

Comparing primate crania: The importance of fossils

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Abstract

Objectives: Extant primate crania represent a small subset of primate crania that have existed. The main objective here is to examine how the inclusion of fossil crania changes our understanding of primate cranial diversity relative to analyses of extant primates. We hypothesize that fossil taxa will change the major axes of cranial shape, occupy new areas of morphospace, change the relative diversity of major primate clades, and fill in notable gaps separating major primate taxa/clades.

Materials and Methods: Eighteen 3D landmarks were collected on 157 extant and fossil crania representing 90 genera. Data were subjected to a Generalized Procrustes Analysis then principal components analysis. Relative diversity between clades was assessed using an *F*-statistic.

Results: Fossil taxa do not significantly alter major axes of cranial shape, but they do occupy unique areas of morphospace, change the relative diversity between clades, and fill in notable gaps in primate cranial evolution. Strepsirrhines remain significantly less diverse than anthropoids. Fossil hominins fill the gap in cranial morphospace between extant great apes and modern humans.

Discussion: The morphospace outlined by living primates largely includes that occupied by fossil taxa, suggesting that the cranial diversity of living primates generally encompasses the total diversity that has evolved in this Order. The evolution of the anthropoid cranium was a significant event allowing anthropoids to achieve significantly greater cranial diversity compared to strepsirrhines. Fossil taxa fill in notable gaps within and between clades, highlighting their transitional nature and eliminating the appearance of large morphological distances between extant taxa, particularly in the case of extant hominids.

KEYWORDS

cranial diversity, geometric morphometrics, human evolution, morphology, primate evolution

1 | INTRODUCTION

Primate crania—indeed, the crania of all vertebrates—are complex structures that are involved in a variety of functions including ingestion, mastication, and respiration, as well as protecting the brain and housing the organs of taste, olfaction, vision, hearing, and balance (Lieberman, 2011). There is considerable diversity in cranial shape across the nearly 500 species of living primates (Mittermeier, Rylands, & Wilson, 2013; Rylands & Mittermeier, 2014). In a previous analysis (Fleagle, Gilbert, & Baden, 2010), we examined the patterns of cranial diversity within and between clades of extant primates using multivariate analyses of cranial landmarks. We identified the major axes of shape differences across the

order, and described the relative amounts of variance in cranial shape. We found that the major axis of cranial shape separated strepsirrhines from anthropoids; that extant strepsirrhines showed significantly less variance in cranial shape than anthropoids, or even individual clades of anthropoids; and that extant hominoids showed the highest variance in overall cranial shape among clades of extant anthropoids.

However, extant primates are just a small fraction of all the primates that have ever lived (Fleagle, 2013), and are a serendipitous sample resulting from the effects of numerous random factors from the past including climate change, tectonics, competition, human predation, and habitat destruction. Thus, the diversity of cranial shapes found among extant taxa is almost certainly only a small subset of

the cranial diversity that has evolved in the order over the past 55 million years. In this contribution, we examine the effects of incorporating the crania of fossil taxa into an analysis of primate cranial diversity. In particular, we address four specific hypotheses of how the addition of fossil taxa will change the results of our previous study based on extant taxa alone.

Hypothesis 1: Incorporating fossil taxa will change the major axes of cranial shape

Any comparative analysis is totally dependent on the sample on which it is based. As numerous authors have emphasized (e.g., see Mitteroecker & Bookstein, 2007; Mitteroecker & Gunz, 2009; Mitteroecker, Gunz, & Bookstein, 2005), principal components axes are statistical calculations that are dependent upon the sample being analyzed and do not necessarily have any biological meaning. Nevertheless, in some instances, the resulting principal components can be readily interpreted in terms of biological factors (e.g., see Sokal & Rohlf, 1995). For instance, in our analyses of extant primate crania, the first principal component separated anthropoids from non-anthropoid primates, and tarsiers from both anthropoids and strepsirrhines. We were therefore able to interpret these results in terms of major phylogenetic events in primate evolution. However, inclusion of additional taxa may well generate a different set of principal components. That is, we predict that the new, larger sample will result in a different morphospace describing primate cranial diversity. This is especially likely since many of the additional taxa are substantially larger than their extant relatives.

Hypothesis 2: Fossil taxa will fill areas of the primate cranial morphospace not occupied by extant taxa

Our second hypothesis is similar, and not unrelated to, *Hypothesis 1*. In our analysis of extant primates, extant clades occupied distinct areas of the morphospace described by the relationships among different aspects of cranial shape such as the relative sizes, shapes, and positions of the neurocranium, the orbits, and the face. It is likely that many of the extinct taxa will show different morphologies and arrangements of cranial features and will not fall within areas of the morphological space enclosing the extant taxa.

Hypothesis 3: Addition of fossil taxa will change the relative diversity of primate clades

A primary goal of the previous study was to examine the relative diversity in cranial morphology among the clades of extant primates in order to determine which extant groups displayed more or less cranial diversity. The addition of extinct taxa is likely to change the amount of documented cranial diversity among the clades for two reasons. First, the relative numbers of extant to extinct taxa can vary greatly among clades of primates, and clades are also likely to differ in the number of well-preserved crania known for extinct taxa. Second, extinct taxa (e.g., subfossil lemurs) are well-known to preserve unique cranial morphologies

not seen among extant taxa, and so we expect that adding extinct taxa will expand the relative morphological diversity of various primate clades.

Hypothesis 4: Fossils will fill the morphological space separating extant taxa and clades

One of the most important contributions of the fossil record for our understanding of evolutionary history is in providing “missing links” or stem taxa that demonstrate how extant taxa and clades obtained their current distinctiveness. Thus we expect that some fossil crania will fall between the morphospaces occupied by extant clades or related extant genera.

2 | MATERIALS AND METHODS

As in our 2010 study, our sample of extant taxa in this study consisted of one male adult cranium and one female adult cranium for 66 genera of extant primates (Table 1). We used a conservative taxonomy in identifying which extant primate genera to include (Fleagle, 1999), rather than more recent taxonomies that recognize additional genera (e.g., see Fleagle, 2013). Because the aim of this study was to analyze cranial morphology across the order and because many extant, as well as extinct, primate species are sparsely represented in museum collections, we largely restricted our sample to a single species of each genus. For most extant genera, we selected a species that was representative of the genus in terms of size and gross morphological appearance and not extreme in size or distinctive in morphology such that it is often placed in a separate genus. However, because of the considerable diversity in size, morphology, and behavior in the genus *Macaca*, we included two species that differ substantially in size, *M. nemestrina* and *M. fascicularis*. Individual specimens of extant taxa were measured in the collections of the American Museum of Natural History (AMNH) in New York, the Museum of Comparative Zoology (MCZ) at Harvard University, Yale Peabody Museum (YPM), and collections at Stony Brook University (SBU). All specimens included in the study were adults with no obvious pathologies and were completely intact on at least one side so that all landmarks (see below) could be identified and measured.

Our fossil sample was limited to complete or nearly complete crania thereby restricting our sample to a fraction of the primate fossil record. Nevertheless, we were able to examine 28 fossil crania from ten families (Notharctidae, Adapidae, Megaladapidae, Indridae, Parapithecidae, Propithecidae, Atelidae, Victoriapithecidae, Cercopithecidae, and Hominidae) spanning over 50 million years of primate evolution (Table 1). Not surprisingly, a large number of the well-preserved fossil crania are drawn from recent subfossil lemurs of Madagascar, and the Plio-Pleistocene record of hominin evolution. However, we also included three important stem taxa, the stem anthropoid *Parapithecus*, the stem catarrhine *Aegyptopithecus*, and the stem cercopithecoid *Victoriapithecus*, as well as two Pleistocene fossil platyrrhines, *Cartelles* and *Caipora*, that are twice as large as any extant platyrrhine. Measurements of fossil crania were made on sharp casts

TABLE 1 Sample used in this study

Taxon	Genus	Species	Specimen #	Male (n)	Female (n)	Unknown sex (n)
STREPSIRRHINES						
Adapoids	<i>Adapis</i>	<i>parisiensis</i>	MHNH 20192 ^{a*}	–	–	1
	<i>Leptadapis</i>	<i>magnus</i>	AMNH 103402 (1893-1) ^{a*}	–	–	1
	<i>Notharctus</i>	<i>tenebrosus</i>	AMNH 127167 ^{a*}	–	–	1
Lemuroids	<i>Eulemur</i>	<i>fulvus</i>	AMNH 100523, 100614	1	1	–
	<i>Haplemur</i>	<i>griseus</i>	AMNH 170693, 170672	1	1	–
	<i>Lemur</i>	<i>catta</i>	AMNH 100596, 100824	1	1	–
	<i>Varecia</i>	<i>variegata</i>	AMNH 100514, 100515	1	1	–
	<i>Avahi</i>	<i>laniger</i>	AMNH 170461, 170494	1	1	–
	<i>Indri</i>	<i>indri</i>	AMNH 185638, 100503	1	1	–
	<i>Propithecus</i>	<i>verreauxi</i>	AMNH 170463, 170473	1	1	–
	<i>Lepilemur</i>	<i>mustelinus</i>	AMNH 100616, 170568	1	1	–
	<i>Cheirogaleus</i>	<i>major</i>	AMNH 100640, MCZ 45123	1	1	–
	<i>Microcebus</i>	<i>sp.</i>	SBU B434, AMNH 174383	1	1	–
	<i>Phaner</i>	<i>furcifer</i>	AMNH 100829	1	–	–
	<i>Daubentonia</i>	<i>madagascariensis</i>	AMNH 100632, 185643	1	1	–
	<i>Archaeolemur</i>	<i>majori</i>	AMNH 30007 ^{a*}	–	–	1
	<i>Babakotia</i>	<i>radofilai</i>	DUPC 95867 ^{a*}	–	–	1
	<i>Hadropithecus</i>	<i>stenognathus</i>	NHMH 1934 IV 1 ^{a*}	–	–	1
	<i>Megaladapis</i>	<i>edwardsi</i>	AMNH 30024 ^{a*}	–	–	1
	<i>Palaeopropithecus</i>	<i>kelyus</i>	UM.8186 AU5T ^{a*}	–	–	1
	<i>Archaeoindris</i>	<i>fontoyntii</i>	Parc Tsimbazaza	–	–	1
Lorisoids	<i>Arctocebus</i>	<i>calabarensis</i>	AMNH 207949, 212954	1	1	–
	<i>Perodicticus</i>	<i>potto</i>	AMNH 52713, 52717	1	1	–
	<i>Loris</i>	<i>tardigradus</i>	AMNH 34256	1	–	–
	<i>Nycticebus</i>	<i>cougang</i>	AMNH 87279, 102845	1	1	–
	<i>Euoticus</i>	<i>elegantulus</i>	AMNH 269911, 241126	1	1	–
	<i>Galago</i>	<i>senegalensis</i>	AMNH 187361, 187355	1	1	–
	<i>Galagoides</i>	<i>demidoff</i>	AMNH 269904, 241121	1	1	–
	<i>Otolemur</i>	<i>crassicaudatus</i>	AMNH 216239, 187364	1	1	–
TARSIIDS						
	<i>Tarsius</i>	<i>spectrum</i>	AMNH 153557, 196486	1	1	–
ANTHROPOIDS						
Early Anthropoids	<i>Parapithecus</i>	<i>grangeri</i>	DPC 18651 ^{a*}	–	–	1
	<i>Aegyptopithecus</i>	<i>zeuxis</i>	CGM 40237 ^{a*}	1	–	–
Platyrrhines	<i>Aotus</i>	<i>lemurinus</i>	AMNH 72057, AMNH 14176	1	1	–
	<i>Cebus</i>	<i>apella</i>	AMNH 136367, 75975	1	1	–
	<i>Saimiri</i>	<i>boliviensis</i>	AMNH 230816, 239868	1	1	–
	<i>Callithrix</i>	<i>argentata</i>	AMNH 94944, 96477	1	1	–
	<i>Callimico</i>	<i>goeldii</i>	AMNH 183289, 183230	1	1	–
	<i>Cebuella</i>	<i>pygmaea</i>	AMNH 72033, 76328	1	1	–
	<i>Leontopithecus</i>	<i>rosalia</i>	AMNH 70316, SBU NLe1	1	1	–
	<i>Saguinus</i>	<i>imperator</i>	AMNH 76012, 76014	1	1	–
	<i>Callicebus</i>	<i>torquatus</i>	AMNH 76927, 78468	1	1	–
	<i>Cacajao</i>	<i>calvus</i>	AMNH 73716, 73719	1	1	–
	<i>Chiropotes</i>	<i>satanus</i>	AMNH 94160, 95867	1	1	–
	<i>Pithecia</i>	<i>pithecia</i>	AMNH 40993, 42418	1	1	–

TABLE 1 (Continued)

Taxon	Genus	Species	Specimen #	Male (n)	Female (n)	Unknown sex (n)
	<i>Alouatta</i>	<i>seniculus</i>	AMNH 76858, 239856	1	1	–
	<i>Ateles</i>	<i>paniscus</i>	AMNH 247694, 211644	1	1	–
	<i>Lagothrix</i>	<i>lagotricha</i>	AMNH 98869, 98366	1	1	–
	<i>Oreonax</i>	<i>flavicauda</i>	AMNH 73222, 112976	1	1	–
	<i>Brachyteles</i>	<i>arachnoides</i>	AMNH 80405	–	1	–
	Cartelles	coimbrafilhoi	MCL 06	–	–	1
	Caipora	bambuorium	MCL 05	–	–	1
Cercopithecoids	<i>Allenopithecus</i>	<i>nigroviridis</i>	AMNH 86856	1	–	–
	<i>Allochrocebus</i>	<i>lhoesti</i>	AMNH 52452, 52458	1	1	–
	<i>Cercopithecus</i>	<i>mitis</i>	AMNH 85199, 1462	1	1	–
	<i>Chlorocebus</i>	<i>pygerythrus</i>	AMNH 27705, 27706	1	1	–
	<i>Erythrocebus</i>	<i>patas</i>	AMNH 34712, MCZ 47018	1	1	–
	<i>Miopithecus</i>	<i>talapoin</i>	AMNH 80779	1	–	–
	<i>Cercocebus</i>	<i>torquatus</i>	AMNH 89383, MCZ 18612	1	1	–
	<i>Lophocebus</i>	<i>albigena</i>	AMNH 52603, 52624	1	1	–
	<i>Macaca</i>	<i>fascicularis</i>	AMNH 103645, 107096	1	1	–
	<i>Macaca</i>	<i>nemestrina</i>	AMNH 106037, 103728	1	1	–
	<i>Mandrillus</i>	<i>sphinx</i>	AMNH 89364, 89361	1	1	–
	<i>Papio</i>	<i>anubis</i>	AMNH 55446, 82097	1	1	–
	<i>Theropithecus</i>	<i>gelada</i>	AMNH 60568, 238034	1	1	–
	Theropithecus	brumpti	NME L345-287^{a*}	1	–	–
	Parapapio	whitei	MP 221^{a*}	1	–	–
	Procercocebus	antiquus	TP-9^{a*}	1	–	–
	<i>Colobus</i>	<i>angolensis</i>	AMNH 52163, 52169	1	1	–
	<i>Piliocolobus</i>	<i>badius</i>	AMNH 54280, 89422	1	1	–
	<i>Procolobus</i>	<i>verus</i>	AMNH 89439, YPM 10375	1	1	–
	<i>Kasi</i>	<i>johnii</i>	AMNH 54639, 163080	1	1	–
	<i>Nasalis</i>	<i>larvatus</i>	AMNH 106272, 85173	1	1	–
	<i>Presbytis</i>	<i>rubicunda</i>	AMNH 106014, 106134	1	1	–
	<i>Pygathrix</i>	<i>nemaeus</i>	AMNH 69555, 87256	1	1	–
	<i>Semnopithecus</i>	<i>entellus</i>	AMNH 54521, 163082	1	1	–
	<i>Simias</i>	<i>concolor</i>	AMNH 103360, 103371	1	1	–
	<i>Trachypithecus</i>	<i>obscurus</i>	AMNH 54970, 119492	1	1	–
Hominoids	Cercopithecoides	williamsi	M3055^{a*}	1	–	–
	Libypithecus	markgrafi	BSM 1914 II 1^{a*}	1	–	–
	Victoriapithecus	macinnesi	KNM-MB 29100^{a*}	1	–	–
	<i>Hylobates</i>	<i>lar</i>	AMNH 54966, 208985	1	1	–
	<i>Symphalangus</i>	<i>syndactylus</i>	AMNH 102728, 102727	1	1	–
	<i>Pongo</i>	<i>pygmaeus</i>	AMNH 140426, 200898	1	1	–
	<i>Gorilla</i>	<i>gorilla</i>	AMNH 167334, 167340	1	1	–
	<i>Pan</i>	<i>troglydites</i>	AMNH 51202, 167343	1	1	–
	Sahelanthropus	tchadensis	TM 266-01-060-1^{a*}	1	–	–
	Australopithecus	afarensis	AL-444^{a*}	1	–	–
	Australopithecus	africanus	STS 5^{a*}	–	1	–
Homo	Paranthropus	boisei	OH-5^{a*}	1	–	–
	Homo	ergaster	KNM-ER 3733^{a*}	–	1	–
	Homo	floresiensis	LB1^{a*}	1	–	–

TABLE 1 (Continued)

Taxon	Genus	Species	Specimen #	Male (n)	Female (n)	Unknown sex (n)
	<i>Homo</i>	<i>heidelbergensis</i>	Kabwe ^a *	1	–	–
	<i>Homo</i>	<i>neanderthalensis</i>	Spy1 ^a *	–	1	–
	<i>Homo</i>	<i>sapiens</i>	Cro-Magnon ^a *	1	–	–
	<i>Homo</i>	<i>sapiens</i>	AMNH 204072, 1363	1	1	–

Note. ^aFossil taxa/specimens; *cast.

with minimal reconstructions except for *Caipora*, *Cartelles*, and *Archaeoindris* for which we measured original fossils.

As in the previous study, we identified 18 landmarks covering all parts of the cranium (Table 2; Figure 1). These include Type 1, Type 2, and Type 3 landmarks (Bookstein, 1991; Slice, 2005) and include/incorporate many aspects of morphology that have been discussed in many decades of research on primate cranial diversity and evolution. These include the size, shape, and orientation of the orbits, facial (or snout) length, breadth and height, palate size and shape, neurocranial size and shape, breadth of the infratemporal fossa and postorbital constriction, the shape and orientation of the occiput and the foramen magnum, as well as flexion of the cranial base and the spatial relationship between the neurocranium and splanchnocranium (Figure 2). We were able to locate nearly all of the landmarks in most of the fossil crania; however, we had to reconstruct the zygomatic arch from its roots in several taxa and parts of the basicranium had been reconstructed in some of the fossil hominins. For the reconstruction of the zygomatic arch, we identified the anterior and posterior roots of the arch and connected them with an arch made of modeling clay approximating an amount of bowing found in related extant taxa, or partial crania of the same fossil taxon in which that feature was preserved. We then identified the midpoint of the arch as the landmark zygion.

The landmarks were digitized on each cranium using a Microscribe G2X digitizer (Baab, McNulty, & Rohlf, 2012; Marcus, Frost, & Delson, 1997). All bilateral landmarks were digitized on the right side of the cranium whenever possible. In the few cases where the right side of the cranium was incomplete or unavailable, landmarks were digitized on the left side of the cranium and reflected over the midline during data processing in Morphologika/Morphologika2 (O'Higgins & Jones, 1998, 2006). Individual crania were stabilized in a bed of clay/Play-Doh® (or foam in the case of the largest crania) and landmarks were digitized in two sets—one from a superior view and another from an inferior view. A set of four landmarks was digitized in both views (see Table 2). The two sets of measurements were then combined using the program DVLR v. 0.4.9 (Raum, 2006) to obtain a single set of 18 three-dimensional coordinates for each cranium.

The digitized coordinates for all of the crania were then subjected to a Generalized Procrustes Analysis which translates the specimens to a common origin, scales each specimen to unit centroid size (i.e., isometrically equalizes size for all specimens while maintaining their distinct shapes), and rotates each specimen to a best-fit by using a least-squares calculation (e.g., Baab et al., 2012; Frost, Marcus, Bookstein, Reddy, & Delson, 2003; Harvati, Frost, & McNulty, 2004; Rohlf & Slice, 1990). The resulting Procrustes coordinates were then subjected to a principal components analysis (PCA) to identify the major axes of cranial shape

among all of the crania in the analysis. All analyses were conducted using Morphologika/Morphologika2 (O'Higgins & Jones, 1998, 2006).

In order to evaluate the measurement error associated with replicability of landmarks on small specimens, and that associated with data collection by different individuals, we performed a small interobserver error study using extant crania (Fleagle et al., 2010). In this analysis, the same primate cranium was digitized several times in succession, alternating among the different authors, and the results compared. The interobserver and replication errors were minimal; digitized specimens of the same taxon always plotted in very similar space on the PCA plots.

Because the results of the PCA on the Procrustes coordinates are often difficult to interpret in terms of individual cranial features, we used two methods to characterize the aspects of cranial shape reflected in the individual axes and to relate these shape differences to standard measures of cranial morphology. First, within the Morphologika software package, we examined wireframe diagrams of the cranial shapes along each of the first few principal components to identify the morphological changes along each axis. We also calculated a series of linear measurements, indices, and angular measurements of individual crania based on the digitized landmarks (Table 3) and then examined

TABLE 2 Landmarks used in this study

Landmark	Definition
1	Rhinion
2	Nasion
3	Bregma
4	Medial orbit border
5	Lateral orbit border
6	Orbitale superior
7	Orbitale inferior
8	"Pterion" (most anterior point on the braincase in the infratemporal fossa)
9 ^a	Zygion
10 ^a	Ectomolare
11 ^a	Euryon
12 ^a	Prosthion
13	Lambda
14	Inion
15	Opisthion
16	Basion
17	Sphenobasion
18	Alveolon

Notes. ^aIndicates landmarks collected in both superior and inferior views. See text for details.

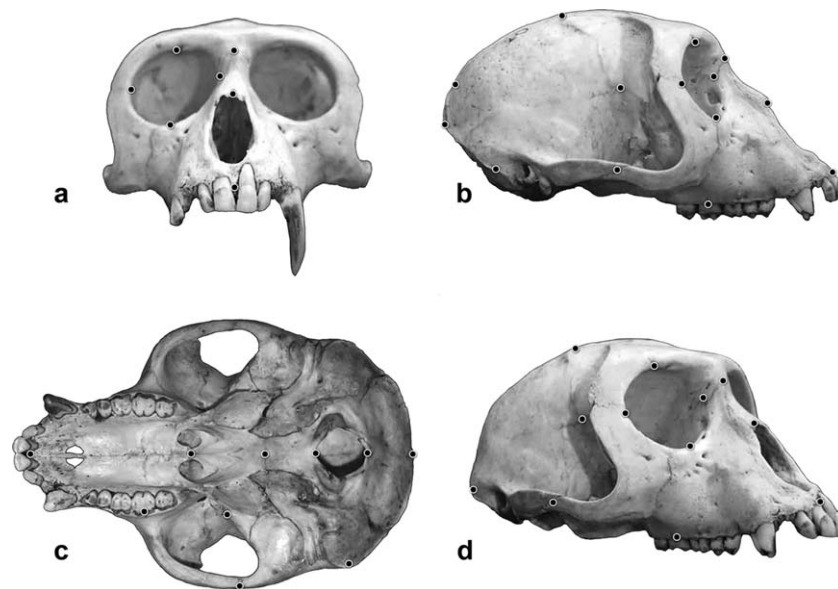


FIGURE 1 Landmarks used in this study. See also Table 2. (a) Frontal view; (b) lateral view; (c) basicranial view; (d) oblique view. Reprinted from Fleagle et al. (2010)

the correlations between the linear dimensions, indices, and angles and the values along individual axes of the PCA using SPSS 22.0.

To compare cranial diversity within clades, we followed methodology as given by Fleagle et al. (2010), using an *F*-statistic for multivariate variance over the first eight principal components. The method essentially weights the variance on the included axes relative to their Eigenvalue scores, and then sums the variance of all included components for each taxon:

$$\sum PC_x * (e_x) + PC_{x+1} * (e_{x+1}) + \dots + PC_{x+n} * (e_{x+n})$$

where PC = the principal component score for component *x* and *e* = the eigenvalue for component *x*. In this analysis, *x* = 1 and *n* = 7.

For calculating the variance of each larger primate grouping (e.g., Superfamily), we summed the weighted variances of each included

genus/species. The variance scores for any two primate groups were then compared using a simple ratio and tested for significance using an *F*-statistic with the appropriate degrees of freedom for the numerator and denominator (Rohlf & Sokal, 1995).

It was impossible to include both male and female crania for the fossil taxa. In most cases crania of both sexes are not known, and often the sex of the fossil cranium available is either unknown or debated. Therefore analyses combining fossils and extant taxa were conducted using different extant samples. We analyzed fossils + extant males, fossils + extant females, and fossils + extant males and females. While the fossils + extant males and females provides the largest sample size and increased statistical degrees of freedom, the fossil taxa are heavily outnumbered by the extant

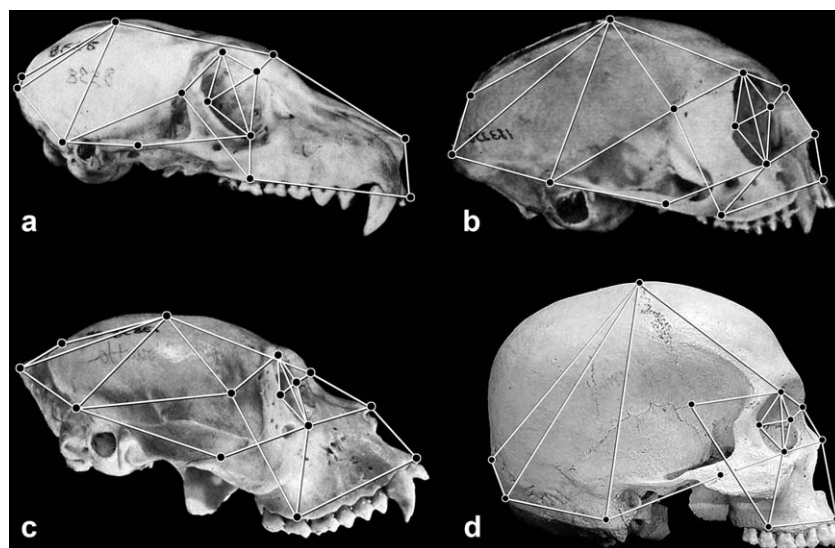


FIGURE 2 Wireframe diagrams of four primate crania demonstrating the extent to which the landmarks capture differences in cranial shape. (a) *Eulemur*; (b) *Callithrix*; (c) *Alouatta*; (d) *Homo*. Reprinted from Fleagle et al. (2010)

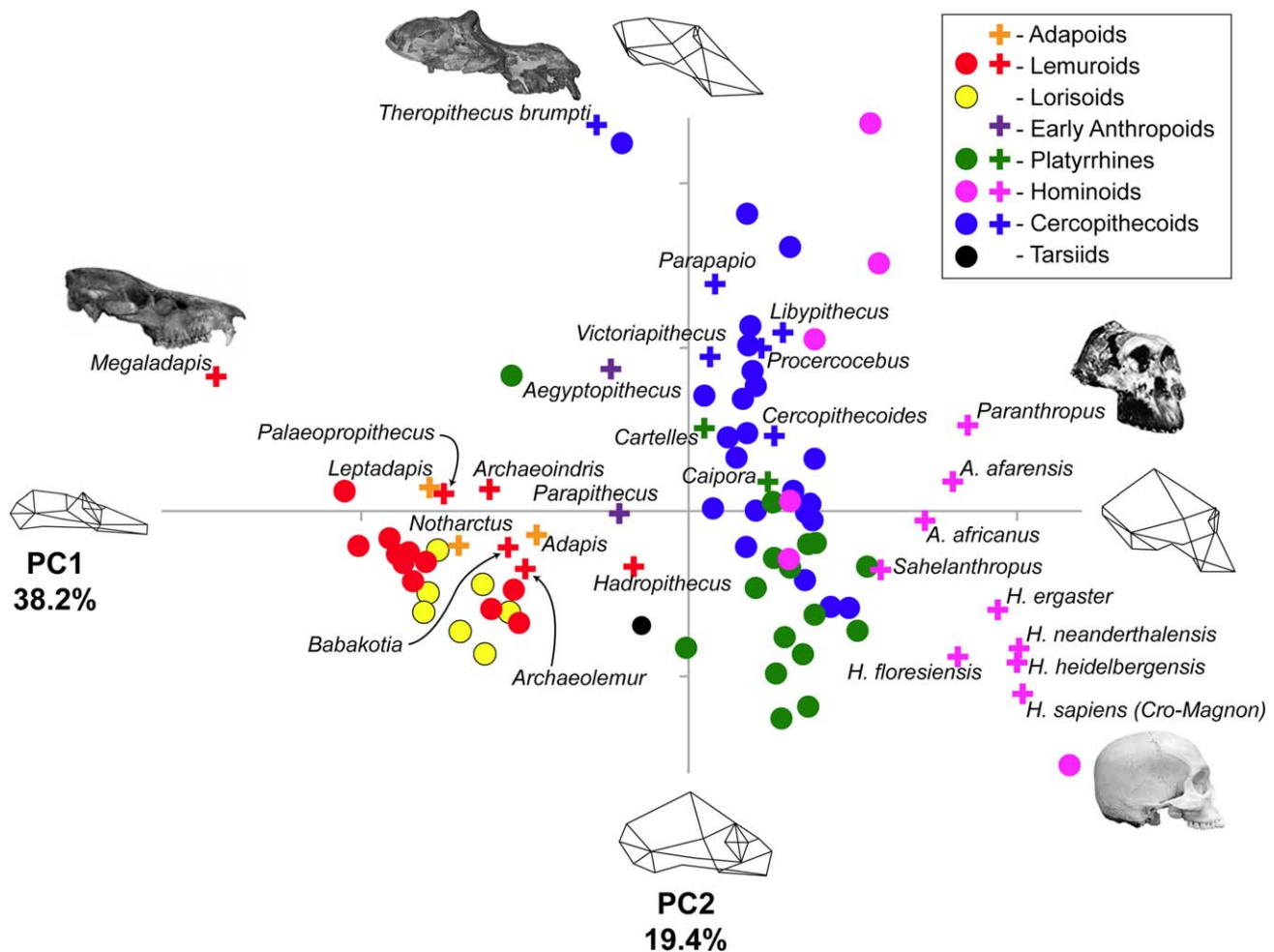
TABLE 3 Definitions of cranial shape variables used in correlation analyses

Variable	Definition
Snout length	nasion-prosthion
Upper facial length	nasion-rhinion
Lower facial length	rhinion-prosthion
Skull flexion	angle between basion-prosthion and basion-nasion
Cranial base flexion	angle between opisthion-basion and opisthion-sphenobasion
Skull length	prosthion-inion
Skull height	basion-bregma
Palate length	alveolare-prosthion
Orbit width	medial orbit border-lateral orbit border
Orbit height	orbitale superior-orbitale inferior
Cranial volume	nasion-inion x basion-bregma x 2 x euryon-opisthion
Facial depth	orbitale inferior-ectomolare
Frontation	angle between orbitale superior-alveolare and orbitale superior-orbitale inferior
Convergence	angle between inion-nasion and inion-lateral orbit border

taxa, so their potential contribution to the analyses should be more limited. In contrast, the analyses using the fossils + extant males and fossils + extant females helps to account for the fact that the fossil taxa are only represented by single specimens, thereby allowing the fossils to have a larger contribution to the resulting analyses compared to the mixed-sex sample, in which each taxon is represented by two crania. We have included results from all of the analyses; however, it turns out that the results are extremely similar in virtually all aspects. We have figured the plots of the analyses of fossils + extant males, and fossils + males and females because the male skulls usually preserve the most extreme morphologies.

3 | RESULTS

Figure 3 illustrates crania from fossils + extant males, with the symbols of the fossil crania labeled. The names of the fossils are not included in later plots, but their symbols remain in the same positions on the plots.

**FIGURE 3** PCA of crania from fossils + extant males, with the symbols of the fossil crania labeled. Extant taxa are denoted by solid circles and extinct taxa by '+'. 3D wireframe models of skulls are shown for several taxa to illustrate shape differences.

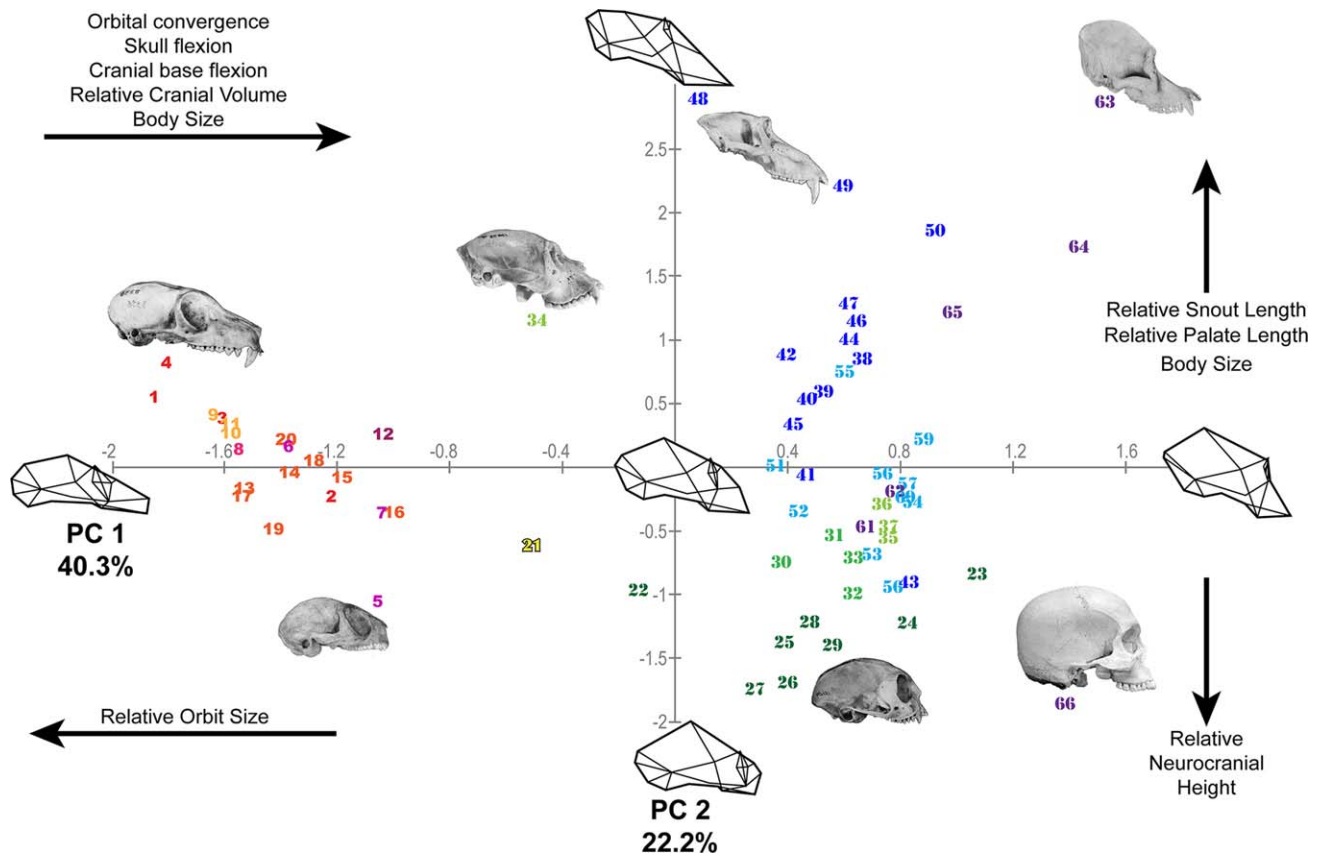


FIGURE 4 PCA of extant male primates demonstrating the extremes of extant primate cranial morphology with both extant crania and wireframes illustrating the principal component axes. The aspects of cranial morphology most highly correlated with each component are noted with arrows on the axes. Colored numbers reference major primate groups. Reprinted from Fleagle et al. (2010). Red = Lemurids, Light purple = Indriids, Magenta = Lepilemurids, Light orange = Cheirogaleids, Maroon = Daubentoniids, Dark orange = Lorids and Galagids, Yellow = Tarsiids, Light green = Atelids, Dark green = Cebids, Light blue = Colobines, Dark blue = Cercopithecines, Dark purple = Hominoids. 1 = Eulemur, 2 = Haplemur, 3 = Lemur, 4 = Varecia, 5 = Avahi, 6 = Indri, 7 = Propithecus, 8 = Lepilemur, 9 = Cheirogaleus, 10 = Microcebus, 11 = Phaner, 12 = Daubentonia, 13 = Arctocebus, 14 = Perodicticus, 15 = Loris, 16 = Nycticebus, 17 = Euoticus, 18 = Galago, 19 = Galagoides, 20 = Otolemur, 21 = Tarsius, 22 = Aotus, 23 = Cebus, 24 = Saimiri, 25 = Callithrix, 26 = Callimico, 27 = Cebuella, 28 = Leontopithecus, 29 = Saguinas, 30 = Callicebus, 31 = Cacajao, 32 = Chiropotes, 33 = Pithecia, 34 = Alouatta, 35 = Ateles, 36 = Lagothrix, 37 = Oreonax, 38 = Allenopithecus, 39 = Allochrocebus, 40 = Cercopithecus, 41 = Chlorocebus, 42 = Erythrocebus, 43 = Miopithecus, 44 = Cercocebus, 45 = Lophocebus, 46 = Macaca fascicularis, 47 = Macaca nemestrina, 48 = Mandrillus, 49 = Papio, 50 = Theropithecus, 51 = Colobus, 52 = Piliocolobus, 53 = Procolobus, 54 = Kasi, 55 = Nasalis, 56 = Presbytis, 57 = Pygathrix, 58 = Semnopithecus, 59 = Simias, 60 = Trachypithecus, 61 = Hylobates, 62 = Symphalangus, 63 = Pongo, 64 = Gorilla, 65 = Pan, 66 = Homo

3.1 | Hypothesis 1

Our first hypothesis predicted that the addition of fossil crania would change the major axes of morphology from those found in our previous analyses of extant primates. A comparison of the first two principal components resulting from the original analysis using only male crania from the extant sample (Figure 4, see also Fleagle et al., 2010), the analysis using extant male crania plus the 28 fossil crania (Figures 3 and 5), and the analysis of male and female extant crania plus fossils (Figure 6) reveals they are all strikingly similar. The axes of the first two principal components, the loadings of individual variables on the axes (Tables 4 and 5), and the positions of the extant taxa are essentially the same despite the addition of almost 30 fossil crania. The only obvious difference is that orbit-size is no longer driving differences among primates on PC 1 (non-significant in the fossils + extant males analysis and a much lower correlation coefficient in the fossils + males and

females analysis compared to extant taxa only), most likely because a large number of extinct (presumably diurnal) strepsirrhines with relatively small orbits (e.g., subfossil lemurs, *Notharctus*, *Adapis*, etc.) have been added to the analysis. Overall, the great similarity between extant and fossil analyses indicates that the morphological relationships and correlations among different parts of the cranium in the fossil taxa are not very different from those that characterize extant primates. This largely falsifies our first hypothesis.

3.2 | Hypothesis 2

Our second hypothesis predicted that some of the fossil taxa would fill parts of the primate morphospace not occupied by the extant taxa. Since there is virtually no difference between the overall morphospace generated by analysis of the extant samples alone and by analysis of the samples of extant plus fossil crania, this hypothesis can be easily

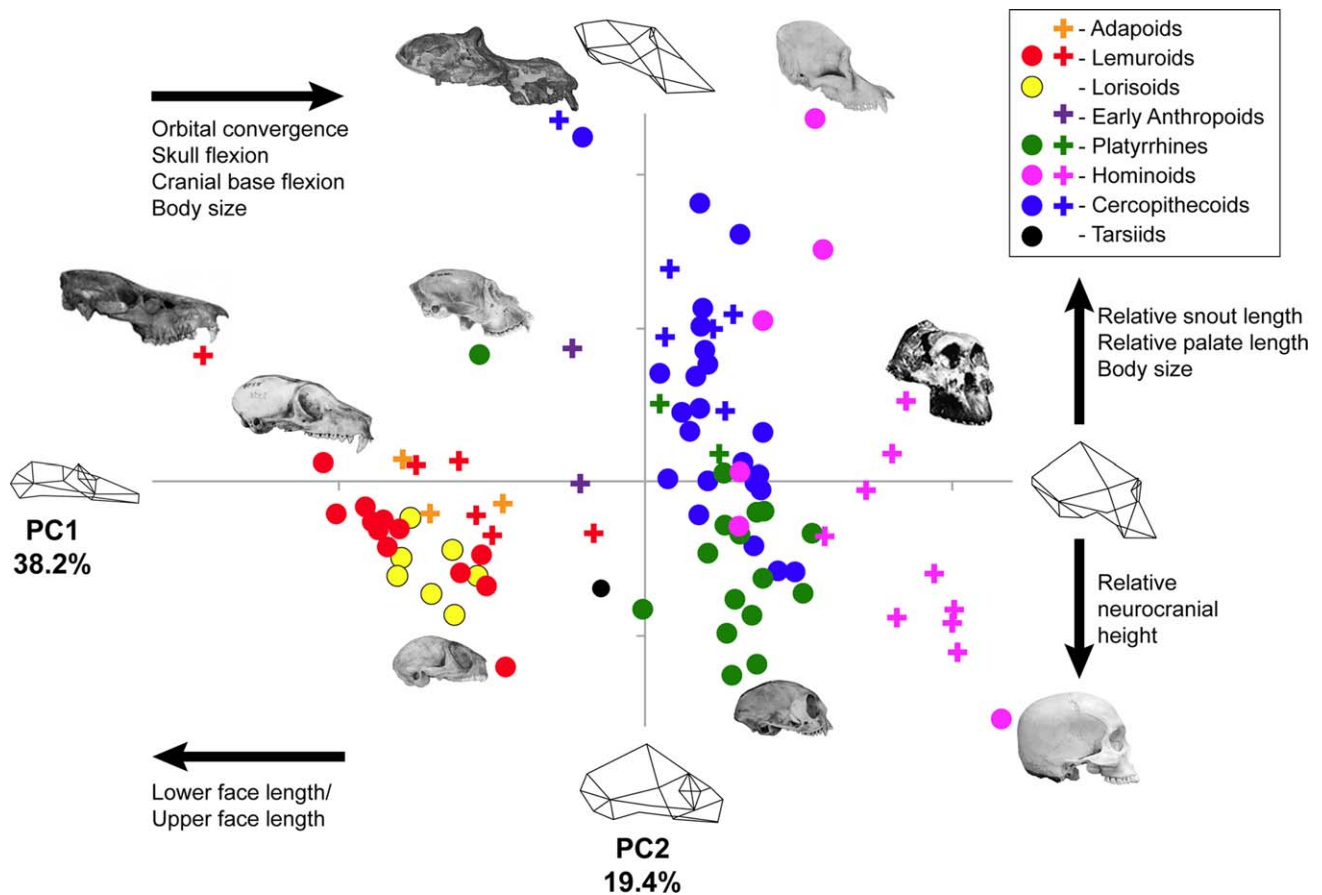


FIGURE 5 PCA of extant males + all fossils demonstrating the extremes of cranial morphology, with images of the extreme crania, and wireframes of the principal component axes, as well as the aspects of cranial morphology most highly correlated with each component. Colored symbols indicate major primate groups as given in Figures 3 and 4

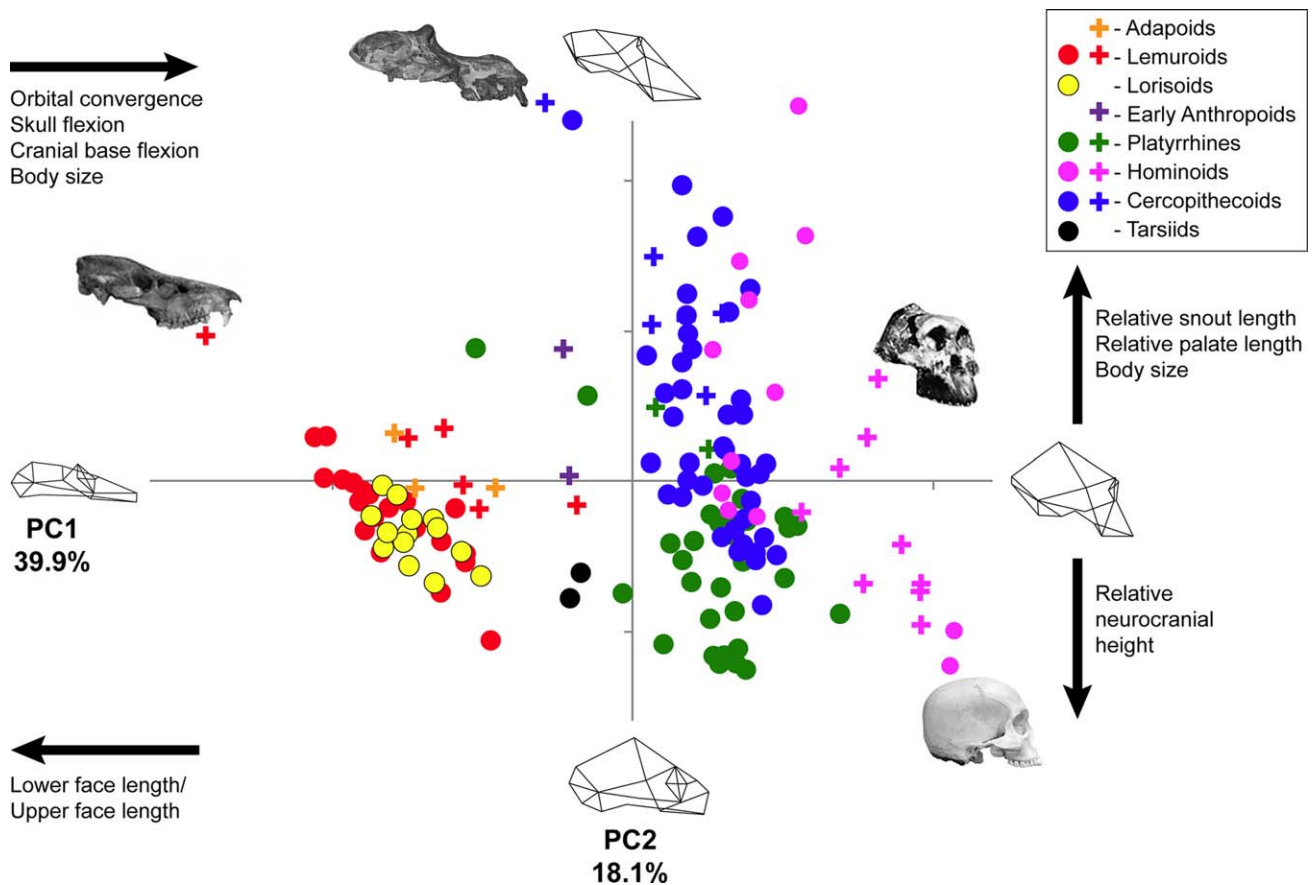


FIGURE 6 PCA of fossils + extant males and females, demonstrating the extremes of cranial morphology, with images of the extreme crania, and wireframes of the principal component axes, as well as the aspects of cranial morphology most highly correlated with each component. Colored symbols indicate major primate groups as given in preceding figures

TABLE 4 Variance loadings for the first eight principal components

		Extant	Eigenvalue	Fossil + Extant	Eigenvalue
		Variance		Variance	
PC 1	Mixed-sex	41.90%	0.0114	39.90%	0.0121
	Males	40.30%	0.0116	38.20%	0.0127
	Females	46.20%	0.0117	42.30%	0.0133
PC 2	Mixed-sex	19.30%	0.0053	18.10%	0.0055
	Males	22.20%	0.0064	19.40%	0.0065
	Females	15.20%	0.0039	15.20%	0.0048
PC 3	Mixed-sex	7.83%	0.0021	8.30%	0.0025
	Males	7.36%	0.0021	8.70%	0.0028
	Females	8.57%	0.0022	8.30%	0.0026
PC 4	Mixed-sex	5.03%	0.0014	5.60%	0.0017
	Males	6.12%	0.0018	5.70%	0.0019
	Females	4.71%	0.0012	6.90%	0.0022
PC 5	Mixed-sex	3.39%	0.0009	4.30%	0.0013
	Males	3.44%	0.0010	5.10%	0.0017
	Females	3.92%	0.0010	4.00%	0.0012
PC 6	Mixed-sex	2.88%	0.0008	3.10%	0.0009
	Males	2.65%	0.0008	3.30%	0.0011
	Females	3.21%	0.0008	3.40%	0.0011
PC 7	Mixed-sex	2.31%	0.0006	2.30%	0.0007
	Males	2.48%	0.0007	2.40%	0.0008
	Females	2.43%	0.0006	2.60%	0.0008
PC 8	Mixed-sex	2.09%	0.0006	1.90%	0.0006
	Males	2.25%	0.0006	2.00%	0.0007
	Females	2.18%	0.0006	1.80%	0.0006
Total	Mixed-sex	84.73%	0.0231	83.40%	0.0253
	Males	86.79%	0.0250	84.70%	0.0280
	Females	88.58%	0.0219	84.40%	0.0265

tested. Although some of the fossil taxa (e.g., *Theropithecus brumpti* and *Paranthropus boisei*) now occupy the extreme positions on the graphs, they are only slightly beyond extant genera (Figures 7–10). In general, the fossil crania tend to fall within or at the edge of the space outlined by the extant genera. The numerous fossil hominins occupy an area of the plot that is distinct from that of other hominoids, but are still within the polygon enclosing extant hominoids (Figures 9 and 10). The major exception to this pattern is the giant subfossil lemur *Megaladapis*, which occupies a place in the primate morphospace quite distinct from that occupied by any extant primates (Figures 7–10). On PC 1, *Megaladapis* lies on the extreme negative side along with other strepsirrhines, despite its large size and small orbits. This position is the result of its unflexed skull, very small neurocranium, relatively divergent orbits, and long lower face. However, *Megaladapis* differs from other strepsirrhines in its high value on PC 2, reflecting its long snout, long palate, large body size, and low neurocranial height, a unique combination of cranial features for a strepsirrhine or any other primate. Thus, the position of the extinct *Megaladapis* supports our second hypothesis, even though the other fossil taxa do not occupy areas of the morphospace dramatically different from those of extant crania.

3.3 | Hypothesis 3

Our third hypothesis predicted that the addition of fossil crania would change the patterns of relative cranial diversity among different clades from those we found in analyses of extant primate genera. This is definitely the case as indicated in Figures 7–10, and Tables 6 and 7. The observed changes are clearly a reflection of our sampling of fossil taxa—lemuroids and hominoids are the taxa with the greatest number of fossil crania included in the analyses and are also the taxa that show the greatest changes in cranial diversity relative to other clades. However, the diversity changes in the best-sampled groups, lemuroids and hominoids, are in opposite directions. In the analyses of extant taxa, lemuroids showed relatively little cranial shape diversity despite a large number of taxa sampled. The addition of the subfossil Malagasy lemurs greatly increased the morphological diversity (and the parts of the morphospace occupied by strepsirrhines and Lemuroidea). This is due to both the unusual cranium of *Megaladapis* noted above, and also the more anthropoid, or “monkey-like” cranial morphology of the archaeolemurines, *Archaeolemur* and *Hadropithecus*.

TABLE 5 Cranial shape loadings for the first four principle components of the males-only, females-only, and combined sex analyses with fossil taxa

Correlation Coefficient												
Measure	PC1		PC2		PC3		PC4		Centroid Size (C.S.)			
	Extant	Fossil + Extant	Extant	Fossil + Extant	Extant	Fossil + Extant	Extant	Fossil + Extant	Extant	Fossil + Extant		
Skull flexion	Mixed-sex	0.631	0.638	0.609	0.600	-0.383	-0.398	0.107	0.105	0.737	0.626	
	Males	0.679	0.642	0.584	0.595	-0.336	-0.397	0.131	-0.119	0.795	0.603	
	Females	0.655	0.667	0.552	0.592	-0.435	-0.381	0.101	-0.014	0.657	0.551	
Cranial base flexion	Mixed-sex	-0.666	-0.695	-0.108	-0.101	0.285	0.324	-0.081	0.029	-0.409	-0.296	
	Males	-0.602	-0.695	-0.026	-0.094	0.377	0.357	-0.003	-0.123	-0.360	-0.272	
	Females	-0.729	-0.747	-0.219	-0.156	0.186	0.211	-0.281	-0.143	-0.490	-0.265	
Relative Snout Length (Snout Length/Skull Length)	Mixed-sex	0.286	0.182	0.844	0.867	-0.278	-0.273	-0.051	0.056	0.673	0.569	
	Males	0.390	0.179	0.816	0.862	-0.239	-0.285	-0.058	-0.123	0.737	0.534	
	Females	0.270	0.146	0.823	0.885	-0.327	-0.266	-0.035	-0.048	0.586	0.505	
Relative Skull Length (Skull Length/C.S.)	Mixed-sex	-0.127	-0.224	0.877	0.874	-0.164	-0.139	-0.215	-0.106	0.487	0.356	
	Males	-0.041	-0.270	0.893	0.859	-0.154	-0.160	-0.248	0.053	0.479	0.281	
	Females	-0.146	-0.289	0.893	0.878	-0.140	-0.060	-0.124	0.070	0.495	0.291	
Relative Neurocranial Height (Skull height/C.S.)	Mixed-sex	0.259	0.352	-0.551	-0.588	-0.013	-0.137	0.551	0.495	-0.063	0.060	
	Males	0.075	0.346	-0.662	-0.671	0.037	-0.135	0.514	-0.398	-0.205	0.056	
	Females	0.439	0.473	-0.343	-0.517	-0.039	-0.254	0.549	-0.367	0.171	0.193	
Relative Palate Length (Palate Length/C.S.)	Mixed-sex	-0.343	-0.476	0.693	0.687	-0.221	-0.214	-0.146	-0.026	0.222	0.166	
	Males	-0.278	-0.479	0.751	0.679	-0.209	-0.240	-0.256	-0.049	0.259	0.148	
	Females	-0.354	-0.485	0.693	0.685	-0.221	-0.201	0.039	0.005	0.173	0.109	
Relative Orbit Size (Orbit Width/C.S.)	Mixed-sex	-0.473	-0.290	-0.371	-0.462	-0.275	-0.340	0.210	-0.261	-0.645	-0.653	
	Males	-0.511	-0.192	-0.336	-0.468	-0.207	-0.326	0.263	0.409	-0.658	-0.657	
	Females	-0.462	-0.156	-0.384	-0.490	-0.371	-0.287	0.114	0.565	-0.637	-0.640	
Relative Cranial Volume (Cranial Volume/C.S.)	Mixed-sex	0.497	0.491	0.316	0.161	-0.118	-0.238	0.420	-0.526	0.864	0.874	
	Males	0.532	0.533	0.235	0.041	-0.128	-0.257	0.449	-0.530	0.850	0.867	
	Females	0.479	0.492	0.368	0.153	-0.087	-0.354	0.382	-0.517	0.882	0.882	
Upper Facial Length/Lower Facial Length	Mixed-sex	-0.806	-0.803	0.072	0.028	-0.271	-0.238	-0.201	-0.207	-0.455	-0.329	
	Males	-0.810	-0.809	0.155	0.007	-0.250	-0.214	-0.162	0.164	-0.446	-0.280	
	Females	-0.797	-0.792	0.081	0.036	-0.300	-0.223	-0.161	0.226	-0.469	-0.272	
Relative Facial Depth (Facial Depth/C.S.)	Mixed-sex	0.668	0.538	0.578	0.641	0.008	0.036	0.020	0.264	0.777	0.730	
	Males	0.730	0.493	0.544	0.661	-0.053	-0.001	0.016	-0.371	0.798	0.711	
	Females	0.667	0.438	0.503	0.630	0.087	0.008	0.028	-0.429	0.746	0.700	

TABLE 5 (Continued)

Measure	Correlation Coefficient									
	PC1		PC2		PC3		PC4		Centroid Size (C.S.)	
	Extant	Fossil + Extant	Extant	Fossil + Extant	Extant	Fossil + Extant	Extant	Fossil + Extant	Extant	Fossil + Extant
Frontation	Mixed-sex	-0.566	-0.601	-0.463	0.312	0.286	0.074	0.135	-0.585	-0.496
	Males	-0.627	-0.637	-0.449	0.336	0.290	-0.006	-0.123	-0.633	-0.502
	Females	-0.533	-0.616	-0.437	0.280	0.156	0.187	-0.219	-0.531	-0.423
Convergence	Mixed-sex	-0.838	-0.753	-0.110	-0.071	-0.242	0.305	0.017	-0.511	-0.517
	Males	-0.833	-0.696	-0.001	-0.016	-0.303	0.374	0.089	-0.500	-0.523
	Females	-0.841	-0.687	-0.200	-0.131	-0.292	0.145	0.249	-0.536	-0.513
Centroid Size (C.S.)	Mixed-sex	0.535	0.415	0.634	0.011	-0.066	0.211	0.439	1.000	1.000
	Males	0.610	0.408	0.580	-0.033	-0.109	0.192	-0.512	1.000	1.000
	Females	0.504	0.341	0.634	0.084	-0.165	0.215	-0.541	1.000	1.000

Notes. Significant correlation coefficients ($p < .05$) are in bold. PC1: skull flexion, cranial base flexion, upper facial length/lower facial length, convergence, frontation, facial depth, cranial volume, body size. PC2: skull flexion, snout length, palate length, orbit size, frontation, facial depth, body size. See Table 3 for definitions of measurements.

In contrast, extant hominoids consist of very few genera (*Pan*, *Gorilla*, *Pongo*, *Hylobates*, *Homo*) with very distinctive crania. Thus, the variance of cranial shape in extant hominoids is very high. However, the addition of numerous fossil hominins which lie within or near the envelope of cranial shape outlined by the extant taxa greatly decreased the variance of hominoid cranial shape. As a result, when the fossils are included, the cranial diversity of lemuroids is no longer less than the cranial diversity of haplorhines, anthropoids, or hominoids, and hominoid cranial diversity is no longer significantly greater than that of lemuroids (Table 6). However, despite these changes, anthropoids (and haplorhines) still show significantly greater cranial diversity than strepsirrhines, and lorisooids (for which we had no complete fossil crania) remain the least diverse primate group. Although the fossil platyrrhines *Cartelles* and *Caipora* have reconstructed body masses roughly twice the size of any extant platyrrhines (Cartelle & Hartwig, 1996; Hartwig & Cartelle, 1996; [Halenar & Rosenberger, 2013](#)), their crania plot barely outside the morphospace occupied by extant platyrrhines.

3.4 | Hypothesis 4

Our fourth hypothesis predicted that, because fossil taxa are likely to preserve ancestral morphologies that gave rise to later, more derived taxa, many of the fossil crania will fill morphological gaps between extant taxa and/or extant clades. Their value as “missing links” and stem taxa is one of the most important roles fossils play in evolutionary biology. As is evident from Figures 9 and 10, the fossil crania do, indeed, fill morphological gaps at many different levels, but only among the anthropoids. The Eocene adapoids (stem strepsirrhines) *Notharctus*, *Adapis*, and *Leptadapis* fall near the center of the cluster of extant strepsirrhines (see also [Bennett and Goswami, 2012](#)). In contrast, the subfossil Malagasy strepsirrhines are generally outside the morphological envelope occupied by extant strepsirrhines (see also [Bennett and Goswami, 2012](#); Griffith & Godfrey, 2013). The short-faced *Hadropithecus* illustrates an interesting phenomenon. Although there is a clear separation between strepsirrhines and anthropoids in the plot of the first two principal components in the analysis of extant crania, in the analysis of extant and fossil crania, *Hadropithecus* falls on the edge of the anthropoid polygon. It has been noted for many years that *Hadropithecus* converged with anthropoids in having a short face and forward-facing eyes, and both *Hadropithecus* and *Archaeolemur* have been described as “monkey-like” lemurs. This is clearly a case of convergence, probably due to dietary adaptations rather than of any phylogenetic link or evolutionary pathway ([Jolly, 1970](#); [Tattersall, 1973](#)).

However, among anthropoids there are clear examples of phylogenetic morphoclines (Figures 9–11). *Aegyptopithecus* from the Early Oligocene of Egypt is a stem catarrhine that shows a combination of cranial features of the ear, dentition, and braincase (as well as postcranial features) that place it intermediate between extant platyrrhines (and early anthropoids) and the two groups of extant catarrhines, cercopithecoid monkeys and hominoids (e.g., [Fleagle, 2013](#)). In the plot of the first two principal components of the extant and fossil crania,

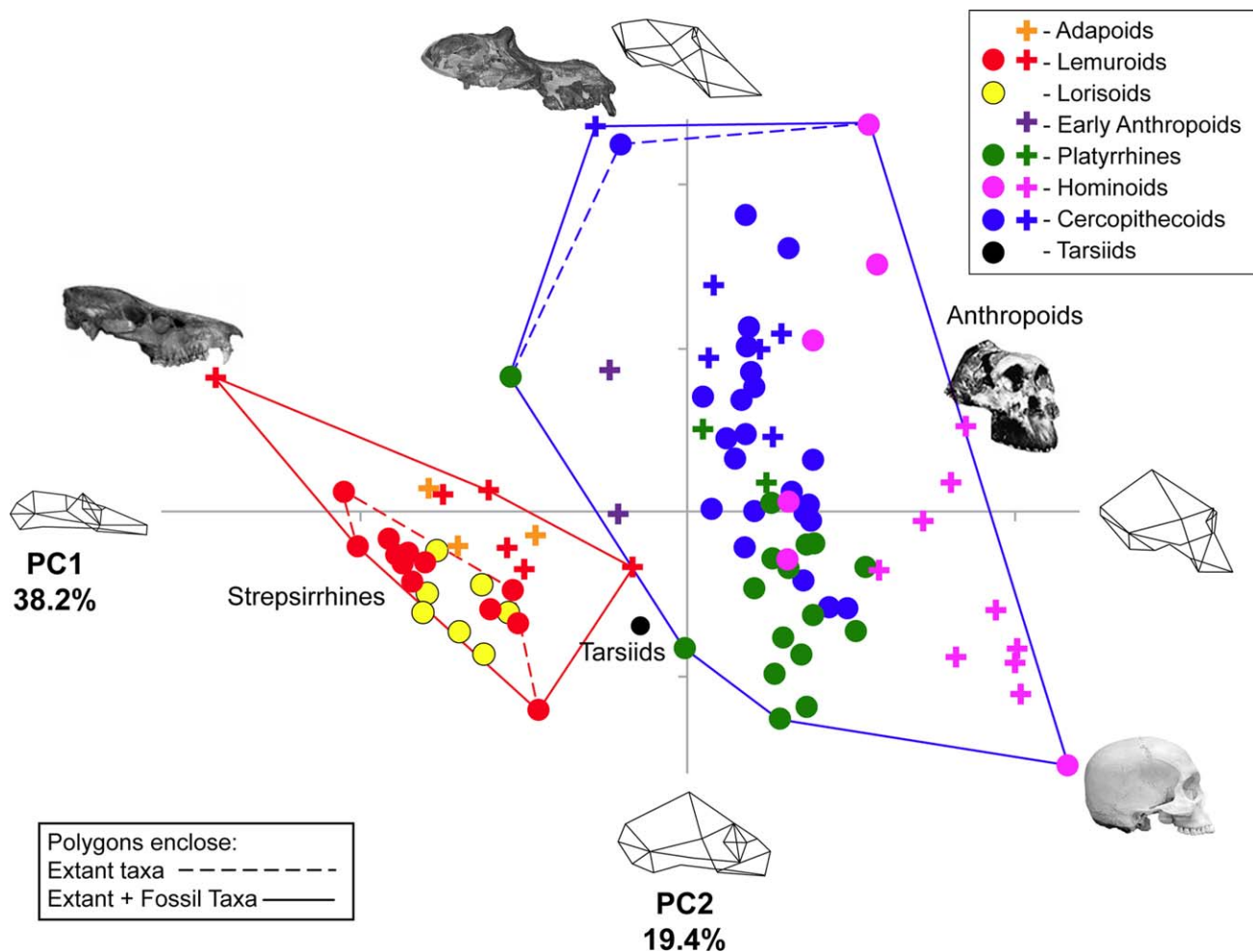


FIGURE 7 PCA of fossils + extant male crania. Polygons outline the distribution of strepsirrhines and anthropoids, with tarsiers labeled in between. Colored symbols reference major primate groups as given in preceding figures

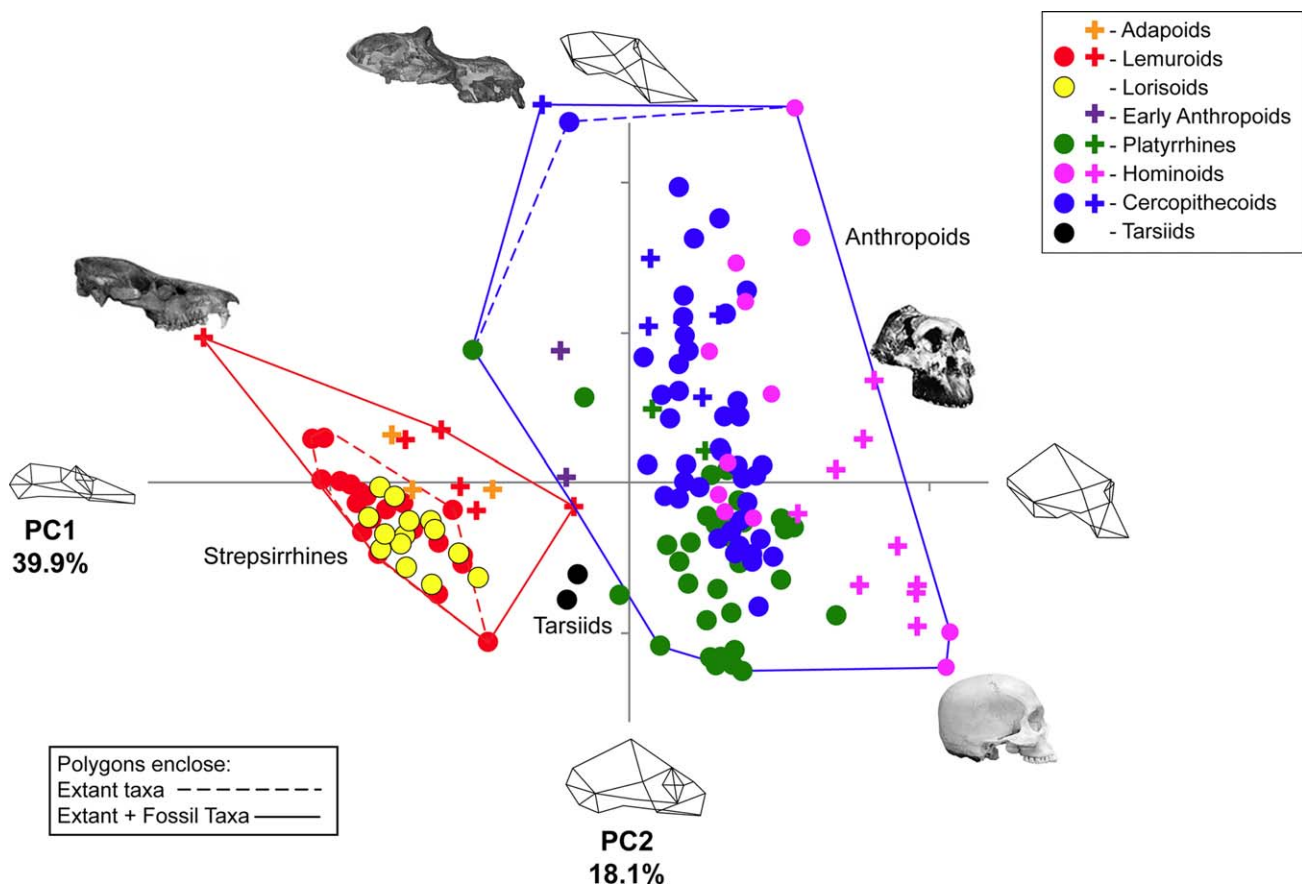


FIGURE 8 PCA of fossils + extant male and female primate crania. Polygons outline the distribution of strepsirrhines and anthropoids, with tarsiers labeled in between. Colored symbols reference major primate groups as given in preceding figures

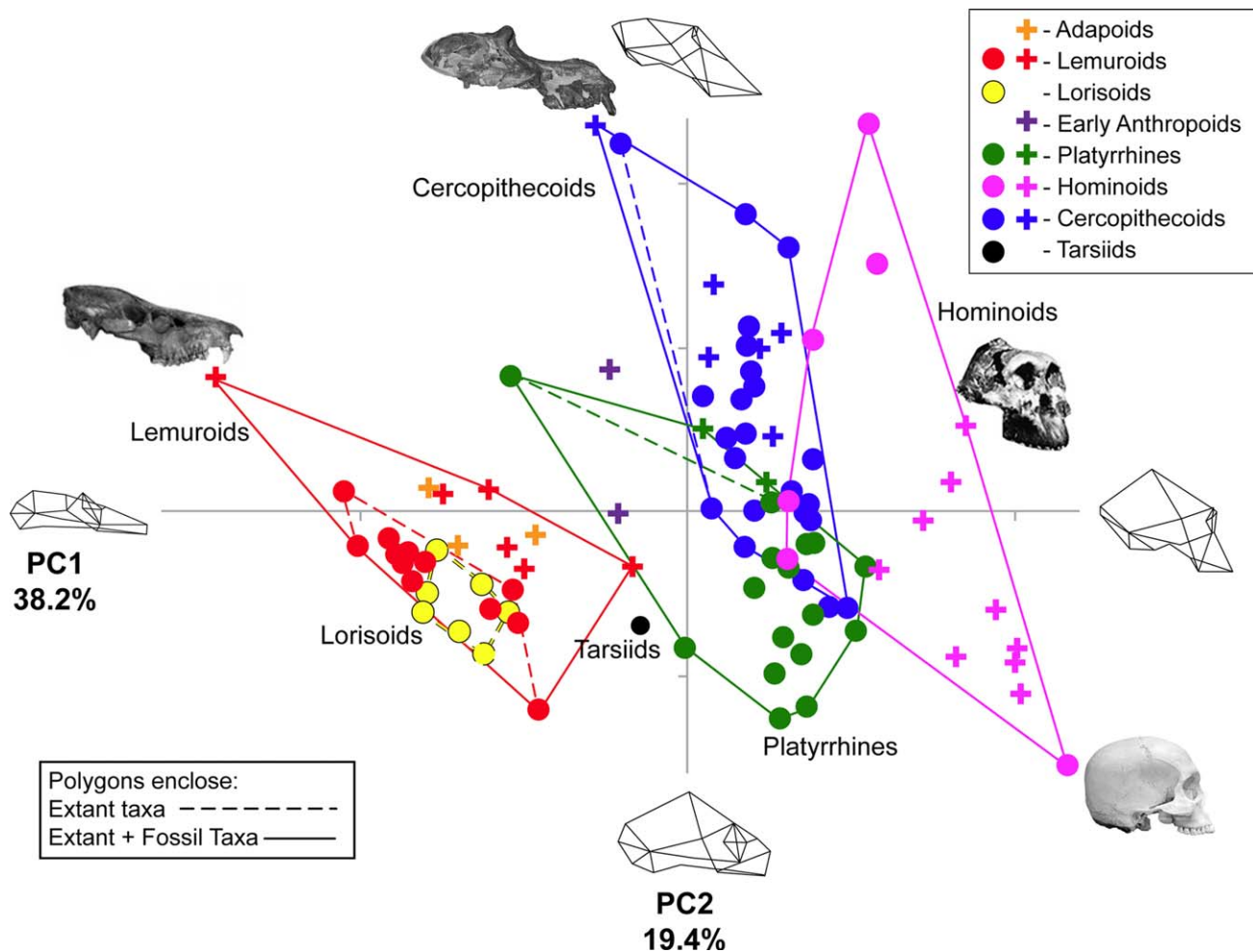


FIGURE 9 PCA of fossils + extant male primate crania. Polygons outline the distribution of major groups among strepsirrhines and anthropoids. Colored symbols reference major primate groups as given in preceding figures

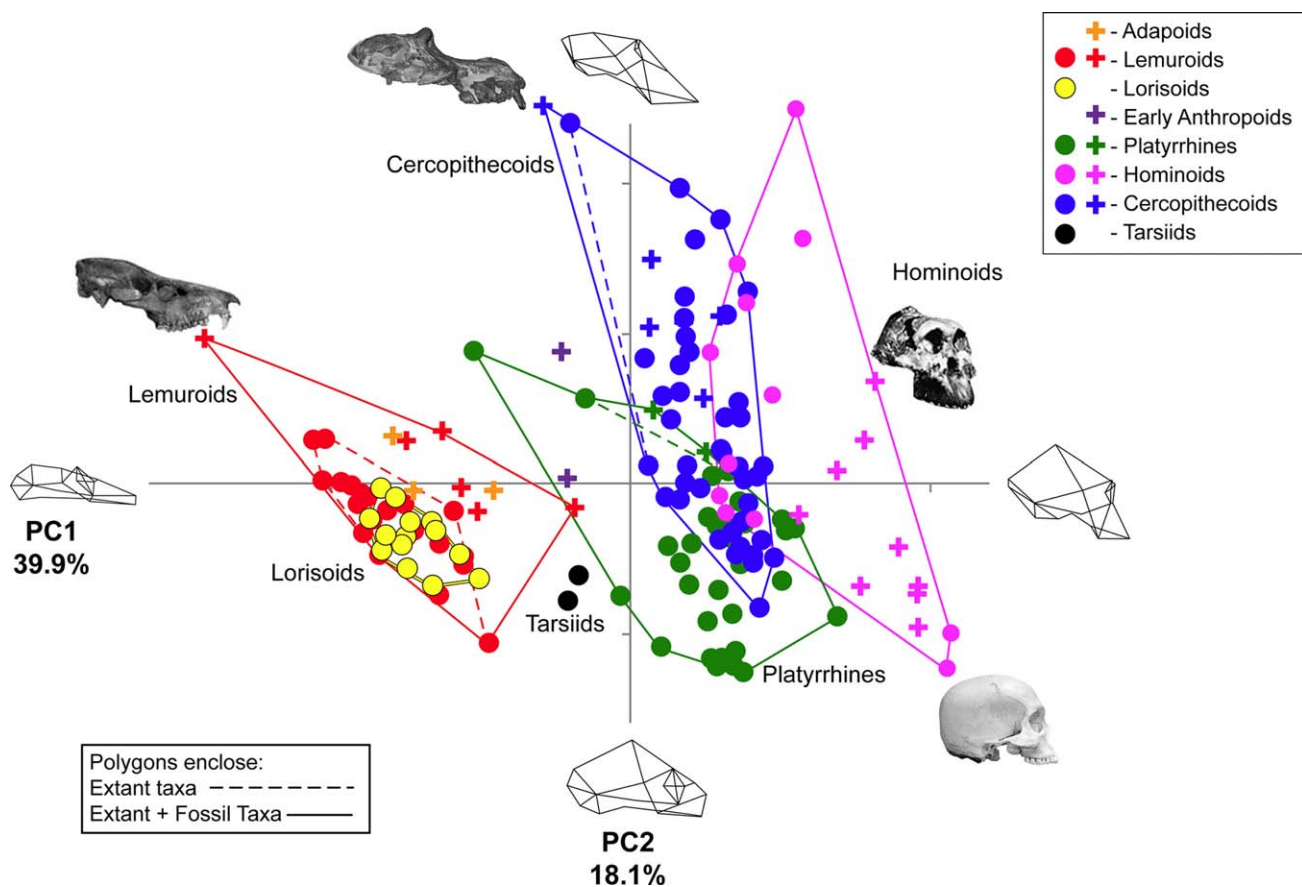


FIGURE 10 PCA of fossils + extant male and female primate crania. Polygons outline the distribution of major groups among strepsirrhines and anthropoids. Colored symbols reference major primate groups as given in preceding figures

TABLE 6 Significant differences in variance between primate groups using an *F*-statistic

Significant pair in extant male analysis	Significant when fossils added?
Anthropoids > Prosimians	YES
Anthropoids > Strepsirrhines	YES
Haplorhines > Strepsirrhines	YES
Haplorhines > Lorisoids	YES
–	Platyrrhines > Lorisoids ^a
Catarrhines > Prosimians	YES
Catarrhines > Strepsirrhines	YES
–	Catarrhines > Platyrrhines ^a
Catarrhines > Lorisoids	YES
Cercopithecoids > Lorisoids	YES
Hominoids > Prosimians	NO
Hominoids > Strepsirrhines	YES
Hominoids > Cercopithecoids	YES
Hominoids > Lemuroids	NO
Hominoids > Lorisoids	YES
–	Lemuroids > Lorisoids ^a

Notes. ^aPair significant in the fossil analysis but not in the original analysis including only extant taxa.

Aegyptopithecus occupies an intermediate position between the platyrrhine *Alouatta* and catarrhines (cercopithecoids and hominoids). Likewise, the basal anthropoid *Parapithecus*, (Fleagle & Kay, 1987; Simons, 2001), like *Aegyptopithecus*, lies outside the morphospace occupied by any extant anthropoids, except *Alouatta*. In contrast, the stem cercopithecoid *Victoriapithecus* (Benefit & McCrossin, 1997) does not occupy any sort of intermediate position either between hominoids and cercopithecoids or between colobines and cercopithecines. Rather, it falls within extant cercopithecines, suggesting that this is the primitive cercopithecoid morphology (Benefit & McCrossin, 1997).

The most striking example of how fossils can fill gaps between very different extant morphologies is found among hominoids. As has been well known for centuries (e.g., Creel & Preuschoft, 1971) and further confirmed metrically in our analysis of extant crania, the human cranium is strikingly different from that of any other hominoid. In our previous study (Fleagle et al., 2010), we found that the morphological difference between a human cranium and that of our closet living primate relative, the chimpanzee, is greater than the difference between any other pair of morphologically divergent sister taxa among extant primates. However, fossil hominin crania from the late Miocene through Recent generally fill that morphological gap (as they are roughly intermediate in many features of relative brain size, neurocranial height, palate length, and snout length). Moreover, the morphological cline from a chimpanzee-like morphology to a human-like morphology follows a rough temporal trend with older fossils being more ape-like and younger fossils more human-like, with a few notable exceptions. The late Miocene *Sahelanthropus* falls closer to *A. africanus* than to *Pan* or early East African taxa such as *A. afarensis*, a pattern also found in the phenetic analyses of Guy et al. (2005). The relatively

young *Homo floresiensis* plots closer to early *Homo erectus* rather than close to *Homo sapiens*, as also found by Baab, McNulty, and Harvati (2013). It is also notable that the robust *Paranthropus boisei*, a derived side-branch in human evolution, plots somewhat away from the main morphological trend line from *Pan* to *Homo sapiens*.

4 | DISCUSSION

Analyses of primate cranial diversity including the fossil record demonstrate that the main morphological factors driving primate cranial evolution and the diversity relationships between major groups have remained remarkably stable over many millions of years. Despite an obvious increase in lemuroid diversity due to the inclusion of subfossil lemur taxa, anthropoids (and haplorhines) maintain a significantly greater amount of diversity than strepsirrhines apparently ever achieved. Unfortunately, we were unable to include any fossil crania from omomyoids, a large group of extinct Paleogene primate usually included among haplorhines. While there are numerous omomyoid crania, all are broken or crushed in ways that preclude use in our analyses.

In any case, the evolution of the anthropoid skull was a significant development in primate (and mammalian) evolution, the reorganization of which led to an incredible radiation spanning the extremes in cranial morphology illustrated by howler monkeys, callitrichines, *Theropithecus brumpti*, orangutans, and modern humans. Within anthropoids, the extant taxa do a remarkable job of sampling the general diversity and extremes of the major radiations of platyrrhines, cercopithecoids, and hominoids, but the fossil taxa are very

TABLE 7 Significant differences in variance between primate groups using an *F*-statistic

Significant pair in extant mixed-sex analysis	Significant when fossils added?
Anthropoids > Prosimians	YES
Anthropoids > Strepsirrhines	YES
Haplorhines > Strepsirrhines	YES
Haplorhines > Lemuroids	NO
Haplorhines > Lorisoids	YES
Platyrrhines > Lorisoids	YES
Platyrrhines > Strepsirrhines	NO
Catarrhines > Strepsirrhines	YES
–	Catarrhines > Prosimians ^a
–	Catarrhines > Platyrrhines ^a
Catarrhines > Lorisoids	YES
Cercopithecoids > Lorisoids	YES
Hominoids > Prosimians	YES
Hominoids > Strepsirrhines	YES
Hominoids > Cercopithecoids	YES
Hominoids > Lemuroids	NO
Hominoids > Lorisoids	YES
–	Lemuroids > Lorisoids ^a

Notes. ^aPair significant in the fossil analysis but not in the original analysis including only extant taxa.

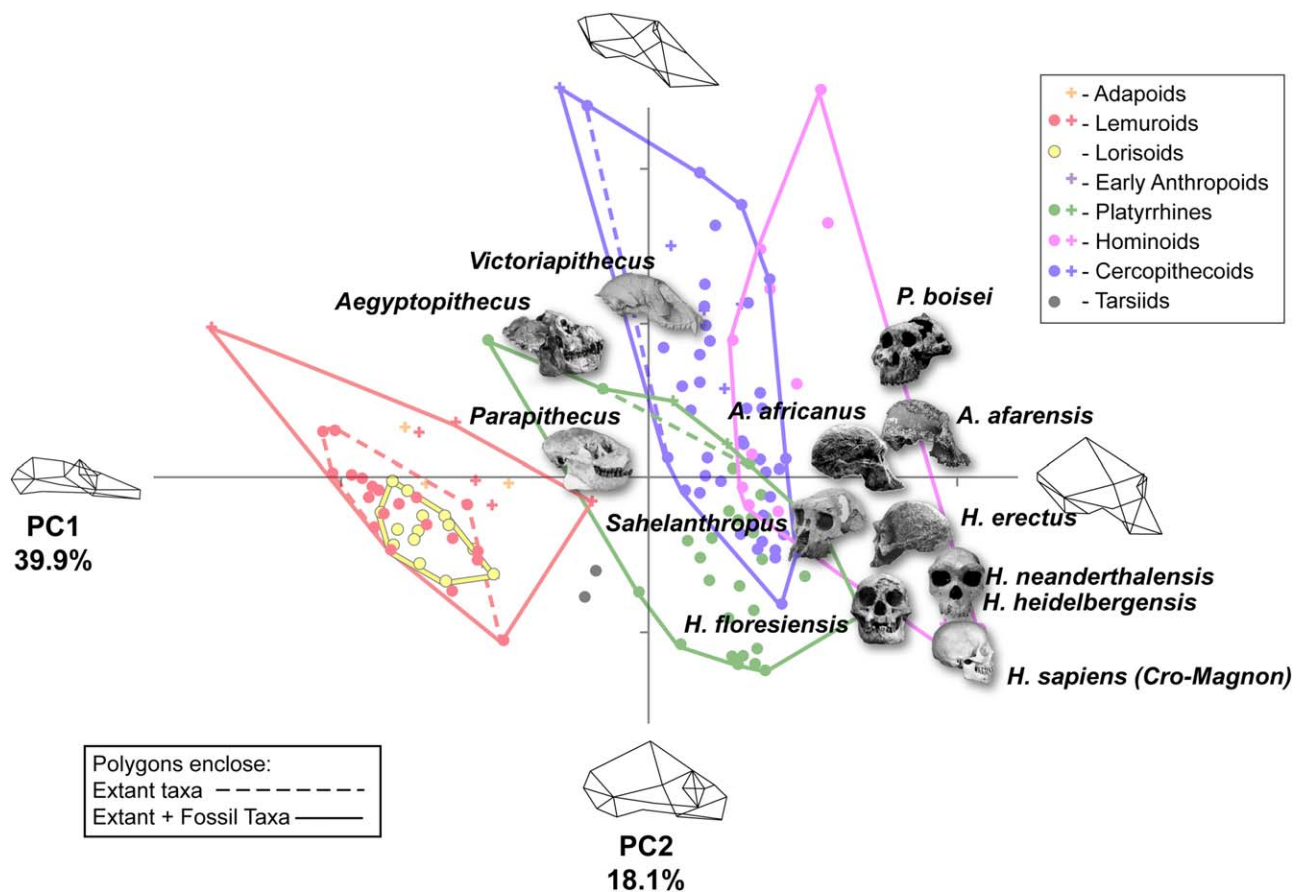


FIGURE 11 PCA of fossils + extant male primate crania. Polygons outline the distribution of major groups among strepsirrhines and anthropoids. Images of fossil specimens illustrate their position on the plot and demonstrate how they fill in notable gaps in morphospace between extant clades or taxa. Colored symbols reference major primate groups as given in preceding figures

important in filling in notable gaps between cranial forms in anthropoid evolution. For example, *Aegyptopithecus* falls between the radiations of platyrrhines and catarrhines, and perhaps most notably, fossil hominins largely occupy the morphospace between extant chimpanzees and modern humans.

The human cranium has an extreme morphology among primate crania. In our previous analyses of cranial morphology among extant primates (Fleagle et al., 2010), we found that the morphological gap between humans and our closest primate relative, *Pan* was greater than the distance between any other pair of closely related taxa. However, once fossil taxa are included, the human cranium, while still very different from any extant hominoids, is just the end of a long evolutionary lineage bridging the gap between ourselves and other great apes.

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