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Abstract

The South African Plio-Pleistocene sites where large numbers of fossil hominid specimens have been discovered in the last 20 years are Sterkfontein, Swartkrans and, most recently, Drimolen. Hominid specimens recovered from these sites have usually been attributed to *A. africanus* (from Sterkfontein), *A. robustus* (Swartkrans, Drimolen and Sterkfontein) and South African early *Homo* (Swartkrans, Drimolen and Sterkfontein). We recently started a research project aimed at characterizing cheek teeth cusp morphology of South African Australopithecinae employing digital photographs of their occlusal surfaces. In this paper an analysis of the basic metrical features of maxillary molar cusp areas and proportions of *A. africanus* and *A. robustus* is presented. We analyzed 92 permanent maxillary molar teeth of South African Australopithecinae. The main results suggest that: a) crown base areas of the three molars are broadly similar in *A. africanus* and *A. robustus*; b) significant differences between the two species in relative cusp areas are evident for the protocone of M^1 (with *A. africanus* larger than *A. robustus*), the paracone of

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M^1, and the protocone of M^2 and M^3 (with *A. robustus* larger than *A. africanus*); c) in the total crown area *A. robustus* shows the sequence $M^1 < M^2 < M^3$ as previously described; d) in *A. africanus* the sequence observed is $M^1 < M^2 > M^3$, as in living apes. This different sequence between *A. africanus* and *A. robustus* appears to be related mostly to differences in mesial cusp size, which in *A. robustus* shows a marked relative expansion from M^1 to M^3. Also, the variability in absolute cusp areas of the *A. africanus* sample seems to be related to the presence of specimens with notably large teeth.

Introduction

The number of fossil hominid specimens recovered from southern African Plio-Pleistocene sites has dramatically increased in the last 20 years. The sites where large numbers of fossil hominid specimens have been discovered include Sterkfontein (e.g., Lockwood and Tobias, 2002; Moggi-Cecchi et al., 2006), Swartkrans (e.g., Brain, 1993) and, most recently, Drimolen (Keyser et al., 2000). Hominid specimens recovered from these sites have usually been attributed to *Australopithecus africanus* (Sterkfontein), *Australopithecus robustus* (Swartkrans, Drimolen and Sterkfontein) and southern African early *Homo* (Swartkrans, Drimolen and Sterkfontein).

Among these, the fossils recovered from the Sterkfontein Formation represent the largest collection of early hominid specimens from a single locality. Hominids from Sterkfontein Member 4 have, with few exceptions, been assigned to *A. africanus*. In recent years, some authors have suggested that, on the basis of the analysis of the cranial anatomy, a few specimens from Sterkfontein Member 4 may represent another taxon (e.g. Clarke, 1988, 1994; Lockwood and Tobias, 2002). However, different studies based on dental metrics have found no evidence for substantial heterogeneity within the Sterkfontein Member 4 hominid dental sample (Suwa, 1990; Wood, 1991a; Calcagno et al., 1999; Moggi-Cecchi, 2003).

It is becoming apparent that analytical studies of the dentition employing traditional linear measurements (mesio-distal and bucco-lingual diameters) may not be the appropriate approach for addressing the issue of morphological variability within the Sterkfontein Member 4 hominid dental sample (Moggi-Cecchi, 2003). For this reason we recently started a research project aiming to characterize the dental morphology of the Sterkfontein hominid sample (in comparison with the other South African fossil hominid species) employing digital photographs of the occlusal surface of the cheek teeth. Although 2D images are just a crude approximation of the complex shape of the tooth crown, they are relatively easy and quick to collect using digital photographs, and they are more informative than the traditional linear measurements. This is because, among other things, they allow measurements of the absolute areas of the individual cusps.

Little work has been carried out on the analysis of cusp areas of the teeth of Plio-Pleistocene hominids since the series of papers by Wood and colleagues two decades ago (Wood and Abbott, 1983; Wood et al., 1983; Wood and Uytterschaut, 1987; Wood and Engleman, 1988). The number of South African dental specimens has vastly increased since then, thus allowing a more detailed analysis of issues pertaining to the intra- and interspecific variability in the fossil samples.

In this paper, we focus on the basic metrical features of maxillary molars cusp areas and proportions of *A. africanus* and *A. robustus*.

Materials and Methods

We analyzed 92 permanent maxillary molar teeth of South African Australopithecinae representing 20 individuals and 15 isolated teeth of *A. africanus* from the sites of Sterkfontein and Makapansgat, and 9 individuals and 30 isolated teeth of *A. robustus* from the sites of Swartkrans, Kromdraai and Drimolen (Table 1). Taxonomic allocation of the specimens for *A. robustus* follows previous studies (e.g., Grine, 1989; Keyser et al, 2000), whereas for *A. africanus*, the specimens recently described from Sterkfontein Member 4 (Moggi-Cecchi et al., 2006), were provisionally considered as belonging to the species *A. africanus*, as all specimens recovered before 1966.

Heavily worn teeth were excluded from the analysis. Teeth in which the fissures between the main cusps were not evident were excluded as well. Each of the selected teeth was positioned with the cusp tips in their approximate anatomical position or, for the worn teeth, with the mesial and the buccal cervical enamel line parallel to the camera lens. A graduated scale was placed next to it, half way between the cusp tips and the cervix. Photographs were taken with a Nikon Coolpix 885 digital camera with a 2048 X 1536 pixel resolution. The images were then stored on a PC and measured with image analysis software (NIH Image J free software) (Boccone, 2004). The intra-observer error was about 2%.

Table 1. Number of maxillary molars of A. africanus *and* A. robustus *analyzed in this study*

	M^1	M^2	M^3
A. africanus			
Sterkfontein	13	16	9
Makapansgat	1	1	1
A. robustus			
Swartkrans	12	11	16
Kromdraai	3	1	2
Drimolen	2	2	2

The four main cusps (paracone, protocone, metacone and hypocone) were defined following Wood and Engleman, (1988), and their absolute areas were measured; the total measured area (TMA) of the crown was computed from the individual cusp areas. One of us (S.B.) measured the cusp areas three times over a six month period, and the average of the three readings was used in the analysis.

A series of univariate non-parametric statistical comparisons, in the form of Mann-Whitney tests, were performed to test for differences in cusp size between *A. africanus* and *A. robustus*.

Results

Tables 2 and 3 present the data on the absolute and relative cusp areas of the teeth assigned to *A. africanus* and *A. robustus*. Mean values for the TMA are also presented in Table 2.

The mean value of TMA of M^1 in *A. africanus* is slightly smaller than *A. robustus*. In M^2 the TMA of *A. africanus* is larger than *A. robustus*, whereas in M^3 the opposite is true. None of the pairwise differences between *A. africanus* and *A. robustus* (TMA M^1 *A. africanus* vs. TMA M^1 *A. robustus*, etc.) is statistically significant.

In *A. africanus*, when the mean values of the total area are examined, we found that the M^2 is the largest tooth, followed by M^3 and M^1, respectively. In *A. robustus*, the M^3 is the largest tooth, followed by M^2 and M^1. This condition results in a molar size sequence $M^1 < M^2 > M^3$ in *A. africanus*, whereas in *A. robustus* it is $M^1 < M^2 < M^3$ (Figure 1).

Inspection of the mean absolute values of the individual cusps showed only minor differences between the two species in the three molars. In M^1, both species have similar values for the lingual cusps (protocone and the hypocone), whereas *A. robustus* shows slightly larger buccal cusps; in M^2, *A. africanus* has slightly larger distal cusps

Table 2. Absolute cusp areas and Total Measured Area (TMA) (in mm^2) of maxillary molars in A. africanus *and* A. robustus

	A. africanus						A. robustus					
	N	x	*Min*	*Max*	*s.d.*	*CV*	*N*	x	*Min*	*Max*	*s.d.*	*CV*
M^1												
Total measured area	14	159.7	115.6	247.7	33.1	20.7	14	163.0	113.4	240.1	32.8	20.1
Protocone	14	51.7	38.2	85.5	11.8	22.9	17	50.8	37.5	66.0	8.6	16.9
Paracone	14	33.8	22.5	51.0	8.1	23.8	16	36.9	25.1	52.7	6.6	17.8
Metacone	14	36.3	26.4	49.9	7.5	20.8	16	39.7	27.4	59.4	8.3	21.0
Hypocone	14	37.4	28.6	62.0	8.4	22.6	15	36.6	20.7	62.2	10.0	27.2
M^2												
Total measured area	14	194.2	130.5	272.8	43.0	22.1	11	183.8	147.3	215.6	22.4	12.2
Protocone	15	64.6	45.5	83.7	12.2	18.9	13	65.6	47.5	82.6	11.5	17.5
Paracone	17	45.9	25.5	68.8	11.5	25.0	13	44.2	31.3	55.2	7.2	16.3
Metacone	16	40.6	23.9	59.5	10.7	26.2	13	35.2	22.2	45.1	8.4	24.0
Hypocone	14	42.9	21.1	68.4	13.2	30.7	13	38.1	23.8	46.7	5.7	15.0
M^3												
Total measured area	9	180.0	137.8	242.0	32.1	17.8	18	195.6	154.3	264.4	31.9	16.3
Protocone	9	61.2	48.2	83.5	10.4	17.0	20	71.3	51.0	130.2	18.3	25.7
Paracone	10	45.6	30.2	68.4	10.4	22.8	19	49.6	38.0	72.1	10.8	21.8
Metacone	10	35.1	21.8	47.1	9.4	26.8	19	35.1	20.2	60.0	10.2	29.2
Hypocone	10	37.7	21.2	53.7	9.0	23.9	19	37.2	18.3	68.3	11.0	29.5

Table 3. Relative cusp areas of maxillary molars in A. africanus *and* A. robustus. (*) *indicates significant differences. See text*

	A. africanus						A. robustus					
	N	x	*Min*	*Max*	*s.d.*	*CV*	*N*	x	*Min*	*Max*	*s.d.*	*CV*
M^1												
Protocone	14	32.4*	27.5	37.0	2.4	7.4	14	30.9	27.5	34.0	1.7	5.5
Paracone	14	21.1	17.8	25.4	2.0	9.6	14	22.9*	20.1	28.0	1.9	8.4
Metacone	14	22.8	19.8	25.5	1.9	8.3	14	24.0	20.2	27.6	2.2	9.1
Hypocone	14	23.5	18.7	25.7	1.9	8.3	14	22.1	17.7	25.9	2.5	11.3
M^2												
Protocone	14	32.9	28.3	37.1	2.6	7.9	11	35.0*	27.5	40.2	3.3	9.5
Paracone	14	24.1	19.7	28.8	2.7	11.2	11	24.8	21.2	29.4	2.8	11.4
Metacone	14	21.3	16.7	25.0	2.0	9.4	11	19.5	11.2	24.3	3.6	18.7
Hypocone	14	21.8	16.2	26.0	2.9	13.3	11	20.7	15.8	26.1	2.5	12.0
M^3												
Protocone	9	34.1	30.6	38.7	2.5	7.4	18	36.9	25.3	49.3	5.7	15.5
Paracone	9	24.8	19.9	28.3	2.5	10.2	18	25.7	19.0	35.8	4.3	16.7
Metacone	9	20.1	15.5	25.7	4.2	20.9	18	18.3	13.1	31.6	4.4	24.2
Hypocone	9	20.6	15.4	26.6	3.4	16.6	18	19.1	9.5	26.4	4.7	24.6

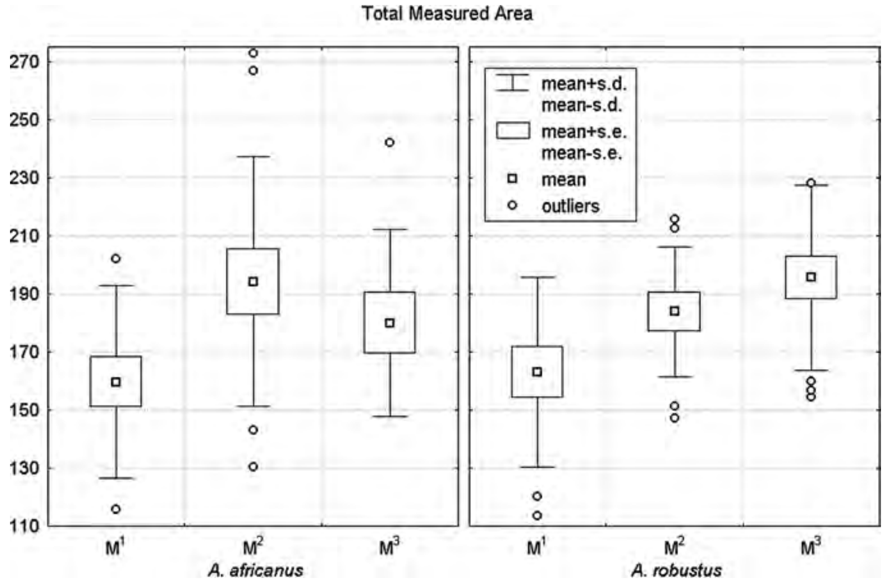

Figure 1. Total crown base area (in mm^2) of maxillary molars of *A. africanus* and *A. robustus*.

than *A. robustus* and similarly sized mesial cusps. In M^3, *A. robustus* shows larger mesial cusps, on average, than *A. africanus*, and distal cusps of the same size. As was the case for TMA, none of the pair-wise differences between *A. africanus* and *A. robustus* is statistically significant.

Both species showed remarkably high levels of variability in absolute cusp areas as expressed by the coefficient of variation (CV), with values always larger than 15. *A. africanus* shows higher CV values than *A. robustus* in the mesial cusps of M^1, and in all four cusps of M^2. However, in M^3 *A. robustus* has higher CV values than *A. africanus* in the protocone, metacone and hypocone. With respect to the TMA, the CV values for *A. africanus* were always larger than for *A. robustus*, especially in M^2.

When absolute mean cusp size is examined along the tooth row (Figure 2) in *A. africanus*, in each cusp the sequence is M^1<M^2>M^3, as was the case for the TMA. Specifically, there is a marked increase (>12 mm^2) from M^1 to M^2 for both mesial cusps, less evident for the distal cusps (~4–5 mm^2). On the other hand, the difference in individual cusp size between M^2 to M^3 is less marked and not statistically significant.

The picture is different in *A. robustus*. The cusp size sequence is M^1< M^2< M^3 for the protocone and the paracone, with a notable increase both from M^1 to M^2 (>14 mm^2 for the protocone and >7mm^2 for the paracone) and less from M^2 to M^3 (> 5 mm^2). The cusp sequence is M^1> M^2 = M^3 for the metacone and M^1<M^2> M^3 for the hypocone, although in the latter case the differences between the three teeth are minimal and not statistically significant.

Analysis of the relative cusp areas showed differences between the two species that were not apparent in the analysis of absolute values. In M^1, the protocone is relatively large in *A. africanus* compared to *A. robustus*, and the difference is statistically significant ($p< 0.05$). A significant difference also emerges in paracone size, with *A. robustus* being significantly larger than *A. africanus* ($p< 0.05$). In M^2 the protocone size is significantly larger in *A. robustus* than in *A. africanus* ($p< 0.05$). In M^3 the protocone size is also larger in *A. robustus*, with a p value close to significant ($p=0.057$).

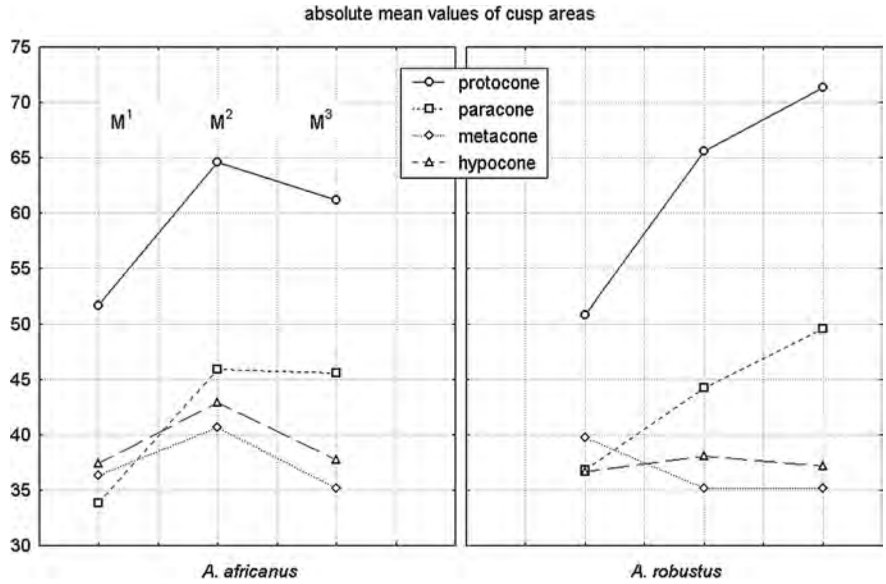

Figure 2. Mean values of absolute cusp areas (in mm^2) of maxillary molars of *A. africanus* and *A. robustus*.

It is also interesting to observe the relative contribution of each cusp to the total area in each molar of both species. For both *A. africanus* and *A. robustus*, in M^2 and M^3 the protocone is the largest cusp, followed by the paracone, hypocone and metacone. In M^1, for *A. africanus* the protocone is the largest cusp, followed by the hypocone, metacone and paracone, whereas in *A. robustus* the sequence is protocone>metacone>paracone>hypocone.

Relative cusp size examined along the tooth row adds complementary information to the analysis of absolute areas (Figure 3). In *A. africanus*, there is an increase in the relative size of the mesial cusps from M^1 to M^2, with a proportional reduction of both distal cusps. From M^2 to M^3, there is also a small increase of the relative size of the mesial cusps, and a decrease in relative size of the distal cusps. In *A. robustus*, on the other hand, the trend for relative cusp area is the same as for absolute cusp area. Moreover, the enlargement of both mesial relative to the distal cusps from M^1 to M^3 becomes more evident.

Discussion

The morphological and metrical characterization of the dental features of early hominids is crucial to the interpretation of their phylogenetic position (e.g., Robinson, 1956; Johanson et al, 1982; Grine, 1989; Tobias, 1991; Wood, 1991b; Ward et al., 2001). In the case of South African Plio-Pleistocene hominids, because of the large number of specimens recovered from long-term excavations, we are now in a position to get a fairly good idea of the characteristics of the dentition of the two most abundant hominid species (*A. africanus* and *A. robustus*). In particular, the large samples allow us to address important issues such as intra- and interspecific variability in the features considered.

The issue of metrical and morphological variability in the dental record of South African hominids is, at the present time, a matter of debate. The existence of different species or different 'morphs' in the fossil sample from Sterkfontein has been suggested by several authors (e.g. Clarke, 1988, 1994; Kimbel and White, 1988, Lockwood

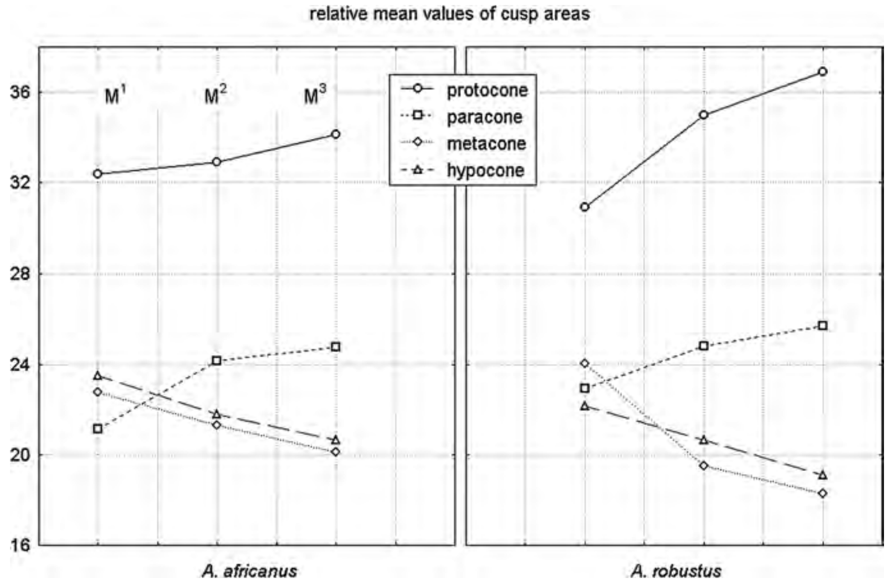

Figure 3. Mean values of relative cusp areas of maxillary molars of *A. africanus* and *A. robustus*.

and Tobias, 2002; Schwartz and Tattersall, 2005), but without reliable information about intraspecific variability these proposals cannot be assessed. On the other hand, previous studies based on dental metrics found no evidence for substantial heterogeneity within the Sterkfontein Member 4 hominid dental sample (Suwa, 1990; Wood, 1991a; Calcagno et al., 1999; Moggi-Cecchi, 2003).

Thus, the detailed metrical analysis of cusp morphology of *A. africanus* and *A. robustus* analyzed in terms of cusp areas of maxillary molars provides a framework within which the existence of a second hominid taxon within Sterkfontein Member 4 can be assessed. Detailed analysis of molar morphology may provide additional information, possibly employing a method of analysis that has been successfully employed to discriminate late Pleistocene taxa (Bailey, 2004).

Results show that broad similarities exist between *A. africanus* and *A. robustus* in terms of TMA of the upper molars. This result confirms observations from previous studies (Robinson, 1956; Sperber, 1973; Wood and Engleman, 1988). In terms of variability in crown size, as expressed by the CV, this is similar for M^1 and M^3 in *A. africanus* and *A. robustus*. However, in *A. africanus* the CV of M^2 is almost twice that in *A. robustus*. This finding will require further investigation in future studies.

In terms of molar size sequence based on TMA values, the uniquely derived condition seen in *A. robustus* described in previous studies (Robinson, 1956; Sperber, 1973; Wood and Engleman, 1988) with $M^1 < M^2 < M^3$ is confirmed. On the other hand, in *A. africanus*, the sequence observed is $M^1 < M^2 > M^3$, which differs from that described by Wood and Engleman (1988), who reported that in their "SAFGRA" sample M^2 and M^3 were subequal in size. Our results indicate the existence of the primitive condition in *A. africanus*, as observed in living apes (Wood and Engleman, 1988).

This different crown size sequence between *A. africanus* and *A. robustus* appears to be related primarily to differences in the size of the mesial cusps. In fact, in *A. africanus* the $M^1 < M^2 > M^3$ sequence of the TMA is also present when the individual cusps are considered in both absolute and in relative terms. On the other hand, in *A. robustus*, the mesial cusps show a marked increase in size from M^1 to M^3, whereas the size of the distal cusps remains the same (in absolute terms) along the molar row (or decreases slightly – in relative terms). This result suggests that the overall increase of the total crown base area from M^1 to M^3 in *A. robustus* is the result of a selective enlargement of the mesial cusps.

This result is interesting, since it differs from the pattern described for mandibular molars of robust australopithecines, where there is a relative expansion of the distal portion of the tooth (the talonid), and relative reduction of the mesial portion (Wood et al., 1983). It will be important to explore this finding in more detail in future studies to discern whether or not a difference between upper and lower molars will be confirmed.

The relative contribution of the different cusps to the total crown area varies between *A. africanus* and *A. robustus*, and from M^1 to M^3. In general, the protocone is the largest cusp. Robinson (1956, p. 97) noted that, in *A. africanus*, the protocone provides a greater contribution to the total area than it does in *A. robustus*. On the basis of the present analysis this statement appears to be confirmed only for the M^1, whereas the opposite is true in M^2 and M^3.

It is interesting to compare cusp area mean values obtained in this study with those published by Wood and Engleman (1988). There are obvious differences in sample size and composition between the two studies (and also there are slightly different measuring techniques), but their comparative analysis provides relevant information.

In *A. africanus*, the mean values of absolute cusp areas obtained in this study are consistently larger that those reported by Wood and Engleman (1988), with the only exception being the hypocone of M^3. In *A. robustus*, the protocone always shows larger mean values in our sample, whereas the distal cusps always have larger mean values in the Wood and Engleman sample. No consistent trend in differences along the tooth row is evident for the metacone. The picture is different when the mean values of relative cusp areas are examined. Differences between the two samples are always minor, with most around 1% and a few less than 3%. Two exceptions are the relative area of the hypocone of M^3 in *A. africanus*, which is 5% larger in the Wood and Engleman sample, and relative area of the protocone of M^2 in *A. robustus*, which is 4.3% larger in our extended sample.

Taken together, this evidence suggests that the large sample used in the present analysis confirms the relative contribution of the main cusps to the total area in *A. africanus* and in *A. robustus* noted by Wood and Engleman (1988). At the same time, analysis of the absolute values suggests that our expanded sample of *A. africanus* includes more individuals with large teeth than were in the Wood and Engleman sample.

The sample of South African fossil hominids used by Wood and Engleman (1988) in their study included almost exclusively specimens recovered from the excavations by Broom and by Robison at Swartkrans and at Sterkfontein (except for Taung and Makapansgat). No specimens included in their study derived from the later excavations conducted by Brain at Swartkrans (labeled SKX and SKW) and by Tobias, Hughes and Clarke at Sterkfontein (labeled Stw – except Stw 6 and Stw 19, used by Wood and Engleman), and, for obvious reasons, the specimens from Drimolen (Keyser et al., 2000).

Among the hominid specimens more recently recovered from Sterkfontein Member 4 (labeled Stw), a few have notably large teeth, as is shown in Figure 4 (comparing the M^2 of Sts 22 and of Stw 183). Some of these Stw specimens are those identified by Clarke (1994) as being distinct from *A. africanus*. (It will be thus essential to perform a more detailed analysis of cusp areas in order to evaluate potential

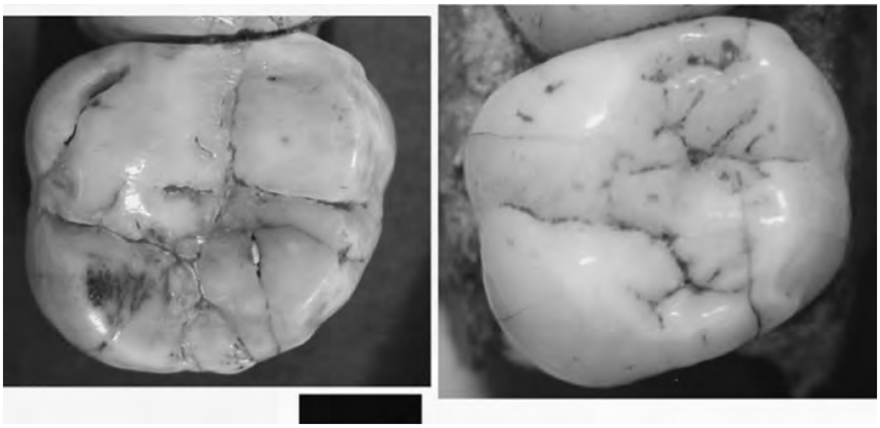

Figure 4. Occlusal photographs of M^2 of Sts 22 (on the left) and Stw 183 (on the right) at the same scale. Note differences in overall crown morphology. Scale = 1 cm.

differences in cusp base areas within the *A. africanus* extended sample.) Further, these larger specimens appear to have a broad based crown relative to the occlusal basin. Such a complex occlusal morphology cannot be captured by standard cusp area analysis and will require a different approach to be quantified (e.g., Bailey, 2004).

Conclusions

Analysis of the maxillary molar cusp areas and proportions of *A. africanus* and *A. robustus* provides the following main results:

1. Crown base areas for the three molars are broadly similar in *A. africanus* and *A. robustus*.
2. Significant differences between the two species in relative cusp areas are evident for the protocone of M^1 (with *A. africanus* larger than *A. robustus*), the paracone of M^1 (with *A. robustus* larger than *A. africanus*), and for the protocone of M^2 and M^3 (with *A. robustus* larger than *A. africanus*).
3. The total crown area sequence for *A. robustus* is $M^1 < M^2 < M^3$ as previously described (Wood and Engleman, 1988).
4. In *A. africanus* the total crown area sequence is $M^1 < M^2 > M^3$, as in living apes (Wood and Engleman, 1988).
5. The different sequences of *A. africanus* and *A. robustus* appear to be related primarily to differences in mesial cusp size, which in *A. robustus* shows a marked expansion from M^1 to M^3 relative to the distal cusps.
6. Differences in the absolute cusp areas of the present expanded *A. africanus* sample and the smaller sample of Wood and Engleman (1988) are likely related to the presence of specimens with notably large teeth in the expanded sample.

Further analysis will specifically address the issue of variability within the *A. africanus* dental sample, with special reference to the specimens from Sterkfontein Member 4.

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