

Morphometric analysis of modern human crania: a framework for assessing early Pleistocene hominids

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Craniofacial measurements have been obtained from modern human skulls from cadavers representing several southern African population groups including Ndebele, Shangaan, Sotho, Swazi, Tswana, Xhosa and Zulu, in addition to European *Homo sapiens*. The measurements were obtained from crania in the Dart Collection housed at the School of Anatomical Sciences of the University of the Witwatersrand. Pairwise comparisons, using least squares linear regression analysis of cranial measurements, were used to calculate the standard error of the m -coefficient associated with the general equation $y = mx + c$, where m is the slope of the regression line. The standard error of the m -coefficient is a measure of the degree of similarity between specimens. Log transformed s.e. _{m} values (log s.e. _{m}) show a normal distribution with a mean value of -1.84 ± 0.087 ($n = 384$ pairwise comparisons). These results can be used as a frame of reference for comparing Early Pleistocene specimens. For example, a comparison between KNM-ER 1813 (attributed to *H. habilis*) and KNM-ER 3733 (attributed to *H. erectus* or *H. ergaster*) is associated with a log s.e. _{m} value of -1.844 . Despite differences in size, these two penecontemporary hominid fossils are associated with a high probability of conspecificity, since the log s.e. _{m} value is identical to the mean log s.e. _{m} value of -1.84 obtained for pairwise comparisons of modern *Homo sapiens*.

Keywords: *Homo sapiens*, *Homo ergaster*, *Homo habilis*, morphology, craniofacial.

INTRODUCTION

Thackeray (2005) has previously examined cranial variation in modern hominoid primates, excluding modern humans, in the context of variation in skulls of extinct African hominins. In this study we obtain cranial data from a sample of modern humans, using more than 100 landmarks, to provide a frame of reference for assessing Plio-Pleistocene hominins.

MATERIALS AND METHODS

The modern comparative human sample in the Dart Collection at the University of the Witwatersrand, from cadavers, includes 24 African crania: Ndebele (two male, two female), Shangaan (two male, two female), Sotho (two male, two female), Swazi (two male, two female), Tswana (one male, one female), Xhosa (two female, two male), Zulu (one male), and one African human cranium; and five crania catalogued as Europeans (Caucasian). The choice of sample size was arbitrary, with the objective of securing a total sample of at least 25 individuals, recognizing that this represents only part of the range of variation that would be expected from a global sample of *H. sapiens*.

The measurements on the modern crania (Table 1) were based on landmarks previously used in Wood's (1991) study of fossil hominins. The landmarks include Prosthion (pr); Nasospinale (ns); Nasion (n); Glabella (g); Bregma (b); Vertex (v); Apex (ap); Lambda (l); Opistocranium (op); Inion (i) Opisthion (o); Basion (ba); Alveolon (alv); Staphylion (sta); Orale (ol); Euryon (eu); Porion (po); Mastoidale (ms); Alare (al); Orbitale (or); Zygion (zy); Ectoconchion (ec); Ectomalare (ecm); Pterion (pt); Endomalare (enm); Frontotemporale (ft).

Measurements were obtained using (1) digital callipers manufactured by the Mitutoyo Corporation (product

name Digimatic Caliper; model no: CD-6 inch CX; code no: 500-171-20; serial no: 09093312; measuring range 0–150 mm; minimum indication 0.01 mm); (2) a two-button digital calliper manufactured by Mitutoyo Corporation, with the same technical specifications (resolution: 0.01 mm); and (3) a Mitutoyo digital linear spreading calliper with a 300 mm digital scale and a throat depth of 150 mm. The modern crania were positioned on a foam base for stability and protection. Measurements were taken using the same calipers throughout the study to minimize measurement error. Curved regions were measured using chord distance.

Statistical method

The method that is used in this study has been developed by Thackeray *et al.* (1997, 2007). Morphological variation within a species can be quantified using least squares linear regression analysis of measurements of pairs of specimens. The degree of similarity between two specimens of the same species can be expressed by comparing measurements of a reference specimen A (associated with the x -axis) and conspecific specimen B (associated with the y -axis). In such cases there is generally little scatter around the regression line, associated with the linear regression equation $y = mx + c$, where m represents the slope of the regression line, and c represents the constant; the log transformed standard error of the slope m is referred to as log s.e. _{m} . The limited scatter around the regression line is associated with similarity in shape of the two conspecific specimens.

The degree of scatter around the regression line is quantified by the standard error of the m -coefficient (s.e. _{m}).

The s.e. _{m} value for pairs of conspecific pairs is relatively low. By contrast, when measurements of two specimens representing two different species are compared, there is

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Table 1. List of craniofacial measurements.

Number	Measurement	Number	Measurement
1	Glabella–opisthocranium	52	Bizygomatic breadth
2	Posthion–inion	53	Bimaxillary breadth
3	Posterior cranial length	54	Outer alveolar breadth
4	Basion–bregma	55	Anterior interorbital breadth
5	Basion–nasion	56	Orbital breadth
6	Porion height	57	Orbital height
7	Mastoid length	58	Orbitale–zygomaxillare
8	Minimum frontal breadth	59	Minimum malar height
9	Maximum parietal breadth	60	Malar thickness
10	Maximum temporal breadth	61	Width temporal gutter
11	Biporionic breadth	62	Vertical thickness of supraorbital torus
12	Supramastoid breadth	63	Anteroposterior thickness of supraorbital torus
13	Maximum breadth across mastoid process	64	Anteroposterior thickness of supraorbital torus
14	Biaterionic breadth	65	Anteroposterior thickness of glabella
15	Interentoglenoid breadth	66	Frontal torus breadth
16	Entoglenoid breadth	67	Frontal torus breadth
17	Glabella–bregma	68	Maximum nasal width
18	Glabella–bregma	69	Nasal height
19	Postglabellar sulcus–bregma	70	Rhinion–nasospinale
20	Postglabellar sulcus–bregma	71	Sagittal length of nasal bones
21	Bregma–left pterion	72	Superior breadth of nasal bones
22	Bregma–left pterion	74	Inferior breadth of nasal bones
23	Bregma–right pterion	75	Infratemporal fossa depth
24	Bregma–right pterion	76	Foramen magnum length
25	Parietal sagittal length	77	Foramen magnum maximum width
26	Parietal sagittal length	78	Occipital condyle maximum length
27	Parietal temporal length	79	Occipital condyle maximum width
28	Parietal temporal length	80	Mandibular fossa length
29	Parietal coronal breadth	81	Mandibular fossa length
30	Parietal coronal breadth	82	Mandibular fossa breadth
31	Parietal lambdoid length	83	Mandibular fossa breadth
32	Parietal lambdoid length	84	Mandibular fossa depth
33	Bregma–asterion	85	Depth of postglenoid process
34	Bregma–asterion	86	Depth of articular eminence
35	Lambda–inion	87	Maxillo–alveolar length
36	Lambda–inion	88	Maxillo–alveolar breadth
37	Inion–opisthion	89	Palate length (orale–staphylion)
38	Inion–opisthion	90	Palate length (orale–palatomaxillary suture)
39	Occipital sagittal length	91	Palate breadth
40	Occipital sagittal length	92	Incisive canal–palatomaxillary suture
41	Biasterionic breadth	93	Internal alveolar breadth at M3
42	Biasterionic breadth	94	I ¹ –I ² alveolar length
43	Superior facial height	95	Canine alveolus breadth
44	Superior facial length	96	P ³ –P ⁴ alveolar length
45	Alveolar height	97	M ¹ –M ³ alveolar length
46	Subnasale–prosthion	98	Inter canine distance
47	Subnasale–prosthion (horizontal projection)	99	P ³ interalveolar distance
48	Subnasale–prosthion (vertical projection)	100	P ⁴ interalveolar distance
49	Superior facial breadth	101	M ² interalveolar distance
50	Biorbital breadth	102	M ³ interalveolar distance
51	Bijugal breadth	103	Palatal height

a greater degree of scatter around the regression line and the $s.e._m$ value is relatively high (Thackeray et al. 1997; Aiello *et.al.*, 2000). The distribution of $s.e._m$ values obtained from pairwise comparisons of extant conspecific pairs of specimens has been examined. Thackeray *et.al.* (1997) showed there is a log normal distribution of $s.e._m$ values when pairwise comparisons are made between conspecific specimens of extant vertebrates including mammals, birds, reptiles and extant invertebrates. In a larger study (Thackeray, 2007), log $s.e._m$ values are inclined to be centrally distributed around a mean log $s.e._m$ value of -1.61 ± 0.23 (including vertebrates and invertebrates where $n = 1424$ specimens), not significantly different from a mean log $s.e._m$ value of -1.66 ± 0.20 for invertebrates ($n = 172$ specimens).

Thackeray (2007) proposed that when comparisons are made between any two specimens of the same species,

the log $s.e._m$ approximates a ‘biological species constant’ ($T = -1.61$) which is considered to prevail over evolutionary time and geographical space. The advantage of this approach is that the mean log $s.e._m$ value of -1.61 ± 0.23 facilitates a definition of a species based on morphometric analysis. It allows for the assessment of probabilities of conspecificity associated with fossil specimens including hominins from South and East Africa, taking into account the fact that there is morphological variation in time and space, and recognizing that there is no clear boundary between hominin species in space and time, and no clear boundary between *Australopithecus* and *Homo*. The method has been used in this study to assess the degree of similarity between a sample of modern specimens of *Homo sapiens*, representing only part of the range of variation that would be expected in a global sample. As an example of the application of this approach, comparisons

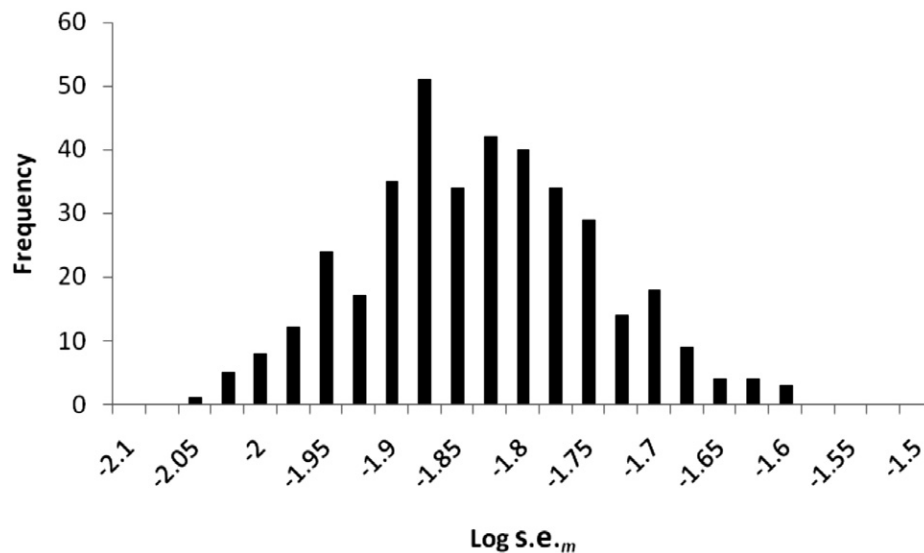


Figure 1. Normal distribution of log s.e._m values obtained from pair-wise comparisons of *Homo sapiens* crania in the Dart Collection. The mean log-transformed s.e._m value based on comparisons of conspecific pairs of *Homo sapiens* is -1.84 ± 0.09 ($n = 384$ comparisons).

are between two penecontemporary Early Pleistocene hominin specimens, KNM-ER 1813 (attributed to *H. habilis*) and KNM-3733 (attributed to *H. ergaster* or *H. erectus*), dated around 1.6 million years, from Koobi Fora (East Turkana) in Kenya (Wood, 1991).

RESULTS

Results obtained from pair-wise comparisons of crania of modern humans (Table 2) are presented in Fig. 1.

Table 2. Human specimens from the Dart Collection, School of Anatomical Sciences, University of the Witwatersrand. This list includes catalogue numbers, population affinities, age and sex.

Catalogue number	Population affinity	Age	Sex
4011	Tswana	54	m
4069	Tswana	20	f
3955	Zulu	56	m
1532	Ndebele	69	f
1549	Ndebele	28	f
1274	Ndebele	39	m
1535	Ndebele	35	m
172	Shangaan	60	m
58	Shangaan	38	m
263	Shangaan	30	f
3057	Shangaan	30	f
2492	Sotho	21	f
2307	Sotho	60	f
2248	Sotho	48	m
2077	Sotho	48	m
1360	Swazi	19	f
1534	Swazi	24	f
2014	Swazi	42	m
1362	Swazi	49	m
1333	Xhosa	48	m
400	Xhosa	36	m
22	Xhosa	30	f
761	Xhosa	37	f
4035	African	22	f
2179	Caucasian	19	f
3902	Caucasian	40	m
3129	Caucasian	29	f
2186	Caucasian	57	m
3545	Caucasian	40	m

COMPARISON BETWEEN FOSSIL CRANIA

A log s.e._m value of -1.84 has been obtained from a comparison of two early Pleistocene hominid crania, KNM-ER 1813 (attributed to *H. habilis*) and KNM-ER 3733 (attributed to *H. ergaster* or *H. erectus*).

DISCUSSION AND CONCLUSION

The results of this study show that the log s.e._m values obtained from 384 pairwise comparisons of human crania display a normal distribution, similar to results obtained from previous studies of both vertebrates and invertebrates (Thackeray *et al.* 1997; Thackeray 2007). The mean log s.e._m value of -1.84 ± 0.09 obtained from the human crania provides a frame of reference for assessing Early Pleistocene hominids.

Thackeray *et al.* (1997) compared conspecific specimens of extant vertebrates including mammals such as primates, rodents and ungulates; birds; reptiles; and invertebrates (Coleoptera and Lepidoptera). In a preliminary study the mean log-transformed s.e._m value calculated by Thackeray *et al.* (1997) from comparisons of measurements of conspecific pairs of vertebrates and invertebrates was -1.78 ± 0.27 for 1260 specimens (70 extant species). Extending this approach Thackeray (2007) provided a statistical definition of a species, taking advantage of a substantially larger sample of vertebrates. Using that enlarged sample Thackeray (2007) calculated a mean log s.e._m of -1.61 ± 0.23 ($n = 1424$ specimens), which is not significantly different from the mean value obtained from the initial study.

The result of -1.84 obtained from *Homo sapiens* crania in this study is lower than the mean log s.e._m value of -1.78 (Thackeray *et al.* 1997) and -1.61 (Thackeray, 2007) obtained for large samples of a diversity of vertebrates and invertebrates.

Despite differences in size, KNM-ER 1813 and KNM-ER 3733 are examples of early Pleistocene hominid fossils which are associated with a high degree of similarity. The log s.e._m value of -1.84 obtained from the comparison of these two specimens is identical to the mean log s.e._m.

value of -1.84 obtained for pairwise comparisons of modern *Homo sapiens*. The implication is that there is a high probability that KNM-ER 1813 and KNM-ER 3733 are conspecifics, despite the fact that they have previously been attributed to different species of *Homo* (*H. habilis* and *H. erectus/ergaster*). This serves as one example demonstrating the applicability of a morphometric approach to assess probabilities of conspecificity in fossil hominids.

Thackeray (2005) has previously suggested that KNM-ER 1813 is a small female of a species also represented by KNM-ER-3733, considered to be a large male. Both are dated to about 1.6 million years before present (BP).

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