Cranial anatomy of the Duchesnean primate *Rooneyia viejaensis*: New insights from high resolution computed tomography

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**Abstract**

*Rooneyia viejaensis* is a North American Eocene primate of uncertain phylogenetic affinities. Although the external cranial anatomy of *Rooneyia* is well studied, various authors have suggested that *Rooneyia* is a stem haplorhine, stem strepsirrhine, stem tarsiiform, or stem anthropoid. Here we describe the internal cranial anatomy of the *Rooneyia* holotype based on micro-computed tomography and discuss the phylogenetic implications of this anatomy. Precise measurements of the natural endocast filling the braincase of the *Rooneyia* holotype reveal that the genus had a relative brain size comparable to some living callitrichines and strepsirrhines. *Rooneyia* was thus probably more encephalized than any other known omomyiform, adapiform, or plesiadapiform. Relative olfactory bulb size in *Rooneyia* was most comparable to some living strepsirrhines and the stem anthropoid *Parapithecus*. The nasal fossa of *Rooneyia* resembled that of living strepsirrhines in retaining an obliquely oriented nasolacrimal canal, four ethmoturbinals, and an olfactory recess separated from the nasopharyngeal meatus by a transverse lamina. The ear region of *Rooneyia* is characterized by large and complete canals for both the stapedial and promontory branches of the internal carotid artery. *Rooneyia* also retains a patent parotic fissure and thus had an extrabullar origin of the stapedius muscle. In most of these respects, *Rooneyia* exhibits the condition that is presumed to be primitive for crown primates and lacks a number of key crown haplorhine synapomorphies (e.g., a dorso-ventrally oriented nasolacrimal canal, loss of the olfactory recess, loss of ethmoturbinals 3–4, loss or extreme reduction of the stapedial canal due to involution of the stapedial artery). These data are consistent with the hypothesis that *Rooneyia* is an advanced stem primate or a basal crown primate but are inconsistent with prior suggestions that *Rooneyia* is a crown haplorhine.

**Introduction**

*Rooneyia viejaensis* is an Eocene primate from the Sierra Vieja of West Texas. The species is known only from the type specimen (TMM 40688–7), which was recovered in 1964 from the Duchesnean Rifle Range Hollow locality in the Chambers Tuff Formation (Wilson, 1966, 1986; Robinson et al., 2004). The *Rooneyia* holotype is a nearly undistorted cranium missing only the premaxillae, postorbital bars, zygomatic arches, and portions of the neurocranium (Fig. 1). The specimen also preserves a complete and undistorted natural endocast of the braincase (Hofer and Wilson, 1967). The endocast is sufficiently well preserved that impressions of the middle meningeal vessels and intracranial venous sinuses are readily visible. Most cranial foramina and sutures are also well marked on the *Rooneyia* holotype. Despite the excellent preservation of the *Rooneyia* holotype, the phylogenetic affinities of this taxon have proved difficult to resolve with a high degree of confidence. Although *Rooneyia* is frequently grouped with fossil omomyoids as a stem tarsiiform (Szalay and Delson, 1979; Seiffert et al., 2010), some analyses have indicated that *Rooneyia* may be unrelated to omomyoids and could instead be a stem haplorhine (Ross, 1994; Ross et al., 1998), a stem strepsirrhine (Kay et al., 2004), or a stem anthropoid (Rosenberger, 2006).
Shortly after the *Rooneyia* holotype was first described, Hofer and Wilson (1967) published a brief qualitative description of the natural endocast. In order to better visualize the surface of the endocast, sections of the neurocranium were mechanically removed, including portions of the frontal, alisphenoid, temporal, and occipital bones on the right side of the specimen.¹ The description provided by Hofer and Wilson (1967) confirmed the existence of a Sylvian fissure and noted that *Rooneyia*’s olfactory bulbs are intermediate in size between those of extant anthropoids and strepsirrhines. These authors also concluded that *Rooneyia* has cerebral morphology similar to *Microcebus* and *Galago* and cerebellar morphology comparable to extant prosimians.² These observations were largely corroborated by Radinsky (1970, 1975), who also compared the morphology of the *Rooneyia* endocast favorably with those of the omomyiforms *Tetonius* and *Necrolemur*. Following the mechanical preparation and exposure of the *Rooneyia* endocast, several authors have estimated its total volume using modeling and double-graphic integration (Jerison, 1973, 1979; Radinsky, 1977; Gurche, 1982). All of these estimates are fairly similar, ranging from 7.0 to 7.5 cm³.

In 1976, Szalay and Wilson published an emended description of the basicranial anatomy of *Rooneyia*. In order to visualize the morphology of the middle ear, the floor of the right auditory bulla and most of the matrix within the right tympanic cavity were mechanically removed. Szalay and Wilson’s (1976) description confirmed that *Rooneyia* possesses promontory and stapedial canals, an aphaneric ectotympanic, an uninflated petromastoid region, and a simple tympanic cavity undivided by major septa (Szalay and Wilson, 1976). Unfortunately, the removed section of the bullar floor is now missing and mechanical preparation of the right middle ear resulted in damage to some bony structures (most notably the stapedial canal; see below).

Since 1976, most novel observations of *Rooneyia* have been based on further examination of the externally visible anatomy of the holotype (e.g., Ross, 1994; Kay and Kirk, 2000) or surface scans of high-resolution casts (e.g., Rosenberger, 2006). The holotype was first scanned using micro-computed tomography (μCT) in 1998, but the anatomy revealed by this scan has only been partly described in two prior publications. Seiffert et al. (1999) published an abstract in which they offered a preliminary assessment of the internal anatomy of *Rooneyia*’s nasal cavity. Most significantly, these authors observed that *Rooneyia* resembles extant strepsirrhines and many non-primate mammals in exhibiting an olfactory recess³ that is separated from the nasopharyngeal meatus by a transverse lamina. More recently, Silcox et al. (2009a) drew inferences regarding

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¹ Compare photographs in Wilson (1966) and Hofer and Wilson (1967). Unfortunately, the removed sections of the neurocranium are highly fragmented and no longer preserve useful anatomical details.

² The exact prosimian species to which *Rooneyia* was stated to bear a resemblance were not specified by Hofer and Wilson (1967).

³ The olfactory recess (Cave, 1973; Smith and Rossie, 2008) is equivalent to the ‘sphenoidal recess’ of Loo (1973) and Rowe et al. (2005). See Table 2 of Smith and Rossie (2008) for additional synonyms of nasal fossa structures.
locomotion in *Rooneyia* based on semicircular canal radius of curvature. This analysis demonstrated that the holotype has moderately large semicircular canal radii of curvature for its estimated body mass, leading Silcox and colleagues to conclude that *Rooneyia* “practiced medium—medium fast locomotion, similar to an omo- myid ... or a derived notharctid” (Silcox et al., 2009a: 324).

The goal of the present analysis is to provide an emended description of the cranial anatomy of *Rooneyia* based on μCT scans. We focus on three regions of particular significance for evaluating the phylogenetic affinities of Paleogene primates: the endocranium, the ear region, and the nasal cavity. These descriptions allow us to evaluate prior claims regarding the anatomy and phylogeny of *Rooneyia* based on previously unobserved evidence.

**Materials and methods**

The holotype cranium of *Rooneyia* was scanned at the High-Resolution X-ray Computed Tomography Facility at The University of Texas at Austin. To visualize the endocast and nasal cavity, the entire cranium was first scanned in a coronal plane (in-plane resolution = 39.1 microns; inter-slice spacing = 86.7 microns; field of reconstruction = 40 mm). A virtual endocast was then constructed by manually selecting a volume of interest in each slice using Amira 3.1.1 software. To better visualize small auditory structures, the partially prepared right ear region of *Rooneyia* was scanned in the coronal plane at higher resolution (in-plane resolution = 11.7 microns, inter-slice spacing = 16.4 microns, field of reconstruction = 12 mm). To facilitate anatomical descriptions of the nasal fossa and ear region of *Rooneyia*, contrast between matrix and bone was enhanced ad libitum in the individual 16-bit tiff files that comprise each scan using the ‘adjust levels’ function in Photoshop CS4 Extended 11.0.2. Planes of the individual coronal μCT slices that are reproduced as figures (i.e., Figs. 7–9) are shown in Fig. 2. Source files for both of the μCT scans of *Rooneyia* used in this analysis are available for download at http://digimorph.org/specimens/Rooneyia_viejaensis/.

To compare endocast morphology in *Rooneyia* and extant primates, virtual endocasts were also constructed using μCT scans of a mouse lemur (*Microcebus rufus*; USNM 328789, adult female), a slender loris (*Loris tardigradus*; USNM 256739, adult male), and a tamarin (*Saguinus geoffroyi*; USNM 301646, adult male). The terminology used here for structures in the nasal fossa follows Smith and Rossie (2008). To illustrate the similarities between nasal structures of *Rooneyia* and *Microcebus*, we relied on published descriptions of *Microcebus murinus* and *Microcebus myoxinus* (Smith et al., 2007, 2011; Smith and Rossie, 2008) and μCT scans of *M. rufus*. A μCT scan of the nasal fossa of *M. rufus* (USNM 328789) is available for download at http://digimorph.org/specimens/Rooneyia_viejaensis/. Estimates of body mass for *Rooneyia* based on cranial length were taken from Silcox et al. (2009a). Comparative data on endocranial volume, olfactory bulb volume, and body mass in both living and fossil taxa follow Bush et al. (2004), Isler

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4 The μCT scan of *Rooneyia* used by Seiffert et al. (1999) and Silcox et al. (2009a) had an in-plane resolution of 36 microns and an inter-slice spacing 120 microns.
et al. (2008), and Silcox et al. (2009b, 2010). Data on endocranial volume and body mass for extant primates were taken from Isler et al. (2008) and include only species represented by at least four adult individuals, and at least two males and two females for anthropoids.

Results

Endocast

The virtual endocast of Rooneyia is shown in Fig. 3, and in Fig. 4 the endocast of Rooneyia is compared with virtual endocasts of Microcebus, Loris, and Saguinus. In most respects, the anatomy of the Rooneyia virtual endocast supports previous descriptions based on the exposed dorsal, lateral and caudal surfaces of the natural endocast (Hofer and Wilson, 1967; Radinsky, 1970, 1979). In its gross morphology, the virtual endocast of Rooneyia closely resembles that of Microcebus. Both genera exhibit (1) similar degrees of overlap of the olfactory bulbs by the frontal lobe of the cerebrum, and (2) similar degrees of overlap of the cerebellum by the occipital lobe of the cerebrum (Fig. 4, superior and lateral views). Rooneyia further resembles Microcebus and Loris and differs from Saguinus in having a frontal lobe that is mediolaterally narrower than the temporal and parietal regions of the endocast (Fig. 4, superior view). However, the frontal lobes of Rooneyia also appear to have been dorso-ventrally narrower than any of the three extant species (Fig. 4, rostral view). The endocast of Rooneyia has only a single visible cerebral sulcus: the Sylvian fissure between the frontal and temporal lobes. In this respect Rooneyia most closely resembles Microcebus, which matches prior descriptions in exhibiting only a Sylvian fissure and a “faint trace” of the superior temporal sulcus (Radinsky, 1974: 785). By comparison, the endocast of Saguinus has impressions of both the Sylvian fissure and a more clearly marked superior temporal sulcus. Loris has the most visibly gyrencephalic endocast illustrated in Fig. 4, with impressions of the Sylvian fissure, the rhinal fissure, the superior temporal sulcus, the orbital sulcus, and the coronal sulcus (cf. Radinsky, 1974). The Sylvian fissure is faintly marked in the endocasts of Rooneyia and Saguinus, and is much deeper in the endocasts of Microcebus and Loris (Fig. 4). These observations suggest that Rooneyia may have resembled some small extant primates like M. murinus, Galagoides demidoff, and Tarsius spectrum in having a largely lissencephalic neocortex (Woolard, 1925; Le Gros Clark, 1931; Radinsky, 1974; Zilles et al., 1979).

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Figure 3. Virtual endocast of Rooneyia viejaensis in dorsal (A), ventral (B), rostral (C), caudal (D), right lateral (E), and left lateral (F) views. Casts or impressions of the following structures are labeled: \( \text{CL} \) = cerebellar lateral lobe, \( \text{CV} \) = cerebellar vermis, \( \text{HF} \) = hypophyseal fossa, \( \text{NC} \) = neocortex, \( \text{OB} \) = olfactory bulb, \( \text{OC} \) = orbitotemporal canal, \( \text{ON} \) = optic nerve, \( \text{OT} \) = olfactory tract, \( \text{PC} \) = piriform cortex, \( \text{PS} \) = petrosquamous sinus, \( \text{SF} \) = subarcuate fossa, \( \text{SG} \) = sigmoidal sinus, \( \text{SS} \) = superior sagittal sinus, \( \text{SY} \) = Sylvian sulcus, \( \text{TS} \) = transverse sinus.

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5 These species are designated as ‘ok’ in the ‘Data quality’ column of Appendix 3 in the supplemental online material of Isler et al. (2008).
As in Microcebus, the temporal region of the Rooneyia endocast demonstrates a well-developed cast of the orbitotemporal canal\(^6\) connecting the orbit with the postglenoid foramen and adjacent intracranial hiatus of the stapedial canal. A similar structure is present but more faintly marked in the endocast of Loris dorsal to the rhinal fissure. The orbitotemporal canal typically transmits the ramus superior of the stapedial artery and the accompanying cranio-orbital venous sinus (Diamond, 1992). In extant lemuriform primates the orbitotemporal canal lies adjacent to the rhinal fissure (Radinsky, 1970; Silcox et al., 2009b), which demarcates the boundary between the neocortex and piriform cortex of the cerebrum (Le Gros Clark, 1959; Jerison, 1973). If one assumes that a similar close relationship between the orbitotemporal canal and rhinal fissure also existed in Rooneyia, then the proportions of the cerebrum dorsal and ventral to the rhinal fissure were roughly comparable in Rooneyia and Microcebus. Nevertheless, in rostral view it is evident that in addition to having proportionally larger frontal lobes, the endocast of Microcebus has its greatest breadth located more dorsally than in Rooneyia (Fig. 4). These observations

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\(^6\) This structure has also been referred to as the ‘sinus canal’ (McDowell, 1958), ‘arteria duralis media’ (Hofer and Wilson, 1967), and ‘cranio-orbital sulcus’ (Diamond, 1992). Here we follow Wible et al. (2004) and Silcox et al. (2010) in our use of the term ‘orbitotemporal canal’. It should be noted, however, that in both Rooneyia and Microcebus the orbitotemporal canal is represented by a groove in the endocranial surface of the temporal squama rather than a fully enclosed bony canal.

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**Figure 4.** Comparison of virtual endocasts in dorsal (top row), right lateral (middle row), and rostral (bottom row) views. Taxa from left to right include: Saguinus geoffroyi (Geoffroy’s tamarin), Microcebus rufus (brown mouse lemur), Rooneyia viejaensis, and Loris tardigradus (slender loris). OC = orbitotemporal canal, PS = petrosquamous sinus, RF = rhinal fissure.

**Figure 5.** Bivariate plot of log10 endocranial volume on log10 body mass. Minimum convex polygons are fit to species means calculated for 134 extant haplorhines and 52 extant strepsirrhines using data provided by Isler et al. (2008). The three data points for Rooneyia represent the mean body mass and upper and lower 95% confidence limits based on cranial length (Silcox et al., 2009a). Extant data points are omitted for clarity. Sources for fossil comparative data include Bush et al. (2004) and Silcox et al. (2009a, b, 2010).
suggest that the cerebrum of *Rooneyia* may have had proportionally more piriiform cortex and less neocortex than in *Microcebus*. Caudal to the postglenoid foramen, the virtual endocast of *Rooneyia* also lacks a well-developed impression for the petrosquamous sinus\(^7\) because this structure primarily traveled in a fully enclosed bony canal (= ’temporal canal’ of Diamond, 1992) for most of its length. By contrast, in the *Microcebus* and *Loris* endocasts (Fig. 4), most of the course of the petrosquamous sinus is marked by the impression of an open groove on the caudal surface of the endocast’s temporal region (= ’petrosquamous sulcus’ of Diamond, 1992). However, the presence and length of a temporal canal for the petrosquamous sinus is highly variable in extant primates (Diamond, 1992).

The total volume of *Rooneyia*’s virtual endcast is 7.234 cm\(^3\). This value agrees well with prior estimates (7.5 cm\(^3\), Radinsky, 1977; 7.0 cm\(^3\), Jerison, 1979; 7.38 cm\(^3\), Gurche, 1982) and is very similar to the absolute endocast volume reported for extant *Callithrix jacchus* (7.24 cm\(^3\); Iser et al., 2008). The estimated body mass for *Rooneyia* based on cranial length is 381 g (95% confidence limits: 197 g – 736 g; Silcox et al., 2009a). These values are shown in Fig. 5, which compares endocast volume and body mass in *Rooneyia*, 176 extant primate species, and seven additional fossil taxa. Fig. 5 demonstrates that *Rooneyia* had a brain size relative to mean estimated body size that was comparable to some living strepsirrhines (e.g., *Microcebus* and *Loris* endocasts) and callithricine anthropoids (e.g., *Callithrix argentata*, *Saguinus fuscicolis*). If the mean body mass estimate of 381 g is accurate, then *Rooneyia* was more encephalized than any other fossil taxon included in Fig. 5. In this case, *Rooneyia* would also be the only fossil taxon in our sample with a relative brain size that falls within the extant anthropoid range.

Alternatively, if the upper body mass estimate of 736 g is accurate, then *Rooneyia* resembled the fossil ommomorph *Necrolemur antiquus* in exhibiting a degree of encephalization near the lower end of the extant strepsirrhine range. In this case, relative brain size in *Rooneyia* would be most comparable to that of extant *Lepilemur leucopus*. Finally, the lower body mass estimate of 197 g would indicate that *Rooneyia* was more encephalized than living platyrhines of similar body mass. However, we regard this latter possibility as unlikely because estimates of body mass for *Rooneyia* based on upper first molar area are larger than those based on cranial length (Silcox et al., 2009a), suggesting that the lower estimate of 197 g derived from cranial length is probably too small.

Based on olfactory fossa size, we further estimate that olfactory bulb volume in *Rooneyia* was 68 mm\(^3\). This value is shown in Fig. 6, which compares olfactory bulb volume and endocranial volume in *Rooneyia*, 39 extant primate species, and seven additional fossil taxa. Fig. 6 demonstrates that *Rooneyia* had an olfactory bulb size relative to brain size that was most comparable to the extant strepsirrhines *Avahi laniger* and *Prolemur simus*, and the stem anthropoid *Parapithecus grangeri*. However, both *Rooneyia* and *Parapithecus* plot outside the living strepsirrhine polygon and in close proximity to the living anthropoid *Aotus trivirgatus* (Fig. 6). As a percentage of total endocranial volume, olfactory bulb volume in *Rooneyia* (0.94%) is similar to that of the living strepsirrhines *Eulemur fulvus* (1.04%) and *P. simus* (0.80%) and the fossil omomyiform *Necrolemur antiquus* (0.86%) (Silcox et al., 2010). This value for *Rooneyia* falls near the lower end of the extant strepsirrhine range (3.38% – 0.39%) and above the values for *Parapithecus* (0.66%), *Tarsius syrichta* (0.53%), *A. trivirgatus* (0.40%), and extant diurnal anthropoids (0.39% – 0.01%; Silcox et al., 2010).

**Nasal cavity**

The anatomy of the nasal cavity in *Rooneyia* is shown in Figs. 7 and 8 (see Fig. 2 for slice planes). Fig. 7 includes three coronal \(\mu\)CT slices through the cranium at the levels of the fourth and third maxillary premolars. These slices were selected to illustrate the inlet, midsection, and incomplete rostral portion of the nasolacrimal canal (Fig. 7A,B and C, respectively). Fig. 8 includes coronal \(\mu\)CT slices through the cranium at the levels of the second and first maxillary molars (Fig. 8A and B, respectively). These slices illustrate the disposition of the turbinals, transverse lamina, and olfactory recess, which were noted by Seiffert et al. (1999) but have not previously been described in detail.

Although the nasal cavity of *Rooneyia* is completely filled with matrix of variable density, many internal nasal structures are nonetheless observable at the scanning resolution used here. Portions of most turbinals are preserved and distinct from the surrounding matrix, but these visible segments are incomplete and no turbinals are visible in their entirety. However, the primary laminae by which turbinals originate from the internal margins of the nasal fossae are generally well preserved bilaterally, allowing many structures to be identified with a high degree of confidence.

The nasolacrimal canals are well preserved bilaterally (Fig. 7). The inlet of each nasolacrimal canal (lacrimal foramen) is located along the suture between the lacrimal bone and the frontal process of the maxilla, about 3.5 mm rostral to the medial margin of the orbit (Fig. 1C). From the lacrimal foramen, the nasolacrimal canal runs rostrally and slightly ventrally for about 3.2 mm until it reaches the primary lamina of the maxilloturbinal. The canal then continuesrostro-ventrally through the base of the maxilloturbinal primary lamina to empty into the inferior meatus. The total length of the nasolacrimal canal is approximately 4.3 mm. However, only the proximal 1.6 mm of each canal is fully enclosed by bone on all sides (Fig. 7B). Shortly before reaching the maxilloturbinal primary lamina, the medial surface of each canal appears to be unossified (Fig. 7C). Although this observation may be the result of breakage or insufficient scanning resolution, the bilaterally symmetrical

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\(^7\) The petrosquamous sinus runs from the transverse sinus to the postglenoid foramen (Butler, 1967; Diamond, 1992).
occurrence of a fenestra in the medial wall of the nasolacrimal canal suggests that the distal portion of Rooneyia’s nasolacrimal canal was not fully ossified. Additionally, the nasolacrimal and infraorbital canals of Rooneyia communicate via a smaller canal (‘communicating canal’, Fig. 7A) that runs rostro-dorsally from the infraorbital canal. This communicating canal merges with the ventral surface of the proximal nasolacrimal canal near the lacrimal foramen.

Figure 7. Coronal μCT sections through the rostrum of Rooneyia at the level of the third and fourth maxillary premolars. Slice A illustrates the lacrimal foramina. Slice B, showing a fully enclosed nasolacrimal canal, is approximately 1.2 mm rostral to slice A. Slice C, showing a partly enclosed nasolacrimal canal, is approximately 1.0 mm rostral to slice B. Contrast enhanced to illustrate anatomical structures.
In most respects, the internal anatomy of the nasal cavity of Rooneyia is fundamentally similar to that of living mouse lemurs (Microcebus spp.). Each nasal fossa of Rooneyia possesses six major turbinals, including one maxilloturbinal, one nasoturbinal, and four ethmoturbinals. In this respect, the nasal cavity of Rooneyia exhibits the condition that is presumed to be primitive for crown primates (Cave, 1948, 1973; Le Gros Clark, 1959; Loo, 1973; Martin, 1990). The primary lamina of the maxilloturbinal is visible on the lateral wall of the nasal fossa near the piriform aperture (Fig. 7C). In the coronal plane, the rostral-most portion of the maxilloturbinal primary lamina is adjacent to the tip of the lateral incisor root in the premaxilla. About 3.5 mm caudal to this point, the primary lamina of the maxilloturbinal shifts from the lateral wall of the nasal fossa to the ventral floor of the nasal fossa (Fig. 7). From this point, the primary lamina of the maxilloturbinal remains visible in this ventral position (Figs. 7A and B) for ~7.8 mm until it merges with the ventro-lateral wall of the nasopharyngeal meatus near the free rostral margin of the transverse lamina.

The primary lamina of the nasoturbinal and semicircular crest in Rooneyia is first visible ~8.8 mm caudal to the piriform aperture on the dorso-lateral surface of the nasal fossa. As in Microcebus, the rostral origin of this lamina lies in close proximity to the inlet of the

Figure 8. Coronal μCT sections through the cranium of Rooneyia at the level of the second maxillary molar (A) and first maxillary molar (B). Slice B is approximately 3.2 mm rostral to slice A (this figure) and 3.6 mm caudal to slice A in Fig. 7. Contrast enhanced to illustrate anatomical structures.
nasolacrimal canal. When viewed moving caudally in the coronal plane, the primary lamina for the nasoturbinal shifts to the superior margin of the nasal fossa by ~3 mm caudal to its rostral origin. The lamina remains in this dorsal position (Fig. 8B) for ~1.8 mm until it merges with the rostral margin of the cribiform plate. In this respect, the nasoturbinal primary lamina of Rooneyia differs from that of Microcebus, in which the caudal-most one-quarter of the nasoturbinal primary lamina originates dorso-medially from the bony nasal septum.

Free medial portions of ethmoturbinal I are visible bilaterally in Rooneyia beginning ~6 mm caudal to the piriform aperture (Fig. 7). About 4.8 mm caudal to this rostral-most visible portion of ethmoturbinal I, the rostral edge of the frontomaxillary septum (i.e., the primary lamina of ethmoturbinal I) is visible on the lateral surface of the nasal fossa. The frontomaxillary septum is robust compared with other turbinal primary laminae (Fig. 8B), and in some µCT slices it projects more than half of the distance from the lateral wall of the nasal fossa to the bony nasal septum. In the left nasal fossa, the frontomaxillary septum is also visibly continuous with more medially positioned scroll-shaped portions of ethmoturbinal I.

About 12 mm caudal to the piriform aperture, a small primary lamina splits from the dorsal surface of the frontomaxillary septum in Rooneyia. When viewed moving caudally in the coronal plane, this lamina migrates dorsally until it merges with the rostro-lateral margin of the cribiform plate. The total rostro-caudal length of this primary lamina is about 2.3 mm, and its relative position and morphology favor the conclusion that it is a frontoturbinal8 (Fig. 8B). Indeed, the only salient morphological distinction between the putative frontoturbinal of Rooneyia and frontoturbinal of Microcebus is that the rostral origin of the mouse lemur frontoturbinal is adjacent to (but not continuous with) the frontomaxillary septum.

About 8.7 mm caudal to the piriform aperture, the frontomaxillary septum of Rooneyia divides into two separate primary laminae on the lateral wall of the nasal fossa. In Microcebus, the dorsal-most of these two laminae may either be (1) the dorsal root of ethmoturbinal I alone, or (2) a common primary lamina for ethmoturbinal II and the dorsal root of ethmoturbinal I. Similarly, the ventral-most of these laminae in mouse lemuris is continuous with the ventro-caudal portion of ethmoturbinal I, the maxilloturbinal, and (variably) the primary lamina of ethmoturbinal II. Due to the lack of preservation or visibility of the medial portions of most ethmoturbinals in Rooneyia, it is not clear what structure(s) may have arisen from the dorsal lamina splitting from the frontomaxillary septum other than the dorsal root of ethmoturbinal I. Nonetheless, the dorsal root of ethmoturbinal I can be seen merging with the cribiform plate ~2.2 mm caudal to the point at which the frontomaxillary septum divides into separate dorsal and ventral laminae. Additionally, about 0.7 mm caudal to this split of the frontomaxillary septum, a new primary lamina appears between the dorsal and ventral divisions of the frontomaxillary septum. By analogy with Microcebus, this new septum could either be the primary lamina of ethmoturbinal II or an interturbinal.9 In the case of Rooneyia, however, it is not possible to determine the identity of this lamina with confidence using the presently available scans. In fact, between the first appearance of a separate dorsal root of ethmoturbinal I and the rostral margin of the transverse lamina, the lateral wall of the nasal fossa of Microcebus is highly complex, with as many as seven separate primary laminae of ethmoturbinals and interturbinals simultaneously visible bilaterally in the coronal plane. Rooneyia exhibits similar structural complexity in this region, and it is therefore not possible at present to resolve some questions regarding the anatomy of the nasal fossa in this taxon (e.g., number of interturbinals). Nevertheless, if our interpretations of the identifiable primary laminae of Rooneyia are correct, then this taxon only possessed one frontoturbinal as in Microcebus spp., rather than two frontoturbinals as in Mirza coquereli and Cheirogaleus medius (Smith and Rossie, 2008).

Despite this current inability to identify all of the nasal structures of Rooneyia, scan resolution in the caudal region of the nasal fossa is sufficient to permit the identification of several key features. About 15.6 mm caudal to the piriform aperture, a complete transverse lamina is visible separating the olfactory recess10 dorsally from the nasopharyngeal meatus ventrally (Fig. 8A). From this point, the nasopharyngeal meatus extends ~3.6 mm caudally to the choanae, and the olfactory recess extends ~5.0 mm caudally to end in a cul-de-sac. As a percentage of the total rostro-caudal distance from the piriform aperture to the end of the olfactory recess, Rooneyia has a proportionally longer olfactory recess (25.4%) than Microcebus (~21.0%). The transverse lamina of Rooneyia is first visibly complete in the same coronal plane as the rostral margin of the second maxillary molar’s lingual root. By comparison, in Microcebus the rostral-most portion of the transverse lamina is visible as a small projection from the bony nasal septum in the same coronal section as the rostral margin of the second maxillary molar crown. When viewed moving caudally in the coronal plane, the transverse lamina extends progressively laterally but does not contact the lateral wall of the nasal fossa until it is caudal to the maxillary third molars. As a result, the transverse lamina of Microcebus is first visibly complete in the same approximate coronal plane as the choanae and the free caudal margins of the horizontal plates of the palatine bones.

In both Rooneyia and Microcebus, the cribiform plate and olfactory fossa lie immediately dorsal to the olfactory recess. Lodged within the olfactory recess of Rooneyia are ethmoturbinals III and IV (Fig. 8A). Medial portions of ethmoturbinal III are visible ~1.0 mm rostral to the inlet of the olfactory recess in Rooneyia. From this point, ethmoturbinal III extends ~2.3 mm caudally and dorsally to merge with the cribiform plate. More than 50% of the visible length of ethmoturbinal III thus occurs within the olfactory recess. Rooneyia differs from Microcebus in this respect, as the olfactory recess in mouse lemur contains only ethmoturbinal IV (Smith and Rossie, 2008). The visible portion of the primary lamina of ethmoturbinal IV in Rooneyia occurs entirely within the olfactory recess and extends caudally ~0.7 mm past the caudal end of ethmoturbinal III. Here again Rooneyia differs from Microcebus, in which the rostral origin of the primary lamina of ethmoturbinal IV lies rostral to the inlet of the olfactory recess.

The anatomy of the ear region in Rooneyia is shown in Supplemental Online Material (SOM) Figure 1 and in Figure 9, which includes five successive coronal µCT slices through the mechanically prepared right middle ear (see Fig. 2 for slice planes). These slices illustrate the course of the canals for the internal carotid artery and its branches, the disposition of the unprepared regions of the right

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8 Frontoturbinals (also called ectoturbinals) are accessory ethmoidal turbinals that arise in the frontal recess and are confined to the lateral portion of the nasal fossa (i.e., they do not project medially to lie in close proximity to the nasal septum; Smith and Rossie, 2008).

9 Interturbinals are accessory ethmoidal turbinals that arise from the orbitonasal lamina caudal to the frontal recess; like frontoturbinals, they are confined to the lateral portion of the nasal fossa (Smith and Rossie, 2008).

10 In our coronal µCT sections, we defined the olfactory recess as being delimited by a complete transverse lamina ventrally.
typanic cavity, and several canals for cranial nerves and their branches that have not been previously described.

Internal carotid canal and branches. The posterior carotid foramen is located on the caudal and medial aspect of the auditory bulla. From this point, the internal carotid canal runs dorsally, rostrally, and laterally for ~2.3 mm to reach the lateral surface of the promontorium adjacent to the basal turn of the cochlear labyrinth (SOM Fig. 1A and B). Near the inlet of the posterior carotid foramen, the internal carotid canal is ~0.8 mm in diameter. However, the internal carotid canal narrows slightly as it runs dorsally, and is ~0.7 mm in diameter as it reaches the promontorium.

Shortly after reaching the promontorium, the internal carotid canal divides into separate promontory and stapedial canals (Fig. 9A and B). The stapedial canal runs dorsally and caudally from this point to reach the ventral margin of the fenestra vestibuli. The most proximal end of the stapedial canal appears to be somewhat smaller than the internal carotid or promontory canals (Fig. 9A and B). However, the precise size of this portion of the stapedial canal is impossible to measure because most of the right stapedial canal between the internal carotid canal and fenestra vestibuli was removed during mechanical preparation of the right middle ear space. However, this segment of the stapedial canal appears to be intact in the unprepared left middle ear. The right stapedial canal is visibly complete near the fenestra vestibuli and measures ~0.25 mm in diameter. The stapedial canal maintains this approximate size as it crosses the fenestra vestibuli as a complete bony canal (Fig. 9C). While passing the fenestra vestibuli, the stapedial canal turns to run dorsally and rostrally. On the dorsal margin of the fenestra vestibuli, the stapedial canal courses in close proximity to the postgunciulate portion of the facial canal. The facial canal, which at this point runs mainly caudally and laterally, passes dorsal to the stapedial canal. Like other primatest with intact stapedial canals, the crossing portions of the stapedial and facial canals appear to have been separated by a thin or incomplete bony lamina (ECK, Personal observation). After passing the facial canal, the distal segment of the stapedial canal runs dorsally, rostrally, and laterally through the epitympanic recess (Fig. 9A). The stapedial canal ultimately reaches the endocranial cavity near the medial margin of the postglenoid foramen's endocanalicular inlet. Along this course, the distal segment of the stapedial canal steadily increases in diameter from ~0.30 mm near the facial canal to ~0.50 mm near the postglenoid foramen. Accordingly, the distal-most portion of the stapedial canal is approximately twice the diameter of the proximal stapedial canal near the fenestra vestibuli.

Like the stapedial canal, the promontory canal is complete throughout its intratympanic course. The most proximal segment of the promontory canal is ~0.55 mm in diameter and runs rostrally across the ventro-lateral surface of the promontorium (Fig. 9A; SOM Figure 1A). At the rostral pole of the promontorium, the promontory canal turns dorsally to reach the roof of the tympanic cavity. As it reaches the tympanic roof, the promontory canal widens to about 0.70 mm in diameter. From this point, the promontory canal runs rostrally and medially on the roof of the tympanic cavity, ultimately merging with the endocranial cavity near the rostral margin of the tympanic cavity and auditory bulla. Tympanic cavity and ectotympanic bone. As in crown lemurs, the tympanic cavity of *Rooneyia* consists of a single large middle ear space that is unidivided by major septa. In this respect, *Rooneyia* differs from crown haplorhines and lorisiforms, which have major intrabullary bony laminae that partition off large accessory air spaces (i.e., the anterior accessory cavity in haplorhines and the medial accessory cavity in lorisiforms; MacPhee, 1981; MacPhee and Cartmill, 1986). In *Rooneyia*, three minor bony laminae are visible bilaterally in the ventral and caudal region of the tympanic cavity. One bony septum (‘broad shelf’ of Szalay and Wilson, 1976:290) runs laterally and caudally from the internal carotid canal to connect the canal with the ventral and caudal portions of the inner bullar wall and ectotympanic (Fig. 9C; ‘CS’ in SOM Figure 1A–C). Two small bony septa (‘vertical struts’ of Szalay and Wilson, 1976:290) also connect the ectotympanic with the lateral bullar wall (‘BS’ in SOM Figure 1A). The tympanic annulus of the ectotympanic bone, which framed the tympanic membrane in life, is well marked on the lateral wall of the middle ear space (Fig. 9B–D). The ectotympanic is fully fused to the lateral bullar wall. However, no sutures are visible between the tympanic annulus, the bulla, and the ossified external acoustic meatus. As a result, it is not possible to delimit the extent of the adult ectotympanic bone as an element separate from the surrounding osseous structures.

The caudal portion of the tympanic cavity proper is continuous with two minor accessory air spaces (SOM Figure 1B,C). One of these accessory air spaces is a caudal prolongation of the epitympanic recess (Fig. 9A and B). This ‘epitympanic accessory air space’ extends ~2.4 mm caudally from the region of the fenestra vestibuli to end as a cul-de-sac lateral to the subarcuate fossa (Fig. 9C–E). The second accessory air space is continuous with the dorso-lateral portion of the tympanic cavity proper through an oval ostium measuring about 1.7 by 1.0 mm. This lateral accessory air space is about 4.1 mm in rostro-caudal length (Fig. 9A–D). Its rostral end is adjacent to the caudal margin of the postglenoid vein. Moving caudally, the lateral accessory air space runs dorsal to the external acoustic meatus and lateral to the epitympanic recess and tympanic cavity proper (Fig. 9A and B). The caudal end of the lateral accessory air space is lateral to the epitympanic accessory air space (Fig. 9D). The most caudal portions of the epitympanic accessory air space and the tympanic cavity proper extend only a short distance more caudally than the lateral accessory air space and the vestibule of the inner ear (Fig. 9E).

Caudal to this terminus of the tympanic cavity and inferior to the subarcuate fossa, the petromastoid and occipital bone contain small voids and trabeculae. These structures appear to represent cancellous bone rather than mastoid air cells because none of the voids are visibly continuous with the tympanic cavity or either accessory air space.

Canals for cranial nerves and stapedius muscle. As in all crown primates, the intratympanic segment of the facial nerve in *Rooneyia* was fully enclosed in a bony canal (Fig. 9A–E; MacPhee, 1981; Wible and Covert, 1987). In most respects, the anatomy of the facial canal is unremarkable. The postgunciulate portion of the facial canal begins in the internal acoustic meatus dorsal to the middle turn of the cochlear labyrinth. From this inlet the facial canal runs a short distance rostrally to the genu, where the facial canal widens to form the cavum supracochleare11(‘CS’ in SOM Figure 1B). The petrosal canal for the greater petrosal nerve exits the facial canal at the rostral margin of the cavum supracochleare. From this point, the petrosal canal runs ~0.35 mm rostrally until it merges with the endocranial cavity at the hiatus Fallopian in the middle cranial fossa. The facial canal proper turns to run caudally and laterally at the genu. As noted previously, the postgunciulate facial canal crosses the stapedial canal near the fenestra vestibuli (Fig. 9C) and continues caudally, laterally, and ventrally to a point ventral to the rostro-lateral margin of the subarcuate fossa. From this point, the facial canal runs rostrally and ventrally to reach the stylomastoid foramen.

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11 The cavum supracochleare housed the geniculate ganglion of the facial nerve.
Figure 9. Five successive μCT sections of the mechanically prepared right middle ear of Rooneyia (A to E – rostral to caudal; See Fig. 2). Slice A includes the cochlear labyrinth and external acoustic meatus. Slice B also includes the cochlear labyrinth and external acoustic meatus and is 0.80 mm caudal to slice A. Slice C includes the vestibule, fenestra vestibuli, and basal turn of the cochlear labyrinth and is 1.03 mm caudal to slice B. Slice D also includes the vestibule and fenestra vestibuli and is 0.39 mm caudal to slice C. Slice E includes
ventral to the caudal margin of the external acoustic meatus (Fig. 9B).

In addition to the canal for the greater petrosal nerve, several other small canals are associated with the much larger facial canal at various points. The extracranial outlet of the canal for the auricular branch of the vagus nerve is located in the tympanomastoid fissure at the caudo-ventral margin of the external acoustic meatus. This canal runs medially and caudally for ~1.0 mm to merge with the canal for the chorda tympani (Fig. 9B–D). The chorda tympani canal is short, running ~0.2 mm from the facial canal to enter the tympanic cavity at the iter chordae posterius dorsal to the caudal-most portion of the tympanic annulus (Fig. 9D). Lateral to the jugular foramen, a structure we interpret as the mastoid canaliculus (by which the auricular branch of the vagus nerve gains entry to the tympanic cavity) enters the caudal-most portion of the tympanic cavity proper (Fig. 9E). If these interpretations are correct, then the auricular branch of the vagus nerve in Rooneyia passed through the mastoid canaliculus to emerge within the caudal portion of the tympanic cavity. The auricular branch of the vagus would then have run rostrally on the inner surface of the tympanic cavity to enter the iter chordae posterior and briefly share a common canal with the chorda tympani and (possibly) receive communicating branches of the facial nerve. From this point, the auricular branch of the vagus nerve would have traveled in its own canaliculus to emerge at the tympanomastoid fissure.

More caudally, the canal for the stapedius muscle begins as an open fossa on the lateral external surface of the petromastoid, ventral to the subarcuate fossa. Rooneyia thus exhibits the likely plesiomorphic condition for eutherians in having a patent parotic fissure and an extrabullar origin for the stapedius muscle (Ross, 1994). In this respect, Rooneyia resembles tarsiers, most omomyiforms, plesiadapiforms, and scandentians but differs from crown anthropoids, crown strepsirrhines, and adapiforms (Ross, 1994). From the parotic fissure, the fully enclosed stapedius canal (Fig. 9E) runs ~1.4 mm rostrally to the intratympanic hiatus for the stapedius tendon at the pyramidal eminence. The pyramidal eminence and stapedius tendon hiatus are located lateral to the caudal margin of the fenestra vestibuli. As the stapedius canal crosses in close proximity to the facial canal, the two canals are bridged by a tiny canaliculus for the motor nerve to the stapedius muscle.

**Discussion**

Our μCT analysis of the Rooneyia holotype provides important new information regarding the internal cranial anatomy and phylogenetic relationships of this enigmatic genus. The virtual endocast of Rooneyia (Fig. 3) exhibits a mosaic of traits that are both primitive and derived relative to the presumed ancestral condition for crown primates. Compared with the plesiadapiforms Plesiadaapis, Ignacius, and Microsyops (Gingerich and Gunnell, 2005; Silcox et al., 2009b, 2010), Rooneyia has a cerebrum with a proportionally larger neocortex and a proportionally smaller piriform cortex. This observation suggests that Rooneyia differs from plesiadapiforms and more closely resembles extant primates in having a smaller percentage of its cerebrum devoted to processing olfactory stimuli. Like omomyiforms and extant primates, Rooneyia further differs from plesiadapiforms in having an endocast with a proportionally larger cerebrum that more extensively overlaps the olfactory bulbs and cerebellum (Fig. 4; Szalay, 1969; Radinsky, 1970, 1975, 1977, 1979; Gingerich and Gunnell, 2005; Silcox et al., 2009b, 2010). Relative to body mass, endocast volume in Rooneyia is substantially greater than that of Ignacius and Microsyops (Fig. 5). To the extent that known plesiadapiform endocasts are representative of brain morphology in stem euarchontans or stem primates, these observations suggest that Rooneyia is derived in exhibiting a relatively large brain, cerebrum, and neocortex.

Despite these synapomorphies shared with crown primates, Rooneyia appears to have exhibited a proportionally smaller neocortex and larger piriform cortex than either of the extant strepsirrhines shown in Fig. 4. Furthermore, although absolute brain size is similar in Rooneyia and some callitrichine platyrhynths, Rooneyia lacks the very large cerebrum, very large neocortex, and small olfactory bulbs that are characteristic of extant anthropoids (Figs. 4 and 6; Radinsky, 1979). Rooneyia also resembles adapiforms (e.g., Smilodectes and Adapis) and omomyiforms (e.g., Tetonius and Necrolemur) in having a cerebrum with a proportionally smaller frontolobe than in extant primates (Fig. 4; Radinsky, 1975, 1979). This combination of a comparatively small neocortex and frontal lobes probably represents the primitive condition for crown primates (Radinsky, 1979).

The endocast of Rooneyia is also primitive in having a single visible neocortical sulcus: the Sylvian fissure (Fig. 3; Hofer and Wilson, 1967). In this respect Rooneyia resembles the omomyiforms Tetonius and Necrolemur but differs from the adapiforms Adapis and Smilodectes, both of which exhibit endocasts with coronalateral sulci (Radinsky, 1970, 1979). Although the degree of neocortical fissurization is strongly influenced by absolute brain size in mammals (Jerison, 1982; Martin, 1990; Macrini et al., 2007), the nearly lissencephalic cerebral endocast of Rooneyia is striking when compared with those of extant primates with smaller absolute brain sizes and greater neocortical gyriation (e.g., Loris in Fig. 4; Radinsky, 1974). As noted by Radinsky (1979:6), “…a modern prosimian brain the size of that of Rooneyia would have other sulci in addition to the Sylvian fissure.”

The primitive retention by Rooneyia of a nearly lissencephalic cerebrum with small frontal lobes stands in stark contrast to the derived size of its brain and olfactory bulbs. When endocranial volume is compared with estimated body mass (Fig. 5), it is evident that Rooneyia has one of the largest relative brain sizes of any known Paleogene primate. If the mean body mass estimate of 381 g based on cranial length is accurate (Silcox et al., 2009a), then the relative brain size of Rooneyia is comparable to living strepsirrhines and callitrichines and is greater than any other Paleogene primate in our sample. Alternatively, if the upper estimated body mass of 796 g is more accurate, then Rooneyia still exhibits a relative brain size comparable to some living primates (e.g., Lepilemur). In this case, the encephalization of Rooneyia would still be greater than that of any other fossil taxon considered here except Necrolemur (Fig. 5). Similarly, when olfactory bulb volume is compared with total endocranial volume (Fig. 6), Rooneyia has olfactory bulbs that are relatively smaller than those of most living strepsirrhines and all fossil taxa considered in this analysis except Necrolemur and Parapithecus. These findings suggest that although Rooneyia retains
an endocast with a fairly primitive morphology compared with living primates, this genus is nonetheless derived compared with the ancestral condition for crown primates in having a large brain relative to body size and small olfactory bulbs relative to brain size. Both features may be related to the fact that *Rooneyia* was probably diurnal (based on relative orbital aperture size; Kay and Kirk, 2000) and may have required a large brain to accommodate increased visual input from a large total population of retinal ganglion cells (based on optic foramen area; Kirk and Kay, 2004; Kirk, 2006). While it is also clear that relative brain size has increased in parallel in multiple primate lineages (Kay et al., 2012; Steiper and Seiffert, 2012), these findings are consistent with the hypothesis that *Rooneyia* is a crown primate.

In contrast to the derived sizes of the brain and olfactory bulbs, the internal anatomy of the nasal cavity in *Rooneyia* does not differ fundamentally from the presumed ancestral condition for crown primates or crown euarchontans (Cave, 1948, 1973; Le Gros Clark, 1959; Loo, 1973; Martin, 1980). Compared with living primates, the nasal cavity of *Rooneyia* most closely resembles that of strepsirrhines and lacks the derived features shared by haplorhines (Cave, 1973; Martin, 1990; Rossie and Smith, 2007). Most notably, *Rooneyia* retains four ethmoturbinals in each nasal fossa, has an olfactory recess separated from the nasopharyngeal meatus by a transverse lamina, and shows no indication of the interorbital septum seen in many small-bodied haplorhines (Ross, 1994). These results suggest that *Rooneyia* was similar to extant strepsirrhines in having a relatively large area of olfactory mucosa in its nasal cavity and a correspondingly sensitive and acute sense of smell (Negus, 1958; Cave, 1973; Smith et al., 2007, 2011). *Rooneyia* also exhibits an obliquely oriented nasolacrimal canal that is unlike the derived vertical canals seen in living haplorhines (Rossie et al., 2006; Rossie and Smith, 2007). In this respect, *Rooneyia* more closely resembles extant strepsirrhines, *Adapis*, *Aziobius*, and *Microchoerus*, which exhibit subhorizontally or obliquely oriented nasolacrimal canals (Rossie and Smith, 2007; Tabuce et al., 2009). Although comparative studies of nasolacrimal canal orientation in extant primates have primarily focused on strepsirrhines, tarsiers, and small-bodied platyrrhines (Rossie and Smith, 2007), the vertically oriented canals of living haplorhines are sufficiently distinctive that nasolacrimal canal orientation provides an important basis for assessing the crown haplorhine status of fossil taxa (Rossie et al., 2006; Tabuce et al., 2009). Furthermore, because a subhorizontally or obliquely oriented nasolacrimal canal irrigates the rhinarium in extant strepsirrhines (Rossie and Smith, 2007), the primitive orientation of *Rooneyia*’s nasolacrimal canal may imply that this genus retained a rhinarium as a collecting surface for semiochemicals analyzed by the vomeronasal organ. These details of internal nasal anatomy suggest that *Rooneyia* maintained well-developed main and accessory olfactory systems similar to those of living strepsirrhines. By comparison, the reorientation of the nasolacrimal canal and derived loss of (1) the olfactory recess, (2) ethmoturbinals III-IV, and (3) the rhinarium in crown haplorhines reflects a fundamental decrease in the ecological importance of olfaction compared with extant strepsirrhines. Accordingly, the absence of these derived features in *Rooneyia* provides compelling evidence that it is neither a stem tarsiform (Szalay and Delson, 1979; Seiffert et al., 2010) nor a stem anthropoid (Rosenberger, 2006).

Additional evidence that *Rooneyia* was not a crown haplorhine is provided by the anatomy of its ear region. Both the stapedial and promontory canals of *Rooneyia* are complete, with the promontory canal following a transpromontorial route through the tympanic cavity. Although the stapedial canal ranges between about 50% and 70% of the size of the promontory canal, the large sizes of both canals suggest that *Rooneyia* retained patent stapedial and promontory branches of the internal carotid artery. In these respects *Rooneyia* resembles most adapiforms and omomyiforms and differs from living haplorhines, in which the promontory artery follows a peribullar course through the middle ear and the stapedial artery involutes during fetal ontogeny (MacPhee, 1981; MacPhee and Cartmill, 1986; Ross, 1994). *Rooneyia* also has a simple tympanic cavity that is undivided by major septa, and thus lacks the transverse lamina and anterior accessory cavity shared by extant haplorhines (MacPhee and Cartmill, 1986; Ross, 1994). *Rooneyia* further differs from extant strepsirrhines, in which either the promontory artery (most lemuriforms) or the entire internal carotid (cheirogaleids and lorisiforms) involute during fetal development (MacPhee, 1981; MacPhee and Cartmill, 1986; Ross, 1994). *Rooneyia* also differs from extant anthropoids in having a patent parotic fissure and an extrabular origin for the stapedius muscle (Ross, 1994). In each of these respects, *Rooneyia* exhibits middle ear morphology that is probably primitive for crown primates. Other features of the ear region of *Rooneyia* described here for the first time are either autapomorphic (e.g., the presence of the lateral accessory air space) or have uncertain phylogenetic significance due to a lack of comparative data (e.g., the disposition of the bony canals for the auricular branch of the vagus nerve).

**Conclusions**

The totality of the new and revised anatomical observations made here on the basis of µCT data suggest that *Rooneyia* retained many cranial features that were presumably present in the last common ancestor of crown primates but are primitive for the clade. At the same time, *Rooneyia* exhibits several important cranial attributes that are derived compared with the condition in putative stem primates like *Ignacius* and *Microsops* (Silcox et al., 2009b, 2010). These derived features of *Rooneyia* include (1) relatively large and forward-facing orbits, (2) a large endocranial volume relative to body mass, and (3) small olfactory bulbs relative to endocranial volume. Significantly, however, none of the evidence considered in this analysis clearly supports a close phylogenetic relationship with any living primate clade. As a result, the new anatomical observations provided by this analysis do not favor the conclusion that *Rooneyia* is a stem tarsiform (Szalay and Delson, 1979; Seiffert et al., 2010) or a stem anthropoid (Rosenberger, 2006). If one of these hypotheses is correct, then either the numerous derived nasal and middle ear features shared by extant tarsiers and anthropoids (MacPhee and Cartmill, 1986; Ross, 1994) were acquired convergently, or *Rooneyia* has undergone multiple reversals to return to the ancestral condition. Both possibilities are less parsimonious than the conclusion that *Rooneyia* is either a very primitive stem haplorhine (Ross, 1994; Ross et al., 1998), a very primitive stem strepsirrhine (Kay et al., 2004), or an advanced stem primate.

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**Appendix A. Supplementary data**

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2014.03.007