



The cranium of Sts 5 ('Mrs Ples') in relation to sexual dimorphism of *Australopithecus africanus*

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KEYWORDS:

Hominini; human evolution; Pleistocene; Sterkfontein; South Africa

HOW TO CITE:

Tawane GM, Thackeray JF. The cranium of Sts 5 ('Mrs Ples') in relation to sexual dimorphism of *Australopithecus africanus*. S Afr J Sci. 2018;114(1/2), Art. #a0249, 4 pages. <http://dx.doi.org/10.17159/sajs.2018/a0249>

Fossil Sts 5 ('Mrs Ples') is a Plio-Pleistocene cranium assigned to *Australopithecus africanus*. It was discovered in April 1947 by Robert Broom and John Robinson at Sterkfontein in the Gauteng Province, situated in the Cradle of Humankind in South Africa.¹ It is thought to date to at least 2.1 mya²⁻⁴, probably closer to 2.5 mya. Broom had initially referred to such specimens from Sterkfontein as *Plesianthropus* (where 'ples' refers to 'almost', and 'anthropus' to 'human').

Broom^{1,5} suggested that the edentulous specimen represented a female individual on the basis of small canine sockets, but in 1947 he did not have a substantial comparative sample for *A. africanus*. He considered Sts 5 to be an adult based on his claim that cranial sutures appeared to be closed, assuming that suture closure could be used to estimate developmental age. The identification of Sts 5 as the cranium of a female adult is still the subject of ongoing debate. Resolution of this issue is important for an understanding of sexual dimorphism and ontogeny in *A. africanus*.

The debate concerning the developmental age and sex of Sts 5 can be summarised in terms of a diversity of views held in recent decades. Rak⁶ used the presence of facial anterior pillars to suggest that Sts 5 represented a male individual. Lockwood⁷ examined variability in facial anatomy in more than 12 specimens of *A. africanus* to try to distinguish between female and male individuals, but was not in a position to be certain as to whether 'Mrs Ples' was the cranium of a female individual, as suggested initially by Broom, or that of a male individual, as contended by Rak.

With regard to the developmental age of Sts 5, Thackeray et al.⁸ used CT scans of the roots of dentition to suggest that the individual was adolescent. By contrast, Bonmati et al.⁹ concluded that the individual was adult at the time of death, while Villmoare et al.¹⁰ suggested that 'Mrs Ples' was senescent. Grine et al.¹¹ stated: 'There is no evidence to contradict the assertion that "Mrs Ples" is an adult female'.

Here, we do not attempt to resolve the issue as to whether Sts 5 represents an adult or an adolescent individual. Instead, we address the question as to whether Sts 5 is the cranium of a small male individual distinct from that of a large female individual, using alveolar canine dimensions and a re-examination of Lockwood's⁷ craniofacial data as an expression of sexual dimorphism in *A. africanus*.

Canine sockets and alveolar bone loss

Broom's^{1,5} suggestion that Sts 5 represents a female individual, based on a small canine socket, needs to be examined in the context of post-mortem damage. After mechanical preparation of the cranium, using hammer and chisel, Broom et al.¹² measured the buccolingual (BL) and mesiodistal (MD) canine socket diameters as 9.0 mm and 7.6 mm, respectively.

Unfortunately, acetic acid was used at some stage of preparation, as is evident from acid damage to the petrosal bones within the cranium. If acid caused such damage to substantially thick petrosal bones, it is likely that (at some time since 1950) acetic acid preparation also caused damage to alveolar bone associated with the canine sockets. Such acid damage would have led to a reduction of canine socket diameters because the roots of the canines (and the associated sockets) are conical.

In 2012, the BL and MD diameters for the right canine alveolar socket were given by Grine et al.¹¹ as 7.2 mm and 6.9 mm, respectively. These values correspond closely to a BL value of 7.0 mm given by Thackeray¹³ and a MD dimension of 6.9 mm obtained in this study. The reduction in the reported BL diameter, from 9 mm to 7.2 mm, could relate to post-mortem damage to the conical sockets, of the kind associated with acid preparation of the fossil. Villmoare et al.¹⁰ confirmed that some degree of alveolar bone loss had occurred in the case of Sts 5.

It is not known to what extent Broom's mechanical preparation of the maxilla contributed to the damage of original alveolar bone adjacent to the canine socket. It is also not certain to what extent some degree of predepositional bone loss may have occurred after the canine teeth had broken, prior to the sockets being filled with sediment which became calcified. However, assuming that original measurements by Broom et al.¹² were accurate, it is apparent that in 1950 the conical canine alveolar sockets were larger than they are currently. We suggest that this difference is a result of acid preparation sometime after 1950. These observations are relevant to the identification of the sex of Sts 5, compared to other cranial specimens of *A. africanus* that have been identified as belonging to either male or female individuals.

The measurement of 9 mm by Broom et al.¹² for the BL diameter of Sts 5 is larger than the BL diameter of 8 mm for a definite male specimen of *A. africanus* (Stw 505), and almost as large as the BL diameters for another male adult, TM 1511, estimated as 10.2 mm for the left canine¹² and 10.5 mm for the right canine¹¹. Discovered in 1936, TM 1511 was not prepared in acetic acid.

Relationships between BL and MD canine diameters for presumed male and female specimens of *A. africanus* are shown in Figure 1, based partly on data presented by Grine et al.¹¹ but (for the first time, in this study) including the position of Sts 5 based on BL and MD diameter measurements published by Broom et al.¹² in 1950 and recorded before the damage associated with acetic acid preparation. According to these data, the canine diameter measurements of Sts 5 are consistent with the hypothesis that 'Mrs Ples' indeed represents a male individual. The

data for BL and MD diameters shown in Figure 1 counter the statement by Grine et al.¹¹ that 'there is no evidence to contradict the assertion' that Sts 5 represents a female individual.

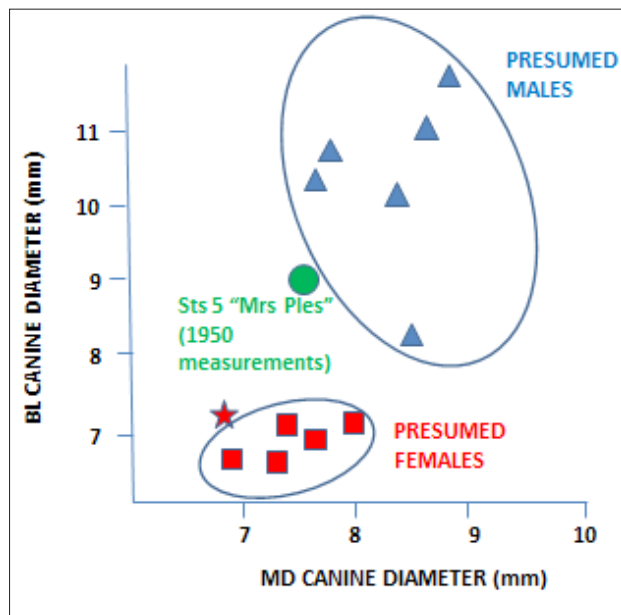


Figure 1: Relationship between buccolingual (BL) and mesiodistal (MD) diameters for conical canine sockets, based in part on data for presumed male individuals (blue triangles) and presumed female individuals (red squares) of *Australopithecus africanus*, published by Grine et al.¹¹ The green circle represents MD and BL measurements for Sts 5 as published by Broom et al.¹², most probably taken before damage and alveolar bone loss occurred. According to these data, Sts 5 is more likely to belong to a small male individual than a female individual, as proposed by Grine et al.¹¹ The red star represents measurements of Sts 5 given by Grine et al.¹¹, probably obtained after damage caused by digestion of cranial bone in acetic acid. Presumed male individuals are Stw 505, TM 1511, Sts 52, Stw 183, Stw 252, Stw 369 and presumed female individuals are Sts 71, Sts 17, Sts 53, Stw 13, Stw 73.¹¹

Sexual dimorphism in *A. africanus*

Sexual dimorphism of the facial anatomy of *A. africanus* was investigated by Lockwood who recognised Sts 71 as a female adult and Stw 505 as a large male adult; and, on the basis of many facial variables taken together, Lockwood⁷ concluded that the sex of the relatively small Sts 5 individual was 'indeterminate'. This problem relates at least in part to the challenge of distinguishing a relatively large female from a small male individual.¹³

Certain features can help to address this problem. Among the most remarkable facial features of Sts 5 is its prominent glabella which Lockwood⁷ described as 'marked' (as in the case of the male Stw 505), distinct from the slight glabellar prominence in Sts 71 (identified as female). In fact, Lockwood⁷ stated that the glabellar as well as the supraorbital morphology of Sts 5 indicated that this specimen was one of the 'best candidates' for being male (our emphasis).

Lockwood⁷ calculated mean values and standard deviations for 21 craniofacial dimensions for a sample of 13 specimens of *A. africanus* housed at the University of the Witwatersrand and the Ditsong National Museum of Natural History (formerly the Transvaal Museum), including Sts 5 (Table 1). We have calculated standardised z-scores for the facial dimensions of Sts 5 using the means and standard deviations for these dimensions in Sts 5 and the other *A. africanus* specimens measured by Lockwood⁷. The z-scores are calculated by:

$$z = [x - \text{mean for } A. \textit{africanus} \text{ dimensions}] / \text{standard deviation for } A. \textit{africanus} \text{ dimensions}$$

where x is the dimension for Sts 5, for each of the 21 variables listed in Table 1.

Table 1: Measurements of 21 craniofacial distances of Sts 5 in relation to the means and standard deviations for corresponding variables for specimens of *Australopithecus africanus* measured by Lockwood⁷. The z-values for Sts 5 in bold are relatively large in relation to the z-values for Sts 5 for other cranial dimensions.

Cranio-facial measurement		Sts 5 (mm)	Mean <i>A. africanus</i> (mm)	Standard deviation (mm)	z for Sts 5
Orbital height	ORBH	30.5	32.2	2.8	-0.607
Glabellar height	GLAH	75.3	82.1	10.7	-0.635
Upper facial height	UPFH	70	77.8	10	-0.789
Nasal height	NASH	47.6	54.1	7.1	-0.915
Orbito-alveolar height	OALH	49	49.1	5.3	-0.019
Orbito-jugal height	OJUH	57.8	53.8	6.6	0.606
Foraminal height	FORH	38	35.9	3	0.700
Malar depth	MALH	25.1	26.4	3.8	-0.342
Alveolar height	ALVH	30	25.7	3.2	1.343
Superior facial breadth	SUFB	95.1	95.5	8.2	-0.048
Anterior interorbital breadth	ITOB	15.5	16	1.5	-0.333
Bimaxillary breadth	BMAB	105	99.7	8.1	0.654
Interforaminal breadth	IFOB	43.6	44.8	6.4	-0.187
Nasal aperture breadth	NASB	27	24.9	2.5	0.840
Snout breadth	SNOB	45.6	47	5	-0.280
Anterior maxillo-alveolar breadth	ANMB	45.4	46.3	3.3	-0.272
Maxillo-alveolar breadth	MAXB	65.4	64.9	4.7	0.106
Anterior palatal breadth	APAB	33	32.5	2.6	0.192
Palatal breadth	PALB	36.4	35.1	3.8	0.342
Maxillo-alveolar length	MAXL	50.4	51.4	2.2	-0.454
Post-canine maxillo-alveolar length	PMXL	42	41.2	2.1	0.380

Five craniofacial dimensions are relatively large in Sts 5: alveolar height (ALVH), foraminal height, nasal breadth, bi-maxillary breadth and orbito-jugal height. Results are presented in Figure 2 for ALVH and bimaxillary breadth, as two examples.

ALVH in Sts 5 has a value of 30 mm compared with a mean value of 25.7 ± 3.2 mm ($n=11$) for specimens of the species examined by Lockwood⁷. ALVH in *A. africanus* ranges between 21.1 mm and 30.0 mm. Thus Sts 5 has the largest ALVH dimension in this sample of the species. ALVH in Sts 5 (30 mm) is not only larger than the ALVH value of 23 mm in Sts 71 (identified as a female adult), but also larger than the ALVH value of 29 mm in Stw 505 identified as a large male adult. This is also reflected by standardised z-scores (Figure 2). Similarly, in terms of bimaxillary breadth, Sts 5 appears to be closer to that of a male individual (Stw 505), as shown in Figure 2.

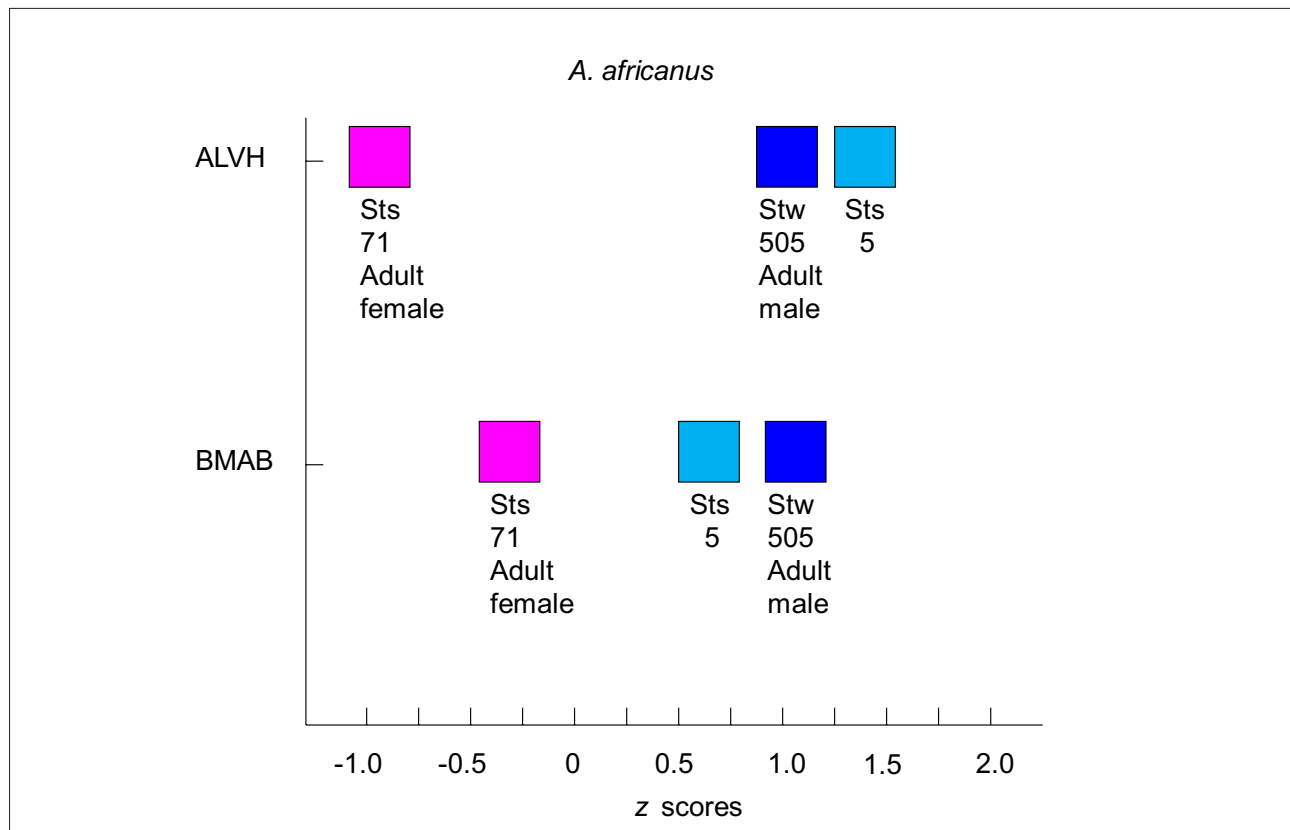


Figure 2: Standardised z-values for Sts 5, compared to other specimens of *Australopithecus africanus*, based on means and standard deviations of alveolar height (ALVH) and bi-maxillary breadth (BMAB).

Conclusion

Both age and sex are factors that would have contributed to variation in growth and development of crania of australopithecines.¹³⁻¹⁶ If Sts 5 was adolescent, as suggested by Thackeray et al.⁸, this would partially account for the relatively small dimensions of some of the facial variables of this specimen, for example nasion height and upper posterior facial height. However, the relatively large values of certain facial variables of 'Mrs Ples' (Figure 2, Table 1) – for example, ALVH as well as other dimensions such as foramina height, nasal breadth, bi-maxillary breadth and orbito-jugal height – can partially be accounted for in terms of Sts 5 belonging to a male individual. The fact that some variables of Sts 5 are relatively large for Sts 5, whereas others are relatively small (as compared to the mean values for *A. africanus*) could be because of a combination of factors associated with both ontogeny and sexual dimorphism.

Despite observations by Villmoare et al.¹⁰ regarding remodelling of anterior maxillary bone, the prominent glabella of Sts 5 and its supra-orbital morphology are not inconsistent with it being male, as noted by Lockwood⁷. Furthermore, the indisputable evidence for open cranial sutures¹⁷ is not inconsistent with the hypothesis that Sts 5 was adolescent at the time of death. These observations, together with the relatively large BL measurement for the canine alveolar diameter (as published originally by Broom et al.¹²), refute the statement that 'there is no evidence to contradict the assertion that 'Mrs Ples' is an adult female'¹¹.

On the basis of the data presented here, we conclude that Sts 5 is a small male rather than a large female individual. This conclusion is relevant to an understanding of Sts 5 in the context of sexual dimorphism in *A. africanus*.

Acknowledgements

J.F.T. thanks the Andrew W. Mellon Foundation, the National Research Foundation (South Africa) and the DST/NRF Centre of Excellence in

Palaeosciences for their support. We thank J. Braga, C. Dean, A.L. Dinat and A.D. Botham for helpful comments.

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