

Primate Cranial Diversity

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KEY WORDS morphometrics; principal components analysis; skull

ABSTRACT Many studies in primate and human evolution focus on aspects of cranial morphology to address issues of systematics, phylogeny, and functional anatomy. However, broad analyses of cranial diversity within Primates as an Order are notably absent. In this study, we present a 3D geometric morphometric analysis of primate cranial morphology, providing a multivariate comparison of the major patterns of cranial shape change during primate evolution and quantitative assessments of cranial diversity among different clades. We digitized a set of 18 landmarks designed to capture overall cranial shape on male and female crania representing 66 genera of living primates. The landmark data were aligned using a Generalized Procrustes Analysis and then subjected to a principal components analysis to identify the major axes of cra-

nial variation. Cranial diversity among clades was compared using multivariate measurements of variance. The first principal component axis reflects differences in cranial flexion, orbit size and orientation, and relative neurocranial volume. In general, it separates strepsirrhines from anthropoids. The second axis reflects differences in relative cranial height and snout length and primarily describes differences among anthropoids. *Eulemur*, *Mandrillus*, *Pongo*, and *Homo* are among the extremes in cranial shape. Anthropoids, catarrhines, and haplorhines show a higher variance than prosimians or strepsirrhines. Hominoids show the highest variance in cranial shape among extant primate clades, and much of this diversity is driven by the unique cranium of *Homo sapiens*. Am J Phys Anthropol 142:565–578, 2010. © 2010 Wiley-Liss, Inc.

Cranial anatomy has long played a central role in studies of systematics (e.g., Groves, 1967, 1970; Creel and Presuschoft, 1984; Frost et al., 2003; Stumpf et al., 2003), phylogeny (e.g., Howells, 1973; Cartmill, 1975; MacPhee and Cartmill, 1986; Rae, 1993; Kay et al. 1997; Strait et al., 1997), and functional anatomy (e.g., Lieberman et al., 2000, 2004; Kirk and Kay, 2004; Heesy et al., 2007; Ross and Kirk, 2007) in primate and human evolution. There are many detailed studies of cranial morphology within clades of closely related primates (e.g., Groves, 1967, 1970; Creel and Presuschoft, 1984; Howells, 1993; Singleton, 2002; Frost et al., 2003; Cardini and Elton, 2008) and other studies of specific aspects of cranial morphology across a wide range of taxa (e.g., Ross, 1995; Lieberman et al., 2000). Although texts in primate morphology or primate evolution offer discussions of primate cranial morphology, they tend to examine cranial morphology in modules such as the olfactory region, the auditory region, the orbital region, the neurocranium, etc. (e.g., Martin, 1990; Fleagle, 1999; Ankel Simons, 2007). While broad overviews of primate cranial evolution are prominent in the older primate literature, these are largely descriptive and qualitative (e.g., Clark, 1959; Biegert, 1963). Although there are a few quantitative studies of overall cranial organization in specific groups of extant primates (Marroig and Cheverud, 2001; Oliveira et al., 2009) or across mammals (Marcus et al., 2000), quantitative studies of overall cranial morphology among all extant primates as a group are essentially absent.

Biodiversity is a topic of major interest to primatologists, as it is to all biologists, and students of primate biology regularly make statements about the relative diversity among different clades of living primates. For example, Old World monkeys have been argued to be relatively uni-

form compared with other clades (e.g., Schultz, 1970). To this point, however, statements about the relative diversity in overall cranial shape among different primate clades have been largely subjective.

In this article, we use 3D geometric morphometrics (e.g., O'Higgins and Jones, 1998; O'Higgins, 2000; Sington, 2002; Frost et al., 2003; Slice, 2005, 2007; Mitteroecker and Bookstein, 2007, 2008; Mitteroecker and Gunz, 2009) to provide a broad quantitative analysis of cranial shape among extant primates to 1) identify major patterns in cranial shape throughout the order; 2) identify correlations among morphological changes in different cranial regions; 3) provide a quantitative assessment of relative cranial diversity among different clades; and 4) identify the most extreme shape differences in cranial shape among closely related extant primates.

MATERIALS AND METHODS

This study is based on one male adult cranium and one female adult cranium for 66 genera of extant prima-

Grant sponsor: LSB Leakey Foundation.

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Received 3 June 2009; accepted 18 December 2009

DOI 10.1002/ajpa.21272

Published online 22 February 2010 in Wiley InterScience (www.interscience.wiley.com).

TABLE 1. Sample used in this study

Taxon code	Genus	Species	Male (n)	Female (n)
Strepsirrhines				
1	<i>Eulemur</i>	<i>fulvus</i>	1	1
2	<i>Hapalemur</i>	<i>griseus</i>	1	1
3	<i>Lemur</i>	<i>catta</i>	1	1
4	<i>Varecia</i>	<i>variegata</i>	1	1
5	<i>Avahi</i>	<i>laniger</i>	1	1
6	<i>Indri</i>	<i>indri</i>	1	1
7	<i>Propithecus</i>	<i>verreauxi</i>	1	1
8	<i>Lepilemur</i>	<i>mustelinus</i>	1	1
9	<i>Cheirogaleus</i>	<i>major</i>	1	1
10	<i>Microcebus</i>	<i>sp.</i>	1	1
11	<i>Phaner</i>	<i>furcifer</i>	1	X
12	<i>Daubentonia</i>	<i>madagascarensis</i>	1	1
13	<i>Arctocebus</i>	<i>calabarensis</i>	1	1
14	<i>Perodicticus</i>	<i>potto</i>	1	1
15	<i>Loris</i>	<i>tardigradus</i>	1	X
16	<i>Nycticebus</i>	<i>coucang</i>	1	1
17	<i>Euoticus</i>	<i>elegantulus</i>	1	1
18	<i>Galago</i>	<i>senegalensis</i>	1	1
19	<i>Galagooides</i>	<i>demidoff</i>	1	1
20	<i>Otolemur</i>	<i>crassicaudatus</i>	1	1
Tarsiids				
21	<i>Tarsius</i>	<i>spectrum</i>	1	1
Platyrrhines				
22	<i>Aotus</i>	<i>lemurinus</i>	1	1
23	<i>Cebus</i>	<i>apella</i>	1	1
24	<i>Saimiri</i>	<i>boliviensis</i>	1	1
25	<i>Callithrix</i>	<i>argentata</i>	1	1
26	<i>Callimico</i>	<i>goeldii</i>	1	1
27	<i>Cebuella</i>	<i>pygmaea</i>	1	1
28	<i>Leontopithecus</i>	<i>rosalia</i>	1	1
29	<i>Saguinus</i>	<i>imperator</i>	1	1
30	<i>Callicebus</i>	<i>torquatus</i>	1	1
31	<i>Cacajao</i>	<i>calvus</i>	1	1
32	<i>Chiropotes</i>	<i>satanus</i>	1	1
33	<i>Pithecia</i>	<i>pithecia</i>	1	1
34	<i>Alouatta</i>	<i>seniculus</i>	1	1
35	<i>Ateles</i>	<i>paniscus</i>	1	1
36	<i>Lagothrix</i>	<i>lagotricha</i>	1	1
37	<i>Oreonax</i>	<i>flavicauda</i>	1	1
37a	<i>Brachyteles</i>	<i>arachnoides</i>	X	1
Cercopithecoids				
38	<i>Allenopithecus</i>	<i>nigroviridis</i>	1	X
39	<i>Allochrocebus</i>	<i>lhoesti</i>	1	1
40	<i>Cercopithecus</i>	<i>mitis</i>	1	1
41	<i>Chlorocebus</i>	<i>pygerythrus</i>	1	1
42	<i>Erythrocebus</i>	<i>patas</i>	1	1
43	<i>Miopithecus</i>	<i>talapoin</i>	1	X
44	<i>Cercocebus</i>	<i>torquatus</i>	1	1
45	<i>Lophocebus</i>	<i>albigena</i>	1	1
46	<i>Macaca</i>	<i>fascicularis</i>	1	1
47	<i>Macaca</i>	<i>nemestrina</i>	1	1
48	<i>Mandrillus</i>	<i>sphinx</i>	1	1
49	<i>Papio</i>	<i>anubis</i>	1	1
50	<i>Theropithecus</i>	<i>gelada</i>	1	1
51	<i>Colobus</i>	<i>angolensis</i>	1	1
52	<i>Piliocolobus</i>	<i>badius</i>	1	1
53	<i>Procolobus</i>	<i>verus</i>	1	1
54	<i>Kasi</i>	<i>johnii</i>	1	1
55	<i>Nasalis</i>	<i>larvatus</i>	1	1
56	<i>Presbytis</i>	<i>rubicunda</i>	1	1
57	<i>Pygathrix</i>	<i>nemeaeus</i>	1	1
58	<i>Semnopithecus</i>	<i>entellus</i>	1	1
59	<i>Simias</i>	<i>concolor</i>	1	1
60	<i>Trachypithecus</i>	<i>obscurus</i>	1	1
Hominoidea				
61	<i>Hylobates</i>	<i>lar</i>	1	1
62	<i>Sympalangus</i>	<i>syndactylus</i>	1	1
63	<i>Pongo</i>	<i>pygmaeus</i>	1	1
64	<i>Gorilla</i>	<i>gorilla</i>	1	1
65	<i>Pan</i>	<i>troglodytes</i>	1	1
66	<i>Homo</i>	<i>sapiens</i>	1	1

X = unavailable.

TABLE 2. Landmarks used in this study

Landmark no.	Landmark
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

^a landmark collected in both superior and inferior views. See text for details.

tes, except for a few rare taxa (Table 1). The results of multivariate analyses are driven by the samples included in the analyses (e.g., Mitteroecker and Bookstein, 2007; Mitteroecker and Gunz, 2009). Thus, unequal sample sizes can greatly affect the results of such analyses. Because the aim of this study was to analyze cranial morphology across the order and many taxa are sparsely represented in museum collections, we restricted our sample to a single individual of each genus rather than having large samples of common genera and small samples of rare genera. For most genera, we examined the cranium of one species that seemed to be near the center of the genus in terms of size and gross morphological appearance. However, because of the considerable diversity in size and behavior in the genus *Macaca*, we examined two species, *M. nemestrina* and *M. fascicularis*, that differ substantially in size. Individual specimens were chosen for inclusion in this study primarily on their completeness and their availability in the American Museum of Natural History in New York, the Field Museum of Natural History in Chicago, the National Museum of Natural History in Washington, D.C., the Harvard Museum of Comparative Zoology, the Yale Peabody Museum, and the Stony Brook Museum of Comparative Anatomy. All specimens included in this study were adults (recognized by the full eruption of the adult dentition and closed sutures) with no obvious pathologies and were completely intact on at least one side so that all landmarks (Table 2) could be identified and measured.

To obtain a relatively simple, but broad characterization of overall cranial shape among the different primate genera, we identified 18 landmarks covering all parts of the cranium (Table 2 and Fig. 1). These include Type 1, Type 2, and Type 3 landmarks (Slice, 2005) and covered many aspects of morphology that have been discussed in decades of research on primate cranial diversity and evolution, including the size, shape and orientation of the orbits, facial length, breadth and height, palate size and shape, neurocranial size and shape, breadth of the zygomatic arch and postorbital constriction, shape and orientation of the occiput and foramen magnum, as well as flexion of the cranial base and the spatial relationship between the neuromorphocranial and splanchnocranial (Fig. 2).

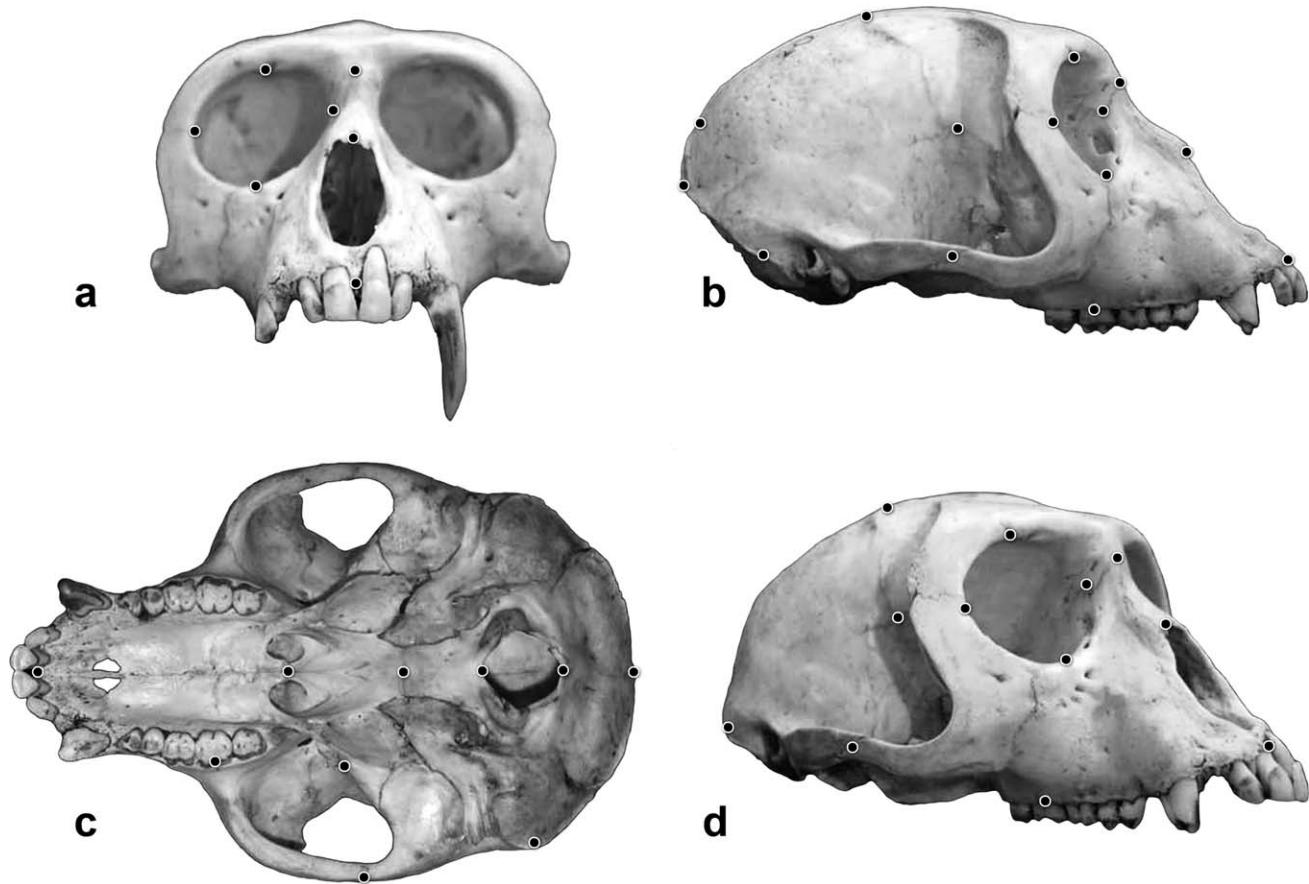


Fig. 1. Landmarks used in this study. See also Table 2. (a) Frontal view; (b) lateral view; (c) basicranial view; (d) oblique view.

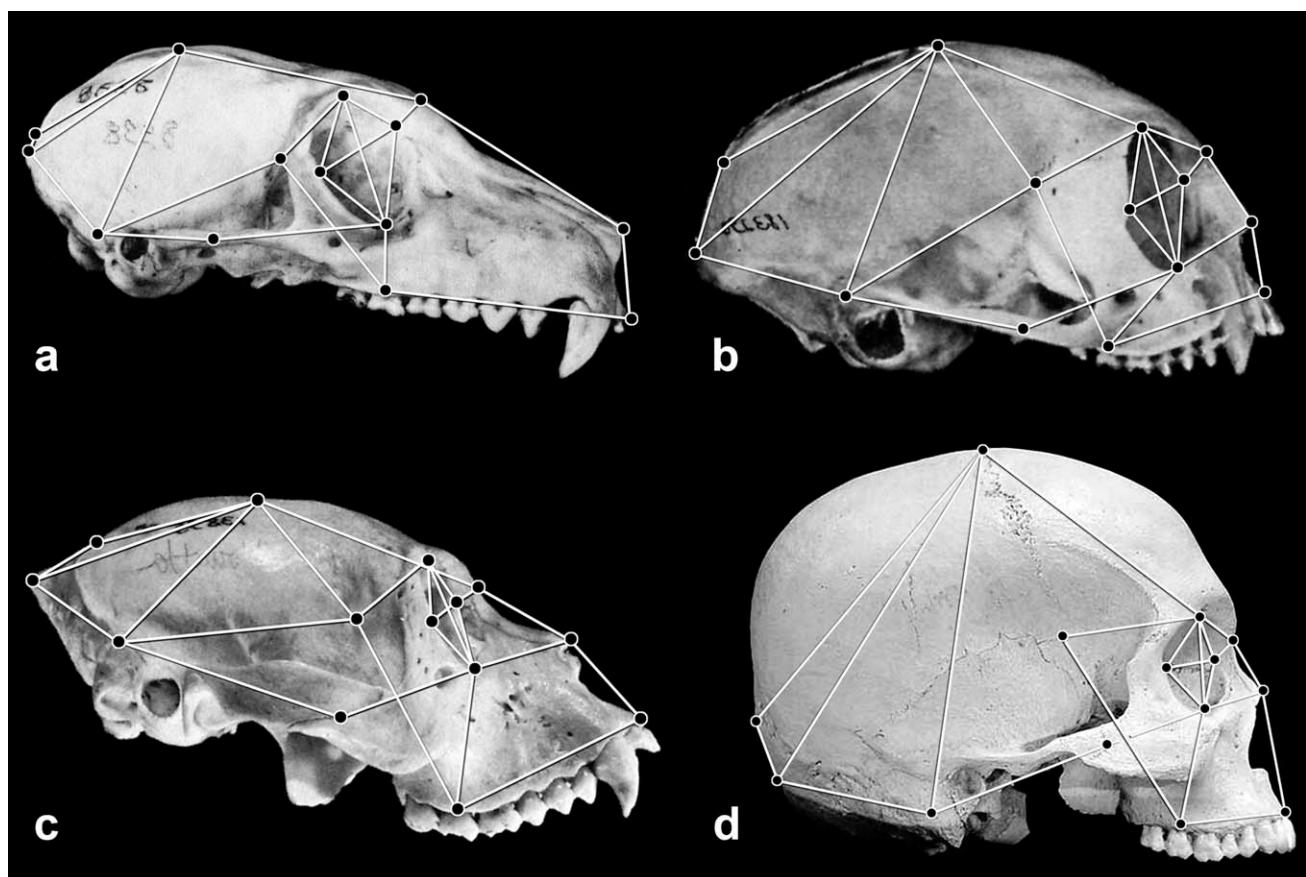


Fig. 2. Wireframe diagrams of four primate crania demonstrating the extent to which the landmarks capture differences in cranial shape. (a) *Eulemur*; (b) *Callithrix*; (c) *Alouatta*; (d) *Homo*.

The landmarks were digitized on each cranium using a Microscribe G2X digitizer (Marcus, 1997). All bilateral landmarks were digitized on the right side of the cranium. The individual crania were stabilized in a bed of clay/Play-Doh, and the 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 (Table 2). The two sets of measurements were then stitched together using the program DVL v. 0.4.9 (Raaum, 2006) to obtain a single set of 18 3D 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 using a least-squares calculation (e.g., see Frost et al., 2003; Harvati et al., 2004). 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 and Jones, 1998, 2006).

There are potential methodological sources of variation in the results of studies of geometric morphometrics other than that in the specimens being studied and many approaches to identifying and addressing these (Singleton, 2002; von Cramon-Taubadel et al., 2007; Lockwood et al., 2002). To evaluate the effect of data collection by different individuals on the replicability of the overall landmark configuration of specimens in our study, we digitized the same male *Hylobates* skull several times in succession, alternating among the different authors. We also digitized three specimens of one species (*Callicebus torquatus*) and three similar species of the same genus (*Aotus*). Our results indicated that any interobserver differences introduced less variation than can be expected within multiple specimens of the same species or genus, and that intrageneric variation is generally less than intergeneric variation. Moreover, the fact that separate analyses of male and female crania yield very similar plots indicates that neither specimen sampling nor measurement variation are distorting our results in any significant way (see also Lockwood et al., 2002).

Because the results of a PCA on 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 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 crania shapes along each of the first four 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 the correlations between the linear dimensions, indices, and angles and the values along individual axes of the PCA using SPSS 13.0. Because cranial base flexion is difficult to characterize on the external skull, we used several measures of this cranial feature (Aiello and Dean, 1990; Lieberman et al., 2000; McCarthy, 2001) and also included species specific values from the literature (Ross and Ravosa, 1993; Lieberman et al., 2000).

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 \times basion-bregma $\times 2 \times$ euryon-opisthion
Frontation	Angle between orbitale superior-alveolare and orbitale superior-orbitale inferior
Convergence	Angle between inion-nasion and inion-lateral orbit border

To compare cranial diversity among clades, we followed methodology similar to Wills et al. (1994) and Kamilar (2006) 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:

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

where PC is the principal component score for component x and e is 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), the variances of weighted PC scores for all included genera/species were summed. 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 and Sokal, 1995).

For calculating the morphological distance between individual taxa, we calculated the Procrustes distance between each specimen in each analysis using the software program TPSSmall (Rohlf, 2003). We then focused our attention on the Procrustes distances between distinctive pairs of sister-taxa throughout the Order Primates.

All analyses were performed on the male sample and the female sample separately as well as on the total sample with both sexes combined. In some cases, the directionality of the principal component axes differs between analyses. This is a commonly seen artifact of PCA calculation because the direction of the principal component axes is arbitrary and has no biological or statistical significance (e.g., Jolliffe, 2002; Macleod, 2006). For convenience, we have plotted all of the axes to match those from the male analysis and presented correlations of individual cranial features on principal component values in a uniform fashion.

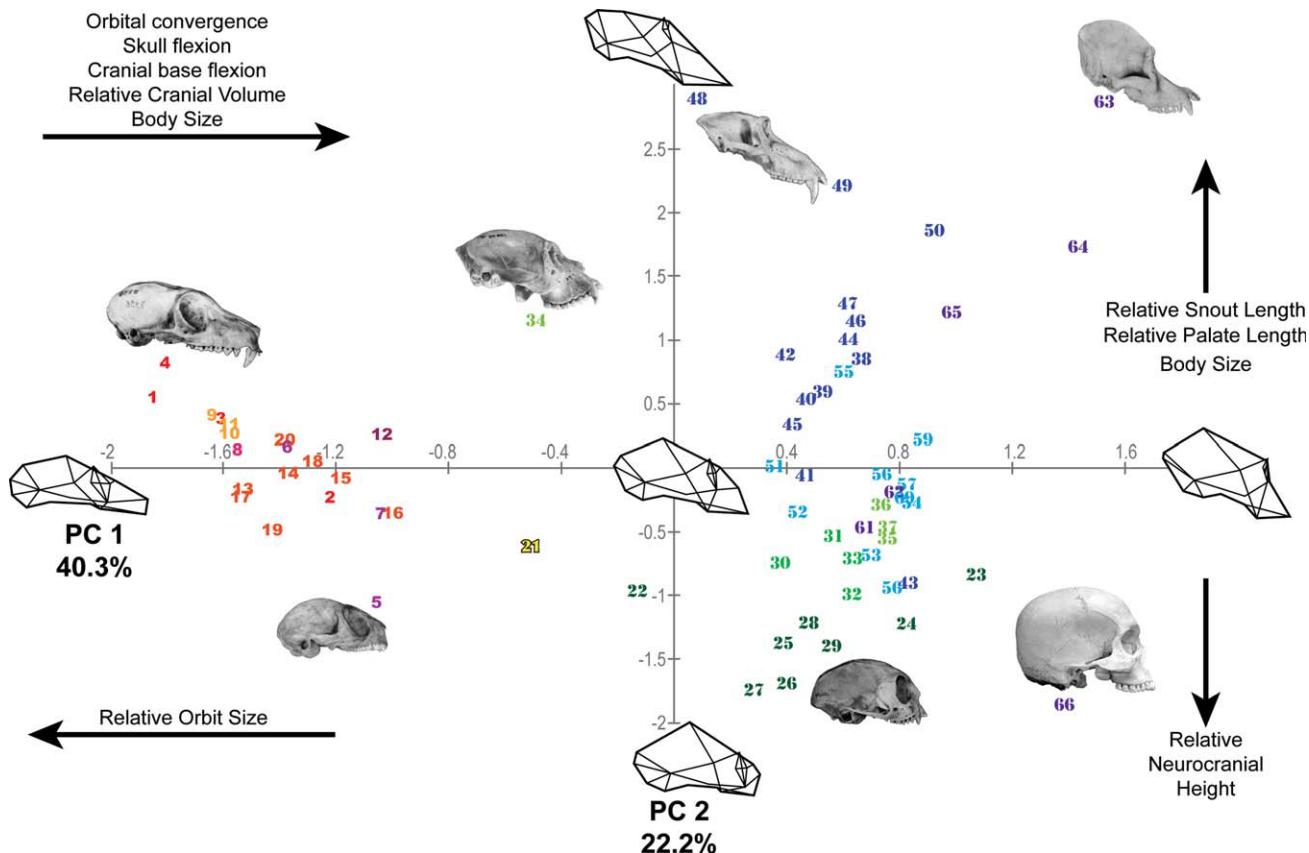


Fig. 3. PCA of male primates demonstrating the extremes of primate cranial morphology, with both extant crania, and wireframes of the principal component axes, as well as the aspects of cranial morphology most highly correlated with each component. Numbers of individual taxa follow Taxon Code in Table 1. Colors reference major primate groups. Red, Lemurids; light purple, Indriids; maroon, Daubentonoids; light orange, Cheirogaleids; dark orange, Lorisoids; yellow, Tarsiids; light green, Atelids; dark green, Cebids; light blue, Colobines; dark blue, Cercopithecines; dark purple, Hominoids.

TABLE 4. Variance loadings for the first eight PCs of the male, female, and mixed-sex analyses

	Males (%)	Females (%)	Mixed-sex (%)
PC 1	40.30	46.20	41.90
PC 2	22.20	15.20	19.30
PC 3	7.36	8.57	7.83
PC 4	6.12	4.71	5.03
PC 5	3.44	3.92	3.39
PC 6	2.65	3.21	2.88
PC 7	2.48	2.43	2.31
PC 8	2.24	2.18	2.09
Total	86.79	88.58	84.73

RESULTS

Major features of primate cranial shape

The first two principal components of the analysis of the 66 male crania are shown in Figure 3. The first component accounts for 40.3% of the overall variance and the second accounts for 22.2%. Component 3 accounts for 7.4% of the variance (Table 4). The first principal component is positively associated with measurements reflecting increased overall size, orbital convergence, relative facial depth, skull flexion, orbital frontation, cranial base flexion, and relative neurocranial volume; it is negatively correlated with relative orbit size. The second principal

component is positively associated with measurements of overall size, relative snout length, and relative palate length, and negatively correlated with relative neurocranial height (Fig. 3 and Table 5). The crania at extremes of the PC 1 are, in the negative direction, *Varecia* and *Eulemur*, with their relatively long, flat crania with a small braincase and laterally facing orbits; and the great apes and humans in the positive direction with their flexed skulls, relatively large braincases, and convergent orbits. On PC 2, in the positive direction, the extreme taxa include mandrills, orangutans, and gorillas with their relatively long maxillae; and callitrichids and humans in the negative direction with their relatively tall braincases and short faces with small maxillae (Fig. 3). Analyses of female crania (Fig. 4) and both male and female crania (Fig. 5) yield similar distributions of taxa and similar correlations between the principal component axes and major aspects of cranial shape (Table 5).

Phylogenetic patterns

The first principal component separates strepsirrhines in the negative direction from anthropoids in the positive direction; *Tarsius* lies in between. Thus, PC 1 separates both strepsirrhines from haplorhines and prosimians from anthropoids (Figs. 6 and 7). Within strepsirrhines, indriids, *Daubentonina*, and lorisoids plot closest to anthropoids, most likely due to their relatively short

TABLE 5. Cranial shape loadings for the first four PCs of the male, female and mixed-sex analyses

	Correlation coefficient (M, F, mixed-sex)				C.S.
	PC1	PC2	PC3	PC4	
Skull flexion	0.679 , 0.655 , 0.631	0.584 , 0.552 , 0.609	-0.336 , -0.435 , -0.383	0.131 , 0.101 , 0.107	0.795 , 0.657 , 0.737
Cranial base flexion	-0.602 , -0.729 , -0.666	-0.026 , -0.219 , -0.108	0.377 , 0.186 , 0.285	-0.003 , -0.281 , -0.081	-0.360 , -0.490 , -0.409
Relative snout length (snout length/skull length)	0.390 , 0.270 , 0.286	0.816 , 0.823 , 0.844	-0.239 , -0.327 , -0.278	-0.058 , -0.035 , -0.051	0.737 , 0.586 , 0.673
Relative skull length (skull length/C.S.)	-0.041 , -0.146 , -0.127	0.893 , 0.893 , 0.877	-0.154 , -0.140 , -0.164	-0.248 , -0.124 , -0.215	0.479 , 0.495 , 0.487
Relative neurocranial height (skull height/C.S.)	0.075 , 0.439 , 0.259	-0.662 , -0.343 , -0.551	0.037 , -0.039 , -0.013	0.514 , 0.549 , 0.551	-0.205 , 0.171 , -0.063
Relative palate length (palate length/C.S.)	-0.278 , -0.354 , -0.343	0.751 , 0.693 , 0.693	-0.209 , -0.221 , -0.221	-0.256 , 0.039 , -0.146	0.259 , 0.173 , 0.222
Relative orbit size (orbit width/skull length)	-0.433 , -0.387 , -0.390	-0.505 , -0.523 , -0.520	-0.164 , -0.318 , -0.223	0.295 , 0.130 , 0.238	-0.685 , -0.672 , -0.677
Relative orbit size (orbit width/C.S.)	-0.511 , -0.462 , -0.473	-0.336 , -0.384 , -0.371	-0.207 , -0.371 , -0.275	0.263 , 0.114 , 0.210	-0.658 , -0.637 , -0.645
Relative cranial volume (cranial volume/C.S.)	0.532 , 0.473 , 0.497	0.235 , 0.368 , 0.316	-0.128 , -0.087 , -0.118	0.449 , 0.382 , 0.420	0.850 , 0.882 , 0.864
Upper facial length/lower facial length	-0.810 , -0.797 , -0.806	0.155 , 0.081 , 0.072	-0.250 , -0.300 , -0.271	-0.162 , -0.161 , -0.201	-0.446 , -0.469 , -0.455
Frontation	-0.627 , -0.533 , -0.566	-0.449 , -0.437 , -0.463	0.336 , 0.280 , 0.312	-0.006 , 0.187 , 0.074	-0.633 , -0.531 , -0.585
Convergence	-0.833 , -0.841 , -0.838	-0.001 , -0.200 , -0.110	-0.016 , -0.131 , -0.071	0.374 , 0.145 , 0.305	-0.500 , -0.536 , -0.511
Relative facial depth (facial depth/C.S.)	0.730 , 0.667 , 0.668	0.544 , 0.503 , 0.578	-0.053 , 0.087 , 0.008	0.016 , 0.028 , 0.020	0.798 , 0.746 , 0.777
CBA4	X , X , -0.357	X , X , -0.169	X , X , 0.313	X , X , -0.472	X , X , -0.527
CBA1	X , X , -0.493	X , X , -0.179	X , X , 0.350	X , X , -0.229	X , X , -0.396
C.S.	0.610 , 0.504 , 0.535	0.580 , 0.634 , 0.634	-0.033 , 0.084 , 0.011	0.192 , 0.215 , 0.211	1.00 , 1.00 , 1.00

M, males; F, females; C.S., centroid size; X, unavailable. CBA1 and CBA4 refer to measures of cranial base angulation as presented by Ross and Ravosa (1993) and Lieberman et al. (2000). Significant correlation coefficients ($P < 0.05$) are in bold. PC1: skull flexion, cranial base flexion, upper facial length/lower facial length, convergence, frontation, facial depth, orbit size, cranial volume, CBA, body size. PC2: skull flexion, snout length, skull length, palate length, neurocranial height, orbit size, frontation, facial depth, body size.

snouts, globular neurocrania, and convergent orbits, respectively. The anthropoids closest to the prosimians are *Alouatta*, distinguished by its low, unflexed skull (airorhynch); see Biegert, 1963; Bruner et al., 2004), and *Aotus* with its large orbits. Within anthropoids, PC1 separates great apes (but not hylobatids) from cercopithecoids and platyrhines.

PC 2 largely separates groups of anthropoids based on aspects of relative facial length, palate length, and cranial height (Figs. 3–7). In contrast to the diversity among major anthropoid groups, there is very little dispersion of extant strepsirrhines on this axis, but among females, it separates long-snouted lemurids from indriids, and lorises from galagos (Fig. 4). Among anthropoids, PC 2 tends to separate cercopithecoids from platyrhines (except *Alouatta*). In addition, PC 2 largely separates the major families and subfamilies within these groups. Thus among platyrhines, atelids are largely separated from cebids and among cercopithecoids, cercopithecines are largely separated from colobines (Fig. 7). The notable exceptions are male *Nasalis* which plots within the longer-snouted cercopithecines and male *Miopithecus* which plots with the short-snouted colobines. While hominoids are separated from other catarrhines on PC 1, most of the differences among hominoids lie on PC 2, where there is very little overlap between the major groups among all plots. Hylobatids, great apes, and humans all occupy separate morphospace on PC 2, with great apes showing very positive scores, hylobatids near the center (among colobines), and humans with very negative values.

The analyses of female crania (Fig. 4) and the combined-sex analysis (Fig. 5) yield similar patterns. Thus, the major morphological differences in the shape of primate crania are largely those that have characterized the evolution of different higher-level clades, such as strepsirrhines, anthropoids, cercopithecoids, and hominoids, rather than evolution within these clades. More detailed analyses of between-sex differences are underway and will be presented in a future study (but see Discussion and Gilbert et al., 2009a).

Relative diversity among primate clades

Like most biologists, primatologists regularly make statements about the morphological diversity of different groups, but these statements are rarely based on any quantitative assessment. We have used the within group variance of the coordinates on the first eight principal components (accounting for ~85% of total information in each analysis) to obtain a quantitative measure of cranial diversity for individual clades (Table 6). The most striking results of these comparisons are the great relative diversity among extant hominoids and the low relative diversity among extant strepsirrhines. The morphological diversity among hominoids is largely a result of the unusual shape of the human cranium, combined with the small number of taxa (Fig. 7). Thus, nonhuman hominoids are not significantly more diverse than other clades (Table 6).

Among males as well as males and females combined, extant strepsirrhines have significantly less cranial diversity than haplorhines, anthropoids, catarrhines, and hominoids. However, there are almost no significant differences among strepsirrhines, platyrhines, or cercopithecoids (one exception: mixed-sex platyrhines vs. strepsirrhines). The fact that many of these significant differences between primate groups disappear in the female analysis demonstrates that male cranial morphology is

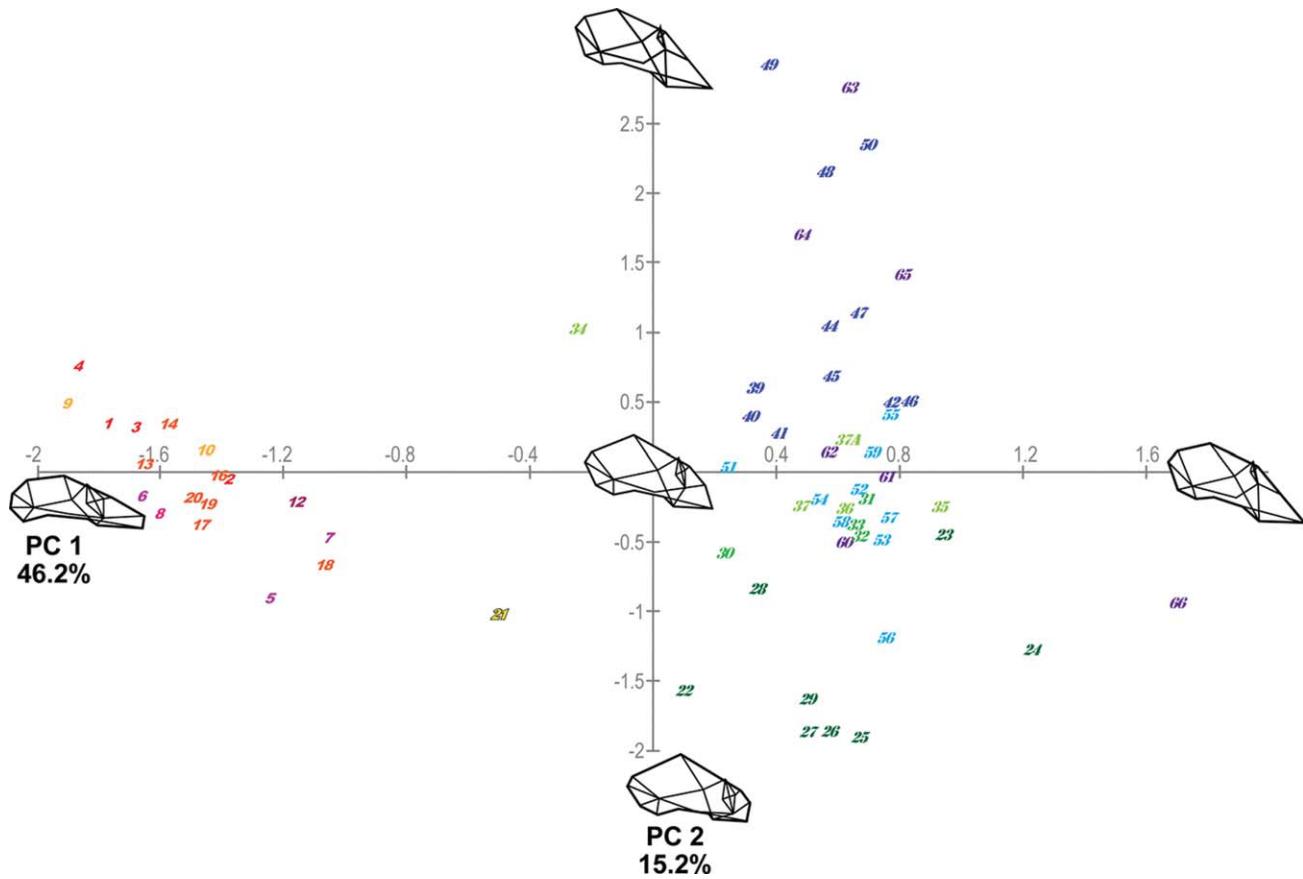


Fig. 4. PCA of female primate crania. Numbers of individual taxa follow Taxon Code in Table 1. See Figure 3 caption for color codes.

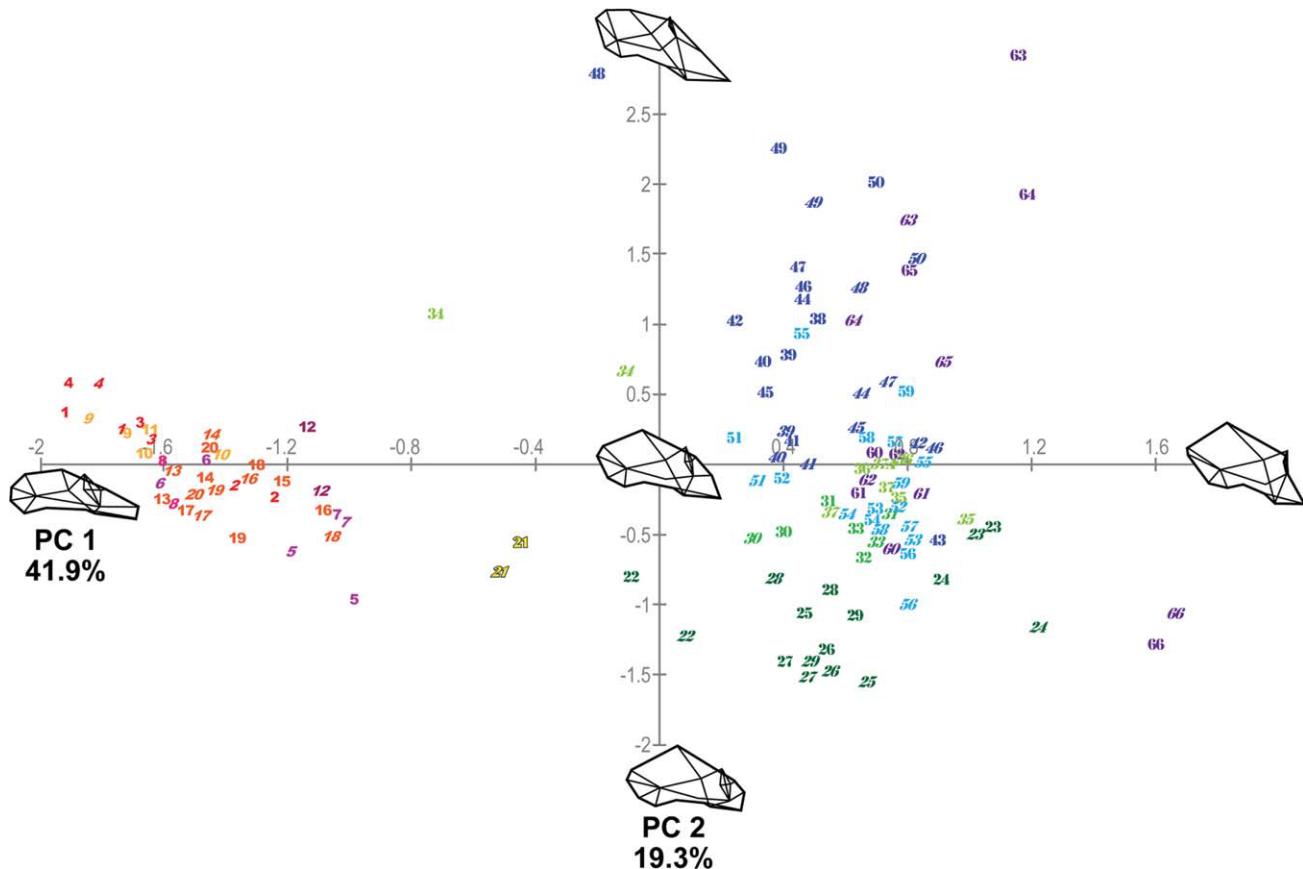


Fig. 5. PCA of male and female primate crania. Males in bold numbers, females in italics. Numbers of individual taxa follow Taxon Code in Table 1. See Figure 3 caption for color codes.

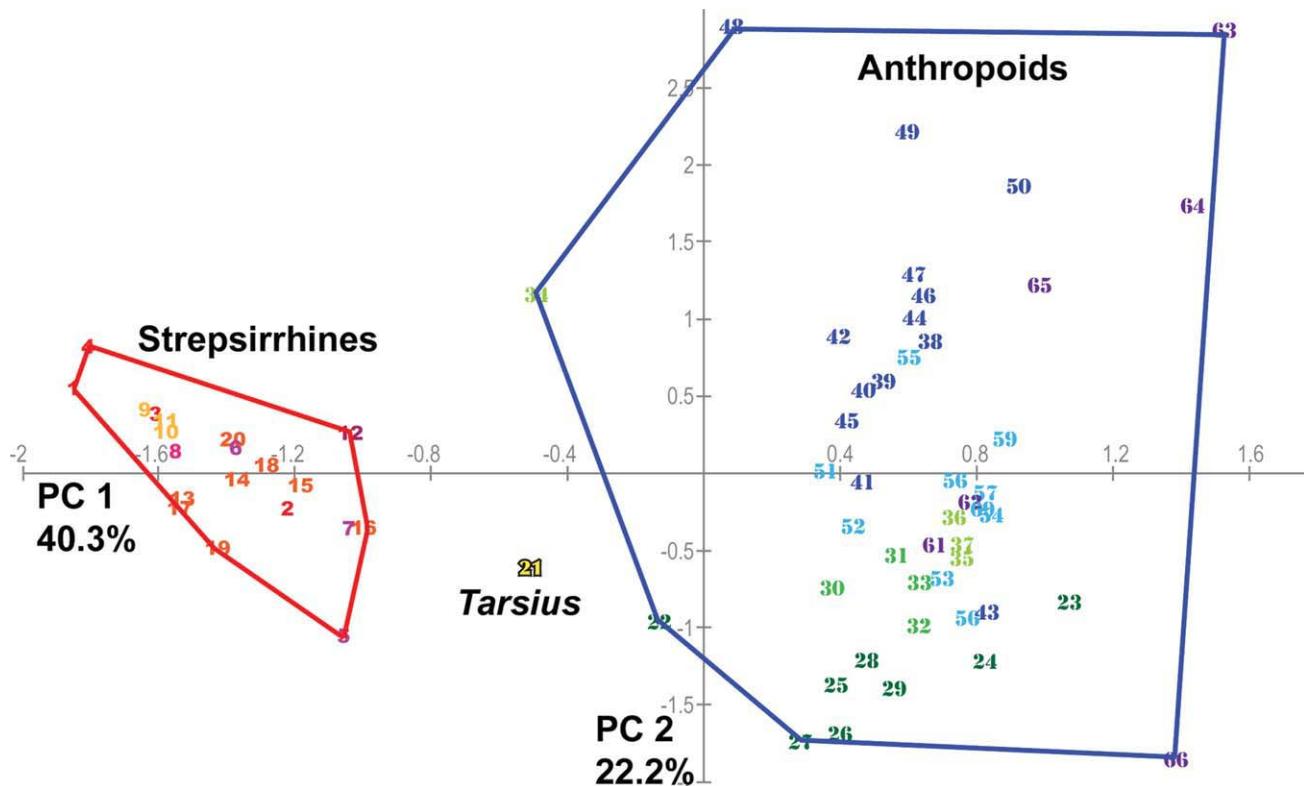


Fig. 6. PCA of male primate crania. Polygons outline the distribution of strepsirrhines and anthropoids, with tarsiers labeled in between. Numbers of individual taxa follow Taxon Code in Table 1. See Figure 3 caption for color codes.

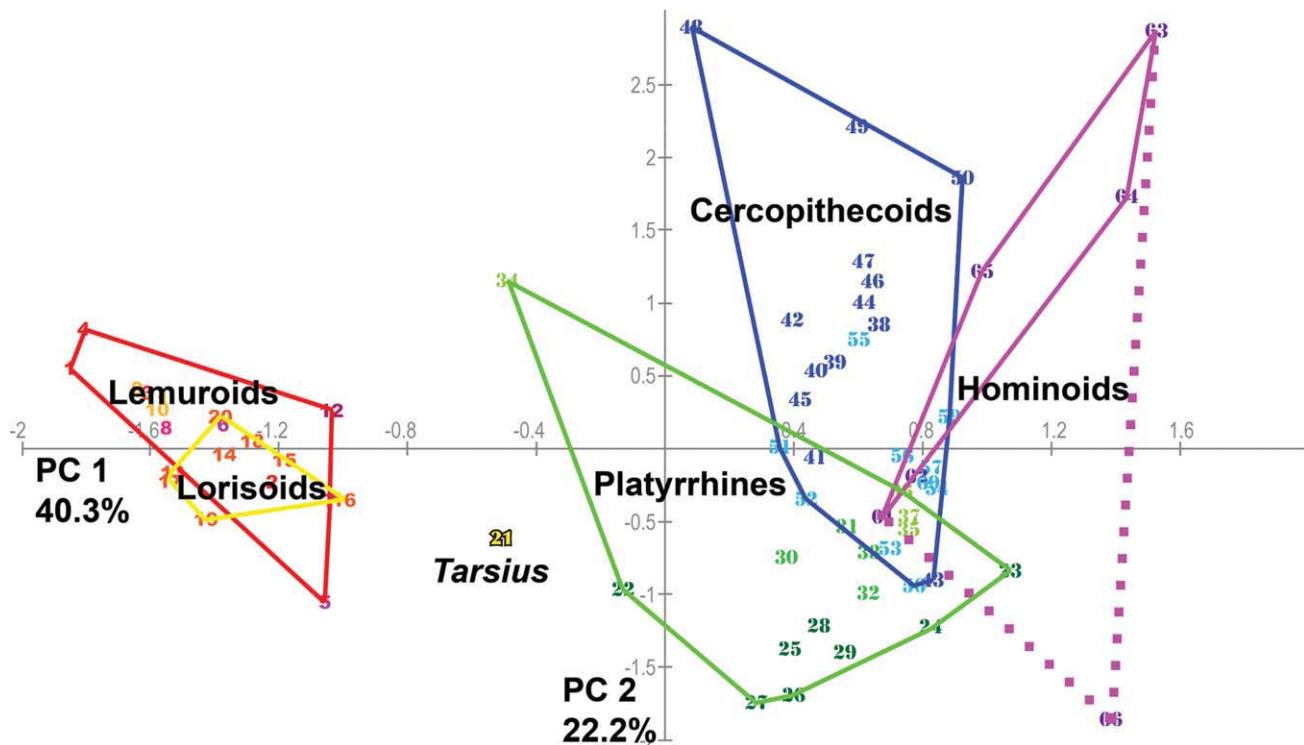


Fig. 7. PCA of male primate crania. Polygons outline the distribution of major groups among strepsirrhines and anthropoids. Numbers of individual taxa follow Taxon Code in Table 1. See Figure 3 caption for color codes.

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

vs.	Prosimians	Anthropoids	Strepsirrhines	Haplorrhines	Platyrrhines	Catarrhines
	(M, F, M-S)	(M, F, M-S)	(M, F, M-S)	(M, F, M-S)	(M, F, M-S)	(M, F, M-S)
Prosimians	> X	0.38, 0.88, 0.53	1.37, 1.67, 1.50	0.36, 0.75, 0.48	0.63, 0.92, 0.71	0.42, 1.01, 0.58
Anthropoids	> 2.64, 1.13, 1.90 X		3.62, 1.90, 2.85 X	0.95, 0.85, 0.92	1.67, 1.04, 1.34	1.11, 1.14, 1.11
Strepsirrhines	> 0.73, 0.60, 0.67	0.28, 0.53, 0.35	X	0.26, 0.45, 0.32	0.46, 0.55, 0.47	0.31, 0.60, 0.39
Haplorrhines	> 2.79, 1.33, 2.07	1.06, 1.17, 1.09	3.83, 2.22, 3.10	X	1.76, 1.22, 1.46	1.18, 1.34, 1.21
Platyrrhines	> 1.58, 1.09, 1.41	0.60, 0.96, 0.74	2.17, 1.83, 2.12	0.57, 0.82, 0.68	X	0.67, 1.10, 0.83
Catarrhines	> 2.37, 0.99, 1.71	0.90, 0.87, 0.90	3.24, 1.66, 2.57	0.85, 0.75, 0.82	1.50, 0.91, 1.21	X
Cercopithecoids	> 1.41, 0.54, 1.12	0.53, 0.48, 0.59	1.93, 0.90, 1.68	0.51, 0.41, 0.54	0.89, 0.49, 0.79	0.60, 0.54, 0.65
Hominoids	> 4.95, 2.47, 3.04	1.88, 2.18, 1.60	6.79, 4.13, 4.56	1.78, 1.86, 1.60	3.13, 2.26, 2.15	2.09, 2.49, 1.77
Non-human Hominoids	> 3.60, 0.53, 1.61	1.36, 0.47, 0.85	4.93, 0.89, 2.42	1.29, 0.40, 0.78	2.28, 0.48, 1.14	1.52, 0.53, 0.94
Lemuroidea	> 0.95, 0.74, 0.85	0.36, 0.65, 0.45	1.29, 1.23, 1.27	0.33, 0.55, 0.41	0.60, 0.67, 0.60	0.40, 0.74, 0.49
Lorisoidae	> 0.37, 0.39, 0.34	0.14, 0.35, 0.18	0.51, 0.66, 0.51	0.13, 0.30, 0.16	0.23, 0.36, 0.24	0.16, 0.40, 0.20
	Cercopithecoids	Hominoids	Non-Human Hominoids	Lemuroidea	Lorisoidae	
	(M, F, M-S)	(M, F, M-S)	(M, F, M-S)	(M, F, M-S)	(M, F, M-S)	
Prosimians	> 0.71, 1.86, 0.89	0.20, 0.41, 0.33	0.28, 1.89, 0.62	1.06, 1.36, 1.18	2.69, 2.55, 2.93	
Anthropoids	> 1.87, 2.10, 1.70	0.53, 0.46, 0.62	0.73, 2.14, 1.18	2.79, 1.54, 2.24	7.11, 2.89, 5.57	
Strepsirrhines	> 0.52, 1.11, 0.60	0.15, 0.24, 0.22	0.20, 1.13, 0.41	0.77, 0.81, 0.79	1.96, 1.52, 1.96	
Haplorrhines	> 1.98, 2.46, 1.85	0.56, 0.54, 0.68	0.78, 2.51, 1.28	2.95, 1.80, 2.44	7.51, 3.38, 6.07	
Platyrrhines	> 1.12, 2.03, 1.27	0.32, 0.44, 0.47	0.44, 2.06, 0.88	1.67, 1.48, 1.67	4.26, 2.78, 4.15	
Catarrhines	> 1.68, 1.84, 1.53	0.48, 0.40, 0.56	0.66, 1.88, 1.06	2.50, 1.35, 2.03	6.38, 2.53, 5.03	
Cercopithecoids	> X	0.28, 0.22, 0.37	0.39, 1.02, 0.69	1.49, 0.73, 1.32	3.80, 1.37, 3.28	
Hominoids	> 3.51, 4.58, 2.72	X	1.38, 4.66, 1.88	5.23, 3.35, 3.59	13.34, 6.28, 8.92	
Non-human Hominoids	> 2.55, 0.98, 1.44	0.73, 0.21, 0.53	X	3.80, 0.72, 1.91	9.69, 1.35, 4.74	
Lemuroidea	> 0.67, 1.37, 0.76	0.19, 0.30, 0.28	0.26, 1.39, 0.52	X	2.55, 1.87, 2.48	
Lorisoidae	> 0.26, 0.73, 0.30	0.07, 0.16, 0.11	0.10, 0.74, 0.21	0.39, 0.53, 0.40	X	

M, males; F, females; M-S, mixed-sex. Significant F-values ($P < 0.05$) are in bold. The table should be read from left to right with the value in each cell indicating whether or not the taxon listed at the left of the table has a significantly greater variance than the taxon listed at the top of the table.

particularly distinctive and driving a large portion of the diversity among anthropoid crania (Gilbert, 2007; Gilbert et al., 2009b).

Cranial differences between closely related taxa

Among primate crania, our human cranium is very distinct as evidenced in the results presented earlier. To put the uniqueness of the human cranium in a broader perspective, we calculated the Procrustes distances between pairs of closely related, but morphologically distinct, taxa in several different clades. Among hominoids, we compared shape differences between the sister taxa *Pan* and *Homo*; among cercopithecoids we compared differences between *Mandrillus* and *Cercocebus*; among platyrrhines, we compared the difference between the morphologically distinctive *Alouatta* and *Ateles*; and among strepsirrhines, we compared the distance between *Daubentonia* and *Eulemur* (Table 7 and Fig. 8). In both males and females the distance in cranial shape between *Pan* and *Homo* is greater than that between any of the other closely related taxa. This is despite the fact that the estimated divergence time between humans and chimpanzees is far less, in many cases, than that between other pairs of taxa. The lack of a particularly large distance between *Daubentonia* and other strepsirrhines is surprising (e.g., Oxnard, 1981; Groves, 2004), but most probably reflects the fact that our measures of cranial morphology do not capture many of the oddities of the aye-aye such as its dental formula, ever-growing incisors, and its elongated, specialized third manual digit.

TABLE 7. Procrustes distances between morphologically extreme sister taxa

Sister-Taxa	Males	Females
<i>Homo-Pan</i>	0.3378	0.2776
<i>Mandrillus-Cercocebus</i>	0.2091	0.1286
<i>Alouatta-Ateles</i>	0.2817	0.1917
<i>Daubentonia-Eulemur</i>	0.2064	0.2050

DISCUSSION

In this study, we undertook to examine the extent to which we could use a relatively small number of cranial landmarks and a powerful morphometric technique to examine gross patterns of cranial morphology and diversity within the Order Primates. Despite a very limited sampling of cranial anatomy, we were able to distinguish and characterize many aspects of cranial evolution within our order. In many respects, our results complement previous research on many major issues in primate evolutionary morphology.

Statistics and biology

To more easily interpret the results of our Procrustes analyses, we used principal components analysis, a multivariate approach that facilitates interpretation by identifying a new series of independent axes containing a relative large amount of the same information (e.g., Sokal and Rohlf, 1995; Tabachnick and Fidell, 2007). As many

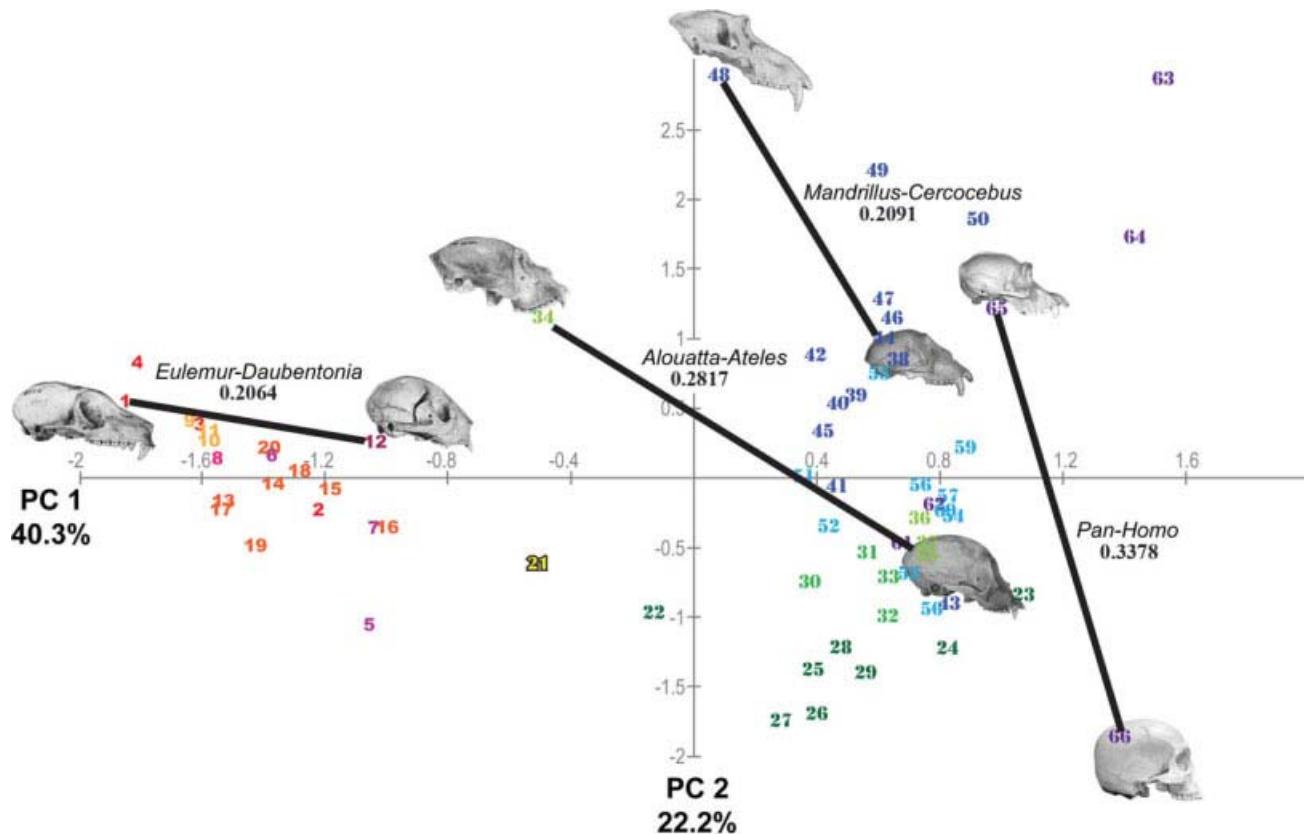


Fig. 8. PCA of male primates demonstrating extreme sister-taxa. See also Table 7. Numbers of individual taxa follow Taxon Code in Table 1. See Figure 3 caption for color codes. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com].

researchers have emphasized (e.g., Mitteroecker et al., 2005; Mitteroecker and Bookstein, 2007; Mitteroecker and Gunz, 2009), 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., Sokal and Rohlf, 1995). Thus, in our analyses, the first principal component clearly separates anthropoids from nonanthropoid primates and tarsiers from both anthropoids and strepsirrhines. Therefore, we can interpret these results both as statistical analyses identifying the major components of cranial shape and in terms of major events in primate evolution. However, it is also true that the separation of anthropoids from other primates, as well as the separation of other clades, was not an obvious and anticipated result of the landmarks we measured. It was quite plausible that the most prominent shape differences among primate crania might well have been simply body size, or cranial differences distinguishing nocturnal taxa with large eyes from diurnal taxa with small eyes, or features related to diet such as palate length and width. This is especially true since our landmarks did not capture many of the features normally used to characterize anthropoids and other groups of primates such as postorbital closure, features of the auditory region, and features of the dentition (e.g., Fleagle, 1999). The fact that the first principal component separated anthropoids from other primates reinforces the common observation

that the evolution of the higher primate cranium involved both a major morphological transformation and a significant cladistic event in primate evolution (e.g., Fleagle and Kay, 1994; Ross and Kay, 2004).

Patterns of morphological diversity and organization

In the analyses described earlier, we were able to identify the aspects of cranial shape that differ among all living primates and how these features are interrelated. In many regards, our results corroborate the findings of previous studies using different techniques. Thus, most of the major morphological differences in primate cranial morphology in our analyses have been widely discussed and debated in the literature.

Size. Size is a factor that affects all aspects of morphological change and organization (e.g., Jungers, 1985), including cranial morphology (e.g., Biegert, 1963; Ross, 1995; Marroig and Cheverud, 2005). In our analyses, size, represented by the Procrustes Centroid Size (CS), is highly correlated with each of the first two principal components (Table 5). Despite a relatively high correlation between centroid size and the first principal component, individual taxa are only loosely arranged by size along this axis. Thus, the smaller lemurs and lorises are on the left side of the plot and the larger great apes on the right. However, marmosets and tamarins, which are similar in size to the smallest lemurs and lorises, also

have high values on the first component. While the major axis of cranial shape change among primates is correlated with size, it is not simply a size factor. This is further evidenced by the fact that the second axis of morphological change is as highly correlated with centroid size as the first. Although allometry certainly plays a role in various features of the primate cranium (see correlations in Table 5), the morphological shift from prosimians to anthropoids documented on the first axis must have been a consequence of factors other than simple allometric scaling. Similarly, the differences among anthropoid taxa on the second axis are not purely due to the effects of allometry.

There is some suggestion from the distribution of individual taxa, from the wireframes, and the correlations in Table 5, that the first two principal components are associated with different aspects of cranial size, with PC1 being more highly correlated with the size of the neurocranium while PC2 is more highly correlated with the size of the palate and dentition (e.g., Figs. 3–5). Many studies of primate morphology and development have dealt with the “independent” nature of these two aspects of the cranium (e.g., Lieberman et al., 2000). Further analyses of both immature and adult specimens, using more landmarks, especially of the neurocranium would help determine more clearly how independent the different aspects of the cranium are in primate evolution and development.

Orbit size. The relative size of the orbits differs considerably among extant primates and has a considerable impact on the shape of the cranium. As many studies have documented, orbit size is highly correlated with body size and is negatively allometric for simple functional reasons (Ross, 1995). Smaller taxa must have relatively larger eyes to have similar numbers of retinal cells and similar visual acuity and sensitivity. However, within the negatively allometric pattern, orbit size is also associated with activity cycle; nocturnal taxa have relatively larger orbits than similar-size diurnal taxa (e.g., Kay and Cartmill, 1977; Martin, 1990). The negative allometry of primate orbit size is evident in our analysis as orbit diameter is negatively correlated with the first principal component and also negatively correlated with centroid size. However, the association with activity pattern does not appear in our results. In the first three components of our study, there is no clear separation between diurnal and nocturnal taxa, with one exception. *Aotus*, the one nocturnal anthropoid, with exceptionally large orbits has an extremely low value on the first component and plots very near to *Tarsius*, the primate with the relatively largest eyes.

Orbit orientation. In addition to differences in size, primates vary considerably in the orientation of their orbits. Two types of orbit orientation are usually identified. Frontation is the degree of verticality of the orbits, i.e., whether they face anteriorly or superiorly; convergence is the degree to which the right and left orbits face in the same direction (e.g., Cartmill, 1972; Martin, 1990; Ross, 1995). While frontation and convergence have been shown to be correlated among primates, the relationships of these measures within different clades and with other aspects of cranial shape are complex (Ross, 1995). However, convergence of the orbits increases with body size, in part because the relatively smaller orbits of larger taxa can more easily be aligned to face forward (Cartmill, 1972; Martin 1990) and a high

amount of orbital convergence, facilitated by a narrow interorbital septum, distinguishes anthropoids from other primates (e.g., Ross, 1995). Our analyses largely accord with these previous studies (e.g., Fig. 3 and Table 5). Both frontation and convergence are highly correlated with the first principal component and with centroid size, and frontation is also correlated with the second principal component. Orbital convergence has an especially high correlation with the first principal component that separates anthropoids from other primates but is not correlated with the second principal component that largely described differences within anthropoids.

Cranial flexion. It has long been recognized that there is considerable variation among primates in the positional relationship of the face and the neurocranium (e.g., Huxley, 1863; Aiello and Dean, 1990) and that these positional differences are related to differences in the angulation of the cranial base and ontogenetic changes in that part of the skull (e.g., Huxley, 1863; Biegert, 1963; Aiello and Dean, 1990; Ross and Ravosa, 1993; Lieberman et al., 2000). In addition, the angulation of the cranial base has also been related to numerous other aspects of cranial anatomy, including brain size, orbit size, orbit orientation, and palate size (e.g., Biegert, 1963; Ross and Ravosa, 1993; Lieberman et al., 2000, 2008).

As many researchers have noted, the orientation of the cranial base is difficult to document with intact crania (Aiello and Dean, 1990) and a variety of measurements have been proposed for describing cranial flexion (e.g., Lieberman et al., 2000; McCarthy, 2001). As discussed earlier, we examined the relationship between several different measure of cranial flexion and estimates of cranial base flexion and the principal components in our analyses (Table 5). All were positively correlated with the first principal component, but only one measure was correlated with the second component. The positive correlations between measures of cranial flexion and the first principal component (Fig. 3), which is also highly correlated with orbital convergence and neurocranial size, supports other studies linking basicranial flexion to these aspects of cranial morphology and, in turn, these features to the cranial reorganization which took place during the evolution of anthropoids (Ross and Ravosa, 1993; Lieberman et al., 2000). Nevertheless, it is important to keep in mind that any correlations of this nature are heavily dependent upon the taxa included in the analysis. The most prominent morphological distinctions in our study are those distinguishing anthropoid from other, nonanthropoid, primates. More detailed study looking at morphological relationships within different clades and within ontogenetic sequences are needed to document solid developmental constraints and interrelationships.

The interplay of morphological and phyletic evolution

In our analyses, as noted earlier, the major morphological differences in primate cranial morphology are those between major clades; more specifically, those that characterize major evolutionary innovations in primate evolution. The evolution of many “new” clades of primates has been characterized by major changes in aspects of cranial shape and organization that still are evident in the extant genera of those clades.

The major division in primate cranial morphology is that between anthropoids and prosimians (Figs. 3–6).

Thus, the aspects of cranial morphology commonly cited as defining anthropoid features—increased orbital convergence (Cartmill, 1972; Ross, 1995, 1996, 2000), increased frontation (Cartmill, 1972; Ross, 1995, 1996, 2000), increased cranial flexion (e.g., Ross and Ravosa, 1993; Ross, 1996; Lieberman et al., 2000; Ravosa et al., 2000), increased neurocranial volume (e.g., Ross and Ravosa, 1993; Ross, 1996; Lieberman et al., 2000), etc.—are highly correlated on the first principal component in all analyses (Table 5). The functional reasons for this morphological reorganization, that is, why anthropoids developed this specific suite of cranial features, remain unclear, although some have suggested that it may be due to a diurnal shift by a visual predator (Ross, 1996, 2000).

Moreover, this same suite of morphological features which separates anthropoids (as a group) from strepsirrhines (as a group) also separates hominoids from cercopithecoids and platyrhines (within anthropoids), suggesting a second shift in overall cranial shape during the evolution of the extant great apes (Figs. 6 and 7). Interestingly, on PC 1, platyrhines, and cercopithecoids (and gibbons) are all at more or less the same “monkey grade.” It is this phylogenetic pattern of successive change along a single morphological gradient from prosimians to hominoids that lay behind the common identification of “trends in primate evolution” that were characteristic of the field through most of the 20th century (e.g., Clark, 1959).

The interplay between morphology and phylogeny on PC 2 is more complex. As noted earlier, there is very little diversity on this axis among extant strepsirrhines. However among anthropoids, there are major separations both between and within major clades (Fig. 7). This axis separates cercopithecines from colobines and, less clearly, cercopithecoids from platyrhines, and among platyrhines, cebids from atelids. Within hominoids it separates great apes, hylobatids, and humans.

In addition, much of the morphological difference between sexes within dimorphic anthropoid taxa lies along PC 2 (Fig. 5). A large portion of the diversity in anthropoid crania is driven by the male morphotypes, and it is the male anthropoids that typically display the most extreme scores on PC 2, particularly in the positive direction, due to their longer snouts. Nevertheless, both the morphological correlations and the separation of clades along PC 2 are essentially the same in all three analyses, so this is not just a result of male morphologies.

The fact that much of the diversity among anthropoid taxa is described by PC 2, and that sexual dimorphism is common among anthropoid species but minimal or nonexistent among most strepsirrhines, suggests that these are somehow interrelated. One particularly intriguing interpretation of this phenomenon is that cladistic differences among groups of anthropoids and differences between sexes among anthropoid species are based on a set of very similar developmental patterns (Gilbert et al., 2009a). This theme of sexual dimorphism in primate crania and its relation to phyletic evolution is currently the subject of a more detailed analysis.

Cranial diversity

In sampling all extant genera of primates in a single analysis, we have been able to obtain a quantitative measure of cranial diversity in the extant members of

many different primate clades. Perhaps surprisingly, it is the taxonomically depauperate hominoids that possess the greatest amount of cranial diversity among the major primate groups (Fig. 7 and Table 6). The majority of this cranial diversity is driven by the unique human cranium, which is undeniably odd if judged by any extant primate and mammalian standards. As noted earlier, nonhuman hominoids are no more diverse than other major anthropoid groups (i.e., platyrhines and cercopithecoids). The addition of *Homo sapiens* to the analysis results in a substantial increase in hominoid cranial diversity. Because our measurement of morphological diversity is a variance measure, the small number of extant hominoids certainly contributes to their high diversity. Nevertheless, it is striking that the great apes and humans span the extremes of PC 2. Moreover, this large difference between great ape and human crania is not just a reflection of the extensive development of secondary features in the crania of male great apes; females occupy only slightly less extreme positions on this axis and the distance between female great apes and female humans also nearly spans the extremes of PC 2. The position of gibbons among colobines (Fig. 7) reflects a morphological similarity that has been noted by numerous primate morphologists (e.g., Vogel, 1966, 1968; Delson and Andrews, 1975). Likewise, although in the 21st century we tend to view humans as another great ape, the striking differences between the human cranium and that of all other primates is a morphological pattern that did not greatly conflict with the efforts of many scholars in previous centuries who wished to place humans in a separate taxonomic group.

At the other end of the diversity spectrum, living strepsirrhines are notable for their comparative lack of cranial diversity compared with anthropoids (Fig. 7 and Table 6). In many ways, this is surprising since extant strepsirrhines are placed in six or seven families: daubentonids, lemurids, indriids, lepilemurids, cheirogaleids, lorisids, and galagids (Fleagle, 1999), and extend over three major biogeographic areas (Africa, Madagascar, and Southern Asia). Nevertheless, despite greater higher level taxonomic diversity, the number of extant strepsirrhine genera is only slightly greater than that of platyrhines and slightly smaller than that of cercopithecoids, clades that are not significantly different in our measure of cranial diversity.

As noted earlier, it is true that our 18 landmarks do not capture some of the oddities of certain primate genera, and that this may help to drive down perceived diversity among certain groups, particularly strepsirrhines. It is also tempting to attribute this apparent lack of diversity among strepsirrhine taxa to the recent extinction of a large portion of the Malagasy strepsirrhine fauna including the giant sloth lemurs, *Megaladapis*, and the archaeolemurids (monkey-lemurs). At least nine genera and approximately 16 species have become extinct in the last few thousand years (Godfrey et al., 1997; Godfrey and Jungers, 2002; Jungers et al., 2008), all larger than extant taxa, and many with very striking cranial morphologies. Certainly, inclusion of the subfossil taxa from Madagascar would increase the diversity of that clade. However, other groups of primates (including platyrhines, cercopithecoids, and especially hominids) have also suffered extinctions during their evolution, during the Pleistocene as well as other epochs (e.g., Leakey, 1982; Cartelle and Hartwig, 1996; Fleagle, 1999). Unfortunately, compared with the Malagasy lemurs, relatively few are

known from complete cranial material. For uniformity, we have restricted this study to extant taxa. The effect of including extinct fossil taxa in comparisons of cranial diversity among primate clades is the subject of another ongoing study. (e.g., Fleagle et al., 2008).

ACKNOWLEDGMENTS

We thank Eileen Westwig (AMNH), Linda Gordon (NMNH), Bill Stanley and Michi Schulenberg (FMNH), Judith Chupasko (MCZ), and Kristof Zyskowski (YPM) and their respective museums for access to the specimens used in this study. Luci Betti-Nash prepared the illustrations. James Rohlfs, Karen Baab, Chris Ruff, and several anonymous reviewers provided valuable comments and suggestions that greatly improved this manuscript. Biren Patel provided access to essential resources.

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