Paleoneuroanatomy of the European lambeosaurine dinosaur
* Arenysaurus ardevoli

Penélope Cruzado-Caballero, Josep Fortuny, Sergio Llacer, José Ignacio Canudo

The neuroanatomy of hadrosaurid dinosaurs is well known from North America and Asia. In Europe only a few cranial remains have been recovered that include 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 it to a subfamily level, 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. Both these characters are present in the endocast of *Arenysaurus*. Osteological features indicate an adult ontogenetic stage while some paleoneuroanatomical features are indicative of a subadult ontogenetic stage. It is hypothesized that the presence of puzzling mixture of 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*. 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.
Paleoneuroanatomy of the European lambeosaurine dinosaur *Arenysaurus ardevoli*

**Corresponding author and first author:**

P. Cruzado-Caballero

CONICET-Instituto de Investigación en Paleobiología y Geología, General Roca (Río Negro, Argentina)
Área de Paleontología, Facultad de Ciencias, Universidad de Zaragoza, Zaragoza (Spain).

**Authors:**

J. Fortuny ¹, ²

S. Llacer ¹

J. I. Canudo ³

¹ Institut Català de Paleontologia, C/ l'Escola Industrial, 23, 08201 Sabadell (Barcelona, Spain);
josep.fortuny@icp.cat; sergio.llacer@icp.cat

² Universitat Politècnica de Catalunya - BarcelonaTech, Terrassa, Spain;

³ Grupo Aragosaurus-IUCA. Área de Paleontología, Facultad de Ciencias, Universidad de Zaragoza.

Pedro Cerbuna 12, 50009 Zaragoza (Spain). http://www.aragosaurus.com, jicanudo@unizar.es
Keywords

Paleoneurology, European lambeosaurine, Hadrosaurid, Dinosauria, inner ear, paleobiology

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 & Hübner, 2013). CT scan techniques are currently common in biology and paleontology as a way of obtaining digital models of inner regions, as in the case of endocranial morphology, where these cavities may sometimes be filled by matrix. One of the great advantages of the CT-scan is also that it makes it possible to access features without destroying the specimen (by contrast with very old methods) with minimum manipulation of the specimen and to create 3D models allowing manipulation or measurement without damage to the specimen. 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 described historically (Nopcsa, 1900).

Arenysaurus forms part of the rich hadrosaurid fauna from the Iberian Peninsula, although 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 complete and uncrushed braincase (Figure 1). The Arenysaurus remains, together with other hadrosaurid and lambeosaurine material, helped to exchange 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 1) to describe the first 3D endocast of a European hadrosaurid, 2) compare the neuroanatomy of the European hadrosaurids with the other Laurasian ones, and 3)
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; Lauters et al., 2013).

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 CT-scan 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 an in-plane pixel
size of 0.24 mm, while in the other part including the right postorbital and right squamosal there were
582 slices, providing an in-plane pixel size of 0.2 mm. Due to the density of the bone and internal
matrix, the CT images present several artifacts such as beam hardening, cupping artifacts and ring
artifacts. These artifacts made automatic thresholding impossible, because the grey pixel value
changes. For example, the beam hardening artifact makes the edge of the object brighter than the
center, and ring artifacts produce bighting and dark concentric circles. Furthermore, the grey levels of
regions of interest are very similar to those of matrix regions. Therefore, the endocast segmentation
was done manually. 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 looking for contact points
in the 3D braincase surfaces. When these were perfectly fitted on the inside the 3D endocast fitted too.
Then digital measurements, including the volume, were obtained using Rhinoceros 4.0 and ImageJ.

Repository of the ct-data sets: Figshare http://dx.doi.org/10.6084/m9.figshare.1287781
http://dx.doi.org/10.6084/m9.figshare.1287779

Cranial endocast

The braincase of Arenysaurus is almost complete, and the individual bones are heavily co-ossified
(Figure 2, see video). It has a slight lateral taphonomic deformation that does not affect the validity of
the three-dimensional digital model (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 digitally rendered, while
those on the right side are poorly preserved and in some cases unable to be reconstructed. As a whole, it is possible to observe the incomplete olfactory bulbs, the cerebral hemisphere, cerebellum, beginning of the medulla oblongata, pituitary (hypophyseal) fossa, inner ear and the canal for 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 116.5 mm from the base of the olfactory tract to the caudal branch of the hypoglossal nerve. The maximum width across the cerebral hemisphere is 48.4 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 65.4 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 31.3 mm in this region, and slightly constricted at the medulla oblongata (26.3 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 hemisphere is very small, close to 10°, 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 anteroventral to the cerebral hemisphere; only the bases of the bulbs are preserved. 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 inverted 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 occurs 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 (measured between the anterodorsal surface of the cerebral hemisphere and the dorsal surface of the olfactory bulb). The total volume of the partially preserved olfactory bulbs is 3.4 cm³.

Several authors have commented on the presence of vascular elements in endocasts (Osmolska, 2004; Evans, 2005; Evans *et al*., 2009, Lauters *et al*., 2013). In the case of *Arenysaurus*, the transverse sinus can be seen on the lateral side of the cerebellum, and on the ventral side of the cerebellum and in part of the medulla oblongata the ventral longitudinal sinus can be discerned (Figure 2). The *Arenysaurus* pituitary (or hypophyseal) fossa is located posterovertrally to the optic nerve. It is deformed on its left side. It has a length of 19.1 mm, a height of 32.8 mm, a width of 14.5 mm, and a volume of 3.6 cm³. The original volume of the pituitary fossa was probably bigger, but taphonomical deformation has
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

The canals for almost all the cranial nerves, excluding nerve I and IV, can be seen to be preserved on
the left side. Through these canals other structures also accompanied the nerves (e.g. meninges, venous
structures, arteries, etc.). The cranial nerves present the same configuration as in other hadrosaurids
(see Hopson, 1979; Evans et al., 2009).

Nerve II, or the optic nerve (CN II), is the most anterior nerve preserved. It is very small, tubular, and
parallels the ventral side of the cerebral hemisphere (with a lateromedial width of 4.8 mm, and a
dorsoventral height of 5.5 mm). It is located under the cerebral hemisphere and is joined to the pituitary
anteriorly. This nerve is very small in comparison with hadrosaurids, for example Hypacrosaurus
(Evans et al., 2009) and Amurosaurus (Lauters et al., 2012; Saveliev et al., 2012). The optic chiasm
can only be seen in left view and is represented by a low, rounded protrusion dorsal to the pituitary
fossa.

Nerve III, or the oculomotor nerve (CN III), is posterior to nerve II. It is located in the middle of
the juncture between the pituitary and the midbrain. It is small and has a very short, tubular
morphology (with a lateromedial width of 4.8 mm, a dorsoventral height of 6.5 mm and an
anteroposterior length of 5.9 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 V₁) and the base of the trigeminal ganglion are preserved.
However, the maxillary and mandibular branches (CN V₂-₃) are not observed. The ophthalmic branch
is 7 mm in height dorsoventrally and 2.4 mm in length anteroposteriorly.
The ventral side of the endocast preserves nerve VI, or the abducens nerves (CN VI). These are joined to the pituitary, and exits from it posteriorly 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 positioned anterior 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. It is ventral to nerve VIII and runs lateroposteriorly with respect to the anteroposterior axis of the endocast.

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 slim in its basal part and is tubular in shape. At its lateral extreme the nerve is extremely expanded dorsomedially (3.1 mm) and lateromedially (3 mm).

Nerves X and XI, the vagus and accessory nerves respectively (CN X and XI), are joined and these possibly also join with a branch of nerve XII to form a single nerve. These joined nerves are very broad anteroposteriorly (6.8 mm) and are clearly lateroposteriorly directed.

Nerve XII, or the hypoglossal nerve (CN XII), is possibly formed by two branches. The more anterior branch could be joined with nerves X and XI. The second branch, which is more posterior presents an anteroposteriorly narrow base (2.2 mm) and a dorsoventral height (3.9 mm) that is expanded distally (with an anteroposterior width of 4.7 mm and a dorsoventral height of 5.58 mm). This nerve is only laterally directed.

**Inner ear**

The digital reconstruction of the inner ear 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 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. The anterior semicircular canal is slightly taller than the posterior semicircular canal (when the lateral canal is oriented horizontally). This difference between the dorsoventral heights of the canals is reflected in the ratio between them, which is 0.98 in Arenysaurus. With regard to their ampullae, the lateral ampulla is larger than the posterior ampulla and the anterior ampulla, as in Parasaurolophus sp. RAM 14000 (Farke et al., 2013) and unlike in Hypacrosaurus altispinus ROM 702 and Lambeosaurus sp. ROM 758 (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 10.7 mm from the foramen vestibulea (Table 3).

Discussion

The endocranial morphology among hadrosaurid dinosaurs is similar and characteristic of the family. Hadrosaurid endocranial possess a greatly inflated, smoothly rounded cerebrum, do not have a pontine flexure and the orientation of the cranial cavity within the skull is obliquely anterodorsal (Hopson, 1979). At a subfamily level (hadrosaurine-lambeosaurine) there are characters that can help to distinguish 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 are consistent with the lambeosaurine affinity of this taxon.
A previous paper (Pereda-Suberbiola et al., 2009b) considered that this *Arenysaurus* specimen belongs to a presumably adult individual on the basis of several osteological characteristics. The paleoneuroanatomical evidence supports this ontogenetic assignment, with the following features referred to adult hadrosaurid animals 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 is usual in adult specimens.

However, some paleoneuroanatomical features herein reported are indicative of a subadult ontogenetic stage for this specimen: the total volume of the endocast without olfactory bulbs; the volume of the cerebral hemispheres without olfactory bulbs; the maximum width of the cerebral hemisphere (see Table 1). This puzzling mixture of 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 120°) while parasaurolophins presented a more acute angle (approximately 90°).

We have observed hadrosaurins and lambeosaurins to display an angle of no less than 100°. In the case of *Arenysaurus*, this angle is approximately 114° (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
an angle less than 100° 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*; the ratio of anterior/posterior semicircular canal height is 1.11 in *Iguanodon*), by contrast with some hadrosaurines, where the posterior semicircular canal is slightly taller than the others (*Edmontosaurus*; the ratio of anterior/posterior semicircular canal height is 0.92). Later, in the Lambeosaurinae subfamily, *Parasaurolophus* and *Arenysaurus* present anterior semicircular canals that are slightly taller (the ratio of anterior/posterior semicircular canal height is 0.97 in *Parasaurolophus* and 0.98 in *Arenysaurus*), while in the lambeosaurini tribe they are similar in proportions to those seen in *Dysalotosaurus* or *Iguanodon* (the ratio of anterior/posterior semicircular canal height is 1.58 in *Hypacrosaurus* and 1.16 in *Lambeosaurus*). 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 in 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 or on behavior.

**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, it presents an optic nerve that is unusually small, indeed very much smaller than that of other known hadrosaurid. 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 a phylogenetic signal.

**Acknowledgements**
We acknowledge the academic editor Dr. Andrew A. Farke (Raymond M. Alf Museum of Paleontology, Claremon, United States of America), Dra. Pascaline Lauters (Department of Palaeontology, Royal Belgian Institute of Natural Sciences, Bruxelles, Belgium and Service d’Anthropologie et Génétique Humaine, Université Libre de Bruxelles, Bruxelles, Belgium) and an anonymous reviewer for their comments on the manuscript. The authors sincerely thank Dr. Andrew A. Farke and Dra. Ariana Paulina Carabajal for valuable discussions, Dra. Elena Santos for the CT-scanning, as well as Rupert Glasgow, who revised the translation of the text into English.

References

Brown, B (1914). Corythosaurus casuarius, a new crested dinosaur from the Belly River Cretaceous, with provisional classification of the family Trachodontidae. Bulletin of the American Museum of Natural History 33:559–565.

Casanovas, ML, Pereda-Suberbiola, X, Santafé, JV, Weishampel, DB (1999). First lambeosaurine hadrosaurid from Europe: palaeobiogeographical implications, Geological Magazine 136:205–211.

Company J, Galobart À, Gaete R (1998). First data on the hadrosaurid dinosaurs (Ornithischia, Dinosauria) from the Upper Cretaceous of Valencia, Spain. Oryctos 1:121–126.

Cruzado-Caballero, P (2012). Restos directos de dinosaurios hadrosáuridos (Ornithopoda, Hadrosauridae) del Maastrichtiense superior (Cretacico Superior) de Aren (Huesca). D. Phil. Thesis, University of Zaragoza.

Cruzado-Caballero, P, Pereda Suberbiola, X, Ruiz-Omeñaca, JI (2010). Blasisaurus canudoi gen. et sp. nov., a new lambeosaurine dinosaur (Hadrosauridae) from the latest Cretaceous of Arén (Huesca, Spain). Canadian Journal of Earth Sciences 47(12):1507–1517.
Cruzado-Caballero, P, Ruiz-Omeñaca, JI, Canudo, JI (2010). Evidencias de la coexistencia de hadrosaurinos y lambeosaurinos en el Maastrichtiano superior de la Península Ibérica (Arén, Huesca, España). *Ameghiniana* 47(2):153–164.

Cruzado-Caballero, P, Canudo, JI, Moreno-Azanza, M, Ruiz-Omeñaca, JI (2013). New material and phylogenetical position of *Arenysaurus ardevoli*, a lambeosaurine dinosaur from the Late Maastrichtian of Arén (Northern Spain). *Journal of Vertebrate Paleontology* 33(6):1376–1384.

Dalla Vecchia, FM (2009). *Tethyshadros insularis*, a new hadrosauroid dinosaur (Ornithischa) from the Upper Cretaceous of Italy. *Journal of Vertebrate Paleontology* 29(4):1100–1116.

Evans, D.C. (2005). New evidence on brain-endocranial cavity relationships in ornithischian dinosaurs. *Acta Palaeontologica Polonica*, 50(3): 617-622.

Evans, DC, Ridgely, R, Witmer, LM (2009). Endocranial anatomy of lambeosaurine hadrosaurids (Dinosauria: Ornithischia): a sensorineural perspective on cranial crest function. *The Anatomical Record* 292:1315–1337.

Farke, AA, Chok, DJ, Herrero, A, Scolieri, B, Werning, S (2013). Ontogeny in the tube-crested dinosaur *Parasaurolophus* (Hadrosauridae) and heterochrony in hadrosaurids. *PeerJ* 1:e182.

Giffin, EB (1989). Pachycephalosaur paleoneurology (Archosauria: Ornithischia). *Journal of Vertebrate Paleontology* 9(1):67–77.

Gilmore CW (1924). On the genus *Stephanosaurus*, with a description of the type specimen of *Lambeosaurus lambei*, parks. *Canada Department of Mines (Geological Survey of Canada) Bulletin* 38:29–48.

Godefroit, P, Bolotisky, YL, Lauters, P (2012). A new saurolophine dinosaur from the latest Cretaceous of far Eastern Russia. *Plos One* 7(5):e36849.

Horner, JR, Weishampel, DB, Forster, CA (2004). *Hadrosauridae*. In: Weishampel, DB, Dodson, P. and Osmólska, H. University of California Press (eds). *The Dinosauria*, 438-463.
Hopson JA (1979). Paleoneurology. In: Gans C, (ed). Biology of the reptilian. New York: Academic Press, vol IX, 39–146.

Knoll, F, Ridgely, RC, Ortega, F, Sanz, JL, Witmer, LM (2013). Neurocranial osteology and neuroanatomy of a Late Cretaceous titanosaurian sauropod from Spain (Ampelosaurus sp.). Plos One 8(1):e54991.

Lambe LM (1920). The hadrosaur Edmontosaurus from the Upper Cretaceous of Alberta. Canada Department of Mines (Geological Survey of Canada) Memoir 120:1–79.

Langston, WJr (1960). The vertebrate fauna of the Selma Formation of Alabama. Pt. VI. The Dinosaurs. Fieldiana Geology Memoirs 3:313–361.

Lautenschlager, S and Hübner, TH (2013). Ontogenetic trajectories in the ornithischian endocranium. Journal of Evolutionary Biology 26(9):2044–2050.

Lauters, P, Vercauteren, M, Bolotsky, YL, Godefroit, P (2013). Cranial endocast of the lambeosaurine hadrosaurid Amurosaurus riabinini from the Amur Region, Russia. Plos One 8(11):e78899.

Lull RS and Wright NE (1942). Hadrosaurian dinosaurs of North America. Especial Paper - Geological Society of America 40:1–242.

McDonald AT (2012). Phylogeny of Basal Iguanodonts (Dinosauria: Ornithischia): An Update. Plos One 7(5):e36745. doi:10.1371/journal.pone.0036745

Nopcsa, F (1900). Dinosaurierreste aus Siebenbergen: Schadel von Limnosaurus transsylvanicus nov. gen. et specie. Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse 65:555–591.

Norman, DB, Witmer, LM, Weishampel, DB (2004). Basal Ornithischia In: Weishampel, DB, Dodson, P. and Osmólska, H. University of California Press (eds). The Dinosauria, 325–334.
Paulina Carabajal A, Sterli J, Müller J, Hilger A (2013). Neuroanatomy of the Marine Jurassic Turtle Plesiochelys etalloni (Testudinata, Plesiochelyidae). Plos One 8(7):e69264. doi:10.1371/journal.pone.0069264

Paulina Carabajal A, Carballido, JL, Currie, P (2014). Braincase, neuroanatomy, and neck posture of Amargasaurus cazauí (Sauropoda, Dicraeosauridae) and its implications for understanding head posture in sauropods. Journal of Vertebrate Paleontology 34(4):870–882

Pereda-Suberbiola, X, Canudo, JI, Company, J, Cruzado-Caballero, P, Ruiz-Omeñaca, JI (2009a). Hadrosaurids from the latest Cretaceous of the Iberian Peninsula: new interpretations. Journal of Vertebrate Paleontology 29(3):946–951.

Pereda-Suberbiola, X, Canudo, JI, Cruzado-Caballero, P, Barco, JL, López-Martínez, N, Oms, O, Ruiz-Omeñaca, JI (2009b). The last hadrosaurid dinosaurs of Europe: A new lambeosaurine from the Uppermost Cretaceous of Aren (Huesca, Spain). Comptes Rendus Palevol 8:559–572.

Prieto-Márquez, A, Dalla Vecchia, FM, Gaete, R, Galobart, À (2013). Diversity, relationships, and biogeography of the lambeosaurine dinosaurs from the European Archipelago, with description of the new aralosurin Canardia garonnensis. Plos One 8(7):e69835.

Osmólska, H. (2004). Evidence on relation of brain to endocranial cavity in oviraptorid dinosaurs. Acta Palaeontologica Polonica, 49(2): 321-324.

Ostrom, JH (1961). Cranial morphology of the hadrosaurian dinosaurs of North America. Bulletin of the American Museum of Natural History 122(2): 186 p.

Saveliev, SV, Alifanov, VR, Bolotsky, YL (2012). Brain anatomy of Amurosaurus riabinini and some neurobiological peculiarities of duck-billed dinosaurs. Paleontological Journal 46(1):79–91.

Serrano-Brañas, CI, Hernández-Rivera, R, Torres-Rodríguez, E, Espinosa Chávez, B (2006). A natural hadrosaurid endocast from the Cerro del Pueblo Formation (Upper Cretaceous) of Coahuila,
Mexico, in Lucas, S G and Sullivan, RM (eds): Late Cretaceous Vertebrates from the Western Interior. *New Mexico Museum of Natural History and Science Bulletin*, vol 35, pp 317–321.

Vila B, Oms O, Fondevilla V, Gaete R, Galobart À, Riera, V, Canudo, JI (2013). The Latest Succession of Dinosaur Tracksites in Europe: Hadrosaur Ichnology, Track Production and Palaeoenvironments. *Plos One* 8(9):e72579. doi:10.1371/journal.pone.0072579

Witmer LM, Ridgely R, Dufeau DL, Semones MC (2008). *Using CT to peer into the past: 3D visualization of the brain and inner ear regions of birds, crocodiles, and nonavain dinosaurs.* In: Endo H and Frey R (eds). *Anatomical imaging: towards a new morphology.* Tokyo: Springer-Verlag, 67–87.

Young CC (1958). The dinosaurian remains of Liayang, Shantung. *Palaeontol Sinica* 142:1–139.

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; dp, dural peak; ie, inner ear; mo, medulla oblongata; ob, olfactory bulbs; pit, pituitary fossa; ts, transverse sinus; vls, ventral longitudinal sinus. 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.
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 & Hübner (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. Measurements were obtained from Lambe (1920), Ostrom (1961), Evans *et al.* (2009), Savaliev, Alifanov & Bolotsky (2012), Farke *et al.* (2013), Lauters *et al.* (2013), and for *Arenysaurus* they were 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 the *Arenysaurus* endocast, Lambe (1920), Ostrom (1961), Evans *et al.* (2009), Savaliev, Alifanov & Bolotsky (2012), Farke *et al.* (2013) and Lauters *et al.* (2013).
Table 3. 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.
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.
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; dp, dural peak; ie, inner ear; mo, medulla oblongata; ob, olfactory bulbs; pit, pituitary fossa; ts, transverse sinus; vls, ventral longitudinal sinus. 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.
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.
Endosseous labyrinths of the inner ears

Endosseous labyrinths of the inner ears redrawn for: *Dysalotosaurus*, Lautenschlager & Hübner (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. Measurements were obtained from Lambe (1920), Ostrom (1961), Evans et al. (2009), Savaliev, Alifanov & Bolotsky (2012), Farke et al. (2013), Lauters et al. (2013), and for *Arenysaurus* they were 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 of the cerebral hemispheres (mm) | Volume total of endocast without olfactory bulbs (cm³) | Cerebral hemispheres without olfactory bulbs (cm³) | % cerebral hemispheres volume with respect total volume | Olfactory bulbs volume (cm³) |
|---------------------|------------------|--------------|----------------------------------------------------|-----------------------------------------------|--------------------------------------------------------|--------------------------------------------------|-------------------------------------------------|-----------------------------|
| 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 14000    | --------                                           | 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 1/123 | 230 | 72 | 400 | 240** | 60**    | --------- |
| 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* |

2 *, incomplete or stimate.
3 **, include the volume of the olfactory bubs.
4 ---, no data.
Table 2 (on next page)

Measurement of the angle of the dural peak for several hadrosaurines and lambeosaurines

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 the *Arenysaurus* endocast, Lambe (1920), Ostrom (1961), Evans *et al.* (2009), Savaliev, Alifanov & Bolotsky (2012), Farke *et al.* (2013) and Lauters *et al.* (2013).
| Taxa                        | Angle of dural peak |
|-----------------------------|---------------------|
| Edmontosaurus regalis       | 110.66              |
| (N.M.C. No. 2289)           |                     |
| Edmontosaurus               | 133.79              |
| (A.M.N.H. No. 5236)         |                     |
| Kritosaurus notabilis       | 132.28              |
| (A.M.N.H. No. 5350)         |                     |
| Corythosaurus sp.           | 130.4               |
| (CMN 34825)                 |                     |
| Hypacrosaurus altispinus    | 139.08              |
| (ROM 702)                   |                     |
| Lambeosaurus sp.            | 106.71              |
| (ROM 758)                   |                     |
| Amurosaurus                 | 123.77              |
| (AENM 1/123)                |                     |
| Amurosaurus                 | 138.56              |
| (IRSNB R 279) |       |
|--------------|-------|
| Arenysaurus  | 117.08|
| (MPZ2008/1)  |       |
| Parasaurolophus sp. | 90 |
| (RAM 14000)  |       |
**Table 3** (on next page)

The maximum length of the digital cochlea of *Arenysaurus* casts and of other lambeosaurines

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               |