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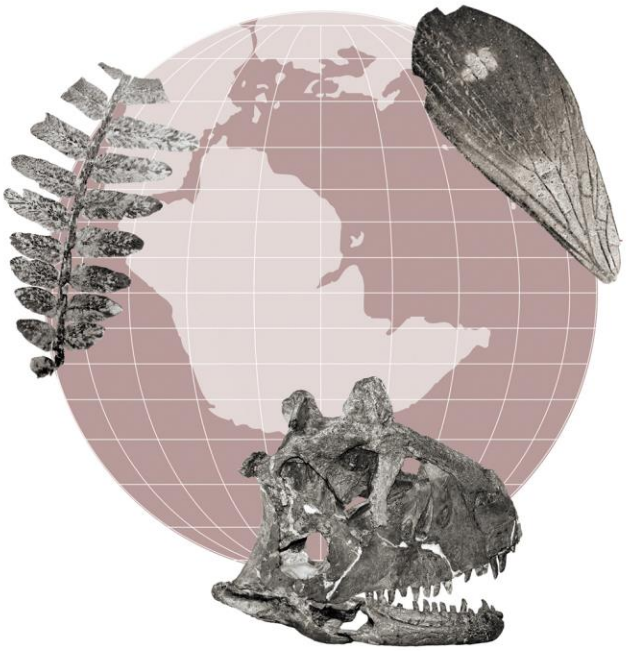

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THE FIRST RECORD OF THEROPOD DINOSAUR REMAINS FROM THE ANGOSTURA COLORADA AND COLI TORO FORMATIONS (CAMPANIAN-MAASTRICHTIAN) IN THE INGENIERO JACOBACCI AREA (RIO NEGRO PROVINCE, ARGENTINA)

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Running Header: PAULINA-CARABAJAL *ET AL.*: FIRST ABELISAURID REMAINS FROM INGENIERO JACOBACCI

Short Description: Theropod dinosaur remains were never found in Angostura Colorada and Coli Toro formations. The first record in both geological units correspond to abelisaurid remains near Ingeniero Jacobacci.

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Abstract. Several unpublished remains of indeterminate Late Cretaceous dinosaurs - collected by Rodolfo Casamiquela during the late 1950s are housed in the paleontological collections of the Museo Histórico Jorge Gerhold (Ingeniero Jacobacci, Rio Negro, Argentina) under the acronym MHJG 189 Pa. Among them, one basicranium and two fragments of the ornamented skull roof of a mid-to-large abelisaurid stand out, representing the first record of Theropoda for the Angostura Colorada Formation. A recent prospection of the same locality produced an isolated abelisaurid tooth, representing the first undoubtedly theropod record for the Coli Toro Formation, a unit overlying the Angostura Colorada Fm. Despite their fragmentary nature, these abelisaurid remains represent the first evidence of theropod dinosaurs not only for the Ingeniero Jacobacci area, but for both Angostura Colorada and Coli Toro formations.

Keywords. Abelisauridae. Basicranium. Tooth. Lacrimal. Postorbital. Upper Cretaceous.

Resumen. EL PRIMER REGISTRO DE RESTOS DE DINOSAURIOS TERÓPODOS DE LAS FORMACIONES ANGOSTURA COLORADA Y COLI TORO (CAMPANIANO-MAASTRICHTIANO) EN EL ÁREA DE INGENIERO JACOBACCI (PROVINCIA DE RÍO NEGRO, ARGENTINA). Varios restos de dinosaurios indeterminados del Cretácico Superior -colectados por Rodolfo Casamiquela a finales de la década de 1950- se albergan en las colecciones paleontológicas del Museo Histórico Jorge Gerhold (Ingeniero Jacobacci, Río Negro, Argentina) bajo el acrónimo MHJG 189 Pa. Entre ellos destacan un basicráneo y dos fragmentos del techo craneano ornamentado de un abelisáurido de tamaño mediano a grande, que representan el primer registro de Theropoda para la Formación Angostura Colorada. Una prospección reciente en la misma localidad produjo un diente aislado de abelisáurido, que representa indudablemente el primer registro de terópodo para la Formación Coli Toro, una unidad suprayacente a la Formación Angostura Colorada. A pesar de su naturaleza fragmentaria, estos restos de abelisáuridos representan la primera evidencia de dinosaurios terópodos no solo para el área de Ingeniero Jacobacci, sino también para las formaciones Angostura Colorada y Coli Toro.

Palabras clave. Abelisauridae. Basicráneo. Diente. Lacrimal. Postorbital. Upper Cretaceous

RODOLFO CASAMIQUELA (1932–2008) was an Argentinean paleontologist, archaeologist, and writer born and raced in the city of Ingeniero Jacobacci, in the centre of Río Negro province in North Patagonia, Argentina. He started collecting Upper Cretaceous dinosaur remains from areas near Ingeniero Jacobacci in 1949, and proper research on extinct reptiles in this province started in the 1960s with his works on the first Cretaceous hadrosaurid dinosaurs found in South America (Casamiquela, 1964). In this area, the localities with sediments bearing dinosaurs correspond to outcrops of the Angostura Colorada Formation (Campanian–Maastrichtian) and the Coli Toro Formation (Maastricthian–Danian). Those dinosaur remains belong to sauropod and hadrosaurid dinosaurs, including few cranial (*e.g.*, hadrosaurid isolate maxillae) and many postcranial (the most common are sauropod and hadrosaurid caudal vertebrae and limb bones) elements. Most of them are hosted in the collections of the Museo Histórico Jorge Gerhold (MHJG) in Ingeniero Jacobacci and others at the Museo Argentino de Ciencias Naturales (MACN) in Buenos Aires, Argentina, among them the first record of Hadrosauridae for the Southern Hemisphere (Casamiquela, 1964). Despite the large number of isolated dinosaur remains hosted in MHJG, few of them have been studied so far (Casamiquela, 1964; Powell, 1987; Cruzado-Caballero, 2015, 2017; Zurriaguz *et al*., 2017; Cruzado-Caballero *et al*., 2018). The sole named dinosaur from the herpetological collection of the MHJG is the titanosaurid sauropod *Aeolosaurus rionegrinus* Powell 1987, collected by R. Casamiquela at the Bajo Colorado site, from outcrops of the Angostura Colorada Formation (Salgado, 2022). On the other hand, numerous hadrosaurid remains have been identified at the family level (Coria, 2009; Cruzado-Caballero, 2017 and references therein). Theropod dinosaur remains were never reported in either Angostura Colorada Formation or in the overlying Coli Toro Formation until recently (Paulina-Carabajal *et al*., 2024).

As mentioned, the dinosaur research in the Ing. Jacobacci area started with R. Casamiquela (particularly during the 1940s-1960s, and later until his death). José Bonaparte (MACN) also led expeditions in the late 80s in the same sites where R. Casamiquela made his findings but with no good results in terms of the recording of better-preserved specimens (Bonaparte & Migale, 2015). In 2015, a team led by two of the authors of this manuscript (APC and AHM) renovated the search for dinosaurs in outcrops of the Angostura Colorada and Coli Toro formations. The research was at an impasse due to the pandemic in 2020-2021 and was resumed in 2023 after acquiring new Government permits to work. However, no significant findings were made until

2024 and 2025 (Becerra *et al.*, 2024; Paulina-Carabajal *et al.*, 2024; Pérez-Moreno *et al.*, 2025).

As part of a larger project, our team members were dedicated to reviewing and digitalizing the dinosaur collection of the MHJG. During this process, we identified unpublished theropod material collected by R. Casamiquela in 1956. The fossils correspond to three cranial fragments of an abelisaurid theropod, grouped with other elements under the collection number MHJG 189 Pa.1-14. All these fossils were collected in Estancia Yuquiche (García brothers farm), Southwest of Ingeniero Jacobacci. Unfortunately, there is no other information in the museum's historical records regarding which of the two outcropping geological units held the fossils. In this regard, Volkheimer (1973: 20) made the following reference supporting the possible Angostura Colorada Formation provenance of these elements "*En el área de la Estancia Yuquiche aflora la parte superior de la Formación Angostura Colorada, rica en restos de dinosaurios (actualmente en estudio por R. Casamiquela)*"/ "In the area of the Yuquiche ranch, the upper part of the Angostura Colorada Formation emerges, rich in dinosaur remains (currently under study by R. Casamiquela)."

More recently, a prospection made by our team at the Estancia Yuquinche site (Fig. 1) produced the record of a second abelisaurid specimen, an isolated tooth. This specimen was undoubtedly collected from sediments of the Coli Toro Formation. Despite their fragmentary nature, these abelisaurid remains represent the first evidence of theropod dinosaurs for the Ingeniero Jacobacci area and for both Angostura Colorada and Coli Toro formations.

(INSERT FIGURE 1 HERE)

Institutional Abbreviations. FMNH, Field Museum of Natural History, Chicago, USA; **MACN**, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; **MAU**, Museo Municipal Argentino Urquiza, Rincón de los Sauces, Argentina. **MCA**; Museo Provincial Carlos Ameghino, Cipolleti, Argentina; **MHJG**, Museo Histórico Jorge Gerlhold (**Pa**, Paleontology, Casamiquela Collection. **NCP**, new paleontological collection), Ingeniero Jacobacci, Rio Negro, Argentina; **MPVN-PV**, Museo Patagónico de Ciencias Naturales "Juan Carlos Salgado", General Roca, Argentina

MATERIALS AND METHODS

Specimen MHJG-NCP 298

The abelisaurid from the Angostura Colorada Formation was collected in 1956 near Cerro Yuquiche and belongs to a cluster of several dinosaur bones under the number MHJG -189 Pa.1-14, registered as "diverse fossil remains" by Casamiquela himself. These fossils correspond mostly to hadrosaurid dinosaur caudal vertebrae. The identification card for the collection number MHJG 189 Pa indicates 14 bones for the cluster, but specimens 189 Pa 3, 8, 11, 12, and 13 are currently missing. The abelisaurid cranial elements are an incomplete basicranium (without collection number), an incomplete right postorbital (without collection number), and a fragment of lacrimal (identified with a partial collection number: "189 Pa…"). There is insufficient information to associate the lacrimal, basicranium, and postorbital with any of the missing specimens (*i.e.*, 189 Pa 3, 8,11-13). Here, we proposed a new nomination to identify the three bones under a single theropod specimen: MHJG-NCP 298, with parts "a" (basicranium), "b" (postorbital), and "c" (lacrimal).

Comparisons were made with other published abelisaurid braincases: *Abelisaurus comahuensis* (Paulina-Carabajal, 2011a), *Arcovenator escotae* (Tortosa *et* *al.*, 2014), *Aucasaurus garridoi* (Coria *et al.*, 2002; Paulina-Carabajal, 2011a), *Carnotaurus sastrei* (Bonaparte, 1985; Paulina-Carabajal 2011b), *Guemesia ochoai* (Agnolín *et al.*, 2022), *Llukalkan aliocranianus* (Gianechini *et al.*, 2021), *Majungasaurus crenatissimus* (Sampson & Witmer, 2007), *Niebla antiqua* (Aranciaga Rolando *et al.*, 2021), *Spectrovenator ragei* (Zaher *et al.*, 2020), V*iavenator exxoni* (Filippi *et al.*, 2016; Paulina-Carabajal & Filippi, 2018), and the abelisaurid MAU-Pv-LI-582 (Méndez *et al.*, 2022). 3D models used for comparisons included *Majungasaurus* (FMNH PR 2100) lacrimal and postorbital, available at www.morphosource.org.

The specimens were photographed using a Nikon D3000 camera, and the figures were created using Adobe Photoshop (PS 2020). One of the authors (KUG) used the photos to create PDF 3D models of MHJG-NCP 298a-c with the photogrammetry software Agisoft PhotoScan (Supp. Inf. 1).

Specimen MHJG-NCP 299

The abelisaurid isolated tooth was collected in 2025 from the Coli Toro Formation outcrops at the Estancia Yuquiche, a few kilometers north of Cerro Yuquiche. The collection GPS data is S 41° 27´ 38.9´´ W 69° 43´ 55.5´´. We followed the terminology proposed by Hendrickx *et al.* (2015) for the anatomical description and measurements of the tooth.

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen 1842

Saurischia Seeley 1887

Theropoda Marsh 1881

Abelisauridae Bonaparte and Novas 1985

Specimen MHJG-NCP 298

Abelisauridae indet (Figs. 2,3)

Specimen MHJG-NCP 299

Abelisauroidea indet

(Fig. 4.1-3)

Locality and Horizon. The specimens described here were collected at the Estancia Yuquiche, located 30 km southwest of Ingeniero Jacobacci (Fig. 1). In this area, the largest outcrops correspond to the upper section of the Angostura Colorada, which is overlaid by smaller outcrops of the Coli Toro Formation (Volkheimer, 1973).

The Angostura Colorada Formation (Campanian-Maastrichtian) is integrated by a succession of facies of continental sandstones, pelites, and conglomerates, arranged according to a decreasing stratum and grain arrangement (Volkheimer, 1973; Manassero & Maggi, 1995). This unit rarely exceeds the 100 m of red to yellow sandstones and clays “bearing dinosaurs strata” extended north and southwest of Ingeniero Jacobacci (Casamiquela, 1969). This geological unit extends in Rio Negro Province from Pilcaniyeu Viejo to Carri Laufquen lagoon at the Somun Cura, and was first recognized by Volkheimer (1973) as represented by rocks outcropping at south of Ingeniro Jacobacci. Posteriorly, outcrops of other localities (*e.g.*, Pilcaniyeu Viejo, Comallo) were included under the same formation (Manassero & Maggi 1995). During the upper Cretaceous the Somun Cura divided two depocenters of continental sedimentation, the basins of Nequen Group towards the north and the Chubut Group towards the south. The Angostura Colorada Formation correlates with the late units of both groups, being the microfossil associations important in determining a Campanian age for this unit (Page *et al.*, 1999, and references therein). Besides the microfossils, the scarcity of plant and animal materials with determinative features recovered so far from the Angostura Colorada Formation prevented more accurate correlates. Hence the importance of continuing to conduct paleontological studies in the area that allow us to better understand the evolutionary history of dinosaur fauna at the end of the Cretaceous.

The Coli Toro Formation (Maastrichtian-Danian) represents the change from a Cretaceous marginal environment to a Danian marine sedimentary environment (Casamiquela, 1964; Bertels, 1969). This formation was named by Bertels (1969) based on marine Maastrichtian deposits northeast of Ingeniero Jacobacci. It correlates with the Allen Formation (continental) and Jagüel Formation (marine), and has been also considered as the inferior member of the Los Alamitos Formation (Coira, 1979). From the Cerro Yeso locality, separated by few km from Estancia Yuquiche, isolated hadrosaurid caudal vertebrae and several other marines and continental cretaceous reptile teeth were recovered in the past by R. Casamiquela, including several plesiosaurid teeth (*Sulcusuchus* Gasparini & Spalletti 1990; O'Gorman, 2015). In the collections, we found one titanosaurid sauropod tooth (MHJG-NCP 300; formerly identified as 5/4/7-3), and one crocodyliform (peirosaurid ?; MHJG Pa 614 106) tooth. Also, lungfish dental plates (*Metaceratodus*?), fish vertebrae and ganoid scales, and turtle plates are commonly found in these sediments (*e.g.*, Gasparini & Spalleti, 1990; Casamiquela, 1992; Pascual & Bondesio, 1976; Apesteguía *et al.*, 2007). The present work adds the first record of a theropod dinosaur (Abelisauridae) to the faunal association of the Coli Toro Formation.

DESCRIPTION

Specimen MHJG-NCP 298.a-c (basicranium, postorbital and lacrimal)

The basicranium (MHJG-NCP 298a; Fig. 2) preserves a partial basioccipital (missing the neck and body of the occipital condyle) and a partial basisphenoid (missing the basipterygoid processes and the surface bone of the floor of the endocranial cavity). The parabasisphenoid is not preserved either, and the anterior fracture exhibits the partial posterior wall of the pneumatic subsellar recess. The preserved basicranium is 58 mm long (incomplete), 69.3 mm maximum wide (complete), and 60 mm tall (incomplete, preserved below the neck of the occipital condyle level). Unfortunately, this specimen has no preserved foramina or grooves associated with cranial nerves or blood vessels.

(INSERT FIGURE 2 HERE)

Basioccipital. The basioccipital is fused to the basisphenoid. The contact between these two bones is evident on the ventral surface of the basicranium, showing that the basisphenoid forms most of the basal tubera, with the basioccipital participating only posteriorly (Fig. 2.3).

The fused basal tubera project ventrally below the occipital condyle, forming a subquadrangular plate in posterior view, as in other abelisaurids. This plate is vertical, and the basituberal web -joining both tubera distally-bears a slight notch mediodistally, indicating a separation between the right and left basal tuber. The low curvature of this notch is similar to that in *Abelisaurus, Carnotaurus*, *Llukalkan* and *Spectrovenator* (in *Arcovenator* and *Majungasaurus* the distal end of the fused basal tubera is flat). In contrast, *Niebla, Viavenator* and the abelisaurid MAU-Pv-LI-582 (Méndez *et al.*, 2022) exhibit well-defined and markedly pronounced notches. Above the notch, there is a median vertical ridge of bone that is more prominent distally where it splits in an inverted V-shape that disappears dorsally, reminding the condition in *Llukalkan*, but unlike other abelisaurids where the ridge is absent (*e.g.*, *Carnotaurus*) or runs along the complete height of the plate almost reaching the neck of the occipital condyle (*e.g.*, *Niebla*, *Abelisaurus*, *Viavenator*). Laterally, symmetrical vertical fractures indicate the basioccipital contact with the ventral rami of each opisthotic. If preserved, the ventral ramus of the opisthotic forming the crista tuberalis would have been attached to the basioccipital, extending ventrally and reaching the distal end of the basal tuber on each side. This feature is typical of the abelisaurid braincase (Paulina-Carabajal, 2009, 2011a, 2011b). The symmetrical absence of both opisthotics indicates that these elements were fragile crests, probably not completely fused to the basioccipital. In *Carnotaurus* and *Viavenator,* the basioccipital-opisthotic contact is not evident, indicating a complete fusion of bones. In other taxa, this contact is clearer (*e.g.*, *Abelisaurus*, *Niebla*, *Llukalkan* (Fig. 5.1,5.2). This lack of fusion seems unrelated to body size, being observed in both large and small abelisaurid specimens.

As mentioned, the neck and occipital condyle are missing. At the base of the neck of the occipital condyle, the dorsal fractures show the osteological correlates of the ventral side of paired elongated pneumatic sinuses that invaded the body of the basisphenoid and part of the basioccipital. These anteroposteriorly elongated pneumatic cavities are separated by a median longitudinal septum and correspond to the internal extent of the lateral tympanic recesses (Fig. 2.6).

Basisphenoid. The main body of the basisphenoid is preserved, missing the dorsal and anteriormost surfaces, including most of both basipterygoid processes and the area where the internal carotid foramen and the preotic pendant would have been (Fig. 2). The basisphenoid forms most of the basal tubera, the basipterygoid processes and the basipterygoid web (transversely joining the base of both basipterygoid processes). As mentioned, the dorsal surface of the basisphenoid (floor of the endocranial cavity) is eroded, exhibiting the ventral walls of the lateral tympanic recesses. The ventral margin of the external opening of the lateral tympanic recess is preserved on the lateral sides of the basisphenoid (Fig. 2.2, 2.6). The basipterygoid processes are missing, being sectioned at their bases. This section is markedly oval, indicating a probable blade-like morphology for the structure. The basipterygoid web -joining both processes- is a wide and low transverse ridge separating the basisphenoid recess posteriorly and the subsellar recess anteriorly (Fig. 2.3). The posterior wall of the subsellar recess is preserved, indicating a good development of this pneumatic cavity (Fig. 2.4).

The external opening of the basisphenoid recess is triangular. This pneumatic recess deeply excavates the body of the basisphenoid ventrally, as in other abelisaurids (*e.g.*, Sampson & Witmer 2007; Paulina-Carabajal 2011a,b, 2015). Internally, there are two small oval pneumatic foramina (Fig. 2.3). These two foramina do not contact dorsally with the paired pneumatic recesses on the neck of the condyle (lateral tympanic recesses).

(INSERT FIGURE 3 HERE)

Postorbital. A partial right postorbital is preserved, missing the posterior branch and the distal portion of the ventral shaft (Fig. 3.1-5). The dorsal and lateral surfaces are highly ornamented. The ornamentation on the dorsal surface is well-defined, and it comprises low ridges, narrow grooves, and circular to oval pits (Fig. 3.2). Unlikely, *Abelisaurus* and *Aucasaurus* exhibit skull roof ornamentation predominantly formed by protuberances, grooves, and valleys.

The preserved fragment of the postorbital is 62 mm long anteroposteriorly and 50 mm lateromedially, whereas the preserved ventral shaft is 42 mm long and 23 mm in section. The shaft section is markedly triangular due to a median vertical crest. The anterolateral contact surface with the lacrimal and the frontal consists of two striated vertical facets (Fig. 3.5). On the medial side, the vertical crest is well-defined, separating anterior and posterior faces (Fig. 3.3). The posteromedial side bears an oval surface of contact for the laterosphenoid. The general morphology of the postorbital is similar to that observed in other abelisaurids (Sampson & Witmer, 2007; Filippi *et al.*, 2016, 2018).

In lateral view, the dorsal margin of this fragment of the postorbital is straight, as in *Arcovenator*, *Llukalkan,* and MAU-Pv-LI-582. However, this straight shape differs from the convex border observed in *Skorpiovenator* and *Viavenator*, or the sigmoid edge present in *Aucasaurus*, *Abelisaurus,* and *Majungasaurus* (Sampson & Witmer, 2007; Novas *et al.*, 2013; Filippi *et al.*, 2016, Gianechini *et al.*, 2021). The postorbital does not have a thickened dorsal margin like that in *Abelisaurus*, *Arcovenator*, *Ekrixinatosaurus*, *Ilokelesia*, and *Skorpioventor*.

Lacrimal. The left lacrimal (MHJG-NCP 298c) preserves the posterior process, missing the anterior process and most of the ventral ramus (Fig. 3.6-9). The posterior process measures 58 mm anteroposteriorly and 48.5 mm lateromedially. This bone exhibits a sculptured external surface, a convex smooth medial surface (orbital), and a large striated surface of contact with the postorbital posteriorly. The fractures in two main regions exposed pneumatic cavities within this bone anteriorly, consisting of at least two cavities, with the largest one subdivided into smaller recesses. This morphology is consistent with the pneumaticity described in other theropod lacrimal bones (*e.g.*, Gold *et al.*, 2013). In particular, within the Abelisauridae, the presence of pneumatic foramina in the lacrimal bone is well documented in Majungasaurus (Sampson & Witmer, 2007) and Carnotaurus (Cerroni et al., 2020). However, the fragmentary nature of MHJG-NCP 298c prevents us from determining the spatial arrangement and morphology of the internal sinuses, thus hindering a comparison with these two taxa.

The dorsal margin of the posterior process is almost flat in lateral view, unlike the margin with protuberances observed in *Abelisaurus*, *Carnotaurus,* and *Majungasaurus*. In this aspect, the lacrimal MHJG-NCP 298 is more similar to that in *Llukalkan*. However, the latter taxon has a posterior process triangular in dorsal view (Gianechini *et al.*, 2021, fig.7D), whereas the process is quadrangular in MHJG-NCP 298, with parallel lateral and medial margins.

The lacrimal ornamentation is similar to that in the right postorbital but deeper, denser, and with more pits. The pits are also larger, and a low ridge separates two regions of the ornamented surface (Fig. 6.7).

Specimen MHJG-NCP 299 (isolated tooth)

The isolated tooth corresponds to a ziphodont tooth, 20 mm long, which is missing the root and part of the enamel in one of the lateral faces (Fig. 4.1-3). In labial/lingual views, the crown has a straight distal margin and a convex mesial margin, which are features of the abelisaurid clade (Hendrickx *et al*., 2015). The tooth is labiolingually compressed with an interpreted crown-to-base ratio (CBR= CBW/CBL) of 0.5 (meaning the labiolingual width is approximately 50% of mesiodistal length). The CBR of this specimen would have lied within the range calculated for other abelisaurids (circa 0.5) (Hendrickx *et al.*, 2015). CBL= 11 mm CBW= 5.5 mm (approx.).

The serrated distal carina is straight and centrally positioned on the crown. In contrast, the serrated mesial carina is straight apically but curves (lingually?) towards the root. Denticles on the distal carina are subrectangular and become smaller apically. They are proximo-distally longer than the mesial denticles and are apically projected. Denticles on the mesial carina are equally longer than wider (quadrangular), hooked, and strongly apically recurved. The interdenticular spaces are narrow, and denticle density is approximately the same in both carinae. The number of denticles per 5 mm at the mid-crown is 11.5 in the distal carina and 10.5 in the medial carina.

(INSERT FIGURE 4 HERE)

COMPARISONS

Abelisauroids are the best-represented theropods in Patagonia (Novas *et al*., 2013). However, the diversity of the group is far from being well-known (*e.g.*, Gianechini *et al*., 2015; Cerroni *et al.*, 2020). Although highly fragmentary, the preserved skull elements of MHJG-NCP 298 and MHJG-NCP 299 bear morphological features of Cretaceous abelisaurids, which allowed the identification of the specimens at a family level. These features include a robust basicranium with fused basal tubera forming a quadrangular vertical plate; the presence of large basisphenoid, subsellar, and lateral tympanic recesses; and a lateromedially compressed basipterygoid process (Paulina-Carabajal, 2011a, 2011b). Grooves, pits, and some protuberances highly sculpt the postorbital and the lacrimal, all features considered a synapomorphy of Abelisauridae (Canale *et al.*, 2009). The sutural surface of contact between postorbital and lacrimal suggests that the frontal was excluded from the orbital rim, another feature considered a synapomorphy of the clade (Carrano & Sampson, 2008).

Abelisaurid tooth traits defined by Hendrickx *et al.* (2015) and shared by this specimen include an almost straight distal profile of the tooth, transversal and short marginal undulations on the crown, denticles with strongly developed interdenticular sulci, distal denticles with an apex pointing towards the tip, a DSDI (denticle size density index) close to one, an irregular enamel texture, and the presence of apically pointed denticles on the distal carina.

Comparisons with other Patagonian Cretaceous abelisaurid basicrania

The general configuration of the basicranium MHJG-NCP 298 is highly reminiscent of that in *Llukalkan* (Fig. 5.7,5.8). However, the basal tuber has a rounded distal end in MHJG-NCP 298, whereas the same margin is flat in *Llukalkan* (in ventral view). Also, *Llukalkan* has a triangular external opening of the basisphenoid recess, but in MHJG-NCP 298, it is markedly narrower and bears a median constriction that gives it a distinct keyhole shape. Although the morphological differences between these two abelisaurids seem minor, there are some important aspects to consider: 1) both specimens come from different formations and ages. *Llukalkan* comes from the Bajo de la Carpa Formation, being Santonian in age, whereas the new specimen is Campanian-Maastrichtian. 2) The basicranial structures tend to be conservative among clades. Although recent research has shown that the braincase is not as conservative as previously thought (*e.g.*, Rauhut, 2007; Paulina-Carabajal, 2009; Bullar *et al*., 2019), dinosaur braincases are, in general, conservative structures compared to other regions of the skull (Currie, 1995). The basicranium is, in turn, the most conservative region of the braincase, which is why non-closely related dinosaur taxa may share basicranial morphology (*e.g.*, Paulina-Carabajal, 2015). Furthermore, the only abelisaurids from Rio Negro Province with preserved braincases are *Abelisaurus comahuensis* (Fig. 5. 1) and *Niebla antiqua* (Fig. 5.2,5.3), both taxa recovered from the Allen Formation (Bonaparte & Novas, 1985; Aranciaga Rolando *et al.*, 2021). The new specimen exhibits morphological variation with them, including a unique trait (the shape and reduction of the external opening of the basisphenoid recess, with the presence of a median constriction) suggesting the presence of a different taxon for the Angostura Colorada Formation at the end of the Cretaceous.

(INSERT FIGURE 5 HERE)

Ornamentation. Generally, the abelisaurid skull roof and craniofacial bones are characterized by marked ornamentations, even presenting ornaments such as crests and horns (Novas *et al*., 2013). The reduction of ornamentation is observed in early abelisaurids, such as *Eoabelisaurus* (Pol & Rauhut, 2012), *Spectrovenator* (Zaher *et al.*, 2020), and small upper Cretaceous taxa, such as *Guemesia* (Agnolín *et al.*, 2022) and indeterminate small abelisaurids from North Patagonia (Paulina-Carabajal *et al*., 2023).

As mentioned above, similar aged (Campanian-Maastrichtian) patagonian abelisaurids preserving the braincase are *Abelisaurus comahuensis, Niebla antiqua* and *Aucasaurus garridoi*. All these taxa, together with other abelisaurid specimens (*e.g.*, isolated maxilla, Gianechini *et al*., 2015), share sculptured bones characterized by well-developed grooves and valleys, similar to those present in the lacrimal and postorbital of MHJG-NCP 298.

Pneumaticity. The presence of large pneumatic cavities in the abelisaurid basicrania was first commented by Paulina-Carabajal (2009, 2011a) regarding the “apneumatic” state scored for the abelisaurid braincase in the phylogenetic analyses carried out at that time. The abelisaurid basicranium is affected by the lateral tympanic recess, basisphenoid recess, subsellar recess, and, in some cases, well-defined paracondylar recess (*e.g.*, *Arcovenator*). The basisphenoid and lateral tympanic recesses are the most expanded cavities within the body of the basisphenoid.

The specimen MHJG-NCP 298 preserves the basisphenoid recess, the posterior wall of the subsellar recess, and evidence of the posterodorsal paired expansions of the lateral tympanic recess on each side. The surface of the floor of the endocranial cavity is eroded, exhibiting dorsally the parallel cavities that affect the neck of the occipital condyle. The latter features are visible externally and through fractures, as in *Ilokelesia* (Paulina-Carabajal 2011a). In other cretaceous abelisaurids such as *Aucasaurus*, *Carnotaurus*, *Guemesia*, *Llukalkan*, *Majungasaurus*, *Niebla*, and *Viavenator*, the basicranial pneumaticity was identified using CT scans (Sampson & Witmer, 2007; Paulina-Carabajal 2011a, Paulina-Carabajal & Filippi, 2018; Paulina-Carabajal & Cerroni, 2019; Aranciaga Rolando *et al*., 2021; Gianechini *et al*., 2021; Agnolín *et al*., 2022; Méndez *et al*., 2022). In the specimen MHJG-NCP 298 the median ridge below the occipital condyle is markedly low, and the paracondylar recesses are poorly defined but evident laterally to the neck of the occipital condyle (Fig. 5).

CONCLUSIONS

Rodolfo Casamiquela found theropod remains in outcrops of the Angostura Colorada Formation, near Ingeniero Jacobacci, as long as the early 1950s. Still, the fossils remained unidentified until 2024 (Paulina-Carabajal *et al*., 2024, present work). These cranial remains are the first evidence of theropod dinosaurs for the Angostura Colorada Formations in North Patagonia and represent the first theropod for the herpetological collections of the MHJG. A second specimen was collected in 2025 from outcrops of the Coli Toro Formation, at the same locality where the first abelisaurid came from. The specimens under study are abelisaurids, based on features of the basicranium, ornamented lacrimal and postorbital, and serrated teeth. The fragmentary nature of the remains prevents further assignation below the Family level.

Some features of the basicranium, such as the shape of the basisphenoid recess, are not shared with other known abelisaurid braincases. This suggests the presence of an unknown mid-to-large-sized abelisaurid taxon in the Angostura Colorada Formation that roamed the region, probably among the top predators in a faunal association dominated by hadrosaurid ornithopods and titanosaurid sauropods. This faunal association coincides with those recorded in correlatable formations of Patagonia, such as the Allen Formation, Los Alamitos Formation, and La Colonia Formation.

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Figure legends

Figure 1. Location map of Argentina. Detail of Ingeniero Jacobacci area (Rio Negro province, Argentina). The star indicates the Estancia Yuquiche locality.

Figure 2. Abelisaurid basicranium (**MHJG-NCP 298a)** in **1**, posterior; **2**, left lateral: **3**, ventral; **4**, anterior and **6**, dorsal views. **5**, diagram of a complete abelisaurid braincase in left lateral view showing in grey the preserved basicranium. Abbreviations: **bsr**, basisphenoidal recess; **bt**, basal tuber; **btp**, basipterygoid process (sectioned base); **btw**, basituberal web; **fecc**, floor of endocranial cavity (eroded); **ltr-eo**, lateral tympanic recess (external opening margin); **ltr**, lateral tympanic recess (internal cavity); **ocn**, occipital condyle neck (base); **p.fo**, pneumatic foramen; **ri**, vertical ridge or crest; **sc-ct**, sutural contact with the crista tuberalis; **ssr**, subsellar recess. Scale bar equals 50 mm.

Figure 3. **1-5**, Abelisaurid right postorbital (**MHJG-NCP 298b**) in **2**, lateral; **3**, posterior; **4**, ventral and **5**, medial views. **6-9**, Abelisaurid left lacrimal (**MHJG-NCP 298c**) in **7**, lateral; **8**, posterior and **9**, ventromedial views. **1** and **6**, diagrams showing the preserved area of the postorbital and lacrimal, respectively. Abbreviations: **orb**, orbit; **orn**, ornamentation; **pn.fo**, pneumatic foramen; **sut.lac-f**, sutural contact with the lacrimal and frontal; **sut.po**, sutural contact with the postorbital; **ve.rim**, vertical rim or crest. Scale bar equals 10 mm.

Figure 4. Abelisaurid tooth (**MHJG-NCP 299**) in **1**, lingual; **2**, mesial; **3**, labial and 4, distal views. Scale bars equal 10 mm.

Figure 5. Comparative basicranial morphology among abelisaurid taxa. **1**, ***Abelisaurus comahuensis*** (**MC** 11078) in posterior view; **2,3**, ***Niebla antiqua*** (**MPVN-PV**-706) in **2**, posterior; and **3**, ventral views; **4**, ***Carnotaurus sastrei*** (**MACN CH**-894) in posterior view; **5,6**, **MHJG** 189 Pa/a in **5**, posterior and **6** ventral views; **7,8**, ***Llukalkan aliocranianus*** (**MAU-Pv-LI**-581) in **7**, posterior; and **8**, ventral views; **9,10**, ***Viavenator exxoni*** (**MAU-Pv-LI**-530) in **9**, posterior; and **10**, ventral views. Abbreviations: **bsr**, basisphenoid recess; **bt**, basal tuber; **btp**, basiptergyoid process; **ct**, crista tuberalis; **cul**, cultriform process; **oc**, occipital condyle; ri, vertical rim or crest below the occipital condyle, **ssr**, subsellar recess. Arrows indicate the contact of the ventral ramus of the opisthotic (crista tuberalis) with the basioccipital. Not to scale.

Suppl. Inf. 1. A 3D model generated using photogrammetry of the specimen MHJG-NCP 298a. Abelisaurid basicranium. Available at The Internet Archive. Link:

Suppl. Inf. 2. A 3D model generated using photogrammetry of the specimen MHJG-NCP 298b. Abelisaurid postorbital (fragment). Available at The Internet Archive. Link:

Suppl. Inf. 3. A 3D model generated using photogrammetry of the specimen MHJG-NCP 298c. Abelisaurid lacrimal (fragment). Available at The Internet Archive. Link:


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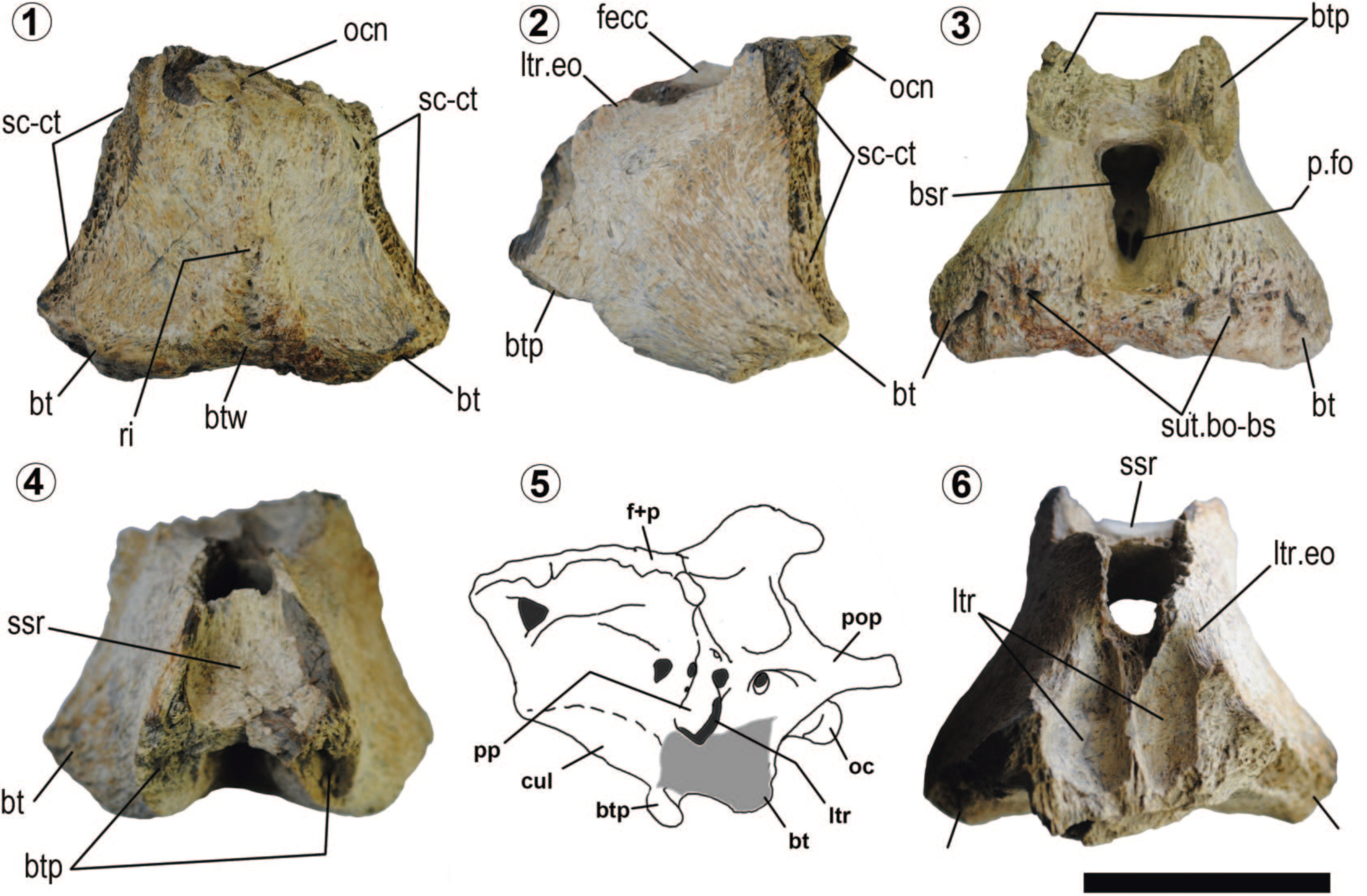
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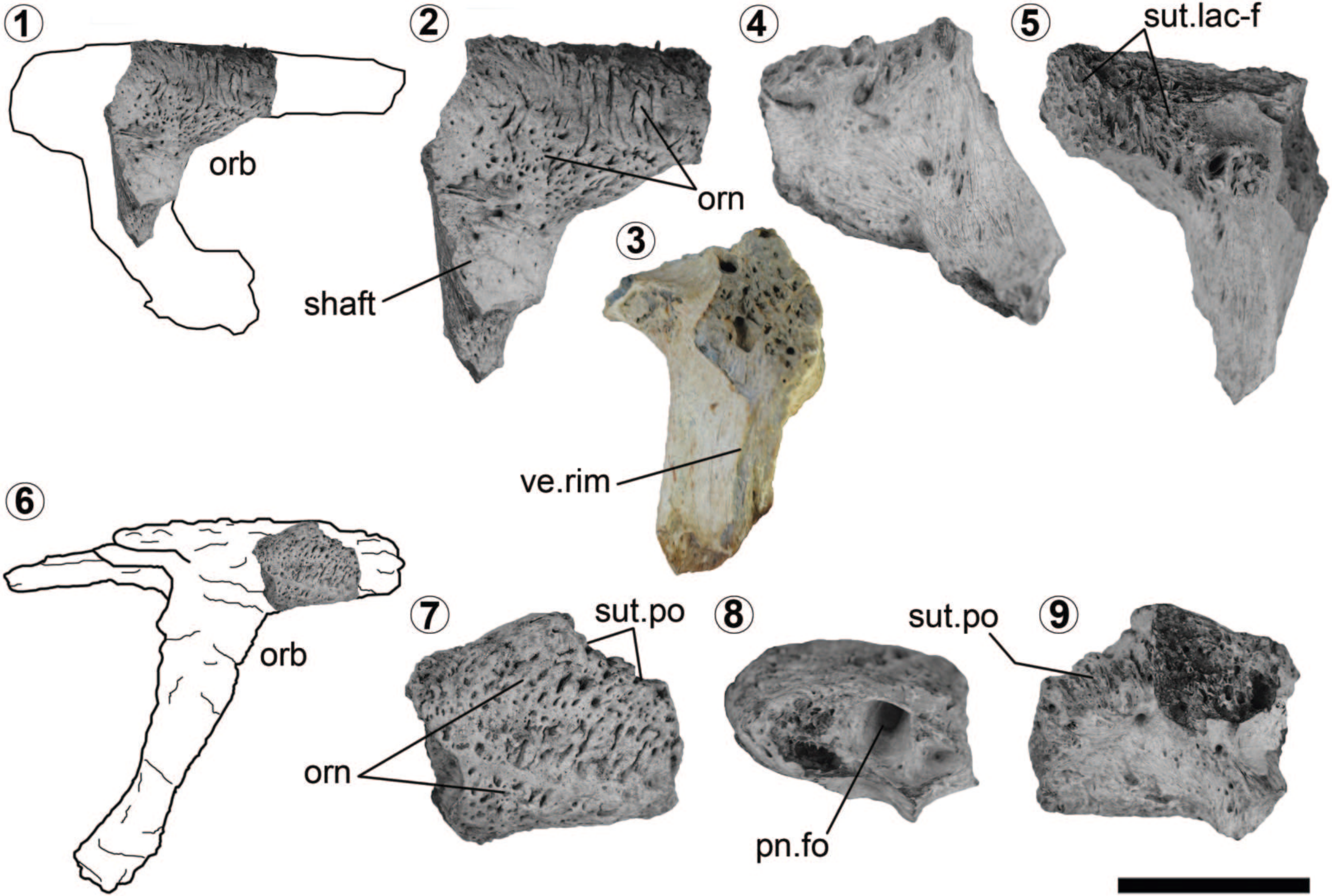
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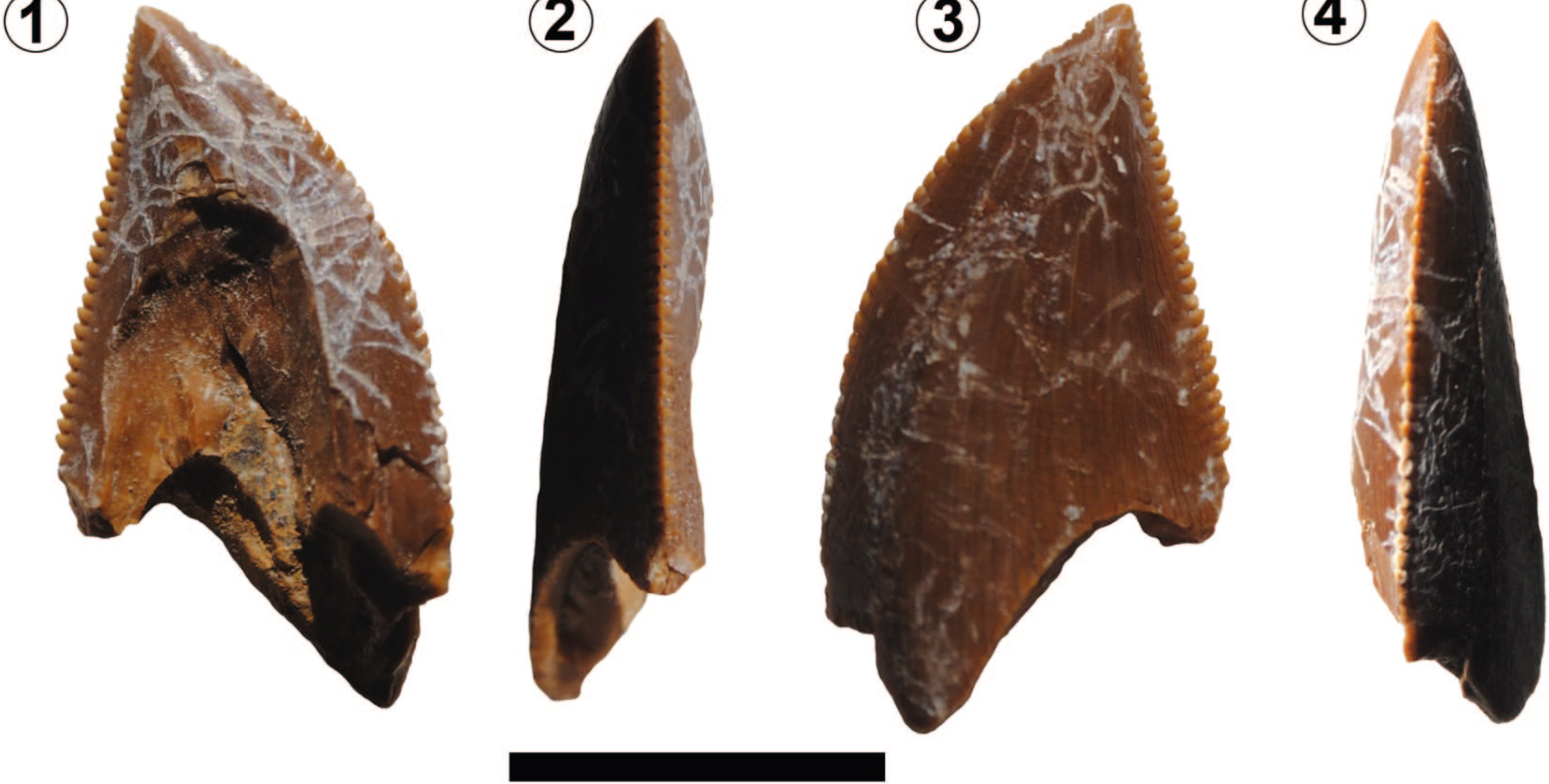
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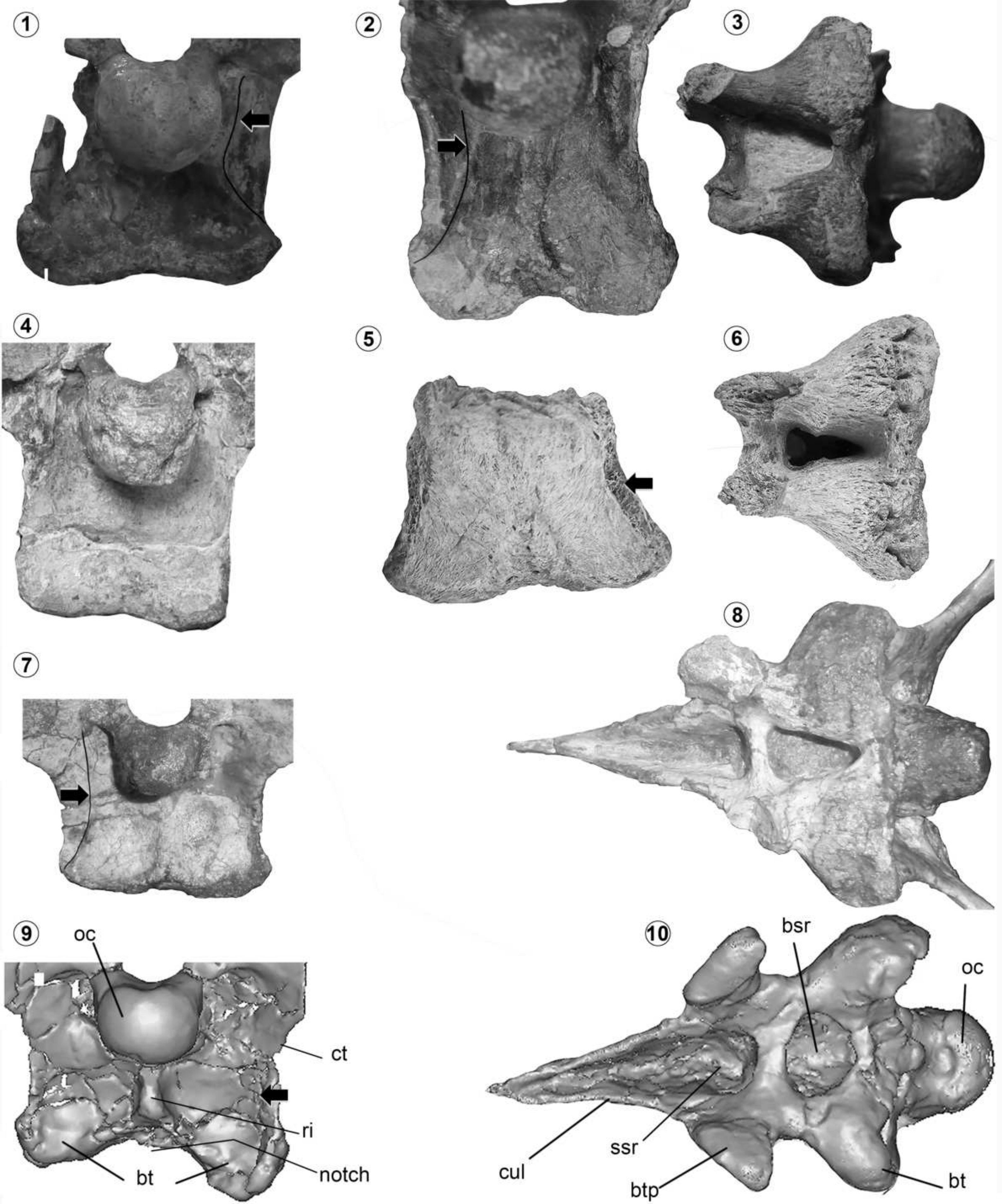
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