Alpha and sigma taxonomy of *Pan* (chimpanzees) and Plio-Pleistocene hominin species

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A fundamental question in biology, and more specifically in palaeontology, is 'how much variation is there within a biological species?' To answer that question, it is necessary to define a species, notably in a way that can be applied in palaeontological contexts. Recognising that boundaries between taxa may not always be clear, an appeal has been made for a probabilistic definition of a species[1-3], based on pairwise comparisons of specimens and morphometric analyses using least squares linear regression analysis associated with a general equation of the form $y=mc+c$, where x and y are linear dimensions of a skeletal element such as a cranium[4]. The degree of scatter around the regression equation (associated with morphology) is quantifiable using the log of the standard error of the m co-efficient (log sem). Here it is shown how this morphometric approach can be applied to cranial specimens attributed to two extant species of *Pan*, and to extinct Plio-Pleistocene hominins in a temporal sequence, indicating the lack of clear boundaries between species, thereby challenging the prevailing concept of alpha taxonomy[5] which assumes discrete entities. An appeal is made for an alternative concept, namely sigma taxonomy.[3]

Applications and a probabilistic definition of a species

The approach has been applied to measurements obtained from more than 70 taxa[1], and more recently to measurements of crania of *Pan troglodytes*, the common chimpanzee, and also to those of *P. paniscus*, the bonobo[2,6]. The results were remarkable in the sense that, in the case of both species analysed separately (using alpha taxonomy), a mean log sem value of -1.6 was obtained for conspecific pairs. The data confirmed a hypothesis proposed by Thackeray[1] that -1.61 for mean log sem values constitutes an approximation of a biological species constant (T), relating to a central tendency for the degree of variation within a species. An associated standard deviation for this proposed biological constant was given as 0.1 when using more than 2000 regression analyses for pairwise comparisons of specimens of the same species.[2]

A mean log sem value of -1.61 ± 0.1 based on log sem statistics was considered to be a probabilistic definition of a species[2], relating to the degree of variability typically expressed within a single (extant) species.

Application to Plio-Pleistocene crania

The approach has been applied to cranial measurements of Plio-Pleistocene hominins.[4] Here, attention is restricted to five well-preserved and almost complete crania which have been attributed either to the genus *Australopithecus* or to the younger genus *Homo*. The five specimens and associated data are given in Table 1, in chronological order, from 1.6 million years ago (mya) to 2.5 mya.

Table 1: The sample of five almost complete Plio-Pleistocene cranial specimens

Specimen	Age	Taxon	Provenance
KNM-ER 3733	1.6 mya	*Homo erectus*	Turkana Basin, Kenya
OH 24	1.8 mya	*Homo habilis*	Olduvai, Tanzania
KNM-ER 1813	1.9 mya	*Homo habilis*	Turkana Basin, Kenya
Sts 5	2.1 mya	*Australopithecus africanus*	Sterkfontein, South Africa
Sts 71	2.5 mya	*Australopithecus africanus*	Sterkfontein, South Africa

A matrix of log sem values, based on pairwise comparisons of cranial measurements of these specimens[4] is given in Figure 1.

	Sts 71	Sts 5	ER 1813	OH 24	ER 3733
Sts 71		-1.691	-1.546	-1.63	-1.526
Sts 5	-1.643		-1.603	-1.506	-1.558
ER 1813	-1.507	-1.627		-1.701	-1.844
OH 24	-1.566	-1.509	-1.685		-1.723
ER 3733	-1.318	-1.399	-1.656	-1.546	

Key	LOG SEM SPECTRUM
	-1.8
	-1.7
	-1.6
	-1.5
	-1.4

Figure 1: Log sem values for pairwise comparisons of five Plio-Pleistocene hominin crania, dated between 1.6 and 2.5 million years ago. The mean log sem for the entire database is -1.59 ± 0.12 which is almost identical to the values for conspecific comparisons of modern *Pan paniscus* (-1.61 ± 0.1) and for *P. troglodytes* (-1.61 ± 0.1).

The mean log sem value for the data set is -1.59±0.12 (n=20 pairwise comparisons). This result for a *temporal* sequence is remarkable in the sense that it expresses almost exactly the degree of variability that is found *spatially* in two modern species of chimpanzees (-1.61±0.1), examined more specifically below.

Four sets of independent data of mean log sem values, published by Gordon and Wood[6] and discussed by Thackeray and Dykes[2], are given in Table 2 for conspecific chimpanzees (male and female individuals are considered separately), to demonstrate consistency in the mean value of log sem for conspecific comparisons.

Table 2: A set of mean log sem values for pairwise comparisons of conspecific *Pan troglodytes* and *P. paniscus*

Log sem	Comparison
-1.61 ± 0.087	Female–female comparisons of *Pan paniscus*
-1.62 ± 0.095	Male–male comparisons of *Pan paniscus*
-1.62 ± 0.100	Female–female comparisons of *Pan troglodytes*
-1.60 ± 0.109	Male–male comparisons of *Pan troglodytes*
-1.61 ± 0.1	**Mean, n>2000 regression analyses**

Comparisons

On the basis of log sem statistics, it is evident that the spectrum of variability through *evolutionary time* (from 2.5 to 1.6 mya) in five Plio-Pleistocene hominins (mean log sem = -1.59±0.12) is comparable to the spectrum of variability in *geographical space* (-1.61±0.1) at the present time in *Pan paniscus* to the south of the Congo River. It is also comparable to the spectrum of variability in geographical space (-1.61±0.1) in *Pan troglodytes* to the north of that river.

Notably, the degree of variability (mean log sem = -1.61±0.1) in each of the two species of *Pan* developed within a period of (at least) one million years since the time of their divergence. However, when *P. troglodyes* and *P. paniscus* were compared with each other, log sem values did not show a clearly distinct separation.[2,6] This finding is consistent with genetic evidence for hybridisation between *P. troglodytes* and *P. paniscus* within the last million years.[7]

Hypotheses and a definition

Using the results presented here for two species of chimpanzees which diverged about 1 million years ago, and also for five Plio-Pleistocene hominins in a sequence within about one million years, the following hypotheses are presented:

H1: There is no clear boundary between *P. troglodytes* and *P. paniscus.*

H2: There is no clear boundary between certain species attributed to *Australopithecus* and *Homo*.

H3: Certain hominin species attributed to *Australopithecus* and to *Homo* were capable of interbreeding within a period of a million years (a spectrum of time between 1.6 and 2.5 million years ago).

These observations and hypotheses serve to underscore the importance of developing a probabilistic definition of a species that relates to sigma taxonomy, where sigma is the Greek letter for S (Σ) standing for the concept of a spectrum[3,8,9], as opposed to alpha taxonomy which assumes clear boundaries between species[5]. A formal definition for sigma taxonomy is: 'The classification of taxa in terms of probabilities of conspecificity, without assuming distinct boundaries between species'.

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References

1. Thackeray JF. Approximation of a biological species constant? S Afr J Sci. 2007;103:489.
2. Thackeray JF, Dykes S. Morphometric analyses of hominoid crania, probabilities of conspecificity and an approximation of a biological species constant. Homo. 2016;67(1):1–10. http://dx.doi.org/10.1016/j.jchb.2015.09.003
3. Thackeray JF, Schrein CM. A probabilistic definition of a species, fuzzy boundaries and 'sigma taxonomy'. S Afr J Sci. 2017;113(5/6), Art. #a0206, 2 pages. http://dx.doi.org/10.17159/sajs.2017/a0206
4. Thackeray JF, Odes E. Morphometric analysis of early Pleistocene African hominin crania in the context of a statistical (probabilistic) definition of a species. Antiquity. 2013;87(335):1–3. Available from: http://antiquity.ac.uk/projgall/thackeray335/
5. Mayr E, Linsley EG, Usinger RL. Methods and principles of systematic zoology. New York: McGraw-Hill; 1953.
6. Gordon AD, Wood BA. Evaluating the use of pairwise dissimilarity metrics in paleoanthropology. J Hum Evol. 2013;65:465–477. https://doi.org/10.1016/j.jhevol.2013.08.002
7. De Manuel M, Kuhlwilm M, Frandsen P, Sousa VC, Desai T, Prado-Martinez J, et al. Chimpanzee genomic diversity reveals ancient admixture with bonobos. Science. 2016;354(6311):477–481. https://doi.org/10.1126/science.aag2602
8. Thackeray JF. Sigma taxonomy in relation to palaeoanthropology and the lack of clear boundaries between species. Proc Eur Soc Stud Hum Evol. 2015;4:220.
9. Thackeray JF. *Homo habilis* and *Australopithecus africanus*, in the context of a chronospecies and climatic change. In: Runge J, editor. Changing climates, ecosystems and environments within arid southern Africa and adjoining regions: Palaeoecology of Africa 33. Leiden: CRC Press/Balkema; 2015. p. 53–58.