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First virtual endocasts of adapiform primates

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ABSTRACT

Well-preserved crania of notharctine adapiforms from the Eocene of North America provide the best direct evidence available for inferring neuroanatomy and encephalization in early euprimates (crown primates). Virtual endocasts of the notharctines *Notharctus tenebrosus* ($n = 3$) and *Smilodectes gracilis* ($n = 4$) from the middle Eocene Bridger formation of Wyoming, and the late Eocene European adapid adapiform *Adapis parisiensis* ($n = 1$), were reconstructed from high-resolution X-ray computed tomography (CT) data. While the three species share many neuroanatomical similarities differentiating them from plesiadapiforms (stem primates) and extant euprimates, our sample of *N. tenebrosus* displays more variation than that of *S. gracilis*, possibly related to differences in the patterns of cranial sexual dimorphism or within-lineage evolution. Body masses predicted from associated teeth suggest that *N. tenebrosus* was larger and had a lower encephalization quotient (EQ) than *S. gracilis*, despite their close relationship and similar inferred ecologies. Meanwhile, body masses predicted from cranial length of the same specimens suggest that the two species were more similar, with overlapping body mass and EQ, although *S. gracilis* exhibits a range of EQs shifted upwards relative to that of *N. tenebrosus*. While associated data from other parts of the skeleton are mostly lacking for specimens included in this study, measurements for unassociated postcrania attributed to these species yield body mass and EQ estimates that are also more similar to each other than those based on teeth. Regardless of the body mass prediction method used, results suggest that the average EQ of adapiforms was similar to that of plesiadapiforms, only overlapped the lower quadrant for the range of extant strepsirrhines, and did not overlap with the range of extant haplorhines. However, structural changes evident in these endocasts suggest that early euprimates relied more on vision than olfaction relative to plesiadapiforms, despite having relatively small endocranial volumes compared to extant taxa.

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1. Introduction

Compared to many other mammal groups, on average the brains of extant primates are large when controlling for body mass (Martin, 1990; Barton, 2006). This is often cited as a potentially diagnostic characteristic of the order Primates (e.g., Cartmill, 1992) and various studies have correlated differences in relative brain size within and outside of Primates with ecological and social variables in attempts to understand the selective pressures that drove the evolution of increased relative brain size in this lineage (e.g., Clutton-Brock and Harvey, 1980; Dunbar, 1998; Healy and Rowe, 2007). Despite the potential importance of this characteristic to understanding primate evolution, the pattern and timing of brain evolution in the earliest fossil euprimates (crown primates) is not well understood. In particular, whether or not brain morphology and relative encephalization of early fossil crown primates differed in significant ways relative to that of stem primates ("plesiadapiforms") is poorly documented. Yet such information is critical for understanding the unifying features of the primate clade and the ecological context of primate origins.

Although soft tissues of internal organs do not typically fossilize, endocranial endocasts, or the casts of the internal cranial cavity

(Jerison, 1973), are one way in which relative brain size and morphology of extinct mammals may be studied. Because the brains of mammals occupy much of the volume of the internal cranial cavity, mammalian endocasts provide a relatively accurate proxy for brain size and external morphology, particularly for small mammals (Jerison, 1973; Macrini, 2007). This paper describes a sample of virtual endocasts of three Eocene adapiform primates, *Notharctus tenebrosus*, *Smilodectes gracilis*, and *Adapis parisiensis*, to assess ontogenetic, temporal, and sexual signals in endocast morphology and to re-evaluate the hypothesis that the earliest crown primates were more encephalized and/or differed in endocranial morphology relative to stem primates.

Crown primates (sometimes also referred to as "primates of modern aspect"; Simons, 1972, Wible and Covert, 1987; but see Boyer et al., 2013b, p. 39 for reasons to avoid this term), include all extant primates and their extinct direct relatives (Hoffstetter, 1977; Szalay and Delson, 1979; Martin, 1990). 'Euprimates' is a specific formulation of crown primates that includes Eocene adapiforms as stem strepsirrhines and omomyiforms as stem haplorhines (Hoffstetter, 1977). Plesiadapiformes is a paraphyletic group of Paleogene stem primates that includes the superfamily Plesiadapoidea, suggested to be the sister group of Euprimates (Bloch et al., 2007). Omomyiformes (also known as Omomyoidea) and Adapiformes (also known as Adapoidea) are two clades of early euprimates that had diverged by the earliest Eocene (Rose, 1994). While omomyiforms are recognized from the earliest Eocene to early Miocene of Asia, Europe, and North America, adapiforms are recognized from the earliest Eocene to late Miocene of Europe, Africa, and Asia (Gebo, 2002; Gunnell and Rose, 2002; Rasmussen, 2007). Adapiformes is typically divided into six families: the Eocene European family Adapidae, the Eocene Asian family Asiadapidae, the Eocene European, African, and Asian family Caenopithecidae, the Eocene through Miocene Asian family Sivaladapidae, the Eocene Asian and European family Cercamoniidae, and the Eocene European and predominantly North American family Notharctidae (Fleagle, 2013). The phylogenetic relationships of adapiforms have long been debated, with suggested affinities to either haplorhines (e.g., Gingerich, 1980; Rasmussen, 1987; Franzen et al., 2009; Gingerich et al., 2010) or to lemuroids, prosimians, or strepsirrhines (Gregory, 1920; Beard et al., 1986; Martin, 1990), with similarities to haplorhines (see Kay et al., 1997; Maiolino et al., 2012) explained as the result of convergent evolution (Seiffert et al., 2009). In the latter phylogenetic context, adapiforms are classified as stem strepsirrhines (Williams et al., 2010a,b; Maiolino et al., 2012), while omomyiforms are classified as stem haplorhines (Williams et al., 2010b).

Within Primates, endocasts of both plesiadapiforms and euprimates are known. These include endocasts produced by natural sediment infillings of the endocranium (e.g., Gazin, 1965), from artificially derived representations of the inner surface made of materials such as latex (e.g., Gingerich and Martin, 1981), and by virtual segmentation of sequential images produced by high-resolution X-ray micro computed tomography (CT) scanning (e.g., Silcox et al., 2009b, 2010; Kirk et al., 2014; Orliac et al., 2014; Ramdarshan and Orliac, 2015). Published plesiadapiform, adapiform, and omomyiform endocasts are summarized in Table 1.

These endocasts have formed the basis of understanding encephalization and endocranial morphology in stem primates and early euprimates and are often discussed in a comparative context (e.g., Radinsky, 1970; Gurche, 1978; Martin, 1990; Silcox et al., 2010), but the different endocast reconstruction methods pose some comparative limitations. Primate endocasts described and analyzed prior to Silcox et al. (2009b) — which include both natural and artificial physical endocasts (or a composite of both) of varying degrees of completeness (e.g., Gazin, 1965; Gingerich and Martin, 1981) — may have obscured morphology due to preservation of overlying bone (e.g., Hofer and Wilson, 1967; Radinsky, 1967; Gurche, 1982), and/or poorer surface resolution compared to virtual endocasts (e.g., Silcox et al., 2009b, 2010; Kirk et al., 2014; Orliac et al., 2014; Ramdarshan and Orliac, 2015). In addition, because of the difficulties in obtaining high quality endocasts from well-preserved skulls, sample sizes for fossil euprimate endocasts have been relatively small.

Recent advances in imaging technology have significantly changed the study of primate endocasts. Virtual endocasts of *Ignacius graybullianus* (Silcox et al., 2009b), *Microsyops annectens* (Silcox et al., 2010), *Rooneyia viejaensis* (Kirk et al., 2014), *Plesiadapis tricuspidens* (Orliac et al., 2014), and *Microchoerus erinaceus* (Ramdarshan and Orliac, 2015) have clearly shown that X-ray CT technology presents an unprecedented opportunity to visualize more complete endocasts of specimens where it would have been previously difficult or impossible without damage to the specimen. Virtual endocast reconstruction also allows for more consistent quantitative comparisons, as volumes and other metrics may be measured precisely using the same 3D imaging software. This is important because past studies on natural and artificial endocasts have utilized disparate methods of volume estimation. In the absence of complete endocasts, brain volumes have been estimated mathematically through double graphic integration (Jerison, 1973; Gingerich, 1976; Radinsky, 1977), infilling of cranial space by mustard seeds (Gingerich and Martin, 1981), or by water displacement of partially artistically reconstructed endocasts (Gurche, 1978, 1982).

Since Jerison's (1973) introduction of the encephalization quotient (or EQ, a comparative ratio of the measured brain size of a mammal to the expected brain size of an average mammal of the equivalent body mass) it has been clear that comparison of brain size in fossils requires both the estimation of endocranial volume and the prediction of body mass. An additional source of variation among

Table 1
Published endocasts of plesiadapiforms and early Euprimates

Taxon	Sources
Megadelphus lundeliusi (Microsyopidae, Plesiadapiformes)	Szalay, 1969; Radinsky, 1977
Microsyops annectens (Microsyopidae, Plesiadapiformes)	Szalay, 1969; Radinsky, 1977; Silcox et al., 2010
Plesiadapis cookei (Plesiadapidae, Plesiadapiformes)	Gingerich and Gunnell, 2005; Orliac et al., 2014
Plesiadapis tricuspidens (Plesiadapidae, Plesiadapiformes)	Orliac et al., 2014
Ignacius graybullianus (Paromomyidae, Plesiadapiformes)	Silcox et al., 2009b
Adapis parisiensis (Adapinae, Adapidae, Adapiformes)	Neumayer, 1906; Gregory, 1920; Le Gros Clark, 1945; Radinsky, 1970; Gurche, 1978, 1982; Gingerich and Martin, 1981; Martin, 1990
Smilodectes gracilis (Notharctinae, Notharctidae, Adapiformes)	Gazin 1965; Radinsky, 1970; Gurche, 1978, 1982; Martin, 1990
Notharctus tenebrosus (Notharctinae, Notharctidae, Adapiformes)	Gregory, 1920; Gurche, 1978, 1982
Tetonius homunculus (Anaptomorphinae, Omomyidae, Omomyiformes)	Radinsky, 1967; Radinsky, 1970; Gurche 1978, 1982
Necrolemur antiquus (Microchoeridae; Omomyiformes)	Hürzeler, 1948; Hofer, 1962; Radinsky, 1970; Gurche, 1978, 1982
Microchoerus erinaceus (Microchoeridae, Omomyiformes)	Ramdarshan and Orliac, 2015
Rooneyia viejaensis (in certae sedis)	Hofer and Wilson, 1967; Radinsky, 1970; Gurche, 1978, 1982; Kirk et al., 2014