Burials and engravings in a small-brained hominin, *Homo naledi*, from the late Pleistocene: contexts and evolutionary implications

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**Abstract:** Data from recent explorations in the Dinaledi subsystem illustrates one of the earliest examples of a mortuary practice in hominins and offers the earliest evidence of multiple interments and funerary actions, as well as evidence of the early creation of meaning making by a hominin. The hominin undertaking these behaviors was the small-brained *Homo naledi*. These data call into question several key assumptions about behavioral and cognitive evolution in Pleistocene hominins. The evidence from Dinaledi push back the temporal origins of mortuary and funerary behaviors and associate the creation of meaning making with a small-brained species and thus challenge key assumptions about the role and importance of encephalization in human evolution. This suggests that the hominin socio-cognitive niche and its relation to meaning-making activities is more diverse than previously thought. The association of these activities in subterranean spaces accessed and modified by the small brained species *Homo naledi*
impacts assertions that technological and cognitive advances in human evolution are associated solely with the evolution of larger brains.

**One-Sentence Summary:** Burials and related meaning making in a small-brained hominin alter our understandings of human evolution.
Main Text:

Scholars have long argued that there is a qualitative difference between the abilities of *Homo sapiens* versus other Pleistocene hominins and that this difference has to do with overall brain size and neurobiological complexity. Complex behavior and the construction and use of “meaning-laden” material, e.g., burial, fire as light, engravings, ornamentation, ochre use, etc. have all been suggested to be signals of “modern” human cognitive capacity tied to a brain well above 1000cc (Kissel and Fuentes 2021; Galway-Witham, Cole, and Stringer 2019). The recent finds from the Dinaledi chamber, Rising Star Cave, South Africa indicate that large-brain-only model for complex hominin behavior no longer holds (Berger et al. 2023a,b).

It is true that overall brain size and Encephalization Quotient (EQ) increased in many populations of the genus *Homo* over the past 2 million years, and that this is generally associated with increased appearance of complex behavior. However, it is now apparent that many of these behaviors are found in places used by, or associated with, hominins that are not traditionally considered to be *Homo sapiens*. For example, engravings are found with non-*H. sapiens* hominins (Joordens et al. 2014; Mania and Mania 1988; Sirakov et al. 2010). Ochre use is documented in samples that predate *H. sapiens* (Ronen et al. 1998; Watts, Chazan, and Wilkins 2016; Dapschauskas et al. 2022) and both fire use and simple mortuary behavior are also found in association with hominins that pre-date *H. sapiens* (Carbonell and Mosquera 2006; MacDonald et al. 2021). However, one might argue that all of these instances are associated with large-brain hominins or could be the result of taphonomic issues or dating issues (Püschel et al. 2021). But this is not accurate. Substantive evidence suggests that approximately 250-350,000 years ago the later Pleistocene hominin, *Homo naledi*, a small-brained hominin, carried deceased conspecifics into difficult to access locations in the Rising Star Cave system and interred them (Berger et al. 2023a,b) and likely produced engravings on cave walls near those areas of interment. Such actions require considerable social collaboration, coordination, and planning. And in the context of the subterranean Dinaledi system also require use of a light source; fire (Berger 2022). *H. naledi* carried out these behaviors with a brain size of less than ~600cc.

Fire use, mortuary behavior, and the evidence of engravings attributed to *H. naledi* falsify the hypothesis that only a large-brained hominin was capable of cognitively complex cultural, possibly symbolic, behavior. Recent discoveries demonstrate that at least a few populations/taxa in the genus were characterized by smaller overall brain sizes (~5-600cc) well into the later Pleistocene. Material evidence associated with these smaller brained populations overlaps with the technology and fire use (*H. floresiensis*, (Moore et al. 2009)), mortuary behavior and the production of engravings (*H. naledi*, Berger et al. 2023a,b) exhibited by their larger brained congenerics (see Fig 1). While these populations were characterized by smaller bodies than temporally sympatric hominins, their brains are not simply allometrically-scaled reductions of the larger forms (Holloway et al. 2018). This suggests that neurobiological organization rather than overall brain size, may have been one part of an early key transition within hominin evolution (8). It may be possible that the apparent gap in distribution of...
Homo/hominin fossils with an endocranial volume under 800cc between 1.0 and .3 mya in Figure 2 may be filled in with future discoveries. The open question introduced by the current evidence for H. naledi, and H. floresiensis, behavior is whether there might be one or more lineages of small brained hominins that flourished alongside larger brained forms and shared at least some aspects of the distinctive socio-cognitive hominin niche of the later Pleistocene (Galway-Witham, Cole, and Stringer 2019; Kissel and Fuentes 2021).

Here we offer an analysis of the recent data reported for complex behavior in the small-brained Homo naledi and suggest a suite of implications this has for our understanding of the relationships between brain size, cognition, complex behavior and the evolution of the genus Homo across the Pleistocene. These implications also query the driving forces behind encephalization and its relationship to the emergence of complex behaviors in hominins and other animals.

H. naledi buried their dead

Recently Pettitt (2022) laid out the three key criteria for assessing whether or not the Homo naledi remains in the Dinaledi subsystem represent actual funerary behavior: a) is there an as-yet unmapped entrance into the Dinaledi Chamber? b) Is there any evidence of artificial lighting in the cave system, and c) Is there evidence that it was dead bodies, rather than body parts that were carried into the chamber? The first query has been repeatedly addressed and no other options for alternative ingress have been found or hypothesized (Elliott et al. 2021). And now Berger et al. (2023a,b) answers both (b) and (c) clearly: there is evidence of fire use in the Dinaledi system (Bower, 2022) and entire bodies rather than body parts make up much of the buried remains. Therefore, one must conclude that the evidence meets Pettit’s (2022) criterion set forth and that H. naledi remains in the Dinaledi subsystem are one of the two earliest examples of a mortuary practice and offer the earliest evidence of multiple interments and funerary actions in a hominin.

The locations, contexts, and the inferred behavior associated with the H. naledi burials, including the appearance of engravings near the interment sites, likely also demonstrate meaning-making activity (Kissel and Fuentes 2017). Mortuary and funerary practices had previously only been attributed to Homo sapiens but more recently are associated with a range of large-brained hominin taxa in later the Pleistocene (Figure 1). Evidence of funerary behavior is assumed to require human-like cognitive capability (Pettitt 2018). Such behavior found in a small-brained hominin suggests that increases in brain size/EQ may not be a necessary precursor for the appearance of meaning-making behavior in the hominins.

The newly described Homo naledi data, and the clear assignation of funerary behavior to the context, and the presence of engravings in the same space, calls into question several key assumptions about behavioral evolution in Pleistocene hominins, and the importance of brain size evolution in general. The data emerging from the Dinaledi subsystem support an emerging argument that individual cognitive
ability related to increased encephalization may not be the primary explanation of certain complex hominin behavior, such as burying of the dead, strategic use of fire for illumination, and the creation of engravings. Rather than wholly relying on increased encephalization, we suggest that a distinctive cultural, empathetic, collaborative niche dependent on increasingly complex and robust relationships between individuals has also been a primary driver in the development of key aspects of human, or human-like, behavior (Galway-Witham, Cole, and Stringer 2019; Kissel and Fuentes 2021; McBrearty and Brooks 2000; Fuentes 2017; Spikins 2022; DeCasien, Barton, and Higham 2022).

The varied treatments of the dead described in Berger et al. (2023a) is certainly indicative of mortuary behavior, defined as specific actions relating to death and to the treatment of the dead, and the presence of dug burials and associated engravings is likely indicative of funerary behavior, defined as specific activities relating to the disposal of the dead and to their subsequent commemoration (Pettitt 2018). The data reflect a scenario where members of the H. naledi community carried the bodies of their dead more than 75 meters underground in an extremely difficult and dangerous subterranean environment (Elliott et al. 2021). Despite bodies being smaller and thus more capable of navigating the Rising Star system than contemporary humans, the carrying of bodies and behavioral actions required to bury or place them in the various locations described would have had high energetic costs and carried substantial risk for H. naledi. There are no clear direct fitness benefits nor any indication of proximate functional stimuli for this suite of behaviors.

The challenges for Homo naledi to bury its dead in remote subterranean contexts are significant. To accomplish this H. naledi had to coordinate their behavior and collaborate to move the bodies to a specific location inside the cave system, excavate an area and place the body in it, and cover it, or place the remains in a specific non-floor area. The data from Berger et al. (2023a) suggest that this is a behavioral sequence that was repeated multiple times in the same location, likely across a long temporal duration. Given the complexity of the cave layout (Elliott et al. 2021), there must have been some form of explicit communication for coordination of movement and actions, and the use of fire as a light source, between the H. naledi undertaking the behavior. Such coordination and specific set of actions around the treatment of deceased conspecifics is more methodologically extensive, energetically costly, with higher risk of injury than any reported for other primates and non-human animals to date (King 2013). This behavior is also more complex and multifactorial than that reported for the one earlier case of hominin mortuary behavior (Sima de Los Huesos, (Carbonell and Mosquera 2006)).

The subterranean environment used by H. naledi is not only physically challenging but is also emotionally and physiologically challenging, reflecting an engagement with difficult underground spaces not seen elsewhere in the archaeological record at this time. Dark enclosed spaces, where visual perception is curtailed, can create a state of emotional arousal profoundly affecting perceptual, cognitive and social systems (Zuccarelli et al. 2019), even with some form of illumination. While we cannot yet be certain of the exact modes, intensity and quality of the fires used by H. naledi in the Dinaledi subsystem, we can assume that they likely provided flickering and, at best, moderate intensity light sources. In
humans, and other diurnal primates, sensory deprivation through reduced or a lack of consistent visual clues creates a heightened sensitivity to other senses as well as prompting experiences of visual disturbances, hallucinations, and disorientation (Hodgson 2021). Experiences of these types of extreme and unusual environments, though often inducing fear responses, can also facilitate powerful bonding experiences (Steidle, Hanke, and Werth 2013). This range of substantive emotional and psychological reactions may explain why experiences in deep dark caves are often associated with a sense of the transcendent in contemporary humans (Montello and Moyes 2012) and given the broad range of sensory commonalities across diurnal anthropoids, and especially apes, they likely had comparable impacts on *H. naledi* and other Pleistocene hominins using subterranean spaces. We argue that careful and coordinated treatment of the dead on several occasions, in these environments, implies particularly strong social and emotional bonds and some shared understanding of meaning (Pettitt and Anderson 2020) in *H. naledi*.

That this high-risk, high-cost, no-overt-direct-fitness-benefit behavior was undertaken repeatedly by multiple members of the *H. naledi* community across time indicates a valued social, and likely cultural, tradition. The combination of features of the behavior (burial and associated engravings), and the context in which it was undertaken (in deep caves with the use of fire for illumination), suggests a level of cognitive/semiotic meaning-making capacity in *H. naledi* (e.g., (Kissel and Fuentes 2017; 2018)) that matches similar assessments of other populations of the genus *Homo* during the same, and later, time periods (Figure 1). This assessment of meaning-making capacity for *H. naledi* is supported by the active transformation of the ‘space’ of the Dinaledi chamber and Hill antechamber to ‘place’ (Low and Lawrence-Zúñiga 2003) through the pattern of mortuary and likely funerary behavior (e.g. (Silverman 2008) involving group collective practice, high levels of social/emotion investment, and some form of communicating the commitment to undertake the endeavor.

Recent research has produced growing evidence of multiple aspects of meaning making earlier in the archaeological record and with a wider range of hominins acknowledged to be responsible for mortuary practices (Table 1 & Fig. 1). This includes meaning making within deep caves by members of the genus *Homo* beginning after 200,000 years ago at Wonderwerk in South Africa and Bruniquel in France, both of which have evidence of fire use as well. The range of examples of meaning making extend our understanding of the cultural complexity of later Pleistocene members of the genus *Homo*. Nonetheless, the Dinaledi subsystem site is the earliest known example of the pattern of mortuary, and likely funerary, behavior that becomes increasingly common in populations of the genus *Homo* in the terminal Pleistocene (Table 1). It is critical to note that *H. naledi* is the least *Homo sapiens*-like of any hominin yet described in the Middle and Late Pleistocene of Africa.

**A role for emotional cognition?**

This pattern of emergence of meaning making in different hominins (Figure 1), to which the *Homo naledi* burial evidence makes an important contribution, also has other implications. Most particularly it may cast light on the question of the evolution of human conscious awareness of emotions and its involvement in the processes of cognitive evolution in the genus *Homo* and in hominins in general.
Humans share many building blocks of emotional cognition with other mammals, and some complex abilities with other apes. We share the same visceromotor and sensorimotor foundation for emotions with other mammals for example (Steklis and Lane 2013). Moreover, a range of common emotional responses to humans has now been documented in other primates, and particularly in apes, through measurement of heart rate and skin conductance as well as more recently pupil mimicry and infrared thermography (Nieuwburg, Ploeger, and Kret 2021). Interpersonal emotional interactions also have a common basis. Emotional contagion is apparent in monkeys and apes, and apes in particular demonstrating a level of empathy through yawning and even sympathy through active consolation (Romeró, Castellanos, and de Waal 2010; Preston and de Waal 2002). Diverse primate species have the cognitive ability to infer emotional meaning from expressions (Nieuwburg, Ploeger, and Kret 2021). Moreover, there is anecdotal evidence for the foundations of cognitive empathy in targeted helping within apes (Koski and Sterck 2010). However, no other mammal demonstrates the emotional conscious awareness of contemporary Homo sapiens. Contemporary humans possess a distinctive cognitive ability to regulate emotions by bringing feelings into “rational” thought (Green and Spikins 2020). As a result humans communicate and engage in shared intentions, and meaning-making, to a degree not seen in other animals, and demonstrate motivations to share emotions, experiences and activities with other persons (Steklis and Lane 2013).

The H. naledi evidence suggests that conscious emotional awareness was present in this hominin despite its small brain size. The shared and planned deposition of several bodies in the Rising Star system is evidence of a shared sets of beliefs or assumptions about meaning and action, something one would term “shared grief” in contemporary humans. The creation of engravings in the same space as the burials suggests a form of shared memorialization, or at least shared attentions and action to alter the locations beyond the interment of the bodies. Regardless of what one terms the underlying cognitive processes associated with the burial activities of H. naledi, they indicate a level of conscious emotional awareness that enables and is associated with extensive shared intentionality, forward planning, and repeated cultural behavior involving bodily risk. Equally complex symbolic use of caves by Neanderthals (Jaubert et al. 2016; Baquedano et al. 2023) demonstrate a similar emotional self-awareness, and production of highly symmetrical stone tools is also potentially indicative of emotional awareness and regulation in early member of the genus Homo (Green and Spikins 2020). However, the fact that a small-brained hominin displays these sorts of behavior suggests that the neurological capacity enabled by a larger than 1000cc brain cannot be the only factor, or necessarily the main factor, enabling the kind of emotional cognition that is considered a central factor in human evolutionary success.

That complex emotional cognition is not unique to Homo sapiens should not be surprising. Social understanding of emotions is widely accepted as adaptive in an evolutionary context (Nieuwburg, Ploeger, and Kret 2021) and moreover emotional awareness is associated with better life outcomes in modern human contexts (Smith et al. 2023). That brain regions associated with socio-emotional processing are relatively enlarged in H. naledi despite a limited overall brain size reinforces this argument, particularly as the medial prefrontal cortex is important in reflective awareness in modern
humans. A specifically *H. naledi* behavioral adaptation, reflected in the burial activities, may have depended on emotional commitments to others combined with a set of cultural beliefs/practices, a high level of emotional awareness to manage these, and in turn collaboration with extensive coordination.

*What does* *H. naledi* burial activity mean for understanding human evolution?*

As outlined in Hawks et al. (Hawks et al. 2017) the phylogenetic relationships between *H. naledi* and other populations/taxa in the genus *Homo* remain unclear. However, *H. naledi* and some other populations of the genus *Homo* overlap temporally in the expression of meaning making behavior indicating some degree of shared socio/emotional/cognitive processes. To date, *H. naledi* is the earliest example of such actions, combining both mortuary and funerary behavior with the creation of likely symbolic engravings. Thus, it is clear that the hominins in the later Pleistocene are typified by a range of brain sizes and cranial and post-cranial morphologies and that the material record in that same time period offers increased evidence for shared meaning-making. This demonstrates that such behavior is neither “modern” nor exclusive to *Homo sapiens* (*sensu latu*). Whilst this adds further evidence to our understanding of the emergence of hominin cognition there are also wider evolutionary implications. Much like potentially independent evolution of social emotional abilities in other primates (Nieuwburg, Ploeger, and Kret 2021) the behavioral evidence for small-brained *H. naledi* may suggest that some degree of analogous rather than homologous evolution underlies social emotional complexity in humans.

The evidence for the burials by *H. naledi* creates two problems for current models of human evolution. The first is: what is the relationships between *H. naledi* mortuary/funerary behavior and that of other *Homo* taxa/populations? This can be clarified via one of three possible explanations.

a) *H. naledi* is not in the human lineage and its mortuary/funerary activities and use of fire are the result of parallel evolution/homoplasy.

b) mortuary practices, use of fire and any related meaning-making capacities are very old dating to the early Pleistocene, or even Pliocene hominins, and thus are a homology between *H. naledi* and *H. sapiens.*

or,

c) *H. sapiens* “borrowed” the mortuary and funerary behavior as a cultural practice from sympatric *H. naledi* or vice versa.

The second problem is how to incorporate the fact that neither absolute brain size nor encephalization quotient are necessarily correlated with the meaning-making capacities and emotional-cognition complexity associated with mortuary and funerary behavior. It is assumed that a large brain was an essential step towards a uniquely human cognition, social relationships and culture (Dunbar 2003; Muthukrishna et al. 2018). However, small-brained hominins were responsible for many key changes in human evolution. Planning and forethought in stone tool production predates the origins of *Homo* (Harmand et al. 2015) and by 1.76 million years ago multiple taxa/populations of relatively small-brained hominins were likely developing separate bifacial tool traditions (Lepre et al. 2011). It is also evident that small-brained hominins (under 800-1000cc) were those who initially expanded around, and out of Africa,
crossing into eastern and Southeastern Asia (Antón, Potts, and Aiello 2014). Additionally, the use of fire emerges in excess of 1.5 million years ago conspecific only with small-brained hominins (Hlubik et al. 2019). This constellation of data is particularly significant as it demonstrates that small-brained hominins are a part of the complex hominin niche that characterizes later Pleistocene members of the genus Homo (Mondanaro et al. 2020).

This new evidence for complexity in *H. naledi* behavior pushes back the origins of mortuary and funerary behaviors, challenges our assumptions about the role and importance of encephalization in human evolution, and suggests that the hominin emotional, socio-cognitive niche is more significant than previously thought. This will structure how we understand and model the origins and patterns of human evolution in the future (Kissel and Fuentes 2021; Spikins 2022; Spikins et al. 2019).

### References and Notes


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Visualization: MK, JH

Funding acquisition: LRB

Project administration: AF, LRB, JH

Supervision: AF, LRB

Writing – original draft: AF, PS, MK

Writing – review & editing: AF, PS, MK, LRB, JH, KM

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**Data and materials availability:** All data, code, and materials used in the analysis are available in the SOM and in Berger et al (2023a,b)

**Supplementary Materials**

references for Table 1 on mortuary practices

supplement for Figure 1

**Figures**
Fig. 1. Archaeological evidence of culturally-mediated, meaning-making, behaviors. Dots represent different sites and the error bars are the maximum and minimum dates when available. See Table for details and See supplemental material for references.
Fig. 2. Endocranial volume estimates for hominin cranium. Error bars represent the maximum and minimum ages for specimens when available. See supplemental material for references. Hawks, John. 2023. Endocranial volumes for fossil hominins (dataset). Figshare
https://doi.org/10.6084/m9.figshare.22743980
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<td>Neandertal</td>
<td>Bischoff et al. 2003</td>
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<td>modification/mortuary behavior?</td>
<td>100</td>
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<td>Defleur et al. 1999</td>
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<td>Herto</td>
<td>open air</td>
<td>no</td>
<td>modification/mortuary behavior?</td>
<td>adult</td>
<td>Homo sapiens</td>
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<td>cave</td>
<td>yes</td>
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<td>adults and children</td>
<td>Neandertal</td>
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<td>Bodo</td>
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<td>White 1986</td>
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<td>na</td>
<td>modification/mortuary behavior?</td>
<td>adult and children</td>
<td>Homo sp.</td>
<td>Fernández Jalvo et al. 1999</td>
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<td>modification/mortuary behavior?</td>
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<td>Australopithecus</td>
<td>Pickering et al 2000</td>
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<td>Krapina</td>
<td>cave</td>
<td>yes</td>
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<td>many age ranges</td>
<td>Neandertal</td>
<td>Russel 1987</td>
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<td>AL-333</td>
<td>open air</td>
<td>yes</td>
<td>mortuary behavior?</td>
<td>adults, juveniles and infants</td>
<td>Australopithecus afarensis</td>
<td>Pettitt 2011</td>
<td></td>
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</table>

**Table 1. Table of evidence of potential mortuary behavior in hominins.** See supplemental material for references.
Supplement for Table 1 on mortuary practices

Refs for table 1


Text for Supplement table 1 on mortuary practices.

Note on table 1: Table 1 was constructed by searching the literature for examples of funerary behaviors in the Paleolithic. The nature of many of these finds are contentious (1). For example, some scholars have rejected Roc-de-Marsal (2, 3) as a burial based on reevaluating the context of the site, while others include it in list of European burials (4). Similarly, experts are divided as to if La Chapelle-aux-Saints should (4) or should not (5, 6) be accepted as an intentional Neandertal burial. We also list sites that are not burials but instead show possible evidence of modifying the body after death. Again, scientists disagree if these are funerary practices or, in the case of cutmarks on hominin bones, cannibalism.

Most archaeologists define burial in a way that lets them detect it archaeologically (excavate a pit, put body in pit, refill pit), but this is only one type of funerary ritual. All cultures must find ways to deal with the beginning of life and with the end of life. How to treat the dead (and how to decide when someone is really dead) is culturally specific. The symbolic practices related to death are also highly varied. Just as with foodways, deathways are mediated by how a culture sees death.

All of this is to say that the symbolic aspects around death are as important as the process of dealing with the body. We might also ask how the death related symbolic behaviors help people mourn.

# Supplementary Material

## Data for Figure 1.

### Table used to create figure 1

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<th>type</th>
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<th>Min. age</th>
<th>Midrange</th>
<th>associated species</th>
<th>references</th>
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<td>unknown archaic</td>
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<td>archaic Homo</td>
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<td>engraved shell</td>
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<td>Mania and Mania 1988</td>
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<td>Diepkloof Rock Shelter</td>
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<td>engraved eggshell</td>
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<td>Hovers et al. 1997</td>
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<td>Sima de los Huesos</td>
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<td>mortuary</td>
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<td>Vandermeersch and Bar-Yosef 2019</td>
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<td>Panga ya Saidi</td>
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<td>Radovčić et al 2016</td>
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</table>
Table X. Data used to create Figure 1.

Refs for Figure 1


31. Berger et al. (2023b) 241,000 to 335,000 Years Old Rock Engravings Made by Homo naledi in the Rising Star Cave system, South Africa. bioRxiv, DOI pending

**Text for notes on table X.**

This table is a sampling of archaeological sites that have been suggested to show signs of what some call “symbolic behavior.” Delimitating what is and what is not symbolic has been the source of contention for many decades now (1–6). Traditionally, archaeologists have defined symbols as objects that have meanings embedded in them. Yet a symbol, by its very nature, must be interpreted within a system of meaning and discerning if something is symbolic becomes difficult without knowing the cultural context within which it has been created (7). We created this table from the published literature to demonstrate that no matter what we choose to call it, culturally-mediated behaviors predate contemporary humans. Such behaviors are found with Homo erectus (8), Neandertals (9) and other archaic populations (10–12).