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Neuroanatomy of the titanosaurian sauropod *Narambuenatitan palomoi* from the Upper Cretaceous of Patagonia, Argentina

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Recibido: 15 de mayo 2019 - **Aceptado:** 21 de mayo 2020 - **Publicado:** 30 de septiembre 2020

Para citar este artículo: Ariana Paulina-Carabajal, Leonardo Filippi, and Fabien Knoll (2020). Neuroanatomy of the titanosaurian sauropod *Narambuenatitan palomoi* from the Upper Cretaceous of Patagonia, Argentina. *Publicación Electrónica de la Asociación Paleontológica Argentina* 20 (2): 1–9.

Link a este artículo: http://dx.doi.org/10.5710/PEAPA.21.05.2020.298

ISSN 2469-0228

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Pe-APA | Publicación Electrónica
ASOCIACIÓN PALEONTOLÓGICA ARGENTINA
Año 2020 - 20(2): 1–9
ARTÍCULO

NEUROANATOMY OF THE TITANOSAURIAN SAUROPOD *NARAMBUENATITAN PALOMOI* FROM THE UPPER CRETACEOUS OF PATAGONIA, ARGENTINA

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Abstract. *Narambuenatitan palomoi* is a titanosaurian sauropod from the Upper Cretaceous of North Patagonia. Considered initially as a basal titanosaur, this taxon has uncertain phylogenetic relationships within the clade. An X-ray Computed Tomography (CT) scan of the holotype braincase allowed the first reconstruction of the brain and inner ear of this taxon, making it possible to compare the neuroanatomy with that of closely related forms. Except for the slightly sigmodal shape of the endocast in lateral view—considered a basal condition—, the brain shows derived titanosaurian traits such as a poorly developed dorsal expansion and a single exit for Cranial Nerve (CN) XII. In contrast, the inner ear exhibits slender and long semicircular canals (the anterior semicircular canal is distinctly longer than the posterior semicircular canal), which is a character present in more basal representatives of the group, such as *Sarmientosaurus*. We consider, however, the morphology of the inner ear as an unreliable indicator of phylogenetic position. Furthermore, there is a remarkable similarity between the morphology of the endocast of *Narambuenatitan* and the possible saltasaurid from (FAM 03.064), from the Upper Cretaceous of Fox-Amphoux-Métisson, France, suggesting saltasaurine affinities for the Argentinean taxon.

Key words. Paleoneurology. Cranial endocast. Inner ear. Dinosauria.

Resumen. NEUROANATOMÍA DEL SAURÓPODO TITANOSAURIO *NARAMBUENATITAN PALOMOI* DEL CRETÁCICO SUPERIOR DE PATAGONIA, ARGENTINA. *Narambuenatitan palomoi* es un saurópodo titanosaurio del Cretácico Superior del Norte de Patagonia. Considerado inicialmente como un titanosaurio basal, este taxón tiene relaciones filogenéticas inciertas dentro del clado. Una Tomografía Computada de rayos X del neurocráneo del holotipo permitió la primera reconstrucción del encéfalo y oído interno de esta especie, otorgando la oportunidad de comparar la neuroanatomía con formas cercanamente emparentadas. Excepto por la forma ligeramente sigmoidal del molde endocraneano en vista lateral—considerada una condición basal—el encéfalo muestra rasgos derivados de titanosaurios, tales como una expansión dorsal pobremente desarrollada y una salida única para el Nervio Craneano (NC) XII. Por su parte, el oído interno muestra canales semicirculares delgados y largos (el canal semicircular anterior es particularmente más largo que el canal posterior), características presentes en representantes más basales del grupo, como *Sarmientosaurus*. Consideramos, sin embargo, que la morfología del oído interno es un indicador poco fiable de la posición filogenética. Además, hay una marcada similitud en la morfología de los moldes endocraneanos de *Narambuenatitan* y el posible saltasaurino de Fox-Amphoux-Métisson, del Cretácico Superior de Francia (FAM 03.064), lo que sugiere afinidades con Saltasaurinae para el taxón argentino.

Palabras clave. Paleoneurología. Endocráneo. Oído interno. Dinosauria.

Narambuenatitan palomoi Filippi, García & Garrido, 2011 is a titanosaurian sauropod from the Upper Cretaceous of North Patagonia, collected from outcrops of the Anacleto Formation (lower–middle Campanian; Dingus *et al*., 2000). The remains include a complete (although slightly distorted) isolated braincase, a region of the skull extremely rare in the fossil record of sauropods. This specimen allowed, by means of CT scans and 3D renderings, the study of the endocranial cavity and inner ear of this species (Figs. 1–3). The neuroanatomy of several titanosaurian dinosaurs from distant parts of the world have been described (*e.g.*, Paulina-Carabajal & Salgado, 2007; Paulina-Carabajal *et al*., 2008;

Paulina-Carabajal, 2012; Knoll *et al.*, 2013, 2015, 2019; Sues *et al.*, 2015; Martínez *et al.*, 2016; Poropat *et al.*, 2016; Andrzejewski *et al.*, 2019), and of these studies correspond to saltasaurines and other eutitanosaurs. Moreover, most taxa are from Argentina, including *Antarctosaurus wichmannianus* Huene, 1929 (Paulina-Carabajal, 2012), *Bonatitan reigi* Martinelli & Forasiepi, 2004 (Paulina-Carabajal, 2012), *Saltasaurus loricatus* Bonaparte & Powell, 1980 (Powell, 2003; Paulina-Carabajal, 2012), *Sarmientosaurus musacchioi* Martínez, Lamanna, Novas, Ridgely, Casal, Martínez, Vita, & Witmer, 2016, and two isolated indeterminate titanosaur braincases (MGPIFD-GR 118, Paulina-Carabajal & Salgado, 2007, and MCF-PVPH 765, Paulina-Carabajal *et al.*, 2008). Paleoneurological investigations have been conducted in other Gondwanan titanosaurs, though: *Malawisaurus dixeyi* (Haughton, 1928) from the Lower Cretaceous of Malawi (Andrzejewski *et al.*, 2019), *Jainosaurus septentrionalis* (Huene & Matley, 1933) from the Upper Cretaceous of India (Huene & Matley, 1933; Wilson *et al.*, 2009), and *Diamantinasaurus* Hocknull, White, Tischler, Cook, Calleja, Sloan & Elliott, 2009 from the Upper Cretaceous of Australia (Poropat *et al.*, 2016). In contrast, the paleoneurology of Laurasian titanosaurs is known only in a few taxa from the Upper Cretaceous of Spain—an indeterminate Lithostrotia and *Lohuecotitan* (= "*Ampelosaurus* sp.")—(Knoll *et al.*, 2013, 2015), France (Knoll *et al.*, 2019), and Uzbekistan (Sues *et al.*, 2015). The aim of the present study is to describe the digitally reconstructed cranial endocast of *Narambuenatitan* and use this novel anatomical information to clarify the phylogenetic position of this taxon. The endocranial data about *Narambuentatitan* presented here are particularly interesting since this taxon represents a basal form within Lithostrotia according to the phylogenetic analysis of Filippi *et al.* (2011), which is mainly based on the scoring of postcranial elements. Although the endocranial anatomy of *N. palomoi* was expected to exhibit a large number of plesiomorphic characters, it is clearly more derived than that of *Sarmientosaurus musacchioi*, which is the only basal titanosaur known so far to be represented by a well-preserved skull, and whose endocranial morphology has been studied (Martínez *et al.*, 2016).

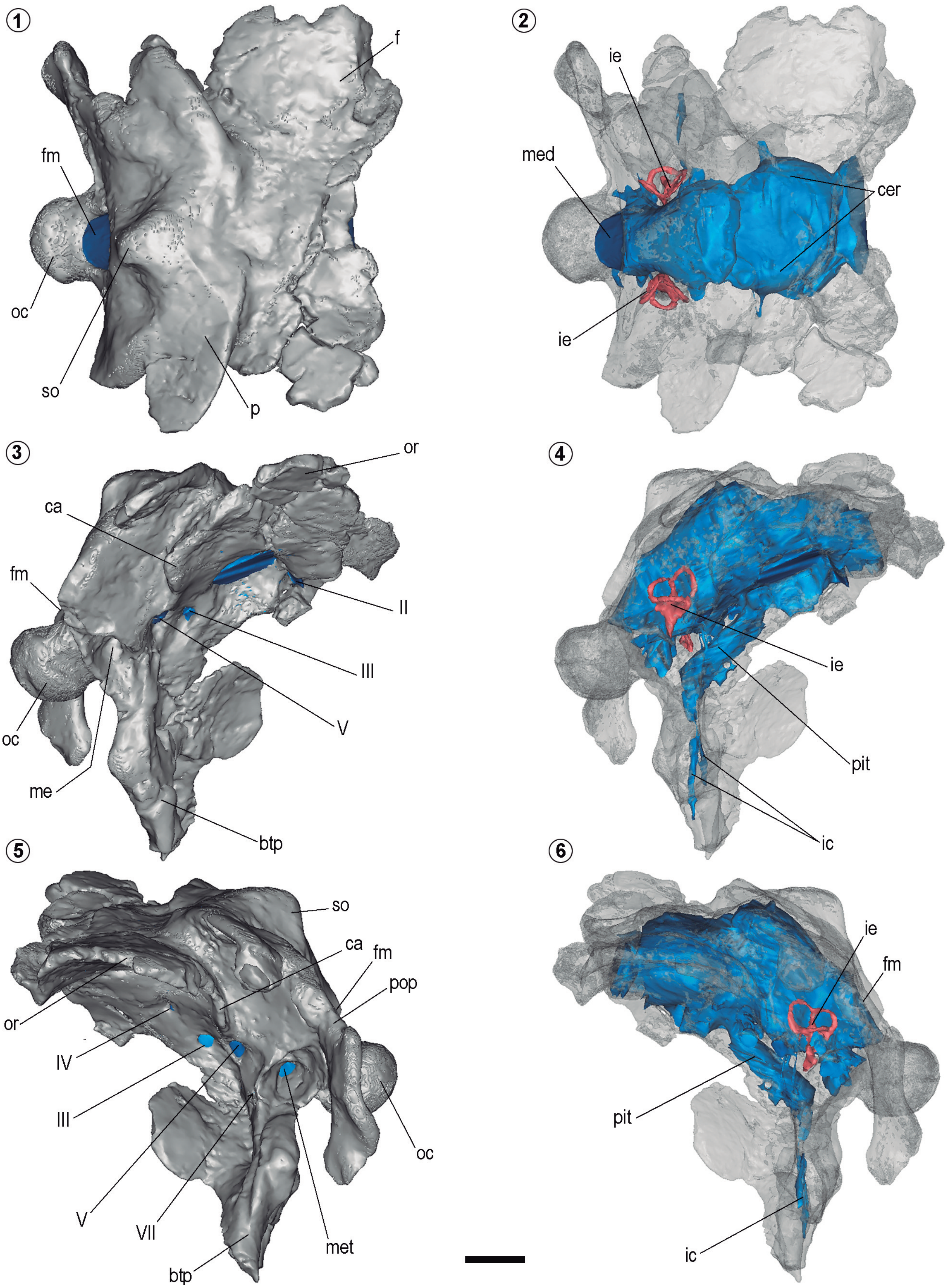
MATERIALS AND METHODS

The braincase of the holotype specimen of *Narambuenatitan palomoi* (MAU-Pv-N-425) has suffered some degree of oblique dorsoventral deformation, which resulted in fractures and the mediolateral displacement of delicate structures on the right side. Also, the orbitosphenoids and laterosphenoids were pushed towards the ventral side of the skull roof as shown in Figure 1.3. This distortion affects to a lesser degree the cranial endocast, except for the forebrain, which is dorsoventrally compressed as a result.

The braincase was X-ray CT scanned at the "Clínica de Imágenes" (Neuquén City, Argentina) using a medical CT machine, a Siemens Sensation 64, with a voltage of 140 kV and a current of 149.8 mA. 336 slices were produced, with a slice increment of 0.59 mm. The CT data were imported into the software Materialise Mimics (18.0) for image segmentation and digital reconstruction of 3D surface models of the braincase and internal spaces. Final illustrations were made using Photoshop (Adobe). Measurements (distance and volumes) were taken using the tools of the software Mimics.

Institutional abbreviations. FAM, Mairie de Fox-Amphoux, Fox-Amphoux, France; **MAU-Pv-N,** Museo Argentino Urquiza, Rincón de los Sauces, Argentina; **MCF-PVPH,** Museo Carmen Funes, Plaza Huincul, Argentina; **MGPIFD-GR,** Museo de Geología y Paleontología del Instituto de Formación Docente Continua de General Roca, General Roca, Argentina; **MPCM-HUE,** Museo de Paleontología de Castilla-La Mancha, Cuenca, Spain.

Figure 1. 1–6, Digital 3D reconstruction of the braincase, brain and inner ear of ***Narambuenatitan palomoi* (MAU-Pv-N-425)**. **1–2,** dorsal view; **3–4,** right lateral view, and **5–6,** left lateral view. In figures **2, 4,** and **6,** the bone was rendered semi-transparent to allow the observation of the endocranial features. Abbreviations: **btp,** basipterygoid process; **ca,** crista antotica; **cer,** cerebral hemisphere; **f,** frontal; **fm,** foramen magnum; **ic,** cerebral branch of internal carotid artery; **ie,** inner ear; **me,** middle ear depression (within which open the metotic foramen and the fenestra ovalis); **med,** medulla oblongata; **met,** metotic foramen (for CNs IX–XI); **oc,** occipital condyle; **or,** orbital roof; **p,** parietal; **pit,** pituitary; **pop,** paroccipital process; **so,** supraoccipital; **II–XII,** cranial nerves. Scale bar= 20 mm.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RESULTS

Cranial endocast

The cranial endocast of *Narambuenatitan* is complete, measuring 102 mm anteroposteriorly and 51.5 mm transversely at the widest region (cerebrum). As in other sauropods, it is bulbous, transversely wide and anteroposteriorly short, with a laterally expanded cerebrum and a well-developed and elongate pituitary. The cranial endocast has a volume of approximately 100.6 cm^3, of which 4.3 cm^3 correspond to the cast of the pituitary fossa (approximately 4.3 % of the total volume of the endocranial cavity). The cranial endocast presents wide angles between the forebrain, midbrain, and hind brain, respectively, so that it appears sigmoidal in lateral view (Fig. 2.1–3). The situation of *Narambuenatitan* in this respect seems to be intermediate between those of basal and more derived forms. In derived titanosaurs (*e.g.*, Paulina-Carabajal, 2012; Knoll *et al.*, 2015) the endocast is more "tubular", whereas an endocast strongly sigmoid in lateral view (*e.g.*, *Giraffatitan*; Knoll & Schwarz-Wings, 2009) is the plesiomorphic condition among sauropods (Knoll *et al.*, 2019). Posterodorsally, the dorsalmost region of the cast is constituted by the dorsal expansion (= dural peak), which is posterior to the cerebral hemispheres. It forms a modest rounded hump dorsal to the cerebellar region of the brain (Figs. 1.4, 2.3). This dorsal expansion is indicative of the presence of a relative large venous sinus (Witmer *et al.*, 2008). The relative size of the dorsal expansion in *Narambuenatitan* is similar to that of lithostrotian titanosaurs from Argentina (*e.g.*, *Antarctosaurus*, *Bonatitan*; Paulina-Carabajal, 2012) and Europe (*e.g.*, *Lohuecotitan* Knoll *et al.*, 2013). The putative basal lithostrotian *Sarmientosaurus* (Martínez *et al.*, 2016) and the Dzharakuduk titanosaur (Sues *et al.*, 2015: fig. 10) have relatively larger and more dorsally projected dorsal expansions. In *Narambuenatitan*, the optic lobe and the flocculus of the cerebellum did not leave any impression on the medial wall of the endocranial cavity. Therefore, these structures are absent in the endocranial cast, as in most sauropods (see Knoll *et al.*, 2015: 14).

The olfactory region of *Narambuenatitan* projects anteriorly from the cerebral hemispheres (Fig. 2.1). The olfactory tracts are markedly short, almost nonexistent, as in other titanosaurs, whereas the olfactory bulbs may have been small and similarly short anteroposteriorly. This is consistent with shortened nasal bones, that is to say external nares with retracted caudal margins, as in other sauropods (Knoll *et al.*, 2019).

The widest part of the cranial endocast is across the cerebral hemispheres, the left one of which is the better preserved. As in other sauropods, the interhemispheric fissure is obscured by a dorsal longitudinal sinus. The passages for the orbitocerebral veins are narrow and project laterally from the lateral side of each cerebral hemisphere (Fig. 2.1–3). These blood vessels were not identified previously in the braincase (Filippi *et al.*, 2011).

The infundibulum is elliptical in transverse section and is well separated spatially from the roots of the optic nerve (Cranial Nerve (CN) II). The pituitary body is large, elongate and posteroventrally oriented, as in other sauropodomorphs. In *Narambuenatitan* the pituitary is particularly strongly posteroventrally projected in comparison with other titanosaurs, except for *Lohuecotitan* (Knoll *et al.*, 2013). The angle formed by the long axis of the pituitary and the lateral semicircular canal of the inner ear as seen in lateral view of the endocast is approximately 40°, similar to the situation in the titanosaur MPCM-HUE-1667 (approximately 45°, Knoll *et al.*, 2015) from Spain. A significantly wider angle is observed in the unnamed titanosaur from France (approximately 65°, Knoll *et al.*, 2019), Argentinean titanosaurs (*e.g.*, approximately 65° in *Bonatitan*, Paulina-Carabajal, 2012), and *Giraffatitan* (approximately 70°, Knoll & Schwarz-Wings, 2009). Although the taphonomic deformation of the braincase of *Narambuenatitan* is less pronounced in the ventral basicranium—in which the pituitary fossa is excavated—, the possibility that the angle observed in this taxon has been altered to some degree cannot be discarded.

In the basicranium of *Narambuenatitan*, a single median passage, presumably for the basilar artery, communicates the floor of the endocranial cavity with the pituitary fossa (Fig. 2.4). Among titanosaurs, the same connection—observed in the endocast as a bridge between the hindbrain and the pituitary—is present in *Bonatitan* (Paulina-Carabajal, 2012), an indeterminate titanosaur from North Patagonia (García *et al.*, 2008), *Malawisaurus* (Andrzejewski *et al.*, 2019), and the titanosaur from Uzbekistan (Sues *et al.*, 2015). Outside Titanosauria, this feature is known at least in *Plateosaurus* (Galton, 1985), the rebbachisaurid *Limaysaurus*

(Paulina-Carabajal & Calvo, 2015); and in the basal sauropod *Spinophorosaurus* (Knoll *et al.*, 2012). The passages for the cerebral branches of the internal carotid artery enter the pituitary fossa separately from one another. They are long, posteroventrally projected, and divergent from the midline by approximately 60° (Figs. 1.4, 2.3).

Cranial nerves

The cranial nerves show the same arrangement as in other sauropods. The roots of the optic nerves (CN II—and probably the optic chiasm region, represented by a small bulge—are observed in the endocast (Fig. 2.2). There was a single median opening for the nerves of both sides at the

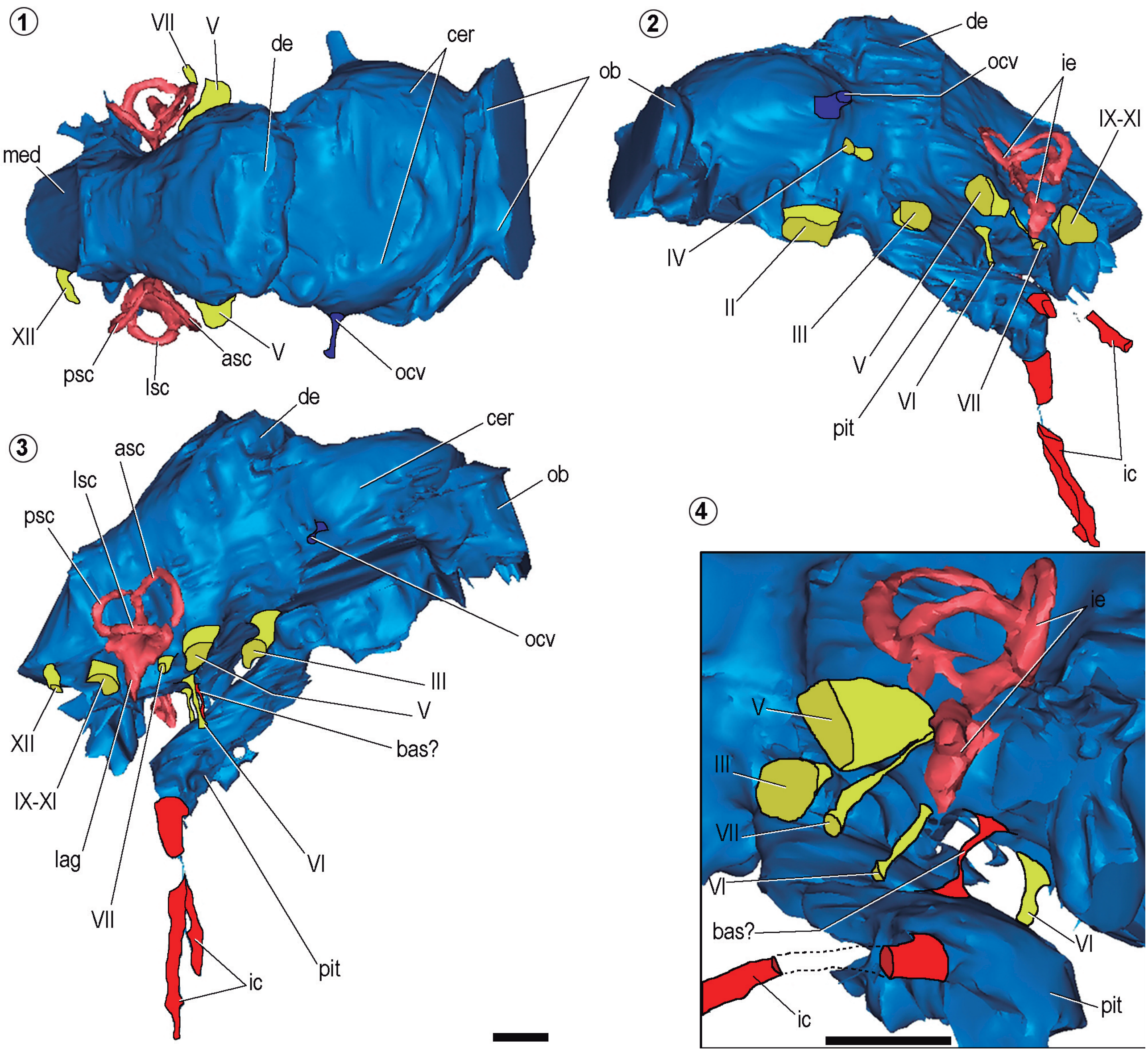

Figure 2. 1–4, Digital 3D reconstruction of the brain and inner ear of ***Narambuenatitan palomoi*** **(MAU-Pv-N-425)**. **1,** dorsal view; **2,** left ventrolateral view; **3,** right lateral view; **4,** close up image of pituitary, cranial nerves and blood vessels in left posteroventral view, to show the course of the basilar artery. Cranial nerves are in yellow and blood vessels are in red (arteries) and blue (veins). Abbreviations: **asc,** anterior semicircular canal; **bas,** basilar artery; **cer,** cerebral hemisphere; **de,** dorsal expansion; **ic,** cerebral branch of internal carotid artery; **ie,** inner ear; **lag,** lagena; **lsc,** lateral semicircular canal; **med,** medulla oblongata; **ob,** olfactory bulb; **ocv,** orbitocerebral vein; **psc,** posterior semicircular canal; **II–XII,** cranial nerves. Scale bar= 10 mm.

medial contact of the orbitosphenoids. The roots of CN III, which are relatively large and circular in section, project laterally from the infundibulum (Fig. 1.2–3). A narrower and anterolaterally projected CN IV is observed posterior to the cerebral hemisphere, and anterodorsal to CN III. This nerve could only be traced on the left side of the cranial endocast (Fig. 2.3). The trigeminal nerve (CN V) is the largest of the cranial nerves. As in other titanosaurs, the three branches of CN V leave the endocranial cavity through a single, large but short passage, which extends mostly laterally. The abducens nerve (CN VI) is narrow. It projects anteroventrally from the ventral side of the brainstem. It does not penetrate the pituitary fossa, as in other titanosaurs, but could not be traced distally in the CT scans due the state of preservation of the braincase ventrally. The facial nerve (CN VII), which is of small diameter, could only be reconstructed on the left side. Quite long, it extends ventrolaterally in such a manner that its exit is much more ventral than that of CN V (Fig. 2.4). Although the exit of CN VII is not observed on the external surface of the braincase due to preservational circumstances (Filippi *et al.*, 2011), its approximate location should be on the ventral region of the well-developed crista prootica, as indicated in Figure 1.5. A similar elongate CN VII, running ventrolaterally, is observed in particular in the saltasaurine *Bonatitan* (Paulina-Carabajal, 2012) within titanosaurs. In most (but not all) sauropods CN VII is relatively shorter and its exit is immediately posterior or posteroventral to that of CN V (Witmer *et al.*, 2008). In *Narambuenatitan*, the metotic group (CNs IX–XI) is large, short, and slightly ventrally projected. On the lateral surface of the braincase, the exit foramen for these nerves (the metotic foramen) opens together with the fenestra ovalis within a deep middle ear recess. Although it is difficult to tell based on the CT scans, it seems that there is only one root for CN XII as in derived titanosaurs (*e.g.*, Paulina-Carabajal, 2012; Knoll *et al.*, 2019), and in contrast with the condition present in *Pitekunsaurus* (Paulina-Carabajal, 2012), *Sarmientosaurus* (Martínez *et al.*, 2016), and the titanosaurs from France and Uzbekistan (Sues *et al.*, 2015; Knoll *et al.*, 2019), which have two branches for this nerve.

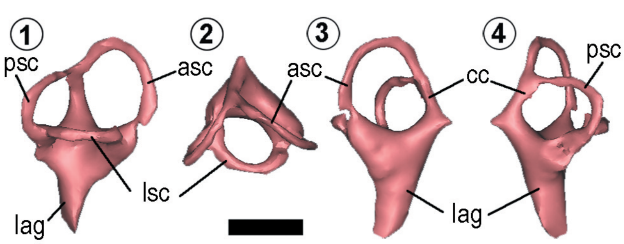

Figure 3. 1–4, Digital 3D reconstruction of the right endosseous labyrinth of ***Narambuenatitan palomoi*** **(MAU-Pv-N-425)**. **1,** lateral view; **2,** dorsal view; **3,** anterior view; **4,** posterior view. Abbreviations: **asc,** anterior semicircular canal; **cc,** crus commune; **lag,** lagena; **lsc,** lateral semicircular canals; **psc,** posterior semicircular canals. Scale bar= 10 mm.

Inner ear

The right endosseous labyrinth of *Narambuenatitan* was completely reconstructed (Figs. 2.3, 3). The three semicircular canals are slender, contrasting with the relatively more robust canals observed in derived titanosaurs. The anterior semicircular canal follows a sub-circular course and raises farther dorsally than the posterior semicircular canal, which also describes a sub-circular path. In contrast, the anterior and posterior semicircular canals are subequal in length in other South American titanosaurs (Paulina-Carabajal & Salgado, 2007; Paulina-Carabajal *et al.*, 2008; Paulina-Carabajal, 2012), except for *Sarmientosaurus* (Martínez *et al.*, 2016). The same holds essentially true for European titanosaurs (Knoll *et al.*, 2013, 2015, 2019). The lateral semicircular canal of *Narambuenatitan* is long, not significantly shorter than the posterior semicircular canal. The angle formed by the planes of the anterior and posterior semicircular canals in this taxon is 90° (Fig. 2.1). The lagena is simple, conical, and short, similar to that of other sauropods, especially derived titanosaurs.

DISCUSSION

Overall, the paleoneuroanatomy of *Narambuenatitan* is in line with those seen in other sauropods, showing as it does an anteroposteriorly short cranial endocast with a long and posteroventrally oriented pituitary, among other characters. Within Titanosauria it is reminiscent of most taxa from the latest Cretaceous of both Gondwana and Laurasia (Paulina-Carabajal, 2012; Knoll *et al.*, 2013, 2015, 2019). This together with the mosaic of primitive and derived characters (Tab. 1) visible on the endocast of *Narambuenatitan* makes it difficult to clarify the precise phylogenetic position of this taxon. If a marked reduction of the anterior semicircular canal is a synapomophy of saltasaurines (see Paulina-Carabajal, 2012), then the long anterior semicircular canal of *Narambuenatitan* suggests a more basal position of this taxon within Titanosauria. Similarly, an anterior semicircular canal longer than the posterior semicircular canal in *Malawisaurus* was interpreted as primitive (Andrzejewski *et al.*, 2019). Nevertheless, the moderate degree of development of the dorsal dural expansion in *Narambuenatitan* makes a basal position within Titanosauria unlikely (see Knoll *et al.*, 2019). The basal titanosauriform *Giraffatitan* (Knoll & Schwarz-Wings, 2009), the basal titanosaur *Sarmientosaurus* (Martínez *et al.*, 2016), and the titanosaur of uncertain position from Uzbekistan (Sues *et al.*, 2015) all show developed dural expansions. In contrast, derived titanosaurs, such as *Bonatitan*, *Lohuecotitan*, and *Jainosaurus*, have moderate dural expansions (Wilson *et al.*, 2009; Paulina-Carabajal, 2012; Knoll *et al.*, 2013). Other derived characters present in the cranial endocast of *Narambuenatitan* include CN VI running laterally to the pituitary space (instead of penetrating it) and CN XII with a single root. Whereas the first of these features is widespread among titanosaurs, a two-rooted CN XII is observed only in some of the most derived titanosaurs (Knoll *et al.*, 2019). Filippi *et al.* (2011: fig. 12) suggested for *Narambuenatitan* a moderately derived phylogenetic position within Titanosauria on the basis of the analysis of a small number of characters and taxa. The topology of Filippi *et al.* (2011) is inconsistent with that recovered by the most recent and comprehensive phylogenetic analyses of Titanosauria, such as that of Gorscak & O'Connor (2019). Pending a new analysis, we surmise that *Narambuenatitan* would nest within Saltasauridae given the

TABLE 1 – Titanosauriformes endocranial traits

Taxon	Brain-shape	DE	CN XII	CN VI/pit	CN VII	vasculature	asc vs psc	lsc vs psc	PIT
Giraffatitan[1]	sigmoid	extra large	two	penetrates	-	ocv/rmcv	>>>	≤	70°
Sarmientosaurus[2]	sigmoid	extra large	two	not	long	ocv/rmcv	>>>	≤	80°
Antactosaurus[3]	tubular	moderate	one	not	short	ocv	≥	<	65°
Bonatitan[3]	tubular	moderate	one	not	long	ocv/rmcv/ba	≥	<	65°
Diamantinasaurus[4]	tubular?	large	one	not	short	-	≥	-	?
Jainosaurus[2]	tubular	moderate	one	not	short	ba	≥	<	?
Lohuecotitan[2]	tubular	moderate	one	not	short	-	>	<	55°
Malawisaurus[5]	-	moderate	one	not	short	ba	>	≤	65°
Narambuenatitan	sub-sigmoid	moderate	one	not	long	ocv/ba	>	≤	40°
MPCM-HUE-1667[2]	tubular	moderate	one	not	long	-	≥	<	45°
FAM 03.064[2]	tubular	moderate	two	not	long	rmcv	≥	<	65°
Uzbekistan titanosaur[2]	tubular	moderate	two	not	short	cmcv/ba	≥	<	60°

Abbreviations: **Brain-shape,** endocast morphology in lateral view; **DE,** dorsal expansion relative size; **CN XII,** number of foramina; **CN VI/pit,** relation between the passage of the nerve and the pituitary; **CN VII,** length of the passage; **vasculature,** blood vessels identified (ocv, orbito-cerebral vein; rmcv, rostral middle cerebral vein; ba, basilar artery?); **asc vs psc,** relative size of anterior and posterior semicircular canals; **lsc vs psc,** relative size of lateral and posterior semicircular canal; **PIT,** angle formed between the lateral semicircular canal and the pituitary in lateral view. Data from: [1]Knoll & Schwarz-Wings (2009), [2]Knoll *et al.* (2019: fig. 4) (and references therein), [3]Paulina-Carabajal (2012), [4]Poropat *et al.* (2016), [5]Andrzejewski *et al.* (2019).

remarkable similarity in endocast morphology with the possible saltasaurid from Fox-Amphoux-Métisson, which appears to be fairly coeval (Knoll *et al.*, 2019).

CONCLUSIONS

The novel data on the neuroanatomy of *Narambuenatitan palomoi* presented in the present work inform our knowledge of the paleoneurology of titanosaurian sauropods. The position of the external foramina for the orbitocerebral vein and some cranial nerves, including CNs III, IV, VI, and VII, were determined or confirmed on the basis of CT data. The study reveals states of characters of possible phylogenetic importance, such as the moderate development of the dural expansion and CN XII with a single root. Although the long anterior and lateral semicircular canals of the inner ear may be considered to be consistent with *Narambuenatitan* being a basal titanosaur, all in all the paleoneurology indicates that it is certainly a significantly more advanced taxon than *Sarmientosaurus* (Sues *et al.*, 2015). In fact, *Narambuenatitan* appears to be fairly comparable, in stage of evolution, to the Métisson titanosaur (Knoll *et al.*, 2019).

ACKNOWLEDGMENTS

The authors warmly thank the "Clínica de Imágenes" (Neuquén, Argentina) for allowing the CT scanning of the specimen, particularly the radiologist G. Diez for her time and assistance. To Secretaria de Cultura of Neuquén Province, for authorizing the transfer and study of the specimen. The editors and reviewers P. Gallina, A. Otero, and S. Poropat greatly improved an early version of the present article. The Project was funded by the Argentinean National Agency for Scientific and Technological Promotion, PICT 2016-0481 (to APC), and FEDER/Spanish Ministry of Science and Innovation-State Research Agency CGL2017-89123-P (to FK). F. Knoll is an ARAID Senior Researcher and a member of the reference research group E04_20R FOCONTUR.

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doi: 10.5710/PEAPA.21.05.2020.298

Recibido: 15 de mayo 2019
Aceptado: 21 de mayo 2020
Publicado: 30 de septiembre 2020