

## Craniofacial sexual dimorphism patterns and allometry among extant hominids

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**Summary.** Craniofacial sexual dimorphism in primates varies in both magnitude and pattern among species. In the past two decades, there has been an increasing emphasis in exploring the correlations of these patterns with taxonomy and the variation in patterns within and among the craniofacial regions.

Scrutinising these relationships for hominids, we decompose the craniofacial morphology in five taxa: *Homo sapiens*, *Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla* and *Pongo pygmaeus*. 3D coordinates of 35 traditional landmarks and 61 semilandmarks, covering five ridge curves, are measured for each of 268 adult and sub-adult specimens and analysed using geometric morphometric methods.

A multivariate analysis in size-shape space shows that ontogenetic scaling contributes to the development of sexual dimorphism in all five taxa, but to a varying extent. In absolute as well as in relative terms *P. pygmaeus* shows the greatest allometric component, followed by *G. gorilla*. *Homo* is intermediate, while in *Pan* the non-allometric constituent part contributes a large fraction to the actual sexual dimorphism, most markedly in the pygmy chimpanzee. An eigendecomposition of the five vectors of sexual dimorphism reveals two dimensions independent of allometry. One separates orang-utan sexual dimorphism from the African apes and *Homo*, and the other differentiates between the great apes and *Homo* with *Pan* mediating.

We discuss these patterns and speculate on their use as characters for taxonomic analysis in the fossil record.

**Key words:** Craniofacial sexual dimorphism pattern – growth allometry – Hominids – Geometric morphometrics

### Introduction

Craniofacial dimorphism in primates has been documented by many authors over the years. Until the 1980s, dimorphism was generally thought to differ among species primarily in degree rather than in pattern (Plavcan 2002). Since then, there have been a number of studies, demonstrating interspecific differences in the *pattern* of craniofacial dimorphism, increasingly in multivariate terms (e.g., Oxnard 1983, 1987; O'Higgins et al. 1990, 2001; Wood et al. 1991; O'Higgins and Dryden 1993; Plavcan 1993, 2002; Masterson and Hartwig 1998).

Understanding the pattern of dimorphism among living species is also important for interpreting the biological and taxonomic significance of variation in the fossil record. There are, for instance, persistent debates about whether variation in early hominins reflects sexual dimorphism or interspecific variation (e.g., Brace 1972; Zihlmann 1985; Kimbel and White 1988; Richmond and Jungers 1995; Lockwood 1999; Reno et al. 2003).

The literature indicates that there is some variation in patterns of dimorphism between species. Also, they seem to agree on a broad association between body mass dimorphism and the overall magnitude of dimorphism among craniofacial dimensions. Apart from these generalisations, neither the degree to which patterns of craniofacial dimorphism are correlated with taxonomy, nor the variation in patterns within and among craniofacial regions, is well understood or agreed on (Plavcan 2002).

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One possible reason for this uncertainty is that few studies actually compare interspecific patterns of craniofacial dimorphism among hominids (Wood 1976; Oxnard 1987; O'Higgins et al. 1990, 2001; Wood et al. 1991; O'Higgins and Dryden 1993; Lockwood 1999) and even fewer among nonhominids. Wood (1976), Ravosa (1991), Ravosa and Ross (1994), Masterson (1997), Richtsmeier and Cheverud (1989), and O'Higgins et al. (2001) are among those comparing pairs of taxa.

To a surprising degree, species-specific sexual dimorphism can be explained by growth allometry itself. The work of Schultz (e.g. 1962) foreshadowed the suggestions made by Shea (1986) that attention should be focussed away from just adult size and shape differences. Shea points out that sexual dimorphism may arise due to female/male differences in growth rates as well as from size-independent shape dimorphism. Then comparing sexual dimorphism patterns in the framework of ontogenetic trajectories would help determine a species-specific role for the allometry component in sexual dimorphism. Such comparisons gain power when more than two taxa are considered, but that is exactly where the literature is weakest: so far, there are only two studies with sufficiently broad scope (Masterson and Hartwig 1998; Plavcan 2002).

Traditional multivariate methods have difficulty in isolating size and in differentiating the shape variables that depend directly on size (allometry) from those that are a function of other factors, such as sex. Geometric morphometrics provide a powerful tool for the in-depth investigation of morphological processes because it allows the multivariate and integrated study of morphological configurations instead of linear measurements (e.g., Bookstein 1991; O'Higgins and Dryden 1993; Bookstein et al. 1999, 2003; O'Higgins 2000; Rosas and Bastir 2002).

Our analysis here attempts to respond to all these methodological critiques.

To document craniofacial dimorphism patterns among hominid species, we compare five extant hominid taxa including juvenile specimens, decomposing the craniofacial dimorphism pattern into an allometric and a non-allometric component, all by use of the geometric morphometric toolkit. There are specific expectations about the outcomes of this study; we expect, for instance, a positive association between the extent of the allometric component in larger species with larger sexual size dimorphism. Yet the aim of this study is not to test particular hypotheses. Instead, we seek a framework for hominid sexual dimorphism which might eventually develop to serve as a reference for hominin fossils as well.

## Material and Methods

*Material.* The cranial material consists of 268 specimens of five extant hominid species: 206 adult (as well as 62 juvenile) individuals of *Homo sapiens*, *Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla* and *Pongo pygmaeus*. The specimens are approximately

**Table 1.** Sampled taxa

Taxa	Adults		Juveniles		Collection*
	♀ N	♂	♀ N	♂	
<i>Pongo pygmaeus</i>	<b>24</b>	<b>23</b>	<b>5</b>	<b>5</b>	
<i>pygmaeus pygmaeus</i>	23	22	5	5	1, 2
<i>pygmaeus abelii</i>	1	1	–	–	1, 2
<i>Gorilla gorilla gorilla</i>	<b>21</b>	<b>23</b>	<b>6</b> (1)	<b>6</b> (4)	2, 3
<i>Pan troglodytes</i>	<b>19</b>	<b>20</b>	<b>6</b> (2)	<b>4</b>	2, 3, 4
<i>troglodytes troglodytes</i>	14	14	1	4	
<i>troglodytes schweinfurthii</i>	0	3	1	–	
<i>troglodytes verus</i>	5	3	2	–	
<i>Pan paniscus</i>	<b>20</b>	<b>16</b>	<b>6</b>	<b>6</b>	4
<i>Homo sapiens</i>	<b>20</b>	<b>20</b>	<b>7</b>	<b>11</b>	5, 6, 7

\* Collection codes: 1 = State Collection for Anthropology and Palaeoanatomy, Department of Anthropology, Munich, Germany; 2 = First Zoological Department of the Natural History Museum, Vienna, Austria; 3 = Institute of Anthropology, University of Zuerich-Irchel, Switzerland; 4 = Royal Museum for Central Africa in Tervuren, Belgium; 5 = Department for Archaeological Biology and Anthropology, Natural History Museum, Vienna, Austria; 6 = Institute for Anthropology of the University of Vienna; 7 = Institute of Anatomy, Medical University of Vienna. Numbers in brackets, when subspecies in not determined.

equally distributed across species and sex, and the ages span the full range from perinatal/early postnatal stages to adulthood. Except for a few infants, all ape specimens are wild-shot. The human sample was selected to cover a wide range of geographic variability (Tab. 1).

*Data acquisition and pre-processing.* For the measuring procedure, each cranium was fixed in plasticine. Except for the basicranial landmarks, all structures to be recorded were taken in the course of one session. To digitise the structures of the base, the crania had to be turned over and embedded again. Five reference points were marked on each cranium and recorded at the beginning of these two successive measuring sessions. By matching the respective reference points, the corresponding two data subsets could be assembled for the statistical analyses.

Three-dimensional co-ordinates of 41 ectocranial anatomical landmarks (Martin and Saller 1957; White 1991) on the face and the cranial base (Tab. 2, Fig. 1), and five ridge curves (Fig. 1) on the left side of the crania were digitized by one of the authors (M.B.) using a MicroScribe 3DX TM scanner. For more detailed information on the sample and data acquisition protocol see Bernhard (2003).

To the series of continuous points digitized along each ridge curve, a cubic spline was fitted and 53 equidistant semilandmarks placed on it. They were allowed to slide along their curves so as to minimise the net bending energy of the data set as a whole around its own Procrustes average. For the statistical analysis these relaxed semilandmarks can be treated as homologous within the sample (Bookstein et al. 1999, 2003; Gunz et al. in press). Because in many forms the neurocranium is concealed beneath a sagittal crest, landmarks in that region had to be omitted. All statistical operations were programmed in MATHEMATICA 4.0 by two of the authors (P.G. and P.M.).

**Table 2.** Cranial osteometric points. No. 1–13 midline points, No. 14–28 bilateral points. Landmarks in italics treated as semi-landmarks in analysis

No.	Landmark
1	prosthion
2	nasospinale
3	rhinion
4	nasion
5	glabella
6	opisthion
7	basion
8	sphenobasion
9	hormion
10	staphylion
11	intersection of medial and lateral palatal sutures
12	foramen incisivum
13	orale
14	point where the nasomaxillary suture meets the nasal aperture
15	intersection of nasomaxillary and frontonasal suture
16	maxillofrontale
17	zygoorbitale
18	frontomolare orbitale
19	zygomaxillare
20	zygion
21	mastoidale
22	auriculare
23	most superior point on the suture separating zygomatic and parietal bone
24	<i>jugale</i>
25	frontomolare temporale
26	frontotemporale
27	point on the most posterior end of the alveolar ridge
28	<i>canine base</i>

## Results

*Plain adult sexual dimorphism of size and shape.* Landmarks and semilandmarks are superimposed using a GLS Procrustes registration that results in a vector of shape co-ordinates and an explicit size variable – centroid size – for each individual. We compare sexual dimorphism in size across the species as the difference of the mean centroid size of males and females for each taxon.

Analogously, a scalar numerical summary of sexual dimorphism in shape is calculated as the Procrustes distance between the male and female consensus configuration.

Figure 2 plots both the estimate for sexual dimorphism in size and the one for shape for the five species under study. They are arranged in the order of decreasing absolute size dimorphism, starting with *Gorilla* and ending with *Pan paniscus*. Males are significantly larger than the females in all five species, though the relative magnitude of this dimorphism ranges from ~2% (for the bonobo) to ~20% (for orang-utan and gorilla). The right side of the graph shows the corresponding sexual dimorphism in

shape for the individual species. The sequence and also the pattern is slightly rearranged here, with *Pongo* showing the greatest difference in shape between females and males, followed by *Gorilla*. *Homo* and *Pan* form a cluster of smaller amounts of shape dimorphism than the other two taxa, but only fall short of the largest value for the whole phalanx by about 50 percent. In all five species, the males are not only larger than the females but also exhibit a significantly ( $p < 0.01$  by permutation test) different shape, although both to varying extents, intra- as well as interspecifically.

So far, this result reflects the well-known fact of hominid sexual dimorphism in craniofacial form. At the same time it enables us to formulate the imperative next step in the analysis: to investigate the extent to which the shape differences found for the sexes may be due to the pure size differences just confirmed.

*Allometric growth in size-shape space.* In order to explore the connection between the difference in shape and in size between the sexes in all five taxa, we add to the sample of adult specimens the corresponding 62 juvenile individuals. Although Procrustes registration separates size and shape information, we can perform an overall analysis of form when analysing Procrustes co-ordinates and the natural logarithm of centroid size together – as principal components of the data in size – shape space (see Mitteroecker et al. this volume).

Figure 3 visualises the whole set according to its differentiation in form. Allometric shape change plotted against scale show a common transition pattern for each of the five species: starting with the juveniles at the lowest values, passing into the females and ending with the males scoring highest. Allometric shape change is linearly strongly correlated with scale (all within-species  $r$  values with centroid size are  $\geq 0.92$ ), confirming an important allometric effect underlying the actual sexual dimorphism in shape in all taxa.

However, apart from the fact that the sexes in the smaller species (*Pan* and *Homo*) almost overlap in this scatter while *Pongo* and *Gorilla* males cluster separately from the females, there is a difference in the deviation from growth allometry comparing gorilla and orang-utan males too. *Pongo* males seem to be aligned straight along the allometric trajectory, while *Gorilla* males – most exceeding their females in size – show relatively less shape change, as evident by their horizontal deviation from the growth trajectory.

*Allometric versus non-allometric component: The angle with species specific allometry.* In order to investigate the proportion to which the allometric component actually accounts for sexual dimorphism, we calculate a vector of sexual dimorphism in size-shape space for each species as the difference vector between the male and female consensus configurations. The angle between this vector of sexual dimorphism and the within-species vector of ontogenetic allometry – computed as the vector of regression coefficients on the log of centroid size – gives a value for the similarity of these two biological factors.

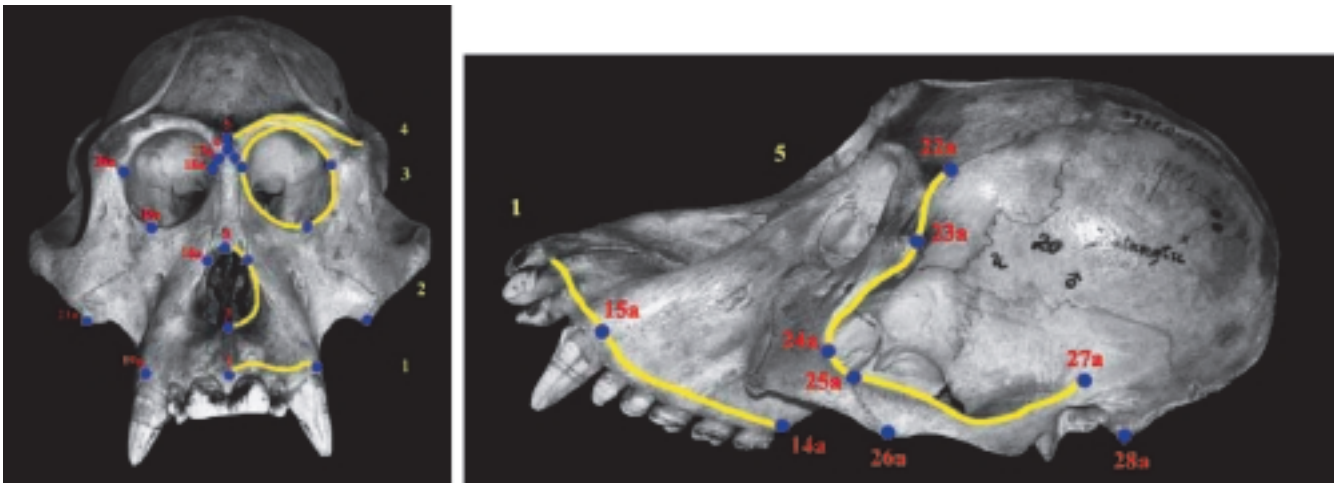


Fig. 1.

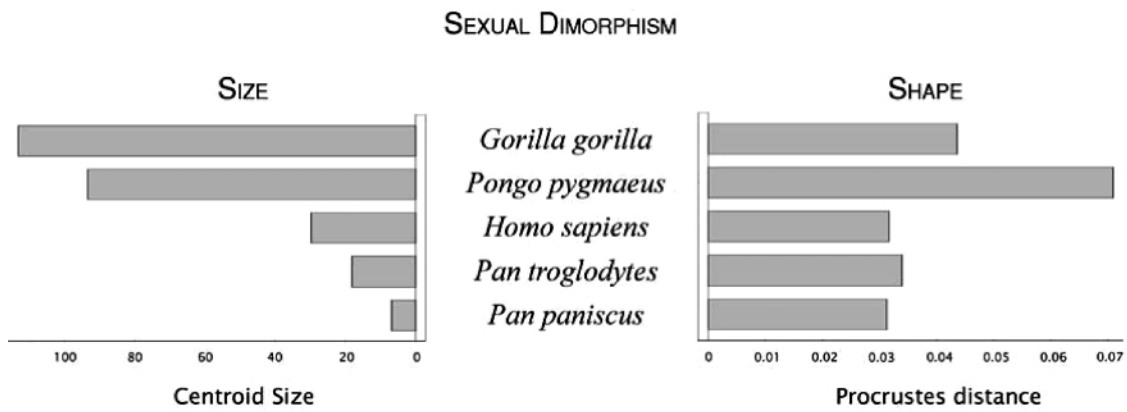


Fig. 2.

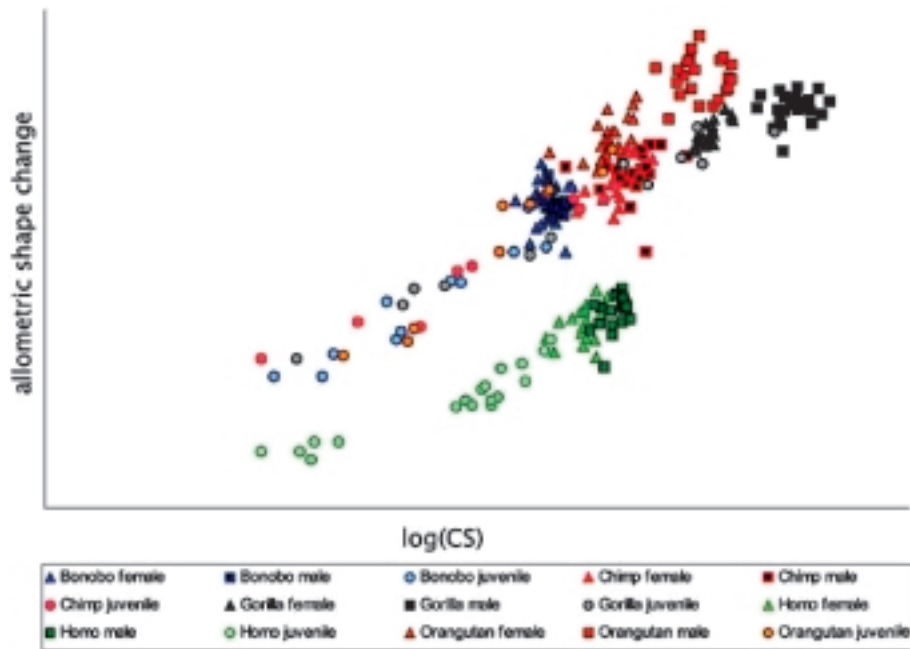
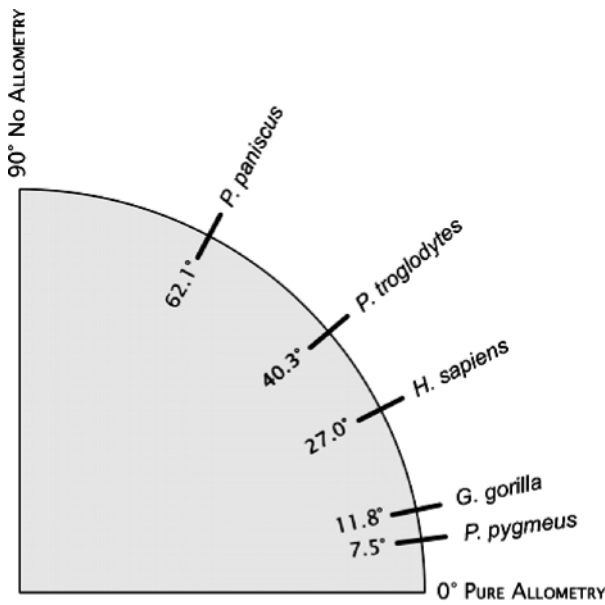


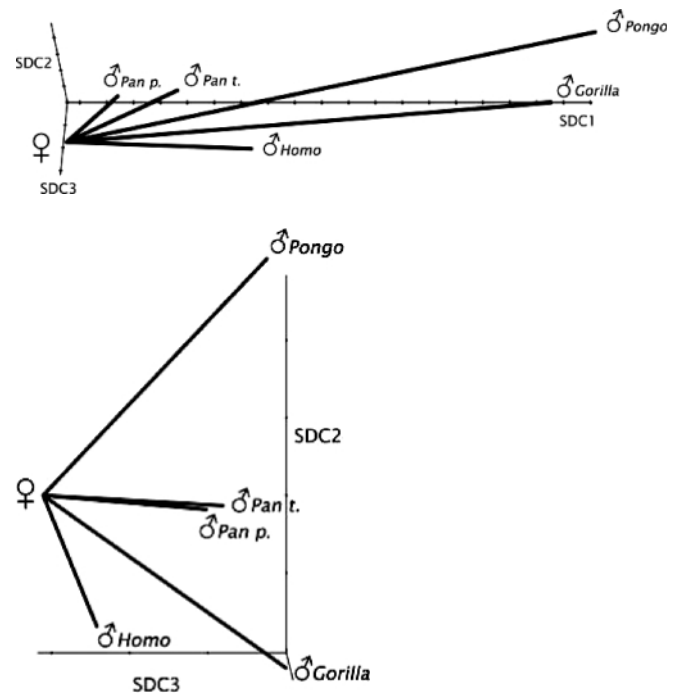
Fig. 3.



**Fig. 4.**

Figure 4 shows these angles of the sexual dimorphism vectors with the within-species allometry vectors. There is nearly no divergence from allometry for *Pongo* sexual dimorphism, only about 12° for *Gorilla*, for *Homo* 27°, for *Pan troglodytes* 40° and more than 60° for the bonobo sexual dimorphism. (These angles are little changed if calculated from the common allometric hominid trajectory instead of the species specific ones.) This result corroborates a strong connection with sexual dimorphism in size, indicating that in hominid sexual dimorphism generally, the proportion that pure growth allometry accounts for increases fundamentally with the difference in centroid size.

*Sexual dimorphism sub-pattern.* In addition to the determination of the extent the allometric and the non-allo-



**Fig. 5 a, b.**

metric components contribute to the full sexual dimorphism for the individual taxa, we also scrutinise their shape patterns. That is, from an eigendecomposition of the five vectors of sexual dimorphism in size-shape space, we present the first three components. To ease interpretation, this three-dimensional subspace is rotated so that the direction of common allometry is aligned with the first axis. This visualisation allows the assessment of similarities in the pattern of sexual dimorphism among hominids – whether attributable to allometry or other effects.

In Figure 5 the lengths of the vectors correspond to the magnitude of full sexual dimorphism in size-shape space.

**Fig. 1.** Ridge curves. Example of a male *P. pygmaeus* cranium in (a) anterior and (b) left lateral view. Ridge curves (yellow): 1. alveolar, 2. nasal, 3. orbital, 4. torus supraorbitalis, and 5. upper zygomatic curve; landmarks (blue): plain numbers: midline points; numbers plus a: bilateral landmarks; see Table 1 for landmark definitions.

**Fig. 2.** Craniofacial sexual dimorphism in size and shape. Bars on the left refer to the difference in mean centroid size between adult male and female configurations per taxon ( $P < 0.05$  in all five species by Student's *t*-test; variance higher in *Gorilla* and *Pongo* males than in the opposite sex,  $P < 0.001$  by permutation test); bars on the right indicate the extent of shape difference, calculated as the Procrustes distance between adult male and female specimens in the consensus configuration after a Procrustes fit ( $P < 0.01$  by permutation test in all five species; variance higher in *Gorilla* males  $P = 0.025$ , and in bonobo females  $P = 0.025$  by permutation test).

**Fig. 3.** Sexual dimorphism and allometry. Scale (abscissa) plotted against the allometric shape change (ordinate) by species. In all five taxa, males score higher than females do but they differ in distance and position to the females and the allometric trajectory: *Pongo* and *Gorilla* Show distinctive clusters (the latter diverging horizontally from the growth trajectory, that is achieving lower allometric shape scores than predicted for their size) whereas *Pan* and *Homo* sexes almost overlap.

**Fig. 4.** Allometric versus non-allometric component. Angles between 1) the vector between male and female consensus configuration for all five taxa separately and 2) the respective species specific allometry vector. *Pongo* shows the greatest allometric component and the bonobo the least.

**Fig. 5.** Eigendecomposition of the five vectors of sexual dimorphism in size-shape space. **a)** Alignment of the pooled allometry with the first component (SDC1, abscissa): Also in absolute terms, *Pongo* shows the greatest allometric component and *P. paniscus* the smallest. **b)** shows figure a) rotated, so as to visually 'partial-out' the allometric component: component 2 separates *Pongo* from the African apes including *Homo*, component 3 rather differentiates between the great apes and *Homo*, with *Pan* mediating.

The first dimension represents the allometric component of sexual dimorphism, reflecting the angles presented above: *Pongo* with allometry contributing greatest to sexual dimorphism, then *Gorilla* followed by *Homo*, *P. troglodytes*, and ending with the bonobo having the smallest amount of allometry of all, and also the shortest vector (Fig. 5 a). The additional two components plotted give evidence of the direction of the *non*-allometric components contributing to sexual dimorphism. In order to further investigate these, we can visually ‘partial out’ allometry by rotating Figure 5 a until the line of vision parallels the direction of the first component of sexual dimorphism (SDC1).

Figure 5 b is arranged in exactly this perspective, so that SDC1 points into the picture and one only sees the dimensions of sexual dimorphism independent of allometry. As indicated by the length of the vectors, in absolute terms, the orang-utan and gorilla slightly exceed the other taxa in this dimension to. Remember, though, that these foreshortened lengths only represent a small fraction of their total sexual dimorphism whereas in *Pan* and *Homo* this *non*-allometric component amounts to more than two thirds of their total sexual dimorphism. It is obvious in the second dimension that *Pongo* separates from the African apes including *Homo*. The third component differentiates between the Great apes and *Homo* with *Pan* mediating.

## Discussion

*Craniofacial sexual dimorphism in hominids.* In this study we have attempted to assess intersexual differences of five hominid crania in three dimensions, using geometric morphometric methods.

*Size and shape.* The result for sexual dimorphism in size confirms earlier studies, males being significantly larger than females in the great ape crania studied (O’Higgins and Dryden 1993) and also in *Homo* (Rosas and Bastir 2002). O’Higgins and Dryden even give a comparable factor for the degree in intersexual size difference in their 2D study investigation among *Pan troglodytes*, *Gorilla* and *Pongo*. Also their results for the size variation correspond to the ones presented here: the males of *Pongo* and *Gorilla* show significantly more phenotypic size variability than do the females, while in *Pan troglodytes* such difference cannot be established, and likewise not in the bonobo and in *Homo*, the two other taxa that had been added for the present study.

Highly significant shape differences between males and females were found only in gorillas and orang-utans, and lesser (but still significant) ones in the remaining three taxa: humans, bonobos and chimpanzees. O’Higgins and Dryden (1993) found statistically significant shape differences in orang-utans and gorillas, but none in chimpanzees. The latter fact contrasts with those from an earlier study of O’Higgins et al. (1990), where significant differ-

ences between male and female chimpanzees were found in a number of facial measurements. O’Higgins et al. presume that it is likely that size contributed to a large degree to the significant differences observed in the earlier study and that any remaining shape differences, when size is removed, are too small to achieve significance. But the present study demonstrates that this does not seem to be the case. It might rather be either the differences in the anatomical regions or the variables depicted or both that lead to contradictory results. Our data yielding significant sexual shape differences in all five taxa may also depend on our extension to 3D. If in *Pan* and *Homo* any lateral dimension (such as cranial width or zygomatic process size) played a role in sexual dimorphism, this information would not be grasped by analyses in the median sagittal plane.

*Growth allometry.* Craniofacial differences in size and shape between the sexes are partially due to allometric scaling. Although contradicting some details in Leutenegger and Masterson (1989) who note from a study of cranial sexual dimorphism in *Pongo pygmaeus* that “only half of the growth allometries are ontogenetically scaled, while the other half exhibits marked departures from ontogenetic scaling” (p. 21), our results concur with them that *Pongo* does indeed show a departure from ontogenetic scaling in sexual dimorphism, but the smallest one of all five studies taxa.

We generally quantified here the outcome of a mechanism Shea has described already 1983 as a ‘time hypermorphism’ *within* gorilla and chimpanzee and a ‘rate hypermorphism’ *between* these species with the gorilla males overgrowing the females for about the same amount of time as the chimpanzee males the chimpanzee females but the gorilla males growing much faster and to much larger sizes in the given time than the chimpanzees. Since, as for gorilla and orang-utan, the social system primarily involves high intensity male-male competition (level 3; Plavcan and van Schaik 1997) and marked differences in weight and size dimorphism (in *Gorilla*, with a factor of ~1.6; in *Pongo*, even as high as ~2.1), this can be obviously achieved optimally in the given amount of time, by strictly continuing ontogenetic growth, at least as long as the morphological outcome does not negatively impact on other basic abilities necessary for survival, such as foraging or food intake. In the genus *Gorilla*, already relatively enormous in body size, this may be the reason for the males not to exhibit 100 percent growth allometry, as one would expect according to their size difference to the females.

Conversely, in the bonobo and the common chimpanzee, the much smaller size dimorphism is basically associated with *non*-allometric shape differences between the sexes. For *Pan troglodytes*, Shea (1983) again has noted that some changes in the male chimpanzee skull do not comply with ontogenetic scaling; and indeed, half of them do not – in the bonobo about two thirds.

A functional mechanical constraint is not very likely as an explanation, nor are these morphological deviations

from allometry likely to be miscellaneous developmental by-products in the course of relatively slower growth. We suspect rather, that they operate in sexual selection. Since the smaller magnitude in (body) size dimorphism is related to low-intensity male-male competition (level 2 in comparison to high-intensity male-male competition in gorilla and orang-utan; Plavcan and van Schaik 1997) more subtle strategies of sexual selection play a role, such as sperm competition and female choice. We surmise the nonallometric components in *Pan* and *Homo* being associated with male sexual attractiveness, such as enlarged cheekbones, 'testosterone markers', which are linked to sexual attractiveness in humans (e.g., Cunningham et al. 1990).

*Distinguishing between sexual dimorphism and interspecies variation in fossil hominins.* We think we can use these results also to make some predictions for distinguishing between sexual dimorphism and interspecies variation in fossil hominin finds.

First, in Figure 3, we expect australopithecines to plot comparably to the scoring of the males and females of the five investigated species. The sexes from the same species should, according to their size difference, be sorted *in the direction* of the common allometric trajectory, and not *against* this direction. Additionally, also the *length* of the vector between a presumed female and a male individual in size-shape space should not exceed the maximum amount found in the five species investigated. This, of course, is only a rough estimate, but may already serve as an orientation.

Under the assumption that sexual dimorphism in fossil hominins does not differ substantially from that one found in the African apes or *Homo*, but rather should be expected somewhere among or between these patterns, the sub-patterns depicted with the eigendecomposition (Fig. 5 b) could also serve as reference. For australopithecines, sexual dimorphism would be expected to range somewhere in the dimension enclosed by the *Homo*, the gorilla, and the chimpanzee vector at the lower part of the figure. However, when we dare to limit australopithecine sexual dimorphism to the pattern found in *Pan* and *Homo* only, its predicted location would become even more precise.

In sum, the next important steps are to test these models empirically, to visualise and examine the actual morphology changes for the components of sexual dimorphism determined in this study, and to search for factors and mechanisms that might induce these sturdy components of the variation of form.

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