The Brain of *Iguanodon* and *Mantellisaurus:* Perspectives on Ornithopod Evolution

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Information on the structure of the brain of the basal iguanodontian dinosaurs *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis,* from the Early Cretaceous of Bernissart, is presented on the basis of computed tomographic scanning and 3D reconstruction of three braincases. The resulting digital cranial endocasts are compared with physical and digital endocasts of other dinosaurs. The orientation of the brain is more horizontal than in lambeosaurine hadrosaurids. The large olfactory tracts indicate that the sense of smell was better developed than in hadrosaurids. The primitive flexures of the midbrain are virtually absent in *I. bernissartensis* but appear to be better developed in *M. atherfieldensis,* which might be explained by the smaller body size of the latter. The brain of *Iguanodon* was relatively larger than in most extant nonavian reptiles, sauropods, and ceratopsians. However, it was apparently smaller than in lambeosaurines and most theropods. The relative size of the cerebrum was low in *Iguanodon.* In *Mantellisaurus,* the cerebrum was proportionally larger than in *Iguanodon* and compares favorably with lambeosaurines. The behavioral repertoire and/or complexity were therefore probably different in the two iguanodontoids from Bernissart, *Iguanodon* and *Mantellisaurus.* The enlargement of the cerebrum appeared independently, together with possible capabilities for more complex behaviors, at least two times during the evolution of Iguanodontoidea.

Introduction

Two natural endocasts of basal Iguanodontia were discovered in England during the eighteenth century. The first one, from the Wealden of Brooke (Isle of Wright), was described by Hulke (1871) and Andrews (1897). In his Ph.D. thesis, Norman (1977) studied a second nicely preserved endocast from the Wealden of Sussex, England. This specimen was subsequently illustrated and briefly discussed in both editions of *The Dinosauria* (Norman and Weishampel, 1990; Norman, 2004) and in the book *Dinosaurs: A Very Short Introduction* (Norman, 2005). As noted by Norman (1980), the skulls of the Bernissart iguanodons are damaged because of oxidation of pyrite, and the matrix inside the endocranial cavities has never been completely removed. Consequently, the skulls of the Bernissart iguanodons are particularly fragile, and for that reason, to date, nobody has tried to study their neurocranial anatomy and reconstruct their endocranial space. However, new medical imaging technologies now allow studying inaccessible areas inside the skull without damaging these fragile fossils.

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During the renovation of the Janlet Wing of the Royal Belgian Institute of Natural Sciences, from 2003 to 2007, all the skeletons of the Bernissart iguanodons were completely dismantled and treated against pyrite deterioration. On this occasion, the best-preserved skulls were scanned by computed tomography (CT) at Gasthuisberg Hospital in Leuven (Belgium). CT scanning generates a three-dimensional image of an object from a large series of x-ray images taken around a single axis of rotation. CT scanning was recently used to reconstruct the endocranial space and inner ear of pterosaurs (Witmer et al., 2003), ankylosaurians (Witmer and Ridgely, 2008a), sauropods (Sereno et al., 2007; Witmer et al., 2008), theropods (Rogers, 1998, 1999, 2005; Brochu, 2000, 2003; Larsson, 2001; Franzosa, 2004; Franzosa and Rowe, 2005; Sanders and Smith, 2005; Norell et al., 2009; Sampson and Witmer, 2007; Witmer and Ridgely, 2009), ceratopsians (Zhou et al., 2007; Witmer and Ridgely, 2008a), and hadrosaurids (Evans et al., 2009).

Here we present the first reconstructions of the endocranial space of *Iguanodon bernissartensis* Boulenger *in* Van Beneden, 1881, and *Mantellisaurus atherfieldensis* (Hooley, 1925) from the Early Cretaceous of Bernissart, based on CT scanning of skulls from the RBINS collection.

Institutional abbreviations. AEHM, Palaeontological Museum of the Institute of Geology and Nature Management, Far East Branch, Russian Academy of Sciences, Blagoveschensk, Russia; CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; MNHN, Muséum national d'Histoire naturelle, Paris, France; RBINS, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; ROM, Royal Ontario Museum, Toronto, Ontario, Canada.

Materials and Methods

Ten skulls were regarded as sufficiently well preserved to be CT scanned:

- RBINS R51 (="IRSNB 1534[Q]" in Norman (1986, appendix 1). Holotype of *Iguanodon bernissartensis* Boulenger *in* Van Beneden, 1881.
- RBINS R52 (="IRSNB 1536[A3]"). Paratype of *I. bernissartensis.*
- RBINS R54 (="IRSNB 1731[F]"). Paratype of *I. bernissartensis.*
- RBINS R55 (="IRSNB 1535[N]"). Paratype of *I. bernissartensis.*
- RBINS R56 (="IRSNB 1561[L]"). Paratype of *I. bernissartensis.*
- RBINS R57 (="IRSNB 1551[T]"). *Mantellisaurus atherfieldensis* (Hooley, 1925).
- RBINS VERT-5144-1562 (="IRSNB 1562[E2]"). *I. bernissartensis.*
- RBINS VERT-5144-1657 (="IRSNB 1657[D2]"). *I. bernissartensis.*
- RBINS VERT-5144-1680 (= »IRSNB 1680[J] »). *I. bernissartensis.*
- RBINS VERT-5144-1715 (= »IRSNB 1715[C2] »). *I. bernissartensis.*

These specimens were CT scanned at the Gasthuisberg Hospital, Leuven, Belgium, with a Siemens Sensation 64 device. All specimens were scanned helically in the coronal plane with a slice thickness of 1 mm and a 0.5-mm overlap. Data were output in DICOM format and imported into Amira 5.1 or Artecore 1.0-rc3 (Nespos, VisiCore Suite) for viewing, reconstruction/analysis, visualization, and measurement. Anatomical features of
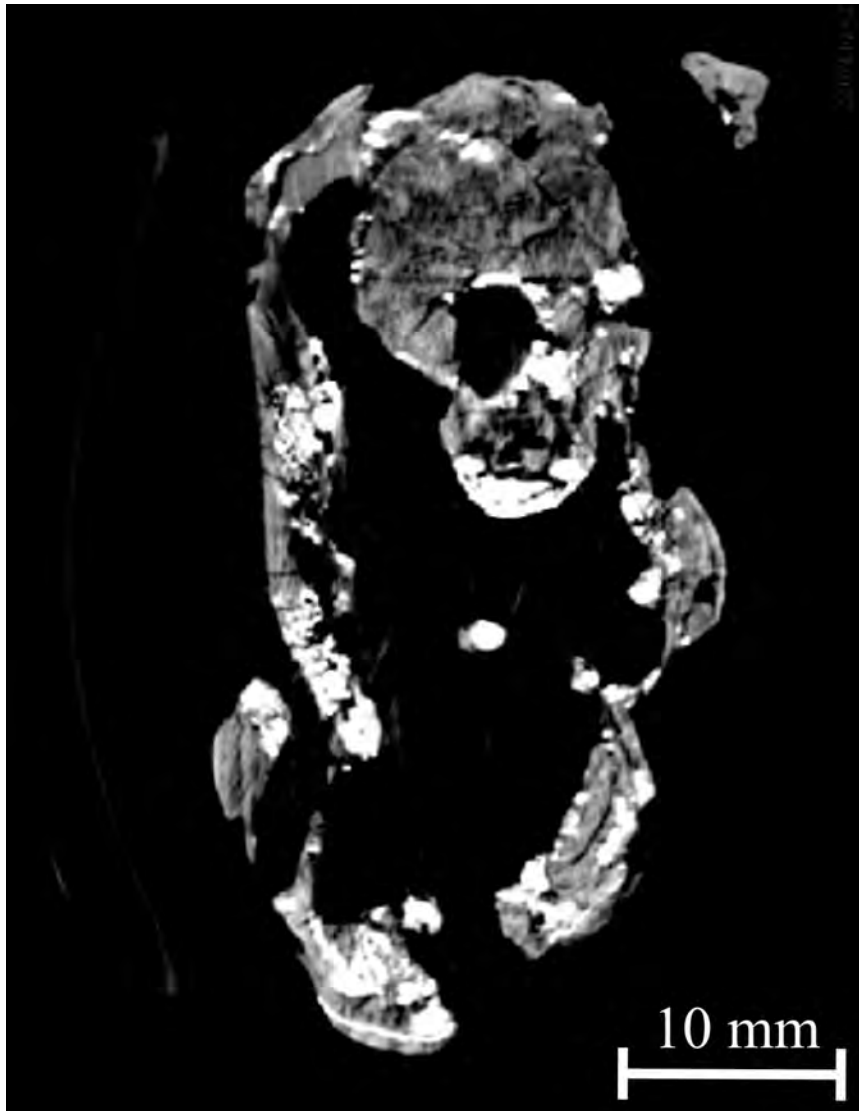
16.1. Coronal CT slice through the skull of *Iguanodon bernissartensis* (RBINS R51, holotype). The white spots are caused by pyrite, which extensively reflects x-rays.

interest (endocranial space) were highlighted and digitally extracted with Artecore's segmentation tools.

Several specimens were highly pyritized (Fig. 16.1) and/or squashed after taphonomic processes. High levels of pyritization cause artifacts, typically long-axis lines that blurred the pictures and prevented the reconstruction of the endocranial space. After close examination, only three data sets were suitable for study: RBINS R51 and RBINS R54 (*Iguanodon bernissartensis*), and RBINS R57 (*Mantellisaurus atherfieldensis*).

The measurements taken on the endocranial endocasts are illustrated in Figure 16.2.

It has often been hypothesized that the brain of sauropsids does not fill the endocranial cavity, and the reasonable assumption has been that the endocast is essentially a cast of the dura mater (Osborn, 1912; Jerison, 1973; Hopson, 1979). In extant reptiles, the endocranium reflects forebrain surface morphology, and thus the endocast is likely a relatively accurate representation of the shape of the telencephalon (Hopson, 1979). In crocodilians,

Brain Cavity Endocasts of *Iguanodon* and *Mantellisaurus*
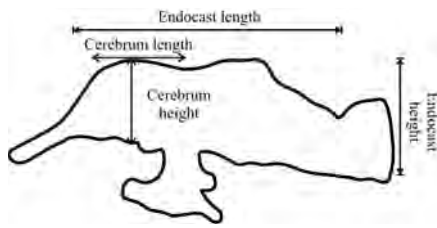
16.2. Explanation of the measurements taken on the cranial endocasts.

the proportion of the endocranial cavity occupied by the brain varies with body size (Hopson, 1979; Rogers, 1999). Traditionally nonavian dinosaurs have been regarded as reptilian in that their brains were thought to have filled a relatively small portion of the endocranial cavity, in contrast to the condition in mammals and birds (Jerison, 1969; Hopson, 1979; Rogers, 1999; Larsson, 2001).
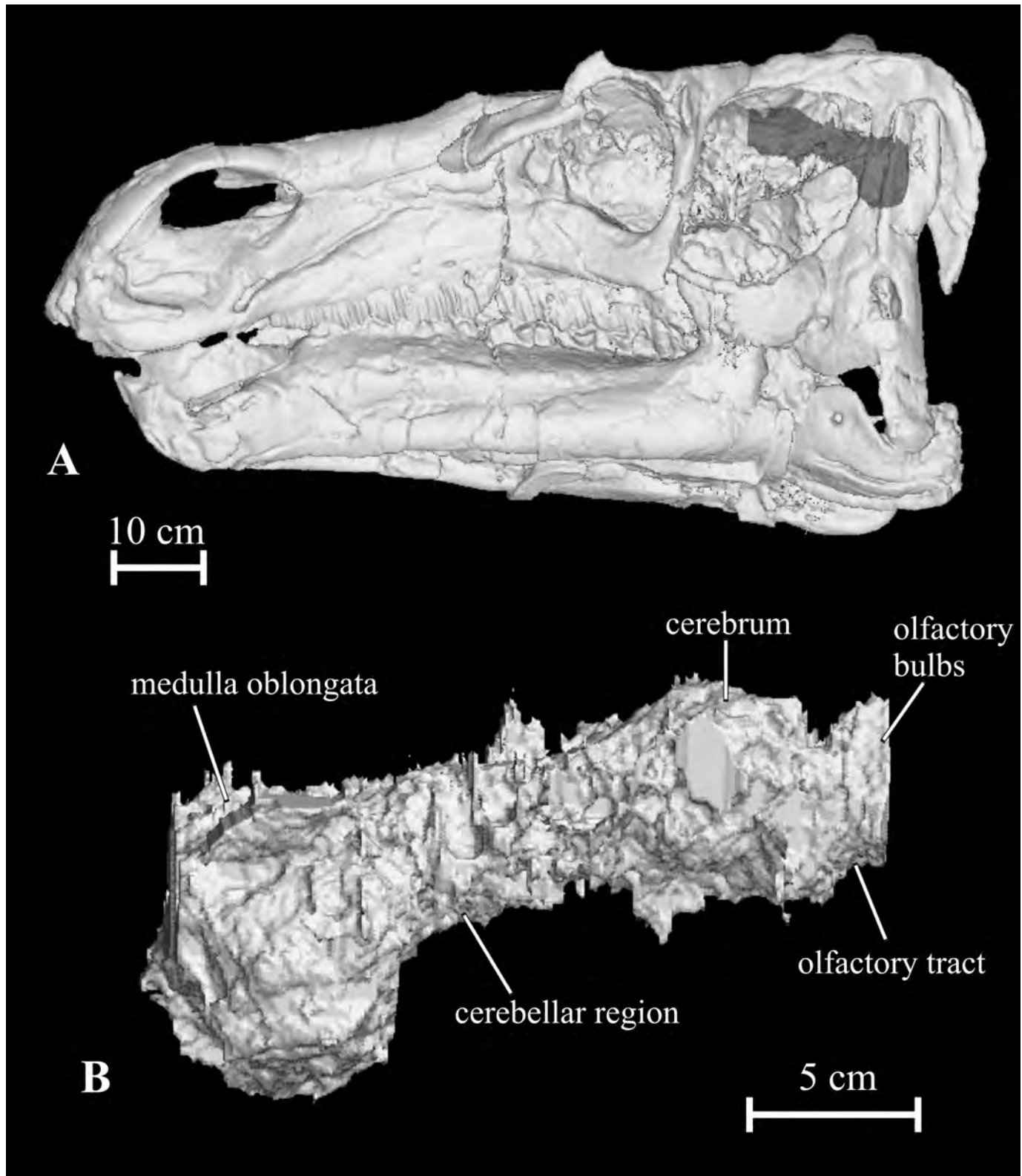
However, previous observations led to the discovery of vascular impressions on the internal surfaces of the braincase of dinosaurs (Hopson, 1979; Osmólska, 2004). These vascular imprints (valleculae) show that the brain was closely appressed to the wall of the braincase. Evans (2005) and Evans et al. (2009) demonstrated for hadrosaurids and pachycephalosaurs that the portion of the endocast corresponding to the telencephalon faithfully represents the contours of the underlying brain. Moreover, valleculae were also observed on endocasts of Russian hadrosaurids (Lauters et al., in prep.) and on the cast of the basal hadrosauroid *Batyrosaurus rozhdestvenskyi* from Kazakhstan (see Chapter 20 in this book). Therefore, we assume that the endocast generally reflects the shape of the rostral and ventral regions of the brain. Evans (2005) and Evans et al. (2009) showed that much of the hindbrain of hadrosaurids was not in close relationship to the endocranial wall. It is also probably the case in *Iguanodon* and *Mantellisaurus* because the dorsal region of the endocast appears largely undefined in these basal iguanodontians.

The digital endocasts of the three studied specimens do not show considerable detail for several reasons. With a slice thickness of 1 mm, the resolution of the CT scan does not allow an accurate reconstruction of smaller anatomical features such as the endosseous labyrinth and the smaller cranial nerves. Moreover, CT scanning revealed that the deformation and the deterioration of the braincases, after taphonomic processes and oxidation of the pyrite, were more important than expected. Finally, the high concentration of pyrite within both the bone and the matrix creates artifacts that obscure smaller details of the endocranial cavities, such as the valleculae.

Iguanodon bernissartensis (RBINS R51 and RBINS R54)

Only two braincases were sufficiently well preserved to allow a suitable reconstruction of the endocranial cavity in *Iguanodon bernissartensis*. The reconstruction of the endocranial cavity was made by Artecore 1.0-rc3. In *Iguanodon*, the major axis of the cerebrum is oriented ~15 degrees to the horizontal plane (as seen in lateral view; Figure 16.3A). This is the usual orientation encountered in hadrosaurines and other ornithopods (Hopson, 1979), as opposed to the more oblique (~45 degrees) orientation observed in lambeosaurine hadrosaurids. According to Evans et al. (2009), the rotation of the cerebrum is certainly related to the caudodorsal expansion of the nasal cavity and crest in the evolution of lambeosaurines.

The endocranial cavity of the holotype RBINS R51 is fairly complete (Fig. 16.3B). The brain endocast measures 183 mm from the foramen magnum to the rostral margin of the cerebrum and has a total volume of 357 cm^3. The olfactory tracts and olfactory bulbs are not included in this measurement. The endocranial cavity of RBINS R54 is less complete (Fig. 16.4). Its estimated volume of 194 cm^3 is probably largely underestimated.

16.3. Cranial endocast of *Iguanodon bernissartensis* (RBINS R51, holotype). A, Position and orientation of the endocranial cavity within the skull in left lateral view. B, Cranial endocast reconstructed from CT scans in right lateral view.

Although their volume cannot be adequately estimated, the olfactory tracts and bulbs appear to be particularly large, reflecting a well-developed sense of smell in *Iguanodon bernissartensis,* as also observed in most dinosaurs, including the ceratopsians *Psittacosaurus* (Zhou et al., 2007) and *Pachyrhinosaurus* (Witmer and Ridgely, 2008b), and virtually all theropods (Hopson, 1979; Zelenitsky et al., 2008). The great proportions of the visible

16.4. Cranial endocast of *Iguanodon bernissartensis* (RBINS R54) reconstructed from CT scans in right lateral view.
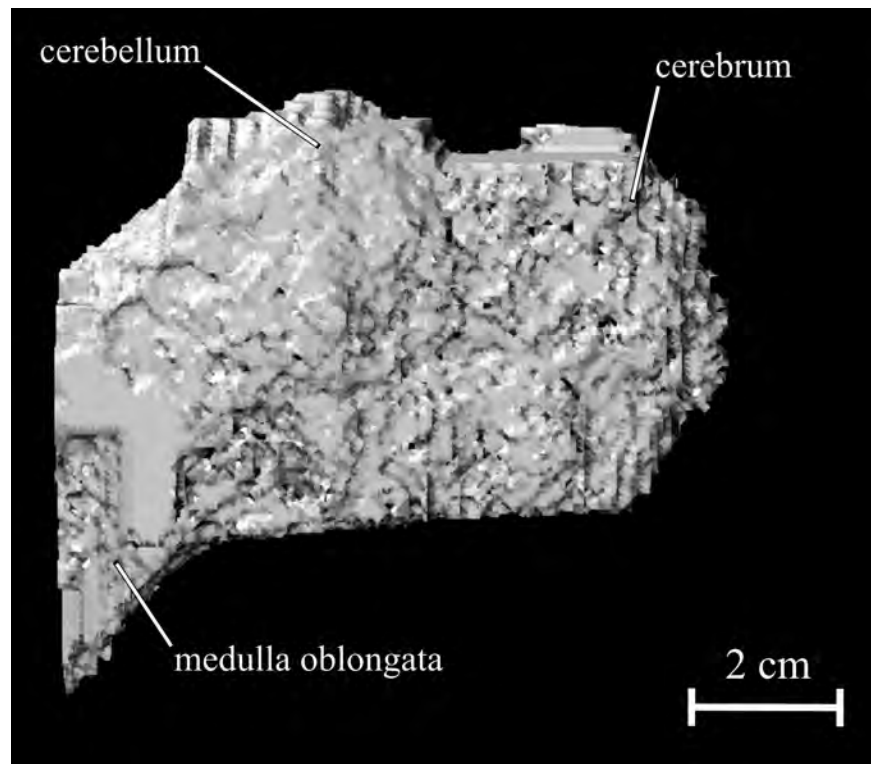
parts of the olfactory system (tracts and bulbs) in *Iguanodon* contrast with the situation observed in adult hadrosaurines and lambeosaurines, in which the bulbs usually form ~5% of the total endocast volume. Evans (2006) and Evans et al. (2009) consider that the small size of the olfactory system in hadrosaurids is a plesiomorphic character. However, it is more plausible that the reduction of the olfactory bulbs and tracts is in fact synapomorphic for hadrosaurids because the olfactory system is well developed in the basal Iguanodontia *Iguanodon* (and also in *Mantellisaurus*; see below) and in ceratopsians.

The cerebrum is enlarged and round, but not proportionally as large as in hadrosaurids (see below). The shape of the cerebrum prefigures the condition observed in later hadrosaurids, in which it is more expanded.

In RBINS R51, the cerebellar region is constricted and elongated. The cranial and pontine flexures are virtually absent, and the endocranial cavity is consequently nearly straight. According to Giffin (1989), these characters are derived for "iguanodontids" and hadrosaurids. The cerebellar region is less constricted in RBINS R54, and a large triangular peak is developed above the midbrain. Similar peaks are observed in a wide variety of dinosaur brains, including the theropods *Allosaurus, Tyrannosaurus* (Hopson, 1979), and *Majungasaurus* (Sampson and Witmer, 2007), and to a lesser extent in the lambeosaurines *Hypacrosaurus, Corythosaurus,* and *Lambeosaurus* (Evans et al., 2009). It is possible that the dural space housed a well-developed pineal apparatus (epiphysis). Pineal glands are present in extant birds (Breazile and Hartwig, 1989), and evidence for pineal-like tissue in alligators was presented by Sedlmayr et al. (2004).

Specimen	Taxon	Skull Length (mm)	Endocast Length (mm)	Endocast Height (mm)	Endocast Max. Width (mm)	Endocast Volume (cm³)
RBINS R51	*Iguanodon bernissartensis*	840	183	105	110	357
RBINS R54	*Iguanodon bernissartensis*	794	>107	100	62	>194
RBINS R57	*Mantellisaurus atherfieldensis*	>540	141	166	89	>131

Table 16.1. Measurements of brain cavity endocasts in three basal Iguanodontia from the Early Cretaceous of Bernissart

Note: Measurements were taken on digital endocasts by means of digital segmentation by the Artecore and Amira programs.

Mantellisaurus atherfieldensis (RBINS R57)

Although the skull appears to be superficially well preserved, the endocranium is partially squashed, and the midbrain is consequently lost. The reconstruction of the endocranial cavity was made by Amira 5.1 (Fig. 16.5). The endocranial cavity is 14.1 cm long from the foramen magnum to the rostral margin of the telencephalon. Its maximal height and width are, respectively, 16.6 cm and 8.9 cm. The volume of the reconstructed endocranial cavity is about 131 cm³. The brain volume of the living animal is, underestimated, however, because a large portion of the midbrain is missing. The cerebrum is only slightly larger than the medulla oblongata. As in *Iguanodon,* the olfactory tract is particularly large, suggesting large olfactory bulbs.

The endocranial cavity is proportionally higher in *Mantellisaurus* than in *Iguanodon* (Table 16.1). Moreover, although a large portion of the midbrain is missing in RBINS R57, the major axis of the hindbrain appears out of line with that of the cerebrum. Therefore, the cerebral cavity does not appear as straight as in *Iguanodon.* It can therefore be hypothesized that the primitive flexures in the midbrain region were better developed in *Mantellisaurus* than in *Iguanodon.* Hopson (1979) and Giffin (1989) hypothesized that the most likely causes of variation in the angles of the primitive flexure pattern are absolute skull size and relative eye size. Smaller genera and individuals tend to have more highly flexed endocasts than do large genera and individuals because of the negative allometry of the brain and eye sizes in reptiles (Hopson, 1979). Brains are therefore less constrained by space limitation in larger reptiles like *Iguanodon.*

Encephalization Quotient

The encephalization quotient (EQ) is an estimation of the relative brain size and represents the actual brain size of an individual divided by the expected brain size for its particular body size, calculated by using an allometric relationship derived from a large extant sample (Jerison, 1969, 1973). According to Jerison (1969) and Hopson (1979), there is a negative allometry in vertebrates between brain size and body size. On the basis of EQ, Jerison (1969) noted that living vertebrates cluster into two groups, endotherms and ectotherms. Hopson (1979) concluded that the EQs of dinosaurs usually fall between those of modern ectotherms and endotherms. Hurlburt

Relative Brain Size in *Iguanodon* and *Mantellisaurus*

16.5. Cranial endocast of *Mantellisaurus ather-fieldensis* (RBINS R57) reconstructed from CT scans in right lateral view.
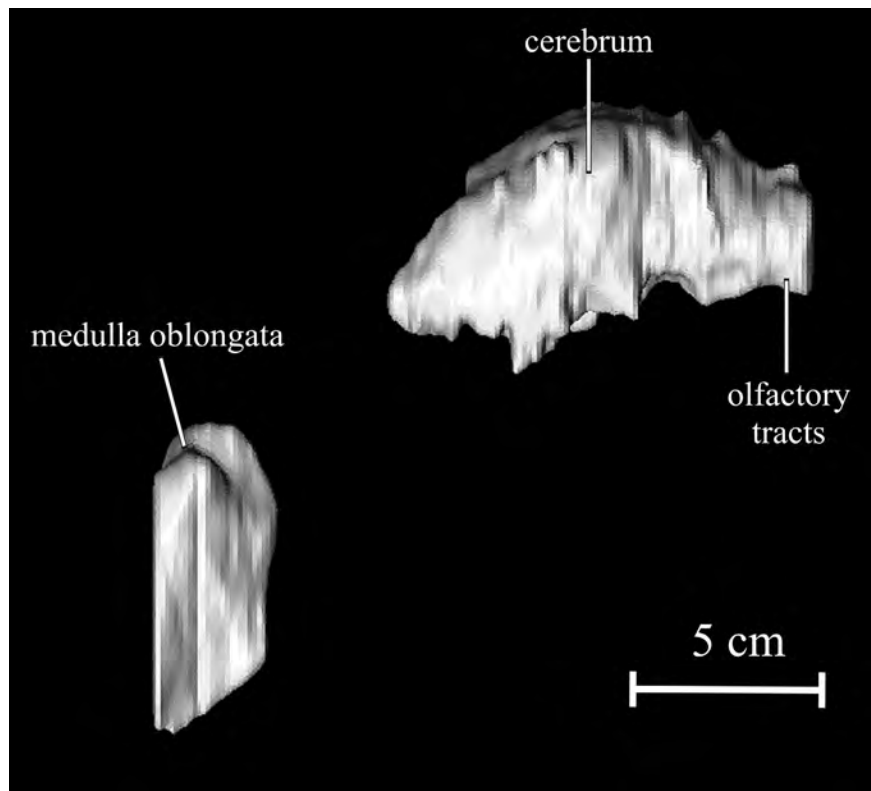
(1996) adapted Jerison's "lower" vertebrate equation for nonavian reptiles and defined a reptile encephalization quotient (REQ) as follows:

$$REQ = M_{Br}/(0.0155 \times M_{Br}^{0.553})$$

where M_{Br} is the mass of the brain (in grams) and M_{Bd} is the mass of the body (in grams). The mass of the brain is obtained by multiplying the volume of the brain by 1.036 g/mL (Stephan, 1960).

In extinct taxa, both the brain and body masses must be estimated, leading to many uncertainties in the calculation of the REQ. REQ calculations for dinosaurs usually estimated the volume of the brain under the assumption that the brain occupied 50% of the endocranial volume (Jerison, 1973; Hopson, 1977; Hurlburt, 1996). According to Evans (2005) and Evans et al. (2009), the extensive valleculae in hadrosaurids imply that the brain occupied a relatively larger portion of the endocranial cavity than in other ornithischians, and they calculated the REQ on the basis of a brain size estimate of 60% of the endocast volume. Because it cannot be decided whether valleculae are present in *Iguanodon* and *Mantellisaurus*, we calculated the REQ for these basal iguanodontians using both the 50% and the 60% estimates (Table 16.2).

The body weight of the specimens was estimated using both the bipedal and quadrupedal regression formulae of Anderson et al. (1985). Indeed, although Norman (1980) suggested that quadrupedality was the predominant posture for adults of *Iguanodon*, subsequent discussions (Alexander, 1985; Norman, 1986, 2004; Norman and Weishampel, 1990; Bultynck, 1993) suggest a semibipedal (sensu Bultynck, 1993) gait and locomotion for *Iguanodon* and *Mantellisaurus*. Therefore, the actual weight for these basal

Specimen	Taxon	Brain Weight	Body Weight	REQ	
				Bipedal	Quadrupedal
RBINS R51	*Iguanodon bernissartensis*	185 g (50%) 222 g (60%)	3,880 kg (bipedal), 7,727 kg (quadrupedal)	2.71 (50%) 3.25 (60%)	1.85 (50%) 2.22 (60%)
RBINS R57	*Mantellisaurus atherfieldensis*	>68 g (50%) >81 g (60%)	926 kg (bipedal), 1,547 kg (quadrupedal)	>2.2 (50%) >2.6 (60%)	>1.66 (50%) >1.97 (60%)

Table 16.2. Brain weight, body weight, and nonavian reptile encephalization quotient (REQ) for two basal Iguanodontia from the Early Cretaceous of Bernissart

Note: Brain weight was calculated based on assumptions that the brain occupied either 50% (Jerison, 1973; Hurlburt, 1996) or 60% (Evans, 2005; Evans et al., 2009) of the endocranial cavity. Body weight was estimated by both the bipedal and quadrupedal regression formulae of Anderson et al. (1985).

iguanodontians probably fell somewhere between the mass estimates for the bipedal and quadrupedal formulae of Anderson et al. (1985).

Depending on the chosen model (50% versus 60% relative brain size; bipedal versus quadrupedal gait), our REQ estimates for *I. bernissartensis* range between 1.88 and 3.3 (Table 16.2). The lowest of our REQ estimates is marginally higher than most extant nonavian reptiles (Hurlburt, 1996), sauropods (*Diplodocus*, 0.53–0.69; *Nigersaurus*, 0.4–0.8; Franzosa, 2004; Witmer et al., 2008), and ceratopsians (*Psittacosaurus*, 1.7; *Triceratops*, 0.7; Zhou et al., 2007; Witmer et al., 2008). Both the lowest and highest REQ estimates are lower than those calculated for the lambeosaurine hadrosaurid *Hypacrosaurus altispinus* (2.3–3.7; Evans et al., 2009). Estimated REQ values for *Iguanodon* also appear significantly lower than most nonavian theropods (*Carcharodontosaurus*, 2.3–3.23; *Ceratosaurus*, 3.31–5.07; *Allosaurus*, 2.4–5.24; *Acrocanthosaurus*, 2.75–5.92; *Citipati* 3.6; *Tyrannosaurus*, 5.44–7.63; *Troodon*, 7.76; Franzosa, 2004).

Cerebrum

According to Evans et al. (2009), the most striking aspect of the brain endocast of lambeosaurine hadrosaurids is the relatively large size of the cerebrum. Its estimated relative volume (CRV = cerebrum volume/endocast volume) calculated for four late Campanian lambeosaurines from North America varies between 35% and 42% (Table 16.3). The cerebrum of lambeosaurines is therefore larger than that of large theropods such as *Carcharodontosaurus* (24%) and *Tyrannosaurus rex* (33%), but compares favorably with the maniraptoran theropod *Conchoraptor* (43%) and even with the basal bird *Archaeopteryx* (45%).

We estimated the volume of the cerebrum in *Iguanodon* and *Mantellisaurus*, in *Lurdusaurus arenatus* Taquet and Russell, 1999 (a basal styracosternan Iguanodontia, according to Norman, 2004), in the basal hadrosauroid *Batyrosaurus rozhdestvenskyi* (see Chapter 20 in this book), and in the basal lambeosaurine *Amurosaurus riabinini* Bolotsky and Kurzanov, 1991 (Table 16.3). Because the cerebrum has roughly the shape of an ellipsoid, its volume can be deduced from the following formula: $V = 4/3\pi \times L \times W \times H$, where L, W, and H are, respectively, half of the maximal length, width, and height of the cerebrum. In RBINS R51, the holotype of *Iguanodon bernissartensis*, the CRV is 19%, as in the basal styracosternan *Lurdusaurus* (Table 16.3). Figure 16.6A shows that the cerebrum is proportionally less developed

Table 16.3. Comparisons of the estimated endocast and cerebrum volume in styracosternan ornithopods

Specimen	Taxon	Endocast Length (mm)	Endocast Volume (cm³)	Cerebrum Volume (cm³)	CRV (%)
RBINS R51	*Iguanodon bernissartensis*	183	357	68	19
RBINS R54	*Iguanodon bernissartensis*	>107	>194	58	—
RBINS R57	*Mantellisaurus atherfieldensis*	141	>131	90	—
MNHN GDF 1700	*Lurdusaurus arenatus*	137	167	32	19
AEHM 4/1	*Batyrosaurus rozhdestvenskyi*	100	—	27	—
AEHM 1/232	*Amurosaurus riabinini*	145	290	88	30
ROM 758a	*Lambeosaurus* sp.	113	94.1	35.1	37
ROM 759a	*Corythosaurus* sp.	110	97.9	41.6	42
CMN 34825a	*Corythosaurus* sp.	142	145.4	51.1	35
ROM 702a	*Hypacrosaurus altispinus*	204	289.9	117.5	41

Note: CRV = cerebrum relative volume (cerebrum volume/endocast volume).
[a] Data from Evans et al. (2009).

in *Iguanodon* and *Lurdusaurus* than in North American lambeosaurines and in the Russian basal lambeosaurine *Amurosaurus* (CRV 30%).

Although the skull of RBINS R57 (referred specimen of *Mantellisaurus atherfieldensis*) is much smaller than that of RBINS R51 (holotype of *Iguanodon bernissartensis*), the volume of the cerebrum is larger in RBINS R57 (90 cm³) than in RBINS R51 (68 cm³). Unfortunately, the CRV of *Mantellisaurus* cannot be adequately estimated because the endocast is squashed at the level of the midbrain region in RBINS R57. However, it is still possible to compare the estimated volume of the cerebrum with the length of the endocast (Fig. 16.6B); the latter measurement is not affected by the squashing of the midbrain region in RBINS R57. The cerebrum is similarly enlarged in *M. atherfieldensis* and in the basal lambeosaurine *Amurosaurus*, and it compares favorably with the North American lambeosaurines. It is proportionally larger than in *Iguanodon* and *Lurdusaurus*.

Enlarged brain and cerebrum relative to body size are usually equated with increased behavioral complexity in vertebrates (Jerison, 1969, 1973; Hopson, 1977; Hurlburt, 1996). According to Evans et al. (2009), the relatively large size of the brain and the cerebrum in lambeosaurines is consistent with the range and complexity of social behaviors inferred from the hypothesis that the supracranial crest was an intraspecific signaling structure for visual and vocal communication. However, a similar increase in the relative size of the cerebellum can be observed in *Mantellisaurus atherfieldensis*. On the other hand, calculated REQ and CRV values remain relatively low in *Iguanodon*. This observation suggests that the behavioral repertoire and/or complexity were different in *Iguanodon* and *Mantellisaurus*, two taxa that most likely occupied the same territories in western Europe during the late Barremian and lower Aptian (see Chapter 15 in this book).

According to Wu and Godefroit (Chapter 19 in this book) and Godefroit et al. (Chapter 20 in this book), *Mantellisaurus* and *Iguanodon* belonged, with *Ouranosaurus*, to a monophyletic clade named Iguanodontidae. Iguanodontidae is the sister taxon of Hadrosauroidea. If this phylogeny is correct, it means that the enlargement of the cerebrum appeared independently, together with possible capacities for more complex behaviors, at least two times during the evolution of Iguanodontoidea.

Acknowledgments

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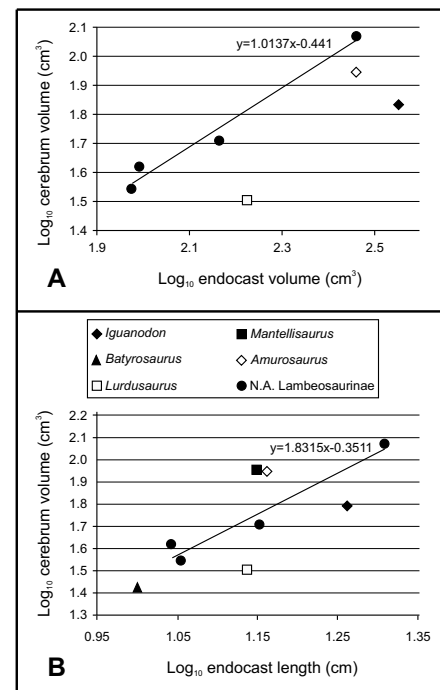
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