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Morphometric ('log sem') analysis of anatomical measurements of Galápagos finches (*Geospiza*), chimpanzees (*Pan*) and Plio-Pleistocene hominins (*Paranthropus*, *Australopithecus* and early *Homo*)

Significance:

- The 'log sem' morphometric method can be shown to be justified in the context of its use in the analysis of anatomical measurements of three sets of data: Galápagos finches (six species of *Geospiza*); two species of chimpanzees (*Pan troglodytes* and *P. paniscus*); and three hominin genera (*Australopithecus*, *Paranthropus* and early *Homo*).

A morphometric method has been used in analyses of linear measurements obtained from crania of modern hominoids[1-3] as well as Plio-Pleistocene hominins,[1,4,5] based on pairwise comparisons associated with least squares linear regression to quantify the degree of scatter around a regression line of the form $y = mx + c$, where m is the slope and c is the intercept. The log-transformed standard error of the m-coefficient, known as 'log sem', serves to quantify the degree of scatter around the regression line, associated with the degree of variability in shape. The effect of size is associated with the m-coefficient.

For many taxa, a mean log sem value of -1.61 has been recognised as a typical degree of intraspecific morphological variation in extant species.[2,3] With a standard deviation of 0.1, it has been used as a frame of reference for assessing probabilities of conspecificity when pairs of specimens are compared (e.g. Thackeray and Dykes[3] and Thackeray[4]).

In this analysis, the results of an UPGMA (unweighted pair group method with arithmetic mean) cluster analysis were obtained from log sem statistics calculated from anatomical measurements from the following three sets of data as examples of method: Galápagos finches (*Geospiza*), chimpanzees (*Pan troglodytes* and *P. paniscus*), and Plio-Pleistocene hominins (*Australopithecus africanus, A. sediba, Homo habilis, H. erectus, H. rudolfensis* and *H. naledi*). The objective was to demonstrate that the log sem statistic has biological significance, reflecting variability in shape in a diversity of taxa.

UPGMA tree for six species of Galápagos ground finches

Using UPGMA, a log sem matrix was analysed for the six generally accepted species of ground finches, namely *Geospiza magnirostris, G. fortis, G. fulginosa, G. difficilis, G. conirostris* and *G. scandens*.[6,7] The log sem matrix was based on measurements of the lengths of wing, tail, culmen, gonys, depth of bill at base, width of mandible at base, tarsus and middle toe with claw, from a database compiled by the California Academy of Sciences. Measurements were obtained from 36 specimens (an equal number of male and female specimens) resulting in more than 1200 regressions. A computer program for analysing large data sets (https://github.com/chdwck9/professorRegressor) was used to calculate log sem statistics.[8]

Figure 1 presents the resulting phenetic tree. This tree corresponds closely to a phylogeny obtained by Burns et al.[9] and Reaney et al.[10] based on genetic data.
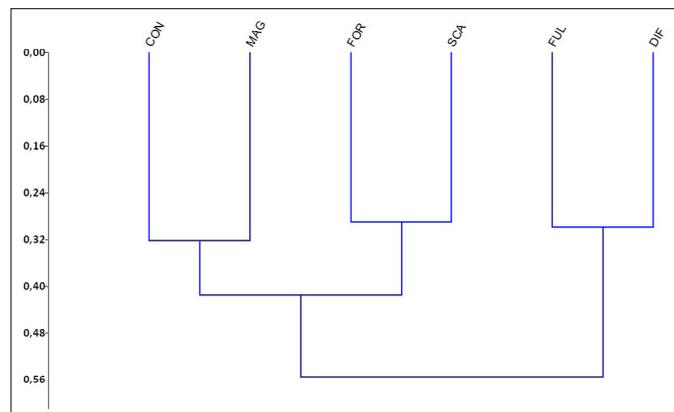
Figure 1: Results of a UPGMA analysis of a log sem matrix based on anatomical measurements of six species of Galápagos ground finches, namely *Geospiza magnirostris* (MAG), *G. fortis* (FOR), *G. fulginosa* (FUL), *G. difficilis* (DIF), *G. conirostris* (CON) and *G. scandens* (SCA). The phenetic tree corresponds closely with a phylogeny presented by Burns et al.[9] and Reaney et al.,[10] based on genetic data. Measurements were obtained from the California Academy of Sciences.
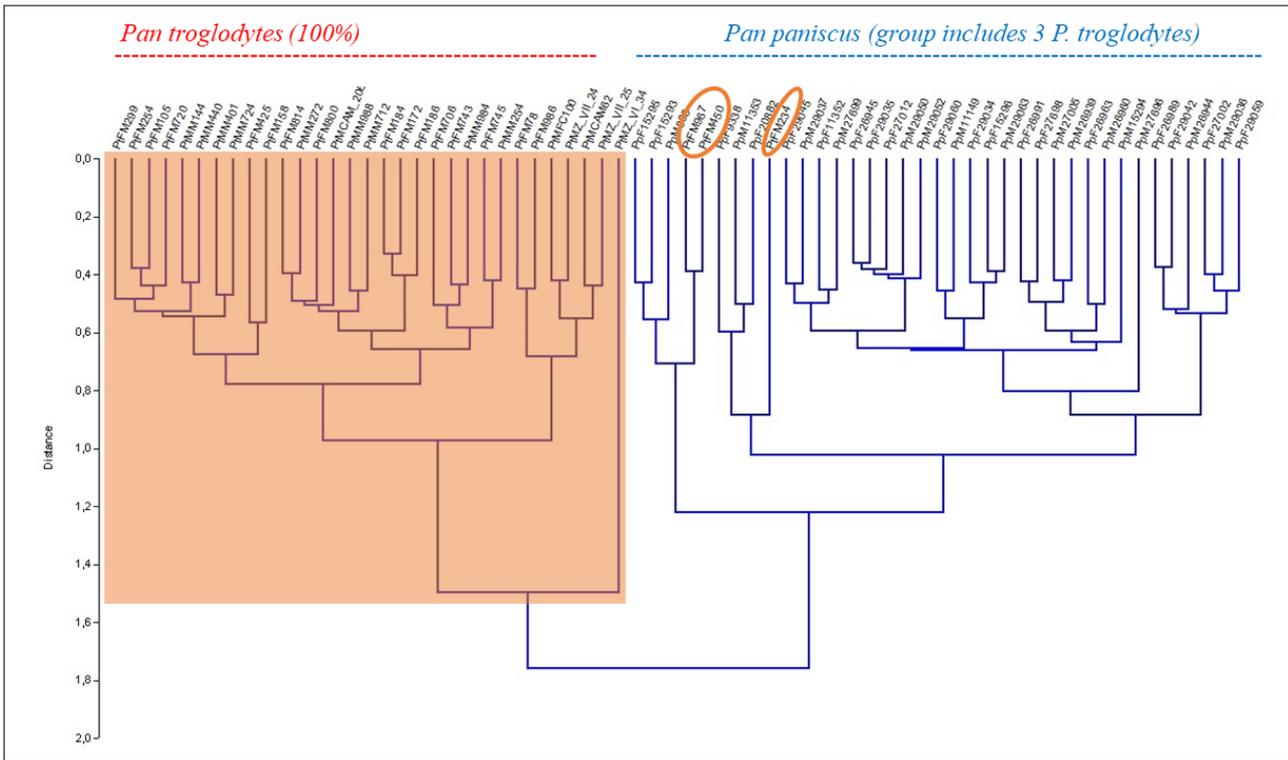
Figure 2: Phenetic tree obtained from UPGMA cluster analysis of log sem statistics based on pairwise linear regression analyses of cranial measurements of two chimpanzee species, *Pan troglodytes* ($n=38$ specimens) and *P. paniscus* ($n=38$ specimens). Measurements for specimens numbered here have been published by Gordon and Wood[11]. Log sem statistics generally distinguish between the two taxa.
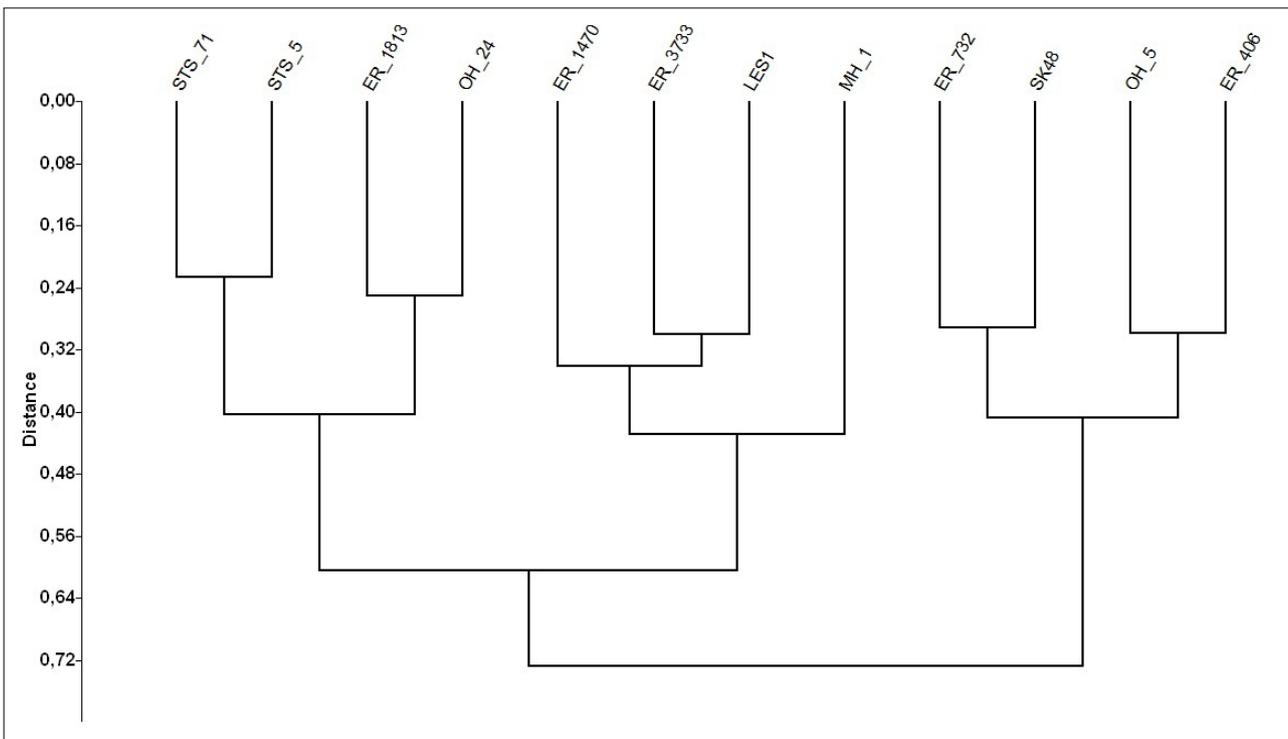
Figure 3: Phenetic tree obtained from UPGMA cluster analysis of log sem statistics based on pairwise linear regression analyses of cranial measurements of Plio-Pleistocene hominins, using measurements published primarily by Wood[14]. Three general groups are distinguished, whereby specimens attributed to *Paranthropus* are distinct from others attributed to *Australopithecus* and *Homo*. Sts 5 and Sts 71 are specimens of *Australopithecus* from Sterkfontein, South Africa. KNM-ER 1813 (Turkana Basin, Kenya) and OH 24 (Olduvai Gorge, Tanzania) have been attributed to *H. habilis* but group with *A. africanus*. KNM-ER 1470 (*H. rudolfensis*) and KNM-ER 3733 (*H. ergaster*) are both from the Turkana Basin. South African specimens LES 1 (*H. naledi*) and MH 1 (*A. sediba*) are from Rising Star and Malapa Caves, respectively. KNM-ER 406 and KNM-ER 732 are specimens of *Paranthropus boisei* from the Turkana Basin. The latter species is also represented by OH 5 from Olduvai Gorge. SK 48 represents *P. robustus* from Swartkrans, South Africa.

UPGMA tree for two chimpanzee species

Figure 2 presents a phenetic tree obtained from UPGMA cluster analysis of log sem statistics based on pairwise linear regression analyses of *Pan troglodytes* and *P. paniscus* cranial measurements (*n*=68 specimens, more than 4500 regressions), using measurements published as supplementary material by Gordon and Wood[11]. The log sem approach generally distinguishes the two taxa, reflecting robusticity of the log sem method. Although 3 out of 34 specimens attributed to *P. troglodytes* group with others attributed to the closely related *P. paniscus,* this lack of a clear boundary is consistent with genetic evidence of hybridisation between chimpanzees and bonobos within the last million years.[12,13]

UPGMA tree for Plio-Pleistocene hominin specimens

Figure 3 presents a phenetic tree obtained from UPGMA cluster analysis of log sem data of the kind published by Thackeray and Odes[5], generated from pairwise comparisons of Plio-Pleistocene hominin specimens attributed to *Australopithecus,* early *Homo* and *Paranthropus,* using measurements published by Wood[14], with the addition of log sem data associated with *A. sediba*[15] and *H. naledi*[16].

Specimens attributed to *A. africanus* (Sts 71 and Sts 5) from South Africa and specimens attributed to *H. habilis* (KNM-ER 1813 and OH 24) from East Africa form a group, consistent with the view that these are closely related. A log sem value of -1.51 calculated from a comparison between OH 24 and Sts 5, combined with a so-called delta log sem[3] value of only 0.003, points to a relatively high probability of conspecificity, despite the fact that OH 24 from Olduvai Gorge in Tanzania has generally been attributed to *H. habilis* whereas Sts 5 ('Mrs Ples' from Sterkfontein in South Africa) is accepted as a specimen representing *A. africanus*. Wood and Collard[17] proposed that *H. habilis* should instead be considered as *A. habilis*. Thackeray[18] suggested that the transition between *A. africanus* and *H. habilis* may constitute a chronospecies.

Robust australopithecines (*Paranthropus*), including specimens SK 48, OH 5, KNM-ER 406 and KNM-ER 732, are separated as a group distinct from specimens attributed to *A. africanus* and others attributed to *Homo*, including *H. ergaster* (KNM-ER 3733) and *H. rudolfensis* (KNM-ER 1470). MH 1 (*A. sediba*, described by Berger et al.[15] as a '*Homo*-like australopith') groups with specimens attributed to *Homo*. Despite differences in age, LES 1 (*H. naledi*) groups with *H. ergaster*.

Conclusion

The three UPGMA analyses of log sem data, calculated for Galápagos finches (*Geospiza*), chimpanzees (*Pan*) and Plio-Pleistocene hominins (*Paranthropus, Australopithecus* and early *Homo*) reflect groups that have biological significance, serving at the same time to demonstrate that the log sem morphometric method has merit, based on anatomical measurements using landmarks.

Acknowledgements

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