The mosaic nature of *Homo naledi*: Behavioural and evolutionary speculations

by Yiorgos Thanos Tsounis

Homo naledi ("Star Man") holds a fascinating morphology of primitive and derived traits, and offers more questions than answers as to their true functions. In this paper, I will attempt to discern some answers by first describing *H. naledi*'s outstanding morphological traits with merit to the researchers who found the specimens, as well as discuss its overarching significance in the field of palaeoanthropology. I will then investigate the theories regarding *H. naledi*'s behavior dissected through comparisons with other hominins, such as contemporary archaic *Homo* members, argue for a semi-rock climbing morphology rather than semi-arboreal, provide evidence for a possible one million year old stasis through the lenses of neurobiology and ecology, and finally question how these attributed to this species' extinction. Although a large portion of this paper is theoretical, it nonetheless stems from evidence directly corresponding to the remains of *H. naledi*.

Discovered exclusively in the Rising Star Cave complex (located in the Cradle of Humankind, South Africa), *Homo naledi* is a hominin with a complex mosaic morphology. Composed of both archaic and derived traits, *H. naledi* loosely resembles both *Homo sapiens* and species of the genus *Australopithecus*. The fossil remains have been dated to roughly 300 thousand years ago (kya), making *H. naledi* one of the youngest species of *Homo* to exhibit a cranial capacity of only approximately 500 cubic centimeters (cc); for context, the modern *Homo sapiens* cranial capacity exhibits approximately 1600 cc (Berger et al. 2015; Berger and Hawkes 2017). In addition, *H. naledi* was a contemporary of both South African *H. sapiens* and *H. heidelbergensis*, hominin species who likely contributed to its extinction, overlapping in both geographic and temporal aspects (Timmermann et al. 2022). The shifting environment of South Africa around 2–0.8 million years ago (mya) likely served as a foundation for the evolution of *H. naledi* and its contemporaries, but in a way that promoted little change to the former's brain size over the millennia, known as a stasis.

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With very little knowledge of its evolutionary past, research on the origins of *H. naledi* has remained speculative and debated. This paper will attempt to construct a new perspective on how this species evolved, lived, and died by way of two theories. The first theory explains why *H. naledi*'s morphology went through an exaptation event from semi-arboreal behavior to rock climbing behavior. Exaptation is defined as the process by which a previously naturally-selected biological character is put into a new role, different from the function it was selected for, but fits the new function (Gould and Verba, 1982). I constructed this theory based on the current morphological research on this species, paleoenvironmental studies indicating that the area in which the species lived in was not suitable for arboreal locomotion, and the idea of possible rock climbing behavior from Voisin et al.'s (2020) research. The second theory will present a scenario for how the species went extinct due to a roughly one-million year cognitive and behavioral stasis. I constructed this theory by amalgamating the evidence and speculations of the previous theory with studies in both brain development and evolution. Overall, the evidence for both theories are presented in the forms of *H. naledi*'s fossil record, palaeoenvironmental reconstructions, and neurological perspectives. The paper will conclude by questioning how *H. naledi* went extinct.

Naledi's Morphology

In order to provide both perspective and the basis of theoretical discussion, it is crucial to highlight the key features from both *H. naledi*'s archaic and derived categories as seen in the fossil record.

Archaic Aspects

In the archaic category, features in the hand bones (metacarpals and phalanges), the bones of the shoulder girdle, and the lower limbs of *H. naledi* attest to this aspect of its morphology and are reminiscent of Australopithecine species.

I will first focus on the nature of the finger bones (fig. 1). Although human-like in shape, the phalanges and metacarpals are quite curved (Berger and Hawkes 2017:191; Berger et al. 2015). Specifically, the first metacarpal (MC1) offers a distinct nature compared to other hominins and will be discussed further in this paper as it is one of the primary sources of inspiration for the theoretical speculation of *H. naledi*'s evolutionary nature. The phalanges have a curvature that is seen in earlier hominins and modern great apes, a result of semi- or fully arboreal behavior, whereby the hands adapted to grasping tree branches.

Because of the relatedness of *H. naledi*'s curved finger bones to other hominins and modern arboreal apes, researchers have speculated that *H. naledi* climbed trees habitually on top of bipedal locomotion, making it a semi-arboreal species (Berger et al. 2015).

Figure 1. The hand of H. naledi. All bones except for the pisiform are presented. Reproduced from Berger et al. (2015).

Figure 2. Paratype of H. naledi's femur represented in (A) the medial view, (B) the posterior view, (C) the lateral view, and (D) the medial view. The scale bar measures 2 cm. Reproduced from Berger et al. (2015).

The upper body of *H. naledi*, specifically the bones of the shoulder girdle and the humeri, are made for climbing: the shoulders have a glenoid fossa canted upwards with climbing-oriented humeri, as well as short and curved clavicles (Berger and Hawkes 2017:192, 214; Berger et al. 2015). Interestingly, Berger et al. (2015) make a connection of *H. naledi*'s archaic finger and upper-body to that of the 4.4 million year old *Ardipithecus ramidus*, illustrating a glimpse of the reach of *H. naledi*'s morphological hands to the archaic side of its traits.

When looking at the lower limbs, Berger identified how the femur's neck and head are similar to the Australopithecines, but with purely unique mediolaterally-running ridges on the neck, creating a sulcus on the superior aspect (fig. 2; Berger and Hawkes 2017:192; Berger et al. 2015).

The pelvis (fig. 3) is flared to the extent that it matches the archaic morphology of the Australopithecines, categorized as such because such flaring is not seen in more derived hominins such as *H. sapiens* (Berger et al. 2015).

Derived Aspects

In the derived category, the carpals and feet are the primary definers for a connection to what

Figure 3. Pelvic specimens representing ilium fragments, showing (A) the lateral view and (B) the anterior view which demonstrates the degree of flare. Reproduced from Berger et al., (2015).

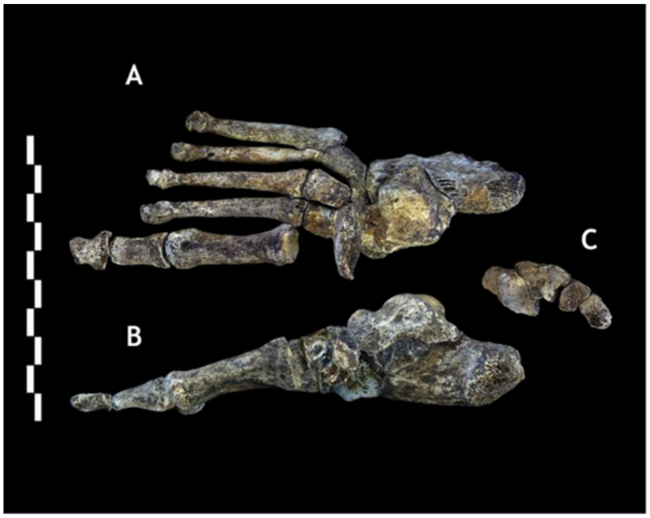

Figure 4. Tarsal and metatarsal specimens placed in the proper shape of *H. naledi*'s foot, shown in (A) the dorsal and (B) medial views. There are also the (C) proximal articular surfaces of the foot that demonstrate its arch. The scale bar measures 10 cm. Reproduced from Berger et al. (2015).

researchers see in the later species of the genus *Homo*, including modern *H. sapiens*.

The carpals are very humanlike and do not suggest an archaic nature (Berger et al. 2015). The same condition is expressed by the feet, as the tarsals and metatarsals (fig. 4) are nearly indistinguishable from those of *H. Sapiens* (Berger and Hawkes 2017:189; Berger et al. 2015), suggesting little to no difference between *H. naledi*'s and *H. sapiens*' striding bipedal locomotion (Harcourt-Smith et al. 2015).

Lastly, the cranial and dental features of *H. naledi* (fig. 5) are predominantly humanlike, with the teeth being adapted for a mixed diet akin to other members of *Homo*, as well as having chipping that relates to a more abrasive diet seen in *Paranthropus robustus* (Berger and Hawkes 2017:196, Berger et al. 2015; Ungar and Berger 2018).

In addition, Berger compared *H. naledi*'s skull with the *H. erectus* skulls from Dmanisi, Georgia, and found that the latter are one of the closest examples to *H. naledi* in cranial capacity: *H. naledi* ranges from 450–550cc with an average of 500cc, and the Dmanisi hominins range from 550–750cc (Berger and Hawkes 2017:193-194; Berger et al. 2015; Lordkipanidze et al. 2013). These similarities in cc have also been identified in other species such as *H. rudolfensis* and *H. habilis* (Berger and Hawkes 2017:195; Berger et al. 2015; Laird et al. 2017), and they have helped researchers place *H. naledi* in the phylogenetic tree.

In essence, *H. naledi*'s morphology is a mosaic of traits that support the analogy of the species' "morphological hands" reaching for and complementing morphological traits from the archaic and derived categories.

H. naledi's significance

H. naledi's mosaic morphology and time period relative to other *Homo* species and their morphologies, particularly with respect to cranial capacities, make this hominin particularly distinct.

The *H. naledi* specimens have been dated to approximately 250–450 thousand years ago (kya), meaning they coexisted alongside other *Homo* species such as *H. heidelbergensis* and *H. sapiens*

Figure 5. The cranial holotype specimens of H. naledi. The cranium is represented in the (A) posterior and (B) frontal views; The maxilla in (C) medial, (D) frontal, (E) superior, and (F) occlusal views; The mandible in (H) occlusal, (I) basal, (J) right lateral, and (K) anterior views; (G) The combination of the cranium, maxilla, and mandible in left lateral view. Reproduced from Berger et al. (2015).

(Grün et al. 2020:372; Dirks et al. 2017). However, compared to other *Homo* species, *H. naledi* exhibits a much smaller brain size. This is crucial because it suggests that time does not equate to brain growth, rather that behavior-altering pressures brought about by the environment do.

Stemming from this understanding arises a speculated capability to grasp the concept of death. No other animal or faunal remains were present at the site of discovery, and there is no indication of water flowing into the cave system to explain how the remains appeared there (Berger and Hawkes 2017:204). There were no teeth marks on any of the fossils (Berger and Hawkes 2017:215), suggesting no predator might have brought them down into the cave system. This led researchers to theorize that this could not have only been a home, but a space for the deceased, suggesting a pivotal step for cultural transformation that would eventually be seen in humans today (Berger and Hawkes 2017:205). However, the evidence for such conclusions remain scarce, and the idea of intentional burial should be treated with skepticism until more evidence is proposed.

Realm of Rocks over Branches: Rock Climbing Theory

This first theory speculates that *H. naledi*'s upper-body morphology is not a reflection of purely arboreal-adapted behaviors, but rather of rock climbing. The evidence for this theory is predominantly paleoenvironmental, suggesting a lack of abundant tree distribution and thus no possibility for a semi-arboreal morphology to have evolved. Additionally, the morphology necessary for climbing, regardless of whether it is tree or rock climbing, allows individuals to increase the efficiency of the muscles of the shoulder during elevation of the upper limb (Voisin et al. 2020:6).

The humanlike shape yet archaic curvature of *H. naledi*'s hand morphology is shared amongst both the adults and juveniles of the specimens found at the Dinaledi site (Kivell et al. 2015), suggesting a constant behavioral pattern of climbing for most, if not all, members of varying ages within *H. naledi* populations. Without looking at the climate of the time and area *H. naledi* lived in, it is easy to claim that, much like the australopithecines, *H. naledi* was partly arboreal. However, this is not likely the case.

Palaeoenvironment

Based on palaeoenvironmental reconstructions of the Southern African region, the climate at approximately 1.5 mya consisted of grasslands; from 1.3–0.8 mya, it was dry but had a significant amount of tree distribution; and from 1.1–0.8 mya, there was a predominant presence of wooded grasslands (Reynolds and Kibii 2011:63, 68): Around 0.5–0.3 mya, when *H. naledi* lived, the climate was akin to the dry, open, and tree-sparse terrain of modern South Africa (Reynolds and Kibii 2011:63, 83).

Additional studies indicate that the shift to open environments could have occurred as early as 1.7 mya (Hopley et al. 2007:620; Hopley and Maslin 2010:43; Luyt and Lee-Thorp 2003:271–272). Based on $\delta^{13}C$ analysis on tooth enamel of faunal remains from Swartkrans and Sterkfontein, the proportion of C4 plant (grass) values outmatched C3 plant (tree and shrub) values in the upper levels of the sites, suggesting that the fauna during this time period (~1.7 mya) relied on a grass-based diet (Hopley and Maslin 2010; Luyt and Lee-Thorp 2003). This means that the environment within this time period was most likely covered in grasses rather than trees and shrubs. Looking at $\delta^{13}C$ analyses of flowstone deposits from Buffalo Cave, C4 values are recorded at a much higher rate than C3, further suggesting a grassy expansion during this time period (Hopley et al. 2007). Although the results from these studies do not show the entirety of South Africa's environment at 1.7 mya and onwards, they nonetheless provide context to the environment *H. naledi* evolved in.

With the understanding that the climate of South Africa was inhospitable to trees during the time period when *H. naledi* was extant, there is little reason to consider this species semi-arboreal: there was little to no tree distribution that would serve as the basis of morphological change to a semi-arboreal state as seen in the individuals' morphologies. However, there were rocky outcroppings and mountainous ranges present in South Africa such as Magaliesburg that could have served as *H. naledi*'s preferred location for habitual activity (Voisin et al. 2020). The presence of these rocky areas could have been the source for *H. naledi*'s preserved climbing morphology.

Naledi's hand: MC1

Figure 6. First metacarpal (MC1) specimens of H. naledi. Reproduced from Berger et al. (2015).

Looking at the hand of *H. naledi*, the distinct first metacarpal (fig. 6) is likely an indicator of habitual rock climbing behavior. Berger connected the MC1's robusticity and large muscle attachment sites to the possibility of tool manufacturing, as such a task requires strong grip and precision (Berger and Hawkes 2017:190). Although it is likely *H. naledi* was capable of using stone tools, its MC1 does not reflect Australopithecine, *Homo*, and modern great ape MC1 morphology (Berger et al. 2015). Due to this distinction, it is possible that the evolution of *H. naledi*'s MC1 likely consisted of adapting to a pressure that required powerful grasping and coordination, such as the practice of rock climbing.

Behaviorally, climbing a mere 4–5 meters up a rocky wall would provide great protection against predators, or even climbing down or into a cave system like Dinaledi's, that could help a group's survival (Voisin et al. 2020:7).

It can therefore be understood that *H. naledi*'s morphology creates an "illusion" of a semi-arboreal morphology due to the similarities seen in older, semi-arboreal hominins. However, due to the palaeoenvironmental reconstructions, the morphology of this hominin is a unique story with links to the realm of rocks rather than branches.

In addition, the "illusion" proposed by the curved phalanges and metacarpals is most likely due to an exaptation event: the vestigial curvature brought about by early *H. naledi* populations living in tree-abundant areas was "replaced" in function by the rock climbing populations and their behaviors as seen in the fossil record; the physiological change from tree to rock climbing would not have shown a drastic morphological change in the upper limbs and body.

The Origins of H. naledi

Having discussed the "illusion" of *H. naledi*'s morphology, this section will observe the likely time range the species arose, its environmental contexts, and the relatedness to other hominins phylogenetically.

Berger and his team estimated the origin of *H. naledi* at around 2 mya (Berger and Hawkes 2017:218), whereas another crew at Simon Fraser University came up with a date of 912 kya via Bayesian analysis (Dembo et al. 2016). It is likely that *H. naledi*'s origin, with influence from the palaeoenvironmental reconstructions, is closest to Simon Fraser University's claim: this paper estimates it at approximately 1–1.2 mya.

H. naledi's date of origin at 1–1.2 mya is more probable than Berger's because it would reflect a pressure—the switch to dry grasslands—sufficient enough to branch off from a common ancestor with other hominins. When the shift to a significant cover of trees occurred, *H. naledi* adapted to the wooded environment and began to morphologically mirror the semi-arborealism seen in other hominin groups prior to their "shift" to the rock climbing morphology present at 500–300 kya.

Turning now to *H. naledi*'s phylogenetic relatedness to other hominin species, many hypothetical propositions for the species' placement in the family tree vary. However, the

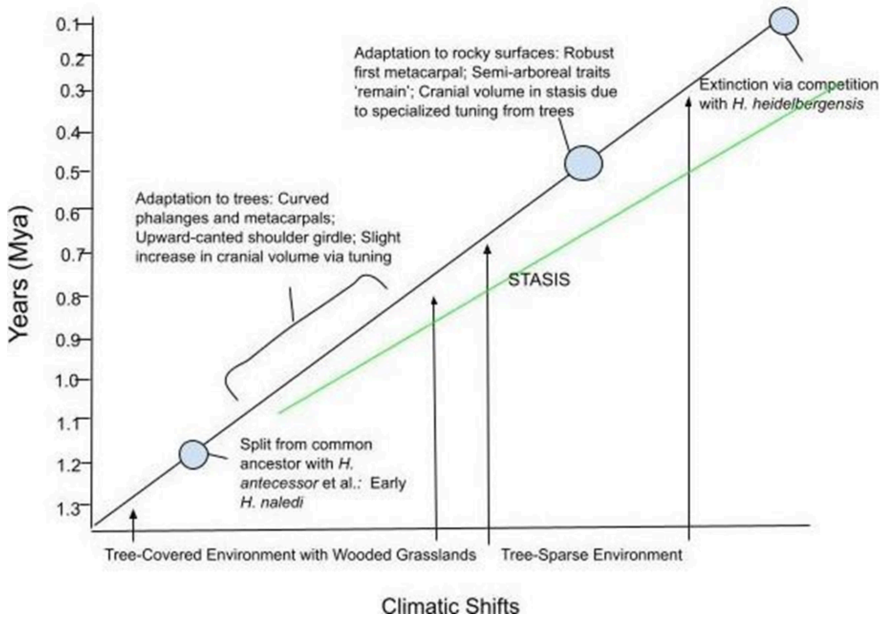

Figure 7. A speculative diagram representing H. naledi's acquisition of climbing characteristics, accompanied by the years (mya) and the two most significant climatic shifts/events that occurred during specific time periods (beginning of shift is indicated by the first arrow, and ended with the second arrow); the stasis is indicated by the green line running across the table. Based on the results from Reynolds and Kibbi (2011).

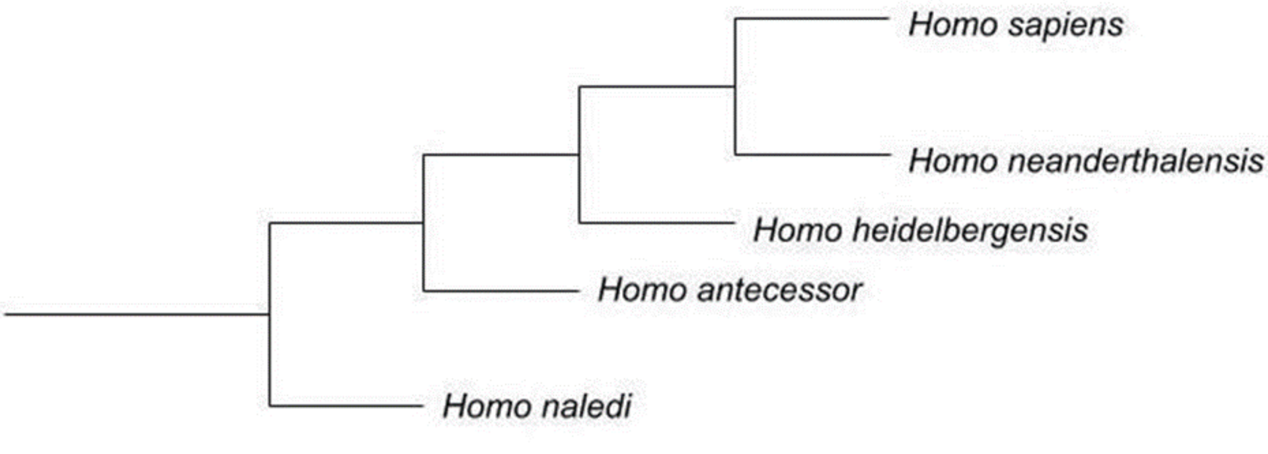

Figure 8. A drawing representing the phylogenetic relatedness of *H. naledi* and its contemporary hominins.

most likely one regards how *H. naledi* forms a clade with *H. antecessor, H. heidelbergensis, H. neanderthalensis,* and our own *H. sapiens* (Dembo et al. 2016). The hominins who are most closely related to this clade are proposed to be *H. erectus, H. rudolfensis, Au. sediba, and H. habilis* (Dembo et al. 2016). A visual depiction of this *H. naledi* clade can be seen in Figure 8.

Following the split from *H. naledi*'s supposed sister taxa's common ancestor, the process of *H. naledi*'s evolutionary path commenced. Although there is presently no genetic evidence for *H. naledi*'s relationships with other hominins, the relations expressed here are likely to be the most probable, but it currently serves as a placeholder for a future genetic-based phylogenetic tree.

Well-Tuned and Hardly Pruned: Stasis Theory

Considering the palaeoenvironmental, morphological, and behavioral aspects of *H. naledi*, the second theory argues that the mosaic morphology is the primary reason for the stasis in cognitive function and brain growth. However, because of this distinct morphology, *H. naledi* could have easily adapted to the shifting environments over time, and thus limited the growth of cranial capacity.

This theory is semi-analogous in nature to a paper by S. M. Stanley (1992). He argued that gracile australopithecines did not expand their brain size, and experienced an evolutionary stasis for more than 1.5 million years, due to their semi-arboreal nature (Stanley 1992:237). This stasis, Stanley maintains, ended with shrinking forests and the onset of expanding grassy habitats, which could have enabled some populations to abandon arboreal activity for semi-terrestrial activity (Stanley 1992:238). In the subsequent 30 years since his work, researchers continue to apply Stanley's proposition to various models on the origin of *Homo*, due to the environmental, morphological, and behavioral implications that he made towards the understanding of *Australopithecus* (Lewis and Harmand 2016; Venkataram, Kraft, and Dominy 2013; McKee 2001; Kimbel and Villmoare 2016). It is thus viable to utilize Stanley's theory in a manner that relates to *H. naledi*, as both *Australopithecus* and *H. naledi* appear to share characteristics (Berger et al. 2017).

The Brain of *H. naledi*

H. naledi's cranial capacity (averaging 500 cc) in comparison to its contemporary *H. heidelbergensis* (averaging 1200 cc) shows great contrast. Because both species were contemporaries in Africa, this difference must be analyzed in order to put the influences of ecology on neurology into context, such that there is an understanding as to what predisposed factors led the latter species to outlive the former.

Ecology

The difference in the hominins' brain size shows how their environments exhibited different pressures. One way to frame this is by understanding that if there is little to no disturbance in an organism's environment, there will be little to no evolutionary changes; if there are great environmental pressures, there will be evolutionary changes (Eldridge 2004:92). That is, little to no environmental pressures equates to little to no brain growth; great environmental pressures equates to brain growth. Therefore, growth entails intensity, rather than just time.

Although *H. naledi*'s environments were shifting throughout its time, the species' distinct morphology and behavior that was honed at approximately 1–0.8 mya could have rendered all subsequent environmental shifts unchallenging, therefore equating to little to no growth or change in brain connectivity and adaptation.

As for *H. heidelbergensis*, because it did not have the same mosaic morphology, its different environmental pressures were greater and more difficult to adapt to, which would have ensured a shift in the organization and size of the brain.

Neurology

As brains grow in size, they reorganize their nutrients to accommodate for the organism's behaviors in response to environmental pressures (Barrett 2020). Not only are the nutrients being reorganized and redistributed, but the neurons are also active through the processes of "tuning and pruning."

Tuning is the strengthening of the connections between neurons, particularly for resource/nutrient management and behavioral aspects which, for "well tuned" connections, are more efficient at carrying out tasks and processing information and will allow the brain to create behavioral patterns that reflect such tuning (Barrett 2020:50–51). What is familiar becomes efficient, and what is efficient becomes familiar. Pruning on the other hand is the process of removing or weakening the connections used the least, colloquially seen in the well-known phrase "if you don't use it, you lose it." Pruning additionally ensures that the tuning process becomes more efficient and stable when adapting to a certain environment (Barrett 2020; Low and Cheng 2006).

Speculation

During the development of *H. naledi*'s morphology, the neural connections could have been tuned to adapt to a mix of tree climbing and bipedal locomotion. When the climatic shift to the 'modern tree-sparse' environment occurred between approximately 1.7–500 kya, the exaptation for the rock climbing morphology would have felt physiologically familiar. This would have eliminated the 'pruning process' of the neural connections. In other words, the motor neurons would have matched the exaptation process described, wherein they were tuned for climbing trees and would not have had to be reallocated and tuned to a great extent when shifting to rock climbing movements.

Overall, it can be summarized that *H. naledi*'s shifting environment did not define its stasis, rather it reflected how the stasis was due to the 'well-tuned and hardly pruned' brain of the species. Essentially, the changing environment caused little disturbance to *H. naledi*, and thus there was little to no change in the brain's growth and evolution as there was no need for it.

Nature of Extinction

H. naledi survived and thrived due to ecological and neurological aspects within the environment. However, the manner of its extinction is up for speculation.

It is probable that the fossils found by Berger and his team were some of the last of the species, yet no factors at the site have indicated a cause of extinction. It is important to recall, however, that the current fossil record for *H. naledi* resides within a single cave system, and nowhere outside of the cave. Currently, researchers are unsure as to how *H. naledi* became extinct, but possibilities constituted from evidence outside of the direct fossil record should be considered.

Possibility: Competition

Based on the discussion in the last section, it is safe to assume that *H. naledi* did not go extinct from climatic shifts. One reason is that the shift to the 'modern day' tree-sparse climate at 500–300 kya is most similar to modern South Africa, such that *H. naledi* was mentally and physically prepared for the shifts in climate. A possibility, however, could be competition with other *Homo* species, particularly *H. heidelbergensis*, whose specimens have been found in the southern parts of Africa (Grün et al. 2020:372); the two species most likely interacted.

In this case, *H. naledi*'s advanced and "tuned" mosaic disposition could have been its downfall in encounters with *H. heidelbergensis*. The former's brain was tuned to be very efficient at climbing to escape predators, and because it never faced challenges to prune out neural pathways in order to solve new problems, a brain like *H. heidelbergensis*' could solve new problems and could have found a way to outmatch *H. naledi* in hunting and gathering resources.

This would mean that over time, possibly up until 150–100 kya—the time period at which I posit *H. naledi* went or was near extinction, *H. heidelbergensis* encumbered the highly tuned *H. naledi* with different behaviors the latter could not adapt to. In Darwinian terms of survival of the fittest, *H. naledi* was the least fit.

Conclusions

This paper has covered the main aspects about what is known of *Homo naledi* morphologically and climatically, highlighting the distinct mosaic nature it held as the basis for the theoretical realm of the two theories presented. This realm explored how *H. naledi*'s morphology reflects a semi-rock climbing morphology that 'replaced' the semi-arboreal morphology the species had prior to the shift to the dry, open environment with little tree distribution at approximately 1.7–0.5 mya. This realm also explored the supposed phylogenetic relationship to other hominin species, and explained *H. naledi*'s fairly successful 'well-tuned and not pruned' stasis through ecological and neurobiological lenses. Finally, there was discussion on how this stasis could have been a factor in its extinction.

Homo naledi is a mysterious species that offers great periods of time to ponder its origin, behavior, and extinction. The remains allow researchers to promote new discoveries that have been and are yet to be released into the public to further give clarity to the species' definition. Ultimately, the search for *H. naledi* reflects paleoanthropology's initiative to formulate a mosaic of hypotheses to unearth the essence of the human condition.

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