



# Locomotor and taxonomic diversity of Sterkfontein hominins not supported by current trabecular evidence of the femoral head

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Based on trabecular microarchitecture of two hominin femoral head fossils, Georgiou et al. (1) advocate for locomotor and taxonomic diversity at Sterkfontein, South Africa. They describe the trabecular pattern of StW 522 (*Australopithecus africanus* from Sterkfontein Member 4, dated to 2.6 to 2.1 Ma) (2) as human-like, while arguing that StW 311 displays a great ape-like pattern and, due to its potential origin from Member 5 (2.0 to 1.8 Ma) (2), warrants classification as either *Paranthropus robustus* or *Homo* sp. We argue that these conclusions are premature and unsupported by their analyses.

First, the two fossils plot close together in the principal component analysis of relative bone volume/total volume (BV/TV) distribution in the femoral head at positions intermediate between recent *Homo* and extant great apes (see figure 5 in ref. (1)). Since the intraspecific difference within all extant comparative taxa is markedly larger than the difference between StW 522 and StW 311, the quantitative analysis of the trabecular distribution does not justify different taxonomic allocations or locomotor classifications.

Conversely, the recognition of qualitative trabecular patterns with a supposed human-like single posterolateral bundle in StW 522 and an ape-like pattern with both an anterolateral and posterolateral bundle in StW 311 largely depends on how the BV/TV values are scaled to their own data range. We suspect that taphonomic processes biased the representation of the trabecular pattern of StW 522, resulting in a visually misleading heat map that undermines the similarity between the fossils by attributing different

colors to comparable densities, thus obscuring the potential presence of an anterolateral bundle.

Furthermore, it remains unclear whether StW 311 actually originates from Member 5 as previously suggested (3). In fact, a reinterpretation of the cave infills demonstrated that Member 4 extends farther to the west than previously thought, while collapses later created cavities and erosional channels, which could have led to an interdigitation of Member 5 infills within Member 4 breccias (3–5). Thus, grid square R53, where StW 311 was found, comes to lie just at the supposed border of Member 5 with Member 4 (which is in the neighboring grid square R52) (3), although it is unknown whether this border between the members also applies to the depth of 14'5" below datum, where StW 311 was unearthed. The complex stratigraphy and the effect of crevices are well demonstrated by the distribution of the StW 431 skeleton remains: 38 of its 39 elements were found in just two adjacent square yards but vertically distributed over 2.1 m (6). Hence, attribution of StW 311 to a specific member is difficult.

Moreover, the classification proposed by Georgiou et al. (1) would be at odds with inferences for a more open paleoenvironment during the time of Member 5 as well as the more modern body proportions of early *Homo* (7, 8).

Collectively, although we do not dismiss the possibility of taxonomic heterogeneity within Sterkfontein, we feel the current data provided by Georgiou et al. (1) are insufficient to confirm locomotor diversity at this locality.

1 L. Georgiou et al., Evidence for habitual climbing in a Pleistocene hominin in South Africa. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 8416–8423 (2020).

2 R. Pickering et al., U-Pb-dated flowstones restrict South African early hominin record to dry climate phases. *Nature* **565**, 226–229 (2019).

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Author contributions: M.H. designed research; M.H., N.M.W., V.A.K., and C.F. performed research; M.H., N.M.W., V.A.K., and C.F. contributed new reagents/analytic tools; M.H., N.M.W., V.A.K., and C.F. analyzed data; and M.H., N.M.W., V.A.K., and C.F. wrote the paper.

The authors declare no competing interest.

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First published October 20, 2020.

- 3 K. Kuman, R. J. Clarke, Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. *J. Hum. Evol.* **38**, 827–847 (2000).
- 4 J. T. Robinson, Sterkfontein stratigraphy and the significance of the extension site. *S. Afr. Archaeol. Bull.* **17**, 87–107 (1962).
- 5 C. A. Ogola, *The Sterkfontein Western Breccias: Stratigraphy, Fauna and Artefacts*, (University of the Witwatersrand, Johannesburg, South Africa, 2009).
- 6 M. Haeusler, C. B. Ruff, "Pelvis" in *Hominin Postcranial Remains from Sterkfontein, South Africa, 1936–1995*, B. Zipfel, B. G. Richmond, C. V. Ward, Eds. (Oxford University Press, Oxford, 2020), pp. 181–201.
- 7 M. Haeusler, H. M. McHenry, Body proportions of *Homo habilis* reviewed. *J. Hum. Evol.* **46**, 433–465 (2004).
- 8 M. Haeusler, H. M. McHenry, Evolutionary reversals of limb proportions in early hominids? Evidence from KNM-ER 3735 (*Homo habilis*). *J. Hum. Evol.* **53**, 383–405 (2007).