



Tracing transformation across 53 million years of euarchontoglires evolution: parallelism in early primate brain shape



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Essential to our understanding of primate brain evolution is the analysis of fossil brain endocasts, which allow us to trace variation through time and provide context for testing evolutionary hypotheses. The broadly held consensus that Primates are members of Euarchontoglires¹ and the growing record of endocasts of living and fossil members of this group^{2–8} allow for the application of new approaches to answer fundamental questions relating to shifts in the shape of the endocranium with evolving function. Using 3D geometric morphometric data of living and fossil Euarchontoglires spanning 53 million years, this analysis overturns previous assumptions about primate brain evolution. We show that: 1) early fossils share a common endocranial shape, with primates diverging towards extant morphologies faster than other clades; 2) Haplorhini and Strepsirrhini share derived endocranial morphologies that evolved independently through parallel evolution; and 3) endocranial shape evolution across Euarchontoglires shows signs of constraint, possibly related to stabilising selection. These analyses demonstrate the necessity of including fossil materials when evaluating long-term evolutionary patterns and should help to form a revised evolutionary and morphological framework within which hypotheses about causality in primate brain evolution can be tested.

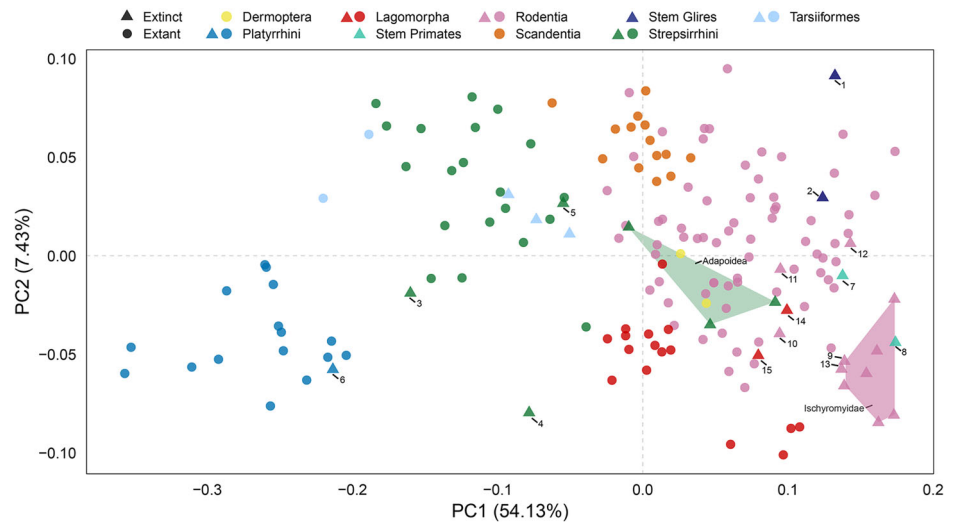
Much of our understanding of early primate brain evolution comes from analyses of brain tissue from living primates and “insectivores”, once thought to be closely related to primates and therefore used as a model for ancestral brain morphology.^{9–13} Soft tissues from extant taxa can be used to test evolutionary hypotheses concerning specific brain regions in living clades. However, in these analyses, it is difficult to examine the origins of innovations and long-term patterns of evolutionary change. Additionally, as “Insectivora” is no longer a valid grouping,¹⁴ the phylogenetic backdrop against which conclusions about primate brain evolution are drawn has been questioned.¹⁵ Though brain evolution among anthropoids and hominins has been the subject of significant research attention,¹⁶ our understanding of early primate brain evolution has been limited by the relative paucity of fossil material and dated phylogenetic comparisons. This gap in our knowledge of early primate brain evolution, has begun to be filled

by analyses framed by our understanding that Primates belong to Euarchontoglires, the superorder containing Euarchonta (Primates, Scandentia, and Dermoptera) and Glires (Rodentia and Lagomorpha),¹ and the use of fossil brain endocasts, reconstructions of the interior surface of the cranial cavity, which in mammals form an accurate representation of brain size and shape.¹⁷ Consequently, brain endocasts (hereafter referred to as *endocasts*) are often used to infer evolutionary changes in the brains of fossil taxa for which no other neurological data are available.¹⁷

This analysis uses 3D geometric morphometrics on the virtual endocasts of living and fossil Euarchontoglires to assess variation in shape across brain regions visible on the endocast surface (Supplementary Information Fig. 1). Our goal is to identify ancestral traits for both primates and Euarchontoglires and trace major morphological transitions that define early primate brain evolution. This analysis places primate brain evolution

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Fig. 1 | PCA of endocranial shape for living and fossil Euarchontoglires. Anthropoidea represented by Platyrrhini and *Simonsius*. Numbers correspond to the following fossils: 1) *Carcinella sigei*, 2) *Anagale gobiensis*, 3) *Archaeolemur sp.*, 4) *Babakotia radofilai*, 5) *Mioeuoticus shipmani*, 6) *Simonsius grangeri*, 7) *Microsyops annectens*, 8) *Ignacius graybullianus*, 9) *Ischyromys typus*, 10) *Cedromus wilsoni*, 11) *Protopsiurus cf. rachelae*, 12) *Mesogaulus paniensis*, 13) *Prospaniomys priscus*, 14) *Palaeolagus haydeni*, 15) *Megalagus turgidus*.



in its appropriate phylogenetic context within Euarchontoglires and is informed by fossils spanning 53 million years of evolution with particular emphasis on Eocene fossils. In doing so, we provide the framework from which hypotheses about early primate brain evolution can be targeted to specific clades, time intervals, and/or brain regions.

Results

There is a clear phylogenetic pattern in endocranial shape across euarchontoglires (Fig. 1). ANOVAs of endocranial shape and clade indicate that up to 41.4% of the variation in endocranial shape follows ordinal membership, and 52.3–55.4% of the variation follows clade membership when Primates is separated into multiple clades (Supplementary Information Table 1a). Post-hoc pairwise tests find significant differences between all tested clades in endocranial shape (Supplementary Information Table 1b). Across the morphospace, extant clades tend to form groups, while fossil taxa are dispersed more broadly (Fig. 1). Phylogenetic signal in endocranial shape across Euarchontoglires is moderate, with a significant K-mult of 0.587 (Supplementary Information Table 2), indicating that related species resemble each other more than expected by chance, but less than under a strict Brownian motion (BM) model. Across all non-primate clades phylogenetic signal in endocranial shape is lower than that of the full sample. In Primates, the phylogenetic signal is very high (K-mult = 1.9) and remains high in the haplorhine and anthropoid (represented by Platyrrhini + *Simonsius* in these analyses) subclades excluding tarsiiforms. This suggests that primates are more similar to each other in endocranial shape than would be expected under BM and shape is therefore strongly influenced by phylogeny.

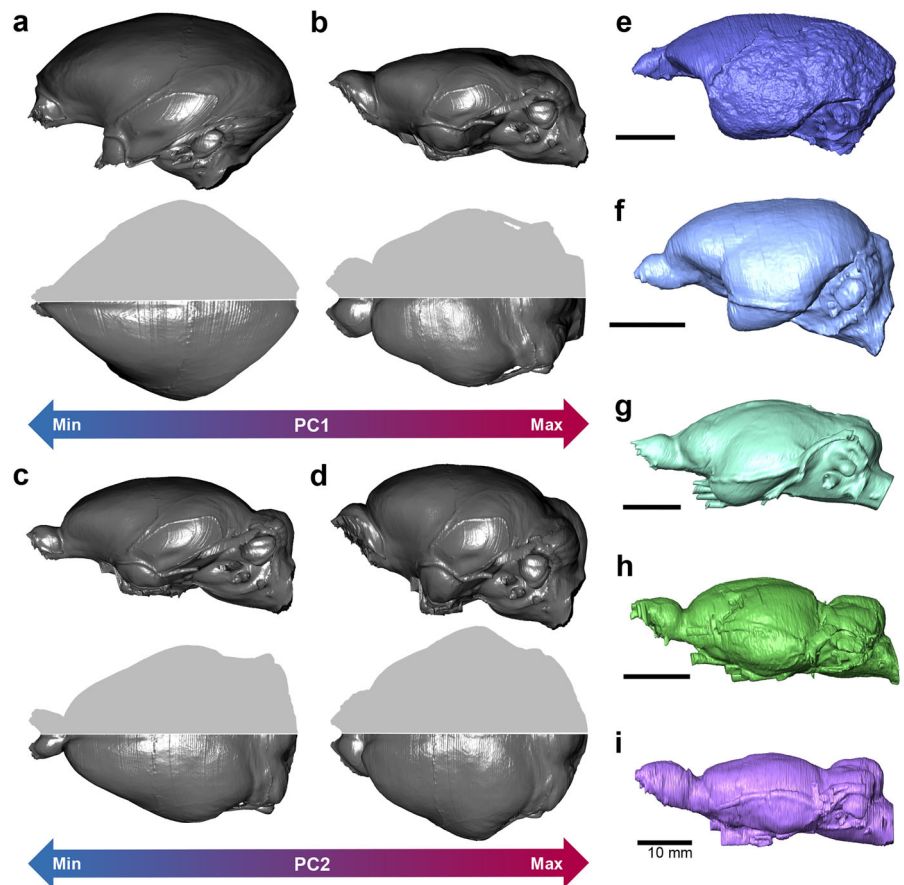
Surface warps of the Principal Component (PC) axes (Fig. 2) suggest that PC1 is capturing variation in the proportion of the neocortex, cerebellum, and olfactory bulbs, temporal lobe morphology, and basicranial flexion. Species that occur on the negative aspect of PC1 (i.e., platyrrhines) have proportionally large neocortices that cover the dorsal aspect of the cerebellum, pronounced temporal lobes, proportionally small olfactory bulbs and cerebelli with both brain regions positioned underneath the neocortex, and a flexed basicranium with an inferiorly projecting brainstem (Fig. 2a). Species that occur on the positive aspect of PC1 (i.e., plesiadapiforms and rodents) have small, shallow neocortices that do not cover the dorsal aspect of the cerebellum, proportionally large olfactory bulbs that sit rostral to the neocortex, and an unflexed basicranium with a caudally projecting brainstem (Fig. 2b). Surface warps suggest PC2 is capturing variation in the endocranial's rostro-caudal compactness such that species on the negative aspect of PC2 (i.e., lagomorphs) tend to have rostro-caudally elongated endocranials with a constricted circular fissure, and a flexed ventral aspect of the endocranial, rostral to the optic foramina (Fig. 2c). Conversely,

species at the positive aspect of PC2 (i.e., scandentans) have deep endocranials dorso-ventrally and large olfactory bulbs with a wide circular fissure; mediolaterally these endocranials also tend to be wider than in species on the negative aspect of PC2 (Fig. 2d). Only 10.13% of the variation is captured by PCs 3 and 4 (Supplementary Information Fig. 2a). Wireframe warps indicate that the negative extreme of PC3 is characterised by an elongated olfactory bulb, whereas the positive extreme shows a rostro-caudally compressed olfactory bulb, expansion of the dorsal neocortex, and an extremely flattened basicranium (Supplementary Information Fig. 2b). Along PC4, the negative extreme is characterised by small olfactory bulbs and expansion of the dorsal neocortex, while the positive extreme shows an elongated olfactory bulb. The cerebellum is more bulbous along PC4 than along PC3 (Supplementary Information Fig. 2c).

Across the morphospace defined by PC1 and PC2, plesiadapiforms (stem primates), early rodents of the Squirrel-Related Clade (SRC; the ischyromyids), and stem Glires all occur at the positive extreme of PC1 (Fig. 1). Plesiadapiforms and ischyromyids occupy a similar location in morphospace across PC2, with negative values on that axis. In contrast, stem Glires have positive PC2 values, with *Carcinella sigei* occurring at the far positive extreme. Extant lagomorphs are separated into two clusters by family (Ochotonidae and Leporidae; Supplementary Information Fig. 2). While fossil lagomorphs overlap with extant ochotonids across PC1 and extant leporids across PC2, they nonetheless occupy a distinct area of the morphospace. Adapoids overlap with the rodent morphospace and are distinct from the rest of euprimates (crown Primates; Fig. 1). Omomyoids overlap in endocranial shape with extant strepsirrhines. The subfossil lemurs, *Archaeolemur sp.* and *Babakotia radofilai*, are distinct from the rest of Strepsirrhini in endocranial shape, with *Babakotia* occupying an area of the morphospace not shared with any other Euarchontoglires. The fossil lorid, *Mioeuoticus shipmani*, sits within the extant strepsirrhine morphospace. The fossil anthropoid, *Simonsius grangeri*, sits on the edge of the extant platyrrhine morphospace. Some of these phylogenetic patterns are also seen in PCs 3 and 4 as anthropoids (Platyrrhini + *Simonsius*), are completely separated from tarsiiforms, scandentians, lagomorphs, with minimal overlap with strepsirrhines, which again form a bridge between these groups and the anthropoids. Rodentia overlaps with all clades across these PCs (Supplementary Information Fig. 2a).

The results of the ANOVAs of endocranial shape and size for Euarchontoglires overall suggest that allometry has a small but significant impact on endocranial shape ($R^2 = 0.107$, $p < 0.0001$). However, within each clade the impact of shape on size is greater, accounting for 17.4% in Rodentia and 45% in Lagomorpha (Supplementary Information Table 3). Results of the homogeneity of slopes test find that the unique allometry model (which assumes different allometric trajectories between clades) is

Fig. 2 | Surface warps from PCA of endocranial shape and endocasts of fossil Euarchontoglires.
a Surface warp of endocranial shape at the negative extreme of PC1 shown in left lateral view (top) and right lateral view (bottom); **b** Surface warp of endocranial shape at the positive extreme of PC1 shown in left lateral view and right lateral view; **c** Surface warp of endocranial shape at the negative extreme of PC2 shown in left lateral view (top) and right lateral view (bottom); **d** Surface warp of endocranial shape at the positive extreme of PC2 shown in left lateral view and right lateral view; **e** endocast of *Simonsius grangeri* (DPC 18651), **f** *Rooneyia viejaensis* (TMM 40688-7); **g** *Adapis parisiensis* (NHM M 1345); **h** *Microsyops annectens* (UW 12362); **i** *Paramys copei* (AMNH 4756). Sample of fossil shown to demonstrate the variation across extinct Euarchontoglires.



best supported (Supplementary Information Table 4a). Post-hoc pairwise tests of allometric mean shape, vector length, and angle find significant differences in these parameters among clades (Supplementary Information Table 4b). These results suggest that while size has a significant impact on shape across Euarchontoglires, it impacts shape differently across these groups. Consequently, performing an allometric correction on these data is not appropriate.

Shifts in evolutionary rate related to shape were identified at several nodes. At 11 nodes, the evolutionary rate is significantly lower than in the rest of the tree, with the rate difference being greatest at the divergence between *Rapamys atramontis* and the rest of Rodentia and the divergence of the Mouse-Related Clade (MRC) from the rest of Rodentia (Supplementary Information Fig. 3, Supplementary Information Table 5). Significantly higher rates are also identified at four points in the primate lineage: at the divergence of Primates from Sundatheria (Scandentia + Dermoptera), at the divergence of *Microsyops annectens* from the rest of Primates, at the divergence of *Ignacius graybullianus* from Euprimates, and at the divergence of Haplorhini and Strepsirrhini, with the largest shift identified at the divergence of plesiadapiforms from the euprimates. (Supplementary Information Fig. 3, Supplementary Information Table 5). These results may suggest that while anthropoids, here represented by platyrrhines and the fossil stem anthropoid *Simonsius*, are morphologically distinct, the greatest shift in evolutionary rates are near the base of the Euprimates, rather than nested within it.

The result of the Disparity Through Time (DTT) plot shows a drop in endocranial disparity in the Late Cretaceous, possibly indicating a diversification event early in this lineage. At each subsequent time interval, endocranial shape is less disparate than would be expected if following neutral evolution (evolving along a BM model) for most of euarchontoglian evolution (Fig. 3). This pattern suggests that endocranial shape evolution may have diversified early then was constrained, potentially due to stabilising selection, directional selection, or other factors limiting trait

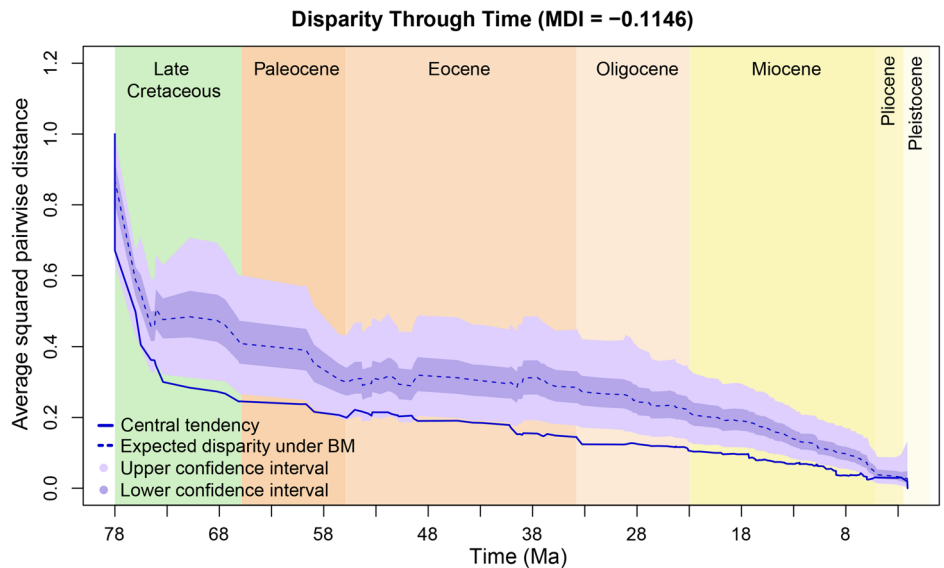
divergence. Of the evolutionary models tested, the best support was found for the OUM model, in which each clade progressed towards its own adaptive optimum based on AICc (Supplementary Information Table 6). Phylogenetic half-lives for PC1-4 are all <1 (PC1 = 0.244, PC2 = 0.22, PC3 = 0.166, PC4 = 0.239), indicating that the strength of the pull towards optima is high and that evolutionary progression is distinct from BM. Additionally, in all of the datasets simulated under BM evolution the BM model was best supported. This indicates that the support for the OUM model for the real data is unlikely to be an artefact of tree structure. These results, together with the DTT analysis, support the argument that these clades are characterised by distinct evolutionary patterns.

Discussion

These results document three significant evolutionary patterns: 1) there is a temporal trend in evolving brain morphology as many early diverging members of euarchontoglian clades possess a shared endocranial shape, with these orders then progressing toward the morphology of their extant relatives; 2) both Haplorhini and Strepsirrhini are derived in endocranial shape relative to the rest of Euarchontoglires, though to differing degrees. Significantly, based on the differing morphology of their stem members, these two clades likely arrived at this similar morphology independently through parallel evolution; and 3) there is evidence that endocranial shape evolution across Euarchontoglires was being constrained, possibly via stabilising selection.

Most of the morphological variation in this dataset is captured by PC1 (54.13%), likely reflecting shape and, to a lesser extent, size. Size accounts for 10.7% of the total morphological variation across all PCs but is typically concentrated in the first principal component. Regarding the first evolutionary pattern, many early fossils occur on the far positive extreme of the morphospace of their closest living relatives along PC1 (Fig. 1). Ischyromyids, a polyphyletic group¹⁸ which, in our sample, date from the early to mid Eocene, do not overlap in endocranial shape with other rodents.

Fig. 3 | Disparity through time (DTT) plot. Disparity calculated at each time interval using average squared pairwise distance for the first four principal components (central tendency). The expected disparity curve is simulated under Brownian Motion, with upper and lower confidence intervals. Morphological Disparity Index (MDI) is reported, representing the difference between the observed central tendency and the expected DTT curve.



Plesiadapiforms also do not overlap with euprimates across the morphospace. These fossils are characterised by a shallower endocranial shape despite its ecological and other anatomical similarities.³²

More recent fossil primates, rodents, and lagomorphs show distinct morphological trajectories. *Ischyromys*, an early Oligocene ischyromyid remains near other fossil rodents in morphospace, while *Cedromus*, a sciurid also from the early Oligocene, approaches the endocranial morphospace of extant SRC species (Supplementary Information Fig. 3). Late Oligocene and Early Miocene SRC rodents (*Protosciurus* and *Mesogaulus*) overlap with their extant relatives, though *Protosciurus* is morphologically distinct from other members of its tribe, Sciurini (Supplementary Information Fig. 3). The morphological similarities between *Cedromus*, *Protosciurus* and *Mesogaulus* and their extant relatives support previous analyses of endocranial shape in the SRC.⁴ Significantly, the shift of these species across the morphospace suggests changes in the shape and relative scale of the neocortex and the overall depth of the endocranial. Previous analyses also document neocortical expansion, which is linked to increased cognitive demands associated with the transition to arboreality.⁵ In primates and rodents, expansion of the occipital lobes, where the primary visual cortex is located is thought to represent a visual adaptation.^{3,33}

Unlike SRC fossils, *Prospaniomys*, a Miocene fossil (Ctenohystriica) rodent, remains near a group of ischyromyids despite its more recent age (Fig. 1). The position of *Prospaniomys* so far from phylogenetically closer species at this time interval contrasts with the pattern seen in SRC fossils, which converge on the endocranial shape of their extant relatives. Both living and fossil ctenohystriicans show significant endocranial diversity,³⁴ but the timing of this transition is not well known. These results suggest that this diversification happened more recently than in other rodent clades. However, this will need to be tested with additional fossils, which have been produced (i.e., *Incamys bolivianus*,³⁴ *Neoeplembia acensis*,³⁵ and *Josephoartigasia monesi*³⁶) but are not preserved in sufficient detail to permit this kind of analysis. Complicating the suggestion that diversification of ctenohystriicans happened more recently is the fact that late Oligocene *Incamys* possesses a mosaic of ancestral and derived traits including an exposed midbrain and expanded neocortex, especially in the temporal region.³⁴

Both fossil lagomorphs are morphologically distinct from their living relatives and morphologically similar in shape to their rodent contemporaries from the Oligocene (*Cedromus* and *Protosciurus*) as well as to some extant rodents. Lagomorph endocranials are characterised by two clusters in the morphospace representing Leporidae and Ochotonidae (Supplementary Information Fig. 3). These families are also markedly different in brain size, which in previous analyses made it difficult to assess whether their

and fossil rodents. As a result, extant Scandentia is not a good morphological model for early euarchontoglian endocranial shape despite its ecological and other anatomical similarities.³²

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morphological differences were the product of phylogeny, adaptation, or purely allometry.³⁷ Interestingly, endocranial volume in *Palaeolagus* (1082.71 mm³) is smaller than that of even the smallest ochotonids (2049.59 mm³), while the endocranial volume of *Megalagus* (7052.78 mm³) is within range of extant leporids (5145.18–17,120.02 mm³) yet neither of these fossils overlap in the morphospace with their extant relatives. Based on these results, the transitions in endocranial shape that are observed in the ochotonids and leporids took place after the Miocene and arguably were not entirely driven by allometry, or else we might have seen more similarities between *Palaeolagus* and the similarly sized ochotonids and *Megalagus* and the similarly sized leporids.

Despite their phylogenetic position as stem Glires, *Carcinella* and *Anagale*, do not follow all aspects of the ancestral morphological pattern observed in the plesiadapiforms and ischyromyid rodents. While they also occur on the positive aspect of PC1, unlike ischyromyid rodents and the plesiadapiforms they occur on the positive aspect of PC2, reflective of a more rostro-caudally compressed endocranial shape with a large olfactory bulb and wide circular fissure. This is especially true for *Carcinella* which occurs on the far positive extreme of this PC. The derived endocranial shape of this species may be linked to adaptations in the brain and/or cranium for extractive foraging and associated specialisations to the olfactory and auditory systems.⁷ Dental wear patterns suggest that *Anagale* and other anagalids were fossorial.³⁸ In support of this, *Anagale* occurs among the fossorial rodents in a generally restricted area of the morphospace (Supplementary Information Fig. 3). As fossorial taxa often use their heads or teeth during excavation,³⁹ this apparent convergence in endocranial shape may reflect adaptations of the cranium rather than the brain itself. These species are also more recent than the plesiadapiforms and ischyromyid rodents (except for *Ischyromys*, which is from the Oligocene), occurring in the late Eocene.^{40,41} Due to the distinct ecological niches occupied by the stem Glires, they are perhaps not an appropriate representation of what is ancestral for early Glires or Euarchontoglires endocranial evolution.

The second identified evolutionary pattern relates to Primates. Though the anthropoids, represented in this analysis by Platyrrhini and the stem anthropoid *Simonsius*, and crown strepsirrhines are found to be morphologically distinct from each other, they are also distinct from the rest of Euarchontoglires, but in similar ways. Effectively, the difference in endocranial shape between these two clades largely reflects a difference in magnitude but not kind. This is evident across PC1 where ~54% of the variation in endocranial shape is captured. Both clades are characterised by an expansion of the neocortex, reduction in the size of the olfactory bulbs, and increased basicranial flexion, though anthropoids are most extreme in this regard.

Within primates, significantly high evolutionary rates are found at several early nodes, including at the separation of Primates from the rest of Euarchonta, the separation of Haplorhini and Strepsirrhini, and the greatest increase in rate occurring at the separations of the plesiadapiforms from the rest of the clade (Supplementary Information Table 4, Supplementary Information Fig. 4). The DTT analysis also indicates that diversification occurred early in the lineage. Importantly, variation within Anthropeoidea is likely underestimated here because hominoids and cercopithecoids were excluded from the analyses due to the challenges posed by their highly derived morphology and pronounced sexual dimorphism (see discussion in the Materials and Methods). Including these taxa also risked obscuring morphological patterns among the remaining groups by expanding the morphospace with highly derived morphologies. Previous primate-focused analyses have identified the greatest accelerations in evolutionary rate within Hominoidea and Papionini in both endocranial morphology^{42,43} and cranial morphology.⁴⁴ The exclusion of these clades means that the complete picture of extant primate variation has not been captured and consequently, the rate of evolutionary acceleration within Anthropeoidea is likely underestimated in the present analysis.

Nevertheless, both infraorders are similarly derived relative to the rest of Euarchontoglires, possessing proportionally large neocortices that cover the dorsal aspect of the cerebellum, small olfactory bulbs and flexed

basicrania, features which distinguish primates from other clades. This pattern also applies to hominoids and cercopithecoids.^{7,42} While adapoids are distinct from the rest of Euprimates, remaining in the rodent morphospace into the Eocene, they moved out of the ancestral morphospace well before the other fossil groups. The evidence of shared morphologies which distinguish both haplorhines and strepsirrhines from the rest of Euarchontoglires emerges from a dataset richer in fossil taxa and from an analysis grounded in a more relevant phylogenetic context than previous analyses.^{42,43} In the context of primate-specific analyses, there is another important caveat. These results suggest that while strepsirrhines are derived relative to the non-euprimate Euarchontoglires, they can nonetheless be described as “primitive” in aspects of overall shape relative to anthropoids. This is because the extant strepsirrhines overlap in the morphospace with the early haplorhine fossils and occupy an intermediate position between the more derived anthropoids and the rest of Euarchontoglires.

The fossil Euprimates (Adapoidea and Omomyoidea) provide essential context regarding how the strepsirrhines and haplorhines arrived at this morphological pattern. Fossil Euprimates are shifted negatively across PC1 having moved towards the extant primate morphospace and away from the plesiadapiform and ischyromyid rodents (Fig. 1). For instance, the stem tarsiiiforms of the middle to late Eocene, Omomyoidea, converge on the endocranial shape of extant strepsirrhines but do not overlap with their extant tarsiiiform relatives. Similarly, the stem strepsirrhines of this same time interval, Adapoidea, while distinct from the plesiadapiforms, occupy an entirely separate region of the morphospace from the crown strepsirrhines. Instead, they are morphologically more similar to many of the extant rodents than they are to the rest of Euprimates as they are entirely within the rodent morphospace. This is surprising, as they are often considered as essentially looking like modern primates based on analyses of relative olfactory bulb size,⁸ the morphology of the temporal lobes, and the expression of major sulci, including the Sylvian sulcus.^{8,45} This highlights the power of shape analyses to identify patterns that qualitative description and other quantitative analyses may miss. Parallelism between the haplorhines and strepsirrhines^{7,46} and possibly between tarsiers and anthropoids depending on the phylogenetic position of the omomyoids,⁴⁷ have been noted in recent analyses of brain size, olfactory bulb size, and in regions of the neocortex; here there is evidence for this trend in overall brain shape. While the analysis of evolutionary rates suggest that the morphological transition began at the euprimate node, it continued in these radiations separately. This information can ultimately be used to tailor analysis of the evolutionary drivers of brain evolution to specific clades, which may help to disentangle contradictory hypotheses about primate brain evolution.^{48,49}

As reflected in the higher evolutionary rate and the distribution across the morphospace, more recent fossil primates arrived at the extant morphotype for their clade sooner than the rodents and lagomorphs. By the early Oligocene, endocranial shape in the stem anthropoid, *Simonsius*, is at the edge of the morphospace of extant platyrrhines. The same occurs with the lorid, *Mioeuticus*, which is within the strepsirrhine morphospace by the early Miocene. The most recent of the fossil primates, however, the subfossil lemurs, which went extinct as recently as 500 years ago,⁵⁰ are morphologically distinct from their closest relatives, which may relate to their unique ecological niches. *Archaeolemur* belongs to a family often referred to as the “monkey lemurs” (Archaeolemuridae) based on ecological similarities with modern Afroeurasian monkeys.⁵⁰ The fact that this species occurs closest to the anthropoid morphospace relative to other strepsirrhines may suggest convergence in endocranial shape related to this anthropoid-like ecology. *Babakotia* belongs to a family often referred to as “sloth lemurs” (Palaeopropithecidae) due to ecological similarities with South American sloths, possessing significant phalangeal curvature and other adaptations for suspensory postures and locomotion,⁵⁰ and exhibiting therefore a suite of adaptations unlike any living primates. Correspondingly, this species occupies an area of the morphospace not shared with any other Euarchontoglires.

Finally, the results of the DTT and evaluation of evolutionary models both suggest that endocranial shape evolution may be constrained relative to

what is expected under neutral evolution. While the results of the DTT might also indicate an early burst of morphological diversification, in the analysis of evolutionary models, the Ornstein-Uhlenbeck model with a unique optimum (OUM) for each clade (Rodentia, Lagomorpha, Scandentia, Dermoptera, Primates) was best supported indicating that each clade is being pulled toward its own adaptive optimum. This is consistent with a pattern of stabilising evolution.⁵¹ Though the OUM model is best supported, this model does not distinguish between a trait evolving toward a fixed adaptive optimum (as in stabilising selection), a trait undergoing directional selection characterised by a consistent trend away from the ancestral state (as modelled by a BMtrend), or temporal variation in evolutionary rates among clades (e.g., early burst dynamics). Consequently, the signal interpreted as evolution toward multiple adaptive optima could instead reflect clade-specific directional selection or early burst dynamics that differ among clades. However, because further subdividing the dataset would reduce statistical power and increase the risk of model overfitting, these alternatives cannot be fully resolved here.

Comparative studies have identified a range of evolutionary modes for brain and endocranial shape across primates. For example, Grabowski et al.⁵² found that while relative brain size followed a BM model in strepsirrhines and haplorhines, platyrrhines exhibited strong directional selection, likely associated with ecological and social factors. Regarding shape, Aristide et al.⁵³ found that endocranial shape in platyrrhines diversified early with several shifts at the family level influenced by ecological factors. In strepsirrhines, López-Aguirre et al.⁵⁴ reported evidence for stabilising selection on endocranial shape. The results of the present study are consistent with these analyses in that the mode of primate brain evolution appears to diverge from neutral evolution. Importantly, it is possible that similar patterns may be occurring in other clades. The identification of distinct evolutionary modes and clade-specific optima in endocranial shape may suggest that different evolutionary pressures have shaped brain morphology across Euarchontoglires, as is also reflected in the differences in allometric scaling patterns reported here and in previous analyses.⁵ These divergent evolutionary modes potentially contributed to the extensive endocranial shape diversity observed across these lineages.

Altogether, these results demonstrate the unique endocranial morphologies of living and fossil Euarchontoglires and elucidate the evolutionary trajectory from the ancestral Euarchontoglires endocranial morphology towards the earliest phases of primate diversification. In doing so, they provide essential context for the morphological transitions within these clades, highlighting the importance of integrating data from the full expanse of primate morphology and evolution.

Methods

Sample

This dataset includes endocranial casts of 168 species of Euarchontoglires (Dermoptera: $n = 2$; Scandentia: $n = 14$; Rodentia: $n = 82$; Lagomorpha: $n = 18$; Primates: $n = 50$ [Haplorhini: $n = 22$; [Platyrrhini $n = 20$; Tarsiiformes: $n = 2$]; Strepsirrhini: $n = 26$; Plesiadapiformes: $n = 2$]; Supplementary Data 1). This sample contains 27 fossil endocranial casts spanning 53 million years of evolution representing all major clades except for fossil members of Dermoptera and Scandentia for which there are no known cranial specimens complete enough to produce endocranial casts. Fossil specimens were selected based on completeness and limited distortion. The fossil endocranial casts and the endocranial casts of 141 extant taxa were landmarked in 3D imaging software AVIZO® 9.1.1 (Visualization and Sciences Group, 1995–2020)⁵⁵ with a set of 27 fixed landmarks, and two curves of sliding semi-landmarks that capture variation along the mid-sagittal aspect of the neocortex and cerebellum. Landmarks (LM) were placed following the protocols published by Lang et al.⁵⁶ As the cribriform plate is delicate and inconsistently preserved in fossils, LM 9 (ventral terminus of the olfactory bulbs) was removed in this analysis. These landmarks were designed to capture variation in major brain regions, including the neocortex, olfactory bulbs, cerebellum, cerebellar petrosal lobules, brainstem, and the ventral surface of the endocranial cast, which largely encompasses the paleocortex and has been rigorously

validated to ensure they are replicable.⁵⁶ Landmarks were applied to the left sides of the endocranial cast. There is discussion about whether landmarking only one side of an object can accurately capture the ‘real’ shape.^{57,58} Furthermore, landmarking only one side of an object means that midline landmarks, where variance is expected to be lower, undergo the same transformations as lateral landmarks during Procrustes superimposition. Significantly however, the loss of information when only landmarking one side of the endocranial cast is minimal in larger macroevolutionary studies such as this.⁵⁸ Single-sided landmarking also allows one to include the best-preserved side of the fossil endocranial casts, limiting the effect of taphonomic damage and distortion on the shape patterns captured by the landmarks.⁵⁹

For three species (*Carcinella sigei* [NMB QH 922], *Cedromus wilsoni* [USNM V 256584], and *Rapamys atramontis* [AMNH 128706]) the endocranial cast was mirrored and the (formerly) right side of the endocranial cast was landmarked and included in analyses as the left side was damaged. In two cases (*Anagale gobiensis* [AMNH 26079/AMNH 26079] and *Megalagus turgidus* [MNH UC 1642]), asymmetrical damage on both sides of the endocranial cast precluded landmarking either the left or right side alone. For these species, a composite endocranial cast was created in which the endocranial cast was duplicated, mirrored, and overlaid so that the damage on the left side was “filled-in” by the complete areas on the right side. Missing landmarks on the endocranial casts of *Necrolemur antiquus* (MaPhQ 289; LM 28) and *Notharctus tenebrosus* (AMNH 127167; LM 3) were estimated with the estimate missing function using the thin plate spline method (R package: geomorph⁶⁰). Extant endocranial casts used for these analyses were obtained from previous publications.^{3,4,32,61} The extant anthropoid sample is comprised solely of Platyrrhini (Panamerican monkeys).

Catarrhini is excluded from these analyses for several reasons. Hominoids (apes and hominins) are highly derived and missing many of the landmarks used to capture ancestral variation. Including them would require removing several landmarks necessary to characterise morphology in other Euarchontoglires. Their inclusion would also likely compress variation across the remaining morphospace due to their extreme morphology, potentially obscuring the evolutionary patterns that are the primary focus of this study. Cercopithecoidea (Afro-Eurasian monkeys) are highly sexually dimorphic⁶² and there is limited research into sexual dimorphism of the primate brain. Recent analyses suggest that some sexually dimorphic primates (i.e., *Gorilla beringei graueri*) show differences between the sexes in brain shape⁶³ a pattern that may also be present in the sexually dimorphic cercopithecoidea. There are three potential ways to overcome this each with their own drawback. First, there is the use of multiple specimens per species across the dataset, however, due to the paucity of CT scans for non-primate Euarchontoglires this is not possible. Second, while mean shapes could theoretically be calculated for male and female specimens, the possibility of allometric differences between the sexes would make the resulting shapes difficult to interpret in relation to allometric patterns observed across the broader sample. Third, many cercopithecoidea exhibit pronounced sexual size dimorphism, with males often substantially larger than females. If endocranial shape varies with size through allometry, representing species using only males or only females could systematically shift taxa along size-related shape axes, potentially confounding interspecific comparisons. Alternatively, Platyrrhini is less sexually dimorphic,⁶² with no statistically significant differences identified in endocranial shape among male and female platyrrhines,⁶⁴ they share many of the derived morphologies that define cercopithecoidea endocranial casts,⁴² and lack many of the derived traits associated with cercopithecoidea endocranial casts, especially related to sulcal arrangements,⁶⁵ making them a more appropriate comparative group for the stem anthropoid *Simonsius*. For the fossils, twenty endocranial casts were obtained from previous publications (for fossil provenance see SD Table 2). Five endocranial casts were produced from CT data for the purpose of this project (e.g., *Archaeolemur sp.* [DPC 7850], *Babakotia radolfilae* [DPC 10994], *Palaeolagus haydeni* [FMNH 9476]) or were produced for concurrent analyses (e.g., *Pseudocylindrodont medius* [CM 10001], and *Mioeoticus shipmani* [KNM RU 2052]). The endocranial casts of the early anthropoid, *Simonsius grangeri* (DPC 18651)⁶⁶, as well as the stem Glires, *C. sigei*,⁴¹ were

re-segmented based on the availability of higher resolution data (for *S. grangeri*) and improved segmenting tools (both taxa).

Statistical analyses

A Principal Component Analysis (PCA) was performed on Procrustes-transformed landmark data. To visualise variation across the morphospace, surface deformations representing the extremes of Principal Components (PCs) 1 and 2 were created from the endocast of the species closest to the mean shape (*Paraxerus cepapi* [USNM 367956]). A broken-stick model was used to determine how many PCs to plot and use in subsequent analyses.⁶⁷ The result of the model indicates that by PC 4 (representing 71.6% of endocranial variation), most of the significant variation is captured (Supplementary Information Fig. 4). To examine the impact of and differences among clades in endocranial shape, ANOVAs were performed on the Procrustes transformed landmark data with groups reflecting: 1) order 2) order with Primates separated into Haplorhini and Strepsirrhini, and 3) Primates further separated into Anthropeidea, Tarsiiformes, and Strepsirrhini, due to the morphological differences in endocranial shape recognised among these clades.^{37,42,68} Significance testing was performed under 10,000 iterations of residuals randomisation. Due to a small sample size, dermopterans and stem Glires were removed from all ANOVAs, and Plesiadapiformes (stem primates) were removed from analyses, with Primates separated into multiple clades. Pairwise comparisons were performed for the ANOVA in which Primates is separated into Haplorhini and Strepsirrhini.

As size is known to impact variation^{37,42} it is commonly corrected for in morphological analyses. To determine whether allometric corrections are appropriate, the impact of size on endocranial shape across Euarchontoglires (evolutionary allometry) was assessed. Allometry of endocranial shape was examined using an ANOVA of endocranial shape and size (centroid size) for all Euarchontoglires as well as each clade individually based on clade-specific Procrustes transformations. A Homogeneity of Slopes test was performed to assess whether allometric slopes were significantly different among clades. In this analysis, Primates are separated into Haplorhini and Strepsirrhini to evaluate allometry between these morphotypes.³⁷ Following this, pairwise comparisons were made to test for significant differences in 1) *common size mean shapes*, the position differences in morphospace after size is controlled; 2) *mean vector lengths*, the amount of shape change per unit of size change (magnitude); and 3) *mean angles*, differences in slope direction measured in degrees among clades. As we are investigating differences among phylogenetic groups, phylogenetic correction methods are not applied to these specific tests. We also performed ANOVAs of size and shape for multiple clades (i.e., Anthropeidea, Strepsirrhini, Scandentia, Rodentia, Lagomorpha) based on separate Procrustes transformations to examine the impact of size within each.

To obtain a time-calibrated tree, a set of trees for extant species only was downloaded from vertlife.org based on 10,000 birth-death node-dated complete trees.⁶⁹ From these trees, a single phylogeny was produced using maximum clade credibility (MCC; R package: phangorn⁷⁰). Fossils were then added to the tree in Mesquite v. 3.70;⁷¹ See Supplementary Data 2 for sources for species' phylogenetic positions). 1000 time-calibrated trees were then created using the bin_cal3TimePaleoPhy function (R package: paleotree⁷²). Minimum ages of all nodes that did not include fossils were provided to the function and incorporated into subsequent trees. These node ages were obtained from the extant-only MCC tree. Fossils were placed into time bins based on the dates of their first and last occurrence (Supplementary Data 3). From this set of 1000 trees, all trees that contained branch lengths equal to 0 were removed ($n = 5$). All trees maintain the same topology and differ only in branching times. A single tree was obtained by averaging branch lengths for each corresponding parent-child node.⁷³

Phylogenetic signal in endocranial shape was assessed for each time-calibrated tree using K-mult with 1000 iterations. The data and trees were then subset according to clade (Primates [Anthropeidea [Platyrrhini + Simonsius], Tarsiiformes, Strepsirrhini, and Haplorhini], Lagomorpha, Scandentia, Rodentia) and phylogenetic signal in these clades were assessed

under the same parameters. Finally, shifts in evolutionary rates were assessed with the RRphylo R package's search.shift function using the auto-recognise feature.⁷⁴ This function uses ridge regression to estimate evolutionary rates for given variables at each branch of a phylogeny and identifies which branches have rates significantly higher or lower than the rest of the tree.

To assess how the level of disparity in endocranial shape across Euarchontoglires accumulated through time we performed a disparity through time (DTT) analysis. Disparity was calculated using the average squared pairwise distance for the first four PCs. This metric takes all the taxa present at a given time slice and computes the squared Euclidean distance (based on the PCs) between all pairs, then produces an average for that time slice.⁷⁵ This disparity metric is then plotted against the level of disparity calculated under a Brownian Motion (BM) model with 1000 simulations (function: dtt.dispRity, R package: dispR⁷⁶).

We also examined the mode of endocranial evolution across this dataset by testing the fit of different evolutionary models for the first four PCs from the PCA of endocranial shape. Using the R package mvMORPH we assessed five different evolutionary models; 1) a BM model which would suggest neutral evolution, 2) a BM model with a trend (BMtrend) which would indicate that there may be directional selection, 3) an Early Burst model (EB) which would suggest endocranial shape diversified early, 4) an Ornstein-Uhlenbeck (OU1) model with a single optimum which would indicate that there is stabilising selection across Euarchontoglires, and 5) an Ornstein-Uhlenbeck model with a unique optimum (OUM) for each clade (Rodentia, Lagomorpha, Scandentia, Dermoptera, Primates). Support for the OUM model may suggest that each clade has its own evolutionary optima and therefore be subject to distinct forms of stabilising selection.

It is important to note, however, some challenges arise when evaluating model fit on this kind of data, especially for OU type models. Type I errors for the OU models are unacceptably high for trees with <200 tips and AIC values may be unreliable to evaluate model fit.⁷⁷ However, these challenges are likely to be mitigated with the inclusion of fossils as is done here.^{77,78} Analyses using the first few PCs, where variance is concentrated, tends to support OU or EB models even when trait evolution is following an BM model.^{79,80} Additionally, while defining OUM regimes based on clade membership may be biologically justified as these clades exhibit distinct morphologies suggestive of different trait optima, when regime assignments follow phylogenetic relationships, support for the OUM model may be artificially inflated due to underlying phylogenetic signal, rather than reflecting true shifts toward distinct adaptive optima.

In light of these challenges, model fit was assessed using AICc and two additional methods. First, when support was found for an OU1 or OUM model the phylogenetic half-life was calculated. The phylogenetic half-life is the amount of evolutionary time it takes for a trait to move halfway from its ancestral state toward its adaptive optimum under an OU.⁸⁰ When branch lengths are rescaled so that the entire tree height is equal to 1 (mvMorph argument: scale.height = TRUE), a half-life of <1 means that traits are evolving quickly towards their optima and are less influenced by phylogeny in their progress towards that optimum. If the half-life is >1 then the trait evolves slowly towards that optimum and the data behave more like a BM model even if an OU model is found to be best supported.^{76,81} Second, 150 simulations of the null hypothesis of BM evolution were performed by evolving traits under a BM model on a tree with the same topology. For each simulation, AICc values were calculated for competing models (BM, BMtrend, EB, OU1, OUM) to assess how often the OU models were supported. Effectively, the data were simulated under a BM model to see how often an OU model was falsely identified as the best supported model using an AICc under this phylogeny. This method will help to determine if support for the OU model is an artefact of the tree structure (i.e., Type I error) rather than a true biological signal.^{82–89}

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All endocasts used for this analysis are available on Morphosource in the following project: <https://www.morphosource.org/projects/000424317?locale=en>.

Code availability

Landmark data and R code used to perform these analyses are accessible from the following link: <https://github.com/madlenlang/Parallelism-in-primate-brain-shape>

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Competing interests

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Additional information

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