

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

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20 **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  
25 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. 2023 a,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 congenics (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 Pettitt'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  
5 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.  
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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)).  
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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  
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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 (Romero, 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.

5 *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  
10 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  
15 “modern” nor exclusive to *Homo sapiens (sensu lato)*. 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.

20 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.

25 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,

30 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  
35 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  
40 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

- 15 Antón, Susan C, Richard Potts, and Leslie C Aiello. 2014. "Evolution of Early Homo : An Integrated Biological Perspective." *Science* 345: 45. <https://doi.org/10.1126/science.1236828>.
- Baquedano, Enrique, Juan L. Arsuaga, Alfredo Pérez-González, César Laplana, Belén Márquez, Rosa Huguet, Sandra Gómez-Soler, et al. 2023. "A Symbolic Neanderthal Accumulation of Large Herbivore Crania." *Nature Human Behaviour* 7 (3): 342–52. <https://doi.org/10.1038/s41562-022-01503-7>.
- 20 Berger, L. (2022) The Future of Exploration in the Greatest Age of Exploration. Carnegie Science Lecture Series. Carnegie Science [https://www.youtube.com/watch?v=kOtX\\_Bcs\\_F4](https://www.youtube.com/watch?v=kOtX_Bcs_F4).
- Berger et al. (2023a) Evidence for deliberate burial of the dead by *Homo naledi*, bioRxiv, DOI pending
- 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
- 25 Bower, Bruce. 2022. "Homo Naledi May Have Lit Fires in Caves at Least 236,000 Years Ago." December 2, 2022. <https://www.sciencenews.org/article/homo-naledi-fire-hominid-cave-human-evolution>.
- Carbonell, Eudald, and Marina Mosquera. 2006. "The Emergence of a Symbolic Behaviour: The Sepulchral Pit of Sima de Los Huesos, Sierra de Atapuerca, Burgos, Spain." *Comptes Rendus Palevol* 5 (1–2): 155–60. <https://doi.org/10.1016/j.crpv.2005.11.010>.
- 30 Dapschaskas, Rimtautas, Matthias B. Göden, Christian Sommer, and Andrew W. Kandel. 2022. "The Emergence of Habitual Ochre Use in Africa and Its Significance for The Development of Ritual Behavior During The Middle Stone Age." *Journal of World Prehistory* 35 (3): 233–319. <https://doi.org/10.1007/s10963-022-09170-2>.
- DeCasien, Alex R., Robert A. Barton, and James P. Higham. 2022. "Understanding the Human Brain: Insights from Comparative Biology." *Trends in Cognitive Sciences* 26 (5): 432–45. <https://doi.org/10.1016/j.tics.2022.02.003>.
- 35 Dunbar, R. I.M. 2003. "The Social Brain: Mind, Language, and Society in Evolutionary Perspective." *Annual Review of Anthropology* 32: 163–81. <https://doi.org/10.1146/annurev.anthro.32.061002.093158>.
- Elliott, M.C., T.V. Makhubela, J.K. Brophy, S.E. Churchill, B. Peixotto, E.M. Fuerriegel, H. Morris, et al. 2021a. "Expanded Explorations of the Dinaledi Subsystem, Rising Star Cave System, South Africa." *PaleoAnthropology* 2021 (1): 16–22.
- Fuentes, Agustín. 2017. *The Creative Spark: How Imagination Made Humans Exceptional*. Dutton.
- Galway-Witham, Julia, James Cole, and Chris Stringer. 2019. "Aspects of Human Physical and Behavioural Evolution during the Last 1 Million Years." *Journal of Quaternary Science* 34 (6): 355–78.
- 45 Green, James, and Penny Spikins. 2020. "Not Just a Virtue: The Evolution of Self-Control." *Time and Mind* 13 (2): 117–39. <https://doi.org/10.1080/1751696X.2020.1747246>.
- Harmand, Sonia, Jason E. Lewis, Craig S. Feibel, Christopher J. Lepre, Sandrine Prat, Arnaud Lenoble, Xavier Boës, et al. 2015. "3.3-Million-Year-Old Stone Tools from Lomekwi 3, West Turkana, Kenya." *Nature* 521: 310–15. <https://doi.org/10.1038/nature14464>.

- Hawks, John, Marina Elliott, Peter Schmid, Steven E Churchill, Darryl J De Ruiter, Eric M Roberts, Hannah Hilbert-wolf, et al. 2017. "New Fossil Remains of Homo Naledi from the Lesedi Chamber, South Africa." *Elife*, 1–63. <https://doi.org/10.7554/eLife.24232>.
- 5 Hlubik, Sarah, Russell Cutts, David R. Braun, Francesco Berna, Craig S. Feibel, and John W.K. Harris. 2019. "Hominin Fire Use in the Okote Member at Koobi Fora, Kenya: New Evidence for the Old Debate." *Journal of Human Evolution* 133: 214–29. <https://doi.org/10.1016/j.jhevol.2019.01.010>.
- Hodgson, Derek. 2021. "Upper Palaeolithic Art as a Perceptual Search for Magical Images." *Time and Mind* 14 (4): 487–99.
- 10 Holloway, Ralph L., Shawn D. Hurst, Heather M. Garvin, P. Thomas Schoenemann, William B. Vanti, Lee R. Berger, and John Hawks. 2018. "Endocast Morphology of Homo Naledi from the Dinaledi Chamber, South Africa." *Proceedings of the National Academy of Sciences of the United States of America* 115 (22): 5738–43. <https://doi.org/10.1073/pnas.1720842115>.
- 15 Jaubert, Jacques, Sophie Verheyden, Dominique Genty, Michel Soulier, Hai Cheng, Dominique Blamart, Christian Burler, et al. 2016. "Early Neanderthal Constructions Deep in Bruniquel Cave in Southwestern France." *Nature* 534 (7605): 111–14. <https://doi.org/10.1038/nature18291>.
- Joordens, Josephine, Francesco D'Errico, Frank P. Wesselingh, Stephen Munro, John de Vos, Jakob Wallinga, Christina Ankjærgaard, et al. 2014. "Homo Erectus at Trinil on Java Used Shells for Tool Production and Engraving." *Nature* 518 (December): 228–31. <https://doi.org/10.1038/nature13962>.
- 20 King, Barbara J. 2013. *How Animals Grieve*. Chicago: University of Chicago Press.
- Kissel, Marc, and Agustín Fuentes. 2017. "Semiosis in the Pleistocene." *Cambridge Archaeological Journal* 0 (0). <https://doi.org/10.1017/S0959774317000014>.
- . 2018. "'Behavioral Modernity' as a Process, Not an Event, in the Human Niche." *Time and Mind* 11 (2): 163–83. <https://doi.org/10.1080/1751696X.2018.1469230>.
- 25 Kissel, Marc, and Agustín Fuentes. 2021. "The Ripples of Modernity: How We Can Extend Paleoanthropology with the Extended Evolutionary Synthesis." *Evolutionary Anthropology* 30 (1): 84–98. <https://doi.org/10.1002/evan.21883>.
- Koski, Sonja E., and Elisabeth H. M. Sterck. 2010. "Empathic Chimpanzees: A Proposal of the Levels of Emotional and Cognitive Processing in Chimpanzee Empathy." *European Journal of Developmental Psychology* 7 (1): 38–66. <https://doi.org/10.1080/17405620902986991>.
- 30 Lepre, Christopher J., H el ene Roche, Dennis V. Kent, Sonia Harmand, Rhonda L. Quinn, Jean-Philippe Brugal, Pierre-Jean Texier, Arnaud Lenoble, and Craig S. Feibel. 2011. "An Earlier Origin for the Acheulian." *Nature* 477 (7362): 82–85. <https://doi.org/10.1038/nature10372>.
- Low, Seta, and Denise Lawrence-Z u niga, eds. 2003. *The Anthropology of Space and Place: Locating Culture*. Wiley-Blackwell.
- 35 MacDonald, Katharine, Fulco Scherjon, Eva van Veen, Krist Vaesen, and Wil Roebroeks. 2021. "Middle Pleistocene Fire Use: The First Signal of Widespread Cultural Diffusion in Human Evolution." *Proceedings of the National Academy of Sciences* 118 (31): e2101108118. <https://doi.org/10.1073/pnas.2101108118>.
- Mania, D., and U. Mania. 1988. "Deliberate Engravings on Bone Artefacts of Homo Erectus." *Rock Art Research* 5: 91–97.
- 40 McBrearty, Sally, and Alison Brooks. 2000. "The Revolution That Wasn't: A New Interpretation of the Origin of Modern Human Behavior." *Journal of Human Evolution* 39: 453–563.
- Mondanaro, Alessandro, Marina Melchionna, Mirko Di Febbraro, Silvia Castiglione, Philip B. Holden, Neil R. Edwards, Francesco Carotenuto, et al. 2020. "A Major Change in Rate of Climate Niche Envelope Evolution during Hominid History." *iScience* 23 (11). <https://doi.org/10.1016/j.isci.2020.101693>.
- 45 Montello, D., and H. Moyes. 2012. "Why Dark Zones Are Sacred." In *In Sacred Darkness: A Global Perspective on the Ritual Use of Caves*, edited by H. Moyes, 161–70. University Press of Colorado.
- Moore, M. W., T. Sutikna, Jatmiko, M. J. Morwood, and A. Brumm. 2009. "Continuities in Stone Flaking Technology at Liang Bua, Flores, Indonesia." *Journal of Human Evolution* 57 (5): 503–26. <https://doi.org/10.1016/j.jhevol.2008.10.006>.
- 50 Muthukrishna, Michael, Michael Doebeli, Maciej Chude, and Joseph Henrich. 2018. "The Cultural Brain Hypothesis: How Culture Drives Brain Expansion, Sociality, and Life History." *PLOS Computational Biology* 14: 1–37. <https://doi.org/10.1371/journal.pcbi.1006504> N.
- Nieuwburg, Elisabeth G. I., Annemie Ploeger, and Mariska E. Kret. 2021. "Emotion Recognition in Nonhuman Primates: How Experimental Research Can Contribute to a Better Understanding of Underlying Mechanisms." *Neuroscience and Biobehavioral Reviews* 123 (April): 24–47. <https://doi.org/10.1016/j.neubiorev.2020.11.029>.
- 55

- Pettitt, Paul. 2018. "Hominin Evolutionary Thanatology from the Mortuary to Funerary Realm: The Palaeoanthropological Bridge between Chemistry and Culture." *Philosophical Transactions of the Royal Society B: Biological Sciences* 373 (1754). <https://doi.org/10.1098/rstb.2018.0212>.
- . 2022. "Did Homo Naledi Dispose of Their Dead in the Rising Star Cave System?" *South African Journal of Science* 118 (11/12). <https://doi.org/10.17159/sajs.2022/15140>.
- Pettitt, Paul, and James R. Anderson. 2020. "Primate Thanatology and Hominoid Mortuary Archeology." *Primates* 61 (1): 9–19. <https://doi.org/10.1007/s10329-019-00769-2>.
- Preston, Stephanie D., and Frans B. M. de Waal. 2002. "Empathy: Its Ultimate and Proximate Bases." *Behavioral and Brain Sciences* 25: 1–20. <https://doi.org/10.1017/S0140525X02000018>.
- Püschel, Hans P., Ornella C. Bertrand, Joseph E. O'Reilly, René Bobe, and Thomas A. Püschel. 2021. "Divergence-Time Estimates for Hominins Provide Insight into Encephalization and Body Mass Trends in Human Evolution." *Nature Ecology & Evolution* 5 (6): 808–19. <https://doi.org/10.1038/s41559-021-01431-1>.
- Romero, T., M. A. Castellanos, and F. B. M. de Waal. 2010. "Consolation as Possible Expression of Sympathetic Concern among Chimpanzees." *Proceedings of the National Academy of Sciences* 107 (27): 12110–15. <https://doi.org/10.1073/pnas.1006991107>.
- Ronen, A, J.-M. Burdukiewicz, S A Laukhin, Y Winter, A Tsatskin, T Dayan, O A Kulikov, V K V;asov, and V V Semenov. 1998. "The Lower Palaeolithic Site Bitzat Ruhama in the Northern Negev, Israel." *Archaeologisches Korrespondenzblatt* 28: 163–73.
- Silverman, Helaine. 2008. "Introduction: The Space and Place of Death." *Archeological Papers of the American Anthropological Association* 11 (1): 1–11.
- Sirakov, N., J.-L. Guadelli, S. Ivanova, S. Sirakova, M. Boudadi-Maligne, I. Dimitrova, Fernandez Ph, et al. 2010. "An Ancient Continuous Human Presence in the Balkans and the Beginnings of Human Settlement in Western Eurasia: A Lower Pleistocene Example of the Lower Palaeolithic Levels in Kozarnika Cave (North-Western Bulgaria)." *Quaternary International* 223 (September): 94–106. <https://doi.org/10.1016/j.quaint.2010.02.023>.
- Smith, Ryan, Horst Dieter Steklis, Netzin Steklis, Karen L. Weihs, John J. B. Allen, and Richard D. Lane. 2023. "Lower Emotional Awareness Is Associated with Greater Early Adversity and Faster Life History Strategy." *Evolutionary Behavioral Sciences* 17: 1–15. <https://doi.org/10.1037/ebbs0000282>.
- Spikins, Penny. 2022. *Hidden Depths: The Origins of Human Connection*. White Rose University Press.
- Spikins, Penny, Andy Needham, Barry Wright, Calvin Dytham, Maurizio Gatta, and Gail Hitchens. 2019. "Living to Fight Another Day: The Ecological and Evolutionary Significance of Neanderthal Healthcare." *Quaternary Science Reviews* 217: 98–118. <https://doi.org/10.1016/j.quascirev.2018.08.011>.
- Steidle, Anna, Eva-Verena Hanke, and Lioba Werth. 2013. "In The Dark We Cooperate: The Situated Nature of Procedural Embodiment." *Social Cognition* 31 (2): 275–300.
- Steklis, Horst Dieter, and Richard D. Lane. 2013. "The Unique Human Capacity for Emotional Awareness: Psychological, Neuroanatomical, Comparative and Evolutionary Perspectives." In *Emotions of Animals and Humans: Comparative Perspectives*, edited by Shigeru Watanabe and Stan Kuczaj, 165–205. The Science of the Mind. Tokyo: Springer Japan. [https://doi.org/10.1007/978-4-431-54123-3\\_8](https://doi.org/10.1007/978-4-431-54123-3_8).
- Watts, Ian, Michael Chazan, and Jayne Wilkins. 2016. "Early Evidence for Brilliant Ritualized Display: Specularite Use in the Northern Cape (South Africa) between ~500 and ~300 Ka." *Current Anthropology* 57 (3): 287–310. <https://doi.org/10.1086/686484>.
- Zuccarelli, Lucrezia, Letizia Galasso, Rachel Turner, Emily J.B. Coffey, Loredana Bessone, and Giacomo Strapazzon. 2019. "Human Physiology during Exposure to the Cave Environment: A Systematic Review with Implications for Aerospace Medicine." *Frontiers in Physiology* 10 (APR). <https://doi.org/10.3389/fphys.2019.00442>.

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5 **Author contributions:**

Conceptualization: AF, LRB, JH, MK, PS

Methodology: AF, MK, LRB, JH

Investigation: AF, PS, MK, LRB, JH, KM

Visualization: MK, JH

10 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

15 **Competing interests:** Authors declare that they have no competing interests.

**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**

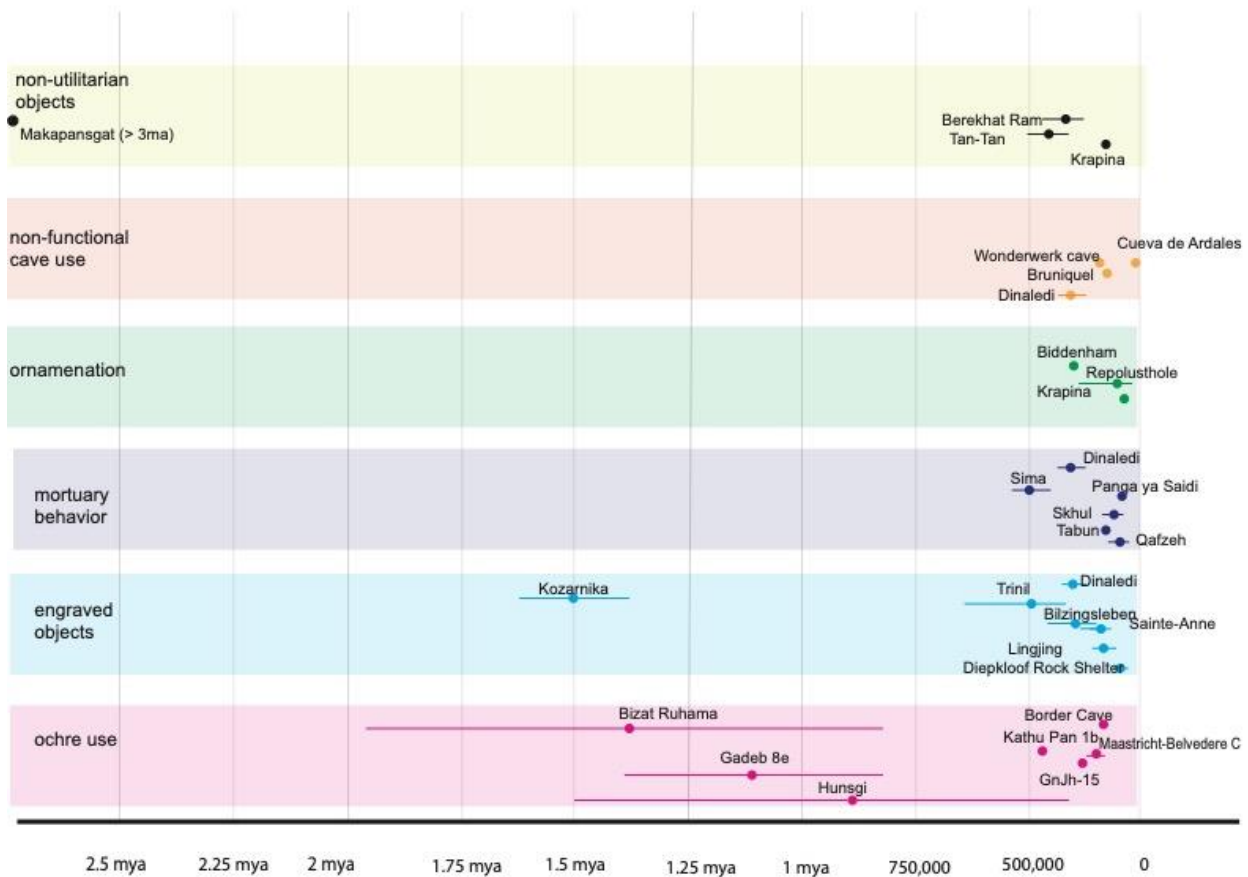
references for Table 1 on mortuary practices

20 supplement for Figure 1

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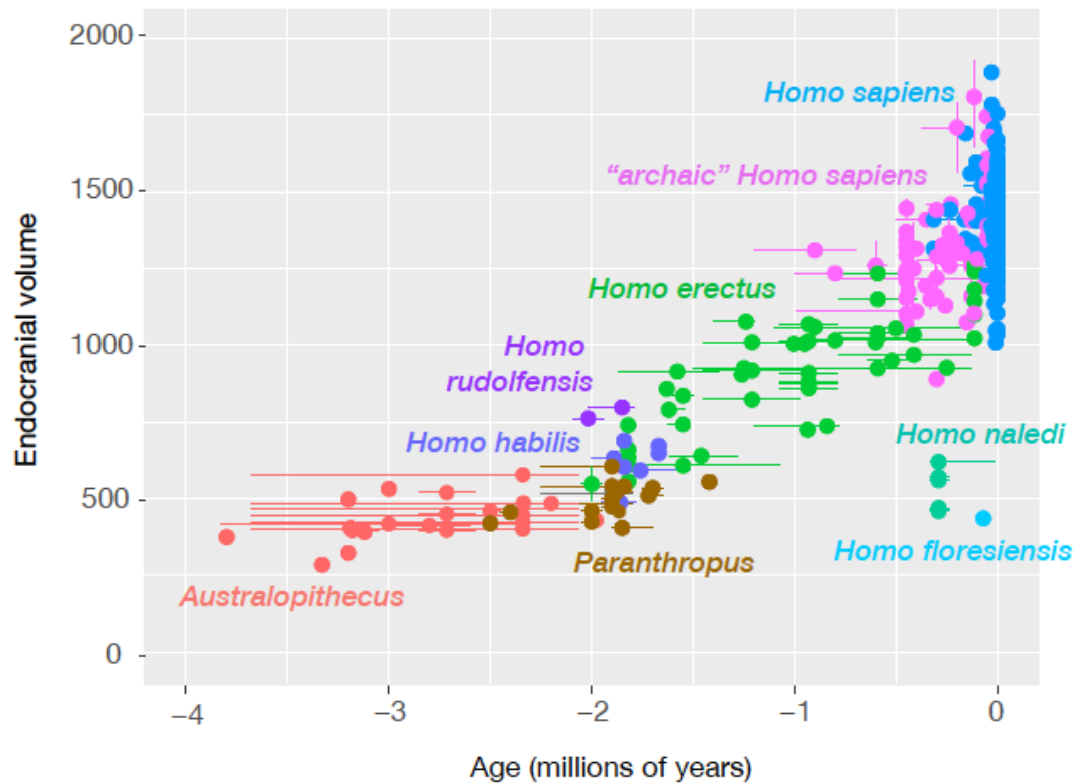
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**Figures**



**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.

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**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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site	type of site	Multiple bodies	type	skeletal age of specimen(s)	Age Estimate (in ka)	species	reference
Krems-Wachtberg	open air	yes	burial	infants	31	Homo sapiens	Teschler-Nicola et al. 2020
Lake Mungo	open air	yes	burial	adults	40	Homo sapiens	Bowler et al 2003
Taramsa hills	open air	no	burial	child (8-10 yrs old)	45	Homo sapiens	Vermeersch et al. 2015
La Ferrassie	cave	yes	burial	children?	45	Neandertal	Gómez-Olivencia et al 2018
Shanidar	cave	yes	burial	adults, infants, 2-3 yr old	45	Neandertal	Pomeroy et al 2020
Mezmaiskaya Cave,	cave	no	burial	infant	45	Neandertal	Golovanova et al 1999
La Chapelle-aux-Saints 1	cave	no	burial	adult	50	Neandertal	Rendu et al 2013
Dederiyeh Cave,	cave	yes	burial	children	50	Neandertal	Akazawa et al 1999.
Régourdou Cave	cave	no	burial	adult	50	Neandertal	Maureille et al 2001
Kebara	cave	yes	burial	child and adult	55	Neandertal	Pettitt 2011
Amud	cave	yes	burial	infant and adults	60	Neandertal	Hovers et al 2000
Roc de Marsal	cave	no	Burial?	child	70	Neandertal	Maureille, B., & Knüsel, C. J. 2022
Panga ya Saidi	cave	no	burial	2.5-3 yrs old	78	Homo sapiens	Martinón-Torres et al
Qafzeh	cave	yes	burial	children and adults	100	Homo sapiens	Vandermeersch & Bar-Yosef 2019
Skhul	cave	yes	burial	adults and children	110	Homo sapiens	Ronen 1976
Tabun	cave	yes	burial	adult (maybe neonate?)	120	Neandertal	Pettitt 2002

Border Cave	cave	yes	burial	adult and infants	74	Homo sapiens	d'Errico & Backwell, 2016
Sima de los huesos	pit	yes	caching/mortuary behavior	adults and children	500	Neandertal	Bischoff et al. 2003
Moula-Guercy	cave	yes	modification/mortuary behavior?		100	Neandertal	Defleur et al. 1999
Herto	open air	no	modification/mortuary behavior?	adult	160	Homo sapiens	White et al. 2003
El Sidron	cave	yes	modification/mortuary behavior?	adults and children	480	Neandertal	Rosas et al. 2006
Bodo	open air	no	modification/mortuary behavior?	adult	600	Homo sp.	White 1986
Gran dolina	cave	na	modification/mortuary behavior?	adult and children	800	Homo sp.	Fernández Jalvo et al. 1999
Sterkfontein	cave	no	modification/mortuary behavior?	adult	1635	Australopithecus	Pickering et al 2000
Krapina	cave	yes	mortuary behavior	many age ranges	130	Neandertal	Russel 1987
AL-333	open air	yes	mortuary behavior?	adults, juveniles and infants	3200	Australopithecus afarensis	Pettitt 2011

**Table1. Table of evidence of potential mortuary behavior in hominins.** See supplemental material for references

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## Supplement for Table 1 on mortuary practices

### Refs for table 1

1. M. Teschler-Nicola, D. Fernandes, M. Händel, T. Einwögerer, U. Simon, C. Neugebauer-Maresch, S. Tangl, P. Heimel, T. Dobsak, A. Retzmann, T. Prohaska, J. Irrgeher, D. J. Kennett, I. Olalde, D. Reich, R. Pinhasi, Ancient DNA reveals monozygotic newborn twins from the Upper Palaeolithic. *Commun. Biol.* **3**, 1–11 (2020).
2. J. M. Bowler, H. Johnston, J. M. Olley, J. R. Prescott, R. G. Roberts, W. Shawcross, N. A. Spooner, New ages for human occupation and climatic change at Lake Mungo, Australia. *Nature.* **421**, 837–840 (2003).
3. P. M. Vermeersch, E. Paulissen, P. Van Peer, S. Stokes, C. Charlier, C. B. Stringer, W. Lindsay, A Middle Palaeolithic burial of a modern human at Taramsa Hill, Egypt. *Antiquity.* **72**, 475–484 (2015).
4. S. I. Berndt, S. Gustafsson, R. Mägi, A. Ganna, E. Wheeler, M. F. Feitosa, A. E. Justice, K. L. Monda, D. C. Croteau-Chonka, F. R. Day, T. Esko, T. Fall, T. Ferreira, D. Gentilini, A. U. Jackson, J. Luan, J. C. Randall, S. Vedantam, C. J. Willer, T. W. Winkler, A. R. Wood, T. Workalemahu, Y.-J. Hu, S. H. Lee, L. Liang, D.-Y. Lin, J. L. Min, B. M. Neale, G. Thorleifsson, J. Yang, E. Albrecht, N. Amin, J. L. Bragg-Gresham, G. Cadby, M. den Heijer, N. Eklund, K. Fischer, A. Goel, J.-J. Hottenga, J. E. Huffman, I. Jarick, A. Johansson, T. Johnson, S. Kanoni, M. E. Kleber, I. R. König, K. Kristiansson, Z. Kutalik, C. Lamina, C. Lecoeur, G. Li, M. Mangino, W. L. McArdle, C. Medina-Gomez, M. Müller-Nurasyid, J. S. Ngwa, I. M. Nolte, L. Paternoster, S. Pechlivanis, M. Perola, M. J. Peters, M. Preuss, L. M. Rose, J. Shi, D. Shungin, A. V. Smith, R. J. Strawbridge, I. Surakka, A. Teumer, M. D. Trip, J. Tyrer, J. V Van Vliet-Ostaptchouk, L. Vandenput, L. L. Waite, J. H. Zhao, D. Absher, F. W. Asselbergs, M. Atalay, A. P. Attwood, A. J. Balmforth, H. Basart, J. Beilby, L. L. Bonnycastle, P. Brambilla, M. Bruinenberg, H. Campbell, D. I. Chasman, P. S. Chines, F. S. Collins, J. M. Connell, W. O. Cookson, U. de Faire, F. de Vegt, M. Dei, M. Dimitriou, S. Edkins, K. Estrada, D. M. Evans, M. Farrall, M. M. Ferrario, J. Ferrières, L. Franke, F. Frau, P. V Gejman, H. Grallert, H. Grönberg, V. Gudnason, A. S. Hall, P. Hall, A.-L. Hartikainen, C. Hayward, N. L. Heard-Costa, A. C. Heath, J. Hebebrand, G. Homuth, F. B. Hu, S. E. Hunt, E. Hyppönen, C. Iribarren, K. B. Jacobs, J.-O. Jansson, A. Jula, M. Kähönen, S. Kathiresan, F. Kee, K.-T. Khaw, M. Kivimäki, W. Koenig, A. T. Kraja, M. Kumari, K. Kuulasmaa, J. Kuusisto, J. H. Laitinen, T. a Lakka, C. Langenberg, L. J. Launer, L. Lind, J. Lindström, J. Liu, A. Liuzzi, M.-L. Lokki, M. Lorentzon, P. a Madden, P. K. Magnusson, P. Manunta, D. Marek, W. März, I. M. Leach, B. McKnight, S. E. Medland, E. Mihailov, L. Milani, G. W. Montgomery, V. Mooser, T. W. Mühleisen, P. B. Munroe, A. W. Musk, N. Narisu, G. Navis, G. Nicholson, E. a Nohr, K. K. Ong, B. a Oostra, C. N. a Palmer, A. Palotie, J. F. Peden, N. Pedersen, A. Peters, O. Polasek, A. Pouta, P. P. Pramstaller, I. Prokopenko, C. Pütter, A. Radhakrishnan, O. Raitakari, A. Rendon, F. Rivadeneira, I. Rudan, T. E. Saariisto, J. G. Sambrook, A. R. Sanders, S. Sanna, J. Saramies, S. Schipf, S. Schreiber, H. Schunkert, S.-Y. Shin, S. Signorini, J. Sinisalo, B. Skrobek, N. Soranzo, A. Stančáková, K. Stark, J. C. Stephens, K. Stirrups, R. P. Stolk, M. Stumvoll, A. J. Swift, E. V Theodoraki, B. Thorand, D.-A. Tregouet, E. Tremoli, M. M. Van der Klauw, J. B. J. van Meurs, S. H. Vermeulen, J. Viikari, J. Virtamo, V. Vitart, G. Waeber, Z. Wang, E. Widén, S. H. Wild, G. Willemsen, B. R. Winkelmann, J. C. M. Witteman, B. H. R. Wolffenbuttel, A. Wong, A. F. Wright, M. C. Zillikens, P. Amouyel, B. O. Boehm, E. Boerwinkle, D. I. Boomsma, M. J. Caulfield, S. J. Chanock, L. A. Cupples, D. Cusi, G. V Dedoussis, J. Erdmann, J. G. Eriksson, P. W. Franks, P. Froguel, C. Gieger, U. Gyllensten, A. Hamsten, T. B. Harris, C. Hengstenberg, A. a Hicks, A. Hingorani, A. Hinney, A. Hofman, K. G. Hovingh, K. Hveem, T. Illig, M.-R. Jarvelin, K.-H. Jöckel, S. M. Keinanen-Kiukaanniemi, L. a Kiemeny, D. Kuh, M. Laakso, T. Lehtimäki, D. F. Levinson, N. G. Martin, A. Metspalu, A. D. Morris, M. S. Nieminen, I. Njølstad, C. Ohlsson, A. J. Oldehinkel, W. H. Ouwehand, L. J. Palmer, B. Penninx, C. Power, M. a Province, B. M. Psaty, L. Qi, R. Rauramaa, P. M. Ridker, S. Ripatti, V. Salomaa, N. J. Samani, H. Snieder, T. I. a Sørensen, T. D. Spector, K. Stefansson, A. Tönjes, J. Tuomilehto, A. G. Uitterlinden, M. Uusitupa, P. van der Harst, P. Vollenweider, H. Wallaschofski, N. J. Wareham, H. Watkins, H.-E. Wichmann, J. F. Wilson, G. R. Abecasis, T. L. Assimes, I. Barroso, M. Boehnke, I. B. Borecki, P. Deloukas, C. S. Fox, T. Frayling, L. C. Groop, T. Haritunian, I. M. Heid, D. Hunter, R. C. Kaplan, F. Karpe, M. F. Moffatt, K. L. Mohlke, J. R. O'Connell, Y. Pawitan, E. E. Schadt, D. Schlessinger, V. Steinthorsdottir, D. P. Strachan, U. Thorsteinsdottir, C. M. van Duijn, P. M. Visscher, A. M. Di Blasio, J. N. Hirschhorn, C. M. Lindgren, A. P. Morris, D. Meyre, A. Scherag, M. I. McCarthy, E. K. Speliotes, K. E. North, R. J. F. Loos, E. Ingelsson, Genome-wide meta-analysis identifies 11 new loci for anthropometric traits and provides

insights into genetic architecture. *Nat. Genet.* **45** (2013), doi:10.1038/ng.2606.

5. A. Gómez-Olivencia, R. Quam, N. Sala, M. Bardey, J. C. Ohman, A. Balzeau, La Ferrassie 1: New perspectives on a “classic” Neandertal. *J. Hum. Evol.* **117**, 13–32 (2018).
  6. E. Pomeroy, P. Bennett, C. O. Hunt, T. Reynolds, L. Farr, M. Frouin, J. Holman, R. Lane, C. French, G. Barker, New Neanderthal remains associated with the ‘flower burial’ at Shanidar Cave. *Antiquity*. **94**, 11–26 (2020).
  7. L. V. Golovanova, J. F. Hoffecker, V. M. Kharitonov, G. P. Romanova, Mezmaiskaya cave: a Neanderthal occupation in the northern Caucasus. *Curr. Anthropol.* **40**, 77–86 (1999).
  8. W. Rendu, C. Beauval, I. Crevecoeur, P. Bayle, A. Balzeau, T. Bismuth, L. Bourguignon, G. Delfour, J. P. Faivre, F. Lacrampe-Cuyaubère, C. Tavormina, D. Todisco, A. Turq, B. Maureille, Evidence supporting an intentional Neanderthal burial at la Chapelle-aux-Saints. *Proc. Natl. Acad. Sci. U. S. A.* **111**, 81–86 (2014).
  9. T. Akazawa, S. Muhesen, H. Ishida, O. Kondo, C. Griggo, New Discovery of a Neanderthal Child Burial from the Dederiyeh Cave in Syria. *Paléorient*. **25**, 129–142 (1999).
  10. Maureille B., H. Rougier, F. Houet, B. Vandermeersch, Les dents inférieurs du Néandertalien Regourdou 1 (site de Regourdou, commune de Montignac, Dordogne). *Anal. Métriques Comp. Paleo.* **13**, 183–200 (2001).
  11. P. Pettitt, *The Palaeolithic Origins of Human Burial* (Routledge, New York, 2010).
  12. E. Hovers, W. Kimblel, Y. Rak, The Amud 7 skeleton — still a burial . Response to Gargett. *J. Hum. Evol.* **39**, 253–260 (2000).
  13. Maureille, B., & Knüsel, C. J. (2022). The Earliest European Burials. In *The Routledge Handbook of Archaeoethanatology* (pp. 140-158). Routledge.
  - 14.
  - 15.
  - 16.
  - 17.
  - 18.
  - 19.
  - 20.
  - 21.
  - 22.
  - 23.
  - 24.
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- M. Martínón-Torres, F. d’Errico, E. Santos, A. Álvaro Gallo, N. Amano, W. Archer, S. J. Armitage, J. L. Arsuaga, J. M. Bermúdez de Castro, J. Blinkhorn, A. Crowther, K. Douka, S. Dubernet, P. Faulkner, P. Fernández-Colón, N. Kourampas, J. González García, D. Larreina, F. X. Le Bourdonnec, G. MacLeod, L. Martín-Francés, D. Massilani, J. Mercader, J. M. Miller, E. Ndiema, B. Notario, A. Pitarch Martí, M. E. Prendergast, A. Queffelec, S. Rigaud, P. Roberts, M. J. Shoaee, C. Shipton, I. Simpson, N. Boivin, M. D. Petraglia, Earliest known human burial in Africa. *Nature*. **593**, 95–100 (2021).
15. B. Vandermeersch, O. Bar-Yosef, The Paleolithic Burials at Qafzeh Cave, Israel. *Paleo.* **30**, 256–275 (2019).
  15. A. Ronen, "The Skhul burials: An archaeological review" in *Colloque XII: Les Sepultures anderthaliennes* (Nice, 1976), pp. 27–40.
  16. P. Pettitt, The Neanderthal dead: exploring mortuary variability in Middle Palaeolithic Eurasia. *Before Farming*. **1**, 1–19 (2002).
  17. F. d’Errico, L. Backwell, Earliest evidence of personal ornaments associated with burial: The Conus shells from Border Cave. *J. Hum. Evol.* **93**, 91–108 (2016).
  18. J. L. Bischoff, R. W. Williams, R. J. Rosenbauer, A. Aramburu, J. L. Arsuaga, N. García, G. Cuenca-Bescós, High-resolution U-series dates from the Sima de los Huesos hominids yields 600–66+∞kyrs: implications for the evolution of the early Neanderthal lineage. *J. Archaeol. Sci.* **34**, 763–770 (2007).
  19. A. Defleur, T. White, P. Valensi, L. Slimak, É. Crégut-Bonnoure, Neanderthal cannibalism at Moula-Guercy, Ardeche, France. *Science (80-. )*. **286**, 128–131 (1999).
  20. T. D. White, B. Asfaw, D. DeGusta, H. Gilbert, G. D. Richards, G. Suwa, F. C. Howell, Pleistocene Homo sapiens from Middle Awash, Ethiopia. *Nature*. **423**, 742–747 (2003).
  21. A. Rosas, C. Martínez-Maza, M. Bastir, A. García-Tabernero, C. Lalueza-Fox, R. Huguet, J. E. Ortiz, R. Julià, V. Soler, T. de Torres, E. Martínez, J. C. Cañaveras, S. Sánchez-Moral, S. Cuezva, J. Lario, D. Santamaría, M. de la Rasilla, J. Fortea, Paleobiology and comparative morphology of a late Neanderthal sample from El Sidron, Asturias, Spain. *Proc. Natl. Acad. Sci. U. S. A.* **103**, 19266–71 (2006).
  22. T. D. White, Cut marks on the Bodo cranium: a case of prehistoric defleshing. *Am. J. Phys. Anthropol.* **69**, 503–509 (1986).
  23. Y. Fernández-Jalvo, C. Diez J., I. Caceres, J. Rosell, Human cannibalism in the Early Pleistocene of Europe (Gran Dolina, Sierra de Atapureca, Burgos Spain). *J. Hum. Evol.* **37**, 591–622 (1999).
  24. T. R. Pickering, T. D. White, N. Toth, Brief Communication: cutmarks on a Plio-Pleistocene hominid from Sterkfontein, South Africa. *Am. J. Phys. Anthropol.* **111**, 579–584 (2000).
  25. M. D. Russell, Mortuary practices at the Krapina Neanderthal site. *Am. J. Phys. Anthropol.* **72**, 381–97 (1987).

26. J. Jaubert, S. Verheyden, D. Genty, M. Soulier, H. Cheng, D. Blamart, C. Burlet, H. Camus, S. Delaby, D. Deldicque, R. L. Edwards, C. Ferrier, F. Lacrampe-Cuyaubère, F. Lévêque, F. Maksud, P. Mora, X. Muth, É. Régnier, J. N. Rouzaud, F. Santos, Early Neanderthal constructions deep in Bruniquel Cave in southwestern France. *Nature*. **534**, 111–114 (2016).

5 *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 (). Similarly, experts are divided as to if La Chapelle-aux-Saints should (4) or should not (5, 6) be accepted as an intentional Neanderthal 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.

10 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.

15 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.

- 20
1. P. Pettitt, *The Palaeolithic Origins of Human Burial* (Routledge, New York, 2010).
  - 25 2. D. M. Sandgathe, H. L. Dibble, P. Goldberg, S. P. McPherron, The Roc de Marsal Neanderthal child: A reassessment of its status as a deliberate burial. *J. Hum. Evol.* 61, 243–253 (2011).
  3. P. Goldberg, V. Aldeias, H. Dibble, S. McPherron, D. Sandgathe, A. Turq, Testing the Roc de Marsal Neanderthal “Burial” with Geoarchaeology. *Archaeol. Anthropol. Sci.* 9, 1005–1015 (2017).
  4. W. Rendu, C. Beauval, I. Crevecoeur, P. Bayle, A. Balzeau, T. Bismuth, L. Bourguignon, G. Delfour, J. P. Faivre, F. Lacrampe-Cuyaubère, C. Tavormina, D. Todisco, A. Turq, B. Maureille, Evidence supporting an intentional Neanderthal burial at la Chapelle-aux-Saints. *Proc. Natl. Acad. Sci. U. S. A.* 111, 81–86 (2014).
  - 30 5. R. H. Gargett, Grave Shortcomings: The Evidence for Neanderthal Burial. *Curr. Anthropol.* 30, 157–190 (1989).
  6. H. L. Dibble, V. Aldeias, P. Goldberg, S. P. McPherron, D. Sandgathe, T. E. Steele, A critical look at evidence from La Chapelle-aux-Saints supporting an intentional Neanderthal burial. *J. Archaeol. Sci.* 53, 649–657 (2015).
- 35

## Supplementary Material

### Data for Figure 1.

5

Table used to create figure 1

site	group	type	Max.age	Min.age	Midrange	associated species	references
Bruniquel	non-functional cave use	cave	-0.176	-0.176	-0.176	Neandertals	Jaubert et al 2016
Wonderwerk	non-functional cave use	cave	n/a	n/a	-0.18	unknown archaic	Chazan and Horowitz 2009
Cueva de Ardales	non-functional cave use	cave	n/a	n/a	-0.66	Neandertals	Martí et al. 2021
Lingjing	engraved objects	engraved bone	-0.125	-0.105	-0.115	archaic Homo	Li et al 2019
Kozarnika	engraved objects	engraved bone	-1.6	-1.4	-1.5	n/a	Sirakov et al. 2010
Trinil	engraved objects	engraved shell	-0.64	-0.38	-0.51	Homo erectus	Joordens et al. 2014
Bilzingsleben	engraved objects	engraved bone	-0.37	-0.23	-0.3	Homo erectus	Mania and Mania 1988
Diepkloof Rock Shelter	engraved objects	engraved eggshell	-0.119	-0.099	-0.109	n/a	Texier et al 2013
Qafzeh	engraved objects	engraved stone	-0.118	-0.075	-0.0965	Homo sapiens	Hovers et al. 1997
Sainte-Anne	engraved objects	engraved	-0.21	-0.17	-0.19	n/a	Raynal and Seguy 1986
Oldisleben	engraved objects	engraved bone	-0.13	-0.08	-0.105	n/a	Bendarik 2006
Sima de los Huesos	mortuary behavior	mortuary	-0.6	-0.4	-0.5	Neandertals	Bischoff et al. 2007
Rising Star Cave	mortuary behavior	mortuary	-0.335	-0.241	-0.29	Homo naledi	Berger et al 2022
Skhul	mortuary behavior	mortuary	-0.13	-0.1	-0.115	Homo sapiens	Ronen 1976
Tabun	mortuary behavior	mortuary	-0.12	-0.12	-0.12	Neandertals	Pettitt, P. B. (2002)
Qafzeh	mortuary behavior	mortuary	-0.13	-0.08	-0.105	Homo sapiens	Vandermeersch and Bar-Yosef 2019
Panga ya Saidi	mortuary behavior	mortuary	-0.082	-0.074	-0.078	Homo sapiens	Martinón-Torres et al. 2021
Berekhat Ram	non-utilitarian objects	art	-0.47	-0.233	-0.35	n/a	d'Errico and Nowell 2001
Makapansgat	non-utilitarian objects	art	n/a	n/a	-3	australopithecus	Bednarik 1998
Tan-Tan	non-utilitarian objects	art	-0.5	-0.3	-0.4	n/a	Bednairk 2003
Krapina	non-utilitarian objects	?	-0.13	-0.08	-0.13	Neandertals	Radovčić et al 2016

Gadeb 8e	ochre use	ochre	-1.45	-0.75	-1.1	n/a	Clark and Kurashina 1979
Bizat Ruhama	ochre use	ochre	-1.96	-0.78	-1.37	n/a	Ronen et al. (1998)
Kathu Pan 1b	ochre use	ochre	-0.417	-0.417	-0.417	n/a	Watts et al. 2016
Hungsi	ochre use	ochre	-1.5	-0.3	-0.9	n/a	Watts et al 2014
Maastricht-Belvedere C	ochre use	ochre	-0.27	-0.2	-0.235	Neandertals	Roebroeks et al 2012
GnJh-15	ochre use	ochre	-0.285	-0.285	-0.285	n/a	Denio and Mcbrearty 2003
Biddenham	ornamentation	ornamentation	-0.3	-0.3	-0.3	n/a	Bednarik 2005
Contrebandiers Cave	ornamentation	ornamentation	-0.115	-0.11	-0.1125	n/a	d'Errico et al 2009
Krapina	ornamentation	ornamentation	-0.13	-0.13	-0.13	Neandertals	Radovicic et al. 2015
Border Cave	ochre use	ochre	na	na	0.2	Homo sapiens	Wadley et al. 2020
Rising Star Cave system	engraved objects	Cave wall	-0.335	-0.241	-0.29	Homo naledi	Berger et al 2023b

**Table X. Data used to create Figure 1.**

### Refs for Figure 1

- 5 1. J. Jaubert, S. Verheyden, D. Genty, M. Soulier, H. Cheng, D. Blamart, C. Burlet, H. Camus, S. Delaby, D. Deldicque, R. L. Edwards, C. Ferrier, F. Lacrampe-Cuyaubère, F. Lévêque, F. Maksud, P. Mora, X. Muth, É. Régnier, J. N. Rouzaud, F. Santos, Early Neanderthal constructions deep in Bruniquel Cave in southwestern France. *Nature*. 534, 111–114 (2016).
- 10 2. M. Chazan, L. K. Horwitz, Milestones in the development of symbolic behaviour: a case study from Wonderwerk Cave, South Africa. *World Archaeol.* 41, 521–539 (2009).
3. A. P. Martí, J. Zilhão, F. d'Errico, P. Cantalejo-Duarte, S. Domínguez-Bella, J. M. Fullola, G. C. Weniger, J. Ramos-Muñoz, The symbolic role of the underground world among Middle Paleolithic Neanderthals. *Proc. Natl. Acad. Sci. U. S. A.* 118, 1–6 (2021).
- 15 4. Z. Li, L. Doyon, H. Li, Q. Wang, Z. Zhang, Q. Zhao, F. d'Errico, Engraved bones from the archaic hominin site of Lingjing, Henan Province. *Antiquity*. 93, 886–900 (2019).
5. N. Sirakov, J.-L. Guadelli, S. Ivanova, S. Sirakova, M. Boudadi-Maligne, I. Dimitrova, F. Ph, C. Ferrier, A. Guadelli, D. Iordanova, N. Iordanova, M. Kovatcheva, I. Krumov, J.-C. Leblanc, V. Miteva, V. Popov, R. Spassov, S. Taneva, T. Tsanova, An ancient continuous human presence in the Balkans and the beginnings of human settlement in western Eurasia: A Lower Pleistocene example of the Lower Palaeolithic levels in Kozarnika cave (North-western Bulgaria). *Quat. Int.* 223, 94–106 (2010).
- 20 6. J. Joordens, F. D'Errico, F. P. Wesselingh, S. Munro, J. de Vos, J. Wallinga, C. Ankjærgaard, T. Reimann, J. R. Wijbrans, K. F. Kuiper, H. J. Mùcher, H. Coqueugniot, V. Prié, I. Joosten, B. van Os, A. S. Schulp, M. Paniel, V. van der Haas, W. Lustenhouwer, J. J. G. Reijmer, W. Roebroeks, *Homo erectus* at Trinil on Java used shells for tool production and engraving. *Nature*. 518, 228–231 (2014).
- 25 7. D. Mania, U. Mania, Deliberate engravings on bone artefacts of *Homo erectus*. *Rock Art Res.* 5, 91–97 (1988).
8. P. Texier, G. Porraz, J. Parkington, J. Rigaud, C. Poggenpoel, C. Tribolo, The context, form and significance of the MSA engraved ostrich eggshell collection from Diepkloof Rock Shelter, Western Cape, South Africa. *J. Archaeol. Sci.* 40, 3412–3431 (2013).
- 30 9. D. Radovčić, D. Japundžić, A. O. Sršen, J. Radovčić, D. W. Frayer, An interesting rock from Krapina. *Comptes Rendus Palevol.* 15, 988–993 (2016).
10. E. Hovers, B. Vandermeersch, O. Bar-Yosef, A Middle Palaeolithic engraved artifact from Qafzeh Cave, Israel. *Israel.* 14, 79–87 (1997).
- 35 11. J. P. Raynal, R. Seguy, Os incisé Acheuléen de Sainte-Anne 1 (Polignac, Haute-Loire) / Acheulean incised bone of Sainte-Anne I (Polignac, Haute-Loire). *Rev. Archeol. Centre France.* 25, 79–81 (1986).
12. R. G. Bednarik, The Middle Paleolithic engravings from Oldisleben, Germany. *Anthropol.* 44, 113–121 (2006).

13. J. L. Bischoff, R. W. Williams, R. J. Rosenbauer, A. Aramburu, J. L. Arsuaga, N. García, G. Cuenca-Bescós, High-resolution U-series dates from the Sima de los Huesos hominids yields 600–66±∞kyrs: implications for the evolution of the early Neanderthal lineage. *J. Archaeol. Sci.* 34, 763–770 (2007).
14. A. Ronen, "The Skhul burials: An archaeological review" in *Colloque XII: Les Sepultures anderthaliennes* (Nice, 1976), pp. 27–40.
15. P. Pettitt, The Neanderthal dead: exploring mortuary variability in Middle Palaeolithic Eurasia. *Before Farming*, 1, 1–19 (2002).
16. B. Vandermeersch, O. Bar-Yosef, The Paleolithic Burials at Qafzeh Cave, Israel. *Paleo.* 30, 256–275 (2019).
17. I. Toro-Moyano, B. Martínez-Navarro, J. Agustí, C. Souday, J. M. Bermúdez de Castro, M. Martínón-Torres, B. Fajardo, M. Duval, C. Falguères, O. Oms, J. M. Parés, P. Anadón, R. Julià, J. M. García-Aguilar, A.-M. Moigne, M. P. Espigares, S. Ros-Montoya, P. Palmqvist, The oldest human fossil in Europe dated to ca. 1.4 Ma at Orce (Spain). *J. Hum. Evol.* in press (2013), doi:10.1016/j.jhevol.2013.01.012.
18. F. d’Errico, A. Nowell, A New Look at the Berekhat Ram Figurine: Implications for the Origins of Symbolism (2001; [http://www.journals.cambridge.org/abstract\\_S0959774300000056](http://www.journals.cambridge.org/abstract_S0959774300000056)), vol. 10.
19. R. G. Bednarik, The “Australopithecine” Cobble from Makapansgat, South Africa. *South African Archaeol. Bull.* 53, 4–8 (1998).
20. R. G. Bednarik, A Figurine from the African Acheulian. *Curr. Anthropol.* 44, 405–413 (2003).
21. D. Radovčić, A. O. Sršen, J. Radovčić, D. W. Frayer, Evidence for Neandertal Jewelry: Modified White-Tailed Eagle Claws at Krapina. *PLoS One.* 10, e0119802 (2015).
22. J. D. Clark, H. Kurashina, Hominid occupation of the East-Central Highlands of Ethiopia in the Plio–Pleistocene. *Nature.* 282, 33–39 (1979).
23. A. Ronen, J.-M. Burdukiewicz, S. A. Laukhin, Y. Winter, A. Tsatskin, T. Dayan, O. A. Kulikov, V. K. V;asov, V. V. Semenov, The Lower Palaeolithic site Bitzat Ruhama in the Northern Negev, Israel. *Archaeol. Korrespondenzblatt.* 28, 163–173 (1998).
24. I. Watts, M. Chazan, J. Wilkins, Early Evidence for Brilliant Ritualized Display: Specularite Use in the Northern Cape (South Africa) between ~500 and ~300 Ka. *Curr. Anthropol.* 57, 287–310 (2016).
25. W. Roebroeks, M. J. Sier, T. K. Nielsen, D. De Loecker, J. M. Parés, C. E. S. Arps, H. J. Múcher, Use of red ochre by early Neandertals. *Proc. Natl. Acad. Sci. U. S. A.* 109, 1889–94 (2012).
26. R. G. Bednarik, Middle Pleistocene beads and symbolism. *Anthropos.* 100, 537–552 (2005).
27. F. d’Errico, M. Vanhaeren, N. Barton, A. Bouzouggar, H. Mienis, D. Richer, J.-J. Hublin, S. P. McPherron, P. Lozouet, Additional evidence on the use of personal ornaments in the Middle Paleolithic of North Africa. *Proc. Natl. Acad. Sci.* 106, 16051–16056. (2009).
28. L. Wadley, I. Esteban, P. De La Peña, M. Wojcieszak, D. Stratford, S. Lennox, F. D’Errico, D. E. Rosso, F. Orange, L. Backwell, C. Sievers, Fire and grass-bedding construction 200 thousand years ago at Border Cave, South Africa. *Science* (80-. ). 369, 863–866 (2020).
29. A. L. Deino, S. McBrearty, <sup>40</sup>Ar/<sup>39</sup>Ar dating of the Kapthurin Formation, Baringo, Kenya. *J. Hum. Evol.* 42, 185–210 (2002).
30. Berger et al, (2023a) Evidence for deliberate burial of the dead by Homo naledi, bioRxiv, DOI pending
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).

1. P. J. Habgood, N. R. Franklin, The revolution that didn’t arrive: A review of Pleistocene Sahul. *J. Hum. Evol.* 55, 187–222 (2008).
2. S. McBrearty, A. Brooks, The revolution that wasn’t: a new interpretation of the origin of modern human behavior. *J. Hum. Evol.* 39, 453–563 (2000).

3. L. Wadley, What is cultural modernity? A general view and a South African perspective from Rose Cottage Cave. *Cambridge Archaeol. J.* 11, 201–221 (2001).
4. T. Hopkinson, ‘Man the symboler’. A contemporary origins myth. *Archaeol. Dialogues.* 20, 215–241 (2013).
5. T. W. Deacon, *The Symbolic Species: The Co-evolution of Language and the Brain* (W. W. Norton, New York, 1997).
6. H. Anderson, Crossing the Line: The Early Expression of Pattern in Middle Stone Age Africa. *J. World Prehistory.* 25, 183–204 (2012).
7. M. Kissel, A. Fuentes, Semiosis in the Pleistocene. *Cambridge Archaeol. J.* 0 (2017),  
doi:<https://doi.org/10.1017/S0959774317000014>.
8. J. Joordens, F. D’Errico, F. P. Wesselingh, S. Munro, J. de Vos, J. Wallinga, C. Ankjærgaard, T. Reimann, J. R. Wijbrans, K. F. Kuiper, H. J. Mûcher, H. Coqueugniot, V. Prié, I. Joosten, B. van Os, A. S. Schulp, M. Panuel, V. van der Haas, W. Lustenhouwer, J. J. G. Reijmer, W. Roebroeks, *Homo erectus* at Trinil on Java used shells for tool production and engraving. *Nature.* 518, 228–231 (2014).
9. D. Radovčić, A. O. Sršen, J. Radovčić, D. W. Frayer, Evidence for Neandertal Jewelry: Modified White-Tailed Eagle Claws at Krapina. *PLoS One.* 10, e0119802 (2015).
10. F. d’Errico, A. Nowell, A New Look at the Berekhat Ram Figurine: Implications for the Origins of Symbolism (2001; [http://www.journals.cambridge.org/abstract\\_S0959774300000056](http://www.journals.cambridge.org/abstract_S0959774300000056)), vol. 10.
11. N. Sirakov, J.-L. Guadelli, S. Ivanova, S. Sirakova, M. Boudadi-Maligne, I. Dimitrova, F. Ph, C. Ferrier, A. Guadelli, D. Iordanova, N. Iordanova, M. Kovatcheva, I. Krumov, J.-C. Leblanc, V. Miteva, V. Popov, R. Spassov, S. Taneva, T. Tsanova, An ancient continuous human presence in the Balkans and the beginnings of human settlement in western Eurasia: A Lower Pleistocene example of the Lower Palaeolithic levels in Kozarnika cave (North-western Bulgaria). *Quat. Int.* 223, 94–106 (2010).
12. Z. Li, L. Doyon, H. Li, Q. Wang, Z. Zhang, Q. Zhao, F. d’Errico, Engraved bones from the archaic hominin site of Lingjing, Henan Province. *Antiquity.* 93, 886–900 (2019).