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NEW REBBACHISAURID (SAUROPODA, DIPLODOCOIDEA) CRANIAL REMAINS FROM THE CRETACEOUS OF PATAGONIA, ARGENTINA, AND THE FIRST ENDOCRANIAL DESCRIPTION FOR A SOUTH AMERICAN REPRESENTATIVE OF THE CLADE

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ABSTRACT—Here we report new rebbachisaurid material (MMCh-PV 71) recovered from the Candeleros Formation (Cenomanian) of northwest Patagonia, Argentina. The cranial remains consist of a partial braincase and a right quadrate. Fractures in the braincase exposed the endocranial cavity, allowing the first study of the brain and inner ear morphologies of a South American rebbachisaurid. The braincase and cranial endocast both exhibit traits similar to those observed in the Cretaceous rebbachisaurids *Nigersaurus* from Africa and *Limaysaurus* from Argentina, although in terms of osteology, the South American taxa are highly similar. The endocast of MMCh-PV 71 is more similar to that of *Nigersaurus* than to those of *Diplodocus* and *Comarasaurus*, suggesting some probable rebbachisaurid features such as the noteworthy presence of the flocculus. The overall morphology of the quadrate shows similarities with *Limaysaurus* and *Nigersaurus*. However, differences such as the broader posterior fossa and the shape and orientation of the head and the pterygoid process indicate that the new specimen could represent a distinct taxon.

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INTRODUCTION

Current knowledge of diplodocoid sauropods in South America is poor, although it has been improving in recent years due to new discoveries, particularly in Argentina (e.g., Carballido et al., 2012; Haluza et al., 2012; Ibiricu et al., 2012, 2013; Gallina et al., 2014). Within this clade, Rebbachisauridae is the basal-most group of Diplodocoidea and the sister group of Flagellicaudata (Diplodocidae + Dicraeosauridae; Wilson, 2002; Harris and Dodson, 2004). Their remains, which usually consist of postcranial elements, are frequently recorded in the lower Upper Cretaceous units (Cenomanian) of the Neuquén and San Jorge basins in Patagonia (Novas, 2009). In particular, the outcrops of the Candeleros and Huincul formations (Garrido, 2010) surrounding the city of Villa El Chocón and Ezequiel Ramos Mexía lake (both Neuquén Province localities) have provided several rebbachisaurid specimens (e.g., Calvo and Salgado, 1995; Calvo, 1999; Gallina and Apesteguía, 2005; Apesteguía, 2007; Simón and Salgado, 2009; Haluza et al., 2012). These discoveries have allowed a relatively good understanding of the postcranial anatomy of this group of basal diplodocoids. However, the cranial morphology is still poorly known because skull remains are rare and braincases even rarer. As such, the complete braincase of *Limaysaurus tessonei* (= *Rebbachisaurus tessonei*; Calvo and Salgado, 1995) represents the only rebbachisaurid braincase described besides that of *Nigersaurus* (Serenó et al., 2007), and the first described from South America. The braincase morphology of the African rebbachisaurid *Nigersaurus* has been

published as a three-dimensional (3D) model that is available at Digital Morphology (www.digimorph.org; Sereno et al., 2007). Its cranial endocast and inner ear were also studied using computed tomography (CT) scans by Sereno et al. (2007:figs. S4–S6) and are used here for comparisons.

In the present study, a partial braincase and right quadrate (MMCh-PV 71) are described. They were recovered from the Candeleros Formation (Cenomanian) at the Barda Atravesada de Las Campanas locality, 25 km southwest from Villa El Chocón, Neuquén Province, Argentina (Fig. 1). The specimens were found in close association with postcranial bones, including a dorsal vertebra that shows clear rebbachisaurid synapomorphies, such as a petal-shaped neural spine and a festooned spinodiapophyseal lamina (Whitlock, 2011). As mentioned above, within rebbachisaurids the braincase of the holotype of *Limaysaurus tessonei* was only briefly described (Calvo and Salgado, 1995), and its endocranial morphology was preliminarily reported by Paulina Carabajal and Calvo (2015). The new specimen, MMCh-PV 71, was recovered from the same formation as the holotype of *Limaysaurus*, but from a different locality. Although the braincase morphology is notably similar in the two specimens, the morphologies of the quadrate and some of the postcranial remains (that are not described here) indicate that the former could represent a new taxon.

The purpose of this study is to provide a detailed description of the braincase and quadrate of this new rebbachisaurid, which includes the first observations on the endocranial anatomy of a representative of the clade from South America. The dinosaur braincase is a rich source of phylogenetically informative data (e.g., Rauhut, 2007; Paulina Carabajal, 2009; Balanoff et al., 2010).

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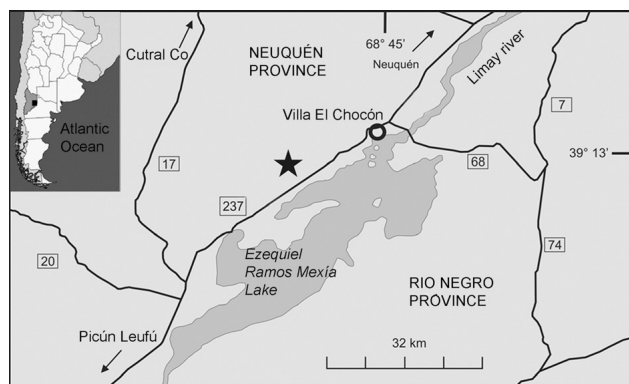


FIGURE 1. Location map for rebbachisaurid specimen MMCh-PV 71.

Because the discovery and description of braincase remains are scarce across Sauropoda, new information—particularly for poorly sampled groups such as Rebbachisauridae—will help to increase our understanding about their anatomy and morphological variation between species.

MATERIALS AND METHODS

The braincase of MMCh-PV 71 is preserved in two halves, as left and right lateral walls, attached to fragmentary pieces of skull roof and basicranium (Fig. 2). There is no preserved median connection between the left and right sides, although the midline is recognizable at the interfrontal region and in the floor of the endocranial cavity. A latex cranial endocast and an inner ear cast were made by one of the authors (A.P.C.) based on the right lateral wall of the braincase, which preserves part of the basicranium. A complete dorsal view of the brain was reconstructed using a specular image of the right side, as shown in Figures 3 and 4. A partial latex cast of the labyrinth of the inner ear is shown in Figure 5. The right quadrate (Fig. 6) was found isolated, 1 m distant from the braincase remains. All the cranial remains were found in close association with part of the postcranium that includes a dorsal vertebra, a partial ilium, and an ungual phalanx, all of which were recovered in an area of no more than 4 m².

The specimen MMCh-PV 71 was compared with the holotype of *Limaysaurus*, from the same stratigraphic age and formation, and with *Nigersaurus*, from the Early Cretaceous (Barremian–Albian) and thus slightly older stratigraphically than the Patagonian forms (Fig. 7). All three specimens represent adult individuals based on relative size and the lack of sutures (personal observation of MMCh-PV 71 and MUCPv 205; Sereno et al., 2007).

Digitally rendered 3D models of the braincase and quadrate of *Nigersaurus* are available at Digital Morphology (http://digitalmorph.org/specimens/Nigersaurus_taqeti).

Institutional Abbreviations—**MMCh-PV**, Museo ‘Ernesto Bachmann,’ Villa El Chocón, Argentina; **MUCPv**, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina.

SYSTEMATIC PALEONTOLOGY

- SAURISCHIA Seeley, 1887
 SAUROPODA Marsh, 1878
 DIPLODOCOIDEA Marsh, 1884
 REBBACHISAUROIDAE Bonaparte, 1997
 REBBACHISAUROIDAE INDET.
 (Figs. 2–7)

DESCRIPTION

Braincase

The braincase of the rebbachisaurid MMCh-PV 71 is preserved in two lateral halves (Fig. 2). Most of the basicranium (including structures such as the occipital condyle and basiptyergoid processes) and the median portion of the skull roof are missing. Structures such as the nuchal crest and the paroccipital processes are incomplete, and the margins of the foramen magnum are not preserved. The lateral walls of the braincase include a partially preserved exoccipital-opisthotic complex, the prootic, laterosphenoid, orbitosphenoid, and a dorsal fragment of the basisphenoid.

Skull Roof—The skull roof is formed by the thick and robust parietal and frontals (Fig. 2B, D). The parietal is fragmentary, and its complete morphology remains unknown. The posterolateral projection of the parietal is firmly fused to the frontal anteriorly and to the dorsal section of the paroccipital process posteriorly. A foramen for the caudal middle cerebral vein, enclosed at least externally by the parietal, is observed on the right side (Fig. 2D). The passage of this vein has a relatively large diameter (3.5 mm) and runs from the posterior section of the dural expansion area of the endocranial cavity (Fig. 2C, F). It is worth noting that this foramen is not observed in *Limaysaurus* (MUCPv 205; Paulina Carabajal and Calvo, 2015), but its passage is reconstructed in the cranial endocast of *Nigersaurus* (Sereno et al., 2007:fig. S4A; Fig. 4).

The frontal forms a more-or-less curved and smooth orbital margin (Fig. 2B), while anteriorly, the nasal process is robust and thick. Endocranially, the cerebral hemisphere is well marked on the ventral aspect of the frontal, although the olfactory bulb does not leave clear impressions (Fig. 2C).

Exoccipital-Opisthotic Complex—Most of the paroccipital processes are missing. The preserved proximal sections indicate that the paroccipital processes were low and posterolaterally projected (Fig. 2B, D). Fractures on both sides of the braincase exposed cavities within the paroccipital processes, suggesting some degree of pneumaticity for the structure, which is usually massive in sauropods (pers. observ., A.P.C.). Although this condition could be the result of erosion, the paired nature of the cavities within the paroccipital processes of MMCh-PV 71 indicate a lower density of the spongy bone compared with other sauropods.

There is a single foramen for cranial nerve (CN) XII preserved on the right exoccipital (Fig. 2D). A single foramen is also observed in *Limaysaurus* (Calvo and Salgado, 1995), whereas there are two foramina in *Nigersaurus* (Sereno et al., 2007). On the lateral side of the braincase, there are no visible sutures between the opisthotic and the prootic. The metotic foramen (for CNs IX–XI) is enclosed by the opisthotic posteriorly and the prootic anteriorly, and is large and oval, as in most sauropods. The crest that anteriorly bounds the metotic foramen (crista interfenestralis) is developed as a low ridge, poorly expanded posterolaterally, differing from the laminar condition observed in *Limaysaurus* (MUCPv 205) and *Nigersaurus* (Knoll, pers. comm., 2015). In *Limaysaurus*, the crest that bounds the metotic foramen posteriorly (crista tuberalis) is well expanded and clearly separates CN XII posteriorly from the metotic foramen anteriorly (Fig. 2A). The fenestra ovalis is not observed in the lateral view of MMCh-PV 71, because it faces posteriorly and is located within a recess together with the metotic foramen, as in *Limaysaurus*. Although the margins of the crista prootica are poorly preserved, it seems that the foramen for CN VII opens on the anterior side and not posterior to the ridge as in *Limaysaurus*, where CN VII, CN XII, and the metotic foramen are clearly visible in posterior view of the braincase (Calvo and Salgado, 1995:fig. 5).

Prootic—The prootic is firmly fused to the opisthotic posteriorly and the laterosphenoid anteriorly, whereas the suture with the parietal is obscured by fractures. The prootic forms at least the posterior

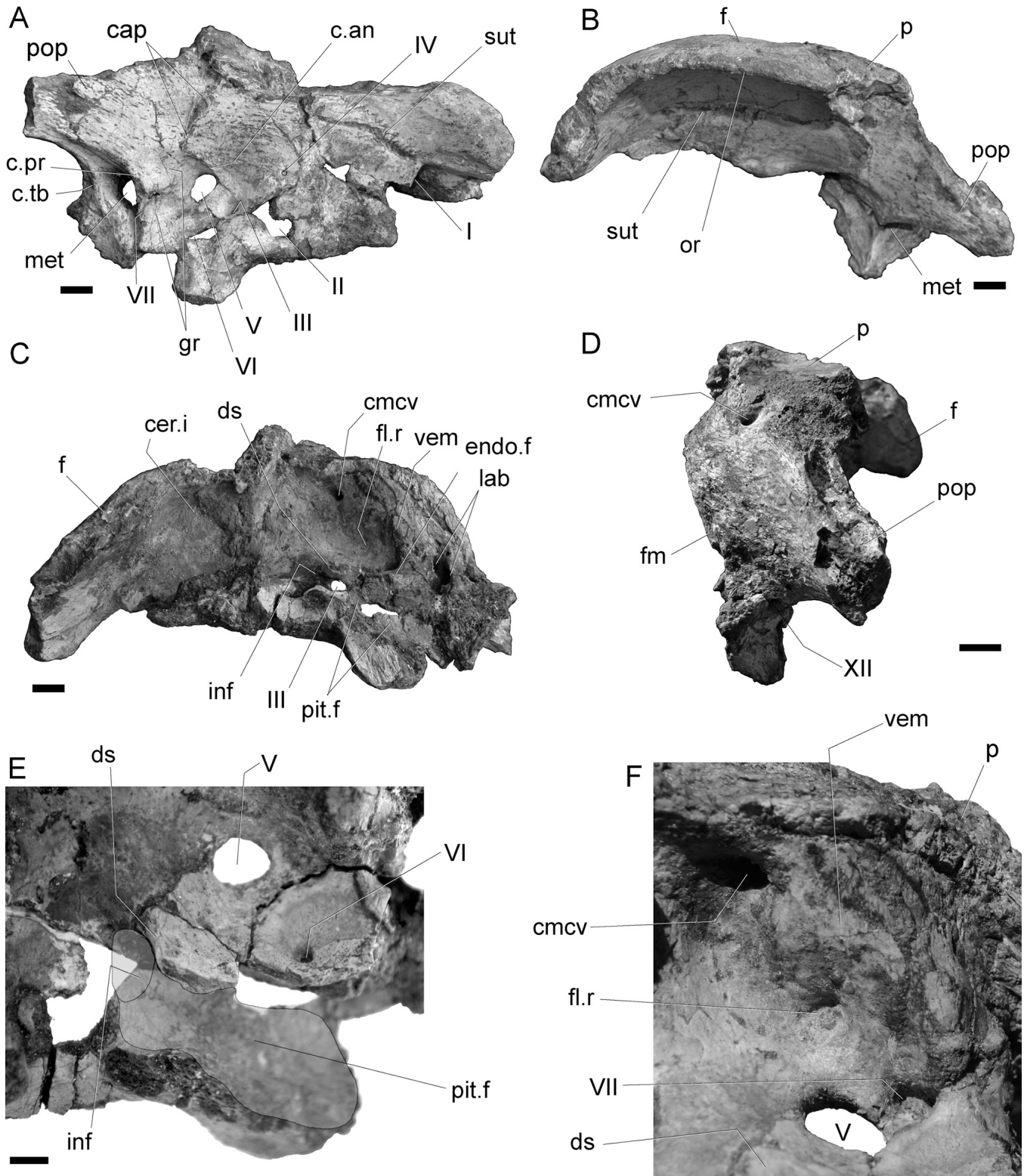


FIGURE 2. Brainscase of rebbachisaurid specimen MMCh-PV 71 in **A**, right lateral view; **B**, left lateral view; **C**, right medial view, and **D**, posterior view. **E**, detail of floor of the endocranial cavity; **F**, detail of right vestibular eminence (not to scale). **Abbreviations:** **c.an**, crista antotica; **cap**, capitate process; **cer.i**, cerebral hemisphere impression; **cmcv**, caudal middle cerebral vein; **c.pr**, crista prootica; **c.tb**, crista tuberalis; **dhv**, dorsal head vein; **ds**, dorsum sellae; **endo.f**, floor of endocranial cavity; **f**, frontal; **fl.r**, floccular recess; **fm**, foramen magnum (preserved margin); **gr**, groove; **inf**, infundibulum; **lab**, labyrinth of inner ear; **met**, metotic foramen; **or**, orbital rim; **p**, parietal; **pit.f**, pituitary fossa; **pop**, paroccipital process; **sut**, suture; **vem**, vestibular eminence; **I–XII**, cranial nerves. Scale bars equal 10 mm in **A–D**. In **E**, which is an enlarged detail, the scale bar equals 20 mm.

margin of the large and oval foramen for CN V, which has a maximum diameter of 9.7 mm, almost equal to the diameter of the metotic foramen (10.7 mm). From the posterodorsal and posteroventral margins of the foramen for CN V, there are two impressions left by the maxillary and mandibular branches of the trigeminal nerve (Fig. 2A). The groove interpreted as the mandibular branch is posteriorly oriented, whereas the groove interpreted as the maxillary branch is posteroventrally oriented. In *Limaysaurus*, the mandibular and maxillary branches also leave clear impressions, oriented posteriorly and ventrally, respectively (MUCPv 205). In *Limaysaurus*, the foramen for CN V has a bilobate contour resulting from a ventral projection of the crista antotica overhanging the dorsal margin of the foramen, unlike the elliptical outline of the foramen in *Nigersaurus* (Knoll, pers. comm.).

Endocranially, a notable feature is the presence of a small and oval floccular recess on the anterior side of the vestibular eminence (Fig. 2C, F). This structure is also present in *Nigersaurus* (Serenó et al., 2007), *Giraffatitan* (Knoll and Schwarz-Wings, 2009), and *Dicraeosaurus* (=‘fossa subarcuata’ in Janensch, 1935), although it is absent in most sauropods.

Laterosphenoid—There are no visible sutures between the laterosphenoid and the surrounding bones, except with the frontal dorsally. The postorbital process of the laterosphenoid (=capitate process) and/or crista antotica is preserved only at its base, indicating a low and markedly thin, crescentic process (Fig. 2A). In *Limaysaurus*, the postorbital process of the laterosphenoid is blade-like, anteroposteriorly short, and markedly projected posteriorly (Calvo and Salgado, 1995).

The laterosphenoid bounds the foramen for CN V anteriorly and the foramina for CNs III and IV posteriorly. These latter two cranial nerves probably indicate the laterosphenoid-orbitosphenoid contact. Cranial nerve III is large and located within a shallow recess posterior to CN II and anterior to CN V. The opening of the foramen for CN III faces posteriorly. The foramen for CN IV is small and opens anterodorsally to CN III and dorsally to CN II (Fig. 2A, C). The shape, size, and disposition of CN III and CN IV are similar to those observed in *Limaysaurus*, but unlike the condition in *Nigersaurus* (Serenó et al., 2007: fig. S4A), where CN III and CN IV share a single exit foramen (Fig. 4).

Endocranially, the laterosphenoid does not form a marked pillar protruding into the endocranial cavity (Fig. 2C), unlike the condition observed in titanosaurid sauropods (e.g., Paulina Carabajal, 2012; Knoll et al., 2013, 2015). There are no visible sutures to indicate if the laterosphenoid forms the dorsal-most section of the dorsum sellae (Fig. 2E).

Orbitosphenoid—The orbitosphenoid is a relatively large element, contacting the laterosphenoid posterodorsally. The suture with the frontal observed on the right side dorsal to CN II, is probably the laterosphenoid-frontal suture, although the most anterior section may correspond to the orbitosphenoid-frontal contact. The foramen for CN II is large (7.4 mm), rounded, and separated from its counterpart by a septum of bone. The foramen indicated in Figure 2 as CN I corresponds to the passage for the olfactory tract, enclosed by the orbitosphenoid and frontal (Fig. 2A).

The orbitocerebral fenestra present in *Nigersaurus* dorsal to CN II (Serenó et al., 2007:fig. S4A) is absent in MMCh-PV 71 and *Limaysaurus* (Figs. 2A, 4A). This might suggest that the two Argentinean taxa form a natural grouping relative to *Nigersaurus* (Knoll, pers. comm.).

Basisphenoid—Only the anterodorsal section of the basisphenoid is preserved on the right side of the floor of the endocranial cavity (Fig. 2C, E). The dorsum sellae is a thin wall that is anterodorsally projected, formed by the basisphenoid and probably by median projections of the laterosphenoids. The foramen for CN VI is small in diameter (1.7 mm), as is usual in sauropods (Knoll et al., 2006), and located far behind the top of the dorsum sellae (Fig. 2E). The passage of CN VI is short and runs laterally

to the pituitary fossa to exit through a small foramen located ventral to CN V (Fig. 2A). This condition resembles that observed in *Limaysaurus* (MUCPv 205) and titanosaur sauropods and is different from that observed in Flagellicaudata, where CN VI usually penetrates the pituitary fossa (e.g., Paulina Carabajal, 2012:table 1, and references therein).

Endocranially, the preserved walls of the infundibulum indicate an oval shape for this opening when complete, with the main axis mediolaterally oriented. The internal foramen for CN III is level with the infundibulum (Fig. 2C). The right lateral wall of the pituitary fossa is preserved (Fig. 2E), indicating that it was large and strongly posteroventrally oriented (Fig. 3A, C).

Cranial Endocast

The complete right side of the endocranial cavity was cast (Fig. 3A, B), and the left side of the complete brain was reconstructed using a specular image (Fig. 3D). The cranial endocast is subhorizontal, with laterally expanded cerebral hemispheres, and the pituitary is markedly enlarged and posteroventrally oriented (Fig. 4C). The specimen MMCh-PV 71 shares with *Nigersaurus* the general shape of the cranial endocast, particularly in dorsal view (Fig. 4B, C). By contrast, in lateral view (Fig. 4A), the dorsal expansion—which was occupied by the dorsal venous longitudinal sinus (Witmer et al., 2008)—is more anteriorly developed than in *Nigersaurus* (Serenó et al., 2007).

Forebrain—In MMCh-PV 71, the olfactory bulbs did not leave a well-defined impression on the ventral surface of the frontal and therefore they are not clearly visible in the endocast (Fig. 3D). The olfactory tracts are clearly discernible from the olfactory bulbs, with both structures at least as long as the cerebral hemispheres (Fig. 3D). This condition is the same in *Nigersaurus*, which has relatively small dural sinuses over the cerebrum (Serenó et al., 2007:fig. 1F), unlike the almost nonexistent olfactory tract observed in titanosaurs (e.g., Paulina Carabajal, 2012). The olfactory tract and bulbs of MMCh-PV 71 are slightly ventrally projected, as in *Nigersaurus*, rather than anterodorsally projecting as in *Diplodocus* and *Camarasaurus* (Serenó et al., 2007:fig. 1G).

The maximum width of the endocast is at the level of the cerebral hemispheres, and is approximately 46 mm (Fig. 3D). The cerebral hemispheres are rounded and laterally expanded, although the fissura inter-hemispherica is obscured by the development of the dorsal longitudinal sinus and the dura, as in most sauropods. In *Nigersaurus* (Serenó et al., 2007) and MMCh-PV 71, the dural sinus is small, allowing the view of the anterior end of the brain, including the olfactory tract, cerebrum, and cerebellar region. In most non-titanosaurians, such as *Apatosaurus* (Balanoff et al., 2010), *Brachiosaurus* (Janensch, 1935; Knoll and Schwarz-Wings, 2009), *Spinophorosaurus* (Knoll et al., 2012), and *Dicraeosaurids* (Janensch, 1935; Knoll et al., 2014; Paulina Carabajal et al., 2014a), and the cast of these structures obscures the dorsal surface of the forebrain.

The pituitary is a long structure, strongly projected posteroventrally from the ventral aspect of the cranial endocast (Fig. 3A, C). The distal end of the pituitary is missing, including the entrances for the internal carotid arteries. Part of the canal of the internal carotid artery is observed in the left side of the basicranium, indicating that the external foramen for this blood vessel was located ventral to the metotic foramen, similar to the condition in *Limaysaurus* (Paulina Carabajal and Calvo, 2015).

Midbrain—The root of CN II is subcircular in cross-section, short, and laterally projected. It is located anterodorsal to the base of the infundibulum (Fig. 3A, C). The two CN II openings are relatively more separated from each other than in *Nigersaurus*, in which they seem to be confluent on the midline and originating from the base of the infundibulum (Serenó et al., 2007: fig. S4C). Cranial nerve III is located posteroventrally relative to

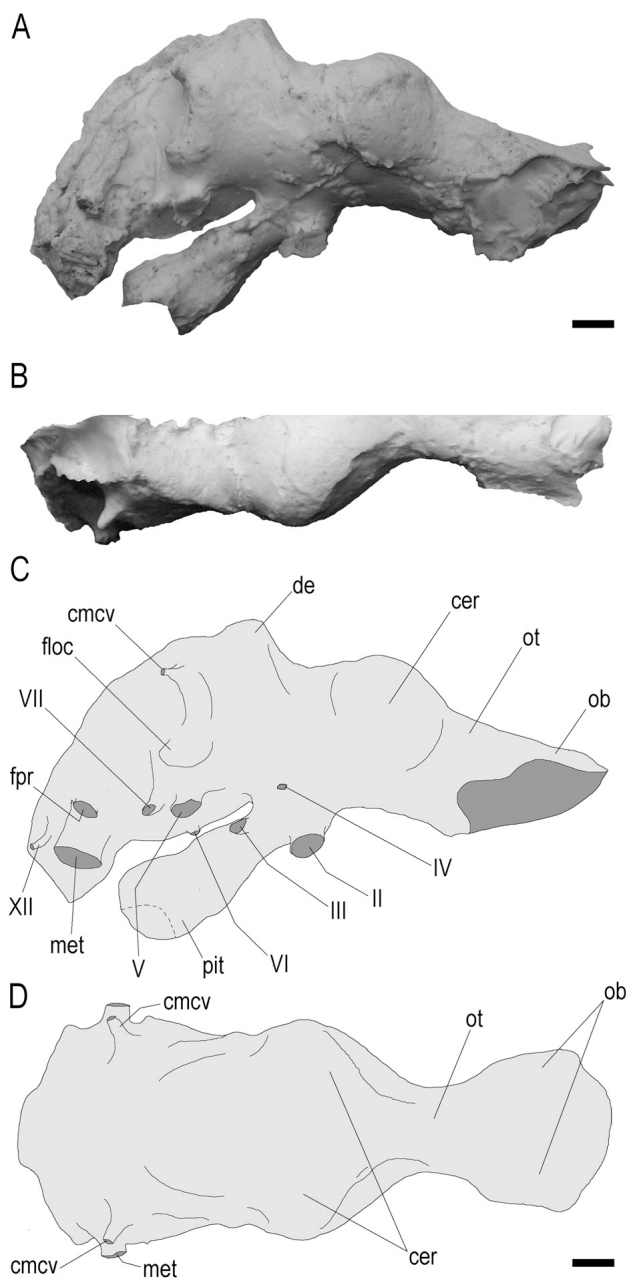


FIGURE 3. Latex cranial endocast of rebbachisaurid specimen MMCh-PV 71 in **A**, right lateral view and **B**, dorsal view. Line drawings of reconstructed cranial endocast in **C**, lateral view and **D**, dorsal view. **Abbreviations:** **cer**, cerebral hemisphere; **cmcv**, caudal middle cerebral vein; **de**, dorsal expansion; **floc**, flocculus; **fpr**, fenestra pseudorotunda; **ie**, inner ear; **met**, metotic passage (for CNs IX–XI); **ob**, olfactory bulb; **ot**, olfactory tract; **pit**, pituitary; **I–XII**, cranial nerves. Scale bar equals 10 mm.

CN II and is confluent with the posterior aspect of the infundibular stalk. The small passage anterodorsal to CN II belongs to a separate CN IV, as in *Limaysaurus*, but unlike *Nigersaurus* where both nerves leave the endocranial cavity through a single large foramen (Serenio et al., 2007:fig. S4A).

Hindbrain—The posterior-most dorsal section of the medulla oblongata is not preserved (Fig. 3A). The dural expansion is a well-defined but small dorsal protuberance (Fig. 4A, C), slightly more marked than that in *Nigersaurus* (Serenio et al., 2007). The caudal middle cerebral vein is located at the posterior section of

the dural expansion. The passage for this vein is relatively large in diameter. It is closely related to a transverse lateral sinus that leaves a half-moon-shaped protuberance on the endocast (Fig. 3A, C). This transverse sinus has a ventral branch that runs towards the root of CN V and probably corresponds to the anterior middle cerebral vein that leaves the endocranial cavity through the trigeminal foramen. In both MMCh-PV 71 and *Nigersaurus* (Serenio et al., 2007:fig. S4A), this lateral sinus is well marked.

The floccular process of the cerebellum is located dorsal to CN V and ventral to the caudal middle cerebral vein (Fig. 3A, C), as in *Nigersaurus* (Fig. 4C). The presence of a developed flocculus that leaves an impression on the anterior wall of the vestibular eminence (floccular recess) is uncommon in sauropods, having been identified in only a few taxa such as the dicraeosaurid *Dicraeosaurus* (Janensch, 1935:pl. XIII, 7) and the titanosauriform *Giraffatitan* (“*Brachiosaurus*” in Janensch, 1935:pl. XIII, 1a; Knoll and Schwarz-Wings, 2009).

The root of CN V is large and oval in cross-section (Fig. 3A, C). It is positioned level with CN II and CN III. As in other sauropods, the passage for this nerve is short and laterally projected.

The passage of CN VI has a small diameter (3 mm), and its root is located posteroventral to CN V, on the ventral side of the hindbrain (Fig. 3A, C). The passage for this nerve runs anteroventrally through the basisphenoid lateral to the pituitary fossa and exits the braincase through a small foramen on the basisphenoid (Fig. 2A), as in *Limaysaurus* (Paulina Carabajal and Calvo, 2015) and *Nigersaurus* (Serenio et al., 2007:fig. S4B). This condition is also present in titanosaurs, although in most Flagellicaudata (derived diplodocoids) CN VI penetrates the pituitary fossa (e.g., Paulina Carabajal, 2012:table 1, and references therein).

The root of CN VII is just posterior to the root of CN V, and both are connected to the transverse venous sinus (Fig. 3A, C). The passage for CN VII has a small diameter (4 mm), and although not reconstructed in the endocast, it is possible to follow it through the prootic (Fig. 2A), as in *Limaysaurus* (Calvo and Salgado, 1995). Cranial nerve VIII is not preserved on the endocast of MMCh-PV 71.

The cast of the metotic passage (for the branches of CNs IX–XI) is large in diameter (13 mm high and 7 mm wide) and oval (Fig. 3C). It is slightly posteroventrally oriented. At the base of the metotic passage, a smaller passage connects anteriorly with the vestibulum of the inner ear, corresponding to the fenestra pseudorotunda (Fig. 3C), as observed in *Nigersaurus* (Serenio et al., 2007:fig. S5A).

There is single root for all the branches of CN XII in the endocast, and a single foramen is observed in the braincase (Figs. 2D, 3C). The same condition is observed in *Limaysaurus* (Calvo and Salgado, 1995), but there are two roots for this nerve in *Nigersaurus* (Serenio et al., 2007).

Inner Ear—A partial endocast of the left inner ear was obtained, including the lagena, the lateral semicircular canal, and partial anterior and posterior semicircular canals (Fig. 5). The inner ear is 35 mm long and approximately 27 mm wide (at the level of the anterior and posterior ampullae). Although the posterior semicircular canal is missing, the angle formed between it and the anterior semicircular canal is approximately equal to or less than 90° in dorsal view (Fig. 5C). In turn, the lateral semicircular canal is oriented upwards, forming an angle with the anterior semicircular canal that is strongly acute (Fig. 5A). This disposition of the lateral semicircular canal is also present in *Nigersaurus* (Serenio et al., 2007:fig. S5A). In MMCh-PV 71, the anterior semicircular canal is subtriangular in shape and has a diameter (of the canal) of approximately 3.4 mm. The lateral semicircular canal is oval in shape and has a diameter of 3.0 mm (Fig. 5). The fenestra ovalis is partially preserved and indicates the limit between the lagena and the vestibulum (Fig. 5). The

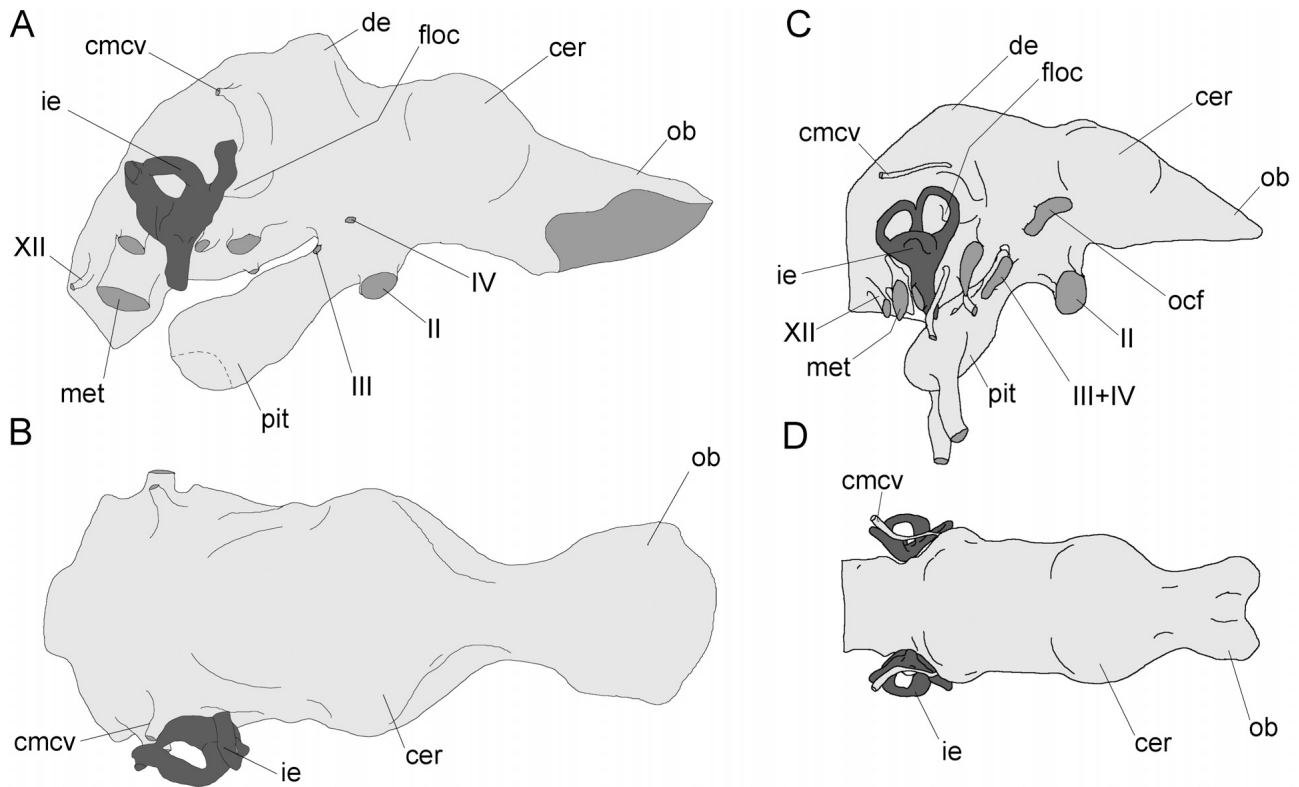


FIGURE 4. Brain and inner ear of rebbachisaurid specimen MMCh-PV 71 in **A**, right lateral view and **B**, dorsal view. Brain and inner ear of *Nigersaurus* in **C**, right lateral view and **D**, dorsal view (after Sereno et al., 2007). **Abbreviations:** **cer**, cerebral hemisphere; **cmcv**, caudal middle cerebral vein; **de**, dorsal expansion; **flocc**, flocculus; **ie**, inner ear; **met**, metotic passage for CNs IX–XI; **ob**, olfactory bulb; **ocf**, orbitocerebral fenestra; **pit**, pituitary; **I–XII**, cranial nerves. Not to scale.

lagna is simple and conical, and, as in *Nigersaurus* (Sereno et al., 2007:fig. S5A), is notably short.

The morphology of the inner ear of MMCh-PV 71 strongly resembles that of *Nigersaurus*, except for the more triangular shape of the anterior semicircular canal. In *Nigersaurus*, the inner ear morphology supports the hypothesis that the skull was held inclined downward in life.

Quadrate

The right quadrate is almost complete. It lacks the head and the dorsal third of the posterior fossa (Fig. 6). The quadrate shaft is relatively robust above the articular region and up to the beginning of the lateral expansion of the quadrate fossa. Dorsal to this point, the shaft is reduced to thin plates of bone, including

the pterygoid wing anteriorly, the inner wall of the quadrate fossa laterally, and a small ventral portion of the posterior projection. In MMCh-PV 71, the quadrate fossa is deep as in other rebbachisaurids, *Giraffaitan*, *Brachiosaurus*, and *Camarasaurus* (Tschopp et al., 2015). In macronarians such as *Camarasaurus*, *Brachiosaurus*, and non-rebbachisaurid diplodocoids such as *Diplodocus* and *Apatosaurus*, the quadrate fossa is mediolaterally slender (Janensch, 1935; Berman and McIntosh, 1978; Madsen et al., 1995). The specimen MMCh-PV 71 has a broad lateral expansion of the quadrate fossa, which is approximately 30% larger than in *Limaysaurus* (Fig. 7) and *Nigersaurus* (Sereno et al., 2007), although in all three rebbachisaurid specimens this expansion is relatively larger than in other sauropods. This condition may constitute a synapomorphy of rebbachisaurids.

Ventrally, the lateral surface of the quadrate exhibits a shallow sulcus for the quadratojugal. This scar continues dorsally over the oblique ventrolateral margin of the posterior fossa of the quadrate. Over the dorsal end of this sulcus and covering the lateral margin of the quadrate, a rugose surface is present that is here interpreted as the articular area for the squamosal. In lateral view, the pterygoid process is moderately anteriorly projected and has a rounded outline, whereas in *Limaysaurus* this process is subtriangular in shape and more anteriorly projected (Fig. 7). A small dorsoventrally oriented pterygoid scar is located on the anteromedial margin of the shaft, ventral to the beginning of the pterygoid process and in the same position as, but smaller than, that of *Rapetosaurus* (Curry Rogers and Forster, 2004).

The articular surface of the quadrate is crescent-shaped in ventral view (Fig. 6E), another synapomorphic trait of Rebbachisauridae (Whitlock, 2011; Tschopp et al., 2015). The quadrate condyle is subdivided by an anteroposterior sulcus, with a medial hemicondyle at least two times mediolaterally larger than the

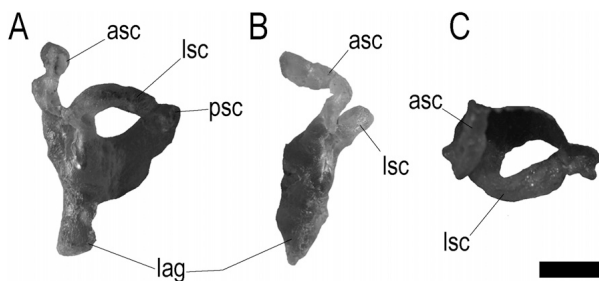


FIGURE 5. Partial left inner ear latex endocast of rebbachisaurid specimen MMCh-PV 71. **A**, lateral view; **B**, anterior view; **C**, dorsal view. **Abbreviations:** **asc**, anterior semicircular canal; **lag**, lagena; **lsc**, lateral semicircular canal; **psc**, posterior semicircular canal. Scale bar equals 10 mm.

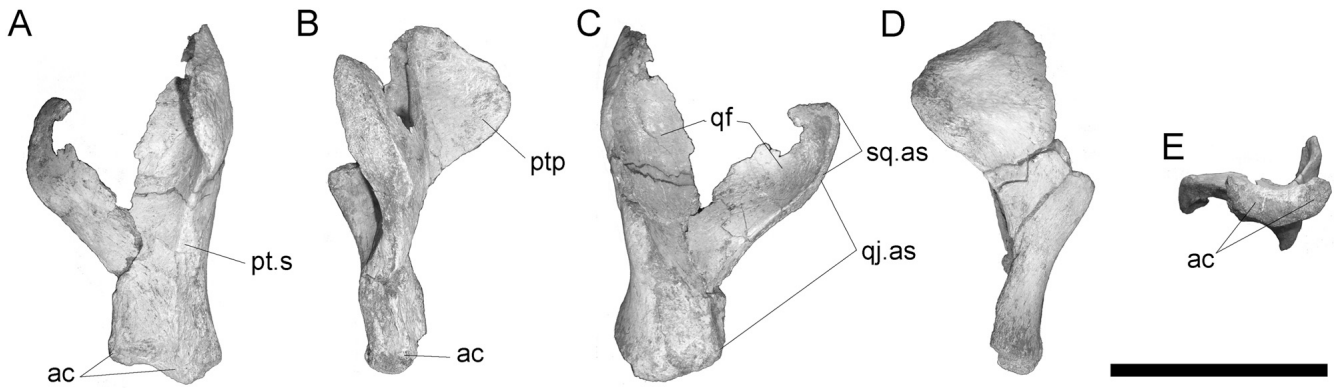


FIGURE 6. Right quadrate of rebbachisaurid specimen MMCh-PV 71. **A**, anterior view; **B**, lateral view; **C**, posterior view; **D**, anterior view; **E**, distal view. **Abbreviations:** **ac**, articular condyle; **ptp**, pterygoid process; **pt.s**, pterygoid scar; **qf**, quadrate fossa; **qj.as**, articular surface for quadratojugal; **sq.as**, articular surface for squamosal. Scale bar equals 10 cm.

lateral one. In *Limaysaurus* (MUCPv 205), the condyle is subdivided but the hemicondyles are subequal in size. A different condition is seen in some macronarians such as *Nemegtosaurus*, where the articular condyle is undivided (Wilson, 2005).

DISCUSSION

Specimen MMCh-PV 71 consists of cranial (present study) and postcranial (currently under analysis) remains that show clear rebbachisaurid features. These include the large lateral expansion of the quadrate fossa and a crescent-shaped articular condyle of the quadrate in ventral view, characters shared with *Limaysaurus* and *Nigersaurus* (Calvo and Salgado, 1995; Sereno et al., 2007).

The lateral expansion of the quadrate in MMCh-PV 71, however, is 30% larger than in *Limaysaurus* (Calvo and Salgado, 1995) and *Nigersaurus* (Sereno et al., 2007), likely representing an autapomorphy of MMCh-PV 71 together with the unequally subdivided articular condyle (see Table 1). The braincase has several non-titanosaurian characters such as a markedly curved orbit vault and a short and laminar crista antotica. Endocranially, there is no pillar of the laterosphenoid, but there is a floccular recess, a well-developed transverse sinus and caudal middle cerebral vein, and a poorly developed dorsal expansion; all these characters shared with *Limaysaurus* and *Nigersaurus* (Sereno et al., 2007). Finally, rebbachisaurid characters present in the postcranial elements of MMCh-PV 71 are the ‘petal-shaped’ neural spine and a ‘festooned’ spinodiapophyseal lamina (Calvo and Salgado, 1995; Wilson, 2002; Whitlock, 2011; Tschopp et al., 2015).

The external braincase morphology of MMCh-PV 71 is very similar to that of *Limaysaurus* (MUCPv 205), showing the same general distribution of cranial and vascular foramina, including the well-marked grooves formed by the maxillary and mandibular branches of the trigeminal nerve, and separate foramina for CNs III and IV (Fig. 2A). Also, CN VI does not penetrate the pituitary fossa, which is an uncommon trait within non-titanosaurid sauropods, suggesting that it is a derived trait of Rebbachisauridae (together with the strongly laterally expanded posterior fossa of the quadrate). The differences with *Nigersaurus* are that the African taxon possesses an orbitocerebral fenestra that is absent in the Patagonian rebbachisaurids, and that CNs III and IV share a single exit foramen (Fig. 4A, C). However, minimal differences are observed between *Limaysaurus* and MMCh-PV 71, including a less expanded crista prootica in the latter specimen (whereas in *Limaysaurus* the crista prootica is large and the foramen for CN VII opens on the posterior side of the crest).

Within rebbachisaurids, only the endocranial morphology of *Nigersaurus* has been studied in detail, whereas a preliminary study has been recently made on the holotype of *Limaysaurus* using CT scans (Paulina Carabajal and Calvo, 2015). So far, it has not been possible to identify a floccular process on the CT scan of *Limaysaurus*, although its presence in MMCh-PV 71 and *Nigersaurus* suggests that it may be characteristic of rebbachisaurids. Development of this cerebellar structure to such an extent that it leaves an impression on the endocranial cavity (floccular recess) is uncommon in sauropods—as discussed above, it has been identified also in *Giraffatitan* (Janensch, 1935; Knoll and Schwarz-Wings, 2009) and *Dicraeosaurus* (Janensch, 1935). Within ornithischians, the flocculus has been identified in even fewer taxa, including some ankylosaurids (Miyashita et al., 2011; Paulina Carabajal et al., 2014c) and *Stegosaurus* (Galton,

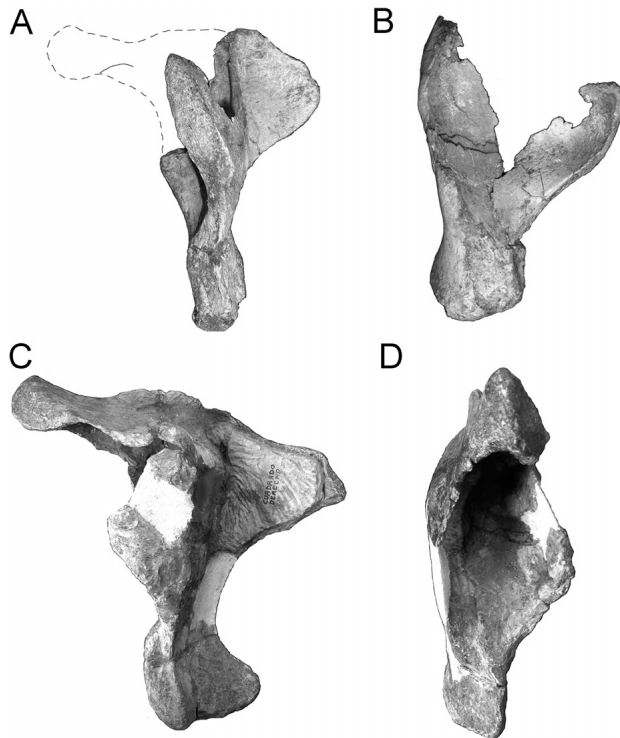


FIGURE 7. Comparison of quadrate morphology of the South American rebbachisaurids. MMCh-PV 71 in **A**, lateral view and **B**, posterior view. *Limaysaurus* (MUCPv 205) in **C**, lateral view and **D**, posterior view. Not to scale.

TABLE 1. Braincase and quadrate character variation within the studied rebbachisaurids.

Character	Rebbachisaurid MMCh-PV 71	<i>Limaysaurus</i> (MUCPv 205)	<i>Nigersaurus</i> *
	Braincase characters		
cmcv	Present	Not visible	Present*
Crista Prootica	Low ridge	Well developed	Well-developed
CN VII, foramen	Anterior to c.pro	Posterior to c.pro	Posterior to c.pro ^a
CN V, shape	Oval	Bilobate	Oval
CN XII, foramina	One	One	Two
flocular process	Present	?	Present
CN III and CN IV	Separate foramina	Separate foramina	Single exit
Orbitocerebral fenestra	Absent	Absent	Present
	Quadrate characters		
Lateral expansion	Extremely broad	Broad	Broad
Pterygoid process	Short and tall	Subtriangular in shape, more rostrally projected	Short and tall
Distal hemicondyles	Medial hemicondyle at least two times larger	Subequal hemicondyles	Medial hemicondyle at least two times larger

*Serenó et al. (2007).

^aKnoll, pers. comm. (2015).**Abbreviations:** cmcv, caudal middle cerebral vein; c.pro, crista prootica.

2001). However, the paleobiological implications of the development of the flocculus in quadrupedal dinosaurs or in other non-archosaurian reptiles remain unknown (e.g., Paulina Carabajal et al., 2014b; von Baczko et al., 2015).

Taxonomic Implications—The holotype of *Limaysaurus tessonei* and the specimen MMCh-PV 71 were both collected from outcrops of the Candeleros Formation, approximately 3 km apart. Comparisons of the neuroanatomy are restricted to the external aspect because the endocranial cavity remains unprepared and filled with sediment in *Limaysaurus*, and has been only preliminarily studied using CT scans (Paulina Carabajal and Calvo, 2015). The quadrate of MMCh-PV 71 shows strong differences with *Limaysaurus*, including the more expanded lateral edge of the quadrate fossa, and the more rounded outline and anteroposteriorly shorter pterygoid process (Figs. 6, 7). As mentioned, the braincase shows few differences. Taking into account the fact that the postcranium of MMCh-PV 71 (including a dorsal vertebra still under analysis) also shows strong differences with *Limaysaurus*, we assume that these differences do not correspond to ontogeny or sexual dimorphism, and therefore the new specimen could represent a new taxon. However, further phylogenetic analyses will be crucial to evaluate the distribution of some of the characters presented here to determine if they are systematically informative.

CONCLUSIONS

The braincase, cranial endocast, and quadrate of MMCh-PV 71 share a number of features with *Limaysaurus* and *Nigersaurus*, suggesting that some endocranial traits, particularly the presence of a large lateral sinus, dorsal head vein, and presence of a floccular recess, together with the laterally expanded quadrate fossa, are characteristic of rebbachisaurids. Although the new specimen comes from the same stratigraphic age and formation as *Limaysaurus*, it exhibits strong differences from *Limaysaurus* in the quadrate and postcranium, suggesting that it may represent a new rebbachisaurid taxon, thereby increasing the sauropod diversity known from the lower Upper Cretaceous of northern Patagonia.

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