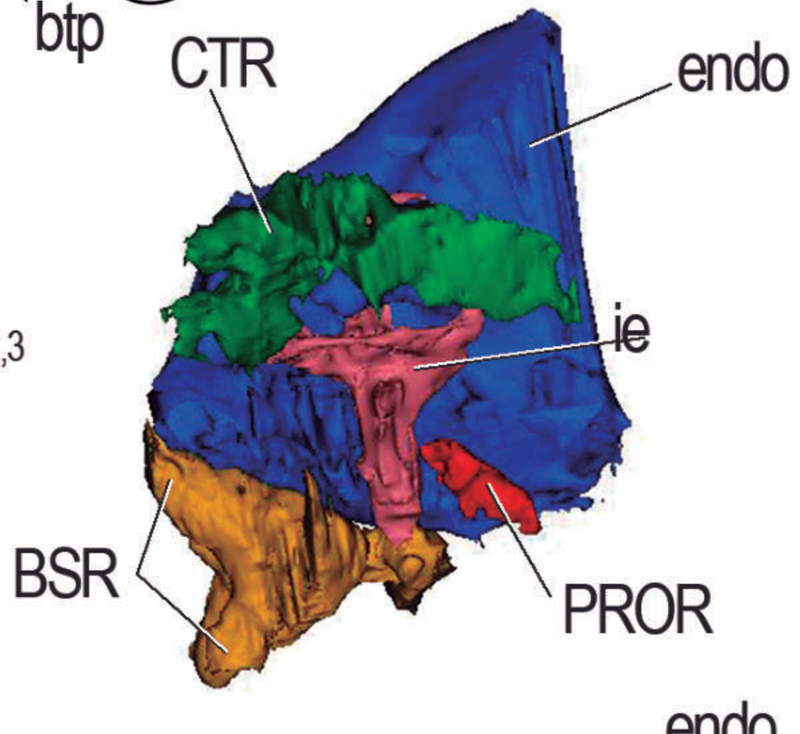
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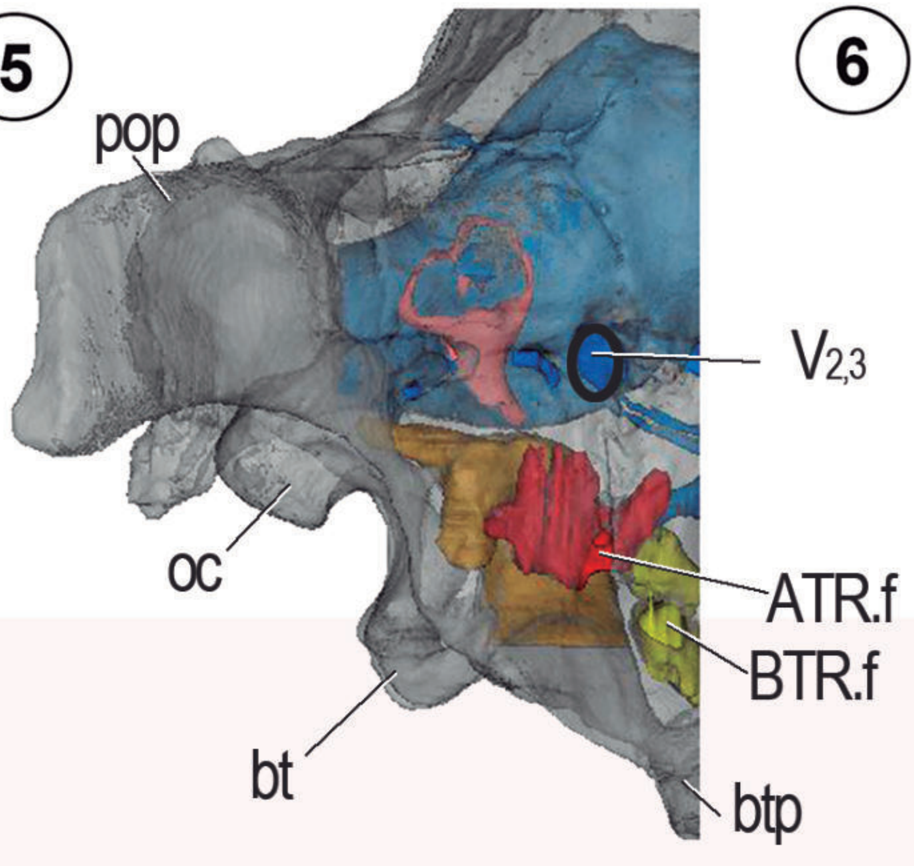
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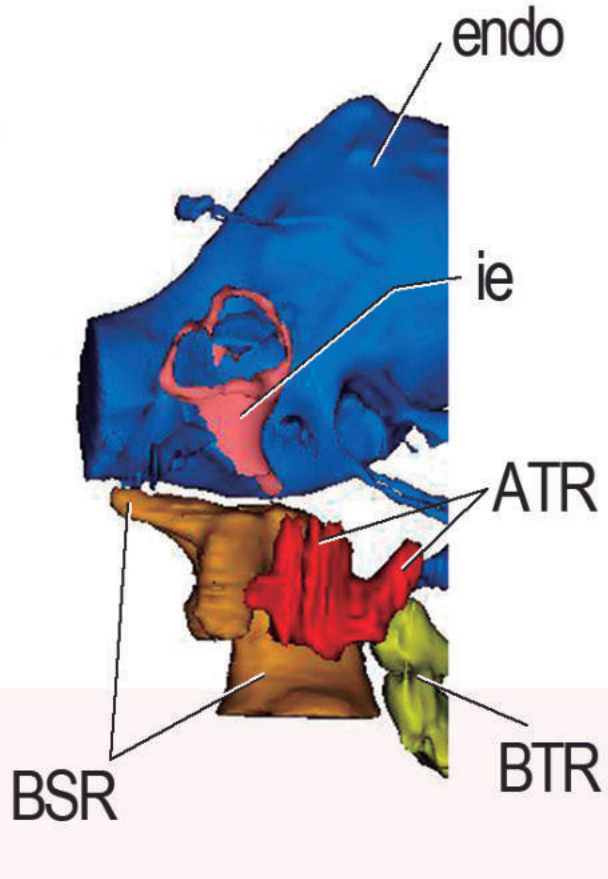
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