

RESEARCH ARTICLE

The Fossil Record of Anthropoid Brain Evolution

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ABSTRACT

Objectives: This study examines brain evolution in early fossil anthropoids using virtual reconstructions of endocranial morphology.

Materials and Methods: We estimated the size of the brain and the proportions of its components using new estimates of body mass and a broad sample of virtual endocasts of extant primates and Oligocene–mid-Miocene anthropoids.

Results: Brain size relative to body mass and brain proportions relative to brain size were evaluated. Compared with body mass, (1) Brain size enlargement has occurred convergently in many anthropoid lineages. (2) Tarsiers and anthropoids evolved smaller olfactory bulbs and larger neocortices than strepsirrhines. (3) Enlargement of tarsier and anthropoid non-frontal regions (occipital, parietal, and temporal lobes), not of the frontal lobe, accounts for larger neocortex size. Considering brain proportions relative to brain size yields similar findings: (1) Tarsiers and extant and fossil anthropoids have smaller olfactory bulbs and larger neocortices than strepsirrhines. (2) Tarsier and anthropoid neocortical expansion occurred principally in regions where visual signals are processed. (3) Correspondingly, species with relatively more visual input also have larger non-frontal neocortex.

Discussion: Shifts in brain proportions found in the stem anthropoid *Simonsius*, and stem platyrrhines and catarrhines were established before brain enlargement. The neocortex was enlarged, with disproportionate expansion of regions where visual signals are processed, emphasizing the heightened importance of the haplorhine visual system. Depending on the phylogenetic position of omomyoid haplorhines, large shifts in neocorticalization either occurred separately in stem tarsiids and anthropoids or once in the stem lineage leading to tarsiids and anthropoids.

1 | Introduction

Anthropoid evolution was marked by numerous changes to the brain, including an increase in overall brain size relative

to body mass, a reduction in the size of the olfactory bulbs and paleocortex, and expansion of the neocortex (Heritage 2014; Le Gros Clark 1959; Radinsky 1973, 1974, 1975). Although fossil and molecular data suggest that anthropoids branched

Summary

- Relative to brain size, the neocortex is larger in haplorhines than in strepsirrhines.
- Most of this enlargement involves regions of the neocortex where visual signals are processed not in the frontal lobes.

from other haplorhines by at least 45 Ma (Beard et al. 1994; Kuderna et al. 2023; Perelman et al. 2011), the earliest complete and well-preserved anthropoid endocasts are those of the stem anthropoid *Simonsius grangeri* and the stem catarrhine *Aegyptopithecus zeuxis*, both from the early Oligocene of Egypt, ~30 Ma (Bush and Allman 2003; Radinsky 1973; Simons et al. 2007). An endocast of the Early Miocene Kenyan stem cercopithecoid *Victoriapithecus macinnesi* has also been described (Gonzales et al. 2015). The oldest hominoid with enough of a neurocranium to permit a full endocast reconstruction is that of Middle Miocene *Nyanzapithecus alesi*, but it has not been described in detail (Nengo et al. 2017). The oldest described endocasts of stem platyrrhines are of *Chilecebus carrascoensis* (~21 Ma, Early Miocene, Chile), and *Homunculus patagonicus* (~17.4 Ma, late Early Miocene, Argentina) (Kay et al. 2004; Kay et al. 2012; Ni et al. 2019; Radinsky 1974; Trayler et al. 2020). The phylogenetic position of these taxa is outlined in Figure 1.

In prior research, cerebral cortical dimensions in fossil primates have been compared with small samples of preserved brains of 27 haplorhine and 15 strepsirrhine genera (Stephan et al. 1981). This approach leaves open questions about how the measurement of preserved cerebral cortex specimens translate to endocast measurements—the only measurements available for fossil species. To better estimate and contextualize the dimensions of fossil anthropoid virtual endocasts, we produced a large, diverse comparative sample of extant primate virtual endocasts representing the first comprehensive dataset of measurements of endocast volume, olfactory fossa volume, surface area of the neocortex, and the surface areas of two regions of the neocortex. Leveraging this comparative dataset, we evaluate a new endocast reconstruction of *Simonsius* and previously published endocasts of *Aegyptopithecus*, *Chilecebus*, and *Victoriapithecus*. We describe the endocranial morphology of two exceptionally well-preserved crania of *Homunculus patagonicus*. Additionally, we describe for the first time a less complete endocast of the stem platyrrhine *Tremacebus harringtoni* (~21 Ma, Early Miocene, Argentina).

An extensive literature exists reconstructing the size of the brain relative to body mass in living and fossil primates using residuals and/or “quotients” (Gurche 1982; Jerison 1973; Martin 1990; Stephan et al. 1981). Using these approaches, *Simonsius* and *Aegyptopithecus* reportedly have strepsirrhine-sized brains relative to body size, both smaller than and outside the range of extant anthropoids (Bush, Simons, and Allman 2004; Radinsky 1973; Simons et al. 2007). The Miocene cercopithecoid *Victoriapithecus* also had a relatively small brain (Gonzales et al. 2015) as did the stem platyrrhines *Chilecebus* (Sears et al. 2008) and *Homunculus* (Kay et al. 2012; Perry et al. 2025)

when compared with extant anthropoids. A recurring problem in these comparisons has been the precision with which body mass is estimated for the fossil species, with differences in approach and comparative datasets leading to a wide range of prior estimates. A key issue is that primate body size and many of its morphological proxies show high phylogenetic covariance, which is negatively correlated with predictive accuracy for body mass models (Pampush et al. 2021). While estimates of this key variable will always necessarily be hampered by caveats in fossils, here we follow the recommendations of Pampush et al. (2021) to produce new estimates of body mass for the extinct taxa using phylogenetic independent contrasts (PIC; Garland et al. 2000), which explicitly incorporates phylogenetic information both into building models and forming predictions from those models, helping to address phylogenetic covariance.

Three areas of focus in past studies of primate brain evolution have been (1) the relative size of the olfactory bulbs, (2) the overall size of the neocortex, and (3) the size of various regions of the neocortex.

Evolutionary trends in the size of the olfactory bulbs relative to body size and brain size have been explored extensively using estimates of the volume of the olfactory fossa as a surrogate for bulb volume. Comparative analyses have consistently demonstrated that living haplorhines have smaller olfactory bulbs than strepsirrhines of similar body mass (Heritage 2014; Lang et al. 2025; Stephan et al. 1981). *Simonsius*, *Aegyptopithecus*, and *Victoriapithecus* have olfactory fossae that are larger than those of extant anthropoids when they are measured relative to endocranial volume but smaller than strepsirrhines (Bush, Simons, Dubowitz, and Allman 2004; Gonzales et al. 2015; Kirk, Kay, et al. 2025; Simons et al. 2007). *Tremacebus*, *Homunculus*, and *Chilecebus* have bulbs within the range of extant diurnal platyrrhines (Kay et al. 2004; Kay et al. 2012; Ni et al. 2019).

In contrast to the robust quantitative data about brain (or endocast) size and olfactory fossa size, the many claims about relative size of the neocortical surface are based mainly on visual inspection of shape and position relative to anatomical landmarks, such as the degree of dorsal bulging and overlap of the rostral part of the neocortex (frontal) surface over the olfactory fossa and the extent of overlapping of the caudal (occipital) neocortex over the cerebellum. On this basis, neocortex size in *Simonsius*, *Aegyptopithecus*, *Victoriapithecus*, *Homunculus*, and *Chilecebus* has been described as small relative to endocast volume compared with living anthropoids. To quantify neocortical size, Jerison introduced a measurement of neocorticalization, defined as the ratio of endocast neocortical surface area to total endocast surface area (Jerison 2007, 2012; Long et al. 2015). Long et al. (2015) extended Jerison's dataset, which was based on plaster and latex casts of a limited number of taxa, to include virtual endocasts of many other taxa pertinent to primate origins. Here we examine changes in neocorticalization in anthropoid primates using a modification of Jerison's approach to account for two potentially confounding effects. First, Jerison used ratios to express relative size of the neocortex. Ratios can be confounded by departures from isometry and therefore systematically influenced by differences in overall size (Albrecht 1978; Gilbert and Jungers 2017; Smith 1984). Second, the denominator in Jerison's ratio—the surface area of the endocast—creates comparative

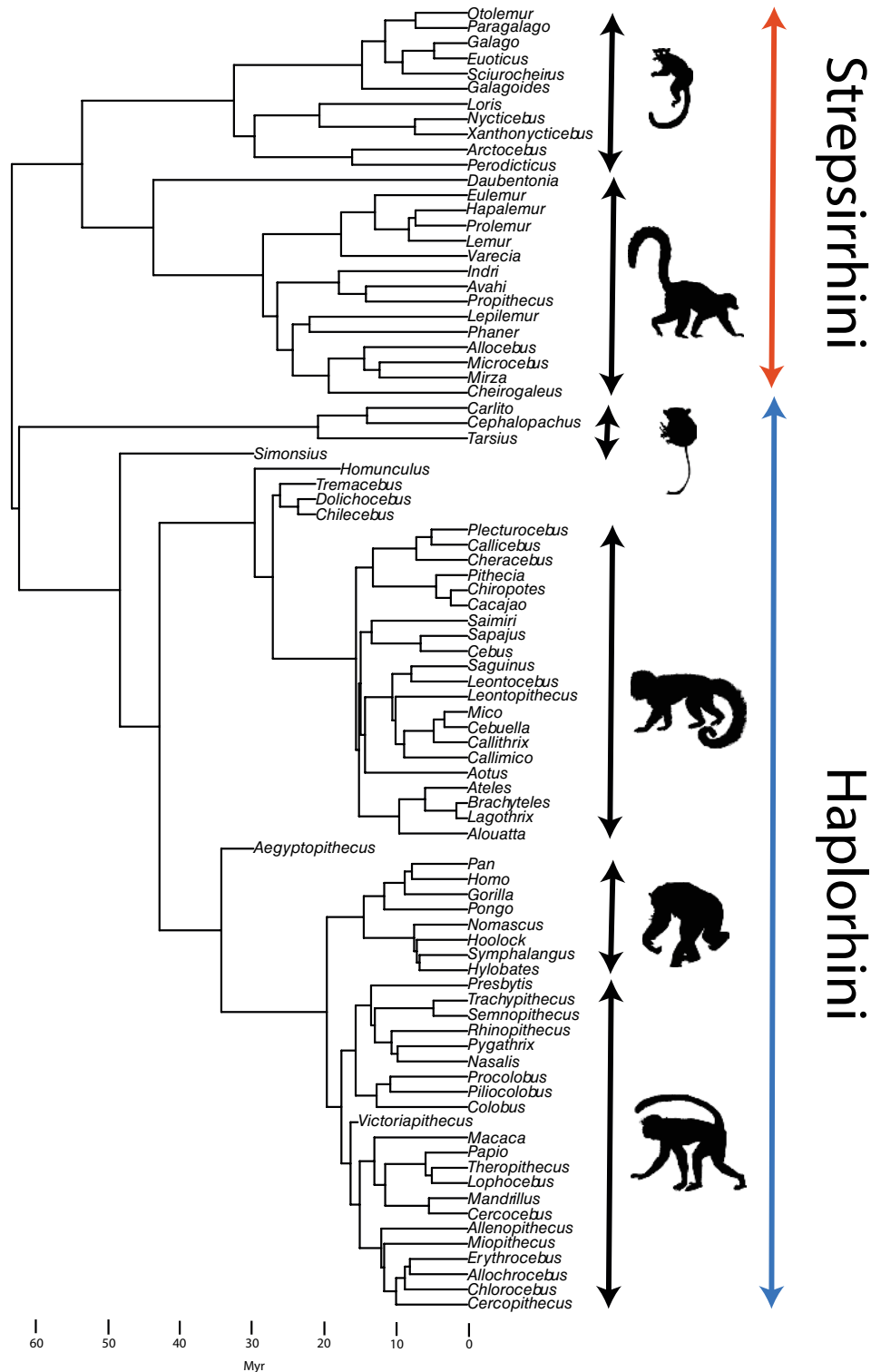


FIGURE 1 | Phylogeny of Primates adopted here for PGLS analyses. Branch lengths are proportional to age and length of separation. The silhouettes of the primates were downloaded from www.phylopic.org and are licensed for free use in the Public Domain without copyright.

and interpretive challenges because basicranial areas of mammalian endocasts include impressions or grooves for various nerves and large arterial and venous channels. Because Jerison's ratio uses the surface area of the entire endocast as its denominator, it is not clear to what extent variability among taxa in the irregularity of the endocranial surface (which does not correspond with brain surface area per se) would affect the ratio.

Moreover, while there is a good rationale for measuring neocortex surface area on an endocast (i.e., the gray matter forms a sheet, so endocast surface offers a plausible, albeit crude, way to approximate that), the remaining endocast surfaces in total do not reflect any uniform underlying brain structure. To address these potentially confounding factors, we introduce a new approach to estimating neocorticalization.

The size of the frontal lobe of the neocortex (or more accurately frontal neocortical shape and surface area as they appear on endocasts) has been commented upon extensively in the literature of fossil anthropoids. The prevailing view is that the frontal lobe (compared with overall endocast size) is smaller in fossil anthropoids, resembling the relationship observed in strepsirrhines. The frontal lobe is said to be small in *Simonsius*, *Aegyptopithecus*, *Victoriapithecus*, *Chilecebus*, and *Homunculus* when compared with endocast volume (Bush, Simons, Dubowitz, and Allman 2004; Gonzales et al. 2015; Kay et al. 2012; Ni et al. 2019; Simons 2004). These conclusions are based mainly on visual inspection without measurement, such as the extent of the frontal's bulging and rostral overlapping of the olfactory bulbs and its flattened dorsal profile in lateral view. In the case of *Aegyptopithecus*, *Victoriapithecus*, and *Chilecebus*, the more rostral position of the central sulcus compared with its position in extant anthropoids is also invoked to claim smaller frontal lobe size. These findings led Wise (2023) to conclude that expansion of the frontal lobes must have occurred several times independently during anthropoid evolution.

Several aspects of these conclusions are subject to challenge: First, the conclusions are not backed up with actual measurements. Second, shape is a notoriously inaccurate way to evaluate size. Consider the obvious and profound effect the size of the orbit must have on frontal lobe shape as it presses against this region of the brain. Paraphrasing Moss and Young (1960), the shape of the frontal lobe is a reflection of the spatial relationship between functionally unrelated cephalic components, the orbit and the brain case, both of which are served by the frontal bone. Third, assumptions based on the position of the central sulcus must also be affected by changes in the position of the orbits and masticatory muscles. Fourth, Bush and Allman (2004) found that strepsirrhine frontal lobe gray matter is larger (as a proportion of total neocortex gray matter) than that of haplorhines. If this finding can be extended to fossil anthropoids, it would suggest that frontal lobes were *larger* relative to neocortex size in the ancestral haplorhine and the frontal lobe has been reduced, not enlarged, in relative size during anthropoid evolution. Finally, confusion is introduced because primate frontal lobes hyperscale with increasing brain or body size (Bush and Allman 2004; Von Bonin 1948). Put another way, the frontal lobe takes up a larger percentage of the neocortex in bigger brains.

The size of remaining parts of the primate neocortex (occipital, parietal, and temporal lobes) is expanded compared with non-primate mammals. Because the occipital lobe houses the striate, or primary visual, cortex, Le Gros Clark (1959) viewed its expansion to be related to accommodating an expanding visual cortex, established early in primate evolution, even in tree shrews, which he regarded as primates. Le Gros Clark identified further “progressive” expansion in the occipital lobe and other areas of visual processing in the temporal and parietal lobes in lemurs compared with treeshrews, and even more so in haplorhines compared with strepsirrhines. As with the frontal lobe, these conclusions are based mainly on visual assessment of the position of the lunate sulcus and the extent to which the occipital lobe's caudal pole covers the midbrain and most or all the cerebellum in dorsal view. *Aegyptopithecus* was considered to resemble modern anthropoids and to be “more advanced”

than most modern strepsirrhines in having an enlarged occipital lobe with relatively more primary visual cortex (as indicated by the position of the lunate sulcus) (Radinsky 1973, 243). Beyond these generalizations, few other attempts have been made to identify the finer details of the evolution of this region. The total surface area of the occipital, parietal and temporal lobes can be delineated on virtual endocasts when a central sulcus, sylvian fissure, and rhinal sulcus can be visualized, but the central sulcus rarely appears in strepsirrhines and never in tarsiers. Here we offer a new approach that can clarify increases in the visual neocortex, although not specifically the occipital lobe.

2 | Background

2.1 | Previous Studies of Early Anthropoid Brain Evolution

Here we concentrate on more complete endocasts of Oligocene and Early Miocene anthropoids from Africa and Early Miocene anthropoids from South America. Other partial endocranial surfaces of fossil anthropoids, summarized in what follows and in Table 2, are too incomplete to offer anything other than rough guesses about endocast size or, in some cases, the size of the olfactory fossa.

2.1.1 | Stem Anthropoids

A fragment of the frontal and parietal of *Ganlea megacania*, a Late Eocene amphipithecoid, may be the oldest record of an Asian anthropoid to preserve any record of endocast shape and size. *Ganlea* had a large olfactory fossa that was “proportionally larger” than that of early Oligocene Afro-Arabian anthropoids *Simonsius grangeri* or *Aegyptopithecus zeuxis* (Jaeger et al. 2020, 5; see below). The endocranial surface of the frontal bone in *Ganlea* also suggests that the olfactory bulbs were pedunculate and the frontal lobes were positioned posterior to the region of greatest postorbital constriction—an anatomical configuration that is otherwise unknown in living or fossil anthropoids (Kirk, Campisano, et al. 2025). The anthropoid status of amphipithecoids has been subject to debate; some regard *Ganlea* to be a strepsirrhine (Ciochon et al. 2001). Intriguingly, *Ganlea* lacks postorbital closure, while its Late Eocene phyletic relative *Siamopithecus* has postorbital closure (Chaimanee et al. 2025).

Two Late Eocene anthropoids from Egypt, *Catopithecus browni* and *Proteopithecus sylviae*, straddling the Eocene–Oligocene boundary are known from crushed and deformed skulls (Simons 1997; Simons and Rasmussen 1996). Simons and Rasmussen (1996) reconstructed the endocranial volume of *Catopithecus*, often regarded as a stem catarrhine (Seiffert et al. 2020), to be very small, at the lower end of the Eocene primate range relative to body mass. The olfactory fossa was not measured but was said to be large compared with those of extant anthropoids and proportionally larger than that of *Aegyptopithecus*. The stem anthropoid *Proteopithecus* has been similarly interpreted as having a smaller endocast than similar-sized platyrrhines (Simons 1997). The endocast sizes of these two genera were estimated by visual comparison with extant platyrrhines of similar size or by modeling a clay

reconstruction of a brain of a size compatible with the crushed braincases and immersing it in water to measure the volume displaced (Simons 1997; Simons and Rasmussen 1996). We regard these estimates to be unreliable given the poor state of preservation of all currently known crania of *Catopithecus* and *Proteopithecus*.

Bush et al. (Bush, Simons, and Allman et al. 2004; Bush, Simons, Dubowitz, and Allman et al. 2004) describe a virtual endocast of the early Oligocene (~30 Ma) parapihthecid stem anthropoid *Simonsius grangeri* (YPM 18651). These authors emphasize the small size of the brain endocast relative to body mass. They also report that, compared with total endocast volume, *Simonsius* has relatively larger olfactory fossa than those of extant anthropoids, though not as large as in extant strepsirrhines. Ni et al. (2019) agreed with this assessment, noting that the olfactory fossa of *Simonsius* is much larger in proportion to body mass than in extant anthropoids. Here we reexamine *Simonsius* based on a new endocast reconstruction.

Apidium phiomense, a parapihthecid contemporary of *Simonsius*, is represented by a partial cranium. Although no measurement was attempted, it evidently had a smaller brain than similar-sized platyrrhines with olfactory fossae intermediate in relative size between anthropoids and strepsirrhines, as in *Simonsius* (Radinsky 1974; Simons 1997).

2.1.2 | Stem Catarrhines

Radinsky (1973) examined a partial natural endocast of the early Oligocene stem catarrhine *Aegyptopithecus zeuxis* (YPM 23975). He reported that the occipital lobes of *Aegyptopithecus* extend more caudally over the cerebellum compared with strepsirrhines. He identified a lunate sulcus, which forms the rostral boundary of the primary visual cortex (=striate cortex) in living anthropoids. Radinsky (1973) noted that this sulcus is located more rostrally than in extant strepsirrhines, suggesting that the primary visual cortex is expanded in *Aegyptopithecus*. Radinsky also identified a central sulcus, which forms the boundary between the parietal somatosensory and frontal motor components of the neocortex. He states that the central sulcus was positioned more rostrally in *Aegyptopithecus*, which may indicate a less expanded frontal lobe compared with extant anthropoids.

A more complete *Aegyptopithecus* specimen (CGM 85785) was studied by Simons et al. (2007). Simons et al. described this specimen as having a small brain for an anthropoid of comparable body mass. Expressed as a ratio of olfactory fossa volume to total endocranial volume, they reported the olfactory fossa of *Aegyptopithecus* to be on the lower end of the range of living strepsirrhines and similar in size to extant anthropoids of its body mass. Ni et al. (2019) agreed, saying that the olfactory fossa of *Aegyptopithecus* is larger relative to body mass than in extant platyrrhines, although they note that *Aegyptopithecus* olfactory fossa size falls within the 95% confidence interval for extant catarrhines. We revisit this specimen in our analysis.

Another stem catarrhine *Saadanius hijazensis* (29–28 Ma, Saudi Arabia) (Zalmout et al. 2010) is a rostrum preserving parts of the

olfactory fossa. The fossa appears small relative to the rest of the face and palate and projects rostral to the anterior cranial fossa.

2.1.3 | Stem Cercopithecoids and Hominoids

The oldest known stem cercopithecoid and hominoid endocranial remains come from the Early and Middle Miocene of East Africa. European hominoid material dates from Middle and Late Miocene. Here, we summarize this material, most of which is too incomplete for inclusion in our metric analysis.

An anthropoid frontal bone from the Early Miocene of Napak Uganda (~19 Ma) of uncertain affinities preserves traces of the frontal parts of the neocortical surface. Radinsky (1974) considered the sulcal impression of this endocast fragment to be like that of hominoids. Falk (1983, 246) instead regarded the sulcal pattern as having a “primitive” anthropoid pattern. Based on its flattened dorsal profile the frontal lobe has been interpreted as less expanded than in extant anthropoids (Pilbeam and Walker 1968).

The earliest stem cercopithecoid endocast is that of *Victoriapithecus macinnesi* (KNM-MB 29100) from the early Middle Miocene (~15 Ma) of Kenya. Gonzales et al. (2015) described and figured a virtual endocast of KNM-MB 29100, showing that it has a distinctively cercopithecoid pattern of cerebral gyrification. These authors interpret the *Victoriapithecus* endocast as indicating a small brain with a small frontal surface and large olfactory fossa compared with those of extant cercopithecoids. This material is sufficiently well preserved to allow estimates of endocast volume and olfactory fossa size as well as a fairly accurate estimate of body mass from postcranial material.

A partial endocast impression of the hominoid *Ekembo heseloni* (= *Proconsul heseloni*) from the late Early Miocene (18–17 Ma) of Kenya was reviewed by Falk (1983), who interpreted the sulcal pattern of the frontal lobe surface as being less derived than the pattern found in any extant catarrhine. Le Gros Clark and Leakey's (1951) suggestion that the endocast features a small frontal lobe for an anthropoid was discounted by Radinsky (1974), although neither author provided any measurements. Based on visual inspection, *Ekembo* had an olfactory fossa within the range of size of extant catarrhines (Fleagle and Kay 1983). A reconstruction from dimensions of the incomplete endocranium by Walker et al. (1983) yielded a brain size estimate of 167.9 cc, which, with an estimated body mass of between 10 and 11 kg, suggests that relative brain size in *Ekembo* was comparable to extant hominoids but greater than extant cercopithecoids of comparable body mass. Manser and Harrison (2000) proposed a smaller brain size of 130.3 cc based on a new estimate from the dimensions of the foramen magnum (FM). With their body mass estimate of 10.9 kg, they concluded that *Ekembo* was more like extant cercopithecoids in relative brain size. Using FM to estimate brains size turns on its head Radinsky's (1967) claim that FM size can substitute for body size, not brain size, when estimating relative brain size in fossils. In any event, Gould (1975) showed that FM size was a function of both brain size and body size, and a suitable substitute for neither. Thus, the available material of *Ekembo* is insufficiently preserved to yield a direct estimate of the size of the brain or its components.

Early Miocene *Turkanapithecus kalakolensis* (17.7–16.6 Ma) is estimated from foramen magnum dimensions to have had an endocranial volume of 84.3 cc with a body size estimated from postcranial material to be ~10 kg (Manser and Harrison 2000). As noted for *Ekembo*, estimates based on FM are unreliable and thus the available material is insufficiently preserved to yield direct estimates of the size of the endocranial or its components. Another Early Miocene east African stem hominoid *Afropithecus turkanensis* (~17 Ma) is represented by a facial skeleton that preserves the olfactory fossa. The fossa is rostrally projecting like in *Aegyptopithecus* and *Victoriapithecus* (Nengo et al. 2017).

The cranium of a young individual of Middle Miocene stem hominoid *Nyanzapithecus alesi* (13 Ma) from Kenya is reported to have an endocranial volume of 101 cc, based on a virtual endocranial corrected for plastic deformation and fractures. Based on Nengo et al.'s (2017) reconstruction of the body mass of ~11.3 kg, this endocranial size, which they think was close to an adult value based on its dental age, would fall within the range of extant cercopithecoids. No data is supplied about the size of the olfactory fossa but it is characterized by those authors as shallow and positioned ventral to the anterior cranial fossa as in extant catarrhines and unlike the larger and more rostrally projecting olfactory fossa of *Aegyptopithecus*, *Victoriapithecus*, and *Afropithecus*.

Endocranial volume and body mass has been estimated for several poorly preserved Middle to Late Miocene hominoids from Europe including: (1) *Pliobates cataloniae* (11.6 Ma): average of 72 cc, based on various external neurocranial measurements; body mass (4.5 kg) (Alba et al. 2015). (2) *Rudapithecus hungaricus* (10.3–9.8 Ma) from a virtual reconstruction of braincase by Gunz et al. 2020 (234 cc); range: 221–247 cc; body mass 15–18.2 kg. (3) *Oreopithecus bambolii* (7–6 Ma) 128.2 cc 22.6 kg based on FM dimensions from a flattened and fragmented cranium (Harrison 1989a).

2.2 | Stem Platyrrhines

Ni et al. (2019) described a virtual endocranial of the stem platyrrhine *Chilecebus carrascoensis* from the Early Miocene (~21 Ma) of Chile, known from a single cranial specimen (SGOPV 3213). They calculated the encephalization quotient (EQ) from a phylogenetic generalized least squares (PGLS) model to evaluate brain endocranial volume relative to body mass, incorporating the effects of phylogeny into the model. On that basis, the endocranial volume of *Chilecebus* falls at the lower end of relative endocranial volume in extant platyrrhines, with some size overlap with extant callitrichines. Ni et al. (2019, 6) also report that the olfactory fossa of *Chilecebus* was “far smaller” than average for extant haplorhines of similar body mass. Based on an evaluation of sulcal patterns, they conclude that the major brain subdivisions of *Chilecebus* and other basal anthropoids exhibit no consistent scaling pattern relative to overall brain size, that sulci appeared in a mosaic fashion in various anthropoid lineages, and that major neocortical subdivisions exhibit many independent instances of size increases and some secondary decreases throughout anthropoid evolution. These conclusions are based solely on observations of brain surface sulci and shape, and Ni et al. (2019) did

not measure the endocranial surface area of the neocortex or its constituent parts. Nevertheless, they note that the frontal part of the neocortex in *Chilecebus* only partially overlaps the olfactory fossa, is less bulging dorsally, and that the central sulcus is more rostrally positioned than in *Aegyptopithecus*. Accordingly, these authors concluded that the frontal lobe of *Chilecebus* is quite small, even smaller than that of *Aegyptopithecus* (Ni et al. 2019).

Two ~21 Ma Early Miocene platyrrhines from Patagonian Argentina, *Dolichocebus gaimanensis* and *Tremacebus haringtoni*, have been examined in much less detail than *Chilecebus*. A battered skull of the stem platyrrhine *Dolichocebus* (MACN 14128) was said by Radinsky (1974) to have expanded occipital lobes, suggesting the presence of an enlarged primary visual cortex like extant anthropoids. The remainder of the *Dolichocebus* natural endocranial was either inaccessible or too damaged for Radinsky to make additional observations.

Kay et al. (2004) made a CT scan of *Tremacebus* (FML 618). They note that relative to endocranial breadth, the olfactory fossa is similar in size to that of extant diurnal platyrrhines but proportionally smaller than that of the only extant nocturnal anthropoid, *Aotus*.

Tauber (1991) described a partial endocranial surface of *Homunculus patagonicus* (CORD-PZ 1130) from the late Early Miocene (~17.4 Ma) of Patagonian Argentina. Tauber identified a sylvian fissure as well as a superior temporal sulcus. He considered the neocortex to be large because it overlaps the cerebellum caudally. Kay et al. (2012) illustrated a virtual endocranial of another *Homunculus* (MPM-PV 3502). They reported that, compared with extant platyrrhines, this specimen had a small brain and a small olfactory fossa relative to its estimated body mass. Here, we describe MPM-PV 3502 in more detail and add a description of another specimen, MPM-PV 17453.

There has been disagreement about the hypodigm of *Homunculus* arising from the naming of a separate taxon, “*Killikaike blakei*” (Tejedor et al. 2006), which has some bearing on our understanding of platyrrhine brain evolution. Type specimens of the two taxa are known from the same locality, but the type specimen of *H. patagonicus* is a mandible (MACN A 635) whereas the type specimen of “*K. blakei*” (MPM PV-5000) is a rostrum with upper teeth, so the two are not directly comparable. Kay et al. (2012) and Perry et al. (2014) concluded that “*Killikaike*” specimens should be included within *Homunculus*. A new specimen of *Homunculus* (MPM PV-17453), the endocranial of which is described here, includes upper and lower jaws and confirms that “*K. blakei*” is a junior synonym of *Homunculus patagonicus* (Perry et al. 2025). This determination is relevant in the present context because Tejedor et al. (2006) estimated the volume of the frontal part of an endocranial in the type specimen of “*Killikaike*” from the volume of its anterior cranial fossa. These authors concluded that the frontal lobe was large for the overall size of the animal, comparing it to the extant cebine platyrrhine *Saimiri*. Tejedor et al. (2006) further claimed that because the frontal lobe was large, the brain must also have been large. However, as Kay et al. (2012) pointed out, their conclusion was based on a misalignment of the rostrum to the braincase. Once this misalignment is accounted for by using more complete cranial material of *Homunculus*, the anterior cranial fossa of the

“Killikake” specimen resembles other *Homunculus* specimens and no longer appears to be expanded.

2.3 | Prior Efforts to Estimate Body Mass

Using an ordinary least squares regression model based on measurements of a wide variety of extant primates, Kay and Simons (1980) estimated the body mass for *Simonsius grangeri* at 1802 g (1632–1990 g). Conroy (1987) gives a much larger mass estimate from the dentition of 2582–3171 g for *Simonsius* based on several different linear regression models using either a sample across all primates (similar to Kay and Simons) or subsets of primates (e.g., anthropoids). Simons et al. (2007) generated a range of body mass estimates for *Simonsius* using equations for orbital area, bizygomatic width, skull length, lower first molar area, and postcranial measurements although neither the measurements nor the equations that produced these estimates were reported. Working from the x–y position of the symbol for *Simonsius* in fig. 4 of their study, a body mass of ~2250 g can be inferred for *Simonsius* cranium DPC 18651.

Using the same data sets and models as for *Simonsius*, Kay and Simons (1980) estimated body mass in *Aegyptopithecus zeuxis* at 5876 g (5346–6450) while Conroy's (1987) estimates range from 6079 to 6716 g. These species average estimates do not take into account the extreme nature of sexual dimorphism of *Aegyptopithecus* and other early Oligocene anthropoids (*Apidium proteopithecus*, *Catopithecus*) (Fleagle et al. 1980; Simons et al. 1999, 2007). Based on fig. 4 of Simons et al. (2007) a body mass of 2735 g was estimated for a female *Aegyptopithecus* cranium CGM 85785, and 6610 g for a male *Aegyptopithecus* cranium CGM 40237.

Various estimates of the body mass of *Victoriapithecus* are summarized in Gonzales et al. (2015). Estimates from cranial dimensions are 6–7 kg, while those from molar dimensions are ~10.5 kg (Delson et al. 2000). The largest postcranial estimates of body mass do not exceed 5.0–5.5 kg (Harrison 1989b).

Early approaches estimated the body mass of *Homunculus patagonicus* from mandibular molar dimensions using the regression equations calculated by Conroy (1987), Meldrum and Kay (1997), and Egi et al. (2004). Kay et al. (2012) produced three added estimates of body mass, ranging from 2152 to 2521 g. Using three skulls (MPM-PV 3501, MPM-PV 3502, and MPM-PV 3503), Kay et al. (2012) generated alternative body mass estimates for *Homunculus* by regressing the cranial dimensions of 47 extant platyrrhine species (data from Hartwig 1993) against mean adult body masses from Smith and Jungers (1997). Two crania (MPM-PV 3501, MPM-PV 3502) were sufficiently complete to provide measurements for 17 and 13 cranial measurements, respectively. A principal components analysis was conducted for these subsets of measurements, with the first principal component used as a proxy for body mass. Kay et al.'s five body mass estimates based on cranial dimensions range from 1854 to 2347 g.

Perry et al. (2014) estimated body mass in *Homunculus* using humeral and femoral articular breadths. Data for extant primates from Runestad (1994) (i.e., 14 species of 11 catarrhine genera and 9 species of 8 platyrrhine genera, covering all the extant

anthropoid families except Pitheciidae) was regressed against body mass. Perry et al.'s (2014) “preferred” estimates combine extant platyrrhine and catarrhine data unless the regressions differed among the clades, in which case they report estimates for each independently. Their four estimates of body mass in *Homunculus* range from 3188 to 4335 g.¹

Other estimates of Miocene platyrrhine body mass include that of *Chilecebus* (SGOPV 3213) at 583 g using a weighted average of 46 models for body mass from craniodental dimensions across extant platyrrhines (Sears et al. 2008). From the dimensions of its first and second lower molars and a variety of previously published regression equations, Kay et al. (2008) estimated the body mass of *Dolichocebus* as between 1149 and 1754 g. The body mass of *Tremacebus* has not previously been estimated, as this species is known only from a cranium that lacks tooth crowns.

3 | Materials and Methods

Our extant comparative sample of anthropoid endocasts consists of 22 genera of platyrrhines and 31 genera of catarrhines. For outgroup comparisons, we measured three genera of tarsids and 26 genera of strepsirrhines. This combined dataset documents all extant primate taxa at the generic level except for the strepsirrhine *Paragalago* and the rare catarrhine *Rungwecebus* (Table 1). The measurements (described in greater detail below) are: (1) endocranial volume, (2) olfactory fossa volume, (3) neocortex surface area, and two subdivisions of the neocortex—(4) the frontal lobe surface area and (5) the area of the remaining parts of the neocortex. Virtual endocasts of many of the extant species examined here were prepared following the methods reported in Sansalone et al. (2020).

Fossil endocasts examined in this analysis are among those listed in Table 2. These include virtual endocasts of *Simonsius*, *Aegyptopithecus*, *Victoriapithecus*, *Tremacebus*, *Dolichocebus*, *Homunculus*, and *Antillothrix*. Institutional abbreviations are listed in Table 2.

The virtual endocast of *Victoriapithecus* (KNM-MB 29100) described in Gonzales et al. (2015) was evaluated here. As noted by these authors, the interior of the braincase is damaged, with the frontal bone depressed ventrally and the left temporal lobe depressed in several places. As a result, although we believe that estimates of the volume of the endocast and olfactory fossa are probably reliable for this specimen, we do not believe that surface area measurements of the neocortex and its components can be estimated accurately on this specimen without further reconstruction.

New virtual endocasts of *Homunculus patagonicus* and *Simonsius grangeri* were created from CT scans. The *Homunculus* scans were made at the Y-TEC laboratory (owned jointly by Yacimientos Petrolíferos Fiscales and Consejo Nacional de Investigaciones Científicas y Técnicas) in La Plata, Argentina on a Bruker SkyScan 1173 CT scanner with a cubic voxel size of 50 µm. The *Simonsius* scans were made at the Duke Shared Materials Instrumentation Facility (SMiF) on a Nikon XTH 225 ST at 140 kV and 200 uA with a voxel size of 35.306 µm. New virtual endocasts were created in Avizo 3D

TABLE 1 | Summary of brain, body mass, neocorticalization, and prosthion-inion dimensions of extant and fossil Anthropoidea, extant Strepsirrhini, and Tarsiiformes.

Genus	Suborder	Higher level group	N	Endocast volume (mm ³)	Neocortex surface area (mm ²)	Frontal lobe area (mm ²)	Occipital–parietal–temporal area (mm ²)	Olfactory fossa volume (mm ³)	Neocorticalization ^a
<i>Allenopithecus</i>	Haplorhini	Catarrhini	3	55,515.8	6663	2010	4653	64	2.14
<i>Allochrocebus</i>	Haplorhini	Catarrhini	1	66,822.4	7535	2520	5015	76	2.14
<i>Cercocoebus</i>	Haplorhini	Catarrhini	3	103,748.3	10,286	3293	6993	109	2.16
<i>Cercopithecus</i>	Haplorhini	Catarrhini	3	66,939	7533	2606	4927	73	2.14
<i>Chlorocebus</i>	Haplorhini	Catarrhini	3	58,551.3	7121	2433	4688	54	2.17
<i>Colobus</i>	Haplorhini	Catarrhini	3	66,795.1	7114	2818	4296	58	2.08
<i>Erythrocebus</i>	Haplorhini	Catarrhini	2	105,723	10,648	3630	7018	75	2.18
<i>Gorilla</i>	Haplorhini	Catarrhini	3	480,913.3	24,515	8238	16,277	587	2.00
<i>Homo</i>	Haplorhini	Catarrhini	5	1,371,706.2	55,144	18,939	36,205	311	2.11
<i>Hoolock</i>	Haplorhini	Catarrhini	2	101,531.8	9330	3214	6116	132	2.07
<i>Hylobates</i>	Haplorhini	Catarrhini	4	99,458.6	9420	3130	6290	82	2.09
<i>Lophocebus</i>	Haplorhini	Catarrhini	3	93,868.5	9481	3361	6120	57	2.14
<i>Macaca</i>	Haplorhini	Catarrhini	3	69,209.7	7813	2774	5039	51	2.15
<i>Mandrillus</i>	Haplorhini	Catarrhini	3	158,300.7	13,664	4318	9346	186	2.16
<i>Miopithecus</i>	Haplorhini	Catarrhini	3	42,621.2	5624	1836	3788	46	2.15
<i>Nasalis</i>	Haplorhini	Catarrhini	3	84,243.6	8419	2867	5552	66	2.09
<i>Nomascus</i>	Haplorhini	Catarrhini	3	107,719.4	9405	3066	6339	86	2.04
<i>Pan</i>	Haplorhini	Catarrhini	5	369,773.2	21,634	7872	13,762	251	2.05
<i>Papio</i>	Haplorhini	Catarrhini	3	140,814.3	12,612	3901	8711	104	2.16
<i>Ptilocolobus</i>	Haplorhini	Catarrhini	3	68,629.8	7413	2878	4535	44	2.10
<i>Pongo</i>	Haplorhini	Catarrhini	3	378,556	21,503	7914	13,589	322	2.03
<i>Presbytis</i>	Haplorhini	Catarrhini	3	64,389.8	6958	2420	4538	38	2.08
<i>Procolobus</i>	Haplorhini	Catarrhini	3	53,823.6	6219	2120	4099	31	2.09
<i>Pygathrix</i>	Haplorhini	Catarrhini	2	90,034.9	9108	3095	6013	47	2.13

(Continues)

TABLE 1 | (Continued)

Genus	Suborder	Higher level group	N	Endocast volume (mm ³)	Neocortex surface area (mm ²)	Frontal lobe area (mm ²)	Occipital–parietal–temporal area (mm ²)	Olfactory fossa volume (mm ³)	Neocorticalization ^a
<i>Rhinopithecus</i>	Haplorhini	Catarrhini	2	110,847	10,194	3524	6670	87	2.10
<i>Sennopithecus</i>	Haplorhini	Catarrhini	3	87,142.7	8388	2875	5513	63	2.07
<i>Simias</i>	Haplorhini	Catarrhini	2	57,289	6428	2115	4313	47	2.08
<i>Symphalangus</i>	Haplorhini	Catarrhini	3	117,813.7	9865	3824	6041	134	2.03
<i>Theropithecus</i>	Haplorhini	Catarrhini	2	132,553	11,558	4090	7468	88	2.11
<i>Trachypithecus</i>	Haplorhini	Catarrhini	3	59,990.5	6720	2335	4385	33	2.09
<i>Alouatta</i>	Haplorhini	Platyrrhini	8	47,261.3	5619	2131	3488	35	2.07
<i>Antillothrix</i> †	Haplorhini	Platyrrhini	1	41,284.8	5112	1653	3459	46	2.07
<i>Aotus</i>	Haplorhini	Platyrrhini	6	15,815.8	2687	893	1794	49	2.07
<i>Ateles</i>	Haplorhini	Platyrrhini	5	104,184.6	9795	3626	6169	61	2.10
<i>Brachyteles</i>	Haplorhini	Platyrrhini	2	111,739.2	9626	3669	5957	69	2.04
<i>Cacajao</i>	Haplorhini	Platyrrhini	6	68,135.4	7344	2439	4905	45	2.10
<i>Callicebus</i>	Haplorhini	Platyrrhini	2	19,221.5	3066	942	2124	19	2.07
<i>Callimico</i>	Haplorhini	Platyrrhini	3	10,629.9	2138	678	1460	19	2.10
<i>Callithrix</i>	Haplorhini	Platyrrhini	2	6622.6	1549	453	1096	16	2.10
<i>Cebuella</i>	Haplorhini	Platyrrhini	1	4205.5	1209	353	856	11	2.15
<i>Cebus</i>	Haplorhini	Platyrrhini	7	65,207	7435	2419	5016	35	2.14
<i>Cheracebus</i>	Haplorhini	Platyrrhini	1	20,530.8	3498	1083	2415	20	2.16
<i>Chitropotes</i>	Haplorhini	Platyrrhini	3	51,519.7	6374	2179	4195	35	2.15
<i>Lagothrix</i>	Haplorhini	Platyrrhini	3	93,868.8	9122	3274	5848	44	2.10
<i>Leontocebus</i>	Haplorhini	Platyrrhini	2	6774.5	1502	480	1022	16	2.05
<i>Leontopithecus</i>	Haplorhini	Platyrrhini	6	11,206.2	2132	711	1421	21	2.06
<i>Mico</i>	Haplorhini	Platyrrhini	3	7319.1	1683	493	1190	13	2.11
<i>Pithecia</i>	Haplorhini	Platyrrhini	3	28,617.5	4132	1417	2715	25	2.10

(Continues)

TABLE 1 | (Continued)

Genus	Suborder	Higher level group	N	Endocast volume (mm ³)	Neocortex surface area (mm ²)	Frontal lobe area (mm ²)	Occipital–parietal–temporal area (mm ²)	Olfactory fossa volume (mm ³)	Neocorticalization ^a
<i>Plecturocebus</i>	Haplorhini	Platyrrhini	5	17,199.8	2953	933	2020	16	2.11
<i>Saguinus</i>	Haplorhini	Platyrrhini	1	9824.2	1984	643	1341	24	2.08
<i>Saimiri</i>	Haplorhini	Platyrrhini	5	22,378.8	3960	1334	2626	17	2.23
<i>Sapajus</i>	Haplorhini	Platyrrhini	7	65,129	7208	2640	4568	44	2.11
<i>Simonsius^b</i>	Haplorhini	Stem Anthropoidea	1	12,166	2220	570	1650	75	2.05
<i>Aegyptopithecus^b</i>	Haplorhini	Stem Catarrhini	1	14,680.9	2541	801	1740	80	2.06
<i>Victoriapithecus^b</i>	Haplorhini	Stem Catarrhini	1	34,528				148	2.24
<i>Chilecebus^{b,c}</i>	Haplorhini	Stem Platyrrhini	1	7862				11	
<i>Dolichocebus^b</i>	Haplorhini	Stem Platyrrhini	1	22,140					
<i>Homunculus^b</i>	Haplorhini	Stem Platyrrhini	2	20,933.5	3256	1001	2255	46	2.07
<i>Tremacebus^b</i>	Haplorhini	Stem Platyrrhini	1	16,297.4	2966.4	874.02	2092.4	21	2.15
<i>Carlito</i>	Haplorhini	Tarsiiformes	2	3551.4	917	200	717	11	1.98
<i>Cephalopachus</i>	Haplorhini	Tarsiiformes	1	3313	924	210	714	17	2.04
<i>Tarsius</i>	Haplorhini	Tarsiiformes	3	3223.8	832	220	612	17	1.95
<i>Allocebus</i>	Strepsirrhini	Lemuriformes	1	2214	503	197	306	37	1.72
<i>Avahi</i>	Strepsirrhini	Lemuriformes	2	9708.1	1474	649	825	97	1.80
<i>Cheirogaleus</i>	Strepsirrhini	Lemuriformes	1	6390.4	1132	433	699	138	1.81
<i>Daubentonina</i>	Strepsirrhini	Lemuriformes	2	41,521.9	4106	1812	2294	541	1.85
<i>Eulemur</i>	Strepsirrhini	Lemuriformes	4	20,974.9	2587	1027	1560	256	1.84
<i>Hapalemur</i>	Strepsirrhini	Lemuriformes	3	12,694.5	1849	756	1093	90	1.84
<i>Indri</i>	Strepsirrhini	Lemuriformes	1	35,888.6	3547	1501.15	2045.9	211	1.81
<i>Lemur</i>	Strepsirrhini	Lemuriformes	3	23,311.7	2800	1139	1661	180	1.85
<i>Lepilemur</i>	Strepsirrhini	Lemuriformes	1	7628.7	1210	487	723	81	1.77
<i>Microcebus</i>	Strepsirrhini	Lemuriformes	3	1791.1	455	161	294	49	1.76

(Continues)

TABLE 1 | (Continued)

Genus	Suborder	Higher level group	N	Endocast volume (mm ³)	Neocortex surface area (mm ²)	Frontal lobe area (mm ²)	Occipital–parietal–temporal area (mm ²)	Olfactory fossa volume (mm ³)	Neocorticalization ^a
<i>Mirza</i>	Strepsirrhini	Lemuriformes	2	5756.9	987	366	621	121	1.75
<i>Phaner</i>	Strepsirrhini	Lemuriformes	1	6344.7	1183	455	728	86	1.86
<i>Prolemur</i>	Strepsirrhini	Lemuriformes	1	27,646.4	2973	1209	1764	199	1.80
<i>Propithecus</i>	Strepsirrhini	Lemuriformes	3	32,980.3	3632	1476	2156	394	1.88
<i>Varecia</i>	Strepsirrhini	Lemuriformes	1	26,304.1	2806	1243	1563	415	1.78
<i>Arctocebus</i>	Strepsirrhini	Lorisiformes	3	5649.7	982	388	594	139	1.76
<i>Euoticus</i>	Strepsirrhini	Lorisiformes	2	5277.6	1008	417	591	64	1.82
<i>Galago</i>	Strepsirrhini	Lorisiformes	4	3962.9	811	299	512	50	1.80
<i>Galagoides</i>	Strepsirrhini	Lorisiformes	1	2418.4	592	201	391	54	1.81
<i>Loris</i>	Strepsirrhini	Lorisiformes	2	5340.1	975	403	572	69	1.79
<i>Nycticebus</i>	Strepsirrhini	Lorisiformes	3	10,073.3	1527	645	882	157	1.81
<i>Otolemur</i>	Strepsirrhini	Lorisiformes	3	10,762.8	1572	668	904	149	1.80
<i>Perodicticus</i>	Strepsirrhini	Lorisiformes	4	9918.4	1392	614	778	199	1.74
<i>Sciurocheirus</i>	Strepsirrhini	Lorisiformes	1	4216.6	798	281	517	85	1.75
<i>Xanthonycticebus</i>	Strepsirrhini	Lorisiformes	1	7172	1275	551	724	106	1.85

^aSquare root of neocortex surface area/cube root endocast volume.

^bIndicates extinct species.

^cData from Ni et al. (2019).

TABLE 2 | Fossil specimens, arranged temporally, examined or mentioned in text.

Taxon	Catalog number	Formation and locality	Age (Myr)	Publications referencing brain anatomy
<i>Antillothrix bernensis</i>	PN-09-01	Padre Nuestro Cave, Dominican Republic	<1	Allen et al. (2012); Halenar-Price et al. (2024); Kay et al. (2011)
<i>Oreopithecus bambolii</i>	NMB BAC 63	Lignite mines of Monte Bamboli, Tuscany, Italy	7–6	Harrison (1989a)
<i>Rudapithecus hungaricus</i>	RUD 200	Rudabánya, Hungary	10.3–9.8	Gunz et al. (2020)
<i>Pliobates cataloniae</i>	IPS 58443	Can Mata landfill (els Hostalets de Pierola, Catalonia, Spain)	11.6	Alba et al. (2015)
<i>Nyanzopithecus alesi</i>	KNM-NP 59050	Napudet, Turkana Basin, Kenya	13	Nengo et al. (2017)
<i>Victoriapithecus macinnesi</i>	KNM-MB 29100	Maboko Island, Kenya	15	Gonzales et al. (2015)
<i>Homunculus patagonicus</i>	MPM-PV 3502	Santa Cruz Formation, Killik Aike Norte	17.4–17.0	Kay et al. (2012); Perry et al. (2010); Trayler et al. (2020)
<i>Homunculus patagonicus</i>	MPM-PV 17453	Santa Cruz Formation, Puesto Estancia La Costa, Argentina	17.4–17.0	Perry et al. (2025)
<i>Afropithecus turkanensis</i>	KNM-WK 16999	Kalodirr site, Lake Turkana, northern Kenya	17.5–17.0	Nengo et al. (2017)
<i>Turkanapithecus kalakolensis</i>	KNM WR 16950	Hiwegi Formation of Rusinga Island, Kenya	17.7–16.6	Manser and Harrison (2000)
<i>Ekembo heseloni</i> (= <i>Proconsul heseloni</i>)	KNM-RU 7290	Rusinga, Island, Kenya	18–17	Simons et al. (2007); Walker et al. (1983)
Napak frontal; Catarrhini	No number	Napak, Uganda	19	Pilbeam and Walker (1968)
<i>Chilecebus carrascoensis</i>	SGOPV 3213	Abanico Formation, Chile	20.09 ± 0.27	Flynn et al. (1995)
<i>Tremacebus harringtoni</i>	FML 618	Sarmiento Formation, Cerro Sacanana, Argentina	21	HersHKovitz (1974); Kay et al. (2004)
<i>Dolichocebus gaimanensis</i>	MACN 14128	Trelew Member, Sarmiento Formation, Gaiman, Argentina	21	Radinsky (1974)
<i>Saadanius hijazensis</i>	SGS-UM 2009–002	Shumaysi Formation, Saudi Arabia	29–28	Zalmout et al. (2010)
<i>Simonsius grangeri</i>	DPC 18651	Quarry I, Jebel Qatrani Formation, Fayum Depression, Egypt	30–29	Bush, Simons, and Allman (2004); Bush, Simons, Dubowitz, and Allman (2004); E. L. Simons (2001)
<i>Aegyptopithecus zeuxis</i>	CGM 85785, CGM 40237	Quarry M, Jebel Qatrani Formation, Fayum Depression, Egypt	30–29	Radinsky (1973, 1974); Simons et al. (2007)

(Continues)

TABLE 2 | (Continued)

Taxon	Catalog number	Formation and locality	Age (Myr)	Publications referencing brain anatomy
<i>Apidium phiomense</i>	DPC 9867, AMNH 14556	Quarry I, Jebel Qatrani Formation, Fayum Depression, Egypt	30.2–29.5	Radinsky (1974); Simons (1997)
<i>Catopithecus browni</i>	CGM 42222, DPC 11594, DPC 11388	Quarry L-41, Jebel Qatrani Formation, Fayum Depression, Egypt	34.7–33.5 (Chron 13r)	Simons and Rasmussen (1996)
<i>Proteopithecus sylviae</i>	CGM 42214, DPC14095	Quarry L-41, Jebel Qatrani Formation, Fayum Depression, Egypt	34.7–33.5	Simons (1997)
<i>Ganlea megacania</i>	NMMP 104	Pondaung Formation, Myanmar	41.0–37.7 (Bartonian)	Jaeger et al. (2020)

v. 2023.1 (FEI, Thermo Fisher Scientific, Waltham, MA) for the former, and VG Studio Max v. 2024.1 (Volume Graphics, Heidelberg, Germany) for the latter. Reconstructed TIFF stacks were imported into these programs with voxel dimensions reflecting scan resolution. A Region of Interest (ROI) called “bone” was created from the histogram of grayscale values, and a threshold value determined using this histogram was applied to include bone and some associated matrix in the ROI. Any remaining matrix occupying the endocranial cavity was removed in the segmentation editor using the paintbrush tool with interpolation where appropriate. Following this process, the bony material layer was locked and any gaps between the endocranial cavity and external environment were filled by hand with an additional material called “air.” These gaps include foramina and sites of specimen breakage, or where the braincase is missing. Once the endocranial cavity was entirely enclosed by materials corresponding to either “bone” or “air” and all matrix within the endocranial cavity was removed, the remaining void representing the endocast was filled and saved as a third “endocast” material. A surface was generated from this material, smoothed, and exported as a PLY file for measurement.

Provenance for previously published specimens of *Homunculus* is given in tab. 1 of Fulwood et al. (2016). The new endocast of *Homunculus patagonicus* described here (MPM-PV 17453) comes from fossil horizon 5.3 of the Santa Cruz Formation (Fleagle et al. 2012; Matheos and Raigemborn 2012; Vizcaino et al. 2012a, 2012b) at the Puesto Estancia La Costa locality (51.2°S, 69.1°W). This is the same locality that also produced CORD PZ1130. MPM-PV 3402 comes from Killik Aike Norte (formerly Felton's Estancia) 51.57°S, 69.45° W on the north bank of the Riá Gallegos. MPM-PV 17453 is particularly important because it includes a nearly complete skull lacking only the zygomatic arches, a complete adult dentition, a complete mandible, both humeri, parts of both scapulae, a left femur lacking the distal end, a partial left os coxa, and a partial sacrum. A full description of the bony elements of this specimen is provided in Perry et al. (2025). Notably, the MPM-PV 17453 specimen of *Homunculus* permits endocranial measurements to be compared with estimates of body mass from postcranial remains

of the same individual. To our knowledge, this represents the first time that such comparisons have been possible for any stem platyrrhine.

The original CT scans and the published endocast reconstruction of *Chilecebus carrascoensis* (Ni et al. 2019) were not made available to us for examination in this article. Accordingly, our observations for *Chilecebus* are restricted to those provided in Ni et al. (2019).

3.1 | Phylogenetic Methods

For analyses employing phylogenetic generalized least-squares regression (PGLS), we used a fully resolved genus-level phylogeny for primates downloaded from *10K trees* (Arnold et al. 2010). Platyrrhine branch lengths follow Beck et al. (2023), except as modified to make the cluster of Patagonian early Miocene platyrrhines into a clade of stem platyrrhines following Kay (2015). Catarrhine branch lengths were adjusted following node dates in Seiffert et al. (2020). Branch lengths for tarsiids and strepsirrhines were scaled following the proposed dates of cladogenesis for Strepsirrhini and Haplorhini following Seiffert et al. (2020). The full phylogeny is illustrated in Figure 1 and a Nexus-formatted time tree is provided in Supplemental Document S1.

Several of the best-supported trees in more recent phylogenetic analyses differ in some respects from the tree we use here (Jensen et al. 2023; Kuderna et al. 2023). To test the robustness of our PGLS results against other phylogenetic arrangements, we ran a second series of PGLS analyses using the Kuderna et al. (2023) tree. This tree lacks the following eight taxa that are represented in our dataset: the lemuroids *Allocebus* and *Phaner*; the lorisooids *Paragalago*, *Sciurocheirus*, and *Euoticus*; the platyrrhines: *Callicebus* and *Brachyteles*; the colobine *Procolobus*; and all fossil taxa. Replicating our PGLS models using the Kuderna et al. (2023) tree topology with these taxa excluded, the differences were extremely minor. For example, the slopes of all PGLS regressions generated using the Arnold et al. (2010) and Kuderna et al. (2023) trees vary by ≤ 0.01 .

3.2 | Measuring Endocast Volumes and Surfaces

We evaluate the size of several brain components from virtual endocasts. Stanford ply files were imported into Avizo 3D. The “Surface Area Volume” module was used to compute the volume of the endocast. To measure the volume of the olfactory fossa (Figure 2A–C), we trace the perimeter of the olfactory fossa using the Surface Editor’s pencil tool and delete that part of the endocranial surface that was outside the trace. The Surface Editor’s “fill hole” option was used to close the resulting gap, creating a “watertight” surface. The remaining olfactory fossa volume was computed with the “Surface Area Volume” module.

Our assessment of neocortex surface area on the endocasts is assisted by the presence of several consistent anatomical landmarks on the endocasts. The rhinal sulcus delimits the neocortex from the paleocortex. Separation of the neocortex from noncortical structures (cerebellum, olfactory fossa, and olfactory tracts) is also readily apparent. On the surface of the neocortex, the sylvian fissure separating the temporal lobe from the frontal lobe is consistently present on all crown primates² (Radinsky 1974, 1975). However, the reliability of other sulci on endocasts does not offer a practical guide for a more detailed assessment of proportions of the major neocortical regions (i.e., the extent of the frontal, parietal, occipital, and temporal lobes).

The exposed surface area of the neocortex on the virtual endocast is measured as follows (Figure 2A,B): using the pencil tool in the Avizo Surface Editor beginning caudally, we highlight and delete all portions of the surface along a line between the cerebrum and the transverse and sigmoid venous sinuses. We then trace along the margins of the base of the endocast reaching rostrally to exclude the optic chiasm and optic nerves. Care is taken to remove the area of the paleocortex on the temporal lobe. The highlighted areas are deleted leaving the exposed neocortex and impressions of the olfactory fossa and tracts. Next, the surfaces of the olfactory fossa and tracts are highlighted and removed. Using the “Surface Area Volume” module, the surface area of the neocortical portion of the endocast is computed.

To estimate the surface area of the frontal lobe, we begin with the whole brain virtual endocast. The surface of the frontal lobe in many anthropoids is delimited by the central sulcus and sylvian sulcus (Le Gros Clark 1959). While the sylvian fissure is always visible on primate endocasts, strepsirrhines lack a central sulcus, and even in anthropoids this sulcus is often not observable on brain endocasts. Accordingly, we first rotate the surface file of the endocast into a lateral perspective and orient it to horizontal along the rostro-caudal axis of the neocortex surface (i.e., Forel’s Axis, see Hofer and Tigges 1963; Lieberman et al. 2000) (blue double-headed arrow in Figure 2C). Second, we delimit the portion of the endocast rostral to the coronal plane drawn through the middle of the hypophysis (i.e., orthogonal to Forel’s Axis) (Figure 2C). Based on published diagrams of Brodmann’s areas³, this plane approximates the position of the central sulcus (when present) and/or the approximate boundary between primary somatosensory cortex (Brodmann area 1–3) and primary motor cortex (Brodmann area 4) (red double-headed arrow, Figure 2C). In other words, when the endocast is oriented along

Forel’s axis, the hypophyseal fossa falls roughly in the same coronal plane as the rostral-most position of the parietal lobe. Neocortical surfaces caudal to this coronal plane through the hypophysis are deleted. Third, we trim away the remaining non-frontal surfaces guided by the position of the sylvian fissure, removing the temporal cortex ventral to the sylvian fissure. Finally, we separate the olfactory fossa and tracts from the frontal lobe surface reconstruction. Once we have an estimate of total neocortex surface area and frontal surface area, we calculate the surface area of the remaining neocortex, which we here refer to as OPT (i.e., occipital + parietal + temporal) cortex. Further neocortical subdivisions beyond frontal and OPT cortex are considered too speculative to measure reliably on endocasts across the full diversity of extant primates.

The optic foramen at the apex of the orbit transmits the optic nerve returning visual sensory information back to the brain. Optic foramen area (OFA), is a validated proxy for total visual input (Kirk 2006). OFA is estimated using optic foramen length and width as the major and minor axes of an ellipse (details in Kirk 2006).

We compare endocast volume, olfactory fossa volume, and surface areas of the neocortex and its components (frontal and OPT) with body mass using PGLS regression implemented in the R package Caper (Orme et al. 2013) using the time tree shown in Figure 1. We also compare olfactory fossa volume, neocortical surface area, and the frontal and OPT surface areas with total endocast volume. All variables are natural log-transformed before regression. To evaluate the reliability of our measures of neocortex size and frontal lobe size, we compared our estimates of neocortex surface area and frontal lobe surface area with published values for neocortex mass and volume of frontal lobe gray matter (Bush and Allman 2004; Stephan et al. 1981).

To test the concordance between OPT size and visual input as measured by OFA, we compare residuals from the PGLS lines of best fit of OPT and OFA versus prosthion–inion length in log space (prosthion–inion and optic foramen dimensions in Table S1).

3.3 | Measuring Neocorticalization and Neocortex Proportions

We chose endocranial volume as a measurement of total brain size against which to compare the relative endocast surface areas of the neocortex and its frontal and OPT subdivisions. The PGLS fit between endocast volume and neocortex surface area indicates an isometric relationship between these two variables (Table 4). As a result, we derive a size-adjusted estimate of “neocorticalization” by dividing the square root of neocortical surface area by the cube root of endocast volume.

3.4 | Estimating Body Mass in Fossil Anthropoids

Estimating the body mass of fossil taxa is complicated by differences in predictive accuracy depending on the morphological proxy employed and the model used to generate predictions. Pampush et al. (2021) compared the predictive accuracy

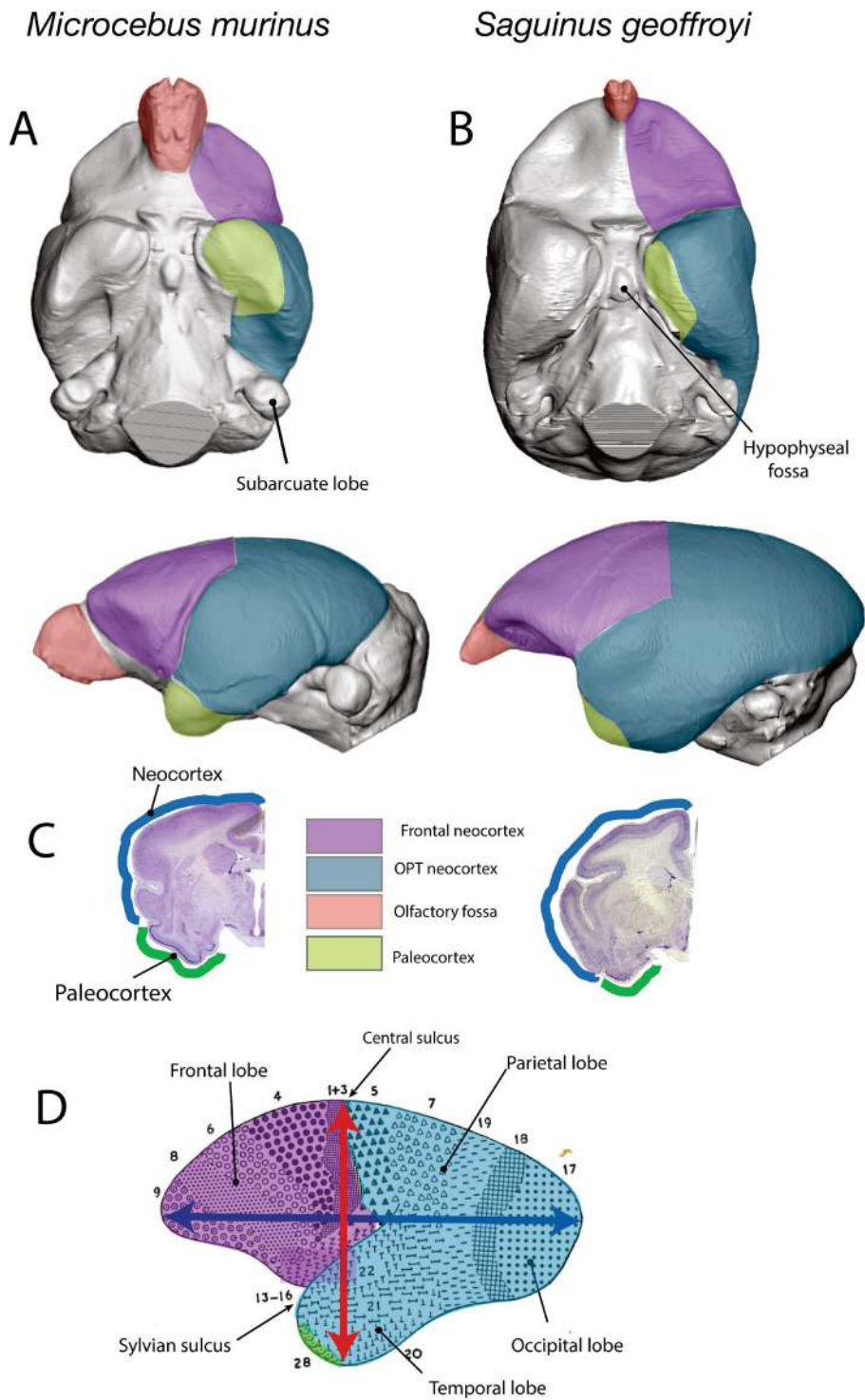


FIGURE 2 | Ventral and lateral views of virtual endocasts of (A) *Microcebus murinus* (DPC 098) and (B) *Saguinus geoffroyi* (USNM 306845) showing parts of the cortex and key anatomical landmarks. (C) Coronal sections through the brains of *Perodicticus potto* (left) and *Aotus trivirgatus* (right) (specimens 62–441 and 69–255; University of Wisconsin-Madison Brain Collection <http://brainmuseum.org/>) with the neocortex (blue ribbon) separated from the paleocortex (green ribbon). (D) Sketch map of regions of the cerebral cortex in *Callithrix*. Lobes and Brodmann's areas are identified. Original image after Le Gros Clark (1959). Area 17 is the primary visual cortex. Areas 5, 7, 17, 18, 19, and 20 take visual inputs from area 17. Alignment for calculating proxy measurement of the frontal lobe shown as arrows in D. The position of the slice through the endocast (red double-headed arrow) with the endocast positioned rostral-caudally along Forel's axis (blue double-headed arrow).

of several common proxies of primate body mass (dental dimensions, long bone midshaft cross-sectional areas, and tarsal facets) across four alternative models for predicting primate

body mass. They found that using PGLS to incorporate phylogenetic structure into the model—but not into the predictions formed by the model—produced body mass estimates with

no greater accuracy than those made using commonplace ordinary least squares (OLS) regression without phylogenetic correction (and occasionally performed worse than OLS). Importantly, they found a correlation between phylogenetic covariance (expressed as Pagel's λ in Pagel 1999) and model prediction error, indicating that body mass proxies that are structured by phylogeny, while potentially producing models with good data fit, will produce inaccurate predictions of body mass unless phylogeny can be explicitly incorporated into the prediction. Two approaches that incorporate phylogenetic relatedness into their model predictions are the PIC method of Garland et al. (2000) and BayesModelS (Nunn and Zhu 2014). Pampush et al. (2021) found that these two methods were considerably more accurate at predicting body mass than were OLS or PGLS, and that their results were largely consistent.

Several of the anatomical proxies investigated by Pampush et al. (2021) produced more accurate body mass estimates than others. In particular, the most accurate results were those based on humeral and femoral cross-sections, and the least accurate were predictions from dental dimensions. This conclusion supports the finding by Campione and Evans (2012) that the relationship between proximal limb bone circumferences and body mass is highly conserved in extant terrestrial mammals and reptiles, in spite of their disparate limb postures, gaits, and phylogenetic histories.

The fossil anthropoids investigated here present challenges for estimating body mass because of the limited morphology known for some taxa. For instance, *Chilecebus* and *Tremacebus* are known solely from cranial material, and *Dolichocebus* is known only from one cranium, several dental specimens, and one talus.

To estimate body mass across all study taxa, including those for which long bone dimensions are unknown, we use skull length (prosthion–inion in mm) (Table S1). These data are available for a large sample of extant and fossil taxa. Average prosthion–inion lengths for 84 extant primate taxa spanning all major primate clades as well as *Galeopterus variegatus* and *Tupaia glis* are from several sources (Heesy and Ross 2001; Kay and Kirk 2000; Kirk 2003; Kirk 2006). Body masses of extant primates are from Smith and Jungers (1997) and Isler et al. (2008) with male and female masses averaged. We selected the species of each genus to agree with the species for which we have endocast, skull length, and optic foramen data. A consensus tree containing all extant primate taxa for which we have prosthion–inion dimensions was downloaded from 10k trees (Arnold et al. 2010) and then modified in Mesquite v. 3.81 (Maddison and Maddison 2023) to include euarchontan outgroups and fossil taxa. As already noted, there are discrepancies between this tree topology and that of Kuderna et al. (2023) but these differences do not have a significant effect on our results.

We place *Galeopterus* as the outgroup to Primates and *Tupaia* as the outgroup to Primatomorpha, consistent with genetic evidence (Janečka et al. 2007; Kuderna et al. 2023; Perelman et al. 2011). To account for differences in divergence times as predicted by genetic data (reflected in the chronogram from 10k trees) and that documented by the primate fossil

record (e.g., Steiper and Seiffert 2012), the deep nodes are adjusted to younger ages. The timing of deep nodes and their subsequent branch lengths are those estimated by Gunnell et al. (2018) from a Bayesian tip-dating analysis that combined molecular and morphological data from across extant and fossil primates to produce a time-calibrated tree. The specific nodes we adjust from the original 10k consensus tree are those for (1) Euarchonta, (2) Primatomorpha, (3) Primates, (4) Strepsirrhini, (5) Lorisiformes, (6) Lemniformes, (7) Haplorhini, (8) Anthropoidea, (9) Platyrrhini, and (10) Catarrhini (Table S2).

A second phylogenetic tree is built from the one described above by adding fossil taxa in Mesquite (Maddison and Maddison 2023). *Simonsius* and *Aegyptopithecus* are added to the tree according to their age and topological position as reported in Gunnell et al. (2018), and the timing and placement of all stem platyrrhines follow that of Kay (2015).

Cranial length (prosthion–inion length) has not been previously evaluated as a proxy of body mass using the robust methods described by Pampush et al. (2021). We therefore assess its performance through evaluation of the natural log-difference of the predicted and observed body masses (lnPE) and success rate at leave-one-out body mass prediction for OLS, PGLS, PIC, and BayesModelS across the extant primate sample. In this way, prosthion–inion length can be compared with the proxies tested by Pampush et al. (2021), albeit with a different phylogenetic dataset than the one employed in their study. Following Pampush et al. (2021), a “successful” body mass prediction was determined as within $\pm 20\%$ of the actual species mean body mass as reported by Smith and Jungers (1997). We also assess the phylogenetic covariance (Pagel's λ) for body mass and prosthion–inion length within the extant data. All body mass modeling and analysis are performed in the open-source statistical computing environment R Core Team (2024). Nexus files for the extant phylogeny and the tree including fossil taxa used to predict body masses are provided in Supplemental Documents S2 and S3, respectively.

4 | Results

4.1 | Endocast Surface Anatomy

The structural details we describe on virtual endocasts are durable positive impressions on the inner surface of the endocranium, expressed as grooves or ridges left by the brain's sulci and gyri, cranial nerves, and endocranial vasculature. Studies of brain evolution using endocasts often refer to endocast surfaces and volumes interchangeably with the brain structures that would have filled them (e.g., “brain” for the entire endocast, “olfactory bulb” for the olfactory fossa, “neocortex” for the neocortical surface of the endocast, “petrosal lobule” or “paraflocculus” for the subarcuate fossa, and “pituitary” for the hypophyseal fossa for pituitary gland). While in general we prefer to use the terms for the actual endocast surfaces or volumes when we are describing or measuring them, in some instances below we refer to portions of the endocast using the corresponding name of the associated soft-tissue structure as a matter of clarity and convenience.

Projecting rostral and ventral to the cerebrum, the olfactory bulbs and tracts are represented by the olfactory fossa and ridges leading caudally from it toward the paleocortex. Endocast representations of the cerebral hemispheres are best visualized in lateral and dorsal view. On the dorsal surface a cleft for the sagittal fissure is visible. In life, this fissure is filled by the superior sagittal venous sinus. The frontal lobe is the most rostral of the lobes of the neocortex; it is separated from the temporal lobe by the sylvian (=lateral) fissure. The separation between the frontal and parietal lobes may be marked on endocasts by a groove corresponding to the central sulcus, but this feature is inconstant on anthropoid endocasts and is absent in strepsirrhines (Radinsky 1979). A groove for the superior temporal sulcus is often visible on the temporal lobe endocast surface separating the superior from the inferior temporal gyri. No clear and consistent separations are visible among temporal, parietal, and occipital lobes of the neocortex, although sometimes in anthropoids a lunate sulcus is visible on the occipital surface of the endocast (De Sousa et al. 2010). When present, the lunate sulcus usually, although not always (Allen et al. 2006; De Sousa et al. 2010; Falk 1976) marks the rostral border of the primary visual cortex. The pre-occipital notch marks the ventrolateral point where the parietal and occipital lobes meet and is the lateral-most point of origin of the tentorium cerebelli, a reflection of dura between cerebrum and cerebellum that is ossified in some taxa (Kay et al. 2008). Traces of other external cerebral sulci and gyri may also be visible on anthropoid endocasts, although their expression on endocasts is variable and often size-dependent (Falk 1980). Inadequate data are available to judge the functional significance, or even homology, of between-species variation in the presence or absence of most cerebral sulci.

In many non-anthropoid primates, there is a pronounced impression left by the orbito-temporal canal on the lateral aspect of the cerebral endocast (e.g., Kirk et al. 2014; Harrington et al. 2016). This structure is interpreted as overlying the rhinal sulcus (Gazin 1965; Martin 1990; Radinsky 1970) and is therefore a key landmark for demarcating the neocortex from the paleocortex (Moini and Piran 2020). In most anthropoids, the temporal part of the neocortex is expanded laterally and ventrally, bringing the separation between the neocortex and piriform lobe onto the ventral surface of the temporal lobe where it is represented by a distinct longitudinal cleft for the rhinal sulcus.

The endocranial surface of the cerebellum is caudal and ventral to the cerebrum and separated from it by ridges that are filled by the transverse and sigmoid venous sinuses running between layers of dura mater. Other details of cerebellar anatomy may also be observed in most endocasts, including two cerebellar lobes, separated from the central vermis by paramedian fissures. The cerebellar endocast also includes a portion that fills the subarcuate fossa (when present) of the petrosal bone, hereafter referred to as the “subarcuate lobe” of the endocast. In life the subarcuate fossa is occupied by the (pedunculate) cerebellar petrosal lobule (Lang et al. 2022).

On the ventral surface of endocasts are the impressions of the optic nerves and chiasm, and the hypophyseal fossa for the pituitary gland and cavernous venous sinus.

4.1.1 | Endocast of *Simonsius grangeri*

The virtual endocast of *Simonsius grangeri* (Figure 3) is based on DPC 18651⁴. The bone on the left side of the braincase is missing and some surface erosion is present on the natural endocast in that region. The endocast is otherwise complete, allowing volumetric and surface area estimates by mirroring the more intact right side. The olfactory fossa of *Simonsius* projects rostrally and is fully visible in dorsal view, as in Eocene omomyids like *Necrolemur* (fig. 4 in Harrington et al. 2020). Despite being of higher resolution than the virtual endocast described by Bush, Simons, and Allman (2004), the new *Simonsius* endocast is lissencephalic save for the sylvian fissure. The rostral pole of the neocortex surface is flattened dorsally, and the caudal pole extends caudally over the cerebellum. The ventral surface of the temporal lobe is creased rostro-caudally, marking the division between neocortex and paleocortex (Figure 3A,B). The cerebellar vermis surface projects almost as far distally as the caudal pole of the cerebrum when viewed laterally. A large spherical subarcuate lobe is connected to the cerebellar endocast by a narrow stalk protruding ventrolaterally on the undamaged right side of the endocast (Figure 3E).

4.1.2 | Endocast of *Aegyptopithecus zeuxis*

Our description of the endocast of *Aegyptopithecus zeuxis* (CGM 85785) is based on the virtual reconstruction illustrated in Simons et al. (2007), and notes about several key anatomical landmarks on a latex mold of the inner table of a dorsal cranial fragment (YPM 23975) described by Radinsky (1973). The olfactory fossa of CGM 85785 is more downturned ventrally than in *Simonsius*, such that it is scarcely visible from a dorsal view (fig. 3 in Simons et al. 2007). On the cerebrum of CGM 85785, impressions of the sylvian fissure can be identified separating the frontal and temporal lobe surfaces, but otherwise the low resolution of the reconstruction provides little surface detail. YPM 23975 preserves impressions of the coronal and lunate sulci on the neocortical surface of the endocast. As in *Simonsius*, the frontal pole of the cerebrum is flattened dorsally. The caudal cerebral pole extends caudally over the cerebellum, but not as far caudally as in *Simonsius*. The ventral surface of the temporal lobe impression is creased rostro-caudally showing the position of the rhinal sulcus between neocortex and paleocortex. A subarcuate lobe is connected to the cerebellar endocast by a narrow stalk that protrudes ventrolaterally on the left side of the virtual endocast.

4.1.3 | Endocast of *Tremacebus harringtoni*

Our description of *Tremacebus* is based on FML 619 (Figure 4). This specimen is missing parts of the posterior neurocranium. Our virtual endocast is based on the better-preserved right posterior and left anterior portions of the braincase. The rostral end of the olfactory fossa in FML 619 is missing (see figures in Kay et al. 2004), but the fossa is clearly rostrally projecting and slightly downturned beyond the frontal lobe. The rostral pole of the neocortex surface is indented by the orbits rostro-ventrally, flattened dorsally, and almost completely overlaps the olfactory fossa in dorsal view. The caudal pole of the cerebrum

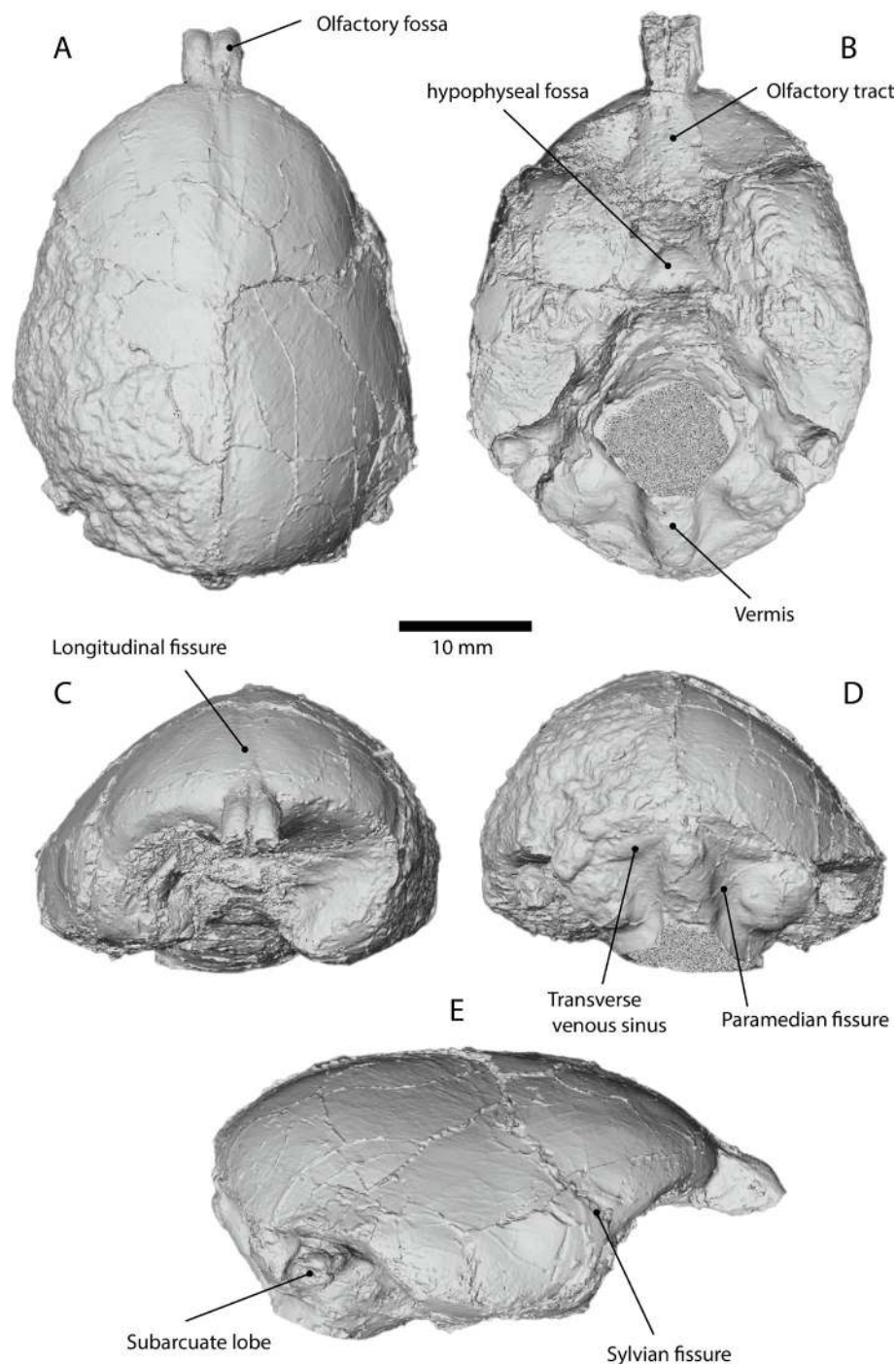


FIGURE 3 | Virtual endocast reconstruction of *Simonsius grangeri* (Anthropoidea) early Oligocene, DPC 18651. (A) Dorsal, (B) ventral, (C) anterior, (D) posterior, and (E) lateral views.

completely overlaps the cerebellum. Ridges are visible on the endocast for the superior sagittal and transverse venous sinuses, as is the Sylvian fissure separating the frontal and temporal lobes. Impressions of the frontal, parietal, and occipital lobes of the endocast lack unambiguous sulci. The surface of the temporal lobe is creased by a pronounced superior temporal sulcus running ventral and parallel to the Sylvian fissure. A rhinal sulcus is observed on the ventrolateral surface of the temporal lobe. The cerebellar portion of the endocast is damaged, but the vermis and a laterally projecting subarcuate lobe are visible.

4.1.4 | Endocasts of *Homunculus patagonicus*

Our description of *Homunculus* is based on virtual endocasts of MPM-PV 3502 (Figure 5) and MPM-PV 17453 (Figure 6). MPM-PV 17453 provides a complete endocast, but substantial damage to the dorsal surface of the braincase obscures surface details of the neocortex in that region. MPM-PV 3502 was eroded by weathering in the field before recovery such that the posterior left dorsolateral portion of the braincase was lost. Most of this region is preserved undistorted on the right side, however,

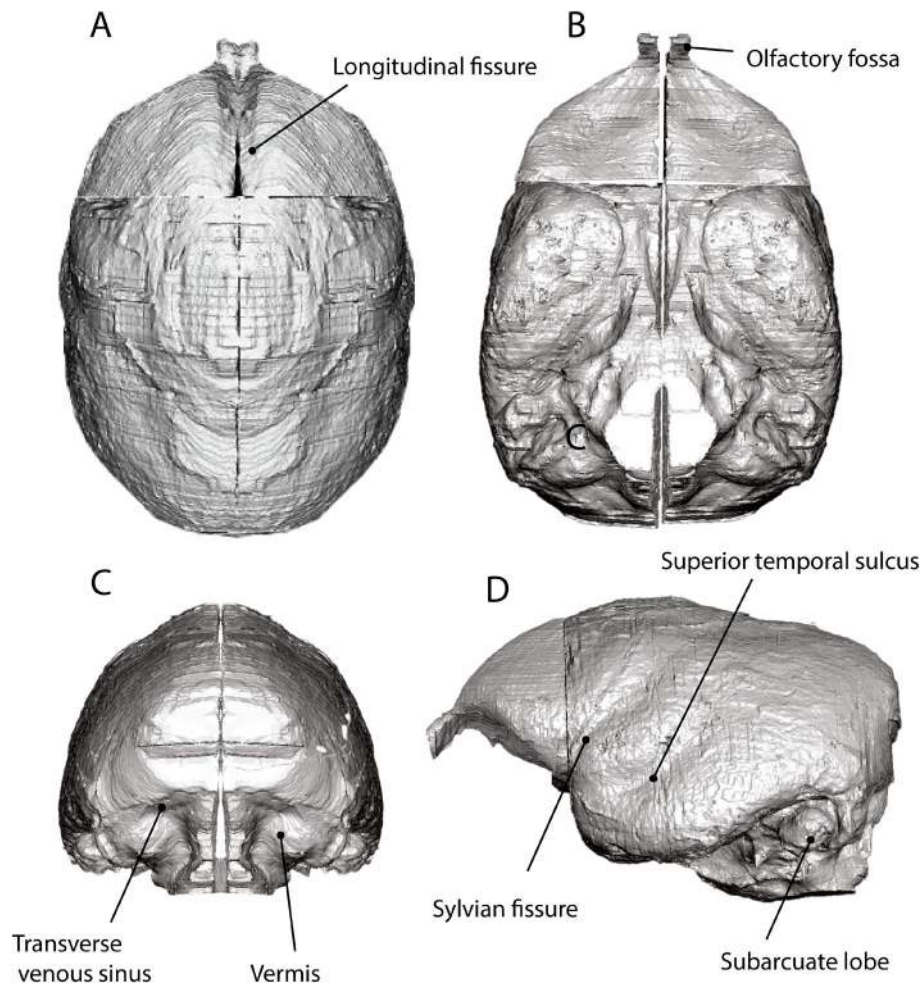


FIGURE 4 | Composite virtual endocast reconstruction of *Tremacebus harringtoni* (Platyrrhini) Early Miocene, FML 619, Rusconi Collection. (A) Dorsal, (B) ventral, (C) posterior, and (D) lateral views.

allowing a complete endocast to be reconstructed by mirroring the right dorsolateral portion of the endocast.

The olfactory fossae of both *Homunculus* specimens project rostrally beyond the cerebrum, but are also slightly downturned ventrally as in *Chilecebus* (Ni et al. 2019) and *Aegyptopithecus*. The rostral pole of the cerebrum is deeply excavated by the orbital cavities and flattened dorsally. The caudal pole of the cerebrum completely overlaps dorsally and extends caudally beyond the cerebellum. The cleft representing the sagittal fissure divides the cerebrum into left and right hemispheres rostrally. Proceeding distally (MPM-PV 17453 only), the sagittal fissure becomes more visible toward the occipital lobe of the endocast, where a raised ridge represents the groove for the superior sagittal sinus. The ridge for the superior sagittal sinus in both specimens terminates caudally at the confluence of sinuses, from which the right and left transverse sinuses course laterally, separating the occipital lobes from the cerebellum. A bulge for the sigmoid sinus is apparent on the right side in MPM-PV 3502 (Figure 5A).

The neocortical surface of *Homunculus* exhibits impressions of multiple sulci, principal among them a pronounced groove for the Sylvian fissure separating the frontal and temporal lobes. The parietal and occipital lobes lack any clear evidence of sulci, and there is no indication of a lunate sulcus. On both specimens,

the temporal lobe surface is creased by a pronounced groove for the superior temporal sulcus running ventral and parallel to the Sylvian fissure. A rhinal sulcus separates the neocortex from the piriform cortex on the ventrolateral surface of the temporal lobe and is best visualized on the ventral aspect of the MPM-PV 17453 endocast (Figure 6A).

Several other anatomical features may be present on the neocortical surface of MPM-PV 17453, but with less certainty. On the right hemisphere, a dimple may indicate the position of the central sulcus. On the left side, a short fronto-orbital sulcus (or possibly the sulcus rectus of HersHKovitz 1970) extends postero-medially along the anterolateral border of the left frontal lobe. An arcuate sulcus, in continuity with the rectus sulcus, is also visible on the left side. MPM PV 3502 also preserves a groove for the orbito-temporal sinus on the right side.

In posterior view on the cerebellar endocast of both specimens of *Homunculus*, the impression for the vermis occupies approximately one-third of its posterior surface. The impressions of the cerebellar hemispheres are set apart laterally from the vermis by deep paramedian sulci (Figures 5D and 6D). Large spherical endocasts of the subarcuate lobe are connected to the cerebellar endocast by narrow stalks in both specimens, although these are truncated in our endocast reconstruction of MPM-PV 17453.

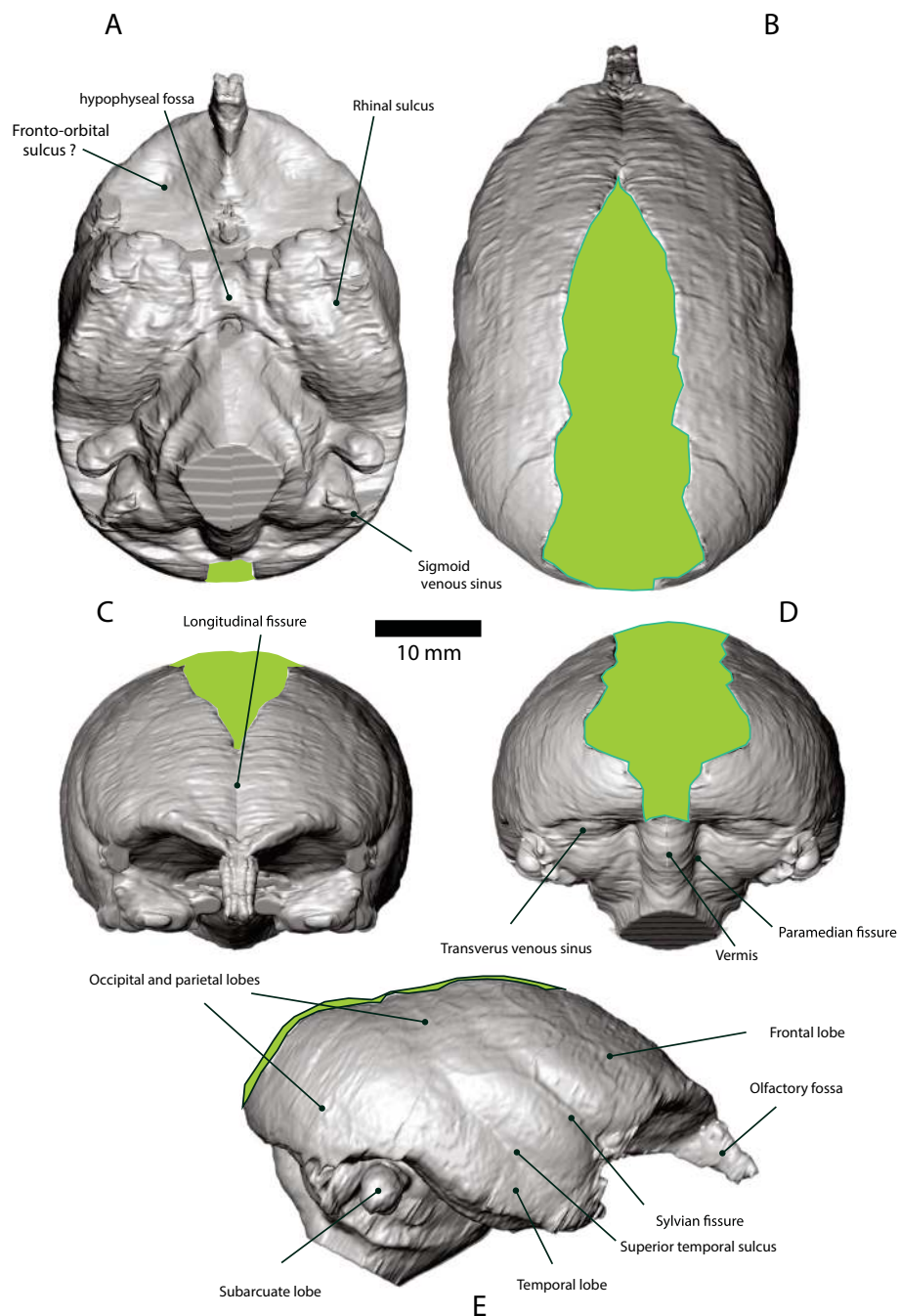


FIGURE 5 | Virtual endocast reconstruction of *Homunculus patagonicus* (Platyrrhini) late Early Miocene, MPM-PV 3502. (A) Dorsal, (B) ventral, (C) anterior, (D) posterior, and (E) lateral views. Green areas reconstructed by mirroring or based on the morphology of MPM-PV 17453.

4.2 | Body Mass Estimates

Prosthion–inion length is strongly influenced by phylogeny in this sample of primates ($\lambda=0.999$), but this metric can nevertheless perform well as a proxy for body mass when those effects are accounted for. The lnPE values for prosthion–inion length (Table S3) are consistently lower than those for dental proxies and higher than those for postcranial proxies calculated by Pampush et al. (tab. 2 in Pampush et al. (2021)), albeit with a different primate phylogeny than the one they used. Unsurprisingly, the lnPE values using PIC and BayesModelS are considerably lower (0.252 and 0.259, respectively), indicating more accurate predictions than those calculated using OLS or

PGLS, which fail to incorporate phylogeny into their predictions. The percentage of species successfully classified to within $\pm 20\%$ of their body mass as reported by Smith and Jungers (1997) further supports the accuracy of PIC and BayesModelS (56.98% and 53.49%, respectively; Table S3). These findings are strong when compared with those reported by Pampush et al. (2021; their tab. 3). Our PIC model of body mass estimation using prosthion–inion length as proxy performs better than any individual proxy or model they tested, apart from calcaneal-cuboid facet area under a BayesModelS model.

Given the above results, we prefer the PIC estimates of fossil anthropoid body mass based on prosthion–inion length

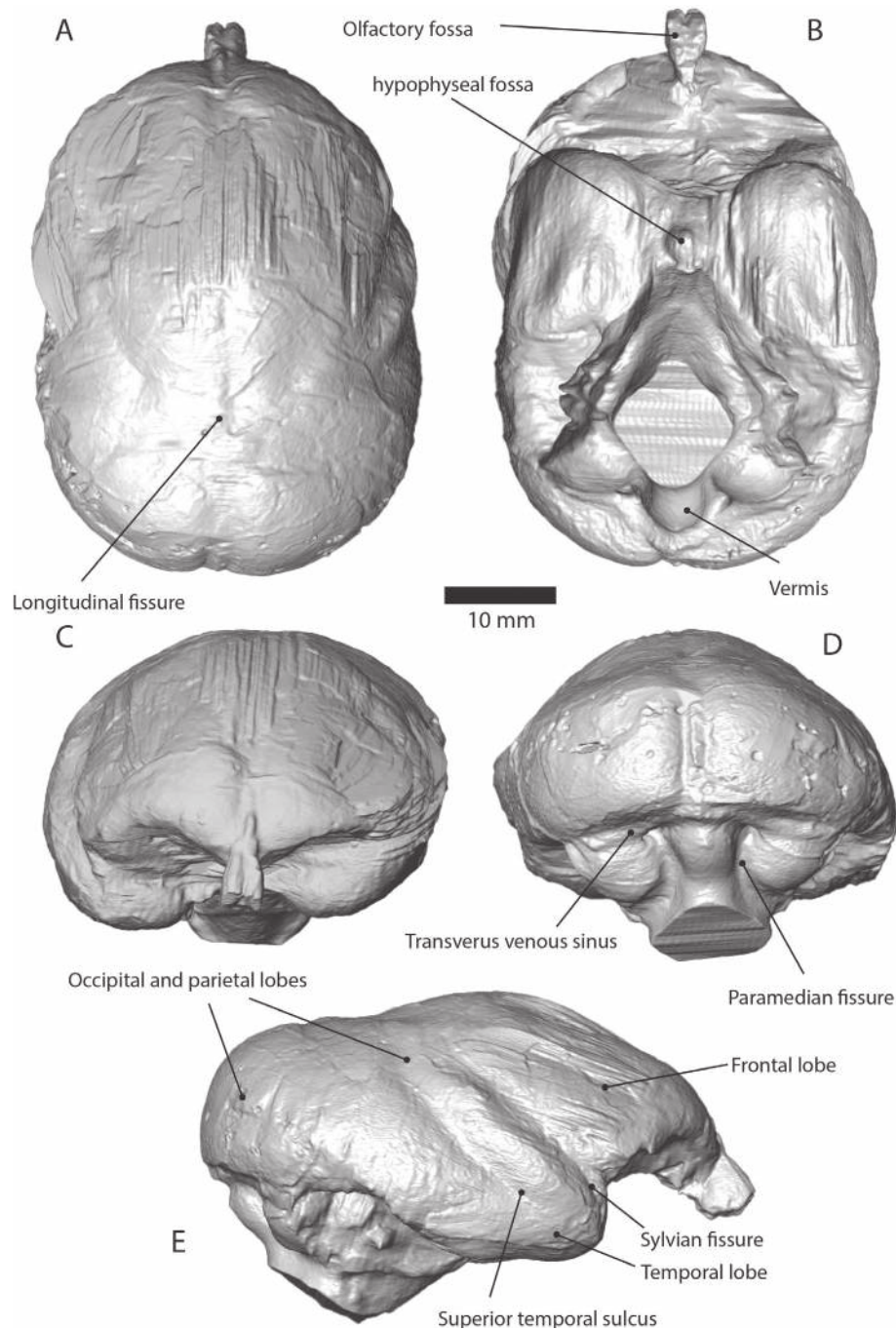


FIGURE 6 | Virtual endocast reconstruction of *Homunculus patagonicus* (Platyrrhini) late Early Miocene, MPM-PV 17453. (A) Dorsal, (B) ventral, (C) anterior, (D) posterior, and (E) lateral views.

over prior estimates made for these taxa using other dimensions (e.g., Dagosto and Terranova 1992; Pampush et al. 2021; Sears et al. 2008; Yapuncich et al. 2015). Body mass estimates based on prosthion–inion lengths for fossil anthropoids investigated in this study are listed in Table 3. The remarkable preservation of *Homunculus* specimen MPM-PV 17453 (Perry et al. 2025), which includes a complete right humerus and most of the right femur in addition to a nearly complete cranium, readily permits body mass estimation using proxies other than prosthion–inion length. To obtain an alternative body mass for this specimen, we used the phylogeny and

dataset of Pampush et al. (2021), which is sufficient for characterizing a stem platyrrhine (but would not be appropriate for making estimations of stem anthropoids or catarrhines). We multiplied midshaft maximum antero-posterior distance by maximum mediolateral distance from humeral and femoral cross-sections obtained digitally in Avizo 3D. Using the same PIC model as Pampush et al. (2021), we estimate the body mass of MPM-PV 17453 to be 1958 g from the humerus and 2369 g from the femur. Based on these alternative approaches, a preferred body mass estimate for this *Homunculus patagonicus* specimen is between 1600 and 2400 g.

TABLE 3 | Body size estimates from PIC models for prosthion–inion length and humeral and femoral cross-sectional areas.

Taxon	PIC prosthion– inion (g)	PIC humeral cross-section (g) ^a	PIC femoral cross-section (g) ^a	Prior body mass estimates (g)	Authority for prior estimate
<i>Homunculus patagonicus</i>	1651.1 ^b	1958 ^c	2369 ^c	Cranial: 2226 ± 209; Dental: 2521 ± 121; Postcranial: 5145 (4274–5923)	Conroy (1987); Gingerich et al. (1982); Kay et al. (2012); Perry et al. (2018)
<i>Chilecebus carrascoensis</i>	670.6	—	—	Weighted average of 46 craniodental dimensions: 583	Flynn et al. (1995); Sears et al. (2008)
<i>Dolichocebus gaimanensis</i>	1356.9	—	—	Dental: 1149–1754	Kay et al. (2008)
<i>Tremacebus harringtoni</i>	1011.1	—	—	No prior estimates	—
<i>Aegyptopithecus zeuxis</i>	4555.7	—	—	Cranial: 2735–6610; Dental: 5876–6716	Conroy (1987); Gingerich et al. (1982); Kay and Simons (1980); Simons et al. (2007)
<i>Simonsius grangeri</i>	1097.8	—	—	Cranial: 2735–6607; Dental: 1802–3171; Postcranial: 1636	Conroy (1987); Gingerich et al. (1982); Kay and Simons (1980); E. L. Simons (2004); Simons et al. (2007)
<i>Victoriapithecus macinessi</i>	—	—	—	Cranial: 6000; Dental: 4824–5476; Postcranial: 3500–4000	Conroy (1987); Gingerich et al. (1982); Gonzales et al. (2015); Harrison (1989b)

^aPIC model for humeral and femoral cross-sectional areas is based on the phylogeny and postcranial dimensions provided in Pampush et al. (2021).

^bThis estimate derived from the average prosthion–inion length of two specimens of *Homunculus*: MPM-PV 3502 and MPM-PV 17453.

^cThis estimate derived from postcranial elements of a single specimen of *Homunculus*: MPM-PV 17453.

4.3 | Size of Brain and Its Components

4.3.1 | Validating the Accuracy of Neocortex Surface Area and Frontal Lobe Surface Area

We find that endocast neocortical surface area is a reliable proxy for the size of the neocortex (data in Stephan et al. 1981).

When we compare residuals from the PGLS lines of best fit of (1) ln neocortex mass versus ln brain mass with residuals of (2) ln neocortical surface area versus ln endocast volume, we find that taxa with relatively large neocortical mass also have relatively large endocast neocortical surface area. The correlation between the residuals is 0.96 ($n = 40$; $p < 0.001$).

Using an analogous procedure, we find that frontal lobe surface area is a reliable proxy for the proportion of frontal lobe gray matter (data in Bush and Allman 2004). When we compare residuals from the PGLS lines of best fit of (1) ln frontal gray matter volume versus ln total neocortex gray matter volume with residuals of (2) ln frontal surface area versus ln neocortical surface area in endocasts, we find that taxa with relatively large frontal gray matter volume also tend to have relatively large frontal lobe endocast surface area. The correlation between the residuals is 0.68 ($n = 10$; $p < 0.016$).

4.4 | Endocast Metrics Compared With Body Mass

4.4.1 | Endocranial Volume

The bivariate plots in Figure 7A–E compare endocranial volume, olfactory fossa volume, neocortical surface area, and its subdivisions (frontal and OPT) with body mass. Endocranial volumes scale with negative allometry relative to body mass (PGLS slope = 0.70 ± 0.04 vs. an expected isometric slope of 1.00 in a volume-to-volume comparison; Table 4, Figure 7A). This result is not surprising, as a negatively allometric relationships between brain mass and body mass has been observed in many prior comparative studies of primates (e.g., Baron et al. 1983; Jerison 1973). Extant anthropoids tend to have larger endocranial volumes compared with living strepsirrhines of comparable body mass. Nevertheless, there is substantial overlap in relative endocranial volume across the shared range of body size represented by extant strepsirrhines and anthropoids. Tarsiers fall within the range of strepsirrhines and have smaller endocranial volumes than *Cebuella*, a platyrrhine of similar body mass. The stem anthropoid *Simonsius* has a relatively small endocast volume for its body mass, and plots outside the lower edge of the envelope encompassing extant anthropoids in Figure 7A but within that of extant strepsirrhines. The stem catarrhine *Aegyptopithecus* has an even smaller endocranial volume for its body mass and plots below the range of all living primates. Previous body mass estimates of these two taxa are larger, which would make their relative endocranial volumes substantially smaller (were these to be accepted, both *Simonsius* and *Aegyptopithecus* would have smaller brains than any Miocene–Recent primate). *Victoriapithecus*, like *Simonsius* and *Aegyptopithecus*, has a very small brain for its body mass,

outside the range of extant primates. Among Early Miocene platyrrhines, *Chilecebus* has a smaller endocranial volume (data from Ni et al. 2019) than extant platyrrhines of comparable body mass and is within the range of extant strepsirrhines. In contrast, *Homunculus Dolichocebus*, and *Tremacebus* mainly fall within the extant anthropoid range and therefore probably had brain sizes that were comparable to extant anthropoids of similar body mass.

For *Homunculus*, the body mass estimate from average prosthion–inion length of three individuals is lower than those estimated from associated humeral and femoral cross-sectional areas of individual MPM-PV 17453. No postcranial material is known for *Chilecebus* or *Tremacebus*, and *Dolichocebus* lacks postcranial elements that have been well-vetted as proxies for body mass outside of a single, unassociated talus (Gebo and Simons 1987). Furthermore, the body mass estimates for *Aegyptopithecus* and *Simonsius* reported here are derived from prosthion–inion dimensions of the same specimens from which we calculate the endocranial volume, not on postcranial measurements of other specimens allocated to those taxa. If a shift of similar magnitude in *Aegyptopithecus* and *Simonsius* toward larger body mass estimates from postcranial measurements compared with prosthion–inion dimensions was also true for these taxa, the result would be to produce even smaller relative endocast values. Additionally, *Aegyptopithecus* exhibits considerable sexual dimorphism (Fleagle et al. 1980), as is true for many of the catarrhines in our body mass estimation models (Smith and Jungers 1997). CGM 85785 is interpreted as female (Simons et al. 2007), and relative endocranial volumes are larger on average in anthropoid females than in males (Isler et al. 2008).

4.4.2 | Olfactory Fossa Volume

Olfactory fossa volume scales with negative allometry relative to body mass (slope = 0.49 ± 0.05 vs. an expected isometric slope of 1.00 in a volume-to-volume comparison; Table 4). Extant anthropoids have relatively smaller olfactory fossa volumes than those of strepsirrhines, with no size overlap across the range of body masses shared by strepsirrhines and anthropoids (Figure 7C). The tarsiid *Carlito* likewise has a small olfactory fossa, although *Cephalopachus* and *Tarsius* have larger fossae than *Cebuella*. Nocturnal or cathemeral *Aotus* (Fernandez-Duque 2003) resembles *Cephalopachus* and *Tarsius* in having much larger olfactory fossae than similar-sized diurnal anthropoids. *Simonsius* falls above the range of extant diurnal anthropoids but below that of strepsirrhines in relative olfactory fossa volume, although its small orbits indicate a likely diurnal activity pattern (Kay and Kirk 2000). The volume of the olfactory fossa of *Aegyptopithecus* falls within the extant diurnal anthropoid range, as do those of *Homunculus* and *Tremacebus*. *Chilecebus* has a very small relative olfactory fossa size (data from Ni et al. (2019)) and plots below the extant anthropoid distribution, although we note that this finding may be the result of damage to the olfactory fossa visible in published images of the SGOPV 3213 endocast (Ni et al. 2019). *Victoriapithecus*, like *Simonsius*, has a large olfactory fossa, above the envelope of extant anthropoids but smaller than in modern strepsirrhines.

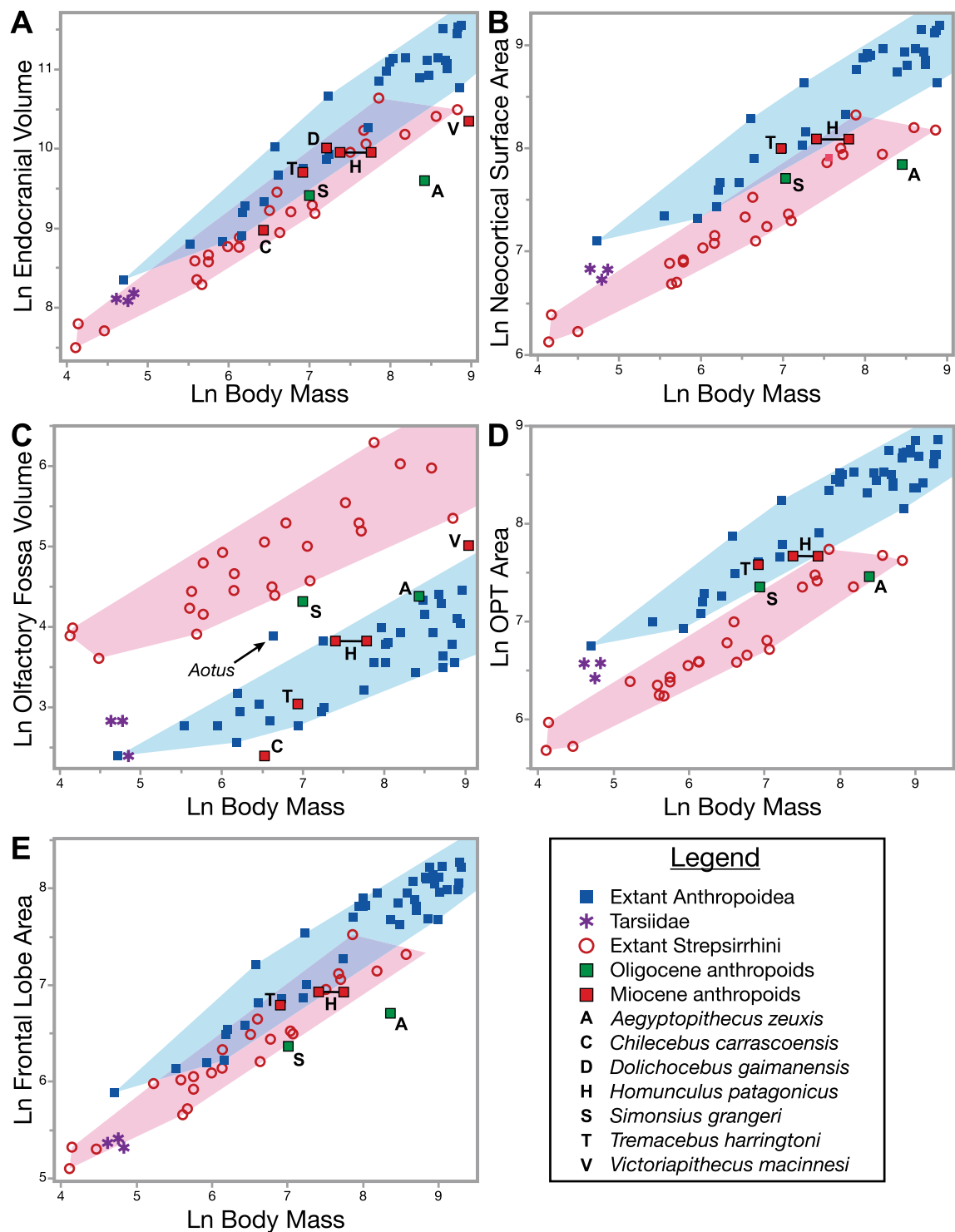


FIGURE 7 | Bivariate plot of ln body mass (as the predictor variable) versus response variables: (A) ln endocranial volume, (B) ln neocortical surface area, (C) ln olfactory fossa volume, (D) ln OPT surface area, and (E) ln frontal lobe surface area. Blue squares are extant anthropoid genera, red open circles are extant strepsirrhine genera, purple asterisks are tarsiid genera. The red envelope represents the range for extant strepsirrhines while the blue envelope represents the range for extant anthropoids. The plotted anthropoid range has been truncated, with larger taxa removed for illustrative purposes. Green squares indicate Oligocene anthropoids (*Simonsius* and *Aegyptopithecus*) and red squares represent Miocene genera. For *Homunculus patagonicus*, two red squares represent PIC body mass estimates from prosthion-inion length and humeral and femoral cross-sections (Table 3).

TABLE 4 | Results of phylogenetic generalized least squares comparisons between body mass and brain variables and among brain variables in log space.^a

Comparison	PGLS slope	Slope standard error	Interpreted relationship	PGLS intercept	Intercept standard error	R-squared	Residual standard error	df	Lambda
Endocast volume vs. Body mass PIC	0.70	0.04	Negative allometry	4.65	0.33	0.78	0.07	83	0.74
Neocortex area vs. body mass PIC	0.41	0.05	Negative allometry	4.68	0.27	0.71	0.06	80	0.98
OPT area vs. body mass	0.40	0.05	Negative allometry	4.57	0.48	0.59	0.07	52	1.00
Frontal lobe surface area vs. body mass	0.44	0.05	Negative allometry	3.36	0.49	0.63	0.07	52	1.00
Olfactory bulb volume vs. body mass PIC	0.49	0.05	Negative allometry	0.97	0.42	0.55	0.09	82	0.94
Olfactory bulb volume vs. endocast volume	0.54	0.07	Negative allometry	-0.80	0.09	0.44	0.09	82	0.87
Neocortex area vs. endocast volume	0.67	0.01	Isometry	1.27	0.08	0.99	0.01	80	0.96
OPT area vs. Endocast volume	0.65	0.01	Isometry	1.08	0.12	0.97	0.02	80	0.98
Frontal lobe surface area vs. Endocast volume	0.72	0.01	Positive allometry	-0.28	0.12	0.98	0.02	80	0.90
OPT Gray Matter volume vs. Endocast volume	0.93	0.06	Positive allometry	-7.48	0.60	0.92	0.06	21	1.00
Frontal gray volume vs. Endocast volume	1.20	0.04	Positive allometry	-11.18	0.41	0.98	0.04	22	1.00
Neocortical Gray Matter vs. Endocast volume	1.17	0.03	Positive allometry	-10.88	0.35	0.98	0.03	21	1.00
Frontal gray matter vs. total gray matter	1.12	0.04	Positive allometry	-1.57	0.11	0.98	0.03	22	0.60
Frontal surface area vs. total neocortical surface area	1.05	0.02	Positive allometry	-1.54	0.16	0.97	0.02	80	0.99
Frontal gray vs. OPT gray	1.20	0.05	Positive allometry	-1.36	0.14	0.97	0.04	22	0.73
Brain mass vs. neocortical mass (data from Stephan et al. (1981))	1.06	0.01	Positive allometry	1.27	0.08	0.99	0.01	80	0.96
Optic foramen area vs. Prosthion-Inion	0.60	0.15	Negative allometry	-0.77	0.51	0.17	0.07	82	0.95
OPT area vs. Prosthion-Inion	0.83	0.19	Negative allometry	4.50	0.67	0.19	0.10	78	1.00

^aBlomberg's kappa for all analyses = 1.00.

4.4.3 | Neocortical Surface Area

Endocast neocortical surface area scales with negative allometry relative to body mass (PGLS slope = 0.41 ± 0.08 , vs. an expected isometric slope of 0.66 in an area-to-volume comparison; Table 4, Figure 7B). Nearly all extant anthropoids have relatively larger endocast neocortical surface areas than extant strepsirrhines (*Daubentonia* excepted). Furthermore, there is almost no overlap (except for *Daubentonia*) in relative neocortical surface area across the range of masses shared by strepsirrhines and anthropoids (Figure 7B). Tarsiids have neocortices that are relatively smaller than that of *Cebuella* but larger than those of similar-sized extant strepsirrhines. *Simonsius* had a relatively small neocortex, outside the anthropoid envelope but within the range of strepsirrhines of similar body mass. *Aegyptopithecus* had an even smaller relative endocast neocortex surface area, outside the range for all living primates of similar body mass. *Homunculus* falls near the smaller (lower) end of the extant anthropoid range, whereas *Tremacebus* neocortical surface areas are well within the extant platyrrhine (and anthropoid) envelope.

4.4.4 | Frontal Lobe Surface Area

Frontal lobe surface area scales with negative allometry relative to body mass (PGLS slope = 0.44 ± 0.05 , vs. an expected isometric slope of 0.66 in an area-to-volume comparison; Table 4, Figure 7E). Extant anthropoids tend to have larger frontal lobe areas than do extant strepsirrhines. However, as with relative endocranial volume (Figure 7A), there is considerable overlap between the two clades in relative frontal lobe area (Figure 7E). This is the case even when accounting for the unusually large frontal lobe of *Daubentonia*. Tarsiids have relatively small frontal lobes for their body size, far smaller than any extant anthropoids. *Simonsius* had a relatively small frontal lobe, outside the anthropoid envelope but near the range of strepsirrhines of similar body mass. *Aegyptopithecus* had an even smaller frontal lobe relative to body mass, outside the range for all living primates of similar body mass. *Homunculus* and *Tremacebus* fall within the range of both extant anthropoids and strepsirrhines in relative frontal lobe size.

4.4.5 | OPT Surface Area

OPT endocast surface area scales with negative allometry relative to body mass (PGLS slope = 0.40 ± 0.05 , vs. an expected isometric slope of 0.66 in an area-to-volume comparison; Table 4). Extant anthropoids all have relatively larger OPT surface areas than extant strepsirrhines, and there is no overlap between the distributions of the two clades (Figure 7D). Tarsiids resemble anthropoids in having relatively large OPT areas. *Simonsius* had a relatively large OPT area, within the anthropoid envelope and outside the range of strepsirrhines of similar body mass. *Aegyptopithecus* had a relatively smaller OPT area than *Simonsius*, within the range for living strepsirrhines of similar body mass. *Homunculus* and *Tremacebus* fall within the range of extant anthropoids (Figure 7D).

4.5 | Endocast Measurements Compared With Endocranial Volume

The relationships between olfactory fossa volume, neocortex surface area, frontal lobe area, and OPT area relative to endocast volume are presented in Table 4 and Figure 8A–D.

4.5.1 | Olfactory Fossa Volume

Olfactory fossa volume scales with negative allometry relative to endocranial volume (PGLS slope = 0.54 ± 0.07 vs. an expected isometric slope of 1.00 in a volume-to-volume comparison; Table 4). Extant anthropoids have small olfactory fossae relative to endocranial volume, and do not overlap the extant strepsirrhine distribution (Figure 8A). Tarsiids all have a relatively smaller olfactory fossa than strepsirrhines, but *Cephalopachus* and *Tarsius* have a proportionally larger fossa than anthropoids. *Simonsius*, *Aegyptopithecus*, and *Victoriapithecus* have a substantially larger olfactory fossae than extant anthropoids of similar endocranial volume, but their olfactory fossae are nevertheless smaller than strepsirrhines of comparable endocranial volume. The olfactory fossa of *Aotus* is also larger than those of other extant anthropoids of similar endocranial volume. *Homunculus* has a relatively large olfactory fossa approaching the size seen in *Aotus*. The olfactory fossa of *Tremacebus* resembles that of extant diurnal anthropoids and is not as large as in *Aotus* (Kay et al. 2004). The fossa of *Chilecebus* follows the general trend for other anthropoids but is below the observed range of extant anthropoids in Figure 8A.

4.5.2 | Neocortical Surface Area and Neocorticalization

Neocortical surface area scales with isometry relative to endocranial volume (PGLS slope = 0.672 ± 0.01 vs. an expected isometric slope of 0.66 in an area-to-volume comparison; Table 4). These two variables are very tightly correlated (coefficient of correlation = 0.99). Nevertheless, relative to endocranial volume, extant anthropoids have larger neocortical surface areas than do extant strepsirrhines, and there is no overlap between the anthropoid and strepsirrhine distributions in Figure 8B. Tarsiids likewise have larger neocortical surface areas than strepsirrhines of similar endocranial volume. *Simonsius*, *Aegyptopithecus*, *Homunculus*, and *Tremacebus* all have relative neocortical surface areas within the range of extant anthropoids (Figure 8B).

A finding of isometry for the relationship between neocortex surface area and endocranial volume permits us to compare taxa using the “modified” neocorticalization ratios described above (i.e., square root of neocortex area divided by cube root of endocranial volume; Figure 9). When measured in this way, there is no overlap in neocorticalization ratio between extant strepsirrhines and extant haplorhines. On average, the neocorticalization ratios of extant strepsirrhines average are 15% smaller than those of haplorhines (Table 1). *Simonsius*, *Aegyptopithecus*, *Homunculus*, and *Tremacebus* all have large neocorticalization ratios, close to the median for extant anthropoids and far larger than any extant strepsirrhine.

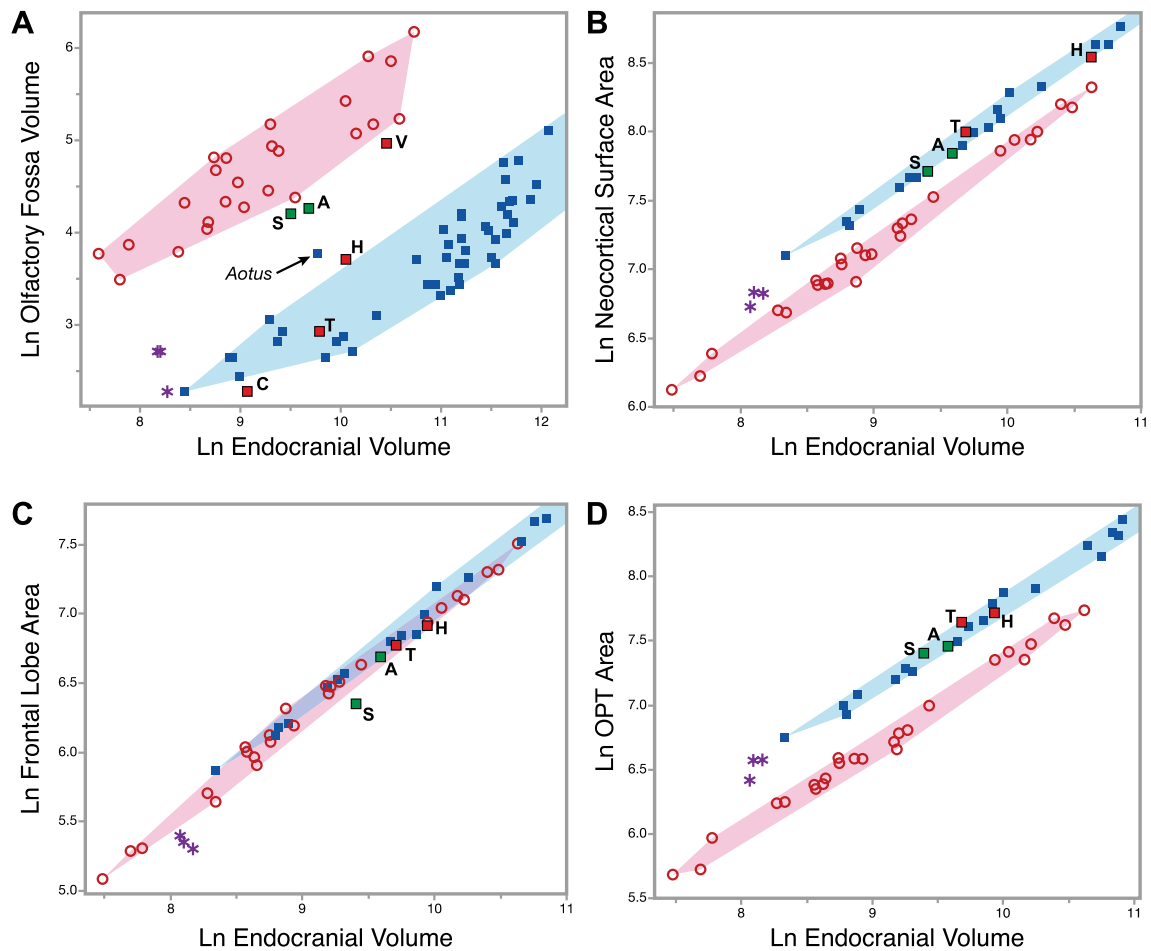


FIGURE 8 | Bivariate plots of Ln endocranial volume (as the predictor variable) versus response variables: (A) Ln olfactory fossa volume; (B) Ln neocortical surface area; (C) Ln frontal lobe surface area; (D) Ln OPT area. Symbols and coloration as in Figure 7.

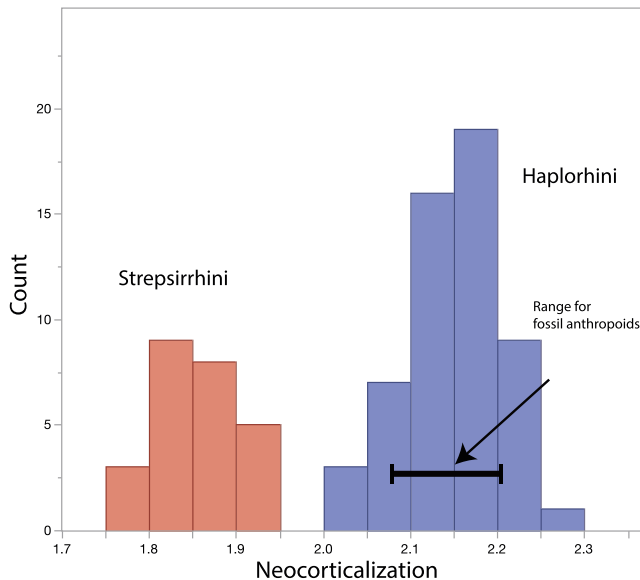


FIGURE 9 | Histogram of neocorticalization ratio (square root of neocortical surface area divided by cube root of endocranial volume) for extant primate genera. Strepsirrhini indicated by red bars ($n=25$, mean=1.80, standard deviation=0.042) and Haplorhini represented by blue bars ($n=58$, mean=2.10, standard deviation=0.048). Range for Oligocene and Miocene anthropoids represented by horizontal black bar. Data in Table 1.

4.5.3 | Surface Areas of Frontal and OPT Neocortical Components Compared With Overall Endocranial Volume

Frontal lobe surface area scales with positive allometry relative to endocranial volume (PGLS slope = 0.72 ± 0.01 vs. an expected isometric slope of 0.66 in an area-to-volume comparison; Table 4). The correlation coefficient between the two variables is 0.989 (Table 4). This positive allometry in frontal lobe surface area relative to brain size agrees with prior studies of actual brains. When Bush and Allman's (2004) data for frontal lobe neocortical gray matter volume in 22 extant primate genera are compared with our data for endocranial volume, the PGLS regression also demonstrates positive allometry (PGLS slope = 1.20 ± 0.04 vs. an expected isometric volume-to-volume ratio of 1.00; Table 4). These results indicate that as the neocortex expands in primates, the frontal lobe undergoes a disproportionate increase in size.

The envelopes of frontal lobe surface area versus endocranial volume for strepsirrhines and anthropoids overlap considerably over their shared range of endocranial volumes (Figure 8C). This similarity also is apparent when we examine the residuals from the PGLS line of fit for members of the two clades (Figure 10A). Tarsiids stand apart from both strepsirrhines and extant anthropoids in having exceptionally small frontal lobe surface areas relative to brain size. The frontal lobe surface area of *Simonsius*

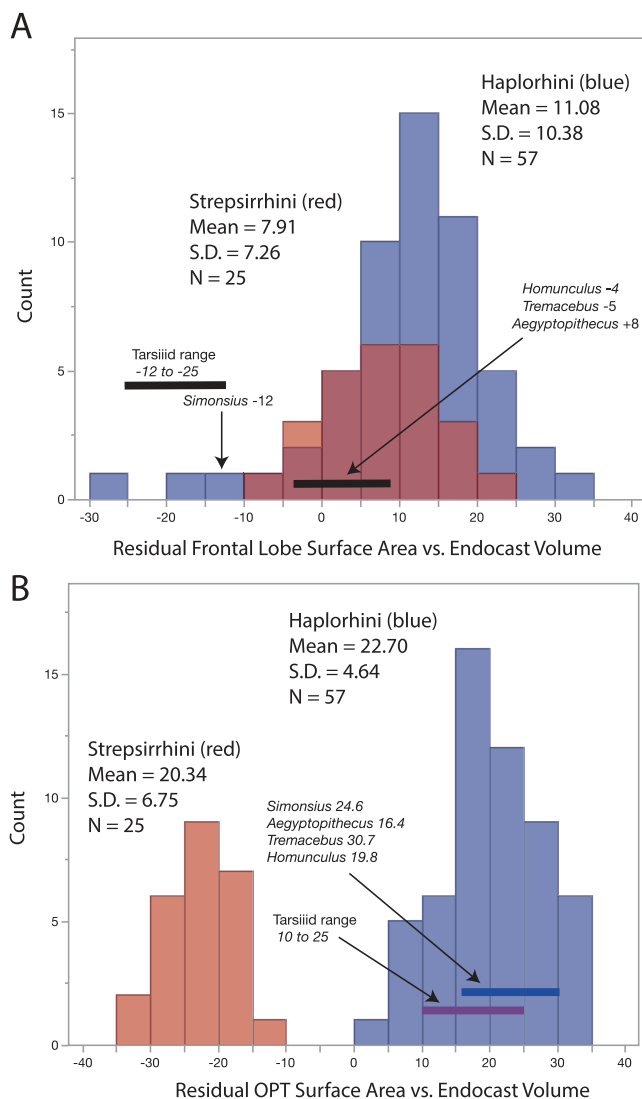


FIGURE 10 | Histograms of residuals from: (A) a PGLS model of ln frontal lobe surface area versus ln endocranial volume, and (B) a PGLS model of ln OPT surface area versus ln endocranial volume. Strepsirrhini indicated by red bars and Haplorhini represented by blue bars. Descriptive statistics for these distributions are denoted in the plots with corresponding colors. Ranges for Tarsiidae and Oligocene and Miocene anthropoids represented by purple and blue horizontal bars, respectively. Residuals are based on equations from PGLS analysis in Table 4.

resembles tarsiids in falling outside and below the range of extant anthropoids and strepsirrhines of comparable endocranial volume. *Aegyptopithecus*, *Homunculus*, and *Tremacebus* fall within the range of overlap between extant anthropoids and strepsirrhines Figures 8C and 10A.

Unlike the positive allometry exhibited by the frontal lobe surface area, the remaining surface of the neocortex (OPT) scales with isometry relative to endocranial volume (slope = 0.65 ± 0.01 vs. an expected isometric slope of 0.66 in an area-to-volume comparison; Table 4). Extant anthropoids also consistently have larger OPT areas than extant strepsirrhines with similar endocranial volumes (Figure 10B). In this respect, extant tarsiids resemble anthropoids in having larger OPT areas than strepsirrhines of similar endocranial volume (Figure 8D). *Simonsius*,

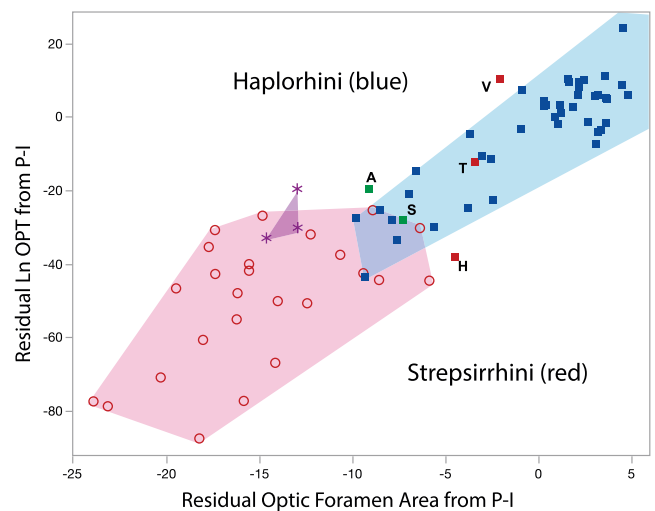


FIGURE 11 | Bivariate plot of residuals from a PGLS model of ln OPT surface area against ln prosthion-inion length (y-axis) versus residuals from a PGLS model of ln optic foramen area against ln prosthion-inion length (x-axis). Symbols and coloration as in Figure 7. Coefficient of correlation = 0.80, $p < 0.001$.

Aegyptopithecus, *Homunculus*, and *Tremacebus* plot with extant anthropoids in Figure 8D.

4.5.4 | Surface Areas of OPT Compared With Optic Foramen Area

Taxa with relatively large ln OPT surface area for their body size also have relatively large ln optic foramen areas when using ln prosthion-inion length as a size proxy to relativize both measurements (Figure 11; formulae for calculating the residuals in Table 4). The correlation between the residuals is 0.802 ($n = 86$; $p < 0.001$). There is some overlap between extant haplorhines and strepsirrhines in these residuals, with 2 tarsiid and 5 anthropoid genera plotting within the upper range of the strepsirrhine distribution. Fossil anthropoid taxa all plot within or near the extant distribution in Figure 11.

5 | Discussion and Conclusions

5.1 | Gyrfication and Its Significance

The sulcal patterns of extant strepsirrhines, tarsiers, and anthropoids differ considerably even though the underlying arrangement of functional regions is similar (Radinsky 1975). In strepsirrhines, a sulcus rectus and longitudinal sulcus cross between the frontal and parietal regions; the latter even extends caudally to the rostral portion of the occipital cortex (Le Gros Clark 1945, 1959). Tarsiids lack useful sulci for delineating neocortical regions on their endocranials (Woollard 1925). In many anthropoids, two sulci not observed in other primates provide important functional neocortical landmarks. The central sulcus separates the primary motor cortex in the frontal lobe from the primary somatosensory cortex in the parietal lobe (Radinsky 1973). The lunate sulcus of the occipital lobe generally delimits the most rostral extent of the primary visual

cortex. However, even in extant anthropoids, the presence and identity of the central and lunate sulci on endocasts is variable (Radinsky 1973).

Oligocene–Early Miocene anthropoids described here are either lissencephalic or have some version of the anthropoid sulcal pattern. The stem anthropoid *Simonsius* had mainly smooth (lissencephalic) neocortical surfaces, although, like all primates (Harrington et al. 2016; Le Gros Clark 1959) a sylvian fissure is apparent. The published endocast reconstruction of *Aegyptopithecus* lacks central and lunate sulci (Simons et al. 2007) but was scanned at low resolution and exhibits few distinguishable neocortical features, but another specimen of *Aegyptopithecus* exhibits an anthropoid-like central and lunate sulci (Radinsky 1973). Early Miocene anthropoid taxa often have endocasts with more readily observable neocortical sulci. *Chilecebus* reportedly has both central and lunate sulci (Ni et al. 2019) as does the Miocene catarrhine *Victoriapithecus* (Gonzales et al. 2015). However, we could not identify central or lunate sulci unambiguously in *Homunculus* or *Tremacebus*.

Although the presence of the central and lunate sulci in anthropoids may signal the size of subcomponents of the neocortex, one should not assume that the absence of sulci on endocasts is meaningful evidence of overall brain organization. The absence of a particular sulcus on an endocast is consistent with two possibilities: either (1) the sulcus was absent on the underlying brain surface or (2) it was present on the brain surface but left no visible trace on the inner bony table of the braincase. Likewise, the general trend with increased brain size for primate endocasts to exhibit greater gyrification (Jerison 1982; Mota and Herculano-Houzel 2015; Rilling 2006) and more prominent sulci may not indicate brain reorganization or a corresponding lack of homology with its smaller-brained relatives. For example, the primary visual cortex (striate cortex; Brodmann area 17) is certainly located in the occipital lobe irrespective of whether a lunate sulcus is present or visible on an endocast (Frahm et al. 1984). Thus, even when not observable based on endocast sulci and gyri, it is reasonable to assume that the underlying neuroarchitecture is similar and homologous in strepsirrhines, tarsiers, and anthropoids.

5.2 | Body Size and Brain Size

Our estimates for body mass in *Homunculus* differ considerably depending on the anatomical proxy employed, with skull length producing an estimate ~16%–30% smaller than those derived from long bone cross-sectional areas of the same individual (Table 3). While our results suggest that skull length is a more accurate predictor of body mass than are dental dimensions, our prediction error values (Table S3) are still higher than those calculated for postcrania by Pampush et al. (Pampush et al. 2021: their tab. 2). Because we estimated body mass for *Simonsius*, *Aegyptopithecus*, *Tremacebus*, and *Chilecebus* on the sole basis of skull length, it is possible that a more accurate proxy would meaningfully alter their estimated body size (although no more accurate proxy has been proposed for *Tremacebus* or *Chilecebus*, which lack postcrania). If the same difference found between limb cross-sections and P-I dimensions for *Homunculus* also applies to these taxa, larger body masses would imply even smaller

relative brain and brain component sizes than what is presented in Figure 7.

Despite these uncertainties, our body size and brain size estimates confirm previous findings that brain size enlargement has occurred convergently in many anthropoid lineages (Flynn et al. 1995; Gonzales et al. 2015; Ni et al. 2019; Radinsky 1975). The stem anthropoid *Simonsius* had a small, strepsirrhine-sized brain (Bush et al. 2004; Simons et al. 2007). The stem catarrhine *Aegyptopithecus* and stem cercopithecoid *Victoriapithecus* had even smaller brains than *Simonsius*. The brain size of stem platyrrhine *Chilecebus* falls below the range for extant anthropoids and within the strepsirrhine envelope. *Tremacebus*, *Dolichocebus*, and *Homunculus* (contra Kay et al. 2012) had brain sizes within the range of values observed in extant platyrrhines but also overlapping the range for larger-brained strepsirrhines.

5.3 | Olfactory Bulbs

As with many prior studies (e.g., Lang et al. 2025; Radinsky 1975), our data shows the olfactory bulbs (as inferred from the size of the olfactory fossa) to be larger in extant strepsirrhines than in anthropoids, whether judged in comparison with body mass (Figure 7C) or endocast volume (Figure 8A). Nocturnal *Aotus* represents an outlier among extant anthropoids in having relatively large olfactory bulbs, although they are still smaller than those of strepsirrhines. When olfactory fossa size is considered relative to body mass, the tarsiids *Cephalopachus* and *Tarsius* resemble *Aotus* in plotting between strepsirrhines and diurnal anthropoids, whereas *Carlito* plots with anthropoids (almost identical in size for both variables to *Cebuella*). The olfactory bulbs of *Simonsius* and *Victoriapithecus* appear to have been proportionally much larger than those of extant anthropoids, but not as large as those of strepsirrhines compared with body mass or endocranial volume. The same is true for *Aegyptopithecus* relative to endocast volume (Figure 8A) but estimated olfactory bulb volume is at the upper edge of the anthropoid range relative to body mass (Figure 7C). The olfactory bulbs of Miocene platyrrhines appear to have been within the range of extant platyrrhines relative to body mass and brain size, or on the trend line extrapolated to smaller body size in the case of *Chilecebus*.

5.4 | Neocortex Size

Aegyptopithecus and *Simonsius* had smaller neocortices (as inferred from the neocortical surface area) relative to body mass than any extant anthropoid, with *Aegyptopithecus* evidently having a smaller neocortex than any extant primate (Figure 7B). In contrast, the neocortices of Miocene platyrrhines were large relative to body mass, resembling extant platyrrhines and other anthropoids. Although the sizes of the brain and neocortex relative to body mass may differ substantially among fossil anthropoid taxa, the *proportion* of the brain comprised by the neocortex nevertheless remains relatively stable among both extant and fossil anthropoids (Figure 8B). Indeed, body mass accounts for ~60% of the variance in endocast neocortex surface area whereas endocranial volume accounts for >99% of the variance in endocast neocortical surface area (Table 4). Accordingly, if

natural selection has favored the evolution of a larger neocortex in multiple anthropoid lineages independently (Heldstab et al. 2022), selection appears to have acted mainly on brain size as a whole rather than neocortex size in isolation (Finlay and Darlington 1995; Krubitzer and Kaas 2005). This conclusion is similar to that of Jerison (2012, 383), who noted the implications for the largest-brained anthropoid species: “The limitation of the increase in *relative* amount of neocortex is similar in all anthropoids. Neocortex is greater in *absolute* area in living humans because the total size of the hominin brain is so much larger than in other primates [*italics in original*].” Similarly, extant tarsiers also exhibit neocortices that are larger relative to both body mass (Figure 7B) and endocranial volume (Figure 8B) compared with extant strepsirrhines.

The isometric relationship (when accounting for phylogeny) between neocortical surface area and endocranial volume permits us to use a ratio—neocorticalization—to compare taxa. We find a complete separation between strepsirrhines and haplorhines in terms of neocorticalization (Figure 9). These results agree with a more limited set of histological data (Frahm et al. 1982; Stephan et al. 1981) that the neocortices of extant haplorhines are larger than those of extant strepsirrhines of equivalent brain size. The new surface data permit us to extend the findings to fossil anthropoids. Relative to endocranial volumes, neocortical surface areas for all fossil anthropoid taxa measured by us, like tarsiers, fall above the range for extant strepsirrhines and within the range of observed values for extant anthropoids (Figure 9). These results may indicate that the last common ancestor of anthropoids and tarsiers (i.e., crown haplorhines) had an enlarged neocortex for its brain size when compared with a strepsirrhine outgroup and that significant increases in neocorticalization occurred in a haplorhine stem lineage. An alternative possibility is that neocortical expansion relative to brain size occurred in parallel in crown tarsiers and crown anthropoids. Choosing between these alternative scenarios depends on the phyletic position of omomyoids in relation to tarsiers and anthropoids. Omomyoids have much smaller endocranial neocortical surface areas relative to endocranial volume compared with extant haplorhines (Kirk, Campisano, et al. 2025). As a result, if omomyoids are stem tarsiiiforms (Ni et al. 2016; Seiffert et al. 2020), then increases in neocortex size relative to brain size would have occurred independently in tarsiers and anthropoids. However, if omomyoids are stem haplorhines (Kirk, Campisano, et al. 2025; Williams et al. 2010), then the increased neocorticalization evident in crown haplorhines is more parsimoniously interpreted as having evolved once in the haplorhine stem lineage.

5.5 | Frontal Lobe Size

The data presented here show that frontal lobe surface area can be estimated in primate endocranial casts using impressions of the Sylvian fissure and the position of the hypophyseal fossa as landmarks even without an identifiable central sulcus. Primate taxa that have endocranial casts with relatively large frontal surface areas compared with total neocortex surface area also have relatively large frontal lobe gray matter volumes relative to total neocortical gray matter volumes. Our results also agree with the histological data (Frahm et al. 1982; Stephan et al. 1981) showing

the same positive allometry in frontal lobe size relative to total brain size (Table 4). These findings give us confidence that we can estimate the size of the frontal lobe (and OPT) in fossil anthropoid endocranial casts.

It is commonly stated that the frontal lobes in primates underwent a “progressive” enlargement from strepsirrhines to extant anthropoids, depicted in the older literature as a *scala naturae* (Le Gros Clark 1934). This perspective is expressed clearly by Le Gros Clark (1959, 232) “The frontal lobes of the brain are commonly assumed to represent the highest functional level of cortical activity. ... [In] the ascending scale of the Anthropoidea, from the monkeys to the apes and finally to man, these lobes show a progressive expansion.” It follows from Le Gros Clark’s interpretation that frontal lobe size in phylogenetically more basal anthropoids should be small and strepsirrhine-like, with frontal lobe enlargement “progressively” increased in various anthropoid lineages, especially that leading to humans. Le Gros Clark mentions body size in his comparisons only with reference to overall brain size, so it is reasonable to assume that he refers to these frontal lobe size increases as being relative to brain size not to body size. As noted previously, the prevailing view of paleontologists today fits within Le Gros Clark’s perspective that strepsirrhines and tarsiers have small frontal lobes relative to brain size and that anthropoids experienced increases in relative frontal lobe size independently in at least three anthropoid lineages: platyrrhines, cercopithecoids, and hominoids. Wise (2023, 132) summarizes these views as follows: “According to the paleontologists who have studied these specimens, all the extinct anthropoids had small frontal lobes compared with modern anthropoids ... at least some expansion of the frontal lobes must have occurred independently in Old World and New World anthropoids.”

Our data present a more nuanced picture. The frontal lobes of anthropoids are somewhat larger *relative to body mass* than in extant strepsirrhines but with substantial overlap between these clades (Figure 7E). On the other hand, extant strepsirrhines and living and fossil anthropoids have similar-sized frontal lobes *relative to brain size*, and tarsiers have small frontal lobes relative both to body size and brain size (Figures 8C and 10A).

Hitherto, the only support advanced for the idea that strepsirrhines had *smaller* frontal lobes for their brain size than haplorhines was provided by qualitative assessments of brain or endocranial morphology. For example, strepsirrhines were purported to exhibit lesser rostral projection of the dorsally flattened frontal lobes in front of the olfactory bulbs compared with greater overlap of the neocortex rostrally over the olfactory bulbs (Le Gros Clark 1945). Authors also noted a perceived narrowness of the frontal surfaces, and a dorsal bulging of the frontal profile in lateral view in anthropoids (Radinsky 1973). Our observations do not support this conventional wisdom. It is far from clear that there is any difference in the lateral profiles of the frontal poles of the neocortex in a strepsirrhine *Eulemur* and a platyrrhine *Plecturocebus* of similar brain size (Figure 12). Variation in the shape of the frontal lobe is more likely a result of structural variations associated with orbit size and the hafting of the braincase onto the face, than an actual size increase in the size of the frontal cortex (Bruner 2017).

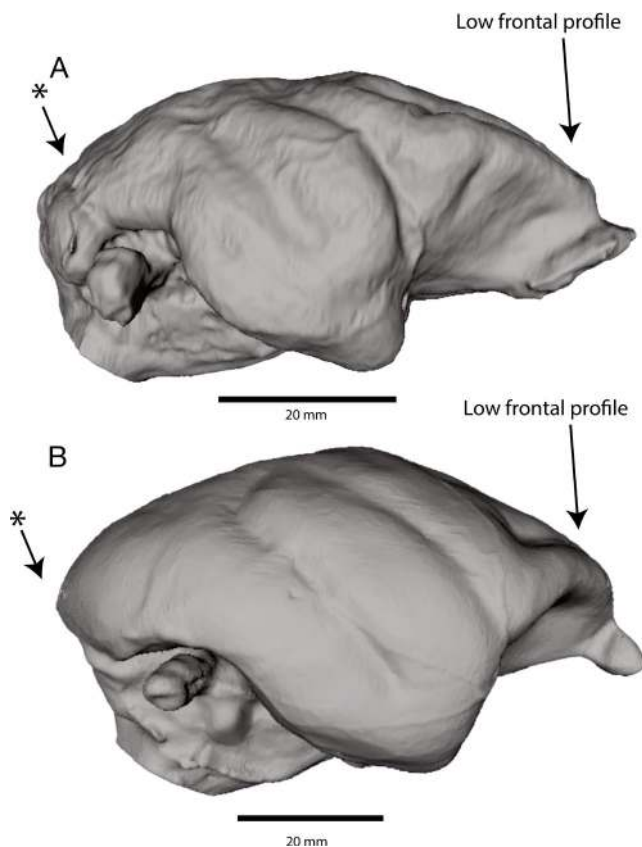


FIGURE 12 | Lateral views of endocasts of (A), a strepsirrhine *Eulemur fulvus* (DPC 057) and (B), a platyrrhine *Plecturocebus moloch* (DPC 39566). The two endocasts are similar in overall size. The frontal poles of the neocortex have similar rostral projection over the olfactory bulbs, and the frontal profiles are similar. Asterisk marks the caudal-most extent of the occipital pole of the neocortex.

We should add that some of this supposed “progressive” tendency for frontal lobe increases in all living primates, including *Homo*, instead is an added consequence of positive allometry of the frontal lobe compared with brain size (Brodmann 1912; Bush and Allman 2004; Jerison 2007; Semendeferi et al. 1997; Semendeferi et al. 2002; Von Bonin 1948). As primate brains get larger, the frontal lobes comprise a larger proportion of total brain size. These scaling factors help to explain the results obtained here for some fossil taxa. For example, in at least one early anthropoid (*Aegyptopithecus*), the small size of the frontal lobe relative to body size (Figure 7E) is presumably a consequence of having a small brain relative to body size (Figure 7A), as frontal lobe size relative to endocranial volume in *Aegyptopithecus* is very similar to that of extant anthropoids (Figure 8C).

This is not to say that there have been no changes in relative frontal lobe size versus brain size among extant anthropoids. For example, cebines *Saimiri*, *Sapajus*, and *Cebus* certainly fall at the upper end of the relative size range of frontal lobe size for platyrrhines and compared with their sister taxa the Aotinae and Callitrichinae. Added to the difficulty of establishing relative size change within these groups is the above noted and well-established positive allometry of frontal lobe size relative to brain volume. It is difficult to disentangle whether frontal lobe hyperscaling can be accounted for by selection (e.g., for

general intelligence, such as memory, problem-solving, etc.) or by increased brain size alone. We suspect that some previously claimed proportional differences between taxa are at least in part related to this hyperscaling. Some Oligocene and Miocene anthropoids will have relatively small frontal lobes by virtue of their small brains, but this is not to be explained by adaptive grade shifts but instead by allometry.

5.6 | OPT Size

Compared with body mass or endocranial volume, endocast OPT areas of extant haplorhines are consistently larger than those of similar-sized strepsirrhines (Figures 7D, 8D, and 10B). Given that relative to brain size and body mass, frontal lobe size overlaps substantially between strepsirrhines, tarsiers, and anthropoids (Figures 7E, 8C, and 10A), this difference in size of the OPT between strepsirrhines and haplorhines largely accounts for the difference in overall neocortex size.

Expanded areas of OPT in extant haplorhines and fossil anthropoids appear to be related to elaboration of visual processing. Primary visual cortex, located in the occipital lobe, is larger relative to brain size in haplorhines compared with strepsirrhines (Stephan 1984; Stephan et al. 1981). Downstream processing of visual signals occurs in the extrastriate cortex in the occipital and parietal cortex via a “dorsal stream” and in the temporal lobe via a “ventral stream” (Kaas et al. 2022). Comparative data on optic nerve size (Kirk 2006) and lateral geniculate parvocellular neuron number (Barton 1998) suggest that differences in visual input may partly explain the greater encephalization of primates relative to the primitive eutherian condition and the high encephalization of extant anthropoids and tarsiers relative to other primates. The data presented here supports these conclusions and refines it to focus on OPT cortex as opposed to the whole brain.

A reorganization of the neocortex with expanded OPT characterizes extant haplorhines as distinct from strepsirrhines, and this reorganization preceded increase in the size of the brain relative to body mass. Early anthropoids had smaller brains for their body size than do extant anthropoids (Figure 7A). Nevertheless, they had already expanded the proportion of the neocortex devoted to visual processing (Figures 8D and 10B). Reliance on acute vision, and the machinery to convert it to motor outputs, has been linked to a variety of selective behavioral factors. But there are conflicting opinions about which behavioral factor(s) may have selected for more emphasis on the sense of vision: Did visual improvements evolve in response to selection for complex social behavior (Byrne 1997; Dunbar 1995), identification (and capture) of food resources (Gibson 1986; Milton 1981), spatial memory (DeCasien and Higham 2019), or some combination of these influences (Healy 2021)? Olfactory information is primarily processed in forebrain regions outside the neocortex in mammals, suggesting that selection for enhanced olfactory abilities was not the reason that anthropoids evolved large neocortices (DeCasien and Higham 2019). This conclusion is supported by a general reduction in the size and complexity of the nasal cavity (Lundeen and Kirk 2019) and the reduced number of functional olfactory receptor genes (Christmas et al. 2023; Niimura et al. 2018) observed in all living haplorhines. The neocortex

generates such a diverse array of functions that it is not possible a priori to determine the potential targets of selection that may have led to increases in anthropoid neocortex size compared with strepsirrhines without more specific comparative data from individual lobes or regions within them. As Barton (2006) noted, “Relative expansion of the neocortex ... reveals comparatively little about which functional systems are involved, and hence what is the adaptive significance of overall brain size As with overall brain size, we still need to identify the specific systems in which selective expansion accounts for the increase in overall neocortex size and hence, in brain size (p. 231).”

6 | Summary

Compared with body mass, extant haplorhines tend to have larger brains than extant strepsirrhines, but the two groups show considerable overlap in relative brain size. These relative brain size differences are mainly attributable to differences in the size of OPT, which is consistently larger in tarsiers and extant anthropoids than in extant strepsirrhines. In contrast, relative to body mass, extant anthropoids have somewhat larger frontal lobes than strepsirrhines and tarsiers, but there is considerable range overlap between these groups.

Compared with brain size: (1) Living haplorhines have larger neocortices than living strepsirrhines. (2) The broadly accepted view that extant haplorhines have larger frontal lobes as a proportion of brain size than extant strepsirrhines is not supported by our data. Instead, we find no consistent difference in frontal lobe size between extant anthropoids and strepsirrhines. Tarsiers and the stem anthropoid *Simonsius* are outliers in our sample in having smaller frontal lobe endocast surface areas than extant primates of comparable endocranial volume. (3) By contrast, we find evidence that tarsiers and anthropoids have larger OPT surface areas relative to brain size. It is therefore an enlargement of OPT, not frontal lobe size, that accounts for the larger size of the neocortex relative to endocranial volume in extant haplorhines and all fossil anthropoids. (4) Many regions of OPT neocortex receive and evaluate visual signals that are relayed (ultimately) from the primary visual cortex, which is larger in haplorhines than in strepsirrhines. Accordingly, the evolution of relatively large OPTs, neocortices, and brains in extant haplorhines may be closely tied to the demands of processing more extensive visual sensory input in a wide variety of socioecological contexts.

There is a much higher correlation between neocortex size and brain size than there is between neocortex size and body size. This result could indicate that evolutionary increases in neocortex size may be most readily achieved by selection to increase the size of the brain as a whole (Finlay and Darlington 1995; Finlay et al. 2001), although the characteristically large neocortex and OPT of extant haplorhines relative to endocranial volume demonstrate that selection may favor disproportionate expansion of these brain regions.

Available published data suggests Eocene Euprimates (both Adapoidea and Omomyoidea) have a mean neocorticalization slightly below that of extant strepsirrhines, and well below that of anthropoids and extant tarsiers. Depending on the phylogenetic position of omomyoids relative to extant haplorhines, large

shifts in neocorticalization either occurred separately in stem tarsiiids and anthropoids or just once in the stem leading to tarsiiids and anthropoids.

Author Contributions

Richard F. Kay: conceptualization, investigation, funding acquisition, writing – original draft, writing – review and editing, data curation, formal analysis, project administration. **E. Christopher Kirk:** conceptualization, investigation, writing – review and editing. **Sergio F. Vizcaino:** investigation, funding acquisition, writing – review and editing. **M. Susana Bargo:** investigation, funding acquisition, writing – review and editing. **Kari L. Allen:** visualization, writing – review and editing, methodology. **Selby Olson:** visualization, writing – review and editing. **Paul E. Morse:** formal analysis, writing – review and editing, visualization, methodology, conceptualization, investigation.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Morphosource at <https://www.morphosource.org/>.

Endnotes

¹ Among the specimens used in Perry et al.'s analysis, we do not consider one specimen (MACN-A 5793) to be a primate. About this specimen, Bluntschli (1931) (in translation) writes, “[MACN-A 5793] is the fragment of a juvenile femur (fig. 40) where the epiphyseal line still exists. To be counted among *Anthropops* [since synonymized with *Homunculus*] as Ameghino did (albeit with a question mark), seems to me highly unlikely. When viewed superficially, the fragment does have a slight resemblance to the corresponding part of the same bone of *Homunculus*; but firstly the width of the epicondyle is almost a fifth less than that of *Homunculus* (19.3 mm, compared with the so-called *Anthropops*, 22.5 mm), but above all there are much wider condyles, a relatively and also absolutely narrower intercondylar fossa, and a much wider and shallower patellar groove in front. It is very likely that this femur fragment does not belong to any monkey at all.” [Emphasis added].

² Radinsky (1970) follows Gazin (1965) in stating that the Middle Eocene notharctid *Smilodectes* lacks a sylvian fissure. However, Harrington

et al. (2016) document a sylvian fissure in at least one specimen (USNM 21815).

³Sources include: (Brodmann 1909) figs. 90 and 91 for *Cercopithecus* and 96 and 97 for *Hapale* (= *Callithrix*) illustrating of areas of primary motor cortex (at the caudal edge of the frontal lobe) vs. somatosensory cortex (caudal margin of the parietal lobe) of *Lemur* and *Macaca*; Le Gros Clark's (1931) diagram of *Microcebus* showing the position of Brodmann's area 4 (primary motor cortex) and 1–3 (primary somatosensory cortex) relative to the hypophysis; and Le Gros Clark's (Le Gros Clark 1959) fig. 116 of *Lemur*, redrawn from figs. 98 and 99 in Brodmann (1909).

⁴In all figures, the endocasts are positioned so that the rostro-caudal Axis of Forel is horizontal (Figure 2D).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.