PROGRESS

Making sense of the first decade of *Homo naledi*

Bernard Wood and Paul Pettitt

It has been just over ten years since the first fossils attributed to *Homo naledi* were recovered from the Rising Star Cave system in South Africa's Cradle of Humankind. The hominin fossil evidence for *H. naledi* shares a distinctive combination of primitive and derived morphology, yet for a time-averaged fossil sample it is remarkable for its relatively low level of variation. Thus—unusually for paleoanthropology—there has been little pushback against the decision to recognize a single novel taxon for all of the material recovered from the Rising Star Cave system. However, almost everything else about *H. naledi*—its age, burial context and behavior—has been controversial. How did the bones find their way into the various subterranean chambers, especially the Dinaledi subsystem that is >70m from the current entrance? How old are the hominin fossils, and are they all broadly of the same age? How and where does *H. naledi* fit into conventional narratives of human evolutionary history? And most controversially, what was *H. naledi*'s cognitive world like? Did it have the capacity for symbolic culture? Despite its small brain, was it capable of deliberately generating and controlling fire? Was it capable of deliberately burying conspecifics? And, finally, what should we conclude about the success, or otherwise, of the unconventional way in which research at the Rising Star Cave system has been disseminated?

The Dinaledi subsystem provides the bulk of the evidence for *H. naledi*, with 1550 fossils from a minimum of 15 individuals recovered from the Dinaledi Chamber (Berger et al., 2015), along with additional fossils from the Hill Antechamber and locality U.W. 110 (Brophy et al., 2021; Elliott et al., 2021). The rest of the evidence, 131 fossils from at least three, and likely four, individuals, comes from the nearby, but separate, Lesedi Chamber (Hawks et al., 2017). Additional hominin discoveries have been reported from the Dinaledi subsystem (Berger et al., 2023a), and from elsewhere in the system (Elliott et al., 2021), but at the time of writing no details of these have been published.

How did the hominin remains get into the cave, and what has happened to them since?

The Rising Star Cave system as currently understood consists of at least 4000 linear meters of passageways, as well as other spaces of differing sizes and shapes (Elliot et al. 2021) all within the Malmani Subgroup dolomites. Currently there are four known entrances to the system, three open and one sealed (Elliot et al. 2021, figure 1). The Dinaledi subsystem, which is 30m below surface and >70m in a straight line from the nearest current opening, is connected to the larger cave system by the Chute (Elliot et al. 2021). The initial report by the project's geologists suggested that the sediment accumulation within the Dinaledi subsystem was the net result of multiple cycles of sediment-flowstone entering the cave followed by its removal and dissolution, with some of the residual sediment finding its way into the Dinaledi Chamber (Dirks. et al., 2015). Most of the hominin evidence in the latter derives from the Unit 3 sediments, and the same authors suggest that the Dinaledi Chamber was relatively isolated when Unit 3 was deposited, with little or no sediment input from other chambers in the subsystem, and they are emphatic that the adjacent Dragon's Back Chamber is unlikely to have been the source of the hominin fossils in the Dinaledi Chamber. All this being said, is it possible, as others (e.g., Val, 2016) have suggested, that another entrance, now sealed, was how the sediments and hominin remains entered the Dinaledi subsystem. Karstic caves are dynamic systems, with the potential that substantial-sized blocks can fall from the roof and block one, or more, of any former entrances, located either to the south (Elliott et al. 2021) or to the west of the Dinaledi chamber.

The densely-packed *H. naledi* fossils in the Dinaledi Chamber, with almost no associated non-hominin fauna (Elliott et al. 2021), contrasts with the sedimentary context of other hominin-bearing cave systems in the Cradle of Humankind, where hominins are but one component of a rich mammal faunal record, that typically accumulated in debris cones subsequently brecciated by flowstone. As suggested by the Rising Star project geologists, because the hominin fossils are mostly contained in unconsolidated reworked muddy sediments, with clear evidence of more than one episode of primary deposition, caution is called for when interpreting both the stratigraphy and the age of the fossils (Dirks et al. 2017).

The question is not whether periodic low-energy water transport occurred—it clearly did—but how effective it was at moving hominin remains around within the cave's subsystems.

The extent and pattern of bone breakage inflicted on the hominin fossils, presumably because the bones were moved around after deposition (Dirks et al. 2016) is inconsistent with minimal transport, but it could be explained if the hominin skeletal remains had entered the cave from another entrance. It is premature to interpret the location of the hominin remains as reflecting a long and arduous journey in the dark, dragging corpses to a favored depositional location. Natural deposition cannot be ruled out.

How old is *Homo naledi*?

The initial paper addressing the geological and taphonomic context of *H. naledi* devoted a single five-line paragraph to the age of the fossils (Dirks et al., 2015). The authors explained that because of the mixed stratigraphic signatures due to the reworking of the sediments, they were reluctant to, in their words, speculate on the age of the deposit, suggesting instead that they were working on developing dating methods that could "circumvent this problem" (Dirks et al., 2015, 30).

Subsequent efforts to address the stratigraphic context and the dating of the *H. naledi* fossils concluded the hominin fossils are relatively recent (Dirks *et al.,* 2017). All of the hominin fossils in the Dinaledi Chamber were recovered from the same horizon, sub-unit 3b. The sediments in that sub-unit were dated using optically stimulated luminescence (OSL), the overlying flowstones were dated using U-Th and paleomagnetism, and three *H. naledi* teeth were dated using U-series and electron spin resonance (US-ESR) methods. The minimum age for the capping flowstones is 242±5 ka BP (sample RS18), and the researchers' best estimate of the age of *H. naledi* is the maximum US-ESR age, which is 253 +82/-70 ka (Dirks *et al.,* 2017), with a more recent study suggesting the age of the *H. naledi* remains is between 335 ka and 241 ka (Robbins *et al*., 2021). But many of these dates are minimum ages, both OSL and US-ESR can be unreliable, and dates for the formation of flowstones in the chamber suggest ages ranging from 500 ka BP to older than 780 ka. This current imprecision seriously impedes understanding of the evolutionary position of *H. naledi.*

The nature and relationships of *Homo naledi*

The overall *bauplan* of *H. naledi* is a distinctive combination of primitive (e.g., small brain and small body mass) and more derived (e.g., reduced body mass dimorphism and elongated lower limbs) features (Garvin *et al*., 2017). The cranium resembles early *Homo/Homo ergaster*, but with an even smaller endocranial volume (*c*.>550 cc). The dentition, both permanent and deciduous, is a mix of modern human-like (Bailey *et al*., 2019), primitive (Davies *et al*., 2019; Kupczik *et al*., 2019) and unusual (Guatelli-Steinberg *et al*., 2019) features. The hand morphology is mostly derived in the direction of modern humans (Kivell *et al*., 2015), the pelvis and hip-joint is relatively primitive, as are the curved foot phalanges (Harcourt-Smith *et al*., 2015), but the femoral morphology is unique among early hominins (Freidl *et al*., 2019).

Given this mix of primitive and derived features both within and among regions, when Dembo *et al.* (2016) used craniodental evidence to reconstruct the age and relationships of *H. naledi*, it was not surprising their suggested date of ~900 ka had a wide error range, and taxa as different as *Australopithecus sediba* and modern humans were equally likely to be the closest relative of *H. naledi*. There is no obvious precursor to *H. naledi*, and no evidence of any later descendant taxon.

The cognitive world of *Homo naledi*

At stake are the suggestions of Berger and colleagues that this small-brained hominin used controlled fire to illuminate a long and difficult-to-negotiate subterranean route, through which it dragged corpses to deliberately bury them near a chamber decorated with engravings (Berger *et al*., 2023a,b; Fuentes *et al*., 2023).

The evidence for fire, deliberate burial and symbolic art is far from compelling. The authors admit to uncertainty about the mode and intensity of any fire used by *H. naledi* in the Dinaledi subsystem (Fuentes et al. 2023, 5) and we must assume this speculative for now. Arguments in favour of deliberate burial of at least one individual rely not on a demonstrable grave cutting but on the disturbance of sediment, an apparent but statistically insignificant distinction between sediments within and without an assumed but invisible 'grave cutting', and very limited skeletal articulation. All of these phenomena can be explained by either disturbance through low-energy water action and/or the process of decay of a corpse. The lack of any clear grave cutting, and the presence within and around the ‘grave’ of isolated remains deriving from other individuals, further weaken the ‘deliberate burial’ hypothesis.

Berger et al. (2023b) interpret linear marks on a natural stone pillar between the Hill Antechamber and the Dinaledi Chamber as “crosshatched etchings” of a deliberate (i.e. engraved) nature. Marks like this, which are made when tectonic activity causes sharp rocks in breccia to score the cave wall, are visible in nearby caves (Martinón-Torres et al. 2023). Berger et al. (2023a) also claim one individual was buried holding a stone tool but sediments in the cave are littered with exfoliated limestone, and a more likely explanation is that this ‘artefact’ is a fortuitously associated spall from the roof of the cave (Martinón-Torres et al. 2023).

Where do things stand with *Homo naledi* after a decade of discovery and analysis?

For several decades now, any increase in our understanding of human evolution from the Cradle of Humankind has come from discoveries at well-established sites such as Kromdraai, Sterkfontein and Swartkrans. Lee Berger should be commended for his success at locating an important new source of evidence, and for taking on the considerable logistical challenge of recovering the evidence of *H. naledi* from deep underground. He has also offered opportunities to early career researchers to take part in the description and analysis of the fossil evidence.

The morphology of *H. naledi* is a puzzling combination of primitive and derived features. Presently, the implications of the fossil evidence have been assessed region-by-region, but a much more challenging task will be combining the regional evidence into a series of hypotheses about where, and how, *H. naledi* fits within existing, or modified, human evolutionary narratives.

Despite the protestations of Berger *et al*. (2015), the geological age of *H. naledi* does influence its interpretation. Reliable dates are not needed for deciding whether *H. naledi* is a good species, but they are needed for working out how *H. naledi* relates to existing hominin species. If its age was between 1 and 2 Ma, its unique mix of primitive and derived features could help us understand the sequence in which regions of the skeleton evolved, but if it is between 300 and 200 kya *H. naledi* likely represents a local relict population whose combination of features owes more to genetic isolation than to deeper human evolutionary history.

More controversial are the ways in which the researchers have approached interpreting the various lines of contextual evidence. Instead of considering the relative likelihood of a series of alternative explanations for each observation, at almost every turn the researchers opted for headline-grabbing exotic explanations instead of more likely prosaic interpretations. The presence in nearby caves of "crosshatched etchings" (Martinón-Torres *et al*. 2023) identical to the ones the Rising Star researchers claim could *only* be created with a hard, sharp tool (Berger et al. 2023b) is perhaps the most obvious example. The preference for explanations that infer the behavior of *H. naledi* in relation to that of modern humans is an example of what Butterfield (1965) referred to as "presentism" - the tendency of historians to reconstruct the past by reference to the present. We need to look at the world of *H. naledi* for its own sake, without constantly comparing it to our world.

This brings us to the way the results of research related to the Rising Star Cave system have been communicated to scientists and to the public. Traditionally, major discoveries at hominin fossil sites are published in high-impact journals that are extensively peer-reviewed. Subsequently, detailed analyses of the hominin fossils are communicated via papers in peer-reviewed specialist journals. Peer-review does not eliminate controversy, but it does place controls on a tendency to over-interpret evidence. The principal researchers involved with the Rising Star research decided to publish the results of their research in unreviewed preprints, or in journals that place the peer-review horse after the evidential cart. Science assumes researchers will work hard at the task of being their own critics – and not just 'ask questions' - and it is not surprising that the recent post-publication peer reviews have been harshly critical of many of the claims made by Berger, Hawks and Fuentes.

The publication strategy of the Rising Star Cave system principal researchers, with its intentional and inevitable media attention, has deflected attention from the real scientific importance of *H. naledi.* Behind all the hoopla is a hominin taxon with a hitherto unknown combination of primitive and derived morphology, that possibly lived alongside the earliest members of our own species. It fully deserves our considered attention. We hope that in the next decade, researchers will turn their attention to the grunt-work involved in trying to understand the real place of *H. naledi* in human evolutionary history.

Word Count: 2305

Berger, L. et al. 2015. *Homo naledi*, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. eLife 2015;4:e09560. DOI: 10.7554/eLife.09560.

Berger, L. et al. 2023a. Evidence for the deliberate burial of the dead by *Homo naledi. bioRxiv* preprint doi: https://doi.org/10.1101/2023.06.01.543127; posted June 5, 2023. Last accessed 16.2.2024.

Berger, L. et al. 2023b. 241,000 to 335,000 Years Old Rock Engravings Made by *Homo naledi* in the Rising Star Cave system, South Africa. Preprint posted at https://doi.org/10.7554/eLife.89102.1. Last accessed 16.2.2024.

Brain, C. K. 1967. Bone weathering and the problem of bone pseudo-tools. *South African Journal of Science* 63, 378-84.

Brophy, J. K., et al. 2021. Immature hominin craniodental remains from a new locality 775 in the Rising Star Cave System, South Africa. *PaleoAnthropology* 2021 (1) 1-14.

Butterfield, H. 1965. *The Whig Interpretation of History*. W.W. Norton, New York.

Dart, R. 1957. The Makapansgat australopithecine osteodontokeratic culture. *Proceedings of the Third Pan-African Congress on Prehistory (Livingstone, 1955).* London: Chatto and Windus.

Davies, T.W. et al. 2019. Endostructural morphology in hominoid mandibular third molars: geometric morphometric analysis of dentin crown shape. *Journal of Human Evolution* 133, 198-213.

Dembo, M. et al. 2016. The evolutionary relationships and age of *Homo naledi:* an assessment using dated Bayesian phylogenetic methods. *Journal of Human Evolution* 97, 17-26.

Dirks, P. H. G. M., et al. 2015. Geological and taphonomic context for the new hominin species *Homo naledi* from the Dinaledi Chamber, South Africa. eLife 2015;4:e09561. DOI: 10.7554/eLife.09561.

Dirks, P. H. G. M., et al. 2016. Comment on 'Deliberate body disposal by hominins in the Dinaledi Chamber, Cradle of Humankind, South Africa?'. *Journal of Human Evolution* 96, 149-53.

Dirks, P. H. G. M., et al. 2017. The age of *Homo naledi* and associated sediments in the Rising Star Cave, South Africa. eLife 2017;6:e24231. DOI: 10.7554/eLife.24231.

Elliott, M. et al. 2021. Expanded explorations of the Dinaledi subsystem, Rising Star Cave System, South Africa. *PaleoAnthropology* 2021:1, 15-22.

Freidl, L. et al. 2019. Femoral neck and shaft structure in *Homo naledi* from the Dinaledi Chamber (Rising Star System, South Africa). *Journal of Human Evolution* 133, 61-77.

Fuentes, O. et al. 2023. Burials and engravings in a small-brained hominin, Homo naledi, from the late Pleistocene: contexts and evolutionary implications. *bioRxiv* preprint posted at https://doi.org/10.7554/eLife.89125.1. Last accessed 16.2.2024.

Garvin, H.M. et al. 2017. Body size, brain size, and sexual dimorphism in *Homo naledi* from the Dinaledi Chamber. *Journal of Human Evolution* 133, 119-138.

Guatelli-Steinberg, D. et al. 2018. Patterns of lateral enamel growth in Homo naledi as assessed through perikymata distribution and number. *Journal of Human Evolution* 121, 40-54.

Harcourt-Smith, W.E.H., et al. 2015. The foot of *Homo naledi*. *Nature Communications* 6, 8432.

Hawks, J., et al. 2017. New fossil remains of *Homo naledi* from the Lesedi Chamber, South Africa. *eLife* 6, e24232.

Kivell, T., et al. 2015. The hand of *Homo naledi*. *Nature Communications* 6, 8431.

Kupczik, K., Delezene, L.K., & Skinner, M.M. 2019. Mandibular molar root and pulp cavity morphology in *Homo naledi* and other Plio-Pleistocene hominins. *Journal of Human Evolution* 130, 85-95.

Martinón-Torres, M. et al. 2023. No scientific evidence that *Homo naledi* buried their deadand produced rock art. *Journal of Human Evolution* published online https://doi.org/10.1016/j.jhevol.2023.103464. Last accessed 16.2.2024.

Robbins, J. L. et al. 2021. Providing context to the *Homo naledi* fossils: constraints from flowstones on the age of sediment deposits in Rising Star Cave, South Africa. *Chemical Geology* 567, https://doi.org/10.1016/j.chemgeo.2021.120108

Thackeray, F.J. 2016. The possibility of lichen growth on bones of *Homo naledi*: Were they exposed to light? *South African Journal of Science* 112(7–8), 1–5.

Val, A. 2016. Deliberate body disposal by hominins in the Dinaledi Chamber, Cradle of Humankind, South Africa? *Journal of Human Evolution* 96, 145–148. https://doi. org/10.1016/j.jhevol.2016.02.004.