Sexual Dimorphism in the Mandible of *Homo Neanderthalensis* and *Homo Sapiens:* Morphological Patterns and Behavioural Implications

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Introduction

In 1980 the Journal of Human Evolution devoted an issue to papers which examined sexual dimorphism in hominid evolution. Two of the contributing authors, Smith and Trinkaus, independently investigated intersexual differences in skeletal patterning in the middle to late Pleistocene species *Homo neanderthalensis*. They also sought to link the patterns they identified to aspects of its behaviour. Surprisingly, they arrived at different conclusions on both counts. Smith (1980) argued his craniometric analyses indicated that the Neanderthals were slightly more dimorphic than anatomically modern humans. From this he inferred that the Neanderthals had a more pronounced sexual division of labour than is common among more recent human groups. In contrast, Trinkaus (1980) suggested his post-cranial analyses indicated that the level of sexual dimorphism exhibited by *H. neanderthalensis* was indistinguishable from that seen in *Homo sapiens*. From this he inferred that the Neanderthals were probably about as polygynous as the majority of ethnographically-known societies.

Since 1980 these conflicting claims have been largely ignored. This is despite the potential contribution an understanding of sexual dimorphism and its associated behavioural inferences could make to our knowledge of Neanderthal bio-cultural evolution (Wood 1985).

In this paper we reconsider both areas of disagreement between Trinkaus (1980) and Smith (1980) over sexual dimorphism in *H. neanderthalensis*. We begin by reporting the results of an analysis of a sample of *H. neanderthalensis* and *H. sapiens* mandibles. This was designed to determine whether the picture of sexual dimorphism presented by mandibular remains was consistent with the findings of the other studies. We then report the results of an analysis of sexual dimorphism in a sample of primate mandibles. This aimed to establish whether the results derived from the fossil mandibular remains were biologically meaningful. Finally we outline a model of sexual differences in behaviour in Upper Pleistocene hominids based on biomechanical principles.

The Nature and Expression of Sexual Dimorphism

Many species of primate are, like the majority of mammalian species, sexually dimorphic. That is, they exhibit sex-based differences in morphology, physiology, and behaviour (Tattersall *et al.* 1988). Over the past 25 years, a number of these intersexual differences have been found to covary among extant species (Crook 1972; Clutton-Brock and Harvey 1977; Clutton-Brock *et al.* 1977; Alexander *et al.* 1979). For example, in primates, differences in body length have been found to correlate with differences in the propensity of males and females to philander and cuckold, respectively (Alexander *et al.* 1977). Species which are monomorphic in body size (i.e. have a low degree of sexual dimorphism), such as the gibbons, are usually monogamous, whereas highly dimorphic species, like the savannah baboons, tend to be polygynous (Clutton-Brock and Harvey 1977; Clutton-Brock *et al.* 1977; Alexander *et al.* 1979). Alexander *et al.* (1977) suggested that this correlation was a consequence of the fact that in polygynous species reproductive success varies more among males than it does among females. The higher degree of inter-male competition relative to inter-female competition selects for traits in the males which are likely to lead to success in combat, such as a large body and large canines, which, in turn, causes the size and shape of male and female bodies to diverge.

Other traits that have been found to covary with body size dimorphism include differences in parental investment, differential patterns of resource acquisition and utilisation, and sexual division of labour. For example, practices which are physically demanding may reduce sexual dimorphism if carried out equally by the sexes and vice versa (Frayer and Wolpoff 1985). In this case dimorphism is a consequence of divergence in muscular or skeletal robusticity. Frayer (1980, 1981, 1984) among others (e.g. Finkel 1982; Wolfe and Gray 1982), has argued that differences in the size of male and female *Homo sapiens* is linked to differences in the economic activities undertaken by the sexes. He has suggested, for instance, that the decline in sexual dimorphism seen as farming became the dominant way of life in Europe was a consequence of the tasks undertaken by the sexes becoming more similar. Mesolithic males would have disproportionately carried out energetically expensive and dangerous activities such as large game hunting, and would therefore have been selected to be larger and more powerful than females. With the adoption of agriculture, the resources supplied by wild animals would gradually have been replaced with those derived from domesticates and cultigens. Since farming plants and animals would have imposed a similar burden on men and women, the selection pressure on males would have relaxed, and the intersexual difference in body size reduced.

1.	Symphyseal height	M-69
2.	Symphyseal breadth	The breadth of the symphyseal region in the sagittal plaine, excluding the spineous process of the genial tubercles
3.	Maximum mandibular length	M-68
4.	Bicondylar maximum breadth	M-65
5.	Bicondylar articular breadth	The distance measured in the coronal plane between the midpoints of the mandibular condyle articular surfaces.
6.	Bicoronoid breadth	M-65-1
7.	Bigonial breadth	M-66.
8.	Bicanine external breadth	The distance between the external alveoli measured at the distal margin of the canines.
9.	Anterior bimolar external breadth	The distance between the external alveoli measured at the distal margin of the first molars.
10.	Anterior bimolar internal breadth	The distance between the internal alveoli measured at the distal margin of the first molars.
11.	Posterior bimolar external breadth	The distance between the external alveoli measured at the distal margin of the second molars.
12.	Posterior bimolar internal breadth	The distance between the internal alveoli breadths measured at the distal margin of the second molars.
13.	Corpus height at the foramen	The height of the corpus measured at the interdental septum level at the location of the mandibular foramen.
14.	Corpus height at the canine	The height of the corpus measured at the canine-third premolar interdental septum.
15.	Corpus height at the molars	The height of the corpus measured at the second-third molar interdental septum.
16.	Condylar height	M-70
17.	Coronoid height	The distance between gonion and the most superior aspect of the coronoid process.
18.	Ramus height	The distance between gonion and the most inferior aspect of the mandibular incisure.
19.	Corpus breadth at the canine	The breadth of the corpus measured at the level of the canine and third premolar.
20.	Corpus breadth at the molars	The breadth of the corpus measured at the level of the second and third molars.
21.	Ramus breadth	M-71a.

Figure 1. Metric measurements used in the analysis [M numbers refer to measurement definition in Martin (1928)].

An Assessment of Sexual Dimorphism in *Homo neanderthalensis* and *Homo sapiens*

In order to assess sexual dimorphism in *H. neanderthalensis* we have utilised the mandible, an anatomical element not incorporated in the studies of Smith (1980) and Trinkaus (1980). The mandible is a good choice for analyses of sexual dimorphism in both extant and extinct taxa for two reasons. Firstly, the mammalian mandible tends to have a higher survival rate in the fossil and sub-fossil records compared to other skeletal aprts (Brain 1981; Lyman 1994). Secondly, the morphology of the mandible is heavily influenced by environmental factors during the life of an individual. Throughout its structure of the mandible there are many regions of localised growth and remodelling. Allof these participate in the development of the shapes and dimensions needed to carry out the multiple functions of the mandible. The morphology and morphogenetic processes in each regional area represent direct adaptations to the localised functional, developmental, biomechanical, and physiological circumstances that are present (Enlow 1992). Consequently, mandibular morphology may reflect life-history patterns including disease, tooth loss, and overall skeletal robusticity.

Materials and Methods

21 measurements were recorded on a sample of mandibles belonging to *H. neanderthalensis* (N = 10), early anatomically modern *H. sapiens* of Pleistocene date (N = 19), and Holocene *H. sapiens* (N = 45) mandibles. The measurements used are given in figure 1. All dimensions were recorded in millimetres rounded to the nearest 0.1 mm. The Holocene *H. sapiens* sample was measured by PSQ and consisted of adult European Mediaeval specimens housed in the Calvin Wells Collection at the University of Bradford. The Neanderthal sample comprised adult remains recovered from Western Asia and Europe. The early anatomically modern human (EAMH) sample was made up of adult remains of upper Pleistocene date from Africa, Europe, Western Asia, and Australia. The measurements were made by PSQ on casts or original specimens. Those recorded from casts were compared against published measurements of the original fossil material. No significant differences were observed (mean difference = 1.4%). The Neanderthal and EAMH specimens examined are listed in figure 2.

Homo neanderthalensis

1.	Amud I	(m)
2.	La Chapelle Aux Saints	(m)
3.	La Ferrassie I	(m)
4.	Le Moustier	(m)
5.	Monte Circeo	(m)
6.	Shanidar I, II & IV	(m)
7.	Tabun II	(m)
8.	Tabun CI	(f)
9.	Spy I	(f)
10.	La Wuina V	(u)

Pleistocene Homo sapiens

1.	Combe-Capelle	(m)
2.	Border Cave V	(m)
3.	Chancelade	(m)
4.	Cro-Magnon I & II	(m)
5.	Gough's Cave I	(m)
6.	Grotte-de-St. Front	(m)
7.	Iwo Eleru	(m)
8.	Kow swamp I & V	(m)
9.	Lake Mungo III	(m)
10.	Oberkassel I	(m)
11.	Pavlov I	(m)
12.	Qafzeh IX	(m)
13.	Skhul V	(m)
14.	Fish Hoek I	(m)
15.	Border Cave II	(f)
16.	Brno III	(f)
17.	Dolni Vestonice III	(f)
18.	Oberkassel II	(f)
19.	Predmosti IV	(f)

Figure 2. Fossil specimens (and their sex) used in the analyses.

The Mediaeval European material was sexed on the basis of associated pelves. The EAMH specimens were also sexed where possible with reference to associated pelvic remains; where this was not possible the sex ascribed to individuals in the literature was assumed to be correct. Given that most of the mandibles are associated with cranial remains (Day 1986; Oakley *et al.* 1971), which can be sexed with a reasonable degree accuracy (St. Hoyme and Iscan 1989), we considered this to be a reasonable assumption. The sex of each of the Neanderthal individuals was based on Trinkaus (1980). Figure 2 gives the sex assigned to each of the fossil specimens.

Male and female means for the three taxa were calculated for each of the 21 measurements. From this a percentage trait dimorphism value (PTD) was then calculated (PTD = [male trait mean/female trait mean] ×100%). The PTDs were then tested for statistical significance using Student's two-tailed t-test, and a percentage overall dimorphism (POD) value calculated for each taxon. This was done by finding the mean of the PTDs for each taxon. A high POD value thus indicates a low level of sexual dimorphism and vice versa. Finally, the differences in POD values between the taxa were assessed for statistical significance (two-tailed t-test).

Results

All 21 measurements produced statistically significant differences between the PTD values for the sexes in each taxon ($P < 0.05$). The POD values calculated from the PTD's for the three taxa were: *H. neanderthalensis* 94%, EAMH 88% and Holocene *H. sapiens* 93%. While the difference between the POD values for Neanderthals and Holocene *H. sapiens* was not significant ($P = 0.68$), the differences between POD value for EAMH and the two other taxa were statistically significant ($P = 0.00$).

As with the results of all analyses of this type, these figures are problematic because they are dependant on the sex of the fossil specimens having been correctly identified. To control for this, a subset of the data was analysed with the 'Means Model', a method of assessing sexual dimorphism in samples of uncertain sex (Plavcan 1994). Metric values recorded for 15 measurements (measurement numbers 1, 2, 8, 9, 10, 11, 12, 13, 14, 15, 17, 18, 19, 20, 21) were taken from the mandibular data set and the sex assignments removed from the specimens.

A mean of the 15 measurements was calculated for each specimen, along with an average value for each of the three taxa. The three groups of specimens were then split into hypothetical sexes about their taxon averages. Aspecimen was considered 'female' if it fell below the taxon average and 'male' if it fell above. Finally, a POD value was calculated for each taxon using the Means Method 'male' and 'female' values, and the differences between the POD values tested for statistical significance.

The Means Method POD calculations produced the following results: *Homo neanderthalensis* 94%, EAMH 89%, and Holocene *H. sapiens* 92% (for a comparison of these and above POD values see figure 3). As in the statistical analysis of the original 21 measurements, the difference between POD values for the Neanderthal and Holocene *H. sapiens* samples was not statistically significant ($P = 0.19$). In contrast, the difference between *H. neanderthalensis* and EAMH POD values was significant ($P = 0.00$), as was the difference between the POD values for the two samples of *H. sapiens* ($P = 0.04$). The fact that the POD values for the three taxa are so similar to those derived from the first analysis suggests that the results of the latter are reliable, at least as far as the relative degree of dimorphism exhibited by the three groups is concerned.

	Sexed Specimen Analysis	Means Method Analysis
Homo neanderthalensis	94%	94%
Homo sapiens (Holocene)	93%	92%
Homo sapeins (Pleistocene)	88%	89%

Figure 3. Comparison of POD values for Hominid specimens and Means Method.

Biological Significance of POD Results

Is the degree of mandibular sexual dimorphism exhibited by our samples of Upper Pleistocene and Holocene hominids biologically meaningful? Is the 5% POD difference between EAMH and the other taxa sufficient to allow defensible inferences to be made about their behaviour?

To answer these questions a third data set was assembled. Our aim was to place the sexual dimorphism exhibited by the three hominid taxa in a comparative primatological context. Data for nine variables were taken from the following taxa: *Gorilla gorilla* (N=37), *Pan troglodytes* (N=35), *Pongo pygmaeus* (N=41), *Papio c. cynocephalus/c. anubis* (N=31), *Colobus guereza* (N=24), *H. neanderthalensis* (N=16), EAMH (N=26), and Holocene *H. sapiens* (75 recent South Africans and 45 Medieval Europeans). The measurements used were numbers 1, 2, 3, 4, 6, 7, 16, 17 and 21 in figure 1. The non-human primate and South African *Homo sapiens* data were taken from Wood (1975) and the Hominid Palaeontology Research Group's Hominid Database. The sub-fossil and fossil hominid measurements were collected by PSQ (see above). Data collected by Wood was conducted on specimens of known sex. The sub-fossil and fossil specimens were sexed in line with the first analysis.

Male and female means of the eight taxa were calculated for each of the nine measurements, and the differences between the male and female means of each taxon tested for statistical significance using Student's two-tailed t-test. The percentage overall dimorphism (POD) value for each of the eight taxa was then calculated, and the significance of the differences in POD values between the taxa assessed.

The nine measurements examined in the analysis produced statistically significant differences between the sexes in all taxa ($P < 0.05$). The results of the POD calculations are given in figure 4, and P values for statistical significance presented in figure 5. The POD values indicate that while *H. neanderthalensis* and Holocene *H. sapiens* fall at the low end of the range of primate mandibular dimorphism, EAMH fall in the middle of the range. The results of the t-tests indicate that the POD values for *H. neanderthalensis* and Holocene *H. sapiens* cannot be distinguished from those of *P. troglodytes* and *C. guereza*. The POD value for EAMH is significantly different from those of *P. troglodytes*, *H. neanderthalensis*, and Holocene *H. sapiens*, but cannot be distinguished from those of *C. guereza* and *P. pygmaeus*. These results suggest that the higher degree of mandibular dimorphism in EAMH relative to *H. neanderthalensis* and Holocene *H. sapiens* is not only statistically significant but probably biologically meaningful.

Pan troglodytes	94%
Homo neanderthalensis	94%
Homo sapiens (Holocene)	93%
Colobus guereza	89%
EAMH	88%
Pongo pygmaeus	85%
Gorilla gorilla	82%
Papio c. cynocephalus/c.anubis	77%

Figure 4. Percentage overall dimorphism values for eight primate taxa.

Comparison with Previous Studies

The finding that Neanderthals exhibited a similar level of mandibular sexual dimorphism to Holocene modern humans is broadly consistent with the picture of Neanderthal dimorphism presented in a number of previous studies. Trinkaus (1980), for example, found that Neanderthal limb bones exhibit a similar level of sexual dimorphism to that seen in a large and geographically diverse sample of Holocene humans. Female *H. neanderthalensis* limb bones were on average 93% the size of those of males, a POD value close to that of Holocene humans. Similarly, Trinkaus (1983) found the difference in his stature estimates for male and female Neanderthals to be comparable to that seen in Holocene humans. Using formulae derived for modern Europeans, he estimated the height of Neanderthal females to have been around 160cm and males about 169 cm. This gives a POD value for the Neanderthals of 95%.

In contrast, Smith (1980), utilising craniometric data, concluded that Neanderthals were markedly more dimorphic than both Pleistocene and Holocene *H. sapiens*, with trait dimorphism values ranging from 89.3 to 97.8%, and a POD of 92.9.

It is worth noting that the differences in POD values found by Trinkaus and Smith may be due to inconsistencies in choice of the skeletal element analysed. Wood (1975, 1976, 1985) has shown that size and shape differences between males and females in primate species are not consistent throughout the skeleton. Canine teeth, for example, tend to be more dimorphic than skeletal elements, which in turn tend to exhibit different degrees of sexual dimorphism from other attributes, such as body length and weight. Thus, different degrees of sexual dimorphism can be discerned for a species depending on which trait, or combination of traits, is examined.

This problem is complicated by the fact that the degrees of sexual dimorphism exhibited by different attributes are not consistent across primate species. Some will, for example, suggest that species A is more dimorphic than species B, whereas others will indicate the reverse. It is impossible, therefore, to circumvent the problem of different traits having different levels of dimorphism by simply assessing the sexual dimorphism of a species relative to other taxa.

To test the possibility that Smith's (1980) and Trinkaus' (1980) conclusions are at odds simply because they examined different skeletal elements, we compared statistically the results of their analyses, along with those from ou rown study. The difference between the results of Smith (1980) and Trinkaus (1980) was found to be statistically insgnificant (P = 0.66). The difference between the dimorphism values from the three studies for *H. neanderthalensis* and Holocene humans were also found to be statistically insignificant (P = 0.68 for the mandibles, P = 0.82 for the crania, and P = 0.82 for the postcrania).

Overall the analyses published to date indicate that (1) the Neanderthals were no more sexually dimorphic than Holocene humans, and (2) the early antomically modern humans were significantly more dimorphic than both the Neanderthals and Holocene humans.

Behavioural Implications of Sexual Dimorphism in *Homo Neanderthalensis* and *Homo Sapiens*

As we noted earlier, it should be possible to infer aspects of the behaviour of *H. neaanderthalensis* and Pleistocene *H. sapiens* from the results of our mandibular anlyses. For instance, using the model of Alexander *et al.* (1979), we should be able to suggest that the Neanderthals were about as polygonous as Holocene humans, whereas early anatomically modern humans were appreciably more so. Alternatively, utilising the model proposed by Frayer (1980, 1981, 1984) we might hypothesise that Neanderthal males and females organised economic tasks differently to Pleistocene anatomically-modern humans.

There are, however, difficulties with these correlation-based models. Most significantly, since not all the relevant neontological studies have included both human and non human primates, it is impossible to determine which of the correlations is most appropriate. Frayer's (1980) sexual division of labour model, for example, is based solely on anatomically modern humans, whereas the harem model of Alexander and colleagues (1979) uses both human and non-human primate data. A decision therefore has to be made whether to treat hominid species like any other primate or like Holocene humans. If the former option is chosen then the dimorphism they exhibit can be linked to harem size. If, however, the latter option is chosen, then the dimorphism they exhibit can be related to differences in the economic roles of the sexes. Crucially, this means that the relative merits of the two models cannot be directly compared.

Given the limitations of the correlation-based method of making behavioural inferences, we developed an alternative approach based on biomechanical principles. Our aim was to develop a functional model, similar to that described by Bock and Von Wahlert (1965), within which the differences seen in the mandibles of male and female hominids could be linked to differences in their behaviour. For the purposes of this paper our discussion is limited to anatomically modern humans, but the approach is readily applicable to other hominid species, including *Homo neanderthalensis*.

Implications of Mandibular Dimorphism from a Biomechanical Perspective

It is evident from a comparison of the EAMH and Holocene *H. sapiens* percentage trait dimorphism values for Data Set A (fig. 5) that the measurement in which the taxa differ most is symphyseal height. The difference between EAMH males and females in symphyseal height is considerably larger (+14%) than the difference between male and female Holocene *H. sapiens* for the same measurement.

During mastication, three primary patterns of mechanical stress are produced within the symphyseal region of the *H.*

Species	B	C	D	E	F	G	H
A	**0.00**	**0.01**	**0.04**	**0.00**	0.08	0.19	0.66
B		0.13	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**
C			**0.04**	**0.00**	**0.00**	**0.00**	**0.02**
D				**0.00**	**0.00**	**0.00**	0.11
E					0.96	0.33	**0.01**
F						0.67	**0.05**
G							**0.01**

Bold = differencs which are stistically significant.

Key

A *C. guereza*
B *G.gorilla*
C *P. c. cynocephalus/c. anubis*
D *P. pygmaeus*
E *P. troglodytes*
F *H. neanderthalensis*
G *H. sapiens* (Holocene)
H *H. sapiens* (Pleistocene)

Figure 5. P values from primate mandibular analysis.

Measurement (from fig. 1)	Pleistocene H. sapiens POD	Holocene H. sapiens POD	% difference
1	80	94	14
2	89	94	5
3	94	94	0
4	89	95	6
5	92	94	2
6	85	95	10
7	89	92	3
8	89	94	5
9	90	92	2
10	91	91	0
11	91	92	2
12	94	91	3
13	85	93	8
14	82	93	11
15	83	95	12
16	82	90	8
17	84	88	4
18	82	90	8
19	89	92	3
20	86	101	5
21	93	96	3

Figure 6. Difference between Pleistocene and Holocene H. sapiens percentage sexual dimorphism values for 21 measurements.

sapiens mandible: (1) lateral bending in the transverse plane, in which the mandibular bodies are pulled apart like a wishbone; (2) vertical bending in the coronal plane, in which the base of the symphysis is pulled apart under tension while the alveolar process is compressed; and (3) dorsoventral shear stress (Daegling 1993). Whereas the level of dorsoventral shear stress is unaffected by the morphology of the symphysis (Hylander 1984, 1985), the relative importance of the two bending stresses depends, in large part, on the size and shape of the symphysis. Lateral transverse bending of the symphysis is produced when the ipsilateral and contralateral bite forces are actively opposed, with the result that the two halves of the mandible are bent in opposite directions in the transverse plane. This 'wish-boning' causes tensile forces to build up on the lingual aspect and compressive forces along the labial aspect of the mandible. Lateral transverse bending thus favours a labio-lingually broad symphysis. Vertical bending of the symphysis is caused by the force moment of the masseter muscles everting the lower borders of the gonial region, producing a bending of the mandible about its long axis. This action results in tensile stress at the lower border of the symphysis, but compressive stress along the alveolar border. Resistance to vertical bending force is maximised by increasing the height of the symphysis, i.e. vertical bending is best resisted by a deep mandibular symphysis.

Overall, therefore, these two mandibular stresses place conflicting adaptational demands on the structure of the symphysis. Lateral transverse bending requires a labio-lingually broad symphysis, whereas vertical bending is best resisted by a deep mandibular symphysis.

The implication of the relationship between these bending stresses and the morphology of the mandible is that the marked difference in symphyseal height dimorphism between Pleistocene and Holocene *H. sapiens* is a result of differential hypertrophication of the masticatory musculature in Pleistocene males relative to Pleistocene females. That is, the higher percentage dimorphism value in symphyseal height in EAMH is a consequence of increased masseter output potential in males relative to females. There are two possible explanations for this. The first is that the greater potential power output of the Pleistocene male masseter relative to those of Pleistocene females is an adaptation. It could, for example, be caused by differences in the masticatory requirements of male and female diets, or alternatively, by differences in the para-masticatory tasks carried out by males and females. Ethnographic data suggest that these activities could have included softening skins, stripping bark from branches, sharpening spears or digging sticks, and pressure flaking stone tools (Barrett 1977; Schulz 1977; Brace *et al.* 1981; Larsen 1985).

The second possibility is that rather than an adaptation, the increased masticatory potential of Pleistocene males relative to Pleistocene females is a consequence of selection for a more general sexual differentiation in skeleto-muscular robusticity levels. In other words it is a by-product of selection for either greater robusticity in males or reduced robusticity in females. If, for example, Pleistocene males had been selected to be generally more skeletally robust and heavily muscled than females it is likely, given the systemic nature of changes involved, that the masticatory musculature would also have increased in size and potential output. Possible behaviours from which this selection pressure could have arisen include intra-male competition for access to females, large game hunting, and long-distance foraging.

Conclusions

Sexual dimorphism in fossil populations is a complex issue. The range of potential factors in the establishment of intraspecific and intrapopulation sexual dimorphism is extensive, and it is with much speculation that we apply primatological or ethnographic models of dimorphism based on sexual selection pressures to extinct culture-bearing hominids. It is perhaps with more reliability that we can analyse sexual differentiation of broad-based, functionally related anatomical characters to these populations in an attempt to explain observed morphological patterns.

In conclusion, we find that using mandibular measurements as a proxy of overall sexual dimorphism indicates that the Neanderthals exhibited a level of dimorphism that is indistinguishable from that of recent humans. Early anatomically modern human populations, in contrast, exhibited a significantly greater degree of morphological sexual dimorphism than either archaic or post-glacial populations of humans. We suggest that this difference is most likely activity related and may indicate that early modern humans adopted either a different approach to their subsistence economy when compared to Neandethal and recent human populations, or had marked sexual differences in diet and/or paramasticatory activities.

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