

# Wide faces or large canines? The attractive versus the aggressive primate

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**Hominids display marked body size dimorphism, suggestive of strong sexual selection, yet they lack significant sex differences in canine size that are commonly associated with intrasexual competition in primates. We resolve this paradox by examining sex differences in hominoid facial morphology. We show that chimpanzees, but not gorillas, exhibit clear sexual dimorphism in face width, over and above that expected based on sex differences in body size. We show that this facial dimorphism, expressed as an index, is negatively correlated with canine dimorphism among anthropoid primates. Our findings suggest that a lack of canine dimorphism in anthropoids is not owing to weak sexual selection, but rather is associated with strong sexual selection for broader face width. Enlarged cheekbones are linked with attractiveness in humans, and we propose that the evolution of a broad face and loss of large canines in hominid males results from mate choice.**

**Keywords:** *Pan troglodytes*; canine dimorphism; facial attractiveness; mate choice

## 1. INTRODUCTION

The phenomenon of weak canine dimorphism associated with the modest to high levels of body weight dimorphism that typify the hominid lineage has long presented a problem when using sexual dimorphism to infer social behaviour within extinct hominid species (Leutenegger & Shell 1987; Plavcan & van Schaik 1997; Plavcan 2001). Whereas weak canine dimorphism is indicative of low levels of intrasexual competition, intense male–male competition in anthropoid primates is usually associated with marked body size dimorphism (Plavcan & van Schaik 1992, 1997). We attempt to resolve this inconsistency by examining how sex differences in facial morphology, detected here in *Pan troglodytes* but absent in *Gorilla gorilla*, relate to canine dimorphism in other anthropoid primates.

Previously, sexual dimorphism in the chimpanzee has been largely associated with differences in body size (Wood 1976; Shea 1983; O'Higgins & Dryden 1993). However, we find in *Pan troglodytes* that some changes in the male chimpanzee skull that relate to the breadth of the

face do not comply with predictions based on ontogenetic scaling. This type of facial dimorphism has been observed in other anthropoid primates (Masterson & Leutenegger 1992; Masterson 1997; O'Higgins & Collard 2002). In the Bornean orang-utan, it has been associated with the large cheek pads that occur in mature males (Masterson & Leutenegger 1992). In the tufted capuchin monkey (*Cebus apella*), the relatively broader male face has been related to the enlargement of the masticatory musculature; however, no significant dietary distinctions have been found to exist between the sexes (Masterson 1997). In *Macaca mulatta* the increased breadth of the male face, with enlargement of the temporalis muscle, has been considered a function of canine size (O'Higgins & Collard 2002). In addition, Wood *et al.* (1991), in a study of intra-specific adult cranial variation across higher primates, demonstrated that cranial breadths were the better sex discriminators compared with measures of facial height. In humans, male cheekbones are enlarged during puberty under the influence of testosterone (Enlow & Hans 1996).

We test the hypothesis that facial breadth dimorphism is related to canine dimorphism using 14 species of anthropoid primate. Given the high incidence of body size dimorphism characterizing different species of primate (Plavcan & van Schaik 1992), it is necessary to control for allometric size differences existing between the sexes. This was achieved by creating indices of facial dimorphism derived from three cranial variables: bizygomatic width, superior facial length and superior facial height. Canine sexual dimorphism is expressed as a ratio of maxillary canine height, as canine dimorphism is usually much greater in the crown height of the tooth than in the occlusal dimensions at the base of the tooth (Plavcan 2001). Furthermore, primate competition levels are better discriminated by canine crown height (Plavcan & van Schaik 1997).

## 2. MATERIAL AND METHODS

### (a) Morphometric analysis

To determine the ontogeny of sex differences in facial morphology in *P. troglodytes* and *G. gorilla*, a postnatal growth series of male and female crania was digitized and inter-landmark distances calculated (see table 1). A comparative ontogenetic analysis of these data was carried out and the results recorded in table 1 and figure 1 (see electronic Appendix A for details of methods and measurement definitions).

### (b) The relation of facial breadth and canine height dimorphism

Data for this part of the study were taken from published sources; all anthropoid species for which data were readily available were included (see electronic Appendix B). Indices of dimorphism were derived from three variables: bizygomatic width, superior facial length and superior facial height; all measures were taken from adult crania. Dimorphism of cranial variables is expressed as the male mean divided by the female mean. The facial indices calculated represent a ratio of these dimorphisms (see table 2). Estimates of primate maxillary canine dimorphism were taken from Plavcan & van Schaik (1992). To assess the influence of phylogeny on correlated trait evolution, phylogenetically independent contrasts were calculated (see electronic Appendix B).

## 3. RESULTS

### (a) Morphometric analysis of Gorilla and Pan crania

Table 1 presents the results of a comparative ontogenetic analysis of ape crania, comparing ontogenetic trajectories between the sexes of *P. troglodytes* and *G. gorilla*. All trait relationships are highly correlated (*Gorilla*,  $r = 0.86–0.99$ ; *Pan*,  $r = 0.79–0.99$ ). In the chimpanzee,

Table 1. *p*-Values for bootstrap tests comparing the major axis slope (above diagonals) and *y*-intercept estimates (below diagonals) between male and female cranial ontogenetic trajectories.

(Abbreviations (see electronic Appendix A for cranial measurement definitions): BCL, basicranial length; FL, superior facial length; FHT, superior facial height; BZW, bizygomatic width; BJW, bijugal width; UCW, upper bicanine width; BMW, bimaxillary width; PMW, bipremaxillary width; MW, bimastoid width; OW, orbital width.)

(a) <i>Pan troglodytes</i>	1 BCL	2 FL	3 FHT	4 BZW	5 BJW	6 UCW	7 BMW	8 PMW	9 MW	10 OW
1 BCL	—	0.595	0.897	0.018*	0.014*	0.131	0.059	0.429	0.746	0.290
2 FL	0.048	—	0.709	0.004*	0.002*	0.077	0.088	0.444	0.967	0.641
3 FHT	0.037	0.404	—	0.010*	0.007*	0.201	0.086	0.418	0.796	0.426
4 BZW	0.782	0.172	0.061	—	0.633	0.205	0.166	0.260	0.009 <sup>a*</sup>	0.564
5 BJW	0.190	0.949	0.417	0.292	—	0.118	0.150	0.174	0.005 <sup>a*</sup>	0.403
6 UCW	0.700	0.206	0.125	0.900	0.279	—	0.800	0.622	0.251	0.952
7 BMW	0.027	0.433	0.907	0.017*	0.342	0.069	—	0.598	0.050	0.894
8 PMW	0.238	0.829	0.763	0.258	0.772	0.087	0.787	—	0.532	0.808
9 MW	0.051	0.000**	0.000**	0.016*	0.000**	0.025	0.000**	0.004*	—	0.325
10 OW	0.558	0.751	0.425	0.685	0.797	0.759	0.520	0.677	0.068	—
(b) <i>Gorilla gorilla</i>	1 BCL	2 FL	3 FHT	4 BZW	5 BJW	6 UCW	7 BMW	8 PMW	9 MW	10 OW
1 BCL	—	0.461	0.772	0.387	0.672	0.814	0.834	0.047	0.325	0.805
2 FL	0.535	—	0.900	0.169	0.278	0.801	0.823	0.049	0.177	0.967
3 FHT	0.767	0.889	—	0.343	0.549	0.911	0.903	0.187	0.333	0.960
4 BZW	0.962	0.655	0.819	—	0.326	0.270	0.083	0.060	0.794	0.472
5 BJW	0.939	0.556	0.741	0.969	—	0.485	0.323	0.061	0.439	0.549
6 UCW	0.359	0.114	0.268	0.299	0.357	—	0.992	0.031	0.303	0.903
7 BMW	0.061	0.076	0.221	0.008*	0.007*	0.003*	—	0.171	0.205	0.993
8 PMW	0.048	0.034	0.090	0.039	0.027	0.000**	0.388	—	0.050	0.153
9 MW	0.017*	0.003*	0.022	0.011*	0.021	0.215	0.000**	0.000**	—	0.387
10 OW	0.558	0.725	0.780	0.583	0.481	0.253	0.578	0.268	0.038	—

<sup>a</sup> Combined effect of mastoid (see intercepts) and facial breadth dimorphism (see slopes) in *Pan*.

\*  $p \leq 0.02$ ; \*\*  $p \leq 0.001$ .

Table 2. Least-squares regression statistics for the relationships of canine height dimorphism, body weight dimorphism and body weight (F) with indices of facial dimorphism for 14 species of anthropoid primate.

(Source data: see electronic Appendix B for sources of data; maxillary canine height dimorphism and body weight data (Plavcan & van Schaik 1992). *d*, dimorphism ratio (adult male mean divided by adult female mean). CHD, canine height dimorphism. See table 1 for cranial measure abbreviations.)

	facial dimorphism index (BZW <sup>d</sup> /FHT <sup>d</sup> )				facial dimorphism index (BZW <sup>d</sup> /FL <sup>d</sup> )			
	slope	<i>r</i>	<i>F</i>	<i>p</i>	slope	<i>r</i>	<i>F</i>	<i>p</i>
canine height dimorphism	−6.359	−0.818	24.183	0.0004	−7.205	−0.767	17.136	0.0014
CHD (independent contrasts)	−5.103	−0.718	12.766	0.0038	−4.766	−0.569	5.743	0.0337
body weight dimorphism	−3.288	−0.491	3.821	0.0743	−2.842	−0.352	1.694	0.2175
body weight (F)	−13.025	−0.029	0.010	0.9219	−18.037	−0.033	0.013	0.9105

the relationships between bizygomatic width (BZW) and bijugal width (BJW) with basicranial length (BCL), superior facial length (FL) and superior facial height (FHT) differ between the sexes (table 1*a*, slope comparisons). However, there is no significant departure from ontogenetic scaling in male and female gorillas for these trait relationships (table 1*b*, slope comparisons). Figure 1 illustrates the type of bivariate relationship that underpins these sexual differences. In chimpanzees, an increase in male facial breadth relative to the length and height of the face is evident. Furthermore, this type of facial dimorphism manifests itself late in postnatal ontogeny, indicative of secondary sexual development that is not evident at birth (figure 1*a*). The significant *y*-intercept comparisons indicate that breadth across the mastoids

(MW) differs between males and females in both *Pan* and *Gorilla*, whereas in *Gorilla* the maxilla (BMW) and the premaxilla (PMW) exhibit sexual variation that is not evident in *Pan*. Ontogenetic trajectories that do not differ indicate that males and females are ontogenetically scaled (variation is associated with growth or size).

#### (b) *The relation of facial breadth and canine height dimorphism in 14 species of anthropoid primate*

Table 2 presents the regression statistics for the relationship of canine height dimorphism, body weight dimorphism and body weight (female) with indices of facial dimorphism. A significant relationship was found between canine height dimorphism and both indices of

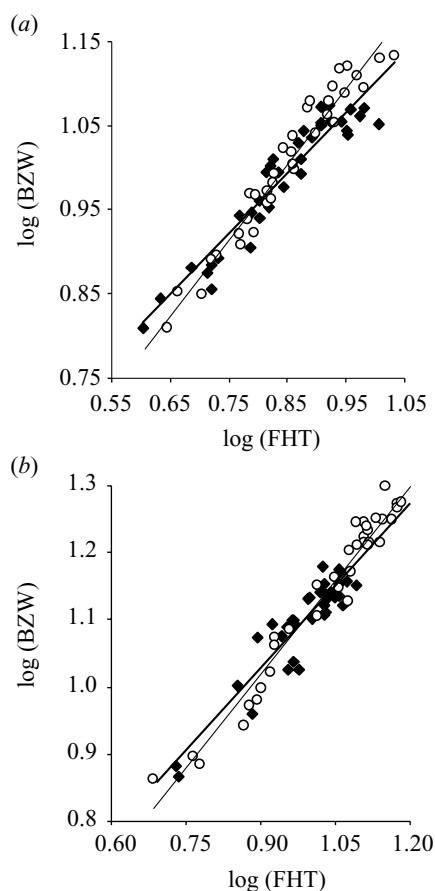


Figure 1. A comparison of male and female ontogenetic trajectories depicting the relationship between bizygomatic width (BZW) and superior facial height (FHT). (a) *Pan troglodytes* (departure from ontogenetic scaling). (b) *Gorilla gorilla* (no departure from ontogenetic scaling). Open circles, males; filled diamonds, females. Major axis slopes and 95% confidence intervals: *P. troglodytes*, male 0.92 (0.85–1.0), female 0.75 (0.67–0.84); *G. gorilla*, male 0.95 (0.88–1.03), female 0.88 (0.75–1.01).

facial dimorphism; for the raw data,  $F_{1,12} = 24.183$ ,  $p = 0.0004$ ;  $F_{1,12} = 17.136$ ,  $p = 0.0014$ ; for the phylogenetically independent contrasts,  $F_{1,12} = 12.766$ ,  $p = 0.0038$ ;  $F_{1,12} = 5.743$ ,  $p = 0.0337$ . Figure 2 illustrates the most significant of these relationships in which the facial dimorphism index is represented as a ratio of the dimorphisms in BZW and superior FHT. This is equivalent to the subtraction of superior FHT dimorphism ( $DI$ ) from BZW dimorphism ( $DI_{BZW} - DI_{FHT}$ ). In consequence, dimorphism indices greater than 1 indicate that  $DI_{BZW} > DI_{FHT}$  and dimorphism indices of less than 1 indicate that  $DI_{FHT} > DI_{BZW}$  (see figure 2a, x-axis). If dimorphism ratios are regressed separately against canine height dimorphism ( $DI_{CHT}$ ), it can be shown that a significant correlation exists between superior FHT dimorphism and  $DI_{CHT}$  ( $F_{1,12} = 12.551$ ,  $p = 0.004$ ,  $r = 0.715$ ), whereas no correlation is evident between  $DI_{BZW}$  and  $DI_{CHT}$  ( $F_{1,12} = 0.192$ ,  $p = 0.6691$ ,  $r = 0.125$ ). Body weight dimorphism and female body weight were also regressed against facial dimorphism indices but these relationships were not significant (table 2). There was no significant relationship between canine height and body weight dimorphism ( $F_{1,12} = 3.915$ ,  $p = 0.0713$ ,  $r = 0.496$ ).

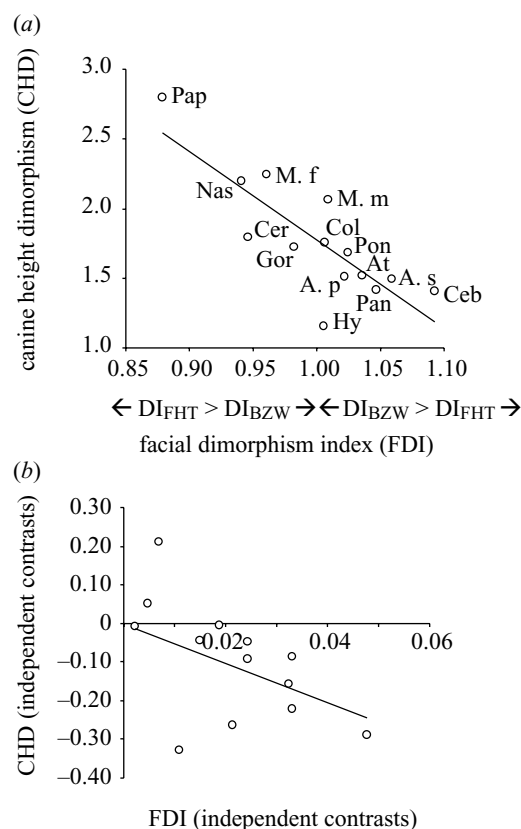


Figure 2. Inverse relationship between canine-height dimorphism and facial dimorphism for 14 species of anthropoid primate. (a) Raw data. Dimorphism indices of greater than 1 indicate that  $DI_{BZW} > DI_{FHT}$ ; dimorphism indices of less than 1 indicate that  $DI_{FHT} > DI_{BZW}$ . (b) Phylogenetically independent contrasts. FDI, BZW dimorphism ratio/FHT dimorphism ratio; A. p, *Alouatta palliata*; A. s, *Alouatta seniculus*; At, *Ateles geoffroyi*; Ceb, *Cebus apella*; Cer, *Cercopithecus aethiops*; Col, *Colobus polykomos*; Gor, *Gorilla gorilla*; Hy, *Hylobates lar*; M. f, *Macaca fascicularis*; M. m, *Macaca mulatta*; Nas, *Nasalis larvatus*; Pan, *Pan troglodytes*; Pap, *Papio cynocephalus*; Pon, *Pongo pygmaeus*. Regression statistics (table 2).

#### 4. DISCUSSION

Contrary to functional expectations, we show that two indices of facial dimorphism are negatively correlated with  $DI_{CHT}$  among anthropoid primates. This suggests that male primates in species without dimorphic canines have proportionally broader, shorter faces relative to females, whereas male primates with highly dimorphic canines have relatively long faces that are not disproportionately broadened relative to females. Generally, in primates a more elongate face facilitates increased gape and the presence of large canines (Plavcan 2001). This observation is corroborated here by the significant correlation shown between superior FHT dimorphism and  $DI_{CHT}$ . However, the finding that facial breadth dimorphism exceeds superior FL and FHT dimorphism in species with low levels of  $DI_{CHT}$  requires an alternative explanation. Canine dimorphism in primates, like body size dimorphism, is strongly associated with intrasexual competition (Plavcan & van Schaik 1992) and is usually attributed to sexual selection. Our findings suggest that some selection for facial breadth dimorphism may also be operating at low levels of  $DI_{CHT}$ .

Sexual selection can operate in two main ways: through mate competition or through mate choice (Plavcan 2001). Although other factors, in addition to sexual selection, can influence sexual dimorphism, considerable support for linking facial dimorphism within hominoids with mate choice is provided through the extensive work done on human attractiveness (e.g. Scheib *et al.* 1999; Fink & Penton-Voak 2002). In men, the cheekbones are enlarged during puberty under the influence of testosterone (Enlow & Hans 1996). Several studies using two-dimensional images of human faces have shown that cheekbone prominence predicts male facial attractiveness, providing evidence that cheekbones are facial cues used in female mate choice (Cunningham *et al.* 1990; Scheib *et al.* 1999). Equally, high cheekbones have been associated with female attractiveness, a finding that has led to considerable confusion in studies that attempt to examine the importance of hormone markers, such as cheekbone prominence, on male and female faces (Fink & Penton-Voak 2002).

However, many studies concerned with human facial attractiveness do not take account of proportional changes that occur during facial growth. Human cheekbone enlargement appears to be a correlate of body size. In humans, male cheekbones grow for a longer period and to a larger size after puberty than those of females. However, in females the cheekbones appear more conspicuous than those of males, as the female nose, forehead and chin do not protrude to the same extent (Enlow & Hans 1996). These examples of allometric shape changes, associated with growth, illustrate why size correction in relation to ontogenetic allometry is fundamental to any procedure used to generate facial stimuli for assessment of attractiveness. Furthermore, it has been shown that female judgement of a male face changes if the face is viewed in profile as opposed to full face (Swaddle & Reiersen 2002). Clearly, additional measures of three-dimensional skull form are needed to assess attractiveness in humans, with cheekbone variability assessed in terms of both prominence and lateral flare.

In *Homo sapiens*, body size dimorphism appears to result in changes in the face that are attractive to both sexes, implying that selection for differences in body size need not be associated with intrasexual competition. However, the re-examination of cheekbone growth in humans is warranted in light of the new evidence presented here showing that facial breadth dimorphism is dissociated from body size dimorphism in *P. troglodytes*.

We propose that facial breadth dimorphism in primates in the absence of canine dimorphism is the result of sexual selection operating mainly through mate choice, a hypothesis corroborated by evidence from facial attractiveness in humans. Female preference for secondary sexual traits in male face shapes can vary across the menstrual cycle in humans, with faces displaying more masculinity being preferable when the probability of conception is highest (Penton-Voak *et al.* 1999). Similarly, female choice has also been reported in the opportunistic mating of wild chimpanzees; in phases of the female oestrus cycle when conception probability was highest, the number of

high-ranking male mating partners increased whereas that of adolescent male mating partners decreased (Matsumoto-Oda 1999).

This study highlights the importance of sexual variation in the zygomatic region of primate faces. The behavioural implications of facial dimorphism may be the key to understanding the paradoxical nature of sexual dimorphism in the hominid lineage. Furthermore, facial structure could have replaced canine size as a sexual selection signal in early hominids, possibly explaining the reduction in size of the canine in humans.

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