

Sexual dimorphism and facial growth in papionin monkeys

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Abstract

Sexual dimorphism in the primate face has been studied intensively lately, but a number of issues remain controversial. For example, some studies have indicated that facial sexual dimorphism arises through ontogenetic scaling, whereas others have found it to be a consequence of both ontogenetic scaling and divergence in male and female growth trajectories. To shed further light on primate facial sexual dimorphism, geometric morphometric methods were applied to crania representing five papionin genera: *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus* and *Papio*. A first set of analyses focused on the pattern and degree of facial sexual dimorphism exhibited by adult specimens. A second set of analyses concentrated on the ontogeny of facial sexual dimorphism in infant-to-adult age series. The first set indicated that the five genera exhibit significant facial sexual dimorphism. These analyses also revealed that the genera share several features of sexual dimorphism. Males are distinguished from females in having a more prognathic mid-face, a relatively more inferiorly and anteriorly positioned prosthion, relatively increased subnasal height and relatively broader zygomatic roots. They are also differentiated from females in their maxillae, which relative to the zygomatics are narrow but vertically deep, especially in the posterior aspect. Also, the first set of analyses indicated that *Macaca* is the most distinctive of the genera in terms of sexual dimorphism. The distinctive features of the *Macaca* sexual dimorphism are that males exhibit relatively wider nasal apertures and premaxillae than females, together with a relative increase in breadth across the inferior zygomatic roots. The second set of analyses demonstrated that in all the genera, sexual dimorphism arises partly through ontogenetic scaling and partly through a late divergence in male and female growth trajectories. The analyses also indicated that the relative contribution of these processes to sexual dimorphism varies among the genera. Ontogenetic scaling is by far the most important process in *Lophocebus* and *Papio*. Late divergence between male and female growth trajectories contributes proportionately more in *Cercocebus* and *Mandrillus*, although ontogenetic scaling still plays the major role. The relative contribution of late divergence between male and female growth trajectories is greatest in *Macaca*, in which it accounts for about half of the facial differences between adult males and females. In all five genera, ontogenetic scaling results in increased prognathism and greater relative maxillary size in males compared to females, whilst the late divergence involves the male mid-face becoming proportionately larger and deeper than the female mid-face, and the male posterior maxilla coming to lie more inferiorly with respect to the zygomatic root than its female counterpart.

Key words: sexual dimorphism, ontogeny, geometric morphometrics, baboon, mangabey, macaque

INTRODUCTION

Sex-linked skeletal and dental variation in humans and other primates has been the focus of considerable anthropological and anatomical research in the past

quarter of a century (e.g. Wood, 1976, 1985; Leutenegger & Kelley, 1977; Leutenegger, 1978, 1982; Leutenegger & Cheverud, 1982; Frayer & Wolpoff, 1985; Jungers, 1985; Leutenegger & Lubach, 1987; Oxnard, 1987; Lieberman, Pilbeam & Wood, 1988; Lovejoy *et al.*, 1989; O'Higgins, Moore *et al.*, 1990; Leigh & Cheverud, 1991; Wood, Li & Willoughby, 1991; O'Higgins & Dryden, 1993; Lague & Jungers,

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1999; Smith, 1999; Tague, 2000). There are two main reasons for this interest. First, sexual dimorphism is one of the major potential sources of variation that must be taken into account when assessing the number of species represented in a fossil sample (e.g. Wood, 1976, 1991, 1993; Lieberman *et al.*, 1988; Wood *et al.*, 1991; Kramer *et al.*, 1995; Richmond & Jungers, 1995; Waddle, Martin & Stock, 1995; Lockwood *et al.*, 1996; Kelley & Plavcan, 1998; Kelley & Alpagut, 1999; Kramer & Konigsberg, 1999; Lockwood, 1999; Miller, 2000). Before concluding that the variation exhibited by such a sample indicates the presence of multiple species, it is first necessary to demonstrate that the variation cannot be attributed to the effects of sexual dimorphism, geography and/or time. Second, reasonably strong correlations have been observed in extant species between sexual dimorphism and ecological variables (e.g. Crook, 1972; Clutton-Brock & Harvey, 1977; Clutton-Brock, Harvey & Rudder, 1977; Leutenegger & Kelley, 1977; Harvey, Kavanagh & Clutton-Brock, 1978; Leutenegger, 1978, 1982; Alexander *et al.*, 1979; Leutenegger & Cheverud, 1982; Frayer & Wolpoff, 1985; Jungers, 1985; Leutenegger & Lubach, 1987; Plavcan & van Schaik, 1992, 1994, 1997; Mitani, Gros-Louisi & Richards, 1995). Thus, by establishing the nature of sexual dimorphism in fossil species it has been possible to make inferences about their social systems and habitat preferences (e.g. Fleagle, Kay & Simons, 1980; F. H. Smith, 1980; Trinkaus, 1980; Jungers, 1988; McHenry, 1994; Plavcan & van Schaik, 1997; Quinney & Collard, 1997; Wrangham *et al.*, 1999).

Since the early 1980s, a number of researchers have investigated the development of sexually distinct morphologies in humans and non-human primates (e.g. Shea, 1983, 1986; Cheverud & Richtsmeier, 1986; Richtsmeier, Cheverud *et al.*, 1993; Richtsmeier, Corner *et al.*, 1993; Masterson, 1997; O'Higgins & Dryden, 1992; O'Higgins & Jones, 1998). In most anatomical elements of extant primates sexual dimorphism becomes more pronounced in later stages of growth and adulthood. For this reason we expect some relationship between growth patterns (the ways in which various anatomical elements change in size and shape during growth) and patterns of sexual dimorphism (the ways in which various anatomical elements differ in size and shape between adult males and females). Several possibilities for this relationship exist but in the extreme we might posit two models. In the first, sexual dimorphism arises simply through relative extension/truncation of a common growth trajectory in one sex (ontogenetic scaling). In the second, sexual dimorphism arises through growth trajectories that differ in pattern between the sexes. If sexual dimorphism in particular anatomical elements of a group of extant species arises exclusively through ontogenetic scaling, it should be possible to use the pattern of adult sexual dimorphism exhibited by fossil members of that group to reconstruct the latter's growth trajectories (O'Higgins & Jones, 1998).

The relationship between sexual dimorphism and

facial growth in humans and other primates has been investigated in several studies (e.g. Shea, 1983, 1986; Cheverud & Richtsmeier, 1986; Corner & Richtsmeier, 1991, 1992, 1993; Leigh & Cheverud, 1991; Richtsmeier, Cheverud *et al.*, 1993; Richtsmeier, Corner *et al.*, 1993; Masterson, 1997; O'Higgins & Jones, 1998; Strand Vidarsdottir, 1999; Cobb & O'Higgins, 2000; O'Higgins, Chadfield & Jones, 2001). These studies indicate that, in general, where sexual dimorphism exists in the primate face, it arises principally through ontogenetic scaling such that male and female adult morphologies represent different endpoints on a single ontogenetic trajectory, with female adults usually being smaller than males (e.g. Shea, 1983, 1986; Cheverud & Richtsmeier, 1986; Corner & Richtsmeier, 1991, 1992, 1993; Leigh & Cheverud, 1991; Richtsmeier, Cheverud *et al.*, 1993; Richtsmeier, Corner *et al.*, 1993). However, ontogenetic scaling does not completely explain adult sexual dimorphism. Several of the studies cited above noted subtle deviations from ontogenetic scaling as did Masterson (1997) in some craniofacial dimensions in two species of the New World monkey genus *Cebus*. Comparable results were obtained by O'Higgins & Jones (1998) in an analysis of facial sexual dimorphism in the papionin species *Cercocebus torquatus*. They found that the sexes of this species follow the same growth trajectory from infancy until eruption of the third permanent maxillary molar, with shape change consisting in the main of increasing maxillary and pre-maxillary prognathism. After the eruption of M³, males and females follow divergent growth trajectories such that they come to differ in the position and relative height of the mid-face with respect to the upper-face, with male maxillae and premaxillae becoming relatively more inferiorly set. Thus, sexual dimorphism in *C. torquatus* arises in part through extension of the size/shape relationship common to younger specimens and in part through sexual divergence in growth pattern.

In this paper we describe a study that was designed to shed further light on sexual dimorphism in the primate face. Building on the work of O'Higgins & Jones (1998), geometric morphometric methods were used to investigate facial sexual dimorphism in five papionin genera: *Macaca*, *Mandrillus*, *Papio*, *Lophocebus* and *Cercocebus*. A first set of analyses focused on the pattern and degree of facial sexual dimorphism exhibited by adult specimens. A second set of analyses concentrated on the ontogeny of facial sexual dimorphism in infant-to-adult age series.

MATERIALS AND METHODS

Data employed in the study comprised 3-dimensional (3-D) landmark coordinates recorded on the faces of mixed sex, infant-to-adult growth series representing five papionin genera. The landmark data were acquired with a Polhemus 3 Space Isotrak II digitizer (Polhemus Incorporated, Colchester, VT, U.S.A.) linked to a laptop computer running a spreadsheet program.

Table 1. Landmark definitions

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 supero-lateral 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 15	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	Naso-frontal 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

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 important anatomical features. To minimize error, the data were collected by just one of us. The data were recorded to an accuracy of 0.05 cm.

The taxa sampled were *Cercocebus* (49 specimens of *C. torquatus* including 7 adult males and 8 adult females), *Lophocebus* (41 specimens of *L. albigena* including 16 adult males and 13 adult females, plus 8 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 7 adult females) and *Papio* (34 specimens of *P. cynocephalus* including 4 adult males and 5 adult females). Adult crania were selected on the basis of completed dentition. Infant and juvenile specimens were aged using standard dental criteria. The ages of the juveniles 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 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 (Dryden & Mardia, 1998). Briefly, these approaches deal with coordinate data as opposed to inter-landmark distances and operate within a non-Euclidean shape space (Kendall, 1984), the geometric and statistical properties of which are well defined and highly desirable

(O'Higgins & Jones, 1998; O'Higgins, 1999, 2000a,b). The approaches offer considerable advantages in terms of statistical analysis and visualization in comparison with other approaches to the analysis of landmarks (Rohlf, 1999, 2000a,b).

The analyses incorporated in this study were conducted with the aid of the geometric morphometrics package *morphologika*. An outline of this package can be found on the world-wide web at <http://evolution.a-nat.ucl.ac.uk/morph/morph.html>. In addition, several recent publications have provided detailed descriptions of *morphologika* (O'Higgins & Jones, 1998; O'Higgins, 1999, 2000a,b; O'Higgins & Strand Vidarsdottir, 1999).

Pattern and degree of facial sexual dimorphism in adults

Seven analyses were carried out that focused on facial sexual dimorphism in the adult specimens. Analysis A1 was undertaken to determine whether the adult males and females within each genus differ significantly in shape. In this analysis, scale, translational and rotational differences among the coordinate data were minimized by a generalized Procrustes analysis (GPA) in which specimen scale was represented by centroid size (Gower, 1975; Bookstein, 1991; Goodall, 1991; Dryden & Mardia, 1998; O'Higgins & Jones, 1998). Mean male and female shapes were estimated for each genus by calculating the arithmetic mean of the appropriate GPA-transformed coordinates. The shape differences exhibited by the sexes of each genus were then quantified by computing the Procrustes chord distance between the male and female mean shapes (Dryden & Mardia, 1998). Also, the significance of the Procrustes chord distances was assessed through a permutation test (Good, 1993), in which the true Procrustes chord distance between means (computed following a pooled-sex GPA) was compared with the distribution of Procrustes chord distances calculated for a large number randomly permuted samples (1000 where the number of individuals permitted).

Having established a significant sex difference in each genus, analysis A2 examined the patterns of variation between male and female means of the five genera. In this analysis, the coordinate data for the mean specimens were subjected to a joint GPA. Patterns of variation amongst the resulting coordinates were examined through principal components analysis (PCA) of the covariance matrix of tangent projected coordinates (Dryden & Mardia, 1993; Kent, 1994). The relationship between size and shape was explored by examining plots and correlations of principal component (PC) scores vs centroid size for the significant principal components. Variations in shape were visualized using back projection from PCA, in which the mean was transformed along the PCs of interest and reconstructed as a 3-D graphic (e.g. Fig. 1). This indicated the shape variability represented by particular vectors (PCs) in the shape space (Dryden & Mardia, 1993; O'Higgins & Jones, 1998).

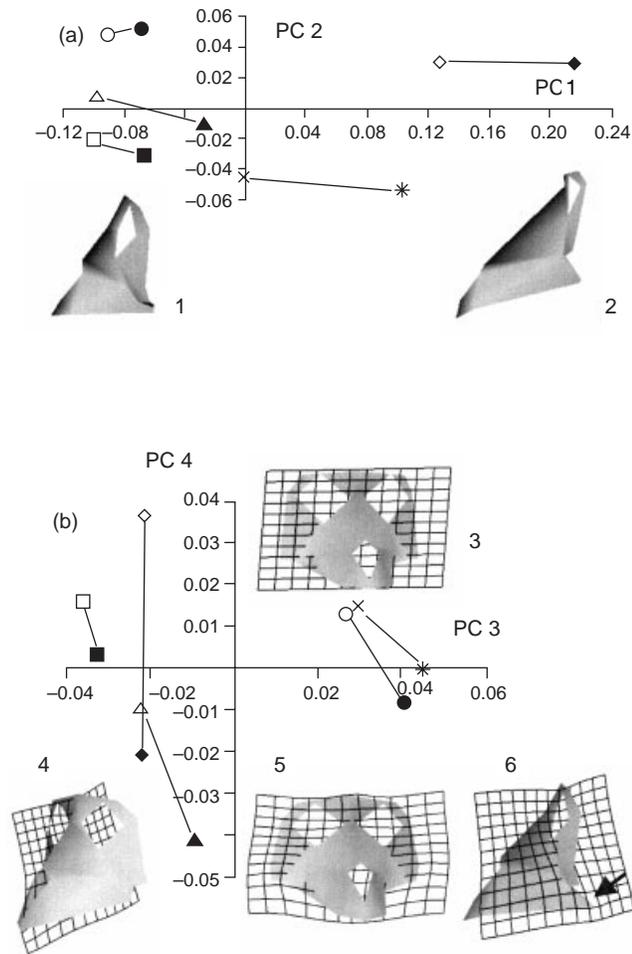


Fig. 1. PCA of adult sex means: (a) PC 1 (horizontal axis) vs PC 2 (vertical axis); (b) PC 3 (horizontal) vs PC 4 (vertical). PC 1 = 77.4%, PC 2 = 9.3%, PC 3 = 6.4%, PC 4 = 3%. Circles, *Macaca*; triangles, *Cercocebus*; rectangles, *Lophocebus*; diamonds, *Mandrillus*; cross, *Papio*; open shapes, female; closed shapes, male (*Papio m* = asterisk). Insets 1 and 2, lateral view of back projected mean face after transformation to the negative (1 = -0.12) and positive (2 = 0.24) limits of PC 1; insets 3, 4, 5 and 6, shape variability represented by positive and negative limits of PC 4: inset 3, mean warped to the positive extreme (0.04) of PC 4, a regular Cartesian grid is drawn vertically through the posterior part of the maxilla; insets 4, 5 and 6, mean warped to the negative extreme (-0.05) of PC 4; inset 5, Cartesian transformation grid in the same location as in inset 3. Insets 4 and 6, left and lateral views with Cartesian grids in the midline and through the zygomatic root, respectively. The deformations of the grids of insets 4, 5 and 6 are multiplied by a factor of 2 to emphasize their features and aid interpretation.

Analysis A3 explored further the differences in sexual dimorphism between the genera by computing Cartesian transformation grids calculated from triplets of thin-plate splines (Bookstein, 1989). These grids indicate how the space surrounding a reference shape can be deformed into that surrounding a target shape such that landmarks in the reference, map exactly into those of

the target; the thin plate spline ensures that the deformation involves minimum bending. The deformation was multiplied by a factor of 2 to aid interpretation.

Analysis A4 examined the extent to which subsets of PCs (defining subspaces of the entire shape space) accounted for the overall differences between sex means in each genus. In this analysis, the Euclidean distance between sex means was computed over the PCs of interest and expressed as a percentage of the full Procrustes distance between them; these figures were taken from analysis A1.

Analysis A5 investigated the patterns of sexual dimorphism through visual inspection of plots of PCs 1–4 showing the vectors connecting the male and female means of each genus. One plot focused on PC 1 and PC 2, the other on PC 3 and PC 4.

Analysis A6 examined further the patterns of sexual dimorphism through comparisons of the angles among the vectors connecting the sex means. The latter were obtained by GPA of the sex means for every possible pair of genera, followed by computation of the angle between the vectors (PCs) connecting the sex means of each pair of genera (Blackith & Reyment, 1971).

Analysis A7 evaluated PCs 2, 3, 5, 6, 7, 8 and 9 in order to identify the components of sexual dimorphism in *Macaca* that are not accounted for by PCs 1 and 4. As in analysis A2, variations in shape described by interesting PCs were visualized using back projection from PCA in which the mean was transformed along the PCs and reconstructed as a 3-D graphic. These visualizations were further interpreted using Cartesian transformation grids calculated from thin-plate spline triplets.

The ontogeny of sexual dimorphism

Nine analyses were also conducted that concentrated on the development of facial sexual dimorphism in the infant-to-adult age series. Analysis B1 separately investigated the growth trajectories within each genus through PCA of tangent-projected coordinates. As in analysis A1, scale, translational and rotational differences among the coordinate data for the specimens within each genus were minimized by GPA. The GPA-transformed coordinates were tangent-projected from the non-Euclidean shape space of Kendall, and a covariance matrix was compiled for each genus from the projected coordinates. Subsequently, the covariance matrices were subjected to PCA, and the relationship between size and shape during growth was explored by computation of correlations of PC scores vs centroid size for the significant principal components derived from the PCA of each generic age series.

Analysis B2 assessed the significance of the differences among the growth trajectories of the five genera through permutation tests of the angles between the first PCs recovered in analysis B1. Other PCs were not examined because they did not correlate to any large degree or significantly with centroid size and therefore

did not represent growth-related change. In the permutation tests the true angles were compared with the distribution of 1000 permuted angles.

Analysis B3 compared the growth trajectories of the five genera using plots of PC 1 against centroid size.

Analysis B4 investigated the absolute degree of ontogenetic scaling of shape in each genus by computing the difference between sex means on PC 1 from analysis B1. The significance of the differences between the male and female scores was assessed using a Student's *t*-test.

Analysis B5 compared the angles between the first PCs from analysis B1 with the angles between adult sex means from analysis A6 with a view to establishing the extent to which ontogenetic scaling accounts for adult sexual dimorphism. The rationale for this analysis was that, if ontogenetic scaling alone accounts for adult sexual dimorphism in each genus, we should expect the angles between the first PCs from the growth series (analysis B1) to mirror the angles between adult sex means (analysis A6). A large and significant correlation among the pairwise angles between first PCs from the growth series and pairwise angles between the adult sex means would indicate that ontogenetic scaling adequately accounts for adult sexual dimorphism. An insignificant correlation or a lack of correlation would indicate that ontogenetic scaling does not fully explain adult sexual dimorphism.

Analysis B6 investigated whether or not aspects of adult sexual dimorphism were the result of divergence in male and female growth trajectories rather than ontogenetic scaling. This was accomplished by *t*-testing the adult sex scores on higher PCs to determine whether significant differences in the mean shape of adult male and female faces are also found on other PCs.

Analysis B7 evaluated the absolute degree of divergence between male and female growth trajectories in each genus by subjecting the differences between the male and female scores on the non-scaling dimorphic PCs to Student's *t*-test.

Analysis B8 assessed the relative contributions of ontogenetic scaling and divergence of male and female growth trajectories to adult sexual dimorphism. This was accomplished for each genus by comparing the distances between males and females on PC 1 with the distances between the sexes on the other dimorphic PC.

Analysis B9 used plots and visualizations of warped means to investigate the nature of the component of sexual dimorphism resulting from ontogenetic scaling (i.e. the first PC-linked dimorphism) and of the component that arises through divergence in male and female trajectories (i.e. the higher PC-linked dimorphism). It also investigated the approximate timing of the divergence between the growth trajectories of the sexes. As in the adult-focused analyses, the visualizations involved back projection from PCA, in which the mean was transformed and reconstructed as a 3-D graphic. These visualizations were further interpreted using Cartesian transformation grids calculated from triplets of thin-plate splines.

RESULTS

The study described here incorporated seven analyses that examined the nature and degree of facial sexual dimorphism in adult specimens of five papionin genera: *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus* and *Papio*. It also incorporated nine analyses that concentrated on the ontogeny of facial sexual dimorphism in infant-to-adult age series representing each of the genera.

Nature and degree of facial sexual dimorphism in adults

Analyses A1 used permutation tests of the full Procrustes distances between male and female mean shapes for each genus to determine whether the five genera exhibit significant facial dimorphism. These distances are presented in Table 2. The permutation tests indicated that the shape differences between the male and female mean shapes are statistically significant. The *P*-value was < 0.001 in all genera except *Papio*, where small adult sample sizes limited the number of permutations and $P < 0.02$. Analysis 1 therefore indicated that all five genera are characterized by significant sexual dimorphism in facial shape.

Analysis A2 investigated the nature of the dimorphisms exhibited by the genera through a PCA of tangent-projected coordinates representing the mean male and female shapes. The PCA yielded nine non-zero principal components. The first of these accounted for 77% of the total variance between means. The other notable PCs were 2, 3, 4 and 8. PC 2 accounted for 9.3% of the variance, PC 3 for 6.3%, PC 4 for 3% and PC 8 for 0.4%. Examination of plots of these PCs indicated that the genera share some features of facial sexual dimorphism but differ in others. The shared features are represented by PC 1 and PC 4, the inter-generic differences by PCs 2, 3, 5, 6, 7 and 9. The nature of the shared features is explored in Fig. 1, which presents a plot of PC 1 vs PC 2 (Fig.1a), and a plot of PC 3 vs PC 4 (Fig.1b). In Fig.1(a), inset 1 is the mean form transformed to the negative limit of PC 1 and inset 2 is the mean form transformed to the positive limit of PC 1. Since males tend to have higher scores than females on PC 1, inset 1 effectively represents female-like aspects of form and inset 2 male-like aspects of form. The forms differ principally in the relative length and height of the maxilla, such that males are generally more prognathic and have a relatively larger maxillae than females. In Fig.1(b), inset 3 is the mean form warped to the positive extreme of PC 4 and insets 4, 5 and 6 are the mean forms warped to the negative extreme of PC 4. These forms differ mainly in the proportioning of the mid-face relative to the upper face. In each genus, males tend to have lower scores than females on PC 4. Thus, the male muzzle is, in general, relatively larger and vertically deeper than the female muzzle.

Analysis A3 explored the common aspects of sexual dimorphism revealed by PC 4 through the computation

Table 2. Proportion of the full Procrustes distance between sexes accounted for by PCs 1 and 4 in the PCA of adult means. M, male; F, female

Genus	Score on PC 1	Score on PC 4	Distance between sex means on PCs 1 and 4	Full Procrustes distance between sex means	% of full Procrustes distance on dimorphic PCs
<i>Macaca</i> F	-0.09007	0.012483			
<i>Macaca</i> M	-0.06783	-0.0091	0.031	0.053	58
<i>Cercocebus</i> F	-0.09824	-0.00996			
<i>Cercocebus</i> M	-0.02688	-0.04199	0.078	0.082	95
<i>Mandrillus</i> F	0.127909	0.036435			
<i>Mandrillus</i> M	0.216011	-0.02055	0.105	0.112	93
<i>Lophocebus</i> F	-0.09867	0.01578			
<i>Lophocebus</i> M	-0.06526	0.002746	0.036	0.039	92
<i>Papio</i> F	-0.0007	0.014869			
<i>Papio</i> M	0.103717	-0.00072	0.106	0.118	89

of Cartesian transformation grids in which the deformation was multiplied by a factor of 2 to facilitate interpretation. These grids are shown in Fig. 1(b). The grids indicated that in males compared to females there is a more vertically deep posterior aspect of the maxilla relative to the zygomatic (arrow, Fig. 1, inset 6). The grids also revealed that in males compared to females there is a relative inferior and anterior positioning of prosthion with increased subnasal height (Fig. 1, inset 4). Lastly, the grids indicated that males show a relative narrowing of the maxilla and broadening of the zygomatic roots compared to females (Fig. 1, inset 5).

Analysis A4 assessed the extent to which PCs 1 and 4 account for sexual dimorphism in each genus. This was accomplished by expressing the Euclidean distance between the sex means based on their scores on PCs 1 and 4 as a percentage of the relevant full Procrustes distance (see Table 2). From these it can be seen that PCs 1 and 4 account for *c.* 90% of the distance between sex means in *Cercocebus*, *Lophocebus*, *Mandrillus* and *Papio*. In contrast, PCs 1 and 4 account for 58% of the distance between sex means in *Macaca*. This indicates that although *Macaca* shares some aspects of sexual dimorphism with the other papionin genera, it also exhibits components of sexual dimorphism that are not accounted for by PCs 1 and 4 and which are more distinctive.

Analysis A5 investigated the patterns of sexual dimorphism through visual inspection of plots of PCs 1–4 showing the vectors connecting the male and female means of each genus. One of the plots focused on PC 1 and PC 2, the other on PC 3 and PC 4. The plot of PC 1 vs PC 2 (Fig. 1a) indicated that the inter-sex vectors of *Cercocebus*, *Lophocebus*, *Mandrillus* and *Papio* trend in roughly the same direction, the female means being slightly above the male means on PC 2. In contrast, the vector connecting the sex means of *Macaca* was disposed in such a way that the female mean is slightly below the male mean. In other words, the PC 1 vs PC 2 plot showed the inter-sex vectors of *Cercocebus*, *Lophocebus*, *Mandrillus* and *Papio* trending in the opposite direction to that of *Macaca*. The plot of PC 3 vs PC 4 (Fig. 1b) indicated that the vectors connecting the sex

means of *Cercocebus*, *Lophocebus*, *Macaca* and *Papio* are roughly parallel, with the female means lying to the left of the male means on PC 3. The vector connecting the means of male and female *Mandrillus* differs slightly from those connecting the sexes of the other genera in that the female mean lies directly above the male mean. In sum, the visual inspection of the plots of PC 1–4 indicated that *Macaca* exhibits the most divergent pattern of sexual dimorphism on PC 2, and that *Mandrillus* displays the most divergent pattern on PC 3, although the divergence is less pronounced than the *Macaca* divergence on PC 2.

Analysis A6 examined the patterns of sexual dimorphism through comparisons of the angles among the vectors connecting the sex means. The angles, which are presented in Table 3, were in line with the findings of the preceding analysis. The angles between the vector connecting the sexes of *Macaca* and the inter-sex vectors of the other genera in the plot of PC 1 against PC 2 are consistently the largest. Likewise, in the plot of PC 3 against PC 4 *Mandrillus* manifests large angles between the vector connecting its sex means and the vectors connecting the sex means of *Lophocebus*, *Cercocebus*, *Macaca* and *Papio*, although these angles are considerably smaller than those between the *Macaca* inter-sex vector and the vectors connecting the sexes of the other genera in the plot of PC 1 against PC 2. Thus, *Macaca* displays the most divergent pattern of sexual dimorphism on PC 2, and *Mandrillus* exhibits the most divergent pattern on PC 3, although the latter divergence is much less pronounced than the former. Note that the angles in Table 3 are generally larger than might be expected from examination of the plots of Fig. 1. This is because PCs 5–9 in the analysis of sex means, whilst accounting for a very small proportion of overall variance between means (~4%), explain a larger proportion of the differences between genera in their patterns (vectors) of sexual dimorphism.

Analysis A7 evaluated PCs 2, 3, 5, 6, 7, 8 and 9 in order to identify the components of sexual dimorphism in *Macaca* that are not accounted for by PCs 1 and 4. This analysis indicated that PC 8, while accounting for a small proportion (0.4%) of the total variance, separated

Table 3. Angles (degrees) between vectors connecting sex means

	<i>Macaca</i>	<i>Cercocebus</i>	<i>Mandrillus</i>	<i>Lophocebus</i>
<i>Cercocebus</i>	60			
<i>Mandrillus</i>	52	36		
<i>Lophocebus</i>	71	35	41	
<i>Papio</i>	73	39	45	38

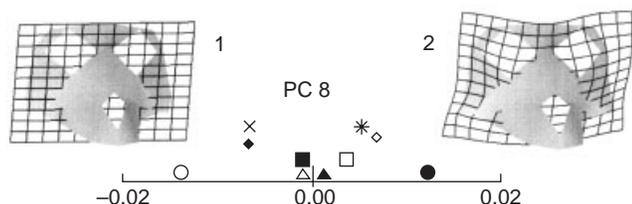


Fig. 2. PC 8 from PCA of adult sex means. PC 8 = 0.4% of total variance. Circles = *Macaca*; triangles = *Cercocebus*; rectangles = *Lophocebus*; diamonds = *Mandrillus*; cross = *Papio*. Open shapes, female; closed shapes, male (*Papio* m = asterix). Inset 1, mean warped to the negative extreme (-0.02) with overlain regular Cartesian grid; inset 2, mean warped to the positive extreme (0.02) with the Cartesian grid deformation multiplied by a factor of 5 to emphasize its features.

Macaca male and female means to the same degree as PC 4. Inspection of the warped means and Cartesian transformation grids (deformation multiplied by a factor of 2) on PC 8 (Fig. 2, insets 1 and 2) indicated that male *Macaca* exhibit a relatively wider nasal aperture and premaxilla compared to female *Macaca*. It also revealed that *Macaca* males display increased relative breadth across the inferior zygomatic roots compared to *Macaca* females.

Ontogeny of sexual dimorphism

Analysis B1 investigated the growth trajectories of the five genera through PCA of tangent-projected coordinates of infant-to-adult age series. In each genus the first PC described growth-related changes in facial shape such that scores on PC 1 showed large and significant correlations with centroid size. No other PCs showed any significant correlation with size over the entire age range. The percentage of total variance explained by PC 1 in each analysis was *c.* 50%, a little more in genera that undergo a lot of shape change during growth and less in those that do not (Table 4).

Analysis B2 assessed the significance of the differences among the growth trajectories of the five genera through permutation tests of the angles among the first PCs. The permutation tests indicated that in all comparisons except *Macaca* vs *Cercocebus* and *Macaca* vs *Lophocebus* the growth trajectory divergence is significant (Table 5).

Analysis B3 compared the growth trajectories of the five genera using plots of PC 1 against centroid size. The

Table 4. Correlations between scores on first PCs of age series and centroid size with significance levels

	Correlation	<i>P</i> -value	% total variance explained by PC 1
<i>Macaca</i>	-0.86	< 0.001	42
<i>Cercocebus</i>	-0.95	< 0.001	52
<i>Mandrillus</i>	0.94	< 0.001	73
<i>Lophocebus</i>	-0.62	< 0.001	40
<i>Papio</i>	0.97	< 0.001	62

Table 5. Angles between first PCs of age series with significance levels for these differences

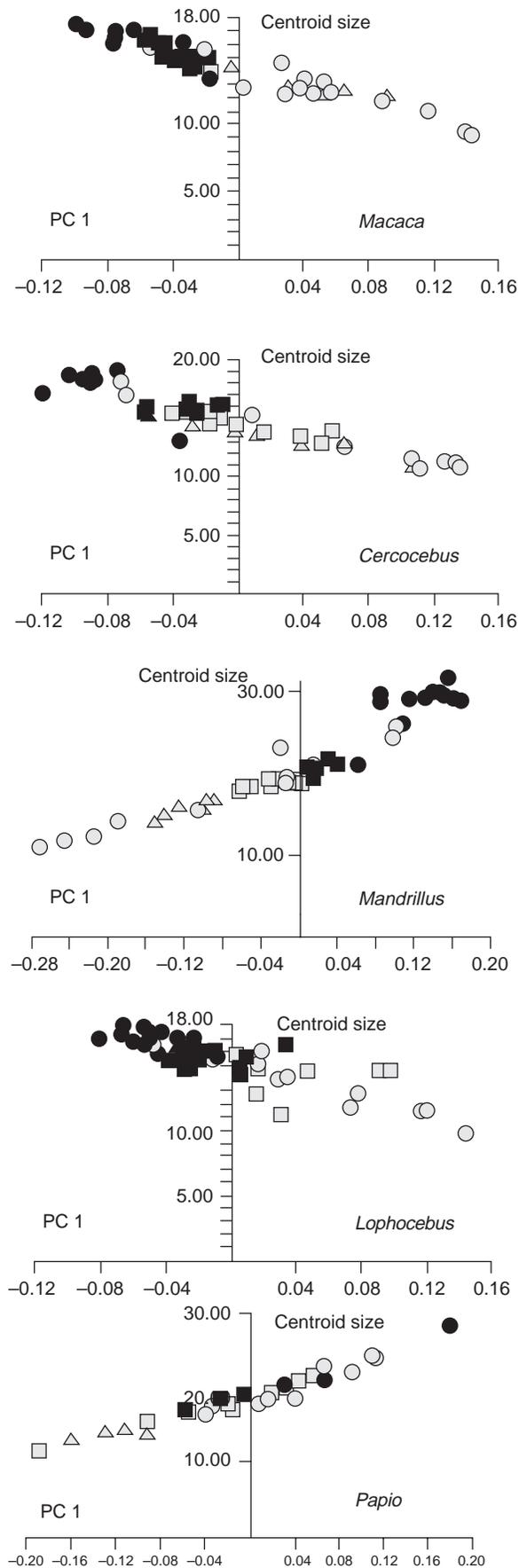
	<i>Macaca</i>	<i>Cercocebus</i>	<i>Mandrillus</i>	<i>Lophocebus</i>
<i>Cercocebus</i>	25 (0.207)			
<i>Mandrillus</i>	32 (< 0.001)	33 (< 0.001)		
<i>Lophocebus</i>	34 (0.499)	29 (0.007)	27 (< 0.001)	
<i>Papio</i>	34 (< 0.001)	36 (< 0.001)	21 (0.002)	32 (< 0.001)

plots, which are shown in Fig. 3, indicated that in each genus the relationship between PC 1 and centroid size is approximately linear, although in *Mandrillus* and possibly *Papio* there is evidence (curvilinearity of the graph) that as males become larger there is a decrease in the rate of change of shape.

Analysis B4 used Student's *t*-test to assess the significance of the absolute differences between the male and female scores on PC 1 in each genus with a view to establishing the absolute degree of ontogenetic scaling of shape exhibited by the genera. (for results of this analysis, see Table 6). The difference between adult male and female mean scores is significant in every genus, but it shows considerable variation in magnitude between genera. In absolute terms, *Papio* and *Mandrillus* exhibit the greatest degree of ontogenetic scaling, *Cercocebus* an intermediate degree, and *Lophocebus* and *Macaca* the least.

Analysis B5 compared the angles between the first PCs from analysis B1 (Table 5) with the angles between adult sex means from analysis A6 (Table 3) with a view to establishing the extent to which ontogenetic scaling accounts for adult sexual dimorphism. No significant correlation was found. The angles between growth vectors were consistently smaller than those between vectors connecting sex means. This indicates that adult sexual dimorphism is at most only partly explained by ontogenetic scaling.

Analysis B6 employed *t*-tests of scores on higher PCs to determine whether significant differences in the mean shape of adult male and female faces are also found on other PCs, and therefore whether sexual dimorphism also arises in part through divergence of male and female growth trajectories. This analysis indicated that a significant difference in the mean shape of adult male and female faces was present on one higher PC in every genus. This PC was PC 5 in *Macaca*, PC 2 in *Cercocebus*,



PC 3 in *Mandrillus* and *Lophocebus*, and PC 4 in *Papio*. As shown in Table 6, the non-growth-related dimorphic PCs accounted for between 8% and 4% of total variance in shape amongst the entire age series.

Analysis B7 evaluated the absolute degree of divergence between male and female growth trajectories in each genus by subjecting the differences between the male and female scores on the non-scaling dimorphic PC to Student's *t*-test. This analysis demonstrated that the late divergence between males and females varies in magnitude among the five genera. It is most pronounced in absolute terms in *Cercocebus* and *Mandrillus*, intermediate in *Macaca*, and least in *Lophocebus* and *Papio*.

Analysis B8 assessed the relative contributions of ontogenetic scaling and divergence of male and female growth trajectories to adult sexual dimorphism. This was accomplished for each genus by comparing the Procrustes distances between males and females on PC 1 with the Procrustes distances between the sexes on the other dimorphic PC. Both sets of Procrustes distances are shown in Table 6. The distance between male and female *Macaca* means on PC 1 is 0.028 and the inter-sex distance on the other dimorphic PC is 0.033. The equivalent distances are 0.066 and 0.049 in *Cercocebus*, 0.107 and 0.034 in *Mandrillus*, 0.034 and 0.019 in *Lophocebus*, and 0.11 and 0.017 in *Papio*. Thus, in *Macaca* divergence between male and female growth trajectories accounts for a larger proportion of sexual dimorphism than ontogenetic scaling, whereas in the other genera the greater part of adult sexual dimorphism is due to ontogenetic scaling. Among the other genera, the role of ontogenetic scaling is greatest in *Lophocebus* and *Papio*.

Analysis B9 used plots and visualizations of warped means to investigate the nature of those aspects of sexual dimorphism that are the result of ontogenetic scaling, and also of those that arise through divergence in male and female trajectories. It also investigated the timing of the late divergence between the growth trajectories of the sexes. Figures 4–8 show the first PC plotted against the other dimorphic PC for *Macaca*, *Cercocebus*, *Mandrillus*, *Lophocebus* and *Papio*, respectively. In each figure, the inset images at left and right depict shape variability along the first PC, whilst those at the top and bottom depict shape variability along the other dimorphic PC.

The right and left insets of Fig. 4 indicate that in *Macaca* the component of sexual dimorphism that arises through ontogenetic scaling consists in the main of a progressive increase in prognathism, plus an increase in size of the maxilla and premaxilla in males relative to females. Comparison of the upper with the lower insets of Fig. 4 suggests that adult males tend to

Fig. 3. PC 1 (horizontal axis) vs centroid size in centimetres (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; grey, sub-adult.

Table 6. PCs which significantly separate adult males and females

Genus	PC	% variance	Absolute difference in sex mean scores	Significance of <i>t</i> -test	Distance between sex means on dimorphic PCs	Full Procrustes distance between sex means	% of full Procrustes distance on dimorphic PCs
<i>Macaca</i>	1	42	0.028	$P < 0.005$	0.043	0.053	81
<i>Macaca</i>	5	4	0.033	$P < 0.0002$			
<i>Cercocebus</i>	1	52	0.066	$P < 0.0001$	0.082	0.089	92
<i>Cercocebus</i>	2	8	0.049	$P < 0.003$			
<i>Mandrillus</i>	1	73	0.107	$P < 0.0001$	0.11219	0.11279	99
<i>Mandrillus</i>	3	4	0.034	$P < 0.002$			
<i>Lophocebus</i>	1	40	0.034	$P < 0.0001$	0.039	0.045	86
<i>Lophocebus</i>	3	6	0.019	$P < 0.004$			
<i>Papio</i>	1	62	0.11	$P < 0.01$	0.011029	0.11813	93
<i>Papio</i>	4	3	0.017	$P < 0.008$			

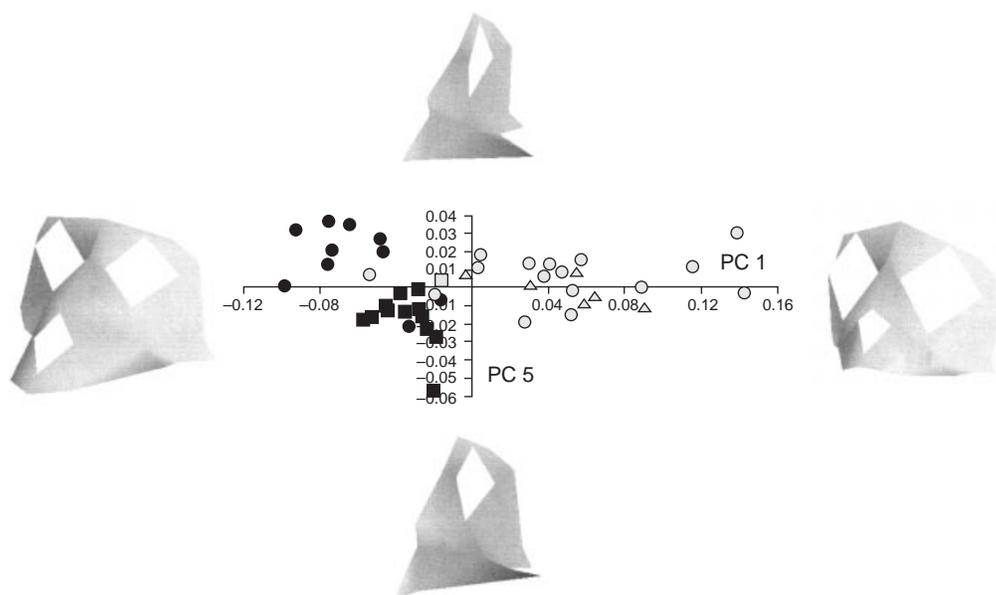


Fig. 4. PC 1 (horizontal axis) vs PC 5 (vertical axis) from analysis of *Macaca*. Circles, males; squares, females; triangles, unknown sex; black, adult; grey, sub-adult. Right inset image, anterior view of mean warped to the positive extreme of PC 1 (this is equivalent to a mean shape of small (= young) faces); left inset image, anterior view of mean warped to the negative extreme of PC 1 (this is equivalent to a mean shape of large (= adult) faces); top inset image, left lateral view of mean warped to the positive extreme of PC 5; bottom inset image, left lateral view of mean warped to the negative extreme of PC 5. On PC 5, the adult male mean has a more positive score than the adult female mean, thus the top and bottom insets indicate the nature of the shape difference between adult male and female means represented by this PC.

have an alveolar border that is relatively more horizontally set than that of adult females. The insets also indicate that adult males tend to have zygomatics that are more superiorly placed with respect to the posterior maxillary alveolar margin than the zygomatics of adult females. In anterior view (not shown) male zygomatics are also positioned more laterally with respect to the posterior maxillary alveolar margin.

The insets at the left and right of Fig. 5 suggest that those features of sexual dimorphism in *Cercocebus* that arise from ontogenetic scaling involve mainly increased prognathism and greater relative size of the mid-face in males compared to females. The insets at the top and

bottom of Fig. 5 indicate that adult males exhibit a different set of the mid-face with respect to the upper face compared to adult females, along with an increase in vertical height of the mid-face relative to the upper face. The upper and lower insets also indicate that adult male maxillae are relatively taller than those of adult females such that the posterior maxilla lies more inferiorly with respect to the zygomatic root.

The left and right insets in Fig. 6 indicate that those aspects of sexual dimorphism in *Mandrillus* that are the result of ontogenetic scaling consist of considerable increase in relative mid-facial size and prognathism in males compared to females. The upper and lower insets

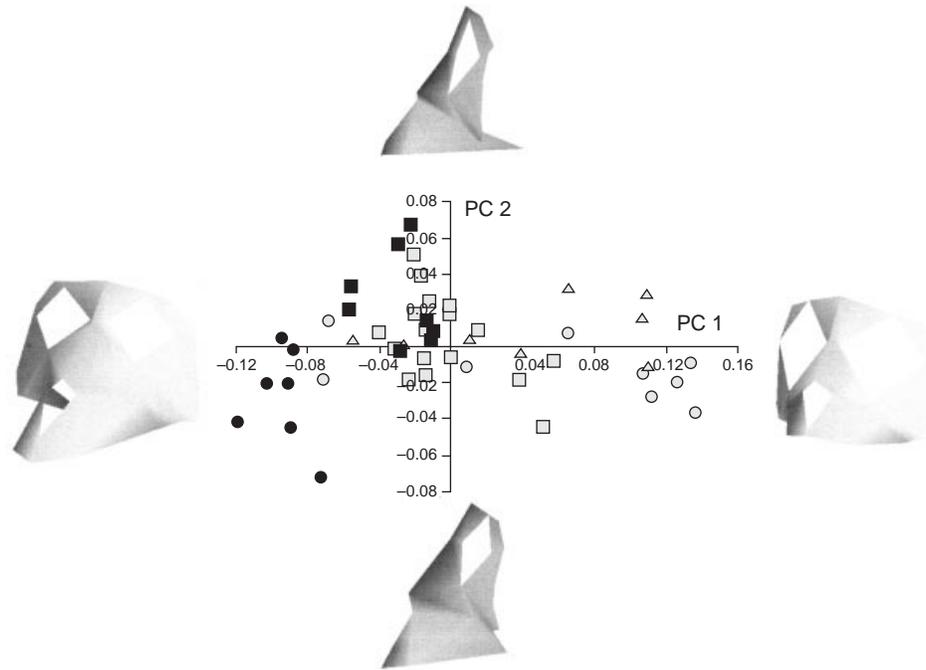


Fig. 5. PC 1 (horizontal axis) vs PC 2 (vertical axis) from analysis of *Cercocebus*. Circles, males; squares, females; triangles, unknown sex; black, adult; grey, sub-adult. Right inset image, anterior view of mean warped to the positive extreme of PC 1 (this is equivalent to a mean shape of small (= young) faces); left inset image, anterior view of mean warped to the negative extreme of PC 1 (this is equivalent to a mean shape of large (= adult) faces); top inset image, left lateral view of mean warped to the positive extreme of PC 2; bottom inset image, left lateral view of mean warped to the negative extreme of PC 2. On PC 2 the adult female mean has a more positive score than the adult male mean, thus the top and bottom insets indicate the nature of the shape difference between adult female and male means represented by this PC.

in Fig. 6 imply that those features of adult sexual dimorphism that arise from late divergence of male and female growth trajectories consist in the main of the maxillae becoming relatively taller in males such that, as in *Macaca* and *Cercocebus*, the posterior maxilla lies more inferiorly with respect to the zygomatic root. Additionally, there is an increase in relative zygomatic width visible on frontal view (not shown).

The insets at the left- and right-hand sides of Fig. 7 indicate that in *Lophocebus* the sexually dimorphic features that are linked to ontogenetic scaling include prognathism in adult males compared to females. The insets at the top and bottom of Fig. 7 suggest that the dimorphism on PC 3 is the result of increased relative maxillary height with the vertical distance between zygomatic and posterior maxilla being relatively greater in males.

The left and right insets in Fig. 8 reveal that those aspects of sexual dimorphism in *Papio* that result from ontogenetic scaling include the male mid-face becoming relatively very large and prognathic compared to the female mid-face. Examination of the upper and lower insets indicates that PC 4 describes a pattern similar to those seen in *Macaca*, *Cercocebus* and *Mandrillus*, namely an increase in relative mid facial height and from frontal view (note shown) zygomatic breadth.

With regard to the approximate timing of the divergence in growth trajectories, the analysis indicated that it occurs late in development in *Cercocebus*, *Macaca*

and *Mandrillus*. The plot of the *Lophocebus* age-series showed the divergence to be late, but the scatter of sub-adults on the relevant PC was similar to that of adults. We consider this to be most likely a consequence of the sample comprising more than one species. The *Lophocebus* sample consists mainly of *L. albigena*, but it also includes eight *L. aterrimus*. Note that all the *L. aterrimus* specimens are sub-adult and two of them have the lowest scores on PC 3 amongst the juveniles. The plot of the *Papio* age-series also showed the divergence to be late, but this too is problematic as the sample of adults was small resulting in several of the older sub-adults having more extreme scores on PCs 1 and 4 than the full adults. However, including these older sub-adults in our computations of degree and significance of dimorphism simply increases their significance.

Since the alignment of adult sexual dimorphism with any particular PC is largely fortuitous and other aspects of sexual dimorphism may be represented to some degree by smaller differences over several higher PCs, it was necessary to assess the extent to which our analyses accounted for the ontogeny of adult sexual dimorphism in the five genera. For each genus, the Procrustes distance between adult sex means was calculated, and for each PCA of the growth series, the Euclidean distance between adult sex means over PC 1 and the other PC that significantly separates adult sex means was computed (see Table 6). The analysis of *Macaca* indicates that the Procrustes distance between adult sex

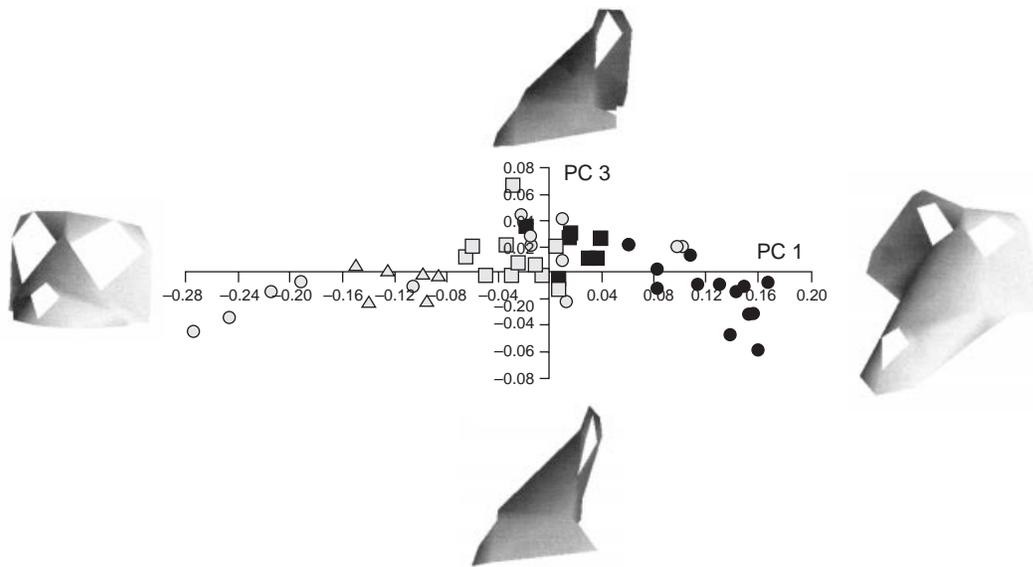


Fig. 6. PC 1 (horizontal axis) vs PC 3 (vertical axis) from analysis of *Mandrillus*. Circles, males; squares, females; triangles, unknown sex; black, adult; grey, sub-adult. Right inset image, anterior view of mean warped to the positive extreme of PC 1 (this is equivalent to a mean shape of large (= adult) faces); left inset image, anterior view of mean warped to the negative extreme of PC 1 (this is equivalent to a mean shape of small (= young) faces); top inset image, left lateral view of mean warped to the positive extreme of PC 3; bottom inset image, left lateral view of mean warped to the negative extreme of PC 3. On PC 3 the adult female mean has a more positive score than the adult male mean, thus the top and bottom insets indicate the nature of the shape difference between adult female and male means represented by this PC.

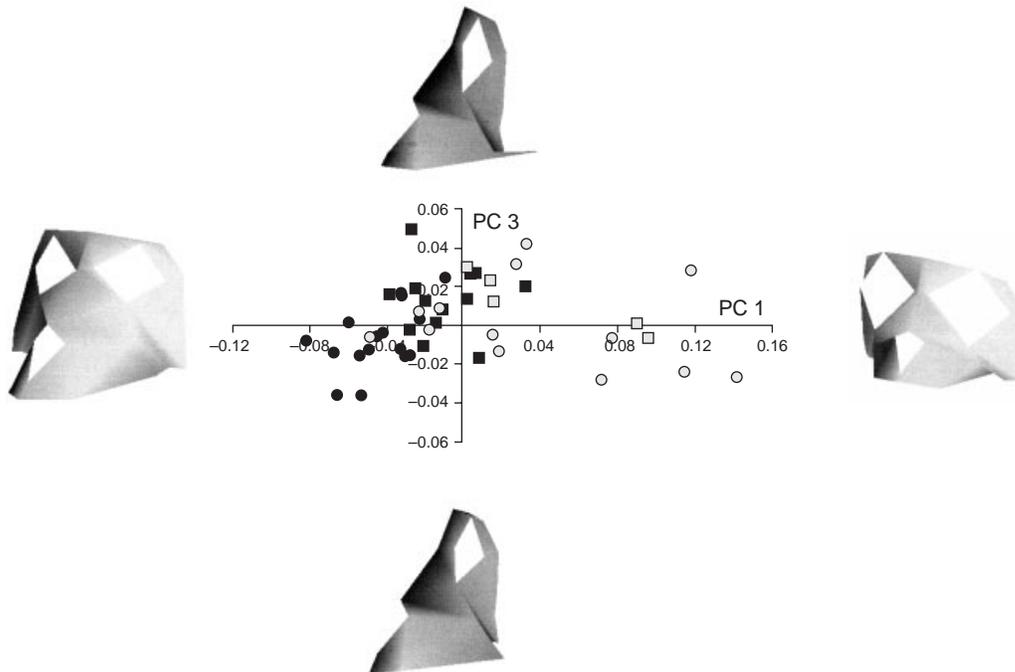


Fig. 7. PC 1 (horizontal axis) vs PC 3 (vertical axis) from analysis of *Lophocebus*. Circles, males; squares, females; triangles, unknown sex; black, adult; grey, sub-adult. Right inset image, anterior view of mean warped to the positive extreme of PC 1 (this is equivalent to a mean shape of small (= young) faces); left inset image, anterior view of mean warped to the negative extreme of PC 1 (this is equivalent to a mean shape of large (= adult) faces); top inset image, left lateral view of mean warped to the positive extreme of PC 3; bottom inset image, left lateral view of mean warped to the negative extreme of PC 3. On PC 3 the adult female mean has a more positive score than the adult male mean, thus the top and bottom insets indicate the nature of the shape difference between adult female and male means represented by this PC.

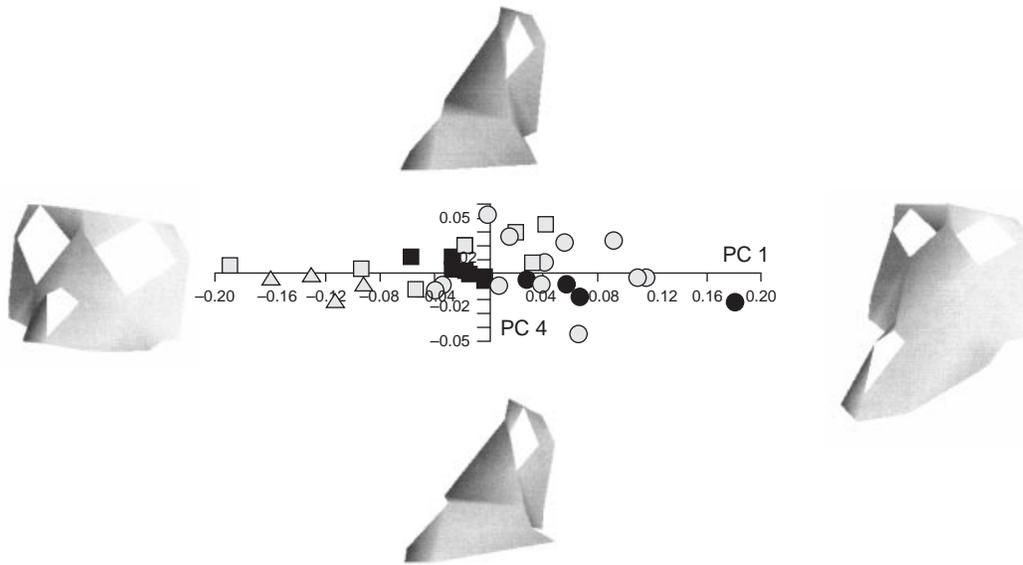


Fig. 8. PC 1 (horizontal axis) vs PC 4 (vertical axis) from analysis of *Papio*. Circles, males; squares, females; triangles, unknown sex; black, adult; grey, sub-adult. Right inset image, anterior view of mean warped to the positive extreme of PC 1 (this is equivalent to a mean shape of large (= adult) faces); left inset image, anterior view of mean warped to the negative extreme of PC 1 (this is equivalent to a mean shape small (= young) faces); top inset image, left lateral view of mean warped to the positive extreme of PC 4; bottom inset image, left lateral view of mean warped to the negative extreme of PC 4. On PC 4 the adult female mean has a more positive score than the adult male mean, thus the top and bottom insets indicate the nature of the shape difference between adult female and male means represented by this PC.

means is 0.053. In the growth series analysis, PC 1 accounts for a distance of 0.028 between adult sex means and PC 5 for a distance of 0.033. The Euclidean distance between adult sex means over PC 1 and PC 5 is 0.043 and this is 81% of the Procrustes distance. Thus the difference between adult sex means evident in Fig. 4 accounts for a significant proportion of the whole. In the other genera this proportion varies between 86% and 99%. Thus, we are confident that our analyses have more or less completely accounted for the ontogeny of adult sexual dimorphism, although in *Macaca* other PCs also represent minor aspects of adult sexual dimorphism.

DISCUSSION

The study described here incorporated seven analyses that investigated the pattern and degree of sexual dimorphism in adult specimens representing five papionin genera: *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus* and *Papio*. These analyses yielded three main findings. First, all the genera exhibit significant sexual dimorphism in facial shape. Inter-sex differences in facial shape were highly significant in *Cercocebus*, *Lophocebus*, *Macaca* and *Mandrillus*. The inter-sex difference in facial shape was large but less significant in *Papio*; this was most likely due to the small size of the adult sample of this genus.

The second main finding of the analyses of adult specimens was that the five genera share some features

of sexual dimorphism. PCA of tangent-projected coordinates representing adult male and female mean shapes resulted in two PCs that consistently ordered the sexes in the same way. Plots and visualizations of these PCs indicated that males are distinguished from females in degree of prognathism and in having relatively larger maxillae. Further common features of sexual dimorphism were revealed through the computation of Cartesian transformations grids. These indicated that males have a vertically deeper posterior aspect of the maxilla relative to the zygomatic than females. The grids also suggested that in males compared to females there is a relative inferior and anterior positioning of prosthion with increased subnasal height. Lastly, the grids revealed that males show a relative narrowing of the maxilla and broadening of the zygomatic roots compared to females.

The third main finding of the adult analyses was that the pattern of sexual dimorphism exhibited by *Macaca* is the most distinctive of the five genera. Although PCs 1 and 4 accounted for *c.* 90% of the full distance between the adult sex means in *Cercocebus*, *Lophocebus*, *Mandrillus* and *Papio*, these PCs accounted for only 58% of the full distance between the adult sex means in *Macaca*. This indicates that the *Macaca* pattern of sexual dimorphism differs from those of the other four genera. The distinctiveness of the *Macaca* pattern of sexual dimorphism was supported by visual inspection of plots showing the vectors connecting the sex means of each genus, and by an analysis of the angles among these vectors. In the sex means of each genus, the vector

of *Macaca* trended in a different direction to those of *Cercocebus*, *Lophocebus*, *Mandrillus* and *Papio*, whilst in the analysis of the angles, the vector of *Macaca* diverged by $c. 20^\circ$ more from the other genera's vectors than those vectors diverged from each other. Examination of the other PCs indicated that the distinctive aspects of sexual dimorphism in *Macaca* were accounted for principally by PC 8. A plot of this PC involving warped means and Cartesian transformation grids indicated that male *Macaca* exhibit a relatively wider nasal aperture and premaxilla compared to female *Macaca*. It also revealed that *Macaca* males display relatively increased breadth across the inferior zygomatic roots compared to *Macaca* females.

The present study also included nine analyses that investigated the ontogeny of sexual dimorphism in *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus* and *Papio*. Six of these analyses focused on the contribution of ontogenetic scaling to the inter-sex shape differences exhibited by each genus. Having established through a PCA of tangent-projected coordinates of infant-to-adult growth series that growth-related shape change was represented only by PC 1, permutation tests were used to assess the significance of the angles among the first PCs. This analysis indicated that growth trajectory divergence among the genera is significant in for all except *Macaca* vs *Cercocebus* and *Macaca* vs *Lophocebus*. Thereafter, plots of PC 1 were examined against centroid size. This analysis revealed that within each genus the relationship between PC 1 and centroid size is approximately linear, with adult males ontogenetically scaled in allometric shape relative to adult females. Subsequently, the absolute degree of inter-sex ontogenetic scaling exhibited by the genera was assessed. This analysis indicated that the absolute degree of ontogenetic scaling varies between genera, with *Papio* and *Mandrillus* exhibiting the greatest, *Cercocebus* intermediate, and *Lophocebus* and *Macaca* the least amount. The fifth analysis compared between genera the angles between the first PCs from the study of the age series with the angles between adult sex means with a view to establishing the extent to which ontogenetic scaling accounts for adult sexual dimorphism. This analysis demonstrated that the angles between growth vectors are consistently smaller than those between vectors connecting sex means, which indicates that ontogenetic scaling explains only a part of adult sexual dimorphism in the five papionin genera.

Two of the age-series analyses concentrated on the contribution of late divergence between male and female growth trajectories to adult sexual dimorphism. The first of these investigated whether significant differences in the mean shape of adult males and females are also found on PCs other than the first PC. This analysis revealed that a significant difference in the mean shape of the adult sexes was present on one higher PC in every genus. The second analysis that focused on the contribution of late divergence among male and female growth trajectories to adult sexual dimorphism evaluated the absolute degree of this divergence among the genera. It

indicated that the late divergence is most pronounced in absolute terms in *Cercocebus* and *Mandrillus*, intermediate in *Macaca*, and least pronounced in *Lophocebus* and *Papio*.

One of the age-series analyses quantified the relative contribution of ontogenetic scaling and divergence between male and female growth trajectories to adult sexual dimorphism. This was accomplished by comparing the Procrustes distances between males and females on PC 1 with the Procrustes distance between the sexes on the other dimorphic PC. The analysis indicated that ontogenetic scaling is by far the most important process in *Lophocebus* and *Papio*. Divergence between male and female growth trajectories contributes more in *Cercocebus* and *Mandrillus*, but ontogenetic scaling still plays the major role. The relative contribution of divergence between male and female growth trajectories is the greatest in *Macaca*, in which it accounts for about half of the facial differences between adult males and females. These findings parallel the greater divergence of the vector connecting sex means in *Macaca* from those connecting sex means of other papionins identified in the analyses of the adult specimens.

The last age-series analysis used plots of the non-scaling dimorphic PCs against the first PCs, together with 3-D visualizations, to investigate the nature of those aspects of sexual dimorphism that are due to ontogenetic scaling and those that arise through divergence in male and female growth trajectories. The analysis indicated that in all the genera the sexual dimorphism resulting from ontogenetic scaling involves a more prognathic muzzle and a larger maxilla in males compared to females. The sexual dimorphism due to divergence between male and female growth trajectories was found to consist in all the genera of males having a proportionately larger and deeper mid-face than females and a posterior maxilla that lies more inferiorly with respect to the zygomatic root, a finding which coincided with the common features of sexual dimorphism represented by PC 4 in the analysis of adult means. The analysis also examined the timing of the onset of the divergence between the growth trajectories of the sexes. It indicated that the divergence occurs late in development in all genera, although the reliability of this finding in *Lophocebus* and *Papio* was limited because of problems with the samples.

Two of the foregoing findings are particularly worthy of further discussion. The first is that facial sexual dimorphism in *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus* and *Papio* is evidently a consequence of both ontogenetic scaling and late divergence of male and female growth trajectories. This finding is in line with an earlier investigation of sexual dimorphism in facial shape in *Cercocebus* by O'Higgins & Jones (1998). It is also consistent with an assessment of sex-linked facial differences in orang-utans (Leutenegger & Masterson, 1989) and an analysis of facial sexual dimorphism in capuchins (Masterson, 1997), both of which noted departures from ontogenetic scaling. However, this

finding conflicts in emphasis with several other studies, most notably Shea's (1983, 1986) investigation of cranial sexual dimorphism in the African apes, Leigh & Cheverud's (1991) examination of the ontogeny of sexual dimorphism in the skull of *Papio*, Corner & Richtsmeier's (1991, 1992, 1993) assessments of cranial growth and sexual dimorphism in the New World monkey genera *Ateles*, *Saimiri* and *Cebus*, and Cheverud & Richtsmeier's (1986), Richtsmeier, Cheverud *et al.*'s (1993), and Richtsmeier, Corner *et al.*'s (1993) analyses of sexual dimorphism in the cranium of *Macaca*. These analyses found that inter-sexual differences in facial form arise in the main through ontogenetic scaling although some departures from this were noted.

Why should some studies indicate that sexual dimorphism in the primate face is principally a consequence of ontogenetic scaling with only minor departures, whilst other studies indicate that late divergence between male and female growth trajectories is an important contributor to dimorphism? One possibility is that the difference in emphasis is a result of different researchers using different methods to examine the ontogeny of facial sexual dimorphism. Cheverud & Richtsmeier (1986), for instance, employed finite elements analysis in their analysis of *Macaca*, whilst in our assessment of *Macaca* we relied heavily on principal components analysis of tangent-projected coordinates. Given that recent studies have indicated that the approaches used in this study offer considerable advantages in terms of statistical analysis and visualization in comparison with other approaches to the analysis of landmarks (Rohlf, 1999, 2000*a,b*), there is clearly a need to revisit Shea's (1983, 1986) analysis of the African apes and Corner & Richtsmeier's (1991, 1992, 1993) studies of *Ateles*, *Saimiri* and *Cebus* using the approaches used here to provide comparability.

The second finding worthy of discussion is the pattern among the five genera in terms of the relative contribution of ontogenetic scaling and divergence between male and female growth trajectories to sexual dimorphism. To recapitulate, ontogenetic scaling is by far the most important process in *Lophocebus* and *Papio*. Late divergence between male and female growth trajectories contributes more in *Cercocebus* and *Mandrillus*, but ontogenetic scaling still plays the major role. The relative contribution of late divergence between male and female growth trajectories is the greatest in *Macaca*, in which it accounts for about half of the facial differences between adult males and females. What is striking about this pattern is its apparent agreement with the molecular phylogeny for Papionini that has been developed over the last few years (Disotell, Honeycutt & Ruvolo, 1992; Disotell, 1994, 1996; Harris & Disotell, 1998; Harris, 2000) and which is becoming increasingly widely accepted as an accurate representation of the tribe's phylogenetic relationships (e.g. Fleagle & McGraw, 1999; Collard & Wood, 2000; Singleton, 2000). Contrary to conventional, morphology-based phylogeny, molecular phylogeny suggests that the mangabeys and

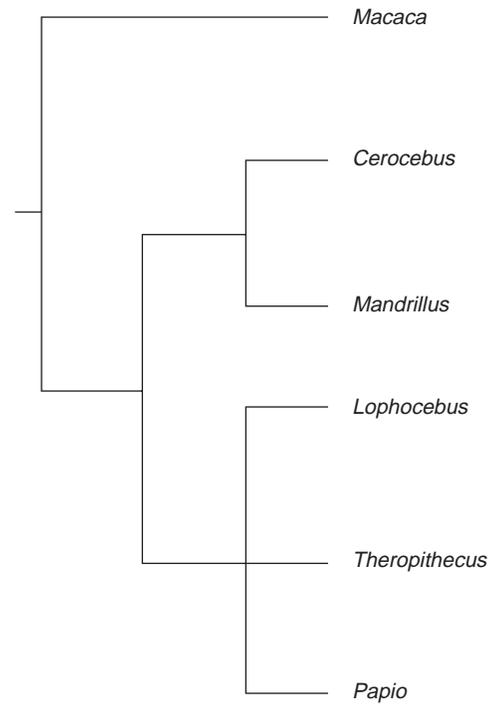


Fig. 9. Consensus molecular phylogeny for Papionini.

baboons are both diphyletic, with the mangabeys of the genus *Cercocebus* being most closely related to the forest baboons of the genus *Mandrillus*, and the mangabeys of the genus *Cercocebus* being most closely related to the savanna baboons of the genus *Papio* and the gelada baboons of the genus *Theropithecus* (Fig. 9). Although a formal analysis has not been carried out, it seems that the relative contribution of ontogenetic scaling and divergence between the growth trajectories of the sexes to sexual dimorphism groups the five genera in line with their molecular phylogeny rather than the morphological one. It may be that the concordance between our finding regarding the relative contribution of ontogenetic scaling and divergence between the growth trajectories of the sexes to sexual dimorphism and the molecular phylogeny is fortuitous. However, it is also possible that the concordance indicates that the processes by which the skeletal similarities and differences among primate taxa arise are more phylogenetically informative than the skeletal similarities and differences themselves. As Lieberman (1998, 1999, 2000) has outlined theoretical reasons why ontogenetic processes may be more reliable for phylogenetic reconstruction than skeletal characters, there is a clear case for examining the ontogeny of sexual dimorphism in other primate groups for which reliable molecular phylogenies are available using the approaches adopted in the present study. The extant hominoids are an obvious focus for such research (Ruvolo, 1997). It would also be useful to apply the approaches used here to an infant-to-adult age-series of the sixth extant papionin genus, *Theropithecus*. If ontogenetic processes are indeed phylogenetically informative, sexual dimorphism in this genus should arise mainly through

ontogenetic scaling, as it does in its sister taxa *Lophocebus* and *Papio*.

One remaining issue that deserves attention is what causes the ontogenetic scaling and the late divergence in male and female growth trajectories that underlie facial sexual dimorphism in the five papionin genera. Given that ontogenetic scaling has been found to be wholly or partly responsible for sexual dimorphism in a wide range of non-human anthropoids (Shea, 1983, 1986; Cheverud & Richtsmeier, 1986; Leutenegger & Masterson, 1989; Corner & Richtsmeier, 1991, 1992, 1993; Leigh & Cheverud, 1991; Richtsmeier, Cheverud *et al.*, 1993; Richtsmeier, Corner *et al.*, 1993; Masterson, 1997; Cobb & O'Higgins, 2000; O'Higgins, Chadfield *et al.*, 2001) and in some human groups (Strand Vidarsdottir, 1999), it seems likely to be a plesiomorphic process for at least the higher primates. As such, we might expect it to be the result of a simple signal with similar manifestations among the taxa in terms of its effect on growth. One likely candidate is the hormonal environment. At puberty, differences in hormones extend growth in males relative to females and trigger changes in functional matrices that stimulate growth divergence. With regard to the late divergence of growth between male and female papionins, which is probably a derived process, the hormonal environment again is a good candidate. The masticatory muscles are among the significant targets for hormones, and it is possible that increased bulk and force generation in males could lead to changes in the growth of the skeletal components of the masticatory apparatus (Moore, 1967; Moore & Lavelle, 1974; Hunt, 1998). An alternative is that differences in dental morphology, and so in skeletal loading, underlie divergence in growth between sexes. Studies of muscular dystrophies, differential force generation, edentulous individuals, and of sexual differences in growth between genera with different degrees of dental sexual dimorphism may be able to distinguish these alternatives.

SUMMARY AND CONCLUSIONS

The study described here sought to shed further light on sexual dimorphism in the primate face through geometric morphometric analyses of five papionin genera, *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus* and *Papio*. Our findings were as follows:

1. All the genera exhibit significant sexual dimorphism in facial shape.
2. The five genera share some features of sexual dimorphism:
 - (a) Males are distinguished from females in their degree of prognathism and in having relatively larger maxillae.
 - (b) Males are also differentiated from females in possessing relatively larger, deeper muzzles, and a vertically deeper posterior aspect of the maxilla relative to the zygomatic.

- (c) Males exhibit a relative inferior and anterior positioning of prosthion with increased sub-nasal height compared to females.
 - (d) Males display a relative narrowing of the maxilla and broadening of the zygomatic roots compared to females.
7. The pattern of sexual dimorphism exhibited by *Macaca* is the most distinctive of the five genera: *Macaca* males exhibit a relatively wider nasal aperture and premaxilla compared to female *Macaca*, and also increased breadth across the inferior zygomatic roots.
 8. Two processes are responsible for sexual dimorphism in *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus* and *Papio*: ontogenetic scaling and late divergence in the growth trajectories of males and females.
 9. *Mandrillus* and *Papio* exhibit the greatest degree of ontogenetic scaling, *Cercocebus* an intermediate degree, and *Lophocebus* and *Macaca* the least amount of ontogenetic scaling.
 10. Late divergence of growth vectors is most pronounced in *Cercocebus* and *Mandrillus*, intermediate in *Macaca*, and least pronounced in *Lophocebus* and *Papio*.
 11. In relative terms, ontogenetic scaling is by far the most important process in *Lophocebus* and *Papio*. Late divergence between male and female growth trajectories contributes more in *Cercocebus* and *Mandrillus*, but ontogenetic scaling still plays the major role. The relative contribution of late divergence between male and female growth trajectories is the greatest in *Macaca*, in which it accounts for about half of the facial differences between adult males and females.
 12. In all five genera, those aspects of sexual dimorphism due to ontogenetic scaling include increased prognathism and greater relative maxillary size in males compared to females.
 13. In all five genera, those features of sexual dimorphism that arise from divergence between male and female growth trajectories consist of the male mid-face becoming proportionately larger and deeper than the female mid-face, and the male posterior maxilla coming to lie more inferiorly with respect to the zygomatic root than its female counterpart.
 14. The divergence in growth trajectories takes place late in development in all the genera.

The finding that facial sexual dimorphism in *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus* and *Papio* is a consequence of both ontogenetic scaling and, to a considerable degree, late divergence of male and female growth trajectories is in line with some earlier studies but conflicts with others. It is possible that the explanation for this state of affairs is methodological. Hence there is reason to reanalyse the taxa on which some of the earlier studies focused using the approaches used in the present study. The pattern among the five genera in terms of the relative contribution of ontogenetic scaling

and divergence between male and female growth trajectories to sexual dimorphism is striking in that it groups the five papionin genera in the same manner as the molecular estimate of their phylogenetic relationships. This suggests that the processes by which the skeletal similarities and differences among primate taxa arise are more phylogenetically informative than the skeletal similarities and differences themselves. This possibility should be tested further by using the approaches adopted in the present study to examine the ontogeny of sexual dimorphism in other primate groups for which reliable molecular phylogenies are available. It should also be tested by applying the approaches to an infant-to-adult age-series of the remaining extant papionin genus, *Theropithecus*. Lastly, it seems likely that the ontogenetic scaling that gives rise to sexual dimorphism in *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus* and *Papio* are driven by changes in the hormonal environment during puberty. The divergence in male and female growth trajectories that also contributes to sexual dimorphism in the five genera may also be linked to puberty-related hormonal changes. Alternatively, they may relate to differences in dental morphology and so in skeletal loading underlie divergence in growth between sexes. Studies of muscular dystrophies, differential force generation, edentulous individuals, and of sexual differences in growth between genera with different degrees of dental sexual dimorphism are required to distinguish these alternatives.

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