A morphometric analysis of hominin teeth attributed to *Australopithecus*, *Paranthropus* and *Homo*

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Teeth are the most common element in the fossil record and play a critical role in taxonomic assessments. Variability in extant hominoid species is commonly used as a basis to gauge expected ranges of variability in fossil hominin species. In this study, variability in lower first molars is visualised in morphospace for four extant hominoid species and seven fossil hominin species. A size-versus-shape-based principle component analysis plot was used to recognise spatial patterns applicable to sexual dimorphism in extant species for comparison with fossil hominin species. In three African great ape species, variability occurs predominantly according to size (rather than shape), with the gorilla sample further separating into a male and a female group according to size. A different pattern is apparent for the modern human sample, in which shape variability is more evident. There is overlap between male and female modern humans and some evidence of grouping by linguistic/tribal populations. When fossil hominin species are analysed using equivalent axes of variance, the specimens group around species holotypes in quite similar patterns to those of the extant African great apes, but six individual fossil molars fall well outside of polygons circumscribing holotype clusters; at least three of these specimens are of interest for discussion in the context of sexual dimorphism, species variability and current species classifications. An implication of this study is that, especially in the case of modern humans, great caution needs to be exercised in using extant species as analogues for assessing variability considered to be a result of sexual dimorphism in fossil hominin species.

Significance:

- Caution should be exercised in using modern analogue species as proxies for fossil hominin species variability.
- Exceptionally wide ranges of molar variability between certain fossil hominin specimens currently allocated to the same species might indicate possible misclassification.
- Molar morphology in gorillas tends to reflect primarily size, rather than shape, variability between the sexes, which is a consideration in the context of assessing possible sexual dimorphism in fossil hominin species.

Introduction

Previous research has established that analyses of dental metrics and morphology on the post-canine dentition of extant hominoids are reasonably successful at differentiating between specimens at the species level and even at the subspecies/regional level.[1-7] Likewise, in the fossil hominin context, molar crown size, shape and cusp arrangements have traditionally been used as diagnostic tools to help to identify specimens attributed to different species of *Australopithecus, Paranthropus* and *Homo.*[8-14] However, taxonomic decisions cannot always be made with accuracy, particularly when the fossil record is incomplete, and boundaries between species are sometimes very indistinct.[15] It is common to use observed variability ranges in extant species as proxies for the quantification of expected variability in similar fossil species (for example, extant hominoids are often used as analogues for extinct hominins), but some caution needs to be observed in doing so.[16] Certain species, such as gorillas and orangutans, are known to be highly sexually dimorphic. In terms of their dental morphometrics, Uchida[1-2] has noted that although teeth vary greatly in size between the sexes, there are no significant differences between male and female gorillas and orangutans in terms of molar shape, in the context of their mean shape indices and cusp proportions. In the case of modern *Homo sapiens*, however, size differences are known to occur along regional or biogeographical lines, and although there may be regional variability and some sexual dimorphism in each region, certain groups globally have extremely large ('megadont') molars, while other groups have very small ('microdont') teeth by comparison.[17-19]

If molar morphology is linked to form and function, as researchers such as Kay[20] and Ungar[21] have postulated, then size reduction and shape changes are more likely to have occurred as a result of selective pressures over time in modern *H. sapiens* as diets and subsistence lifestyles have diverged between groups over millennia. Indeed, studies conducted on femora of modern human groups with differing lifestyles (e.g. hunter–gatherer; sedentary/farming; small-scale farmers) have noted that variability occurs as a function of subsistence lifestyle.[22,23] Other researchers have confirmed that this form–function variation along subsistence lifestyle lines is also found in molar metric variability as a result of long-standing divergences in diet in some groups after the Neolithic Revolution. As diets have become predominantly based on soft cereals and higher levels of cooking and food processing, tooth reduction has generally occurred in these groups[19,24-27], while other groups, such as Australian Aboriginal hunter–gatherers/terrestrial foragers, have retained large, robust molars[17,18,28]. Dietary and subsistence-lifestyle histories may not be the only factors at play in determining the wide variability in size and shape of modern human molars, but the fact remains that although there may be measures of sexual dimorphism within biogeographical groups individually,[29] if molar morphology were to be viewed in morphospace in the same way as that of other

hominoids, while gorilla teeth should separate (by species/sub-species) into a male group and a female group primarily by size,[1] modern human teeth would be expected to group by biogeographical population or by historical subsistence lifestyle divergences initially, and by sex thereafter.

In the case of *Pan* species, variation between the lower first molars of common chimpanzees and bonobos is linked to allometry, such that when the effects of allometry are factored out, 'chimpanzee and bonobo molars are not morphometrically distinguishable'[7]. It is not within the scope of this study to correct for allometry, but because mandibular molar morphometrics are strongly correlated with size in *Pan,* a visualisation in morphospace using size as the first principal component axis should achieve a good degree of discrimination between these two closely related species.

The aim of this study was to build upon previous studies by using geometric morphometric methods to provide a visual analysis of size-versus-shape variability patterns in the post-canine dentition of extant hominoid species and their implications for the analysis of molar variability within and between fossil hominin species. The goal was to obtain a general understanding, not only of patterns of size-versus-shape variability in the lower first molars of African ape species, but also of how these African ape variability patterns differ to those observed in *H. sapiens*. Understanding this difference is important because the typically high ranges of variability in modern human skeletal elements (including teeth) are often used as benchmarks for quantifying the expected range of variability in skeletal elements of fossil hominin species, and further, in species such as *Australopithecus afarensis,* modern human-like sexual dimorphism is cited as the primary factor to explain such high variability between specimens of this species.[30,31] In this context, Ferguson[32] strongly emphasises the need to take into account factors such as globalisation and differences in self-domestication between modern human populations before comparing dental variation between a fossil hominin species such as *Au. afarensis* and modern *H. sapiens.* His conclusion is that dental variation in modern *H. sapiens* is 'not evidence of normal dental variation in hominids'[32]. The aim of the present study was to provide a visualisation of both the range of variability and, more importantly, the pattern of general size/shape variability that would be expected of selected hominoid species, in the context of sexual dimorphism.

In particular, the following specific questions are addressed:

- Do specimens of selected extant hominoids group in morphospace in a way that confirms previous research (using a size-versus-shape principal components analysis to visualise the main axes of variability), particularly in the context of sexual dimorphism?
- Does the pattern of variability in morphospace (size versus shape) of modern *H. sapiens* differ from that of extant African great apes?
- Using equivalent principal components axes (size versus shape), do fossil hominin lower first molars group in morphospace in a similar way to those of gorillas, other African great apes, or modern *H. sapiens,* and if so, what conclusions should be drawn from these groupings?
- Are there certain instances in the fossil hominin record where the lower first molars of individual specimens attributed to a particular hominin species differ so significantly in size and/or shape from those of the other specimens in the group (including the type specimen or holotype of the species) that these specimens warrant further discussion in respect of species variability, sexual dimorphism or potential misclassification?

The aim of the present study was thus to test the predictions (1) that sexual dimorphism should be observable between lower first molars of male and female *Gorilla gorilla gorilla,* primarily according to size*;* (2) that variability between lower first molars of male and female modern humans may follow a different pattern in morphospace to that of African great ape species, possibly being observable primarily along biogeographical lines, and only secondarily according to sex; and (3) that certain specimens in the fossil hominin record may appear as outliers from the typical individuals of their species, raising the possibility of misclassification.

Materials and methods

Digital two-dimensional images of 40 lower first molars (occlusal crown images) from 20 (10 male, 10 female, both antimeres) individuals each of *Gorilla gorilla gorilla, Pan troglodytes schweinfurthii, Pan paniscus* (from the Royal Museum for Central Africa in Tervuren, Belgium), and modern *Homo sapiens* (from the R. A. Dart Collection of the University of the Witwatersrand, Johannesburg, South Africa) were analysed to determine variability within and between species, and between sex within species, for comparison with 36 African Plio-Pleistocene lower first molars from 27 individuals [including five holotypes (*Australopithecus afarensis, Australopithecus africanus, Paranthropus robustus, Homo habilis and Homo erectus*) as well as Peninj 1, which is a mandibular proxy for the holotype of *Paranthropus boisei*]. Because all of the fossil specimens were from African Plio-Pleistocene hominin species, African great apes and modern humans from southern Africa were selected for comparative purposes.

Two-dimensional imagery was chosen for the study because holotypes of certain of the fossil hominin species were extremely worn (e.g. *Au. afarensis* and *P. boisei*), and would not have been able to be included in a three-dimensional analysis, but these specimens were still usable in a study relying on landmark analyses wherein homologous cusp intersections at the perimeter of the occlusal crown view were still discernible. Coupled with a geometric approach to landmarking the surfaces of the crowns, this enabled more fossil specimens (including holotypes and proxies thereof) to be included in the study, even if most of the topography and surface features on the crowns were worn or obliterated. Right antimeres were mirrored to appear as left molars.

Where possible, antimeres were included, because in many individuals there is odontometric asymmetry, which has been linked to tooth eruption patterns, masticatory loads and laterality (handedness) in modern humans.[33-35] As this asymmetry is generally manifested in the form of dimension differences between the two sides, the inclusion of antimeres enabled observations of the potential cause of spatial patterning differences to be controlled for, between sex as well as hemisphere, because for the fossil sample (where sex is unknown but laterality is known), in some cases only left lower molars or right lower molars were available, and to select only left or right specimens would cause a significant reduction in *n* for an already limited fossil hominin sample. Details for the specimens used are given in Tables 1–3.

Table 1: Lower first molar specimens included in the comparative study: Modern *Homo sapiens*

Catalogue number Dart Collection	Population/language group (as stated in the catalogue)	Sex	Age at death
A1263	Sotho (South Africa)	F	18
A1483	Tswana (South Africa or Botswana)	F	19
A3607	Mixed (European & African)	F	40
A84	Amafengu (South Africa)	F	38
A27	San ('Bushman' – South Africa)	F	N/A
A281	Sotho (South Africa)	M	18
A1264	Tswana (South Africa or Botswana)	M	23
A3421	Mixed (European & African)	M	60
A861	Amafengu (South Africa)	M	34
A173	San ('Bushman' – South Africa)	M	N/A

Table 2: Lower first molar specimens included in the comparative study: Extant African great apes

Species	RMCA (Tervuren) catalogue number	Sex
Gorilla gorilla gorilla	7732M15	F
Gorilla gorilla gorilla	7732M8	F
Gorilla gorilla gorilla	7732M5	M
Gorilla gorilla gorilla	7318M3	F
Gorilla gorilla gorilla	7732M7	M
Gorilla gorilla gorilla	7732M6	M
Gorilla gorilla gorilla	7732M3	F
Gorilla gorilla gorilla	7732M2	M
Gorilla gorilla gorilla	7732M1	M
Gorilla gorilla gorilla	7556M2	F
Pan troglodytes schweinfurthii	91060M422	F
Pan troglodytes schweinfurthii	91060M414	M
Pan troglodytes schweinfurthii	91060M410	F
Pan troglodytes schweinfurthii	91060M406	F
Pan troglodytes schweinfurthii	83006M37	F
Pan troglodytes schweinfurthii	83006M32	F
Pan troglodytes schweinfurthii	83006M22	M
Pan troglodytes schweinfurthii	83006M21	M
Pan troglodytes schweinfurthii	83006M17	M
Pan troglodytes schweinfurthii	83006M15	M
Pan paniscus	84036M11	F
Pan paniscus	84036M03	M
Pan paniscus	29055	F
Pan paniscus	29053	M
Pan paniscus	29050	M
Pan paniscus	29027	F
Pan paniscus	29028	M
Pan paniscus	29026	F
Pan paniscus	13021	F
Pan paniscus	11354	M

Table 3: Lower first molar specimens included in the comparative study: Fossil hominin specimens

Specimen number	Side	Marker used	Current taxonomic designation	Location	Comments	Geological paper reference	Estimated geological age (Ma) (latest estimate)	Reference for estimated date
AL 145-35	L	♦	*Australopithecus afarensis*	Wits cast collection, Johannesburg	Cast	36	3.35	58
AL 128-23	R	♦	*Au. afarensis*	Wits cast collection, Johannesburg	Cast	36	3.25	58
AL 266-1	L	♦	*Au. afarensis*	Wits cast collection, Johannesburg	Cast	36	3.2	58
AL 266-1	R	♦	*Au. afarensis*	Wits cast collection, Johannesburg	Cast	36	3.2	58
AL 288-1	R	♦	*Au. afarensis*	Wits cast collection, Johannesburg	Cast	37	3.18	58
AL 333-W60	L	♦	*Au. afarensis*	Wits cast collection, Johannesburg	Cast	38	3.2	58
LH 2	R	♦	*Au. afarensis*	National Museums of Kenya, Nairobi	Cast	39,40	3.77	59
LH 4	L	♦	*Au. afarensis*	National Museum, Dar es Salaam	Holotype – original	39, 40	3.77	59
LH 4	R	♦	*Au. afarensis*	National Museum, Dar es Salaam	Holotype – original	39 40	3.77	59
MLD 2	L	▲	*Au. africanus/ (Au. prometheus)*	Wits fossil collection, Johannesburg	Original	41, 42	2.8	59
MLD 2	R	▲	*Au. africanus/ (Au. prometheus)*	Wits fossil collection, Johannesburg	Original	41, 42	2.8	59
Sts 52b	R	▲	*Au. africanus*	Ditsong National Museum, Pretoria	Original	43	2.3	60
Taung 1 (U.W. 1-1)	L	▲	*Au. africanus*	Wits fossil collection, Johannesburg	Holotype – original	44	2.7	59
Taung 1 (U.W. 1-1)	R	▲	*Au. africanus*	Wits fossil collection, Johannesburg	Holotype – original	44	2.7	59
OH 22	R	●	*Homo erectus*	National Museum, Dar es Salaam	Original	45	0.875	59
KNM-ER 806c	L	●	*H. erectus*	National Museums of Kenya, Nairobi	Original	46	1.49	9
KNM-ER 820	L	●	*H. erectus*	National Museums of Kenya, Nairobi	Original	46	1.6	9
KNM-ER 820	R	●	*H. erectus*	National Museums of Kenya, Nairobi	Original	46	1.6	9
KNM-ER 992	L	●	*H. erectus*	National Museums of Kenya, Nairobi	Holotype – *Homo ergaster* (African *Homo erectus)* original	47	1.49	59,61
KNM-ER 992	R	●	*H. erectus*	National Museums of Kenya, Nairobi	Holotype – *Homo ergaster* (African *Homo erectus)* original	47	1.49	9,61
OH 7	L	●	*H. habilis*	National Museum, Dar es Salaam	Holotype – original	48, 49	1.84	59
OH 7	R	●	*H. habilis*	National Museum, Dar es Salaam	Holotype – original	48, 49	1.84	59
OH 16	R	●	*H. habilis*	National Museum, Dar es Salaam	Original	50	1.74	59
KNM-ER 1802	L	●	*H. rudolfensis*	National Museums of Kenya, Nairobi	Original	51	1.89	9
KNM-ER 1802	R	●	*H. rudolfensis*	National Museums of Kenya, Nairobi	Original	51	1.89	9
KNM-ER 15930	L	■	*Paranthropus boisei*	National Museums of Kenya, Nairobi	Original	52	1.78	9
Peninj 1	L	■	*P. boisei*	National Museum, Dar es Salaam	Mandibular proxy for holotype (OH 5) – original	53	1.4	59
Peninj 1	R	■	*P. boisei*	National Museum, Dar es Salaam	Mandibular proxy for holotype (OH 5) – original	53	1.4	59
SK 6	L	■	*P. robustus*	Ditsong National Museum, Pretoria	Original	54	1.75	59
SK 6	R	■	*P. robustus*	Ditsong National Museum, Pretoria	Original	54	1.75	59
SK 23	L	■	*P. robustus*	Ditsong National Museum, Pretoria	Original	54	1.75	59
SK 23	R	■	*P. robustus*	Ditsong National Museum, Pretoria	Original	54	1.75	59
SK 63	L	■	*P. robustus*	Ditsong National Museum, Pretoria	Original	55	1.75	59
SK 63	R	■	*P. robustus*	Ditsong National Museum, Pretoria	Original	55	1.75	59
SKW 5	R	■	*P. robustus*	Ditsong National Museum, Pretoria	Original	56	1.75	59
TM 1517	R	■	*P. robustus*	Ditsong National Museum, Pretoria	Holotype – original	57	1.75	59

Photographic and image-processing methods

Digital photographs were taken using a Nikon D3200 digital SLR 24-megapixel camera, with an adjustable scale bar placed in each image at the height of the plane of the occlusal crown surface. The tooth being photographed was centred orthogonally below the lens of the camera, well in the centre of the frame of the image, and was aligned in the horizontal using the cervical plane as a horizontal guide; however, because it was not always possible to verify this plane, particularly along the buccolingual axis, and where immersion in levelled sand was not advisable because of the delicate nature of the specimens, visual alignment of the vertical lingual and buccal crown edges was used. The accuracy of the horizontal/vertical alignment of the tooth was tested by using three- to two-dimensional image superimpositions, wherein three two-dimensional digital images, taken for the same tooth at different times, were each inserted into the correct plane of a three-dimensional image of the same tooth using Amira® software, after which differences in the *x*-, *y*- and *z*-axes between the three alignments were measured. The resultant error (averaging 0.014° along the *x*-axis, 0.107° along the *y*-axis and 0.098° along the *z*-axis) was considered to be within acceptable limits, after correlations of landmark measurements at varying degrees of tilt had previously established that errors of tilt of up to 2° from the horizontal produced a correlation coefficient of 0.99 in relation to the same measurements at zero tilt. For purposes of the analyses and the landmark placements, the digital images were each aligned horizontally on screen along the longitudinal axis of the tooth, using the protocols of Wood[9] and Goose[62] as guidelines for this alignment (taking into account the 'normal' alignment[62] of the tooth in question as well as that of its immediate neighbours). A rectangle was superimposed over the image in the form of a bounding box (using Adobe Illustrator®) to act as a proxy for the mesiodistal (minimum) diameter and the buccolingual (maximum) diameter, respectively, according to definitions by Wood[9]. The centre of the bounding box was then calculated for purposes of a fan overlay placement, which would serve as a basis for the placement of landmarks at each 15° interval around the perimeter of the occlusal crown shape. The alignment and the position of this mathematical centre point were subjected to inter-observer tests for accuracy (average error: 0.295% in the *x*-axis and 0.316% in the *y*-axis).

Landmarking method

Five Type I (homologous or 'anatomical') landmarks[63] were sited at the intersection of each of the cusps at the perimeter outline of the occlusal crown surface in the image, and a further 44 Type III (mathematical or 'constructed') landmarks[63] were placed in such a way as to define (1) the buccolingual and mesiodistal diameters of each tooth (four landmarks placed on a bounding box enclosing the tooth plus a fifth at the mathematical centre of the bounding box); (2) the peripheral shape of the tooth (24 landmarks, every 15° around the tooth perimeter); and (3) the orientation of the cusps (five landmarks denoting the midpoint between cusp intersections and five landmarks measured equidistantly from the central landmark to the centre of the cusp arc at the perimeter, along the midline of the cusp, with a further five landmarks equidistant between these central cusp landmarks; in cases where a diagnostic sixth cusp was evident, the landmark normally sited midway between the landmarks at the centre points of the entoconid and the hypoconulid was sited instead at the midpoint between the landmark at the centre of the entoconid and the landmark at the intersection between the sixth cusp and the hypoconulid at the perimeter, so that the landmark would be sited over the sixth cusp). The position of the landmarks is shown in Figure 1.

The images were scaled and landmarks digitised using ImageJ® software and processed via Microsoft Excel® into IBM SPSS® and Morphologika® for purposes of performing Procrustes superimposition, principal components analyses and discriminant function analyses. Lastly, a custom-written macro for MS Excel®, named 'Professor Regressor'[64] was created to produce a high-speed throughput of pairwise regressions for purposes of conducting log se_m analyses to determine average conspecific variation.[65]

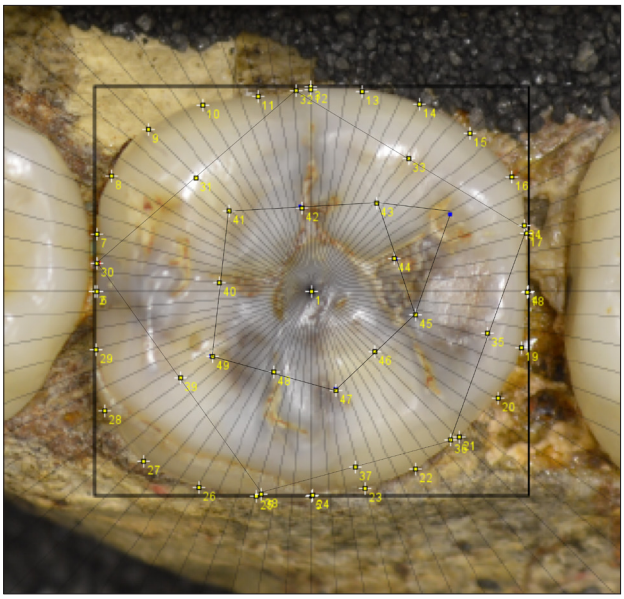

Figure 1: Landmark placements. The first five landmarks describe mesiodistal/buccolingual measurements. Landmarks 6–29 are sited to describe points every 15° along the outline of the perimeter of the tooth in the occlusal view. Landmarks 30–39 are sited at the points at which cusps intersect at the perimeter, together with the midpoints of the cords drawn across the arcs that are described by these cusps and describe an outer pentagon denoting peripheral widths and orientations of cusps. Landmarks 40–49 describe an inner pentagon (or hexagon in the case of a C6) denoting the geometric centre of each cusp as calculated from Landmark 1 to the perimeter of the tooth along the midline of each cusp arc. Thus general proportions (breadth/length), cusp size and cusp orientations are able to be landmarked, even if the crown surface is devoid of diagnostic features, provided that the five cusp intersections at the peripheral outline of the tooth are visible (Type 1 landmarks: 30, 32, 34, 36 and 38).

Methods: Analyses

A principal components analysis (PCA) was first performed on the sample from the four extant species' lower first molars in Morphologika after performing a generalised Procrustes superimposition wherein specimens are translated, rotated and scaled and then plotted on a graph showing the main axes of differentiation from a 'consensus' tooth; a second PCA was conducted using 'Procrustes form space', wherein size is factored back into the analysis by including the log of the centroid size for each shape as a variable in the analysis.[66] This second PCA thus provides a 'size–shape' analysis, aimed at visualising differentiation between similarly shaped, but differently sized, molars (e.g. male and female gorilla molars) on the graph. In a form space analysis, size becomes the predominant factor of variance along the first principal component (PC) axis (the *x*-axis). The second PC axis (the *y*-axis) summarises the main shape differences between specimens, statistically independently of size.[67] In the case of the extant species, PC2 summarised the primary shape variation to be a function mainly of relative breadth of the occlusal surface (high to low mesiodistal:buccolingual ratios), together with aspects of cusp orientation and perimeter shape differences. When fossil specimens were added to the analysis, examination of the thin plate spline warps for higher-order PCs showed that PC3 accounted for almost exactly the same variability factors as PC2 had done in the analysis for the extant species alone (relative breadth, cusp orientation and perimeter shape), and for all PC plots involving fossil specimens PC3 was selected as the *y*-axis component of the plot.

Thereafter, a discriminant function analysis (DFA) was carried out using the first eight PC scores on the four extant species and fossils together. The number of PC scores to include was decided on the basis

of a sensitivity test to determine the minimum number of PC scores needed before the four extant species in the analysis were classified 100% correctly. The data were previously verified as being normally distributed, using a Shapiro–Wilk test.

A further analysis of intra-species variability was carried out using the 'log se_m' methodology pioneered by Thackeray et al.[68] The basic premise behind this analysis is that within any one species, skeletal variability falls within a certain range, and although the range varies from species to species, there is an average range or central tendency of variability across species in general, that approaches what Thackeray et al.[15,65,69] call an approximation of a biological species constant (T=-1.61), and a comparison between any two specimens of unknown species group can be compared against this figure to establish a statistical probability of conspecificity[68,70]. To calculate the log se_m values, pairwise regressions of measurements for specific skeletal elements are conducted, firstly with specimen A on the *x*-axis and specimen B on the *y*-axis, and then with specimen B on the *x*-axis with specimen A on the *y*-axis. The standard error of the slope *m* is calculated for the regression equation $y=mx+c$, and this is then log transformed to provide two paired log se_m values, with the difference between the two values being designated as 'delta log se_m'.[64,65] Specimens of a similar size from the same species will be expected to have very low log se_m values, because the standard error of the slope is a measure of 'scatter' around the regression slope between the two specimens, and there should be a high degree of correlation between points along a regression line for two specimens with similar shape, with more predictable expected *y*-values as a result; and because the specimens are similarly sized, both of the slopes would approach a gradient of 1, and the *x*-on-*y* and *y*-on-*x* values would be barely distinguishable from each other, thus the delta value should also be low. However, two specimens from different species with large shape and size differences between them will not only be poorly correlated in terms of shape (the standard error of the slope would be larger, as a result of the large amount of scatter around both lines), giving a high log se_m value in at least one of the two slopes, but the delta value between the two log se_m values would be high, as the two slopes for each pairwise comparison would have very different gradients as a result of the size differences.

A total of 760 pairwise comparisons of conspecific pairs of lower first molars of *G. gorilla, P. troglodytes, P. paniscus* and *H. sapiens* were analysed using measurements taken radially from the centre of the tooth to the landmark points as described above. A further 252 pairwise comparisons of conspecific pairs of lower first molars of the fossil hominin species were analysed, and the average species variability was compared against the average obtained for the extant species groups. After exclusion of any atypical (potentially misclassified) outlier specimens from the analysis, the remaining 176 pairwise comparisons of conspecific pairs were averaged and the results again compared with the results for the extant species groups.

Results

Sexual dimorphism in gorillas identified in morphospace

Three main clusters in morphospace are detectable from the four extant species' samples using a shape-only PCA (Figure 2). Modern *H. sapiens* exhibit a high degree of shape variability, and have generally relatively wider lower first molars than those of the great apes (Figure 2). Gorilla molars exhibit a distinctive shape, while those of bonobos and common chimpanzees exhibit overlap in the PCA because their molars are less distinguishable between species in terms of shape when scaling is used (Figure 2).

As expected, sexual dimorphism is not evident even within the highly sexually dimorphic gorilla sample in the shape-only analysis, which suggests that lower first molars of male and female gorillas do not vary significantly in their shape. This finding confirms those of previous studies.[1,2] The second PCA, in which size was factored back into the analysis, is shown in Figure 3.

In Figure 3 (size versus shape), all four species are now relatively separate (as the inclusion of size now allows a better separation of bonobos from common chimpanzees). Additionally, there is a very clear separation between male gorillas and female gorillas as a result of differences in size of lower first molars (but as has been seen, not in overall shape).

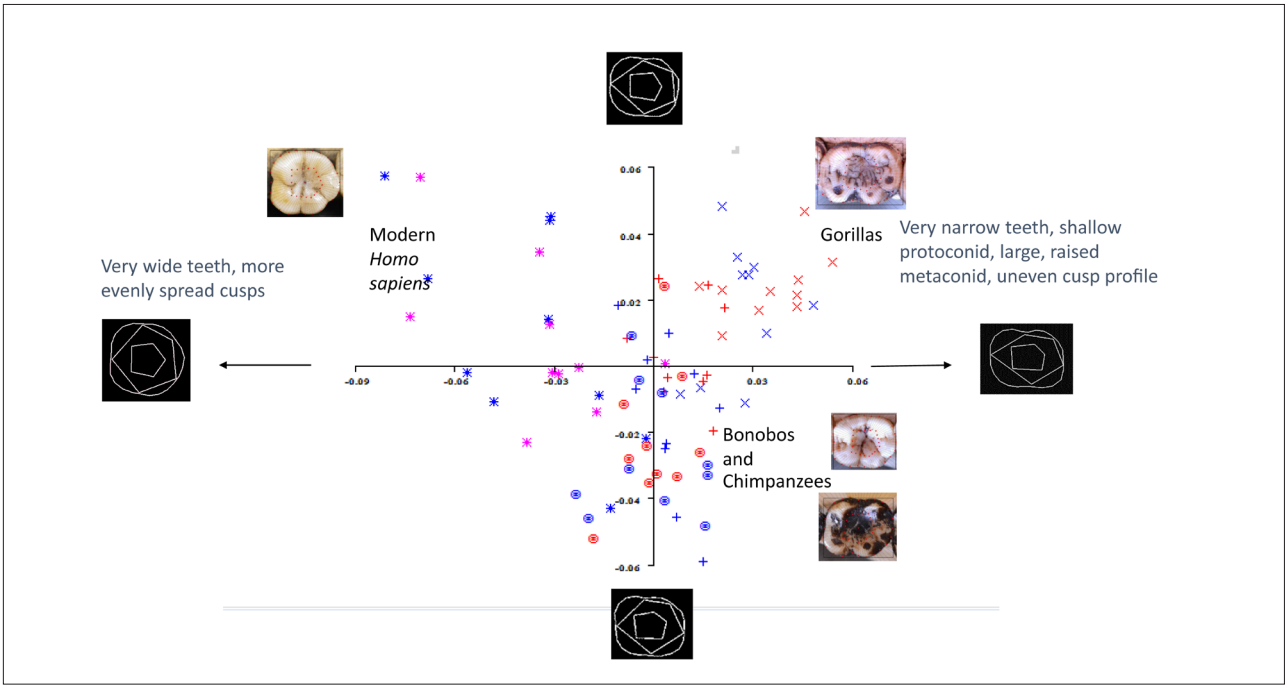

Figure 2: Principal components analysis of four extant species' lower first molars, based on Procrustes shape space (shape-only analysis). PC1 in this plot mainly accounts for the relative width of the tooth with some shape variability (28% of covariance). PC2 principally accounts for tooth shape variability and cusp orientations. *Homo sapiens* is represented by stars; *Gorilla gorilla gorilla* by diagonal crosses; *Pan paniscus* by upright crosses and *P. troglodytes* by circled target markers (pink/red=female and blue=male specimens). In this shape-only analysis, male and female gorilla specimens are not separated by sex, and there is considerable overlap between bonobo and common chimpanzee specimens.

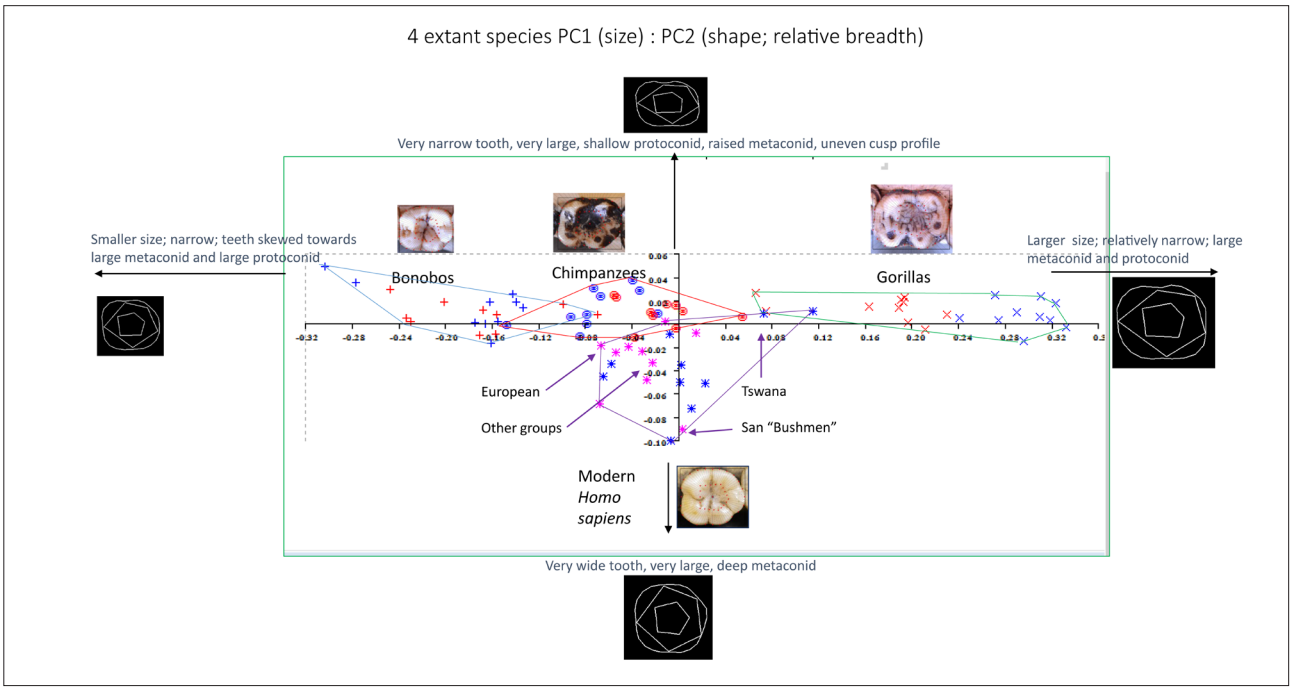

Figure 3: Principal components analysis (PCA) of four extant species' lower first molars, based on Procrustes form space (size-versus-shape analysis). PC1 in this plot mainly accounts for size differences; PC2 principally accounts for relative width of the tooth with some shape and cusp-orientation variability, formerly represented by PC1 in the shape-only PCA (Figure 2). *Homo sapiens* is represented by stars; *Gorilla gorilla gorilla* by diagonal crosses; *Pan paniscus* by upright crosses and *P. troglodytes* by circled target markers (pink/red=female and blue=male specimens). The three African great ape species vary predominantly along the *x*-axis direction (variability predominantly by size rather than by shape); male and female gorillas in the sample are separated into two distinct groups predominantly by size rather than shape; modern humans vary greatly by shape as well as size, and to a certain extent by population/linguistic groupings: the lower first molars of male and female San individuals are of medium overall size but very 'square' in occlusal crown shape; those of Tswana individuals are the largest and narrowest (the lower first molar of the male individual groups alongside that of female gorillas); lower first molars of specimens with European heritage are among the smallest and narrowest of molars in this sample.

Modern Homo sapiens*: Shape variability by population group*

All three African great ape species seem to have a limited range of shape variability within the species/subspecies selected for this study, which fall within narrow limits in terms of their relative length:breadth ratio (relative breadth of crown and cusp arrangements being the primary factors of variation shown along the *y*-axis). It is evident that the most variable within-species group is the modern *H. sapiens* sample, which varies mostly in overall proportion and shape (*y*-axis), rather than overall size (*x*-axis). On further analysis, the variability within this group appears to occur not primarily by sex (as in the gorilla sample, falling as it does into two distinct groups according to sex) but by biogeographical groupings, with teeth from the African San population being relatively square in shape (those from both male and female individuals), and those from the African Tswana group being very large and relatively very narrow in overall proportion – in fact, the teeth from two male Tswana individuals, chosen to represent megadont populations for the analysis, group with the female gorilla sample on the size-shape PC analysis because they are much larger and narrower.

When the same size-shape PC analysis as that applied to extant hominoid species is then applied to include the fossil hominin lower first molar sample (with the same shape parameters selected for the *y*-axis as were used for the extant species alone), the African great apes all group similarly as they had before – largely above the *x*-axis (narrow teeth), with size being the main source of variance between species and between male and female gorillas. The modern human sample again varies largely along the *y*-axis (wider range of shape variance – from wide to narrow across the breadth of the tooth) and most of the fossil specimens group in the bottom right quadrant (larger and wider teeth, as would be expected). *Paranthropus* species seem to follow a gorilla-like grouping parallel to the *x*-axis (variability being predominantly according to size), with this species exhibiting tight cohesion as a well-defined group on the plot, while *Au. afarensis* specimens exhibit wider variance along both size and shape axes, with individuals overlapping with modern *H. sapiens, H. erectus* and *Au. africanus* (Figure 4).

After removing the extant species from the PCA plot, a much clearer picture of shape versus size variability in morphospace is obtained for the fossil hominin species. There is generally good discrimination between species, around their holotypes or holotype proxies (Figure 5).

The distribution of specimens within species groups in this plot shows groupings visually akin to those in the shape-size analysis of the PCA plot of the extant African ape species. The group of *Paranthropus* spp. (*P. robustus* in green squares and *P. boisei* in brown squares) cluster along the *x*-axis in a similar pattern to the gorilla sample (predominantly varying in size rather than shape). The fact that they seem additionally to group in two size clusters (smaller teeth on the left, larger on the right) might possibly hint at sexual dimorphism within this group, as with the gorillas. Specimens from *H. erectus,* the species with the smallest molars in the analysis, cluster visually in morphospace in a similar manner to bonobos.

In the case of *Au. afarensis,* the majority of specimens cluster horizontally around the holotype (varying mainly by size, parallel to the *x*-axis, in a similar manner to the gorilla grouping in morphospace), but two specimens fail to cluster with their group.

Anomalous 'outliers'

Six specimens among the 36 fossil hominin lower first molars failed to group in morphospace with the clusters located around the holotypes for each species.

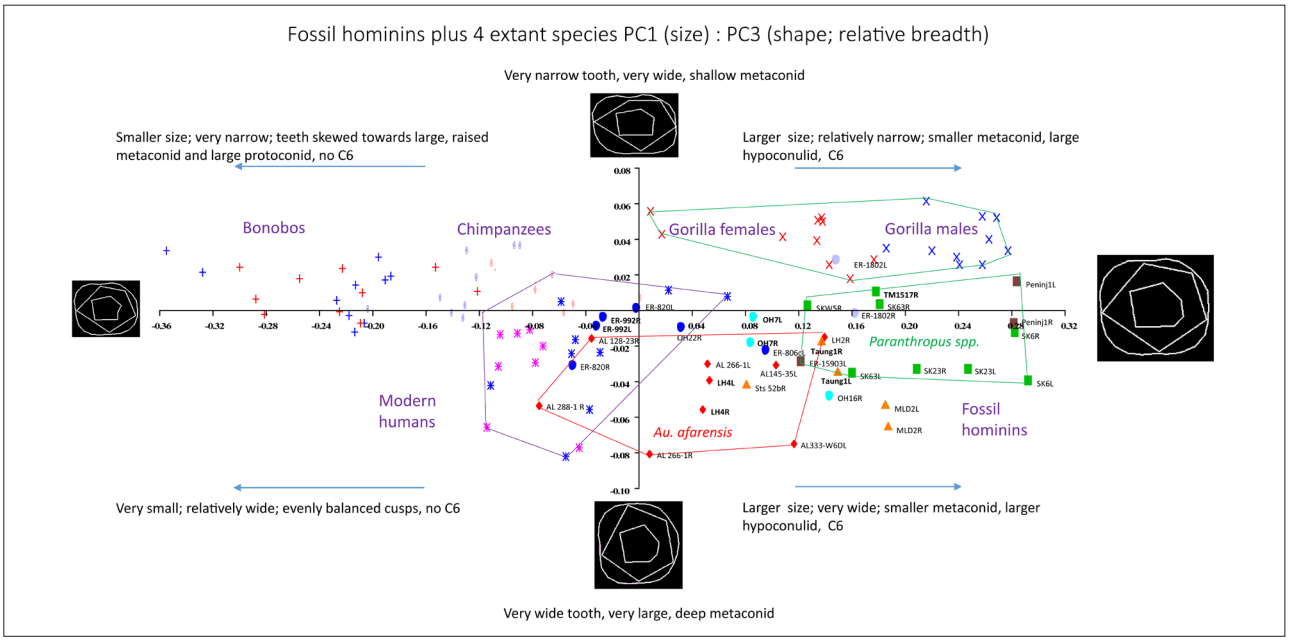

Figure 4: Principal components analysis of extant hominoid and fossil hominin species' lower first molars, based on Procrustes form space (size-versus-shape analysis). PC1 in this plot mainly accounts for size differences. PC3 principally accounts for relative width of the tooth with some shape and buccolingual cusp-orientation variability (the equivalent axis of variance that had been described along PC2 in the analysis for the extant species alone). Species markers are: red diamonds, *Australopithecus afarensis*; orange triangles, *Au. africanus*; lilac circles, *Homo rudolfensis*; turquoise circles, *H. habilis*; blue circles, *H. erectus*; green squares, *Paranthropus robustus*; brown squares, *P. boisei*. *Paranthropus* species plot in morphospace in a cohesive group with little overlap with other species, predominantly parallel to the *x*-axis (size differences as opposed to shape variability) and compare very well, spatially, to the patterning of the gorilla or other great ape samples. *Au. afarensis* specimens form a less cohesive group in morphospace, with individuals overlapping with numerous other species; there is a higher measure of shape variability alongside size variability in this species.

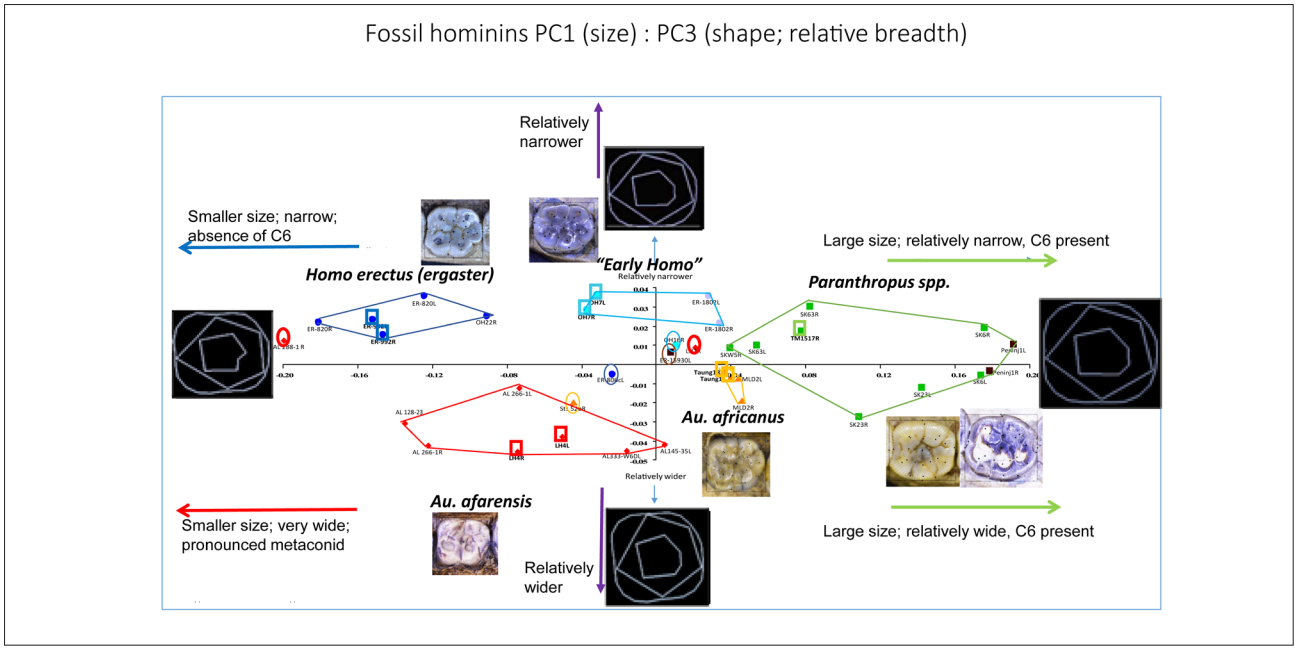

Figure 5: Principal components analysis of fossil species' lower first molars, based on Procrustes form space (size-versus-shape analysis). PC1 in this plot mainly accounts for size differences together with the presence or absence of a sixth cusp, with smallest specimens (lacking C6) at the negative extreme of the *x*-axis and largest specimens (C6 present) at the positive extreme of the *x*-axis; PC3 again principally accounts for relative width of the tooth with some shape and buccolingual cusp-orientation variability. Holotypes of species are marked by rectangular boxes. Species markers are: red diamonds, *Australopithecus afarensis*; orange triangles, *Au. africanus*; lilac circles, *Homo rudolfensis*; turquoise circles, *H. habilis*; blue circles, *H. erectus*; green squares, *Paranthropus robustus*; brown squares, *P. boisei*. Six specimens are marked with circles to illustrate that they do not group with the specimens of their currently allocated species that cluster around their holotype: AL 288-1 (currently allocated to *Au. afarensis* but groups more closely with *H. erectus*); Sts 52b (currently allocated to *Au. africanus* but groups more closely with *Au. afarensis*); KNM-ER 806c (currently allocated to *H. erectus* but groups more towards *Au. africanus* in general dimension, although smaller in size); OH 16 (currently allocated to *H. habilis*; wider buccolingually than the holotype); KNM-ER 15930 (currently allocated to *P. boisei*; extremely small in size for this group); LH 2 (currently allocated to *Au. afarensis* but groups closely with *Au. africanus*).

One outlier from the main cluster of *H. erectus* in morphospace is KNM-ER 806c, a specimen with wider buccolingual dimensions than the generally smaller and narrow molars typical of this species. This specimen also has a sixth and seventh cusp, a protostylid and a morphology extremely similar to that of the lower first molar of MLD 2, currently classified as *Au. africanus.*

Other specimens that do not seem to be typical of their species (which otherwise cluster well in morphospace) are Sts 52b, which groups with *Au. afarensis* rather than with *Au. africanus;* OH 16, which is wider, buccolingually, than the holotype of *H. habilis,* into which it has been classified; and KNM-ER 15930, which has been attributed to *P. boisei* but which is well outside of the normal size range for this species, being closer to the 'early *Homo*' group.

Notably, there are two specimens from *Au. afarensis* which group well away from the cluster around the holotype of the species in morphospace. At first glance, the *Au. afarensis* sample seems to mirror the spatial distribution of *Paranthropus* and gorillas, with several specimens clustering around the holotype (LH 4) in a polygon suggesting more size variability than shape variability. The first atypical outlier, LH 2, which is from a juvenile from the Laetoli area of Tanzania, groups closely with the *Au. africanus* cluster, being larger than the remaining specimens in the species group, and relatively more narrow in overall dimension. The second, AL 288-1, 'Lucy', groups into the quadrant in which *H. erectus* is located, but is even smaller in dimension than specimens clustering in this group.

A DFA conducted on all 116 specimens in the study confirmed that for the four extant species, the most variability was exhibited between specimens in the modern *H. sapiens* group as demonstrated by the mean squared Mahalanobis distance from the group centroid (modern *H. sapiens*: mean = 9.69±4.41 (n=20); *G. g. gorilla*: mean = 6.0±3.51 (n=20); *P. t. schweinfurthii*: mean = 4.51±1.94 (n=20); *P. paniscus*: mean = 5.36±3.20 (n=20)). For the fossil hominin species, the DFA confirmed that as a group, *Au. afarensis* was most variably distributed, with a mean squared Mahalanobis distance of specimens from their group centroid at 12.075±5.52 (n=9). *P. robustus*, with a mean of 6.49±3.11 (n=8) seems again to parallel the gorilla sample in terms of variability. *P. boisei*, with only three specimens in the sample, had a high mean Mahalanobis distance from the group centroid at 8.22±5.49 (n=3), as a result of the huge size difference between the smallest in the group (KNM-ER 15930) and the large Peninj molars that are more typical of this megadont species. The *H. erectus* group's mean squared Mahalanobis distance was also fairly high at 7.28±5.76 (n=6), but, if the one outlier (KNM-ER 806c) is excluded from the sample, this group, otherwise very homogeneous, would have a much lower mean distance from the centroid, as this single outlier's distance from the group centroid was 18.20. Another fossil hominin group with a high mean Mahalanobis distance from the group centroid was *Au. africanus* at 8.87±2.07 (n=5).

With respect to group classification predictions for individual specimens in the fossil hominin species, the DFA output confirms the anomalous status of AL 288-1 (grouped with *H. sapiens* because of its narrowness and relatively tiny size). KNM-ER 806c is predicted to classify, unsurprisingly, with the *Au. africanus* group*,* because of its extreme similarity with MLD 2. The third potential misclassification in this analysis is Sts 52b, which is more predictably classified as *Au. afarensis,* confirming the PCA plot results. One other instance of potential misclassification according to the DFA was that of Taung 1 (left and right antimeres), which classifies more readily with *Paranthropus.* However, this apparent anomaly is because this specimen has an obvious sixth cusp, and was landmarked with six cusps accordingly. The C6 or 'tuberculum sextum'[10,71-73] is diagnostic of *Paranthropus* spp., and all the specimens attributed to *P. robustus* and *P. boisei* were landmarked for this cusp, so it is not surprising that Taung 1 groups with the paranthropines.

Table 4 presents the summary of the results for the fossil hominin specimens. The full table, including the 80 extant species specimens, is provided in the supplementary material.

The results of the log se_m pairwise comparisons for the four extant hominoid species confirmed the results of the PCA plot: the widest ranges of values were shown by *G. g. gorilla* (low degree of shape, but high degree of size, and disparity between the smallest female and the largest male specimen, i.e. low average log se_m value coupled with high delta value) and by *H. sapiens* (most variability in shape, rather than size, of all four species, i.e. high average log se_m value with lower delta value). The average log se_m value for all conspecific comparisons was -1.6208, which is only a very slightly lower value than the average central tendency of average log se_m values for conspecific specimens of -1.61 as calculated by Thackeray[69]. The results are presented in Table 5.

Log se_m results similarly calculated for the lower first molars of fossil hominins included in the study also confirmed the PCA results and the DFA species-wide distributions of squared Mahalanobis distances. *Au. afarensis,* with its main 'holotype-like' group and two outliers/anomalies – one significantly tiny and narrow by comparison with the holotype, and the other more in the range of *Au. africanus* in dimension – had the highest average log se_m and delta values of all the species (indicating both shape and size disparity within the group as currently classified). Specifically, AL 288-1 ('Lucy') had a log se_m value of -1.278 in a pairwise comparison with LH 4 (the holotype of the species) and the equivalent value for LH 2 against LH 4 was -1.486. This result confirms the DFA results, in that the group mean log se_m showed extreme variability between specimens in the species sample, but that AL 288-1 was the specimen most likely not to be conspecific with LH 4. *H. erectus* and other early *Homo* species were the most cohesive of the groups, despite anomalous specimens in each group that both tended more towards *Au. africanus* in dimension. In particular, KNM-ER 806c was the main anomaly in the *H. erectus* group, with a log se_m value of -1.396, in comparison to KNM-ER 992 (the holotype of the species). The mean value for this group is -1.625±0.16 (n=30 pairwise comparisons), but if KNM-ER 806c had been excluded from the group, the mean value would have been -1.727.

The results for the species groups including and excluding the six anomalous specimens as identified by the PCA are presented in Table 6. Once the anomalous specimens are removed from the analysis, the mean log se_m value for conspecific comparisons is -1.607, with a standard deviation of 0.102 (n=176 pairwise comparisons), which is very much in line with Thackeray's mean log se_m value of -1.61 with a standard deviation of 0.230 for 70 species.[69]

Discussion

Sexual dimorphism evident in gorilla lower first molars

Lower first molars of male and female gorillas are undifferentiated in morphospace in a shape-only PCA (Figure 2), but are well separated when size is factored back into the analysis in a shape-and-size PCA (Figure 3). There was no overlap at all along the *x*-axis (PC1 accounting mainly for size) between male and female gorillas in the sample used for this analysis, with molars of all female gorillas being smaller than all molars belonging to male gorillas. The implication is that shape is not a determining factor in distinguishing between sexes within this sample from *G. g. gorilla*, but rather, the main difference is in the size of the molars. Bonobo lower first molars and common chimpanzee lower first molars similarly group together in morphospace in a shape-only analysis (Figure 2); but in a shape-and-size analysis (Figure 3), while separation is achieved between the species on the basis of size differences, there is no marked separation evident between male and female individuals, as there is with gorillas.

Variability between molars of Homo sapiens

The modern human molars included in the analysis showed the greatest within-species variability of the four species included in the study (Figure 2). When size was included in the analysis (Figure 3), these molars still failed to cluster closely, because of differences in relative mesiodistal:buccolingual ratios (relative width of the teeth) and in overall shape. Not only do modern human molars vary more in shape than the other modern African ape species according to the PC analyses, but molars belonging to male and female humans are not differentiated in the same way as gorilla molars are in morphospace within the species as a whole (distinct groups of male and female individuals).

Table 4: Results of discriminant function analysis for fossil hominin species

Specimen	Actual group	Predicted group	Probability	Squared Mahalanobis distance to centroid
AL 145-35 L	*Australopithecus afarensis*	*Au. afarensis*	1.000	18.235
AL 228-23 R	*Au. afarensis*	*Au. afarensis*	0.984	14.045
AL 266-1 L	*Au. afarensis*	*Au. afarensis*	0.939	11.886
AL 266-1 R	*Au. afarensis*	*Au. afarensis*	0.997	11.573
AL 288-1 R	*Au. afarensis*	*Homo sapiens*	0.547	11.957
AL 333-W6D L	*Au. afarensis*	*Au. afarensis*	0.989	6.529
LH 2 R	*Au. afarensis*	*Au. afarensis*	0.545	8.580
LH 4 L	*Au. afarensis*	*Au. afarensis*	0.958	21.809
LH 4 R	*Au. afarensis*	*Au. afarensis*	0.998	4.063
MLD 2 L	*Au. africanus*	*Au. africanus*	0.992	8.650
MLD 2 R	*Au. africanus*	*Au. africanus*	0.402	11.916
Sts 52b R	*Au. africanus*	*Au. afarensis*	0.498	6.568
Taung 1 L	*Au. africanus*	*Paranthropus robustus*	0.817	9.692
Taung 1 R	*Au. africanus*	*P. robustus*	0.958	7.498
OH 22 R	*H. erectus*	*H. erectus*	0.694	8.763
KNM-ER 806c L	*H. erectus*	*Au. africanus*	0.843	18.196
KNM-ER 820 L	*H. erectus*	*H. erectus*	0.960	5.324
KNM-ER 820 R	*H. erectus*	*H. erectus*	0.995	4.556
KNM-ER 992 L	*H. erectus*	*H. erectus*	0.986	2.097
KNM-ER 992 R	*H. erectus*	*H. erectus*	0.956	4.750
OH 7 L	*H. habilis*	*H. habilis*	0.970	3.534
OH 7 R	*H. habilis*	*H. habilis*	0.962	1.566
OH 16 R	*H. habilis*	*H. habilis*	0.992	8.395
KNM-ER 1802 L	*H. rudolfensis*	*H. rudolfensis*	0.995	1.601
KNM-ER 1802 R	*H. rudolfensis*	*H. rudolfensis*	0.964	1.601
KNM-ER 15930 L	*P. boisei*	*P. boisei*	0.729	14.276
Peninj 1 L	*P. boisei*	*P. boisei*	0.972	6.799
Peninj 1 R	*P. boisei*	*P. boisei*	0.991	3.584
SK 6 L	*P. robustus*	*P. robustus*	0.961	8.061
SK 6 R	*P. robustus*	*P. robustus*	1.000	5.432
SK 23 L	*P. robustus*	*P. robustus*	0.994	2.935
SK 23 R	*P. robustus*	*P. robustus*	0.881	7.439
SK 63 L	*P. robustus*	*P. robustus*	1.000	6.193
SK 63 R	*P. robustus*	*P. robustus*	1.000	3.367
SKW 5 R	*P. robustus*	*P. robustus*	1.000	12.829
TM 1517 R	*P. robustus*	*P. robustus*	0.983	5.639

Table 5: Log se_m results for four extant hominoid species

	Gorilla gorilla	*Pan troglodytes*	*Homo sapiens*	*Pan paniscus*	Average of four species
Average log se_m	**-1.6428**	**-1.6577**	**-1.5389**	**-1.6439**	**-1.6208**
Standard deviation	0.13	0.09	0.13	0.10	0.12
Minimum value	-2.1135	-1.9291	-1.9035	-1.9142	
Maximum value	-1.2357	-1.4207	-1.2854	-1.3859	
Delta value	0.0707	0.0483	0.0469	0.0563	0.0555
n	190	190	190	190	760

Table 6: Log se_m results for extinct hominin species groups

	Australopithecus afarensis	*Australopithecus africanus*	*Homo erectus*	*Homo habilis/ H. rudolfensis*	*Paranthropus boisei/ P. robustus*	Average conspecifics
	(all specimens)					
Average log se_m (all specimens)	-1.437	-1.521	-1.625	-1.701	-1.566	-1.570
Standard deviation	0.125	1.134	0.160	0.096	0.110	0.125
Delta value	0.071	0.050	0.040	0.036	0.058	0.034
n	72	20	30	20	110	252
	Au. afarensis	***Au. africanus***	***H. erectus***	***H. habilis/ rudolfensis***	***P. boisei/ robustus***	**Average conspecifics**
	(corrected for anomalies)					
Average log se_m (corrected for anomalies)	**-1.584**	**-1.500**	**-1.727**	**-1.756**	**-1.602**	**-1.607**

(n= 176; s.d. = 0.102)

On further inspection, shape and size variability of both male and female humans is noted at the level of individual population groups: the male and female San individuals in the sample both have molars with almost equal mesiodistal and buccolingual diameters (they appear almost square in the occlusal view), while the molars of the megadont male Tswana individual in this study were large and relatively narrow and overlapped with the smallest female gorilla teeth in the shape-and-size PCA. Molars of individuals with European heritage were among the smallest in the sample.

This finding would seem to fit with previous studies which have suggested that because modern humans have migrated globally and different populations have followed variable histories of subsistence lifestyles and diet, tooth size has evolved biogeographically.[17,26,28] Tooth size reduction, in particular, has occurred in specific regions (particularly Europe, North Africa, the Levant and the Anatolian area) as a result of changes from hunter–gatherer lifestyles to semi-sedentary herding, and particularly to large-scale farming lifestyles. This change in lifestyle involving sedentary or urban living has resulted in increased consumption of soft cereals and more efficient food-processing and cooking technologies, which set these groups on a different dietary trajectory from hunter–gatherer societies since the Neolithic Revolution.[24-27] Stark odontometric differences are also reflected in other skeletal elements such as femora (with European groups having long, gracile femora, with hunter–gatherers and certain Bantu groups having more robust, shorter femora.[22,23]) In the small sample chosen for this study, there are representatives from populations whose lifestyles, until recently, have revolved around hunter–gathering (the San), small-scale subsistence herder-–agriculturalists (Tswana and Sotho), and sedentary/ post-Neolithic large-scale farmers (individuals with European heritage).

Fossil 'outliers'

In all, from the PCA plot, there appears to be six lower first molar specimens that do not seem to cluster in morphospace with their own species groups: (1) AL 288-1 and (2) LH 2 (from *Au. afarensis*); (3) Sts 52b, which has been allocated to *Au. africanus* but whose classification has been questioned within this group by other researchers[74,75]; (4) OH 16, classified as *H. habilis* but which is notably larger and wider than the holotype and has been likened to molars of *Au. africanus* in size[50]; (5) KNM-ER 15930, which is classified into *P. boisei* but which is extremely tiny by comparison with the typically megadont examples of this species; and (6) KNM-ER 806c, classified as *H. erectus*,[9] but visually almost identical to (albeit slightly smaller than) MLD 2 – this particular specimen is currently classified as *Au. africanus* but has been identified as a 'larger-toothed' specimen,[42] and one of a group of specimens being considered for reclassification into a 'second species', *Au. prometheus.*[42]

Three of these specimens – Sts 52b, OH 16 and KNM-ER 15930 – are in species groups with low sample numbers in this study, and so it is difficult to draw firm conclusions. *H. habilis* as a species has been challenged since its first introduction into the literature; KNM-ER 15930 may represent extreme sexual dimorphism in *P. boisei,* as postulated by Leakey and Walker[52]. The status of the specimens representing *Au. africanus* in general warrants some further comment, as Taung 1 appeared to be anomalous in the context of the DFA, alongside Sts 52b. Unfortunately, the species in this particular study was represented by only five molars from three individuals, each of which has been the object of some discussion as to its inclusion within the species. Firstly, Taung 1, which is the holotype, has a sixth cusp more typical of *Paranthropus*, and its inclusion within the group of 'robust australopithecines' has

been previously discussed by researchers.[76] MLD 2 has characteristics associated with *Au. africanus*, including a protostylid, but its attribution to *Au. africanus* has recently been reconsidered by Clarke[42]. Sts 52b is a slightly damaged molar with a great deal of wear, but certain researchers have confirmed the anomalous status noted in this study of the specimen.[42,74,75] The high mean Mahalanobis distance for this species might be explained by the heterogeneity of this sample.

The other three anomalous specimens from the PCA are interesting for further discussion regarding potential misclassification and/or unusually high variability within one single species, as currently defined.

The striking morphological similarities between KNM-ER 806c (currently attributed to *H. erectus* but grouping closely with *Au. africanus* both on the PCA and the DFA) and MLD 2 (*Au. africanus* – or possibly *Au. prometheus*[42]) can be seen in Figure 6. In view of this similarity, and the dissimilarity of KNM-ER 806c with its current species holotype, KNM-ER 992, it would be interesting in future to look at comparisons of other molars of KNM-ER 806 to see with which species they group best.

Two of the atypical specimens identified from the shape-and-size PCA are currently classified into *Au. afarensis.* The first of these, LH 2, is from a juvenile mandible from Laetoli. In the PCA plots, LH 2 groups consistently towards *Au. africanus* in morphospace, being more robust in size and less square in relative dimensions in the occlusal view than the typical *Au. afarensis* molars, as shown in Figure 7. Morphologically, LH 2 shares lower first molar occlusal crown characteristics similar to those of Taung 1, the holotype of *Au. africanus.*

The second atypical specimen currently classified as belonging to the *Au. afarensis* species group is AL 288-1, or 'Lucy'. This molar clusters well away from the holotype of *Au. afarensis* (LH 4) in all of the PCAs, and this apparent misclassification is supported by the DFA and the log se_m analysis.

Donald Johanson, the team leader for the discovery of this specimen and whose PhD thesis was on primate molars, remarked that 'Lucy' was more chimpanzee-like[37,77] than the other specimens ultimately attributed to *Au. afarensis*, with an 'odd lower jaw', which he initially assigned to a different species than that assigned to the typically larger and squarer Hadar molars and those of the mandible from Laetoli, LH 4 (eventually designated as the holotype for *Au. afarensis*). Without wishing to suggest that the mandible of AL 288-1 is indeed from a chimpanzee, what is clear from the PCA plots of the occlusal crown morphometrics of the relatively tiny and narrow lower first molar of this specimen, is that the positions where this specimen consistently plots, away from the holotype group, would seem to add a point of initial agreement with Johanson that 'Lucy is different'[77]. Figure 8 shows occlusal views of the lower first molar of AL 288-1 between LH 4 *(Au. afarensis* holotype) on the one side, and of a chimpanzee and a modern human on the other side.

With these two outliers grouping in different directions in morphospace away from the holotype cluster, it might be interesting to revisit the question of how much variability is normal within any one species. Leonard and Hegmon[78] have suggested that, based on P3 morphology, vast differences between certain specimens can be explained if female individuals of the species were subject to different selective pressures than male individuals. This conclusion is rejected by Ferguson[32]. Perhaps, as Schmid argues[79], Lucy does not belong to the same species as the presumed 'males' of the species; or there may be more than one morphotype in this hypodigm.

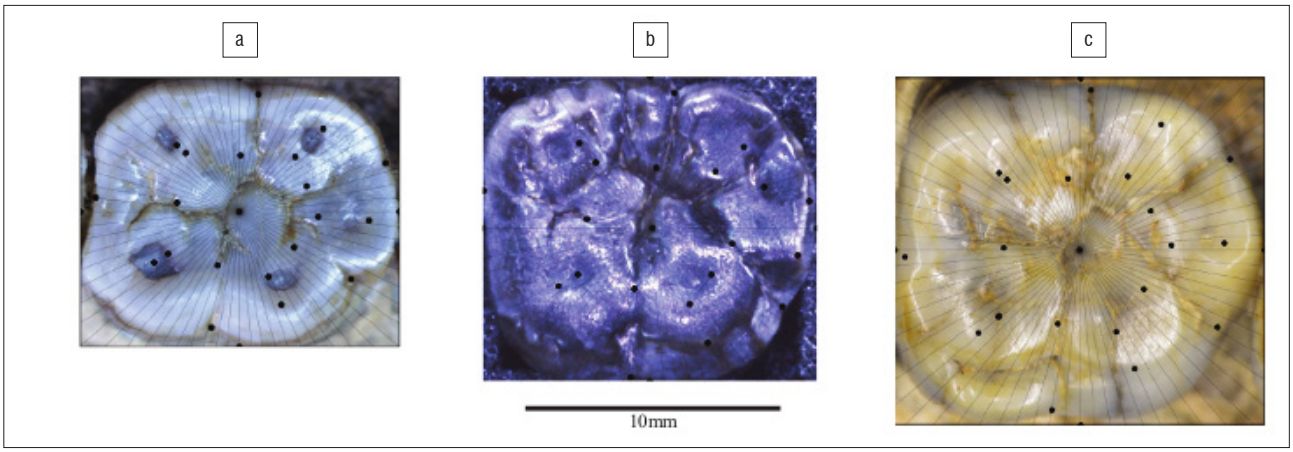

Figure 6: Comparison of lower first molar of KNM-ER 806c with other specimens. (a) KNM-ER 992, the *Homo erectus (ergaster)* holotype; (b) KNM-ER 806c (*Homo erectus*) and (c) MLD 2 (*Australopithecus africanus*). The occlusal views of KNM-ER 806c and MLD 2 show close affinities in morphology and in relative dimension.

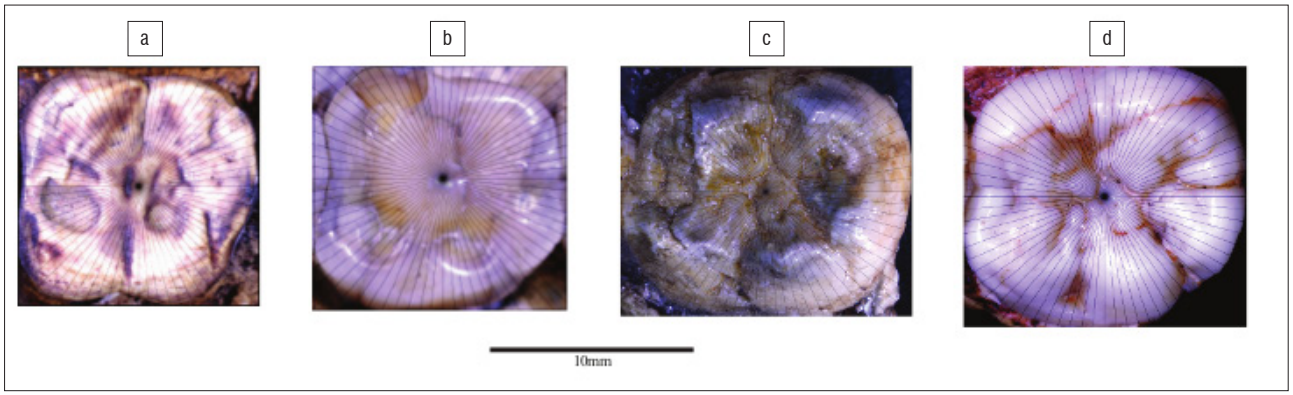

Figure 7: Comparison of lower first molar of LH 2 with other specimens. (a) AL 266-1 (*Australopithecus afarensis*), (b) *Au. afarensis* holotype LH 4, (c) LH 2 (*Au. afarensis*) and (d) Taung 1, the holotype of *Au. africanus*. In size and relative dimension, LH 2 has close affinities with *Au. africanus*, with a small metaconid and large entoconid, whereas the more 'typical' specimens of *Au. afarensis* are more 'square' in dimension (buccolingual diameters are almost equal to mesiodistal diameters), and have a very lingually oriented, large metaconid, coupled with a small entoconid.

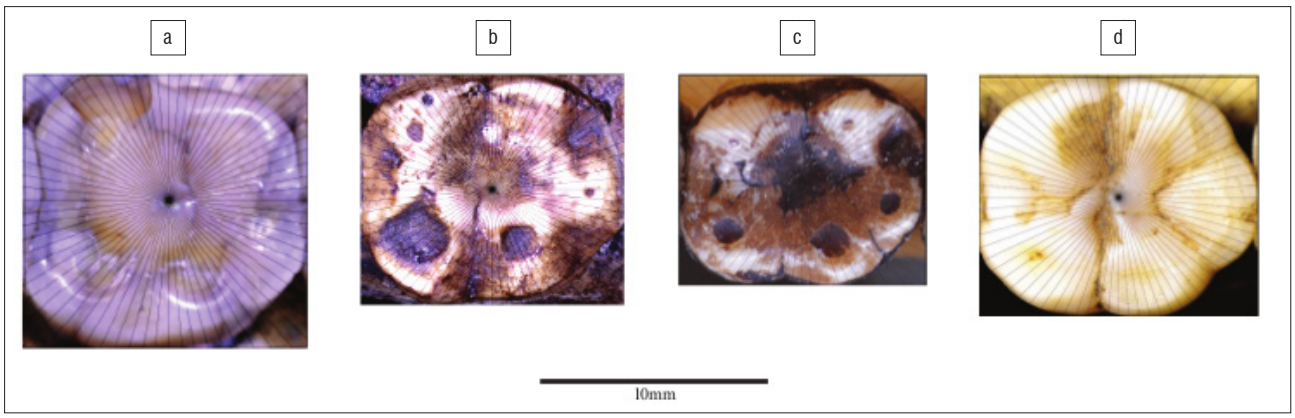

Figure 8: Comparison of lower first molar of AL 288-1 with other specimens. (a) Holotype of *Australopithecus afarensis*, LH 4, (b) AL 288-1 (*Au. afarensis*), (c) lower first molar of a modern chimpanzee and (d) lower first molar of a modern human. In size, relative dimension and in wear pattern, the lower first molar of AL 288-1 appears to resemble the chimpanzee lower first molar more closely than it does the holotype of the species to which it is allocated.

Conclusions

Gorilla gorilla gorilla is well established as a highly sexually dimorphic species, and in the analyses the lower first molars demonstrate well-defined size differences between male and female individuals. However, as with the other two African great ape species in the study, the degree of shape variability is reasonably limited, particularly with respect to the mesiodistal:buccolingual proportions of the teeth in general. When extinct hominin species' lower first molars are landmarked and plotted in a similar analysis, species such as *H. erectus* and other early *Homo* specimens seem to follow the spatial variability patterning of extant ape species such as *P. paniscus* and *P. troglodytes. Paranthropus* species' lower first molars group together in morphospace within a limited range in respect of shape, but show some size disparity that is reminiscent of the way *G. g. gorilla* specimens clustered laterally on the shape-versus-size PCA plot. At first glance, *Au. afarensis* also shows signs of gorilla-like shape similarity, clustering around the very square-shaped holotype, the main difference being size variability (therefore possibly showing some sexual dimorphism observable by size differences rather than excessive shape variance between specimens), but on closer analysis, two very significant anomalies are plotted well away from the main cluster. The only other extant species group that displays such stark within-species shape and size differences in the analysis as a whole is the modern *H. sapiens* group, but unlike the African ape species and the fossil hominin species, modern *H. sapiens* has migrated globally, with individual groups exploiting extremely diverse environments and practising subsistence lifestyles that diverged from each other at least 12 000 years ago. In areas where farming groups have been exposed to soft cereals and have utilised more varied food-processing and cooking technologies than hunter–gatherers since the Neolithic Revolution, facial and tooth-size reduction have been reported (for example in Europe, the Middle East, North Africa and Anatolia). As this kind of dietary and subsistence lifestyle divergence within a single species cannot be applied by proxy as the cause of the range of variability seen between the molars of *Au. afarensis,* it might be argued that some measure of caution should be exercised before using modern *H. sapiens* as an analogue species for comparisons of ranges of variability in molar size and shape in fossil hominin species. If a more cautious approach is taken, a species with an arguably similar-sized range and dietary options available to it should ideally be chosen upon which to assess a likely range of variability of molar shape and the effects thereon of sexual dimorphism within a species. Based on the manner in which the molars of gorillas (the most sexually dimorphic species in the study) plot in morphospace, it could therefore be argued that anomalies or outliers from main species groupings that do not follow a similar clustering pattern (size variability, with limited shape variability) might indicate that some fossil hominin species as currently defined either consist of two (or three) distinct morphotypes within the same species, or that specimens currently attributed to single species belong, in fact, to several different species, or simply that certain specimens may have been wrongly classified. Future studies should include sample sizes that are enlarged sufficiently to encompass the full range of variability of extant species included in the study before confirming such conclusions. The sample representing the fossil species should also be expanded so that each species is adequately represented.

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