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The use of Z-scores to facilitate morphometric comparisons between African Plio-Pleistocene hominin fossils: An example of method

South Africa and East Africa each have a rich palaeoanthropological heritage, but the taxonomy of fossil hominins from these regions is controversial. In this study, two morphometric methods related to the quantification of variability in morphology have been applied to pairwise comparisons of linear measurements of hominoid crania and mandibles. The log-transformed standard error of the m-coefficient ('log sem') is calculated from linear regressions. Like Procrustes Distances (PD), log sem statistics can serve to quantify variation in the shape of a cranium or mandible in the context of a constellation of landmarks. In this study, PD and log sem statistics are integrated and standardised using Z-scores, and applied probabilistically to Plio-Pleistocene hominins. As a test case, OH 7 and OH 24 as reference specimens of *Homo habilis* are compared to fossils representing other taxa. There is a wide spectrum of variation in Z-scores for specimens attributed to early *Homo* dated within the period between circa 1.8 Ma and 2 Ma. In terms of morphometric variation predating 1.8 Ma, Z-scores ($Z < 2$) for *Australopithecus afarensis*, *A. africanus* and *Homo habilis* display a small range of variability. This study serves as a demonstration of a method whereby log sem and PD can be used together to facilitate an objective assessment of morphological variability, applicable in palaeontological contexts.

Significance:

- Using a probabilistic approach, two morphometric methods are integrated to quantify morphological variability in Plio-Pleistocene African hominin mandibles and crania.
- Two Tanzanian specimens of *Homo habilis* (the OH 7 mandible of the holotype specimen, and the OH 24 skull) can be used as reference material for morphometric comparisons with other fossils (mandibles or crania) attributed to *Australopithecus africanus*, *A. afarensis*, *H. erectus* and *H. rudolfensis*.
- The results of these comparisons are expressed as standardised probabilistic Z-scores such that these statistics for skulls and mandibles can be expressed on a common scale.

Introduction

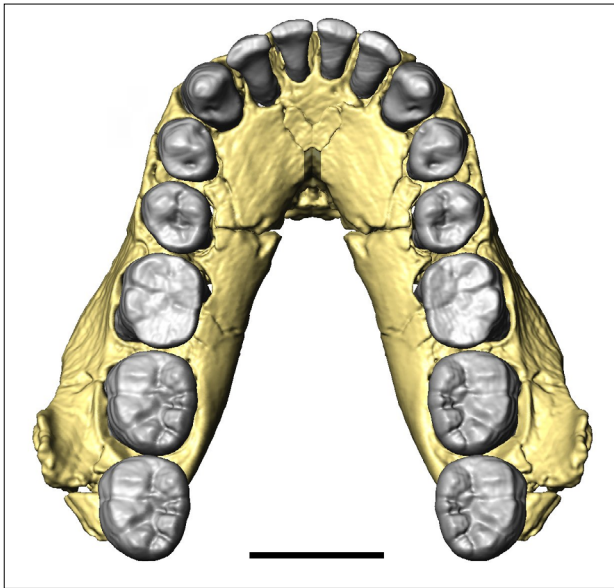
The taxonomy of fossil hominins appears increasingly more complex given recent discoveries and announcements of new species.¹ This is true for early hominins, with new *Australopithecus* species recently named, and also with respect to questions about the emergence of the genus *Homo* and of modern humans. Taxonomic attributions and affiliations are therefore one of the major issues in palaeoanthropology, including, for example, the debate between Tobias and Robinson regarding specimens attributed to *Australopithecus* or early *Homo*.²⁻⁵ By 1992, Tobias⁶ triumphantly declared that *Homo habilis* was 'widely accepted as a good taxon'. However, just a few years later, Wood and Collard⁷ suggested that *H. habilis* as well as *H. rudolfensis* should be placed within *Australopithecus*. The development of analytical and statistical tools is required to help clarify the complex picture such as this (as an example), notably for fossil specimens that cannot be sampled for DNA analyses.

In this study, our aim was to present a methodological approach combining two morphometric methods to quantitatively assess the degree of variability among individuals and provide a probabilistic reference that can be applied to the hominin fossil record for clarification of taxonomic attribution. This approach has the potential to add value for taxonomic debates. As a test case, it is applied to specimens attributed to *H. habilis* and other Plio-Pleistocene taxa. The primary objective of our current morphometric analyses was to demonstrate the novel approach without as yet attempting to resolve particular problems of taxonomy.

Materials

A hominin mandible catalogued as OH 7 (virtual reconstruction⁸ shown in Figure 1), attributed to *H. habilis* (the holotype), was discovered at Olduvai Gorge (Bed I) in Tanzania from deposits dated at 1.8 Million years ago (Ma).⁹ OH 24 is a contemporaneous skull of the same species from the same site.^{10,11} The two specimens can be used as reference material for morphometric comparisons with other fossils (mandibles or crania) attributed to *Australopithecus africanus*, *A. afarensis*, *H. erectus* and *H. rudolfensis*.

The materials used in this study (Table 1) relate primarily to fossils from three general time periods: firstly, specimens attributed to *A. afarensis*, circa 3 million years ago; secondly, specimens attributed to *A. africanus*, circa 2.5 Ma; and, thirdly, specimens attributed to early *Homo*, between circa 1.8 Ma and 2 Ma. *A. afarensis* mandibles from Ethiopia¹²⁻¹⁴ include AL 288-1 ('Lucy'), AL 200, AL 822 and AL 400-1. A mandible of *A. africanus* from Sterkfontein in South Africa is Sts 52b, while Sts 5 (the skull of 'Mrs Ples') from the same site also represents the latter species.¹⁵ Sts 71 (a partial skull) from Sterkfontein was originally attributed to *A. africanus* but has also been referred to as *A. prometheus*.¹⁶⁻¹⁸ AL 666-1 is a maxilla (*Homo* sp.) from Hadar in Ethiopia, circa 2.3 Ma.^{19,20} KNM-ER 1482 (mandible), KNM-ER 60000 (mandible) and KNM-ER 62000 (maxilla) are Kenyan specimens attributed to *H. rudolfensis* from the Turkana Basin, dated between 1.8 Ma and 2.0 Ma.²¹⁻²³ OH 65 (maxilla) is a specimen of early *Homo* from Olduvai, circa 1.8 Ma.²⁴ Early *Homo* specimens from Dmanisi in Georgia (including mandibles



Scale = 2 cm

Figure 1: Virtual reconstruction of the mandible of OH 7, holotype of *Homo habilis*. Reconstruction from Spoor et al.⁸ with permission.

D 211, D 2600 and D 2735), circa 1.8 Ma, have been attributed to *H. erectus* or *H. georgicus*.^{25,26} East African specimens considered to represent *H. habilis* include the KNM-ER 1813 skull and possibly the KNM-ER 1802 mandible as part of the hominin assemblage from the Turkana Basin^{23,27} as well as OH 13 (mandible and maxilla) as part of the hominin assemblage from Olduvai.^{11,28} OH 7 is a reference specimen in this study, but for purposes of the record (Table 1), we include OH 7 MAX which is a virtual representation of the maxilla, as reconstructed by Spoor et al.⁸ using a technique whereby mandibular morphology can facilitate the reconstruction of a maxilla, and vice versa.

Methods

In a morphometric approach based on pairwise comparisons, Thackeray and Odes²⁹ calculated 'log sem' statistics associated with regression analyses to compare OH 24 with other crania, based on measurements from original specimens published by Wood.²³ The log sem results reflect variability in skull shape. In the case of the comparison between OH 24 and Sts 5 (almost complete skulls), 54 measurements are in common. In the instance of OH 24 and Sts 71 (partial skull), 44 measurements are common to both specimens.

A log sem value was obtained from a comparison between our measurements of OH 7 and Sts 52b mandibles, using landmarks based mainly on points associated with mesiodistal and bucco-lingual diameters (excluding third lower molars because the specimens do not represent fully adult individuals). Forty measurements per specimen

Table 1: Specimen numbers, taxonomic nomenclature, approximate date, skeletal element (mandible or cranium) and Z-score

Specimen	Species	Age (Ma)	Skeletal element	Z-score
AL 288-1	<i>Australopithecus afarensis</i>	Ca. 3 Ma	Mandible	1.43
AL 400-1	<i>Australopithecus afarensis</i>	Ca. 3 Ma	Mandible	0.71
AL 822	<i>Australopithecus afarensis</i>	Ca. 3 Ma	Mandible	0.47
AL 200	<i>Australopithecus afarensis</i>	Ca. 3 Ma	Mandible	0.71
Sts 5	<i>Australopithecus africanus</i>	Ca. 2.5 Ma	Cranium	1.00
Sts 71	<i>Australopithecus africanus</i> or <i>A. prometheus</i>	Ca. 2.5 Ma	Cranium	0.10
Sts 52b	<i>Australopithecus africanus</i>	Ca. 2.5 Ma	Mandible	1.60
AL 666-1	<i>Homo</i> sp.	2.3 Ma	Maxilla	3.86
OH 7	<i>Homo habilis</i>	1.8 Ma	Mandible	-
OH 7 MAX	<i>Homo habilis</i>	1.8 Ma	Maxilla (virtual)	-0.90
OH 24	<i>Homo habilis</i>	1.8 Ma	Cranium	-
OH 13	<i>Homo habilis</i>	1.8 Ma	Mandible	0.33
KNM ER 1813	<i>Homo habilis</i>	1.9 Ma	Cranium	1.95
KNM ER 1802	<i>Homo rudolfensis</i> or <i>H. habilis</i>	1.9 Ma	Mandible	-0.90
KNM ER 60000	<i>Homo rudolfensis</i>	1.9 Ma	Mandible	2.90
KNM ER 1482	<i>Homo rudolfensis</i>	2.0 Ma	Mandible	4.33
KNM ER 62000	<i>Homo rudolfensis</i>	2.0 Ma	Partial face	5.29
OH 65	<i>Homo rudolfensis?</i>	1.8 Ma	Maxilla	4.81
D 211	<i>Homo erectus</i>	1.8 Ma	Mandible	1.95
D 2600	<i>Homo erectus</i>	1.8 Ma	Mandible	2.90
D 2735	<i>Homo erectus</i>	1.8 Ma	Mandible	2.43

were taken from virtual reconstructions of OH 7 and Sts 52b by Spoor et al.⁸ and Benazzi et al.³⁰ respectively. Sts 52b was selected for comparison in this study because of an apparent degree of morphological similarity with OH 7, as discussed by Tattersall.³¹

Using Procrustes Distances (PD), Spoor et al.⁸ compared Plio-Pleistocene hominin specimens with a focus on OH 7, based on more than 50 landmarks. For purposes of our study, we used PD data made available through Spoor and Gunz (personal communication to JFT, 2020). Here we integrate the two kinds of shape-related statistics (PD and log sem) by expressing them as standardised Z-scores in relation to data obtained from humans and extant great apes.

The AL 400-1 mandible of *A. afarensis* has been compared with OH 7 on the basis of the PD method. AL 400-1 has also been compared with OH 7 using the log sem statistic. The difference between Z-scores is expected to be relatively small if the approaches yield consistent results.

Log sem statistics for crania

The log sem statistic has been previously used in analyses of linear measurements obtained from crania of modern specimens in natural history museums³²⁻³⁴ and Plio-Pleistocene hominins.^{29,32,34} In this method, measurements are subjected to pairwise comparisons, using least squares linear regression to generate an equation of the form $y = mx + c$, where m is the slope and c is the intercept. In an initial study of pairs of specimens of the same (extant) species in 1997, Thackeray et al.³² reported central tendency of the log-transformed standard error of the m -coefficient, known as 'log sem' which is a measure of the degree of scatter around the regression line, reflecting variability in shape. Central tendency of log sem was also discovered using larger samples, associated with a mean log sem value of -1.61 reported in 2007 by Thackeray.³³ At least for hominoids, the mean log sem value of -1.61 ± 0.1 was recognised in 2016 as a typical degree of intraspecific morphological variation in extant species.³⁴

In response to views expressed by Gordon and Wood,³⁵ Thackeray and Dykes³⁴ emphasised the need to make pairwise comparisons with specimen A on the x -axis and specimen B on the y -axis, and vice versa. Two log sem values are obtained. The absolute difference between these values is termed 'delta log sem'. The mean delta log sem is small (generally ≤ 0.03) when pairs of specimens of the same species are compared. By contrast, delta log sem values are large (generally $\gg 0.03$) when specimens of different species are compared.³⁴ Thackeray and Dykes³⁴ stated that the number of measurable dimensions (k) obtained from pairs of specimens should be maximised as far as possible to ensure robusticity of the log sem statistic. When this is done, with the number of measurements for pairwise comparisons being

greater than 20, there is a tendency for the mean log sem to stabilise around a value of circa -1.6.^{34,35}

In their analyses of cranial measurements of *Pan troglodytes*, *P. paniscus*, *Gorilla gorilla* and *H. sapiens* (using more than 20 measurable dimensions as published by Gordon and Wood³⁵), Thackeray and Dykes³⁴ obtained the following results from pairwise comparisons:

1. Mean log sem = -1.612 ± 0.129 ($n=8072$ pairwise regressions) reflects what is considered to be a typical degree of *intraspecific variation* within hominoids.
2. Mean log sem = -1.063 ± 0.126 ($n=26\ 780$ regressions), reflecting the degree of variability from *interspecific comparisons*.

These results, based on a very large number of regressions, clearly show that there is indeed a significant difference between the log sem values calculated for intraspecific and interspecific comparisons, which is related to similarity (or dissimilarity) in shape.

A criticism that has been levelled against the log sem approach relates to which variables are being measured. Remarkable as it may seem, the degree of intraspecific variability reflected by a mean log sem value of *circa* -1.61 ± 0.1 has been obtained, not only from cranial variables, but also from measurements from teeth.³⁴

Procrustes Distances for mandibles

Bookstein³⁶ and Duta³⁷ have described the method whereby PD are calculated, reflecting differences in shape between objects (in this case, mandibles). PD statistics serve to quantify the difference between landmarks by using the square root of the sum of squared differences in positions of those landmarks.

Spoor et al.⁸ calculated PD values from pairwise comparisons of OH 7 and other hominins, using landmarks indicated in their Fig. 2f and 2g. PD were also calculated for purposes of comparisons with *H. sapiens*, *P. troglodytes* and *G. gorilla*. The mean PD for the extant hominoids, based on data obtained by Spoor and Gunz (personal communication to JFT, 2020), provides a 'within group' (conspecific) frame of reference.

Z-scores

The mean and standard deviation for PD for pairwise comparisons of extant hominoids (0.089 ± 0.021) are analogous to the mean and standard deviation for log sem values for extant hominoids (-1.61 ± 0.1). These two means can both be related to probabilistic Z-scores, where the Z value of 0 corresponds to the mean value of 0.089 (PD) and also to the mean log sem value of -1.61. One standard deviation above or below the mean is circa 1 and -1, respectively. Likewise, two standard deviations above or below a mean Z-value of 0 correspond to Z-score values of

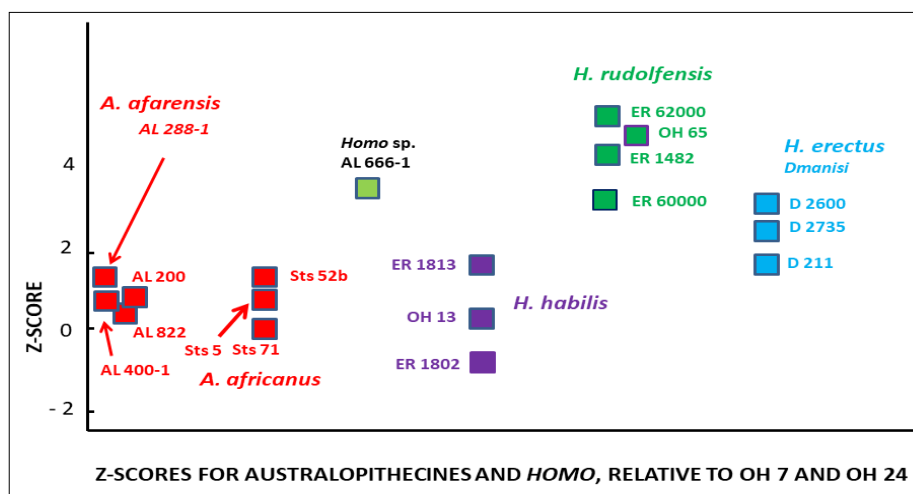


Figure 2: Visualisation of Z-scores for hominins based on data in Table 1. OH 7 and OH 24 are the reference specimens for pairwise comparisons with other hominins.

circa 2 and -2, respectively. In this way, log sem statistics (including those calculated for a comparison between OH 24 and skulls of other hominins) and PD values (including those calculated for comparisons between OH 7 and other hominin mandibles) can be expressed on a common (Z) scale.

Results

Results from this study are presented in Table 1. Figure 2 is a visualisation of the results without a time scale.

The AL 400-1 mandible of *A. afarensis* has a Z-value of 0.71 when it is compared with OH 7 using the PD statistical method. A Z-value of 1.0 is obtained when AL 400-1 is compared to OH 7 using the log sem statistical method. The difference of only 0.29 is relatively small, reflecting consistency.

As indicated in Table 1 and Figure 2, the Z-score for the Sts 52b jaw (compared to the OH 7 mandible) is similar to that which has been obtained for the Sts 5 skull (compared to the OH 24 cranium), and similar also to the Z-score for the Sts 71 skull (also compared to OH 24).

In Figure 2 there is a clear separation between specimens attributed to *H. habilis* (including KNM-ER 1813 and OH 13) and others attributed to *H. rudolfensis* (e.g. KNM-ER 62K and KNM-ER 1482). In terms of Z-scores, specimens from Dmanisi attributed to *H. erectus* are intermediate between *H. habilis* and *H. rudolfensis*.

Discussion and conclusions

We integrated two statistics (PD and log sem) by expressing them as standardised Z-scores. As the important type specimen of *H. habilis*, the OH 7 mandible has been used as a frame of reference for quantifying PD between it and other hominin mandibles. The contemporary OH 24 skull has been used for purposes of calculating log sem statistics in the context of pairwise comparisons between it and other hominin skulls (notably Sts 5 and Sts 71) from South Africa. With OH 7 and OH 24 representing the same species, measurements of mandibles and skulls have been used to obtain PD and log sem statistics, respectively, expressed on a common Z-score scale relative to values for conspecific extant hominoids.

There is a wide spectrum of variation in Z-scores for Tanzanian and Kenyan specimens attributed to early *Homo* dated within the period between circa 1.8 Ma and 2 Ma. By contrast, in terms of variation through time predating 1.8 Ma, Z-scores for *A. afarensis*, *A. africanus* and *H. habilis* display a relatively small range of variability. Put another way, the Sterkfontein specimens are a similar morphological distance to the Olduvai hominins using Z-score measurements. The Z-scores of the specimens from Hadar fall within the range of those determined for specimens from Sterkfontein (0.10–1.60).

We do not intend to say that all specimens attributed to *A. afarensis*, *A. africanus*, and *H. habilis* are necessarily conspecific. The Z-scores serve to quantify the degree of morphological distance between specimens in relation to OH 7 (mandibles) and OH 24 (cranium). We note, however, the suggestion raised by Wood and Collard⁷ that specimens attributed to *H. habilis* could be referred to *A. habilis*. If this were to be the case, a Z-score of approximately 2 would at least potentially constitute a 'fuzzy boundary' between specimens attributed to *Australopithecus* and *Homo*. In addition, we note Thackeray's³⁸ suggestion that the transition between *A. africanus* and *H. habilis* (*A. habilis*) might constitute a chronospecies,

We recognise that our study is based on data derived from only a few specimens within the hypodigms of certain taxa (especially with respect to the two *Australopithecus* species). In addition, we are including only data from the cranium and mandible, and, more narrowly, the mandibular data only reflect the shape of the dental arcade in the context of a constellation of landmarks. However, we have demonstrated a method whereby Z-scores allow us to integrate data from mandibles such as OH 7, Sts 52b and AL 288-1 ('Lucy') and skulls such as OH 24, Sts 71 and Sts 5 ('Mrs Ples'), in a probabilistic context.

Ideally, probabilistic approaches (as in the use of Z-scores) can be used to support one potential taxonomic attribution over another, as examples of sigma taxonomy,³⁹ defined as 'the classification of taxa in terms of probabilities of conspecificity, without assuming distinct boundaries between species', whereas alpha taxonomy generally does assume clear limits.^{39,40} The probabilistic method of the kind presented in this study can supplement alpha taxonomy by providing an objective assessment of morphological variability, applicable in palaeontological contexts. One of the limitations relates to the fact that fossils are often fragmentary such that the number of measurable dimensions (k) is relatively small. Ideally log sem and PD values should be calculated from complete and undistorted specimens. Despite these limitations, we recommend that our approach using Z-scores should be explored further in the context of additional cases, to include assessment of the transition between *Australopithecus* and *Homo*.

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Competing interests

We have no competing interests to declare.

Authors' contributions

J.F.T.: Conceptualisation, methodology, writing and data analysis. O.K.: Writing and revision.

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