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Constraining the Likely Technological Niches of Late Middle Pleistocene Hominins with *Homo naledi* as Case Study

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Abstract

We develop a framework to differentiate the technological niches of co-existing hominin species by reviewing some theoretical biases influential in thinking about techno-behaviours of extinct hominins, such as a teleological bias in discussing technological evolution. We suggest that some stone-tool classification systems underestimate technological variability, while overestimating the complexity of the behaviours most commonly represented. To model the likely technological niches of extinct populations, we combine ecological principles (*i.e.* competitive exclusion) with physical anthropology and the archaeological record. We test the framework by applying it to the co-existence of *Homo naledi* and *Homo sapiens* during the late Middle Pleistocene in southern Africa. Based on our analysis, we suggest that tool use was probably not an essential part of *H. naledi*'s niche, but that technology occasionally provided caloric benefits. In contrast, tool use was a structural part of the *H. sapiens* way of life. We provide reasoning for our interpretation that the latter population is associated with more sophisticated reduction strategies and the development of prepared core technology. The method also has applicability to cases such as the co-existence of different toolmakers during the Earlier Stone Age (ESA) in East Africa and the co-existence of Neanderthals and *H. sapiens* in Eurasia.

Keywords Sympatric hominins · Techno-behaviours · Teleological bias · Technological niches · Extinct hominins · Caloric benefits · Obligatory tool use

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Introduction

Throughout the Pleistocene hominin species frequently co-existed (Wood and Boyle 2016). This poses an archaeological dilemma: As all members of the genus *Homo* are assumed to occupy a technologically-assisted niche, how do we tie archaeological remains to specific hominin species in situations of co-existence? To understand hominin lifeways, especially when they occur sympatrically, insight into their techno-behaviours is required (Shea 2003; Susman 1994; Tocheri *et al.* 2008).

With this contribution, we explore how archaeology can deal with the co-occurrence of different hominins. We first highlight theoretical positions that influence archaeological hypothesis building and may lead us to underestimate the variability exhibited in the archaeological record. We also explore the mechanisms responsible for the transmission of stone tool technology in hominins. We argue that archaeological thinking often exhibits subtle biases that are problematic. We propose that detailed ecological niche modelling, combined with anatomical information on hominin adaptations, can constrain interpretations of a specie's technological repertoires. Our main assumption is that to understand the development of technology, a focus on its adaptive role is key (Shea 2017). Although non-human primates and other animals occasionally use tools, the human niche differs from theirs as it fully depends on technology (Shea 2017), and in hunter-gatherer societies, technology pervades all aspects of life and varies from simple tools to large installations.

We illustrate our approach with a case study of the Middle Pleistocene archaeology of South Africa, where early *Homo sapiens* may have co-existed with *Homo naledi* (Berger *et al.* 2015; Berger *et al.* 2017; Dirks *et al.* 2017; Lombard *et al.* 2018). Based on its estimated age, small-brained *H. naledi* has been considered a potential producer of Middle Stone Age, prepared core technology (Berger *et al.* 2017). Hawks and Berger (2020) argue that the temporal and geographic overlap of *H. naledi* with that of evolving *H. sapiens* confounds current scientific thinking about niche development for the two species, claiming a largely similar niche for both. Our aim is to evaluate hypotheses on the techno-behaviours of *H. naledi* and its ecological niche using three strands of evidence: ecology, anatomy, and archaeology. Our approach constrains interpretations of the likely technological repertoire of *H. naledi*—resulting in a parsimonious, best-fit hypothesis. We contextualise this within the wider archaeological record to further specify the role of stone tools in likely *H. naledi* techno-behaviours. By explicitly considering the fitness benefits of stone tool use in combination with the ecological context and the specific anatomical features of different hominins, we suggest that the archaeological record can be more productively associated with different species. We touch on other instances of co-existence such as the European Middle-to-Upper Palaeolithic transition to illustrate the wider relevance of our approach.

Co-existing Hominins—Niche Differentiation

To co-exist in a geographic area in the longer term, the ecological niches of distinct hominin groups must be differentiated. If their niches overlap significantly, one of the two species will go (locally) extinct. This principle of competitive exclusion is well-established (see discussion in Foley 1987). Unfortunately, the geographical and temporal extent of hominin co-existence is difficult to determine. Archaeological dating methods have been combined with Bayesian statistics to determine whether cultural entities overlap (*cf.* Higham *et al.* 2014). Such models rely on the attribution of lithic industries to specific populations (*e.g.* Benazzi *et al.* 2014; Cortés-Sánchez *et al.* 2019; Ruebens *et al.* 2015). These attributions are often contested (*e.g.* Bar-Yosef and Bordes 2010; Villa *et al.* 2018), and in many cases, taphonomic circumstances preclude a determination of authorship (Gravina *et al.* 2018; Gravina *et al.* 2005; Zilhão *et al.* 2006). These complicating factors led to the search for alternative approaches to investigate the extent of, for example, Neanderthal and *H. sapiens* coexistence. The principle of competitive exclusion is a suitable starting point to make sense of the archaeological record of co-existing hominins. Unless the characters are captured 'tool in hand', attribution to specific species can only be achieved if we know how the tools were used within a given hominin niche.

Encephalising Trends Inferred from the Fossil Record

Evolutionary discourse in archaeology exhibits gradualist and teleological tendencies, which influences how the fossil and lithic records are studied. The evolution of the genus *Homo* is generally characterised by increasing brain size across different species (Gómez-Robles *et al.* 2017; Potts 2011; Galway-Witham *et al.* 2019). Large brains are seen as integral to the human niche (Kaplan *et al.* 2000).

Extensive variability in both body and brain size of, for example, African *H. erectus* populations (Potts *et al.* 2004) have been mostly ignored. Extreme cases such as *Homo floresiensis*, a small-brained, small-bodied species, were initially seen as due to island biogeography (Morwood *et al.* 2004). More recent work, however, suggests that the species is a long-surviving relict of an early (> 1.75 Ma), as yet unknown 'out of Africa' hominin lineage (Argue *et al.* 2017), further complicating the question of how a late-surviving species may relate to an archaeological industry. The Middle Pleistocene age of another small-brained species, *H. naledi* (estimated brain size 465–610 cm^3) in southern Africa also challenges standard interpretations of the fossil record (Berger *et al.* 2015; Dirks *et al.* 2017; Hawks *et al.* 2017). Different from island-isolated *H. floresiensis*, it shows that small-brained hominins co-existed with large-brained ones on the same landscape.

Brain size is an influential concept in human evolution, also used as a criterion for the inclusion of species in the genus *Homo* (Wood 2014). Increasing brain size is often assumed to confer greater cognitive ability (but see Lombard and Högberg 2021 for later humans). As a result, subsistence strategies, technological repertoires, and social systems are thought to become more elaborate (Foley and Gamble 2009). However, large brains also entail significant evolutionary costs, due to high energetic demands (*e.g.* Aiello and Key 2002; Isler and van Schaik 2009; Navarrete *et al.* 2011). This suggests encephalising hominins faced strong selection pressures favouring brain growth.

The very few known Middle Pleistocene African hominin fossils are usually placed within the trend of a gradual increase in brain size (Table 1). Exactly how some descendants of *H. erectus/ergaster* ultimately develop into *H. sapiens* in Africa is

Table 1 Key Middle Pleistocene hominin fossils from Africa according to brain volume, age, and suggested group (references pertain mainly to brain volume and group)

Brain volume (cm^3)	Date and group	Site	Reference
1550–1600	~ 150–90 ka (*H. sapiens*)	Singa, Sudan, northeast Africa	Schwartz and Tattersall 2003
1450	~ 160 ka (*H. sapiens*)	Herto, Ethiopia, eastern Africa	White *et al.* 2003
1450 (Jebel Irhoud 2)	~ 300 ka (archaic-modern *H. sapiens*)	Jebel Irhoud, Morocco, northwest Africa	Holloway 1981; Holloway 1985; Hublin *et al.* 2017; Richter *et al.* 2017
1430 (Omo 2)	~ 195 ka (*H. sapiens*)	Omo, Ethiopia, eastern Africa	McDougall *et al.* 2005; Rightmire 2013
1400 (KNM-ER 3884)	~ 270 ka	Ileret, Kenya, eastern Africa	Bräuer *et al.* 2004
1400 (Omo 1)	~ 195 ka (*H. sapiens*)	Omo, Ethiopia, eastern Africa	McDougall, *et al.* 2005; Rightmire 2013
1305 (Jebel Irhoud 1)	~ 300 ka (archaic-modern *H. sapiens*)	Jebel Irhoud, Morocco, northwest Africa	Holloway 1981; Holloway 1985; Richter *et al.* 2017
1280	~ 299 ka (*H. rhodesiensis/heidelbergensis*)	Kabwe, Zambia, southern Africa	Bräuer 2012; Grün *et al.* 2020; Klein 1973; Montgomery *et al.* 1994
1280	~ 259 ka (archaic-modern *H. sapiens*)	Florisbad, South Africa, southern Africa	Grün *et al.* 1996; Kappelman 1996
1280	~ 300 ka (archaic *H. sapiens*)	Eyasi, Tanzania, eastern Africa	Bräuer 2012
1250	~ 600 ka (*H. sapiens/heidelbergensis*)	Bodo, Ethiopia, eastern Africa	Clark *et al.* 1994; Conroy *et al.* 2000
1225	~ 1.0 Ma–600 ka, likely in later part of range (*H. heidelbergensis*)	Elandsfontein, South Africa, southern Africa	Klein *et al.* 2007; Rightmire 2013; Singer 1954
1212	~ 300–150 ka, estimated from reworked deposits; most parsimonious estimate	Eliye Springs, Kenya, eastern Africa	Bräuer, *et al.* 2004; Bräuer and Leakey 1986
1200 (Hominid 18)	>500–200 ka?, younger age of ~ 130 ka also proposed (archaic-modern *H. sapiens*)	Laetoli, Tanzania, eastern Africa	Cohen 1996; Magori and Day 1983; McBrearty and Brooks 2000
1100	~ 400–200 ka (*H. erectus/sapiens*)	Ndutu, Tanzania, eastern Africa	Clarke 1990
880	~ 400 (*H. erectus/sapiens*)	Salé, Morocco, northwest Africa	Holloway 1981; Holloway 1985; Clarke 1990; Wood 2011
465–610	~ 335-236 ka, *H. Naledi*	Rising Star, South Africa, southern Africa	Berger *et al.* 2015; Dirks *et al.* 2017; Hawks *et al.* 2017

unclear. Some suggest that a group of African and European fossils can be attributed to *H. heidelbergensis*, while others group the African fossils in the separate taxon of *H. rhodesiensis*. It appears that distinct large-brained taxa co-existed in Africa (Hublin *et al.* 2017; Grün *et al.* 2020). This is supported by genetic indications for archaic admixture in contemporary genomes (Hammer *et al.* 2011). For the purposes of our study, we regard these fossils as belonging to an evolutionary lineage with a last common ancestor that lived at a more recent time than the last common ancestor of *H. naledi* and the larger-brained populations. Both early *H. sapiens* and *H. heidelbergensis/rhodesiensis* have been found associated with Middle Stone Age stone artefacts (Richter *et al.* 2017; Grün *et al.* 2020). The specimens of Elandsfontein, Kabwe, and Florisbad demonstrate that the encephalising lineage was present in southern Africa during the Middle Pleistocene. The age estimate of *H. naledi* implies that the encephalising lineage co-existed with a small-brained species—challenging notions of s steady temporal increase in brain size across different hominin species. This suggests the existence of up-to-now unexplored alternative solutions to the ecological problems faced by African hominins.

The South African Fossil Record

In addition to the *H. naledi* findspot, only four late Middle Pleistocene sites have yielded hominin fossils, Florisbad, Cave of Hearths, Hoedjiespunt, and Lincoln Cave at Sterkfontein (also see Berger *et al.* 2017; Dusseldorp *et al.* 2013). The Florisbad cranium belongs to one of the earliest representatives of the *H. sapiens* clade (Richter *et al.* 2017). Found in spring deposits in the Free State, it may be associated with Middle Stone Age lithic technology (Kuman *et al.* 1999) and combines a substantial brain size with a robust build (Rightmire 1978; Bruner and Lombard 2020) (Fig. 1).

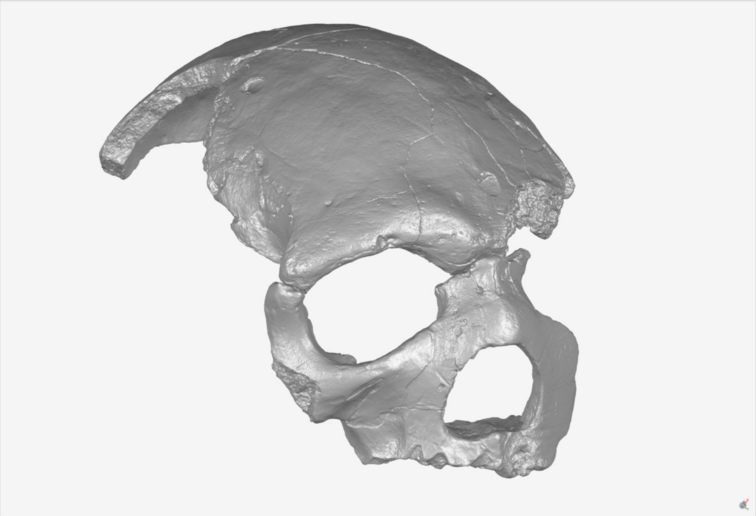

Fig. 1 3D scan on the Florisbad cranium (scan produced by I. Djakovic, reconstruction of skullcap and facial part by Matt Caruana, University of Johannesburg, image © Marlize Lombard).

A radius and a robust jawbone with a number of teeth were found at Cave of Hearths, initially ascribed to archaic *H. sapiens* (Hawks *et al.* 2017; Tobias 1971). Dental analysis shows the teeth to be allied to *H. heidelbergensis*, and different from *H. naledi* (Davies *et al.* 2019). The mandible is associated with a late Acheulean industry; whereas the provenance of the radius is not known exactly, it has been associated with either late Acheulean or early Middle Stone Age (Tobias 1971). A large tibia from Hoedjiespunt has been attributed to *H. heidelbergensis* (Churchill *et al.* 2000). Its dimensions demonstrate a much larger body size than *H. naledi*, but no archaeological remains are associated with it (Stynder *et al.* 2001). At Lincoln Cave in Sterkfontein, isolated teeth and a small cranial fragment were found in Middle to Late Pleistocene deposits. However, there is evidence of post-depositional mixing, with material assigned to *H. ergaster* and archaic *H. sapiens* co-occurring with Acheulean and Middle Stone Age artefacts (Reynolds *et al.* 2007). Because the context of the hominin fossils was not directly dated and post-depositional mixing is attested, we omit the site from our analysis.

Despite the small amount of hominin material, the estimated age of *H. naledi* suggests that at least two very different populations existed in South Africa during the early phase of the Middle Stone Age. Both the Hoedjiespunt and the Florisbad fossils, and likely the Cave of Hearths maxilla demonstrate the presence of a large-bodied, large-brained hominin in South Africa at the same time as the diminutive *H. naledi*.

Challenges for the Archaeological Study of Technological Niches

Archaeological understanding of the adaptive significance of hominin tool use is hampered by taphonomic and epistemic factors. First, the archaeological visibility of hominin techno-behaviours is biased towards knapped stone tools. However, the ability to use other types of artefacts, either unmodified stones or organic tools may have exerted equally strong selection pressures on evolving hominins. Organic tools are widely used by contemporary hunter-gatherers and by non-human primates. Although their use was likely ubiquitous throughout hominin evolution, their archaeological visibility depends on serendipitous discoveries in rare circumstances. Yet, from such discoveries, we can document a long and varied record of organic tools from bone digging implements in South Africa at 2.3 Mya (Backwell and d'Errico 2008; Stammers *et al.* 2018), to in Indonesian *H. erectus* shell tools at 500 ka (Joordens *et al.* 2015), and wooden spears (~ 300 ka) and digging sticks (~ 170 ka) used by Neanderthals (Aranguren *et al.* 2018; Milks *et al.* 2019). Taphonomy thus largely obscures a major component of hominin tool use.

Similarly, the use of unmodified stones is understudied, due to a lack of sound methodological approaches (Caruana *et al.* 2014). Nevertheless, it is clearly in evidence in later populations that exhibit obligatory tool use such as Neanderthals (Pop *et al.* 2018). The oldest knapped stone tools may date back to 3.3 Mya although the stratigraphic provenance of the published artefacts has been critiqued (Harmand *et al.* 2015; Lewis and Harmand 2016; Domínguez-Rodrigo and Alcalá 2017; Archer *et al.* 2020). In any event, it appears that knapped stone tool use was occasional until ~ 1.7 Mya (Shea 2017). And knapping was not practised equally by all hominin populations.

This is illustrated by the potential ‘loss’ of knapped stone tool technologies by *Homo erectus* populations inhabiting the Far East (Joordens *et al.* 2015). The use of archaeologically less visible tool types likely exerted important selective pressures on hominin lifeways.

Trends Inferred from the Archaeological Record

Technology is often taken as a proxy of hominin cognition. As with developing brain size, gradualist and teleological tendencies are exhibited in the study of stone tools. Technological complexity is generally assumed to increase over time, thus progressively gaining in the lengths and numbers of nested steps involved in their manufacture. However, this assumption is poorly supported (Hoffecker and Hoffecker 2018; Vaesen and Houkes 2018). Similar to increases in brain size, increased technological complexity is assumed to take place across different species. We discuss the basic classifications of lithic technology (as the most prolific remnants of Pleistocene techno-behaviours) and examine variability that is overlooked by focussing on so-called complexity.

The assumed increasing complexity of knapped stone tool technology is reflected in Clarke’s (1969) widely used classification of lithic industries. Knapping strategies are divided into five modes from basic to complex. These modes are sometimes envisaged as a sequential development, with mode 1 being replaced by mode 2, *etc.* Alternative descriptions of toolmaking strategies without underlying cognitive implications have been proposed (Shea 2013, 2017). Because Clarke’s modes 1–5 are in near-universal use, we use this terminology. However, we view the sequential replacement of modes as too simplistic. The utilisation of different modes of knapping is better described by time-transgressive scenarios with different modes simultaneously used (see Foley and Lahr 2003; Shea 2011, 2017; also see Shipton 2018 on trends in Acheulean biface knapping), and we use the modal terminology in this context.

Modes 1 to 3 characterise the main subdivisions of the Stone Age and Palaeolithic. The Earlier Stone Age (roughly equivalent to the Lower Palaeolithic outside of Africa) is characterised by mode 1 and mode 2 technologies. Mode 1 technology centres on knapping flakes (*débitage*). Unstandardised flakes are struck from cores without platform preparation. This mode is exemplified by the Oldowan Industry (Leakey 1971), but also includes later industries such as the Clactonian in Europe (MIS 11: ~ 425–375 ka) (Wenban-Smith *et al.* 2006; White 2000). The initial use of mode 1 technology is associated with small-brained early *Homo*, such as *H. habilis* and potentially late Australopithecines and *Paranthropus*, but mode 1 was also produced later by *H. ergaster/erectus*, *H. antecessor*, and others.

Mode 2 is characterised by shaped tools (*façonnage*). Its central feature is the production of roughly symmetrical large cutting tools (LCTs) such as handaxes and cleavers. This mode is represented by the Acheulean complex, distributed across Africa and parts of Eurasia between ~ 1.7 and 0.3 Mya (Lepre *et al.* 2011; Lycett and Gowlett 2008). In the early Acheulean, the LCTs are unstandardised and show few removals (Beyene *et al.* 2013; Diez-Martín *et al.* 2015). They become gradually more carefully shaped, showing larger numbers of flake removals, soft hammer percussion, and purposeful thinning using platform preparation (Diez-Martín *et al.* 2015; Stout *et al.* 2014). The initial use of mode 2 technology is associated with *H. ergaster* in Africa.

The Middle Stone Age (roughly equivalent to the Middle Palaeolithic in Eurasia) is characterised by mode 3 technology. Mode 3, or prepared core technology, focuses on producing flakes of predetermined form from hierarchically organised cores. This technology is associated with routine platform preparation. It takes many different forms and was probably independently invented at different places across the Old World (Adler *et al.* 2014). The Levallois technique is most synonymous with mode 3. By ~ 300 ka, mode 3 technology was in wide-spread use, continuing to ~ 40–20 ka (Barton *et al.* 2016; Osypiński and Osypińska 2016). The use of prepared core technology is associated with large-brained hominins such as Neanderthals, *H. heidelbergensis*, and *H. sapiens* (Adler *et al.* 2014).

Teleological bias is revealed when the classification of assemblages is made based on the most complex mode/s of production represented. But the time-transgressive occurrence of different modes of knapping blinds us to variability in the archaeological record. Artefacts deposited in a high-resolution stratigraphic context are only rarely available. In South Africa for example, the land surface has been stable throughout the Earlier and Middle Stone Ages, leading to the formation of many palimpsest surface collections containing artefacts of vastly different ages (Klein 2000). In many assemblages, both from the surface and excavated contexts, prepared core forms are accompanied by a host of other forms, often characterised as ‘informal’ (Kiberd 2006, table 3; Thompson *et al.* 2010, table 6).

Teleological tendencies are also apparent in the way in which chronological information and lithic classifications are used to reinforce each other. Mode 1 and mode 2 occurrences without direct dates are sometimes suggested to represent ancient occupations and prepared core occurrences in the same area are thought to reflect more recent hominin activities (*e.g.* Terry 2005). However, in regions with better chronostratigraphic control such as East Africa, mode 2 (bifacial) and mode 1 (irregularly flaked) assemblages continue to occur throughout the Middle Stone Age (Foley and Lahr 2003; McBrearty 2005; Shea 2011). Acheulean (mode 2) and Clactonian (mode 1) assemblages also co-occur in the United Kingdom during MIS 11 (Wenban-Smith *et al.* 2006; White 2000). In reverse, assemblages lacking diagnostic artefacts are sometimes assigned to an industry on the basis of radiometric dates only (*e.g.* Clark 1993; de la Peña 2019).

Technologies are part of a larger ecological niche, and increased complexity is not necessarily universally beneficial. Especially when different hominins co-exist, these biases leading to the underestimation of techno-cultural variability are problematic. Overlooking variability and using ‘circumstantial factors’, such as the age of assemblages to classify them, hamper a deeper understanding of the formation of lithic assemblages and differences in hominin niches.

Computer Simulation—Teleology in Action

Computer simulations of the potential co-existence of different hominins exemplifies the subtle but pervasive teleological bias in archaeological thinking. This analytical approach is increasingly favoured as an ‘objective’ tool to simulate situations of hominin co-existence and extinction. Models of reproducing hominin populations (usually *H. sapiens* and Neanderthals) are formulated, based on assumed characteristics. A simulation is run to calculate if, and for how long, populations will co-exist. Such simulations invariably end in Neanderthal extinction. They attempt to recreate the actual history, but do not necessarily illuminate the reasons for the known outcome, because the input generally features differences in the characteristics of the populations. An early and ground-breaking simulation, for example, modelled the life-expectancy of Neanderthals as dependent on the life-expectancy of *H. sapiens* populations (Zubrow 1989). However, this model only allowed for one-way traffic; changes in Neanderthal life expectancy could not affect that of *H. sapiens*. Such models present a foregone conclusion as one population is handicapped and will inevitably go extinct (Scherjon 2019; Vaesen et al. 2019).

In addition to demographic models, some models focus on various assumed behavioural differences between Neanderthals and *H. sapiens*, for example, trade between groups and a more explicit division of labour (Horan *et al.* 2005). Other models focus on assumed differences in 'culture level' or learning ability (Gilpin *et al.* 2016), or in caloric requirements and differences in fire use (Goldfield *et al.* 2018). Again, the assumed advantages of *H. sapiens* over Neanderthals invariably cause the demise of the latter.

Some recent models do not assume selective differences and focus on demographic processes (Kolodny and Feldman 2017). However, such models still handicap Neanderthals in subtle ways. One version stipulates that bands of each species periodically go extinct, but with continuous in-migration of *H. sapiens* groups into Neanderthal territory. This ensures *H. sapiens* never go extinct altogether in the simulation. In another version, bidirectional migration is allowed. However, the simulation stipulates that at least as many *H. sapiens* individuals migrate into Europe as Neanderthals move into Africa. In addition, the initial *H. sapiens* population is modelled to be larger than the Neanderthal population, again leading to the likely extinction of Neanderthals (Kolodny and Feldman 2017). Hence, Neanderthals are still modelled as handicapped in so-called neutral models (Scherjon 2019; Vaesen et al. 2019).

The assumptions of simulations are not necessarily incorrect. However, taking one outcome as virtually inevitable, and ignoring gene-flow between populations (see discussion in Lombard and Högberg 2021), is of limited value in testing hypotheses on the causes and likelihood of that outcome. This excursion illustrates the kind of gradualist, teleological thinking that dominates ideas on hominin anatomic, behavioural, and technological evolution. To move forward, we should leave open idiosyncratic options, such as Neanderthal and *H. sapiens* co-existence, even adaptive advantages for Neanderthals, as well as late-surviving small-brained species that may or may not have used stone tools.

Stone Tools and Hominin Cognition

The character of stone tools, if studied with care, can be used to determine aspects of their function and make inferences about their authors. Below we focus on two aspects of cognition connected to lithic technology. First, we look at the cognitive performance of knappers; secondly, we review the available evidence for the trans-generational transmission of knapping strategies.

Cognitive Requirements of Lithic Technology

Non-human animals modify stones. Capuchin monkeys have been observed to break stones; grasping them with both hands as 'hammers' to pound on rocks lodged in alluvial deposits. They unintentionally produce flakes while doing this (Profitt *et al.* 2016). This shows that the cognitive abilities required to modify stones should not be overestimated.

Recent finds in Kenya suggest that basic knapping was perhaps not done by *Homo* in the region, because thus far the only species found in West Turkana at the same time as the Lomekwian artefacts (~3.3 Mya) is *Kenyanthropus platyops* (Harmand *et al.* 2015; but see Archer *et al.* 2020 for contextual issues), which some authors group with the australopithecines (*e.g.* Williams 2017). While the cognitive requirements involved in the production of these stone tools (dubbed Lomekwian) clearly exceed those of the monkeys' pounding behaviour (Lombard *et al.* 2019), they demonstrate a less thorough understanding of conchoidal fracture and the absence of freehand percussion characteristic of Oldowan (mode 1) assemblages from ~ 2.6 Mya.

Although analyses of cognitive performance during stone tool manufacture are debated, a consensus view is emerging that mode 1 assemblages represent some cognitive advances (*e.g.* Hovers 2012; Toth and Schick 2018; Stout *et al.* 2019). For example, PET scans of Oldowan toolmaking show that although it is not cognitively challenging, compared with ape tool use, it requires increased visuo-motor demands (Toth and Schick 2018), and it has been suggested that Mode 1 knapping uses an ancestral system dubbed the Anthropoid Object Manipulation Network (Herzlinger *et al.* 2017). Compared with mode 3 assemblages that require enhanced cognitive capacities (Faisal *et al.* 2010; Wynn *et al.* 2017), mode 1 tools are relatively easy to produce.

On the other hand, the cognitive requirements of mode 2 technology are more difficult to characterise because of the great differences in sophistication between early and late LCTs (compare Díez-Martín *et al.* 2015; Stout *et al.* 2014). Even though expert modern flint knappers produce a finely retouched handaxe in less than 15 min (Hallos 2005), neurological experiments show that the production of Late Acheulean bifaces requires considerably more cognitive control than mode 1 knapping, as well as a certain level of working memory (Faisal *et al.* 2010; Putt *et al.* 2017).

Prepared core, or mode 3 technology is associated with large-brained hominins such as Neanderthals and *H. sapiens*. Experimental research suggests that the hierarchical organisation of Levallois technology requires different cognitive capacities compared with modes 1 and 2. Mode 3 knapping uses the same neurological mechanisms as language (Eren and Lycett 2012), and may also be cognitively more challenging than mode 4 blade production. For example, Muller et al. (2017) showed that Levallois production consistently required greater hierarchical depth and breadth, as well as more phases through the knapping sequence compared with blade production. In short, mode 3 serves as a prime example of expert cognition, whereas mode 1 and 2 knapping require less expert cognition (Wynn *et al.* 2017).

Expert cognition draws on long-term memory and some (as opposed to enhanced) working memory. Specifically, it allows the expert to draw on a store of behavioural chains from long-term memory for hierarchical knapping procedures (Wynn *et al.* 2017). Chimpanzee nut-cracking shows elements of expert cognition, which could indicate that it draws on features already present in our last common ancestor—unless it was independently evolved. Mode 1 knapping shows a modest increase for expert cognition, causal cognition, and cognition associated with teaching compared with nut-cracking behaviour (Lombard *et al.* 2019; Wynn *et al.* 2017). For (esp. later) mode 2 technology, a significant expansion of both long-term and working memory appears necessary (Herzlinger *et al.* 2017). Further increases in working memory and long-term memory are implicated with the advent of mode 3 technology. Semantic long-term memory also appears necessary (Wynn *et al.* 2017). These observations indicate how changes in stone tool knapping may have stimulated the development of working memory—or *vice versa* in a feedback loop—perhaps also effecting changes in brain morphology in both *H. sapiens* and Neanderthals (Haidle 2010; Wynn and Coolidge 2011; Lombard and Högberg 2021).

Mechanism of Transmission of Lithic Technology

The inter-generational transmission of knapping strategies is another domain where cognitive skills are key. The mechanisms of transmission are the subject of much debate. For some, the assumption that stone tool knapping is a culturally transmitted phenomenon is weakly supported at best, especially for early industries such as the Oldowan (*e.g.* Tennie *et al.* 2017). Even for mode 2 technologies, the standard assumption of a culturally transmitted artefact is contested (Corbey *et al.* 2016; Tennie *et al.* 2016). Gärdenfors and Högberg (2017, pp. 188; also see Uomini and Meyer 2013), however, conclude "that stable transmission of the Oldowan technology requires at least teaching by demonstration and that learning the late Acheulean hand-axe technology requires at least communicating concepts".

The production of Oldowan, or mode 1 technology, may represent a 'latent solution', continuously being reinvented due to individual learning, supplemented with weak forms of social learning such as stimulus enhancement (Morgan *et al.* 2015; Shea 2017; Tennie *et al.* 2017). However, experimental knapping research suggests that demonstration and voluntary practicing of knapping skills are essential to attain mastery also for mode 1 knapping (Gärdenfors and Högberg 2017). Both these elements are unknown in great apes. When compared directly, the teaching modes suggested for bipolar knapping as a form of mode 1 practised at Lomekwi outrank those required for chimpanzee nut-cracking behaviours (Lombard, *et al.* 2019).

The required transmission mechanisms for mode 2 technology likely vary between early and late variants. Experiments suggest that handaxe shape is too stable to be culturally transmitted because variability is smaller than expected taking copying error into account (Kempe, *et al.* 2012). Genetic control has been suggested as potential explanation for this phenomenon (*e.g.* Corbey *et al.* 2016). However, the same stable transmission has been used to suggest that a cognitive threshold was crossed with the advent of mode 2 technology (Muller *et al.* 2017). The hierarchical organisation of knapping goals and subgoals is then assumed to point not only to planning ahead but also to the existence of concepts of these goals that would be transmitted semantically (Gärdenfors and Högberg 2017; Herzlinger *et al.* 2017).

During the Late Acheulean in East Africa, Levallois flake production appears at some sites. At Kapthurin for example, preferential Levallois cleaver flakes are produced using the preferential Levallois technique (Tryon *et al.* 2005). The knapping of mode 3 prepared core technology is cognitively demanding. Moreover, different, discrete variants of prepared core technology are sometimes used concurrently (*e.g.* Boëda 1988), for example, at Kapthurin, from the early Middle Stone Age, preferential and recurrent Levallois methods co-exist (Tryon *et al.* 2005). This suggests the active teaching of specific knapping strategies (Gärdenfors and Högberg 2017). Yet, even in the late Middle Palaeolithic, allometric reduction sequences result in the production of a range of typological tool types, which are all expressions of a single functional concept (Weiss *et al.* 2018). This is reinforced by experiments demonstrating core-forms resembling prepared cores can be produced using very simple knapping methods (Moore and Perston 2016). The ratio between prepared cores and preferential removals in assemblages is sometimes low (Akhilesh *et al.* 2018, supplementary table 1), suggesting that typological mode 3 cores did not always function in a mode 3 *chaîne opératoire*.

The foregoing suggests that cultural control of toolmaking cannot always be assumed and that hierarchically organised engineering could be under genetic control (Allen *et al.* 2003). Hence, hierarchically organised reduction sequences *per se* may not be sufficient evidence to support cultural transmission mechanisms, unless we assume that prehistoric hominins were so similar to modern test subjects that modern knapping experiments give a reliable impression of required transmission mechanisms. Even if artefacts are products of cultural transmission, some types may not represent a mental template, but may be an emergent property of basic knapping practices (McPherron 2000). We can therefore not assume that one single transmission mechanism was used and elaborated across hominin species. Different species likely employed different transmission strategies for similar-looking stone tool assemblages. Mode 1 assemblages may have been a latent solution in Australopithecines or *H. habilis*, while the evolution of more elaborate transmission systems may have been associated with the need for increased fidelity of transmission in other species such as *H. ergaster*.

The South African Archaeological Record

The Middle Pleistocene has been dubbed 'the muddle in the middle' due to the lack of cultural and technological trends (Isaac 1975). In southern Africa, much of the Middle Pleistocene record is represented in surface contexts, complicating interpretation. Nonetheless, South African Acheulean assemblages have been studied for over a century (Goodwin and Van Riet Lowe 1929; Peringuey 1911). Chronological advances are being made, especially with assemblages coming from fluviatile contexts (*e.g.* Lotter and Kuman 2017; Lotter 2020a,b), and technological studies reveal important insights into the development of prepared core technology in South Africa (*e.g.* Li *et al.* 2017; Porat *et al.* 2010; Wilkins *et al.* 2010), which was introduced across the region during the timeframe proposed for *H. naledi*. However, the beginning of the Middle Stone Age was not a simple technological replacement of one industry by another. Other modes of toolmaking continued to be practised. A synthesis of the South African Stone Age techno-cultural sequence based on dated sites only (Lombard, *et al.* 2012), reveals that multiple industries are present in South Africa (Table 3).

The early Middle Stone Age (dated to ~ 300–130 ka) represents an informally designated group of assemblages with limited information on their characteristics (Lombard *et al.* 2012). A common factor of the assemblages is the presence of some form of prepared core technology and blade production (*i.e.* discoidal and/or Levallois). Four sites across South Africa have dates overlapping with *H. naledi*, including Florisbad (Kuman *et al.* 1999; Meiring 1956). Another notable occurrence is Sterkfontein in the Cradle of Humankind, not far from where *H. naledi* was found, with an age estimate of 294–210 ka (Ogola 2009; Reynolds *et al.* 2007).

Second, the Earlier-Middle Stone Age transition (dated to ~ 600–200 ka) contains so-called Sangoan and Fauresmith industries that may be transitional between the Earlier and Middle Stone Ages. A re-appraisal suggests that such assemblages contain many Middle Stone Age technological characteristics (Herries 2011). The assemblages have evidence for the use of prepared core technology, combined with the production of large bifacial cutting tools. Only five dated sites in South Africa have been assigned to this phase (Lombard, *et al.* 2012). However, many undated sites/contexts with both early Middle Stone Age and Earlier-Middle Stone Age transitional assemblages are present on the broader landscape. Some of the assemblages show signs of mixing and dating is problematic; in some cases, the material may be younger than the dates proposed for *H. naledi* (Herries 2011 also see discussion on the Fauresmith at Wonderwerk in Chazan 2015).

Finally, some Earlier Stone Age Acheulean assemblages (dated to 1.5 Mya to approximately 300 ka) overlap with the dating of the *H. naledi* remains, notably those at Duinefontein (Cruz-Uribe *et al.* 2003; Feathers 2002) and Rooidam (Szabo and Butzer 1979). Within the Acheulean, the poorly dated and described Victoria West technology has been proposed to represent the earliest prepared core technology (Li *et al.* 2017), which could suggest deep roots for such technologies in southern Africa. For example, Beaumont and Vogel (2006) proposed that proper Victoria West cores are always preferential cores and that they could date to 1 Ma (also see Lotter 2020b). However, these cores are also argued to be similar to Acheulean bifaces, and as such an extension of mode 2 knapping strategies (Lycett *et al.* 2010).

This brief overview shows that the late Middle Pleistocene record contains much variability. Mode 3 and mode 2 assemblages were both produced between 330 ka and 230 ka in southern Africa, while stratified contexts further afield (McBrearty 2005; Shea 2011) suggest that expedient mode 1 knapping continued to be produced/used. Moreover, we should not reify the Acheulean and Middle Stone Age. The presence of prepared-core-like technologies such as Victoria West in the Acheulean shows that these entities were not homogeneous across the subcontinent (Mercader *et al.* 2016; Lotter 2020b; Lotter *et al.* 2016).

Case Study: *Homo naledi* and *Homo sapiens* in Southern Africa

The discovery and dating of *H. naledi* complicate the interpretation of the southern African archaeological record because it implicates that a small-brained species (Berger *et al.* 2015; Dirks *et al.* 2015), was sympatric with large-brained *H. sapiens sensu lato* in southern Africa (Lombard *et al.* 2018). The species was discovered in a deep cave context near Johannesburg, South Africa. Based on its primitive anatomical characters it was originally anticipated that *H. naledi* would shed light on the “early evolution of humans and their close relatives” (Berger *et al.* 2015, pp. 3). A dating programme subsequently constrained the likely age of the fossil deposit to between 335 and 236 ka—the late Middle Pleistocene (Dirks *et al.* 2017).

Berger et al. (2017) argue that *H. naledi* is a potential author of prepared core technology typical of the Middle Stone Age. For example, they say: "*H. naledi* has traits that were long considered to be adaptations for creating material culture. Its wrist, hand and fingertip morphology share several derived features with Neanderthals and modern humans that are absent in *H. habilis*, *H. floresiensis*, and *Au. sediba* (Kivell *et al.*, 2015). If these features evolved to support habitual tool manufacture in Neanderthals and modern humans, then it is reasonable to conclude that *H. naledi* was also fully competent in using tools" (Berger *et al.* 2017: 9). "MSA variants are characterized by the manufacture of blades and by the presence of the Levallois flaking technique and hafted implements […]" (Berger *et al.* 2017:10). "Considering the context, it is possible that *H. naledi* sustained MSA traditions" (Berger *et al.* 2017: 10). Yet, as already mentioned, large-brained taxa (Neanderthals, *H. sapiens*, *H. heidelbergensis*) are widely accepted as makers of such Levallois (mode 3) technologies (*e.g.* Eren and Lycett 2012).

Here we review the available anatomical, ecological and archaeological information and consider the ecological niches of both *H. naledi* and *H. sapiens* to constrain the likely techno-behaviours of *H. naledi*. We do not suggest that both species evolved sympatrically. *H. naledi* may have evolved in geographic isolation from the encephalising African populations. However, based on the radiometric age estimates, by the Middle Pleistocene, they were sufficiently differentiated to co-exist in the same biome.

Homo naledi Taphonomy and Dating

The co-existence of *H. sapiens* (archaic and/or modern) and very small-brained *H. naledi* in South Africa's grassland biome, depends on the taphonomic context and accuracy of the dating of the Rising Star skeletal material. The context of the initially reported remains of *H. naledi* is unique. They were found in a hard-to-reach location deep within the Rising Star cave (the Dinaledi Chamber), in non-brecciated deposits devoid of other macro-vertebrate remains and with no cultural remains (Dirks *et al.* 2015; Dirks *et al.* 2017). The discoverers suggest this is the result of intentional disposal of the bodies (Dirks *et al.* 2015). However, a comparison of the Dinaledi skeletal element representation with that of bone assemblages of known origin suggests it could also be a natural death assemblage or a scavenged assemblage (Egeland *et al.* 2018; Nel *et al.* in press). As most bones' surfaces are badly preserved, and only a subset of the material has been microscopically examined for carnivore damage a definitive assessment cannot be made (Egeland *et al.* 2018, also see Val 2016). Natural mechanisms of deposition, for example water-borne deposition of the remains, have also been mooted (Val 2016: 146). Nonetheless, conditions in the Dinaledi chamber appear to have been dry for a considerable period (estimated at least 300 ka) as gauged from the rate of *in situ* ongoing brecciation of the sediments (Wiersma *et al.* 2020).

Subsequent discoveries of *H. naledi* remains in a different location of the same cave system (the Lesedi chamber) are in open association with faunal remains—but no cultural objects (Hawks *et al.* 2017). The faunal assemblage, which may not be contemporary with the *H. naledi* remains, is dominated by medium-sized carnivores (*Canis*, *Vulpes*, *Felis*); micro-mammals were also recovered (Hawks, *et al.* 2017). The remains were only announced at genus-level and do not yet provide specific environmental or age-related information.

Several methods were employed to arrive at an age estimate of the *H. naledi* remains from the Dinaledi Chamber. Direct assays on *H. naledi* remains were conducted using radiocarbon, U-Th and U-series ESR dating; flowstones related to the depositional context of *H. naledi* were dated using U-Th estimates and palaeomagnetism, while OSL dating was used on a quartz-bearing layer. Collectively, these approaches yielded an estimated age of between 335 and 236 ka for the deposition of the remains in the Dinaledi Chamber (Dirks *et al.* 2017).

Radiocarbon dating yielded ages of ~ 33 ka and ~ 35 ka instead of the expected infinite ages, possibly as a result of late precipitation of calcite in the fossils. Based on the results of other techniques, these dates appear too young. U-series ESR dates obtained independently in two different laboratories yield an estimated age range of 335–139 ka for the deposition of *H. naledi* remains. U-Th dating places *H. naledi* teeth between 200 and 70 ka (Dirks *et al.* 2017). OSL dates were taken from multiple-grain aliquots and represent averages of the grains in these aliquots. The difference between aliquots suggests that not all grains were fully bleached. As incompletely bleached grains would yield too early ages the team prefers a minimum age model. The OSL dates suggest the Dinaledi skeletal material was deposited between 353 ka and 241 ka (Dirks *et al.* 2017).

Flowstones overlying and encasing *H. naledi* bone yield ages from 242 ka, suggesting that their deposition occurred prior to that time. A potential problem is that erosion and re-deposition is evidenced in the deposits (Dirks *et al.* 2015, and see comments by Val 2016). However, conditions in the chamber are estimated to have been dry for at least the last 300 ka (Wiersma *et al.* 2020). Further, the flowstone-encased bone suggests the *terminus ante quem* is valid. Moreover, some remains are in anatomical context and the sample of studied bone surfaces is not severely weathered (although this sample only forms a small part of the assemblage, see Val 2016: 147; also see Nel et al. in press). This suggests that, although the remains may not be in primary depositional context, they were deposited in the Dinaledi chamber relatively quickly after death and hence this does not invalidate the terminus post-quem. Makhubela et al. (2019), however, draw attention to possible complications regarding the effects of long soil surface residence times on cosmogenic nuclide denudation rates in the Cradle of Humankind. Based on the published age assessments, which have not yet been empirically challenged, we see a late Middle Pleistocene age for the Dinaledi chamber remains as a plausible scenario, and stimulus for consequential speculation/theorising.

Anatomical Features of *Homo naledi* and Their Implications

H. naledi is one of the best described hominins to-date, with information from multiple specimens for all physiological traits (Hawks *et al.* 2017). It presents a mosaic of primitive and derived anatomical characteristics. We review the ecological and technological implications of its anatomy, summarised in Table 2.

Body Size *H. naledi*'s reconstructed body mass overlaps with the lower range of *H. erectus*, but its mean weight (37.5 kg) is much lower than that of other Late and Middle Pleistocene *Homo* species (Pleistocene *H. sapiens* mean 67.2 kg). Its stature was also much smaller (142.2 cm) than that of other Late and Middle Pleistocene *Homo*

Table 2 Published anatomical regions, the types of information that they provide and possible behavioural inferences

Phylogenetic and ontogenetic information	Behavioural inference	Reference
Brain case		
Small	Constraints on knowledge-intensity of foraging niche, technology, group size	Berger *et al.* 2015; Hawks *et al.* 2017
Teeth		
Size reduction High-crowned Heavy wear chipping	Diet with much grit Reduced size of dentition in genus *Homo* attributed to tool-use externalising part of processing.	Berthaume *et al.* 2018; Ungar and Berger 2018
Thorax		
Funnel-shaped Wide lower thorax	Bipedal walking, climbing important; unsuitable for endurance running; reduced activity radius	Williams, *et al.* 2017
Shoulder girdle		
Primitive scapula and clavicle Low humeral torsion High position pectoral girdle	Not a competent thrower Unknown implications for knapping precision Prevents effective "counter-swing" for endurance running Reduced activity radius compared with *H. sapiens*.	Feuerriegel, *et al.* 2017
Hand		
Derived morphology shared with AMH and Neanderthals indicative of habitual tool use Curved phalanges	Likely tool-user Uncertain stone tool knapper Climbing important: densely vegetated facets of environment?	Kivell, *et al.* 2015 but see Wallace *et al.* 2020
Leg		
Femur shape between *Homo* and the australopithecines Elongated tibiae	Suitable for bipedal walking	Marchi, *et al.* 2017
Foot		
Curved phalanges	Bipedal locomotion Elevated grasping ability	Harcourt-Smith, *et al.* 2015

species (*H. sapiens* mean 170.3 cm) and overlaps with the lower range of *H. erectus* (Berger *et al.* 2015; Hawks *et al.* 2017; Will *et al.* 2017). The small body size has implications for land-use and foraging strategies.

Brain Size The estimated endocranial volume of *H. naledi* specimens is 465–610 cm^3 (Fig. 2) (Berger, *et al.* 2015; Hawks *et al.* 2017). *H. naledi* thus had smaller brains than *Homo habilis* (Spoor *et al.* 2015). However, its brain anatomy shares derived morphology with *H. habilis*, *H. erectus* and *H. floresiensis*. This is interpreted as a result of reliance on tool use in the genus *Homo* (Holloway *et al.* 2018). Prior to *H. naledi*'s discovery, only large-brained hominin fossils (Table 1) were known from the African Middle Pleistocene. The persistence of a small-brained species until the late Middle Pleistocene challenges ideas on the importance of encephalisation for hominin niches. Encephalising hominins faced strong selective pressure favouring increased brain size, as large brains come at a cost. They are so-called expensive tissues, accounting for a large proportion of human energy expenditure (Aiello and Wheeler 1995). Energetic demands are highest for pregnant and lactating females (Aiello and Key 2002; Kaplan *et al.* 2000; Leonard *et al.* 2003). To 'finance' larger brains, improved dietary quality, likely resulting in increased meat consumption, and provisioning of pregnant and lactating females were needed (Leonard *et al.* 2003). As a result, hunter-gatherers rely much more than apes on extracted foods (*e.g.* underground storage organs, honey, *etc.*) and meat (Kaplan *et al.* 2000). Increased dietary quality in turn may have resulted in an increased basal metabolic rate and increased fat storage to accommodate bigger brains (Kaplan *et al.* 2000; Leonard *et al.* 2003; Navarrete *et al.* 2011; Pontzer *et al.* 2016).

Two main driving forces have been proposed for hominin encephalisation, namely an expanding social network (Dunbar 1992), and an increasingly multi-dimensional foraging niche (DeCasien *et al.* 2017). Reliance on complex technology forms an

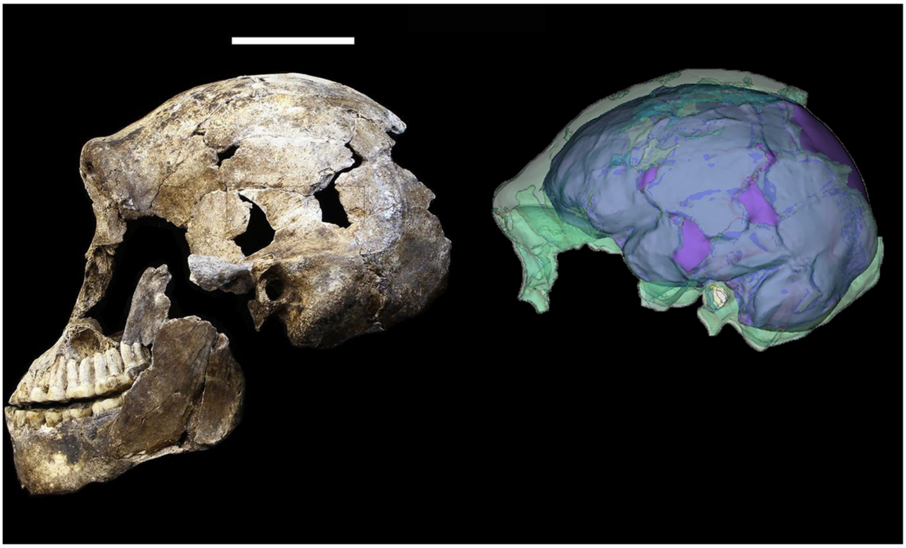

Fig. 2 *Homo naledi* skull illustrated by Lesedi 1 fossil and virtual reconstruction of endocranial volume of 610 ml. Modified from Hawks et al. (2017, Fig. 5, Fig. 6), published under CC-BY licence https://creativecommons.org/licenses/by/4.0/

extension of the foraging niche hypothesis. Toolmaking ability was likely targeted by selection as tool-use became crucial in determining foraging success (*cf.* Shea 2017; Stout and Khreisheh 2015). *H. naledi*'s small brain suggests that its niche was much less social and/or knowledge-intensive than that of early *H. sapiens*. Its shared morphology with *H. habilis*, *H. erectus* and *H. floresiensis* may be the result of tool use (but also see Bruner 2021 and Lombard and Högberg 2021 for aspects of the sapient brain and technology). However, it could also be an inherited feature from an early *Homo* ancestor, no longer actively under selection.

Dentition Dentition preserves both phylogenetic and ontogenetic information. Dental anatomy informs on inherited dietary adaptations (Irish *et al.* 2018), but tooth wear also reveals evidence for the realised diets of the sampled individuals (Berthaume *et al.* 2018; Towle *et al.* 2017). The genus *Homo* exhibits reduced postcanine dentition compared with australopithecines, possibly due to increased external food processing with tools. *H. naledi* conforms to this trend, exhibiting reduced molar size (Berger *et al.* 2015; Berthaume *et al.* 2018). Further, their teeth are high-crowned and wear-resistant; the likely result of selection for increased longevity of the teeth (Berthaume *et al.* 2018). Also, some anatomic features suggest that compared with apes and Plio-Pleistocene *Homo* sp. fossils, *H. naledi* (together with *Paranthropus* and *Australopithecus*) teeth produced larger shear forces. This points to processing of foods higher in structural fibres (Berthaume *et al.* 2018). Analysis of *H. naledi* tooth wear reveals a high degree of chipping on both premolars and molars. This is likely related to dietary quality, not to object manipulation. The chipping indicates lower dietary quality than in *Australopithecus africanus* and *Paranthropus robustus* (Towle *et al.* 2017). The probable cause is a diet containing tough materials such as nuts or shells, or a high incidence of contaminants, such as grit (Towle *et al.* 2017). Further analysis of the wear patterns confirms this (Ungar and Berger 2018). On the whole, *H. naledi*'s dental evidence suggests the consumption of hard plant foods, grit adhering to foodstuffs, and likely a lower degree of processing of foods compared with other *Homo* species.

Limb Anatomy and Locomotion *H. naledi*'s limb anatomy shows a mosaic of adaptations to bipedal walking and climbing. The shoulder girdle was in an ape-like position and the humerus had low torsion—both adaptations towards habitual climbing, preventing counter-rotation of the arms needed to stabilise the trunk during endurance running (Feuerriegel *et al.* 2017). The anatomy of the upper limb also excludes competent overarm throwing in *H. naledi* (Feuerriegel *et al.* 2017). The vertebra and ribs reveal a funnel-shaped thorax that also complicates endurance running and can be interpreted as a climbing adaptation (Williams *et al.* 2017). Climbing was therefore important throughout *H. naledi*'s evolutionary history and may have counteracted selection pressures favouring a barrel-shaped thorax for more effective bipedal locomotion.

Similar to that of apes, *H. naledi*'s phalanges are long and curved, which is a response to climbing and suspension. The degree of curvature is generally thought to develop ontogenetically, suggesting that *H. naledi*'s phalanges demonstrate that the excavated individuals actively engaged in climbing (Kivell *et al.* 2015). However, the phalanges of a chimpanzee raised in a human home and trained to walk on two legs with limited climbing opportunities, show a similar degree of curvature to those of wild chimpanzees (Wallace *et al.* 2020). It is therefore possible that the curved phalanges in *H. naledi* represents an inherited feature instead of definitive evidence that the individuals recovered in the Dinaledi chamber were intensive climbers. The retention of this feature by *H. naledi* (in contrast to other *Homo* species), however, suggests that climbing played an important role in their evolutionary history while the lower limb anatomy demonstrates derived morphology enabling efficient bipedal locomotion. The femur shape clusters between *Homo* and the australopithecines, with elongated tibiae, indicative of long lower limbs (Marchi, *et al.* 2017; also see Steudel-Numbers and Tilkens 2004). The foot of *H. naledi* exhibits a morphology that is similar in many respects to the *H. sapiens* foot and is suitable for striding bipedalism. However, the proximal phalanges of the foot are notably more curved than in *H. sapiens* (Harcourt-Smith *et al.* 2015).

In short, *H. naledi*'s limb anatomy indicates that they relied on both bipedal locomotion and habitual climbing. Lack of evidence for endurance running, which is critical for both active scavenging and endurance hunting in open environments (Blumenschine 1987; Liebenberg 2006; Lieberman *et al.* 2007), points to a more limited foraging radius for *H. naledi* compared with *H. sapiens* and its large-brained forebears. The upper limb demonstrates that *H. naledi* was better adapted to climbing than other members of *Homo*, which could imply a dependence on resources, or resting locations that were 'hard-to-reach' for other hominins or predators.

Limb, Hand Anatomy and Tool Use The derived morphology of the *H. naledi* wrist and hand show a mixture of derived and primitive features, and is one of the main arguments put forward in favour of its 'habitual' tool use (Feuerriegel *et al.* 2017, pp. 171). Characteristics such as a long thumb and a wrist configuration shared with Neanderthals and *H. sapiens* imply to some that *H. naledi* was a committed, habitual tool-user capable of forceful precision grips (Kivell *et al.* 2015). Yet, other features associated with behaviours such as tool use and throwing are lacking, for example, the absence of a styloid process in the 3rd metacarpal (Key 2016; Kivell *et al.* 2015) to stabilise the 'central part of the palm against external volar forces' during knapping with hand-held hammerstones (Marzke 2013, pp. 4). Further upper limb anatomy also has implications for tool use and manufacture, and experimental work suggests that knapping precision shows parallels to throwing when it comes to upper limb kinematics and the role of the wrist (Williams *et al.* 2010). *H. naledi* likely had limited throwing capabilities (Feuerriegel *et al.* 2017, pp. 172), and although the exact advantages of derived *H. sapiens* upper limb morphology in knapping remain under-researched (Williams *et al.* 2014, pp. 53), it is possible that the shoulder configuration of *H. naledi* and the limited amount of humeral torsion could have impacted knapping precision.

The combination of derived features facilitating tool use and indications for intensive arboreal locomotion is unknown in other hominins. As such, it is unclear if there is a loss of functionality implied for either behaviour in *H. naledi* (Kivell *et al.* 2015). Some of the derived anatomy was likely inherited from the common ancestor of *H. naledi* and its closest relatives *H. antecessor* and *H. erectus* (Dembo, *et al.* 2016). But due to the rarity of fossil hands (Kivell, *et al.* 2015), it is unclear to what degree

H. naledi's wrist anatomy was inherited and to what degree *H. naledi* was itself under selection for an effective precision grip.

Homo naledi and *Homo sapiens* as Sympatric During the Late Middle Pleistocene

The relevant fossils and dated artefact assemblages are sparsely distributed (see Table 3). Aside from the *H. naledi* remains, the Florisbad skull is most informative. Florisbad is located about 300 km southwest of the Cradle of Humankind where *H. naledi* was found; both sites are in the current Grassland Biome (Fig. 3) (Mucina and Rutherford 2006). Moreover, the Middle Stone Age stone tools from the Florisbad site occur widely on the Grassland Biome including the Cradle of Humankind (esp. taking into account the open air record [Caruana 2017; Moll 2017]) (for overviews see Lombard, *et al.* 2012; Mason 1962; Volman 1981; Wadley 2015; also see Sampson 1974). It is, however, relevant to note that the location in Florisbad where the hominin was recovered is a redistributed spring deposit, so that its direct association with the archaeological material remains to be verified. The only other African hominins with a radiometrically determined age contemporaneous to that of *H. naledi* are the archaic *H. sapiens* individuals from Jebel Irhoud, Morocco, dated to 286 ± 32 ka (Hublin *et al.* 2017), and the Broken Hill skull in Zambia dated to 299 ± 25 ka (Grün *et al.* 2020).

The presence of multiple hominin lineages on the African continent during the late Middle Pleistocene has also been established by the introgression of archaic DNA into *H. sapiens* genomes (Hammer *et al.* 2011). Previously, it was assumed that these populations were not sympatric (Scerri *et al.* 2018). Further, it was assumed that the populations living in different parts of Africa derived from a relatively large-brained common ancestor (Hammer *et al.* 2011). Reconstruction of the full genome of Holocene Later Stone Age individuals from KwaZulu-Natal in South Africa indicates that *H. sapiens* was present in sub-Saharan Africa from perhaps as early as 350 ka (Schlebusch *et al.* 2017; Schlebusch *et al.* 2020).

However sparse the fossil record, if the Rising Star age estimate is correct, it suggests that *H. naledi* and *H. sapiens sensu lato* were sympatric in the Grassland Biome during the Late Middle Pleistocene. Competitive exclusion would lead to the local extinction of overlapping hominins, unless their niches were sufficiently differentiated (Banks *et al.* 2008). Hence, some form of niche separation must have existed. We do not know the duration of co-existence, as the rich *H. naledi* assemblage from the Dinaledi chamber is thus far the only record of this species with an age estimate. We also do not know where either species evolved, nor do we assume that the Grassland Biome was their core habitat. The two species may have developed separately only to become sympatric after a period of geographic separation. This increases the likelihood of divergent niche development allowing subsequent co-existence in South Africa during the Late Middle Pleistocene.

Middle Pleistocene Ecological Context

The late Middle Pleistocene date places *H. naledi* in the Florisian land mammal age, although such placement would be more secure once associated fauna is found. During

Table 3 Inventory of dated South African contexts (sites, associated technocomplexes and fossil remains) overlapping in age range with *H. naledi* at Rising Star, arranged from youngest to oldest ranges within each current biome. Note: Whereas Gladysvale yielded age estimates that may overlap with that of Rising Star (*e.g.* Pickering *et al.* 2007), the published material from the site is from contexts with ESR ages of 650 ± 63 ka and 779 ± 51 ka ESR (Lacruz *et al.* 2002), and therefore not included below

Age range	Site	Technocomplex	Taxonomic ID	Source/s
Grassland biome				
~ 252–115 ka	Lincoln Cave North at Sterkfontein	Mixed ESA and MSA	None	Reynolds *et al.* 2007
~ 684–251 ka	Sterkfontein Post Member 6	Middle Stone Age	*Homo* sp.	Herries 2011, Reynolds and Kibii 2011
~ 335–236 ka	Rising Star	None	*H. naledi*	Berger *et al.* 2015; Dirks *et al.* 2017; Hawks *et al.* 2017
~ 259–121 ka	Florisbad	Early MSA	*H. sapiens*	Grün *et al.* 1996; Kuman *et al.* 1999
Savanna biome				
~ 227–217 ka	Border Cave	Early MSA	None	Grün *et al.* 2003; Herries 2011
~ 394–144 ka	Bundu Farm	Early MSA/ESA-MSA transitional	None	Kiberd 2006
~ 348–276 ka	Wonderwerk Cave	ESA-MSA transitional	None	Chazan 2015
~ 291 ± 54 ka	Kathu Pan	Early MSA	None	Porat *et al.* 2010
Fynbos biome				
~ 292–125 ka	Duinefontein	Early MSA/ESA-MSA transitional, Acheulean	None	Cruz-Uribe *et al.* 2003; Feathers 2002
~ 300–200 ka	Hoedjiespunt	None	*H. heidelbergensis*	Churchill *et al.* 2000; Stynder *et al.* 2001

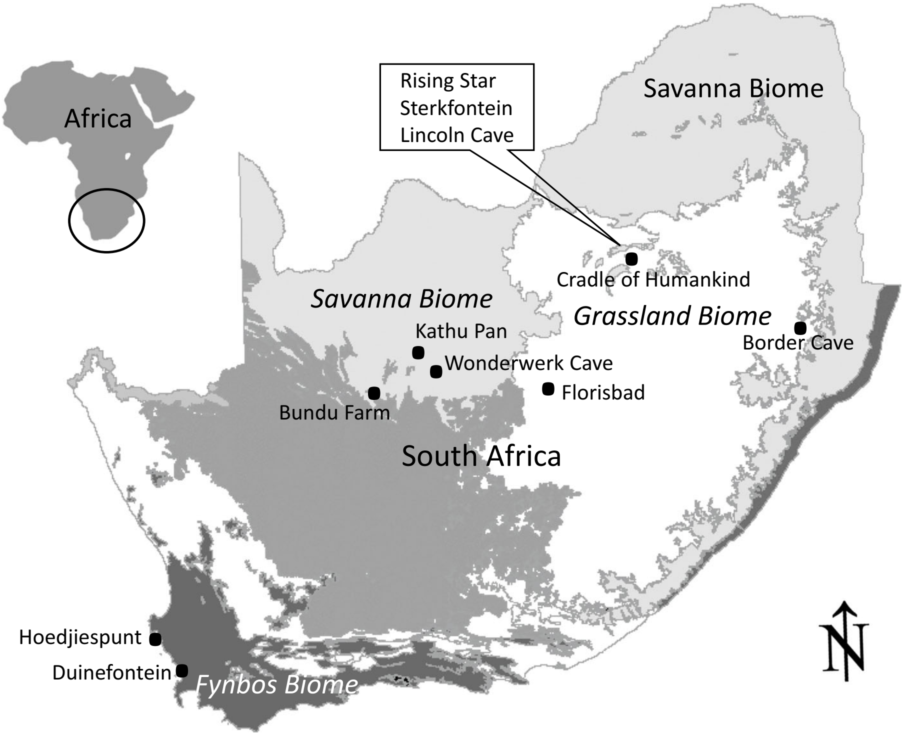

Fig. 3 Map of the South African biomes following Mucina and Rutherford (2006) with important fossil and archaeological sites mentioned in the text.

the Florisian, South Africa's central interior environment was characterised by extensive grasslands. Compared with the late Lower Pleistocene, the Middle Pleistocene saw a progressive opening up of the vegetation and increased importance of C4 plants in ungulate diets, reflecting a dominance of grasslands (Codron *et al.* 2008). Today, the central grasslands are comparatively dry, but by correlating the pollen stratigraphy at the Florisbad site, Scott et al. (2019) found that the lower layers containing the Florisbad fossil and its associated Middle Pleistocene fauna, experienced cool moist and grassy conditions. The contemporaneous occurrence of nine extant (*Equus quagga*, *Ceratotherium simum*, *Phacochoerus aethiopicus*, *Ph. africanus*, *Hippopotamus amphibius*, *Syncerus antiquus*, *Damaliscus pygargus*, *Alcelaphus buselaphus*, and *Connochaetes gnou*) and six extinct species of grazers (*Equus capensis*, *E. lylei*, *Megalotragus priscus*, *Pelorovis antiquus*, *Damaliscus niro*, and *Antidorcas bondi*) reflect a highly productive open grassland ecosystem (Manegold and Brink 2011). It has been suggested that these species interacted in a system of grazing succession similar to what has been described for the Serengeti (Brink 2005; Codron *et al.* 2008).

Together with geological evidence, the wetland component of the Florisian faunas can be interpreted to reflect the presence of perennial lakes (Brink 2005), with the seasonal pans of the modern grassland a relict of the Florisian palaeolake system (Manegold and Brink 2011). The Middle and early Late Pleistocene grasslands of central southern Africa were therefore considerably more productive than today, so that a number of water-loving taxa were present where they are currently unknown (Brink

2016). Two Middle Pleistocene faunal assemblages are known from the immediate vicinity of Rising Star Cave, namely the Gladysvale external deposits and Lincoln Cave at Sterkfontein (Lacruz *et al.* 2002; Reynolds *et al.* 2007). Both support the presence of extensive grasslands. The Lincoln Cave Sterkfontein fauna suggests that part of the assemblage was accumulated in a wet period (Reynolds *et al.* 2007).

Constraining *H. naledi* Techno-behaviours

Based on the foregoing review we move on to an evaluation of *H. naledi*'s likely technological niche. We follow Shea's (2017) suggestion of connecting evolutionary selective pressures to stone tool knapping abilities represented in archaeological assemblages. We assess three distinct hypotheses. First, *H. naledi* did not knap stone tools, but used organic technology or unmodified stones to aid in the exploitation of extracted resources. Secondly, *H. naledi* practised tool use as a routine (habitually), but stereotyped part of their adaptation (*sensu* Shea 2017). This could have been associated with mode 1 or 2 technology. Thirdly, knapped tool use was obligatory for *H. naledi*, with severe negative fitness consequences for individuals that were not taught to produce stone tools (Shea 2017). This crucial role for the technological niche is associated with mode 3 technology, a hypothesis considered a distinct possibility by Berger et al. (2017).

Hypothesis 1. *Homo naledi did not produce knapped stone tools, but used unmodified tools*

From an archaeological point of view this ought to be the null hypothesis since *H. naledi* remains are thus far not associated with any stone artefacts (Dirks *et al.* 2017; Hawks *et al.* 2017) although its hand shares many derived characteristics with the hands of habitual tool users (Hawks *et al.* 2017; Kivell *et al.* 2015). Many of these features have long been "considered adaptations for creating material culture" (Berger *et al.* 2017, pp. 9). This derived anatomy suggests that at some point during *H. naledi*'s evolutionary history, its hands were under selective pressure for effective tool use. However, selective pressures for efficient tool use do not automatically imply the production of knapped stone tools. It could simply indicate the use of organic tools and/or unmodified stones as seen in living primates. Percussive technology (in the form of unmodified hammerstones) is pervasive in the archaeological record, comprising "one of the longest-standing traditions of tool use in human evolution" (Caruana *et al.* 2014, pp. 2). Such tool use could yield important fitness benefits and hence selection pressures favouring changes in hand anatomy.

To us, it is important to distinguish between 'using' tools and 'knapping' stone tools, because habitually using tools may affect hominin body and brain morphology (cf. Holloway *et al.* 2018), as well as cognition, but it does not automatically imply the production or knapping of stone artefacts. Taking the phylogeny of *H. naledi* into account as well as the derived features of its hand—shared with *H. neanderthalensis* and *H. sapiens*—it is likely that they were occasional or habitual tool 'users' (Kivell *et al.* 2015), perhaps also of unmodified organic wood or bone artefacts. We contend that there is a long way to go before a conflation between 'tool use and manipulation' and ‘deliberate technical production’ can be considered robust. Archaeologically, this hypothesis is difficult to evaluate. More research on non-knapped and organic object use is needed.

Hypothesis 2. *Homo naledi used simple knapped stone tools*

The derived features of *H. naledi*’s hand could indicate that they were occasional or habitual tool users, corresponding to the production of mode 1 or mode 2 lithic technologies (*sensu* Shea 2017). Shea (2017) suggests that occasional and habitual tool use brings fitness benefits. He associates occasional tool-use with the use of bipolar technology, pebble core reduction, and simple platform core reduction, resulting in stone artefacts strongly constrained by raw material availability. Habitual tool use is associated with more elaborate reduction sequences that modern novices generally cannot ‘reverse engineer’, needing instruction for successful production (Shea 2017; see also Gärdenfors and Högberg 2017; Morgan, *et al.* 2015). Even today many people are adept tool users—but not so much when it comes to technical conceptualisation and/or production. Hence these abilities may represent distinct aspects of any hominin’s niche.

We argue that the derived wrist anatomy in itself is not sufficient evidence to demonstrate the production of knapped stone tools in *H. naledi* as it may not have been under active selection but rather an inherited feature. Also, the use of non-knapped tools may produce similar selective pressures. This hypothesis is archaeologically challenging because current classification underestimates the variability of lithic reduction sequences that were used. And because bipolar technology, pebble core reduction, and simple platform core reduction strategies associated with habitual tool use, are all found within the area where *H. naledi* lived (*e.g.* Caruana 2017). Their dating and association with hominin groups is ambiguous at best.

Hypothesis 3. *Homo naledi was an obligatory tool user*

Temporally, *H. naledi* overlaps with Middle Stone Age assemblages and its potential authorship should be considered. However, there are multiple technocomplexes and hominin populations on the South African landscape (Table 3; Dusseldorp *et al.* 2013). Until *H. naledi* is stratigraphically associated with diagnostic Levallois-type stone artefacts, we cannot be certain about their producing and using them, and have to consider the use of other tools as best-fit scenarios.

Prepared core knapping requires more than derived hand and wrist anatomy. The knowledge intensity of Levallois reduction sequences is much greater than that of modes 1, 2, and 4 (see discussion above). With an average brain size smaller than *H. habilis* (a Mode 1 producer) we deem this hypothesis unlikely. Our reading is reinforced by the fact that mode 3-type artefacts were often hafted to be utilised effectively as hunting spears or butchery knives (*e.g.* Lombard 2005; Lenoir and Villa 2006; Wilkins *et al.* 2012; Sahle *et al.* 2013), representing an intricate and knowledge-intensive procedure (Barham 2013; Haidle *et al.* 2015; Kozowyk *et al.* 2016; Lombard and Haidle 2012; Wadley *et al.* 2009). The temporal overlap with the occurrence of mode 3 artefacts is insufficient evidence to confirm the hypothesis that *H. naledi* produced such artefacts. We contend that there is not enough archaeological nor other supporting evidence to classify *H. naledi* as an obligatory tool user and a knapper of mode 3 technology. To us, the previously discussed hypotheses of non-knapped tool use or very basic knapping better fit explanations that adhere to the principle of parsimony, and therefore require the fewest possible unverified assumptions.

On *Homo sapiens* and *Homo naledi* Ecological Niches in South Africa

Any consideration of the production and or use of stone tools by late Middle Pleistocene *H. sapiens* (archaic or modern) and *H. naledi* should take into account their eco-functional role. Knapped stone tool production is not automatic in *Homo*. It may be 'lost' in hominin lineages and tools from other materials may be fashioned, as happened in some *H. erectus* populations (Joordens *et al.* 2015). Below, we expand our suggestions on *H. naledi* tool use by fleshing out their ecological niches.

Homo sapiens

The Florisbad fossil is currently the only hominin specimen of similar age to *H. naledi* (Table 3), but South Africa boasts the richest *H. sapiens* record dated between ~ 120 ka and 50 ka on the African continent (Grine 2000; Grine and Henshilwood 2002; Marean *et al.* 2004; Millard 2006; Verna *et al.* 2013; Grine *et al.* 2017; Riga *et al.* 2018; Will *et al.* 2019). All archaeological sites with human remains dating to this time have *bona fide* mode 3 and/or mode 4 technologies. Thus, there can be no question about the association between *H. sapiens* and the production of mode 3 technology. *H. sapiens* was an obligate tool-user, reliant on activities that could not be accomplished otherwise; their tools brought them considerable fitness benefits.

One activity requiring sophisticated tool use is hunting. Based on the archaeological record, ecological modelling and experimental work, active hunting was an important strategy for *H. sapiens*. The regular consumption of meat likely enabled increases in brain size in the *Homo* lineage (Aiello and Wheeler 1995; Kaplan *et al.* 2000; Navarrete *et al.* 2011). Stone tools are associated with bone assemblages demonstrating early access to carcasses in the later Earlier Stone Age (Forrest 2017; Pickering *et al.* 2008; Smith *et al.* 2019). During the Middle Stone Age, *H. sapiens* routinely hunted large ungulates (Clark and Kandel 2013; Dusseldorp 2010; Faith 2008). Hunting is also the most knowledge-intensive foraging technique practised by contemporary foragers (Kaplan *et al.* 2000; Lombard 2015).

Middle Stone Age points are ubiquitous in many assemblages (and often produced using Levallois technology). Their dimensions regularly fit those of ethnographic spear points and points of atlatl darts (Brooks *et al.* 2006; Rots *et al.* 2011; Sahle *et al.* 2013; Sisk and Shea 2011). Some such points are fractured in ways suggesting hunting impact damage (Lombard 2005; Sahle *et al.* 2013; Wilkins *et al.* 2012; but see Rots and Plisson 2014). These suggestions are reinforced by the fact that the ability to throw accurately at high speeds evolved in encephalising hominins (Larson 2015; also see Gärdenfors and Lombard 2018 on spear hunting and cognition). The routine exploitation of mobile animal prey is reflected in other aspects of *H. sapiens* anatomy. Effective bipedal walking was likely present in the common ancestor of archaic *H. sapiens* and *H. naledi*. However, the development of endurance running, allowing ranging over large distances is only evident in *H. sapiens*. Ethnographically, hunting is associated with a far greater foraging range than plant exploitation (Binford 2001; Kelly 1983).

Increases in brain size also led to changes in social structure and cooperation (Boyd and Richerson 2009). As brains' energy consumption increased, provisioning became important—likely prior to the appearance of *H. sapiens* (Aiello and Key 2002; Kaplan, *et al.* 2000; Navarrete, *et al.* 2011). Because hunted meat comes in relatively large 'packages', the increased importance of hunting stimulates food sharing (also see Blurton Jones 1987; Jaeggi and Gurven 2013; Kaplan and Hill 1985), which in turn may have fostered increased cooperative behaviour and a division of labour (Aiello and Key 2002). In *H. sapiens* such a division of labour is universal (Kaplan, *et al.* 2000; Marlowe 2007). These changes may have also stimulated a social environment where effective teaching of tool production and other knowledge-intensive strategies played an increasing role (*cf.* Gärdenfors and Högberg 2017).

Plant food exploitation was probably calorically more important than hunting (Dusseldorp 2014), and tool-assisted. Ethnographic analyses show that Kalahari hunter-gatherers largely rely on plant foods (Lee 1979; Wilmsen 1989). *H. sapiens* exploitation of plant foods likely also depended on the use of fire as a processing strategy (Larbey *et al.* 2019; Wadley *et al.* 2020). Fire control further allows for additional food storage strategies such as smoking and drying, and can play a role in social transmission by increasing time available for social interaction (Dunbar and Gowlett 2014). As the food supply in the Grassland Biome is unreliable, hominin populations need to develop strategies to deal with the challenges. Modern hunter-gatherers rely on long-term planning with food storage and food sharing (Dusseldorp 2014; Johnson 2014), and hunted meat is critical for dealing with food shortages in the dry season (Lee 1978). Technological investment in hafted Levallois-type stone tool technologies demonstrates that hunting was also a key component of the ecological niche of Middle Stone Age *H. sapiens*. We therefore argue that Pleistocene *H. sapiens* dealt with the Grassland Biome through a combination of knowledge-intensive food-gathering and hunting strategies. This type of 'foraging niche' requires considerable planning depth and cognitive astuteness, and tool use for a multitude of tasks is obligatory (Shea 2017).

Homo naledi

By the late Middle Pleistocene, the niches of *H. naledi* and *H. sapiens* diverged sufficiently for them to coexist in the same biome. This does not mean that the Grassland Biome represented the core of *H. naledi*'s range. However, to successfully occupy it and be visible in the fossil record, it co-existed with large-bodied *H. sapiens* and also the chacma baboon (*Papio ursinus*), another generalist primate on the landscape (see Nel *et al.* in press). As *H. naledi* is one of the best represented hominin species anatomically, we can constrain its likely ecological niche. The anatomical indications for a lifeway combining efficient bipedal walking and habitual climbing activity suggest that *H. naledi* spent much time in different facets of the landscape than *H. sapiens*. Perhaps *H. naledi* existed mostly in a mosaic of grassland-forest environments with rocky outcrops and caves—such as the area surrounding the Cradle of Humankind today. This contrasts with the surrounding open grasslands, and those where Florisbad is located. Such a mosaic ecology could have provided a diverse range of plant, insect, and small animal food packages for exploitation.

It is our contention that *H. naledi* was a habitual, but not an obligate tool user (Shea 2017). This is supported by their derived hand anatomy as well as by their evolutionary relationships within the genus *Homo*. The last common ancestor of *H. naledi* and its closest relatives (*H. antecessor*, *H. heidelbergensis*, *H. sapiens*, and Neanderthals) likely knapped stone tools (Dembo et al. 2016). The production and use of prepared core technology require depth of planning, communication, and deliberate social transmission, all of which remains to be established for *H. naledi*. However, relatively simple tools confer important fitness benefits on individuals, especially in the realm of plant exploitation. Pounding and shelling plant foods for example brings sizeable increases in foraging yield (Henry *et al.* 2014). Similarly, digging implements open up a rich variety of underground resources, whose consumption is supported by the chipping seen on *H. naledi* teeth.

In their analysis of *H. naledi* tooth wear, Berthaume et al. (2018) rightly caution that we should not revert to simplistic models, proposing an Australopithecus-like niche for Middle Pleistocene *H. naledi*. There are, however, functional anatomical similarities between australopithecines and *H. naledi*. The relatively small brain of *H. naledi* could mean that the knowledge-intensity of their foraging strategies was similar to those of australopithecines, even though the foraging strategies themselves may have differed. The dental evidence points to the consumption of underground storage organs with adhering sand grains and/or eating hard abrasive plant foods including nuts (Ungar *et al.* 2006; Ungar and Berger 2018). We have no reason to think that *H. naledi* could/did not use anvils and hammerstones for cracking nuts. This techno-behaviour would have been well within the reach of the whole *Homo* lineage, both physically and cognitively (see Lombard *et al.* 2019).

H. naledi likely dealt with seasonal paucity in resource availability in a less knowledge-intensive way than *H. sapiens*. Food sharing was probably unimportant to *H. naledi* as this behaviour is associated with foods that come in large package sizes such as animal carcasses (Blurton Jones 1987). Also, as food storage requires a great degree of planning depth, we suggest this strategy was unimportant for *H. naledi*. As an alternative, we propose that *H. naledi* focused on relatively densely distributed resources, specifically extracted plant foods and perhaps insects and eggs. A reliance on plant underground storage organs literally opens up tonnes of food per hectare (Youngblood 2005) and is in line with their dental wear (Ungar and Berger 2018). We also think that *H. naledi* concentrated on grassland and forest mosaics within rocky outcrops on the greater Grassland Biome to buffer seasonal changes in food availability.

Likely living in smaller groups (Dunbar 1992), we think complex social mechanisms like teaching were limited in scope, and hence, transmission of elaborate behavioural strategies was restricted. Also, social learning mechanisms represent a form of cooperation that comes at a cost and is liable to exploitation by free-riders (Boyd and Richerson 2009; Hoppit *et al.* 2008). Instead, we propose the small-brained lineage likely evolved a reliance on simple transmission mechanisms and latent solutions (Tennie, *et al.* 2017), which could lead to the habitual use of tools, and to expedient ways of shaping them, such as grinding down the tips of digging implements or producing flakes with bipolar reduction. We therefore hypothesise that *H. naledi* occupied a niche focusing on the efficient exploitation of plant foods, insects, and probably small prey such as birds, lizards, rodents, *etc.* They likely relied on their fat reserves and on low-quality vegetable fallback foods to deal with uncertainty in food supply (Navarrete *et al.* 2011). In such a niche, the use of relatively simple, perhaps non-knapped tools, would result in important caloric and fitness benefits, differentiating their niches from both knowledge-intensive foraging by *H. sapiens* and the generalist, omnivore chacma baboon.

Currently, only a few archaeological occurrences are radiometrically dated to the temporal window occupied by the Dinaledi skeletal assemblage. Although no specific archaeological assemblages can be referred to it at this point, relatively simple stone artefacts are present in the late Middle Pleistocene archaeological record, especially in open-air occurrences on the Cradle of Humankind landscape such as Elandsdrift and Maropeng (Caruana 2017; Caruana *et al.* 2019; Moll 2017).

Competition, Niche Differentiation, and Extinction

The differentiating aspect of *H. naledi* and *H. sapiens* did not lie in the exploitation of plant foods *per se*. After all, *H. sapiens* also exploited plants (*e.g.* Henry *et al.* 2014; Larbey *et al.* 2019). Instead, we suggest there were three decisive differentiating factors:

1. *H. sapiens* concentrated on the more open facets of the landscape while *H. naledi* was likely present in more mosaic areas;
2. *H. sapiens* was able to greatly increase its meat intake as a fallback food (*cf.* Lee 1978), while *H. naledi* likely was a hard-object fallback feeder (Ungar and Berger 2018);
3. *H. sapiens* employed multi-step processing including roasting to process starchy tubers (Larbey *et al.* 2019; Wadley *et al.* 2020), leading to increased efficiency of food exploitation on the grassland.

Differences in body size, energetic requirements, and anatomy ensured that the overlap between *H. naledi*'s and *H. sapiens*' niches was small enough to enable successful co-existence. In our view it is unnecessary to invoke *H. sapiens* as a cause for the extinction of *H. naledi*. The latter has been cast as a remnant population (Spoor 2016), and in South Africa this may have been the case. The species was not primarily adapted to open grasslands that steadily expanded in South Africa's interior (Codron *et al.* 2008), leading to a decrease of suitable habitat for *H. naledi* in our model, and perhaps playing a role in its disappearance.

Further Applications

Our approach also works in cases of hominin co-existence with small anatomical differences such as Neanderthals and *H. sapiens*, hence applying to the transition between the Middle Palaeolithic and Upper Palaeolithic in Europe and the Near East. The assignation of different industries to either Neanderthals or *H. sapiens* is complex and in some cases still controversial (Bar-Yosef and Bordes 2010; Villa, *et al.* 2018; also see Lombard and Högberg 2021). Partly because of this, and partly due to taphonomic and dating problems, the process of Neanderthal extinction remains unclear.

Earlier we showed that modelling on Neanderthal and *H. sapiens* co-existence often contains a built-in 'handicap' for Neanderthals, frequently based on assumed anatomical or behavioural differences. In a formalised model, this makes only one outcome possible. Nevertheless, recent reviews show that the known outcome (Neanderthal extinction) was potentially not the only possible outcome (Roebroeks and Soressi 2016; Villa and Roebroeks 2014, also see Langbroek 2012). Archaeological models should incorporate this. Some ingredients of a solution are available. Like *H. naledi*, Neanderthals are well-known anatomically. Some functional differences between Neanderthals and *H. sapiens* are known. Their lower limbs are shorter relative to *H. Sapiens*, impacting their cost of locomotion (Steudel-Numbers and Tilkens 2004). This likely had implications for their land-use strategies (MacDonald *et al.* 2009). Differences in land-use strategies are also suggested by analyses of raw material transports (Féblot-Augustins 1993; Roebroeks *et al.* 1988). Such land-use strategies have been interpreted to result in subtle differences in core reduction strategies in the Levant (Wallace and Shea 2006), so that in an area where typologically the products of *H. sapiens* and Neanderthals are indistinguishable from each other, an understanding of the ecological niche and the technological role therein may still allow differentiation of the archaeological remains of both populations.

Whereas the general shape of *Homo* brains is similar regardless of size, subtle variations are coming to light. For example, for at least one brain region—the precuneus—there exists evidence for recent, *sapiens*-exclusive expansion (Bruner 2010; 2021). Documented functions associated with the precuneus include visuospatial integration, category recognition, praxis, numerical processing, and speech decoding. What is more, the variation in morphological details of the region suggests neurofunctional differences in visuospatial integration. One potential behavioural consequence is variation in techno-behaviours such as the production and use of hunting weapons between the two species (Lombard and Högberg 2021). Although Neanderthals were capable of using ranged weapons (Milks *et al.* 2019), high-velocity projectile weapon systems such as bow-and-arrow sets, and perhaps also spearthrowers and darts, appear to be Middle to Late Pleistocene African developments by *H. sapiens* (Lombard 2020; Sahle and Brooks 2019).

Whereas variation in cognitive reasoning may have played a role in certain contexts between the species (Lombard and Högberg 2021), we propose that in the case of these large-brained hominins, contextual differences such as social structure, group size, and cultural dynamics must be included in any explanation for differences in their knapping strategies and tool-use. After all, both species were dependent on the production of mode 3 technologies for much of their existence (and modes 4 and 5 are not necessarily more cognitively challenging to knap). Both species were also capable of producing composite technology using adhesives to haft. This latter technology requires more than expert cognition, tapping into enhanced memory processes (Wynn *et al.* 2017). We thus argue that a better eye for subtle anatomical and technological differences, as well as cross-disciplinary approaches between two populations and the abandonment of teleological bias can lead to an improved understanding, also in this case. The anatomical differences in lower limb structure suggest Neanderthals exploited the landscape in a different way than *H. sapiens*. This combined with a different social system likely led to differing lithic adaptations.

Conclusion

Archaeology as a discipline is still coming to terms with interpreting a record produced by multiple species on the same landscape. By taking on board anatomical and ecological evidence and combining it with a thorough understanding of the technological behaviours present in a region, it is possible to propose testable hypotheses for the behaviours of co-existing hominin populations. Understanding the association between techno-behaviours and hominins must be rooted within the context of the fitness benefits of these behaviours. This means abandoning gradualist and unilinear approaches. The discoveries of Neanderthal complexity and the discontinuous presence of so-called modern behaviours in the African archaeological record demonstrate that the development of complex behaviours is not a universal driving force of hominin behaviour. Complex behaviour is a situational phenomenon; its development and archaeological visibility depends on ecological and cultural circumstances (see Lombard and Högberg 2021).

The discovery and the surprisingly young age estimate of *H. naledi* bring into focus problems with the archaeological classification of stone tool assemblages. Most classificatory schemes mask the variability in the archaeological record and overestimate the requirements of the dominant blank production strategies. Based on the well-founded assumption of niche differentiation and a review of the archaeological record, the fossil record, and *H. naledi*'s anatomy, we developed a parsimonious, best-fit scenario to interpret the southern African record. We conclude that it is currently most prudent to think of *H. naledi* as a habitual tool user, who possibly shaped implements. No stone tools are thus far associated with a *H. naledi* skeletal collection, which is insufficient reason to discount tool use altogether. Yet, we caution against a hasty assumption that they engaged in mode 3 tool production and use, simply because of their contemporaneity. Instead, anatomical arguments, among others a relatively small brain, suggest a different technological niche for *H. naledi* than for *H.* sapiens. It is our current understanding that *H. naledi* occupied mosaic areas in the landscape potentially exhibiting more climbing behaviour than large-brained hominins, and conclude that relatively simple tools, perhaps resulting from effective but cognitively undemanding mechanisms such as latent solutions, provided them with important fitness benefits. As such, their foraging niche relied on the tool-assisted exploitation of plant foods, and perhaps small prey (*e.g.* digging for insects). However, relatively minimal processing of these foods was practised, as reflected in their tooth wear.

We reconstruct the *H. sapiens* niche in the South African Middle Pleistocene as focused on open areas, and heavily technology assisted. They relied on well-developed expert and causal cognition for behavioural strategies, both in tool production, but also in knowledge-intensive foraging strategies. These included successful large mammal hunting and sharing of meat, especially as a fallback food. Their social relations also provided mechanisms to deal with temporary shortfalls in food and mechanisms aiding the transmission of complex behavioural strategies. Our reasoning is applicable to similar situations in the archaeological record, such as the study of the technological repertoire of early Plio-Pleistocene hominins with at times more than two sympatric hominin species (Wood and Boyle 2016), and also in cases of more closely-related populations such as the Neanderthals and *H. sapiens* in western Asia and Europe. Here, some form of competitive exclusion has often been assumed (Banks *et al.* 2008).

Recent work emphasises the similarity of the knowledge-intensity of Neanderthal and *H. sapiens* behavioural strategies (Kolodny and Feldman 2017; Villa and Roebroeks 2014), whereas advances in palaeoneurology and studies in causal cognition highlight some variation between the two groups in terms of visuospatial integration and reasoning (Bruner 2010; Gärdenfors and Lombard 2018). In areas where their assemblages are not easily distinguished, such subtle anatomical differences may still provide ways to move forward. Further development could focus on more detailed studies, such as the examination of the spatial distribution of different technologies inside a specific region such as the Cradle of Humankind.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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