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Braincase, neuroanatomy, and neck posture of Amargasaurus cazaui (Sauropoda, Dicraeosauridae) and its implications for understanding head posture in sauropods

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ARTICLE

BRAINCASE, NEUROANATOMY, AND NECK POSTURE OF *AMARGASAURUS CAZAUI* (SAUROPODA, DICRAEOSAURIDAE) AND ITS IMPLICATIONS FOR UNDERSTANDING HEAD POSTURE IN SAUROPODS

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ABSTRACT—The braincase of *Amargasaurus cazaui* from the Lower Cretaceous of Argentina represents the only dicraeosaurid sauropod neurocranial material known from South America. It has been computer tomographically (CT) scanned and three-dimensional digital reconstructions of the endocranium and inner ear have been made. The cranial endocast is complete, with a volume of approximately 94–98 ml, excluding the dorsal sinuses. The labyrinth of the inner ear is dorsoventrally taller than the lagena, which is conical, and relatively short. The anterior semicircular canal is longer than the posterior and lateral semicircular canals, as in most non-titanosaurid sauropods. When the braincase is oriented with the lateral semicircular canal positioned horizontally, the occipital condyle is oriented posteroventrally, suggesting that the head was held with the muzzle pointing downward. The morphology of the atlas and axis, together with the reconstruction of the osteological neutral pose of the neck, supports this neck and head position, and also indicates the presence of the proatlas in this taxon. The evidence presented here for the skull and neck position of *Amargasaurus* fits with a midheight food-gathering strategy. The presence of titanosauriforms and rebbachisaurids, together with *Amargasaurus*, supports the niche partitioning hypothesis for the La Amarga Formation sauropods.

INTRODUCTION

Dicraeosauridae is a family of mid-sized sauropod dinosaurs characterized until recently by their Gondwanan paleobiogeographic distribution; this situation changed after the inclusion of a Jurassic form from North America within the clade (Whitlock, 2011a). Dicraeosaurids are known from the Upper Jurassic to the middle Cretaceous and four genera are recognized at present: *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, Remes, Fechner, Cladera, and Puerta, 2005, from Cañadón Calcáreo Formation (Tithonian) of Chubut Province, southern Patagonia, and *Suuwassea* Harris and Dodson, 2004, from the Morrison Formation (Tithonian) of Montana, U.S.A. The braincase of the type species of *Amargasaurus cazaui* (MACN-N 15; Salgado and Calvo, 1992) represents the only known dicraeosaurid neurocranial material from South America for the dicraeosaurid family (Fig. 1).

Cranial endocasts of neosauropod dinosaurs are known for the non-titanosaurian macronarians *Camarasaurus* Marsh, 1877 (Marsh, 1880; Osborn and Mook, 1921; Ostrom and McIntosh, 1966; Zheng, 1996; Chatterjee and Zheng, 2005; Knoll et al., 2006; Witmer et al., 2008), and *Giraffatitan* (Janensch, 1935–1936; Knoll et al., 2006; Knoll and Schwarz-Wings, 2009), and the diplodocoids *Tornieria* Fraas, 1908, *Dicraeosaurus* (Janensch, 1935–1936), *Diplodocus* Marsh, 1884 (Holland, 1906; Osborn, 1912; Galton, 1985; Zheng, 1996; Knoll et al., 2006; Witmer et al., 2008), *Nigersaurus* Sereno, Beck, Dutheil, Larsson, Lyon, Moussa, Sadleir, Sidor, Varricchio, Wilson, and Wilson, 1999 (Sereno et al., 2007), and *Apatosaurus* Marsh, 1877 (Balanoff et al., 2010).

Among dicraeosaurids, the endocranial anatomy of *Dicraeosaurus* was described by Janensch (1935–1936), based on plaster endocasts of two specimens. The braincase of *Amargasaurus* is almost complete and even delicate structures such as the basipterygoid processes are preserved (Fig. 1). It was described in some detail by Salgado and Calvo (1992) and its endocranium was preliminarily described using computed tomographic (CT) scanning (Paulina Carabajal, 2012a). The present study provides a redescription of the braincase in light of new technologies, includes a detailed description of the endocranial morphology of *Amargasaurus*, and provides the first insights on dicraeosaurid inner ear morphology. Additionally, the atlas and axis are described as another source of information about neck-head posture and the range of movements of the neck in this taxon.

MATERIALS AND METHODS

CT scans of the braincase of *Amargasaurus* (MACN-N 15) were performed at the Hospital Alejandro Posadas, city of Buenos Aires, Argentina, using a Toshiba Aquilion 64 multidetector medical tomographer. The slices were taken at 0.5-mm intervals. Virtual three-dimensional inner ear and cranial endocasts were made using the software Mimics (version 14.0) and Geomagic at the University of Alberta Laboratory of Vertebrate Paleontology.

Comparisons with the *Dicraeosaurus* braincase and endocast were based on the literature (Janensch, 1935–1936) and photos of the specimens MB.R.1916.1 (endocast of MB.R.2379.1) and MB.R.1917 (endocast of MB.R.2378.3).

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*Corresponding author.

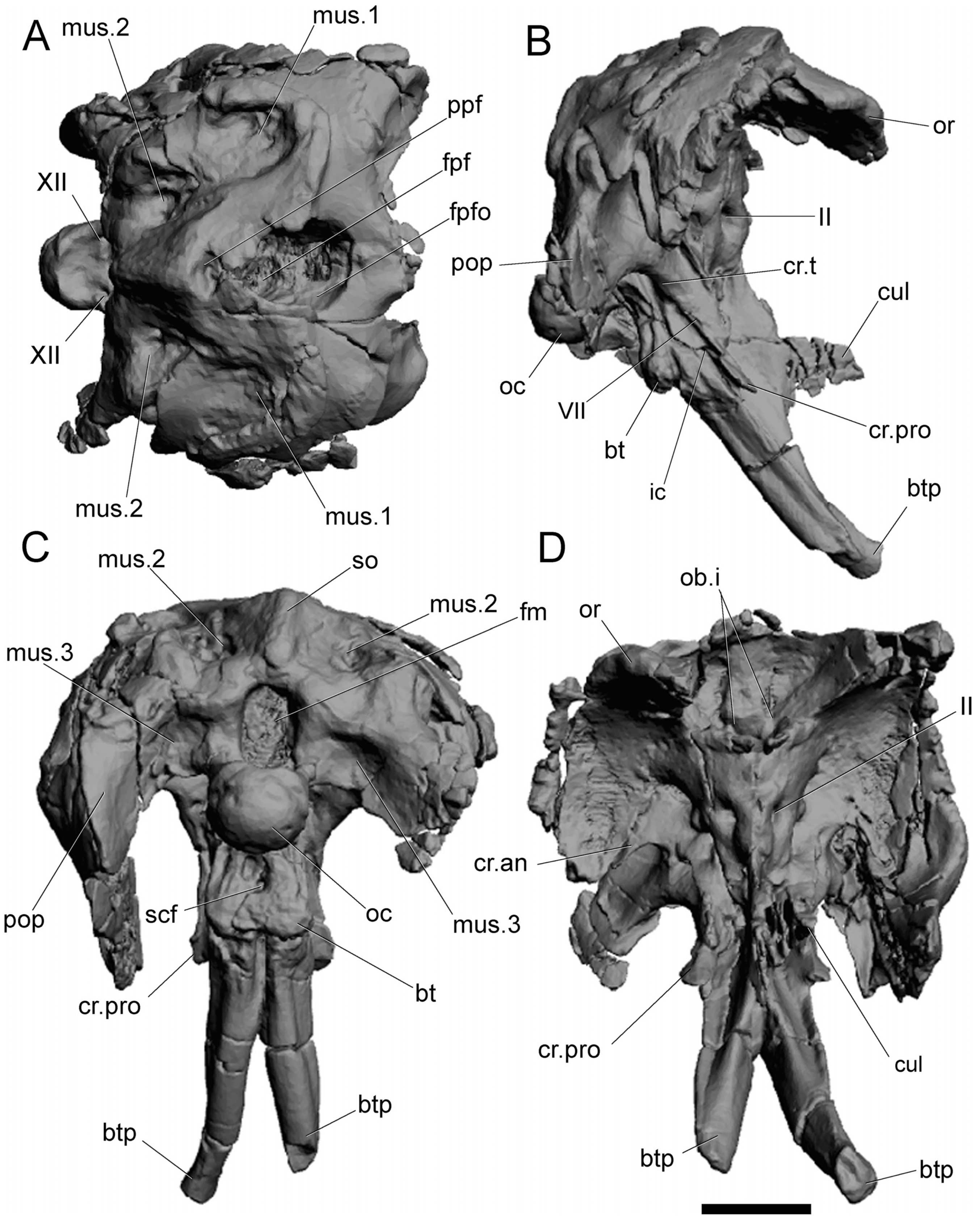


FIGURE 1. Volume rendering of the braincase of *Amargasaurus cazaui* (MACN-N 15). **A**, dorsal; **B**, right lateral; **C**, posterior; and **D**, anterior views. **Abbreviations**: **bt**, basal tuber; **btp**, basipterygoid process; **cr.an**, crista antotica; **cr.pro**, crista prootica; **cr.t**, crista tuberalis; **cul**, cultriform process; **ic**, internal carotid artery foramen; **fm**, foramen magnum; **fpf**, frontoparietal foramen; **fpfo**, frontoparietal fossa; **mus.1**, **2**, **3**, sets of muscle impressions on parietal (**1**), supraoccipital-parietal (**2**), and opisthotic (**3**); **ob.i**, olfactory bulb impression; **oc**, occipital condyle; **or**, orbital rim; **pop**, paroccipital process; **ppf**, postparietal foramen; **scf**, subcondylar foramen; **I**–**XII**, cranial nerves. Scale bar equals 50 mm.

Comparisons with other sauropod endocasts were based on published descriptions of the basal sauropod *Shunosaurus* (Chatterjee and Zheng, 2002) and *Spinophorosaurus* Remes, Ortega, Fierro, Joger, Kosma, Marín Ferrer, Ide, and Maga, 2009 (GCP-CV-4229; Knoll et al., 2012), the macronarian *Camarasaurus* (DNM 28 and GMNH-PV 101; Zheng, 1996), and the diplodocids *Apatosaurus* (BYU 17096; Balanoff et al., 2010), *Tornieria* (Janensch, 1935–1936), and *Diplodocus* (CM 11161; Witmer et al., 2008).

To facilitate discussion, the digital casts of structures are referred to as if they are the structures themselves (e.g., 'olfactory bulb' instead of 'olfactory bulb cavity endocast').

Institutional Abbreviations—ANS, Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.; **BYU**, Brigham Young University, Paleontology collections, Provo, Utah, U.S.A.; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; **DFMMh**, Dinosaurier-Freilichtmuseum Münchehagen/Verein zur Förderung der Niedersächsischen Paläontologie (e.V.), Rehburg, Germany; **DNM**, Dinosaur National Monument, Vernal, Utah, U.S.A.; **GCP**, Grupo Cultural Paleontológico de Elche, Museo Paleontológico de Elche, Elche, Spain; **GMNH**, Gunma Museum of Natural History, Gunma, Japan; **MACN**, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina; **MB.R.**, Collection of fossil Reptilia, Museum für Naturkunde, Berlin, Germany; **SMA**, Sauriermuseum Aathal, Zurich, Switzerland.

DESCRIPTION

Braincase

Skull Roof—The skull roof is wider than long, as in most sauropods (Martinelli and Forasiepi, 2004). On each parietal, there is a deep depression delimited anteriorly by a concave ridge of bone, just in front of the anterior border of the nuchal crest (Figs. 1A, 2A). The depression is anteroposteriorly elongate and subdivided into two sections, corresponding probably to the impressions left by large neck muscle insertions that are identified in theropod dinosaurs as the m. splenius capitis (Snively and Russell, 2007). These insertion marks are equivalent to the m. articuloparietalis in lepidosaurs, the m. transversospinalis capitis lat. in crocodiles, and the m. complexus in aves (Tsuihiji, 2005). In *Amargasaurus*, the muscle insertion scars on the supraoccipital and parietals are larger than in *Dicraeosaurus* (Fig. 2).

There are two conspicuous fenestrae on the midline of the skull (Fig. 2A). The postparietal foramen (Salgado and Calvo, 1992; Harris, 2006; Whitlock, 2011a) is a small opening bounded by the supraoccipital posteriorly and the parietal anteriorly. In the endocast, the cast of the postparietal foramen is just in front of the dural expansion.

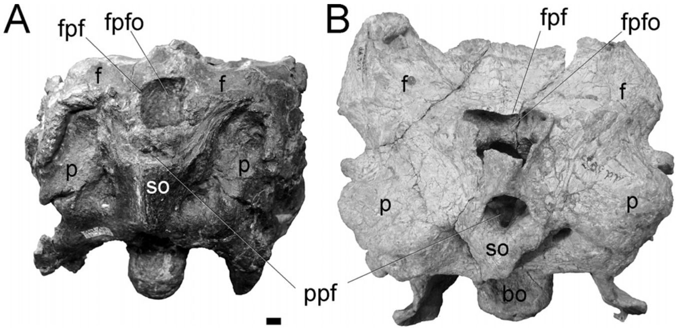


FIGURE 2. **A**, *Amargasaurus cazaui* (MACN-N 15); **B**, *Dicraeosaurus hansemanni* (MBR 279.1). Braincases in dorsal view. **Abbreviations**: **bo**, basioccipital; **f**, frontal; **fpf**, frontoparietal foramen; **fpfo**, frontoparietal fossa; **p**, parietal; **ppf**, postparietal foramen; **so**, supraoccipital. Scale bar equals 10 mm.

The frontoparietal foramen, which has also been referred to as the parietal, pineal, postfrontal, or interfrontal foramen (Salgado and Calvo, 1992; Harris, 2006; Knoll et al., 2012), is a large fenestra, bounded anteriorly by the frontal and posteriorly by the parietal. The frontal is deeply excavated by the frontoparietal fossa, and forms the ventral and lateral walls of the space that was occupied at least in part by the pineal body (Fig. 2A). The frontoparietal recess extends anteroposteriorly, and deeply excavates the frontal to form the ventral and lateral walls of the cavity for at least 37 mm. The posterior portion of the cavity is dorsal to and aligned with the olfactory tract. The frontal extends 46 mm anteriorly to the olfactory tract, roofing the paired oval cavities that are separated by a low ridge of bone.

The frontoparietal fossa is connected posteriorly with the postparietal cavity, which is similar to the condition described for *Apatosaurus* (Balanoff et al., 2010). In *Amargasaurus* and *Dicraeosaurus*, however, the volumes of these spaces are larger, which are evident in the endocasts as markedly dorsal projections that occupy approximately the 35% of the endocranial cavity.

The frontoparietal foramen is a large opening in *Amargasaurus*, and is similar to that in *Dicraeosaurus*, but unlike the smaller foramen present in *Suuwassea* (Harris, 2006). This fenestra is also present in the basal sauropods *Shunosaurus* and *Spinophorosaurus*, and the diplodocids *Apatosaurus* (frontoparietal fenestra in Balanoff et al., 2010), *Diplodocus*, and *Tornieria*. In *Europasaurus* (DFMNh/FV 581.1, 581.2, and 581.3) and *Shunosaurus* (Chatterjee and Zheng, 2002), however, the frontoparietal foramen is enclosed by the parietal only. White (1958) and Zheng (1996) mentioned the presence of a 'pineal foramen' in *Camarasaurus*, but this foramen is not present in other specimens that have been studied (Witmer et al., 2008). Salgado et al. (2005) stated that in dicraeosaurids, the foramen remains open in adults, whereas in other sauropod taxa it is apparently only present in immature individuals.

In *Amargasaurus*, the postparietal foramen is smaller than the frontoparietal foramen, as in *Dicraeosaurus* and *Suuwassea*. The presence of this opening is usually recognized as a dicraeosaurid synapomorphy (Salgado and Bonaparte, 1991; Wilson and Sereno, 1998; Wilson, 2002; Whitlock, 2011a). Among non-dicraeosaurid sauropods, this foramen is now known for *Spinophorosaurus* (Knoll et al., 2012), and the diplodocids *Kaatedocus* (from the Morrison Formation; Tschopp and Mateus, 2013) and *Apatosaurus* (Balanoff et al., 2010). Although Upchurch et al. (2004) described a postparietal foramen in *Torneria*, this fenestra is solely present in a single smaller braincase (MB.R.2387) that cannot be clearly assigned to this taxon and is now recognized as an indeterminate flagellicaudatan sauropod (Remes, 2006; Tschopp and Mateus, 2013). In *Apatosaurus*, the postparietal fenestra is broadly confluent with the frontoparietal fenestra; this is different than the fully or nearly fully anteriorly closed fenestrae of dicraeosaurids, *Spinophorosaurus*, and *Kaatedocus*. Among macronarians, the postparietal fenestra is present solely in *Europasaurus* (DFMNh/FV 581.1 and 581.2; Sander et al., 2006). In *Amargasaurus*, the postparietal fenestra is markedly smaller than in *Dicraeosaurus* (e.g., MB.R.2379.1–3).

As mentioned above, the frontoparietal and postparietal foramina connect internally via a large space, which is expressed in the endocast as an enlarged dorsal outgrowth of the brain. This space partially enclosed the parietal-pineal complex, which includes the pineal gland and the parietal organ (the photoreceptive body) (Harris, 2006). The pineal gland is found between the cerebral hemispheres and the cerebellum, and plays a role in thermoregulation (Schweitzer and Marshall, 2001), and in circadian and other biological rhythms (Franzosa, 2004). In *Amargasaurus* and *Dicraeosaurus*, the anterior section of the cavity may have housed the pineal body, whereas the posterior dorsal peak may have housed part of the superior sagittal sinus (Witmer and Ridgely, 2009). As noted by Witmer et al. (2008), the volume of the dorsal outgrowth exceeds that required for a pineal gland; therefore, the hypothesis that it includes extensive dural sinuses is probably correct (and does not preclude presence of the pineal gland).

Supraoccipital—On the occiput, the exoccipitals and basioccipital are aligned, vertical elements, whereas the supraoccipital is inclined. The supraoccipital is oriented posteroventrally when the lateral semicircular canal (LSC) is held horizontally. Because of this, it is widely exposed in the dorsal view of the braincase, unlike the supraoccipital of *Dicraeosaurus* (Figs. 1A, 2B).

Exoccipital-Opisthotic Complex—The paroccipital process projects posterolaterally at the base and posteroventrally distally. The distal end of the paroccipital process is ventral to the occipital condyle. Lateral to the foramen magnum, the exoccipital-opisthotic complex has an oval depression, whose dorsal margin divides the paroccipital process into dorsal and ventral sections. The ventral section corresponds to another muscle insertion, probably the m. iliocostalis capitis, as described for theropod dinosaurs (Snively and Russell, 2007).

Lateral to the occipital condyle, there is a single foramen for cranial nerve (CN) XII, which is 4.5 mm in diameter (Fig. 3). Unlike in other sauropods, this foramen is posterior to the foramen magnum, indicating that the posterior section of the medulla oblongata was not covered dorsally by braincase bones.

Posterior to the crista prootica, which projects posterolaterally, the metotic foramen and the oval window open within a shallow depression. The metotic foramen is large and oval, whereas the oval window is small and circular. On the left side of the braincase, there is a small additional foramen posterior to the metotic foramen. The CT scans show that the passage of this smaller foramen connects internally with the metotic foramen canal (Fig. 4A), indicating a separate CN XI.

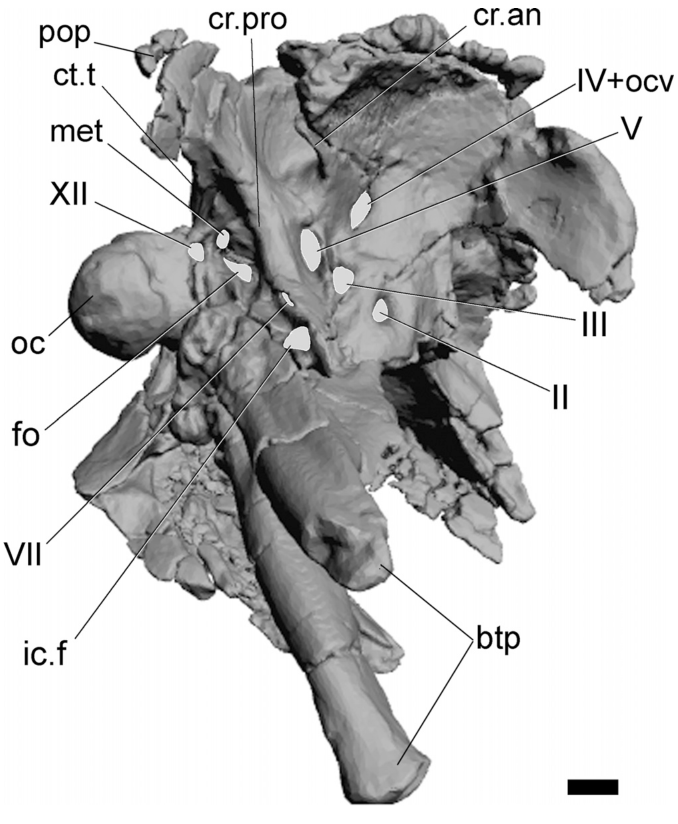


FIGURE 3. Volume rendering of the braincase of *Amargasaurus cazaui* (MACN-N 15), in right posterolateroventral view. **Abbreviations**: **btp**, basipterygoid process; **cr.an**, crista antotica; **cr.pro**, crista prootica; **cr.t**, crista tuberalis; **fo**, fenestra ovalis; **ic.f**, internal carotid foramen; **met**, metotic foramen; **oc**, occipital codyle; **ocv**, orbitocerebral vein; **pop**, paroccipital process; **I–XII**, cranial nerves. Scale bar equals 10 mm.

Basioccipital—The basioccipital forms most of the basal tubera, which are fused and subquadrangular in shape, and projects ventrally below the occipital condyle. There is a single foramen between the basal tubera (Fig. 1C), which communicates internally with a long and vertical pneumatic(?) recess between the basal tubera and the basipterygoid processes.

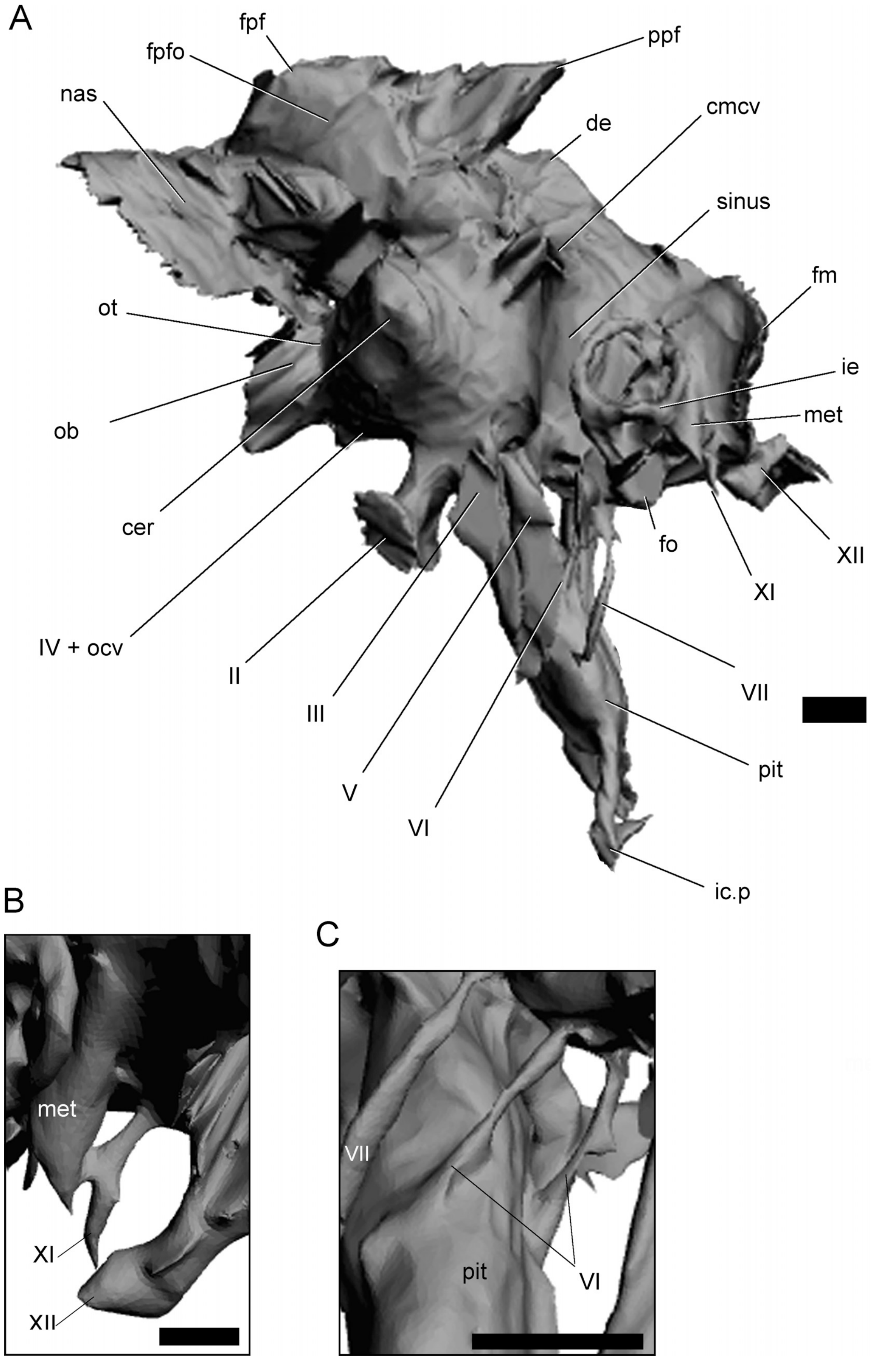
Basisphenoid—The basisphenoid forms the basipterygoid processes, which are solid structures. The external foramen for the internal carotid artery is located on the lateral aspect of the base of each basipterygoid process, at the level of the distal end of the basal tuber (Fig. 3). Because of this, the internal carotid foramen of the basicranium is visible in lateral view in *Amargasaurus*, which seems to be a conservative character within Sauropodomorpha (Paulina Carabajal, 2012b).

The CT scans show a vertical passage between the basipterygoid processes that connects the subcondylar foramen posteroventrally with the pituitary fossa dorsally (Figs. 1C, 5B). The passage for CN VI pierces the floor of the basicranium and enters the pituitary fossa laterally (Figs. 4C, 5B). Although it is not possible to confirm the existence of an external foramen for CN VI on the basicranium, it definitely does not open anteroventral to the foramen for CN III as illustrated by Salgado and Calvo (1992).

Prootic—The prootic delimits the large foramen for CN V posteriorly, whereas the anterior margin of this opening is probably formed by the laterosphenoid, although there are no visible sutures. The small foramen for CN VII is posteroventral to the foramen for CN V, and is probably enclosed only by the prootic (Fig. 3). This foramen is below the level of the occipital condyle, indicating that there is a relatively long passage compared with other sauropods. The crista prootica is elongate and wing-shaped, and is formed mainly by the prootic. It runs ventrally from the crista antotica anterior to the foramen for CN V, and reaches the lateral side of the basipterygoid process. The robust crista tuberalis is formed by the opisthotic and extends behind the opening for CN V (Fig. 3).

Laterosphenoid—The laterosphenoid is firmly fused to the prootic. The crista antotica is slender and projects posteriorly, and anteriorly delimits a relatively small supratemporal fossa (Fig. 1D). Posteriorly, the laterosphenoid encloses the foramina for CNs III and IV, which are similar in size. Cranial nerve III is anterior to CN V and posterior to CN II, whereas CN IV is dorsal to CN III close to the contact with the frontal (Fig. 3). Unlike *Dicraeosaurus* (Janensch, 1935–1936) there is no 'epioptic fenestra' in *Amargasaurus*. In the Argentinean taxon, the foramen for CN IV is probably also the exit of the orbitocerebral vein, which has a separate foramen in some other sauropods (see Paulina Carabajal, 2012b:table 1).

Orbitosphenoid—The orbitosphenoids are elongate and subtriangular in shape, and meet ventrally on the midline in a clear interorbital suture (Fig. 1D). The foramina for CN II are enclosed by the orbitosphenoids. The orbitosphenoid also forms the lateroventral wall of the foramen for CN I, which is also bordered by two small triangular lateral projections that probably correspond to ethmoidal fragments (Fig. 1D). The foramen for CN II is subcircular with a diameter of 6.2 mm. Each foramen is separated from its counterpart by 12 mm of bone. The CT scans show long passages for these nerves (Fig. 4A). The olfactory bulbs are not well defined in the CT scans (Fig. 5A), but the impressions left on the ventral aspect of the frontals are clear. They are 12.8 mm wide and slightly divergent anteriorly.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Cranial Endocast

The cranial endocast of *Amargasaurus* is 95 mm in total anteroposterior length, measured from the back of the olfactory tract to the foramen magnum, and 70 mm in maximum dorsoventral depth (at the level of the dural expansion), making it relatively short and deep as in most sauropods (Hopson, 1979; Figs. 4, 5). The greatest mediolateral breadth of the endocranial space lies across the cerebral hemispheres of the forebrain and is 62 mm, whereas the narrowest point lies in the hindbrain just posterior to the cerebellum. The most conspicuous trait is the dural expansion over the forebrain and midbrain (Fig. 4A). The dural expansion represents a space that was probably occupied by the longitudinal venous sinus (see Witmer et al., 2008, and discussion herein) and is markedly taller than the forebrain. The anterior protuberance corresponds to the spaces related to the frontoparietal and postparietal foramina, and was occupied by the pineal gland and probably other tissues (Fig. 4A). The volume of the complete endocranial cavity is approximately 150.5 ml (Fig. 4A).

Forebrain—The outstanding features of the forebrain include the olfactory tract (CN I), the cerebral hemispheres, optic nerves (CN II), and the pituitary body.

As in most sauropods, the olfactory tract is almost nonexistent (Fig. 5A). The olfactory bulbs are not clearly visible in the endocast. They are oval, 12.8 mm wide and 12 mm long, and diverge from the midline at an angle of approximately 110°, similar to those observed in other sauropods (Balanoff et al., 2010; Paulina Carabajal, 2012b). The maximum transverse width of the combined olfactory bulbs is 32 mm. The impressions of the olfactory bulbs are lateroventrally delimited by thin triangular projections of bone, probably representing remains of the lateral ossified ethmoidal elements (sphenethmoids).

Cranial nerves II exit the endocranial cavity through separate foramina that are enclosed by the orbitosphenoids. The passages of CNs II are 19 mm long and 13 mm in diameter. They extend posteromedially to converge at the midline of the anteroventral margin of the main body of the diencephalon (Fig. 4A).

The cerebral hemispheres are not completely visible in dorsal view due to the development of the dorsal expansion and the pineal protuberance over the forebrain and midbrain. However, if the protuberance is digitally removed, the lateral expansion of the cerebral hemispheres can be clearly defined (Fig. 5A). The lateral border of the cerebrum is pyramidal, unlike the rounded one observed in most sauropods, especially in titanosaurids (Paulina Carabajal, 2012b). In *Dicraeosaurus*, the cerebrum is laterally expanded but not as much as in *Amargasaurus* (Fig. 5A). This pointed projection is probably related to the presence of a well-developed sinus derived from the dorsal longitudinal sinus.

Also part of the diencephalon, the pituitary body descends from the ventral surface of the endocast and exhibits hyperdevelopment, as in other sauropods (Balanoff et al., 2010). The pituitary body is 66.5 mm long and projects posteroventrally at an angle of approximately 70° from the floor of the medulla oblongata (Fig. 4A). The infundibular stalk is not well differentiated, and has the same diameter of the proximal section of the pituitary body. The pituitary endocast does not exhibit any constriction separating the anterior (adenohypophysis) and posterior (neurohypophysis) portions of the pituitary fossa, unlike titanosaurids where the pituitary fossa is clearly divided into two sections (Paulina Carabajal, 2012b). The pituitary cast of *Amargasaurus* has more or less the same diameter along all its length, except distally, where it is slightly expanded. There are no visible pituitary vessels associated with the endocast, but this is probably due to the poor preservation of this region of the specimen and the quality of the CT scan data. The volume of the pituitary fossa cast is approximately 87–90 ml, which represents 6% of the total volume of the endocast.

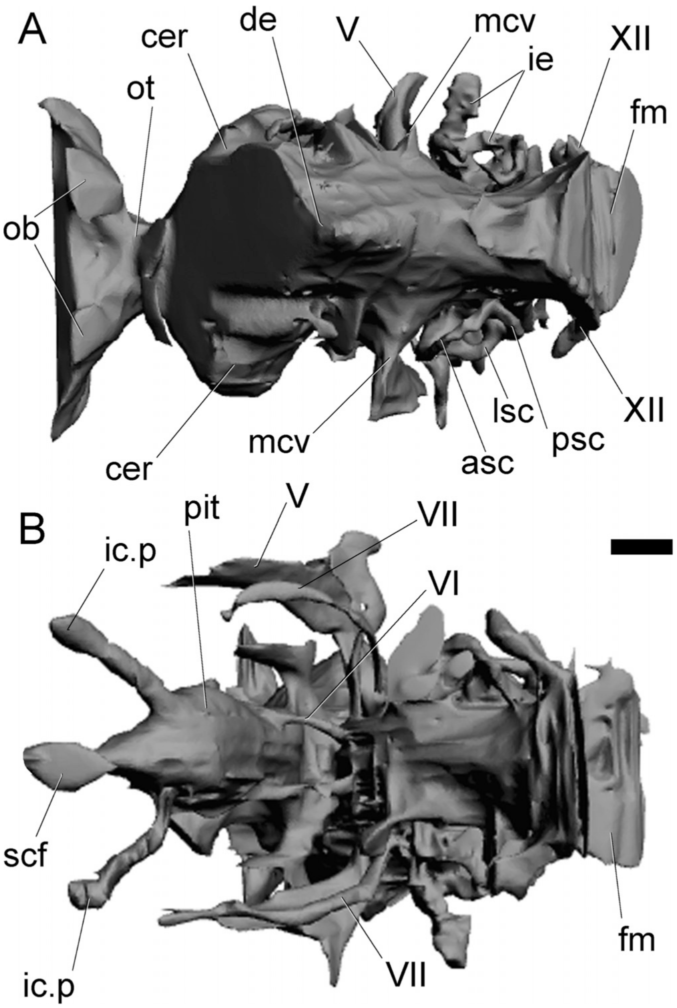

FIGURE 5. Surface rendering of the cranial endocast of *Amargasaurus cazaui* (MACN-N 15). **A**, dorsal view (the dorsal extracranial space was eliminated to facilitate visualization of the cerebral hemispheres); **B**, ventral view. **Abbreviations**: **asc**, anterior semicircular canal; **cer**, cerebral hemisphere; **de**, dorsal expansion; **fm**, foramen magum; **ie**, inner ear; **ic.p**, internal carotid passage; **lsc**, lateral semicircular canal; **mcv**, middle cerebral vein; **ob**, olfactory bulb; **ot**, olfactory tract; **pit**, pituitary body; **psc**, posterior semicircular canal; **scf**, subcondylar foramen cast; **V**, **VI**, **VII**, **XII**, cranial nerves. Scale bar equals 10 mm.

← FIGURE 4. Surface rendering of the cranial endocast of *Amargasaurus cazaui* (MACN-N 15). **A**, left lateral view; **B**, detail of CNs IX–XII in posterodorsal view; **C**, pituitary and CNs VI–VII in posteroventral view. **Abbreviations**: **cer**, cerebral hemisphere; **cmcv**, caudal middle cerebral vein; **de**, dorsal expansion; **fm**, foramen magnum; **fo**, fenestra ovalis; **fpf**, frontoparietal foramen; **fpfo**, frontoparietal fossa; **ie**, inner ear; **ic.p**, internal carotid passage; **med**, medulla oblongata; **met**, metotic foramen cast for CNs IX–XI; **nas**, nasal capsule; **ob**, olfactory bulb; **ot**, olfactory tract; **p**, parietal; **pit**, pituitary body; **ppf**, postparietal foramen; **scf**, subcondylar foramen cast; **sinus**, venous sinus (caudal middle cerebral vein plus rostral middle cerebral vein)?; **I**–**XII**, cranial nerves. All scale bars equal 10 mm.

There are three passages entering the tip of the pituitary cast, two of them corresponding to the internal carotid arteries (Figs. 4B, 5B). The single passage is oriented posteriorly and corresponds in the braincase with a subcondylar foramen, which is present in many other sauropods (Fig. 5B). The internal carotid arteries enter the pituitary fossa through separate foramina. The passages for the arteries are 66.5 mm long, 4 mm in diameter, and diverge from the midline at an angle of 37.5° (Fig. 5B). As mentioned previously, the external foramen in the basicranium for the internal carotid artery opens laterally at the base of the basipterygoid process, as in other diplodocoids; this is different in titanosaurids, which have a foramen for the internal carotid artery that opens medial to the basipterygoid process (Paulina Carabajal, 2012b).

Midbrain—The mesencephalic structures visible in a dinosaur endocast consist of the optic lobes and CNs III and IV (Franzosa, 2004). Cranial nerve III is aligned posteriorly to CN II, whereas CN IV is posterodorsal to CN II (Fig. 4A). The distance between CN II and CN III is slightly larger than the distance between CN III and CN IV, and this ratio is the same in the endocast of *Giraffatitan* (‘*Brachiosaurus*’ in Knoll and Schwarz-Wings, 2009). In *Dicraeosaurus*, the distances between CN II and CN III, and between CN III and CN IV are subequal, as in *Diplodocus* (Hopson, 1979), *Shunosaurus* (Chatterjee and Zheng, 2002), and some titanosaurs (Paulina Carabajal, 2012b).

The passage for CN IV is not completely discernible in the CT scans. However, the foramen for this nerve can be identified in the braincase (Fig. 3) and is therefore indicated in the endocast illustration (Fig. 4A). In *Dicraeosaurus*, there is a large opening for the combined exit of CN IV and the orbitocerebral vein (Witmer et al., 2008; Knoll and Schwarz-Wings, 2009) that is called the ‘epioptic fenestra’ by Janensch (1935–1936). The reduction of this fenestra into a foramen in *Amargasaurus* is an important difference between the two taxa.

Hindbrain—The visible features in the hindbrain region of the cranial endocast include the cerebellum, medulla oblongata, and CNs V–XII. The endocast shows one root for the branches of CN V, which leave the endocranial cavity through a single foramen (Fig. 3). In the endocast, the root of CN V is posteriorly aligned with CN III (Fig. 4A). However, the nerve passes lateroventrally so that the external foramen of CN V is markedly posteroventral to the foramen of CN III in the lateral view of the braincase (Fig. 3).

There is a large vertical protuberance on the endocast that is dorsal to the exit of CN V. It corresponds with an infilling of the dorsal head/caudal middle cerebral vein system—as described for *Spinophorosaurus* (Knoll et al., 2012). Just dorsal to the sinus is the rostral middle cerebral vein, the external opening of which is not visible in the braincase, probably because it is located posterior to the crista antotica close to the laterosphenoid-frontal suture. These two large structures, the dorsal head vein sinus and the middle cerebral veins, are also present in the endocast of *Dicraeosaurus*.

On the ventral side of the hindbrain, the two canals for CN VI are 35 mm long and project anteroventrally (Fig. 4A, C). The canals penetrate the ventral section of the pituitary fossa laterally (Fig. 5B). Cranial nerve VII has a small diameter compared with the other cranial nerves, but the most astonishing characteristic is its extremely long canal through the bone, which is twice the length of the canal of CN V (Fig. 4A). Unlike the condition observed in most sauropods (Knoll et al., 2006), in *Amargasaurus* the canal of CN VII extends ventrolaterally within the prootic (and probably the basisphenoid) to exit through a foramen ventral to that of CN V and a few millimeters dorsal to the exit of the internal carotid artery at the base of the basipterygoid process (Fig. 3).

Cranial nerves IX and X leave the braincase through the same opening, the metotic foramen (Figs. 3, 4C), whereas CN XI has a separate foramen, unlike most sauropods in which the metotic foramen is often for CNs IX–XI. The passage of CN XI is connected transversely to the metotic canal by means a short canal (Figs. 3, 4B, C). In the braincase, there are three foramina lateral to the occipital condyle (Fig. 3). The largest and most anterior foramen is delimited anteriorly by the crista tuberalis (opisthotic) and corresponds to the metotic foramen for CN IX, CN X, and the jugular vein. The other two foramina, which pierce the exoccipital, correspond to foramina for CN XI and CN XII. The CT scans confirm that there is a single foramen for the branches of CN XII (Figs. 3, 4B, 5A).

In other sauropod braincases, including those of titanosauriforms (Curry Rogers and Forster, 2004; Wilson, 2005, 2009; Calvo and Kellner, 2006; Paulina Carabajal and Salgado, 2007; García et al., 2008; Paulina Carabajal et al., 2008; Paulina Carabajal, 2012b) and diplodocoids (Janensch, 1935–1936; Harris, 2006; Balanoff et al., 2010), the internal opening for CN XII always lies in front of the edge of the foramen magnum, within the limits of the endocranial cavity proper. In *Amargasaurus*, however, this foramen is posterior to the edge of the foramen magnum and is clearly visible in dorsal view (Fig. 1A). The neck of the occipital condyle is excavated dorsally by a shallow oval depression that reaches the basioccipital-exoccipital sutures. This depression and the posterior position of the CN XII foramina suggest that the posterior extension of the medulla oblongata was not enclosed dorsally and laterally by braincase bones. Instead, it was probably covered by the proatlas.

The cerebral and pontine flexures are similar to those in *Dicraeosaurus* (Janensch, 1935–1936). *Amargasaurus* shares with *Dicraeosaurus* the presence of a large dorsal longitudinal sinus and an enlarged endocranial space for the frontoparietal fenestra; however, the latter seems to be different from that illustrated by Janensch (1935–1936;lam. XIII) for *Dicraeosaurus*. In *Amargasaurus*, the enlarged endocranial space is dorsal to the forebrain (Fig. 5A).

Inner Ear

The inner ear is 30 mm tall and 22 mm wide (Fig. 6). The labyrinth is dorsoventrally taller than the lagena, which is tubular and markedly short. The lagena housed the cochlear tube, which had the function of converting acoustic stimuli into neural signals. The length of this structure is directly correlated with the length of the sensorial epithelium, and the measurement is used to estimate the auditory capacity (Witmer and Ridgely, 2009). In most sauropods studied, except *Giraffatitan* (Clarke, 2005), the length of the auditory part of the inner ear (the lagena) plus the vestibulum is at least the height of the labyrinth (Knoll et al., 2012; Paulina Carabajal, 2012b). This condition suggests relatively lower auditory capabilities for *Amargasaurus* than in other sauropods in which the inner ears are known.

Although the vestibulum is not well defined, the fenestra ovalis is clearly visible in the CT scans. It is oriented posterolaterally and continuous with the short passage of the columellar recess. The common trunk is robust (Fig. 6A) and the anterior ampula is larger than the posterior ampula.

The anterior semicircular canal (ASC) is longer than the posterior semicircular canal (PSC), and the lateral semicircular canal (LSC) is markedly shorter than the PSC. This is similar to the morphology described for *Diplodocus* and other diplodocoids (Hopson, 1979; Wilmer et al., 2008). Basal macronarians (e.g., *Camarasaurus*, *Giraffatitan*; Sereno et al., 2007; Knoll and Schwarz, 2009) retain the same plesiomorphic configuration. Titanosaurids have a different pattern in which the semicircular canals are shorter and are subequal in length (Paulina Carabajal, 2012b). In dorsal view, the angle formed by the ASC and PSC is slightly larger than 90° (Fig. 6B). In sauropod dinosaurs, short and small semicircular canals suggest a decrease in the compensatory movements of eyes and head (Witmer et al., 2008; Knoll et al., 2012, 2013). On the other hand, the development of large semicircular canals has been associated with behavioral patterns that require agility in the head movements (Sereno et al., 2007).

Cervical Vertebrae

Although *Amargasaurus* was discovered in articulation (Salgado and Bonaparte, 1991; Bonaparte, 1996), the proatlas was not reported. Among neosauropods, the proatlas is rarely preserved but was recovered for *Dicraeosaurus* (Janensch, 1929) and non-titanosaurian macronarians such as *Camarasaurus* and *Giraffatitan* (Gilmore, 1925; Janensch, 1950). When preserved in anatomical position, the proatlas articulates with the exoccipital-opisthotic complex on the rim of the foramen magnum. This has been observed in *Camarasaurus* (CM 11338) and *Kaatedocus* (SMA 004; Tschopp and Mateus, 2013). In *Amargasaurus*, there are no facets lateral to the foramen magnum that indicate this contact. However, the position of the foramina for CN XII behind the edge of the foramen magnum indicates that there was an element dorsally enclosing the posterior part of the medulla oblongata. The articulation of the atlas with the occipital condyle leaves a space between the vertebra and the occipital table of the braincase, which suggests the presence of a proatlas in *Amargasaurus*.

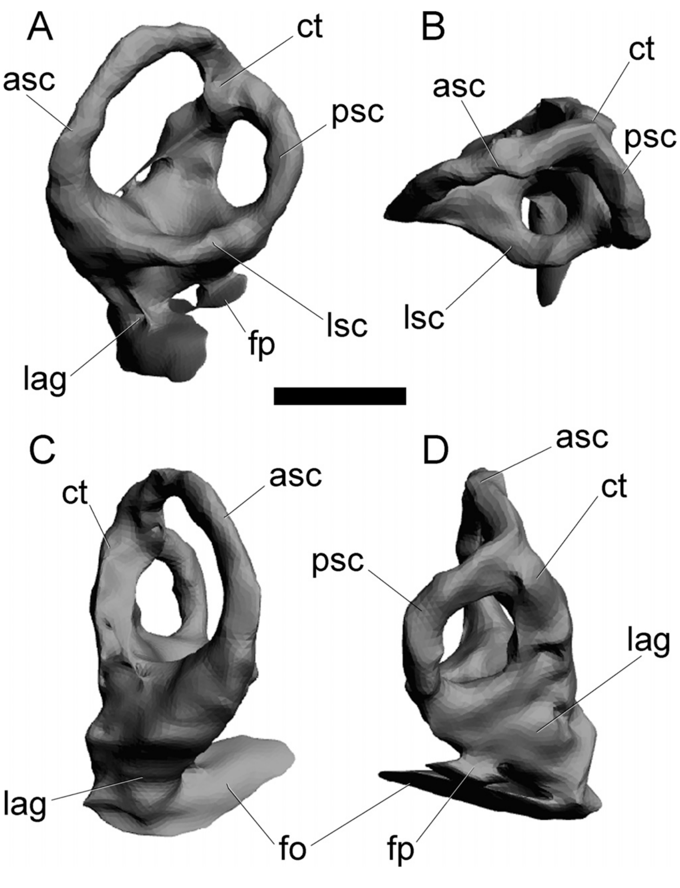

FIGURE 6. Digital left inner ear of *Amargasaurus cazaui* (MACN-N 15). **A**, lateral; **B**, dorsal; **C**, anterior; and **D**, posterior views. **Abbreviations**: **asc**, anterior semicircular canal; **ct**, common trunk; **fo**, fenestra ovalis + columellar recess; **fp**, fenestra pseudorotunda; **lag**, lagena; **lsc**, lateral semicircular canal; **psc**, posterior semicircular canal. Scale bar equals 10 mm.

Atlas—As in other sauropods, the intercentrum is crescentic in anterior view, being 64 mm wide and 35 mm high (Fig. 7). Dorsally, it has a concave region that supports the odontoid process of the axis. This region does not deeply invade the intercentrum, and most of the odontoid would have been bounded by the medial edges of the neurapophyses (Fig. 7C). The odontoid fossa of the axis occupies around one-quarter of the total intercentrum height as in *Dicraeosaurus* and *Suuwassea*, but unlike the deeper odontoid fossa in *Diplodocus* (Hatcher, 1901:fig. 4). In lateral view, both the anterior and the posterior articular surfaces project ventrally approximately to the same degree (Fig. 7B). This is a similar morphology to that observed in non-neosauropod sauropods, non-diplodocid diplodocoids, and titanosauriforms (Janensch, 1929, 1950; Ouyang and Ye, 2002; Harris, 2006; Curry Rogers, 2009). However, it differs from the more developed anteroventral expansion observed in diplodocids (Hatcher, 1901) and basal macronarians (e.g., *Camarasaurus*, *Europasaurus*; Osborn and Mook, 1921; Carballido and Sander, 2014). The anteroposterior length of the dorsal surface of the intercentrum (24 mm) in *Amargasaurus* is shorter than that of its ventral surface (33 mm) (Fig. 7B). This was recognized as a synapomorphy of Flagellicaudata (Wilson, 2002; Whitlock, 2011a), although a more widespread distribution (Diplodocoidea?) cannot be discarded because no information is available for rebbachisaurid sauropods. In anterior view, the condyloid fossa of the intercentrum is crescentic. Although the posterior articular surface is not well seen, because sediment obscures this region, this surface seems to be slightly convex dorsally but with a slight ventral bump (Fig 7B). Ventrally, the intercentrum is transversally concave (Fig. 7D). The neurapophyses of the atlas are almost completely fused with the intercentrum, probably because of an advanced ontogenetic stage of the specimen. Nevertheless, the unfused condition of the cervical ribs indicates that the holotype of *Amargasaurus* is not senescent; an example of an osteologically mature animal is the specimen CM 3018 (*Apatosaurus*), in which the atlas and axis are coossified, as well as the cervical ribs (Gilmore, 1936). The ventral contact of the neurapophyses with the centrum can only be barely recognized as a low crest, and lacks a clear suture scar (dotted lines in Fig. 7B). When the axis is horizontally oriented, the atlas takes a slightly dorsal inclination towards its articulation with the occipital condyle. Because the neurapophyses of the atlas are strongly ossified with the axis, this seems to have been the true inclination of these elements instead product of taphonomic process. As in other sauropods, the neurapophyses are wing-like structures that are oriented posterodorsally. The posterodorsal arm of the neurapophysis supports the postzygapophysis, which articulates with the prezygapophysis of the axis (Fig. 7B). The posterior arm of the neurapophysis is almost as long anteroposteriorly (55 mm) as its maximum dorsoventral height (63 mm). Contrary to the condition of some sauropods such as *Rapetosaurus* (Curry Rogers, 2009) and *Europasaurus* (Carballido and Sander, 2014), no foramina were observed on the dorsolateral surface of the neurapophyses.

Axis—The axis of *Amargasaurus* is well preserved except for the neural spine, which was restored (Fig. 7). The centrum is 105 mm long and 66 mm high at the posterior articular surface. The anterior intercentral articular surface is almost completely flat, with a small anteroventral expansion, whereas the posterior articular surface is markedly concave (Fig. 7A, B). The large pleurocoel that covers most of its lateral surface lacks the bony crest that subdivides the pleurocoel of more posterior cervical vertebrae. Nevertheless, a small anteriorly positioned deep zone can be identified, just dorsal to the diapophysis (Fig. 7B). In other dicraeosaurids, such a depression is absent, and this difference in the major development of pneumatic structures in *Amargasaurus* was also noted by Schwarz and Fritsch (2006). Part of the ventral surface of the centrum has a narrow keel, whereas the

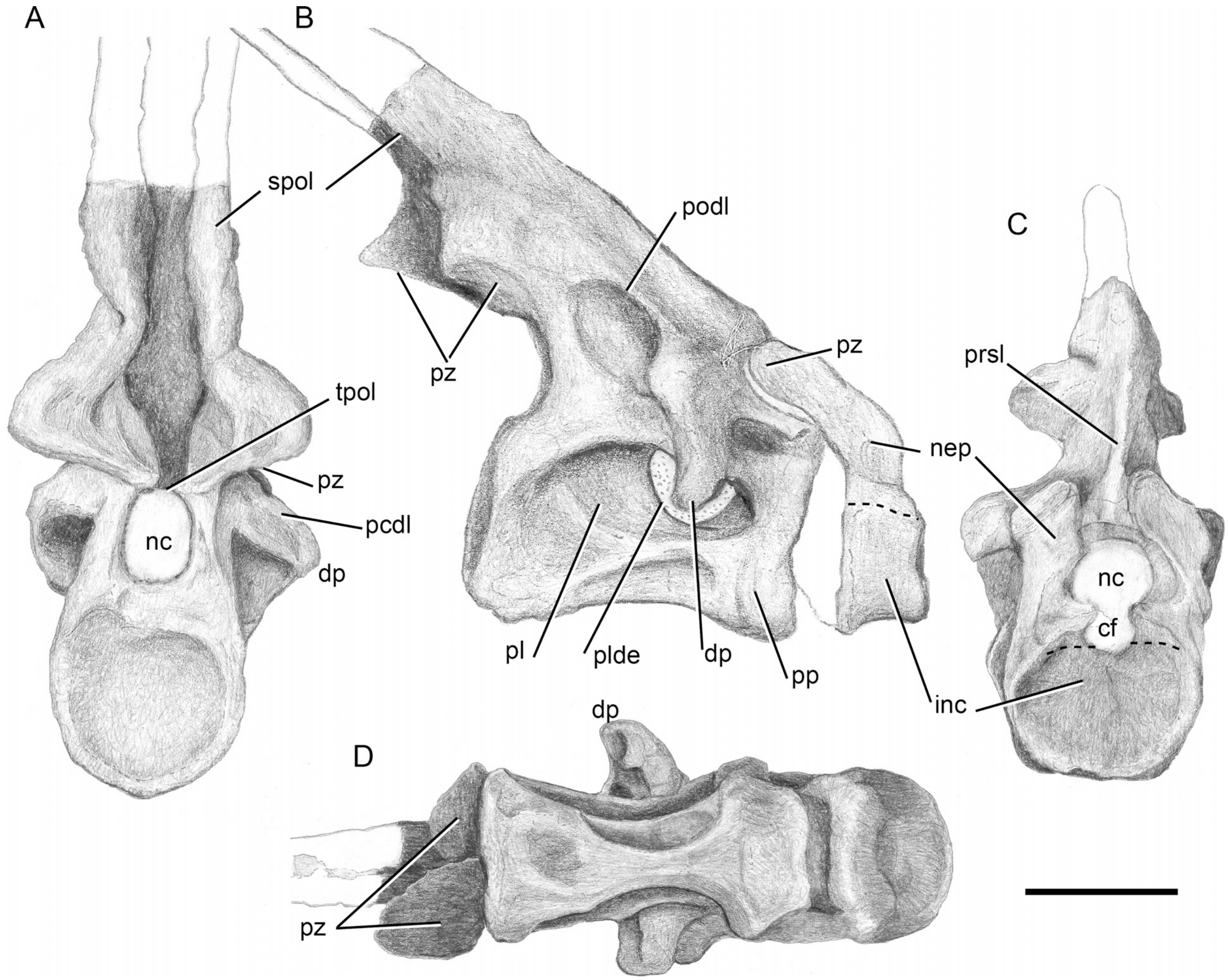

FIGURE 7. Atlas-axis of *Amargasaurus cazaui*, (MACN-N 15). **A**, posterior; **B**, lateral; **C**, anterior; and **D**, ventral views. **Abbreviations**: **cf**, condyloid fossa; **dp**, diapophysis; **inc**, intercentrum; **nc**, neural canal; **nep**, neurapophysis; **pcdl**, posterior centrodiapophyseal lamina; **pl**, pleurocoel; **plde**, pleurocoel deepest excavation; **podl**, posterior centrodiapophyseal lamina; **pp**, parapophysis; **pz**, postzygapophysis; **spol**, spinopostzygapophyseal lamina; **sprl**, spinoprezygapophyseal lamina. Scale bar equals 10 cm.

anterior-most and posterior-most ventral zones are wider and slightly concave transversally, as in other dicraeosaurids (Fig. 7D).

The parapophysis is slightly marked in the centrum (Fig. 7B). The short transverse process of the axis is positioned low on the neural arch and ends in a small diapophysis. Dorsally, the transverse process supports the posterior centrodiapophyseal and prezygodiapophyseal laminae. Below the transverse process, a deep centrodiapophyseal fossa (sensu Wilson et al., 2011) is present. Posteriorly, the single centropostzygapophyseal lamina bounds the neural canal (Fig. 7A). The postzygapophysis has a low angle (around 20°) to the horizontal; a short horizontal intrapostzygapophyseal lamina connects the pair, and forms the ventral limit of the spinopostzygapophyseal fossa.

The axial neural spine was restored during preparation (Fig. 7). It is triangular in transverse section. A single prespinal lamina extends posterodorsally from the midpoint of the neural arch, between the prezygapophyses; however, it lacks any division or expansion, and therefore does not represent the union of paired spinoprezygapophyseal laminae. The prespinal lamina extends past the postzygapophysis, but its more dorsal section is not preserved (Fig. 7B). Above the postzygapophysis, a well-developed spinopostzygapophyseal lamina extends posterodorsally. The left and right spinopostzygapophyseal laminae form the lateral edges of the spinopostzygapophyseal fossa, which is incomplete dorsally (Fig. 7A). Although we are more inclined to consider that the neural spine of the axis was not divided because its dorsal section is not preserved, it is impossible to determinate if it has a small dorsal notch (incipient bifurcation), as observed in *Suuwassea* (Harris, 2006); alternatively, it may have been divided, as in *Dicraeosaurus* (Janensch, 1929). Furthermore, it is not possible to determinate the degree of lateral expansion of the neural spine of the axis. Nevertheless, the preserved section is comparatively much narrower than the same section in *Dicraeosaurus* and *Suuwassea*, and probably the dorsal section of the neural spine does not differ from the reconstruction made by Salgado and Bonaparte (1991).

HEAD AND NECK POSTURE

Head and neck positions in dinosaurs have been discussed by several authors, based mainly on morphology of the cervical

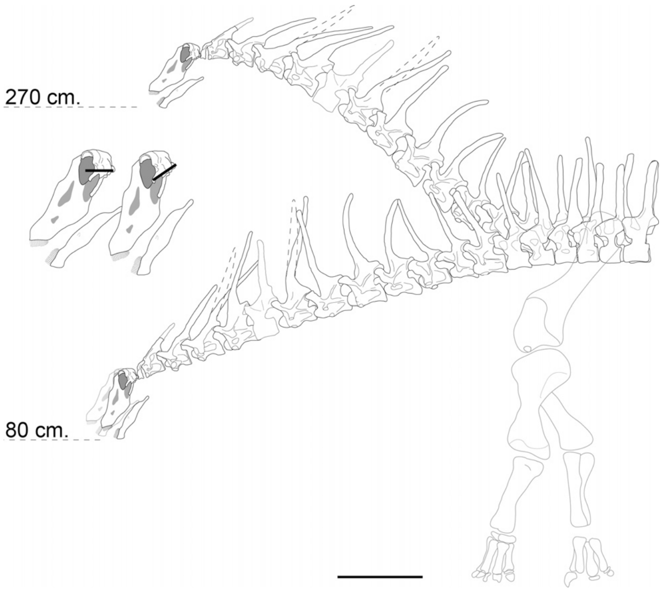

FIGURE 8. Reconstruction of the neck and head postures in *Amargasaurus cazaui*. **A**, in alert position, with the neck upwardly directed with the head at around 270 cm from the floor and the lateral semicircular canal in a horizontal position; **B**, in osteological neutral position, with the neck downwardly directed and the tooth row at around 80 cm from the floor. Scale bar equals 50 cm.

vertebrae and muscle attachments (Stevens and Parrish, 1999, 2005; Dzemski and Christian, 2007; Taylor et al., 2009; Christian, 2010). More recently, these studies have been based on the position of the LSC of the inner ear (Sereno et al., 2007; Witmer et al., 2008; Taylor et al., 2009).

The osteological neutral pose (ONP) is obtained when the zygapophyses of successive vertebrae are aligned and the deflection at the central articulation is minimal (Stevens and Parrish, 1999, 2005). The neutral position of the head with respect to the neck is that which accommodates the occipital condyle being parallel with the atlas-axis complex (Stevens and Parrish, 2005; Taylor et al., 2009). Using this approximation, Steven and Parrish (2005) concluded that sauropods such as the diplodocids *Apatosaurus* and *Diplodocus*, the dicraeosaurid *Dicraeosaurus*, and the macronarians *Euhelopus* and *Brachiosaurus* hold their necks almost horizontally in the ONP with a gently ventral orientation. These authors mentioned that in some extant avian and equine necks, a more vertical orientation is possible solely because of the presence of a 'keystone-shaped' cervicothoracic vertebra; in sauropods, this has only been described for the first preserved (third?) dorsal vertebra of the basal macronarian *Tehuelchesaurus* (Carballido et al., 2011b). Even though Stevens and Parrish (1999, 2005) considered that the ONP was commonly adopted in life (as observed in extant animals), this hypothesis was recently refuted by Dzemski and Christian (2007), Christian and Dzemski (2007), Taylor et al. (2009), and Christian (2010). Nevertheless, the ONP can give a good idea of the midpoint between extremes of dorsiflexion and ventriflexion movements (Taylor et al., 2009), and can resemble the neck posture employed during locomotion (Christian and Dzemski, 2007; Dzemski and Christian, 2007). Although sauropods surely employed different neck postures during different activities (Sander et al., 2011), the ONP provides an easy and reliable method to be used as a proxy to assess neck and head posture in extinct animals.

Recently, the position of the LSC was used to infer the habitual head posture (HHP) in sauropods (Sereno et al., 2007; Witmer et al., 2008). The HHP is related with the alert posture, which is that when animals' senses are heightened (Witmer et al., 2008). In a HHP, the lateral semicircular canal is roughly horizontally placed providing a reliable guide to skull orientation in life (Sereno et al., 2007). Nevertheless, Taylor et al. (2009) noted that some extant birds and mammals typically hold the skull such that the lateral semicircular canal is anterodorsally inclined at angles between 15° and 20°. Therefore, as for the ONP, the HHP can only give a general idea of the head posture, which is logical when a wide range of movements are expected for any animal that need to walk, eat, drink water, and be alert. In this study, the neck and head postures of *Amargasaurus* are explored by the combined use of both techniques: the reconstruction of the osteological neutral position of the neck and anterior dorsal vertebrae, and using the orientation of the LSC.

The new information on the inner ear morphology obtained from the CT scans indicates that when the braincase is oriented with the lateral semicircular canal of the inner ear positioned in the horizontal plane: (1) the occipital condyle is posteroventrally (more posteriorly than ventrally) projected; and (2) the skull roof and principally the basipterygoid processes are anteroventrally oriented at an angle of approximately 65° from the horizontal. Under these conditions, the orientation of the reconstructed skull has the muzzle inclined anteroventrally at an angle of 40°, similar to the position recently postulated for *Diplodocus* (Sereno et al., 2007).

In order to reconstruct the osteological neutral posture, line drawings of each neck vertebrae were made in lateral view. The individual drawings were adjusted to the same scale, and then were rotated and translated into the neutral position using the protocol described by Stevens and Parrish (2005). Although most of the pictures were taken in left lateral view (as in Fig. 8), some pictures were taken from the right (if this was the best preserved side). The braincase was positioned in its neutral position following Stevens and Parrish (2005; see above) and based on figures of both sides, and the direct manipulation of the braincase and atlas-axis casts. Finally, the total forelimb and hind limb heights were taken into account, using the measurements provided by Salgado and Bonaparte (1991), with the pectoral girdle articulated as suggested by Schwarz et al. (2007). As in other sauropods, except *Tehuelchesaurus* (Carballido et al., 2011b), no 'keystone-shaped' element was observed. It must be noted that the centrum of the sixth cervical vertebra is heavily damaged, as well as the centra of several middle and posterior dorsal vertebrae. The ONP restored (Fig. 8) does not greatly differ from that recently proposed for *Dicraeosaurus* (Stevens and Parrish, 2005:fig. 10.2). A major problem is observed in the neural spines of the fourth and seventh cervicals, which are strongly inclined posteriorly and respectively overlap the neural spines of the fifth and eighth cervicals, which are vertically oriented. Nevertheless, the inconsistent orientations of the neural spines (Fig. 8) seem to be the result of postmortem deformation and restoration during specimen preparation. Therefore, a smoother transition from the posteriorly oriented neural spines of the anterior cervicals to the vertically oriented neural spines of the dorsal vertebrae is expected. It must be noted that a horizontally or slightly ventrally inclined position of the neck, at least in its more anterior section, is also supported by atlas-axis fusion; given that when the axis is horizontally positioned, the atlas is dorsally oriented and articulating, therefore, in an almost neutral position with the occipital condyle. Taking into account the forelimb height, the skull of *Amargasaurus* is placed at around 80 cm from the ground when it is in the ONP (Fig. 8A). In the ONP, the lateral semicircular canal is not horizontally placed but inclined at an angle of 20°, which is probably a common variation in the inclination of the lateral semicircular canal based on some extant animals (see Taylor et al., 2009, and references herein). With a more traditional position of the pectoral girdle, with the scapula more dorsally positioned and less vertically oriented (e.g., Wilson and Sereno, 1998), the calculated height for the skull should be around 45 cm from the ground.

Despite the tall neural spines of *Amargasaurus*, dorsal flexure of the neck is also possible with either the current neural spine orientations or the smoother transitional shapes (Fig. 8B). Nevertheless, more dorsal flexion of the neck is precluded by the neural spines of *Amargasaurus* (Salgado, 1996), which would prevent the head from reaching, in the case of *Amargasaurus*, heights greater than 270 cm (Fig. 8B), or 235 cm if the scapula is articulated following the traditional posture. As reconstructed (Fig. 8B), the LSC is horizontal when the neck is dorsally flexed; this has been described as the alert position (Witmer et al., 2008). Such a position was probably taken to allow a wider range of vision of the landscape. The ecological relevance of raising the neck was also noted by Dzemski and Christian (2007), who considered that keeping the neck in low position is very unlikely for any sauropod (see also Taylor et al., 2009). These authors noted that whereas maintaining the neck in a low position was possible without much muscle force (Alexander, 1985; Stevens and Parrish, 1999, 2005), sauropods needed little energy to raise the neck because much of it was stored in the ligaments. The neck and head reconstruction presented by Salgado (1996:fig. 9) is an intermediate position between the ONP and the possible maximum dorsal flexion here presented.

Differences observed in the dental morphology among sauropods, which range from the plesiomorphically broad, spoon-shaped crowns with ‘V’-shaped wear patterns of non-neosauropod sauropods and basal macronarians to the narrow pencil-like crowns of diplodocoids and titanosaurs, were traditionally assumed to reflect differences in their ecological niches (Bakker, 1986; Calvo, 1994; Upchurch and Barrett, 2000, 2005; Sander et al., 2011; Whitlock, 2011a). Ecological differences were also proposed on the basis of carbon isotopic differences (Tütken, 2011). Diplodocoid feeding habits were recently analyzed by Whitlock (2011b) using a combination of different approaches, including body size, snout shape, and dental microwear. Worn teeth are known only for *Dicraeosaurus* (Whitlock, 2011a, 2011b). The proportion of pits with respect to scratches in this taxon represents an intermediate value between the wear facets of *Nigersaurus* (with the higher proportion of pits) and the titanosauriform *Brachiosaurus* (with the smaller pit:scratch ratio; Whitlock, 2011b). This intermediate ratio, together with the round snout of *Dicraeosaurus* and *Suuwassea* made Whitlock (2011b) hypothesize a midheight selective browsing behavior for these dicraeosaurids. As large herbivores that probably had a tachymetabolic endothermic thermometabolism (see Sander et al., 2011, and references herein), sauropod dinosaurs had to forage for long periods of their day, which depends on several factors, such as the morphology of the cropped plants (Gee, 2011; Hummel and Clauss, 2011). However, they perhaps did not spend as much of the day as elephants (80%) due to the absence of oral processing in sauropods (Sander and Clauss, 2008). Although the osteological neutral posture proposed here for *Amargasaurus* fits well with the feeding habitats proposed for dicraeosaurid sauropods (midheight; Whitlock, 2011b), the most common position of the neck and head is difficult if not impossible to known, and different postures were surely adopted, including a raised neck into an alert position (Fig. 8), and movements of the head independently of the neck position, which will affect the orientation of the LSC but not the skull heights here proposed.

NICHE PARTITIONING IN THE LA AMARGA FORMATION SAUROPODS

The long neck of sauropods has been interpreted as a key adaptation (Upchurch and Barrett, 2000) that allowed them to increase the horizontal and vertical feeding ranges (Bakker, 1978; Martin, 1987; Stevens and Parrish, 1999). Sander et al. (2011) concluded that the selective advantage of long necks in sauropods included both the possibility of niche partitioning (between young and adult specimens of the same species, and with other sympatric herbivores) and as a method to save energy, which allowed these gigantic animals to cover a wide area without moving the whole body. Dicraeosaurids are usually characterized by their short necks and relatively small sizes (Rauhut et al., 2005; Whitlock, 2011a); nevertheless, this seems to be the plesiomorphic morphology, because similar sizes and proportions of the bodies and necks are observed among other non-diplodocid diplodocoids and basal macronarians. In contrast, large body sizes are attained independently by diplodocids and titanosauriforms, two lineages of long necked sauropods (e.g., *Giraffatitan*, *Diplodocus*; see Sereno et al., 2007).

Sauropods from the Antigual Member of the La Amarga Formation (Barremian) are represented by ‘short-necked’ basal rebbachisaurids and the dicraeosaurid *Amargasaurus*, and by the ‘long-necked’ titanosauriforms (Apesteguía, 2007). The presence of at least three different sauropod taxa in the same member strongly suggests that these were sympatric sauropods; therefore, niche partitioning can be hypothesized.

Whereas basal titanosauriforms are characterized by their long necks and broad-crowned teeth with ‘V’-shaped wear facets, diplodocoids have shorter necks and narrow-crowned teeth with apical wear facets. Crown shape differences are correlated with differences in food-gathering strategies and with differences in properties of the plants eaten by the different taxa (Upchurch and Barrett, 2000; Stevens and Parrish, 2005). Additionally, basal titanosauriforms are characterized by relatively longer humeri (Carballido et al., 2011a), whereas diplodocoids have short humeri (compared with the femora), which lowers the height of the forelimbs with respect to the hind limbs. Therefore, niche partitioning is strongly suggested between diplodocoids and titanosauriforms, based on both general morphological differences and differences in their crown shapes and wear facets (Upchurch and Barrett, 2000, 2005). Thus, whereas high browsing is expected for basal titanosauriforms (Upchurch and Barrett, 2000; and as described for *Brachiosaurus* and *Euhelopus* by Christian and Dzemski, 2007; Christian, 2010), rebbachisaurids and dicraeosaurids probably browsed at lower levels (Sereno et al., 2007; Whitlock, 2011b). In the case of *Amargasaurus* and based on the evidence presented here for the skull and neck positions, a midheight food-gathering strategy is expected. Although a ground level food-gathering strategy was recently suggested for nigersaurine rebbachisaurids (Sereno et al., 2007; Whitlock, 2011b), the absence of skull information on basal rebbachisaurids precludes fully knowing the food-gathering strategy adopted by basal members of this clade. Therefore, a complete understanding of niche partitioning awaits skull descriptions of the basal forms of this clade. Nevertheless, it seems probable that during the Barremian, the fauna recorded from the La Amarga Formation (Antigual Member) would have made good use of food resources at ground level (basal rebbachisaurids), mid-level (*Amargasaurus*), and high level (titanosauriforms).

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