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BRAINCASES OF ABELISAURID THEROPODS FROM THE UPPER CRETACEOUS OF NORTH PATAGONIA

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Abstract: The braincases of the abelisaurid theropod dinosaurs *Abelisaurus comahuensis* and *Aucasaurus garridoi* are described and compared. These two taxa share the presence of a floccular recess that is '8'-shaped, the absence of a medullar eminence in the floor of the endocranial cavity and the possession of a well-developed, narrow and tall dorsal longitudinal sinus. The basisphenoidal recess is continuous dorsocaudally with two pneumatic cavities, which are separated medially by a thin septum. A connection between the metotic canal and the columellar recess that probably represents the exit of cranial nerve IX is observed in *Abelisaurus*. *Aucasaurus* has a skull roof with a wide sagittal crest and a low parietal eminence that differentiates it from other derived abelisaurids such as *Abelisaurus*, *Carnotaurus* and *Majungasaurus*. The abelisaurid braincases described herein show strong consistency in their general morphology and structure. However, there is some variation, and these detailed descriptions are important for understanding the variation and distribution of braincase characters within Abelisauridae.

Key words: *Abelisaurus*, *Aucasaurus*, basicranial pneumaticity, Argentina.

ABELISAURIDS are a family of theropod dinosaurs with Gondwanan affinities (Bonaparte 1991; Novas 1997; Sereno *et al.* 2004). Although some of these taxa are represented by complete skeletons, braincases are rare and seldom described (Novas *et al.* 2004; Sereno *et al.* 2004; Sampson and Witmer 2007; Paulina Carabajal 2011). The highest diversity of abelisaurids is found in Patagonia, and at least five braincases have been assigned to Patagonian taxa. *Abelisaurus comahuensis* (Bonaparte and Novas 1985), *Carnotaurus sastrei* (Bonaparte *et al.* 1990; Paulina Carabajal in press) and *Ekrixinatosaurus novasi* (Calvo *et al.* 2004) possess the most complete braincases. *Aucasaurus garridoi* (Coria *et al.* 2002) and *Ilokelesia aguadagrandensis* (Coria and Salgado 1998) include more fragmentary material, such as the occipital condyle and associated fragments of exoccipitals and basisphenoid (Paulina Carabajal 2009).

One remarkable characteristic of the abelisaurid skull is the ornamentation of the dermal bones of the skull roof, such as the horn-like structures on the frontals in *Carnotaurus sastrei* (Bonaparte *et al.* 1990) and *Majungasaurus crenatissimus* (Sampson and Witmer 2007). The ornamentation, thickness of the skull roof and the robustness of the supraorbital processes are characteristic of derived abelisaurids (Sereno *et al.* 2004). With the exception of the skull roof and occipital region, braincase morphology in this group was poorly known until the description of the braincase of *Majungasaurus crenatissimus* (Sampson and Witmer 2007) and *Carnotaurus sastrei* (Paulina Carabajal 2011).

In this contribution, the braincases of *Abelisaurus* and *Aucasaurus* are described in detail, complementing previous descriptions of *Abelisaurus* (Bonaparte and Novas 1985; Bonaparte 1991). In spite of incomplete preservation in both species, this study provides new anatomical information on the abelisaurid braincase.

MATERIAL

The abelisaurid *Abelisaurus comahuensis* (MPCA 11.098) is known from a partial skull, which was fully reconstructed for exhibition purposes. The reconstructed skull is 87 cm long, from the tip of the premaxillae to the distal end of the paroccipital process. The material is highly fractured resulting in some deformation that is evident in posterior view. The partial braincase is in contact with other skull elements (quadrates, postorbitals, lacrimals, prefrontals and nasals), which obscure the lateral aspect of the braincase. The preservational quality of the material is good, allowing the identification of delicate structures and some cranial and vascular foramina. The bones are highly fused, indicating that the braincase pertains to an adult specimen.

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The braincase of *Aucasaurus garridoi* (MCF-PVPH 236) is less complete. The best preserved region corresponds to the skull roof, with attached fragments of the prootics, basisphenoid, exoccipital–opisthotics, laterosphenoids, orbitosphenoids and supraoccipital. Fragments of the exoccipitals, basioccipital and basisphenoid are preserved along with the detached occipital condyle. Despite the fractures, the fragmented walls of the braincase and the basicranium are informative. The sutures are obscured by fusion, indicating that the braincase corresponds to an adult individual, as also inferred from the study of the postcranial elements (Coria *et al.* 2002).

Institutional abbreviations. IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires; MPCA, Museo Provincial 'Carlos Ameghino', Cipolletti, Río Negro; MCF-PVPH, Museo 'Carmen Funes', Plaza Huincul, Neuquén; MUCPV, Museo de la Universidad Nacional del Comahue, Neuquén; MUCPV-CEPALB, Centro paleontológico Lago Barreales, Neuquén; MWC, Museum of Western Colorado, Grand Junction; PVL, Instituto Miguel Lillo, Tucumán; TMP, Royal Tyrrell Museum, Drumheller; UA, Université d'Antananarivo, Madagascar; UUVP, University of Utah, Salt Lake City.

COMPARATIVE DESCRIPTION

Parietal

In *Abelisaurus*, the parietals are firmly fused to form a single midline element in the skull roof that is excavated by the supratemporal fossae. The medial margins of the fossae are parallel to the midline along the parietals but diverge along the frontals, as in other abelisaurids (Rauhut 2003). The supratemporal fossae are very close to each other and separated by a narrow sagittal crest, which is 4 mm wide (Text-fig. 1A). The posterior section of the sagittal crest is rostrodorsally oriented and lies in front of the tall parietal eminence, as in *Carnotaurus* (MACN-CH 894) and *Majungasaurus* (Sampson and Witmer 2007). In *Aucasaurus*, the sagittal crest is flat and 10 mm wide and projects forward subhorizontally at least 30 mm from the parietal eminence (Text-fig. 1B). The parietal eminence is low, unlike the markedly taller projection present in the aforementioned taxa.

The parietal eminence in *Abelisaurus* and *Aucasaurus* is situated caudal to the supratemporal fossae and is rhomboid in dorsal view, as in other abelisaurids (Novas *et al.* 2004; Sampson and Witmer 2007; Paulina Carabajal 2011). Its surface is ornamented, although this is less marked than on the frontals. In *Abelisaurus*, the parietal eminence extends 20 mm above the rest of the skull roof. It emits a tongue-shaped process caudally that overlaps the supraoccipital tuberosity, as in *Carnotaurus* (Paulina Carabajal 2011) and *Majungasaurus* (Sampson and Witmer 2007). In *Abelisaurus*, the supraoccipital tuberosity extends caudally 30 mm beyond the caudal tongue of the parietal (Text-fig. 1A). A similar caudal projection of the parietal, overlapping the supraoccipital, is present in carcharodontosaurids (Coria and Currie 2002*a*), although carcharodontosaurids lack a parietal eminence (Paulina Carabajal 2009).

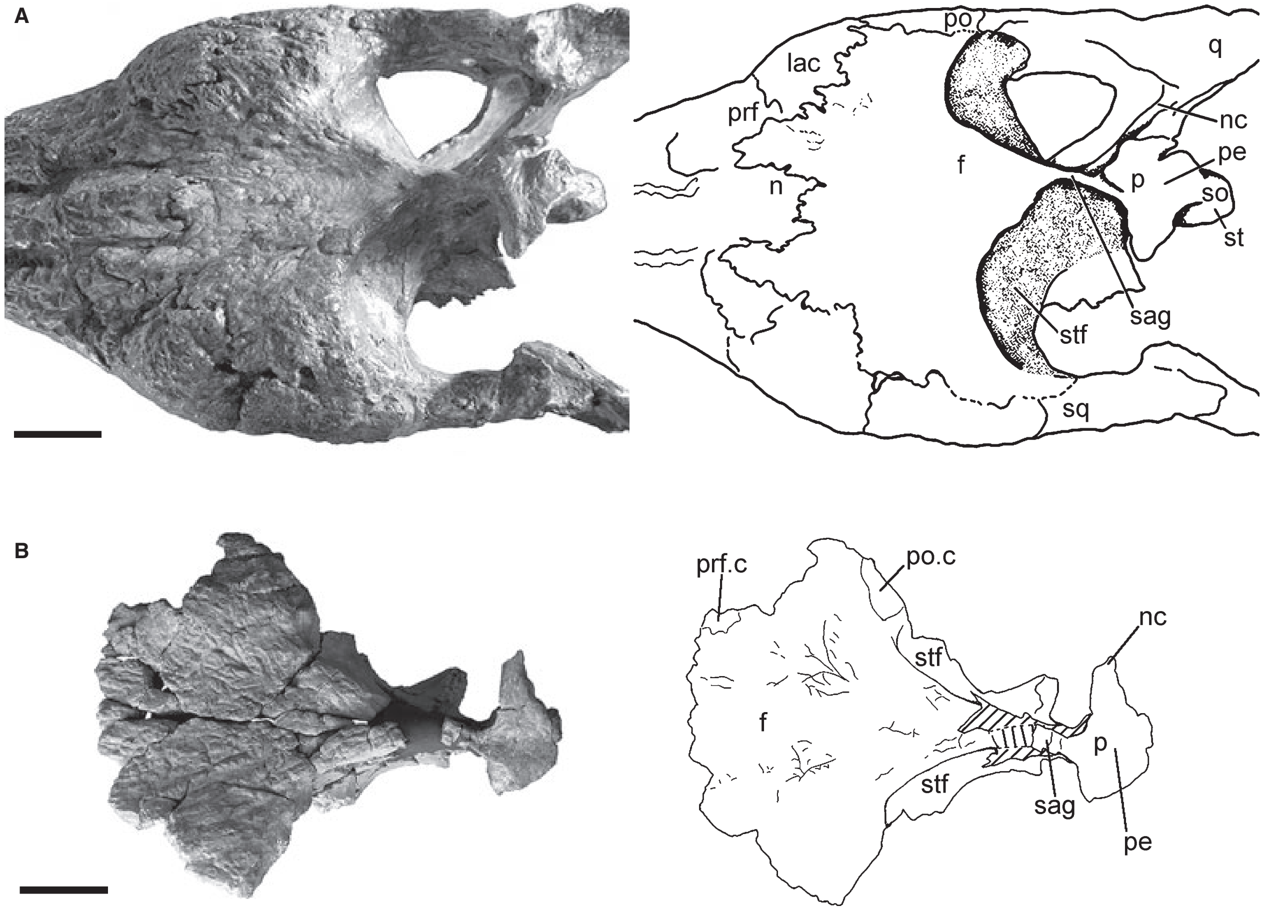
The transverse nuchal crest is incomplete in both specimens. In *Abelisaurus*, the nuchal crest is tall, more than three times the height of the foramen magnum, as in *Carnotaurus* (Paulina Carabajal 2011) and *Majungasaurus* (Sampson and Witmer 2007; Text-fig. 2A). Caudally, the nuchal crest has two wide and shallow ovoid depressions, separated by the supraoccipital crest, which are more clearly defined than in *Carnotaurus* (Paulina Carabajal 2011). The dorsal margins of those depressions delimit a rim in the border of the nuchal crest that is 19 mm high (Text-fig. 2B). The rim corresponds to the attachment area for muscles involved in dorsiflexion of the head (Snively and Russell 2007). The partially preserved posterolateral wing of the parietal overlaps the opisthotic at the base of the paroccipital process (Text-fig. 2A, B). In *Aucasaurus*, the transverse posterior walls of the supratemporal fossae are slightly concave. The preserved segment of the nuchal crest is straight and transversely oriented, as in other abelisaurids (Text-fig. 1A).

The frontoparietal suture is obscured by fusion in all of the studied specimens (Text-fig. 1). In *Aucasaurus*, the region of the frontoparietal contact is thickened by the deposits of bone. In *Abelisaurus*, this contact is probably just in front of the parietal eminence, as described for *Majungasaurus* (Sampson and Witmer 2007; Text-fig. 3A).

Frontal

In both taxa, the frontals are relatively large, robust and anteroposteriorly long, thereby forming a quadrangular skull roof, as in other abelisaurids (Text-fig. 1). In *Abelisaurus*, the frontal sutures with the nasal, prefrontal, lacrimal and postorbital are strongly interdigitated, whereas the sutures with the laterosphenoid, orbitosphenoid and sphenethmoid are obscured by fusion. The ornamentation of the frontal in *Abelisaurus* is well developed, as in *Aucasaurus*, *Majungasaurus* (Sampson and Witmer 2007) and *Carnotaurus* (Paulina Carabajal 2011). The sculpturing consists of small rugosities and corpuscular protuberances of different size separated by a web of small grooves (Text-fig. 1A). The ornamentation is asymmetrical between the left and right frontals. On each frontal, rugosities are concentrated on the anterior and median sectors of the bone, but they are less conspicuous in the lateral borders and caudally, between the supratemporal fossae.

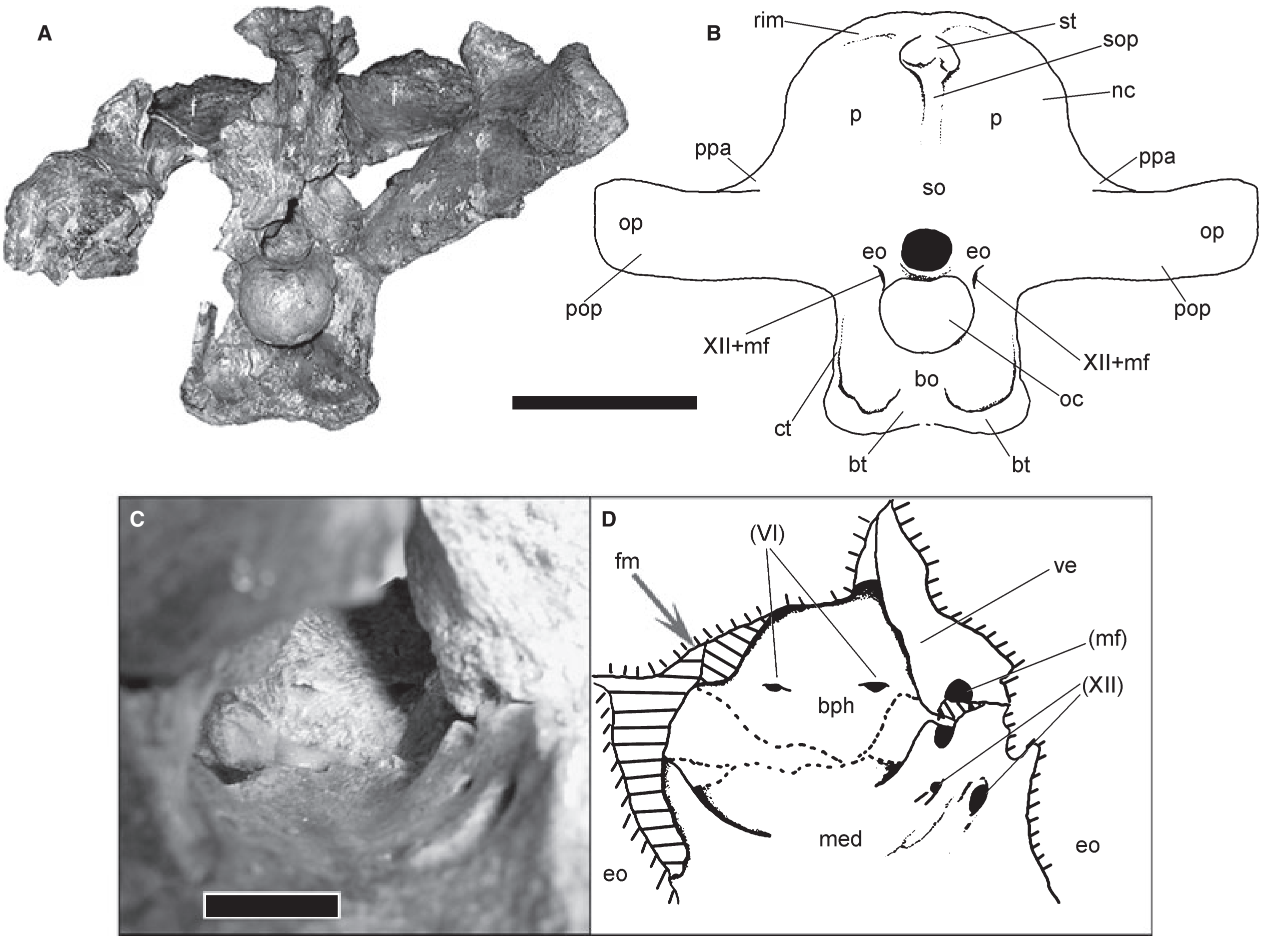
In *Aucasaurus*, the frontals are almost complete, except for the missing nasal processes (Text-fig. 1B). The frontal is robust and 23 mm thick at the interfrontal contact. Externally, the interfrontal suture is indistinct: however, the frontals were originally separated when collected and were seen to possess a clear median sutural surface, consisting of deep dorsoventrally orientated striations. In *Majungasaurus*, CT scans of the specimens also revealed that the frontals were unfused and that a thin superficial and ornamented layer of bone obscures the interfrontal suture, which probably corresponds to the mineralization of some subcutaneous layer (Hieronymus and Witmer 2004; Sampson and Witmer 2007).



TEXT-FIG. 1. A, skull roof of *Abelisaurus comahuensis* (MPCA 11.098). B, skull roof of *Aucasaurus garridoi* (MCF-PVPH 236). f, frontal; lac, lacrimal; n, nasal; nc, nuchal crest; p, parietal; pe, parietal eminence; po, postorbital; po.c, surface of contact with postorbital; prf, prefrontal; prf.c, surface of contact with prefrontal; q, quadrate; sag, sagittal bar separating the supratemporal fossae; so, supraoccipital; sq, squamosal; st, supraoccipital tuberosity; stf, supratemporal fossa. Scale bars represent 50 mm.

The frontals of *Abelisaurus* and *Aucasaurus* are similar in shape, although not in size (Table 1). The absence of hypertrophied ornamental 'horns' differentiates these two taxa from *Carnotaurus* and *Majungasaurus* (Sampson and Witmer 2007). Although the skull roof is predominantly flat, each frontal is dorsally expanded near the orbital rim to form a dome. This dome is situated medial to the lacrimal–postorbital contact, which excludes the frontal from the orbital rim. In basal ceratosaurs such as *Coelophysis* (Raath 1977; Colbert 1989; Tykoski 1998), the frontal participates in the dorsal orbital margin. In *Aucasaurus*, the orbital bulges are present but less prominent. The orbital bulges of *Abelisaurus* and *Aucasaurus* are topographically identical to the frontal 'horns' of *Carnotaurus* (MACN-CH 894). Caudally, the frontals are excavated by the supratemporal fossae. Each supratemporal fossa is wide and slightly more developed rostrocaudally than transversely. The supratemporal fossa occupies approximately 40% of the total length of the frontal, as in other abelisaurids. The medial margins of the supratemporal fossae lie closest to each other at the frontoparietal contact, but diverge strongly from the midline rostrally where the fossae are separated by a triangular section of the frontals (Text-fig. 1). This occurs in most ceratosaurs and might represent a synapomorphy of the clade (Sampson and Witmer 2007). In *Abelisaurus*, the anterior margins of the supratemporal fossae are slightly curved and clearly excavated. In *Aucasaurus*, the surface of the fossa is smooth, with some small striations that probably correspond to muscular attachments. The floor of the supratemporal fossa in front of the supratemporal fenestra is strongly lateroventrally inclined, indicating that the supratemporal fenestra was slightly smaller than the supratemporal fossa. In the rostromedial wall of the supratemporal fossa, there is a curved bony rim that forms the caudal border of an oval depression (Text-fig. 3A). This shallow depression generates a step in the anterior wall of the fossa, which is also present in *Carnotaurus* (Paulina Carabajal 2011) and *Majungasaurus* (L. M. Witmer, pers. comm. 2009) and less clearly marked in *Abelisaurus*. This rim of bone probably indicates a separation of the muscles in this area or, alternatively, might mark the position of the frontoparietal contact.

In *Abelisaurus*, the frontal–prefrontal suture is strongly interdigitated. The frontal contacts the nasal via a short anterior nasal process. Each nasal process is triangular in shape and 45 mm



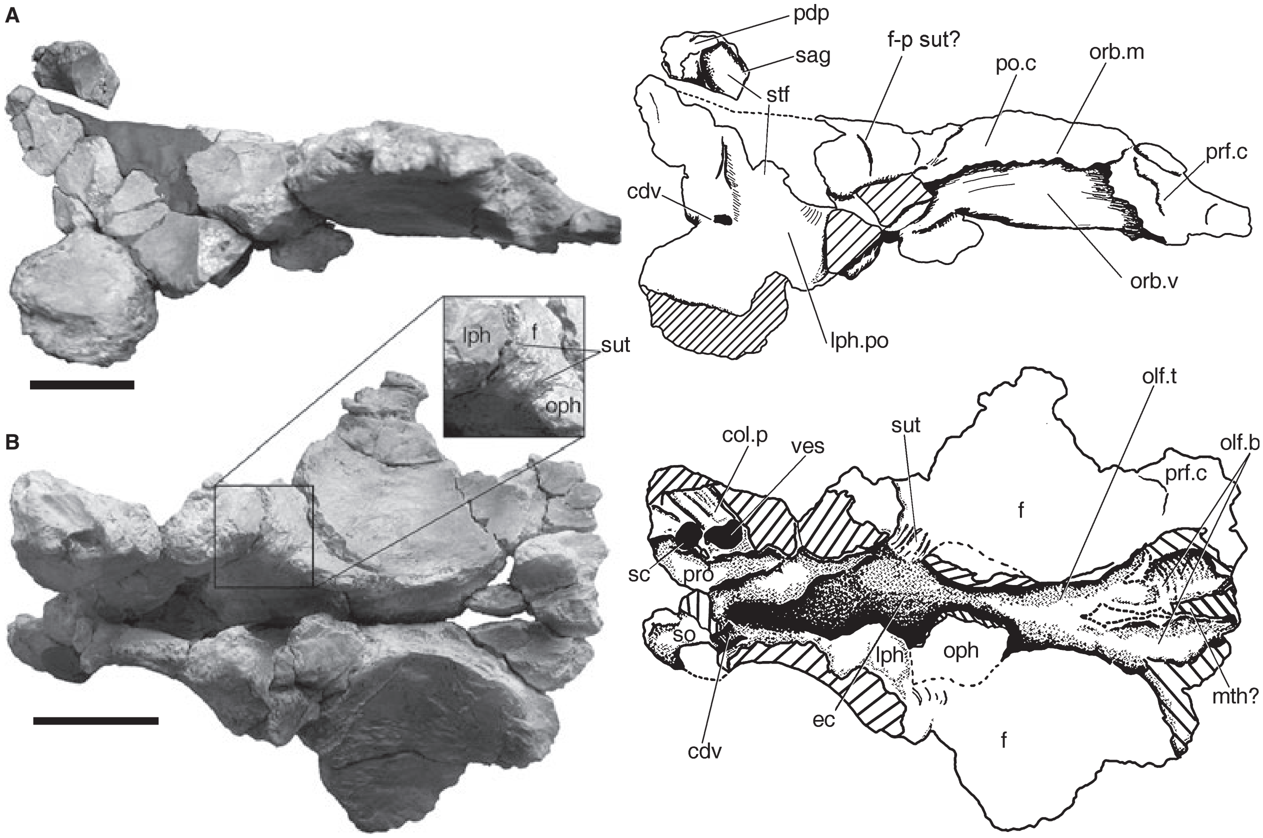
TEXT-FIG. 2. A–D, braincase of *Abelisaurus comahuensis* (MPCA 11.098). A, braincase in posterior view and B, restoration based on A. C, detail of endocranial cavity through the foramen magnum and D, interpretive drawing of C. bo, basioccipital; bph, basisphenoid; bt, basal tuber; ct, crista tuberalis; eo, exoccipital; fm, foramen magnum; med, medullar fossa; mt, metotic foramen for cranial nerves IX–XI; nc, nuchal crest; oc, occipital condyle; op, opisthotic; p, parietal; pop, paroccipital process; ppa, posterolateral wing of the parietal; so, supraoccipital; sop, supraoccipital prominence or crest; st, supraoccipital tuberosity; ve, vestibular eminence; VI and XII, cranial nerve foramina. Endocranial cavity traits indicated between brackets. Scale bars represent 100 mm (A, B) and 10 mm (C, D).

long and is separated from the other by a transverse frontonasal suture that is 28 mm long (Text-fig. 1A). The nasal processes are missing in *Aucasaurus*, and only a small fragment of the contact surface for the nasal is preserved on the right side (Text-fig. 1B). This is a smooth triangular surface that is excavated on the rostrodorsal surface of the frontal that corresponds with the bony platform described in *Majungasaurus* (Sampson and Witmer 2007). In *Abelisaurus*, the extensive frontal sutures with the lacrimal and postorbital are strongly interdigitated. In *Aucasaurus*, the laterosphenoid is broken, making it possible to observe its articulation on the ventral surface of the frontal. The articulation is an elongated surface bearing thin and transverse, parallel grooves (Text-fig. 3B).

Supraoccipital

In *Abelisaurus*, the supraoccipital height is approximately three times the height of the foramen magnum (Text-fig. 2A). As in *Carnotaurus* (Paulina Carabajal 2011) and *Majungasaurus* (Sampson and Witmer 2007), the supraoccipital is a vertically oriented element and the supraoccipital crest has straight, sharp lateral borders. The supraoccipital is fragmentary and eroded in the braincase of *Aucasaurus*, but the supraoccipital crest is partially preserved (Text-fig. 3A). In *Abelisaurus*, the supraoccipital crest is dorsally thickened behind the nuchal crest. A 30-mm-long conical projection extends caudally from the supraoccipital crest, as in *Carnotaurus* (MACN-CH 894) and *Majungasaurus* (Sampson and Witmer 2007). This supraoccipital protuberance is partially overlapped by a caudal projection of the parietal (Text-figs 1A, 2A). The lack of sutures between the supraoccipital and exoccipitals obscures the extent of the supraoccipital in the dorsal margin of the foramen magnum. In *Majungasaurus*, the small contribution of the supraoccipital to that margin has been confirmed by CT scanning (Sampson and Witmer 2007).

In the braincase of *Abelisaurus*, the foramina for the dorsal head veins are not visible as a result of damage. However, in *Aucasaurus*, these two foramina lie very close to the midline and



TEXT-FIG. 3. A, B, *Aucasaurus garridoi* (MCF-PVPH 236). Braincase in A, right lateral and B, ventral views. cdv, dorsal head vein (caudal middle cerebral vein) foramen; col.p, columellar recess passage; ec, endocranial cavity; f, frontal; lph, laterosphenoid; lph.po, laterosphenoid postorbital process; mth, mesethmoid; olf.b, olfactory bulb cavities; olf.t, olfactory tract cavity; oph, orbitosphenoid; orb.m, orbital margin; orb.v, orbital vault; p, parietal; pdp, parietal dorsomedial process; po.c, surface of contact with postorbital; prf.c, surface of contact with prefrontal; pro, prootic; sag, sagittal bar separating supratemporal fossae; sc, semicircular canal of inner ear; so, supraoccipital; stf, supratemporal fenestra; sut, suture; ves, vestibule of inner ear. Scale bar represents 50 mm.

TABLE 1. Braincase measurements (in mm).

	f L	sr L	sr orb	stf L	oc W	oc H	fm A	fm H	bt D	btp D	bt–btp D	bsc H	bc H	so H	pop L	pop H	sag W	olf t L
Abelisaurus MPCA 11.098	135*	184	189	77.5	54	47	30	19†	98	120	88	90	230†	95†	142	45	6	69
Aucasaurus MCF-PVPH 236	115*	165*	140	75‡	35	32	?	?	?	?	?	?	?	55‡	?	?	10	45
Carnotaurus MACN-CH 894	148*	220	200*	96	48	45	38	31	93	85	52	100	230	88	97	55	8	70

f L, length of the frontal without the nasal process; sr L, length of the skull roof; sr orb, interorbital width of the skull roof; stf L, length of the supratemporal fossa; oc, occipital condyle (W, width, H, height); fm, foramen magnum (W, width, H, height); bt D, transversal distance the between basal tubera; btp D, transversal distance between the basipterigoid processes; bt–btp D, anteroposterior distance between basal tubera and basiperigoid process; bsc H, basicranium height; bc H, braincase height; so H, supraoccipital height; pop L, paroccipital process length; pop H, paroccipital process height; sag W, width of the sagittal bar at the frontoparietal contact; olf L, olfactory tract length. *Estimated; †deformed; ‡incomplete.

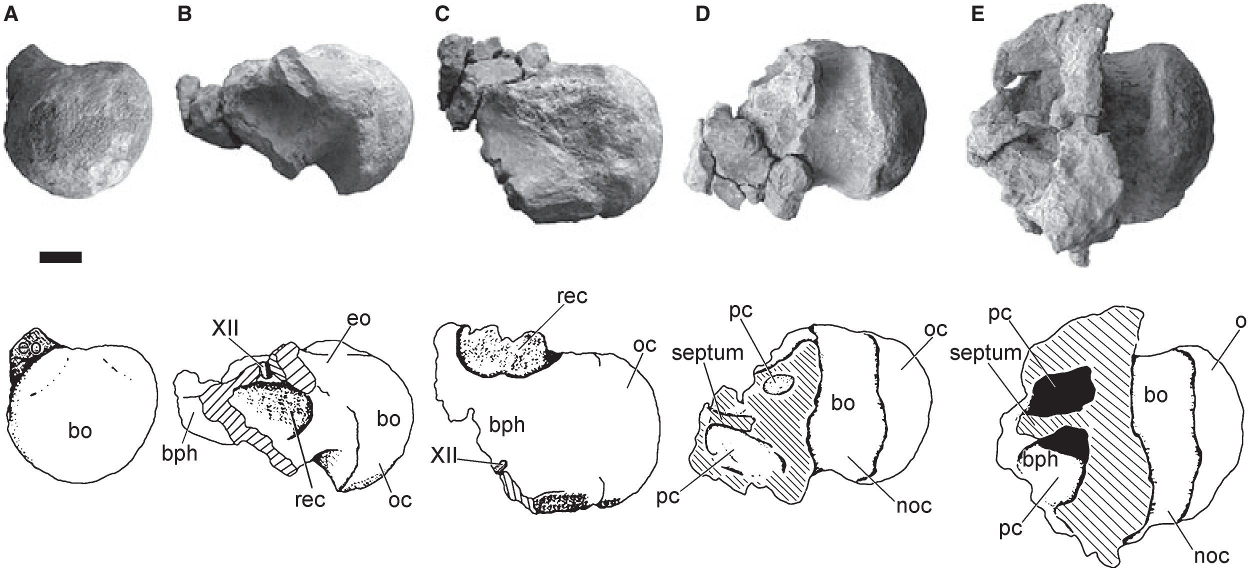
are located on either side of the supraoccipital crest, as in *Majungasaurus* (Sampson and Witmer 2007). These vascular foramina indicate the position of the parietal–supraoccipital contact (Text-fig. 3A). The dorsal head vein foramina communicate with a passage that crosses the supraoccipital rostroventrally, converging internally in the caudodorsalmost sector of the endocranial cavity, which hosts the dorsal longitudinal sinus (Sedlmayr 2002; Sampson and Witmer 2007). The foramina for these veins are 4 mm in diameter. The passage for the dorsal head veins in *Aucasaurus* is relatively shorter than in other theropods, such as the carcharodontosaurid *Giganotosaurus* (MUCP-CH 1) and tyrannosaurids (Witmer and Ridgely 2009, figs 1–3).

Exoccipital–opisthotic

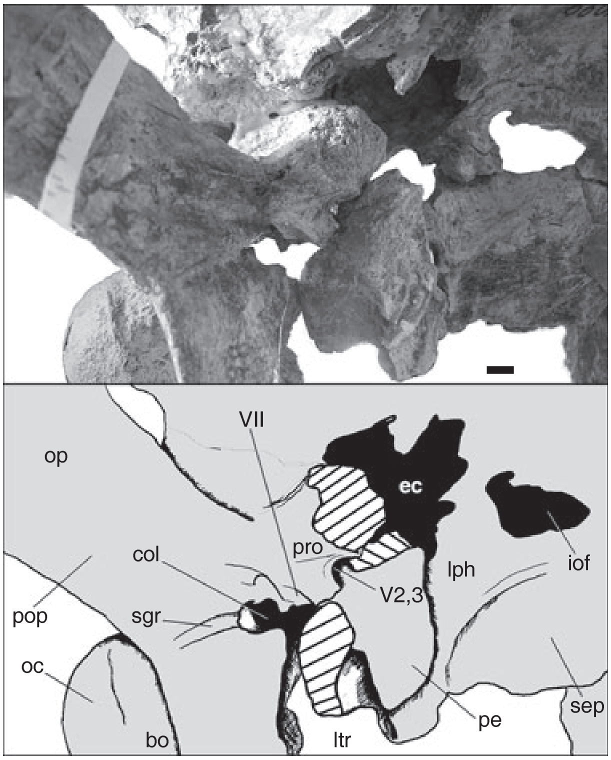
The exoccipitals form the laterodorsal margins of the foramen magnum, which is deformed by fractures in *Abelisaurus*. Although it is difficult to determine the height of the foramen owing to this deformation, its width is approximately 50 mm (Text-fig. 2A). There is a small and shallow ovoid recess lateral to the occipital condyle, as in *Carnotaurus* (Paulina Carabajal 2011) and *Aucasaurus* (Text-fig. 4B, C). This recess houses the foramina for cranial nerve (CN) XII and the metotic foramen (for CN IX–XI), although the latter openings are poorly preserved. In medial view, three aligned foramina are present in this region of the exoccipital–opisthotic. The two more caudally situated are 3 and 2 mm in diameter and correspond to the branches of CN XII. The third opening, which is 6 mm in diameter, corresponds to the internal metotic foramen, which is unlike the deep oval recess (fovea ganglii vagoglossofaryngealis) in other theropods (Paulina Carabajal 2009: Text-fig. 2B). The exoccipitals in *Aucasaurus* are partially preserved along with the occipital condyle. A small foramen, 3 mm in diameter, for CN XII opens in the dorsomedial wall of the partially preserved recess (Text-fig. 4B, C). Endocranially, this foramen opens just rostral to the margin of the foramen magnum. The rest of the exoccipitals are eroded, and the presence of a second foramen for CN XII cannot be confirmed or rejected. In *Majungasaurus*, the endocranial cast showed only one exit for CN XII (Sampson and Witmer 2007).

The opisthotic is fused to the exoccipital to form the exoccipital–opisthotic complex (‘otoccipital’: Sampson and Witmer 2007). It is the main element forming the paroccipital process, which is partially preserved in *Aucasaurus* (Text-fig. 3A). The right paroccipital process of *Abelisaurus* is complete, although it has been displaced by deformation. In the latter taxon, it is long, thin and low, its height being approximately twice the height of the foramen magnum (Text-fig. 2A, B). Fractures show that the process is a solid structure. The paroccipital process is expanded distally and is vertical along its entire length, unlike the caudodorsally oriented paroccipital processes of *Carnotaurus* (Paulina Carabajal 2011) and *Majungasaurus* (Sampson and Witmer 2007). The ventral border of the base of the paroccipital process lies slightly below the level of the dorsal border of the occipital condyle (Text-fig. 2A, B). Rostrally, the paroccipital process is flat and smooth, and there is no caudal tympanic recess, a trait shared with other neoceratosaurs (Sanders and Smith 2005; Sampson and Witmer 2007; Paulina Carabajal 2011).

The opisthotic contacts the prootic rostrally to form the lateral wall of the braincase, although the sutures are obliterated by fusion. In *Abelisaurus*, the caudodorsal and ventral borders of the columellar recess are better preserved on the right side (Text-fig. 5). There is a columellar groove (stapedial groove) on the opisthotic. Ventral to the columellar recess is another groove that communicates with a small foramen, which communicates caudally with the passage of the metotic foramen. A similar configuration is observed in an unnamed coelurosaur from the Cretaceous of Patagonia (Coria and Currie 2002*b*), in which the foramen is interpreted as the exit of CN IX through the lateral wall of the braincase (Paulina Carabajal 2009). This foramen is



TEXT-FIG. 4. A–D, *Aucasaurus garridoi* (MCF-PVPH 236) and E, *Ilokelesia aguadagrandensis* (MCF-PVPH 35). Occipital condyle and neck in A, posterior, B, lateral, C, dorsal and D–E, ventral views. bo, basioccipital; bph, basisphenoid; eo, exoccipital; noc, occipital condyle neck; oc, occipital condyle; pc, pneumatic cavity; re, recess lateral to the occipital condyle hosting CN XII foramen; XII, CN foramen. Scale bar represents 10 mm.



TEXT-FIG. 5. *Abelisaurus comahuensis* (MPCA 11.098). Prootic and laterosphenoid in right lateral view. bo, basioccipital; col, columellar recess; ec, endocranial cavity; iof, interorbitary fenestra; lph, laterosphenoid; ltr, lateral tympanic recess; oc, occipital condyle; op, opisthotic; pe, preotic pendant; pop, paroccipital process; pro, prootic; sep, interorbitary septum; sgr, columellar or stapedial groove; VII, facial nerve foramen; and $V_{2,3}$, maxilomandibular foramen. Scale bar represents 10 mm.

absent in *Carnotaurus* and was not mentioned in the description of *Majungasaurus* (Sampson and Witmer 2007). In *Abelisaurus*, the crista tuberalis is firmly fused laterally to the fused basal tubera, and there are no visible sutures between the opisthotic and the basioccipital. The crista tuberalis in *Abelisaurus* is slightly curved caudally, unlike the vertical crest present in *Carnotaurus* (Paulina Carabajal 2011: Text-fig. 2A).

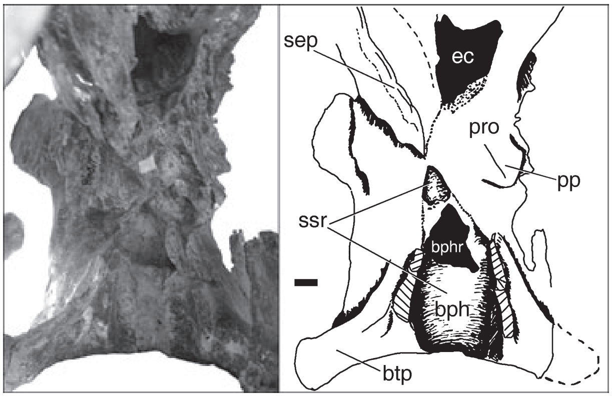
Basioccipital

In *Abelisaurus*, the basioccipital provides a small median contribution to the ventral border of the foramen magnum, as indicated by changes in the surface of the floor of the medullar cavity. The occipital condyle in *Abelisaurus* is circular in posterior view and is wider than the foramen magnum (Text-fig. 2A). In *Aucasaurus*, the basioccipital forms the main part of the occipital condyle (Text-fig. 4). It is a hemispherical structure, slightly wider than tall and relatively smaller than the occipital condyle of *Abelisaurus*, *Carnotaurus* (MACN-CH 894) and *Ilokelesia* (MCF-PVPH 35). In both *Abelisaurus* and *Aucasaurus*, the ventral border of the condyle is sharply defined by an abrupt constriction of the condylar neck, which is short and dorsally flat (Text-fig. 4). In *Abelisaurus* and *Carnotaurus* (Paulina Carabajal 2011), the condylar neck possesses a low longitudinal median crest ventrally, which is absent in *Aucasaurus* and *Ilokelesia* (MCF-PVPH 35). In *Aucasaurus*, the neck of the occipital condyle is massive, and the paired pneumatic cavities developed between the basioccipital and the basisphenoid are not as deep as in *Ilokelesia* (Text-fig. 4E).

In *Abelisaurus*, the basal tubera are completely fused to form a bony plate that is quadrangular in posterior view and projects ventrally from the occipital condyle (Text-fig. 2A, B). The lateral borders of this plate are parallel and fused indistinguishably with the crista tuberalis, as in *Carnotaurus* (Paulina Carabajal 2011) and *Majungasaurus* (Sampson and Witmer 2007). Caudally, the bony plate possesses a shallow depression on either side of the midline, generating a vertical rim below the condyle that does not reach the ventral border of the plate. The location of these depressions corresponds to the positions of the subcondylar and paracondylar pneumatic recesses present in some other theropods (Witmer 1997), including *Majungasaurus* (Sampson and Witmer 2007). Distally, the basal tubera possess a thickened, textured surface that offers a wide caudally facing surface for the attachment of the cervical muscles (Snively and Russell 2007). The transverse width of the bony plate is wider than the occipital condyle (Table 1).

Basisphenoid

In *Abelisaurus*, the basisphenoid forms the main part of the floor of the medullary fossa, which lacks a medullary eminence. The sutures between the basisphenoid and surrounding elements (basioccipital, parasphenoid, opisthotic, prootic and laterosphenoid) have been obliterated by fusion, but the positions of the contacts between them can be determined by using cranial nerve foramina as landmarks (Currie 1997). The basisphenoidal recess deeply excavates the body of the basisphenoid ventrally (Text-fig. 6).

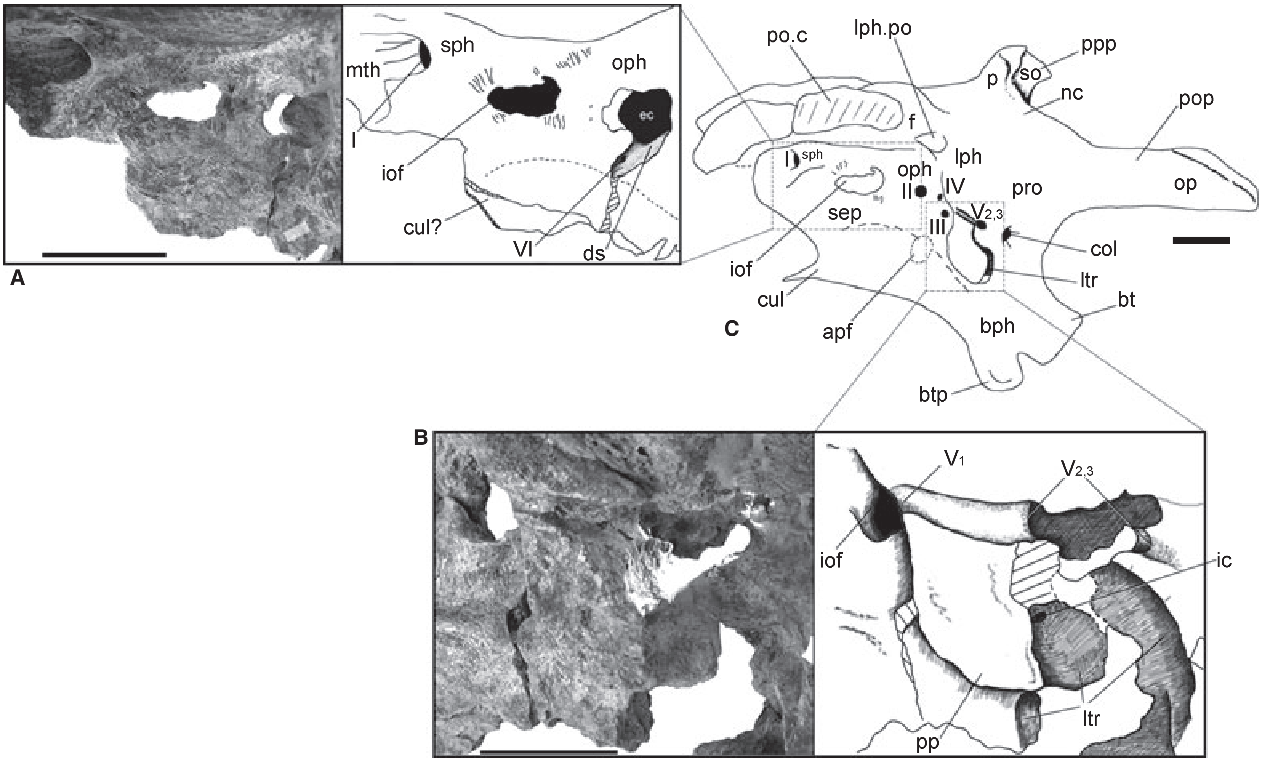


TEXT-FIG. 6. *Abelisaurus comahuensis* (MPCA 11.098). Basicranium in anterior view. bph, basisphenoid; bphr, basisphenoidal recess; btp, basipterygoid process; ec, endocranial cavity; pp, preotic pendant; sep, interorbitary septum; ssr, subselar recess. Scale bar represents 10 mm.

The basisphenoidal recess is a wide and conical pneumatic cavity that narrows dorsally. The ventral opening of the recess, delimited between the basal tubera and the basipterygoid processes, is transversely wide, as in *Carnotaurus* (Paulina Carabajal 2011; Table 1). The rostral wall of the basisphenoid recess is a thin transverse lamina that unites the basipterygoid processes, delimiting the subselar recess caudally. In *Aucasaurus*, the preserved portion of the basisphenoid has a pair of pneumatic cavities that are separated by a narrow median septum (Text-fig. 4D). The caudodorsal parts of the preserved walls of these cavities are smooth and ovate, with slightly concave surfaces. In *Ilokelesia* (MCF-PVPH 35), a larger fragment of basisphenoid is preserved, showing the same deep pneumatic cavities, separated by a median septum, which reach the level of the neck of the condyle (Text-fig. 4E). Paired pneumatic cavities in the basicranium are known in several taxa, including the basal tetanurans *Piatnitzkysaurus* (PVL 4073), *Sinraptor* (IVPP 10600), *Giganotosaurus* (MUCPV-CH 1) and the coelurosaur MCF-PVPH 411. In the latter, CT scans showed that the cavities are extensions of the basisphenoidal recess (Paulina Carabajal 2009).

In *Abelisaurus*, the subselar recess is positioned in the basisphenoid rostral to the basisphenoidal recess, as in *Carnotaurus* (Paulina Carabajal 2011) and *Majungasaurus* (Sampson and Witmer 2007). Only the posterior wall and fragments of the lateral walls enclosing the subselar recess are preserved. This is a deep pneumatic cavity ventral to the cultriform process. Because of this, the recess is also visible partially in anterior view. The posterior wall of the subselar recess is fractured and preserved in two sections, one dorsal and other ventral, which are 33 and 11 mm in height, respectively, suggesting a total height of 45 mm for the recess (Text-fig. 6). The subselar recess is a conical cavity oriented vertically in the basisphenoid, located just below the pituitary fossa.

The basipterygoid processes of *Abelisaurus* project lateroventrally and are markedly divergent, and the distance between them is wider than the distance between the fused basal tubera (Text-fig. 6; Table 1). The same is observed in *Majungasaurus* (L. M. Witmer, pers. comm. 2009), but not in *Carnotaurus*, where the distance between the basipterygoid processes is less than the width of the fused basal tubera (Paulina Carabajal in press). Each basipterygoid process is laterally flat and smooth with the distal end gently curved caudally and possesses two ventral articular surfaces for the pterygoid (Text-fig. 7C).

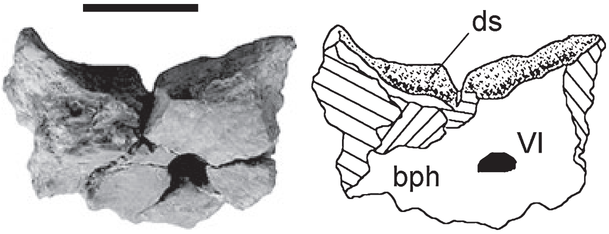


TEXT-FIG. 7. A–C, *Abelisaurus comahuensis* (MPCA 11.098). A, ethmoidal elements and interorbitary septum in left lateral view, and interpretive drawing of A. B, prootic and laterosphenoid in left lateral view, and interpretive drawing of B. C, restoration of the braincase in left lateral view. apf, anterior pituitary fenestra; bph, basisphenoid; bt, basal tuber; btp, basipterygoid process; col, columellar recess; cul, cultriform process; ds, dorsum sellae; sph, sphenethmoid; f, frontal; ic, internal carotid foramen; iof, interorbitary fenestra; mth, mesethmoid; lph, laterosphenoid; lph.po, laterosphenoid postorbital process; ltr, lateral tympanic recess; nc, nuchal crest; op, opisthotic; oph, orbitosphenoid; p, parietal; pp, preotic pendant; po.c, surface of contact with postorbital; pop, paroccipital process; ppp, parietal posteromedial projection; pro, prootic; sep, interorbitary septum; so, supraoccipital; sph, sphenethmoid; I–VI, CN foramina; V_1, ophthalmic branch foramen; $V_{2,3}$, maxillomandibular foramen. Scale bars represent 50 mm.

Only the base of the cultriform process is preserved in *Abelisaurus*, with small fragments of the dorsal border of the process preserved fused to the bony interorbital septum (Text-fig. 7A, B).

In *Abelisaurus*, the caudal and lateral walls enclosing the pituitary fossa are preserved. The pituitary fossa is a vertical cavity and is slightly caudoventrally oriented. In the posterior wall (the dorsum sellae), there is a small, deep depression, which was probably occupied by the pituitary gland. Within this depression, the internal carotid arteries enter the pituitary fossa through two separate large foramina, each of which is 4 mm in diameter. The external foramen for the internal carotid is situated in the rostrodorsalmost chamber of the lateral tympanic recess (Text-fig. 7B). CN VI pierces the basisphenoid, diverging in the floor of the endocranial cavity (Text-fig. 2B), and penetrates the pituitary fossa on its path to the exterior, opening dorsal to the foramina for the internal carotid (Text-fig. 7A). Because of this, the CN VI foramina are not present on the lateral surfaces of the basicranium, a trait shared with *Carnotaurus* (Paulina Carabajal 2011) and *Majungasaurus* (Sampson and Witmer 2007). Endocranially, in the rostral part of the floor of the medullary cavity, the two internal foramina for CN VI open approximately 15 mm behind the dorsum sellae. These foramina are lenticular, 3 mm in diameter and situated 10 mm apart from each other (Text-fig. 2B). In *Aucasaurus*, a small isolated fragment of the left border of the dorsum sellae is preserved. The fragment corresponds to the laterodorsal part of the caudal margin of the infundibular foramen. The dorsum sellae is low and continuous with the floor of the endocranial cavity, as in *Abelisaurus*. This fragment of basisphenoid is pierced by the passage for CN VI, which is 4 mm in diameter (Text-fig. 8). This passage starts in the floor of the endocranial cavity and extends 10 mm, diverging from the midline, to exit on the posterior wall of the pituitary fossa, as in *Abelisaurus* and *Carnotaurus* (Paulina Carabajal 2011).

The lateral (anterior) tympanic recess is a pneumatic cavity that excavates the lateral wall of the basisphenoid and partially covered by the preotic pendant. In *Abelisaurus*, the recess has clear borders and is subdivided by a septum into two depressions or chambers, one rostrodorsal and the other smaller and caudoventral (Text-fig. 7B, C). The smaller chamber is divided by a horizontal septum into dorsal and ventral sections. The internal carotid artery penetrates the basicranium through a foramen located in the median wall of the rostrodorsal chamber of the lateral tympanic recess (Text-fig. 7B). The clear separation of the lateral tympanic recess into subrecesses is also observed in the basal tetanuran *Piatnitzkysaurus* (PVL 4073; Rauhut 2004) and the troodontid *Troodon formosus* (TMP 82.19.23; Currie and Zhao 1993*a*). The basal tetanuran *Eustreptospondylus* has a less pronounced preotic pendant and lateral tympanic recess (Bonaparte 1986; Sadleir *et al.* 2008).



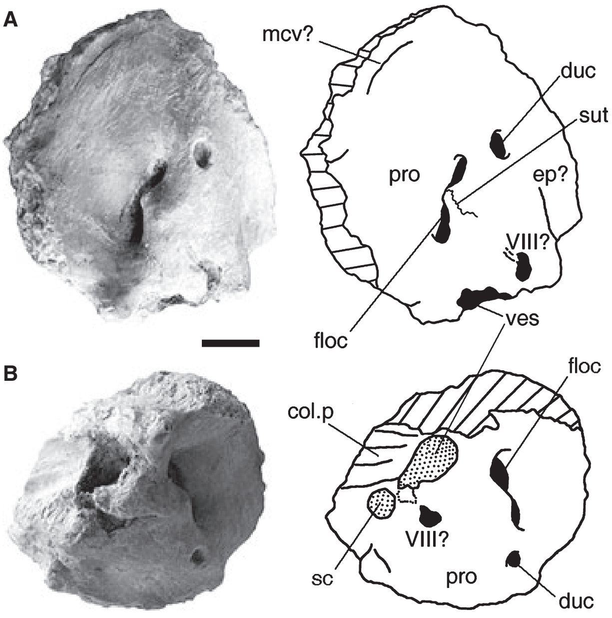
TEXT-FIG. 8. *Aucasaurus garridoi* (MCF-PVPH 236). Isolated fragment of basisphenoid in anterior view, with left CN VI preserved. bph, basisphenoid; ds, dorsum sellae; VI, abducens nerve foramen. Scale bar represents 10 mm.

Prootic

In *Abelisaurus*, the prootic is fragmentary. As in other theropods, the prootic–opisthotic contact is inferred on the basis of the position of the columellar recess (Currie 1997). The columella passes trough the columellar recess to reach the oval window of the inner ear (Text-fig. 5). The prootic–laterosphenoid contact is indicated by the maxillomandibular foramen (CN $V_{2,3}$) of the trigeminal nerve. The ophthalmic branch (CN V_1) has a separate foramen, as in *Carnotaurus* (Paulina Carabajal 2011) and *Majungasaurus* (Sampson and Witmer 2007). In *Abelisaurus*, the CN $V_{2,3}$ foramen (10 mm in diameter) is partially preserved caudodorsal to the preotic pendant (Text-fig. 7B, C). Rostrodorsal to the CN $V_{2,3}$ foramen, the ophthalmic branch leaves a deep horizontal groove (Text-fig. 7C). There was probably a small bar of laterosphenoid lateral to the ophthalmic groove that is now broken, as also noted in *Majungasaurus* (Sampson and Witmer 2007). If true, this implies a separated ophthalmic foramen in the laterosphenoid. The CN VII foramen, which is completely enclosed by the prootic, is partially preserved caudoventral to CN $V_{2,3}$ on the right side of the braincase. The dorsal margin of the foramen is preserved, suggesting a diameter of approximately 4 mm. In *Abelisaurus*, the preotic pendant is formed mainly by the prootic and is almost completely preserved on both sides of the braincase. The structure forms a laminar projection, as in *Carnotaurus* (MACN-CH 894: Text-figs 5, 7C).

Endocranially, the vestibular eminence that encloses the osseous labyrinth of the inner ear is partially preserved. The floccular recess, which housed the floccular projection of the cerebellum, opens on the rostral surface of the vestibular eminence (Text-fig. 2B). The floccular recess is caudodorsally elongated and shaped like a figure ‘8’, as in *Aucasaurus* (Text-fig. 9). In *Abelisaurus*, the floccular recess is 9 mm long, but the constriction dividing the floccular recess is less marked than in *Aucasaurus*. In *Aucasaurus*, the floccular recess is 15 mm long. At the level of the constriction, there is a suture, thickened by a secondary deposit of bone, which corresponds to the medial contact between the prootic and another element, probably the epiotic (Text-fig. 9A). The ‘8’-shaped morphology of the floccular recess has also been observed in the basal tetanuran *Sinraptor* (Paulina Carabajal 2009) and the tyrannosaurid *Daspletosaurus* (TMP 2001.36.0). In the endocranium of other theropods, the floccular recess is circular or oval in outline, as in *Giganotosaurus* (Paulina Carabajal and Canale 2011), *Piatnitzkysaurus* (PVL 4073), the coelurosaurid MCF-PVPH-411 (Paulina Carabajal 2009) and *Troodon* (TMP 86.36.457).

In *Aucasaurus*, the prootic is a robust element. Caudoventral to the floccular recess, there is a poorly preserved foramen for CN VIII (Text-fig. 9). The dorsal margin of the CN VII foramen



TEXT-FIG. 9. A, B, *Aucasaurus garridoi* (MCF-PVPH 236). A, prootic in medial and B, ventral views. col.p, columellar recess passage; duc, endolymphatic duct; ep, epiotic; floc, floccular recess; mcv, medial cerebral vein groove; pro, prootic; sc, semicircular canal of inner ear; sut, suture; ves, vestibule of inner ear. VIII, Auditory nerve foramen. Scale bar represents 10 mm.

is preserved as a shallow groove, situated rostroventral to the floccular recess. In *Abelisaurus*, the CN VII foramen is badly preserved and is not observed on the lateral surface of the prootic. In *Aucasaurus*, the rostroventral margin of the foramen for the dorsal head vein is caudodorsal to the floccular recess and the endolymphatic foramen and delimited by the parietal and supraoccipital–epiotic. From this foramen, a groove curves rostroventrally, which probably housed the middle cerebral vein (Text-fig. 9A). The dorsal half of the columellar recess is ventrally exposed by a fracture in the prootics, allowing the examination of its internal features and some aspects of the inner ear (Text-figs 3B, 9). The margins of the oval window are not preserved, but the transverse fracture shows a circular cavity that corresponds to the vestibule of the inner ear, which is 11 mm long rostrocaudally and 5 mm wide transversely. In the left prootic, the contour of the vestibule is circular because of the plane of the fracture. The lateral (or external) margin of the vestibule is continuous with the columellar recess and the position of the oval window. The smaller foramen medial to the vestibule corresponds to a transverse section of the anterior semicircular canal, with a diameter of 3.7 mm (Text-fig. 9). Including the vestibular eminence, the endolymphatic foramen and the probable location of the oval window, the osseous labyrinth in *Aucasaurus* was approximately 28 mm in height.

Laterosphenoid

Unfortunately, the laterosphenoid is fragmentary in *Abelisaurus* (Text-fig. 5). The postorbital process of the laterosphenoid is a depressed, finger-like structure, projecting transversely from the wall of the braincase. It is separated ventrally from the preotic pendant by the groove of the ophthalmic branch of CN V (V_1). In *Aucasaurus*, only the base of the postorbital process of the laterosphenoid is preserved, which is an inverted triangle in cross-section (Text-fig. 3A). In *Abelisaurus*, the process is finger-shaped and is somewhat dorsoventrally depressed. The laterosphenoid–prootic suture is not visible, but its position is indicated by the foramen for CN $V_{2,3}$. The ophthalmic branch (V_1) extends forward from the anterior border of CN $V_{2,3}$ leaving a groove on the laterosphenoid that is 10 mm in diameter and 45 mm long (Text-fig. 7C). This groove corresponds to the medial wall of the passage of the ophthalmic branch that pierces the laterosphenoid exiting through the CN V_1 foramen. The ophthalmic branch is long compared with that in *Carnotaurus*, in which the CN V_1 foramen opens immediately in front of the CN $V_{2,3}$ foramen (Paulina Carabajal 2011).

In *Aucasaurus*, only fragments of the laterosphenoid contacting the frontals and prootics are preserved (Text-fig. 3B). The laterosphenoid–frontal articulation is preserved on the ventral surface of the frontal (Text-fig. 3C). In the left laterosphenoid, a small vascular foramen is present caudoventral to the base of the postorbital process, near to the laterosphenoid–frontal contact. Endocranially, the internal opening of this foramen is positioned rostrodorsal to the floccular recess and its position corresponds to the course of the middle cerebral vein, which is also seen in *Carnotaurus*, *Abelisaurus* and *Majungasaurus* (Sampson and Witmer 2007; Paulina Carabajal 2009).

Orbitosphenoid

In *Abelisaurus*, there are no visible sutures between the orbitosphenoid, the laterosphenoid and the ossified ethmoidal elements. The limits of this bone can be identified close to the CN II foramina, which are enclosed by this bone in all theropods (Currie 1997). The anterior margin of the CN II foramen is observed in the left side of the braincase and is not confluent with its counterpart, as in *Carnotaurus* (Paulina Carabajal 2011) and *Majungasaurus* (Sampson and Witmer 2007; Text-fig. 7A). This separation is also a consequence of the presence of an ossified interorbital septum, as in *Giganotosaurus* (MUCPV-CH 1) and *Ceratosaurus* (Sanders and Smith 2005).

In *Aucasaurus*, the orbitosphenoids are fragmentary, preserved rostral to the laterosphenoids and contact the frontals dorsally (Text-fig. 3B). None of the foramina for CN II, III or IV are preserved, and the designation of these fragments as orbitosphenoid is based on their topographic position and their relationship to the other braincase elements. The orbitosphenoids converge ventromedially, probably contacting each other, delimiting the ventrolateral margins of the opening for CN I rostrally, as this nerve passes from the endocranial cavity to the olfactory tract (Text-fig. 3B). The contact between the orbitosphenoid and the frontal is observed in those sectors where the orbitosphenoid is not preserved. On the ventral side of the frontal, there is a suture formed by transverse striations and grooves, similar to the contact described for the laterosphenoid.

Ossified interorbital septum

In *Abelisaurus*, the ossified interorbital septum forms a lamina that is fused dorsally to the ethmoidal complex and caudally to the orbitosphenoid and basisphenoid (Text-fig. 7). The septum is incomplete rostroventrally, near the cultriform process, and has a maximum thickness of 12 mm. The ventral fracture of the interorbital septum shows that the lamina is formed there by two fused thin layers of bone, representing probably the most dorsal fragments of the cultriform process (Text-fig. 7A). There is a longitudinal rim on both sides of the interorbital septum that is rostrocaudally oriented and slightly concave downwards. Dorsal to this rim, the surface of the bone is deeply striated near to the contact with the sphenethmoid. In *Carnotaurus* (Paulina Carabajal in press) and *Majungasaurus*, the interorbital septum also presents a different texture, which seems to be a product of the mineralization of a cartilaginous septum (Sampson and Witmer 2007).

The interorbital septum delimits the anterior margin of a large fenestra, which communicates transversely with both orbital spaces (Text-fig. 7A, B). This fenestra corresponds with the interorbital window (*fonticulus interorbitalis*) described in *Majungasaurus* by Sampson and Witmer (2007), which is absent in *Carnotaurus* (Paulina Carabajal 2011). Caudoventrally, the septum delimits the ventral, anterior and dorsal borders of the fenestra that leads into the pituitary fossa, as in *Carnotaurus* (Paulina Carabajal 2011) and *Majungasaurus* ('sphenoidal artery foramen': Sampson and Witmer 2007). A small foramen that communicates with the pituitary fossa lies dorsal to the anterior pituitary fenestra and probably corresponds to the pituitary vein.

Ossified ethmoidal complex

The ethmoidal complex, formed by the fused sphenethmoids and mesethmoid, encloses the cavities of the olfactory tract and olfactory bulbs. The olfactory bulb cavity is divided rostrally by a longitudinal internasal septum that is constituted by the mesethmoid (Ali *et al.* 2008). In *Abelisaurus*, the ethmoidal bones are fused to the orbitosphenoid and the interorbital septum, as in *Carnotaurus* (Paulina Carabajal 2011) and *Majungasaurus* (Sampson and Witmer 2007).

The sphenethmoid is fused to the frontal dorsally and to the interorbital septum ventrally. In *Abelisaurus*, CT scans showed that the sphenethmoid is 'U'-shaped in the olfactory tract section, with the frontals roofing that cavity dorsally. The olfactory bulbs, however, are enclosed by the sphenethmoids, which form a ring that excludes the frontal from the roof. The internasal septum (mesethmoid) is firmly fused to the sphenethmoid and frontal, extending 40 mm rostrally (Text-fig. 7A). In *Abelisaurus*, the CN I foramen is large and subtriangular, with the opening rostrally oriented. It is rostrocaudally separated from the CN II foramen by 75 mm of bone, a relatively shorter distance than in *Carnotaurus* (Paulina Carabajal 2011). In the sphenethmoid, laterodorsal to CN II, there is a small vascular foramen that pierces the olfactory tract. Similar foramina are observed in the braincases of *Carnotaurus* (Paulina Carabajal 2011) and the carcharodontosaurid *Giganotosaurus* (Paulina Carabajal and Canale 2011).

Endocranial cavity

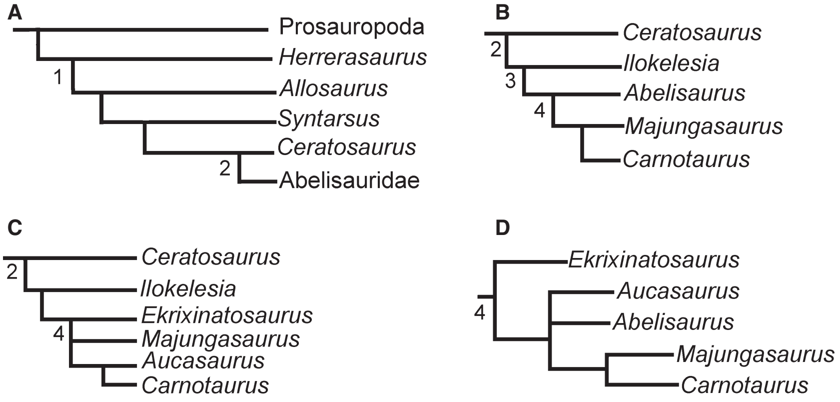
In *Aucasaurus*, the basicranium is not preserved, allowing the observation of the endocranial cavity ventrally (Text-fig. 3B). The endocranial cavity is caudodorsally deep, reaching its maximum height at the level of the supraoccipital–parietal contact, where it enclosed the dorsal sagittal sinus. Ventrolaterally on the frontal, near the orbitosphenoid–laterosphenoid contact, several vascular impressions are observed. The presence of important vascular marks in the endocranial cavity of troodontids and oviraptorids is recognized as an indication that the brain was filling the cavity (Osmólska 2004), although its presence is not common in other basal tetanurans and ceratosaurs. The endocranial cavity is rostrocaudally long and transversely narrow. In front of the orbitosphenoid, the frontal roofs the olfactory tract cavity, which rostrally diverges into a pair of cavities occupied by the olfactory bulbs. The impressions of the olfactory bulbs are clearly visible in ventral view of the frontal (Text-fig. 3B). They diverge slightly rostrally, being separated by the internasal septum, which is incompletely preserved (Text-fig. 3B). This septum tapers caudally. The impressions of the olfactory bulbs are elongated and oval (40 mm long and 14 mm wide), although the olfactory bulb probably did not fill the cavity completely, as mentioned for other theropods (Ali *et al.* 2008). The impression of the olfactory tract in the frontal is 43 mm long and approximately 19 mm wide. The cavity of the olfactory tract is relatively longer than the one observed in the unnamed coelurosaur MCF-PVPH 411 (Paulina Carabajal 2009).

ABELISAURID BRAINCASE CHARACTERS

Features of the abelisaurid braincase

The best known abelisaurid braincases are those of *Majungasaurus* (Sampson and Witmer 2007) and *Carnotaurus* (Paulina Carabajal 2011). *Aucasaurus* and *Abelisaurus*, two related taxa from the early Campanian (Bonaparte and Novas 1985; Coria *et al.* 2002; Carrano and Sampson 2008) of north Patagonia (Text-fig. 10), are represented by adult individuals, as indicated by the lack of sutures in the braincases.

Comparisons with the braincases of the Argentinean abelisaurs *Carnotaurus* (Paulina Carabajal 2011) and *Ilokelesia* (MCF-PVPH 35), and the Madagascan *Majungasaurus* (Sampson and Witmer 2007), show a marked consistency in general morphology. As mentioned by Paulina Carabajal (2011), potentially taxonomically useful abelisaurid braincase features include thickened frontals and parietals, with ornamentation (Sereno *et al.* 2004); parietal length more than 50 per cent of the frontal



TEXT-FIG. 10. Cladograms showing the phylogenetic relationships of *Aucasaurus* and *Abelisaurus*. Simplified cladograms of A, Theropoda (after Tykoski and Rowe 2004); B, Ceratosauria (after Sereno *et al.* 2004; Carrano and Sampson 2008); C, Abelisauria (after Calvo *et al.* 2004); D, Abelisauria, analysis based on braincase characters (after Paulina Carabajal 2009). 1, Theropoda; 2, Neoceratosauria; 3, Abelisauroidea; 4, Abelisauridae.

length (after Maryanska *et al.* 2002); parietal eminence in the skull roof with a caudal projection that overlaps the supraoccipital (Sampson and Witmer 2007); frontal postorbital process that is not strongly projected laterally (Currie 1995); length of frontals equal to their transversal width (Sampson and Witmer 2007); supratemporal fossa comprising 50 per cent of the frontal length (Paulina Carabajal 2009); frontal excluded from the orbital rim by the postorbital and lacrimal (Bonaparte 1991); nuchal crest tall and transverse to the main axis of the skull; paroccipital process expanded distally; ossified interorbital septum and ethmoidal elements present; supraoccipital with a caudomedial projection; fused basal tubera forming a quadrangular plate in occipital view in combination with the ventral ramus of the opisthotic; presence of a large basisphenoid recess that is observed only in ventral view; well-developed preotic pendant and lateral tympanic recess present (Paulina Carabajal 2008); exit for the ophthalmic branch of the trigeminal nerve separate from the exit for the maxillary and mandibular branches (Currie and Carpenter 2000); CN $V_{2,3}$ aligned vertically with the nuchal crest (after Coria and Currie 2002*a*); and CN VI that penetrates the pituitary fossa. Despite the incompleteness of the braincases of *Abelisaurus* and *Aucasaurus*, several endocranial traits can be confirmed in both specimens, such as the presence of an elongated, '8'-shaped floccular recess; separate internal carotid foramina penetrating caudally the pituitary fossa; the presence of a middle cerebral vein foramen in the laterosphenoid; and the absence of a medullar eminence in the floor of the endocranial cavity.

Distribution of braincase characters within Abelisauria

Variable features in the abelisaurid braincase are observed in the skull roof, comprising the ornamentation (e.g. the development of horn-like structures or their absence) and the disposition of parietal structures (e.g. the relative width and inclination of the sagittal crest and height of the parietal eminence). Two morphotypes of abelisaurid skull roof are recognized based on the width and inclination of the sagittal crest and the height of the parietal eminence. In one, the sagittal crest is narrow and strongly rostroventrally inclined, with a tall parietal eminence projecting markedly from the skull roof, as in *Abelisaurus*, *Carnotaurus* (Paulina Carabajal 2011) and *Majungasaurus* (Sampson and Witmer 2007). In the second, the sagittal crest is wider and flat and lies at the same level as the parietal eminence, as in *Aucasaurus* and probably *Ekrixinatosaurus* (MUCPv 294). The variation observed in the sagittal crest, parietal eminence, paroccipital process and basipterygoid process in the studied abelisaurs is related to musculature attachment (Snively and Russell 2007) and the relative positions of the elements of the palate.

The presence of ossified ethmoidal elements and an interorbital septum in abelisaurids and *Ceratosaurus* (MWC 1) suggests that this is a feature of neoceratosaurs, although it is also present in adult carcharodontosaurids such as *Giganotosaurus carolinii* (MUCPv-CH-1), *Carcharodontosaurus saharicus* (SGM-Din 1) and *C. iguidensis* (Brusatte and Sereno 2007).

The ophthalmic branch of the trigeminal nerve has a separate foramen in the studied abelisaurids, as in tyrannosaurids (Witmer and Ridgely 2009) and troodontids (Currie and Zhao 1993*a*). An incipient separation of the ophthalmic branch from the trigeminal foramen is mentioned in *Sinraptor* (Currie and Zhao 1993*b*), *Poekilopleuron*? *valesdunensis* (Allain 2002) and *Eustreptospondylus* (Sadleir *et al.* 2008), whereas in the coelophysoid *Coelophysis*, the ophthalmic branch leaves a groove on the laterosphenoid (Raath 1977). In abelisaurids, the CN VI foramina open in the caudal wall of the pituitary fossa, as in *Coelophysis* (Raath 1977), *Piatnitzkysaurus* (Rauhut 2004), carcharodontosaurids (Paulina Carabajal 2009) and tyrannosaurids (Witmer and Ridgely). Within abelisaurids, the foramina for the dorsal head veins were only identified in *Majungasaurus* (Sampson and Witmer 2007) and *Aucasaurus*.

Final considerations

The braincase of *Abelisaurus* differs from that of *Aucasaurus* in several anatomical structures, although the incompleteness of the braincase in the latter taxon prevents the comparison of most basicranial traits. The comparison of the studied abelisaurid braincases showed a marked consistency in the general morphology of the structure (Paulina Carabajal 2011), reflected also in the high support values for the node Abelisauridae in a cladistic analysis based exclusively braincase characters (Paulina Carabajal 2009). However, the relationships within the clade remain unclear (see Carrano and Sampson 2008 and references cited therein). The new braincase descriptions provide morphological information that allows the determination of several potentially useful taxonomic and systematic characters for abelisaurids. However, further descriptions of complete braincases are needed to enhance our understanding of the distribution of braincase characters and the evolution of this part of the skull within the clade.

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REFERENCES

ALI, F., ZELENITSKY, D., THERRIEN, F. and WEISHAMPEL, D. B. 2008. Homology of the 'ethmoid complex' of tyrannosaurids and its implications for the reconstruction of the olfactory apparatus of non-avian theropods. *Journal of Vertebrate Paleontology*, **28**, 123–133.

ALLAIN, R. 2002. Discovery of megalosaur (Dinosauria, Theropoda) in the middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. *Journal of Vertebrate Paleontology*, **22**, 548–563.

BONAPARTE, J. F. 1986. Les dinosaurés (Carnivoures, Allosauridés, Sauropodes, Cetiosauridés) du Jurassique Moyen de Cerro Cóndor (Chubut, Argentine). *Annales de Paleontologie*, **72**, 247–289.

—— 1991. The Gondwanan theropod families Abelisauridae and Noasauridae. *Historical Biology*, **5**, 1–25.

—— and NOVAS, F. E. 1985. *Abelisaurus comahuensis* n. gen. n. sp. Carnosauria del cretácico superior de Patagonia. *Ameghiniana*, **21**, 259–265.

—— —— and CORIA, R. A. 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Contributions to Science, Natural History Museum of Los Angeles County*, **416**, 1–42.

BRUSATTE, S. L. and SERENO, P. C. 2007. A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and revision of the genus. *Journal of Vertebrate Paleontology*, **27**, 902–916.

CALVO, J. O., RUBILAR-ROGERS, D. and MORENO, K. 2004. A new Abelisauridae (Dinosauria: Theropoda) from northwest Patagonia. *Ameghiniana*, **41**, 555–563.

CARRANO, M. T. and SAMPSON, S. D. 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Paleontology*, **6**, 183–236.

COLBERT, E. 1989. The Triassic dinosaur *Coelophysis*. *Museum of Northern Arizona, Bulletin*, **57**, 1–160.

CORIA, R. A. and CURRIE, P. J. 2002*a*. The braincase of *Giganotosaurus carolinii* from the Upper Cretaceous of Argentina. *Journal of Vertebrate Paleontology*, **22**, 802–811.

—— —— 2002*b*. Un gran terópodo celurosaurio en el Cretácico de Neuquén. *Ameghiniana*, **39**, 9R.

—— and SALGADO, L. 1998. A basal Abelisauria Novas, 1992 (Theropoda-Ceratosauria) from the Cretaceous of Patagonia, Argentina. *Gaia*, **15**, 89–102.

—— CHIAPPE, L. and DINGUS, L. 2002. A new close relative of *Carnotaurus sastrei* (Theropoda: Abelisauridae) from Upper Cretaceous of Patagonia. *Journal of Vertebrate Paleontology*, **22**, 460–465.

CURRIE, P. J. 1995. New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). *Journal of Vertebrate Paleontology*, **15**, 576–591.

—— 1997. Braincase anatomy. 81–83. *In* CURRIE, P. J. and PADIAN, K. (eds). *Encyclopedia of dinosaurs*. Academic Press, New York, 896 pp.

—— and CARPENTER, K. 2000. A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas*, **22**, 207–246.

CURRIE, P. J. and ZHAO XI-JIN 1993*a*. A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. *Canadian Journal of Earth Sciences*, **30**, 2231–2247.

—— —— 1993*b*. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences*, **30**, 2037–2081.

HIERONYMUS, T. and WITMER, L. 2004. Cranial rugosity and dinosaur 'horns': rhino and giraffe as model systems for skin reconstruction in fossil taxa. *Journal of Vertebrate Paleontology*, **24** (3 Suppl.), 70A.

MARYANSKA, T., OSMÓLSKA, H. and WOLSAN, M. 2002. Avialan status for Oviraptorosauria. *Acta Palaeontolgica Polonica*, **47**, 97–116.

NOVAS, F. E. 1997. Abelisauridae. 1–2. *In* CURRIE, P. J. and PADIAN, K. (eds). *Encyclopedia of dinosaurs*. Academic Press, New York, 896 pp.

—— AGNOLIN, F. L. and BANDYOPADHYAY, S. 2004. Cretaceous theropods from India: a review of specimens described by Huene and Matley (1933). *Revista Museo Argentino de Ciencias Naturales*, **6**, 67–103.

OSMÓLSKA, H. 2004. Evidence on relation of brain to endocranial cavity in oviraptorid dinosaurs. *Acta Palaeontologica Polonica*, **49**, 321–324.

PAULINA CARABAJAL, A. 2008. Abelisaurid theropod braincase pneumaticity: phylogenetic implications based on Argentinean specimens. *Ameghiniana*, **45**, 30R.

—— 2009. *El neurocráneo de los dinosaurios Theropoda de la Argentina. Osteología y sus implicancias filogenéticas*. Unpublished Doctoral Thesis, Universidad Nacional de La Plata, Facultad de Ciencias Naturales y Museo, 540 pp.

—— 2011. The braincase anatomy of *Carnotaurus sastrei* (Theropoda: Abelisauridae) from the Upper Cretaceous of Patagonia. *Journal of Vertebrate Paleontology*, **31**, 378–386.

—— and CANALE, J. I. 2011. Cranial endocast of the carcharodontosaurid theropod *Giganotosaurus carolinii* Coria and Salgado. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **258**, 249–256.

RAATH, M. A. 1977. *The anatomy of the Triassic theropod Syntarsus rhodesiensis (Saurischia: Podokesauridae) and a consideration of its biology*. Unpublished Doctoral Thesis, Rhodes University, Grahamstown, South Africa, 233 pp.

RAUHUT, O. W. M. 2003. The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Paleontology*, **69**, 1–213.

—— 2004. Braincase structure of the Middle Jurassic theropod dinosaur *Piatnitzkysaurus*. *Canadian Journal of Earth Sciences*, **41**, 1109–1122.

SADLEIR, R. W., BARRETT, P. M. and POWELL, H. P. 2008. The anatomy and systematics of *Eustreptospondylus oxoniensis*, a theropod dinosaur from the Middle Jurassic of Oxfordshire, England. *Palaeontographical Society Monographs*, **160** (627), 1–82.

SAMPSON, S. D. and WITMER, L. M. 2007. Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Memoir of the Society of Vertebrate Paleontology*, **8**, 32–102.

SANDERS, K. R. and SMITH, D. K. 2005. The endocranium of the theropod dinosaur *Ceratosaurus* studied with computed tomography. *Acta Palaeontologica Polonica*, **50**, 60–616.

SEDLMAYR, J. C. 2002. *Anatomy, evolution, and functional significance of cephalic vasculature in Archosauria*. Unpublished PhD thesis, Ohio University, USA, 398 pp.

SERENO, P. C., WILSON, J. A. and CONRAD, J. L. 2004. New dinosaurs link southern landmasses in the mid-Cretaceous. *Proceedings of the Royal Society of London, Series B*, **271**, 1325–1330.

SNIVELY, E. and RUSSELL, A. P. 2007. Functional variation of neck muscles ad their relation to feeding style in Tyrannosauridae and other large theropod dinosaurs. *The Anatomical Record*, **290**, 934–957.

TYKOSKI, R. S. 1998. *The osteology of Syntarsus kayentakatae and its implications for ceratosaurid phylogeny*. Master's Thesis, University of Texas, Austin, 217 pp.

—— and ROWE, T. 2004. Ceratosauria. 47–70. *In* WEISHAMPEL, D. B., DODSON, P. and OSMOLSKA, H. (eds). *The Dinosauria*, Second edition. University of California Press, Berkeley, 833 pp.

WITMER, L. M. 1997. Craniofacial air sinus system. 151–159. *In* CURRIE, P. J. and PADIAN, K. (eds). *Encyclopedia of dinosaurs*. Academic Press, New York, 896 pp.

—— and RIDGELY, R. C. 2009. New insights into the brain, braincase, and ear region of tyrannosaurs, with implications for sensory organization and behavior. *Anatomical Record*, **292**, 1266–1296.