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The partial skeleton StW 431 from Sterkfontein – Is it time to rethink the Plio-Pleistocene hominin diversity in South Africa?

Gabriele A. Macho¹, Cinzia Fornai², Christine Tardieu³, Philip Hopley⁴, Martin Haeusler⁵ & Michel Toussaint⁶

1) *Earth and Planetary Science, Birkbeck, University of London, London WC1E 7HX, England; School of Archaeology, University of Oxford, Oxford OX1 3QY, England*

email: Gabriele.A.Macho@gmail.com; G.Macho@bbk.ac.uk

2) *Institute of Evolutionary Medicine, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland; Department of Anthropology, University of Vienna, Althanstraße 14, 1090 Vienna, Austria*

3) *Muséum National d'Histoire Naturelle, 55 rue Buffon, 75005 Paris, France*

4) *Earth and Planetary Science, Birkbeck, University of London, London WC1E 7HX; Department of Earth Sciences, University College London, London, WC1E 6BT, England*

5) *Institute of Evolutionary Medicine, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland*

6) *retired palaeoanthropologist, Belgium*

email: mtoussaint1866@hotmail.com

Summary - *The discovery of the nearly complete Plio-Pleistocene skeleton StW 573 Australopithecus prometheus from Sterkfontein Member 2, South Africa, has intensified debates as to whether Sterkfontein Member 4 contains a hominin species other than Australopithecus africanus. For example, it has recently been suggested that the partial skeleton StW 431 should be removed from the A. africanus hypodigm and be placed into A. prometheus. Here we re-evaluate this latter proposition, using published information and new comparative data. Although both StW 573 and StW 431 are apparently comparable in their arboreal (i.e., climbing) and bipedal adaptations, they also show significant morphological differences. Surprisingly, StW 431 cannot be unequivocally aligned with either StW 573 or other hominins from Sterkfontein commonly attributed to A. africanus (nor with Paranthropus robustus and Australopithecus sediba). This finding, together with considerations about the recent dating of Plio-Pleistocene hominin-bearing sites in South Africa and palaeoecological/palaeoclimatic conditions, raises questions whether it is justified to subsume hominins from Taung, Makapansgat and Sterkfontein (and Gladysvale) within a single taxon. Given the wealth of fossil material and analytical techniques now available, we call for a re-evaluation of the taxonomy of South African Plio-Pleistocene hominins. Such an endeavour should however go beyond the current (narrow) focus on establishing an A. africanus-A. prometheus dichotomy.*

Keywords - *Plio-Pleistocene hominins, Sterkfontein, South Africa, StW 431, Australopithecus prometheus, Australopithecus africanus, Hominin species diversity.*

Introduction

Our understanding of early hominin species diversity is complicated by a number of taxonomic and stratigraphic uncertainties (Du *et al.*, 2020; Maxwell *et al.*, 2018). Current estimates of taxic diversity are likely underestimates of true

hominin diversity, as implied by phylogenetic diversity estimates (Maxwell *et al.*, 2018) and by the continued announcements of new species over time (e.g., Foley, 2005). Furthermore, new fossil discoveries, especially rarely preserved partial skeletons, such as StW 573 (Clarke, 2019) and StW 431 (Toussaint *et al.*, 2003), will have

Tab. 1 - Compilation of the taxonomy originally proposed for South African Plio-Pleistocene hominins commonly attributed to *Australopithecus africanus*.

DATE	SITE	SPECIES	REFERENCE
1925	Taung	<i>A. africanus</i>	Dart, 1925
1936	Sterkfontein	<i>A. transvaalensis</i>	Broom, 1936
1938	Sterkfontein	<i>Plesianthropus transvaalensis</i>	Broom, 1938
1948	Makapansgat	<i>A. prometheus</i>	Dart, 1948
1950	Taung	<i>A. africanus</i>	Broom, 1950
	Sterkfontein	<i>Plesianthropus transvaalensis</i>	
	Makapansgat	1. (<i>Australopithecus</i>) <i>prometheus</i> Subfamily: Archanthropine 2. <i>Plesianthropus transvaalensis</i>	
1951	Taung, Sterkfontein, Makapansgat	<i>A. africanus</i>	Washburn and Patterson, 1951
1954	Taung	<i>A. africanus</i>	Robinson, 1954
	Sterkfontein	<i>A. africanus transvaalensis</i>	
	Makapansgat	<i>A. africanus transvaalensis</i>	

significant ramifications for the alpha taxonomy and species diversity of poorly-represented fossil groups (e.g. Brocklehurst *et al.*, 2012), like hominins. Here we explore the implications for *Australopithecus* species diversity within South Africa, following propositions that StW 573 and StW 431 should be placed into the same species, separate from *Australopithecus africanus* (Crompton *et al.*, 2018).

The holotype of *A. africanus*, the Taung child (Dart, 1925), is the only hominin fossil from that site. Other specimens traditionally assigned to *A. africanus* are from Sterkfontein and Makapansgat and, more recently, from Gladysvale (Berger *et*

al., 1993). The Taung child was deposited during a period of normal polarity, most likely the Gauss Chron (3.60-2.58 Ma), with the most recent age estimate ~3.03-2.58 Ma (Kuhn *et al.*, 2016). Sterkfontein Member 4 hominin fossils accumulated during the reversed polarity of the Matuyama Chron 2.58-1.95 Ma (Herries *et al.*, 2013, 2019). This potentially makes *A. africanus* the longest-lived Plio-Pleistocene hominin species (Fig. 1), particularly if one considers StW 53 from Sterkfontein Member 5 (Herries & Shaw, 2011: 1.8-1.5 Ma; Granger *et al.*, 2016: 2.18±0.21 Ma) to be *A. africanus* too (Kuman & Clarke, 2000).

Despite initial uncertainty, the scientific community settled in the 1950s that fossils from Taung, Makapansgat and Sterkfontein should be subsumed into a single species (Tab. 1), largely as a means of rationalisation (Wood & Richmond, 2000); it is now “conventional palaeoanthropological wisdom” to do so (Grine, 2019, p. 336). However, in 1988 Clarke began to argue for a second taxon at Sterkfontein, a proposition which has gained traction with the discovery of StW 573 ‘Little Foot’ at Sterkfontein Member 2 (Clarke, 2019; Clarke & Tobias, 1995; Clarke & Kuman, 2019; Partridge *et al.*, 1999, 2003). Clarke assigned StW 573 to *Australopithecus prometheus*, the species name originally proposed for the Makapansgat material (Dart, 1948; Tab. 1). A large proportion of dento-cranial hominin remains from all three sites have since been attributed to either *A. africanus* or *A. prometheus* (Clarke & Kuman, 2019; Fornai *et al.*, 2015), but others have grouped the material differently or have rejected the existence of a second species altogether (for review see Grine, 2013, 2019); some raised the possibility of more than two morphs/species (excluding *Homo*) at Sterkfontein Member 4 (e.g., Lockwood & Tobias, 2002; Schwartz & Tattersall, 2005).

In 1987 the partial skeleton StW 431 was discovered by Alun R. Hughes and his field team and was dated to the late Pliocene by Tim Partridge. In 1988, Michel Toussaint, then Senior Research Officer at the Palaeoanthropology Research Unit, prepared and led a short report about the skeleton for publication in *Nature*. Although the manuscript was accepted (subject to revision) with

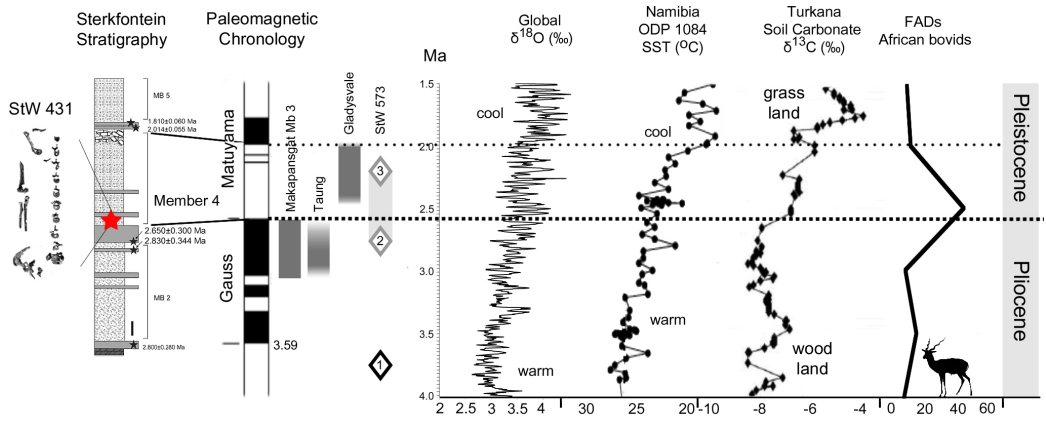


Fig. 1 - Presumed deposition of StW 431 (Toussaint *et al.*, 2003) within the stratigraphy of Sterkfontein (Pickering *et al.*, 2011) and its relation to paleomagnetic chronology. Here we use the ratified definition of the Plio-Pleistocene boundary at 2.58 Ma (Gibbard *et al.*, 2010). The dates for Makapansgat Member 3 (Herries *et al.*, 2019: 3.0–2.6 Ma), Taung (Kuhn *et al.*, 2016), Gladysvale (Herries *et al.*, 2013: 2.4–2.0 Ma) and StW 573 (Granger *et al.*, 2015 [1]: 3.67 ± 0.16 Ma; Kramers & Dirks, 2017 [2] for the maximum age: 2.8 Ma, Walker *et al.*, 2006 [3] for the minimum age: 2.2 Ma) are also shown. These dates are contrasted with the stacked global isotope record (Lisiecki & Raymo, 2005), Atlantic Sea Surface Temperature (SST) off the coast of Namibia (raw data from Marlow, 2000, calculated by deMenocal, 2004), soil carbonates from the Turkana basin (adapted from Bonnefille, 2010) and first appearance data for African bovids (Vrba, 1995). The colour version of this figure is available at the JASs website.

Michel Toussaint as senior author, Tobias withdrew the manuscript from *Nature*. Some 14 years later Tobias published the article with minor alterations under his lead and with no further input from the present authors (Toussaint *et al.*, 2003). Like the original manuscript, the 2003 article concludes that “Stw 431 represents most probably the genus *Australopithecus*, although there is little direct morphological evidence as to the species”, to which Tobias had added that “on grounds of its provenance, morphology and Occam’s razor [...] the new skeleton most likely represents the species *A. africanus*” (Toussaint *et al.*, 2003, p. 222). We contend that the second conclusion does not logically follow from the first, nor from the evidence provided in the article. Hence, we note with interest that Clarke and colleagues suggested removing the partial skeleton StW 431 from the *A. africanus* hypodigm (Clarke & Kuman, 2019; Crompton *et al.*, 2018); they placed it into *A. prometheus*. Yet, taxonomic distinction between *A. africanus* and *A. prometheus* is based on cranio-dental features (Clarke & Kuman, 2019), which StW 431 lacks.

Species attribution on the basis of the postcranium is notoriously difficult however, due to the paucity of hominin postcrania overall and its propensity to high degrees of variability and homoplasy (e.g., Ward, 2013). Moreover, Crompton *et al.* (2018) used the pelvis of StW 431 to make inferences about the positional behaviour of StW 573. These facts call into question whether StW 431 should indeed be attributed to *A. prometheus*, or any other known species (Toussaint *et al.*, 2003). To shed light on this issue here we re-evaluate StW 431 in the context of what is currently known, present some preliminary new data and discuss the results within a broader palaeobiological framework that may inform the taxonomy of South African hominins.

The StW 431 skeleton

StW 431 was the third partial skeleton discovered at Sterkfontein (Toussaint *et al.*, 2003). It comprises an undeformed incomplete pelvis,

the last ten vertebrae, a rib head, and fragments of the right scapula, clavicle, distal humerus and proximal radius and ulna (see Toussaint *et al.*, 2003: Tab.1; Kibii & Clarke, 2003). It is derived from the base of Member 4, i.e. “an older level of Member 4 than Bed D” (Toussaint *et al.*, 2003, p. 217) (Fig. 1). Since 2003 various comparative studies have included StW 431 (usually as a representative of *A. africanus*) in their analyses of the upper limb and shoulder (Bacon, 2000; Drapeau, 2008; Drapeau & Menter, 2020; Green, 2020; Lague, 2014, 2015; Lague & Menter, 2020; Larson, 2007, 2013), while the pelvis has been reconstructed physically (Haeusler, 2002; Kibii & Clarke, 2003) and virtually (Haeusler, 2006), and analysed (Berge *et al.*, 2007; Haeusler, 2002, 2006; Haeusler & Ruff, 2020). Curiously though, an appraisal of the total morphological pattern within StW 431 remains wanting. To redress the balance, here we compile the latest information available on StW 431; our aim is not to assess of the postcranial variation at Sterkfontein *per se* (see Zipfel *et al.*, 2020).

The StW 431 **humerus** and its preservation has been described in several publications (Lague & Menter, 2020; Menter, 2002; Toussaint *et al.*, 2003). In its overall morphology, the StW 431 distal articular surface is comparable to StW 573 (Crompton *et al.*, 2018: Fig. 10, top), StW 602 from Jacovec Cavern (Partridge *et al.*, 2003) and *A. afarensis* (see Johanson *et al.*, 1982). Although joint shape varies considerably among hominins (Hill & Ward, 1988; McHenry & Brown, 2008), the StW 431 trochlear morphology, which combines equal partitioning of its articular surface with a salient lateral margin, would be well-suited to provide stability to the elbow during suspension (Senut, 1981a). Furthermore, the marked supracondylar ridge indicates the presence of a well-developed *m. brachioradialis* and, hence, the capability for powerful pronation and elbow flexion; the insertion area for the digital extensor muscle (i.e. the lateral epicondyle) lies within the upper range of modern humans. Together, these morphologies are in line with propositions that the StW 431 distal humerus was adapted to arboreality (climbing), like StW 573 (Crompton *et al.*, 2018).

As regards morphometric, i.e., taxonomic, diversity of Sterkfontein humeri Lague carried out a number of multivariate statistical analyses that included StW 431. He used either linear measurements taken at the distal articular surface (Lague & Jungers, 1996; Lague, 2015; Lague & Menter, 2020) or 2D cross-sectional shape, i.e. landmark, data of the distal diaphysis (Lague, 2014, 2015; Lague & Menter, 2020). Cross-sectional shape is deemed more useful for taxonomic purposes than linear measurements (Lague, 2015; Senut, 1981b; Susman *et al.*, 2001). As a case in point, a multivariate statistical study of the distal humerus joint morphology of IB-7594 from Melka Kunture, Ethiopia (Di Vincenzo *et al.*, 2015) showed StW 431 to be variably clustered with *Homo ergaster* KNM-WT 15000, to fall between *A. afarensis* (A.L. 288-1, AL 322-13), *A. anamensis* (KNM-KP 271) and *H. ergaster*, to show affinities with *Paranthropus boisei/Homo* sp. (KNM-ER 1504) or to be closest to *Paranthropus robustus* TM 1517 from Kromdraai, South Africa. Conversely, in their cross-sectional shape analyses Lague & Menter (2020) consistently identified two morphological groups within the Sterkfontein Mb4 assemblage (Fig. 2A); a third group probably represents early *Homo* from Sterkfontein Mb5 (Lague & Menter, 2020). In diaphyseal shape StW 431 clusters with StW 38 and StW 124 from Sterkfontein, with the Pliocene *A. anamensis* and *A. afarensis* from East Africa (Toussaint *et al.*, 2003) and with the Pleistocene *P. robustus* from South Africa. When linear measurements of the distal joint surface were used to calculate Procrustes distances, StW 431 and StW 602 are closer to one another than are any other possible pairs of hominins (save for the left and right humerus of A.L. 288-1); compared to samples of five extant hominoids, the distance between StW 431 and StW 602 falls in the lower 3%. This is noteworthy, as StW 602 from Jacovec Cavern has previously been dated to the Pliocene and has been associated with StW 573 (Partridge *et al.*, 2003); Herries *et al.* (2013), however, dated Jacovec Cavern to the Pleistocene. Regardless, MLD 14, presumably the geologically oldest humerus from South Africa used in Lague’s study, and StW 339 from Sterkfontein

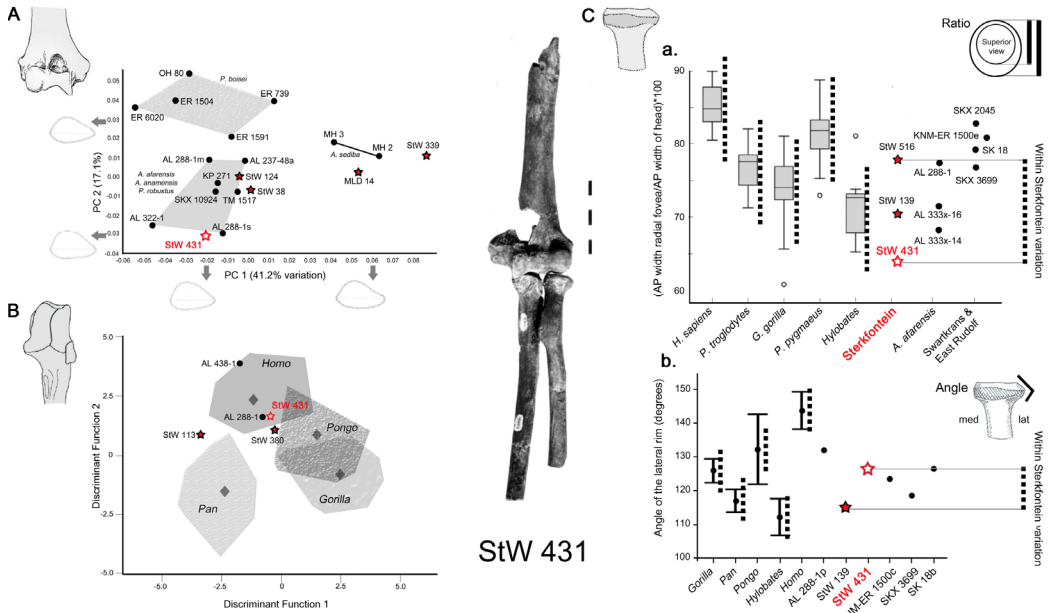


Fig. 2 - Compilation of various comparative quantitative studies that have included StW 431 in their analyses. A. Summary graph of the results obtained for the cross-sectional shape of the distal humerus, modified from Lague & Menter (2020: Fig. 6.6). B. Discriminant analysis of the ulna, using 12 linear measurements, modified from Drapeau & Menter (2020: Fig. 7.14). C. (a) The ratio between the fovea of the radial head and its articular surface, modified from Drapeau & Menter (2020: Fig. 7.21). (b) Angle at the lateral aspect of the head, adapted from Patel (2005: Fig. 6f). To highlight the potential taxonomic significance of the morphological difference(s) within the Sterkfontein material, the maximum difference is mapped out in C (stippled) and is then superimposed onto the plots of extant species [N.B. this is for illustrative purposes only and should not be regarded a statistical analysis]. The colour version of this figure is available at the JASs website.

Mb4 align with *Australopithecus sediba*, which is dated to 1.95-1.78 Ma (Dirks et al., 2010). It thus follows that shape variation of presumed “*A. africanus*” humeri is not only greater than it is for any other hominin taxon, but that this variation does not follow a temporal morphocline. Although a bootstrap analysis found the Sterkfontein humerus variation to exceed the mixed australopithecus sample, it fell within the variation of extant hominoids. Lague & Menter (2020) thus refrained from rejecting the single-species hypothesis, but stressed that the probability of sampling such extreme morphologies is very low, especially when other australopithecine species are used as a yardstick (*ibid.*). As regards functional inferences, humeral cross-sectional shapes are uninformative due to extant hominoids with different locomotor

behaviours overlapping considerably in humerus cross-sectional shapes (*ibid.*).

A comprehensive morphological description of the StW 431 **ulna**, including comparative measurements for all Sterkfontein ulnae currently available for study, is given in Drapeau & Menter (2020). Sterkfontein ulnae, where at least one measurement could be compared with StW 431 are: StW 108, StW 113, StW 326, StW 340, StW 349, StW 380, StW 398a/b, StW 568, StW 571. None of the linear measurements vary greatly among Sterkfontein (CV ranges from 2.07 to 13.51), but there are a few dimensions, where StW 431 falls at the upper/lower end of the range. Notably, the angle defining the orientation of the olecranon and, hence, the *m. triceps brachialis* lever length, is smaller than it

is in the Sterkfontein ulnae StW 113 and StW 380. The angle approaches the modern human condition and is considered advantageous when the forearm is habitually loaded in a flexed position (Drapeau, 2008), perhaps during manipulation (Drapeau & Menter, 2020). However, the trochlear notch in *A. afarensis* KSD-VP-1/1 and A.L. 288-1 also faces antero-superiorly (Lovejoy *et al.*, 2016), as it does in *Ardipithecus*, an above-branch quadruped (Lovejoy *et al.*, 2009). This led Lovejoy *et al.* (2009) to suggest that an anteriorly-facing trochlear notch is the ancestral condition from which great apes diverged. Consistent with propositions that the proximal ulna (or at least aspects thereof) are plesiomorphic is the reduced keeling angle in early hominins like StW 431, StW 113 (Drapeau, 2008), StW 573 (Heaton *et al.*, 2019), *A. afarensis* (A.L. 288-1n, A.L. 438-1, L40-19, KSD-VP-1/1) and BOU-VP-12/1 (Asfaw *et al.*, 1999); all share this condition with modern humans. If apes are indeed derived in ulna morphology, as suggested by Lovejoy *et al.* (2009), simple morphological comparisons for the purpose of determining locomotion in extinct taxa would thus be hampered and, furthermore, it must be considered that early hominin arboreality may not have a modern equivalent. Despite this caveat, on the basis of StW 431 joint morphology, combined with its clear muscle markings that indicate great muscle strength in the upper arm (also seen in StW 113) (Senut & Tobias, 1989; Toussaint *et al.* 2003), we concur with Crompton *et al.* (2018) that StW 431 probably engaged in hand-assisted locomotor behaviours, e.g. arboreality/climbing. The other morphology where StW 431 clearly diverges from the Sterkfontein sample is the large size of its radial facet, although the functional significance (if any) of this feature remains unclear. Overall thus, some few linear dimensions inform functional aspects and, perhaps, character polarity in hominoids (i.e., trochlear notch orientation), but linear measurements are largely silent as regards taxic heterogeneity within Sterkfontein Mb4. Conversely, the case for homogeneity cannot necessarily be sustained when multivariate statistical analyses

are employed (Fig. 2B). A discriminant analysis revealed StW 113 to differ from both, StW 380 and StW 431, as well as from *A. afarensis* (A.L. 438-1, A.L. 288-1). Using posterior probabilities to assign the fossil hominins to an extant species (Drapeau & Menter, 2020:Table 7.7), StW 431 aligned with *Pongo* with a probability of 100%. The figures for StW 380 are: *Pongo* $p=0.64$, *Homo* $p=0.34$, *Pan* $p=0.002$, while StW 113 was assigned to *Pan* or *Homo* with probabilities of 0.68 and 0.32, respectively. StW 431 thus appears to be the most primitive of the Sterkfontein ulnae analysed.

The StW431 **radius** has been described in Toussaint *et al.* (2003) and, recently, in Drapeau & Menter (2020), where comparative data can also be found. Excluding the juvenile StW 105 radius, metric comparisons with StW 431 are possible for Sts 68, Sts 2198b, StW 139, StW 431, StW 516 and StW 528. Again, in linear dimensions the variation among Sterkfontein Mb4 radii is moderate with coefficients of variation (CV) ranging from 0.87 to 15.44; StW 431 generally falls within the Sterkfontein range. Only proximodistal neck length and diaphyseal diameters (medio-lateral and antero-posterior) are larger in StW 431 and are comparable to *A. anamensis* KNM-ER 20419 (Drapeau & Menter, 2020: Tab. 7.2); both specimens fall within the range of chimpanzees in this dimension. This is functionally relevant, as the radial neck length affects the lever length of the *m. biceps brachii*. Overall therefore, and similar to the ulna, some linear dimensions potentially provide information about function, but they are uninformative about taxonomic diversity. Compound measures, on the other hand, provide insights to both, function and taxic heterogeneity (Patel, 2005). Specifically, the extent to which the fovea occupies the articular surface of the radial head differs among extant species with different locomotor modes, but also shows a greater amount of variation at Sterkfontein Mb4 than it does for any other extant group (Fig. 2Ca). StW 431 is closest to *Hylobates* in this ratio, followed by StW 139 and *A. afarensis* (A.L. 333x-16, A.L. 333x-14) (Fig. 2Ca). Other specimens exhibiting reduced

fovea sizes are Sts 68, *A. anamensis* KNM-ER 20419 (Drapeau & Menter, 2020, Heinrich *et al.*, 1993), StW 573 (Heaton *et al.*, 2019) and *P. boisei* OH 80 (Dominguez-Rodrigo *et al.*, 2013). A small fovea in relation to the articular surface increases the stability of the elbow joint by preventing proximo-ulnar displacement (Patel, 2005), which may occur during suspension and during other activities that necessitate powerful wrist and finger flexor muscle action. The distinct joint morphology of the StW 431 radius is further highlighted by the angled lateral rim of its head (Patel, 2005) (Fig. 2Cb); in its degree this angle is comparable to StW 573 (pers. observ.). Although only two Sterkfontein specimens were used in Patel's study, it is noteworthy that the difference between StW 431 and StW 139 exceeds the entire 95% confidence interval of every single comparative species analysed, except *Pongo*. Overall therefore, the radial head morphology clearly sets StW 431 apart from other hominins and aligns it with *A. anamensis*/*A. afarensis*, on the one hand, and with species that are engaged in suspensory behaviours, on the other (Fig. 2Cb).

Published studies on the **axial skeleton** are limited (Benade, 1999; Haeusler *et al.*, 2002; Ward *et al.*, 2020). Like other australopithecines and *Homo*, the lumbar column of StW 431 consists of five vertebrae (Haeusler *et al.*, 2002; Toussaint *et al.*, 2003), whereby the trapezoidal shapes of L1-L3 suggest an effective lumbar lordosis, important for erect trunk posture (Haeusler *et al.*, 2002; Tardieu *et al.*, 2017; Tardieu & Haeusler, 2019). However, the relatively small vertebral cross-sectional areas compared to later hominins (Fig. 3A) point towards limited adaptations to permanently maintain erect postures.

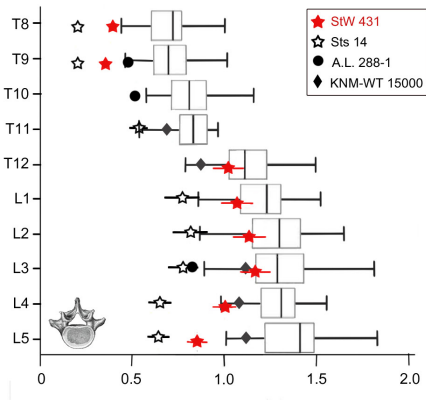
The StW 431 **sacrum** is human-like in its crescent-shaped auricular surface, that reaches the third sacral vertebra. The lateral angles of the alae are strongly developed in both StW 431 and Sts 14 compared to A.L. 288-1, suggestive of powerful sacro-iliac ligaments (Stern & Susmann, 1983). Moreover, the dorsal aspect shows the presence of three well-developed fossae adjacent to the auricular surface for the insertion

of the interosseous ligament, which is similar to Sts 14, but contrasts A.L. 288-1. Yet, the relatively small superior joint sizes of the StW 431 and Sts 14 sacrum compared to later hominins imply that these australopithecines engaged less frequently in upright bipedalism than modern humans (Tardieu *et al.* 2017; Tardieu & Haeusler, 2019).

A recent geometric morphometric analysis of the StW 431 sacrum suggests that its morphology is significantly different from that of Sts 14 (Fornai *et al.*, 2020). The probabilities of sampling morphologies as distinct as Sts 14 and StW 431 from a single species were less than 5% for modern humans, *Pan troglodytes*, *Gorilla gorilla* and *Pongo pygmaeus*. These differences in sacrum morphology between StW 431 and Sts 14 could not completely be explained by developmental age or sexual dimorphism. The results thus provide convincing statistical evidence for taxic heterogeneity at Sterkfontein Mb4.

StW 431 preserves parts of the undistorted **ossa coxae** with the majority of the right ilium, the right and left acetabulum and the left pubis (Haeusler & Ruff, 2020). Further fragments of the left ilium with the auricular surface and the right posterior superior iliac spine were retrospectively identified and joined with StW 431 (Kibii & Clarke, 2003). Although the pelvis of StW 573 is badly crushed (Clarke, 2019), our visual inspection revealed the shapes of the undistorted anterior iliac margin, the anterior inferior and superior iliac spines and the posterior superior iliac spine to be much more chimpanzee-like, i.e. thinner than in StW 431 and Sts 14. The anterior iliac margin of StW 573 also appears straighter and forms almost a right angle with the anterior aspect of the iliac crest. In size, StW 431 (possibly male) and StW 573 (female; Clarke & Kuman, 2019) are comparable and differ from the much smaller sub-adult Sts 14 (possibly female). Superimposition of the StW 431 pelvis reconstruction (Haeusler, 2006; Fornai *et al.*, 2019; Haeusler & Ruff, 2020) onto that of Sts 14 (Haeusler & Schmid, 1995), after scaling to the same pelvic inlet size, reveals the StW 431 sacrum positioned higher

A. Scaled superior endplate area of vertebrae



B. StW 431 vs. Sts 14 pelvis morphology

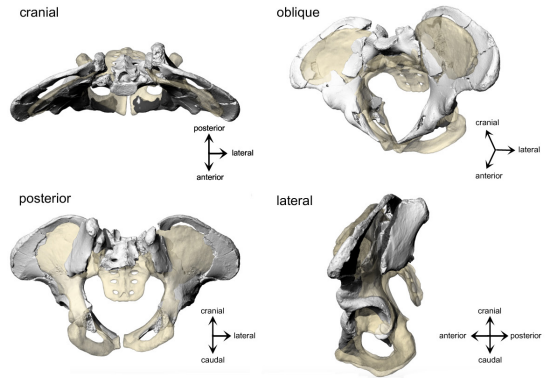


Fig. 3 - A. Vertebral cross-sectional areas were normalized to femur subtrochanteric sizes, i.e. a proxy for body mass, and plotted against a sample of modern human sub-adults (box-plots; $n=42$), showing that StW 431 aligns with *Homo erectus* in relative vertebral size (adapted from Tardieu & Haeusler, 2019). As StW 431 lacks a femur, estimates were derived from regression equations using acetabulum size. B. Superimposition of the reconstruction of the StW 431 pelvis (Haeusler, 2006; Fornai et al., 2019; Haeusler & Ruff, 2020; light grey) with that of Sts 14 (Häusler & Schmid, 1995; transparent yellow) at the pelvic inlet and scaled to the same size of the inlet. Cranial, oblique, posterior, and lateral views. Note the higher position of the sacral base and the wider iliac blades in StW 431. The colour version of this figure is available at the JASs website.

within the pelvis, while the iliac blades are wider and somewhat more posteriorly oriented (Fig. 3B). The difference in relative position of the sacrum seems to exceed the degree expected for sexual dimorphism in modern humans. Because of its higher position relative to the iliac crest, compared to Sts 14, the lumbar spine could have been more mobile. Conversely, the StW 441/465 ilium fragment closely matches the shape of the anterolateral portion of the StW 431 iliac blade, although its size is comparable to Sts 14 (Häusler & Berger, 2001). Hence, body size discrepancies alone cannot explain the morphological differences between StW 431 and Sts 14. Importantly, the partial hipbone Sts 65 (Robinson, 1972) allies with Sts 14 in general morphology, but it is intermediate in size between StW 431 and Sts 14; its relatively narrow greater sciatic notch, robust iliac pillar and marked pubic pecten suggest a male sex (Haeusler & Ruff, 2020; *contra* Claxton et al., 2016). Such high pelvic diversity is unexpected and could imply taxic heterogeneity.

Berge and colleagues (2007) suggested that StW 431 shared the majority of ilium traits with *Paranthropus robustus* from Swartkrans and Kromdaai. However, when the StW 431 ilium is superimposed (and scaled) onto SK 3155 and SK 50 from Swartkrans, this suggestion is not borne out. Accounting for the deformation of SK 50, both *Paranthropus* ilia exhibit similar anterior ilium morphology, distinct from StW 431: their ilia are elongated antero-posteriorly, their anterior inferior iliac spines are weaker and the anterior superior iliac spines are positioned lower.

Discussion

Taxonomic heterogeneity of postcranial remains is commonly assessed on the basis of whether the observed variability among hominin fossils exceeds the within-species variation of an extant species (Fig. 2). An established character polarity, necessary for cladistic analyses, is however lacking for hominins (but see discussions about

the ulnar trochlear notch orientation above). Such a lack is not unusual where closely-related taxa are concerned. Bone, unlike teeth, responds plastically to loading *in vivo*, especially during development and growth, which may ultimately explain the high levels of variability and homplasy in the hominin postcranium (Ward, 2013). For example, in modern humans, the bicondylar angle of the femur develops during childhood as the child learns to walk; the angle, which permits the adduction of the knee-joint is the combined result of growth and gravity (Tardieu & Trinkaus, 1994). This morphological change is accomplished through differential metaphyseal apposition at the distal end of the femoral diaphysis during length growth, with an additional medial metaphyseal apposition on the medial, i.e. more compressed, side (Tardieu, 1999, 2010; Tardieu & Trinkaus, 1994; Shefelbine *et al.*, 2002). However, such ontogenetic changes can only occur if the distal metaphyseal plane of the femur has become flat and, consequently, horizontal during walking, as in the case of australopithecines (Jenkins, 1972; Tardieu & Preuschoft, 1996; Tardieu, 2010). This highlights the complex interplay between genetic determinism (flat metaphyseal plane) and plastic modifications (bicondylar angle) in the postcranium. What is more, evolutionary responses to changing ecological conditions and, specifically, to substrate use can be quite rapid, as exemplified in the *Gorilla* (e.g., Dunn *et al.*, 2014; Schultz, 1927; Tocheri *et al.*, 2016; see also Macho, 2018 for a wider discussion). In case of *G. beringei graueri* and *G. beringei beringei*, for example, the population split occurred only some 10 ka years ago with geneflow persisting for another 5 ka at least (Roy *et al.*, 2014), yet the two (sub)species show distinct, at times non-overlapping, hand and foot morphologies (Dunn *et al.*, 2014; Tocheri *et al.*, 2016). To recall, Sterkfontein Member 4 accumulated over some 500 ka, during which time South Africa experienced many changes/fluctuations in climate and ecology. Hence, increased morphological variability and microevolutionary processes are expected, especially in those skeletal elements that are directly involved in substrate use, i.e. the limbs (Fig. 2) and in food processing,

i.e. the masticatory apparatus (see Martin *et al.*, 2020 for an example in South African *P. robustus*). Sampling biases would further influence the observed variation. Against this backdrop, the variability in upper limb morphology at Sterkfontein Mb4 is unremarkable. Of course, convergence is also possible as, perhaps, in the case of MLD 14 and *A. sediba* humeral cross-sections; the two specimens are separated by >500 ka (Figs. 1, 2A). Despite these caveats, it is noteworthy that Stw 431 consistently clusters with *A. anamensis* and *A. afarensis* (and South African *P. robustus*) and, frequently, appears even more primitive than any of these (Fig. 2). Hence, we continue to maintain that StW 431 should only be assigned to *Australopithecus* at the genus level (Toussaint *et al.*, 2003; see discussion above). Inspection of the pelvis confounds the issue of possible species attribution even further.

Both the partial skeleton StW 431 (this study) and StW 573 (Clarke, 1999, 2013; Clarke & Tobias, 1995; Crompton *et al.*, 2018) exhibit morphologies that are compatible with adaptations to a partially arboreal environment (i.e., climbing) or, alternatively, that had not yet been selected against climbing adaptations. However, inferences drawn from the pelvis are equivocal, not least because Crompton *et al.* (2018) used the pelvis of StW 431 to make inferences about the locomotor and positional behaviour of StW 573. On morphological grounds we tentatively conclude that the pelvis of these two individuals are not comparable. Regardless, what is unexpected, and arguably more important here, is the amount of pelvic variation found **within** the Sterkfontein Mb4 assemblage. From a macroevolutionary standpoint, primate pelvic morphology integration is relatively low and evolvability is high (e.g., Betti, 2017; Grabowski, 2013; Lewton, 2012), but at the micro-level the pelvis is likely more constrained than is the appendicular skeleton (see above). Although hominins appear to share a common pelvis bauplan, that is established early during ontogeny (Zirkle & Lovejoy, 2019), some plastic responses occur, especially during ontogeny as the infant learns to sagittally balance the trunk on the lower limbs (Boulay *et al.*, 2005;

Tardieu *et al.*, 2013). During this process, the angle of pelvic incidence increases from about 25° in new-borns to 54° in adults, concomitant with an increase in the curvature of the sacrum. This angle increases in association with the increase of the lordosis, leading to a tight correlation between these two parameters in adults. The result is a more and more backwards positioning of the sacral plate in relation to the acetabulae, essential for an efficient sagittal balance. In the pelvis of Sts 14 and MH2 (*A. sediba*) this angle almost reaches the mean values of humans (Tardieu *et al.*, 2017, 2019). The strong lumbar curvature of Sts 14 is concordant with its quite high value of incidence, but in Stw 431 the lumbar curvature appears less expressed and would suggest a lower incidence. This supports suggestions that StW 431 was less well adapted to bipedality (see above). This, and bearing in mind the more constrained nature of the pelvis relative to the limbs, together with the results obtained for the sacrum (Fornai *et al.*, 2020), raises the possibility that South Africa supported a greater hominin diversity during the Plio-Pleistocene than is currently recognised.

It has long been considered that the morphological variation within Sterkfontein Member 4 (Fig. 1) is likely due to the temporal mixing of various fossil assemblages (Vrba, 1982), accumulated over hundreds of thousands of years and many precessional cycles (Hopley & Maslin, 2010), which resulted in recurrent ecological shifts and paraphyletic speciations (Brain, 1985). Conversely, *A. prometheus* was originally assigned to the Pliocene material from Makapansgat (Dart, 1948; Tab. 1). Debate over the age of the *A. prometheus* partial skeleton StW 573 (Fig. 1; see also Grine, 2019) has seen the skeleton attributed to the Pliocene at 3.67±0.16 Ma (Bruxelles *et al.*, 2019; Granger *et al.*, 2015; Stratford *et al.*, 2017) and also to the early Pleistocene at ~2.2 Ma (Kramers & Dirks, 2017; Walker *et al.*, 2006); StW 431 may straddle the Plio-Pleistocene boundary (Fig. 1).

The Plio-Pleistocene transition is associated with considerable global climatic changes, notably cooling, climatic unpredictability and an increase in seasonality (e.g., deMenocal, 2004;

Potts, 2013). Major shifts in low-latitude insolation started with the onset of the Northern Hemisphere glaciation around 3.3 Ma and intensified ~2.8 Ma (deMenocal, 1995). This latter date coincides with the turnover in many mammalian lineages (e.g., Bobe *et al.*, 2002; Bobe & Behrensmeyer, 2004; Vrba, 1995), the emergence of the earliest *Homo* at ~2.8 Ma (Villmoare *et al.*, 2015) with the oldest flaked stone tool technology emerging shortly afterwards at ~2.6 Ma (Braun *et al.*, 2019), the emergence of *Paranthropus aethiopicus* at around 2.73 Ma and the extinction of *A. afarensis* at 2.88 Ma (Wood & Boyle, 2016; Du *et al.*, 2020). In southern Africa, changes in Atlantic sea surface temperatures during the Plio-Pleistocene (Marlow *et al.*, 2000) also led to increased climate variability and an extension of arid vegetation after 2.7 Ma (Dupont *et al.*, 2005; Fig. 1). It seems improbable that South African Plio-Pleistocene hominins remained unaffected by these environmental trends. Instead, hominin species turnover is expected although, as in other eurybiomic taxa, there may have been some time lag (Macho, 2014). Whether the morphological differences between StW 573 and StW 431 suffice to invoke species distinction or, perhaps, represent a morphocline from the presumably older (StW 573) to younger (StW 431) hominins cannot be resolved at present. Attribution of StW 431 to *A. africanus* is not warranted either, not only because of the morphological evidence (Figs. 2, 3).

In 1988, Tobias assessed the synapomorphies of South African hominins and concluded that the holotype of *A. africanus*, the Taung child, is derived and “approximates...the apomorphic state of *A. robustus/A. boisei* and *H. habilis*” (Tobias, 1988, p. 303); he assumed Taung to be no older than the material from Swartkrans and Kromdraai (~1.6–2 Ma). Paleomagnetic evidence now revealed Taung to have accumulated during normal polarity (Herries *et al.*, 2013; 2019; Hopley *et al.*, 2013; Kuhn *et al.*, 2016). Hence, Taung is likely contemporary with Makapansgat Member 3 between 3.03–2.58 Ma. It is noteworthy that Clarke has consistently argued for *A. prometheus* to be derived towards, and ancestral to, the robust lineage (Clarke, 1988, 1994, 2013). If the Taung child is

derived towards the robust condition too (Tobias, 1988) and radiometric dating further confirm a Pliocene age, the taxonomy of Plio-Pleistocene hominins in South Africa will need to be revisited (Tab. 1). At present, we reserve judgement on this issue, not least because of the different ecological settings in which these hominins were found. Although eurybiomic, it is questionable whether a hominin species could have successfully navigated such varied habitats in the Pliocene and/or whether (and when) ecological corridors between these locations existed in the past. Suffice to say, in order to attribute StW 431 (and other specimens) to *A. africanus*, we first need to ascertain whether the holotype of *A. africanus* differs in morphology and ecological specificity from Sterkfontein Member 4 fossils, as well as in geological age (Fig. 1). If it does, the lumping of specimens into *A. africanus* in the 1950s (Tab. 1) may have been counterproductive for scientific progress. It may ultimately be found that Broom (1929) was not only right about the Pliocene age of Taung, but also about its uniqueness (Broom, 1950).

In summary, the unexpected morphological variation found here shines new light on three unresolved issues in palaeoanthropology: (1) the effects of the Plio-Pleistocene transition on species turnover in South Africa, (2) the morphological variation expected if species diverge and then fuse over relatively short (geological) time scales and (3) the effects of microevolutionary changes in response to ecological changes/fluctuations.

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Author contributions

Conceptualization (GAM, MT); Methodology (GAM, CF, MH); Formal analysis (GAM, CT, MT, pelvis: CF, MH); Investigation (GAM, CF, CT, PH, MH, MT); Management (GAM); Visualization (GAM, pelvis: CF, MH); Validation (PH); Writing, review and editing (GAM, CF, CT, PH, MH, MT).

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