We the hunted

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Classic depictions of human evolutionary ecology cast *Homo* as predator and other hominins, including *Paranthropus robustus*, as prey. Such hypotheses rest on a small number of fossils that exhibit evidence of carnivore predation, including the iconic SK 54 cranium from Swartkrans in South Africa. Here we demonstrate that the SK 54 cranium shares its closest affinities with *H. erectus* sensu lato rather than *P. robustus.* Demonstrating that *Homo* was prey for leopards at Swartkrans weakens the historically significant hypothesis that *Homo* was better able to avoid predation because of being behaviourally and technologically advanced compared to *Paranthropus*. Subsequent ideas about hominin palaeobiology derived from this hypothesis warrant reconsideration.

Significance:

- The small sample of early *Homo* from southern Africa is increased by the allocation of the SK 54 cranium to that genus.
- Evidence from Swartkrans suggests that *Homo* was prey for leopards.
- Hypotheses concerning the biology, behaviour, and technological capabilities of *Homo* and *P. robustus* stemming from Brain's seminal work, *The Hunters or the Hunted?*, should be reassessed.

Introduction

SK 54 is a partial hominin cranium that was recovered from the ~1.9–1.8 Ma palaeocave deposits of Swartkrans Member 1 Hanging Remnant in South Africa in 1949 and subsequently prepared by John T. Robinson.[1-3] This specimen is an iconic hominin fossil that has influenced both the development of the discipline of cave taphonomy and narratives concerning how multiple hominin species shared the landscape of Pleistocene southern Africa.[1] Brain[1,2] described two carnivore puncture marks on its left and right parietal bones (Figure 1) whose location, size, and spacing indicate strongly that they were inflicted by a leopard (famously, the marks conform well to the canines of leopard fossil SK 349 from the same deposit).[4] Leopards are known to be predators rather than scavengers[1,5], and thus this specimen preserves direct evidence of the predation of hominins. Even if future taphonomic analyses conclude that these puncture marks were not caused by a predator, the historical significance of Brain's[4] assessment remains. For this reason, although there are other hominin fossils from Swartkrans that exhibit carnivore modification marks[1,2,6,7], no other specimen has figured as centrally in hypotheses concerning carnivore predation on hominins than SK 54[1,2,6,8-17]. The specimen has previously been attributed to *Paranthropus robustus*[1], and that taxonomy has remained largely unchallenged and current[18-21]. Brain[1] did not explain the reasoning underlying this taxonomic decision, although he did note that the specimen appeared to possess a relatively small brain. Tobias[22] and Clarke[23] noted that SK 54 lacked certain derived circumorbital morphology characteristic of *P. robustus,* but did not assign the specimen to a different species and interpreted the variation as a product of ontogeny. We do, however, note that Braga et al.[24] have recently questioned SK 54's attribution to *P. robustus* based on differences between its circumorbital and postorbital morphology and that of the juvenile *P. robustus* specimen KW 9000/9600 from Kromdraai, and we largely agree with their conclusions. Notwithstanding this recent reassessment, SK 54's attribution to *P. robustus* has underwritten hypotheses that australopiths were prey while early *Homo* were transforming into predators, as elucidated in Brain's[2] classic monograph, *The Hunters or The Hunted?* Here we provide further taxonomic evidence that challenges this narrative.

Materials and methods

Our analysis of SK 54 results principally from morphological observations conducted in South Africa in 2018, 2019 and 2022 on original fossil specimens of *Australopithecus africanus* (Taung 1; Sts 5, Sts 71, Stw 505), *A. sediba* (MH 1), *P. robustus* (DNH 7, DNH 155, DNH 152, SK 46, SK 48 and SK 52) and early *Homo* (Stw 53, SK 847) curated at the Evolutionary Studies Institute of the University of the Witwatersrand, and the Ditsong Museum of Natural History. Because SK 54 is a subadult, we closely compared SK 54 to available subadult specimens of *H. erectus* sensu lato (DNH 134) and a description of *P. robustus* (KW 9000/9600) from southern Africa. We additionally utilised published descriptions and/or casts of subadult specimens attributed to *H. erectus* (Mojokerto 1 and KNM-ER 42700) and *P. aethiopicus* (L338y-6).

Results

SK 54 is a fragmentary neurocranium preserving parts of the occipital, frontal, and left and right parietal bones. The degree of sutural fusion suggests that the specimen may have been a juvenile at the time of death. The specimen is plasticly deformed such that it is not possible to assess overall neurocranial shape, and this deformation precludes meaningful quantitative analysis. One measurement that can be confidently taken on the specimen is cranial vault thickness, which we assess as being minimally 3.3 mm at the posterior aspect of the parietal bone just above the squamosal suture. This measurement compares favourably to that of the subadult *H. erectus* specimen DNH 134 (3.2 mm) and is thinner than that of the subadult *P. robustus* specimen KW 9000 / 9600 at 4.0 mm.[24] Although *H. erectus* specimens are often characterised as having thick vaults, this characteristic is more strongly expressed in Asian rather than early African specimens[25] and in any case the taxonomic valence of this trait is compromised by SK 54's likely young ontogenetic age (see also Antón[26]). Notably, vault thickness in the vicinity of bregma is qualitatively thin in Modjokerto[27], a juvenile specimen conventionally attributed to *H. erectus*[26]. SK 54's

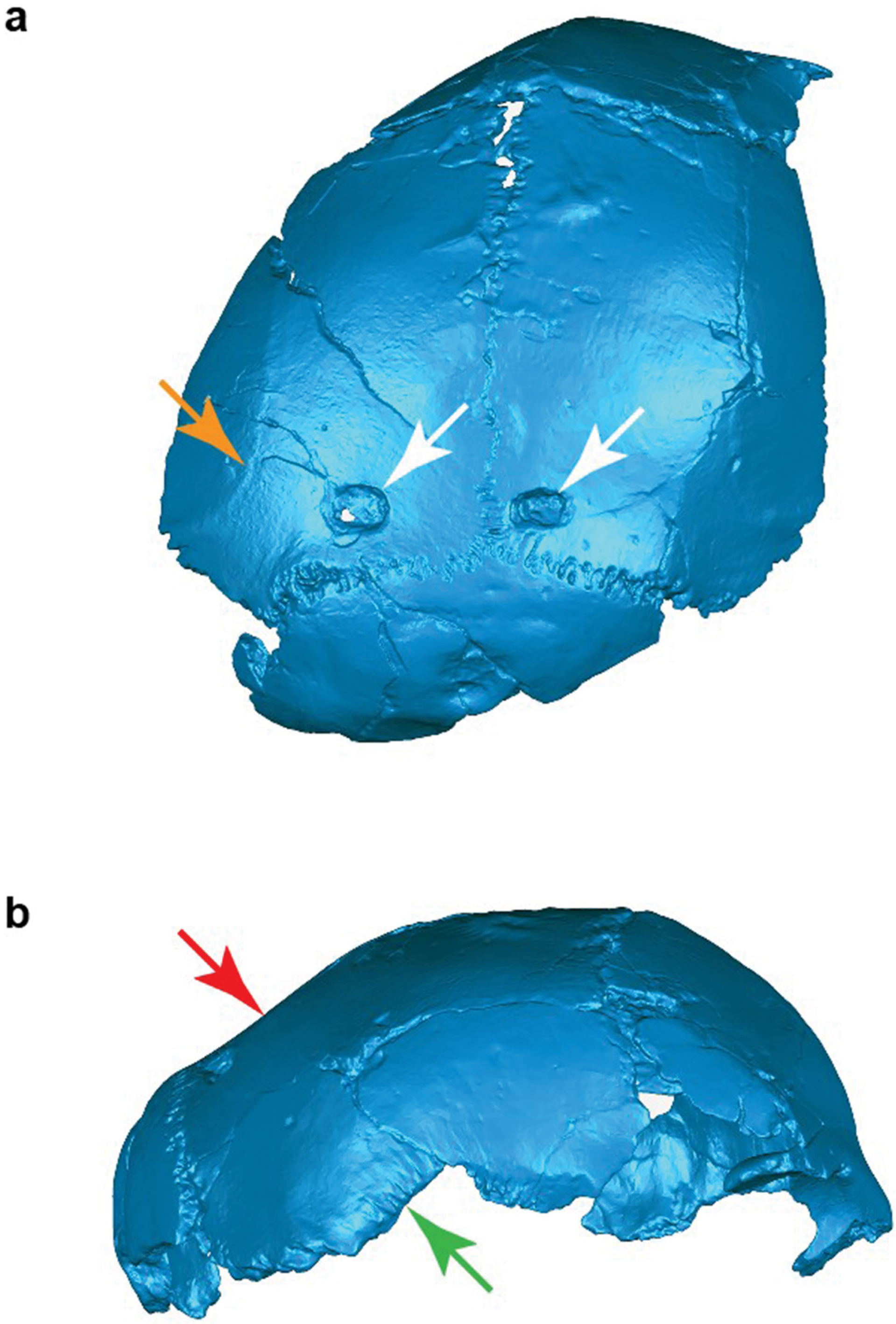

Figure 1: Three-dimensional surface scans of SK 54 shown in (a) superoposterior and (b) lateral views. White arrows indicate puncture marks. Orange arrow indicates the left superior temporal line positioned laterally far from the sagittal suture. Red arrow indicates likely pre-lambdoidal flattening. Green arrow indicates the posterior aspect of the parietal portion of the squamosal suture that is straight and shows minimal overlap with the temporal bone.

neurocranial vault is distorted on both the right and left sides, making a digital reconstruction highly subjective and of little diagnostic value. The individual evidently had a generally small brain, but estimates of its cranial capacity cannot be made with confidence.[28] Nonetheless, aspects of preserved morphology challenge its traditional taxonomic attribution to *Paranthropus* and suggest affinities with *Homo.* The temporal lines are well separated and laterally positioned (Figure 1) – a configuration that is incompatible with adult *P. robustus* specimens that exhibit either a sagittal crest (in putative male specimens) or nearly convergent temporal lines (in female specimens).[29] The KW 9000/9600 fossil from Kromdraai provides the only evidence for temporal line configuration in a subadult *P. robustus*, and the superior temporal line is clearly closer to midline in the vicinity of bregma[24] than the weakly expressed and more laterally positioned temporal lines exhibited by SK 54. Similarly, the juvenile *P. aethiopicus* specimen L338y-6 (whose sutures are as or more open than those of SK 54, implying a coarse similarity in age) exhibits well-developed, strongly convergent temporal lines[30], further suggesting that SK 54 may not be *Paranthropus.* Kimbel et al.[20] have previously argued that SK 54 preserves rugose *striae parietalis* that they suggest are correlated with a high degree of overlap between the temporal squama and parietal at the squamosal suture. They based their inference on the observation by Rak[31] that juvenile *H. sapiens* from a Holocene population

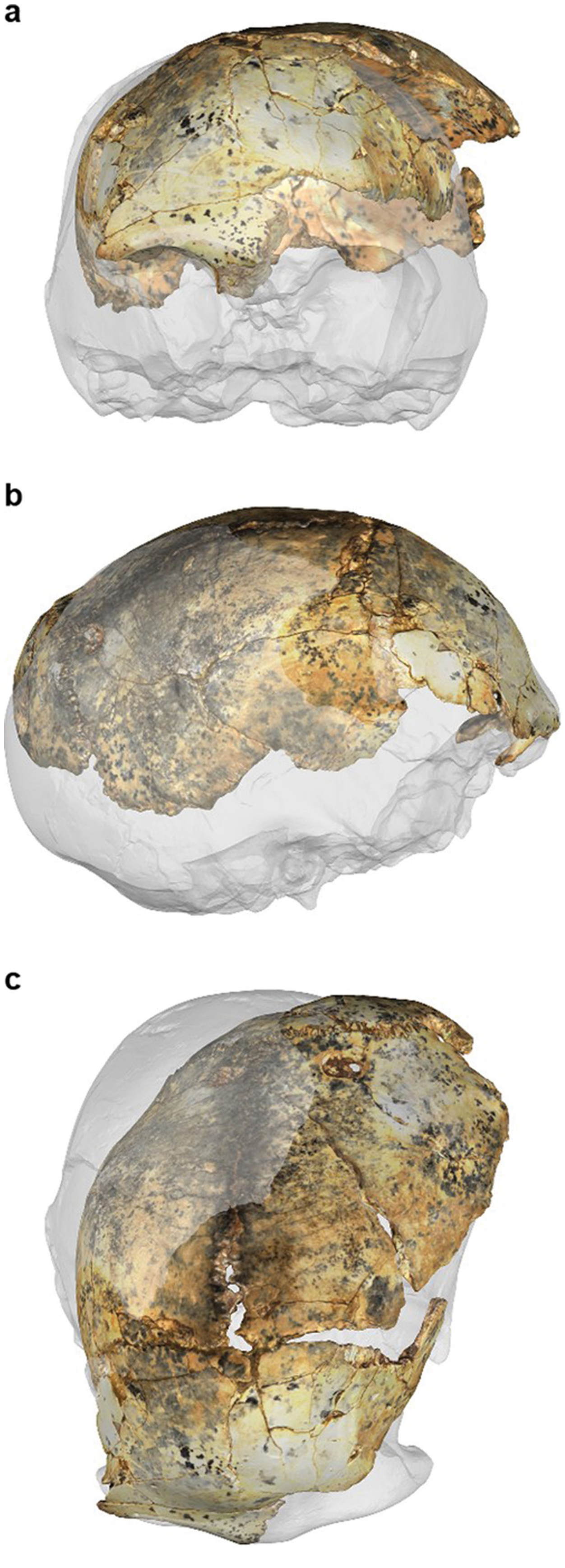

Figure 2: Superimposition of a three dimensional surface scan of SK 54 onto a cast of KNM-ER 42700 (transparent, scaled to 90% of its size) in (a) frontal, (b) right lateral, and (c) superior views. The specimens are aligned at their right orbital margins and circumorbital regions, which are the least distorted portions of SK 54.

exhibited fine rather than rugose striae. However, the length of the *striae parietalis* preserved in SK 54 (Figure 1) are notably less than those of L338y-6 and adult *P. robustus* specimens DNH7, DNH152, and DNH155, and both the length and rugosity of SK 54's striae closely resemble the condition in the juvenile *H. erectus* sensu lato specimen DNH 134. In our assessment, enough of the inferior bevelled edge of the right parietal (Figure 1) is preserved to indicate that the temporal and parietal portions of the squamosal suture would not have overlapped extensively, unlike the extensive overlap seen in both adult and juvenile *Paranthropus*.[30-32] Finally, *contra* Kimbel et al.[20], the very wide separation of the superior temporal lines on the frontal bone argues against the inference that a frontal trigon would have developed in adulthood.

Two discrete traits of SK 54 may suggest affinities with *Homo erectus* sensu lato. The preserved posterior portion of the squamosal suture is straight as it rises anteriorly and superiorly (Figure 1). Rightmire et al.[33] note that, "A low temporal squama with a straight upper border passing downward toward asterion is a consistent marker for [H. erectus]." Moreover, SK 54's parietal bones are flattened anterior to the lambdoidal suture (Figure 1), although there is distortion present in this region. Pre-lambdoidal flattening is a derived characteristic of many *H. erectus* specimens; in their description of the skulls from Dmanisi, Rightmire et al.[33] state that:

> *There are also good indications that the Dmanisi skulls share at least a few (specialized?) characters with populations from the Far East. An example is provided by parasagittal flattening of the posterior vault. Flattening or even depression of the parietal surfaces is pronounced at Dmanisi, and it is common in the [H.] erectus crania from Sangiran in Java.*

The fragmentary and deformed nature of SK 54 precludes a definitive taxonomic allocation but, heuristically, superimposing SK 54 onto *H. erectus* sensu lato specimen KNM-ER 42700[34] demonstrates a striking similarity between the two specimens (Figure 2). We agree with Braga et al.[24] that a provisional assignment of SK 54 to *Homo* seems warranted, and we argue that a tentative species-level allocation to *H. erectus* sensu lato is plausible. This assignment adds to the evidence for *Homo* at Swartkrans Member 1 Hanging Remnant that includes the juvenile cranium SK 27 that Clarke[35] reclassified from *P. robustus* to *Homo*, and the suggested partial skull consisting of individual fossils SK 80, SK 846b, SK 847[36] and sometimes also the mandible fragment SK 45[2] . At 1.9–1.8 Ma[3], these fossils are slightly younger than the 2.04–1.95 Ma DNH 134 cranium from Drimolen Main Quarry that also shows affinities to *Homo erectus*[32].

Discussion

Brain's work on cave taphonomy remains seminal, and his taphonomic assessment linking SK 54 with leopard predation is currently unchallenged. Assuming that those taphonomic conclusions remain valid, our taxonomic reassessment of SK 54 demonstrates that *Homo* was also prey for leopards in the early Pleistocene, and this characterisation could not be further removed from classic depictions of *Homo* the hunter and *Paranthropus* the hunted. Allocating SK 54 to *Homo* tempers the impetus for supposing that early *Homo* and *P. robustus* were differentially predated because of the former's behavioural and technological advancement.

It is impossible to know with certainty how the history of palaeoanthropology might have been different had SK 54 been recognised as *Homo* when it was first discovered, but it is reasonable to infer that the impact of such a realisation would have been significant. Only 6 years prior to the publication of Brain's[1] now-classic paper, the description of the newly discovered *H. habilis*[36] included an assessment of the relative tool-making skills and trophic positions of the new species and its contemporary, *Zinjanthropus boisei* (i.e. *P. boisei*):

> *While it is possible that Zinjanthropus and Homo habilis both made stone tools, it is probable that the latter was the more advanced tool maker and that the Zinjanthropus skull represents an intruder (or a victim) on a Homo habilis living site.*[37]

Shortly thereafter, the highly influential *Man the Hunter* conference was held, followed by the publication of its accompanying edited volume[38,39] that described hunting as a fundamentally important human adaptation. Brain's[2,3] interpretation of SK 54, based on an incorrect taxonomy, was therefore compatible with the thinking of the time, but it could have instead been a powerful challenge to conventional wisdom. Ideas, like species, evolve and have descendants, so the evidence presented here should prompt a reassessment of hypotheses concerning the biology, behaviour, and technological capabilities of *Homo* and *Paranthropus* that are derived from earlier ideas positing *Homo* as predator and *Paranthropus* as prey (for example, Lockwood et al.[29]). Our findings complement a recent zooarchaeological analysis showing that the appearance of *H. erectus* is not associated with increased evidence for hominin carnivory.[38]

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Competing interests

We have no competing interests to declare.

Authors' contributions

J.M.M., A.B.L., A.I.R.H., S.E.B., and D.S.S. wrote the paper. J.M.M. and D.S.S. additionally participated in conceptualisation, data collection, sample analysis, and data analysis.

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