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ARTICLE

DIGITAL CRANIAL ENDOCAST OF *PUCADELPHYS ANDINUS*, A PALEOCENE METATHERIAN

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ABSTRACT—A digital cranial endocast of *Pucadelphys andinus*, a Paleocene metatherian from Bolivia, is described. This is the first cranial endocast described for the taxon and the only one (to date) from a stem marsupial (i.e., non-marsupial metatherian). The *Pucadelphys* endocast is compared with others generated from skulls from six taxa of extant marsupials (*Monodelphis domestica*, *Didelphis virginiana*, *Dasyurus hallucatus*, *Vombatus ursinus*, *Phascolarctos cinereus*, and *Dromiciops australis*). The *Pucadelphys* endocast is generally similar to the didelphid marsupial *Monodelphis*. However, the olfactory bulb casts and the cerebellar space (approximated using vermis cast length) of *Pucadelphys* are relatively large in comparison to those of these extant marsupials. The cerebral hemisphere casts of *Pucadelphys* are dorsoventrally thin in comparison to those of the extant marsupials examined here. With other dimensions of the cerebral hemisphere casts being comparable between *Pucadelphys* and the extant marsupials, this suggests that the overall volume of the cerebral hemispheres was smaller in *Pucadelphys*. Thus, two possible synapomorphies for crown Marsupialia are a decrease in size of the cerebellar space and an increase in cerebral hemisphere volume.

INTRODUCTION

A cranial endocast is the three-dimensional representation of the endocranial space or space within the endocranial cavity of a particular skull. Endocranial space in mammals is bounded anteriorly by the cribriform plate and comprises the confluent ethmoidal, cerebral, and cerebellar cavities. The brains of most mammals largely fill this endocranial space leaving an impression on the internal surfaces of skull bones (Jerison, 1973). Besides the brain, the endocranial cavity also houses other soft tissue structures such as the meninges, blood vessels, and nerves, and therefore, 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.

The study of cranial endocasts is important for at least a couple of reasons. First, the brain is the organ in which sensory information and motor functions are coordinated and study of the sensory systems of organisms is important for understanding behavior of those organisms. Therefore, the evolution of behavior is tied to the evolution of the brain, and cranial endocasts are useful for studying the behavior of extinct animals, particularly mammals. Second, cranial endocasts represent a potentially large amount of unexplored phylogenetic data. The majority of morphological data for mammal and cynodont phylogenetic analyses comes from the exterior of the skull, including the dentition (e.g., Luo et al., 2001a, b, 2002, 2003; Kielan-Jaworowska et al., 2004; Luo and Wible, 2005). Internal cranial morphology is poorly represented in phylogenetic analyses because of the difficulty in visualizing and studying this anatomy. High-resolution computed tomography (CT) makes the internal cranial osteology and cranial cavities of fossil or unique specimens more accessible for study (e.g., Rowe et al., 1995; Brochu, 2000; Larsson et al., 2000; Tykoski et al., 2002, Witmer et al., 2003; Maisey, 2004, 2005; Van Valkenburgh et al., 2004; Franzosa and Rowe, 2005).

One goal of this article is to explore the evolution of sensory structures in the brain in early marsupial phylogeny. This is accomplished in part through a description of a digital cranial endocast of *Pucadelphys andinus* from the early Paleocene of Bolivia (Marshall and Muizon, 1988; Muizon, 1992; Marshall et al., 1995). *Pucadelphys andinus* is a member of Metatheria, the lineage that includes Marsupialia and its closest extinct relatives (herein we use a crown definition of Marsupialia, to include the last common ancestor of all living taxa, plus all of its descendants). Metatheria extends back to at least the Early Cretaceous with the earliest members of this clade represented by fossils from North America, Mongolia, and China (Luo et al., 2003; Kielan-Jaworowska et al., 2004).

Pucadelphys is arguably the best preserved stem marsupial (i.e., non-marsupial metatherian), represented by multiple, nearly complete, three-dimensional skulls and skeletons (Muizon, 1992; Marshall and Muizon, 1995; Marshall and Sigogneau-Russell, 1995; Muizon, 1998). A recent phylogenetic analysis places *Pucadelphys* in a polytomy with other stem marsupials and crown Marsupialia (Luo et al., 2003). Other stem marsupials, such as *Asiatherium reshetovi* from the Late Cretaceous of Mongolia (Szalay and Trofimov, 1996) and *Sinodelphys szalayi* from the Early Cretaceous of China (Luo et al., 2003), are fairly complete but are not known from three-dimensional specimens. *Deltatheridium* is represented by specimens that only preserve the rostral portion of the skull, dentition, and incomplete tarsals (Rougier et al., 1998; Horovitz, 2000; Luo et al., 2002).

The extracranial anatomy and postcranial osteology of *Puca-*

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delphys andinus are well documented in the literature (Muizon, 1992; Marshall and Muizon, 1995; Marshall and Sigogneau-Russell, 1995; Muizon, 1998), but the internal cavities of its skull, including the endocranial cavity, are undescribed. In fact, no cranial endocast (natural or artificial) has yet been described for any stem marsupial. The digital cranial endocast of *Pucadelphys andinus* described in this paper represents the oldest and most basally diverging taxon within the metatherian lineage for which a cranial endocast can be studied. Therefore, this endocast is useful for polarizing phylogenetic characters pertaining to endocranial space with respect to Marsupialia. To this end, the *Pucadelphys* endocast was compared with endocasts extracted from skulls of extant marsupials. Optimization of these characters on a phylogenetic framework is part of a larger effort to study the evolution of endocranial space and the brain in mammals (Macrini, 2006).

Institutional Abbreviations—**FMNH**, Field Museum, Chicago, Illinois, U.S.A.; **MHNC**, Museo de Historia Natural de Cochabamba, Cochabamba, Bolivia; **TMM M**, Recent mammal collections of the Vertebrate Paleontology Laboratory, Texas Memorial Museum, Austin, Texas, U.S.A; **UTCT**, University of Texas High-Resolution X-ray Computed Tomography Facility, Austin, Texas, U.S.A.

MATERIALS AND METHODS

Specimens Examined

The digital endocast described below was extracted from a skull of *Pucadelphys andinus* (MHNC 8266). The specimen was collected from a site called "the Quarry" in the lower Paleocene Santa Lucía Formation at Tiupampa, Mizque Province, Department of Cochabamba, south-central Bolivia (Marshall and Muizon, 1988; Marshall et al., 1995). The skull is essentially complete with minor damage to the palate, the right zygomatic portion of the squamosal, and the nasals and surrounding bones of the roof of the snout (Fig. 1). There is very little distortion to the skull. This skull measures 30.64 mm from the anterior tip of the premaxillae to the back of the occiput. Based on its full set of dentition, this specimen represents an adult individual at the time of death.

Body mass for the individual represented by this specimen of *Pucadelphys andinus* was estimated at 49 g. The estimate was derived by taking an average of masses of several specimens of 90-day-old *Monodelphis domestica*, gray short-tailed opossum, which have nearly identical skull lengths with that of this specimen of *Pucadelphys*.

The *Pucadelphys* endocast was compared to digital endocasts extracted from skulls of the following extant marsupials: *Monodelphis domestica* (gray short-tailed opossum; Didelphidae), *Didelphis virginiana* (Virginia opossum; Didelphidae), *Dasyurus hallucatus* (northern quoll; Dasyuromorphia), *Vombatus ursinus* (common wombat; Diprotodontia), *Phascolarctos cinereus* (koala; Diprotodontia), and *Dromiciops australis* (monito del monte; Microbiotheriidae). See Table 1 for specimen numbers.

About Computed Tomography Scanning

All skulls for this study were scanned at UTCT. High-resolution CT uses differential attenuation of X-rays passed through a specimen to differentiate between bone and other material to produce two-dimensional images (i.e., slices) that reveal internal details of specimens (for a detailed description of CT, see Denison et al., 1997 and Table 2). Consecutive equidistant two-dimensional slices provide a three-dimensional digital map of the specimen that can be manipulated using a variety of image processing techniques and software.

The *Pucadelphys* skull was scanned in its entirety in the horizontal slice plane from top to bottom. The scanning resulted in 114 slices with dimensions of 512 x 512 pixels. The images are 0.1 mm thick with an interslice spacing (the space between consecutive slices) of 0.1 mm. The field of reconstruction for the two-dimensional slices is 35.1 mm.

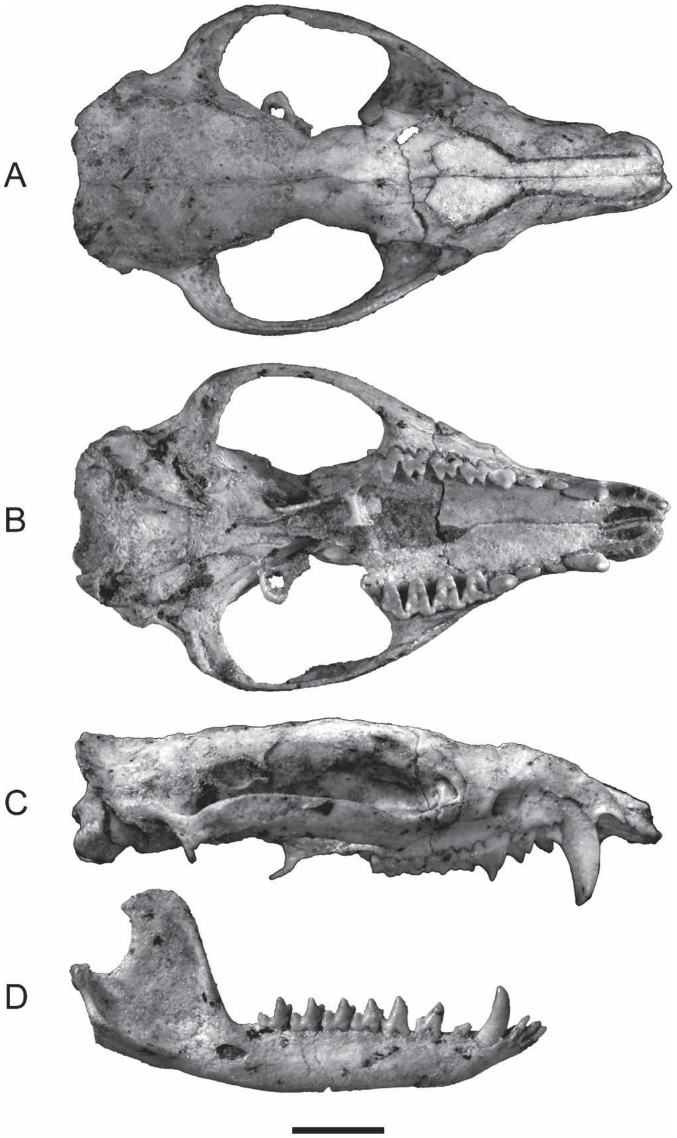

FIGURE 1. The skull of *Pucadelphys andinus* (MHNC 8266). **A**, dorsal; **B**, ventral; **C**, right lateral views of skull; **D**, right lateral view of the mandible. Scale bar equals 5 mm.

Extraction of Endocasts

The digital endocasts were generated using the program VGStudioMax© (version 1.2; Volume Graphics GmbH, 2004). VGStudioMax© is a program designed for the analysis and visualization of voxel data that allows the user to digitally segment (in the jargon of informatics) portions of volumetric datasets. We used the magic wand tool of the 'segmentation menu' of VGStudioMax© to select the endocranial space of each skull, and we used the lasso tool, also of the segmentation menu, to fine-tune the selections. Lines were drawn to seal off openings in the braincase, 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

TABLE 1. Volumes from endocasts used in this study.

Taxon	Specimen no.	Gender	BM	EF	EV	OB volume*	PF volume*	HP volume
Pucadelphys andinus	MHNC 8266	?	49.0^{A}	26°	311.506	36.41	2.971	1.687
Dasyurus hallucatus	TMM M-6921	♀	401.0	34°	3339.751	265.761	45.512	1.264
Didelphis virginiana	TMM M-2517	♂	2800^{B}	40°	6608.008	729.531	39.166	31.375
Dromiciops australis	FMNH 127463	♀	21.5	36°	820.999	29.684	11.867	0.277
Monodelphis domestica	TMM M-7599	♀	80.4^{C}	46°	954.777	76.401	10.544	5.558
Monodelphis domestica	TMM M-8271	♀	89.5	46°	987.894	80.249	11.491	2.871
Monodelphis domestica	TMM M-8273	♂	110.0	38°	956.059	80.582	11.343	2.358
Phascolarctos cinereus	TMM M-2946	?	9500^{D}	24°	26275.291	671.817	110.780	18.228
Vombatus ursinus	TMM M-2953	?	25000^{E}	36°	63553.504	1995.414	n/a	42.579

Body mass given in g. Volumes given in mm^{3}.

Abbreviations: $^{\mathbf{A}}$, mass estimate based on *Monodelphis domestica* of similar size (see Materials and Methods); $^{\mathbf{B}}$, average mass for adult males from McManus (1974); $^{\mathbf{C}}$, mass estimate based on equation derived from plot of skull length vs. body mass in adult *M. domestica* (Macrini, 2006); $^{\mathbf{D}}$, mass average of adults from Nowak (1991); $^{\mathbf{E}}$, mass average of adults from Nowak (1991); **BM**, body mass; **EF**, endocast flexure; **EV**, endocranial volume for entire endocast, including hypophyseal fossa, olfactory bulb casts, and parafloccular casts; **HP**, hypophyseal fossa; **OB**, olfactory bulb cast; **PF**, parafloccular cast; *, volume data presented are combined for bilateral structures.

bone. The same procedure was used to segment portions of the endocast representing distinctive structures such as the olfactory bulb casts, parafloccular casts, and hypophyseal fossa casts.

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. Measurements are given to the third decimal place in this paper because this is how VGStudioMax© provides numbers. Bony markers in the braincase serve as proxies for boundaries of soft tissue structures (e.g., cribriform plate for anterior edge of olfactory bulbs). The anterior end of the olfactory bulb casts of *Pucadelphys* was estimated from the broken cribriform plate. 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 (= transverse of some authors) plane. 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 measurements of the vermis and cerebral hemisphere casts were taken using the linear measurement tool in Amira 3.1™ (Zuse Institute Berlin, 2004).

The relative proportions of different regions of the endocasts are expressed as percentages of the total endocranial volume (e.g., percent of endocranial space composed of the olfactory bulb casts). Although proportions and ratios are often criticized in the literature, their use is appropriate in this situation because the intention is to determine the relationship between two variables (e.g., olfactory bulb cast volume and endocranial volume) to express proportionality and not to provide statistical control for the variance of one factor in relation to another (Smith, 2005).

Endocast flexure was measured in lateral view by taking the acute angle between two lines, both of which pass through the hypophyseal cast (Fig. 2). 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.

Movie frames were exported to National Institutes of Health ImageJ where they were cropped and rotated as necessary. The frames were then exported to QuickTime™ 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 (see Table 2).

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 paper for aesthetic purposes only. We obtained all volume measurements prior to smoothing the endocasts.

DESCRIPTION

The overall morphology of the *Pucadelphys* endocast (Fig. 3) is similar to that of the didelphid marsupial *Monodelphis domes-*

TABLE 2. Relevant web page addresses.

Description	Web address
UTCT web site	www.ctlab.geo.utexas.edu/index.php
Digimorph homepage	www.digimorph.org
Pucadelphys CT movies	www.digimorph.org/specimens/Pucadelphys_andinus
Monodelphis (TMM M-7599) CT movies	www.digimorph.org/specimens/Monodelphis_domestica/adult/
Monodelphis (TMM M-8273) CT movies	www.digimorph.org/specimens/Monodelphis_domestica/whole/
Didelphis CT movies	www.digimorph.org/specimens/Didelphis_virginiana/
Dasyurus CT movies	www.digimorph.org/specimens/Dasyurus_hallucatus/
Dromiciops CT movies	www.digimorph.org/specimens/Dromiciops_gliroides/
Phascolarctos CT movies	www.digimorph.org/specimens/Phascolarctos_cinereus/
Vombatus CT movies	www.digimorph.org/specimens/Vombatus_ursinus/

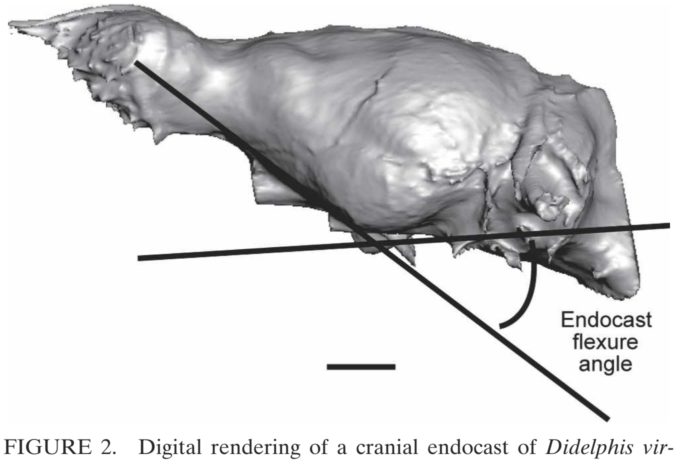

FIGURE 2. Digital rendering of a cranial endocast of *Didelphis virginiana* (TMM M-2517) shown in left lateral view and illustrating how endocast flexure was measured. Scale bar equals 5 mm.

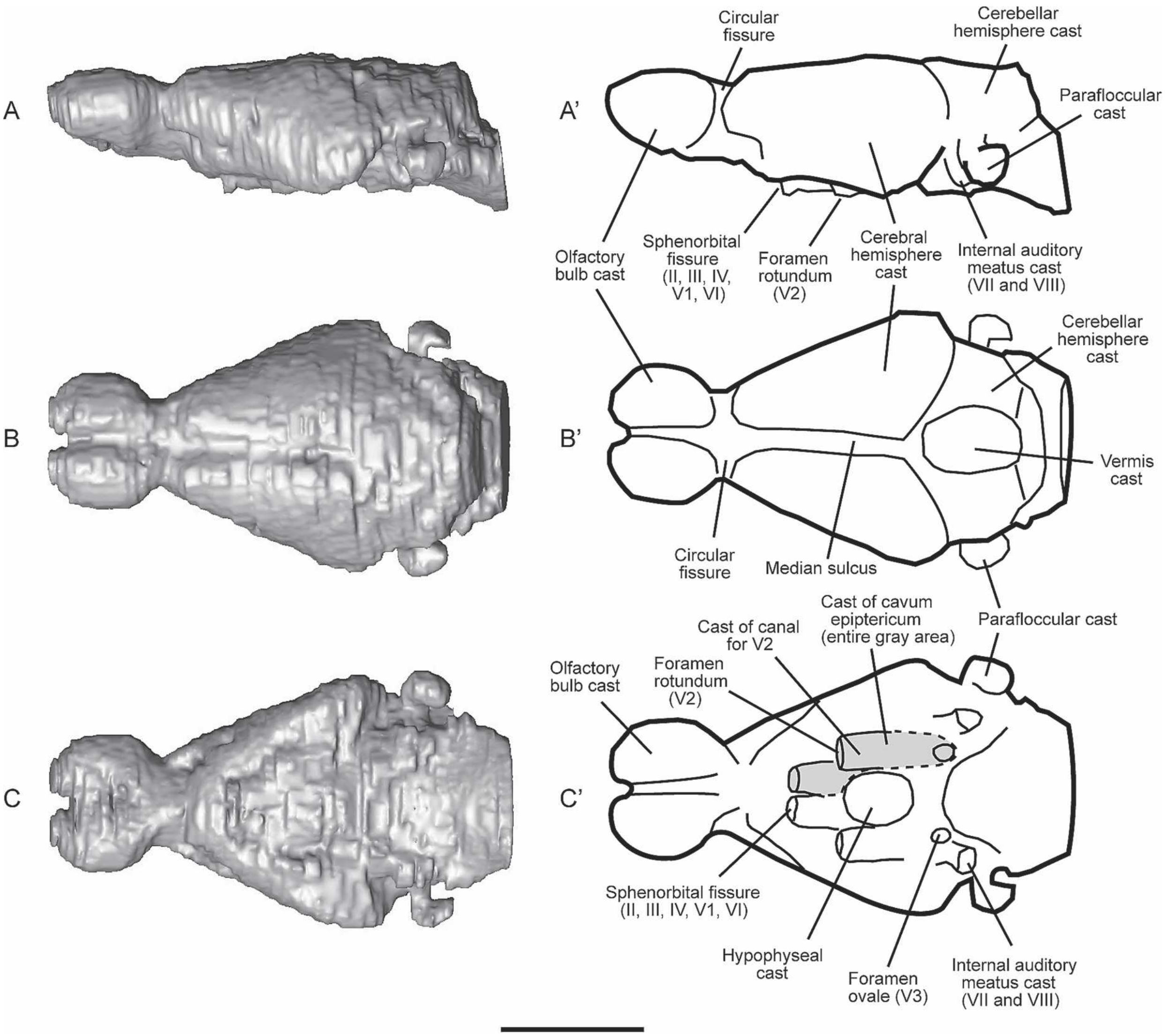

FIGURE 3. Digital rendering of the cranial endocast of *Pucadelphys andinus* (MHNC 8266). **A**, left lateral view; **B**, dorsal view; **C**, ventral view. Line drawings of the cranial endocast with anatomical labels. **A'**, left lateral view; **B'**, dorsal view; **C'**, ventral view. Scale bar equals 5 mm.

tica (Fig. 4). In dorsal view, the *Pucadelphys* endocast is wedge-shaped with large, spherical olfactory bulb casts on its anterior terminus (Fig. 3). In lateral view, the endocast is low and shows flexure of 26º around the hypophyseal cast (see Table 1; Fig. 3A). A rhinal fissure is not visible on the lateral surface or anywhere else on the endocast. The width/length endocast aspect ratio is 0.58, the height/length ratio is 0.44, and the height/width ratio is 0.75. See Table 1 for volumes and partial volumes of *Pucadelphys* and other endocasts used in this study. Table 3 provides linear measurements from all endocasts used in this study.

The olfactory bulb casts are relatively large (see Fig. 3), together composing about 11.69% of the total endocranial space. The casts are ovoid in shape with a width/length aspect ratio of 0.62. The circular fissure (sensu Loo, 1930; Rowe 1996a, b; = transverse fissure of Krause and Kielan-Jaworowska, 1993) separating the olfactory bulb casts from the rest of the cerebral hemisphere casts is well developed (Figs. 3A, 3A', 3B, 3B'). The olfactory tracts from the bulbs and leading to the telencephalon do not leave an impression on the ventral surface of the endocast (Fig. 3C).

The cerebral hemisphere casts of *Pucadelphys* are lissencephalic (= smooth) and are divided by a deep median sulcus (Figs. 3A, 3A', 3B, 3B'). It is noteworthy that the sulcus is deeper in *Pucadelphys* (Fig. 3B) than in *Monodelphis* (Fig. 4B). The two cerebral hemispheres are triangular when viewed dorsally, being narrow anteriorly and expanding laterally toward their posterior ends (Figs. 3B, 3B'). The cerebral hemisphere casts of *Pucadelphys* do not expand as far laterally as in *Monodelphis*, whose casts extend beyond the lateral extent of the parafloccular casts of the cerebellum (compare Figs. 3, 4). The height/length aspect ratio of the cerebral hemisphere casts of *Pucadelphys* is 0.62. This ratio is much larger in the *Monodelphis* endocasts examined (range = 0.74–0.86; mean = 0.79; n = 3). However, the combined width/length aspect ratio for the cerebral hemisphere casts of *Pucadelphys* is 1.12, which is significantly different from the ratio in *Monodelphis* (range = 1.24–1.38; mean = 1.29; n = 3). The cerebral hemisphere cast length/total endocast length ratios are quite similar between *Pucadelphys* (0.51) and *Monodelphis* (range = 0.42–0.50; mean = 0.47; n = 3).

A large bulge on the posterior surface of the endocast covers the midbrain (Figs. 3B, 3B'); this structure is interpreted as the cast of the vermis of the cerebellum. The vermis cast of *Puca-*

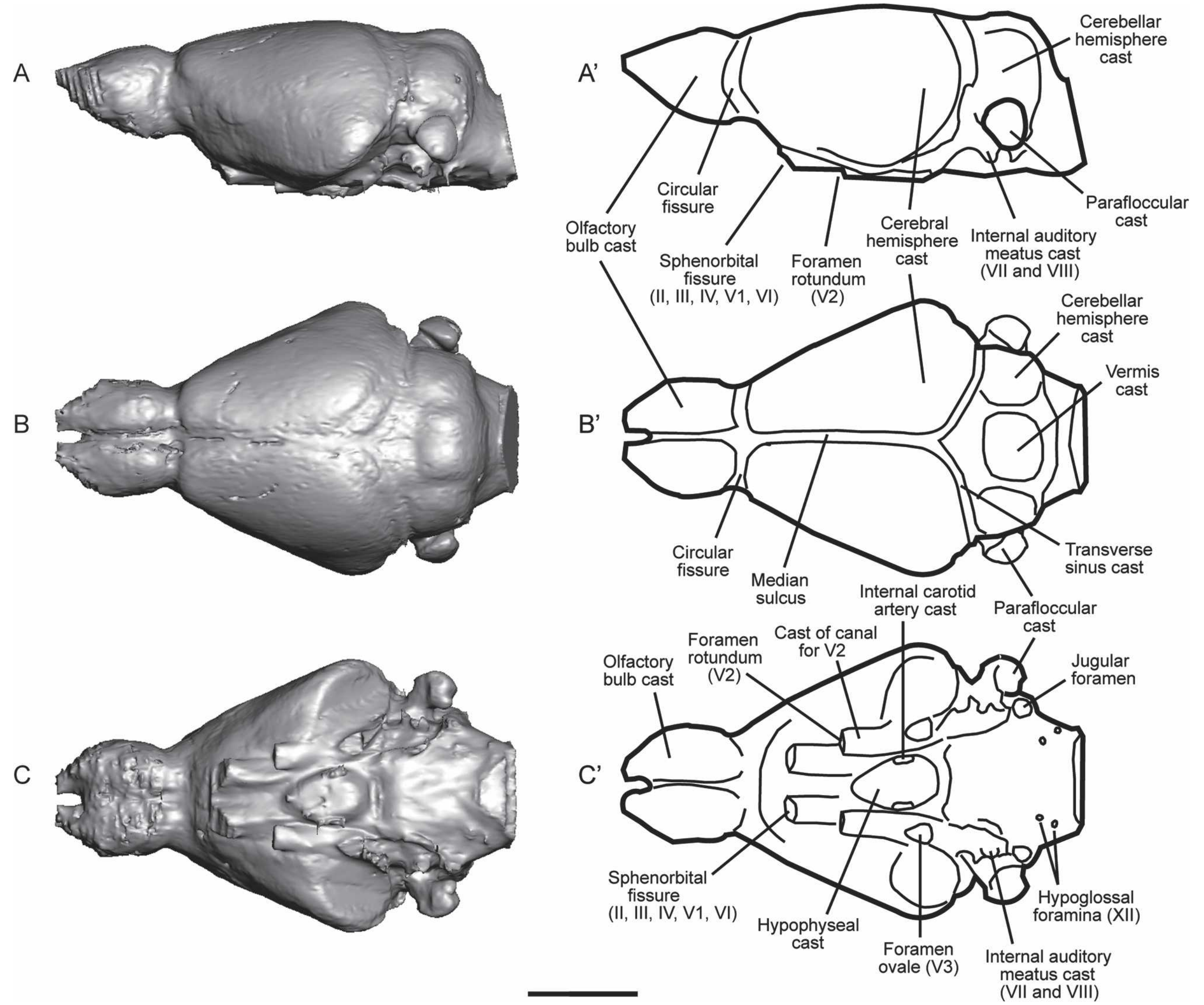

FIGURE 4. Digital rendering of a cranial endocast of *Monodelphis domestica* (TMM M-7599). **A**, left lateral view; **B**, dorsal view; **C**, ventral view. Line drawings of the cranial endocast with anatomical labels. **A'**, left lateral view; **B'**, dorsal view; **C'**, ventral view. Scale bar equals 5 mm.

delphys extends anterior to the casts of the paraflocculi and has a width/length ratio of 0.81, indicating that the structure has a somewhat anteroposteriorly elongate oval shape. Cerebellar hemisphere casts are also visible on the endocast (Figs. 3A, 3A', 3B, 3B'), but distinctive superior (dorsal) sagittal, transverse, and sigmoid sinuses are not visible. The parafloccular casts of the cerebellum are prominent (see Fig. 3), together constituting 0.95% of the endocranial space.

TABLE 3. Linear measurements from endocasts used in this study.

Taxon	Endocast: Length, Width, Height	Olfactory Bulb Casts: Length, Width,* Height	Hypophysis: Length, Width, Height	Vermis Cast: Length, Width	Cerebral Hemisphere Cast: Length, Width,† Height
Pucadelphys andinus	16.042, 9.323, 7.000	3.976, 4.936, 3.700	2.674, 2.948, 0.700	3.498, 2.816	8.107, 9.056, 5.025
Dasyurus hallucatus	32.222, 19.784, 16.153	7.448, 8.751, 7.401	1.264, 2.509, 2.002	4.059, 4.115	17.799, 19.185, 13.773
Didelphis virginiana	45.672, 26.211, 29.785	14.916, 12.708, 11.835	5.544, 4.527, 3.336	5.399, 3.926	23.015, 18.821, 16.320
Dromiciops australis	16.748, 12.633, 10.807	3.397, 5.156, 3.781	1.501, 0.881, 0.559	4.947, 3.543	11.028, 12.537, 9.000
Monodelphis domestica[a]	20.790, 13.156, 10.102	5.220, 5.747, 4.714	3.960, 3.143, 1.257	2.417, 3.367	10.466, 13.056, 8.090
Monodelphis domestica[b]	21.105, 13.073, 9.062	5.040, 5.625, 4.792	3.780, 2.552, 0.833	2.191, 3.021	10.283, 12.709, 7.657
Monodelphis domestica[c]	22.692, 13.188, 8.850	5.000, 6.014, 4.765	3.188, 2.536, 0.820	2.752, 3.068	9.490, 13.091, 8.130
Phascolarctos cinereus	64.260, 36.533, 29.535	8.568, 11.338, 13.857	4.522, 3.499, 2.100	7.208, 6.816	35.284, 34.275, 25.718
Vombatus ursinus	66.150, 52.078, 56.203	10.350, 22.172, 19.250	6.750, 5.328, 5.156	12.175, 8.317	46.087, 50.483, 33.905

All measurements given in mm.
Abbreviations: [a], specimen no. TMM M-7599; [b], specimen no. TMM M-8271; [c], specimen no. TMM M-8273.
*Combined olfactory bulb width.
†Combined cerebral hemisphere cast width.

A conspicuous wide, circular, shallow hypophyseal cast is present in the center of the ventral surface of the *Pucadelphys* endocast (Figs. 3C, 3C'). The hypophyseal cast composes about 0.54% of the entire endocranial space. The hypophyseal fossa is wider than long, with a width/length aspect ratio of 1.10.

The right and left casts of the canals that transmitted the maxillary branches of the trigeminal nerve (V_2) are widely separated and are located just anterolateral to the hypophyseal cast (Fig. 3C'; Marshall and Muizon, 1995). The foramen rotundum (Figs. 3A', 3C') is the opening in the skull through which passed V_2. The sphenorbital fissure (= optic-orbital foramen), which transmitted cranial nerves II, III, IV, V_1, VI, the ophthalmic artery, and a vein (Marshall and Muizon, 1995), is located anteromedial to the foramen rotundum (Fig. 3C'). The right and left casts for the exit of these nerves in the endocast are in proximity to each other but are not confluent.

The foramen ovale lies anteromedial to the internal auditory meatus cast and posterolateral to the hypophyseal cast (Fig. 3C'). This opening transmitted the mandibular branch of the trigeminal nerve (V_3; Marshall and Muizon, 1995). The cavum epiptericum (Fig. 3C'), which housed the trigeminal ganglion, is not confluent with the cavum supracochleare for the geniculate ganglion in *Pucadelphys*. The cava epipterica of *Pucadelphys* have a combined volume of 0.521 mm^3 together constituting 0.17% of the total endocranial space. The cast of the internal auditory meatus for passage of cranial nerves VII and VIII is visible on the right side of the endocast (Figs. 3A', 3C'). The rectangular cast for the ventral surface of the hindbrain is located posterior to the foramen ovale. The hindbrain cast is unremarkable in *Pucadelphys*; the medulla oblongata and pons did not leave distinctive impressions on the endocast (Figs. 3C, 3C').

DISCUSSION

Comparisons of *Pucadelphys andinus* are made below using digital endocasts of *Monodelphis domestica*, *Didelphis virginiana*, *Dasyurus hallucatus*, *Vombatus ursinus*, *Phascolarctos cinereus*, and *Dromiciops australis*. Phylogenetic relationships of these taxa and other marsupials are presented by Horovitz and Sánchez-Villagra (2003).

The olfactory bulb casts are relatively larger in *Pucadelphys* (together composing 11.69% of endocranial space) than in any of the extant marsupials examined in this study but are probably within the range of variation of *Didelphis virginiana* whose olfactory bulb casts together constitute 11.04% of endocranial space (n = 1). The olfactory bulb casts are much smaller in the other marsupials examined here: 8.00% to 8.43% of endocranial space in *Monodelphis domestica* (n = 3), 7.96% in *Dasyurus hallucatus*, 3.62% in *Dromiciops australis*, 3.14% in *Vombatus ursinus*, and 2.56% in *Phascolarctos cinereus*. A preliminary survey of many mammalian species suggests that olfactory bulb size is correlated with endoturbinal surface area and olfactory acuity (Rowe et al., 2005). The large relative size of olfactory bulb casts in *Pucadelphys* and didelphids suggests that this was the ancestral condition for marsupials (Luo et al., 2003).

The circular fissure is deep in all of the extant marsupial taxa examined here except for *Phascolarctos*. The circular fissure forms around the annular ridge, a bony ventral projection from the internal surface of the frontal. The circular fissure marks the posterior extent of the olfactory bulb space in most mammalian endocasts. The fissure is deeper in *Pucadelphys* than in *Monodelphis*. Presence of a relatively deep circular fissure was likely the ancestral condition for marsupials.

The cerebral hemisphere casts of *Pucadelphys* are lissencephalic (= smooth). The ancestral condition of marsupials, and of mammals in general, is presence of lissencephalic cerebral hemispheres. Presence of gyrencephalic hemispheres, the condition of having a convoluted cerebrum, has evolved at least three times within Marsupialia (Macrini, 2006), once in *Sarcophilus* (Tasmanian devil, Dasyuridae), once among wombats, and at least once in Macropodidae (kangaroos and wallabies). The conditions of the cerebral hemispheres are confirmed on the actual brains of these taxa. It is important to point out that cranial endocasts do not always accurately reflect the condition of cerebral hemispheres in mammals. For example, the brain of *Tursiops truncatus*, the bottlenose dolphin, is very convoluted, but its cranial endocast is smooth (Colbert et al., 2005). Ossification of the surrounding meninges of the brain is one explanation for this discrepancy (Colbert et al., 2005). This character is also affected by the overall volume of the brain, as larger brains are more likely to be convoluted than smaller-sized brains. Volume increases as the cube of a linear unit but surface area only increases by the square of the linear unit as the overall size of a sphere increases. Assuming that a brain is roughly spherical in shape, convolutions increase the amount of cortical surface area relative to volume for increasing brain size.

It is nearly impossible to obtain accurate volumetic measurements for some regions of the brain that are represented on mammalian endocasts. For example, it is difficult to get a volume for the cerebral hemisphere casts by themselves because there are no bony markers between the forebrain and midbrain, especially because the midbrain does not show up on the endocast. In addition, it would be impossible to distinguish the telencephalon (cerebral hemispheres) from the diencephalon. Because of this, linear measurements (length, width, height) of the cerebral hemisphere casts taken on the exterior of endocasts serve as an estimate of the size of these structures.

The cerebral hemisphere cast length/total endocast length aspect ratio of *Pucadelphys* (0.51) falls within the range of this aspect ratio for the extant marsupials examined here (range = 0.42–0.70; mean = 0.55; n = 8). Similarly the combined width/length ratio of the cerebral hemisphere casts of *Pucadelphys* (1.12) falls within the range of this aspect ratio for the extant marsupials (range = 0.82–1.38; mean = 1.13; n = 8). However, the height/length aspect ratio of the cerebral hemisphere cast is smaller in *Pucadelphys* (0.62) than in the extant marsupial endocasts studied here (range = 0.71–0.86; mean = 0.77; n = 8). These ratios indicate that although the relative length and width/length aspect ratio of the cerebral hemisphere casts is similar in *Pucadelphys* and the extant marsupials, the hemisphere casts are much thicker in these extant marsupials than in *Pucadelphys*. This suggests that the cerebral hemispheres were relatively smaller in *Pucadelphys* than in extant marsupials. Increase of the relative size of the cerebral hemispheres (and corresponding isocortex) is a possible synapomorphy for crown Marsupialia. Presumably, the relative amount of isocortex for sensory projections is greater in extant marsupials than in *Pucadelphys*.

The median sulcus separating the cerebral hemispheres is deep in *Pucadelphys* compared with taxa on the therian stem. Similarly, a relatively deep median sulcus is present in the endocasts of *Dromiciops*, *Vombatus*, and *Dasyurus*. The *Didelphis, Monodelphis*, and *Phascolarctos* endocasts, however, exhibit a distinctly shallower sulcus than that of *Pucadelphys*. The median sulcus of *Pucadelphys* is wider than that of *Monodelphis*, but narrower than the sulcus of *Phascolarctos*. The ancestral condition for Marsupialia for the relative depth of the median sulcus is equivocal.

The rhinal fissure is typically used as an indication of the ventral boundary of isocortex (= neocortex) in mammals and thus can be used to record the expansion of the isocortex in extinct taxa (Jerison, 1991). The rhinal fissure is not visible anywhere on the endocast of *Pucadelphys*. In addition, none of the endocasts of *Monodelphis* (see Fig. 4) examined so far exhibit a rhinal fissure, despite the distinctive mark of this fissure on the lateral surface of the cerebral hemispheres in dissected adult specimens

(Macrini and Rowe, 2002, 2005). In contrast, a distinctive rhinal fissure is visible on the lateral surfaces of endocasts of *Didelphis*, *Phascolarctos*, *Vombatus*, *Dasyurus*, and *Dromiciops*. The ancestral condition in Mammalia is that the rhinal fissure is not exposed on the endocast (Kielan-Jaworowska, 1986). However, the ancestral condition for this character in Marsupialia is equivocal. This character might not have phylogenetic significance, because presence or absence of the rhinal fissure on an endocast might be related to the overall size of the endocast (Rowe, 1996a, b), such that an endocast with a small surface area to volume ratio might not show the rhinal fissure.

The midbrain does not show dorsal exposure on *Pucadelphys* or on any marsupial endocasts examined in this study. Reasons for lack of midbrain exposure on the dorsal surface of mammal endocasts include being covered by a blood sinus, posterior expansion of the cerebral hemispheres, anterior expansion of the cerebellum, or some combination of two or more of these causes (Edinger, 1964). The venous sinus system covers the midbrain in *Monodelphis* (see Fig. 4), *Didelphis*, *Dromiciops*, *Dasyurus*, and *Phascolarctos*. The confluens sinuum and the sinus transversus cover the midbrain of *Didelphis* in dorsal view (Dom et al., 1970). In *Vombatus*, the expanded gyrencephalic cerebral hemispheres overlap its midbrain. However, in *Pucadelphys* it appears that an anteriorly expanded vermis of the cerebellum obscures the dorsal surface of the midbrain on the endocast. Therefore, the ancestral condition in Marsupialia is for the midbrain to be covered on the endocast by some other structure, likely a venous sinus.

Similar to the problem with the cerebral hemispheres, it is difficult if not nearly impossible to obtain accurate volumetric measurements of the cerebellar space from mammalian endocasts. However, the anteroposterior length of the cast of the vermis on the endocast can serve as a proxy for the anteroposterior length of the cerebellum. The vermis is not a separate organ of the cerebellum with a specific identifiable function but rather is a topographical feature signifying expansion of the cerebellum in the anteroposterior and dorsoventral directions. A ratio of the vermis cast length to total endocast length thus provides a relative size estimate of the cerebellar space.

The cast of the vermis of the cerebellum in *Pucadelphys* is relatively longer than most of the other marsupial endocasts examined here. The vermis length/endocast length aspect ratio of 0.22 for *Pucadelphys* is similar to that of *Vombatus* (0.18), but smaller than that of *Dromiciops* (0.30). This ratio is significantly larger in *Pucadelphys* than in the remaining extant marsupials examined here (mean = 0.12; range = 0.10–0.13; n = 6). This suggests that the cerebellum was relatively larger in *Pucadelphys* in comparison to the other marsupials examined here with the exception of *Dromiciops*. Presence of a relatively anteroposteriorly short cerebellum is a possible synapomorphy for crown Marsupialia. However, similar to extant marsupials, *Pucadelphys* had distinctive cerebellar hemispheres as is evident from the cranial endocast (see Figs. 3A, 3A', 3B, 3B'). This suggests that the cerebelli of crown marsupials do not show significant lateral expansion compared to the cerebellum of *Pucadelphys*.

The parafloccular casts of *Pucadelphys* together compose 0.95% of the endocranial space. This is within the range of the extant marsupials we examined. The parafloccular casts of *Dromiciops* and *Dasyurus* are larger: 1.45% and 1.36% of endocranial space, respectively. *Monodelphis* is most similar to *Pucadelphys* in this respect; the parafloccular casts constitute 1.10% to 1.19% of endocranial space (n = 3). *Phascolarctos* and *Didelphis* have the smallest relative parafloccular casts (0.42% and 0.59% of endocranial space, respectively) among the taxa examined here. Paraflocculi are completely absent in *Vombatus*. Presence of relatively large parafloccular casts is the likely ancestral condition for Marsupialia.

The paraflocculus is a lateral extension of the cerebellum that is housed in the subarcuate fossa of the petrosal bone. The paraflocculus is involved with coordination, balance, and vestibular sensory acquisition. Presence of well-developed paraflocculi is probably plesiomorphic for Marsupialia and Mammalia (Kielan-Jaworowska, 1986). However, the extent to which the subarcuate fossa correlates with parafloccular size is largely untested. One study suggests that the paraflocculus does not completely fill the subarcuate fossa in adult *Monodelphis domestica* (Sánchez-Villagra, 2002), but the effects of desiccation of dead specimens on brain shape are unexplored.

The hypophyseal fossa composes 0.54% of the entire endocranial space of *Pucadelphys*. This is relatively large compared with the marsupials examined here. *Monodelphis* and *Didelphis* have relatively large hypophyseal fossae, constituting 0.25% to 0.58% of endocranial space in *Monodelphis* (n = 3) and 0.47% in *Didelphis* (n = 1). *Dromiciops*, *Dasyurus*, *Phascolarctos*, and *Vombatus* all have relatively small hypophyseal fossae, composing 0.03%, 0.04%, 0.07%, and 0.07% of endocranial space, respectively. Although it is evident that the hypophyseal fossa does not give a perfect estimate of the entire volume of the pituitary gland, it might serve as a reasonable proxy for the gland's size in fossil taxa (Edinger, 1942).

The pituitary gland regulates growth and effectively overall body size through the release of hormones. Larger glands are expected to release more hormones resulting in larger body size. Among the taxa examined here, hypophyseal fossa volume correlates weakly with both endocranial volume and body mass. Relative hypophyseal fossa size; that is, hypophyseal volume expressed as a percentage of endocranial volume, is not correlated with either body mass or endocranial volume. The largest taxa examined here, *Phascolarctos* and *Vombatus* (4–15 kg, 15–35 kg, respectively; Nowak, 1991), do not have the largest relative hypophyseal fossae. Instead the extant taxon with the largest relative hypophyseal fossa (*Monodelphis*) has a relatively small body mass (~100 g). Perhaps the pituitary gland is significantly larger than the hypophyseal fossa in some marsupials such that the gland extends above the fossa. Alternatively, maybe there really is a positive correlation between relative hypophyseal fossa size and body size, but the taxonomic sampling here is too small.

The pons and medulla oblongata are not visible on the ventral surface of *Pucadelphys* or on any of the endocasts of extant marsupials examined here. Presumably, these structures are obscured by meninges of the brain and/ or blood sinuses that sit below the brain.

In addition to the neural characters discussed above based on endocast material, another synapomorphy of marsupials is based on comparative study of brains (Johnson et al., 1982a, b). The arteries of the central nervous system of marsupials terminate in individual non-anastomotic capillary loops (Wislocki and Campbell, 1937; Sunderland, 1941; Johnson et al., 1982a, b). This condition was observed in *Didelphis virginiana*, *Dasyurus viverrinus*, *Macropus giganteus*, *Pseudochirus* sp., *Trichosurus vulpecula*, and *Phascolarctos cinereus* (Wislocki and Campbell, 1937; Sunderland, 1941). This is in contrast to the ancestral condition found in other mammals in which the arterioles form free capillary anastomoses with a number of different venules (Johnson et al., 1982a, b).

The encephalization quotient (EQ) of *Pucadelphys* is smaller than any of the extant marsupials examined here, but most similar to that of *Didelphis virginiana* (Table 4). The EQ of *Dromiciops* is significantly higher than the other metatherians examined in this study. This indicates that the endocranial volume (EV) of *Dromiciops* is relatively large compared to other mammals of its size, whereas both *Pucadelphys* and *Didelphis* have relatively small EVs for mammals of their size. The reason for this large relative brain size in *Dromiciops* is unclear. *Dromiciops* is a small (16.7-31.4 g body mass), scansorial marsupial

TABLE 4. Encephalization quotient values calculated from endocranial volumes including and excluding the olfactory bulbs using three different equations (denoted by superscripts).

Taxon	$EV/(0.12[Wt]^{0.67})^{A}$	$EV/(0.055[Wt]^{0.74})^{B}$	$EV/(0.047[Wt]^{0.79})^{C}$
Pucadelphys andinus[1]	0.19	0.32	0.31
Pucadelphys andinus[2]	0.17	0.28	0.27
Dasyurus hallucatus[1]	0.50	0.72	N/A
Dasyurus hallucatus[2]	0.46	0.66	N/A
Didelphis virginiana[1]	0.27	0.34	N/A
Didelphis virginiana[2]	0.24	0.30	N/A
Dromiciops australis[1]	0.88	1.54	1.55
Dromiciops australis[2]	0.84	1.49	1.49
Monodelphis domestica[1]	0.34–0.42	0.54–0.68	0.50–0.63
Monodelphis domestica[2]	0.31–0.39	0.49–0.62	0.45–0.58
Phascolarctos cinereus[1]	0.47	0.54	N/A
Phascolarctos cinereus[2]	0.46	0.53	N/A
Vombatus ursinus[1]	0.60	0.64	N/A
Vombatus ursinus[2]	0.58	0.62	N/A

Equation A from Jerison (1973). Equation B from Eisenberg (1981). Equation C from Hurlburt (1996) for extant mammals with body masses under 300 g.

Abbreviations: **EQ**, encephalization quotient; **EV**, endocranial volume; **Wt**, weight or body mass; [1], EQ calculated with olfactory bulbs; [2], EQ calculated without olfactory bulbs.

found at high elevations in central Chile and western Argentina (Marshall, 1978). Arboreal and scansorial didelphids have relatively larger brains than terrestrial didelphid species (Eisenberg and Wilson, 1981). Arboreal and scansorial mammals might require a larger brain, and in particular a larger isocortex, to map additional sensory information to allow for navigation in a complex habitat (Eisenberg and Wilson, 1981). Perhaps the same holds true for *Dromiciops*.

In summary, examination of the endocast of *Pucadelphys* provides insight into polarizing endocast characters of marsupials. The *Pucadelphys* endocast confirms some ancestral conditions for marsupials. These include: presence of relatively large olfactory bulb casts; distinctive circular fissure; smooth cerebral hemisphere casts; relatively large parafloccular casts; and features of the ventral hindbrain (e.g., pons and medulla oblongata) not visible on the endocast. These characters are also likely plesiomorphic for Mammalia. Presence of a relatively large hypophyseal fossa as seen in *Pucadelphys* and *Monodelphis* is a potential ancestral condition for Marsupialia, but this character is unexplored for most members of Mammalia. The presence or absence of exposure of a distinctive rhinal fissure on the endocast is an equivocal character for Marsupialia. The relative depth of the median sulcus is also an equivocal character for Marsupialia.

The cerebral hemispheres of *Pucadelphys* were relatively smaller than those of the extant marsupials examined in this study as estimated by the height/length aspect ratio of the right cerebral hemisphere cast. This suggests that presence of relatively large cerebral hemispheres is a synapomorphy for Marsupialia.

The cerebellum is relatively large in *Pucadelphys* in comparison to the extant marsupials examined here, as approximated by the vermis cast length/total endocast length aspect ratio. Presence of a reduced cerebellum is a possible synapomorphy for Marsupialia.

The endocast characters and measurements presented in this paper need to be examined in a larger taxonomic context (Macrini, 2006) in order to more rigorously determine their polarity with respect to Marsupialia.

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