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Mechanical loading of primate fingers on vertical rock surfaces

Mechanical loading of finger bones (phalanges) can induce angular curvature, which benefits arboreal primates by dissipating forces and economising the recruitment of muscles during climbing. The recent discovery of extremely curved phalanges in a hominin, *Homo naledi*, is puzzling, for it suggests life in an arboreal milieu, or, alternatively, habitual climbing on vertical rock surfaces. The importance of climbing rock walls is attested by several populations of baboons, one of which uses a 7-m vertical surface to enter and exit Dronkvlei Cave, De Hoop Nature Reserve, South Africa. This rock surface is an attractive model for estimating the probability of extreme mechanical loading on the phalanges of rock-climbing primates. Here we use three-dimensional photogrammetry to show that 82–91% of the climbable surface would generate high forces on the flexor tendon pulley system and severely load the phalanges of baboons and *H. naledi*. If such proportions are representative of vertical rock surfaces elsewhere, it may be sufficient to induce stress-mitigating curvature in the phalanges of primates.

Significance:

- We present the first three-dimensional photogrammetric analysis of a vertical rock surface climbed by a non-human primate, the chacma baboon (*Papio ursinus*).
- Our results show that a large proportion of a vertical rock wall would compel crimp and slope hand positions during climbing – grips that could explain the extraordinary phalangeal curvature expressed by a Middle Pleistocene hominin, *Homo naledi.*

Introduction

Bone is a dynamic tissue, and repeated mechanical loading can induce changes to its density and angular curvature. For example, loading stresses from vertical climbing and suspensory locomotion can increase the curvature of primate finger bones (phalanges) during growth and development.[1-3] Greater curvature is advantageous to arboreal primates because it dissipates forces and dampens recruitment of muscles during finger flexion, thus economising energetic costs and simultaneously lowering the risk of falling. Phalangeal curvature is therefore widely viewed as a measure of arboreality among primates – it is a classic form-functional trait that informs our interpretations of behaviour and ecology in the fossil record[1-7] (but see Wallace et al.[8] for a counterexample).

Upsetting this orthodoxy is the hand of *Homo naledi*, recovered from Rising Star Cave, South Africa, in 2013–14 and described in 2015.[9] The degree of phalangeal curvature is astounding, with an included angle (θ) that far exceeds that of modern humans (Figure 1). Such curvature would normally and unequivocally suggest an arboreal milieu[3], but there are at least two reasons to doubt such an inference for *H. naledi*. First, the phalanges are relatively short, resulting in humanlike hand proportions.[9] No arboreal primate has phalanges that are both short and curved; it is an aberration that confounds conventional interpretation. Second, existing specimens of *H. naledi* are dated to the Middle Pleistocene between 335 kya and 241 kya.[12] Nearby faunal assemblages of comparable age – those of Gladysvale[13] and Lincoln Cave, Sterkfontein[14] – favour habitat conditions that resemble those of today, i.e. a mix of acacia woodland and grassland, neither of which would incentivise a strongly arboreal ecology.[15]

So, what was *H. naledi* doing with its hands? Voisin et al.[16] examined the shoulder girdle of *H. naledi* and reported morphological traits associated with vertical climbing and suspension. But given the inferred habitat conditions, they discounted arboreal activities and argued instead for 'movement across and climbing on rocky walls'[16(p.2)]. Voisin et al.'s hypothesis is intriguing given that rock climbing puts high forces on finger flexor tendons, especially during the 'crimp' position (Figure 2).[17-20] This position puts extreme stress on the flexor tendon pulley system, a series of five annular (A1–A5) and three cruciate ligaments (C1–C3) that resist bowstringing of the tendons. In other words, the pulley system holds the tendons close to the bone, effectively converting linear force into torque that produces flexion at the metacarpophalangeal and interphalangeal joints (Supplementary figure 1).

Ruptures of A2[17] and other severe pulley injuries are common among human rock climbers[21], and a testament to the mechanical loading of phalanges. Indeed, frequent rock climbing is known to cause geometric and cortical thickening of the phalanges[22] and it may induce greater curvature, at least hypothetically. Tan et al.[18] calculated the benefits of greater phalangeal curvature for reducing tendon and pulley stresses of fingers in the crimp position; however, affirming increased curvature among rock climbers is difficult because it is challenging to measure angles from radiographs of living subjects. Another model system is needed.

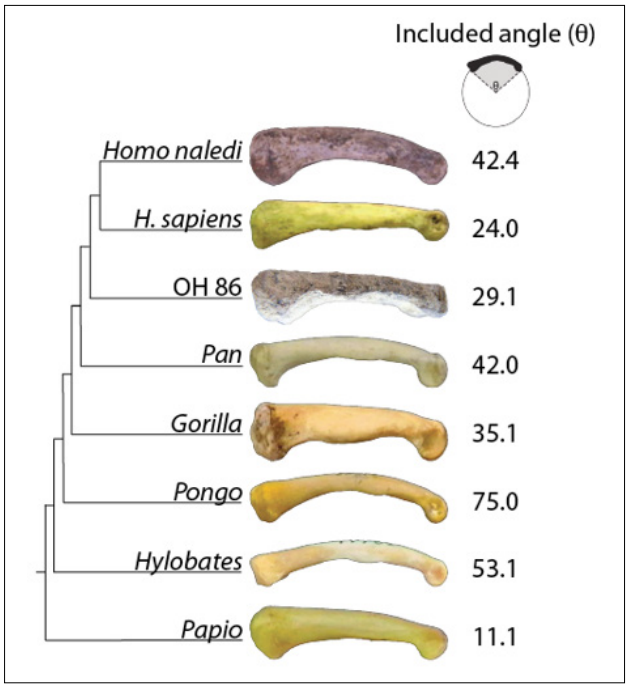


Figure 1: Cladogram of baboons (*Papio*), gibbons (*Hylobates*), orangutans (*Pongo*), gorillas (*Gorilla*), chimpanzees (*Pan*), an indeterminate hominin (OH 86), and genus *Homo*. The branches are tipped with representative photographs of manual proximal phalanges in lateral view, together with mean degrees of curvature of the proximal phalanx, as measured by computing the included angle (θ). Data sources for θ: Stern et al.[10] (humans), Jungers et al.[6] (non-human primates), and Domínguez-Rodrigo et al.[11] (OH 86). The θ value for *H. naledi* was calculated by one of us (S.M.S.) as the mean of digits II (42.71), III (46.49), IV (48.44), and V (31.88) of hand 1, the right hand of an adult (see Kivell et al.[9] for further details).

Some populations of baboons and chimpanzees enter cave systems to avoid predators and/or regulate body temperature.[23-34] Some caves are only accessible by climbing sheer cliffs.[28] For example, Marais[23] described a group of chacma baboons (*Papio ursinus*) and their daily ascent to a cliffside cave opening ≈150 m high. His vivid account speaks to the mechanical loading of fingers: 'they had to go more than a mile hanging only by their fingers to the [cliff] ledge; their hind feet against the smooth surface'[23(p.63)]. In some cases, baboons must negotiate vertical rock surfaces within a cave. For example, at Misgrot Cave in Thabazimbi, South Africa, baboons face a perilous 17-m vertical descent from ground level (Figure 3)[32], whereas those entering Dronkvlei Cave, De Hoop Nature Reserve, South Africa, descend 7 m to access the interior (Figure 4). Baboons use both caves regularly as overnight sleeping sites; Dronkvlei is used on 28% of nights.[30]

Study aims and design

Dronkvlei Cave is an appealing model system for exploring the topography of a vertical rock surface and its potential to load primate fingers. Here we ask a basic question: what proportion of a vertical rock wall would, when climbed, force the distal phalanges of *P. ursinus* (and, hypothetically, *H. naledi)* into a crimp or slope grip position? It is a thought experiment that leaves formal comparative measures of phalangeal curvature in *P. ursinus* as a priority for future research. To answer our question, we used three-dimensional (3D) photogrammetry to detect and quantify concavities in the surface that range from a minimum graspable depth (determined as the length of the third distal phalanx) to a minimum crimpable depth (determined as the sum length of the third intermediate and distal phalanx) – i.e. depths of 11–25 mm for *P. ursinus* and 14–37 mm for *H. naledi* (Table 1).

Methods

Data acquisition

Photogrammetry is a low-cost method for extracting accurate measurements from photographs. It is well suited for producing 3D models of irregular surfaces, such as cave walls.[36] To obtain photographs of the rock surface climbed by baboons, we used metal irrigation piping to construct a temporary T-shaped scaffold. The cross pipe was mounted

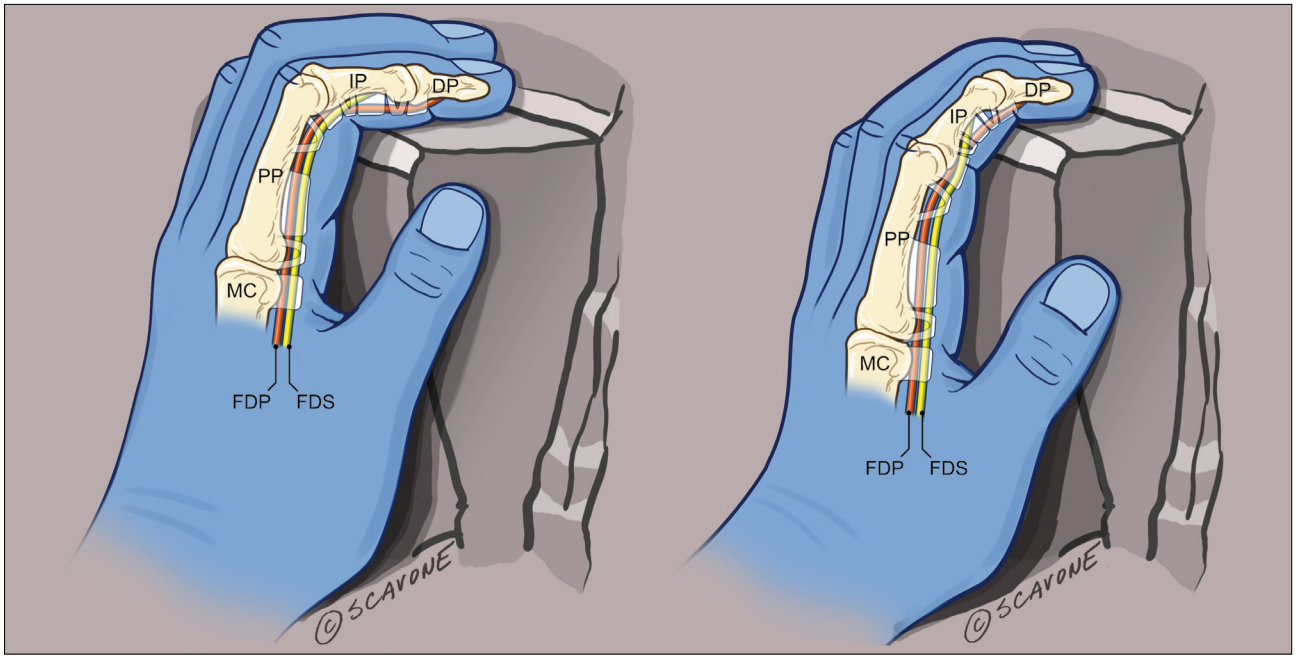
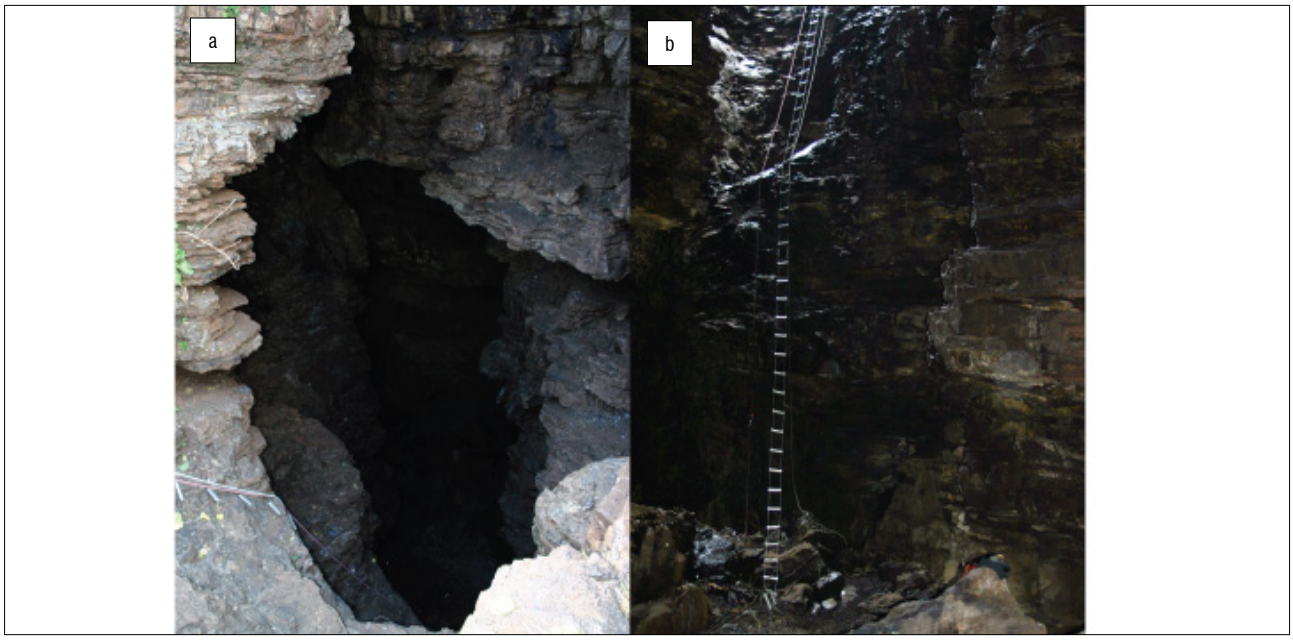


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Anatomical labels: MC, metacarpal; PP, proximal phalanx; IP, intermediate phalanx; DP, distal phalanx; FDS, flexor digitorum superficialis; FDP, flexor digitorum profundus

Figure 2: Common handholds on rock surfaces and the underlying flexor tendon pulley system. Up to 90% of climbers use the crimp grip (*left*), where the proximal interphalangeal (PIP) joints are flexed from 90° to 100° and the distal interphalangeal (DIP) joints are either fully extended or hyperextended.[17] The second most common grip is the slope grip or open hand grip (*right*), which is distinguished by extended or slightly flexed PIP joints and flexion (50° to 70°) of the DIP joints.[17]



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Figure 3: Misgrot Cave in Thabazimbi, South Africa. Chacma baboons (a) enter the cave at ground level before negotiating (b) a steep vertical descent of 17 m.

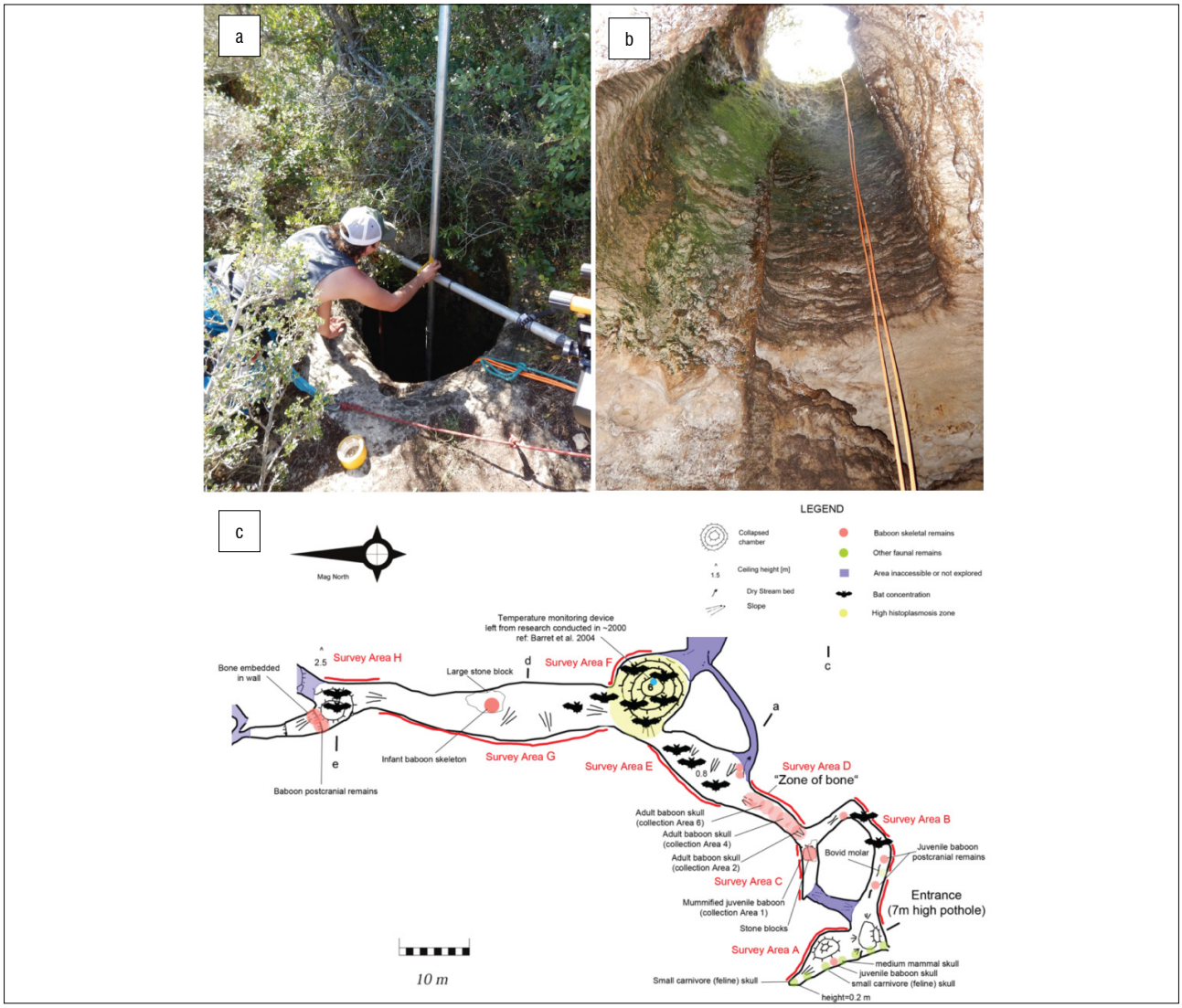


Figure 4: Dronkvlei Cave, De Hoop Nature Reserve, South Africa. Chacma baboons (a) enter the cave through a 1-m opening at ground level before negotiating (b) a vertical descent of 7 m. The preferred surface of the baboons is clearly differentiated by a dark patina. This surface area is the focus of our analysis. In addition, we produced (c) a map of the interior, noting the presence of skeletal remains. Some remains are now accessioned at the University of the Witwatersrand (repository prefix U.W., site designation 116, see Zipfel and Berger[35] for cataloguing details).

at the cave opening and fixed to a vertical pipe that extended to the shaft floor (Figure 4a), where it was weighted to minimise lateral excursions. We hitched a digital camera to this pipe so that photography occurred from a fixed central axis, and we mounted ground control points to the rock surface. We abseiled into the cave to operate the camera, aiming for 80% overlap between serial photos in the horizontal and vertical planes.

Table 1: Lengths (in mm) of the third intermediate and distal phalanx of the hand. Most measures of *Papio ursinus* were obtained from specimens in the School of Anatomical Sciences, University of the Witwatersrand (see Supplementary table 1 for catalogue numbers and corresponding measurements).

Species (*N* individuals)	Intermediate phalanx mean ± 1 SD (range)	Distal phalanx mean ± 1 SD (range)	Source
Papio ursinus (19)	14.4 ± 1.7 (12.2–19.7)	10.8 ± 1.3 (9.2–13.8)	This study
Homo naledi (2)	22.2 (21.8–22.6)	14.4	Kivell et al.[9], Kivell, unpublished

Photogrammetry

We processed the image set (n=354) with Agisoft Metashape Pro (formerly Photoscan Pro), a common package used in archaeological research.[37-39] Due to logistical constraints in the field, we did not record spatial data for each ground control point, so the model was scaled to real-world dimensions by using the targets as scale bars, and manually oriented. Manual orientation is suboptimal for any calculations that rely on the slope of the wall, but it should not affect the local depth calculations described below. After alignment, dense cloud construction, and texture application, we trimmed the 3D model to the area used for climbing (Figure 4b) and exported it as an orthophoto (Figure 5a) and digital elevation model (DEM) with an arbitrary local coordinate system. We brought the resulting geotiffs, both with sub-millimetre resolution, into ArcGIS and SAGA GIS for further processing and visualisation.

Depth processing

In ArcGIS, the DEM raster treats the surface of the rock wall as vertical elevation data. To calculate the local relative depth of each raster cell in the rock wall, we used focal statistics with a small neighborhood, and maximum elevation as the statistics type, to create a raster of the local maximum height of the wall, and then smoothed that raster again with focal statistics over a wider neighborhood, creating a smoothed idealised model of the maximum height of the local surface of the cave. We subtracted the original DEM from this idealised surface to find the local difference between each cell and the average nearest 'maximum' value. Finally, we queried this raster of local depths for cells in two ranges (11–25 mm for *P. ursinus* and 14–37 mm for *H. naledi*) and used this value to calculate the total area of each range.

Results and discussion

The entrance to Dronkvlei Cave is a useful model for exploring potential stresses on the flexor tendon pulley system and phalanges of primates. We focused our analysis on the surface area climbed by baboons – representing 5.98 m^2 (Figure 5a) – and we show that crimp- and slope-inducing handholds are distributed relatively evenly across a nearly vertical plane (Figure 5b). However, the total area of such holds differed between the two species.

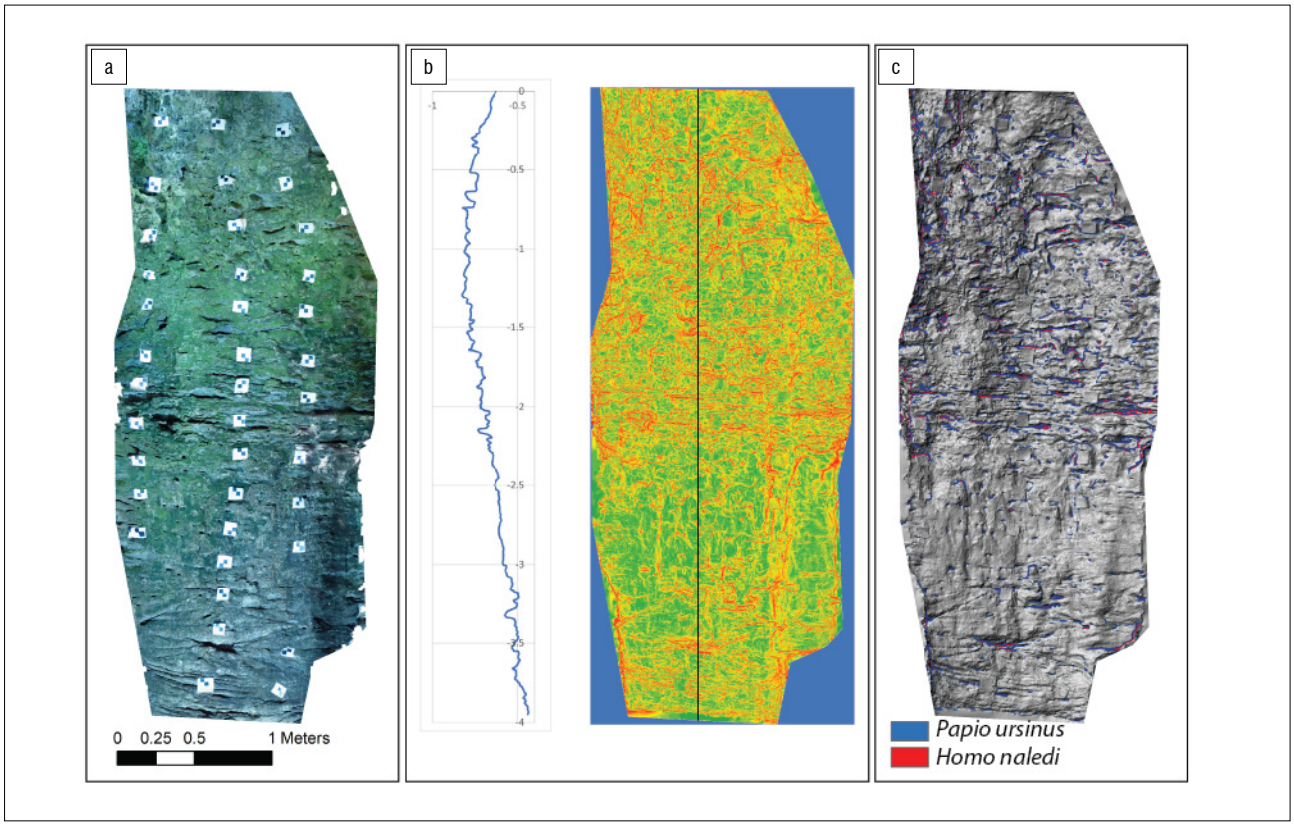


Figure 5: Section of vertical rock wall at the entrance to Dronkvlei Cave, South Africa. It is a surface that baboons climb regularly (Figure 4b) and the focus of our analysis. (a) Composite orthophoto and ground control points. (b) Digital elevation model to visualise the rugosity and verticality of the surface (the cross-sectional profile on the left corresponds to the black line). Red surfaces slope outward, whereas green surfaces are relatively flat. (c) Hillshaded visualisation; the colours correspond to handholds that are likely to compel weight-bearing finger flexion by chacma baboons (*Papio ursinus*) and *Homo naledi*. The 3D mesh and raw photo are available in MorphoSource (https://www.morphosource.org/projects/000348582).

For *P. ursinus*, we calculated an area of 0.494 m^2 (2 514 603 cells of 0.44 mm x 0.44 mm), and for *H. naledi* an area of 0.353 m^2 (1 795 106 cells of 0.44 mm x 0.44 mm), with an overlap of 0.282 m^2 (Figure 3c). Thus, 6–8% of the total surface area, when gripped, is expected to generate high forces on the flexor tendon pulley system and severely load the phalanges of both primate species. Such an estimate is conservative, however, as a large proportion of the rock surface is smooth and unclimbable. When we subtract surface depths of <11 mm and <14 mm from the total, the total graspable surface area is reduced to 0.602 m^2 and 0.390 m^2, respectively, meaning that as much as 82% (*P. ursinus*) or 91% (*H. naledi*) of usable handholds would produce forces that would favour greater phalangeal curvature.

The significance of our finding is a matter of speculation – even at 8% of the total surface area, the rock wall of Dronkvlei Cave is a non-trivial source of phalangeal loading when extrapolated over a lifetime. The average life expectancy of a female baboon that survives to adulthood is 12.1 years in Amboseli, Kenya, and 19.7 years in Gombe, Tanzania (with record longevities of 27 years at both sites).[40] If we use these parameters to estimate an average life expectancy of ≈16 years for *P. ursinus*, and given that animals climb 12 m to enter and exit Dronkvlei Cave on 28% of days[30], an individual would encounter ≈1.6 km of crimp- and slope-grip-inducing surfaces over its lifetime [(16 years × 365 days × 0.28) × (12 m × 0.08 m)]. It is a crude estimate of mechanical 'loading' on the flexor tendon pulley system and distal phalanges, but it invites an analysis of phalangeal curvature in this population.

More instructive perhaps are the mummified/skeletal remains of baboons in Misgrot Cave.[34] These individuals climb greater distances than those at Dronkvlei (Figure 3b), but the frequency of overnight use is unknown. Still, each climbing bout carries great risk. Falling from heights as high as 17 m is likely to cause severe morbidity or outright mortality[15], although the rugosity of the dolomitic surface may differ from the limestone surface of Dronkvlei Cave in crucial ways, affecting risk. Misgrot Cave is a promising site for studying the natural history of why, and the mechanics of how, baboons climb vertical rock surfaces, as well as the effects on their finger bones. Another promising study system lies in the lava tubes of Mount Suswa, Kenya, the site of an oft-cited analysis by Simons[24], who described the skeletal remains of baboons (*P. anubis*) and leopards, sometimes commingled, at the base of vertical shafts. Remains of baboons continue to accumulate there, serving as a tourist attraction.

So, did *H. naledi* climb vertical rock surfaces regularly? Answering this question is beyond reach at present, but their bodies, alive or dead, negotiated at least two steep walls of dolomite to arrive in the Dinaledi Chamber of Rising Star Cave: an entry point through the roof of Postbox Chamber and a 12-m fissure ('The Chute').[12] Our results suggest that climbing these surfaces would have compelled the use of crimp or slope grips to some extent, and Tan et al.'s[18] model of flexor tendon pulley forces suggests that *H. naledi* would have enjoyed a 23% reduction in phalangeal forces compared to modern humans (Supplementary figure 2). Such findings indicate that high phalangeal curvature – whether mechanically induced or genetically mediated[8] – would have conferred advantages to *H. naledi* during rock climbing.

A limitation of our model system approach is that *H. naledi* (weighing ~40 kg[41]) was heavier than *P. ursinus* is now and probably longer-lived, factors that would load its fingers to a greater extent. Yet the pedal phalanges of *H. naledi* express the same curvature as those of *Papio*, which is '[possibly] indicative of elevated pedal grasping ability'[42(p.4)]. Thus, both species are equipped to grip vertical rock surfaces with their feet – a prudent means of distributing body mass and mitigating forces on the fingers during climbing.

We conclude by acknowledging that rock-climbing baboons are an imperfect model for interpreting the curious anatomy of *H. naledi*, but we would argue that detailed studies of their functional anatomy and climbing kinematics, together with systematic measures of the rock surfaces used, are promising areas of future research.

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Competing interests

We have no competing interests to declare.

Authors' contributions

M.C.Everett: Conceptualisation, methodology, data collection, data curation, data analysis, writing – the initial draft, writing – revisions, project leadership. M.C.Elliott: Methodology, data collection, writing – revisions. D.G.: Methodology, data collection, writing – revisions. A.C.H.: Methodology, data analysis, writing – the initial draft. S.M.S.: Data collection. J.C.: Methodology, writing – the initial draft. B.Z.: Data curation, data collection, writing – revisions. J.M.D.: Conceptualisation, student supervision, writing – the initial draft, writing – revisions. N.J.D.: Conceptualisation, student supervision, writing – the initial draft, writing – revisions.

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