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We report an isolated left frontal (MCF-PVPH 320) corresponding to a medium-sized theropod dinosaur from the Portezuelo Formation (Coniacian) of northern Patagonia. It shows a unique combination of traits that are not present in any other known Cretaceous theropod from South America. MCF-PVPH 320 is robust and anteroposteriorly short, with a flat and smooth dorsal surface largely excavated by the supratemporal fossa. Endocranially, the olfactory bulb impression is elongate, and the olfactory tract impression is markedly shortened anteroposteriorly. MCF-PVPH 320 differs greatly from the frontals of Late Cretaceous theropods, such as abelisaurids, megaraptorines and carcharodontosaurids. In contrast, character states including the thickness of the bone, V-shaped frontoparietal suture, reduced participation on the orbital margin and markedly short olfactory tract impression suggest the presence of an unknown mid-sized to large allosauroid for the Portezuelo Formation.

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Key words: frontal, skull roof, theropod, Coniacian, Argentina.

THE CRANIAL roof of theropod dinosaurs is morphologically variable, possibly in conjunction with modifications in the rostral part of the skull for feeding and other behaviours (Currie 1997). Although not typically considered character-rich (Sereno & Brusatte 2008, Cau *et al*. 2012), the frontal as a singular element does have diagnostic value, even in some cases up to species level (Currie 1987).

Here we describe an isolated left frontal (MCF-PVPH 320) collected from the Portezuelo Formation at Sierra del Portezuelo (Coniacian; Leanza *et al*. 2004), 22 km west of the town of Plaza Huincul in Neuquén Province, Argentina. This locality has yielded a diverse assemblage of theropods including the large-bodied neovenatorid *Megaraptor namunhuaquii* (Novas 1998), the small to mid-sized dromeaosaurs *Neuquenraptor argentinus* (Novas & Pol 2005) and *Unenlagia comahuensis* (Novas & Puerta 1997), and the alvarezsaurid *Patagonykus puertai* (Novas 1997). However, none of these taxa shares diagnostic features with the specimen described here. MCF-PVPH 320 bears sufficient information to allow for both comparisons and a phylogenetic analysis with other taxa. We suggest that MCF-PVPH 320 represents an as-yet unknown theropod from Cretaceous rocks of South America.

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Institutional abbreviations. MCF, Museo Carmen Funes, Plaza Huincul, Argentina; SMNS, Staatliches Museum fur Naturkunde, Stuttgart, Germany; TPM, Royal Tyrrell Museum, Alberta, Canada; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Systematic palaeontology

DINOSAURIA Owen, 1842
THEROPODA Marsh, 1881
TETANURAE Gauthier, 1986
ALLOSAUROIDEA Marsh, 1878

Genus et species indet.

Description. MCF-PVPH 320 is a well-preserved, almost complete isolated left frontal that lacks only the nasal process. Part of the sutural contact for the nasal is preserved near the midline (a shallow V-shaped smooth surface) indicating that both frontals formed a short median triangular projection between the nasals, resulting in a W-shaped frontonasal suture (Figs 1A, 2A). MCF-PVPH 320 is robust and markedly thickened along the midline (30 mm) at the level of the postorbital process, a characteristic mentioned for carcharodontosaurs (Currie & Zhao 1993, Cau *et al*. 2012) and abelisaurids (Carrano & Sampson 2008; Fig. 1C).

In dorsal view, the frontal is rather rectangular: 66 mm long from the frontoparietal suture to the base of

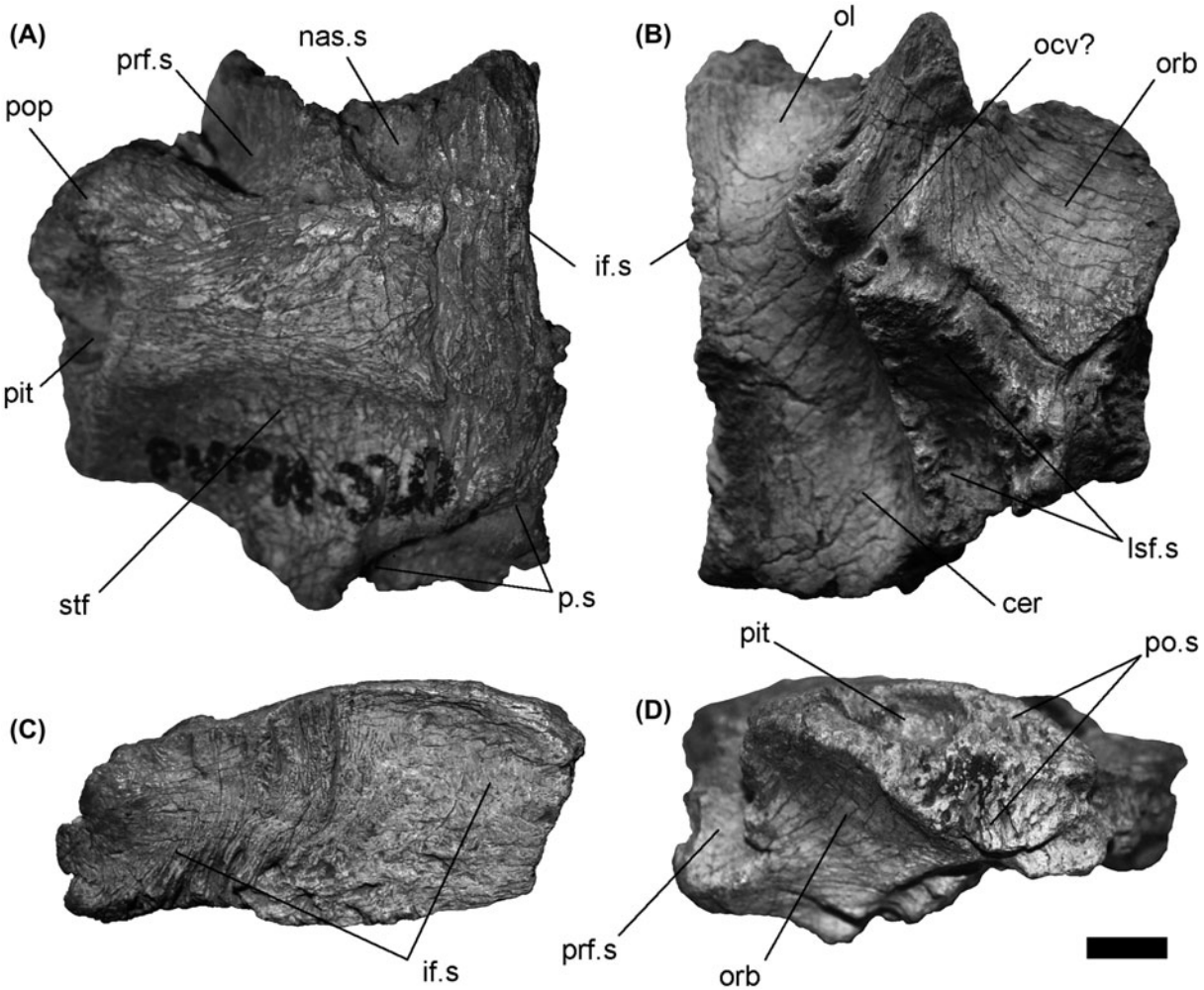

Fig. 1. Theropod frontal MCF-PVPH-320 in dorsal (**A**), ventral (**B**), medial (**C**) and lateral (**D**) views. Abbreviations: cer, cerebral hemisphere impression; lsf.sut, sutural contact for the laterosphenoid; nas.sut, sutural contact for the nasal; ol.b, olfactory bulb cavity; ol.tr, olfactory tract cavity; orb.v, orbital vault; p.sut; sutural contact for the parietal; po.sut, sutural contact for the postorbital; prf.sut, sutural contact for the prefrontal; stf, supratemoporal fossa; stf.am, anterior margin of supratemporal fossa. Scale bar = 10 mm.

the nasal process; 61 mm wide from the interfrontal suture to the end of the postorbital process. The dorsal surface is flat and smooth, without any ornamentation, unlike the markedly sculptured frontals of abelisaurids (e.g., Paulina Carabajal 2011a, fig. 2; Paulina Carabajal 2011b, fig. 1). The width/length ratio (length measured from the frontoparietal suture to the prefrontal suture) is approximately 0.9 in MCF-PVPH 320, whereas it is approximately 0.7 in abelisaurids and carcharodonotosaurids (Sereno & Brusatte 2008, Cau *et al*. 2012). This indicates that the frontal section of the skull roof was transversely broad and anteroposteriorly short (Figs 1A, 2A). The supratemporal fossa is shallow but well defined, with a transversely straight anterior margin; this is unlike the concave anterior margin of *Megaraptor* (Porfiri *et al*. 2014) or the anterolaterally oriented edge of the probable megaraptorid frontal MCF-PVPH 411 (Coria & Currie 2002, Paulina Carabajal 2009). In MCF-PVPH 320, the supratemporal fossa is largely excavated for more than the 50% of the frontal length. The tabular postorbital process is poorly projected laterally and, therefore, obscured in dorsal view (Fig. 1A). The reconstructed sagittal bar, delimited between both supratemporal fossae, was low, flat and 24 mm wide (Fig. 2A).

Anteriorly, part of the sutural surface of contact with the nasal is preserved. The nasal process is only preserved posteriorly and projects more anteriorly on the medial edge. The reconstructed frontonasal suture is W-shaped (Figs 1A, 2A). Posteriorly, the frontoparietal suture is V-shaped in dorsal view (Figs. 1A, 2A) but transversally oriented on the ventral side (endocranial surface), indicating that the parietals bore an anterodorsal projection that wedged between the dorsal surfaces of the frontals but not extending to the ventral (endocranial) surface. This V-shaped dorsal view of the frontoparietal suture is thought to be characteristic of tyrannosaurids (e.g., Currie 2003) in which an anterodorsal process of the parietal separates both frontals posteriorly. However, in a few tyrannosaurid crania, the frontoparietal sutural contact is also V-shaped on the ventral side (e.g., TMP 81.09.01), because the parietal forms a median tongue-like projection that entirely separates the frontals posteriorly (Paulina Carabajal

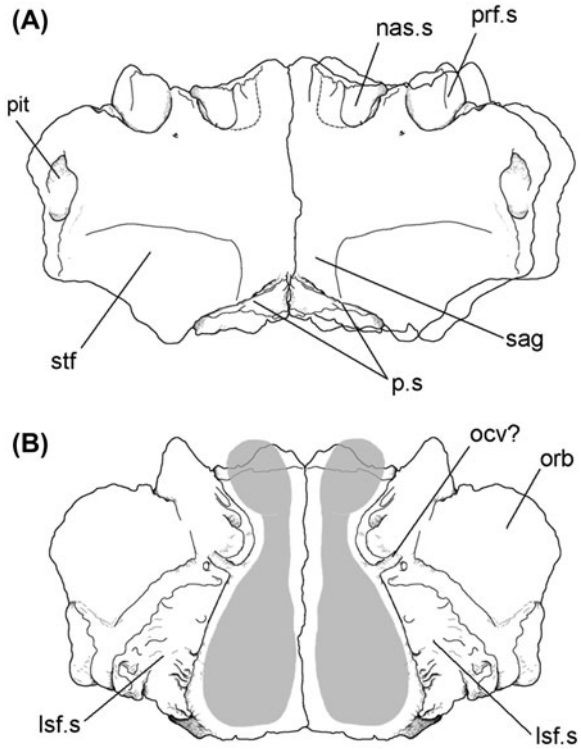

Fig. 2. Reconstructed skull roof of the theropod MCF-PVPH-320, in dorsal (**A**) and ventral (**B**) views. Abbreviations: cer, cerebral hemisphere impression; lsf.sut, sutural contact for the laterosphenoid; nas.sut, sutural contact for the nasal; ol.b, olfactory bulb cavity; ol.tr, olfactory tract cavity; orb.v, orbital vault; p.sut; sutural contact for the parietal; po.sut, sutural contact for the postorbital; prf.sut, sutural contact for the prefrontal; sag, sagittal bar; stf, supratemoporal fossa; stf.am, anterior margin of supratemporal fossa. Scale bar = 10 mm.

2009). The opposite situation is evident in the unnamed megaraptorid MCF-PVPH 411, in which the frontoparietal suture is transverse dorsally but V-shaped endocranially (Paulina Carabajal 2009).

In medial view, the interfrontal suture of MCF-PVPH 320 has a maximum/minimum height of 30/18 mm. The contact surface is mostly flat, having an almost vertical ridge (Fig. 1C). In lateral view, the postorbital contact is oval, with a low horizontal ridge separating two distinct striated areas. The anterodorsal section forms a shelf, flooring a deep oval pit that was probably part of the postorbital contact. In front of the postorbital process, there is a triangular slit for the prefrontal contact that corresponds to the 'peg-and-socket' condition described in *Allosaurus*, *Baryonyx* and carcharodonotosaurids (Carrano *et al*. 2012).

In ventral view, the laterosphenoid contact is concave with a triangular outline (Fig. 1B). The section of the frontal that contributes to the orbital vault between the prefrontal and postorbital contacts is a small, fan-like smooth surface that is poorly developed laterally. The frontal seems to have been almost excluded from the orbital rim by the postorbital and the prefrontal (Fig. 1D).

On the ventral side of the frontal, the impressions left by the cerebral hemisphere and the olfactory tract and bulb are preserved (Figs 1B, 2B). The cerebral hemisphere impression is relatively small and oval, narrower (16 mm) than long (35 mm). The impression of the olfactory tract is markedly short and transversely wide. The oval olfactory bulb impression is complete, slightly divergent from the midline anteriorly, and relatively large when compared with the size of the cerebral hemisphere impression (Fig. 2B). This morphology differs from the long and robust olfactory tract and bulbs (enclosed by ossified ethmoidal elements) observed in abelisaurids (e.g., Sampson & Witmer 2007, Paulina Carabajal & Succar 2015) and carcharodontosaurids (e.g., Larsson 2000, Paulina Carabajal & Canale 2010).

Discussion

The morphology of MCF-PVPH 320 indicates that it is neither an abelisaurid nor a carcharodontosaurid. Nevertheless, it resembles these taxa in the thickness of the frontal and its exclusion from the orbital margin. In contrast to Abelisauridae (see Paulina Carabajal 2011b and references herein), the surface of the frontal is not ornamented. In contrast to both abelisaurids and carcharodontosaurids, which have an olfactory tract and bulb anteroposterior length that surpass the length of the cerebral hemispheres (e.g., Sampson & Witmer 2007, Paulina Carabajal & Canale 2010, Paulina Carabajal & Succar 2015), MCF-PVPH 320 has endocranially olfactory tract and bulb impressions that are shorter than the cerebral hemisphere's length (Fig. 2B). This is also the case in the probable megaraptorid MCF-PVPH-411 and in the allosauroid *Allosaurus* (e.g., USNM 544100). Within Allosauroidea, *Acrocanthosaurus* and *Sinraptor* also have relatively short (anteroposteriorly) olfactory bulb impressions (Paulina Carabajal & Currie 2012, fig. 7D, E); however, the length of the olfactory tract plus the olfactory bulbs surpasses the length of the cerebral hemisphere, as in abelisaurids (i.e., Sampson & Witmer 2007; Paulina Carabajal 2011b) and carcharodontosaurids (e.g., Paulina Carabajal & Canale 2010, Paulina Carabajal & Currie 2012). *Megaraptor* (Novas 1998), *Neuquenraptor* (Novas & Pol 2005), *Patagonykus* (Novas 1997) and *Unenlagia* (Novas & Puerta 1997) have been recorded from the Sierra del Portezuelo locality. *Megaraptor* is the only taxon of similar body size that is represented by skull roof material (Porfiri *et al*. 2014) and is currently the only non-abelisaurid and non-carcharodontosaurid mid-sized theropod recorded from the Portezuelo Formation. *Megaraptor* was first identified as a basal coelurosaurian (Novas 1998) but was reassigned to basal Tetanurae following the discovery of additional material (Calvo *et al*. 2004, Benson *et al*. 2010). Currently, *Megaraptor* belongs to an endemic radiation of medium-sized theropods, together with *Aerosteon* and *Orkoraptor* (Benson *et al*. 2010). However, their phylogenetic status is disputed, being considered either members of Neovenatoridae

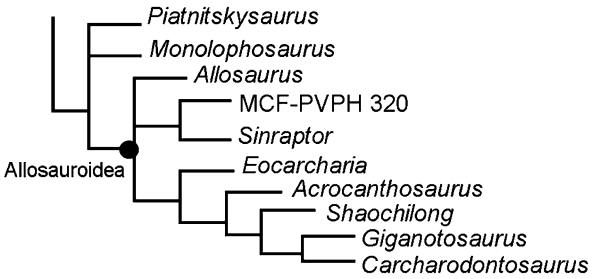

Fig. 3. Detail of the Consensus Cladogram showing the position of the specimen MCF-PVPH-320 within Theropoda. CI = 0.394 and RI = 0.506.

(Benson *et al*. 2010, Carrano *et al*. 2012) or basal tyrannosauroids (Novas *et al*. 2013). A recently discovered juvenile skeleton attributed to *Megaraptor* (Porfiri *et al*. 2014) includes an isolated left frontal that shows a larger participation in the supratemporal fossa, a less-developed postorbital process and a stepped nasal process similar to MCF-PVPH 320. The probable megaraptorid MCF-PVPH 411 (Coria & Currie 2002), exposed at Sierra Barrosa, 30 km east from Sierra del Portezuelo, also corresponds to a mid-sized specimen with preserved skull roof. Although its frontal shares some traits with MCF-PVPH 320 (e.g., thickness of the bone, reduced participation on the orbital margin, and markedly short olfactory tract impression), other characteristics (i.e., lateroventrally inclined dorsal surface of the bone) imply taxonomic distinction.

A phylogenetic analysis of MCF-PVPH 320 using the published matrix of Cau *et al*. (2012), with characters 809, 810 and 811 modified from Carrano *et al*. (2012) and additional scores for character 808 (see supplementary data), was conducted with a traditional search in *TNT* (Goloboff *et al*. 2003). This placed MCF-PVPH 320 within Allosauroidea and closely related to *Sinraptor*, forming a sister group with Carcharodontosauridae (Fig. 3). Therefore, we conclude that MCF-PVPH 320 might derive from a basal Tetanurae, more closely related to spinosauroidea and allosauroidea than abelisaurids and Coelurosauria. The large extent of the supratemporal fossa on the surface of the frontal constitutes a specific synapomorphy for Allosauroidea.

Conclusion

Comparisons with South American theropods do not support affinity of MCF-PVPH 320 with any coeval theropod taxa currently documented from cranial remains. Our phylogenetic analysis suggests attribution to a basal tetanuran, perhaps closely related to Allosauroidea. In terms of mid-sized to large theropods, the Late Cretaceous of northern Patagonia is characterized by the presence of abelisaurids, megaraptorids and carcharodontosaurids. However, we conclude that MCF-PVPH 320 does not belong to any of these clades but rather suggests the presence of an as-yet undetected large allosauroid in the Portezuelo Formation.

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