

Ontogeny and homoplasy in the papionin monkey face

Mark Collard^{a*} and Paul O'Higgins^b

^aDepartment of Anthropology and AHRB Centre for the Evolutionary Analysis of Cultural Behaviour, University College London, Gower Street, London WC1E 6BT, UK

^bDepartment of Anatomy and Developmental Biology, University College London, London WC1E 6BT, UK

*Author for correspondence (email: m.collard@ucl.ac.uk)

SUMMARY Recent molecular research has provided a consistent estimate of phylogeny for the living papionin monkeys (*Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus*, *Papio*, and *Theropithecus*). This phylogeny differs from morphological phylogenies regarding the relationships of the mangabeys (*Cercocebus* and *Lophocebus*) and baboons (*Mandrillus*, *Papio*, and *Theropithecus*). Under the likely assumption that the molecular estimate is correct, the incongruence between the molecular and morphological data sets indicates that the latter include numerous homoplasies. Knowledge of how these homoplasies emerge through development is important for understanding the morphological evolution of the living papionins, and also for reconstructing the phylogenetic relationships and adaptations of their fossil relatives. Accordingly, we have used geometric morphometric techniques and the molecular phylogeny to investigate the ontogeny of a key area of morphological homoplasy in papionins, the face. Two analyses were carried out. The first compared allometric vectors of *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus*, and *Papio* to determine which of the facial resemblances among the genera are homoplastic and which are plesiomorphic. The second analysis focused on early post-natal facial form in order to establish

whether the facial homoplasies exhibited by the adult papionins are to some degree present early in the post-natal period or whether they develop only later in ontogeny. The results of our analyses go some way to resolving the debate over which papionin genera display homoplastic facial similarities. They strongly suggest that the homoplastic facial similarities are exhibited by *Mandrillus* and *Papio* and not by *Cercocebus* and *Lophocebus*, which share the putative primitive state with *Macaca*. Our results also indicate that *Mandrillus* and *Papio* achieve their homoplastic similarities in facial form not through simple extension of the ancestral allometric trajectory but through a combination of an extension of allometry into larger size ranges and a change in direction of allometry away from the ancestral trajectory. Thus, the face of *Mandrillus* is not simply a hypermorphic version of the face of its sister taxon, *Cercocebus*, and the face of *Papio* is not merely a scaled-up version of the face of its sister taxon, *Lophocebus*. Lastly, our results show that facial homoplasy is not restricted to adult papionins; it is also manifest in infant and juvenile papionins. This suggests that the homoplastic facial similarities between *Mandrillus* and *Papio* are unlikely to be a result of sexual selection.

INTRODUCTION

The tribe Papionini comprises the macaques, mangabeys, and baboons. Paraphrasing Fleagle (1999), macaques are medium- to large-sized monkeys (3–10 kg) with robust limbs, moderately long faces, high-crowned but low-cusped molar teeth, and long third molars. There are some 19 extant species of macaque, all of which are assigned to the genus *Macaca*. Macaques are found throughout much of temperate and tropical Asia, as well as in parts of North Africa and on Gibraltar, to which they were introduced. Macaques occupy a broad range of habitats, from lowland secondary forests to upland hilly environments. Mangabeys are large (6–10 kg), stout-limbed monkeys that have elongated molars, very large incisors, prognathic faces, and deeply excavated suborbital fossae. There are four species of mangabey, two of which are assigned to the genus *Cercocebus* and two to the genus *Lophocebus*. Mangabeys are found in many of the forests of

sub-Saharan Africa, from Kenya in the east, to Equatorial Guinea in the west, and to Angola in the south. Baboons are the largest Old World monkeys (12–50 kg). They are characterized by long, robust limbs, elongated faces, pronounced supraorbital tori, long molars, broad incisors, and, in males, daggerlike canines. Most taxonomists now divide baboons into three genera: *Papio*, the savannah baboon; *Mandrillus*, the forest baboon; and *Theropithecus*, the gelada baboon. *Papio* is widely distributed throughout the woodlands and grasslands of sub-Saharan Africa, whereas *Mandrillus* is restricted to the forests of western Africa and *Theropithecus* is limited to the grasslands of the Ethiopian highlands.

Molecular and morphological analyses of papionin phylogeny have reached different conclusions regarding the affinities of the mangabeys (*Cercocebus* and *Lophocebus*) and baboons (*Mandrillus*, *Papio*, and *Theropithecus*). The consensus molecular phylogeny (Fig. 1) suggests that the mangabeys of the genus *Cercocebus* are most closely related to the

forest baboons of the genus *Mandrillus*, whereas the mangabeys of the genus *Lophocebus* are most closely related to the savannah baboons of the genus *Papio* and the gelada baboons of the genus *Theropithecus* (Disotell 1994, 1996, 2000; Disotell et al. 1992; van der Kuyl et al. 1994; Harris and Disotell 1998; Harris 2000). In contrast, the majority of morphological phylogenies have supported a sister-group relationship between *Papio* and *Mandrillus* and a sister-group relationship between *Cercocebus* and *Lophocebus* (Jolly 1966, 1967, 1970; Delson 1975, 1993; Szalay and Delson 1979; Strasser and Delson 1987; Delson and Dean 1993). One recent morphology-based phylogenetic analysis of the papionins supported a sister-group relationship between *Cercocebus* and *Mandrillus* (Groves 2000), but another, more comprehensive, analysis published in the same year found strong support for phylogenetic relationships that are incompatible with the consensus molecular phylogeny (Fig. 2) (Collard and Wood 2000).

It has been argued recently that there are several reasons for considering the molecular estimate of papionin phylogeny to be more accurate than the morphological one (Collard and Wood 2000, 2001). Firstly, in phylogenetics, morphology can never be more than a proxy for genetic data as phylogenetic relationships are essentially genetic relationships.

Secondly, because osseous characters can be highly influenced by external stimuli, such as the forces generated by habitual activities (Murray 1934; Currey 1968, 1984; Lieberman 1995, 1997, 1999, 2000; Lieberman et al. 1996), they can be expected to provide misleading information about phylogeny more frequently than genetic characters, which are less subject to such stimuli. Thirdly, the methods of molecular phylogenetics have been successfully tested on taxa of known phylogeny, whereas comparable tests of morphological phylogenetic methods have proved unsuccessful (Fitch and Atchley 1987; Atchley and Fitch 1991; Hillis et al. 1992). It may be argued that because these tests are based on subspecific taxa (e.g., inbred strains of mice), they are of little significance regarding the relationships among the papionin genera. However, we contend that since subspecific phylogenies can be expected to be more difficult to reconstruct than genus-level phylogenies, the tests actually provide strong reason to favor the molecular phylogeny for the papionins over any of the phylogenies based on their morphological characteristics. Lastly, the consensus molecular cladogram for the extant papionins is supported by several sets of independent data (Disotell 1994, 1996, 2000; Disotell et al. 1992; van der Kuyl et al. 1994; Harris and Disotell 1998; Harris 2000). These data sets differ regarding the rela-

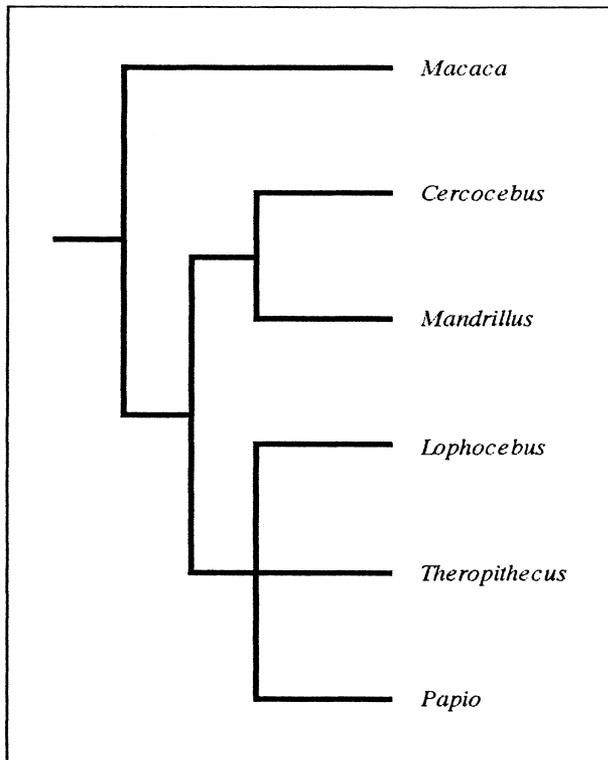


Fig. 1. Consensus molecular phylogeny for Papionini (Disotell 1994, 1996, 2000; Disotell et al. 1992; van der Kuyl et al. 1994; Harris and Disotell 1998; Harris 2000).

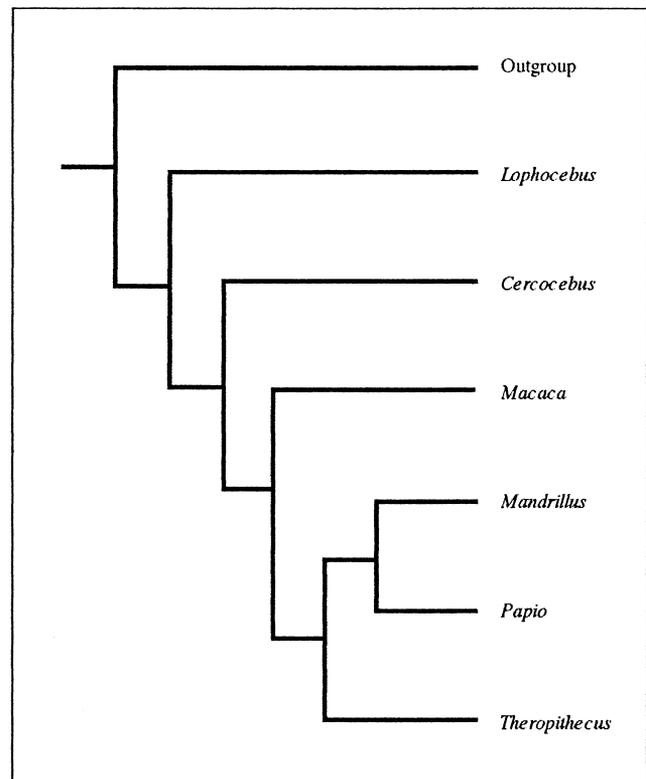


Fig. 2. Collard and Wood's (2000) morphology-based phylogeny for the papionin monkeys.

tionships among *Lophocebus*, *Papio*, and *Theropithecus*, but they agree that *Lophocebus*, *Papio*, and *Theropithecus* form one clade within Papionini and that *Cercocebus* and *Mandrillus* form a second. Agreement among multiple independent data sets is the strongest support possible for a phylogenetic hypothesis.

If the consensus molecular phylogeny is accepted as accurate (cf. Fleagle and McGraw 1999; Collard and Wood 2000, 2001), then the disagreement between the phylogenies derived from the molecular and morphological data sets indicates that the latter contain a large number of homoplasies—similarities resulting from mechanisms other than descent from a common ancestor, such as behavior-induced morphogenesis, convergence, parallelism, and reversal (Willey 1911; Simpson 1961; Cain 1982; Patterson 1982; Sober 1988; Sanderson and Hufford 1996; Lieberman 1999; Lockwood and Fleagle 1999). Knowledge of how these similarities emerge through development is necessary to further our understanding of the morphological evolution of the living papionins (Harris 2000). Such knowledge is also relevant to the reconstruction of the phylogenetic relationships and adaptations of their fossil relatives, such as *Procynocephalus*, *Paradolichopithecus*, and *Dinopithecus* because it may assist in choice of characters. Additionally, improved understanding of the developmental basis of papionin facial homoplasy may aid phylogenetic analyses of other extinct primate taxa (e.g., Rae 1997). Since the face has been argued to be a key area of homoplasy in the papionins (Disotell 1994; Harris and Disotell 1998; Harris 2000), we have used geometric morphometric techniques (Bookstein 1991; Goodall 1991; Dryden and Mardia 1998; O'Higgins 1999, 2000a, 2000b; O'Higgins and Jones 1998; O'Higgins and Collard 2001 in press) to investigate the post-natal ontogeny¹ of the face in five papionin genera, *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus*, and *Papio*. Specifically, we investigated similarities and differences in allometric vectors and in early post-natal facial form in order to elucidate the origins and nature of the facial homoplasies.

The aim of the analysis of allometric vectors was to ascertain whether the facial similarities between *Mandrillus* and *Papio* are homoplastic and those between *Cercocebus* and *Lophocebus* plesiomorphic (shared-primitive), or whether the facial similarities between *Cercocebus* and *Lophocebus* are homoplastic and those between *Mandrillus* and *Papio* plesiomorphic. The incongruence between the molecular and morphological phylogenies indicates that facial homoplasy is present, but it does not indicate which of the similarities among the genera are homologous and which are homoplastic. Both possibilities have been supported in the

literature. Disotell (1994) and Harris (2000) have suggested that the long faces of *Mandrillus*, *Papio*, and *Theropithecus* are independently derived from a common ancestor that exhibited a similar facial form to *Cercocebus* and *Lophocebus*, whereas Groves (1978) and Kingdon (1997) have argued that the common ancestor of *Cercocebus*, *Lophocebus*, *Mandrillus*, *Papio*, and *Theropithecus* was long-faced like *Mandrillus*, *Papio*, and *Theropithecus* and that *Cercocebus* and *Lophocebus* have independently reevolved shorter faces.

It has been argued frequently that ontogenetic data can be used to distinguish homologies from homoplasies (e.g., Nelson 1978; Reidl 1978; Patterson 1982; Roth 1984; Wood 1988; Wagner 1989; Lieberman 1995, 1999; Lieberman et al. 1996; Lovejoy et al. 1999; McCollum 1999; but see Cartmill 1994; Hall 1998). Under this hypothesis, difference in developmental process is evidence for homoplasy. Thus, in the simplest case, if the similarities between *Mandrillus* and *Papio* are homoplastic and those of *Cercocebus*, *Lophocebus*, and *Macaca* are plesiomorphic, then the allometric vectors of *Mandrillus* and *Papio* should be significantly different from each other and from those of *Cercocebus*, *Lophocebus*, and *Macaca*, which should be identical in statistical terms. Conversely if the similarities between *Cercocebus* and *Lophocebus* are homoplastic and those of *Macaca*, *Mandrillus*, and *Papio* are plesiomorphic, then the allometric vectors of *Cercocebus* and *Lophocebus* should be significantly different from each other and from those of *Macaca*, *Mandrillus*, and *Papio*, which should be statistically indistinguishable.

The analysis of early post-natal facial form sought to establish whether the facial homoplasies exhibited by adult papionins are to some degree present early in the post-natal period or whether they develop only later in ontogeny. The analysis was undertaken in part to test Harris' (2000) suggestion that the trend toward disproportionate facial lengthening in *Mandrillus*, *Papio*, and *Theropithecus* is related to a general social system in which there is strong sexual dimorphism with intense intermale competition. Given that significant sexual differences in the papionin facial skeleton do not emerge until the eruption of M² (O'Higgins and Jones 1998; O'Higgins and Collard 2001 in press), if Harris' hypothesis is correct the homoplasies should occur only late in development. Conversely if Harris' hypothesis is incorrect, the homoplasies should arise early in development. The latter finding would suggest that the similarities are likely to be due to some other process, presumably natural selection and/or developmental canalization.

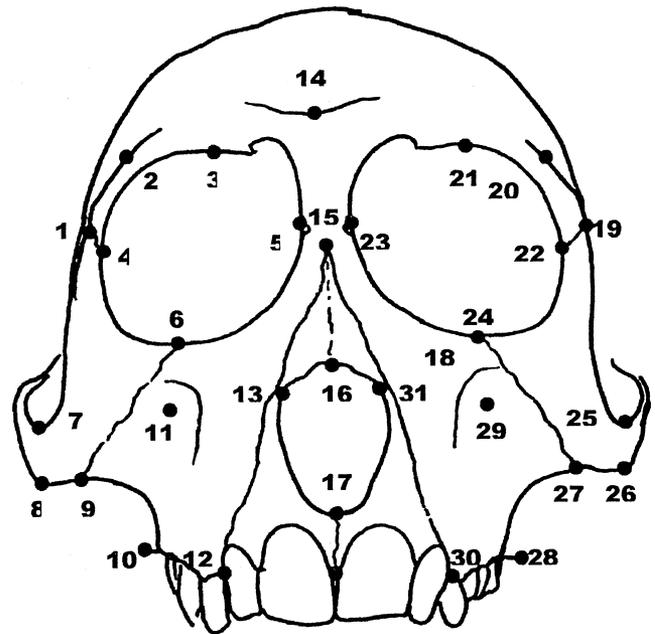
MATERIALS AND METHODS

The data employed in the study comprised three-dimensional (3-D) landmark coordinates recorded on the faces of mixed sex, infant-to-adult ontogenetic series representing five papionin genera. The

¹During ontogeny, the face changes in size and shape over time. Here we use "allometry" to refer to changes in shape with size, "growth" to refer to changes in size over time, and "development" to refer to changes in shape over time.

Table 1. Landmark definitions. (See Fig. 3 for locations).

Number	Definition (based on anatomical orientation of the face)
1 and 19	Most lateral point on zygomatico-frontal suture on orbital rim
2 and 20	Most superolateral point on supraorbital rim
3 and 21	Uppermost point on orbital aperture
4 and 22	Zygomatico-frontal suture at the lateral aspect of the orbital aperture
5 and 23	Fronto-lacrimal suture at medial orbital margin
6 and 24	Zygomatico-maxillary suture at inferior orbital margin
7 and 25	Superior root of zygomatic arch
8 and 26	Inferior root of zygomatic arch
9 and 27	Zygomatico-maxillary suture at root of zygomatic arch
10 and 28	Most posterior point on maxillary alveolus
11 and 29	Deepest point in maxillary fossa
12 and 30	Maxillary-premaxillary suture at alveolar margin
13 and 31	Nearest point to maxillary-premaxillary suture on nasal aperture
14	Upper margin of supraorbital rim in the midline
15	Nasofrontal suture in the midline
16	Tip of nasal bones in the midline
17	Premaxillary suture at the inferior margin of the nasal aperture in the midline
18	Premaxillary suture at alveolar margin

**Fig. 3.** Location of landmarks used in study. See Table 1 for definitions.

landmark data were acquired with a Polhemus 3 Space Isotrak II digitizer (Polhemus Incorporated, Colchester, VT) linked to a laptop computer running a spreadsheet program. Thirty-one landmarks were employed (Table 1). These were chosen to represent the locations of sutural junctions, maxima of curvature, and a number of other anatomical features (Fig. 3). The data were collected by a single observer and were recorded to the nearest 0.05 cm.

The taxa sampled were *Cercocebus* (49 specimens of *C. torquatus* including seven adult males and eight adult females), *Lophocebus* (41 specimens of *L. albigena* including 16 adult males and 13 adult females, plus eight specimens of *L. aterrimus*, none of which was adult), *Macaca* (46 specimens of *M. mulatta* including 10 adult males and 12 adult females), *Mandrillus* (31 specimens of *M. leucophaeus* including 13 adult males and seven adult females), and *Papio* (34 specimens of *P. cynocephalus* including four adult males and five adult females). Unfortunately we were unable to measure a sufficient number of infant and juvenile gelada specimens to include *Theropithecus* in the analysis. Adult crania were selected on the basis of completed dentition. Infant and juvenile specimens were aged using standard dental criteria. It should be noted that the ages of the specimens were used only to ensure evenness of sampling within the available collections. Specimens were sexed on the basis of field records. Most of the *Cercocebus* specimens we examined are housed in the Department of Anatomy and Developmental Biology, University College London. The other specimens form part of the primate collection maintained by the Mammals Section of the Natural History Museum, London.

The analytical approaches used in this study are from the field of geometric morphometrics (Bookstein 1991; Goodall 1991; Dryden and Mardia 1998; O'Higgins 1999, 2000a, 2000b; O'Higgins

and Jones 1998; O'Higgins and Collard 2001 in press). These methods allow patterns of variation in shape and size to be investigated within a well understood statistical framework that yields easily interpreted numerical and visual results. The methods deal with coordinate data as opposed to the interlandmark distances of traditional morphometrics, and operate within a non-Euclidean shape space (Kendall 1984), the geometric and statistical properties of which are both well defined and highly desirable (O'Higgins 1999, 2000a, 2000b). The methods have been argued to offer considerable advantages in terms of statistical analysis and visualization in comparison with other approaches to the analysis of landmark data (Rohlf 1999, 2000a, 2000b).

Two analyses were carried out. The first focused on the allometric trajectories of the five genera. Shape variation in the mixed age/sex series of each genus was examined using the geometric morphometrics package *morphologika* (O'Higgins and Jones 1998; O'Higgins 1999, 2000a, 2000b; O'Higgins and Strand Vidarsdottir 1999). The pooling of sexes is justified since other studies of sexual dimorphism using these data indicate that male and female allometric trajectories only diverge to a significant degree after M² completion but even then continue to share important aspects of allometry (O'Higgins and Jones 1998; O'Higgins and Collard 2001 in press). Since we concern ourselves in this study with comparison of intergeneric patterns of allometry, and not with the mechanism by which sexual dimorphism arises, combined sex samples are appropriate.

Scale, translational, and rotational differences were minimized by generalized procrustes analysis (GPA) (Gower 1975; O'Higgins and Jones 1998; Rohlf and Slice 1990; Bookstein 1991; Goodall 1991). In the GPA specimen scale was represented by centroid size, which is defined as the square root of the sum of squared Euclidean distances from each landmark to the centroid (Bookstein 1991;

Goodall 1991; Dryden and Mardia 1998; O'Higgins and Jones 1998; O'Higgins 1999, 2000a, 2000b). The resulting shape coordinates were subject to Principal Components Analysis (PCA) in the tangent space to Kendall's shape space (Kent 1994; Dryden and Mardia 1998; O'Higgins and Jones 1998; O'Higgins 2000a, 2000b). The principal component (PC) scores for each ontogenetic series were examined for evidence of a significant relationship between shape and centroid size in order to identify which represented size-related shape changes during ontogeny. In all genera only the first PC was found to describe allometric changes in facial shape (see below). Thereafter, the angles between the first PCs of pairs of genera were calculated by PCA of coordinates derived from joint Procrustes fitting, and the significance of the differences between the angles was then assessed using a permutation test (Good 1993), in which the true angles were compared with the distribution of angles calculated for 1000 random samples. Lastly, the similarities and differences between the angles between the allometric vectors were interpreted in the light of the papionin consensus molecular phylogeny (Fig. 1).

The aim of this analysis was to ascertain whether the facial similarities between *Mandrillus* and *Papio* are homoplastic and those between *Cercocebus* and *Lophocebus* plesiomorphic, or vice versa. Under the hypothesis that difference in developmental process is evidence for homoplasy (Nelson 1978; Reidl 1978; Patterson 1982; Roth 1984; Wood 1988; Wagner 1989; Lieberman 1995, 1999; Lieberman et al. 1996; Lovejoy et al. 1999; McCollum 1999), if the similarities between *Mandrillus* and *Papio* are homoplastic and those of *Cercocebus*, *Lophocebus*, and *Macaca* are plesiomorphic, then the allometric vectors (PC1s) of *Mandrillus* and *Papio* should be significantly different from each other and from those of *Cercocebus*, *Lophocebus*, and *Macaca*, which should be identical in statistical terms. Conversely if the similarities between *Cercocebus* and *Lophocebus* are homoplastic and those of *Macaca*, *Mandrillus*, and *Papio* are plesiomorphic, then the allometric vectors of *Cercocebus* and *Lophocebus* should be significantly different from each other and from those of *Macaca*, *Mandrillus*, and *Papio*, which should be statistically indistinguishable.

The second analysis concentrated on early post-natal facial form and sought to establish whether the facial homoplasies exhibited by adult papionins are to some degree present early in the post-natal period or whether they develop only later in ontogeny. The analysis employed the PC1 scores obtained in the first analysis. Early post-natal facial form was estimated using *morphologika's* warp function. The overall mean for each genus was warped to the score on PC1 consistent with a centroid size of 11 cm. The overall differences in shape of these means were then summarized by computing a matrix of Procrustes chord distances and deriving from these a UPGMA dendrogram. The Procrustes chord distances were calculated in *morphologika*; the UPGMA dendrogram was produced using NTSYS-PC (Applied Biostatistics Inc.). Lastly, the dendrogram was compared with the papionin consensus molecular phylogeny (Fig. 1).

The analysis was undertaken in part to test Harris' (2000) suggestion that the trend toward disproportionate facial lengthening in *Mandrillus*, *Papio*, and *Theropithecus* is related to a general social system in which there is strong sexual dimorphism with intense intermale competition. Given that significant sexual differences in the papionin facial skeleton do not emerge until the eruption of M²

(O'Higgins and Jones 1998; O'Higgins and Collard 2001 in press), if Harris' hypothesis is correct then the homoplasies should occur only late in development and the dendrogram of early post-natal facial shape should be compatible with the molecular phylogeny regarding the relationships of *Cercocebus*, *Lophocebus*, *Mandrillus*, and *Papio*. It should group *Cercocebus* with *Mandrillus*, and align *Lophocebus* with *Papio*. Conversely if Harris' hypothesis is incorrect, then the homoplasies should arise early in development and the dendrogram of early post-natal facial shape should disagree with the molecular phylogeny.

RESULTS

The first PC was judged to be an adequate description of size-related changes in facial shape in all five genera. In *Macaca*, the correlation between scores on the first PC and centroid size was -0.86 , $P < 0.001$ and the first PC accounted for 42% of the total variance in the sample. For *Cercocebus* these figures were $r = -0.95$, $P < 0.001$ and 52%; for *Lophocebus*, $r = -0.62$, $P < 0.001$, 40%; for *Mandrillus*, $r = 0.94$, $P < 0.001$, 73%; and for *Papio*, $r = 0.97$, $P < 0.001$, 62%. No other PC showed evidence of a significant relationship between size and shape in any genus. It should be noted that there is no a priori reason to expect a strong correlation between PC1 and centroid size. Unlike classic allometric methods (Jolicouer 1963), the analytical approach used here prescales coordinates such that the strong correlation between shape variation described by PC1 and centroid size indicates that ontogenetic allometry explains a considerable proportion of adult facial morphology and dominates all other influences on face shape in the five ontogenetic series. Figure 4 shows PC1 versus centroid size from the analyses of the five age series.

The angles between the first PCs indicate the degree of overall similarity of allometric changes in facial shape. They are given in Table 2, along with an estimate of their significance. The angle between the PC1s of *Mandrillus* and *Papio* is significant, as are the angles between the PC1 of *Mandrillus* and the PC1s of *Cercocebus*, *Lophocebus*, and *Macaca*, and the angles between the PC1 of *Papio* and the PC1s of *Cercocebus*, *Lophocebus*, and *Macaca*. The angle between the PC1s of *Cercocebus* and *Lophocebus* is also significant. However, the angle between the PC1s of *Cercocebus* and *Macaca* is not significant and neither is the angle between the PC1s of *Lophocebus* and *Macaca*. This indicates that the allometric vectors in shape of *Mandrillus* and *Papio* are significantly different from each other and from those of *Cercocebus*, *Lophocebus*, and *Macaca*. It also indicates that while the allometric vectors of *Cercocebus* and *Lophocebus* are significantly different from one another, the allometric vectors of these genera are not significantly different from the allometric vector of *Macaca*.

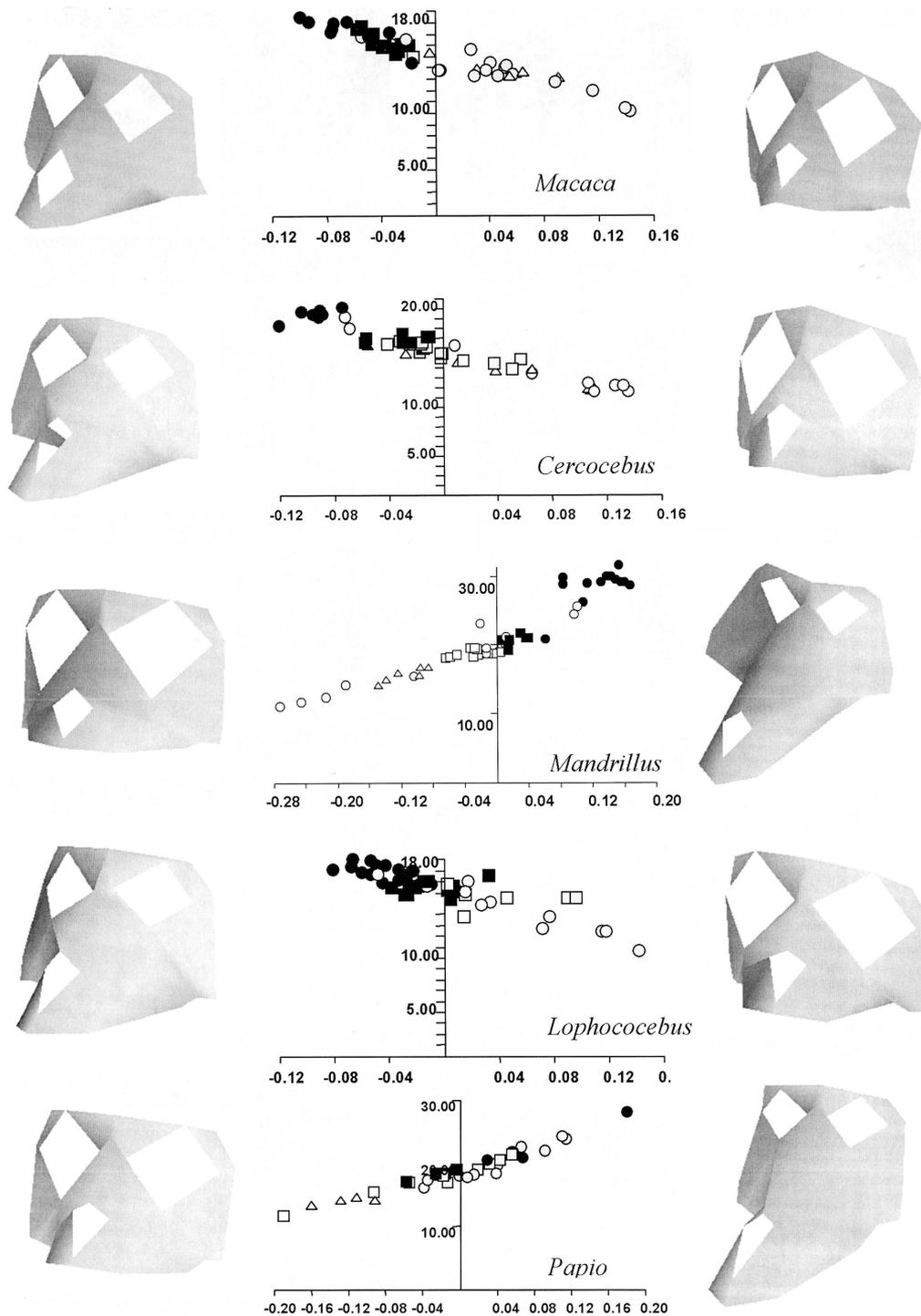


Fig. 4. PC1 (horizontal axis) versus centroid size in cm (vertical axis) from analyses of each genus. Row 1 = *Macaca*, 2 = *Cercocebus*, 3 = *Mandrillus*, 4 = *Lophocebus*, 5 = *Papio*. Circles = males, squares = females, triangles = unknown sex, black = adult, gray = subadult. Inset to left and right of each plot is a surface-rendered representation of the generic mean shape warped to the left and right extremes of PC1, respectively. These insets (not to scale) indicate the aspects of shape variation represented by the first principal component.

Table 2. Angles between first principal components of age series with significance levels in brackets.

	<i>Macaca</i>	<i>Cercocebus</i>	<i>Mandrillus</i>	<i>Lophocebus</i>
<i>Cercocebus</i>	25 (0.207)			
<i>Mandrillus</i>	32 (<0.001)	33 (<0.001)		
<i>Lophocebus</i>	34 (0.499)	29 (0.007)	27 (<0.001)	
<i>Papio</i>	34 (<0.001)	36 (<0.001)	21 (0.002)	32 (<0.001)

Figure 5 shows the estimate in each genus of post-natal shape at centroid size 11 cm and a dendrogram indicating the clustering order between the genera based on Procrustes chord distances between these estimates (Table 3). The branching pattern of the dendrogram differs from that of the molecular phylogeny. It places *Cercocebus* and *Lophocebus* in one group and *Mandrillus* and *Papio* in another, and there-

fore agrees with the majority of morphology-based analyses of papionin phylogeny. It should be noted that additional analyses not reported here found comparable results over a range of centroid sizes typical of young faces. The finding was further supported by unreported analyses of selected infant faces from each genus.

DISCUSSION

Two geometric morphometric analyses were undertaken to investigate facial homoplasy among the papionin monkeys. The aim of the first analysis was to compare allometric vector trajectories in order to ascertain whether the facial similarities of *Mandrillus* and *Papio* are homoplastic and those of *Cercocebus* and *Lophocebus* plesiomorphic, or vice versa. This was accomplished by calculating the significance of the

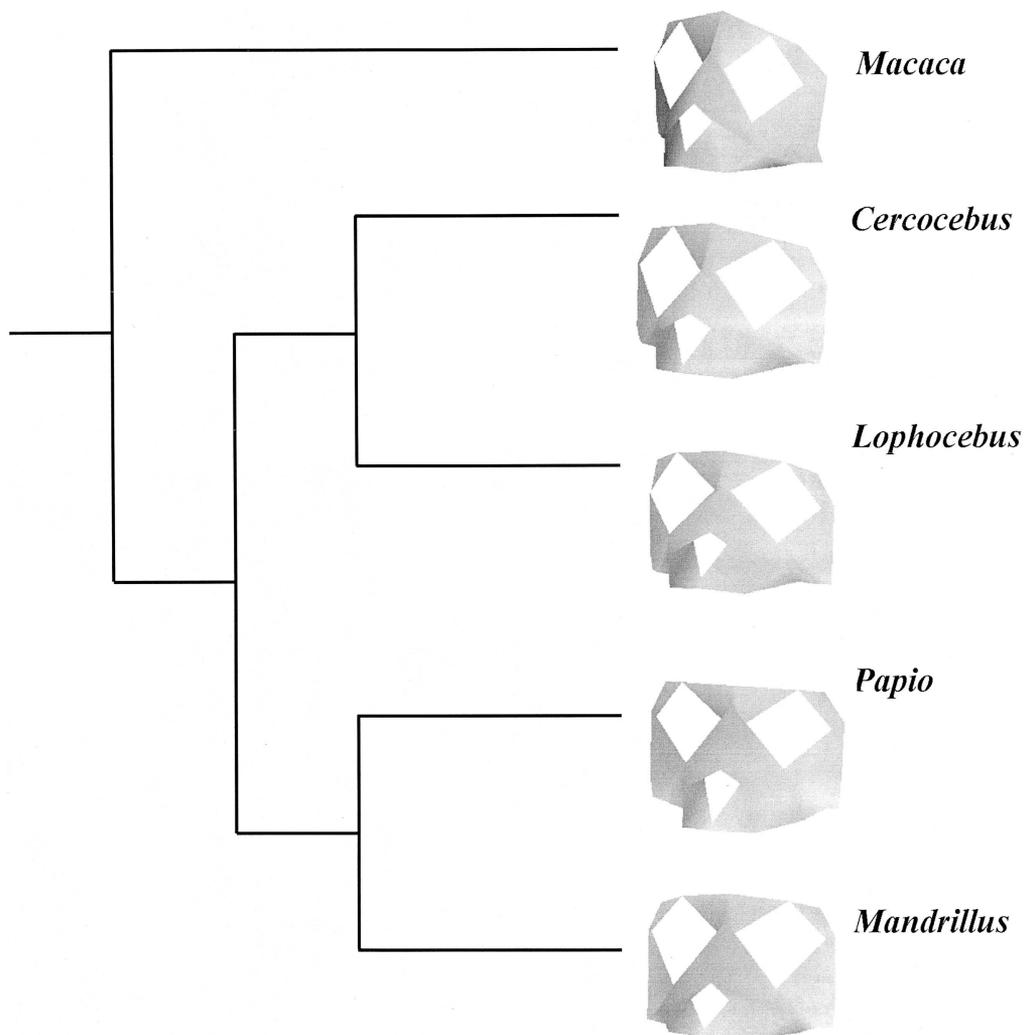


Fig. 5. Dendrogram derived from Procrustes chord distances between estimates of early post-natal facial form in five papionin genera.

Table 3. Procrustes chord distances between estimated juvenile specimens.

	<i>Macaca</i>	<i>Cercocebus</i>	<i>Mandrillus</i>	<i>Lophocebus</i>
<i>Cercocebus</i>	0.106067			
<i>Mandrillus</i>	0.120509	0.096705		
<i>Lophocebus</i>	0.123534	0.092086	0.100977	
<i>Papio</i>	0.124346	0.105597	0.094626	0.101647

angles between the first PCs derived from PCAs of the age series (PC1 in each genus was the only PC to correlate significantly with size). The analysis indicated that the allometric trajectories of *Mandrillus* and *Papio* differ significantly from the shape allometric trajectories of *Cercocebus*, *Lophocebus*, and *Macaca*. It also indicated that *Cercocebus* and *Lophocebus* differ significantly in their ontogenetic allometries. Lastly, the analysis indicated that the PC1s of *Cercocebus* and *Lophocebus* are statistically indistinguishable from the scaling PC of *Macaca*. Assuming that *Macaca* displays the primitive condition, this result suggests that the facial similarities between *Mandrillus* and *Papio* are homoplastic, being derived from different allometric trajectories, whereas the facial similarities between *Cercocebus* and *Lophocebus* are plesiomorphic. This strongly supports Disotell's (1994) and Harris' (2000) hypotheses regarding facial homoplasy among the African papionins and fails to support those of Groves (1978) and Kingdon (1997). It is worth noting that Steven Leigh of the Department of Anthropology, University of Illinois, has recently reached the same conclusions using different allometric methods (personal communication 2000).

In addition to clarifying which of the African papionins display homoplastic facial similarities, the results of the first analysis shed light on the nature of those similarities. Harris' (2000) support for the hypothesis that *Mandrillus* and *Papio* exhibit facial homoplasy was based on work suggesting that there is a general allometric trend among the papionins for disproportionate lengthening of the face to be correlated with increasing body size (Freedman 1962; Jolly 1970). However, the results of our first analysis indicate that simple extension of ontogenetic allometry does not fully account for the facial similarities between *Mandrillus* and *Papio*. The significant difference between the allometric trajectories of *Cercocebus* and *Mandrillus* indicates that the face of *Mandrillus* is not simply a hypermorphic version of the face of *Cercocebus*. Likewise, the significant difference between the allometric trajectories of *Lophocebus* and *Papio* indicates that the face of *Papio* is not merely a scaled-up version of the face of *Lophocebus*. Thus the similarities in facial form between *Mandrillus* and *Papio* are achieved through a combination of an extension of allometry into larger size ranges (allometric change) and an alteration in direction away from the ancestral allometric trajectory.

The second analysis assessed whether the facial homoplasy exhibited by adult papionins is to some degree present early in the post-natal period or whether it only develops later. This was accomplished by comparing the branching pattern of a dendrogram summarizing intergeneric similarities and differences in estimated early post-natal facial form with the branching pattern of the group's molecular phylogeny. The dendrogram's branching pattern was found to differ in placing *Cercocebus* and *Lophocebus* in one group and *Mandrillus* and *Papio* in another. This is consistent with the phylogeny favored by the majority of morphology-based analyses of papionin phylogeny. Since there are grounds for considering the molecular phylogeny to be a reliable estimate of papionin phylogeny, this result indicates that facial homoplasy is not restricted to adult papionins; it is also manifest in infant and juvenile papionins.

One important implication of this result concerns the role of sexual selection in the evolution of the homoplastic similarities in the faces of *Papio* and *Mandrillus*. Harris (2000) has suggested that the trend toward disproportionate facial lengthening in *Mandrillus*, *Papio*, and *Theropithecus* is related to a general social system in which there is strong sexual dimorphism with intense intermale competition. However, this hypothesis is not supported by the agreement between the early post-natal dendrogram and the majority of phylogenies derived from adult morphology. Given that significant sexual differences in the facial skeleton do not emerge until the eruption of M² (O'Higgins and Jones 1998; O'Higgins and Collard 2001 in press), if Harris' hypothesis is correct we would have expected a better fit between the early post-natal dendrogram and the molecular phylogeny than between the early post-natal dendrogram and the phylogeny derived from adult morphology. In other words, if Harris' hypothesis is correct we would not have expected infant *Mandrillus* and *Papio* to have exhibited facial homoplasy. Yet this is precisely what the comparison between the early post-natal dendrogram and the molecular phylogeny revealed. *Mandrillus* and *Papio* exhibit homoplasy at all stages of ontogeny. Thus, the analysis of early post-natal facial form does not support the suggestion that sexual selection is responsible for the homoplastic similarities exhibited by *Mandrillus* and *Papio*. It suggests instead that the similarities are likely to be due to some other process, presumably natural selection and/or developmental canalization.

One further issue that deserves consideration is the impact of the results of this study on current understanding of the phylogenetic relationships of the fossil papionin species. These relationships are contested (e.g., Delson and Dean 1993; Jablonski 1993), but the consensus view is that *Macaca prisca*, *Macaca majori*, *Macaca libyca*, *Macaca anderssoni*, *Macaca palaeindica*, *Macaca jiangchuanensis*, *Paradolichopithecus arvenensis*, *Procynocephalus subhimalayensis*, and *Procynocephalus wimani* are members of

the macaque lineage and that *Parapapio broomi*, *Parapapio jonesi*, *Parapapio whitei*, *Parapapio antiquus*, and *Parapapio ado* form a lineage close to the ancestry of the mangabeys and baboons (Fleagle 1999). The consensus view also holds that *Papio robinsoni*, *Papio izodi*, *Papio quadratirostris*, *Dinopithecus ingens*, and *Gorgopithecus major* are members of the savannah baboon lineage and that *Theropithecus oswaldi*, *Theropithecus delsoni*, *Theropithecus darti*, *Theropithecus brumpti*, and *Theropithecus baringensis* are members of the lineage leading to the gelada baboon (Fleagle 1999).

Our finding that the similarities in facial form between *Mandrillus* and *Papio* are homoplastic rather than homologous suggests that a number of these hypothesized relationships may need to be reconsidered. In particular, if a prognathic face has evolved independently in *Mandrillus* and *Papio*, which belong to lineages that separated around 11 million years ago (Harris 2000), then it is possible that such a face may have evolved several times in the putative lineage comprising *Papio*, *Dinopithecus*, *Gorgopithecus*, *Lophochebus*, and *Theropithecus*. Given that molecular analyses have so far been unable to resolve the relationships among the extant members of this lineage (Fig. 1), it is entirely possible that, contrary to the current consensus, the two extinct genera, *Dinopithecus* and *Gorgopithecus*, do not form a monophyletic group with *Papio* but instead represent one or more additional long-faced lineages that arose from the ancestral *Lophochebus*-like lineage. Likewise, it is feasible that some of the extinct species assigned to *Papio* and *Theropithecus* in fact may have arisen independently from the *Lophochebus*-like lineage or from the lineage(s) to which *Dinopithecus* and *Gorgopithecus* belong. There is, we suggest, a pressing need for analyses designed to evaluate these possibilities. In the meantime, the results of this study indicate that the character “long face” should be given little weight in phylogenetic analyses of the fossil papionins.

CONCLUSIONS

In the study described here we used geometric morphometric techniques to investigate homoplasy in the papionin monkeys. Specifically we investigated the origins and nature of the facial homoplasy exhibited by the tribe through analyses of allometric vectors and analyses of early post-natal facial form. Our results indicate that the homoplastic facial similarities are exhibited by *Mandrillus* and *Papio* rather than by *Cercocebus* and *Lophochebus*, which are hypothesized to share the plesiomorphic state with *Macaca*. Our results also suggest that *Mandrillus* and *Papio* achieve their homoplastic similarities in facial form not through simple extension of the ancestral allometric trajectory but through a combination of allometric change and change in direction of allometry away from the ancestral trajectory. As such, the face of *Man-*

drillus is not simply a larger version of the face of its sister taxon, *Cercocebus*, and the face of *Papio* is not merely an enlarged version of the face of its sister taxon, *Lophochebus*. Lastly our results show that facial homoplasy is not restricted to adult papionins; it is also manifest in infant and juvenile papionins. This suggests that the homoplastic facial similarities between *Mandrillus* and *Papio* are most likely not a consequence of sexual selection. Overall, this study demonstrates how analyses of allometry using 3-D morphometric techniques can be combined with molecular phylogenetic information to produce new insights about the evolution of the nonhuman primate face. This approach may well have utility for investigating the evolution of other groups of animals.

Acknowledgments

We thank the Natural History Museum, London, for providing access to the specimens in its care and Nicholas Jones for his programming efforts. We also thank David Degusta, Phyllis Lee, Steven Leigh, and Bernard Wood for their comments on earlier versions of the manuscript. This work was funded in part by The Wellcome Trust.

REFERENCES

- Atchley, W. R., and Fitch, W. M. 1991. Gene trees and the origin of inbred strains of mice. *Science* 254: 554–558.
- Bookstein, F. L. 1991. *Morphometric Tools for Landmark Data: Geometry and Biology*. Cambridge University Press, Cambridge.
- Cain, A. J. 1982. On homology and convergence. In K. A. Joysey and A. E. Friday (eds.), *Problems of Phylogenetic Reconstruction*. Academic Press, London, pp. 1–19.
- Cartmill, M. 1994. A critique of homology as a morphological concept. *Am. J. Phys. Anthropol.* 94: 115–123.
- Collard, M., and Wood, B. A. 2000. How reliable are human phylogenetic hypotheses? *Proc. Natl. Acad. Sci. USA* 97: 5003–5006.
- Collard, M., and Wood, B. A. 2001. How reliable are current estimates of fossil catarrhine phylogeny? An assessment using extant great apes and Old World monkeys. In L. de Bonis, G. D. Koufous, and P. Andrews (eds.), *Hominoid Evolution and Climate Change in Europe*, Vol. 2: Phylogeny of the Neogene Hominoid Primates of Eurasia. Cambridge University Press, Cambridge, pp. 118–150.
- Currey, J. D. 1968. The adaptation of bones to stress. *J. Theor. Biol.* 20: 91–106.
- Currey, J. D. 1984. *The Mechanical Adaptations of Bones*. Princeton University Press, Princeton, New Jersey.
- Delson, E. 1975. Evolutionary history of the Cercopithecidae. *Contrib. Primatol.* 5: 167–217.
- Delson, E. 1993. *Theropithecus* fossils from Africa and India and the taxonomy of the genus. In N. G. Jablonski (ed.), *Theropithecus: Rise and Fall of a Primate Genus*. Cambridge University Press, Cambridge, pp. 157–189.
- Delson, E., and Dean, D. 1993. Are *P. baringensis* R. Leakey, 1969, and *P. quadratirostris* Iwamoto, 1982, species of *Papio* or *Theropithecus*? In N. G. Jablonski (ed.), *Theropithecus: Rise and Fall of a Primate Genus*. Cambridge University Press, Cambridge, pp. 125–156.
- Disotell, T. R. 1994. Generic level relationships of the Papionini (Cercopithecoidea). *Am. J. Phys. Anthropol.* 94: 47–57.
- Disotell, T. R. 1996. The phylogeny of Old World monkeys. *Evol. Anthropol.* 5: 18–24.
- Disotell, T. R. 2000. Molecular systematics of the Cercopithecidae. In P. F. Whitehead and C. J. Jolly (eds.), *Old World Monkeys*. Cambridge University Press, Cambridge, pp. 29–56.
- Disotell, T. R., Honeycutt, R. L., and Ruvolo, M. 1992. Mitochondrial DNA phylogeny of the Old World monkey tribe Papionini. *Mol. Biol. Evol.* 9: 1–13.

- Dryden, I. L., and Mardia, K. V. 1998. *Statistical Shape Analysis*. John Wiley, London.
- Fitch, W. M., and Atchley, W. R. 1987. Divergence in inbred strains of mice: a comparison of three different types of data. In C. Patterson (ed.), *Molecules and Morphology in Evolution: Conflict or Compromise?* Cambridge University Press, Cambridge, pp. 203–216.
- Fleagle, J. G. 1999. *Primate Adaptation and Evolution*, 2nd ed. Academic Press, London.
- Fleagle, J. G., and McGraw, W. S. 1999. Skeletal and dental morphology supports diphyletic origin of baboons and mandrills. *Proc. Natl. Acad. Sci. USA* 96: 1157–1161.
- Freedman, L. 1962. Growth of muzzle length relative to calvaria length in *Papio*. *Growth* 26: 117–128.
- Good, P. 1993. Permutation tests: a practical guide to resampling methods for testing hypotheses. Springer-Verlag, New York.
- Goodall, C. R. 1991. Procrustes methods and the statistical analysis of shape. *J. Roy. Statist. Soc. B* 53: 285–340.
- Gower, J. C. 1975. Generalised Procrustes analysis. *Psychometrika* 40: 33–50.
- Groves, C. P. 1978. Phylogenetic and population systematics of the mangabeys (Primates: Cercopithecoidea). *Primates* 9: 1–34.
- Groves, C. P. 2000. The phylogeny of the Cercopithecoidea. In P. F. Whitehead and C. J. Jolly (eds.), *Old World Monkeys*. Cambridge University Press, Cambridge, pp. 77–98.
- Hall, B. K. 1998. *Evolutionary Developmental Biology*. Chapman and Hall, London.
- Harris, E. E. 2000. Molecular systematics of the Old World monkey tribe Papionini: analysis of the total available genetic sequences. *J. Hum. Evol.* 38: 235–256.
- Harris, E. E., and Disotell, T. R. 1998. Nuclear gene trees and the phylogenetic relationships of the Mangabeys (Primates: Papionini). *Mol. Biol. Evol.* 15: 892–900.
- Hillis, D. M., Bull, J. J., White, M. E., Badgett, M. R., and Molineux, I. J. 1992. Experimental phylogenetics: generation of a known phylogeny. *Science* 255: 589–592.
- Jablonski, N. G. 1993. The phylogeny of *Theropithecus*. In N. G. Jablonski (ed.), *Theropithecus: Rise and Fall of a Primate Genus*. Cambridge University Press, Cambridge, pp. 209–224.
- Jolicouer, P. (1963). The multivariate generalisation of the allometry equation. *Biometrics* 19: 497–499.
- Jolly, C. J. 1966. Introduction to the Cercopithecoidea, with notes on their use as laboratory animals. *Symp. Zool. Soc. Lond.* 17: 427–457.
- Jolly, C. J. 1967. The evolution of baboons. In H. Vagtborg (ed.), *The Baboon in Medical Research*, Vol. II. University of Texas Press, Austin, pp. 23–50.
- Jolly, C. J. 1970. The large African monkeys as an adaptive array. In J. R. Napier and P. H. Napier (eds.), *Old World Monkeys: Evolution, Systematics, and Behaviour*. Academic Press, New York, pp. 139–174.
- Kendall, D.G. 1984. Shape manifolds, procrustean metrics and complex projective spaces. *Bull. Lond. Math. Soc.* 16: 81–121.
- Kent, J. T. 1994. The complex Bingham distribution and shape analysis. *J. Roy. Statist. Soc. B* 56: 285–299.
- Kingdon, J. 1997. *The Kingdon Field Guide to African Mammals*. Academic Press, San Diego.
- Lieberman, D. E. 1995. Testing hypotheses about recent human evolution from skulls: integrating morphology, function, development, and phylogeny. *Curr. Anthropol.* 36: 159–197.
- Lieberman, D. E. 1997. Making behavioral and phylogenetic inference from hominid fossils: considering the developmental influence of mechanical forces. *Annu. Rev. Anthropol.* 26: 185–210.
- Lieberman, D. E. 1999. Homology and hominid phylogeny: problems and potential solutions. *Evol. Anthropol.* 7: 142–151.
- Lieberman, D. E. 2000. Ontogeny, homology, and phylogeny in the Hominid craniofacial skeleton: the problem of the browridge. In P. O'Higgins and M. J. Cohn (eds.), *Development, Growth and Evolution*. Academic Press, London, pp. 85–122.
- Lieberman, D. E., Wood, B. A., and Pilbeam, D. R. 1996. Homoplasy and early *Homo*: an analysis of the evolutionary relationships of *H. habilis sensu stricto* and *H. rudolfensis*. *J. Hum. Evol.* 30: 97–120.
- Lockwood, C. A., and Fleagle, J. G. 1999. The recognition and evaluation of homoplasy in primate and human evolution. *Ybk. Phys. Anthropol.* 42: 189–232.
- Lovejoy, C. O., Cohn, M. J., and White, T. D. 1999. Morphological analysis of the mammalian postcranium: a developmental perspective. *Proc. Natl. Acad. Sci. USA* 96: 13247–13252.
- McCollum, M. A. 1999. The robust australopithecine face: a morphogenetic perspective. *Science* 284: 301–305.
- Murray, P. D. F. 1934. *Bones*. Cambridge University Press, Cambridge.
- Nelson, G. J. 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. *Syst. Zool.* 27: 324–345.
- O'Higgins, P. 1999. Ontogeny and phylogeny: morphometric approaches to the study of skeletal growth and evolution. In M. A. J. Chaplain, G. D. Singh, and J. McLachlan (eds.), *On Growth and Form: Spatio-Temporal Patterning in Biology*. John Wiley and Sons, London, pp. 373–393.
- O'Higgins, P. 2000a. Quantitative approaches to the study of craniofacial growth and evolution: advances in morphometric techniques. In P. O'Higgins and M. Cohn (eds.), *Vertebrate Ontogeny and Phylogeny: Implications for the Study of Hominid Skeletal Evolution*. Academic Press, London, pp. 163–185.
- O'Higgins, P. 2000b. Advances in approaches to the study of morphological variation in the hominid fossil record: biology, landmarks and geometry. *J. Anat.* 197: 103–120.
- O'Higgins, P., and Collard, M. 2001. Sexual dimorphism and facial growth in papionin monkeys. *Journal of Zoology*. In Press.
- O'Higgins, P., and Jones, N. 1998. Facial growth in *Cercocebus torquatus*: an application of three dimensional geometric morphometric techniques to the study of morphological variation. *J. Anat.* 193: 251–272.
- O'Higgins P., and Strand Vidarsdottir, U. 1999. New approaches to the quantitative analysis of craniofacial growth and variation. In R. Hoppa and C. Fitzgerald (eds.), *Human Growth in the Past*. Cambridge University Press, Cambridge, pp. 128–160.
- Patterson, C. 1982. Morphological characters and homology. In K. A. Joysey and A. E. Friday (eds.), *Problems of Phylogenetic Reconstruction*. Academic Press, London, pp. 21–74.
- Rae, T. C. 1997. The early evolution of the hominoid face. In D. Begun, C. Ward, and M. Rose (eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. Plenum Press, New York, pp. 59–77.
- Reidl, R. J. 1978. *Order in Living Organisms*. Wiley, New York.
- Rohlf, F. J. 1999. Shape statistics: Procrustes superimpositions and tangent spaces. *Journal of Classification* 16: 197–223.
- Rohlf, F. J. 2000a. On the use of shape spaces to compare morphometric methods. *Hystrix* 11: 9–25.
- Rohlf, F. J. 2000b. Statistical power comparisons among alternative morphometric methods. *Am. J. Phys. Anthropol.* 111: 463–478.
- Rohlf, F., and Slice, D. E. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Syst. Zool.* 39: 40–59.
- Roth, V. L. 1984. On homology. *Biological Journal of the Linnean Society* 22: 13–29.
- Sanderson, M. J., and Hufford, L. (eds.). 1996. *Homoplasy: The Recurrence of Similarity in Evolution*. Academic Press, San Diego.
- Simpson, G. G. 1961. *Principles of Animal Taxonomy*. Columbia University Press, New York.
- Sober, E. 1988. *Reconstructing the Past: Parsimony, Evolution and Inference*. MIT Press, Cambridge, MA.
- Strasser, E., and Delson, E. 1987. Cladistic analysis of cercopithecoid relationships. *J. Hum. Evol.* 16: 81–99.
- Szalay, F., and Delson, E. 1979. *Evolutionary History of the Primates*. Academic Press, New York.
- van der Kuyl, A. C., Kuiken, C. L., Dekker, J. T., and Goudsmit, J. 1994. Phylogeny of African monkeys based upon mitochondrial 12S rRNA sequences. *J. Mol. Evol.* 40: 173–180.
- Wagner, G. P. 1989. The biological homology concept. *Ann. Rev. Ecol. Syst.* 20: 51–69.
- Wiley, A. 1911. *Convergence in Evolution*. John Murray, London.
- Wood, B. A. 1988. Are "robust" australopithecines a monophyletic group? In F. E. Grine (ed.), *Evolutionary History of the "Robust" Australopithecines*. Aldine de Gruyter, New York, pp. 269–284.