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Syeda, Samar M., Tsegai, Zewdi J., Cazenave, Marine, Dunmore, Christopher J., Skinner, Matthew M. and Kivell, Tracy L. (2022) *Reconstructing hand use in Australopithecus sediba and Homo naledi: mapping variation in cortical thickness across the proximal and intermediate phalanges*. In: *PaleoAnthropology. 12th Annual Meeting of the European Society for the Study of Human Evolution. Abstracts. Tübingen, 22-24 September 2022. Podium Presentation Session 3. 2022 (2)*. p. 588. Paleoanthropology Society

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Poster Presentation Number 82, Session 2, Friday 18:15

Reconstructing hand use in *Australopithecus sediba* and *Homo naledi*: mapping variation in cortical thickness across the proximal and intermediate phalanges

Samar M. Syeda¹, Zewdi J. Tsegai¹, Marine Cazenave^{1,2,3}, Christopher J. Dunmore¹, Matthew M. Skinner^{1,4}, Tracy L. Kivell^{1,4}

1 - Skeletal Biology Research Centre, School of Anthropology and Conservation, University of Kent, Canterbury, UK · 2 - Division of Anthropology, American Museum of Natural History, New York, New York, USA · 3 - Department of Anatomy, Faculty of Health Sciences, University of Pretoria, South Africa · 4 - Centre for the Exploration of the Deep Human Journey, University of the Witwatersrand, Johannesburg, South Africa

The inferred diversity of manual behaviors within the hominin lineage is exemplified by the mosaic morphology of the hands of *Australopithecus sediba* and *Homo naledi* [1-2]. Derived morphological features present in both fossil hominins point to human-like manipulation abilities, while curved fingers with well-developed flexor sheath ridges (FSRs) suggest the continued use of their hands for climbing and grasping [1-2]. The internal bone structure may reflect habitual locomotor and/or manipulative loading of the fingers due to bone's ability to (re)model throughout life in response to mechanical load [3], and thus variation in phalangeal cortical bone distribution holds the potential for reconstructing hand use among fossil hominins.

We investigated the distribution of phalangeal cortical thickness in extant great apes, *A. sediba* and *H. naledi* to inform our reconstruction of fossil manual behaviours. The sample included microCT scans of the proximal and intermediate phalanges of rays II-V of *Gorilla gorilla* (N=21), *Homo sapiens* (N=37), *Pongo pygmaeus* (N=9), *Pan* sp. (N=24), *A. sediba*, and *H. naledi* (Hand 1). We used the R package morphomap [4] to map diaphyseal cortical thickness and conducted a principal component analysis (PCA) on the cortical thickness values to explore patterns across species.

Results show clear separation among extant taxa across all phalanges. The extant taxa are separated along PC1, with some overlap between the African apes reflecting a pattern of thickness localised to the FSRs, with a different pattern of overall thickness of the shaft in *Pongo* and in humans. PC2 reflects differences in the location of greatest thickness; in African apes this occurs in the FSRs throughout the shaft, whereas in *Pongo* this is distally located with some dorsal thickening, and in humans it is primarily in the dorsodistal region of the shaft. The proximal phalanges of *A. sediba* consistently fall close to the African apes, reflecting maximum thickness localised to the FSRs, while *H. naledi* consistently falls close to humans, reflecting thickening of the dorsal region of the shaft and the FSRs distally. The intermediate phalanges of both fossil species fall between the African ape and human distribution, reflecting a thickening of the dorsal region of the bone and the FSRs, which are located in the proximal-to-midshaft region. The distribution of the *A. sediba* intermediate phalanges differs from those of *H. naledi* in that the thickening on the palmar surface extends further distally. This is consistent with external morphology of *A. sediba* intermediate phalanges that possess unusually long and prominent FSRs.

Overall, we show that variation in phalangeal cortical bone distribution clearly separates extant hominoid taxa that differ in their locomotor and manipulative behaviours. Within this comparative context, *A. sediba* proximal phalanges are most similar to the African ape cortical signal and intermediate phalanges are intermediate between all extant taxa. Along with a high degree of phalangeal curvature and prominent FSRs, this morphology better distributes stress and reduces strain on the bone during flexed finger loading (e.g., during climbing or suspension) [5]. In contrast, while *H. naledi* phalanges are most similar to humans in their cortical distribution, this appears to contradict their high degree of curvature, which may be a functional indication of arboreal locomotion [5]. The *H. naledi* phalanges indicate a hand uniquely adapted for arboreal behaviours in the degree of curvature but not cortical distribution, differing to that of extant great apes and *A. sediba*.

For access to specimens we thank the following individuals/institutions: Max Planck Institute for Evolutionary Anthropology (C. Boesch), J.-J. Hublin (College de France); Museum für Naturkunde - Leibniz Institute for Evolution and Biodiversity Science (F. Mayer, C. Funk); Powell-Cotton Museum (I. Livne); Royal Museum for Central Africa (E. Gilissen); University of Florence (J. Moggi-Cecchi, S. Bortoluzzi); Johann-Friedrich-Blumenbach-Institute for Zoology and Anthropology, Georg-August University, Göttingen (B. Grosskopf); Frankfurt Senckenberg Museum (V. Volpato); University of the Witwatersrand (L. Berger, B. Zipfel); Science Academy of the Czech Republic (J. Svoboda). This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No. 819960 and No. 101025719).

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