

## Short communication

## A natural cranial endocast with possible dicraeosaurid (Sauropoda, Diplodocoidea) affinities from the Lower Cretaceous of Patagonia

A. Paulina Carabajal<sup>a, \*</sup>, R.A. Coria<sup>b</sup>, P.J. Currie<sup>c</sup>, E.B. Koppelhus<sup>c</sup><sup>a</sup> Instituto de Investigaciones en Biodiversidad y Medioambiente (Consejo Nacional de Investigaciones Científicas y Técnicas-Universidad Nacional del Comahue), Quintral 1250 (R8400FRF), San Carlos de Bariloche, Río Negro, Argentina<sup>b</sup> CONICET – Subsecretaría de Cultura de Neuquén – Museo Carmen Funes, Av. Córdoba 55 (8318), Plaza Huinca, Neuquén, Argentina<sup>c</sup> University of Alberta, CW405 Biological Sciences Building, Edmonton, Alberta, Canada

## ARTICLE INFO

## Article history:

Received 21 December 2016

Received in revised form

24 November 2017

Accepted in revised form 2 December 2017

Available online 12 December 2017

## Keywords:

Dicraeosauridae

Neurocranium

Natural endocast

Valanginian

Patagonia

## ABSTRACT

A partially preserved sauropod natural cranial endocast (MLL-003) was collected from the Lower Cretaceous Mulichinco Formation in Argentina. The cast consists of cemented sandstone that has preserved in detail the general endocranial morphology, but not the cranial nerves. The dural expansion, the dorsal portion of the medulla oblongata, the cerebrum and the optic lobes are preserved, and suggest the specimen belongs to a sauropod dinosaur. The presence of the pineal foramen, and possibly post-parietal foramen and floccular process, suggests this specimen is more likely related to dicraeosaurids than it is to Titanosauriformes. This makes specimen MLL-003 particularly relevant because the paleoneurology of Dicraeosauridae is poorly known.

© 2017 Elsevier Ltd. All rights reserved.

## 1. Introduction

The Dicraeosauridae are mid-sized, short-necked sauropods with a fossil record that extends from the Upper Jurassic to the mid-Cretaceous, and their remains are known in Africa, South America and North America (Janensch, 1914; Salgado and Bonaparte, 1991; Harris and Dodson, 2004; Gallina and Apesteguía, 2005; Rauhut et al., 2005; Sereno et al., 2007; Lovelace et al., 2008; Coria et al., 2012). The stem-based clade is defined as the Diplodocoidea sauropods more closely related to *Dicraeosaurus* than to *Diplodocus*, and is characterized by their relatively short necks and extreme elongation of doubled presacral neural spines (Upchurch et al., 2004). Most authors recognize that the current members of the family are the genera *Dicraeosaurus* (Janensch, 1914) from the Tendaguru Formation (Kimmeridgian) of Tanzania, *Amargasaurus* (Salgado and Bonaparte, 1991) from La Amarga Formation (Barremian) of northern Patagonia, *Brachytrachelopan* (Rauhut et al., 2005) from the Cañadon Calcáreo Formation (Tithonian) of southern Patagonia, and *Suuwassea* (Harris and Dodson, 2004; Salgado et al., 2006; Witlock, 2011) from the Morrison Formation (Tithonian) of North America.

Braincase and neurocranial anatomical information of dicraeosaurids has been gathered from the preserved braincases of *Amargasaurus*, *Dicraeosaurus* and *Suuwassea* (Janensch, 1935–1936; Paulina-Carabajal et al., 2014; Knoll et al., 2015a). These braincases are characterized (except in the North American taxon, Harris, 2006) by co-ossified frontals, the presence of a postparietal fenestra, a leaf-shaped dorsolaterally directed process on the crista prootica, basiptyergoid processes diverging at an angle of 20°, and a deep pit between the bases of the basiptyergoid processes (Upchurch et al., 2004). The braincase and endocranial morphology of *Dicraeosaurus hannsemani* was described and illustrated in detail on the basis of two complete braincases and endocasts, and an isolate basicranium (Janensch, 1935–36, figs. 94–98, tab. 13, figs. 6, 7; Knoll et al., 2014, 2017). The complete braincase of the type species of *Amargasaurus cazau* (MACN-N 15) was described by Salgado and Calvo (1992), and its endocranial morphology has been recently studied using CT scans (Paulina Carabajal et al., 2014). The braincase of *Amargasaurus* represents the only dicraeosaurid neurocranial material recorded in South America (Salgado and Calvo, 1992).

Recently, a partial natural cranial endocast (MLL 003, Paulina Carabajal et al., 2012) was collected from terrestrial deposits of the lower section of the Mulichinco Formation (Valanginian, Leanza, 2009) that outcrops in central Neuquén Province, northern

\* Corresponding author.

E-mail address: [a.paulinacarabajal@conicet.gov.ar](mailto:a.paulinacarabajal@conicet.gov.ar) (A. Paulina Carabajal).

Patagonia (Fig. 1). The specimen MLL 003 was collected from the same strata that contained a dicraeosaurid dorsal vertebra, a diplodocid caudal vertebra, indeterminate postcranial elements and petrified wood remains (Coria et al., 2012; locality in fig. 1 of Gnaedinger et al., 2017). Although incomplete, the cranial endocast MLL 003 preserves the dural expansion, the dorsal portion of the medulla oblongata, the cerebrum, and the region corresponding to the optic lobes (which are not well distinguishable in sauropods). All these structures exhibit typical sauropod dinosaur affinities.

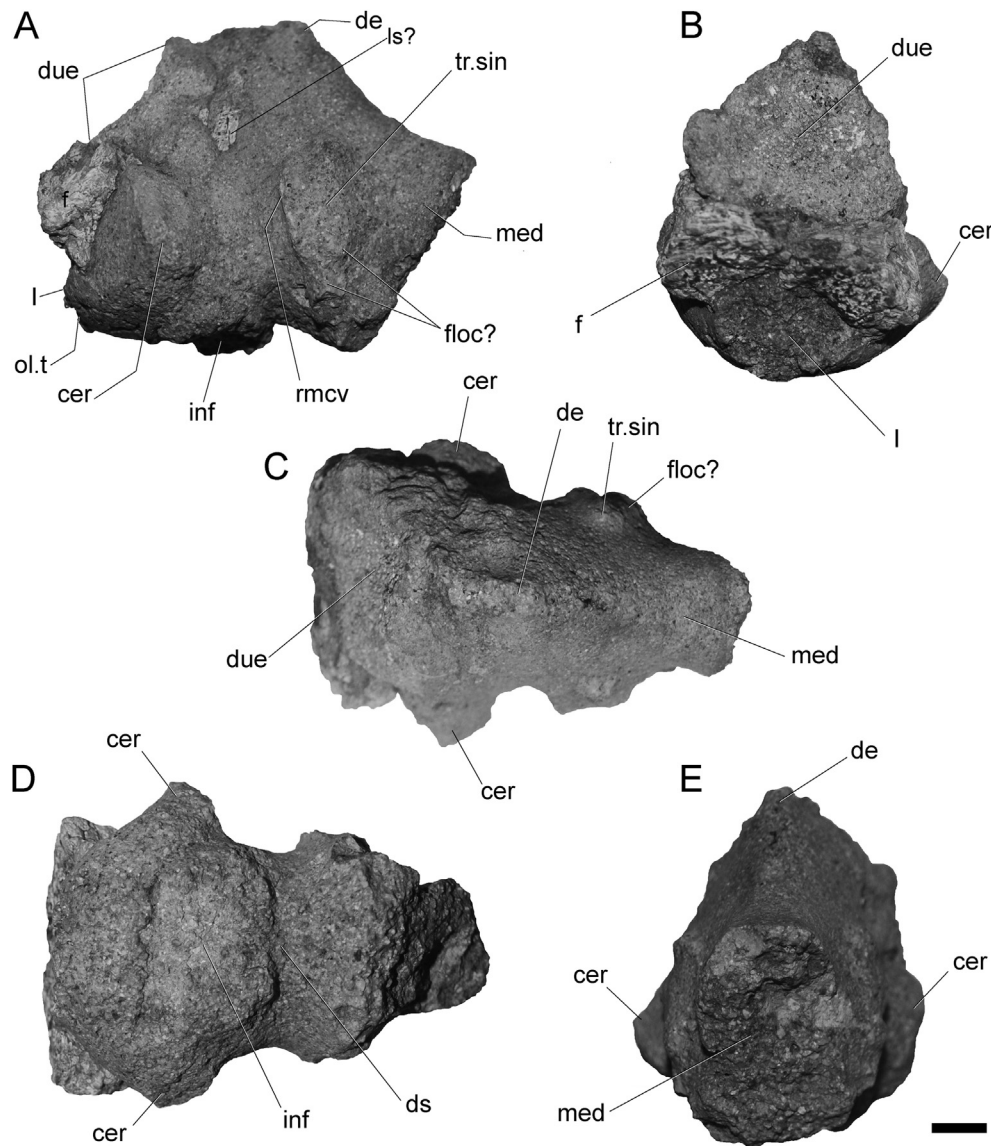
Natural cranial endocasts of reptiles are rare in the fossil record. For example, they are known for a pterosaur (Newton, 1888; Edinger, 1941), a few marine turtles (e.g., Edinger, 1938; Gaffney, 1977), and several other marine reptiles, such as metriorhynchids (e.g., Koken, 1887; Edinger, 1938, 1975). Furthermore, dinosaur natural cranial endocasts are extremely rare, and are known for few saurischian and ornithischian taxa (Hopson, 1979; Jerison, 2004). The new specimen MLL 003 is not only unique by its nature, but also, in spite of its incomplete preservation, contributes to a better

understanding and characterization of the endocranial morphology of dicraeosaurids, and of the paleoneurology of this group of peculiar sauropod dinosaurs.

## 2. Material and methods

MLL 003 consists of a partially preserved natural cranial endocast. It is formed by cemented sandstone that shows the dorsal morphology of the endocranial cavity in all details (the region corresponding to the roots of the cranial nerves is not preserved) (Fig. 1). All the braincase bones that enclosed the endocranial cavity are missing, except for small pieces of the frontal and the laterosphenoid that remain attached to the cast (Fig. 1A,B; Supplementary information 1).

Comparisons were made with the digital cranial endocast of *Amargasaurus* (Paulina Carabajal et al., 2014); and photos of two cranial endocasts of *Dicraeosaurus*: MBR 1916.1 (cranial endocast of specimen MBR 2379.1 (= dd 307, in Janensch, 1935–36)), and MBR



**Fig. 1.** Natural cranial endocast of dicraeosaurid MLL 003 in left lateral (A), anterior (B), dorsal (C), ventral (D), and posterior (E) views. Abbreviations: I, cranial nerve I (olfactory nerve); **cer**, cerebral hemisphere; **de**, dorsal expansion; **ds**, impression of dorsum sellae; **due**, dural expansion correlated externally with the frontoparietal and postparietal fenestrae; **f**, frontal; **floc?**, probable floccular process; **inf**, infundibulum; **med**, medulla oblongata; **ol.t**, olfactory tract; **rmcv**, anterior middle cerebral vein; **tr.sin**, transverse venous sinus. Scale bar = 10 mm [planned for 1.5 column].

1917 (cranial endocast of specimen MBR 2378.3 (= dd 495 in Janensch, 1935–36)).

**Institutional abbreviations.** **MACN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; **MBR**, Museum für Naturkunde, Berlin, Germany; **MLL**, Museo Municipal de Las Lajas, Las Lajas, Argentina.

### 3. Description

The cranial endocast MLL 003 preserves most of the dorsal and lateral aspects of the endocranial cavity. The fragments of the frontal frame posteriorly what seems to be a large frontoparietal foramen, which is a feature also present in *Amargasaurus* Salgado and Bonaparte 1991, *Amargasaurus* Cope 1877 (APC, pers. obs.), *Dicraeosaurus* Janensch 1914, *Diplodocus* Marsh 1878 (Hopson, 1979; Zheng, 1996), and *Suuwassea* (Harris, 2006). These feature, however, is highly inconsistent within sauropods (being variation among *Diplodocus* specimens), although the opening is probably genuine in *Dicraeosaurus* (Knoll, pers. Comm). In MLL 003 it is not possible to determine the presence of the postparietal foramen, which is present in known dicraeosaurids and in several early sauropodomorphs.

The narrowest point of the endocast lies in the hindbrain immediately posterior to the cerebellum, in between the right and left optic capsules (Fig. 1C). The angles between forebrain, midbrain and hindbrain are similar to those observed in *Amargasaurus* (Paulina Carabjal et al., 2014) and *Dicraeosaurus* (Janensch, 1935–36), resulting in a slightly sigmoid cranial endocast (excluding the region corresponding to the dorsal expansion) in lateral view (Fig. 2).

In MLL 003, the more remarkable features of the forebrain include the olfactory tract (CN I) and the cerebral hemispheres. The ventral section of the diencephalon suggests that there was a wide infundibulum. As in most sauropods, the olfactory tract is almost nonexistent. The olfactory bulbs are not preserved. The greatest mediolateral breadth of the endocranial space lies across the cerebral hemispheres of the forebrain, and is 62 mm. The cerebral hemispheres are well-marked. The lateral border of the cerebrum is pyramidal in shape (Fig. 1A,D) as in *Amargasaurus* (Paulina Carabjal et al., 2014) and *Dicraeosaurus* (Fig. 2C), which is unlike the rounded cerebral hemispheres observed in derived titanosaurs (e.g., Paulina Carabjal, 2012; Knoll et al., 2013, 2015b, in press) and rebbachisaurids (Serenó et al., 2007; Paulina Carabjal and Calvo, 2015; Paulina Carabjal et al., 2016).

The dorsal expansion of MLL 003 is prominent, forming a pointy triangular prominence (Fig. 1A). It is posterior to the region occupied by the dural expansion. The infilling of the dural expansion (which was probably occupied by venous sinuses) is missing. The transverse section of the dural expansion suggests it was similar in size to the one present in *Amargasaurus*, in which the dural expansion obscures the dorsal surfaces of the cerebral hemispheres (Paulina Carabjal et al., 2014) (Fig. 2D,E). In *Dicraeosaurus*, the enlarged dural expansion obscures the dorsal surfaces of the cerebral hemispheres (Fig. 2F). In both *Amargasaurus* and *Dicraeosaurus*, the dural expansion correlates externally with the frontoparietal and the postparietal fenestrae (Paulina Carabjal et al., 2014, fig. 2). Differentiation of both fenestrae in MLL 003 it is not possible because the corresponding region is not preserved in the endocast. In neither *Amargasaurus* nor MLL 003 cranial endocasts, there is any large orbitocerebral foramen (for the orbitocerebral vein) lateral to the cerebral hemisphere, unlike the condition in *Dicraeosaurus* (Janensch, 1935–36) (Fig. 2C).

The mesencephalic structures visible in dinosaur endocasts consist of the optic lobes and cranial nerves III and IV (Franzosa, 2004). As in other sauropod endocasts (Serenó et al., 2007; Knoll

and Schwarz-Wings, 2009; Paulina Carabjal, 2012), the optic lobes of MLL 003 are not visible, whereas the casts of cranial nerves III and IV are not preserved because the ventral region of the cranial endocast is missing.

The visible hindbrain features in the endocast of MLL 003 include the cerebellum and the medulla oblongata. There is a large vertical protuberance on the endocast dorsal to CN V. This structure corresponds with an infilling of the space that was occupied with a venous sinus related to the middle cerebral vein system (Fig. 1A, Supplementary information 1), specifically to the anterior middle cerebral vein (=transverso trigeminal vein, in Leahey et al., 2015). This protuberance is present in titanosaurs (Paulina Carabjal, 2012) and was described for *Spinophorosaurus* (Knoll et al., 2012) and *Amargasaurus* (Paulina Carabjal et al., 2014). In MLL 003, the relative development of this vertical protuberance is similar to those observed in the dicraeosaurids *Amargasaurus* and *Dicraeosaurus*, the rebbachisaurids *Limaysaurus* (Paulina Carabjal and Calvo, 2015) and MMCh-PV 71 (Paulina Carabjal et al., 2016). However, in the rebbachisaurid sauropods, the protuberance is markedly crescentic (Paulina Carabjal et al., 2016). On the other hand, in *Dicraeosaurus* (Janensch, 1935–36) and the rebbachisaurid MMCh-PV 71 (Paulina Carabjal et al., 2016), the ventral distal section of the protuberance turns laterally, and represents the cast of a small floccular recess. It is highly probable that the enlarged transverse sinus is as well related to a small floccular process in *Amargasaurus*, as observed in MLL 003 (Fig. 2A–C). In MLL 003 the anterior margin of this transverse protuberance seems to be the cast of the impression left by the anterior middle cerebral vein, which in this case has no independent exit foramen and, therefore, leaves the endocranial cavity through the trigeminal foramen (Fig. 1A).

The medulla oblongata is partially preserved and has the same lateral outline observed in *Amargasaurus*, although is slightly more taller and transversely wider than that of *Dicraeosaurus* (Fig. 2).

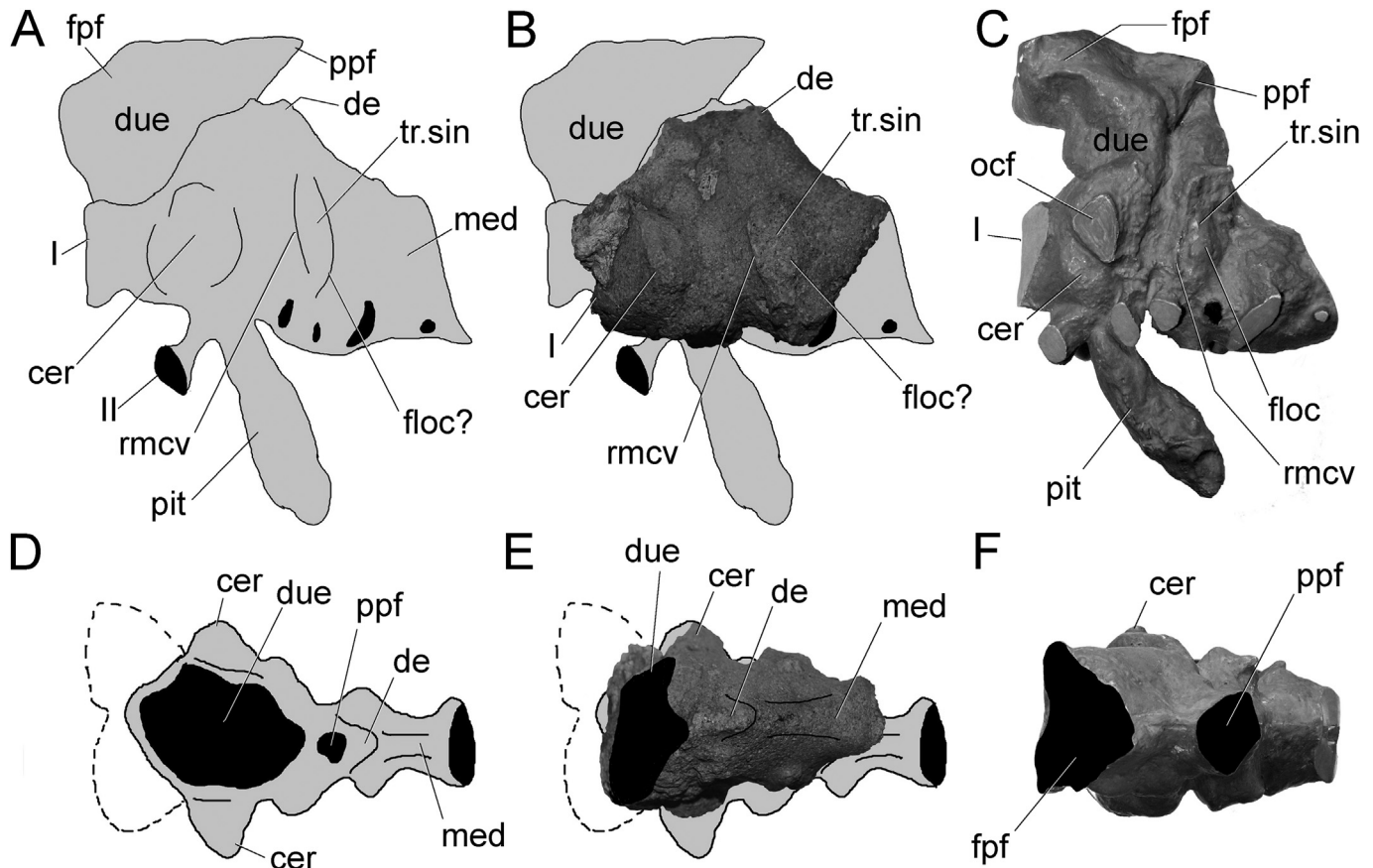
### 4. Discussion

Unlike dicraeosaurids (Janensch, 1936; Salgado and Bonaparte, 1991), rebbachisaurids and titanosaurs do not have fenestrated skull roof (e.g., postparietal or postfrontal fenestrae). The inferred presence of a markedly large anterior dural expansion related with at least one skull roof fenestra indicates that MLL 003 can be identified either as a dicraeosaurid or an indeterminated non-rebbachisaurid diplodocoid. Notwithstanding, the general morphology of the endocast is markedly similar to those observed in *Amargasaurus* (Paulina Carabjal et al., 2014) and *Dicraeosaurus* (Janensch, 1935–36). These similarities include the development of the pyramidal cerebral hemisphere (which expands markedly laterally), the development of the transverse sinus, the presence of a floccular process, and the outline of the medullar region (Fig. 2). The absence of an extremely large orbitocerebral foramen and a smaller dural expansion that does not obscure the pointed dorsal expansion are traits shared between *Amargasaurus* and MLL 003 (Fig. 2A,B).

The greatest mediolateral breadth of the endocranial space of MLL 003 is across the cerebral hemispheres and is 62 mm, which is approximately the same width observed in the 95 mm long endocast (from the back of the olfactory tract to the foramen magnum) of the *Amargasaurus cazaui* holotype. The complete cranial endocast of MLL 003 would have probably had the same encephalic proportions as *Amargasaurus* (excluding the venous and infilled sections of the frontoparietal and parietal fenestrae) and probably represents a sub-adult or adult specimen.

Moreover, the natural cast exhibits non-titanosaur endocranial features (Paulina Carabjal, 2012; Knoll et al., 2013), suggesting





**Fig. 2.** Compared dicraeosaurid endocranial morphology in left lateral (A–C) and dorsal (D–F) views. *Amargasaurus cazau* (after Paulina Carabajal et al., 2014) (A,D); dicraeosaurid MLL 003 (outline of complete endocranial morphology based on *Amargasaurus*) (B,E), and *Dicraeosaurus* (MBR 1916.1) (C,F). Abbreviations as in Fig. 1, plus: II, cranial nerve II; **fpf**, frontoparietal fenestra; **ocf**, orbitocerebral fontanelle; **pit**, pituitary; **ppf**, postparietal foramen. Not to scale. [planned for 1.5 column].

diplodocoid affinities for the new specimen (e.g. Hopson, 1979; Harris, 2006; Balanoff et al., 2010). In particular, characters such as a markedly large dorsal space in the endocranial cavity (inferred in MLL 003 from what seems to be partially preserved margins of openings in the skull roof such as the parietal/frontoparietal fenestra and the postparietal fenestra), together with the presence of a well-developed transversal venous sinus (which is probably related to the presence of a floccular process) are features shared with *Amargasaurus* and *Dicraeosaurus* (Janensch, 1935–36; Paulina Carabajal et al., 2014).

## 5. Conclusions

Despite recent advances (Paulina Carabajal et al., 2014; Knoll et al., 2014, 2015a, 2017), dicraeosaurid paleoneurology is poorly known. The cranial endocast and inner ear of *Amargasaurus* represent the only available dicraeosaurid endocranial information in South America. This makes the new specimen particularly relevant from both morphologic and phylogenetic points of view. Characters of MLL 003 such as the presence of a large frontoparietal fenestra (related to a large longitudinal dorsal venous sinus), a large transverse sinus and a floccular process, suggest dicraeosaurid affinities. The specimen described here together with other postcranial remains currently under study indicates a continuous presence of dicraeosaurids in South America from the Late Jurassic up to the mid-Cretaceous. The forthcoming detailed anatomical analysis of these specimens will shed light to both the phylogeny and biogeography of the Dicraeosauridae.

## Acknowledgments

Photographs of the braincases and cranial endocasts of *Dicraeosaurus* were kindly provided by J. Canale and F. Knoll. We thank the comments and corrections made by the editor E. Koutsovkos and the reviewers F. Knoll and V. Diez-Diaz, which greatly improved this manuscript. The 3D PDF based on photogrammetry of the specimen MLL 003 was made by G. Windholtz and I. Díaz Martínez (Universidad Nacional de Río Negro). This research was supported by PIP-CONICET 0233 and University of Río Negro PI 40-A-157 and 378 (to R.A.C), and Dinosaur Research Institute grant (Alberta, Canada to P.J.C.).

## References

- Balanoff, A.M., Bever, G.S., Ikejiri, T., 2010. The braincase of *Apatosaurus* (Dinosauria, sauropoda) based on Computed Tomography of a new specimen with comments on variations and evolution in sauropod neuroanatomy. *American Novitates* 3677, 1–29.
- Cope, E.D., 1877. On a gigantic saurian from the Dakota epoch of Colorado. *Paleontological Bulletin* 25, 5–10.
- Coria, R.A., Ortega, F., Succar, C., Currie, P., Koppelhus, E., 2012. First record of a dicraeosaurid sauropod from the Lower Cretaceous (Valanginian) of Neuquén Basin, Ameghiniana, Suplemento Resúmenes 49, R44.
- Edinger, T., 1938. Über steinkerne von hirn-und ohr-höhlen der Mesosuchier *Goniopholis* und *Pholidosaurus* aus dem Bückeburger Wealden. *Acta Zoologica* 19, 467–505.
- Edinger, T., 1941. The brain of *Pterodactylus*. *American Journal of Science* 239, 665–682.
- Edinger, T., 1975. Paleoneurology 1804–1966. An annotated bibliography (with a foreword by Bryan Patterson). *Advances in Anatomy, Embryology and Cell Biology* 49, 1–258.

- Franzosa, J.W., 2004. Evolution of the brain in Theropoda (Dinosauria) (Unpub. PhD Thesis). The University of Texas at Austin, Austin, 357 pp.
- Gaffney, E.S., 1977. An endocranial cast of the side-necked turtle, *Bothremys*, with a new reconstruction of the palate. *American Museum Novitates* 2639, 1–12.
- Gallina, P.A., Apesteguiá, S., 2005. *Cathartesaura anaeróbica* gen. et sp. nov., a new rebbachisaurid (Dinosauria, Sauropoda) from the Huincul Formation (Upper Cretaceous), Río Negro, Argentina. *Revista Museo Argentino De Ciencias Naturales* 7, 153–166.
- Gnaedinger, S., Coria, R.A., Koppelhus, E., Casadío, S., Tunik, M., Currie, P.J., 2017. First Lower Cretaceous record of Podocarpaceae wood associated with dinosaur remains from Patagonia, Neuquén Province, Argentina. *Cretaceous Research* 78, 228–239.
- Harris, J.D., Dodson, P., 2004. A new diplodocoid sauropod dinosaur from the Upper Jurassic Morrison Formation of Montana, USA. *Acta Palaeontologica Polonica* 49, 197–210.
- Harris, J.D., 2006. Cranial osteology of *Suuwassea emilieae* (Sauropoda: Diplodocoidea: Flagellicaudata) from the Upper Jurassic Morrison Formation of Montana. *Journal of Vertebrate Paleontology* 26, 88–102.
- Hopson, J.A., 1979. Paleoneurology. In: Gans, C. (Ed.), *Biology of the Reptilia*. Academic Press, New York, pp. 39–146.
- Janensch, W., 1914. Übersicht über die Wirbeltierfauna der Tendaguru-Schichten, nebst einer kurzen Charakterisierung der neu aufgeführten Arten von Sauropoden. *Archiv für Biontologie* 3, 81–110.
- Janensch, W., 1935–1936. Die Schädel der Sauropoden *Brachiosaurus*, *Barosaurus* und *Dicraeosaurus* aus den Tendaguru-Schichten Deutsch-Ostafrikas. *Palaeontographica* 2, 147–298.
- Jerison, H.J., 2004. Dinosaur brains. In: Adelman, G., Smith, B.H. (Eds.), *Encyclopedia of Neuroscience*. CD Edition. Elsevier, Amsterdam [CD EDITION].
- Knoll, F., Schwarz-Wings, D., 2009. Palaeoneuroanatomy of *Brachiosaurus*. *Annales de paléontologie* 95 (3), 165–175.
- Knoll, F., Witmer, L.M., Ortega, F., Ridgely, R.C., Schwarz-Wings, D., 2012. The braincase of the basal sauropod dinosaur *Spinophorosaurus* and 3D reconstructions of the cranial endocast and inner ear. *PLoS One* 7 (1), e30060. <https://doi.org/10.1371/journal.pone.0030060>.
- Knoll, F., Ridgely, R.C., Ortega, F., Sanz, J.L., Witmer, L.M., 2013. Neurocranial osteology and neuroanatomy of a Late Cretaceous titanosaurian sauropod from Spain (*Ampelosaurus* sp.). *PLoS One* 8, e54991. <https://doi.org/10.1371/journal.pone.0054991>.
- Knoll, F., Ridgely, R.C., Schwarz-Wings, D., Witmer, L.M., 2014. The brain and inner ear of the sauropod dinosaurs from Tendaguru (Tanzania) in the context of sauropod evolution: a unique glimpse into the sensory world of Gondwanan Jurassic giants. *Journal of Vertebrate Paleontology*, Program and Abstracts: 160.
- Knoll, F., Ridgely, R.C., Witmer, L.M., 2015a. Comparative paleoneurology of the basal dicraeosaurid sauropod *Suuwassea emilieae*. *Journal of Vertebrate Paleontology*, Program and Abstracts: 156.
- Knoll, F., Witmer, L.M., Ridgely, R.C., Ortega, F., Sanz, J.L., 2015b. A new titanosaurian braincase from the Cretaceous "Lo Hueco" locality in Spain sheds light on neuroanatomical evolution within Titanosauria. *PLoS One* 10 (10), e0138233.
- Knoll, F., Ridgely, R.C., Schwarz, D., Witmer, L.M., 2017. Brain and labyrinth anatomy of the Gondwanan Jurassic sauropod *Dicraeosaurus*. In: 15th Annual Meeting of the European Association of Vertebrate Palaeontologists.
- Knoll, F., Lautenschlager, S., Valentin, X., Díez Díaz, V., Pereda Suberbiola, X., Vilanova, G., García, G., 2017. Palaeoneurology of a titanosaurian sauropod from the Late Cretaceous of Fox-Amphoux-Métisson (southern France) and its systematic significance. *Journal of Vertebrate Paleontology*, Program and Abstracts, 2017 in press.
- Koken, E., 1887. Die Dinosaurier, Crocodiliden und Sauropterygier des norddeutschen Wealden. *Palaeontologische Abhandlungen* 3, 309–419.
- Leahey, L.G., Molnar, R.E., Carpenter, K., Witmer, L.M., Salisbury, S.W., 2015. Cranial osteology of the ankylosaurian dinosaur formerly known as *Minmi* sp. (Ornithischia: Thyreophora) from the Lower Cretaceous Allaru Mudstone of Richmond, Queensland, Australia. *PeerJ* 3, e1475.
- Leanza, H.A., 2009. Las principales discordancias del Mesozoico de la Cuenca Neuquina según observaciones de superficie. *Revista del Museo Argentino de Ciencias Naturales* 11, 145–184.
- Lovelace, D.M., Hartman, S.A., Wahl, W.R., 2008. Morphology of a specimen of *Supersaurus* (Dinosauria, Sauropoda) from the Morrison Formation of Wyoming, and a re-evaluation of diplodocid phylogeny. *Arquivos Do Museu Nacional, Rio De Janeiro* 65, 527–544.
- Marsh, O.C., 1878. Principal characters of American Jurassic dinosaurs. *American Journal of Science* 95, 411–416.
- Newton, E.T., 1888. On the skull, brain and auditory organ of a new species of pterosaurian (*Scaphognathus purdoni*) from the Upper Lias near Whitby, Yorkshire. *Proceedings of the Royal Society* 43, 436–440.
- Paulina Carabjal, A., 2012. Neuroanatomy of titanosaurid dinosaurs from the Upper Cretaceous of Patagonia, with comments on endocranial variability within Sauropoda. *The Anatomical Record* 295, 2141–2156.
- Paulina Carabjal, A., Calvo, J.O., 2015. Nueva información sobre la neuroanatomía del saurópodo *Limaysaurus* basada en Tomografías computadas. Simposio Nuevas perspectivas en el estudio de la anatomía endocraneana de vertebrados en América del Sur, 5° Congreso Latinoamericano de Paleontología de Vertebrados (Colonia), Abstracts, 99.
- Paulina Carabjal, A., Coria, R.A., Currie, P.J., Koppelhus, E.B., 2012. A possible dicraeosaurid (Sauropoda, Diplodocoidea) cranial endocast from the Early Cretaceous of Patagonia. XXVI Jornadas Argentinas de Paleontología de Vertebrados. *Ameghiniana* 49 (Suppl. 4), R54.
- Paulina Carabjal, A., Carballido, J.L., Currie, P.J., 2014. Braincase, neuroanatomy, and neck posture of *Amargasaurus cazaui* (Sauropoda, Dicraeosauridae) and its implications for understanding head posture in sauropods. *Journal of Vertebrate Paleontology* 34 (4), 870–882.
- Paulina Carabjal, A., Canale, J.L., Haluza, A., 2016. New rebbachisaurid cranial remains (Sauropoda, Diplodocoidea) from the Cretaceous of Patagonia, Argentina, and the first endocranial description for a South American representative of the clade. *Journal of Vertebrate Paleontology*. <https://doi.org/10.1080/02724634.2016.1167067>.
- Rauhut, O.W.M., Remes, K., Fechner, R., Cladera, G., Puerta, P., 2005. Discovery of a short-necked sauropod dinosaur from the Late Jurassic period of Patagonia. *Nature* 435, 670–672.
- Salgado, L., Bonaparte, J.F., 1991. Un nuevo saurópodo Dicraeosauridae, *Amargasaurus cazaui* gen. et sp. nov., de la Provincia del Neuquén, Argentina. *Ameghiniana* 28, 333–346.
- Salgado, L., Calvo, J.O., 1992. Cranial osteology of *Amargasaurus cazaui* Salgado and Bonaparte (Sauropoda, Dicraeosauridae) from the Neocomian of Patagonia. *Ameghiniana* 29, 337–346.
- Salgado, L., Carvalho, I.S., Garrido, A.C., 2006. *Zapalasaurus bonapartei*, a new sauropod dinosaur from La Amarga Formation (Lower Cretaceous), north-western Patagonia, Neuquén Province, Argentina. *Geobios* 39, 695–707.
- Sereno, P.C., Wilson, J.A., Witmer, L.M., Whitlock, J.A., Maga, A., Ide, O., Rowe, T.A., 2007. Structural extremes in a Cretaceous dinosaur. *PLoS One* 2, e1230.
- Upchurch, P., Barrett, P.M., Dodson, P., 2004. Sauropoda. In: Weishampel, D.B., Dodson, P., Osmolska, H. (Eds.), *The Dinosauria*. University of California Press, Berkeley and Los Angeles, pp. 259–322.
- Witlock, J.A., 2011. A phylogenetic analysis of Diplodocoidea (Saurischia: Sauropoda). *Zoological Journal of the Linnean Society* 161, 872–915.
- Zheng, Z., 1996. Cranial anatomy of *Shunosaurus* and *Camarasaurus* (Dinosauria: Sauropoda) and the phylogeny of sauropods (Doctoral thesis). Texas Tech University, 194 pp.

## Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.cretres.2017.12.001>.