Arenysaurus ardevoli, first paleoneuroanatomical description of a European hadrosaurid

The neuroanatomy of hadrosaurid dinosaurs is well known from North America and Asia. In Europe only a few cranial remains have been recovered with the braincase. *Arenysaurus* is the first European endocast for which the paleoneuroanatomy has been studied. The resulting data have enabled us to draw ontogenetic, phylogenetic and functional inferences. *Arenysaurus* preserves the endocast and the inner ear. This cranial material was CT-scanned, and a 3D-model was generated. The endocast morphology supports a general pattern for hadrosaurids with some characters that distinguish to a subfamily level, such as a brain cavity anteroposteriorly shorter or the angle of the major axis of the cerebral hemisphere to the horizontal in lambeosaurines. Both characters are present in the endocast of *Arenysaurus*. Moreover, osteological features indicate an adult ontogenetic stage while some paleoneuroanatomical features are indicative of a subadult ontogenetic stage and even a juvenile ontogenetic stage. Finally, a comparison with other hadrosaurids reveals that the low values for the angle of the dural peak may be an autapomorphy exclusive to the *Parasaurolophus* genus. It is hypothesized that the presence of puzzling characters that suggest different ontogenetic stages for this specimen, may reflect some degree of dwarfism in *Arenysaurus*. Regarding the inner ear, its structure shows differences from the ornithopod clade with respect to the height of the semicircular canals. These differences could lead to a decrease in the compensatory movements of eyes and head, with important implications for the paleobiology and behavior of hadrosaurid taxa such as *Edmontosaurus, Parasaurolophus* and *Arenysaurus*. These differences in the vestibular system could be used as a phylogenetical signal. The endocranial morphology of European hadrosaurids sheds new light on the evolution of this group and may reflect the conditions in the archipelago where these animals lived during the Late Cretaceous.

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Introduction

Hadrosaurids are the most abundant ornithopod dinosaurs from the Late Cretaceous of Laurasia with a very complete record including ontogenetic series, mummies, eggs, ichnites, etc. (see Lull & Wright, 1942; Horner, Weishampel & Forster, 2004 for reviews). This rich record also includes natural cranial endocasts or complete skulls allowing the generation of silicone or latex rubber models of the endocast (Lambe, 1920; Gilmore, 1924; Ostrom, 1961; Serrano-Brañas *et al.*, 2006; Lauters *et al.*, 2013). The endocranial morphology of hadrosaurids has been studied since the first quarter of the 20th century (as in the case of *Edmontosaurus regalis* (Lambe, 1920) or *Lambeosaurus* (Gilmore, 1924)). Nowadays, non-invasive techniques such as CT scans shed new light on the paleoneurology of dinosaurs and other extinct taxa (Witmer *et al.*, 2008; Evans *et al.*, 2009; Godefroit, Bolotsky & Lauters, 2012; Lautenschlager & Hubner, 2013). CT scan techniques are currently common in biology and paleontology in a considerable variety of studies as a way of obtaining digital models of inner regions, as in the case of endocranial morphology, where these cavities are surrounded by matrix. Interestingly, the CT scan allows a 3D visualization with a high or very high resolution depending on the type of CT scan used and the goal of the study.

To date, endocranial morphology is mainly known from North American specimens (Lull & Wright, 1942; Ostrom, 1961; Hopson, 1979; Evans *et al.*, 2009; Farke *et al.*, 2013) and to a lesser extent from Asian remains (Young, 1958; Saveliev *et al.*, 2012; Godefroit, Bolotsky & Lauters, 2012; Lauters *et al.*, 2013), including isolated individuals and ontogenetic series. In Europe, however, the cranial record of hadrosaurids is very scarce, and no paleoneurological analyses have yet been performed. The European hadrosaurids with cranial material are *Tethyshadros*, *Telmatosaurus* and *Arenysaurus* (Nopcsa, 1900; Dalla Vecchia, 2009; Pereda-Suberbiola *et al.*, 2009b). In the case of *Telmatosaurus* a latex rubber model of poor quality was historically described (Nopcsa, 1900).

Arenysaurus forms part of the rich hadrosaurid fauna from the Iberian Peninsula, although the cranial remains are scarce (Cruzado-Caballero, Pereda Suberbiola & Ruiz-Omeñaca, 2010; Cruzado-Caballero, Ruiz-Omeñaca & Canudo, 2010, Cruzado-Caballero *et al.,* 2013; Prieto-Márquez *et al.*, 2013). It was described by Pereda-Suberbiola *et al.* (2009b) as the first European lambeosaurine hadrosaurid preserving most of the cranial elements, including an almost 3D complete braincase (Figure 1). The *Arenysaurus* remains, together with other hadrosaurid and lambeosaurine material, helped to change the vision of a primitive European fauna for one that is more diverse, permitting osteological comparison with derived hadrosaurid faunas from North America and Asia and studies of the phylogenetic relations between them (Company, Galobart & Gaete, 1998; Casanovas-Cladellas *et al*., 1999; Pereda-Suberbiola *et al*., 2009a; Cruzado-Caballero, Pereda Suberbiola & Ruiz-Omeñaca, 2010; Cruzado-Caballero, Ruiz-Omeñaca & Canudo, 2010; Cruzado-Caballero, 2012). Recently, Cruzado-Caballero *et al*. (2013) and Prieto-Márquez *et al*. (2013) have raised the possibility of a North American influence on the European lambeosaurine fauna.

The main goals of the present paper are A) to describe the first 3D endocast of a European hadrosaurid, B) to compare the neuroanatomy of the European hadrosaurids with the other Laurasian ones, and C) to provide new insights into the paleobiology of the lambeosaurines, for which there has up to now been a scarcity of information in comparison with hadrosaurines (Evans, Ridgely & Witmer, 2009).

Material and methods

Studied material: MPZ2008/1 (Figure 1), skull remains of the holotype of the taxon *Arenysaurus* (Pereda-Suberbiola *et al.,* 2009b). The remains are from the Blasi 3 locality in the town of Arén (Huesca province, NE Spain). Postcranial remains of *Arenysaurus* have also been recovered (see Cruzado-Caballero *et al*., 2013).

Institutional abbreviation: AEHM, Amur Natural History Museum, of the Amur Complex Integrated Research Institute of the Far Eastern Branch of the Russian Academy of Sciences, Blagoveschensk, Russia (Amur KNII FEB RAS); CMN, Canadian Museum of Nature, Ottawa, Canada; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MPZ, Museo de Ciencias Naturales de la Universidad de Zaragoza, Zaragoza, Spain; RAM, Raymond M. Alf Museum of Paleontology, Claremont, California, USA; ROM, Royal Ontario Museum, Toronto, Canada.

Computed Tomography: The cranial material of *Arenysaurus* was CT-scanned at the "Laboratorio de Evolución Humana" (LEH) of the Universidad de Burgos (Spain) using an industrial Yxlon Compact. The braincase is broken into two pieces (one including the frontal, parietal, left postorbital and left squamosal while the other includes the right postorbital and right squamosal), and these were scanned separately. In both cases, the material was scanned at 200 kV and 2.8 mA and an output of 1024 x 1024 pixels per slice with an inter-slice space of 0.3 mm. In the part of the skull with the frontal, parietal, left postorbital and left squamosal there were 543 slices, providing a pixel size of 0.24 mm, while in the other part including the right postorbital and right squamosal there were 582 slices, providing a pixel size of 0.22 mm. Due to the hard properties of the bone elements, and especially of the internal matrix, the CT images present several artifacts such as beam hardening, cupping artifacts and ring artifacts that made the segmentation of the different elements of the skull difficult, but not impossible.

The segmentation was done in the 3D Virtual Lab of the Institut Català de Paleontologia using Avizo 7.1 (VSG, Germany), generating a 3D mesh of each CT scan. After the segmentation, the two 3D surfaces were united using the same software, and then digital measurements including the volume were obtained using Rhinoceros 4.0 and ImageJ.

Cranial endocast

The braincase of *Arenysaurus* is almost complete and fused (Figure 2). It presents a slight taphonomic lateral deformation that affects the inner structures of the three-dimensional endocast (see osteological description in Pereda-Suberbiola *et al.*, 2009b). By means of the CT scan, an almost complete three-dimensional endocast has been reconstructed. The structures on the left side of the endocast are well preserved and have been 3D digitally rendered, while those on the right side are poorly preserved and in some cases unable to be 3D reconstructed. As a whole, it is possible to observe the incomplete olfactory bulbs, the cerebral hemisphere, cerebellum, beginning of the medulla oblonga, pituitary (hypophyseal) fossa, inner ear and almost every nerve from II to XII (Figure 2).

The *Arenysaurus* endocast, as is typical in hadrosaurids, is elongate anteroposteriorly with an anteroposterior length of 116.48 mm from the base of the olfactory tract to the caudal branch of the hypoglossal nerve. The maximum width across the cerebral hemisphere is 48.38 mm, and the estimated volume of the endocast (including the olfactory bulbs) is 126.2 cm^3. The total volume of the cerebral hemisphere is 65.42 cm^3, comprising 53.3% of the total endocranial volume (excluding the olfactory bulbs). This volume value is close to the results obtained by Saveliev *et al*. (2012) for the adult specimen of the lambeosaurine *Amurosaurus* AENM1/123 (see Table 1). On the other hand, the *Arenysaurus* endocast is considerably constricted lateromedially at the cerebellum level with a maximum width of 31.32 mm in this region, and slightly constricted at the medulla oblonga (26.26 mm). Unfortunately, the vallecula system, described in the anterior part of the endocast of other hadrosaurids, cannot be observed in *Arenysaurus* due to the hard matrix that covers this area.

The angle of the major axis of the cerebral hemisphere to the horizontal is close to 45° in the endocast. According to Evans *et al.* (2009), this high angle corresponds to a lambeosaurine shape as opposed to that of hadrosaurines and other ornithopods, where the cerebral hemisphere is positioned more horizontally (Hopson, 1979).

The angle of flexure between the cerebellum and the cerebral hemispehere is very small, close to 10º, revealing that in this respect the endocast is similar to previously described adult Laurasian lambeosaurines (e.g. *Hypacrosaurus altispinus* ROM 702, *Amurosaurus riabinini* IRSNB R 279, AENM nos. 1/232 and 1/240; Evans *et al.*, 2009; Saveliev *et al.*, 2012; Lauters *et al.*, 2013).

According to Giffin (1989), pontine flexures are virtually absent and the possession of a nearly straight endocranial cavity is derived for “iguanodontids” and hadrosaurids. Further, in lateral view the cerebral hemisphere is not very strongly arched, as is the case in adult lambeosaurines and unlike young individuals (e.g. *Parasaurolophus* sp. RAM 14000). These different angles are possibly a consequence of more strongly arched frontals in young individuals (Farke *et al.*, 2013).

In *Arenysaurus* the angle of the dural peak is close to 114º (Lautenschlager & Hübner, 2013; Farke *et al.*, 2013).

The olfactory bulbs are located anteroventrally to the cerebral hemisphere and only preserve their base. It has not been possible to reconstruct them completely, because the skull is broken in the anterior part of the frontals. The left bulb is the more complete one, while the right bulb only preserves its ventral part. In anterior view, the left olfactory bulb has an inside-out L-shaped morphology. In this view, it is also possible to observe that the left olfactory bulb is almost half the height of the cerebral hemisphere, as also happens in the adult of *Amurosaurus* (IRSNB R 279, AENM nos. 1/232 and 1/240; Saveliev *et al.,* 2012; Lauters *et al.*, 2013) and the subadult of *Corythosaurus* sp. (CMN 34825; Evans *et al.*, 2009). The olfactory bulbs are turned downward with an angle on the dorsal side of 127.6º. The total volume of the partially preserved olfactory bulbs is 3.44 cm^3.

Several authors have commented on the presence of vascular elements in endocasts (Evans *et al.*, 2009 and references therein). In the case of *Arenysaurus,* the opening of the caudal middle cerebral vein can be seen on the dorsal side of the cerebellum, and on the lateral side the dorsal head vein can be recognized (Figure 2). On the ventral side of the cerebellum at the beginning of the medulla oblonga, vascular elements can be made out.

The *Arenysaurus* pituitary (or hypophyseal) fossa is located posteroventrally to the optic nerve. It is deformed on its left side. It has a length of 19.07 mm, a height of 32.84 mm, a width of 14.53 mm, and a volume of 3.64 cm^3. The original volume of the pituitary fossa was probably bigger, but taphonomical deformation caused a volume artifact. The size of the pituitary body appears relatively large, as in other hadrosaurids (Lauters *et al.*, 2013). Posteroventrally, it is possible to observe the joining of two big cerebral carotid arteries (Figure 2).

Cranial nerves

Almost all the cranial nerves, excluding nerve I and IV, can be seen to be preserved on the left side.

Nerve II, or the optic nerve (CN II), only preserves its base. This nerve is the most anterior nerve preserved. It is very small, tubular-like and runs parallel to the ventral side of the cerebral hemisphere (with a lateromedial width of 4.84 mm, and a dorsoventral height of 5.48 mm). It is located under the cerebral hemisphere and is joined to the pituitary anteriorly.

Nerve III, or the oculomotor nerve (CN III), is posterior to nerve II. It is located in the middle of the bonding area between the pituitary and the midbrain. It is small and has a button-like morphology (with a lateromedial width of 4.85 mm, a dorsoventral height of 6.5 mm and an anteroposterior length of 5.89 mm).

The next nerve preserved towards the posterior portion is nerve V, or the trigeminal nerve (CN V). From this nerve the ophthalmic branch (CN V_1) and the base of the trigeminal ganglion are preserved. However, the maxillary and mandibular branches (CN $V_{2\text{-}3}$) are not observed. The ophthalmic branch is 7 mm in height dorsoventrally and 2.36 mm in length anteroposteriorly.

The ventral side of the endocast preserves the nerves VI, or the abducens nerves (CN VI). This joins the pituitary, which their exits from the posterior to connect ventrally with the cerebellum. The nerves are flattened lateromedially and are wider than high.

Nerve VII, or the facial nerve (CN VII), is present and positioned anteriorly to the cochlea and near nerve VIII. This nerve is tube-like, very small and thin, with a slight widening dorsomedially on its distal side. This nerve is ventral to nerve VIII and runs lateroposteriorly.

Nerve VIII, or the vestibulocochlear nerve (CN VIII), is dorsal to nerve VII. This nerve is only partially preserved, showing a very small portion of the base dorsoventrally flattened.

Nerve IX, or the glossopharyngeal nerve (CN IX), is posterior to the cochlea and runs laterally, touching the cochlea in its anteriormost part. This nerve is very slight in its basal part and is tubular-like in shape. At its lateral extreme the nerve is extremely expanded dorsomedially (3.08 mm) and lateromedially (3.02 mm).

Nerves X and XI, the vagus and accessory nerves respectively (CN X and XI), are separated at their base, but then they join to form a single nerve. This joined nerve is very broad anteroposteriorly (6.8 mm) and is clearly lateroposteriorly directed.

Nerve XII, or the hypoglossal nerve (CN XII), is the most posterior one. It presents an anteroposteriorly narrow base (2.19 mm) and a dorsoventral height (3.94 mm) that is expanded distally (with an anteroposterior width of 4.69 mm and a dorsoventral height of 5.58 mm). Unlike the joint nerves X and XI, nerve XII is only laterally directed.

Inner ear

The digitally reconstructed vestibular apparatus is complete on the left side whereas the right side just conserves part of the cochlea and the anterior and posterior semicircular canals. The general form of the inner ear is similar to that described in other hadrosaurids (Brown, 1914; Langston, 1960; Ostrom, 1961; Evans *et al.*, 2009; Farke *et al.*, 2013), and, as discussed in Evans *et al.* (2009), it resembles the condition in extant crocodilians. The three semicircular canals are oriented in an approximately the three planes of space, where the anterior semicircular canal is slightly higher dorsoventrally and longer (Figure 3). This configuration is the most common one in vertebrates (Knoll *et al.*, 2013). The arch of the anterior and lateral semicircular canals is circular in shape while the posterior semicircular canal is ellipsoidal.

With regard to their ampullae, the lateral ampulla is larger than the posterior ampulla and the anterior ampulla, as in Farke *et al*. (2013) and unlike in Evans *et al*. (2009) (where the anterior ampulla is the largest, followed by the lateral ampulla). Moreover, in lateral view, the cochlea is boomerang-like, convex laterally and concave medially. In anterior view, it presents an S-shape with a sharp distal border and it has a length of 10.72 mm from the foramen vestibulea (Table 4).

Discussion

The endocranial morphology among hadrosaurid dinosaurs is similar and characteristic of the family (Hopson, 1979). At a subfamily level (hadrosaurine-lambeosaurine) there are characters that can help to distinguish between them, such as a brain cavity that is anteroposteriorly shorter or the angle of the major axis of the cerebral hemisphere to the horizontal in lambeosaurines (Evans *et al*., 2009). Both characters are present in the endocast of *Arenysaurus* and confirm the lambeosaurine affinity of this taxon.

A previous paper (Pereda-Suberbiola *et al*., 2009b) considered that this *Arenysaurus* specimen belongs to a presumably sole adult individual on the basis of several osteological characteristics. The paleoneuroanatomical evidence supports this ontogenetic assignation, with features referred to adult hadrosaurid animals that are present in this specimen: an angle of flexure between the cerebellum and cerebral hemisphere that is very small as in lambeosaurine adults, as described by Evans *et al*. (2009), and the cranial sutures that are difficult to discern in the CT scan as usual in adult specimens.

However, some paleoneuroanatomical features herein reported are indicative of a subadult ontogenetic stage for this specimen (see Table 1 and 3) and even a juvenile ontogenetic stage in the case of the total length of the endocast. According to Evans *et al*. (2009), however, this difference in the length of the endocast may be due to phylogenetic rather than ontogenetic considerations, as in the case of *Hypacrosaurus.* Moreover, when we compare the femur length of juvenile and adult lambeosaurines with the femur of *Arenysaurus*, the latter is nearer to the average for adult Asian than for adult North American lambeosaurines (see Table 3). This puzzling mixture characters from adult and subadult stages may reflect a possible first case of a certain degree of dwarfism evidenced by a hadrosaurid endocast*.* The hypothesis of a reduction in size due to insularism in European hadrosaurids has been proposed by several authors in the last decade and is supported by bone as well as track records (Vila *et al*., 2013 and references).

Moreover, Farke *et al*. (2013) have hypothesized that hadrosaurids such as the small ornithopod *Dysalotosaurus lettowvorbecki* present a dural peak (the angulation of the dorsal margin of the cerebellum, not its prominence) that is mostly unchanged through the ontogenetic stages. These authors suggest that the phylogenetic differences between the lambeosaurini and parasaurolophini tribes could be assessed in the light of the angle of the dural peak. In these terms, the lambeosaurins presented a wider angle (around 120º) while parasaurolophins presented a more acute angle (approximately 90º). We have observed that angles up to 100º are present for several hadrosaurins and lambeosaurins. In the case of *Arenysaurus*, this angle is approximately 114º (see Table 2). In sum, the angle of the dural peak may indeed be informative, suggesting that the condition with a greater angle could be a basal character and a lesser angle of 100º may be exclusive to the genus *Parasaurolophus*. Regarding the inner ear, although the general form is similar to the other hadrosaurids, it is possible to observe small differences in the semicircular canals with respect to the ornithopod clade (see Figure 4). The anterior semicircular canal is tallest at the base of the clade (*Dysalotosaurus* and *Iguanodon*), by contrast with some hadrosaurines, where the posterior semicircular canal is slightly taller than the others (*Edmontosaurus*). Later, in the Lambeosaurinae subfamily, *Parasaurolophus* and *Arenysaurus* present anterior semicircular canals that are slightly taller, while in the lambeosaurini tribe they are similar in size to *Dysalotosaurus* or *Iguanodon*. In addition, *Parasaurolophus* and *Arenysaurus* share a lateral ampulla that is larger than the posterior and the anterior ampullae.

The vestibular system is involved in the coordination of movement, gaze control and balance, detecting head movement (sensing angular acceleration) in space and maintaining visual and postural stability (Paulina Carabajal *et al*., 2013). The morphology and size of the semicircular canals are related to locomotor agility and neck mobility and a decrease in the compensatory movements of eyes and head (see references in Knoll *et al*., 2012 and Paulina Carabajal, Carballido & Curie, 2014). According to Witmer *et al*. (2008), the reduction in the difference between the length of the anterior and posterior semicircular canals, and perhaps also of the height of these canals, may reflect a decrease in the compensatory movements of eyes and head in *Edmontosaurus*, *Parasaurolophus* and *Arenysaurus*. If true, this could be related with behavioral patterns that require less agility in the head movements (Sereno *et al*., 2007).

Likewise, we hypothesize that these differences in the vestibular system, i.e. the different ratios between the height of the anterior and posterior semicircular canal and the size of the ampullae, could be used as a phylogenetic signal to differentiate *Edmontosaurus, Parasaurolophus* and *Arenysaurus* from the rest of the hadrosaurids. However, more data are necessary to know the possible influences that these differences could have on phylogenetic interpretations.

Conclusion

We provide the first complete 3D reconstruction of the brain cavity and inner ear of a European lambeosaurine, *Arenysaurus*. This cranial endocast presents the general pattern known for hadrosaurids and add to the record of hadrosaurid brain cavities from Laurasia. The osteological and paleoneuroanatomical data suggest that *Arenysaurus* was an adult individual that probably presented a certain degree of dwarfism due to insularity. Thus, *Arenysaurus* could be the first evidence of how dwarfism could affect hadrosaurid paleoneuroanatomy. Moreover, the paleoneuroanatomical data suggest that the presence of the low angle of the dural peak could be an autapomorphy of the *Parasaurolophus* genus. Furthermore, the structure of the inner ear shows differences from the ornithopod clade with respect to the height of the semicircular canals. These differences can be explained principally in terms of a probable decrease in the compensatory movements of eyes and head, which would affect the paleobiology and behavior of these animals. We hypothesize that these differences in the vestibular system could be used as are a phylogenetic signal.

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Figure 1. A 3D reconstruction of the braincase of *Arenysaurus ardevoli*. A) Braincase opaque, B) Semitransparent braincase with the brain cavity endocast opaque.

Figure 2. Cranial endocast in A) right lateral, B) left lateral, C) dorsal, D) ventral, and E) anterior views. Abbreviations: car, cerebral carotid artery canal; cer, cerebral hemisphere; cll, cerebellum; cmcv, caudal middle cerebral vein; ie, inner ear; mo, medulla oblongata; ob, olfactory bulbs; pit; pituitary fossa. II-XII, nerves: II, optic nerve; III, oculomotor nerve; V, trigeminal nerve; V_1, ophthalmic branch of nerve V; g V, trigeminal ganglion of nerve V; VI, abducens nerve; VII, facial nerve; VIII, vestibulocochlear nerve; IX, glossopharyngeal nerve; X, vagus nerve; XI, accessory nerve; XII, hypoglossal nerve.

Figure 3. Left inner ear in A) lateral, B) anterior, C) posterior, and D) dorsal views. Abbreviations: asc, anterior semicircular canal; asca, ampulla of anterior semicircular canal; c, cochlear duct (= lagena); crc, crus communis; fv, fenestra vestibuli (=oval window); lsc, lateral semicircular canal; lsca, ampulla of lateral semicircular canal; psc, posterior semicircular canal; psca, ampulla of posterior semicircular canal; ve, vestibule of inner ear.

Figure 4. Endosseous labyrinths of the inner ears redrawn for: *Dysalotosaurus,* Lautenschlager & Hubner (2013; fig. 2 h); *Iguanodon,* Norman, Witmer & Weishampel (2004; fig. 19.9); *Edmontosaurus*, Ostrom (1961; fig. 59 a); *Lophorhothon*, Langston (1960; fig. 163 a); *Parasaurolophus,* Farke *et al*. (2013; fig. 16 d); *Hypacrosaurus* and *Lambeosaurus,* Evans *et al*. (2009; fig. 8 a, e) and *Arenysaurus ardevoli*, displayed on a cladogram redrawn from Horner, Weishampel & Forster (2004), with additional data from McDonald (2012) and Cruzado-Caballero *et al*. (2013). Left inner ear: *Edmontosaurus, Arenysaurus, Hypacrosaurus* and *Lambeosaurus*; right inner ear: *Dysalotosaurus, Iguanodon, Lophorhothon* and *Parasaurolophus.*

Table 1. Measurements of length and volume for complete brain cavity and various brain regions, calculated from the digital endocasts using digital segmentation in the Avizo 7.1 program.

Table 2. Measurement of the angle of the dural peak for several hadrosaurines and lambeosaurines calculated from drawings and digital endocasts using ImageJ. Measurements were obtained from Lambe (1920), Ostrom (1961), Evans *et al*. (2009), Savaliev, Alifanov & Bolotsky (2012), Farke *et al*. (2013) and Lauters *et al*. (2013).

Table 3. Average measurements of the length and volume of the brain cavity with and without olfactory bulbs, the maximum width of the cerebral hemisphere and the length of the femur from lambeosaurines in relation to the ontogenetic stage. Average length, width and volume of the brain measurements were obtained from Evans *et al*. (2009), Savaliev, Alifanov & Bolotsky (2012), Farke *et al*. (2013) and Lauters *et al*. (2013). Average length from femur measures were obtained from Brett-Surman (1989), Godefroit *et al*. (2001, 2004, 2012), Mo *et al*. (2007) and Brinkman (2011).

Table 4. The maximum length of the digital cochlea of *Arenysaurus* casts determined using the Avizo 7.1 program, and of other lambeosaurines from Evans *et al*. (2009). *, not complete

Figure 1

A 3D reconstruction of the braincase of *Arenysaurus ardevoli*

A 3D reconstruction of the braincase of *Arenysaurus ardevoli*. A) Braincase opaque, B) Semitransparent braincase with the brain cavity endocast opaque.

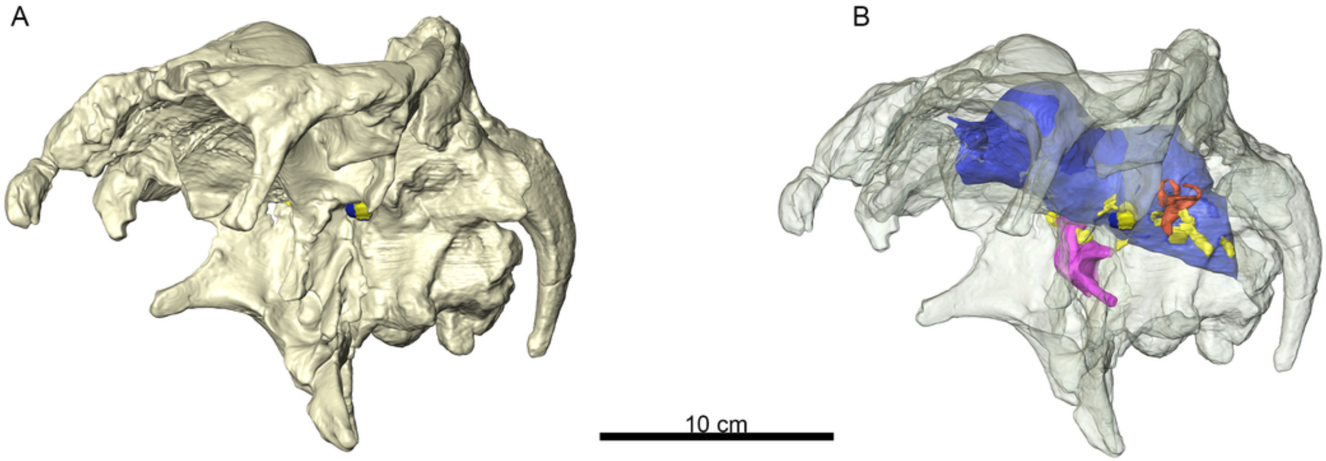

Figure 2

Cranial endocast

Cranial endocast in A) right lateral, B) left lateral, C) dorsal, D) ventral, and E) anterior views. Abbreviations: car, cerebral carotid artery canal; cer, cerebral hemisphere; cll, cerebellum; cmcv, caudal middle cerebral vein; ie, inner ear; mo, medulla oblongata; ob, olfactory bulbs; pit; pituitary fossa. II-XII, nerves: II, optic nerve; III, oculomotor nerve; V, trigeminal nerve; V1, ophthalmic branch of nerve V; g V, trigeminal ganglion of nerve V; VI, abducens nerve; VII, facial nerve; VIII, vestibulocochlear nerve; IX, glossopharyngeal nerve; X, vagus nerve; XI, accessory nerve; XII, hypoglossal nerve.

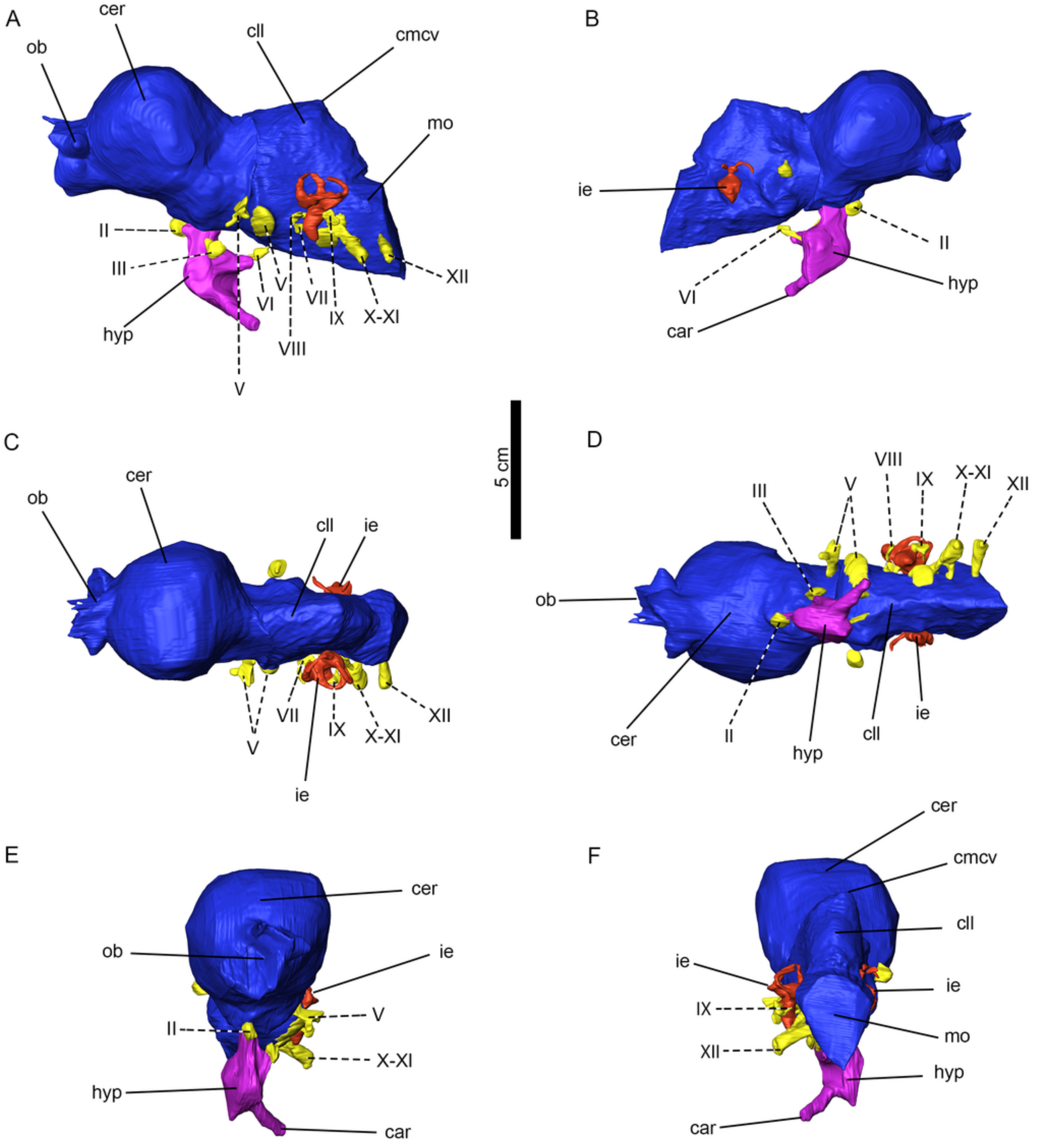
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Figure 3

Left inner ear

Left inner ear in A) lateral, B) anterior, C) posterior, and D) dorsal views. Abbreviations: asc, anterior semicircular canal; asca, ampulla of anterior semicircular canal; c, cochlear duct (= lagena); crc, crus communis; fv, fenestra vestibuli (=oval window); lsc, lateral semicircular canal; lsca, ampulla of lateral semicircular canal; psc, posterior semicircular canal; psca, ampulla of posterior semicircular canal; ve, vestibule of inner ear.

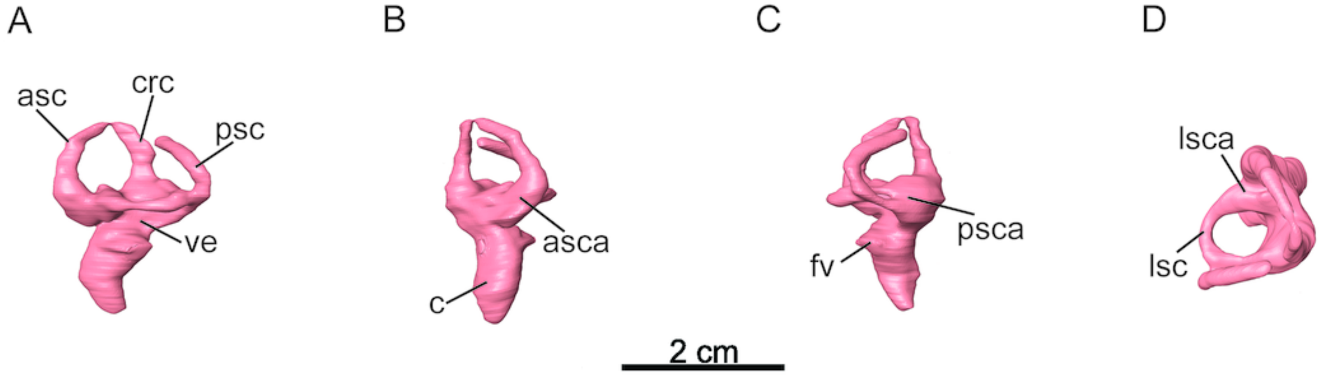

Figure 4

Endosseous labyrinths of the inner ears

Endosseous labyrinths of the inner ears redrawn for: Dysalotosaurus, Lautenschlager & Hubner (2013; fig. 2 h); Iguanodon, Norman, Witmer & Weishampel (2004; fig. 19.9); Edmontosaurus, Ostrom (1961; fig. 59 a); Lophorhothon, Langston (1960; fig. 163 a); Parasaurolophus, Farke et al. (2013; fig. 16 d); Hypacrosaurus and Lambeosaurus, Evans et al. (2009; fig. 8 a, e) and Arenysaurus ardevoli, displayed on a cladogram redrawn from Horner, Weishampel & Forster (2004), with additional data from McDonald (2012) and Cruzado-Caballero et al. (2013). Left inner ear: Edmontosaurus, Arenysaurus, Hypacrosaurus and Lambeosaurus; right inner ear: Dysalotosaurus, Iguanodon, Lophorhothon and Parasaurolophus.

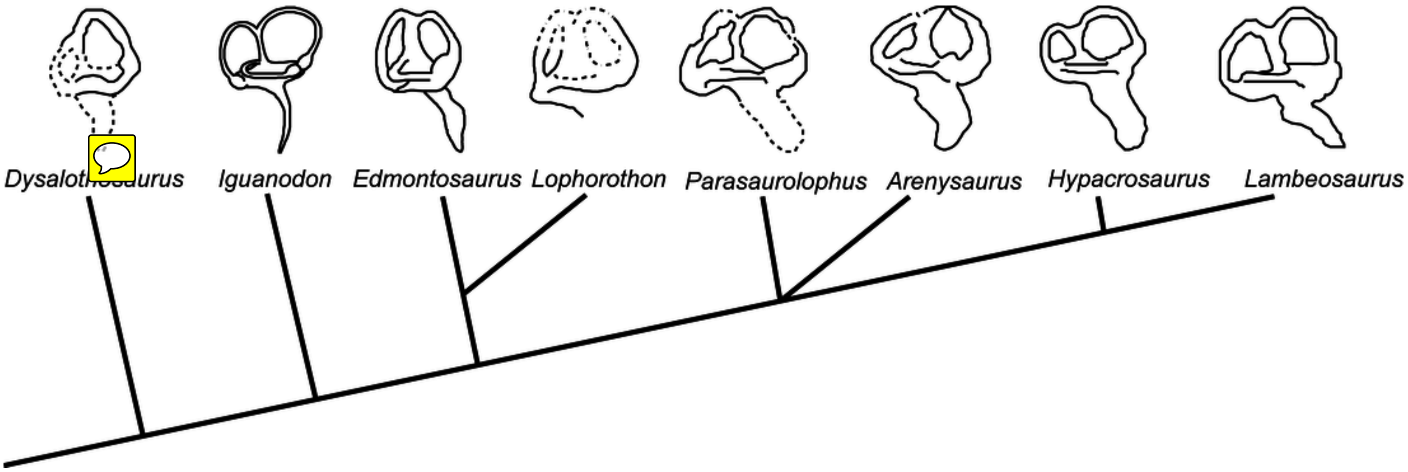

Table 1(on next page)

Measurements of length and volume for complete brain cavity and various brain regions

Measurements of length and volume for complete brain cavity and various brain regions, calculated from the digital endocasts using digital segmentation in the Avizo 7.1 program.

Taxa	Ontogenetic state	Specimen no.	Total length endocast without olfactory bulbs (mm)	Maximum width (mm)	Volume total without olfactory bulbs (cm^3)	Cerebrum volumen (cm^3)	% cerebrum volumen with respect total volume	Olfactory bulbs volumen (cm^3)
Lambeosaurus sp.	Juvenile	ROM 758	113.2	43	88.32	35.1	39.74	2.9
Corythosaurus sp.	Juvenile	ROM 759	110.1*	46.5	91.7	41.6	45.36	6.2*
Parasaurolophus sp.	Juvenile	RAM 1400	----------	36*	----------	----------	----------	----------
Corythosaurus sp.	Subadult	CMN 34825	142	44.7	134.2	51.1	38.08	11.2*
Hypacrosaurus altispinus	Adult	ROM 702	204	63.2	275.9	117.5	42.59	14*
Amurosaurus	Adult	AENM 1/123	230	72	370	210**	56.76**	----------
Amurosaurus	Adult	AENM	230	72	400	240**	60**	----------

		1/123						
Amurosaurus	Adult	IRSNB R 279	154	65	290	87	30	----------
Arenysaurus	Subadult-Adult	MPZ2008/1	116.48	48.38	122.8	65.42	53.27	3.44*

*, incomplete or stimate.

**, include the volume of the olfactory bubs.

---, no data.

Table 2(on next page)

Average measurements of the length and volume of the brain cavity with and without olfactory bulbs, the maximum width of the cerebral hemisphere and the length of the femur

Average measurements of the length and volume of the brain cavity with and without olfactory bulbs, the maximum width of the cerebral hemisphere and the length of the femur from lambeosaurines in relation to the ontogenetic stage. Average length, width and volume of the brain measurements were obtained from Evans et al. (2009), Savaliev, Alifanov & Bolotsky (2012), Farke et al. (2013) and Lauters et al. (2013). Average length from femur measures were obtained from Brett-Surman (1989), Godefroit et al. (2001, 2004, 2012), Mo et al. (2007) and Brinkman (2011).

Taxa	**Subfamily**	**Ontogenetic state**	**Specimen no.**	**Angle of dural peak**
Edmontosaurus regalis	Hadrosaurine	Adult	N.M.C. No. 2289	110.66
Edmontosaurus	Hadrosaurine	Adult	A.M.N.H. No. 5236	133.79
Kritosaurus notabilis	Hadrosaurine	Adult	A.M.N.H. No. 5350	132.28
Corythosaurus sp.	Lambeosaurini	Subadult	CMN 34825	130.4
Hypacrosaurus altispinus	Lambeosaurine	Adult	ROM 702	139.08
Lambeosaurus sp.	Lambeosaurine	Juvenile	ROM 758	106.71
Amurosaurus	Lambeosaurine	Adult	AENM 1/123	123.77
Amurosaurus	Lambeosaurine	Adult	IRSNB R 279	138.56
Arenysaurus	Lambeosaurine	Subadult-Adult?	MPZ2008/1	117.08
Parasaurolophus sp.	Lambeosaurine	Juvenile	RAM 1400	90

Table 3(on next page)

Average measurements of the length and volume of the brain cavity with and without olfactory bulbs, the maximum width of the cerebral hemisphere and the length of the femur

Average measurements of the length and volume of the brain cavity with and without olfactory bulbs, the maximum width of the cerebral hemisphere and the length of the femur from lambeosaurines in relation to the ontogenetic stage. Average length, width and volume of the brain measurements were obtained from Evans et al. (2009), Savaliev, Alifanov & Bolotsky (2012), Farke et al. (2013) and Lauters et al. (2013). Average length from femur measures were obtained from Brett-Surman (1989), Godefroit et al. (2001, 2004, 2012), Mo et al. (2007) and Brinkman (2011).

Ontogenetic state	**Total volumen without olfactory bulbs (cm^3)**	**Cerebrum volumen with out olfactory bulbs (cm^3)**	**Total length endocast (mm)**	**Maximum width of the cerebral hemisphere (mm)**	**Femur length (mm)**
Juvenile average	90.01	38.35	111.65	44.75	555
Subadult average	134.2	51.1	142	44.7	----------
Adult average	333.97	163.62	204.5	68.05	960
North American adult average	275.9	117.5	204	63.2	1074
Asian adult average	353.33	179	204.67	69.67	715
Arenysaurus	122.8	65.42	116.48	48.38	711

Table 4(on next page)

The maximum length of the digital cochlea of *Arenysaurus* casts

The maximum length of the digital cochlea of Arenysaurus casts determined using the Avizo 7.1 program, and of other lambeosaurines from Evans et al. (2009). *, not complete

Taxa	Ontogenetic state	Specimen no.	Cochlea length (mm)
Lambeosaurus sp.	Juvenile	ROM 758	9.2
Corythosaurus sp.	Juvenile	ROM 759	11.9
Parasaurolophus sp.	Juvenile	RAM 1400	7.6*
Corythosaurus sp.	Subadult	CMN 34825	12.3
Hypacrosaurus altispinus	Adult	ROM 702	16.7
Arenysaurus	Subadult-Adult?	MPZ2008/1	10.72