

Description of a Cranial Endocast From a Fossil Platypus, *Obdurodon dicksoni* (Monotremata, Ornithorhynchidae), and the Relevance of Endocranial Characters to Monotreme Monophyly

Thomas E. Macrini,^{1*} Timothy Rowe,¹ and Michael Archer²

¹Jackson School of Geosciences and University of Texas High-Resolution X-ray Computed Tomography Facility, University of Texas at Austin, Austin, Texas 78712, USA

²School of Biological Science, University of New South Wales, Sydney, New South Wales 2052, Australia

ABSTRACT A digital cranial endocast of the Miocene platypus *Obdurodon dicksoni* was extracted from high-resolution X-ray computed tomography scans. This endocast represents the oldest from an unequivocal member of either extant monotreme lineage and is therefore important for inferring character support for Monotremata, a clade that is not well diagnosed. We describe the *Obdurodon* endocast with reference to endocasts extracted from skulls of the three species of extant monotremes, particularly *Ornithorhynchus anatinus*, the duckbill platypus. We consulted published descriptions and illustrations of whole and sectioned brains of monotremes to determine which external features of the nervous system are represented on the endocasts. Similar to *Ornithorhynchus*, well-developed parafloccular casts and reduced olfactory bulb casts are present in the *Obdurodon* endocast. Reduction of the olfactory bulbs in comparison with tachyglossids and therian mammals is a potential apomorphy for Ornithorhynchidae. The trigeminal nuclei, ganglia, and nerves (i.e., trigeminal complex) are enlarged in *Obdurodon*, as evidenced by their casts on the endocast, as is the case in the extant platypus. The visibility of enlarged trigeminal nucleus casts on the endocasts of *Obdurodon* and *Ornithorhynchus* is a possible synapomorphy of Ornithorhynchidae. Electroreception and enlargement of the trigeminal complex are possible synapomorphies for Monotremata. *J. Morphol.* 267:1000–1015, 2006.

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Monotremes are generally held to comprise two extant clades, Ornithorhynchidae, represented by the duckbill platypus (*Ornithorhynchus anatinus*), and Tachyglossidae, with two extant species of echidnas (*Tachyglossus aculeatus* and *Zaglossus bruijnii*). These three taxa are very different morphologically and ecologically, and were initially united based on plesiomorphic characters (e.g., presence of a cloaca, ovipary, presence of an interclavicle, and a procoracoid in the shoulder girdle; Griffiths [1978]). *Ornithorhynchus anatinus* is aquatic, has webbed feet, and a bill-shaped snout. Echidnas are terrestrial

and have rounded and dorsoventrally compressed bodies that are mostly covered by hollow spines that are essentially modified hairs. The most prominent feature on the echidna head is the elongated, hairless snout.

Whereas monotreme monophyly is virtually unquestioned, there are relatively few unequivocal morphological synapomorphies for Monotremata described in the literature; most of these are osteological (as summarized by Gregory, 1947; Rowe, 1986). However, some of these were subsequently shown to be equivocal. For instance, the presence of a tarsal spur, found in all three extant species of monotremes, was a suggested synapomorphy for the group (Ax, 1987). A tarsal spur is now known from a number of fossil mammals, including *Gobiconodon*, some multituberculates, *Zhangheotherium*, and *Henkelotherium* and therefore is plesiomorphic for Monotremata (Luo et al., 2002, 2003, and references therein).

Moreover, the differences between the platypus and echidnas are profound and the fossil record suggests both had diverged from a common ancestor with therian mammals by the mid-Jurassic (Rowe, 1986; Messer et al., 1998; Luo et al., 2001, 2002; Rauhut et al., 2002). A poor pre-Pleistocene fossil record for crown Monotremata (Archer et al., 1985; Pascual et al., 1992) raises the possibility that monotreme monophyly could be a manifestation of long-branch attraction. A nearly complete skull of a

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*Correspondence to: T.E. Macrini, University of Texas at Austin, Geoscience Department, 1 University Station C1100, Austin, TX 78712-0254. E-mail: tmacrini@mail.utexas.edu

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fossil platypus, *Obdurodon dicksoni*, from Miocene deposits of Riversleigh, Australia, represents the oldest record of an unequivocal member of either monotreme clade and is therefore significant for monotreme systematics (Archer et al., 1992, 1993; Musser and Archer, 1998).

We explore the question of monotreme monophyly by examining the nervous system, an anatomical system that is poorly represented in phylogenetic analyses (but notable exceptions include: Johnson et al., 1982a,b, 1994; Kirsch, 1983; Kirsch and Johnson, 1983; Kirsch et al., 1983; Northcutt, 1984, 1985). Because soft tissue anatomy such as the brain rarely, if ever, fossilizes, cranial endocasts are often the best material that paleontologists have to study the central nervous system of fossil mammals (Jerison, 1973). An endocast is any three-dimensional representation of the space within a particular cavity. A cranial endocast represents the space within the braincase or cranial cavity. Besides the brain, the cranial cavity also houses other soft tissue structures such as the meninges, blood vessels, and nerves, and therefore, at best cranial endocasts only provide approximations of external features of the brain. Even so, the general shapes and volumes of some external features of the brain can be inferred from endocasts. However, cranial endocasts do not provide any direct information about the internal structure of the brain such as morphology of the neurons, number of neurons, neuron density, or neuron connectivity.

In this article we describe a digital cranial endocast of the fossil *Obdurodon dicksoni* in reference to endocasts of the three extant species of monotremes and their brains as described in the literature. Including these new data from the *Obdurodon* endocast allows us to sample from all members of crown Monotremata, with at least one well-preserved skull, in order to explore new potential apomorphies for Ornithorhynchidae and Monotremata.

MATERIALS AND METHODS

Specimens Examined

The only known skull of *Obdurodon dicksoni* (QM F20568) (QM F = fossil collection of Queensland Museum, Brisbane, Australia) was collected from the middle Miocene Ringtail Site on the Riversleigh World Heritage property in Queensland, Australia (Musser and Archer, 1998). *Obdurodon dicksoni* was collected from freshwater carbonate deposits at sites well known for aquatic vertebrates including crocodiles, turtles, and lungfish (Archer et al., 1992). Based on this, it is assumed that *O. dicksoni* was aquatic, like its extant relative *Ornithorhynchus anatinus*.

The skull of *Obdurodon dicksoni* is nearly complete but is missing a large, oblique section of the cranial roof that extends from the lambdoidal crest on the right dorsum of the skull to anterior of the orbit on the left side (Musser and Archer, 1998). The *Obdurodon* skull measures 134.4 mm from the anterior tip of the premaxillae to the back of the occiput (Archer et al., 1992) and is presumed to belong to an adult, because of fusion of the cranial sutures. In addition, the *Obdurodon* skull is about 30% larger than skulls of adult *Ornithorhynchus*.

When the *Obdurodon* skull was first discovered, the endocranial cavity was filled with a natural limestone endocast that was only partially exposed through breaks in the skull (Fig. 1). The skull was subsequently acid-prepared, resulting in the destruction of the natural endocast (Fig. 2).

Digital endocasts from two skulls of *Ornithorhynchus anatinus*, one of *Tachyglossus aculeatus*, and one of *Zaglossus bruijnii*, were compared to the *Obdurodon* endocast. The platypus sample includes one skull from a juvenile (AMNH 252512) (AMNH = American Museum of Natural History, New York, NY) retaining all of its deciduous dentition and measuring 59.05 mm from the anterior tip of the premaxillae to the back of the occiput, and one adult skull (AMNH 200255) with a total length of 91.60 mm. Both echidna skulls are from adults; the *Tachyglossus* skull has a total length of 99.00 mm and the *Zaglossus* skull length is 164.00 mm.

About CT Scanning

All skulls were computed tomography (CT)-scanned at the University of Texas High-Resolution X-ray CT Facility (UTCT) in Austin, TX. High-resolution X-ray CT (HRXCT) is a proven technique for studying the internal cranial osteology and cavities of fossil or unique specimens (e.g., Rowe et al., 1995; Brochu, 2000; Tykoski et al., 2002; Witmer et al., 2003; Franzosa and Rowe, 2005). HRXCT utilizes differential attenuation of X-rays passed through a specimen to differentiate between bone and other material to produce 2D images (i.e., slices) that reveal internal details of specimens (for a detailed description of CT, see Denison et al., 1997, and Table 1). Consecutive equidistant 2D slices provide a 3D digital map of the specimen that can be manipulated using a variety of image processing techniques and software. All skulls were scanned in their entirety in the coronal (=transverse of some authors) slice plane. Scan parameters for these specimens are presented in Table 2.

Extraction of Endocasts

The digital endocasts were generated using the program VGStudioMax (v. 1.2; Volume Graphics, Germany, 2004). VGStudioMax is a program designed for the analysis and visualization of voxel data that allows the user to digitally individuate or segment (in the jargon of informatics) portions of volumetric datasets. The magic wand tool was used to select the endocranial space and the lasso tool to fine-tune the selections. Lines were drawn to seal off openings in the braincase (e.g., foramen magnum, foramina for passage of nerves and vessels), when necessary, to establish boundaries of the endocranial space. For the most part, lines were drawn through the center of openings to match the contours of the surrounding bone.

The same procedure was used to segment portions of the endocast representing distinctive structures such as the olfactory bulb casts, parafloccular casts, hypophyseal casts, and cavum epiptericum casts. The geometric shapes of these endocast features do not precisely reflect the histological boundaries of soft tissue structures, but rather serve as reasonable proxies.

The cribriform plate serves as the anterior boundary of the olfactory bulb space in mammals. *Ornithorhynchus* (Zeller, 1988) and *Obdurodon* have a partially ossified cribriform plate, with the anterodorsal portion remaining unossified in adults. In these two taxa the anterior end of the olfactory bulb casts was determined by the curvature of the bones surrounding the ethmoidal fossa (e.g., frontal, lamina obturans). A distinctive, complete cribriform plate is present in *Tachyglossus* and *Zaglossus*. The posterior end of the olfactory bulb casts was determined by the medial inflection of the endocast at the anterior edge of the circular fissure (sensu Loo, 1930; Rowe 1996a,b; =transverse fissure of Krause and Kielan-Jaworowska, 1993), as viewed dorsally. This surface was treated as a coronal plane. However, the cribriform plate of *Tachyglossus* (Fig. 7) and *Zaglossus* extends posterior to the circular fissure, as do the corresponding olfactory nerve fibers. The olfactory bulb surface area and volume are



Fig. 1. Photograph of the *Obdurodon dicksoni* skull at the time of discovery, showing the natural limestone cranial endocast. A skull of an *Ornithorhynchus anatinus* is held up for comparison.

correlated to the surface area of the cribriform plate (Rowe et al., 2005) and, therefore, the olfactory bulb casts of echidnas extend beyond the circular fissure. There are no distinctive bony markers to segregate the posterior portion of the olfactory bulb space from the rest of the endocranial cavity and, therefore, the volumes of the olfactory bulb casts in the two species of echidnas are underestimated.

The medial end of each parafloccular lobe cast was treated as an oblique sagitto-coronal cut plane. Its location was determined as the point of constriction of the parafloccular casts into a neck but prior to the connection with the main body of the cerebellum. The dorsal cut plane of the hypophyseal fossa was determined by the dorsalmost horizontal slice in which the lateral walls, dorsum sella, and clinoid processes of the sella turcica are all visible. The cavum epiptericum was determined as the space posterior of the sphenorbital fissure to the posterior end of the foramen ovale. A horizontal line was drawn across the top of this space in each coronal slice.

Endocast flexure was measured in lateral view by taking the acute angle between two lines, both of which pass through the hypophyseal cast. The first line passes through the middle of the olfactory bulb casts to the middle of the hypophyseal cast. The second line passes from the middle of the hypophyseal cast to the middle of the foramen magnum.

VGStudioMax was also used to calculate volumes and partial volumes, to take linear measurements of the extracted endocast segments, and to generate movie frames of the rotating endocasts. VGStudioMax provides measurements with accuracy to the third decimal place (e.g., 0.001). The movie frames were exported to National Institutes of Health (Bethesda, MD) ImageJ and/or Adobe Photoshop (San Jose, CA), where they were cropped and rotated as necessary. The frames were then exported to QuickTime (Apple, Cupertino, CA) and compiled into self-contained movies. The movies of the endocasts along with CT slices of the skulls of these specimens are available on the Digimorph website (Table 1). Isosurface models of the endocasts were generated using VGStudioMax and then exported to Amira 3.1 (Zuse Institute, Berlin, 2004), where the surfaces of the endocasts were smoothed. Images of the smoothed endocasts are used in the figures of this article.

Anatomical Terminology

The anatomical terminology for the cranial foramina of monotremes is not standardized (see Musser and Archer, 1998, for discussion) because of questions about homology with foramina in nonmonotreme mammals (e.g., therians, multitubercu-

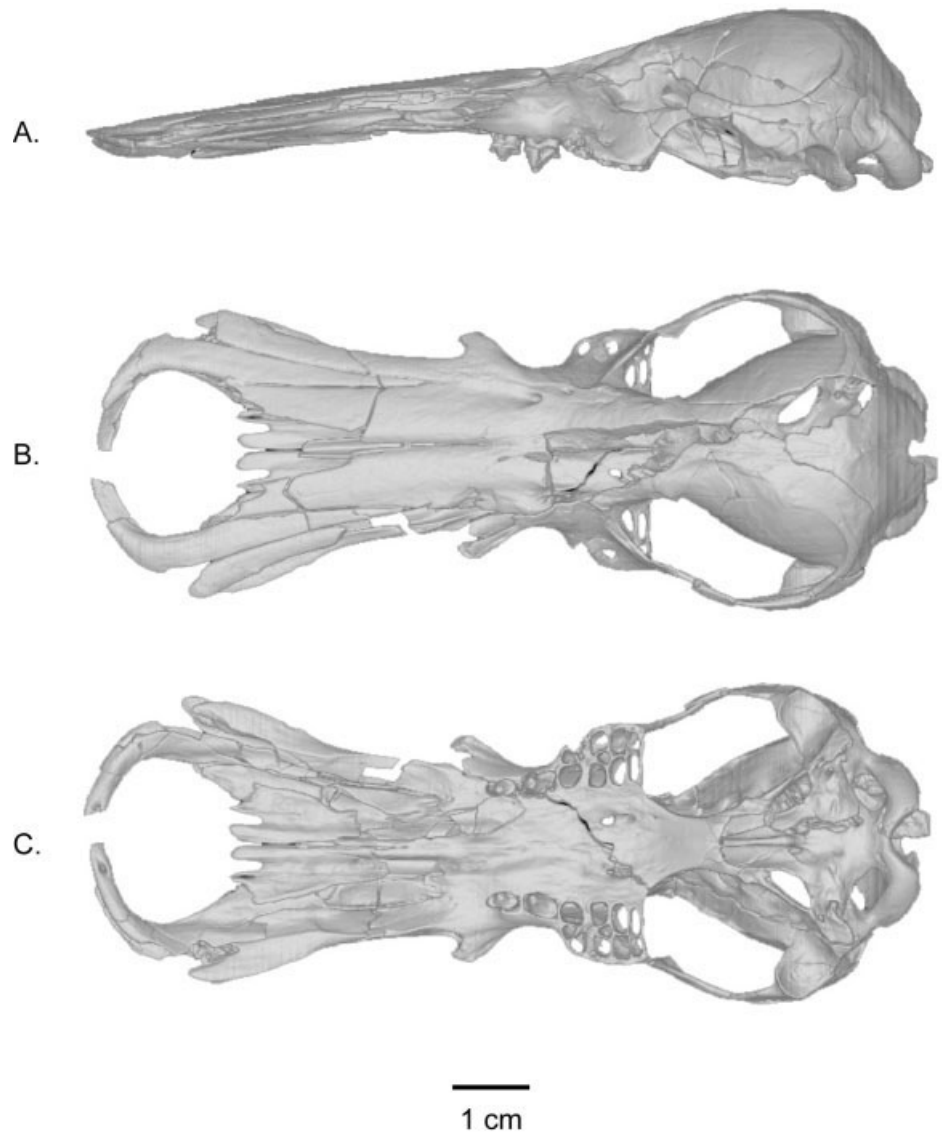


Fig. 2. Digital rendering constructed from CT images of the acid prepared skull of *Obdurodon dicksoni* shown in left lateral (A), dorsal (B), and ventral (C) views.

lates, triconodonts). For instance, the foramen for the exit of cranial nerves II, III, IV, V₁, and VI is referred to by the following names in the literature: foramen sphenor-orbitale + opticum, foramen sphenopticum, optic foramen, and sphenorbital foramen (list compiled in Musser and Archer, 1998). In this article we adapt the terminology used for nonmonotreme mammals for foramina that transmit the same soft tissue structures in monotremes and other mammals. This practice follows the attempts of others (e.g., Wible and Rougier, 2000; Wible, 2003) to standardize anatomical terminology for Mammalia. Thus, the

foramen for the exit of cranial nerves II, III, IV, V₁, and VI in the platypus is referred to as the sphenorbital fissure in this article.

RESULTS

The cranial endocast of *Obdurodon dicksoni* (Fig. 3) is similar in overall morphology to that of the extant platypus, *Ornithorhynchus anatinus*, but size

TABLE 1. Relevant web addresses

Description	Web address
UTCT website	http://www.ctlab.geo.utexas.edu/overview/index.html
Digimorph homepage	www.digimorph.org
Adult <i>Ornithorhynchus</i> CT movies	www.digimorph.org/specimens/Ornithorhynchus_anatinus/adult/
Juvenile <i>Ornithorhynchus</i> CT movies	www.digimorph.org/specimens/Ornithorhynchus_anatinus/juvenile/index.phtml
<i>Obdurodon</i> CT movies	www.digimorph.org/specimens/Obdurodon_dicksoni
<i>Tachyglossus</i> CT movies	www.digimorph.org/specimens/Tachyglossus_aculeatus/skull
<i>Zaglossus</i> CT movies	www.digimorph.org/specimens/Zaglossus_bruijnii

TABLE 2. Scan parameters for skulls examined

Taxon	Specimen no.	No. of slices	Slice resolution	Slice thickness	Interslice spacing	FR
<i>Obdurodon</i>	QM F20568	612	512 × 512	0.260	0.2200	53.0
<i>Ornithorhynchus</i> (adult)	AMNH 200255	438	512 × 512	0.210	0.2100	43.5
<i>Ornithorhynchus</i> (juvenile)	AMNH 252512	522	512 × 512	0.157	0.1178	33.0
<i>Tachyglossus</i>	AMNH 154457	693	1024 × 1024	0.150	0.1500	47.0
<i>Zaglossus</i>	AMNH 157072	909	1024 × 1024	0.175	0.1750	55.0

"No. of slices" indicates number of images reconstructed from coronal (= transverse of some authors) slice plane. Interslice spacing is the space between consecutive slices; if the interslice spacing value is less than slice thickness for a particular scan, this indicates that there is overlap between consecutive slices. FR, field of reconstruction for the two dimensional slices. Slice resolution is reported in pixels; slice thickness, interslice spacing, and field of reconstruction are reported in mm.

is a major difference. The *Obdurodon* endocast is significantly larger than that of the adult *Ornithorhynchus* (Fig. 4) and aspect ratios of endocast width/length and height/length vary between the two taxa. The height/width aspect ratio is well conserved between the three specimens examined here. The width/length aspect ratio of the *Obdurodon* endocast is 0.77, the height/length ratio is 0.57, and the height/width ratio is 0.74. In contrast, the adult *Ornithorhynchus* endocast has a width/length ratio of 0.93, a height/length ratio of 0.69, and a height/width ratio of 0.74. The juvenile *Ornithorhynchus* endocast has a width/length ratio of 0.97, a height/length ratio of 0.73, and a height/width ratio of 0.75. Volume and linear measurements for the endocasts described here are presented in Tables 3 and 4, respectively. Endocast flexure is also presented in Table 3. The endocast volumes presented here compare favorably with published brain volumes and partial volumes for extant monotremes (Pirlot and Nelson, 1978; Ross et al., 2004).

The endocast of *Obdurodon* is dominated by massive, lissencephalic (=smooth) cerebral hemisphere casts that are separated dorsally by a deep median sulcus (Fig. 5). A prominent ossified falx cerebri (Fig. 6), an ossification of a portion of the dura mater of the meninges, sits in the median sulcus. Damage to the dorsal surface of the skull of *Obdurodon* prevents an accurate reconstruction of the shape of the anterodorsal surface of the olfactory bulb casts, giving the appearance that the cerebral hemisphere and olfactory bulb casts are not separated by a deep circular fissure (sensu Loo, 1930; Rowe 1996a,b; =transverse fissure of Krause and Kielan-Jaworowska, 1993; Figs. 2, 3A). Each *Ornithorhynchus* endocast also has massive, lissencephalic hemisphere casts and a prominent median sulcus resulting from a conspicuous ossified falx cerebri (Fig. 6).

The anterodorsal portion of the lamina cribrosa is unossified in the adult *Ornithorhynchus*, such that foramen olfactorium advehens remains open (Zeller, 1988). However, the posterior portion of the cribriform plate of *Ornithorhynchus* is ossified. This ossified portion of the cribriform plate is formed by the coalescence of endoturbinals I, II, and III of the ethmoid bone, as is the case in other mammals (see

CT movies on the web, Table 1; Rowe et al., 2005). A hint of the ossified posterior cribriform plate of *Obdurodon* is also visible on the CT slices (see CT movies on the web, Table 1). The cribriform plate of *Obdurodon* also appears to be formed by coalescence of the ossified turbinal elements of the ethmoid bone.

The olfactory bulbs of *Obdurodon* are relatively small, together comprising about 1.90% of the endocast volume. The olfactory bulb casts of the extant platypus specimens are even smaller. In the adult *Ornithorhynchus* the olfactory bulb casts together comprise 0.95% of the total endocranial space and are about half the relative size of the corresponding structures in *Obdurodon*. In the juvenile *Ornithorhynchus* the olfactory bulb casts together compose 1.80% of its endocranial space.

The mesencephalon is not visible on the dorsal surface of the *Obdurodon* endocast or on the exterior of extant monotreme brains (Griffiths, 1978) or endocasts (Macrini and Rowe, 2004). A cast of the vermis of the cerebellum of *Obdurodon* and all the extant monotremes is well developed on the dorsal surface of the endocasts (Macrini and Rowe, 2004; Figs. 1, 2). Casts of the paraflocculi and cerebellar hemispheres are also conspicuous on the *Obdurodon* and *Ornithorhynchus* endocasts (Figs. 3–5). The parafloccular casts are small and spherical but distinct, similar to those of *Ornithorhynchus*. The parafloccular casts comprise about 0.57%, 0.71%, and 0.58% of the endocranial volume in *Obdurodon*, the juvenile *Ornithorhynchus*, and the adult *Ornithorhynchus*, respectively.

On the ventral surface of the *Obdurodon* endocast, the cast of the hypophyseal fossa is prominent (Fig. 3C). The hypophyseal cast of *Obdurodon* is more pronounced than that of the adult *Ornithorhynchus* endocast, which is much narrower transversely (Fig. 4C). The hypophyseal fossa of the adult *Ornithorhynchus* is confluent anteriorly with a long, narrow groove in the basisphenoid. At least some of this groove is occupied by the pituitary gland (Zeller, 1989a). The hypophyseal fossa in *Obdurodon* composes 0.17% of the endocast volume, while in *Ornithorhynchus* the hypophyseal fossa comprises 0.10% and 0.08% of the total endocranial space for the adult and juvenile endocasts, respectively.

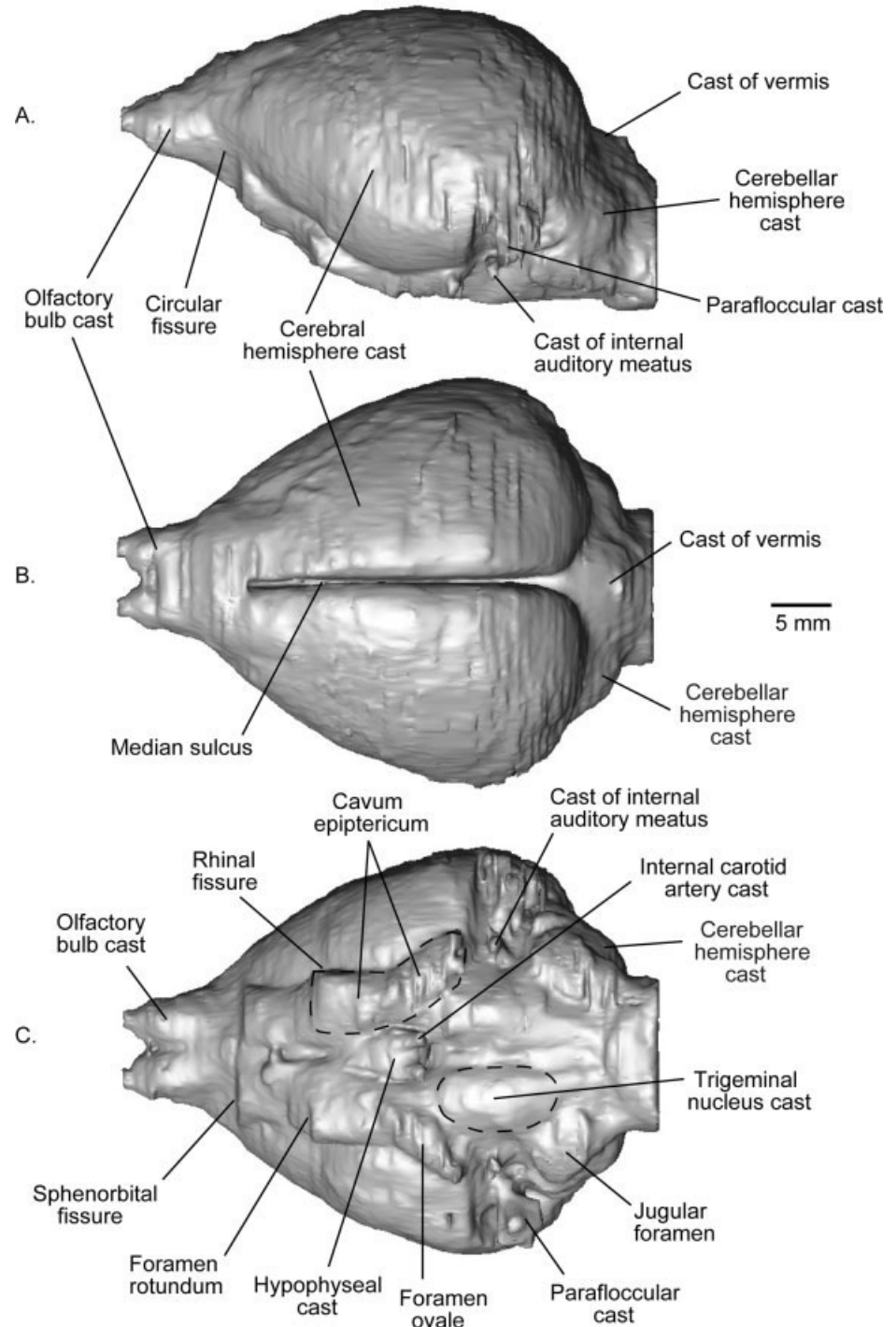


Fig. 3. Digital rendering of the cranial endocast of *Obdurodon dicksoni* shown in left lateral (A), dorsal (B), and ventral (C) views.

The maxillary branch of the trigeminal nerve (V_2) passes through the foramen rotundum of the skull of *Ornithorhynchus*; large casts of the canals transmitting these nerves are visible on the endocast immediately anterior and lateral to the hypophyseal cast. Cranial nerves II, III, IV, V_1 , and VI pass through the sphenorbital fissure of the skull of *Ornithorhynchus* (Zeller, 1989a,b); casts of the canals transmitting these nerves

are smaller and anterior to the maxillary branch casts. The cast of the canal for V_2 is much thinner transversely in the adult *Ornithorhynchus* compared to *Obdurodon*. The paired canal casts for cranial nerves II, III, IV, V_1 , and VI are confluent in the adult *Ornithorhynchus* endocast (Fig. 4C), but not in *Obdurodon* (Fig. 3C). That is, there is no bony septum between the paired sphenorbital fissures in *Ornithorhynchus* (fig. 53 in Zeller,

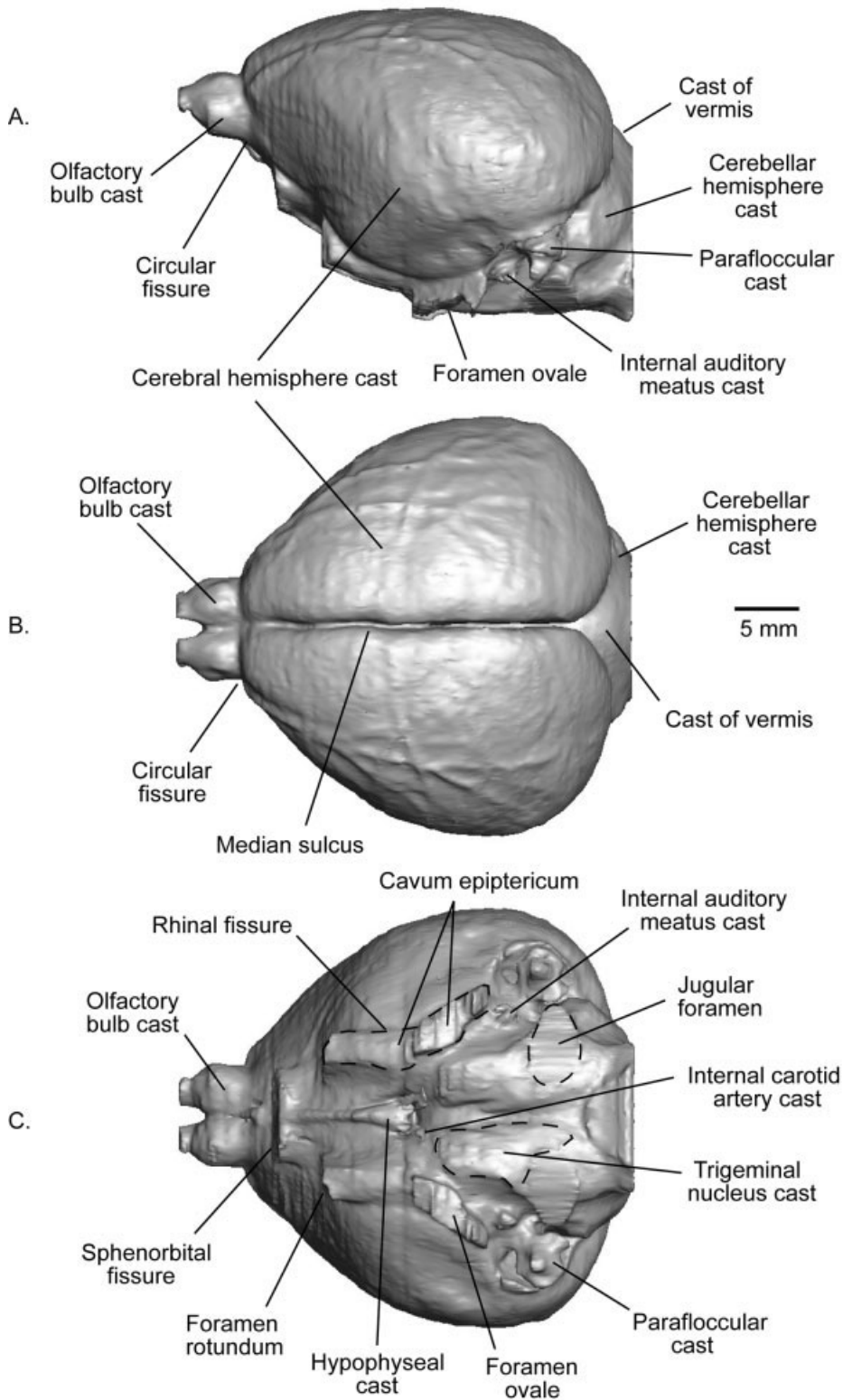


Fig. 4. Digital rendering of the cranial endocast of an adult *Ornithorhynchus anatinus* (AMNH 200255) shown in left lateral (A), dorsal (B), and ventral (C) views.

1989a) but a bony division is clearly visible in *Obdurodon*.

Casts of massive trigeminal nuclei sit posterior to the hypophyseal cast of *Obdurodon* (Fig. 3C). The trigeminal nucleus casts of *Obdurodon* are flatter

and less pronounced than those of *Ornithorhynchus*. Neither echidna endocast shows any indication of a trigeminal nucleus cast. The large jugular foramen lies posterior and lateral to the trigeminal nucleus cast in *Obdurodon* and *Ornithorhynchus*. Cranial

TABLE 3. Volumes from endocasts

Taxon	Specimen no.	Body mass	EV	OB volume*	PF volume*	HP volume	CE volume*
<i>Obdurodon</i>	QM F20568	2038 ^a	15443.661	293.077	88.484	26.962	207.510
<i>Ornithorhynchus</i> (adult)	AMNH 200255	1389 ^b	9732.844	92.140	56.633	9.530	106.201
<i>Ornithorhynchus</i> (juvenile)	AMNH 252512	895 ^a	4456.047	80.359	31.608	3.383	55.238
<i>Tachyglossus</i>	AMNH 154457	4250 ^c	20013.875	456.046	n/a	32.385	260.505
<i>Zaglossus</i>	AMNH 157072	7500 ^c	36049.008	1108.623	n/a	15.108	398.766

Body mass given in g. Volumes given in mm³. *, Volume data presented are combined for bilateral structures; CE, cavum epiptericum; EV, endocranial volume; HP, hypophyseal fossa; OB, olfactory bulb cast; PF, parafloccular cast.

^aBody mass estimated by scaling from adult *Ornithorhynchus* average, based on differences in skull length.

^bMass average of adults from Pasitschniak-Arti and Marinelli (1998).

^cMass average of adults from Nowak (1991).

nerves IX, X, XI, and XII pass through this opening in *Ornithorhynchus* (Zeller, 1989a,b).

The cavum epiptericum is quite large in *Obdurodon* (comprising 1.34% of endocranial space) as well as in *Ornithorhynchus* (comprising 1.24% of endocranial space in the juvenile and 1.09% in the adult). The cavum epiptericum in both taxa extends from just posterior of the foramen rotundum to just posterior to the foramen ovale, therefore including the cast of the V₂ canal (Figs. 3, 4; Zeller, 1989a). There is no clear separation between the cavum epiptericum and the cavum supracochleare space in *Obdurodon* or *Ornithorhynchus*; therefore, the geniculate ganglion is incorporated within the space of the cavum epiptericum. In addition to the geniculate ganglion, the trigeminal ganglion, the rostral portion of the otic ganglion, and portions of several cranial nerves are located in the cavum epiptericum of *Ornithorhynchus* (Zeller, 1989b).

The pons and medulla oblongata do not leave distinctive marks on the ventral surface of the endocasts of *Obdurodon* or *Ornithorhynchus*. The rhinal fissure is poorly represented on the ventral surface of the endocasts of *Obdurodon* and *Ornithorhynchus*. It is most visible on the juvenile platypus endocast. Lateral to the anterior portion of the trigeminal nucleus is the cast of the internal auditory meatus for cranial nerves VII and VIII (Archer et al., 1992). In posterior view, the foramen magnum appears relatively taller in the adult *Ornithorhynchus* compared to *Obdurodon* (Fig. 5).

The average adult monotreme encephalization quotient (EQ; Jerison, 1973) calculated using the

equation of Eisenberg (1981) is 0.87 (range: 0.75–1.00; Table 5), which is fairly close to the average for mammals (1.00). Comparing adult monotremes only, Ornithorhynchidae has a higher average EQ than Tachyglossidae (0.92 vs. 0.82; Table 5). The EQ of *Obdurodon* is 1.00, which is higher than the adult extant platypus (0.84; Table 5). The juvenile platypus has an EQ that is nearly half that of the adult sampled, suggesting that the endocranial volume (EV) shows positive allometry with body size from the stage when all teeth are present throughout adulthood.

DISCUSSION

Potential Synapomorphies for Monotremata and Ornithorhynchidae

Similarities between the cranial endocasts of *Obdurodon* and *Ornithorhynchus*, suggest that *Obdurodon* shared many neurological features with its extant relative; some of these features are possibly unique to Ornithorhynchidae. Similarly, the endocasts of the two extant species of echidnas are nearly identical except for differences in size, hence only the endocast of *Tachyglossus* is figured here (Fig. 7). At first glance, the brains and endocasts of echidnas (Fig. 7) and platypuses (Figs. 3, 4) look very different (e.g., echidna brains and endocasts are gyrencephalic [=convoluted], while those of platypuses are lissencephalic [=smooth]); however, upon further examination it is evident that Tachyglossidae and Ornithorhynchidae share

TABLE 4. Linear and angle measurements from endocasts

Taxon	Endocast flexure	Endocast length, width, height	Olfactory bulb casts length, width,* height	Hypophysis length, width, height
<i>Obdurodon</i>	40°	44.880, 34.678, 25.672	7.480, 11.490, 9.213	6.600, 4.555, 2.277
<i>Ornithorhynchus</i> (adult)	52°	32.760, 30.501, 22.685	4.620, 7.647, 5.353	4.410, 2.634, 2.209
<i>Ornithorhynchus</i> (juvenile)	42°	25.798, 25.008, 18.756	4.241, 6.961, 6.188	3.416, 2.320, 1.289
<i>Tachyglossus</i>	43°	47.100, 39.350, 28.212	8.400, 21.419, 7.711	9.450, 5.324, 2.142
<i>Zaglossus</i>	49°	53.550, 50.560, 35.592	12.425, 28.216, 12.174	7.000, 5.085, 1.432

All linear measurements given in mm.

*, Combined olfactory bulb width.

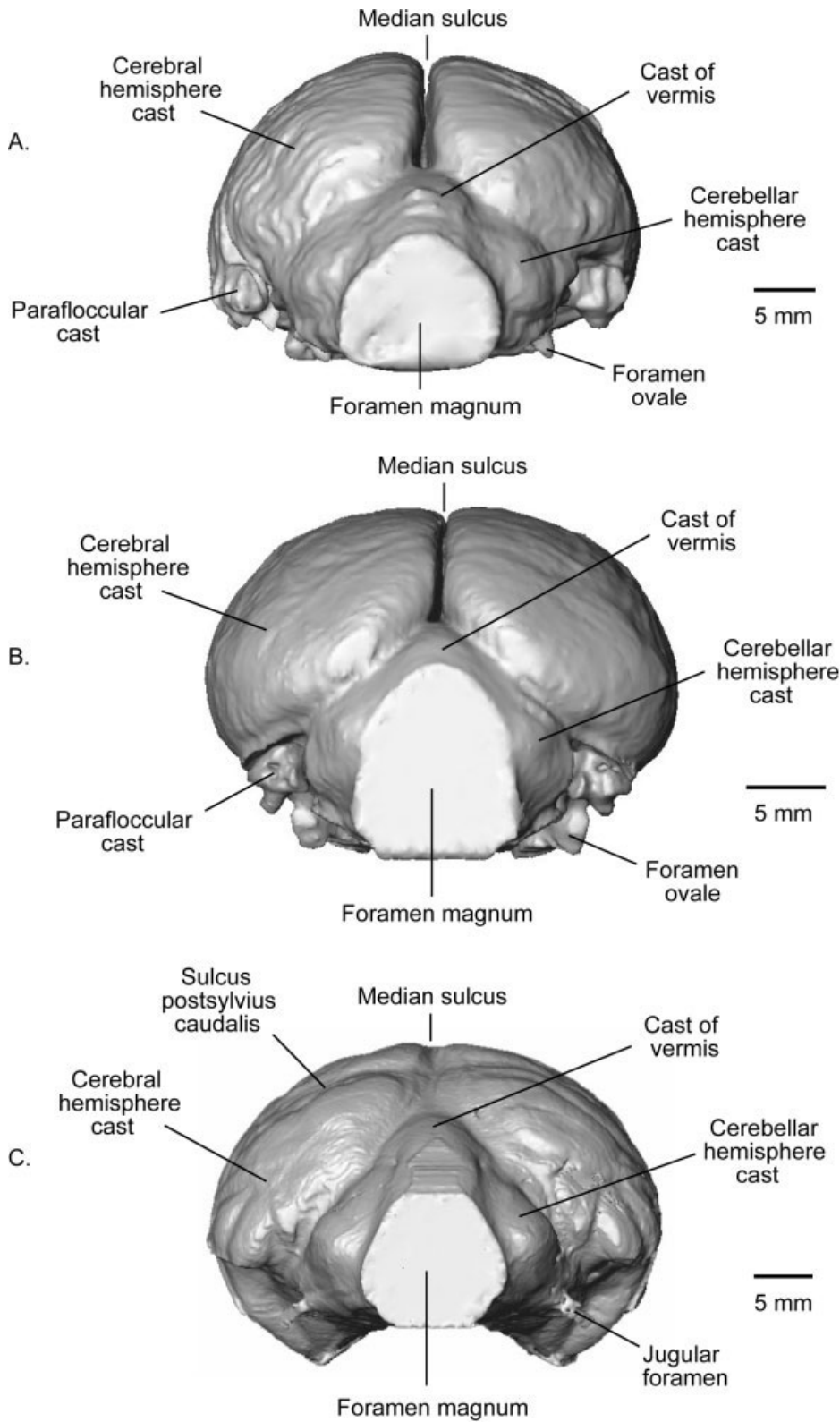


Fig. 5. Digital renderings of posterior views of cranial endocasts: (A) *Obdurodon dicksoni*, (B) adult *Ornithorhynchus anatinus* (AMNH 200255), (C) *Tachyglossus aculeatus* (AMNH 154457). Note that scale is different for each image.

some neurological characters that are potential synapomorphies for crown Monotremata.

Both *Obdurodon* and *Ornithorhynchus* have relatively small olfactory bulb casts. The terrestrial

tachyglossids, however, have relatively larger olfactory bulbs comprising 2.28% of the EV of an adult *Tachyglossus aculeatus* and 3.08% of the EV of an adult *Zaglossus bruijnii* (Table 3). The olfac-

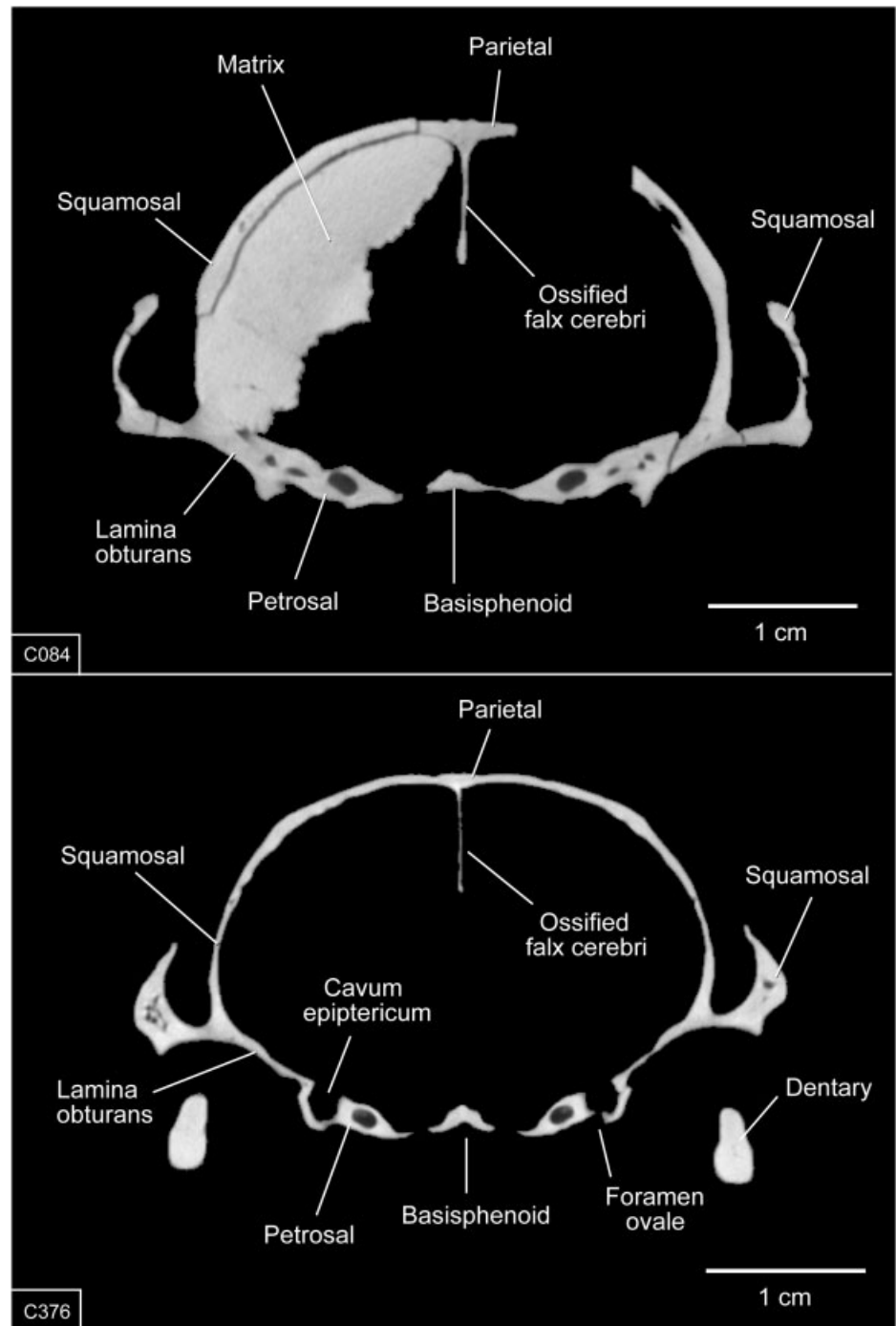


Fig. 6. Coronal CT images through the skull of *Obdurodon dicksoni* (top image) and an adult *Ornithorhynchus anatinus*, AMNH 200255 (bottom image) showing the ossified falx cerebri.

tory bulb casts of an adult female *Monodelphis domestica*, the gray short-tailed opossum, comprise 8.43% of the EV (Macrini, unpubl. obs.). Several fossil mammals outside crown Theria have large olfactory bulb casts (Kielan-Jaworowska, 1986) but the condition for nonmammalian cynodonts is somewhat uncertain, partly a result of lack of ossification of the cribriform plate in those taxa (Rowe, 1996a,b). However, a reconstruction of the endocast of *Morganucodon*

(Zielan-Jaworowska et al., 2004) and other unpublished data suggest that the presence of relatively large olfactory bulbs is the primitive condition for Mammalia.

In addition to reduced olfactory bulb casts, both *Ornithorhynchus* and *Obdurodon* have three endoturbinals, but *Tachyglossus* has seven (Paulli, 1900). A preliminary survey of many mammalian species suggests that endoturbinial surface area corresponds to olfactory acuity and olfactory bulb size

TABLE 5. Encephalization quotient values calculated from endocranial volumes including and excluding the olfactory bulbs using two different equations

Taxon	EV/(0.12[Wt] ^{0.67}) ^A	EV/(0.055[Wt] ^{0.74}) ^B
<i>Obdurodon dicksoni</i> ¹	0.78	1.00
<i>Obdurodon dicksoni</i> ²	0.77	0.98
<i>Ornithorhynchus anatinus</i> (adult) ¹	0.64	0.84
<i>Ornithorhynchus anatinus</i> (adult) ²	0.63	0.83
<i>Ornithorhynchus anatinus</i> (juvenile) ¹	0.39	0.53
<i>Ornithorhynchus anatinus</i> (juvenile) ²	0.38	0.52
<i>Tachyglossus aculeatus</i> ¹	0.62	0.75
<i>Tachyglossus aculeatus</i> ²	0.60	0.73
<i>Zaglossus bruijni</i> ¹	0.76	0.89
<i>Zaglossus bruijni</i> ²	0.74	0.86

Equation A from Jerison (1973). Equation B from Eisenberg (1981). Endocranial volumes and body mass estimates are listed in Table 3. EQ, encephalization quotient; EV, endocranial volume; Wt, weight or body mass.

¹EQ calculated with olfactory bulbs.

²EQ calculated without olfactory bulbs.

(Rowe et al., 2005). Reduction of the olfactory bulbs is therefore a potential apomorphy of Ornithorhynchidae, possibly correlated with reduced olfactory turbinates as a result of aquatic habitat use (Pirlot and Nelson, 1978; Zeller, 1988). Many aquatic placental mammals, in particular cetaceans and sirenians, also have great reduction or complete loss of the main olfactory bulb (Meisami and Bhatnagar, 1998; Colbert et al., 2005). Thus, reduction or loss of olfactory bulbs has occurred independently in multiple lineages of mammals.

The trigeminal nerve of monotremes passes through 14 foramina in the skull and mandible of both the platypus and echidnas en route to innervating the upper and lower jaws or bills (Huber, 1930; Musser and Archer, 1998). Enlargement of the trigeminal nerve is evident on the cranial endocasts of *Obdurodon* and *Ornithorhynchus* by the large cast of the canal transmitting V₂ and the large foramen ovale for passage of V₃. The canal leading to the sphenorbital fissure is also enlarged, but besides V₁ a number of other nerves and vessels pass through this canal. In addition, the maxillary canal is large in *Obdurodon* and *Ornithorhynchus* to accommodate the infraorbital branch of V₂ along with the infraorbital artery and vein (Zeller, 1989a; Fig. 8). The trigeminal nerve and corresponding canals are also enlarged in the two extant species of echidna but not to the extent seen in members of Ornithorhynchidae. A large trigeminal nerve is also present in other secondarily aquatic mammals (Zeller, 1988) and, therefore, it is possible that this character in Ornithorhynchidae is convergent with an aquatic lifestyle.

The axons of the trigeminal nerve project to the trigeminal nucleus and the cell bodies are bundled in the trigeminal ganglion, a structure that sits in the cavum epiptericum (Butler and Hodos, 1996). The trigeminal nerve, ganglion, and nucleus together comprise the trigeminal complex. The presence of a trigeminal complex that is enlarged com-

pared to that in other mammals is a possible synapomorphy for monotremes.

Obdurodon and *Ornithorhynchus* both have large trigeminal nucleus casts. In *Ornithorhynchus* the trigeminal sensory nuclei are responsible for these bulges off the medulla oblongata of the hindbrain (Hines, 1929). These nuclei presumably account for the bulges on the *Obdurodon* endocast as well. The trigeminal sensory nucleus is also enlarged in *Tachyglossus* but not to the extent seen in the extant platypus (Abbie, 1934). The trigeminal nucleus does not leave a noticeable impression on the endocast of either species of echidna, unlike the condition seen in the *Ornithorhynchus* and *Obdurodon* endocasts (Abbie, 1934; Brauer and Schober, 1970; Fig. 7). Therefore, the presence of an enlarged trigeminal nucleus cast that is visible on endocasts is a synapomorphy for Ornithorhynchidae.

The monotreme specimens measured in this study all have large cava epipterica that comprise greater than 1% of endocranial space (range, 1.09–1.34%). *Ornithorhynchus* has a large trigeminal ganglion that fits into a correspondingly large cavum epiptericum. *Obdurodon* also has a large cavum epiptericum and presumably had a large trigeminal ganglion. The cavum epiptericum can only be used as a proxy for the size of the trigeminal ganglion in *Obdurodon* because other ganglia and nerves likely occupied portions of this space. The geniculate ganglion (nerve VII), the rostral portion of the otic ganglion (nerve VIII), and segments of nerves III, IV, V, VI, and VII occupy portions of the cavum epiptericum in *Ornithorhynchus* (Zeller, 1989b), and presumably the same is also true for *Obdurodon*. The cavum epiptericum and corresponding trigeminal ganglion are large in echidnas as well (Abbie, 1934; Fig. 7) but, unlike in the platypus, this space does not encompass the geniculate ganglion (Kuhn, 1971; Zeller, 1989a).

The extant platypus has electroreceptors in its bill that are innervated by the large trigeminal nerve

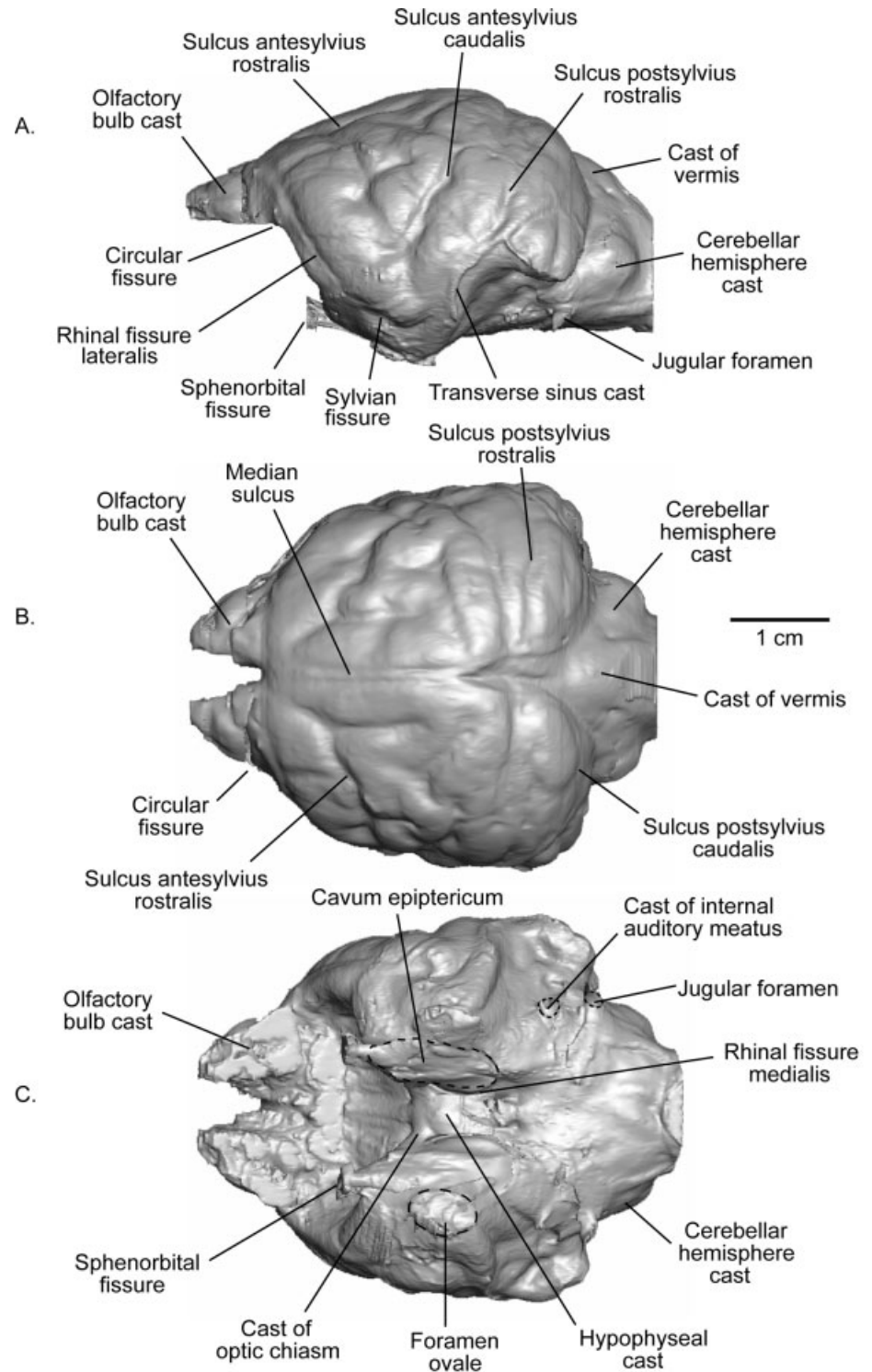


Fig. 7. Digital rendering of the cranial endocast from a *Tachyglossus aculeatus* (AMNH 154457) shown in left lateral (A), dorsal (B), and ventral (C) views.

(Scheich et al., 1986; Bohringer, 1992). *Ornithorhynchus* relies on electroreception as well as tactile receptors in its bill for underwater navigation, because the eyes, ears, and olfactory organs are covered while the animal is submerged (Griffiths, 1978; Scheich et al., 1986; Bohringer, 1992). Behavioral and histological studies suggest that both *Tachy-*

glossus and *Zaglossus* also have electroreceptors that are innervated by the trigeminal nerve (Abbie, 1934; Griffiths, 1968; Augée and Gooden, 1992; Manger et al., 1997; Proske et al., 1998). The presence of an electroreception system in *Obdurodon* remains speculative, although the similarities in casts of the trigeminal complex and facial skeleton

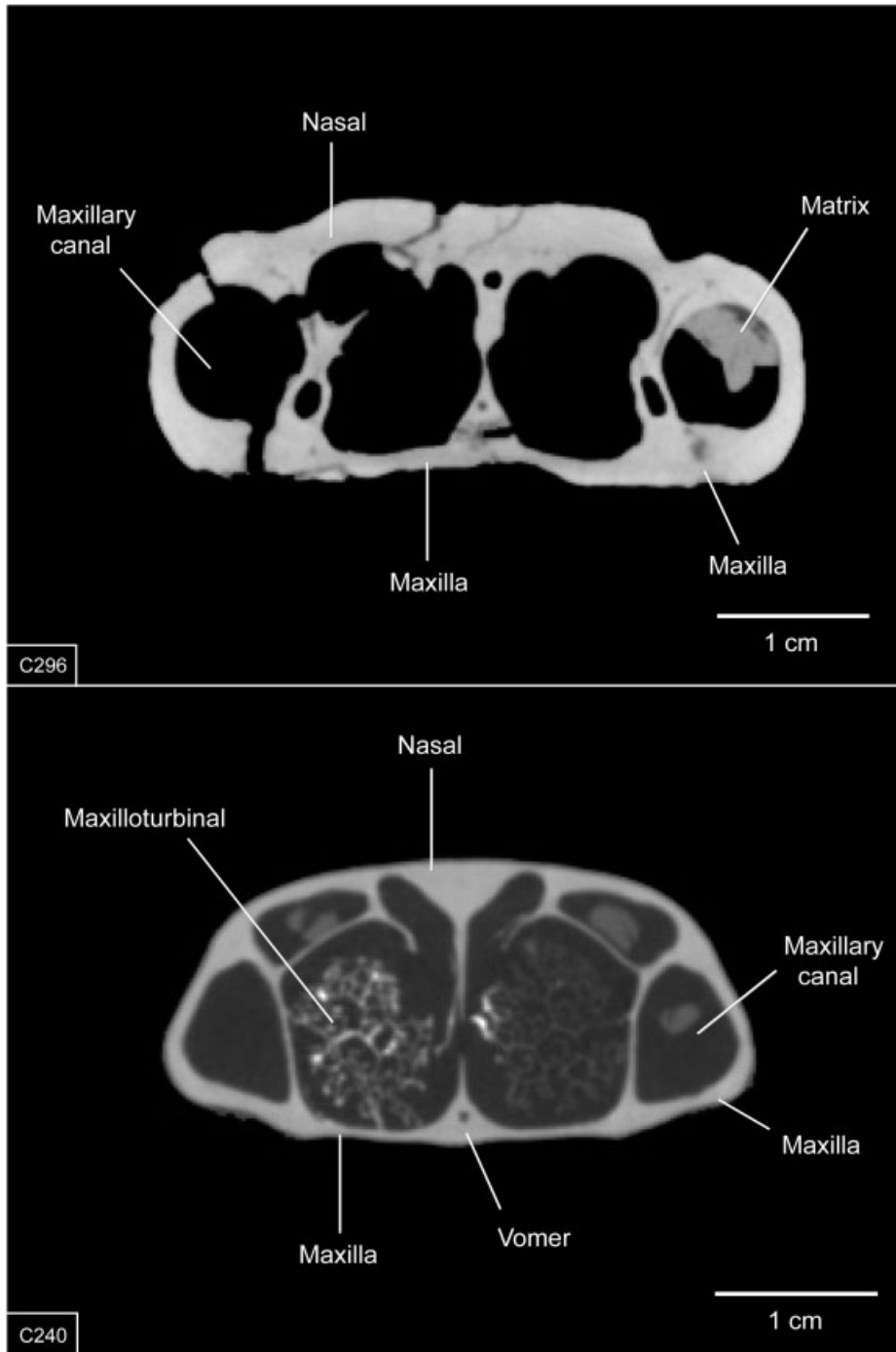


Fig. 8. Coronal CT images through the snout of *Obdurodon dicksoni* (top image) and an adult *Ornithorhynchus anatinus*, AMNH 200255 (bottom image) showing the maxillary canal.

in the extant and extinct platypus suggest that *Obdurodon* had a bill that was well innervated by the trigeminal nerve that was also involved in electroreception.

Electroreception is a synapomorphy for Vertebrata but has been lost and reacquired multiple times within the lineage. In anamniote vertebrates with a lateral line system (e.g., lampreys, chondrichthyans, crossopterygians, polypterids, some teleosts, lungfish, some amphibians), the electrorecep-

tors are innervated by accessory cranial nerves (i.e., lateral line nerves; Bullock et al., 1983; Fritzsche and Münz, 1986; Feng, 1991). The lateral line system and electroreception was lost in Amniota ancestrally (Schlosser, 2002).

Electroreceptors in monotremes are associated with specialized cutaneous glands and are innervated by the trigeminal nerve (Andres and von Düring, 1988). Electroreception is not known for any therian mammal. However, electroreception was re-

ported in the semiaquatic and fossorial star-nosed mole, *Condylura cristata*, based on limited behavioral data (Gould et al., 1993). Subsequent behavioral studies have not corroborated these results nor have anatomical studies (Catania, 2000). The enlarged trigeminal nerve and Eimer's organs in the snout of *C. cristata* are involved in mechanoreception, but there is no evidence of exposure of nerve terminals to the environment, a component of electroreceptor systems (Catania, 2000). Thus, electroreception in monotremes is independently derived from that of amniotes and an electroreception system innervated by the trigeminal nerve is a probable synapomorphy for crown Monotremata.

Another potential synapomorphy for Monotremata is the location of the pons behind the insertion of the trigeminal nerve (Griffiths, 1968, 1978). In all placental and marsupial taxa studied so far the pons lies in front of the trigeminal nerve insertion. Cranial endocasts from two multituberculate mammals (*Chulsanbaatar* and *Nemegtbaatar*) were reported to also show the pons lying completely behind the insertion of the trigeminal nerve (Kielan-Jaworowska, 1986). However, the casts of the pons are not conspicuous on these specimens (based on the description and illustrations presented in Kielan-Jaworowska [1986]) and their exact positions are open to interpretation. The pons also does not leave a pronounced signature on monotreme endocasts and therefore this character cannot be assessed for *Obdurodon*.

SUMMARY AND CONCLUSIONS

This description of the cranial endocast of the fossil species *Obdurodon*, which is represented by a single specimen, was made possible by the nondestructive nature of CT technology. This technology also allows for the relatively easy acquisition of accurate volume and linear measurements and is therefore useful for studying endocasts of both fossil and extant specimens alike. The measurements reported here may prove valuable in future comparative studies of mammalian endocasts; however, the variability of these endocast measurements within a single species (e.g., *Ornithorhynchus anatinus*) remains to be explored.

The new data from this description of the *Obdurodon* endocast allows us to sample endocasts from all of the taxa of crown Monotremata from which braincase material is known. The potential neurological synapomorphies for Monotremata resulting from this comparison are the presence of a relatively large trigeminal complex, the presence of electroreceptors that are innervated by the trigeminal nerve, and the pons lying completely behind the point of insertion of the trigeminal nerve into the hindbrain. Examination of these characters in a broader taxonomic context (Mammalia and its closest extinct outgroups) will more rigorously determine their po-

larity with respect to Monotremata. Because all of these characters are related to the trigeminal nerve complex, it is also possible that they are phylogenetically correlated. This can also be addressed in future analyses.

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