One or two species? A morphometric comparison between robust australopithecines from Kromdraai and Swartkrans

Authors:
Zachary Cofran[1]
J. Francis Thackeray[2]

Affiliations:
[1]Department of Anthropology, University of Michigan, United States of America

[2]Institute for Human Evolution, University of the Witwatersrand, Johannesburg, South Africa

Correspondence to:
Zachary Cofran

email:
zacharoo@umich.edu

Postal address:
Department of Anthropology, University of Michigan, 101 West Hall, 1085 S. University Ave, Ann Arbor, MI 48109, United States of America

Keywords:
Kromdraai; Swartkrans; *Paranthropus robustus*; *Paranthropus crassidens*; STET

Dates:
Received: 15 July 2009
Accepted: 05 Nov. 2009
Published: 11 Mar. 2010

How to cite this article:
Cofran Z, Thackeray JF. One or two species? A morphometric comparison between robust australopithecines from Kromdraai and Swartkrans. S Afr J Sci. 2010;106(1/2), Art. #15, 4 pages. DOI: 10.4102/sajs.v106i1/2.15

This article is available at:
http://www.sajs.co.za

ABSTRACT

The type specimen of *Paranthropus robustus* (TM 1517, including a partial cranium) was discovered at Kromdraai near Sterkfontein in 1938 and described by Robert Broom as a new species. Subsequently, more robust australopithecines were discovered at the nearby site of Swartkrans. These Swartkrans hominins were described by Broom as *Paranthropus crassidens*. Many palaeoanthropologists currently regard the robust australopithecines from Kromdraai and Swartkrans as one species, but consensus has not been reached on this issue. A morphometric analysis has been undertaken to assess the probability that specimens attributed to *P. crassidens* represent the same species as that which is represented by TM 1517, the holotype of *P. robustus*. Our results failed to reject the null hypothesis that both sites sample the same, single species of robust australopithecine.

INTRODUCTION

The type specimen of *Paranthropus robustus* (TM 1517, see Figure 1) was discovered at Kromdraai B in the Cradle of Humankind World Heritage Site in South Africa and described by Broom[1] as a new genus and species. Subsequently, additional specimens of 'robust' australopithecines were discovered at Swartkrans, within four kilometers of Kromdraai B, and described as a distinct species, *P. crassidens*.[2] Many palaeoanthropologists such as Tobias[3], Brain[4], Fuller[5], and Kaszycka[6], regard the Kromdraai B and Swartkrans 'robust' australopithecine specimens as representing a single species. Others such as Grine[7,8,9,10] and Howell[11], and more recently, Schwartz and Tattersall[12], regard the two as distinct at a species level, *P. robustus* and *P. crassidens*, respectively. To date, this issue has not been addressed by a morphometric analysis of both cranial and dental material. The objective of this study is to test the hypothesis that the robust australopithecine crania from Swartkrans and Kromdraai are morphometrically similar enough to belong to the same species, *P. robustus*.

MATERIALS

Craniodental measurements were taken on original specimens: TM 1517a from Kromdraai, and SK 12, SK 46, SK 48, SK 79, SK 83, and SKW 11 from Swartkrans. The set of cranial measurements was adapted from that of Lockwood[13], and is listed in Table 1. Dental measurements included only the maximum labiolingual/buccolingual breadth, because heavy interproximal wear obscures maximum mesiodistal lengths in most specimens.[5,14] Where a trait was present on both the right and left sides, the average of the two values was taken.

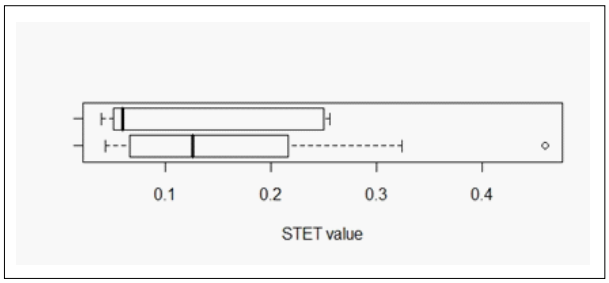
METHODS

Thackeray and colleagues[15,16] described a method whereby measurements of pairs of specimens were compared to one another, in order to assess probabilities of conspecificity. Measurements obtained from extant, conspecific male-female pairs were plotted against each other, with the female on the *x*-axis and male on the *y*-axis. Morphometrically similar pairs tended to exhibit a relatively low degree of scatter about a least-squares regression line associated with the equation $y = mx + c$. This degree of scatter, or degree of dissimilarity, was quantified by calculating the standard error of the slope, *m* (here, "se_m"). Using modern conspecifics as a frame of reference, Thackeray and colleagues[15] found that this se_m statistic displayed a normal distribution when log-transformed (base 10). Thus, pairs of specimens that were morphometrically very different from one another – specimens of different species – can be expected to have a relatively high degree of scatter about the regression line, and so a relatively high se_m. Conversely, pairs of conspecifics tended to have a lower degree of scatter and hence a relatively low se_m. Using an extant reference sample of over 1 400 specimens of vertebrates and invertebrates, Thackeray[16] presented a log se_m value of -1.61 ± 0.23 as a statistical definition of a species expressed in terms of probabilities.

The log se_m method described by Thackeray and colleagues[15] was developed further by Wolpoff and Lee[17,18], who used a statistic which they referred to as the 'standard error test of the null hypothesis' (STET). Like log se_m, STET is based on the standard error of the slope of the least-squares regression line in bispecimen comparisons. However, Wolpoff and Lee[18] argued against the dampening effects of logging the se_m statistic. Additionally, they noted that regressing specimen *x* on specimen *y* produced different slopes and therefore different standard errors, as compared to regressions of *y* on *x*. Thus, STET utilises the standard error of the slopes of both possible pair-wise regressions: $STET = [(s.e._{mx})^2 + (s.e._{my})^2]^{1/2}$, where *mx* and *my* are the least-squares slopes of each possible regression. In this way, the STET statistic is invariant of how specimens are regressed on one another, and makes no assumptions about sex, which is often difficult to determine in fossil specimens. Low STET values indicate very similar overall shape (low scatter about the regression lines).

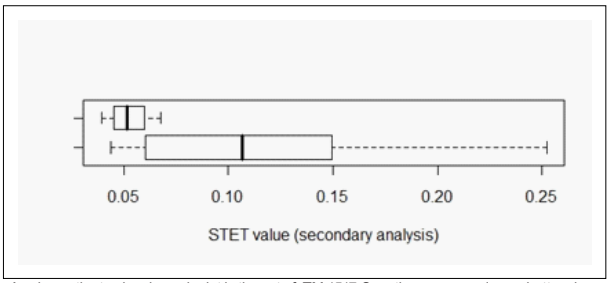
For this analysis, we used the STET statistic to assess the likelihood that TM 1517 and the Swartkrans crania represent the same species. If TM 1517 represents a different species from that which is represented by the Swartkrans robust australopithecines, STET values computed for Swartkrans specimens (compared

FIGURE 1
Left lateral view of the TM 1517a cranium



Top plot is the set of TM 1517-Swartkrans comparisons, bottom are the Swartkrans-only comparisons. The thick black band in the box is the median.

FIGURE 2
Boxplot of the distributions of STET values



As above, the top box in each plot is the set of TM 1517-Swartkrans comparisons, bottom is the Swartkrans-only set.

FIGURE 3
Boxplot of the distribution of STET values for the secondary analysis with reduced dataset

against each other) should be significantly lower than the STETs derived from TM 1517-Swartkrans comparisons. A ranked-sums test[19] was used to determine whether the Swartkrans-only STET values were significantly different from the values computed for the TM 1517-Swartkrans comparisons. This non-parametric test was appropriate in this case because the two samples were not independent: The same Swartkrans crania were used to compute STET values for within-Swartkrans and TM 1517-Swartkrans comparisons.

Finally, because the STET statistic is more reliable with increasing numbers of variables,[18] the above procedure was repeated in a secondary analysis, omitting pair-wise comparisons that share less than ten variables, as in the case of the following pairs: TM 1517-SK 12, TM 1517-SK 79, SK 79-SK 12, and SK 12-SK 83. An advantage of the methods developed by Thackeray and colleagues[15,16] and Lee and Wolpoff[17,18] is that they facilitate assessment of fossil assemblages when certain specimens do not preserve all of the traits under study. Additionally, these methods provide a means of testing hypotheses about taxonomy, based on metric similarity. It should be noted that these methods only test null hypotheses – hypotheses of no significant difference.

RESULTS

The mean STET value for Swartkrans-only was 0.156 ± 0.118, and that of TM 1517-Swartkrans was 0.119 ± 0.104 (see Table 2). The Wilcoxon test showed the distributions are not significantly different (p = 0.3) The TM 1517-Swartkrans distribution was within the range of the Swartkrans distribution, with the exception of the TM 1517-SKW 11 comparison, which had a lower STET value than any comparison within Swartkrans alone (see Figure 2). That the TM 1517-Swartkrans distribution had a lower mean STET value than the Swartkrans-only distribution, highlights the morphological similarities of TM 1517 with many specimens from the Swartkrans sample.

Figure 2 shows that within the Swartkrans-only distribution there is a major outlier, the comparison of SK 12-SK79; this is one of the comparisons preserving fewer than 10 variables in common. The secondary analysis, omitting the comparisons with less than 10 variables in common, produced similar results to the whole-sample analysis (see Figure 3). The mean STET for Swartkrans-only was 0.120 ± 0.070, and that of TM 1517-Swartkrans was 0.053 ± 0.012. In the reduced dataset, the TM 1517-Swartkrans STET values span an even smaller part of the lower range of the within-Swartkrans variation, further underscoring the similarity between TM 1517 and the Swartkrans fossils. A Wilcoxon ranked-sums test on this reduced dataset showed the TM 1517-Swartkrans and Swartkrans-only STET distributions to be significantly different (p = 0.02) at the $p < 0.05$ level. Because the TM 1517-Swartkrans STET values were generally lower than those within Swartkrans, this significant result is surprising, and further emphasises the morphological similarity between the crania from these two sites, as well as the great variation within Swartkrans itself.

DISCUSSION

The results show that one cannot reject the null hypothesis: That TM 1517 from Kromdraai and crania from Swartkrans sample the same species, *Paranthropus* (or *Australopithecus*) *robustus*. The TM 1517-Swartkrans STET values were generally lower than the within-Swartkrans values, indicating that not only is TM 1517 within the Swartkrans-only range of variation, but also that TM 1517 is generally more similar to Swartkrans crania than the Swartkrans crania are to each other. In fact, the lowest STET value from the analysis, indicating the two most similar specimens, is that of TM 1517 from Kromdraai and SKW 11 from Swartkrans Member 1's Hanging Remnant. In light of the fairly large variation displayed by the Swartkrans fossils, our results point to a relatively stable lineage of robust australopithecine in the Sterkfontein valley in the lower Pleistocene.

Our results indicate that the Kromdraai and Swartkrans robust australopithecines represent the same species. This is contrary to findings of Howell[11], Grine[7,9,10], and Schwartz and Tattersall[12], whose conclusions were based largely on differences in dental sizes, proportions, and gross morphology between the two sites. Two issues arose with these authors' conclusions. Firstly, the decisions to make specific distinctions appear to be have been made from gross inspection of each site's summary statistics for given dental traits (e.g. M_3 mesiodistal length), rather than from statistical tests. Along these lines, Fuller[5] used a resampling procedure to compare the pooled Swartkrans-Kromdraai dental coefficients of variation (CV) to the CVs of modern humans, African apes, and fossil hominins. Her results showed that variation within the pooled Swartkrans-Kromdraai sample was statistically no greater than in most of the modern and fossil referents, leading her not to reject the hypothesis of a single species represented at the two sites.

Article #15
South African Journal of Science

TABLE 1
List and description of cranial measurements used in this analysis

1	*Orbital height: maximum distance from the superior to the inferior orbital margin, perpendicular to the orbital breadth.
2	*Orbito-alveolar height: minimum distance from the inferior orbital margin to the alveolar margin.
3	*Orbito-jugal height: minimum distance from the inferior orbital margin to the alveolar margin of the maxilla between the canine and third premolar; the inferior terminus of the measurement is the same as that used for anterior maxillo-alveolar breadth and postcanine maxillo-alveolar length.
4	*Foraminal height: minimum distance from the superior margin of the infraorbital foramen to the maxillary alveolar margin.
5	*Malar depth: minimum distance from the inferior orbital margin to the inferior margin of the zygomatic arch.
6	*Alveolar height: nasospinale to prosthion.
7	*Anterior interorbital breadth: left maxillofrontale to right maxillofrontale.
8	*Bimaxillary breadth: left zygomaxillare to right zygomaxillare.
9	*Interforaminal breadth: minimum distance between the medial margins of the left and right infraorbital foramina.
10	*Nasal aperture breadth: maximum distance between the lateral margins of the nasal aperture in the same horizontal plane .
11	*Snout breadth: distance between the lateral margins of the canine buttresses (or anterior pillars, where appropriate) at the level of the inferior nasal margin.
12	*Anterior maxillo-alveolar breadth: distance between the alveolar margins of the maxillae, measured at the outer margin of the septum between the canine and third premolar on either side.
13	*Maxillo-alveolar breadth: distance between the most lateral points on the alveolar margins of the maxillae at the midpoint of the second molar.
14	*Anterior palatal breadth: distance between the lingual alveolar margins of the palate, measured at the most medial point on the septum between the canine and third premolar on either side.
15	*Palatal breadth: distance between the lingual alveolar margins of the palate at the midpoint of the second molar.
16	*Maxillo-alveolar length: distance from prosthion to the midpoint of a line across the palate and alveolar processes at the level of the outer surface of the interalveolar septa between the second and third molars; the value is calculated by triangulation from two measurements: 1) the measurement of the distance between the left and right outer interalveolar septa (not the same as the maxillo-alveolar breadth described above) and 2) the distance from prosthion to the midpoint of the outer interalveolar septum.
17	*Postcanine maxillo-alveolar length: distance from the outer surface of the interalveolar septum between the canine and third premolar to the corresponding point between the second and third molar on the same side.
18	*Zygomatic process to porion distance: distance from porion to the anterior limit of the zygomatic process.
19	*Postorbital breadth: maximum breadth across the greatest postorbital constriction of the frontal bones.
20	*External auditory meatus height: maximum superoinferior diameter of the external acoustic meatus, taken at its internal, most lateral margin.
21	*Infraorbital foramen-zygo-orbitale: distance from superior margin of infraorbital foramen to zygo-orbitale.
22	*Width of the temporomandibular joint: the distance from the inferolateral-most articular eminence to the medial-most entoglenoid process.
23	*Porion-prosthion distance.
24	*Prosthion to the M2-3 interalveolar septum.
25	*Porion to the C1-P3 interalveolar septum.
26	*Superior-inferior palate thickness: superoinferior height, taken just posterior to the nasal exit of the incisive canal.
27	*Maximum length of the temporal gutter, taken at the gutter's confluence with the temporal squama, posteriorly to the posterior extent of the suprameatal crest.
28	*Width of the temporal gutter, taken from the posterior junction of the gutter with the temporal squama, to the base of the (medial) vertical wall of the zygomatic process.
29	*Vertical height of the zygomatic process, taken from just anterior of the articular eminence.

Variables indicated by (*) are quoted from the Appendix of Lockwood[13].

Secondly, some Kromdraai specimens contributing to the seemingly specific differences between the two sites may actually relate to the presence of early *Homo*. For example, Grine[9,10] suggested that the teeth of a sub-adult from Kromdraai, KB 5223, represented a robust australopithecine species different from that which was represented at Swartkrans. However, Braga and Thackeray[20] have shown, using qualitative and quantitative criteria, that KB 5223 is probably attributable to early *Homo*. Placing all other Kromdraai B dental specimens in the *P. robustus* sample along with Swartkrans specimens, these authors found it improbable that the KB 5223 postcanine dentition came from the same *P. robustus* sample, but rather more likely indicated the presence of *Homo* at Kromdraai. In some non-metric traits, this specimen is similar to the TM 1536 M_1 and dm_1, also from Kromdraai. However, the authors noted that TM 1536 lacked the key diagnostic features of *Homo* molars, such as the absence of the hypoconulid on the dm_1 and C6 on the dm_2, present in KB 5223. Thus, the results of Braga and Thackeray[20] corroborated those of Fuller[5], indicating a high probability that the 'robust' dental specimens from Kromdraai and Swartkrans, with the exception of the KB 5223 dentition, sample a single species. Our results further demonstrate the craniodental affinities of the Kromdraai and Swartkrans robust australopithecine fossils.

CONCLUSION

From our morphometric analysis, we failed to reject the null hypothesis, therefore there is a very high probability that the type specimen of *P. robustus*, TM 1517, is the same species of robust australopithecine that is present at Swartkrans. Moreover, TM 1517 fit comfortably within the range of craniodental variation

TABLE 2
STET values for all pair-wise Comparisons

COMPARISON	STET
SKW11-SK46	0.077
SKW11-SK48	0.072
SKW11-SK79	0.252
SKW11-SK83	0.106
SKW11-SK12	0.15
SK46-SK48	0.053
SK46-SK79	0.212
SK46-SK83	0.06
SK46-SK12	0.127
SK48-SK79	0.132
SK48-SK83	0.044
SK48-SK12	0.057
SK79-SK83	0.221
SK12-SK79	0.459
SK12-SK83	0.324
1517-SKW11	0.039
1517-SK46	0.052
1517-SK48	0.068
1517-SK83	0.052
1517-SK12	0.25
1517-SK79	0.256

seen in Swartkrans, and is indeed morphometrically very similar to many of the Swartkrans fossils. Hence, the Swartkrans 'robust' australopithecines and TM 1517 can be considered conspecific, representing a single species, *Paranthropus* (*Australopithecus*) *robustus*.

ACKNOWLEDGEMENTS

Support for this research was provided by the Rackham Graduate School and the University of Michigan Department of Anthropology (ZC), and by the French Embassy in South Africa, the National Research Foundation (South Africa) and the Andrew Mellon foundation (JFT). We thank Dana Begun and Milford Wolpoff for helpful comments on earlier manuscripts, as well as two anonymous reviewers for helpful and insightful comments on an earlier draft. Our gratitude also goes to Stephany Potze, Lazarus Kgasi and Tersia Perregil at the Transvaal Museum for helpful access to the fossil material.

REFERENCES

1. Broom R. The Pleistocene anthropoid apes of South Africa. Nature. 1938;142:377–379.
2. Broom R. Another new type of fossil ape-man. Nature. 1949;163:57.
3. Tobias PV. The cranium and maxillary dentition of *Australopithecus* (*Zinjanthropus*) *boisei*, Olduvai Gorge. Cambridge University Press, Cambridge; 1967.
4. Brain CK. The hunters or the hunted? An introduction to African cave taphonomy, University of Chicago Press, Chicago; 1981.
5. Fuller K. An analysis of the probability of multiple taxa in a combined sample of Swartkrans and Kromdraai dental material. Am J of Phys. Anthropol. 1996;101:429–439.
6. Kaszycka KA. Status of Kromdraai: cranial, mandibular, and dental morphology, systematic relationships, and significance of the Kromdraai hominids, CNRS Editions, Paris; 2002.
7. Grine FE. New craniodental fossils of *Paranthropus* from the Swartkrans formation and their significance in 'robust' Australopithecine evolution. In: Grine FE. Evolutionary history of the 'robust' Australopithecines. New York: Aldine, 1988; p. 223–246.
8. Grine FE. New hominid fossils from the Swartkrans formation (1979-1986 excavations): Craniodental specimens. Am J Phys Anthropol. 1989;79:409–449.
9. Grine FE. Description and preliminary analysis of new hominid craniodental fossils from the Swartkrans formation. In: Brain CK. Swartkrans: A cave's chronicle of early man. Pretoria: Transvaal Museum, 1993; p. 75–116.
10. Grine FE. A new juvenile hominid (Mammalia: Primates) from Member 3, Kromdraai Formation, Transvaal, South Africa. Ann Transvaal Mus. 1982;33:165–239.
11. Howell FC. Hominidae. In: Maglio VJ, Cooke HBS, editors. Evolution of African Mammals. Cambridge: Harvard University Press, 1978; p. 154–248.
12. Schwartz JH, Tattersall I. The human fossil record vol. 4. craniodental morphology of early hominids (*Genera Australopithecus, Paranthropus, Orrorin*), and overview. Hoboken: John Wiley & Sons Inc.; 2005.
13. Lockwood CA. Sexual dimorphism in the face of *Australopithecus africanus*. Am J Phys Anthropol. 1999;108:97–127.
14. Wolpoff MH. Interstitial wear. Am J Phys Anthropol. 1971;34:205–228.
15. Thackeray JF, Bellamy CL, Bellars D, et al. Probabilities of conspecificity: application of a morphometric technique to modern taxa and fossil specimens attributed to Australopithecus and Homo. S Afr J Sci. 1997;93:195–196.
16. Thackeray JF. Probabilities of conspecificity. S Afr J Sci. 2007;103:1.
17. Wolpoff MH, Lee SH. The Late Pleistocene human species of Israel. Bull Mem Soc Anthropol Paris. 2001;13:291–310.
18. Lee SH, Wolpoff MH. Habiline variation: A new approach using STET. Theory Biosci. 2005;124:25–40.
19. Siegel S. Nonparametric statistics for the behavioral sciences. New York: McGraw-Hill; 1956.
20. Braga J, Thackeray JF. Early homo at Kromdraai B: probabilistic and morphological analysis of the lower dentition. C R Palevo. 2003;2:269–279.