A Southern African Perspective on Human Origins Research between 500 000 and 50 000 Years Ago: Current Dilemmas and Questions for the Future

Marlize Lombard

1 Introduction

Africa – a continent rich in mineral resources, ecological settings and variation in human populations regarding languages spoken, socio-economic and political institutions as well as genetic composition. It is a continent with ancient civilisations not yet understood fully, from the Egyptian dynasties in the north, to Great Zimbabwe, Mapungubwe and Thulamela in the south. Its contemporary history and current socio-political ideologies remain plagued by the aftermath of the slave trade, the age of imperialism during which foreign capitalist economies divided the continent amongst themselves, and recent colonial authoritarianism. In the post-colonial era, whilst being the continent with the lowest per-capita carbon footprint, the effect of greenhouse gas emissions spreading from the global north has profound consequences for Africa – most severely felt in the aridification of vast regions, resulting in widespread famine. Notwithstanding these recent challenges, the variation contained in the continent's human DNA, and the rich array of languages and socio-economic structures of its peoples translate into the evolutionary roots of all living humans today.

When we think about human origins it is key to think about what makes us human (*Homo sapiens*), and how, where and when we gained our humanness, with its prolific variations – or as the buzzword want to have it, in all our 'diversity'. Thus, we need to ask what sets our species apart from other animals. Not because we are special in a biblical sense, but to understand our species' evolutionary trajectory in a similar way that one might want to understand why giraffes evolved into the only mammal with an exceptionally long neck, or why hominins became bipedal. I therefore reject any notion of superiority, scientific racism or social Darwinism (e.g., Dennis, 1995; Leonard, 2009).

One aspect that sets us apart from other living animals is the way we think and reason about ourselves, each other and the world around us – our cognition. Today, the pan-human experience, regardless of level of education,

socio-political or socio-economic context, is of a world continuously shaped and reshaped by our socially shared ideas and imaginings, perceived and expressed through our senses, our languages, and our technologies or material cultures. This is as true for the 'illiterate' Kalahari hunter-gatherer, as it is for the WEIRD (western, educated, industrialized, rich, and democratic) professor of cognitive science in Denmark. The remarkable thing about the sapient mind is its flexibility (Barrett, 2009; Lombard, 2016). So that when the Kalahari hunter changes places with the WEIRD professor, they will both be able to survive and function within their new contexts in due time. Both will learn new languages. The one will learn how to read and write, and how to make use of public transport and central heating. The other will learn where to dig for roots to extract drinking water in the desert, how to hunt, how to track animals and how to find his way home without a GPS. Both their brains and ways of thinking will change in the process (Maguire et al., 2000; Draganski et al., 2006; Hill et al., 2006; Osterhout et al., 2008).

This socio-cognitive flexibility was in all probability what allowed for the successful spread of *Homo sapiens* out of Africa sometime before ~50 ka (ka = thousand years ago or old) (Lombard and Haidle, 2012; Lombard, 2012; 2016). It could also explain our species' interaction with other, closely related, human populations such as the Neanderthals when we encountered them on new landscapes, as well as our ultimate survival as the only hominin in most ecological niches on earth today (Pearce, 2018; Lombard and Högberg, 2021). Exactly how, why or when we became such flexible socio-technical thinkers, and the precise role of the southern African sub-continent in these developments remain open questions.

From an archaeological point of view, the tangible outflow of this development is our technologies and other forms of material culture. I argue that including technology, and therefore archaeology, in exploring human evolution is critical, because we have become the only species completely dependent on technology for our survival (Shea, 2017). The artefacts we excavate reflect past humans' knowledge about how the world works, how they thought about it, interacted with it, and to some extent can indicate how people thought about and interacted with each other. Human socio-technical contexts become extensions of ourselves, contributing to the shaping of our bodies, brains, neurological structures and our DNA (Malafouris, 2010; 2019; Bruner and Lozano, 2014; Pearce, 2018; Kuhlwilm and Boeckx, 2019; Lombard, 2019). They embody our identities, connect us with each other, and allow us to manipulate and control our socio-ecological contexts. All because sometime during our evolution on the African plains, our ancestors became reliant on what they learnt from each other socially and technically (see Högberg and Lombard (2020)

for discussion on the socio-technical framework). It is therefore the interplay between, and co-evolution of, human ecology, biology, society and technology through time that resulted in the mind of *Homo sapiens* as we know it today (Lombard and Högberg, 2021).

2 The 'Origins' of 'Human Origins' Research in Southern Africa

Until the late 1960s, evolutionists generally thought that our human roots lay in Eurasia. The African palaeo-anthropological and archaeological records amassed during the last century, however, started to rewrite human history. During the last few decades, new dating methods and the human genetic record added to the suite of approaches that identify Africa as humanity's birthplace with groups wandering out of, and probably back into, the continent through time. Africa's legacy in human origins research started almost a century ago in South Africa. In 1924, quarrymen at a lime mine, near Taung in the North-west Province, found the fossil now known as the Taung Child (Figure 1.1).

FIGURE 1.1 Left: Facial forensic reconstruction of the Taung Child, the first African hominin fossil described as *Australopithecus africanus*
 IMAGE FROM THE FREE WIKIMEDIA COMMONS MEDIA REPOSITORY.
 PROVIDED BY ARC-TEAM, ANTROCON NPO, CICERO MORAES,
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 Right: Stephanie Baker from the University of Johannesburg, co-director/permit holder of the Drimolen hominin site, with the reconstructed skull of a *Homo erectus* infant who lived ~2 million years ago in the Cradle of Humankind, South Africa
 PHOTO WITH PERMISSION OF MATT CARUANA

Raymond Dart (1925) described the fossil in *Nature* as a new hominin species – *Australopithecus africanus*. For the first time, southern Africa revealed its potential for studying human origins through a child who lived between about 3 and 2.5 million years ago (Kuhn et al., 2016), and who was three-and-a-half years old when attacked and killed by an eagle (Berger and Clarke, 1995).

The place of this first African hominin fossil in human evolutionary research did not come without resistance, because at the time only Neanderthal fossils from Eurasia were known as a possible ancestral population to *Homo sapiens*. British authorities on palaeo-anthropology, some of whom were associated with the Piltdown fraud (De Groote et al., 2016), questioned Dart's interpretation in the ensuing issue of *Nature* (Keith et al., 1925). They argued that the fossil represented an extinct ape species, not a hominin. Only by the second half of the 20th century, and largely because of the Leakeys' work in eastern Africa (Leakey and Walker, 1997), did the African hominin fossil record become so convincing that it could no longer be brushed aside.

To counter an African origins scenario, a multi-regional model for human origins was suggested (Wolpoff, 1989; Thorne and Wolpoff, 1992), holding on to the Eurasian ideal of a local evolution into *Homo sapiens*. Today we know that becoming human was a process more complex than what could be imagined, and that our *Homo sapiens* ancestral populations successfully produced fertile offspring with archaic humans both in Africa and in Eurasia (Hammer et al., 2011; Pääbo, 2013). Thus, our biological heritage “was not a package that had a single African origin in one time, place, and population, but was a composite whose elements appeared, and sometimes disappeared, at different times and places and then coalesced to assume the form we see in extant humans. However, during the past 400 000 years, most of that assembly took place in Africa, which is why a recent African origin still represents the predominant (but not exclusive) mode of evolution for *Homo sapiens*” (Stringer, 2014: 251). But, I digress ...

Returning to southern Africa's first fossil, Robert Broom saw the Taung fossil a few weeks after Dart's publication, and was convinced that it was a hominin. A decade or so later, he was appointed at the then Transvaal Museum (now part of the Ditsong Museum amalgamation in Tshwane and Johannesburg), and went on to work in what is today the UNESCO World Heritage Site, known as the Cradle of Humankind on the Gauteng Highveld of South Africa. Here he discovered *Paranthropus robustus* and adult specimens of *Australopithecus africanus* such as Mrs Ples at Sterkfontein caves, validating the morphological affinities of the Taung Child as species-level morphology. Broom and Scheepers (1946) published the first synthesis of the then known hominins of South Africa, cementing the place of the subcontinent in the epic of human

evolution. To date, the dolomitic palaeo-caves of the relatively small area (~51.5 thousand hectares) known as the ‘Cradle of Humankind’ have yielded one of the richest and most varied early hominin records worldwide with more than 3300 hominin fossil pieces including *Australopithecus africanus*, *Australopithecus sediba*, *Paranthropus robustus*, *Australopithecus prometheus*, early *Homo*, and *Homo erectus* (Table 1.1).

TABLE 1.1 The known hominin sites of the cradle of humankind with numbers of fossil specimens (pers. comm. Bernhard Zipfel and Stephanie Baker, January 2020), and associated hominins

Hominin-bearing site	Number of fossil pieces	Associated hominins
Cooper’s Cave	30	<i>Paranthropus robustus</i>
Drimolen Main Quarry	166	<i>Paranthropus robustus</i> , early <i>Homo</i>
Gladysvale	10	<i>Australopithecus africanus</i> , early <i>Homo</i>
Gondolin	2	<i>Paranthropus robustus</i>
Haasgat	2	<i>Australopithecus</i> sp. or early <i>Homo</i>
Kromdraai	70	<i>Paranthropus robustus</i> , early <i>Homo</i>
Malapa	230	<i>Australopithecus sediba</i>
Plover’s Lake	11	<i>Homo sapiens</i>
Rising Star Dinaledi Chamber	1751	<i>Homo naledi</i>
Rising Star Lesedi	150	<i>Homo naledi</i>
Sterkfontein	680	<i>Australopithecus africanus</i> , <i>Australopithecus prometheus</i> , <i>Paranthropus robustus</i> , <i>Homo habilis</i> , <i>Homo ergaster/erectus</i> , <i>Homo sapiens</i>
Swartkrans	266	<i>Paranthropus robustus</i> , early <i>Homo</i> , <i>Homo</i> sp., <i>Homo sapiens</i>

More than 150 additional pre-50 ka human fossils come from sites across South Africa such as Blind River, Blombos Cave, Border Cave, Cave of Hearths, Cornelia Uitzoek, Die Kelders, Diepkloof Rock Shelter, Elandsfontein, Equus Cave, Florisbad, Hoedjiespunt, Klasies River, Makapansgat, Pinnacle Point, Sea Harvest, Sibudu Cave, Taung, and Witkrans (e.g., Dusseldorp et al., 2013). The latest finds from the Cradle of Humankind continue in the region’s tradition with the newly published *Paranthropus robustus* and *Homo erectus* fossil skulls

from Drimolen, dating to between ~2.04 and 1.95 million years ago (Herries et al., 2020). Here an infant skull now represents the earliest known occurrence of a cranium with clear affinities to *Homo erectus* at ~2 million years (Figure 1.1), questioning the previous account of an exclusively eastern African origin for *Homo* (Herries et al., 2020; see Semaw et al., 2020 for the most recent on eastern African *Homo erectus*).

Although the South African fossil record roughly spans the last 3 million years, many gaps remain. The dated Stone Age archaeological record, however, attests to hominin presence on the landscape throughout the last 2 million years (Lombard et al., 2012 for synthesis; also Caruana et al., 2020). Whilst some previous interpretations suggested breaks in the archaeological record (e.g., Singer and Wymer, 1982; Jacobs et al., 2008), recent work does not support such scenarios (Wurz, 2013; Kandel et al., 2016; Lombard et al., 2019; Lombard and Högberg, 2021). Population genomics also point to Khoe-San populations now living in southern Africa as the most varied groups, and therefore indicating the most ancient roots of *Homo sapiens* populations (e.g., Schlebusch et al., 2012; Barbieri et al., 2016). Moreover, the DNA from a child who lived at what is now Ballito Bay, along the east coast of South Africa, recently modified the genetic time depth of *Homo sapiens* to between 350 ka and 260 ka (Schlebusch et al., 2017; Lombard et al., 2018).

Not one of the three records (fossil, archaeology, DNA) can provide ultimate arguments on their own. Fossils can sometimes answer questions about who, when and where, but apart from problems in identification and dating, they are too few to provide a comprehensive reconstruction of human evolution. Archaeology can fill many spatiotemporal occupational gaps left by the fossil record, but unless directly associated with hominin fossils, the authors of the record remain open to interpretation (e.g., see Dusseldorp and Lombard (2021) for discussion). The DNA record reveals detailed population identities/histories, and increasingly robust time depths for genetic split scenarios between populations, but not the exact locations of such events. Most recent work, however, consistently include southern Africa as one of the 'hotspots' within a complex framework for the evolution of *Homo sapiens* on the continent (Schlebusch et al., 2017; Scerri et al., 2018; Mounier and Lahr, 2019).

3 Becoming Human in Southern Africa

Here I do not aim to offer ultimate answers, but rather highlight some aspects in the various records, revealing the most pertinent gaps and questions for

future multi-disciplinary research. To do so, I provide a brief overview of mainly the South African Pleistocene record between 500 and 50 thousand years ago – starting at the time just after the Neanderthal split from other populations and spanning the period during which *Homo sapiens* evolved in Africa (Figure 1.2). I use this record only as a window into what is known because, as an artefact of historical research focus, it is the most complete, and I am the most familiar with it. Geo-political boundaries are, however, meaningless in our evolutionary history, so that we may assume similar trends across southern Africa (roughly the region south of the Zambezi River), and possibly sub-Saharan Africa. For some global contextualisation, I also briefly touch on fossil and other records from elsewhere. Below are a few additional pointers for cross-disciplinary readers:

1. The use of species names in association with any of the records reflects classifications chosen for scientific discussion, not past realities. In Iain Davidson's (2020: 36) words: "[T]here can be no hard and fast boundaries between species through time, much less between genera. A mother (of any species past or present) could not have given birth to a male offspring to whom she was so distantly related that they would not have been able, give or take an incest taboo, to have produced offspring. So, the boundaries are things that are created in the process of study depending on what is being studied and why, and on the assumptions that are brought to bear on the study" (also see Antón et al., 2014). The same principle applies to archaeological categories.
2. *Homo rhodesiensis* is now mostly accepted as synonymous to *Homo heidelbergensis*, and I use the latter for specimens previously identified as the former.
3. Even though I present a chronological discussion, it does not imply a teleological progression in human evolutionary history, but merely provides the temporal context as presently understood.
4. Both the fossil and archaeological records are heavily sampled. As a result, we find exponentially less than what was there originally the deeper we go in time. Presence of absence does therefore not translate into absence of presence – the records merely indicate what is currently known/confirmed.
5. I mostly refer to dated material, again fractioning the existing records, but in so doing I provide relatively secure anchor points within the fitness landscapes of populations (see Lombard (2012 and 2016) for discussion).

FIGURE 1.2 Top graph: Effective population sizes estimated for single individuals (i.e. two chromosomes) for the Khoe-San (average over the five individuals in each population), the HGDP individuals and the boy from Ballito (baa001) who lived 2000 years ago. Below the graph, the San group represents the southern African population in comparison with other African and non-African populations. Second from top graph: Isotopic values (derived from Cohen et al., 2019 by Matt Caruana) and sea-surface temperatures just off the east coast of southern Africa (reconstructed by Matt Caruana after Caley et al., 2018) as broad climatic indicators. Green lines below the climatic indicators represent the broad Stone Age archaeological sequence for South Africa and Lesotho with overlaps based on dated assemblages (LSA = Later Stone Age, MSA = Middle Stone Age, ESA = Earlier Stone Age). Bottom: Some key fossil finds in South Africa spanning 500–50 ka

4 Human Occupation and Populations ~500 000 to >350 000 Years Ago

It is not yet clear when the Neanderthals and Denisovans of Eurasia split from earlier populations. The current consensus lies somewhere between 600 ka and 400 ka, and suggests that the last common ancestor was likely *Homo heidelbergensis* (e.g., Stringer, 2012, but also see Mounier and Caparros 2015 on the status of *Homo heidelbergensis*). A recent study on teeth, however, suggests that the Neanderthal-*Homo sapiens* split may have been much earlier (>800 ka), implying that *Homo heidelbergensis* was perhaps not the common ancestor, but rather another sympatric or sister population (Gómez-Robles, 2019). Eurasian fossil sites falling within the 500–350 ka window are mostly associated with *Homo heidelbergensis*, with some possible Neanderthals in Italy and Portugal, and a Neanderthal population at Swanscombe in the UK dating to ~400 ka. It therefore seems that both *Homo heidelbergensis* and Neanderthal populations were present in Eurasia during this time (Table 1.2).

African fossils with relatively secure age estimates around 400 ka, have been interpreted as *Homo heidelbergensis*/late *Homo erectus*/early *Homo sapiens*, at Ndutu in Tanzania, and as *Homo heidelbergensis* at Salé in Morocco (Table 1.2). In southern Africa, a skullcap ascribed to *Homo heidelbergensis* from Elandsfontein has an estimated age range of 600–500 ka, and a partial mandible from Cave of Hearths that could date to anything between 500 ka and 200 ka is thought to be transitional between *Homo erectus* and early *Homo sapiens* (Figure 1.2). The current African fossil record is therefore too sparse to resolve any of the questions surrounding the timing of a split, and whether *Homo heidelbergensis*, *Homo erectus* or another population could represent our last common ancestor with the Neanderthals.

By 500 ka the archaeology of South Africa is characterised by the transition of the Earlier Stone Age (ESA – roughly corresponding to the Lower Palaeolithic in Eurasia) into the Middle Stone Age (MSA – roughly corresponding to the Middle Palaeolithic in Eurasia). These assemblages often have a hybrid appearance consisting of large blades, small bifaces, and sometimes Levallois-like points. We still see the Acheulean techno-complex at the beginning of the period at sites such as Elandsfontein (Table 1.2). A recent re-analysis of the faunal assemblage at this site revealed interesting behavioural aspects about its human occupants. Bunn (2019) found that here *Homo heidelbergensis* used the marshland for ambush hunting large ungulate prey. Such early hunting, was possibly practiced in the form of stoning or clubbing animals that were already at a disadvantage, such as being slowed down by natural funnels or being stuck in mud at drinking holes or grazing marshlands (Liebenberg, 2006; Lieberman et al., 2009).

TABLE 1.2 Key dated archaeological sites and fossil finds in south africa and elsewhere that reflect human occupation and populations at ~500 000 to >350 000 years ago

Dated archaeology, South Africa	Fossils with age estimates, South Africa	Fossil sites elsewhere
Elandsfontein , ~600–500, ESA Acheulean/ESA- MSA transitional	Elandsfontein , <i>H. heidelbergensis</i> (<i>rhodesiensis</i>), ~600– 500 ka?	Mauer 1 , Germany, <i>H. heidelbergensis</i> , ~500 ka
Kathu Pan , Fauresmith/ESA- MSA transitional, ~550–460 ka	Cave of Hearths , transitional <i>H. erectus</i> /early <i>H.</i> <i>sapiens</i> ~500–200 ka?	Mala Balanica , Serbia, <i>H. heidelbergensis</i> 525–>395 ka
Bundu Farm , ESA- MSA transitional, ≤390 ka		Boxgrove , UK, <i>H. heidelbergensis</i> , ~500 ka
Fauresmith , Fauresmith/ESA- MSA transitional, 500–200 ka? (based on lithic assemblage)		Fontana Ranuccio , Italy, <i>H. neanderthalensis</i> / <i>H.</i> <i>heidelbergensis</i> , ~460 ka
Canteen Kopje , Fauresmith/ESA- MSA transitional, 500–200 ka? (based on lithic assemblage)		Argil/Ceprano , Italy, <i>H. cepranensis</i> / <i>H. heidelbergensis</i> , ~450 ka
Van der Elst Donga , Fauresmith/ESA- MSA transitional, 500–200 ka? (based on lithic assemblage)		Aroeira 3 , Portugal, <i>H. heidelbergensis</i> /Neanderthal-like, ~400 ka
		Miguelón 5 , Spain, <i>H. heidelbergensis</i> , ~400 ka
		Ndutu , Tanzania, <i>H. heidelbergensis</i> (<i>rhodesiensis</i>)/late <i>H. erectus</i> /early <i>H. sapiens</i> , ~400 ka
		Salé , Morocco, <i>H. heidelbergensis</i> , ~400 ka
		Swancombe , UK, <i>H. neanderthalensis</i> , ~400 ka.
		Arago 21 , France, <i>H. erectus</i> , ~400–350 ka
		Gawis , Ethiopia, <i>H. erectus</i> / <i>H. sapiens</i> , ~350 ka
		Steinheim , Germany, <i>H. heidelbergensis</i> , ~350 ka

If this was the case, there are certain cognitive inferences that can be made for the Elandsfontein hunters. For example, in setting up an ambush scenario, the hunters understood that their common goal was to kill a prey animal, and that they have different roles in the execution of this joint intention, indicating third-order theory of mind. Their understanding of the predictable patterns of animal movement, conducive of such ambush hunting, might also indicate non-conspecific theory of mind, also described as grade 5 causal reasoning (Lombard and Gärdenfors, 2017; Gärdenfors and Lombard, 2018; Lombard and Gärdenfors, 2021). The same cognitive implications would apply to Neanderthal ambush hunting with wooden spears, at sites such as Schöningen in Germany, and Clacton in the UK dating to ~400–300 ka (e.g., Thieme, 2005; Voormolen, 2008; Allington-Jones, 2015).

More advanced forms of technological-assisted hunting have been suggested for ~500 ka at Kathu Pan 1 in the South African interior (Wilkins et al., 2012). Here, stone points, excavated some decades before the dating and chronological reconstruction of the site were re-aligned with a newly exposed stratigraphic context dated to between 542 ± 40 – 107 ka and 464 ± 46 ka, directly underlying a layer with an age estimate of 291 ± 45 ka. Wilkins and colleagues (2012) interpreted these artefacts as hafted spear tips, but questions about the relationship between the dated geological horizon and the previously curated artefacts remain (Wadley, 2013; Wurz, 2013). Similar artefacts and evidence for the use of stone-tipped spears become widespread in sub-Saharan Africa since ~300 ka (Tryon et al., 2005; Sahle et al., 2013; Lombard, 2021).

Shea's (2017) discussion on differentiating between occasional, habitual and obligatory stone tool use in human evolution situates the 500–350 ka slot towards the end of the hominin habitual stone tool use phase, which started at ~1.7 million years ago. According to him: "Habitual tool use engages tools in stereotyped ways in activities with variable periodicities and evolutionary consequences. Individuals who use tools in one way reap fitness rewards differently than do those who use tools in other ways or not at all, but these benefits vary along with the periodicity in the need for tool use across time and space" (Shea, 2017: 209). The mixed appearance of the ESA-MSA transitional assemblages in South Africa may well reflect human adaptation towards becoming obligatory tool users that was probably a contributing factor to the cognitive evolutionary trajectories of subsequent human populations, including *Homo sapiens*. However, both the fossil and archaeological records for this period in southern Africa still leave us with more questions than answers. Nothing is known yet about the human DNA record apart from the back-calculation of population sizes that shows a slow and consistent rise from just less than 20 000 to about 30 000, with numbers for the ancestral populations of current southern African populations slightly below that of other Africans (Figure 1.2).

5 Human Occupation and Populations ~350 000 to >250 000 Years Ago

It is, however, the DNA of a young boy who lived on the coast of KwaZulu-Natal about 2000 years ago (Lombard et al., 2018), that brings us to the 350–250 ka time slice in human evolution. This was not a healthy child, dying at the age of six or seven from a combination of ailments including anaemia, possibly caused by a parasitic infection such as schistosomiasis (Pfeiffer et al., 2019), and/or typhus-like flea-borne rickettsioses caused by the *Rickettsia felis* bacterium (Rifkin et al., 2020). Yet, his remarkably complete genome, together with that of two other Stone Age hunter-gatherer men buried close to him, provided the unique opportunity to recalculate the genetic time depth for *Homo sapiens* (Schlebusch et al., 2017). At the same time, the interpretation of fossil material from Morocco in North Africa, dated to ~286 ka was announced as that of early *Homo sapiens* (Hublin et al., 2017). So that two completely different datasets published almost simultaneously revealed a similar outcome – African *Homo sapiens* lived on the continent much earlier than previously thought. These finds support the interpretation of the material from Ileret, Kenya, as early *Homo sapiens* with an age estimate of 300–270 ka (Bräuer, 2016). The dilemma, however, is that the fossil data come from the far northwest and central east of the continent, whilst the DNA comes from the far south. So that once again, even though we now have a better grasp on timing, we can still not pinpoint the place where *Homo sapiens* first appeared on the continent. But then again, looking for such a place might be as flawed in principle as the notion of pin-pointing a singular speciation event.

In South Africa, the younger end of the new genetic split-time estimate for *Homo sapiens* coincides with the Florisbad skull from the Free State dated to 259 ka (Grün et al., 1996). Different authors proposed a taxonomic affinity with early *Homo sapiens*, Neandertals or late *Homo heidelbergensis*. In a recent analysis (Bruner and Lombard, 2020), we found that the endocranial anatomy of the Florisbad cranium displays a mosaic of derived and plesiomorphic features, which makes this fossil central to the questions about the possible anagenetic evolution from *Homo heidelbergensis sensu lato* to *Homo sapiens*. The archaeology in general also seems to shift from ESA-MSA transitional assemblages to early MSA ones during this phase (Table 1.3). With the MSA largely including characteristic discoidal and Levallois flake technologies.

On an Old World global scale, the 350–250 ka window spans the introduction of obligatory tool use, “which engages tools in tasks that are otherwise difficult or impossible to accomplish, [and] has serious and immediate fitness consequences. Individuals who do not use tools in such circumstances either

TABLE 1.3 Key dated archaeological sites and fossil finds in South Africa and elsewhere that reflect human occupation and populations ~350 000 to >250 000 years ago

Dated archaeology, South Africa	Fossils with age estimates, South Africa	Fossil sites elsewhere
Duinefontein, ESA Acheulean/ESA-MSA transition/early MSA, 292–265 ka	Rising Star, <i>H. naledi</i> , 335–236 ka	Ileret, Kenya, early <i>H. sapiens</i> , 300–270 ka
Wonderwerk Cave, ESA-MSA transition, 349–276 ka	Florisbad, <i>H. helmei</i> / <i>H. heidelbergensis</i> /early <i>H. sapiens</i> , 259 ka	Eliye Springs, Kenya, 300–200 ka
Sterkfontein, early MSA, 294–252 ka	Hoedjiespunt, <i>H. heidelbergensis</i> , 300–200 ka	Jebel Irhoud 1–5, Morocco, early <i>H. sapiens</i> , 286 ka
Kathu Pan, early MSA 295 ka		Samu, Hungary, <i>H. heidelbergensis</i> , 275 ka
Florisbad, early MSA, 281–265 ka		Dali, China, <i>H. erectus</i> / <i>H. heidelbergensis</i> /early <i>H. sapiens</i> 260 ka
Border Cave, early MSA, 280–217 ka		Galilee, Israel, <i>H. heidelbergensis</i> , 250 ka
Lincoln Cave, early MSA, 252 ka		Saccopastore 1, Italy, <i>H. neanderthalensis</i> , 250 ka
Rooidam, Fauresmith/ESA-MSA transitional, ~200 ka?		

die immediately or suffer other adverse effects in the near term” (Shea, 2017: 204). It is therefore perhaps not surprising that this is also the time during which our ancestors became increasingly proficient stone-tipped weapon makers and spear and javelin hunters (Lombard and Haidle, 2012; Sahle et al., 2013; Lombard, 2021). Together with these techno-behaviours they developed an understanding that allows for the attribution of causal roles to inanimate objects such as hafting agents in the form of twine and/or adhesives for making their composite tool kits (Gärdenfors and Lombard, 2018; Niekus et al., 2019; Lombard and Gärdenfors, 2021).

Other human remains from South Africa dating to this period include *Homo heidelbergensis*/early *Homo sapiens* from Hoedjiespunt with an age estimate of 300–200 ka, also associated with MSA artefacts (Berger and Parkington, 1995; Churchill et al., 2000). At this point, the South African record seems consistent with the notion of a slow and steady evolution of one big-brained population (*Homo heidelbergensis*) into another with an even bigger cranial capacity (*Homo sapiens*) (see Galway-Witham et al., 2019; Bruner and Lombard, 2020). This scenario seems reinforced by the fact that there are no obvious breaks in technological developments, as is palpable in the Eurasian record when *Homo sapiens* groups start to appear on a landscape previously dominated by Neanderthal populations and their traditions.

But then there is *Homo naledi*. At first thought to have lived more than a million years ago, the context of this small-brained hominin, thus far only found at a single cave site in the Cradle of Humankind was recently dated to 335–236 ka (ka = thousand years old/ago) (Dirks et al., 2017). Directly preceding this time, there is no obvious ancestral population for this hominin. Although its brain may show a structure similar to that of the *Homo* clade (Holloway, 2018), its cranial capacity of 465–610 cc is well below that any of its hominin contemporaries (Galway-Witham et al., 2019; Dusseldorp and Lombard, 2021). Instead, it is more akin to that of the Australopithecines who disappeared from the Cradle of Humankind >1.5 million years ago. Thus, if the dates for *Homo naledi* are correct, its existence poses a real conundrum (see Dusseldorp and Lombard, 2012).

Whereas the other fossil hominins for the period in South Africa have been associated with MSA assemblages, *Homo naledi* thus far remains without archaeology. Yet, it is claimed that: “We can no longer assume that we know which species made which tools, or even assume that it was modern humans that were the innovators of some of these critical technological and behavioral breakthroughs in the archaeological record of Africa” (<https://www.maropeng.co.za/news/entry/historic-new-homo-naledi-discoveries-unveiled-at-maropeng>; Lee Berger, accessed 25/02/2020).

One way to assess the age of *Homo naledi* and its affinity with other hominins would be to conduct DNA analyses on some of the well-preserved material. The risk is of course that such research may produce unexpected outcomes such as those obtained for Plovers Lake (Lombard et al., 2019), a site previously published as having human remains from an MSA context (de Ruiter et al., 2008). In this instance, we hoped to gain genetic insight about people who were supposed to live >60 ka in the Cradle of Humankind. Our cross-disciplinary work, however, provided at least four strands of independent evidence revealing that the deposits were not exclusive to the MSA. Our

data included: *i*) Direct C14 dates that were only a few hundred years old; *ii*) bovid mtDNA profiles that were consistent with domestic cattle instead of buffalo; *iii*) human mtDNA profiles that were strongly associated with current-day Bantu-speakers, instead of hunter-gatherers from southern Africa; and *d*) isotope values that were consistent with a farming way of life (Lombard et al., 2019).

Until its genetic affinity and archaeology can be resolved empirically, one way to approach the *Homo naledi* dilemma is from a theoretical point of view. Its age estimate poses interesting questions about sympatric hominin niche construction on the southern African grasslands for the period associated with the morphological and genetic emergence of *Homo sapiens*. For example, to co-exist in a geographic area in the longer term, the ecological niches of distinct hominin groups had to be differentiated. If their niches overlap significantly, one of the two species will go extinct locally. This principle of competitive exclusion is well-established (see discussion in Foley, 1987), and should be thoroughly explored for the potentially co-existing *Homo naledi* and *Homo sapiens* in southern Africa (Dusseldorp and Lombard, 2021). Resulting hypothetical frameworks could also be useful in a broader African context.

Mounier and Lahr (2019), for example, found evidence of a complex process for the evolution of *Homo sapiens*, wherein not all African populations associated with its so-called origins contributed equally. Instead, based on skull morphology, they suggest that: “*Homo sapiens*’ origin may have resulted from the coalescence of South and, possibly, East-African source populations. In this scenario, the North-African hominins may represent a population which introgressed into Neandertals” (Mounier and Lahr, 2019: 1). What is more, it is often thought that by this time the Neanderthals were dominating in Eurasia, yet the fossil record remains diverse (Table 1.3). Genetically derived population numbers are, however, relatively stable during this period, showing a slight rise in the ancestry of all groups to around 30 ka (Figure 1.2). This could reflect the relatively stable climate subsequent to the marine isotope stage (MIS) 9e peak at ~340–330 ka.

6 Human Occupation and Populations ~250 000 to >150 000 Years Ago

These relatively steady climatic conditions continue throughout the 250–150 ka window, but we do see a drop in population numbers associated with the lower temperatures of MIS 6 (Figure 1.2). The drop is especially pertinent in

the non-African ancestry populations. The population ancestry representing the current southern African component remains the most stable, with its drop in numbers also less dramatic than that of other African populations. This raises the question of the southern tip of Africa potentially being a crucible or refuge for hominins and mammals during certain climatic conditions. Especially aridification of the landscape would have resulted in expansive deserts or semi-deserts void of enough fresh water to sustain some types of mammal populations or prevent them from crossing the continent (Shackley, 1985; Castañeda et al., 2009), limiting cross-continental gene flow. Additional records highlight fluctuating climates during the Quaternary in southern Africa that would have affected the distribution of both people and bio-ecologies (Tyson and Partridge, 2000; Dupont et al., 2005; Dupont, 2006; Scott and Neumann, 2018).

Scott and Neumann's (2018) pollen-interpreted palaeo-environments show that during MIS 7 (~245–190 ka), vegetation along the Indian Ocean of southern Africa started to change from cool and humid conditions with widespread forests, to warmer conditions with expanding woodlands between ~230 ka and ~191 ka. This is followed by the MIS 6 glacial (~190–130 ka) with colder and moister conditions in the eastern regions of southern Africa. By ~185 ka, a global drop in sea levels is indicated, and by ~170 ka generally cool conditions. In the interior of the sub-continent, the record is typical for the drying out of lakes or the forming of salt pans – a condition that lasted throughout MIS 6, indicating aridification of central southern Africa. This drying out could correlate with the development of grassland at interior sites such as Florisbad (Scott and Neumann, 2018). Pollen records for the south-western part of southern Africa are not currently available. But both Parkington (2010) and Marean (2011) suggested that, based on its plant diversity and resource-rich coastline, the south coast was key to the development of *Homo sapiens* in the region as “a refuge during the long cold MIS 6” (Marean, 2011: 434), similar to what Basell (2008) argued for eastern Africa.

Archaeologically, assemblages of ESA-MSA transitional nature persist at some sites, but most dated sites in South Africa is typical of the early MSA during this phase. *Homo naledi* may still be present in the Cradle (depending on the accuracy of its age range), the Hoedjiespunt material is interpreted as *Homo heidelbergensis* based on its robusticity, and *Homo sapiens* was present at the inland site of Border Cave accompanied by MSA archaeology (Table 1.4). It is also here at Border Cave where Wadley and colleagues (2020) found the earliest known evidence of cooked starchy rhizomes at ~170 ka, and along the south coast at Pinnacle Point 13B, humans expanded their diet to include marine resources by ~164 ka (Marean, 2010). We know that these people were also efficient hunters, because ungulate taxa dominate the Pinnacle Point

TABLE 1.4 Key dated archaeological sites and fossil finds in South Africa and elsewhere that reflect human occupation and populations ~250 000 to >150 000 years ago

Dated archaeology, south Africa	Fossils with age estimates, south Africa	Fossil sites elsewhere
Rooidam , ESA-MSA transition, 174 ka	Rising Star Dinaledi Chamber, <i>H. naledi</i> , 335–236 ka	Bontnewydd , UK, <i>H. neanderthalensis</i> , ~230 ka
Duineforntein , ESA-MSA transition, 168–151 ka	Hoedjiespunt , <i>H. heidelbergensis</i> , 300–200 ka	Apidima 1 , Greece, <i>H. sapiens</i> , 210 ka
Wonderwerk Cave , early MSA, 182 ka	Border Cave , <i>H. sapiens</i> , 171–152 ka	Petralona 1 , Greece, <i>H. heidelbergensis</i> , ~200 ka
Sterkfontein , early MSA, 252–210 ka		Ngaloba Beds , Tanzania, <i>H. sapiens</i> , ~200 ka
Pinnacle Point , early MSA, 166–150 ka		Omo Kibish , Ethiopia, <i>H. sapiens</i> , ~195 ka
Florisbad , early MSA, 159–259 ka		Hexian , China, <i>H. erectus</i> , ~195 ka
Duinefontein , early MSA, 151–168 ka		Tamil Nadu , India, <i>H. erectus</i> / <i>H. sapiens</i> , ~190 ka
Border Cave , early MSA, 183–141 ka		Misliya 1 , Israel, <i>H. sapiens</i> , ~187 ka
		Apidima 2 , Greece, <i>H. neanderthalensis</i> , ~170 ka
		Herto , Ethiopia, <i>H. sapiens</i> , ~160 ka
		Xiahe , China, <i>Homo</i> sp. Altai/Denisovan, ~160 ka
		Altamura , Italy, <i>H. neanderthalensis</i> , 151 ka

faunal assemblage, and stone points indicate the use of hunting weapons (Lombard, 2021). Yet, shifting subsistence practices towards including denser, more predictable and nutritious resources, such as starchy rhizomes and oily shellfish, has far-reaching evolutionary consequences – not only in terms of

subsistence behaviour. Marean (2016), for example, explains the adaptation in terms of economic defendability, where maintaining access and control of such beneficial resources result in costly behaviours such as competition, aggression and territoriality amongst groups (also see Chabot-Hanowell and Smith 2012). Resulting pressure for conflict resolution within and amongst groups, may have stimulated selection towards cooperative networks of unrelated individuals, such as seen amongst recent hunter-gatherer groups (Wiessner, 1982), and suggested for Pleistocene *Homo sapiens* (Pearce, 2018), stimulating the evolution of higher order theory of mind (Barrett et al., 2010; Lombard and Gärdenfors, 2021).

African hominin fossils from Tanzania and Ethiopia for this window in time are all identified as *Homo sapiens*, and for the first time we see this species also in Greece and perhaps in India (Table 1.4). Neanderthals are present in Greece, Italy and the UK, but some fossils in Eurasia are still interpreted as *Homo heidelbergensis* and *Homo erectus*. When we consider the possible presence of *Homo naledi* in southern Africa, and Denisovans in China, together with the complete fossil record spanning the ~250–150 ka window, it is clear that whilst *Homo sapiens* may be on the rise, human populations in general are still morphologically diverse (Table 1.4). On the other hand, this is also the time during which we see the last identifications of *Homo erectus* globally, and the demise of *Homo naledi* and *Homo heidelbergensis* in southern Africa.

7 Human Occupation and Populations ~150 000 to >50 000 Years Ago

By 150 ka, temperatures start to rise amidst a continuing drop in population numbers or reproducing groups (Figure 1.2). After the warmest peak during MIS 5e, the climatic indicators become increasingly unstable. It is during this period that *Homo sapiens* became the only remaining human population in the South African fossil record (Table 1.5), so that we may assume that modern humans now produced the resulting archaeology. The last ESA-MSA transitional assemblages are described for one coastal and two inland sites, and the early MSA is present in the interior at Border Cave, Florisbad, Wonderwerk Cave, and also Lincoln Cave in the Cradle of Humankind – these assemblages all pre-date 105 ka (Table 1.5). It is, however, also since ~150 ka that knappers in southern Africa start to develop clearly distinguishable techno-complexes through time and across space, and that a broad lithic sequence becomes apparent (Lombard et al., 2012), notwithstanding a few outliers mostly related to dating issues.

TABLE 1.5 Key dated archaeological sites and fossil finds in South Africa and elsewhere that reflect human occupation and populations ~150 000 to >50 000 years ago

Dated archaeology, South Africa	Fossils with age estimates, South Africa	Fossil sites elsewhere
Bundu Farm, ESA-MSA transition, 145 ka	Klasies River, <i>H. sapiens</i> , 120 ka	Liujiang, China, <i>H.</i> sp., 139–111 ka
Border Cave, early MSA, 141 ka	Blind River, <i>H. sapiens</i> , 118 ka	Singa, Sudan, <i>H. sapiens</i> , 133 ka
Wonderkrater, MSA, 138–56 ka	Klasies River, <i>H. sapiens</i> , 110 ka	Mumba, Tanzania, <i>H. sapiens</i> , 130 ka
Florisbad, early MSA, 133–125 ka	Witkrans, <i>H. sapiens</i> , 103–86 ka	Kabwe (Broken Hill 1), Zambia, <i>H.</i> <i>rhodesiensis</i> / <i>H. heidelbergensis</i> , 125 ka
Ysterfontein, MSA (Klasies River), 132–71 ka	Blombos Cave, <i>H. sapiens</i> , 100 ka	Ngaloba, Tanzania, <i>H. sapiens</i> , 120 ka
Diepkloof, MSA (Still bay), 129–70 ka	Pinnacle Point, <i>H. sapiens</i> , 100–90 ka	Tabun C1, Israel, <i>H. neanderthalensis</i> , ~120 ka
Pinnacle Point, MSA (Klasies River), 128–110 ka	Klasies River, <i>H. sapiens</i> , 100–80 ka	Krapina 3, Croatia, <i>H. neanderthalensis</i> , 113 ka
Duinefontein, ESA-MSA transition, 125 ka	Border Cave, <i>H. sapiens</i> , 90–66 ka	Denisova 8, Russia, <i>Homo</i> sp. Altai, 110 ka
Wonderwerk Cave, early MSA, 118 ka	Seaharvest, <i>H. Sapiens</i> , 85 ka	Aduma, Ethiopia, <i>Homo</i> sp/ Neanderthaloid, 105–79 ka, 77–60 ka
Lincoln Cave, early MSA, 115 ka	Sibudu Cave, <i>H. sapiens</i> , 77 ka	Sladina, Belgium, <i>H. neanderthalensis</i> , 103 ka
Rooidam, ESA-MSA transition, 108 ka	Blombos Cave, <i>H. sapiens</i> , 72 ka	
Klasies River, MSA (Klasies River), 108–106 ka	Border Cave, <i>H. sapiens</i> , 72–61 ka	
Blombos Cave, MSA (pre-Still Bay), 100–85 ka	Die Kelders, <i>H. sapiens</i> , 70–60 ka	
Pinnacle Point, MSA (Mossel Bay), 99–90 ka		
Diepkloof, MSA (Howiesons Poort), 96–58 ka		
Rose Cottage Cave, MSA (pre-Still Bay), 95–27 ka		
Melikane (Lesotho), MSA (Mossel Bay), 83–79 ka		

TABLE 1.5 Key dated archaeological sites and fossil finds in South Africa and elsewhere that reflect human occupation and populations ~150 000 to >50 000 years ago (*cont.*)

Dated archaeology, South Africa	Fossils with age estimates, South Africa	Fossil sites elsewhere
Klasies River, MSA (Mossel Bay), 85–82 ka	Klasies River, <i>H. sapiens</i> , 65–60 ka	Skhul 5 & 9, Israel, <i>H. sapiens</i> , 100 ka
Hollow Rock Shelter, MSA (Still Bay), 80–72 ka	Sibudu Cave, <i>H. sapiens</i> , 64 ka	Qafzeh 6 & 9, Israel, <i>H. sapiens</i> , 100–90 ka
Sibudu Cave, MSA (pre-Still Bay), 77–73 ka	Diepkloof, <i>H. sapiens</i> , 60 ka	Denisova, Russia, <i>H. neanderthalensis</i> / <i>H. sapiens denisova</i> , 90 ka
Blombos Cave, MSA (Still Bay), 77–72 ka	Klasies River, <i>H. sapiens</i> , 60–40 ka	Porc-Epic, Ethiopia, Neanderthaloid,
Border Cave, MSA (Howiesons Poort), 76–58 ka	Diepkloof, <i>H. sapiens</i> 57–46 ka	Obi-Rakhmat, Uzbekistan, <i>H.</i> <i>neanderthalensis</i> , 75 ka
Sibudu Cave, MSA (Still Bay), 72–70 ka		Teshik-Tash, Uzbekistan, <i>H.</i> <i>neanderthalensis</i> , 70 ka
Klipdrift, MSA, 71 ka		La Ferrassie 1, France, <i>H.</i> <i>neanderthalensis</i> , 70 ka
Umhlatuzana, MSA (Still Bay), 70 ka		Shanidar 1, Iraq, <i>H.</i> <i>neanderthalensis</i> , 70 ka
Klein Kliphuis, MSA (Howiesons Poort), 66–60 ka		La Chapelle-aux- Saints 1, France, <i>H.</i> <i>neanderthalensis</i> , 60 ka
Boomplaas, MSA (Howiesons Poort), 66–58		Kebara 2, Israel, <i>H.</i> <i>neanderthalensis</i> , 60 ka
Klasies River, MSA (Howiesons Poort), 65–53 ka		
Rose Cottage Cave, MSA (Howiesons Poort), 65–63 ka		
Sibudu Cave, MSA (Howiesons Poort, 65–62 ka		
Border Cave, MSA (Sibudu), 63–41 ka		
Melikane (Lesotho), MSA (Howiesons Poort), 61 ka		
Ntloana Tsoana (Lesotho), MSA (Howiesons Poort), 60 ka		
Klipdrift, MSA (Howiesons Poort), 60–59 ka		

TABLE 1.5 Key dated archaeological sites and fossil finds in South Africa and elsewhere that reflect human occupation and populations ~150 000 to >50 000 years ago (cont.)

Dated archaeology, South Africa	Fossils with age estimates, South Africa	Fossil sites elsewhere
Klasies River, MSA (Sibudu), 60–50 ka		Amud 7, Israel, <i>H. neanderthalensis</i> , 55 ka
Umhlatuzana, MSA (Howiesons Poort), 60 ka		Liang Bua, Indonesia, <i>Homo floresiensis</i> , 55 ka
Sibudu Cave, MSA (Sibudu), 59–46 ka		Manot 1, Israel, <i>H. sapiens</i> , 55 ka
Klein Kliphuis, MSA (Sibudu), 58–53 ka		Tam Pa Ling, Laos, <i>H. sapiens</i> , 54 ka
Diepkloof, MSA (Sibudu), 57–55 ka		La Quina 5 & 18, France, <i>H. neanderthalensis</i> , 52 ka
Sehonghong (Lesotho), MSA (Sibudu), 57–46 ka		Mungo, Australia, <i>H. sapiens</i> , 50 ka
Rose Cottage Cave, MSA (Sibudu), 56 ka		Mt. Circeo 1, Italy, <i>H. neanderthalensis</i> , 50 ka
Ntloana Tsoana (Lesotho), MSA (Sibudu), 56 ka		
Klipdrift, MSA (post-Howiesons Poort), 51 ka		

By ~80 ka the precocious Still Bay techno-complex is introduced together with a suite of other complex behaviours followed by the Howiesons Poort. Jointly, these two industries represent a proliferation in techno-behaviours and symbolic material culture as never seen before in the archaeological record (Henshilwood, 2012; Lombard, 2012; Wadley, 2015; Högberg and Lombard, 2020). They span ~80–58 ka, starting by the end of MIS 5 and last throughout the MIS 4 glacial until the beginning of MIS 3. This timing coincides with both archaeological and genetic evidence for the successful spread of *Homo sapiens* from Africa into Eurasia (Groucutt et al., 2015; Nielsen et al., 2017). Throughout this period, the climatic indicators remain erratic. Population numbers are at their lowest across the board during MIS 5, but during the MIS 4 glacial, the

numbers for southern African populations start to rise, whilst those for other groups remain at their lowest.

From analysing and interpreting the archaeological record, it is also ever more apparent that, by at least 100 ka, the cognition of *Homo sapiens* populations in southern Africa became increasingly complex, and in some ways similar to that of humans today (e.g., Henshilwood, 2012; Lombard, 2012; Wadley, 2015). Cumulatively, their techno-behaviours reveal high levels of working memory, episodic memory, mental time travel, analogical reasoning, intentionality, theory of mind, relational complexity, social cognition, cognitive flexibility and causal cognition (Lombard and Gärdenfors, 2021; Lombard and Högberg, 2021). These behaviours include, amongst others, the processing of pigments (Henshilwood et al., 2011), the patterning of beadwork (Vanhaeren et al., 2013), using snares, synthetic adhesives and insect repellents (Wadley et al., 2009; 2011; Wadley, 2010), heat treating rocks to improve knappability (Brown et al., 2009; Wadley and Prinsloo, 2014; Schmidt and Högberg, 2018), and bow hunting (Lombard and Haidle, 2012; Gärdenfors and Lombard, 2018, 2020; Lombard, 2019; 2021). It is also during this time that the oldest known human burial in Africa, that of a four- to six-month-old infant with conus shell ornamentation, took place at Border Cave at ~74 ka (d'Errico and Backwell, 2016).

Neanderthals are now dominant in Eurasia (Table 1.5) with their own forms of possible burial and symbolic use of marine shells and mineral pigments, so that there is an increasing call for Neanderthal cognition to be considered the same as that of *Homo sapiens* (e.g., Zilhão et al., 2010; Galway-Witham et al., 2019). Yet, it is also becoming ever more evident that a considerable suite of brain-selective genetic variants in *Homo sapiens* evolved differently compared to that of the Neanderthal genome (Lombard et al., 2013; Doan et al., 2016; Neubauer et al., 2018; Kuhlwilm and Boeckx, 2019; Lombard and Högberg, 2021), not implying superiority in either instance, but pointing to alternatives in their cognitive evolutionary histories. These variants include gene regions medically associated with brain development, skull shape and plasticity, a range of cognitive and memory regulators, aspects of language inheritance the development of the nervous system associated with axonal and dendritic growth and synaptic transmission, as well as social behaviours.

Based on the genomes of living and ancient Khoe-San populations from southern Africa, Schlebusch and colleagues (2020) also found new variations in early *Homo sapiens* subsequent to their split from the Neanderthals, but before their split from other African populations at more than 300 ka. These findings include a brain-related region on chromosome 4, which plays an important role in determining the connectivity rates between the principal

neurons of the cortex. Thus, based on the nature of brain-selective genetic distinctions, the notion that Neanderthals as a population were cognitively identical to *Homo sapiens* seems unlikely. Instead, they probably evolved their own unique way of thinking subsequent to the split that allowed them to be a very successful hominin population for several hundred thousand years in Eurasia (also see discussion in Lombard and Högberg, 2021).

Developments in palaeo-neurology highlight both similarities and distinctions between Neanderthal and *Homo sapiens* brain regions. As hominin brain size increased, they generally display a relative flattening in non-modern humans, but Neanderthals display wider superior parietal lobules, with *Homo sapiens* having an even larger parietal lobe expansion resulting in the bulging of the parietal profile and a more rounded skull shape. This bulging is partly caused by the enlargement of the precuneus (e.g., Bruner et al., 2018). *Homo sapiens* fossils with developed parietal bulges are the Skhul 5 cranium at ~130–100 ka (Mercier et al., 1993; Grün et al., 2005), and the Qafzeh 9 cranium at ~120–90 ka (Valladas et al., 1988; Grün and Stringer, 1991), both from Israel in the Levant. Since the ancestors of these individuals originated from Africa, we may accept that the modifications started in African *Homo sapiens* sometime subsequent to their genetic divergence by ~350–260 ka (Schlebusch et al., 2017). Although African *Homo sapiens* fossil crania dating to >100 ka are scarce, we see that the early specimens from Jebel Irhoud and Kabwe lack extensive parietal bulging (Figure 1.3). The Florisbad cranium from South Africa at 260 ka is too fragmented to assess in this respect (Bruner and Lombard, 2020), but by ~160 ka the Herto 1 cranium from Ethiopia clearly shows the bulging trend in some African populations (Pearson 2008; Mounier and Lahr, 2019) (Figure 1.3).

The precuneus is a region that plays a central role in modern human brain organization. For example, it forms part of the default-mode network, amongst others (Margulies et al., 2009). Cognitively, it has strong associations with several traits that, in their enhanced forms, are unique to the human way of thinking today. These include episodic memory, working memory, planning and response inhibition, language network reorganization and verbal fluency, event processing and attention-related neural activity, age-associated executive

FIGURE 1.3 *Homo Sapiens* Fossil Crania >100 ka

function, brain connectivity during associative emotional learning and emotional processing, empathy, theory of mind, social cognition, visuospatial processing and higher grade causal cognition (Bruckner et al., 2008; Laursen et al., 2014; Bruner and Iriki 2016; Sormaz et al., 2018; Gärdenfors and Lombard, 2018; Lombard and Gärdenfors, 2021). There is thus a distinct correlation between the development of the precuneus in *Homo sapiens* and some of the cognitive traits associated with the archaeological record of South Africa from ~100 ka. This record, apart from some aspects of symbolic behaviour, is distinct from that produced by Eurasian Neanderthals before ~50 ka. The different records therefore show contextual adaptive variation, and that Neanderthal-specific cognitive developments deserve more attention, instead of simply being equated to the *Homo sapiens* mind when they display certain forms of complex cognition (Lombard and Högberg, 2021).

For example, Pearce and colleagues (2013) point out that the large Neanderthal brains (sometimes surpassing that of *Homo sapiens* in volume), and variation in parietal lobe shape indicate that they may have had neurological and cognitive specialisations related to visual areas in the occipital lobe that surpassed those of *Homo sapiens*. The parietal expansion in both populations that include the temporal region, in combination with a prefrontal cortex that is modern-like already in *Homo heidelbergensis* (e.g., Robson and Wood, 2008), may account for similarities in symbolic material culture as observed in the archaeological records of both species (also see Henshilwood and Dubreuil, 2011). This may well indicate that in terms of some aspects in our social behaviour the two populations were similar (Zilhão, 2019). Such an interpretation would explain the propensity for genetic admixture between these groups (e.g., Nielsen et al., 2017), and probably also for material culture exchanges (Flas, 2011; Hingam et al., 2014; Lombard and Högberg, 2021).

8 Conclusions

It is not yet certain to which extent the technical, cognitive or genetic developments that happened during our evolution in southern Africa affected the *Homo sapiens* groups that ultimately moved into Eurasia to meet up with the Neanderthals and Denisovans. In this respect, a major challenge is to start understanding population structures throughout Africa during the last 500 thousand years or so by asking:

- When and how did the groups interact with each other?
- How and under what circumstances did they exchange knowledge, technologies and/or genes?

- To which extent did socio-technical frameworks influence the ebb and flow of their techno-behaviours?
- What were their systems for maintaining and controlling resources?
- How did aspects of competition, aggression and territoriality play out amongst groups?
- Did they have structured practises for conflict resolution and risk management?

We can only address these questions with sustained work across the different disciplines, aiming to enrich the various empirical records as well as to improve our theoretical thinking about, and understanding of, the records. Only when we are able to bring the lines of evidence and reasoning together, will we be able to build increasingly robust reconstructions of our diverse, yet shared, human past. Notwithstanding the recent overemphasis on eastern Africa, southern Africa remains the region in Africa with the longest history in human origins research. Not all countries of the region are currently equally represented. This is a result of complex and nuanced circumstances reflected in historical bias, differences in chronological schemes, excavation, analytical and curatorial practices, and in challenging infrastructure and socio-political dynamics.

It is however certain that, whilst sometimes controversial and contested, the cross-disciplinary insight gained into the rich archaeological, fossil and genetic records of southern Africa, forever changed, and are continuously changing, how we think about the origins of our species.

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