

FIRST RECORD OF AN ABELISAURID (DINOSAURIA, THEROPODA) NATURAL ENDOCAST, AND COMMENTS ON SKULL ROOF ORNAMENTATION

ARIANA PAULINA-CARABAJAL^{1,*}, KAREN ULLOA-GUAIQUÍN¹, LEONARDO S. FILIPPI²,
ARIEL H. MÉNDEZ³, and YUONG-NAM LEE⁴

¹Instituto de Investigaciones en Biodiversidad y Medioambiente (CONICET-Universidad Nacional del Comahue), S. C. de Bariloche (8400), Argentina, a.paulinacarabajal@conicet.gov.ar; ulloaka@comahue-conicet.gob.ar;

²CONICET-Museo Municipal “Argentino Urquiza”, Chos Malal 1277, 8319, Rincón de los Sauces, Neuquén, Argentina, lsfilippi@gmail.com;

³Instituto Patagónico de Geología y Paleontología (CCT CONICET-CENPAT), Bv. Brown 2915, 9120, Puerto Madryn, Chubut, Argentina, amendez@cenpat-conicet.gob.ar;

⁴School of Earth and Environmental Sciences, Seoul National University, Seoul 08826, South Korea

ABSTRACT We present here a natural cranial endocast assigned to an abelisaurid theropod found in Cretaceous rocks of the outcropping Bajo de la Carpa Formation (Santonian) in Neuquén Province, Northern Patagonia, Argentina. The specimen was found in association with fragmentary braincase remains, which include an otic capsule and part of the skull roof. These fragments bear abelisaurid features that support the taxonomic assignment. The general shape of the endocast is similar to that in other abelisaurids, being anteroposteriorly elongated with long and robust olfactory tract and olfactory bulbs, rounded cerebral hemispheres, and pronounced and triangular dural peak. It is the second natural endocast described for a dinosaur in Argentina and the first for a theropod. The comparison with other Patagonian abelisaurids indicates the endocast belonged to a small to mid-sized specimen that highly resembles that of *Viavenator* and *Llukalkan*. However, the skull roof ornamentation is markedly different, and comments are made on certain features of the ornamentation of the frontal in the new specimen and other close relatives.

KEYWORDS Paleoneurology, Abelisauridae, Argentina

INTRODUCTION

Natural cranial endocasts (*Steinkern*) are rare in the fossil record of vertebrates in general but are even rarer for terrestrial taxa, especially for reptiles (e.g., Hopson, 1979; Jerison, 2009; Dozo et al., 2023 and references therein). This particular kind of endocast corresponds to physical casts of the endocranial cavity (the space occupied in life by the brain and related soft tissues), which were formed naturally during the taphonomic process. Isolated natural endocasts result when the sediment filling the endocranial cavity is lithified, becoming hard enough to survive the erosion of the surrounding skull bones. However, in the face of the systematic and widespread absence of natural endocasts, paleoneurologists have been constructing physical endocasts for well over a century (e.g., *Stegosaurus*, Marsh 1880; *Iguanodon*, Andrews 1897; *Tyrannosaurus*, Osborn 1912).

These early endocasts were initially cast using plaster first, and later took advantage of latex and silicone as casting materials. It was Othniel C. Marsh, a pioneer worker in dinosaur paleoneurology, who studied around a dozen of dinosaur cranial endocasts, including sauropods, theropods, and ornithischians from North America (e.g., Marsh, 1881, 1884a,b, 1890, 1894, 1896). Nowadays, digital techniques, such as computed tomography, allow paleontologists to construct digital 3D models that, in turn, can be made into physical objects using 3D printing--regardless of whether or not the endocranial cavity is filled with sediment.

Today, the neuroanatomy of more than 150 dinosaur taxa have been studied using both natural and artificial (physical or digital) endocasts (see an actualized list of studied dinosaur endocasts in Paulina-Carabajal et al., 2023; Burch et al., in press). Natural endocasts, however, represent less than 5 percent of the total sample, and thus, paleoneurology

*Corresponding author

studies based on natural endocasts of dinosaurs are remarkably few. These include the ceratopsian *Anchiceratops* (Brown, 1914), two iguanodontids (Serrano Barañas et al., 2006; Brasier et al., 2016), the duckbill *Edmontosaurus* (Jerison, 2009), the partially exposed dorsal cerebrum of the ornithomimid *Leaellynasaura amicagraphica* (Rich and Rich, 1989), an indeterminate dicraeosaurid sauropod (Paulina-Carabajal et al., 2018), and the theropods *Allosaurus* (Rogers, 1998) and *Ceratonykus oculatus* (Alifanov and Barsbold, 2009).

Here, we present the first record of a natural cranial endocast of a representative of the abelisaurid family found in the Cretaceous rocks of North Patagonia, Argentina (Fig. 1). The specimen comes from an area near the city of Rincón de los Sauces, where an elevated number of dinosaur braincase remains have been recovered from the Bajo de la Carpa Formation, and from the underlying sedimentary rocks (i.e., the titanosaurids *Narambuenatitan* and *Pitekunsaurus* from the Anacleto Formation). This “hot spot”, known as Cerro Overo-La Invernada, has provided from Bajo de la Carpa Formation only, braincase remains of four abelisaurids (the complete braincases of *Llukalkan aliocraniumus* (Gianechini et al., 2021), *Viavenator exxoni* (Filippi et al., 201), MAU-Pv-LI-582 (Méndez et al., 2021), the fragmentary fused frontals of MAU-Pv-LE-620, and three titanosaurid sauropods (MAU-Pv-LI-595, MAU-Pv-CO-687 and MAU-Pv-CO-688) (Fig. 2).

The comparison of the new specimen, MAU-Pv-CO-725, with the abelisaurids mentioned above — in particular, the

isolated skull roof MAU-Pv-LE-620 — shed some light on our understanding of the morphological disparity within the clade and the possible presence of an unknown group.

MATERIAL AND METHODS

The specimen MAU-Pv-CO-725 was collected from continental deposits of the Bajo de la Carpa Formation (Santonian, Upper Cretaceous; Garrido 2010), which outcrops at the Cerro Overo locality, 50 km west of the city of Rincón de los Sauces, Neuquén Province, Argentina (Fig. 1). It corresponds to a fragmentary skull roof (preserving a pair of frontals), the right otic capsule (formed by a partial prootic and opisthotic), and a natural cranial endocast that is missing the anterior end of the forebrain and most of the hindbrain mostly at the brainstem region. Thus, the endocast does not preserve most of the cranial nerves (V–XII). The natural endocast is made of very fine clastic material (only single crystals) cemented by calcium carbonate.

The specimen fragments (bone and endocast) exhibit considerable damage produced by erosion, indicating that they have been fractured and exposed, probably for a long time (can be years in a desert climate as in North Patagonia). As a result, the endocast exhibits several small punctuations on its surface produced by friction with surrounding rocks.

Comparisons of this natural endocast were made with the digital endocasts of other studied abelisaurids collected from Argentina, including *Aucasaurus garridoi* (Paulina-Carabajal and Succar, 2015), *Carnotaurus sastrei* (Cerroni and Paulina-

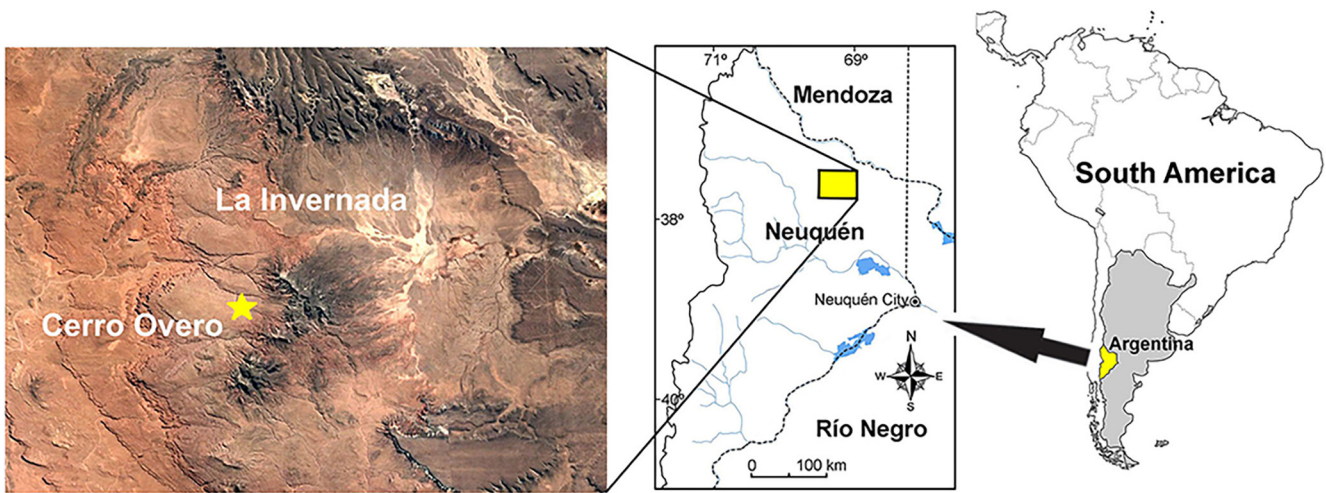


FIGURE 1. Location map. The star indicates the fossil site at the Cerro Overo locality that yielded the specimen MAU-Pv-CO-725. [planned for column]

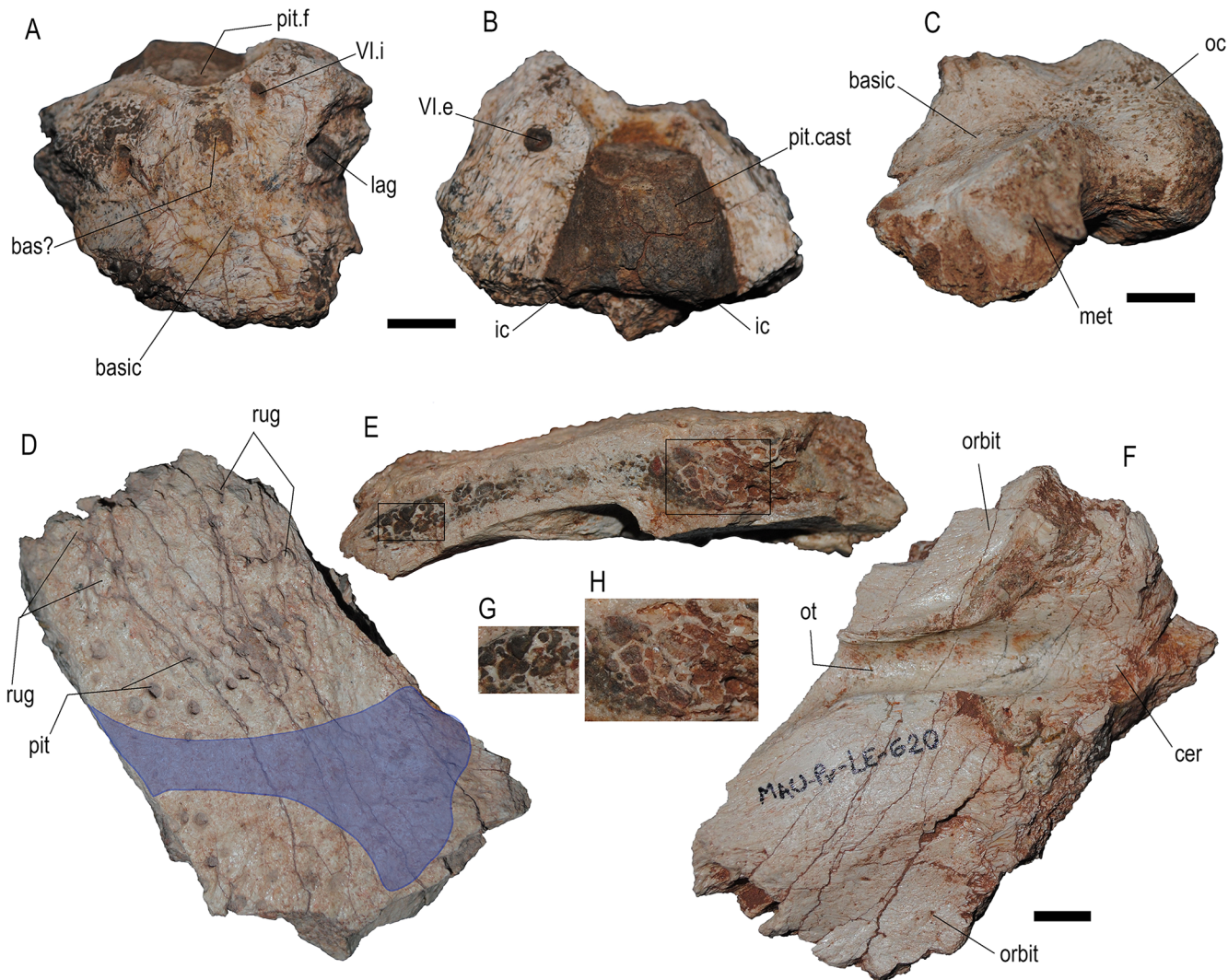


FIGURE 2. Previously unpublished dinosaur braincase remains from Cerro Overo-La Invernada sites (Bajo de la Carpa Formation). These materials include the titanosaurid basicrania MAU-Pv-CO-687 (A, B) and MAU-Pv-CO-688 (C), and the abelisaurid theropod skull roof MAU-Pv-LE-620 (D-F). A and D) dorsal view, B) anterior view, C) left lateroventral view, F) ventral view. E) transverse fracture along the right frontal and details (G, H) of the internal pneumaticity. The impression of the forebrain is on the ventral side of the frontals. To facilitate the orientation of the fragmentary skull roof, a blue shade indicates the forebrain size and position in a dorsal view of the frontals. Abbreviations: **bas?**, basilar artery; **basic**, basicranium (floor of the endocranial cavity); **cer**, osteological correlate of the cerebral hemisphere; **ic**, cerebral branch of the internal carotid artery; **lag**, lagena (section); **met**, metotic passage (for CN IX-XI and jugular vein); **oc**, occipital condyle; **orbit**, orbital part of the frontal; **ot**, osteological correlate of the olfactory tract; **pit**, blind circular pits on dorsal surface of the frontals (ornamentation); **pit.cast**, pituitary cast; **pit.f**, pituitary fossa. **II**, Cranial Nerve II. Scale bar equals 10 mm. [planned for page width]

Carabajal, 2019), *Guemesia ochoai* (Agnolín et al., 2022), *Llukalkan* (Gianechini et al., 2021), *Niebla antiqua* (Aranciaga Rolando et al., 2021), *Viavenator* (Paulina-Carabajal and Filippi, 2018), and an indeterminate abelisaurid MAU-Pv-LI-582 (Méndez et al., 2021), as well as *Majungasaurus crenatissimus* (Sampson and Witmer, 2007) from Madagascar.

The natural specimen was photographed using a Nikon

D3000 camera, and the figures were created using Adobe Photoshop (PS 2020). Photos were used to create a PDF 3D model of the natural endocast using the photogrammetry software Agisoft PhotoScan (see Supplementary information).

Institutional Abbreviations — MAU, Museo Municipal Argentino Urquiza, Rincón de los Sauces, Argentina.

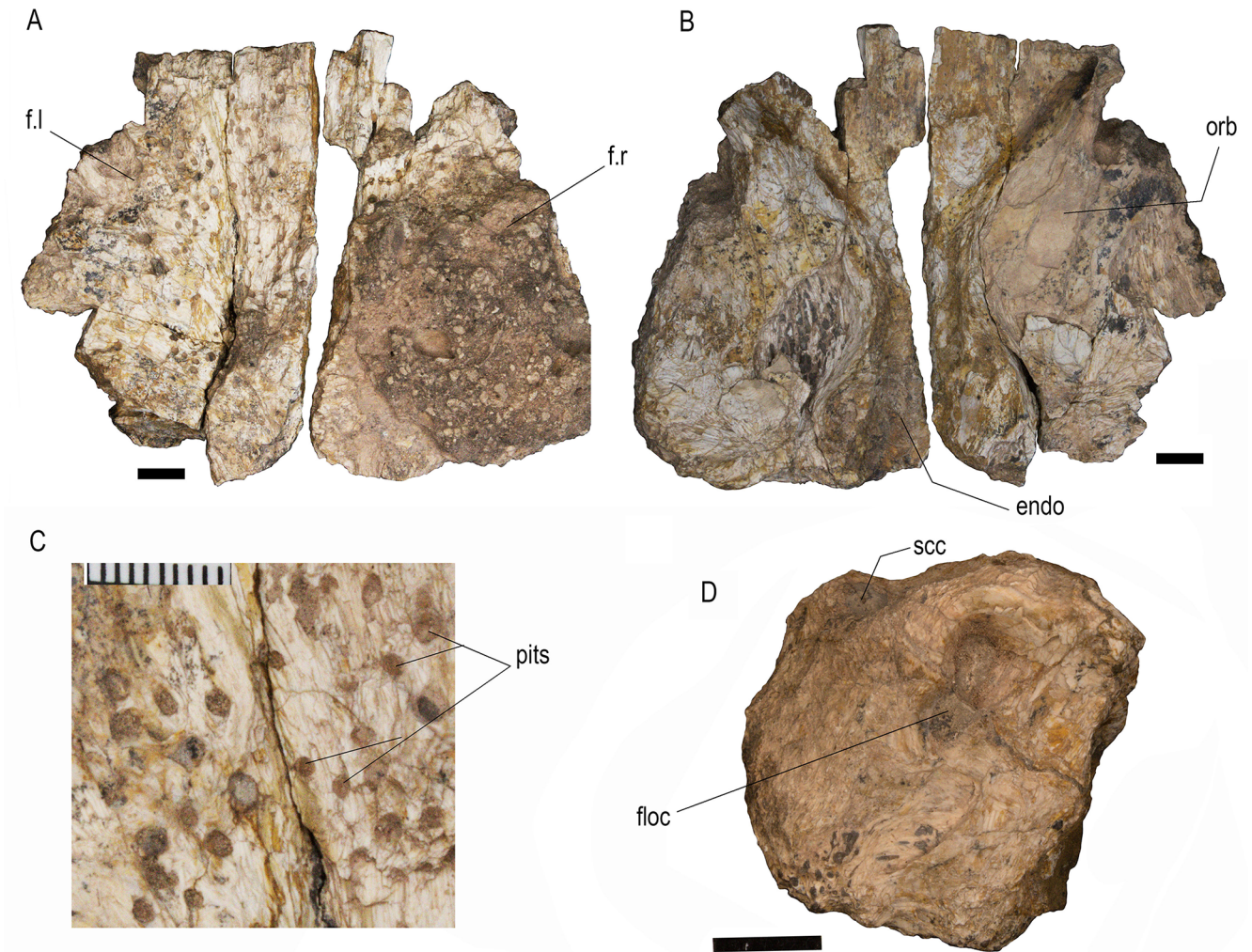


FIGURE 3. MAU-Pv-CO-725, frontals (A-C), and right otic capsule (D), in dorsal (A), ventral (B), and medial (D) views. (E) detail of the frontal ornamentation formed by pits. Abbreviations: **endo**, endocranial cavity (osteological correlates of olfactory apparatus and anterior region of the cerebrum); **f.l.**, left frontal; **f.r.**, right frontal; **floc**, floccular recess; **orb**, orbital part of the frontal; **scc**, semicircular canal of the inner ear, in section (probably anterior semicircular canal). Scale bar equals 10 mm. [planned for page width]

DESCRIPTION

Skull roof

Both frontals were recovered (Figs. 3A, B). They form a flat plate approximately 120 mm wide, 90 mm long, and 21 mm in maximum thickness. Unlike most abelosaurids, the frontals in the specimen MAU-Pv-CO-725 are not especially dorsoventrally tall and exhibit a low degree of ornamentation. This particular ornamentation is formed not by grooves, crests, and rugosities as in most abelosaurids (e.g., *Abelisaurus*, *Aucasaurus*, *Carnotaurus*, *Viavenator*; Bonaparte 1985; Tykoski and Rowe 2004; Paulina-Carabajal 2011a, b), but formed by sparsely spaced circular pits distributed on an almost flat

surface (Figs. 3A, C).

On the ventral surfaces of the frontals, osteological correlates of the olfactory tracts and olfactory bulbs are preserved (Fig. 3B). This anatomical information completes the missing anterior region of the natural endocast, allowing a complete reconstruction of the brain in dorsal view.

Cranial endocast

The natural cranial endocast is missing the anterior region of the forebrain (olfactory tract and bulbs), the distal end of the hindbrain, and the pituitary ventrally. Small fragments of supraoccipital/parietal and orbitosphenoid/mesethmoid bones are still attached to the posterodorsal and ventromedial sides,

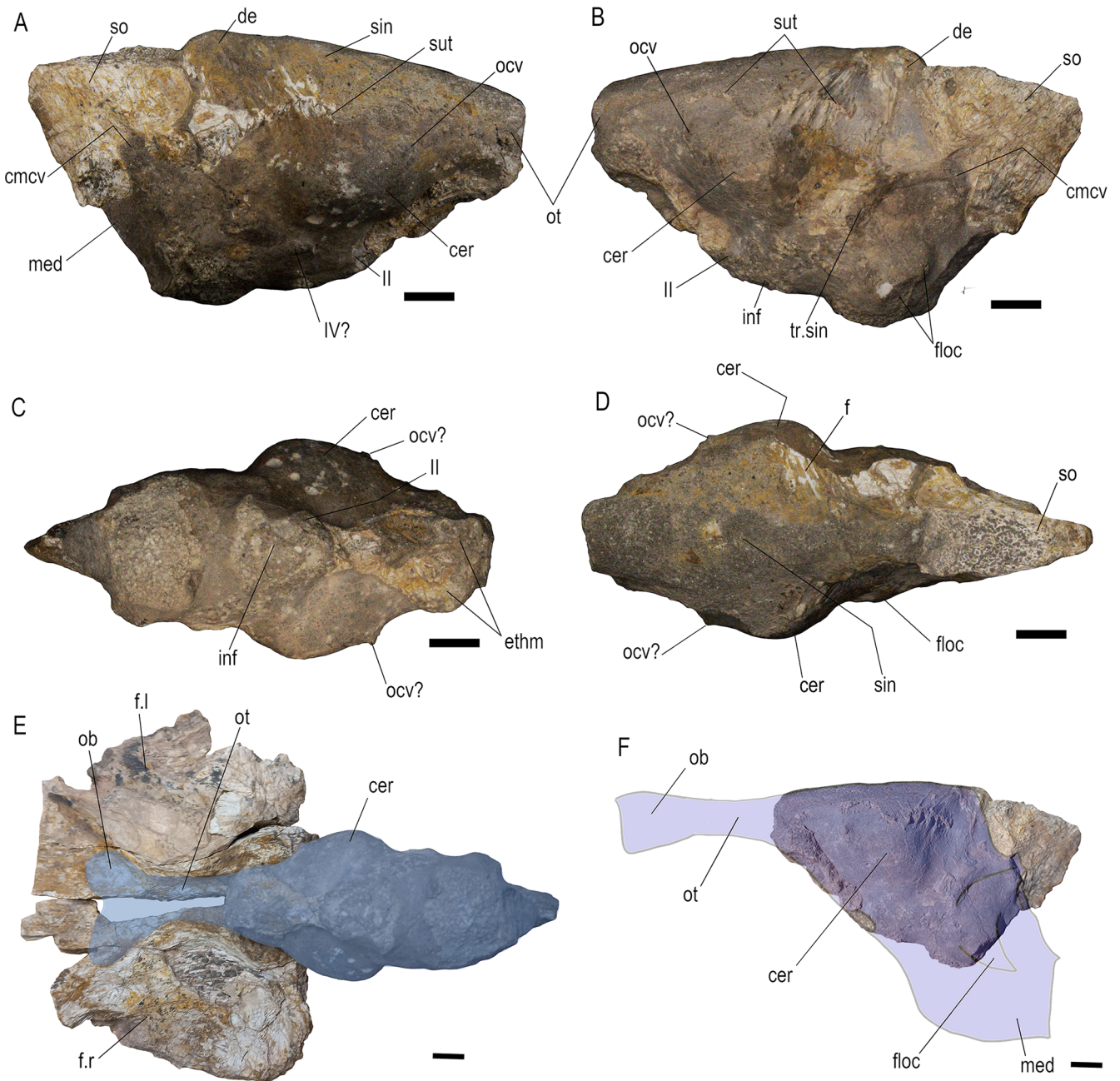


FIGURE 4. MAU-Pv-CO-725 natural cranial endocast (A-D) in right lateral (A), left lateral (B), ventral (C), and dorsal (D) views. Reconstructions (blue shades) of the complete endocast in ventral (E) and left lateral (F) views. Abbreviations: **de**, dorsal expansion or dural peak; **cer**, cerebral hemisphere; **cmcv**, caudal middle cerebral vein; **f**, frontal fragments; **f.l**, left frontal; **f.r**, right frontal; **floc**, base of flocculus of cerebellum; **inf**, proximal section of the infundibulum; **med**, medulla oblongata; **ob**, olfactory bulb; **ocv**, orbitocerebral vein; **ot**, olfactory tract; **sin**, dorsal longitudinal venous sinus; **so**, supraoccipital fragment; **sut**, suture marks between frontal and laterosphenoid-prootic; **tr.sin**, transverse venous sinus. Scale bar equals 10 mm. [planned for page width]

respectively (Figs. 4A-D). The osteological correlates of the olfactory tract and bulbs are preserved on the ventral surface of the frontals, allowing the reconstruction of the complete forebrain morphology (Fig. 4E).

The general shape of the endocast is reminiscent of that of other basal theropods, being anteroposteriorly long, with elongate olfactory tract and bulbs, the maximum transverse width lying across the cerebral hemispheres, and a pronounced

and triangular dorsal expansion (dural peak) dorsoposteriorly overlying the hindbrain. The angles between the forebrain, midbrain, and hindbrain result in a sigmoid shape in the lateral view (Fig. 4F).

Forebrain — The natural endocast is missing the anterior region. However, osteological correlates of the olfactory tract and bulbs on the ventral surface of the frontals allow the reconstruction of the olfactory region (Figs. 3B, 4E).

The olfactory tract is approximately 30 mm long and 15 mm transversely wide, resulting in a relatively robust structure, as is a common feature among abelosaurids (e.g., Sampson and Witmer, 2007; Paulina-Carabajal and Succar, 2015; Paulina-Carabajal and Filippi, 2018, and references therein) and carcharodontosaurids (Larsson, 2001; Paulina-Carabajal and Canale, 2010; Paulina-Carabajal and Nieto, 2020). The olfactory bulbs are relatively large, oval, and markedly divergent from the midline, as in other abelosaurids (e.g., *Majungasaurus*, *Viavenator*) (Figs. 3B, 4E). The Olfactory Ratio (OR) for MAU-Pv-CO-725 is approximately 58%, similar to that of *Viavenator* (57%, Paulina-Carabajal and Filippi, 2018), while *Majungasaurus* OR is 48.3% (Sampson and Witmer, 2007; Cerroni and Paulina-Carabajal, 2019). The OR is calculated by comparing the size of the olfactory bulb with the size of the cerebral hemisphere, a measurement that can be used with body size to estimate olfactory acuity (Zelenitzky et al., 2009). The body mass of MAU-Pv-CO-725 remains unknown, thus preventing further calculation of olfactory acuity.

The cerebral hemispheres are well marked, rounded, and laterally expanded, as in other abelosaurids (Figs. 4A-D). The lateral border of the cerebral hemisphere is rounded.

Based on known abelosaurid neuroanatomy, the entire endocast of MAU-Pv-CO-725 would have had a length of approximately 130 mm from the tip of the olfactory bulbs to the end of the medulla oblongata (Fig. 4F).

Midbrain — The only structures that can be observed in non-avian dinosaur brains are the optic lobes and cranial nerves III and IV (Franzosa, 2004). As in other non-coelurosaur theropods, the optic lobes of MAU-Pv-CO-725 are not visible in the endocast. As for the roots of CNs III and IV, they are not preserved in the endocast, except for a possible short passage for CN IV observed on the right side of the endocast (Fig. 4A).

Hindbrain — A part of the cerebellum (i.e., the floccular

process) and the proximal part of the medulla oblongata are observed in the endocast. The main body of the cerebellum, located just posterior to the optic lobes, is obscured on the endocast by the dorsal longitudinal venous system, which covers the dorsal surface and forms a dorsal expansion in this region (Fig. 4B). This dural expansion, located above the anterior margin of the floccular process, does not project over the dorsal surface of the forebrain, as in *Viavenator* and *Llukalkan* (Fig. 4D). In contrast, the dural expansion is more anteriorly placed in MAU-Pv-LI-582 and *Majungasaurus*, level with the root of the trigeminal nerve (CN V) and resulting in a different sigmoidal shape of the endocast.

The floccular process of the cerebellum is broken at the base on both sides, so its complete length and shape remain unknown. The proximal section of the flocculus is oval and markedly lateromedially compressed (Fig. 4B), as in other abelosaurids. Moreover, the right otic capsule exhibits the floccular recess on the anterior surface of the vestibular eminence, which is figure eight-shaped (Fig. 3D), similar to that described in *Aucasaurus* (Paulina-Carabajal and Succar, 2015). Nevertheless, the figure eight-shaped floccular recess is not limited to abelosaurids among theropods (i.e., the tyrannosaurid *Daspletosaurus*; Paulina-Carabajal et al., 2021)

The medulla oblongata is partially preserved. Unfortunately, the brainstem region is missing, preventing the preservation of the roots of the remaining cranial nerves (CNs V-XII). The caudal middle cerebral vein is the only blood vessel observed in this region (Figs. 4A, B). This large passage projects posterodorsally from the intersection with the transverse sinus to exit the braincase posteriorly. The caudal middle cerebral vein has a larger diameter proximally than distally, where the passage becomes more flattened. The impression left on the supraoccipital indicates that the exit foramen for this vein was near the midline, separated from its counterpart by a vertical crest, as commonly observed in other abelosaurids (e.g., *Aucasaurus*, *Niebla*).

DISCUSSION

Endocast and bone features supporting abelosaurid designation

The general shape of the natural endocast from the Cerro Overo site resembles most non-maniraptoran theropods, being longer than wide and lacking observable anatomical definition from the optic lobes and the cerebellum. The

markedly elongated and robust olfactory tracts and bulbs are typical features of ceratosaurs and carcharodontosaurids (e.g., Larsson, 2001; Sanders and Smith, 2005; Sampson and Witmer, 2007; Paulina-Carabajal and Canale, 2010; Paulina-Carabajal and Filippi, 2018).

The general morphology of the endocast of MAU-Pv-CO-725 largely resembles that of *Viavenator* and *Llukalkan* but not that of MAU-Pv-LI-582, which shares more similarities with *Majungasaurus*. MAU-Pv-CO-725 also represents a smaller specimen than *Viavenator* and slightly smaller than *Llukalkan* and *Niebla*.

Luckily, the endocast was recovered with fragmentary but very informative bones. Thus, extra data supports the taxonomic assignment of this specimen and includes the morphology of the frontals and otic capsule (e.g., the shape of the floccular recess).

The frontals of MAU-Pv-CO-725 are transversely wider than longer, not particularly thick at the midline (frontals of abelisaurids are, in general, markedly engrossed at the midline, Tykoski and Rowe, 2004). More recently, relatively low frontals have been described for the small taxon *Guemesia*, and the basal abelisaurid *Spectrovenator* from Brazil (Zaher et al., 2020), but not for *Niebla*, suggesting that this feature is not directly related to body size. Internally the frontals in MAU-Pv-CO-725 exhibit some degree of pneumaticity, as observed through fractures, a feature also present in MAU-Pv-LE-620 and observed through CT scans in *Guemesia* (Agnolín et al., 2022).

The frontals exhibit an ornamented surface, a characteristic feature of the abelisaurid skull roof, although much less developed in MAU-Pv-CO-725 than in most other representatives of this clade. Moreover, the ornamentation in this specimen is particular regarding both, the large amount of pits and its irregular distribution on the surface of the frontals. In this regard, the particular type of ornamentation present in MAU-Pv-CO-725 is also observed in MAU-Pv-LE-620 (another skull roof from Bajo de la Carpa Formation) and in the non-Patagonian abelisaurid *Guemesia*, which exhibit a lower number of pits near the midline and some rugosities laterally, near the orbital rim. The complete lack of ornamentation is observed in the Jurassic taxon *Euabelisaurus*, and the early Cretaceous *Spectrovenator*, which suggests that the reduction of ornamentation in derived late Cretaceous forms may represent the retention of a primitive character in adult specimens or possibly a younger ontogenetic stage.

The isolated right otic capsule exhibits on the anterior surface of the vestibular eminence a figure eight-shaped floccular recess. A similar morphology has been described for *Aucasaurus* (Paulina-Carabajal, 2009; Paulina-Carabajal and Succar, 2015), although it is observed in non-ceratosaurian theropods as well (Paulina-Carabajal, 2009; Paulina-Carabajal et al., 2021).

Comparisons with other abelisaurids of the Bajo de la Carpa Formation

The abelisaurids collected from sites near Cerro Overo that preserve braincases are *Llukalkan*, *Viavenator*, MAU-Pv-LI-582, and MAU-Pv-LE-620, the latter corresponding to a previously unpublished isolated skull roof. *Llukalkan*, *Viavenator*, and MAU-Pv-LI-582 are mid-to-large-sized abelisaurids, with *Viavenator* being the largest. The surface of the bone in the skull roof of the three specimens has been damaged by erosion, obscuring the nature of the ornamentation. However, fragments of skull roof preserved in each specimen indicate the presence of “normal” abelisaurid ornamentation, this is, the presence of well-marked grooves and rugosities, in *Llukalkan* and MAU-Pv-LI-582, and most likely also in *Viavenator*. Other abelisaurids with marked ornamentations (and even with cornual structures) are *Abelisaurus comahuensis* (Bonaparte and Novas, 1985), *Aucasaurus garridoi* (Coria et al., 2002), *Carnotaurus sastrei* (Bonaparte, 1985), *Ekrixinatosaurus novasi* (Calvo et al., 2004), *Niebla antiqua* (Aranciaga-Rolando et al., 2020), *Skorpiovenator bustingorryi* (Canale et al., 2008) from Argentina, *Majungasaurus crenatissimus* from Madagascar (Sampson et al., 1998), *Arcovenator escotae* from France (Tortosa et al., 2014), and the Indian *Indosaurus matleyi* and *Rajasaurus narmadensis* (Huene and Matley, 1933; Wilson et al., 2003; Carrano and Sampson, 2008).

Guemesia and *Niebla* are the smaller abelisaurids with preserved braincases from the Upper Cretaceous of Northwestern Argentina and Patagonia, respectively, followed by *Llukalkan*, also from Patagonia. *Niebla* and *Llukalkan*, however, have an engrossed skull roof with marked ornamentation formed by grooves and rugosities, whereas *Guemesia* has a non-engrossed frontal and exhibits a low degree of ornamentation formed by few pits near the midline and “normal” ornamentation (grooves and rugosities) near the orbital rim. The holotype of *Niebla* also is considered an adult specimen (Aranciaga Rolando et al., 2020). The isolated braincase of *Guemesia*, however, bears no evidence

enough to discard it as a juvenile individual, and therefore is not possible to associate its small size to any ontogenetic state. Regarding skull roof morphology, the Jurassic abelisaurid *Eoabelisaurus* has a skull roof that is not markedly engrossed and has no ornamentation (Pol and Rauhut, 2012). This suggests that the lack of ornamentation represents a primitive character within the clade Abelisauridae. So far, the secondary reduction of the ornamentation in the Cretaceous abelisaurid forms described here, seem to be related to body size. Also, although it is difficult to determine if *Guemesia*, MAU-Pv-LE-620, and MAU-Pv-CO-725 represent juvenile specimens, the lack of ornamentation may represent a paedomorphic character.

Finally, MAU-Pv-LE-620 and MAU-Pv-CO-725, although from different sites (apart 13 km away from each other), are from the same geological formation and share a relatively small size and the reduction of ornamentation, suggesting that both specimens belong to the same unknown taxon.

CONCLUSION

The endocast and the associated braincase fragments bear features that support the taxonomical assignment of the specimen to Abelisauridae. The endocranial morphology of the abelisaurids from Cerro Overo-La Invernada sites indicates the presence of two morphotypes, with *Viavenator*, *Llukalkan*, and the natural endocast MAU-Pv-CO-725 sharing the same general morphology. The relative size of the latter is interpreted here as similar to that of *Llukalkan*. The marked reduction of ornamentation in MAU-PV-CO-725 and MAU-Pv-LE-620 (the two isolate skull roofs) is, however, a distinctive pattern that differentiates them from *Llukalkan* and *Viavenator*, which exhibit well-developed ornamentation formed by grooves and rugosities.

The natural endocast and skull roof described here correspond to a small-sized individual, but due to its incompleteness, it is impossible to rule out that it may be a juvenile. Are MAU-Pv-CO-725 and MAU-Pv-LE-620 juvenile specimens or representatives of sexual dimorphism of known taxa? Or do they represent an unknown group of small-sized abelisaurids characterized by the reduction of the skull roof sculpturing? Further findings and studies are needed to answer these questions.

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AUTHOR CONTRIBUTIONS

APC designed the project and drafted the manuscript; LF and KUG took photographs; APC created the illustrations, and KUG made the 3D photogrammetry model. All authors analyzed the data and edited the manuscript.

SUPPLEMENTARY INFORMATION

Supplemental-3D model (photogrammetry) of natural endocast.pdf

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