



PALEONTOLOGY

Re-description of the braincase of the rebbachisaurid sauropod *Limaysaurus tessonei* and novel endocranial information based on CT scans

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Abstract: CT scans of the type braincase of *Limaysaurus tessonei* (MUCPv-205) allowed the first study of the endocranial cavities (brain and inner ear) for this South American taxon. Comparisons of the cranial endocast of *L. tessonei* with other sauropods indicate that 1) South American rebbachisaurids are more similar to each other than to *Nigersaurus*, and 2) certain association of traits are present in all known rebbachisaurid cranial endocasts, such as lack of an enlarged dorsal expansion, poorly laterally projected cerebral hemispheres, presence of a small flocculus of the cerebellum, markedly long passage for the facial nerve (CN VII), markedly inclined pituitary, and presence of a passage for the basilar artery communicating the floor of the endocranial cavity and the pituitary fossa. The relatively enlarged olfactory region indicates that smell was an important sense for this group of dinosaurs, suggesting different olfactory capabilities when compared to coeval titanosaurs.

Key words: Braincase, endocranial cavity, inner ear, paleoneurology.

INTRODUCTION

Knowledge of diplodocoid sauropods in South America is scarce, although it has been improved in recent years, particularly due new findings in Argentina (e.g. Salgado et al. 2006, Apesteguía 2007, Carballido et al. 2012, Haluza et al. 2012, Ibiricu et al. 2012, 2013, Gallina et al. 2014, 2019, Rauhut et al. 2015). Within this group, Rebbachisauridae is a family of sauropod dinosaurs that lived from the early Cretaceous to the late Cretaceous of South America, Europe and Africa (Bonaparte 1997, Carvalho et al. 2003, Upchurch et al. 2004, Apesteguía et al. 2010, Whitlock 2011, Mannion & Barret 2013, Torcida Fernandez-Baldor et al. 2011). The family includes a dozen genera, from which *Rayososaurus agrionensis* (Bonaparte 1997, Carballido et al. 2010), *Limaysaurus tessonei* (=

Rebbachisaurus tessonei in Calvo & Salgado 1995, Salgado et al. 2004), *Cathartesaura anaerobica* (Gallina & Apesteguía 2005), *Nopcsaspondylus alarconensis* (Apesteguía 2007), *Comahuesaurus windhausenii* (Carballido et al. 2012), *Katapultasaurus goicoecheai* (Ibiricu et al. 2013, 2015), *Zapalasaurus bonapartei* (Salgado et al. 2006) and *Lavocatisaurus agrioensis* (Canudo et al. 2019) were registered in Argentina. Most rebbachisaurid remains correspond in general to postcranial elements, which are frequently recorded in the lower - upper Cretaceous units (Cenomanian) of Neuquén and San Jorge Basins in Patagonia (Calvo & Salgado 1995, Calvo 1999, Gallina & Apesteguía 2005, Apesteguía 2007, Novas 2009, Simón & Salgado 2009, Paulina-Carabajal et al. 2016). However, rebbachisaurid skulls and particularly braincase remains are

scarce, being known for *Nigersaurus taqueti* from the Aptian-Albian of Africa (Sereno et al. 1999, 2007), and *Limaysaurus tessonei* (Calvo & Salgado 1995) and an unnamed rebbachisaurid (MMCH-PV 71; Paulina-Carabajal et al. 2016) from the Cenomanian of North Patagonia, Argentina. From these, paleoneurology has been explored only in *Nigersaurus taqueti* using CT scans (Sereno et al. 2007, figs. S4-S6), and MMCG-PV 71 using latex endocasts (Paulina-Carabajal et al. 2016).

The skull of *L. tessonei* preserves the braincase, which is the most complete found in South America -for a rebbachisaurid sauropod- so far. The purpose of the present study is to re-describe the braincase osteology of *L. tessonei* (Fig. 1) under the light of new anatomical information based on CT scans, providing the first descriptions of the brain and inner ear for this taxon (Figs. 2, 3).

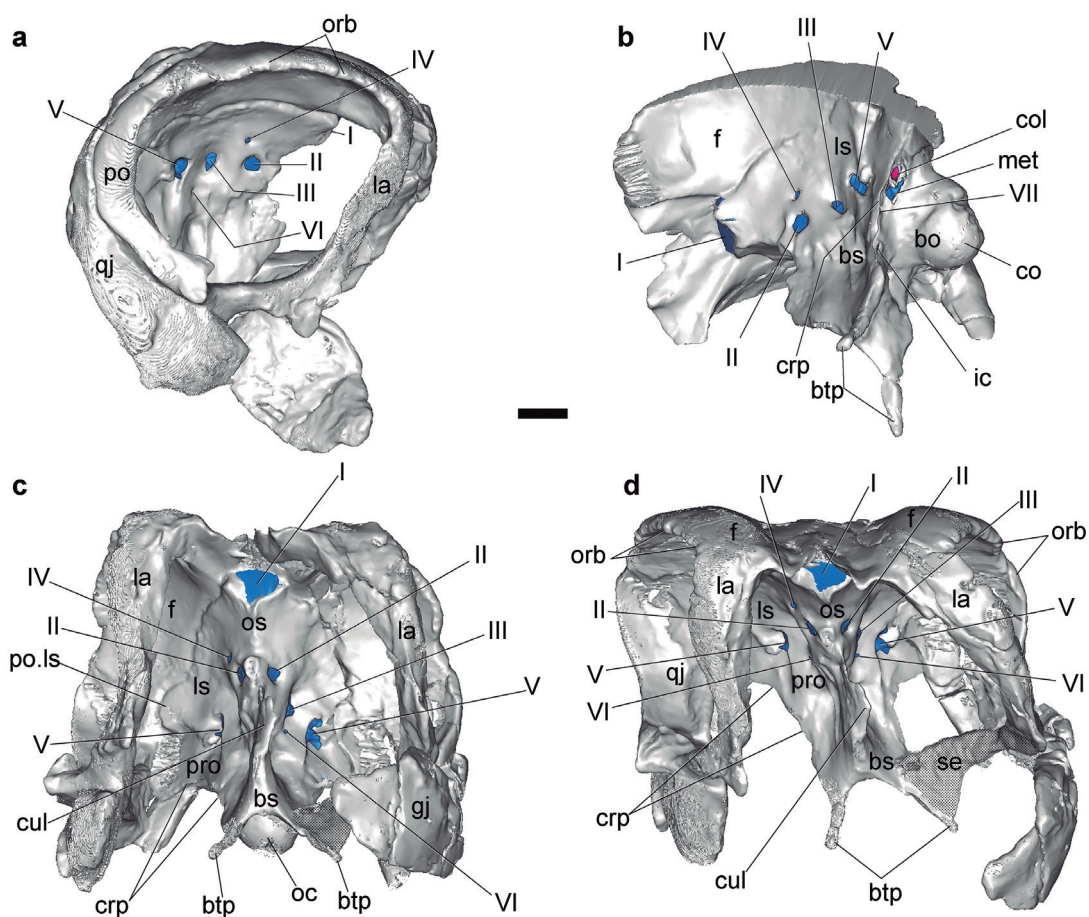


Figure 1. Segmentation of the braincase and articulated skull bones of *Limaysaurus tessonei* (MUCPv-205) in a, right lateral; b, left lateroventral; c, ventral and d, anterior views. In b, lacrimal, postorbital and the margin of the orbital rim formed by the frontal were longitudinally sectioned and removed to allow better observation of the lateral wall of the braincase. Abbreviations: bo, basioccipital; bs, basisphenoid; bt, basal tuber; btp, basipterygoid process; col, columellar recess; crp, crista prootica; cul, cultriform process; f, frontal; ic, cerebral branch of internal carotid artery; la, lacrimal; met, metotic foramen for CNs IX-XI; oc, occipital condyle; orb, orbital rim; os, orbitosphenoid; p, parietal; po, postorbital; po.ls, postorbital process of laterosphenoid; pro, prootic; gj, quadratojugal; se, sediment attached to bone; I-VII, cranial nerves. Scale bar= 10 mm.

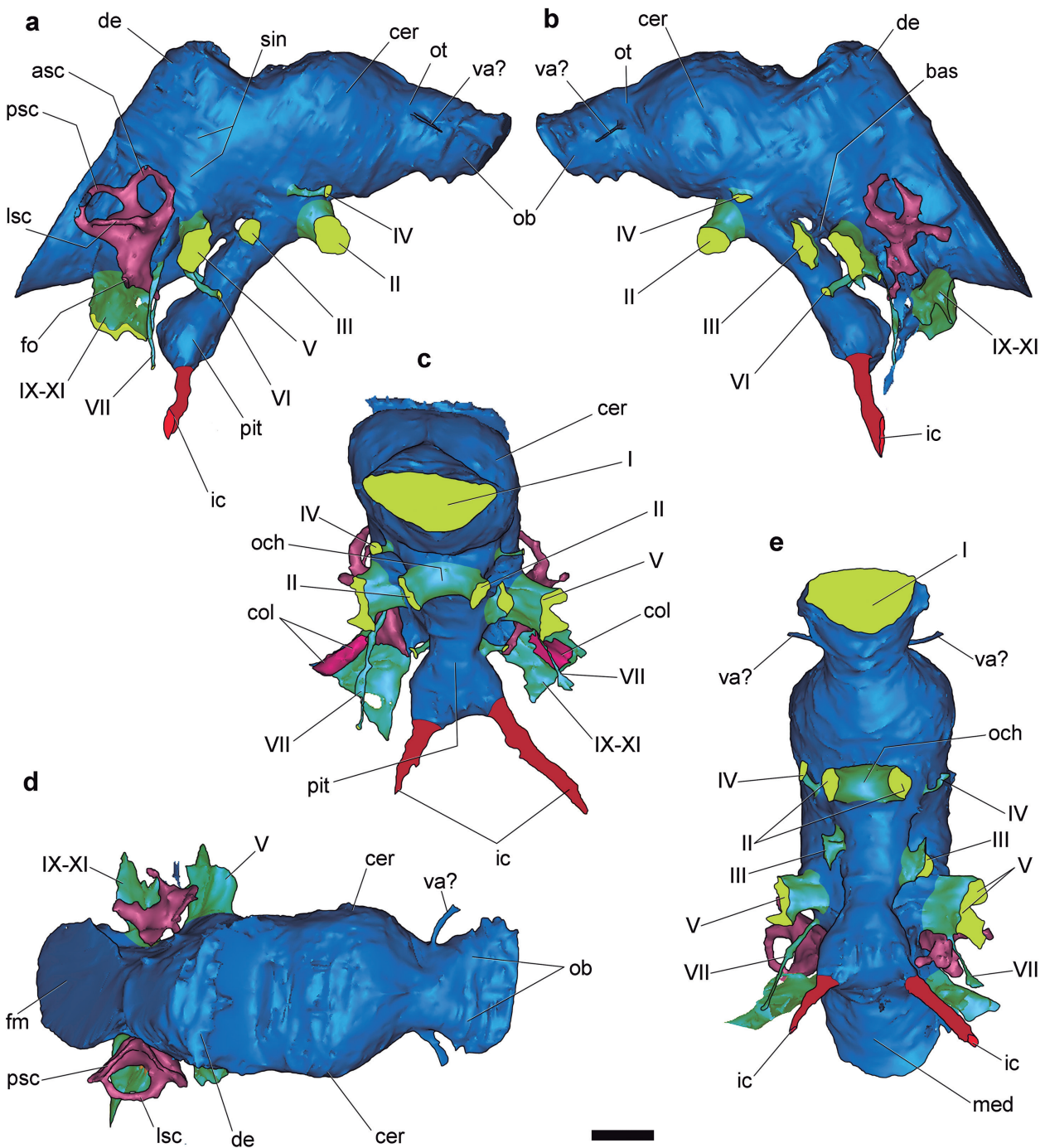


Figure 2. Segmentation of the brain and inner ear of *Limaysaurus tessonei* (MUCPv-205) in a, right; b, left; c, anterior; d, dorsal and e, ventral views. Cranial nerves are in yellow, internal carotid arteries are in red and the cast of the columellar recess (Fig. 3c) is in magenta. Abbreviations: asc, anterior semicircular canal; cer, cerebral med, medulla oblongata hemisphere; de, dorsal expansion; fo, fenestra ovalis; ic, internal carotid artery; lsc, lateral semicircular canal; ob, olfactory bulb; och, optic chiasm; ot, olfactory tract; pit, pituitary; psc, posterior semicircular canal; sin, transversal venous sinus; va, vascular element (unidentified blood vessel); I-XI, cranial nerves. Scale bar= 10 mm.

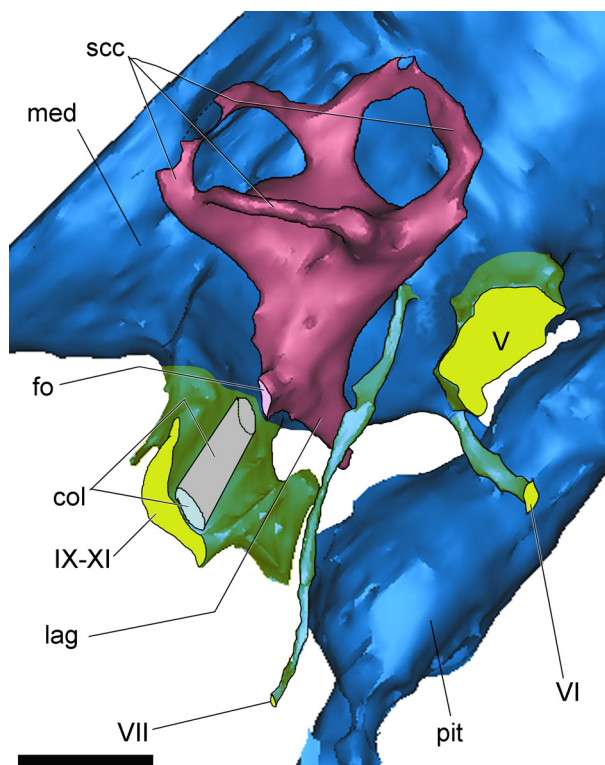


Figure 3. Detail of posterior region of the cranial endocast and inner ear in right lateral view, showing three-dimensional reconstruction of the columellar recess. Abbreviations: col, columellar recess; fo, fenestra ovalis; lag, lagena; med, medulla oblongata; pit, pituitary; scc, semicircular canals of the inner ear; V-XI, cranial nerves. Scale bar = 10 mm.

MATERIALS AND METHODS

The CT scan of the holotype braincase of *L. tessonei* (MUCPv-205) was performed at Clínica Moguillansky (Neuquén City, Argentina), using a General Electric Medical Systems BrightSpeed tomographer. A number of 362 slices were obtained applying an energy of 120 kv and 96.15 mAs, with a slice increment of 0.62 mm. The segmentations of the braincase, brain and inner ears were made using the software Materialise Mimics (18.0); whereas, final images for publication were made using Adobe Photoshop. Renderings of the braincase, brain and inner ear were published in MorphoMuseum A. Paulina-Carabajal & J.O. Calvo, in press.

Comparisons with *Nigersaurus taqueti* are based on the endocranial morphology published by Sereno et al. (2007), and their 3D braincase reconstruction available online at the site Digimorph (http://digimorph.org/specimens/Nigersaurus_taqueti/basicranium/).

Regarding the endocranial morphology and following other authors (e.g. Witmer et al. 2008), and to facilitate discussion along the text, the digital casts of structures will be referred as if they were the structures themselves (e.g. “olfactory bulb” instead of “cast of olfactory bulb cavity”, etc.).

Brain based calculations

Reptile Encephalization Quotient calculation (REQ).

The REQ of *L. tessonei* was calculated after Hulburt et al. (2013), using the following equation: $REQ = MBr / (0.0155 \times MBd^{0.553})$, where **MBr** is the brain mass (calculated from brain volume of approximately 125cm³) and **MBd** is the body mass (7000 kg, calculated by Paul 2010, and 11.688 kg, calculated by Benson et al 2018). Since the brain did not fulfill the endocranial cavity completely, the 50% and 100% of the total volume of the cranial endocast was used in the calculations, resulting in REQs of 0.66 and 1.32 (using 7000 kg), and 0.49 and 0.99 (using 11.688 kg) respectively.

Olfactory ratios. Olfactory ratio allows interpreting the olfactory acuity in extinct forms. It is calculated as the ratio between the longest diameter of the olfactory bulb and the longest diameter of the cerebral hemisphere, regardless of orientation, and multiplied by 100 (see Zelenitsky et al. 2009).

RESULTS

Braincase

The braincase is complete and preserves delicate structures, such as the laminar cultriform process

and the slender basipterygoid processes. It is in natural articulation with other skull bones (i.e. lacrimal, postorbital and quadratojugal, Fig. 1), and shows little oblique dorsoventral compression that results in a slight asymmetry as seen in anterior view (Fig. 1d).

Parietals and frontals are transversely wider than long in dorsal view, delimiting slit-shaped supratemporal fossae, and there are no postfrontal or parietal fenestrae (see Calvo & Salgado 1995, fig. 3). The nuchal crest is low and anteroventrally inclined (Supplementary Material - Figure S1a). Posteriorly, and laterally to the supraoccipital knob, there are marked oval depressions on each side for the insertion of the muscles involved on dorsiflexion movements of the head, probably the *m. transversospinalis capitis* (see Snively & Russell 2007, Button et al. 2014). Similar although slightly larger insertion marks are observed in dicraeosaurids, such as *Amargasaurus cazaui* (Salgado & Calvo 1992, Paulina-Carabajal et al. 2014) and *Dicraeosaurus hansemanni* (Janensch 1935-36).

The supraoccipital is a vertical short element, contacting the parietals dorsoalterally and the exoccipital-opisthotics lateroventrally. It participates on the dorsal margin of the foramen magnum, which is oval-shaped (Calvo & Salgado 1995, fig. 3). The supraoccipital knob is robust but has no well-marked margins. It bears a median longitudinal and shallow depression.

The exoccipital is fused to the opisthotic on each side, forming the exoccipital-opisthotic complex, as in most dinosaurs (Currie 1997). The paroccipital processes of *L. tessonei* are delicate long and thin blade-shaped structures which are markedly projected ventrally (Calvo & Salgado 1995, fig. 5). They are straight projections with dorsal and ventral margins more or less parallel along their entire length, and being slightly expanded distally. The base of the paroccipital process bears dorsally a rounded

protuberance divided by a small channel that delimits –together with the supraoccipital knob– another depression, probably for the insertion of musculature involved in dorsiflexion of the head (Snively & Russell 2007, “*m. splenius capitis*” in Button et al. 2014). Lateral to the occipital condyle is the foramen for the exit of Cranial Nerve (CN) XII, as illustrated by Calvo & Salgado (1995). The passage for this nerve is not observed in the CT scans. Contrarily, the metotic passage and its external foramen are large and clearly traceable on the CT scans (Figs. 1b, 2a). The metotic foramen, for CNs IX–XI and the internal jugular vein, opens within an oval recess delimited between the crista prootica anteriorly and the ventral ramus of the opisthotic posteriorly, which corresponds to the middle ear region of the braincase. Within this recess, and anterodorsal to the metotic foramen, opens also the columellar recess that leads internally to the fenestra ovalis (Figs. 1b, 3).

The prootic contacts with the opisthotic posteriorly (probably at the metotic foramen level) and the laterosphenoid anteriorly, probably forming the posterior margin of the trigeminal (CN V) foramen. The prootic forms the conspicuous crista prootica, which is a delicate and deep crest of bone posterolaterally projected (Fig. 1b) and obscuring the observation of the metotic foramen in a lateral view of the braincase, as in *N. taqueti* (Sereno et al. 2007, image available at Digimorph). In MMCh-PV 71 the crista prootica is eroded (Paulina-Carabajal et al. 2016), and it is not possible to determine if it was as deep as in *L. tessonei* and *N. taqueti*. The crista prootica is also well developed in other diplodocoids, such as dicraeosaurids (Janensch 1935-36, Paulina-Carabajal et al. 2014) and the diplodocid *Diplodocus* (USNM V 2673, Paulina-Carabajal 2015, fig. 9.4). Contrarily, in titanosaurs the crista prootica is low (even forming a shallow ridge in some specimens) and

the metotic foramen and the fenestra ovalis are clearly observed in lateral view of the braincase (e.g. Calvo & Kellner 2006, Paulina-Carabajal 2015). All the branches of the trigeminal nerve leave the endocranial cavity through a single foramen located within the anterior lobe of a large and deep heart-shaped recess on the lateral wall of the braincase (Fig. 1a, b). This recess is the osteological correlate of the Gasserian (= trigeminal) ganglion. The heart-shaped dorsal margin of the recess is produced by a ventrally projected protuberance that divides the trigeminal foramen proper anteriorly and the dorsal lobe of the recess posteriorly. This protuberance seems to indicate the insertion surface for the *M. levator pterygoideus* (Holliday 2009). A similar constitution is also present in *N. taqueti* (Serenio et al. 2007, lateral view of the braincase, available image at Digimorph) and in MMCh-PV 71, although in the later the recess is not well marked. In *L. tessonei*, the ophthalmic branch (V_1) probably passed through the anterior lobe of the gasserian recess, whereas the maxillomandibular branches ($V_{2,3}$) passed ventrally and posteriorly, as indicated by the grooves/impressions left by the nerves. In *L. tessonei*, the exit foramen for CN VII is not just posterior CN V as in most dinosaurs, but far ventrally displaced (it probably opens within the basisphenoid) and clearly separated from the later by the crista prootica (Calvo & Salgado 1995, fig.5; Fig. 1b). Therefore, CN VII is only visible in posterior view of the braincase.

The laterosphenoid is firmly fused to the orbitosphenoid anteroventrally and to the prootic posteriorly. It forms a delicate and poorly differentiated capitate process (= postorbital process of laterosphenoid) attached to the ventral side of the frontal (Fig. 1c). The foramina for CNs III and IV are probably indicating the laterosphenoid-orbitosphenoid contact, as in other dinosaurs (Currie 1997). In the

rebbachisaurid MMCh-PV 71 (Paulina-Carabajal et al. 2016), CNs III and IV have also separated foramina; whereas these two nerves leave the endocranial cavity through a single opening in *N. taqueti* (Serenio et al. 2007).

Cranial Nerve II is completely enclosed by the orbitosphenoid and separated from its counterpart (Fig. 1a). This foramen is circular and slightly larger than the foramen for CN V, as in MMCh-PV 71, but different from *N. taqueti*, where CN II is larger than CN V (Serenio 2007, image available at Digimorph). The sub-triangular opening delimited between both orbitosphenoids lateroventrally and the frontals dorsally corresponds to the space occupied by the olfactory tracts and bulbs, indicated however in figures as CN I (Fig. 1). In *L. tessonei* and the rebbachisaurid MMCh-PV 71 there is no foramina for the orbitocerebral vein in the orbitosphenoid-laterosphenoid region, meaning this blood vessel uses the foramen for CN IV to exit the endocranial cavity. Contrarily, there is a large “epioptic fenestra” on the lateral wall of the braincase in *N. taqueti* (Serenio et al. 2007, image available at Digimorph), which was probably used by cerebral blood vessels.

The basicranium of *L. tessonei* is complete, including delicate structures such as the basiptyergoid processes and the cultriform process (Fig. 1). The basioccipital forms most of the occipital condyle and the ventrally projected basal tubera. The basal tubera are fused medially forming a rectangular surface in posterior view, which bears a large subcondylar depression (Calvo & Salgado 1995, fig. 5). The basisphenoid forms elongate and divergent pen-shaped basiptyergoid processes, which are ventrally projected when the lateral semicircular canal is oriented horizontally. The external foramen for CN VI is small in diameter and is located ventral to CN III, as indicated in Figure 1a. It is piercing the basisphenoid, indicating

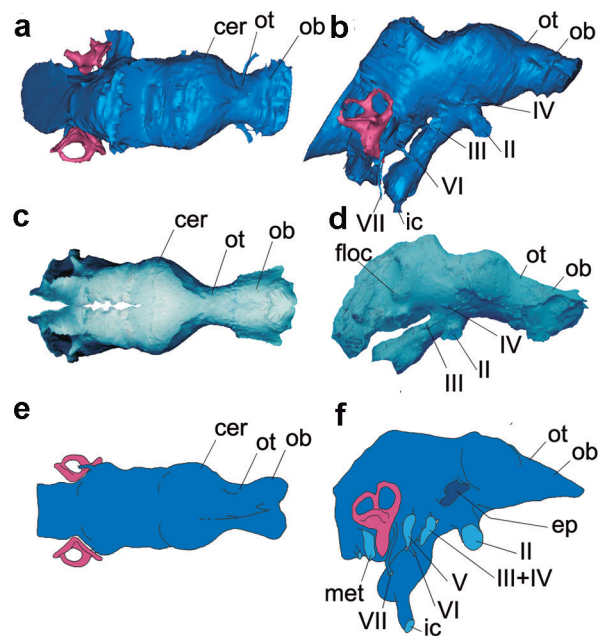


Figure 4. Endocranial casts of *Limaysaurus* (a, b), rebbachisaurid MMCh-PV 71 (c, d), and *Nigersaurus* (e, f) compared; in dorsal (left column) and right lateral (right column) views. Abbreviations: cer, cerebral hemisphere; ep, epiotic fenestra; flocc, flocculus of cerebellum; ic, cerebral branch of internal carotid artery; met, metotic passage; ob, olfactory bulb; ot, olfactory tract; I-XI, cranial nerves. (c, d, modified from Paulina-Carabajal et al 2014; e, f, modified from Sereno et al. 2007). Not to scale.

that CN VI runs laterally to the pituitary fossa, as in titanosaurids (e.g. Paulina-Carabajal 2012). The foramen for the internal carotid artery is located laterally to the end of the basal tuber, within a small groove delimited between the ends of the crista tuberalis and the crista prootica (Fig. 1b). Therefore, the internal carotid foramen is observed mainly in posterior view of the basicranium, whereas it is observed in ventral view in titanosaurs, and in lateral view in most non-titanosaur sauropodomorphs, the latter being the plesiomorphic condition.

Cranial endocast

The general morphology of the cranial endocast of *L. tessonei*—excluding the olfactory bulbs—is reminiscent of that of that in other

studied sauropods. The cranial endocast is anteroposteriorly short and transversely wide (also behind the cerebral hemispheres); the cerebral hemispheres are not markedly projected laterally but they are clearly observed protuberances, and the hypertrophied pituitary is posteroventrally projected (Fig. 2). The cranial endocast measures approximately 130 mm from the olfactory bulbs to the foramen magnum, whereas the maximum transversal width (44.3 mm) is across the cerebral hemispheres. The dorsal expansion is a protuberance expanded dorsally from the endocast, similar in size and volume to that in other rebbachisaurids and titanosaurs (Sereno et al. 2007, Paulina-Carabajal et al. 2016, Knoll et al. 2019 and references therein).

The visible regions of the forebrain in the cranial endocast correspond to the olfactory bulbs and olfactory tracts, the cerebral hemispheres, the pituitary and CN II (Fig. 2). In *L. tessonei*, the olfactory tract is short and transversely wide. The olfactory bulbs are slightly projected ventrally, as in *N. taqueti* (Sereno et al. 2007) and the rebbachisaurid MMCh-PV 71 (Fig. 2a, b). The olfactory bulbs are oval-shaped and markedly divergent from the midline (Fig. 2d). A strong constriction anterior to the cerebral hemispheres indicates the beginning of the olfactory tracts. At this level, there is a blood vessel on each side that runs anterolaterally from the olfactory tract (Fig. 2a, d). The exit foramen for these vascular passages are not observed in the CT scans, and locate near the orbitosphenoid-frontal suture on each side of the braincase, representing probably vascularization of the ethmoid region. The cerebral hemispheres are not markedly expanded laterally and although the maximum transversal width of the endocast is across the cerebral hemispheres, it is slightly wider than the hindbrain, as observed in *N. taqueti* and MMCh-PV 71. In *L. tessonei*,

the pituitary is hypertrophied, as in other sauropods (Hopson 1979). It is elongated and markedly posteroventrally projected (Fig. 2a), forming an acute angle of approximately 50° with the lateral semicircular canal (see Knoll et al. 2015), similar to the angles observed in the other two studied rebbachisaurids (Sereno et al. 2007, Paulina-Carabajal et al. 2016) and in the titanosaurs *Lohuecotitan pandaflandi* (55°, Knoll et al. 2013), an indeterminate titanosaur from Spain (45° Knoll et al. 2015) and *N. palomoi* (40°, Paulina-Carabajal et al. 2020). The internal carotid arteries merge with the distal end of the pituitary as separate passages. These blood vessel passages are relatively long and small in diameter, divergent from the midline (Fig. 2c, e). Cranial Nerve II has a robust and short passage that merges with its counterpart medially in an enlarged protruded region on the ventral side of the endocast that we identify as the optic chiasm (Fig. 1e). This region is also well differentiated in the cranial endocasts of *N. taqueti* and MMCh-PV 71.

The only structures of the midbrain recognized in the cranial endocast of *L. tessonei* correspond to CN III (oculomotor nerve) and CN IV (trochlear nerve). The passage for CN III is posterior to the infundibular region, at the base of the pituitary region. It is short and laterally projected (Fig. 2a, b). The base of the passage for CN IV is posterodorsal to CN II, and has a smaller diameter than CN II. This is an elongate passage that runs anteriorly so that the exit foramen is dorsal to CN II, as observed in the right side of the brain (Fig. 2a, c). As mentioned, separate passages for CNs III and IV are also present in MMCh-PV 71 (Paulina-Carabajal et al. 2016), but they leave the endocranial cavity through a single opening in *N. taqueti* (Sereno et al. 2007).

The structures of the hindbrain observed in the cranial endocast of *L. tessonei* correspond to the cerebellar region, the medulla oblongata

and CNs V–XII. The osteological correlate of the flocculus of the cerebellum, identified in *N. taqueti* (Sereno et al. 2007) and MMCh-PV 71 (Paulina-Carabajal et al. 2016) is not observed in the CT scans of *L. tessonei*. However, since this structure is a small protuberance in rebbachisaurid cranial endocasts, its presence in *L. tessonei* cannot be discarded. Moreover, the flocculus in the rebbachisaurid MMCh-PV 71 is converged with a well-developed vertical venous sinus that protrudes on the posterodorsal region of the endocast reaching the base of the trigeminal nerve (Paulina-Carabajal et al. 2016). In *L. tessonei*, a similar vertical protuberance –although less marked– is clearly observed on the right side of the endocast (Fig. 2a). The medulla oblongata is ventrally smooth and slightly concave in lateral view. The foramen magnum is anteroventrally inclined, unlike the vertical one in *N. taqueti* (Sereno et al. 2007). The passage for CN V is large, short and laterally projected. Cranial Nerve VI has a passage of small diameter that runs anteroventrally from the base of the medulla oblongata and passes laterally to the pituitary (Fig. 3). The base of the passage for CN VII is small in diameter and locates just posterior CN V. However, it is markedly long and ventrolaterally projected so that the exit foramen for this nerve locates posteriorly to the crista prootica (Figs. 2, 3). The cast of the metotic passage (CNs IX–XI) is large in diameter, anteroposteriorly compressed and posteroventrally oriented (Fig. 3). The passages for CN XII are not visible in the CT scans, although a single opening is observed externally in the braincase (Calvo & Salgado 1995).

Inner ear

The right inner ear of *L. tessonei* was completely reconstructed (Fig. 3). It has slender semicircular canals, short and robust crus commune. The anterior semicircular canal (asc) is circular,

whereas the posterior semicircular canal (psc) and the lateral semicircular canal (lsc) are oval (Fig. 1a, d). The asc is slightly larger than the psc, unlike the markedly larger asc observed in other eusauropods, such as *Diplodocus* sp., *Giraffatitan braincai* and *Spinophorosaurus nigerensis* (Knoll et al. 2012). In dorsal view, the angle formed between the asc and psc in *L. tessonei* is approximately 82°. The lagena is simple, short and conical, and slightly ventromedially projected (Fig. 3). The fenestra ovalis is small in diameter and posterolaterally oriented, indicating the trajectory of the columella. The CT scans showed a tubular recess running parallel and adjacent to the metotic passage, which corresponds to the columellar recess (Fig. 3).

Endocranial morphology compared and paleobiological implications

The cranial endocast and the inner ear morphologies of *L. tessonei*, *N. taqueti* (Serenó et al. 2007) and the rebbachisaurid MMCh-PV 71 (Paulina-Carabajal et al. 2016) are strongly similar, showing a combination of certain endocranial traits that may be characteristic for the clade Rebbachisauridae (Fig. 4). Although these characters are individually shared with other sauropods, they are present together in all known rebbachisaurid cranial endocasts. They include: 1) poorly developed dorsal expansion (it represents the cast of the dorsal longitudinal venous sinus, e.g. Witmer et al. 2008), which does not obscure dorsally the general shape of the forebrain allowing the observation of the cerebral hemispheres, olfactory tract and olfactory bulbs in dorsal view of the endocast (Fig. 4a). This development is comparable to the shallow dorsal expansion observed in titanosaur cranial endocasts (e.g. Wilson et al. 2009, Paulina-Carabajal 2012, Knoll et al. 2013, 2015, 2019) except *Sarmientosaurus musacchioi* (Martínez et al. 2016), and contrasts with basal

sauropods and diplodocoids (e.g. Janensch 1935-36, Knoll & Schwarz-Wings 2009, Knoll et al. 2012, Paulina-Carabajal et al. 2014) where this venous sinus develops largely dorsally and also anteriorly, and thus obscuring the morphology of most of the forebrain in dorsal view of the endocast. 2) poorly laterally expanded cerebral hemispheres. In dorsal view of the endocast, the lateral margins of the cerebral hemispheres are convex but do not expand laterally overpassing the level of the anterior and posterior ampulae of the inner ear (whereas, in the titanosaurid *Botanitan* the lateral expansion of the cerebral hemisphere reaches the level of the lateral semicircular canal of the inner ear (Fig. 4a, e). Also, in dorsal view there is a poorly marked constriction separating the cerebral hemisphere from the cerebellar region, resulting in a more or less rectangular shape for the rebbachisaurid cranial endocast (Fig. 4a, c, e). In most titanosaurs—in which this region is observable due the reduction of the dorsal expansion—there is a noticeable constriction or separation between these two regions of the endocast (e.g. Paulina-Carabajal 2012, Knoll et al. 2019); 3) The flocculus of the cerebellum (structure that has been related to gaze stabilization capabilities, see Walsh et al. 2013 and references therein) leaves a small osseous correlate on the endocranial cavity of *N. taqueti* and MMCh-PV 71 (Fig. 4d), suggesting there is a high probability of its presence in *L. tessonei*, in which this trait is not observed in the CT scans. In this region of the endocast of *L. tessonei*, there is a large vertical venous sinus (continuous dorsally with the dorsal longitudinal venous sinus) in connection with the dorsal margin of CN V ventrally (Fig. 4b, d). This vertical “ridge” on the lateral side of the endocast represents a vascular sinus, and is also clearly observed in other sauropod endocasts, such as the basal sauropodomorph *Spinophorosaurus* (Knoll et al. 2012), *Diplodocus*

(Witmer et al. 2008), and some titanosaurs (e.g. Paulina-Carabajal 2012, Martínez et al. 2016). 4) Relatively elongate olfactory tracts and olfactory bulbs (if compared with the extremely short ones present in titanosaurs), which are slightly ventrally oriented (Fig. 4b, d, f). The relatively elongate olfactory region of the forebrain is probably related to the relative position of the nares in the skull, as in other sauropods (Knoll et al. 2019). Although compared with other dinosaurs rebbachisaurids seem to have relatively smaller olfactory bulbs, they are however, relatively larger than those observed for example in titanosaurids and dicraeosaurids. The calculated Olfactory Ratio (Zelenitsky et al. 2009) for *L. tessonei* is approximately 50%, and approximates 47% in MMCh-PV 71 and in *N. taqueti*, contrasting with the approximately 36% calculated for the saltasaurid *Bonatitan reigi*. If the olfactory ratios and body masses of *L. tessonei* and *B. reigi* are plotted in the regression calculated for theropods by Zelenitsky et al. (2009, fig. 2), both sauropods lay below predicted olfactory ratios, with the titanosaur laying outside the 95% confidence interval. This suggests different olfactory capabilities for rebbachisaurids and titanosaurids. However, the olfactory acuity (see Zelenitsky et al. 2009) has not been calculated for sauropods so far, and further paleoneurological studies are needed in order to allow a more comprehensive analysis regarding the sense of smell within the clade. 5) extremely elongate passage for CN VII, which exits the endocranial cavity through a foramen largely separated ventrally from CN V. In *L. tessonei* (Calvo & Salgado 1995) and *N. taqueti* (Serenó et al. 2007) -in MMCh-PV 71 this region is badly preserved- this foramen opens on posterior side of the crista prootica and thus is not observed in lateral view of the braincase. A similar condition is also observed in the dicraeosaurid *Amargasaurus cazau* (Paulina-Carabajal et al.

2014, fig. 3). Rebbachisaurid and dicraeosaurid basicrania have elongate and delicate basiptyergoid processes, which indicate the relative position of the palate and may be related with the posteroventral orientation of the facial nerve. Within titanosaurs, a relatively elongate passage for CN VII is present in *Narambuenatitan palomoi* (Paulina-Carabajal et al. 2020), although the exit foramen opens on the lateral side of the braincase. 6) acute angle of approximately 45°-50° between the pituitary and the lsc of the inner ear (Fig. 4b, d, f). All sauropods have posteroventrally oriented pituitary, however the mentioned angle (measurement proposed by Knoll et al. 2015) approximates 60°-70° in most studied taxa, as observed in basal sauropodomorphs (e.g. Knoll et al. 2012), diplodocoids (e.g. Hopson 1979, Witmer et al. 2008, Paulina-Carabajal et al. 2014) and titanosaurs (e.g. Paulina-Carabajal 2012, Knoll et al. 2019 and references therein) except in *N. palomoi* and *L. pandafilandi* (Knoll et al. 2013, A. Paulina-Carabajal et al. in press), which exhibit strongly acute angles (approximately 45°) between the pituitary and the lsc. 7) The REQ of *L. tessonei* (calculated at 50% of total endocranial volume and using 7000 kg and 11.688 kg of body size) varies between 0.49 and 0.66, falling within the range calculated previously for other sauropods, such as *Giraffatitan brancai* (e.g. 0.62–0.79; Knoll & Schwarz-Wings 2009).

The cranial endocasts of South American rebbachisaurids *L. tessonei* and MMCh-PV 71 share between them (but not with *N. taqueti*) few other endocranial characters including: 1) a marked depression forming a “valley” separating the cerebral hemispheres and the dorsal expansion in lateral view of the endocast (Fig. 4b, d). This depression is less marked in *N. taqueti*, where the dorsal surface of the cerebral hemispheres is more or less continuous posteriorly with the dorsal expansion as shown in the reconstruction

made by Sereno et al. (2007). However, since the supraoccipital and parietals are not preserved in this taxon, the posterodorsal aspect of its cranial endocast remains hypothetical, and thus, the possibility that this region is similar to that in South American representatives of the group, cannot be discarded (Fig. 4f); 2) separate foramina and passages for CNs III and IV (Fig. 4b, d), whereas these nerves exit the endocranial cavity through a large single opening in *N. taqueti* (Fig. 4f); 3) absence of the orbitocerebral vein foramen (Fig. 4b, d), whereas there is a large opening -epioptic fenestra- in the braincase of the African form (Fig. 4f). Interestingly, the same difference is observed between the braincases of the dicraeosaurids *Amargasaurus* and *Dicraeosaurus*, where there is no orbitocerebral vein foramen in the former but there is a large epioptic fenestra in latter respectively (Paulina-Carabajal et al. 2014). In this regard, even in the case that we were misidentifying the foramen for CN IV in *L. tessonei*, and this nerve leaves in fact the endocranial cavity together with CN III as in *N. taqueti* (the remnant foramen corresponding then to the orbitocerebral vein), there is yet a lack of epioptic fenestra in the South American specimens. These characters shared only by *L. tessonei* and MMCH-PV 71 may be synapomorphic of the Limaysaurinae group (e.g. Whitlock 2011).

CONCLUSION

The CT scans allowed to corroborate the identification of braincase neurovascular foramina made by Calvo & Salgado (1995), adding new information regarding the internal disposition of passages for almost all cranial nerves, internal carotid arteries, basilar artery, and the orbitocerebral veins. In general terms, the cranial endocast and inner ear morphologies

of *L. tessonei*, *N. taqueti* (Sereno et al. 2007) and the rebbachisaurid MMCh-PV 71 (Paulina-Carabajal et al. 2016) are strongly similar. The combination of certain endocranial traits –which however, individually are shared with other sauropods– may be characteristic for the clade Rebbachisauridae. Furthermore, South American specimens share a few characters differing from *N. taqueti*, which represent qualitative morphological characters with potential use in taxonomy and or phylogeny.

Interesting characters of the rebbachisaurid cranial endocast include the presence of flocculus of cerebellum (which is associated to gaze stabilization) and a relatively enlarged –when compared to other upper Cretaceous Gondwanan sauropods– olfactory region in the forebrain. In this regard, the rebbachisaurid olfactory ratio is almost 30% higher than that in titanosaurs, suggesting markedly different olfactory capabilities between this two coeval sauropod groups.

ABBREVIATIONS: **MMCh-PV**, Museo 'Ernesto Bachmann' Villa El Chocon, Argentina; **MUCPv**, Museo de la Universidad Nacional del Comahue, Argentina; **USNM**, Smithsonian National Museum of Natural History, Washington, United States of America.

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SUPPLEMENTARY MATERIAL

Figure S1. Segmentation of the braincase and articulated skull bones of *Limaysaurus tessonei* (MUCPv-205) in a-b, posterior; c-d, ventral, and e-f, anterior, views. In the figures at the right column the bone is rendered semitransparent to allow the observation of internal structures (brain and inner ear). Abbreviations: bo, basioccipital; bs, basisphenoid; bt, basal tuber; btp, basipterygoid process; cer, cerebral hemispheres; col, columellar recess; crp, crista prootica; cul, cultriform process; end, endocranial cavity; eo-op, exoccipital-opisthotic complex; f, frontal; fm, foramen magnum; ic, cerebral branch of internal carotid artery; la, lacrimal; ls, laterosphenoid; m1, muscular attachment area; met, metotic foramen for CNs IX-XI; ob, olfactory bulb (CN I); oc, occipital condyle; orb, orbital rim; os, orbitosphenoid; p, parietal; pit, pituitary; po, postorbital; po.ls, postorbital process of laterosphenoid; pro, prootic; qj, quadratojugal; se, sediment attached to bone; sok, supraoccipital knob; I-VII, IX-XII, Cranial Nerves. Scale bar= 10 mm.

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