Chimpanzee subspecies and 'robust' australopithecine holotypes, in the context of comments by Darwin

J.F. Thackeray[a*] and S. Prat[b,c]

On the basis of comparative anatomy (including chimpanzees, gorillas and other primates), Darwin[1] suggested that Africa was the continent from which 'progenitors' of humankind evolved. Hominin fossils from this continent proved him correct. We present the results of morphometric analyses based on cranial data obtained from chimpanzee taxa currently recognised as distinct subspecies, namely *Pan troglodytes troglodytes* and *Pan troglodytes schweinfurthii*, as well as *Pan paniscus* (bonobo). Our objective was to use a morphometric technique[2] to quantify the degree of similarity between pairs of specimens, in the context of a statistical (probabilistic) definition of a species.[3–5] Results obtained from great apes, including two subspecies of chimpanzee, were assessed in relation to same-scale comparisons between the holotypes of 'robust' australopithecine (Plio-Pleistocene hominin) taxa which have traditionally been distinguished at a species level, notably *Paranthropus robustus* from South Africa, and *Paranthropus (Australopithecus/Zinjanthropus) boisei* from East Africa. The question arises as to whether the holotypes of these two taxa, TM 1517 from Kromdraai[6] and OH 5 from Olduvai,[7] respectively, are different at the subspecies rather than at the species level.

Key words: **hominin taxonomy, Pleistocene, *Australopithecus, Paranthropus,* chimpanzee**

Darwin was among the first to recognise difficulties in distinguishing taxa at the species or genus level. Even in 1851, and again in 1854, he was finding problems in expressing differences between barnacle species, especially as sample sizes available for study became large, as is the case today with hominin fossils from Africa and elsewhere in the world.[8] Darwin[9] noted that 'after considerable experience, when numerous varieties of a species have been carefully examined, the eye acquires a sort of instinctive knowledge by which it can recognise the species, though the character cannot be defined by language'. In *The Origin* published 150 years ago,[10] he stated that it would not be a 'cheering prospect' if it was necessary to treat 'species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations of convenience'. He recognised the need to quantify the 'amount of difference' between species.

Recognition of boundaries between species is problematic, particularly in palaeoanthropological contexts. Indeed, depending on the criteria used to define a species, hominin specimens in some cases have been recognised as either distinct species, or classified instead at a subspecies level. For example, specimens from Dmanisi in Georgia include the holotype of *Homo georgicus*[11] but have alternatively been classified as *Homo erectus georgicus*[12] using criteria for the recognition of extant subspecies[13] (geographical separation and morphological discontinuity). Another example is the classification of *Ardipithecus kadabba* from Ethiopia, initially described as a subspecies of *Ardipithecus ramidus* (*Ardipithecus r. kadabba*)[14] but raised to species level after the discovery of new dental material.[15]

Boundaries between the fossil hominin taxa are not clear, but morphometric analyses can facilitate the assessment of probabilities of conspecificity, in the context of a statistical definition of a species. The morphometric technique we used is based on least-squares linear regression analysis of cranial measurements of pairs of specimens, in this case equal numbers of males and females of *Pan troglodytes troglodytes*, *Pan troglodytes schweinfurthii* and *Pan paniscus.* Cranial measurements were used, based on anatomical landmarks (Table 1). A frame of reference for morphometric comparisons has been presented by Thackeray[3] who reported that the standard error (s.e.) of the coefficient m (associated with the regression equation $y = mx + c$) shows a log-normal distribution in the case of pairwise comparisons of conspecific pairs of extant mammals, birds, reptiles, lepidoptera and coleoptera (n = 1 424 specimens). In this instance, the log-transformed standard error of the coefficient m (designated log s.e.$_m$) for pairwise comparison of conspecific pairs is –1.61 ± 0.23, constituting a morphometric definition of a species,[3] expressed in terms of probabilities (95% confidence limits for log s.e.$_m$ values, around a mean of –1.61, range between –2.07 and –1.15). The quantification of the 'amount of differences' (as expressed by log s.e.$_m$ values) is relevant for purposes of assessing the probability that any two specimens are conspecific, without assuming that all hominin fossils can be pigeon-holed into discrete taxa.[3–5]

This approach was used in an exploratory study of the crania of the holotype specimens of *Paranthropus robustus* (TM 1517) and *Paranthropus boisei* (OH 5). It was necessary to select measurements that were obtainable from both specimens, recognising that TM 1517 is a partial cranium. The 16 dimensions that were used in this study are listed in Table 1, based on standard anatomical landmarks. The same dimensions were measured on crania of *Pan t. troglodytes*, *Pan t. schweinfurthii* and *Pan paniscus.*

The mean log s.e.$_m$ value obtained for comparisons between pairs of specimens of *Pan t. troglodytes* was –1.41 ± 0.14 (n = 42

Table 1. The dimensions, used in this study, of TM 1517 (holotype of *Paranthropus robustus* from Kromdraai), OH 5 (holotype of *Paranthropus/Australopithecus/Zinjanthropus boisei* from Olduvai Gorge), *Pan troglodytes troglodytes, Pan troglodytes schweinfurthii* and *Pan paniscus.* Anatomical features are described in standard manuals. The definitions of White and Folkens[16] are used in this case.

Measurement
1. Alveolar height
2. Palate length
3. Temporal length
4. Temporal squama length
5. Temporal squama height
6. Articular eminence height
7. Root of the zygomatic process height
8. Postglenoid height
9. P3 mesiodistal crown diameter
10. P3 buccolingual crown diameter
11. P4 mesiodistal crown diameter
12. P4 buccolingual crown diameter
13. M1 mesiodistal crown diameter
14. M1 buccolingual crown diameter
15. M2 mesiodistal crown diameter
16. M2 buccolingual crown diameter

[a]Institute for Human Evolution, University of the Witwatersrand, P.O. WITS 2050, Johannesburg, South Africa.
[b]UPR 2147 du CNRS, 44 rue de l'Amiral Mouchez, 75014 Paris, France.
[c]Human Origins and Past Environments Research Unit (HRU), Transvaal Museum, P.O. Box 413, Pretoria 0001, South Africa.
*Author for correspondence E-mail: mrsples@global.co.za

pairwise comparisons). This was not significantly different ($P = 0.05$) from the mean log s.e.$_m$ value of –1.58 ± 0.19 obtained from 36 pairwise comparisons of crania of *Pan t. schweinfurthii.* The main difference was the greater degree of morphological variability expressed by the higher standard deviation in the case of the latter taxon, but in both cases the mean log s.e.$_m$ values were (as expected) within the 95% confidence limits for log s.e.$_m$ for conspecific pairs.[3]

A mean log s.e.$_m$ value of –1.44 ± 0.17 ($n = 90$ pairwise comparisons) was calculated when pairwise comparisons were made between specimens of *Pan t. schweinfurthii* and *Pan t. troglodytes.* A mean log s.e.$_m$ value of –1.32 ± 0.17 was obtained when *Pan troglodytes* and *Pan paniscus* were compared ($n = 100$ comparisons). As expected, this mean value was higher (more positive) than that obtained when subspecies of *Pan troglodytes* were compared against each other.

These results can be assessed in the relation to results obtained from morphometric analyses of African hominins. TM 1517 (type specimen of *Paranthropus robustus* from Kromdraai, South Africa) and OH 5 (type specimen of *Paranthropus (Australopithecus/Zinjanthropus) boisei* from Olduvai Gorge, Tanzania) were compared using measurable dimensions common to both specimens (Table 1), resulting in a log s.e.$_m$ value of –1.15. This value was not significantly different ($P = 0.05$) from the corresponding value obtained when two species of chimpanzee (*Pan troglodytes* and *Pan paniscus*) were compared.

Thackeray[4] indicated previously that TM 1517 and OH 5 are potentially conspecific. Analyses of measurements (Table 1) included in the current study of chimpanzees do not contradict the possibility that TM 1517 and OH 5 may be conspecific. However, it should be emphasised that the log s.e.$_m$ value for the comparison between TM 1517 and OH 5 is close to the upper 95% confidence limit for conspecific extant pairs.

As indicated in our morphometric study, the boundaries between taxa are difficult to determine. In addition to the methodology used here, further analyses based on morphological differences between TM 1517 and OH 5 will be undertaken to assess probabilities of conspecificity.

We thank the National Research Foundation (South Africa), the French Embassy in South Africa, the Fyssen and the Singer-Polignac Foundations (France) for financial support and the curators of the Musée Royal d'Afrique Centrale (Belgium) and the Powell-Cotton Museum (U.K.) for access to the collections. We also thank the National Museum of Tanzania and the Ministry of Culture of Tanzania for access to OH 5, the Transvaal Museum for access to TM 1517 and two referees for useful comments on an earlier version of the manuscript.

Received 19 January. Accepted 13 July 2009.

1. Darwin C. (1871). *The Descent of Man, and Selection in Relation to Race.* John Murray, London.
2. Thackeray J.F., Bellamy C.L., Bellars D., Bronner G., Bronner L., Chimimba C., Fourie H., Kemp A., Krüger M., Plug I., Prinsloo S., Toms R., van Zyl A.J. and Whiting M.J. (1997). Probabilities of conspecificity: application of a morphometric technique to modern taxa and fossil specimens attributed to *Australopithecus* and *Homo. S. Afr. J. Sci.* **93**, 195–196.
3. Thackeray J.F. (2007). Approximation of a biological species constant? *S. Afr. J. Sci.* **103**, 489.
4. Thackeray J.F. (1997). Probabilities of conspecificity. *Nature* **390**, 30–31.
5. Thackeray J.F. (2006). Darwin, South Africa and the emergence of the genus *Homo. Trans. R. Soc. S. Afr.* **61**, 127–130.
6. Broom R. (1938). The Pleistocene anthropoid apes of South Africa. *Nature* **142**, 377–379.
7. Tobias P.V. (1967). Olduvai Gorge, Vol. 2: *The Cranium and Maxillary Dentition of* Australopithecus (Zinjanthropus) boisei. Cambridge University Press, Cambridge.
8. Thackeray J.F. (1999). Alternative views on hominid diversity in the context of Darwin's assessment of barnacles. In *Towards Gondwana Alive. Promoting Biodiversity and Stemming the Sixth Extinction,* ed. J.M. Anderson, pp. 100–109. National Botanical Institute, Gondwana Alive Society, Pretoria.
9. Darwin C. (1854). *A Monograph of the Sub-Class Cirripedia with Figures of all the Species. The Balanidae (or Sessile Cirripedes); The Verrucidae, etc.*, pp. 1–684. Ray Society, London.
10. Darwin C. (1859). *The Origin of Species by Means of Natural Selection.* John Murray, London.
11. Gabunia L., de Lumley M.A., Vekua A., Lordkipanidze D. and de Lumley H. (2002). Découverte d'un nouvel hominidé à Dmanissi (Transcaucasie, Gérogie). *Comptes Rendus Palévol* **1**, 242–253.
12. Rightmire G.P., Lordkipanidze D. and Vekua A. (2006). Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisi, Republic of Georgia. *J. Hum. Evol.* **50**, 115–141.
13. Mayr E. (1969). *Principles of Systematic Zoology.* McGraw Hill, New York.
14. Haile-Selassie Y. (2001). Late Miocene hominids from Middle Awah, Ethiopia. *Nature* **412**, 178–181.
15. Haile-Selassie Y., Suwa G. and White T.D. (2004). Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. *Science* **303**, 1503–1505.
16. White T.D. and Folkens P.A. (2005). *The Human Bone Manual.* Elsevier Academic Press, Burlington, MA.