

## Probabilities of conspecificity: application of a morphometric technique to modern taxa and fossil specimens attributed to *Australopithecus* and *Homo*

A morphometric method of analysis is applied to specimens attributed to the same species, using museum collections of mammals, birds, reptiles and insects. We demonstrate a central tendency of the log-transformed standard error of the  $m$ -coefficient ( $\log_{10} s.e._m$ ), derived from linear regression analyses associated with equations of the form  $y = mx + c$ , when measurements of one specimen are compared against corresponding measurements of another specimen attributed to the same species. As indicated previously, this approach has potential application in palaeontological contexts where there is uncertainty about any two specimens being conspecific. We recommend that  $s.e._m$  statistics be used in exploratory studies to quantify probabilities of conspecificity when any two hominid specimens are compared.

In a morphometric study of males and females of 25 extant mammalian species, based on comparison of measurements of variables from a female of any one taxon against corresponding data for the same variables in a male of the same species,<sup>1</sup> it was noted from linear regression analyses that standard errors of the  $m$ -coefficient ( $s.e._m$ ) associated with equations of the form  $y = mx + c$  displayed a strong central tendency, not correlated with body size. More recently, we have extended this approach to allow comparison of sets of measurements obtained from larger samples, including conspecific vertebrates (Aves, Reptilia and Mammalia) and invertebrates (Arthropoda). Our objective is to confirm whether a pattern of central tendency is discernible from morphometric studies of conspecific birds, reptiles, insects as well as mammals, and if so, to show how this method may be cautiously applied to the study of extinct hominid fossils.

In this study, skeletal or external body measurements are explored by means of least-squares linear regression analysis, based on data from 1260 specimens, including mammals, reptiles, birds and insects, altogether representing 70 taxa. As

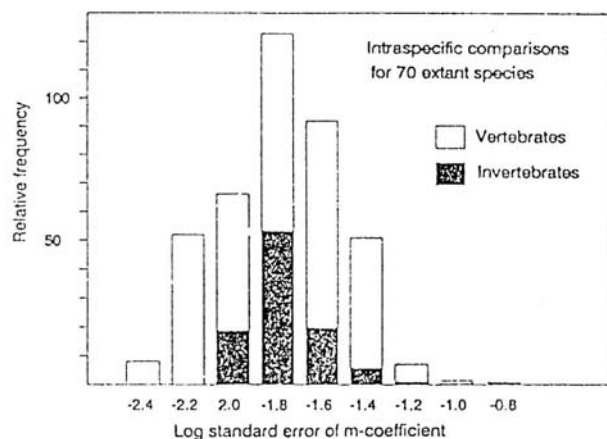


Fig. 1. Histogram of values of log-transformed  $s.e._m$ , the standard error of the  $m$ -coefficient associated with equations of the form  $y = mx + c$ , calculated from regression analyses, where measurements for 10 variables in a male of one species were compared against corresponding data for a female of the same extant species (1260 specimens, 70 taxa including mammals, reptiles, birds and insects). Differences in sample size are controlled by expressing  $\log_{10} s.e._m$  values as percentages of the total for each group (mammals, reptiles, birds, and insects).

Table 1. Measurement definitions for 10 variables measured in modern mammals, for purposes of intraspecific comparisons and the calculation of  $s.e._m$  values.<sup>1</sup>

1. Maximum cranial length: greatest length of the skull from the anterior edge of the nasal aperture to the most posterior point on the occipital.
2. Maximum cranial width: greatest width of the braincase at the dorsal root of the squamosals.
3. Interorbital breadth: least breadth between the orbits.
4. Zygomatic arch length: greatest arch length.
5. Greatest cranial height: greatest height of skull perpendicular to the horizontal plane and through the bullae.
6. Mandibular height: height of the mandible taken from the alveolus between last two molars.
7. Foramen magnum height: widest part of the foramen magnum in the vertical plane.
8. Length of mandible: from the posterior surface of the condylar process to the anteroventral edge of incisor alveolus.
9. Tooth row length: maximum length of the maxilla, from the anterior edge of incisor alveolus (where present; alternatively, from the most anterior extent of mid-sagittal maxillary bone, as in ruminants without incisors), to the posterior surface of M3 (or last molar) alveolus.
10. Greatest length of the mandible in a straight line from the anterior edge of  $I_1$  to the posterior surface of the angular process.

before, comparisons are made between linear measurements obtained from pairs of adult specimens known to belong to the same (extant) species.<sup>1</sup> Attention is focused on standard errors of the slope  $m$  associated with general equations of the form  $y = mx + c$ , determined from linear regression analyses. In all instances, measurements of 10 variables in a male of one species are compared against corresponding data for the same variables measured from a female of the same extant species.

Variables chosen for conspecific comparison of mammals in this analysis include those listed in Table 1. The selection of variables for conspecific comparisons of other taxa (birds, reptiles and insects) has been based on identification of those variables that are readily measurable and which are considered to reflect general variability in size and shape.

By way of example, the technique has been applied to early Pleistocene hominid fossils from the Sterkfontein valley in South Africa, using measurable variables as defined by Martin.<sup>2</sup>

### Results

Results obtained from this study of modern taxa are plotted as a histogram of log-transformed  $s.e._m$  values in Fig. 1. A log-normal distribution is evident. The mean  $\log_{10} s.e._m$  value is  $-1.78$  with a standard deviation of  $0.27$ , based on conspecific comparisons for vertebrates and invertebrates (1260 specimens, 70 extant species).

We have applied this approach to an analysis of cranial measurements of two penecontemporaneous hominid fossils, SK 48 and SK 847, both from Member 1 at Swartkrans in the Sterkfontein valley and considered to be about 1.7 million years old.<sup>3,4</sup> SK 48 has been described as *Australopithecus robustus*; SK 847 has been generally attributed to early *Homo*,<sup>3-6</sup> although part of this fragmentary specimen was formerly attributed to *A. robustus*.<sup>5</sup> Sixteen cranial measurements obtainable from both of these specimens, using Martin's<sup>2,6</sup> variable numbers 41, 43, 43.1, 45, 46, 48, 48.1, 48.3, 49a, 50, 51a, 52, 55, 55a, 56, 56.1, 57, 57.1 and 57.3, are plotted in relation to each other in Fig. 2. The standard error of the  $m$ -coefficient determined from regression analysis is  $0.048$ .

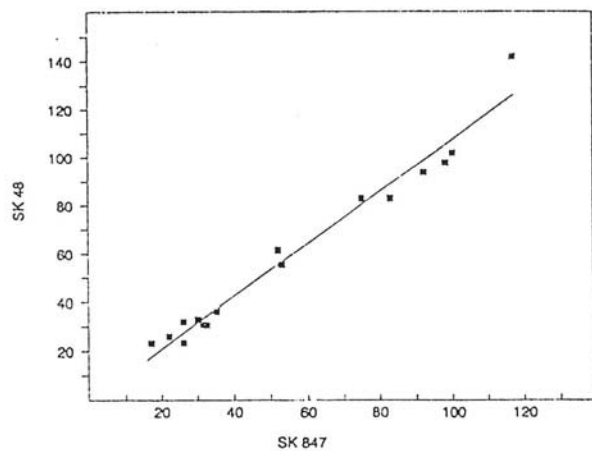


Fig. 2. Relationships between cranial dimensions of SK 48 and SK 847 from Swartkrans, both from Member 1 at Swartkrans in the Sterkfontein valley, considered to be c. 1.7 million years old. Regression equation:  $y = 1.08x - 0.025$  ( $s.e._m = 0.048$ ). Limited scatter around the regression line reflects general similarities in shape; greater scatter would reflect greater differences in morphology, which would be expected between any two specimens that belong to different species. The possibility that SK 847 represents a small, female individual of the species to which SK 48 belongs has been considered in previous studies.<sup>1,7-11</sup>

#### Discussion and conclusion

High  $s.e._m$  values relate to high morphological variability when measurements of any two specimens are compared, reflected also by a high degree of scatter of measurements around a regression line. Relatively low  $s.e._m$  values can be expected in situations where there is only a small degree of morphological difference, associated with limited scatter around a regression line, reflecting similarities in shape of two specimens being compared.

Differences in slope ( $m$  coefficient in  $y = mx + c$ ) relate to differences between males and females, and relatively high  $s.e._m$  values are associated with instances of pronounced sexual dimorphism, but log-normal distributions of  $s.e._m$  with similar central tendencies are indicated from conspecific comparisons in the case of both invertebrates and vertebrates (Fig. 1). We consider this to be significant for purposes of using modern taxa as a general frame of reference for assessing probabilities of conspecificity when any two specimens are compared.

Recognition of boundaries between species is problematic, particularly in palaeontological contexts. On the basis of comparisons between pairs of modern specimens known to be conspecific, however, we suggest that log-transformed  $s.e._m$  values can be cautiously used to facilitate the quantification of probabilities of conspecificity when anatomical measurements of any two specimens are compared.

In this study, where we have dealt with modern specimens known to belong to the same taxon, 95% of all comparisons have log  $s.e._m$  values falling between  $-2.32$  and  $-1.24$ , within 2 standard deviations on either side of the mean value of  $-1.78$ . Where measurements of any two fossil specimens are compared, we expect a high probability of conspecificity if the log-transformed  $s.e._m$  value determined from regression analysis falls between these values (within 2 standard deviations of the mean for extant taxa).

In an example of the application of this approach to the study of penecontemporaneous hominid fossils from Swartkrans, SK 847 and SK 48, we have obtained a log  $s.e._m$  value of  $-1.32$  from least-squares linear regression analysis. This value is within the

95% confidence limits for conspecificity as determined from our study of modern vertebrates and invertebrates. Without asserting that this result means that SK 847 and SK 48 are necessarily conspecific, we conclude that this possibility deserves further attention, especially in the context of other data that have suggested that SK 847 might represent a small individual, a female, of a species also represented by penecontemporaneous specimens from Swartkrans attributed to *A. robustus*.<sup>1,7-11</sup>

The log  $s.e._m$  value of  $-1.32$  obtained from comparison between SK 48 and SK 847 is close to the upper limit of variability associated with the 95% confidence intervals of log-transformed  $s.e._m$  values determined from this study of modern taxa. The fact that it is within the 95% confidence limit points to similarities between certain specimens attributed to *Australopithecus* and *Homo*.

We do not intend to use 95% confidence limits associated with  $s.e._m$  values to determine boundaries between taxa, but if there is no clear boundary between *Australopithecus* and *Homo*, we suggest that  $s.e._m$  values may be used cautiously as one potential way of assessing the degree to which pairs of hominid specimens are similar to each other, in the context of quantifying probabilities of conspecificity, rather than 'pigeon-holing' specimens into one or other taxon.

We recognise that the approach illustrated here is limited by its dependency on measurements of anatomical rather than behavioural and other features that are not preserved in the fossil record. However, noting that  $s.e._m$  distributions for vertebrates and invertebrates are almost identical (Fig. 1), we draw attention to the potential advantage of this method as one general means of quantifying probabilities of conspecificity in palaeontological contexts. Further applications of this approach to inter-specific comparisons of closely related extant taxa are necessary to refine the potential application of this technique to hominid fossils.

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