174 Truman, J. W., Development and hormonal release of adult behavior patterns in silk moths. J. comp. Physiol. *107* (1976) 39–48.
175 Truman, J. W., and Morton, D. B., The mechanism of steroid regulation of peptide action on the insect nervous system, in: Molecular Entomology, pp. 165–177. Ed. J. H. Law. Alan R. Liss, Inc., New York 1987.
176 Truman, J. W., and Riddiford, L. M., Neuroendocrine control of ecdysis in silkmoths. Science *167* (1970) 1624–1626.
177 Tyndale-Biscoe, M., Effects of ovarian condition on nesting behaviour in a brood-caring dung beetle, *Copris diversus* (Waterhouse (Coleoptera: Scarabaeidae). Bull. ent. Res. *73* (1983) 45–52.
178 Wada, Y., Effect of larval density on the development of *Aedes aegypti* (L.) and the size of adults. Quaest. Ent. *1* (1965) 223–249.
179 Wallis, R. C., and Lang, C., Egg formation and oviposition in blood-fed *Aedes aegypti* (L.). Mosq. News *16* (1956) 283–286.
180 Washino, R. K., The physiological ecology of gonotrophic dissociation and related phenomena in mosquitoes. J. med. Ent. *13* (1977) 381–388.
181 Watson, R. D., Williams, T. K., and Bollenbacher, W. E., Regulation of ecdysone biosynthesis in the tobacco hornworm, *Manduca sexta:* Titre of the haemolymph stimulatory factor during the last larval instar. J. exp. Biol. *128* (1987) 159–173.
182 Williams, R. W., Hagan, N. K. B., Berger, A., and Despommier, D. D., An improved assay technique for matrone, a mosquito pheromone, and its application in ultrafiltration experiments. J. Insect Physiol. *24* (1978) 127–132.
183 Woke, P. A., Ally, M. S., and Rosenberger, C. R. Jr, The numbers of eggs developed related to the quantities of human blood ingested in *Aedes aegypti* (L.) (Diptera: Culicidae). Ann. ent. Soc. Am. *49* (1956) 435–441.
184 Young, A. D. M., and Downe, A. E. R., Male accessory gland substances and the control of sexual receptivity in female *Culex tarsalis*. Physiol. Ent. *12* (1987) 233–239.
185 Young, A. D. M., and Downe, A. E. R., The action of male accessory gland fluids in the control of sexual receptivity in *Culex tarsalis* Coq., in: Host Regulated Developmental Mechanisms in Vector Arthropods, pp. 206–211. Eds D. Borovsky and A. Spielman. University of Florida, Vero Beach 1989.
186 Zóltowski, Z., Stejgwillo-Laudanska, B., and Kazmierczuk, J., Physiological and behavioural interpretation of the presence of micro-traces of mixed host blood in alimentary tracts of mosquitos of the genus *Aëdes* Meigen, 1818 (Diptera: Culicidae). Acta parasit. pol. *25* (1978) 351–357.

0014-4754/90/070660-11$1.50 + 0.20/0

Research Articles

The variability of patterns of sexual dimorphism in the hominoid skull

P. O'Higgins[a], D. R. Johnson[a], W. J. Moore[a] and R. M. Flinn[b]

[a]*Morphometrics Laboratory, Department of Anatomy, University of Leeds, Leeds, W. Yorks (UK) and* [b]*Centre for Computer Studies, University of Birmingham, Birmingham, Warwks (UK)*
Received 16 October 1989; accepted 27 February 1990

Summary. Univariate and multivariate statistical analyses are applied to a number of cranial dimensions and angles from living hominoids in order to investigate the patterns of sexual dimorphism in these groups. Clear differences in patterns of cranial sexual dimorphisms are demonstrated not only between genera but also within a single species *(Homo)*. These differences overlay the common finding of a sexual size difference in all groups. The results imply that caution is required in using the sexual dimorphisms of living hominoids as models for those anticipated in fossils.
Key words. Hominoids; crania; sexual dimorphism; discriminant analysis.

Several recent studies[1–5] have focused attention on patterns of sexual dimorphism in the primate skull. Sexual dimorphism results from the interaction of natural selection and a number of reproductive, social and other factors[6–10]. Wood[2], in a study of patterns of cranial and post-cranial sexual dimorphism amongst a range of primate genera concluded that "Apart from a few exceptions variables are consistently sexually dimorphic in all groups, differences between primates being one of degree of dimorphism rather than due to a different pattern of dimorphism". In this context, the term 'pattern' refers to the shape change encountered in going from a female to a male form. It is distinct from 'degree' of dimorphism which implies size rather than shape differences though pattern differences may well be allometrically linked to size differences. It may be possible for the same size difference between sexes in two species to be associated with different shape differences by virtue of the existence of different allometric phenomena in each.

More recently Uytterschaut[4] and Johnson et al.[11] have suggested that patterns of cranial size related shape differences and cranial sexual dimorphism[4,5] show a degree of dissimilarity amongst geographic subgroups of a single species, man. Likewise Oxnard[5] has shown that differences exist between hominoids in the patterns of sexual dimorphism exhibited by the dentition.

The complex of factors involved in the evolution of sexual dimorphisms might lead us to expect that the pattern of morphological differences between the sexes of a particular primate species should be unique to that species[3–5] (and ref. cited in Oxnard[5]). The extent to which different groups show similarities in their patterns of

sexual dimorphism might, in turn, be expected to reflect the degree to which they are similarly adapted and phylogenetically related [5].

The contradiction between the findings of Wood [1, 2] and other workers [4, 5, 11] suggests that cranial sexual dimorphism needs to be re-examined in order to determine if there does indeed exist a degree of dissimilarity between hominoid groups. If this turns out to be the case then it is worth considering if there is any element of cranial sexual dimorphism which is shared by different hominoids and which might provide the basis of a useful model for the study of fossils.

The present study is based on a collection of 165 skulls of extant apes (54 *Pongo*, 50 *Pan*, 61 *Gorilla*) and 75 skulls of extant *Homo* (30 caucasoid and 45 mongoloid). Sexes of *Pan* and *Gorilla* were taken from field records and checked against skins. *Pongo* was sexed on the basis of size, cresting and muscular markings (confirmation of the accuracy of sexual attributions was provided by principal components analyses which showed no overlap between the 'male' and 'female' distributions). The sexes of the human crania were known from burial records.

A series of 24 linear dimensions and 7 angles were taken between 18 cranial landmarks [11, 12]. Each dimension was examined for bimodality of distribution. The mean ± SE of each variable was then calculated for each sex and the significance of any difference between means noted. A stepwise discriminant analysis [13] was used to determine the six variables which, in combination (= shape), best discriminated between sexes in each sample. A series of discriminant analyses were then undertaken in which the variables shown to be optimal in discriminating between sexes in one group were applied in turn to each other group in order to judge the degree to which overall patterns of sexual dimorphism are shared. In each group 10 pairs of analyses were undertaken: in each analysis a randomly selected 90 % of the individuals were used to construct a discriminant function and the remainder classified by the function (see Johnson et al. [11] for full details of the method).

Table 1 lists those variables which show a significant ($p < 0.05$) difference between means for males and females in each group. In all cases the males are larger than the females. These dimorphisms differ between species and even within *Homo*. The number of dimorphic variables is greatest in *Gorilla* and *Pongo* confirming that sexual dimorphism is most marked in species with the largest absolute size difference between crania. Stepwise discriminant analysis allows us to list those six variables which, in combination, best discriminate between the sexes within each species (table 1). The differences between these lists strengthen the impression gained from the univariate data that patterns of sexual dimorphism vary between and even within species. Repeated discriminant analyses (table 2) demonstrate that optimal rates of sexual identification of crania are obtained when the six variables produced by the stepwise procedure are employed. The use of 'foreign' discriminators (i.e., the best six for one group used to classify another group) usually decreases this accuracy. There is, however, a degree of interchangeability of variables, e.g., the best six variables for *Pan* classify *Pongo* and *Gorilla* rather better than they do *Pan* (because there is a greater degree of sexual dimorphism in the larger apes), and allow correct identification in the majority of human subjects. This suggests that

Table 1. Means which are significantly different between sexes and the best six combined discriminators for sex in each group. Significant differences in means are indicated by: O = $p < 0.05$, X = $p < 0.01$. Best combined discriminators are indicated, in order of efficacy, by the numbers in brackets.

Variable[a]	*Gor*	*Pon*	*Pan*	Cau	Mon
maximum length	X	X	X	X(2)	X(2)
max. cranial breadth	X	X	X(3)	O	X
basi – bregmatic ht.	X	X		X	X
auricular ht.	X	X	(6)	X	X
post – orbital brdth.	X	X	(2)	X	X
frontal chord	X	X			O
parietal chord	X(6)				
occipital chord	X	X			(6)
foraminal length					O(4)
foraminal breadth	X				(3)
upper facial ht.	X	X(4)	X	X	
palatal length	X	X	X	O(5)	
palatal breadth	X	X(3)	(4)	O	
nasal breadth	X(5)	X(5)	X	(3)	
nasal height	X	X	X	X	
subnasal height	(3)	X		(4)	(5)
orbital height	X	X			O
orbital breadth	X(4)	X			O
infraorbital brdth.	X	X	O		X
bizygomatic breadth	X	X(1)	X(1)	X(1)	X
basi – infraorbital l.	X	X	O	O	
basi – nasal length	X	X	X	X	X
basi – prosthion l.	X(1)	X	X	X	
basi – staphylion l.	X	X	O		
angle b – la – o	X	(2)			
angle la – o – ba	X(2)		(5)		X
angle ba – n – b	X	O	X		
angle ba – n – pr	X	X			
angle n – b – la	X	X(6)			
angle o – ba – n		O		(6)	X(1)
angle n – ba – pr	X				

[a] See references 11 and 12 for definitions

Key: b = bregma, ba = basion, la = lambda, n = nasion, o = opisthocranion, pr = prosthion, brdth. = breadth, l. = length, ht. = height.

Note: the six best discriminators in each group were selected by a stepwise discriminant analysis [13]. This analysis takes due account of differences between variable means, variable intercorrelations and variance ratios (between-group relative to pooled-within-group). Variables which singly are not significantly different between sexes may, in combination (when shape is being considered), contribute markedly to discrimination.

Table 2. The percentage of crania correctly identified in discriminant analyses using different sets* of variables

Group	Best discriminating variables for:				
	Gorilla	*Pongo*	*Pan*	Mon	Cauc
Gorilla	100	97	97	77	100
Pongo	100	100	100	87	100
Pan	70	82	87	66	80
Mon	69	76	87	89	87
Cauc	63	83	83	73	97

* Sets of variables as numbered in table 1, see text for explanation.

there are certain features of cranial sexual dimorphism (we suggest principally a size difference and any shared allometric effects) common to all groups.

The results presented here strongly suggest that there is a degree of variation between the studied hominoid groups (even within a single species, *Homo*) in their patterns of cranial sexual dimorphism (contra 2). Whilst a male – female size difference is a common finding (indeed, it may account for the degree of interchangeability of variables), with males being larger than females, there are differences in the shape transformations between the sexes. We conclude that these differences in cranial sexual dimorphisms must be attributable to differences between the groups in their mechanisms (e.g. allometry) of development of sexual dimorphism, to similar mechanisms acting upon different ontogenies or to a combination of these. The present study casts no light upon the mechanism of development of the hominoid sexual dimorphisms but it does imply that great caution should be taken in using the sexual dimorphisms of living hominoids as models for the 'expected' dimorphisms of fossils.

Acknowledgments. The authors would like to thank the staff of British Museum (Natural History), University College London, The Duckworth Laboratory of Physical Anthropology, University of Cambridge, The Royal Scottish Museum, Edinburgh, The Powell Cotton Museum, Birchington, the rector of St. Bride's Church, Fleet St., London, and the staff of the Department of Anatomy, University of Hong Kong, for allowing us access to the material in their care. The authors thank two anonymous referees for their helpful comments. We all owe a special debt of gratitude to our late colleague and collaborator, Professor E. H. Ashton, formerly of the University of Birmingham, who was responsible for collecting and collating much of the data and sexing the orang utan crania.

1 Wood, B. A., Ph. D. Thesis, University of London, 1975.
2 Wood, B. A., J. Zool., Lond. *180* (1976) 15.
3 Holland, T. D., Am. J. phys. Anthrop. *70* (1986) 203.
4 Uytterschaut, H. T., in: Sexual Dimorphism in Living and Fossil Primates, p. 193. Eds M. Pickford and B. Chiarelli. Pub. Il Sedicesimo, Firenze 1986.
5 Oxnard, C. E., Fossils, Teeth and Sex: New Perspectives on Human Evolution. University of Washington Press, Seattle 1987.
6 Clutton-Brock, T. H., Harvey, P. H., and Rudder, B., Nature, Lond. *269* (1977) 797.
7 Leutenegger, W., Nature, Lond. *272* (1978) 610.
8 Leutenegger, W., and Cheverud, J., Int. J. Primat. *3* (1982) 387.
9 Clutton-Brock, T. H., in: Size and Scaling in Primate Biology, p. 51. Ed. W. Jungers. Plenum Press, New York 1985.
10 Leutenegger, W., and Cheverud, J., in: Size and Scaling in Primate Biology, p. 33. Ed. W. Jungers. Plenum Press, New York 1985.
11 Johnson, D. R., O'Higgins, P., Moore, W. J., and McAndrew, T. J., For. Sci. Int. *41* (1989) 41.
12 Trevor, J. C. T., Anthropometry. Chamber's Encyclopaedia, Vol. I, pp. 458–462, 1950.
13 SAS Users Guide: Statistics, p. 163. SAS institute. Cary, N.C. 1982.

0014-4754/90/070670-03$1.50 + 0.20/0

Muscle lipofuscin content and satellite cell volume is increased after high altitude exposure in humans

M. Martinelli[a], R. Winterhalder[a], P. Cerretelli[b], H. Howald[c] and H. Hoppeler[a]

[a]Department of Anatomy, University of Bern, Bühlstrasse 26, CH-3000 Bern 9, [b]Department of Physiology, University of Geneva, CMU, 1 rue Michel Servet, CH-1211 Genève 4, and [c]Ciba-Geigy AG, CH-4002 Basel (Switzerland)
Received 10 August 1989; accepted 10 January 1990

Summary. Muscle ultrastructural changes during a typical expedition to the Himalayas were analyzed by taking muscle biopsies from seven climbers before and after their sojourn at high altitude (over 5000 m for 8 weeks). M. vastus lateralis samples were analyzed morphometrically from electron micrographs. A quantitative evaluation was made of lipofuscin, satellite cells and myonuclei. Significant increases of the volume densities of lipofuscin (+ 235%) and satellite cells (+ 215%) were observed.
Key words. Muscle; morphometry; human; hypoxia; lipofuscin; satellite cell; high altitude.

Recent studies on humans exposed to high altitude during traditional long-lasting expeditions to Mt. Everest and Lhotse have shown signs of muscle deterioration[4, 13]. The main observation made in these studies was that there was a significant reduction of muscle cross-sectional area, mainly due to a decrease in muscle fiber size. A loss of muscle oxidative capacity was also evident, as indicated by a decrease in the volume of muscle mitochondria. The capillary network was mostly unchanged, so that oxygen transport to the remaining muscle mitochondria appeared to be improved after prolonged high altitude exposure (fig. 1). These studies further showed qualitative evidence of lipofuscin accumulations, which were considered to be possible signs of degeneration of mitochondria and other membrane-rich cell organelles. However, these findings were not quantitated.

The first goal of the present study was to measure the previously suggested increase of lipofuscin granules with high altitude exposure[13], using muscle biopsy specimens of the same individuals described in the previous reports[9, 13]. In a survey of the literature we found quantitative measurements of lipofuscin in central nervous tissue, kidney and myocardial cells, but not in skeletal muscle tissue[2, 12, 23, 25, 30]. This study is thus, to the best of our