The North African Middle Stone Age and its place in recent human evolution

Eleanor M. L. Scerri[1, 2]

[1]Research Laboratory for Archaeology and the History of Art, School of Archaeology, University of Oxford, 36 Beaumont Street, Oxford OX1 2PG, U.K.

[2]Department of Archaeology, Max Planck Institute for the Science of Human History, Jena, Germany.

eleanor.scerri@rlaha.ox.ac.uk

Number of double spaced pages: 47

Number of Tables: 3

Number of Figures: 4

Number of Boxes: 1

Key Words: Out of Africa, symbolic material culture, African Multiregional evolution, Middle Stone Age, North Africa, Human Evolution

This research was supported by a postdoctoral fellowship from the British Academy of Arts and Social Sciences.

ABSTRACT

The North African Middle Stone Age (NAMSA, ~250-24 thousand years ago, or ka) features what may be the oldest fossils of our species as well as extremely early examples of technological regionalization and 'symbolic' material culture. The geographic situation of North Africa and an increased understanding of the wet/dry climatic pulses of the Sahara Desert also show that North Africa played a strategic role in continental-scale evolutionary processes by modulating human dispersal and demographic structure (Drake et al., 2011; Blome et al., 2012). However, current understanding of the NAMSA remains patchy and subject to a bewildering array of industrial nomenclatures that mask underlying variability. These issues are further compounded by a geographic research bias skewed towards non-desert regions. As a result, it has been difficult to test long-established narratives of behavioral and evolutionary change in North Africa and to resolve debates on their wider significance. In order to evaluate existing data and identify future research directions, this paper provides a critical overview of the component elements of the NAMSA and shows that the timing of many key behaviors have close parallels with others in sub-Saharan Africa and Southwest Asia.

Key words: Middle Stone Age, North Africa, human evolution

INTRODUCTION

The North African MSA (henceforth NAMSA) began in Marine Isotope Stage 8 (MIS 8, ~300-245ka) and lasted at least until the end of MIS 3 (~57-30ka), and possibly MIS 2 (~29-15ka) in localized areas. The record is largely known from a small number of moderately deep sequences at coastal and hinterland cave sites, mostly located in Morocco. Only a handful of these dated sites extend into the early NAMSA. Currently, the oldest optically stimulated luminescence (OSL) dating estimates come from Jebel Irhoud in Morocco (~300ka) and Benzu Cave in Ceuta (~250ka) (McPherron et al., *in press*); Ramos et al., 2008). These dates are closely followed by chronometric estimates from the northeast African sites of Saï Island in Sudan and Kharga Oasis in Egypt (both ~220ka) (Hawkins et al., 2001; Van Peer et al., 2003). No continuous record covering the entire chronological range of the NAMSA from MIS 8-3 has yet been discovered. The archaeological record of North Africa is therefore constructed from a mixture of dated sites and spatially dispersed sites with no chronometric dating.

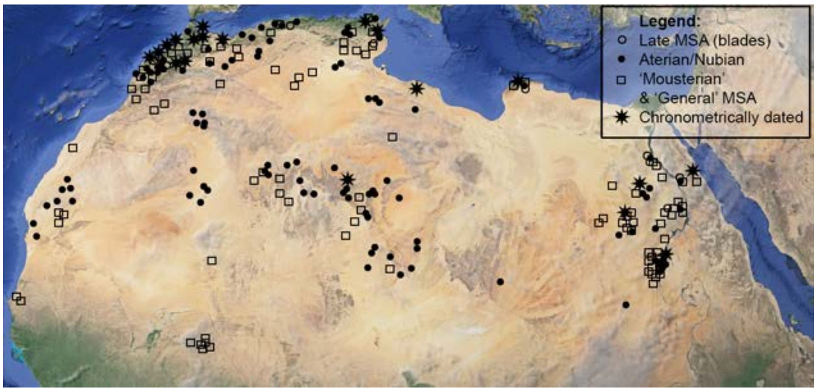

Figure 1: Map of NAMSA sites, marking key chronometrically dated sites and sites assigned to particular industries in the literature. Dense concentrations can be observed in the Maghreb, and to a lesser degree, the Nile Valley, illustrating where research has been most intensively conducted.

The construction of the record is also strongly affected by the terminology historically used to describe it. The NAMSA record is interchangeably described as "Middle

Palaeolithic", which emphasizes Eurasian links, or "Middle Stone Age" (MSA), which emphasizes sub-Saharan African links. While the term MSA is used here to reflect the convention for Anglophone 'African' archaeology, in reality these heuristic divisions break down in North Africa, which forms part of a biogeographically continuous zone including the Arabian, Iranian and Thar Deserts (Groucutt & Blinkhorn, 2013).

Lithics, the most abundant source of material culture from the NAMSA, are also frequently categorized using a range of different industrial nomenclatures. These can be extremely varied, reflecting diverse research traditions and a long-established custom of stamping assemblage groups recovered by different field campaigns with individual names (see Box 1). Therefore, in order to minimize the impact of research history and heuristics on data interpretation, the component parts of the NAMSA record will each be considered in turn, with material culture described in terms of its variability. This is then followed by a re-evaluation of the NAMSA's place in recent human origins.

PALAEOENVIRONMENT

Today, North Africa comprises the Sahara Desert, itself about 25% of the African continent, and the coastal and hinterland regions. These latter non-desert regions consist of Mediterranean forest, mountainous steppe, plateaus, intermontane valleys and rich coastal plains. West of the Gulf of Sirte, these regions are referred to as the Maghreb. East of the Gulf of Sirte to the East, the Jebel Akhdar Mountains of Cyrenaica form a similarly forested and fertile coastal and upland region. In contrast, the Sahara Desert is hyperarid, featuring some of the driest places on earth. However, the Saharan landscape is diverse, consisting of dry mountainous regions, gravel plains, stone plateaus and sand seas (ergs). The only significant currently fertile and well-watered area in the Sahara is the Nile River Valley, which extends across a south- north axis to the Mediterranean Sea.

More disparate opportunities for water in the desert are provided by rare oases fed by underground aquifers. At the southern borders, the desert is bounded by the Sahel, a dry band of tropical savannah.

Today's conditions in North Africa represent a dry phase during the current (Holocene) interglacial, whose warmest period peaked at ~10-8ka. Like the rest of the mid-latitude arid belt, North Africa is subject to dramatic environmental changes primarily linked to eccentricity-modulated precession, which forced variability in low-latitude summer insolation (Drake et al., 2011; Blome et al., 2012). These changes, on orbital timescales, result in a northwards shift of the African monsoon, and when coincident with interglacial periods (regulated by cyclic changes in the earth's orbit), trigger a significant northwards expansion of savannah environments into the Sahara, along with the development of lake and river networks (Figure 3). The interglacial periods associated with the NAMSA are MIS 7 (~243-192ka) and 5e (~130-116ka). During these times, climatic changes were broadly synchronous with those in the Arabian Peninsula and the southern Levant (Drake et al., 2013; Breeze et al., 2016).

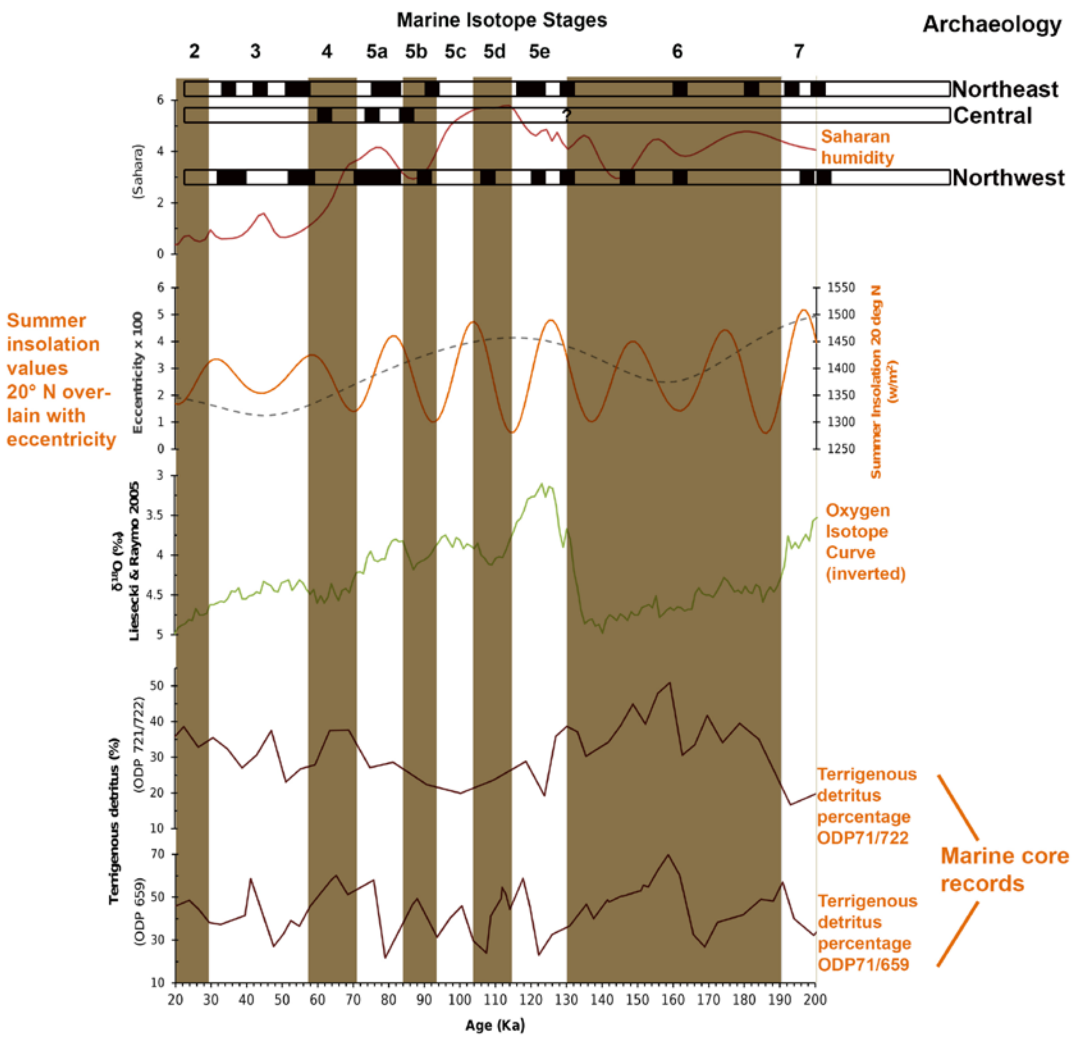

Figure 2: Regional probability density function (PDF) plots for 200-20ka, adapted from Drake et al., 2016 showing the relationship between environmental and human dynamics in the North African MSA. Occupations can be broadly correlated with humid periods, and exceptions are associated with sites in the refugial margins or along the Nile (see also Table 2).

Within these broad climatic cycles, North Africa was also affected by smaller scale fluctuations, at a sub-regional scale (Blome et al., 2012) (Figure 2). For example, brief episodes of heightened humidity within MIS 3 have been identified in the Maghreb, but not yet elsewhere at ~37ka (Drake et al., 2013). Similarly, enhanced Nile flow and humid conditions in northeast Africa and the Levant, but not elsewhere in North Africa, have been identified at ~150ka. Both the Maghreb and the Nile region experienced enhanced humidity between ~180-170ka (Drake et al., 2013, Williams et al., 2015; Breeze et al., 2016). Humid conditions are identified across North Africa at ~138-135ka, and following the Last Interglacial, again between ~105-92ka (MIS 5c) and between ~84-72ka (MIS 5a). Smaller, millennial-scale changes are also apparent (e.g., as Heinrich and Dansgaard/Oeschger events), but their effects on the North African record remain poorly understood.

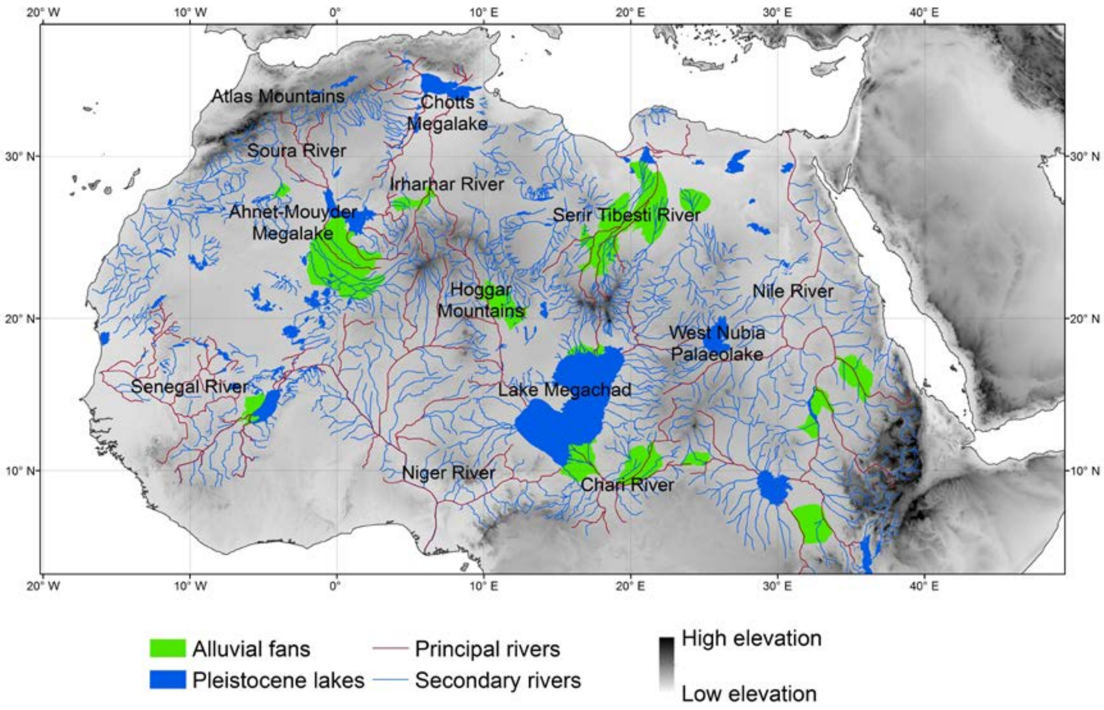

Figure 3: Major lake and river networks identified as active North Africa during the interglacial period, Marine Isotope Stage 5e (from Scerri et al., 2014a). These hydrological networks are likely to have been activated repeatedly during each interglacial period.

Models of vegetation cover suggest that during humid phases, enhanced Mediterranean Westerlies drove the domination of Mediterranean C_3 types in the Mediterranean coastal and hinterland regions, together with plentiful groundwater and moderate temperatures (Castañeda et al., 2009; Breeze et al., 2016). Such models are corroborated by microfaunal studies in Morocco pointing to a relatively humid climate with open grassland and some wooded areas (Stoetzel et al., 2014). Further inland, in the

Mediterranean/Saharan transition zone, the vegetation was a mixed C_3 and C_4 savannah biome during humid periods, with upland regions and areas closer to water likely to have been more densely forested. **Enhanced rainfall at least during the Last Interglacial also activated several major fluvial systems and augmented others (Figure 2, Figure 3), aiding the dispersal of biota from refuge areas outside the Sahara region (Scerri et al., 2014a).** However, palaeoclimate models also indicate that a band of desert continued to exist, representing a gap between intensified Mediterranean Westerlies in the north and the monsoon in the south.

Punctuated humid episodes in the Sahara alternated with periods of varying degrees of aridity. Increased sediment mobility during arid periods has limited the number of detailed climate archives for such times. Extreme hyperarid conditions are thought to have occurred throughout MIS 4 (~71-58ka) and the Last Glacial Maximum (LGM, peaking ~22ka). During these periods it seems likely that even the Nile was reduced to an intermittent seasonal flow (Lamb et al., 2007). Elsewhere in the Sahara, the central mountains remained habitable for longer than the lowland regions during aridification, together with major oases, such as Kharga in the Western Desert (Smith, 2012; Cancellieri & di Lernia, 2013). Further north, Mediterranean Westerlies may have remained relatively stable throughout these environmental fluctuations. However, during hyperarid periods, the Westerlies may have had a more limited impact in the southern Mediterranean, perhaps permitting only the most northerly coastal and hinterland regions of North Africa to remain habitable (e.g., northern Tunisia and the Jebel Akhdar region of Cyrenaica) (Reade et al., 2016). It is unclear whether millennial-scale occupation gaps in the archaeological record at several sites in Morocco indicate patchy habitation or other factors (Jacobs et al., 2012). Microfaunal studies at the same sites have also indicated brief arid conditions during MIS 5 (Stoetzel et al., 2014).

Despite the intensive rainfall required to feed the hydrological systems of North Africa during humid periods such as MIS 5e, the environment would have been strongly seasonal, with a short, pronounced rainy season and a longer dry season. This is the case in today's sub-Saharan savannah belt, reflecting the current most northerly location of the African monsoon system. Today, such pronounced seasonality frequently results in a high degree of environmental risk, particularly drought, if the rains are late or if they fail. Such seasonal fluctuations may partly explain the differing dynamics of an apparently 'arid adapted' (and time-averaged) archaeological record (Garcea, 2012; Scerri, 2013a) and the palaeoenvironmental record of a 'Green Sahara' (Drake et al, 2011).

HUMAN FOSSILS

Human fossil remains from the NAMSA primarily come from cave sites (Table 1). This fossil record is currently limited compared to sub-Saharan Africa and the Levant, and comprises of a significant geographical and chronological range, from at least as early as ~300ka until ~70ka (Table 1). Furthermore, fossils discovered during older excavations often remain undated, and there is variation in the chronological reliability of the dated specimens associated with MSA technology.

Description	**Site**	**Chronology**	**Reference**
Juvenile skeleton, partial loss to weathering, skull preserved	Taramsa Hill	As old as ~69ka, but may be considerably younger if intrusive	Vermeersch et al., 1998 Van Peer et al., 2010
Juvenile maxilla fragment, isolated adult teeth	Mugharet el Aliya	Undated – MIS 5?	Senyurek, 1940
Two fragmentary mandibles, one adult, one juvenile	Haua Fteah	~73-65ka	Douka et al., 2014

1. Mandible	Contrebandiers	1. Undated, associated with "Ouljian breccias" (MIS 5)	1. Vallois & Roche, 1958
2. Occipital and frontal fragments		2. Undated	2. Ferembach, 1976
3. Juvenile skull and partial skeleton		3. ~108ka	3. Balter, 2011
Partial adult skull and associated hemimandible, immature calvaria, mandible, isolated teeth	Dar es Soltane II	~85-75ka	Raynal & Occhietti, 2012
Isolated canine and mandible	Grotte Zourah/El Harhoura 1	?	Débenath, 1980
Parietal fragment	Taforalt	?	Roche, 1953
Seven specimens, principal are two adult skulls (Irhoud 1&2), juvenile mandible (Irhoud 3), juvenile humerus (Irhoud 4)	Jebel Irhoud	~300ka	Richter et al., *in press*

Table 1: Hominin fossils associated with the NAMSA.

The earliest NAMSA-related fossils come from the Middle Pleistocene site of Jebel Irhoud in Morocco (Table 1). These fossils may be the earliest *H. sapiens* fossils in Africa, a group generally characterized by an enlarged cranial capacity, a modern cranial vault, a greater reduction in the size of the supraorbital torus, and a modern face (see Stringer, 2006 for discussion; Richter et al. *in press*). The near complete Jebel Irhoud 1 cranium meets most of these criteria, with the exception of a few archaic features, such as well-developed brow ridges (supraorbital torus, see Rightmire, 2009 and Bräuer, 2012 for discussion). Jebel Irhoud 2 lacks a face, but shows similarities to Jebel Irhoud 1 in terms of having a long, rather than globular (i.e. modern), vault morphology. Differences between Jebel Irhoud 1 and 2 have been ascribed to intra-population variability (see Mbua & Bräuer, 2012).

Late Pleistocene fossils are more abundant. In Morocco, dated fossils represent relatively robust modern humans and span MIS 5-3 (Table 1) (Vallois & Roche, 1958; Hublin, 2001; Balter, 2011; Harvati & Hublin, 2012). All the specimens display morphological similarities and are associated with 'Aterian' technology (see below section on stone tools). Primitive traits associated with this group include a pronounced supraorbital profile, a broad brain case and a strikingly large teeth, which includes the development of traits which added to the overall tooth mass, such as extra crests, distal cuspules, Carabelli's cusp, as well as large, often divided, hypocones on the upper teeth (Hublin, 2000; Hublin et al., 2012). Such traits link the Aterian fossils with the earlier Jebel Irhoud fossils, which have been used to suggest a degree of regional population continuity (Hublin, 2000).

Further east, human fossils are documented at Haua Fteah Cave in MIS 4 (Table 1). Two fragmentary mandibles were discovered associated with the 'Levalloiso-Mousterian' (see below section on stone tools). The first, HF1, is a left ramus and the posterior portion of the left corpus bearing M1 and M2 and the second, HF2 is a juvenile mandibular fragment comprising the same parts as HF1, but with a non-erupted M3 (Hublin, 2000). Both fragments are considered to be *H. sapiens* and although too partial to yield further information, they cluster with the Jebel Irhoud specimens in the character of their differences from contemporary non-African populations (Harvati & Hublin, 2012).

Importantly, they evidence a *H. sapiens* presence in North Africa during the time when Neanderthals were present in nearby areas such as the Levant.

The youngest human fossil that has been proposed as a NAMSA specimen is a juvenile *H. sapiens* from the site of Taramsa Hill (Table 1). However, the dating of this skeleton is not secure. Although a date of ~69ka was proposed, sand from within the skull were dated to an average of 24.3ka and information by which to evaluate results from the dating program (e.g. radial plots) are limited (Van Peer et al. 2010). The apparent association with MSA lithics is also complicated by repeated prehistoric quarrying, as the skeleton was found on top of a layer of extraction debris mixed with MSA artifacts. With these caveats in mind, preliminary observations of the skeleton include the large size of the teeth and their similarity to the Aterian specimens from Morocco. The face has been described as large and apparently prognathic, with some similarities to the Jebel Irhoud fossils (Vermeersch et al., 1998). The humerus shaft also exhibits medio-lateral flattening, a plesiomorphic trait associated with archaic *Homo* juveniles, but present in a clearly *H. sapiens* child.

Unfortunately, further information by which to evaluate the Taramsa child specimen is unlikely to become available. Due to administrative issues, the fossils have not yet been studied in detail and the skeleton itself was mostly lost to weathering. Only the skull and some long bone shafts could be saved, and it is unclear where these fossils are currently stored (Vermeersch et al., 1998). However, it should be noted that a later skeleton from the Nile Valley, dated to ~38ka, also retains some archaic characteristics. Nazlet Khater 2 is associated with an 'Upper Palaeolithic' technology and features a thick cranial vault, prominent zygomatic arches and a powerful masticatory system that is rare in present human populations (Crevecoeur, 2012). Furthermore, particular features of the skeleton (e.g., middle and inner ear structures) place this skeleton at the edge of the variation seen amongst modern humans today, again emphasizing the greater variability of Pleistocene *H. sapiens* in Africa.

The limited fossil evidence from North Africa emphasize broad similarities between the late Middle Pleistocene and Late Pleistocene fossils associated with MSA technology, in contrast to later populations in the region associated with the Later Stone Age (LSA, e.g., the 'Iberomaurusians', see Box 1). The small sample sizes of fossils from the NAMSA, as indeed from elsewhere in Africa during the MSA, prevent any sureties in discussions of nuanced similarity and difference in morphology. With this caveat in mind, from among the Middle Pleistocene fossils, Jebel Irhoud 1 is similar to the *H. sapiens* fossils from Herto and Omo 1 in Ethiopia, in terms of features such as bidacryal and biorbital height (Stringer, 2006). The large and near complete Herto cranium is also similar to Jebel Irhoud 2, once the effects of size are considered (Rightmire, 2009). Large teeth are also observed in in East African specimens, but not in Southern African MSA teeth, suggesting a possible link between populations in North and East Africa (Bräuer, 2012; Hublin et al., 2012).

The Jebel Irhoud and Late Pleistocene human fossils from North Africa have in turn been linked with Late Pleistocene populations in the Levant, at Skhul and Qafzeh, as have other early African *H. sapiens*, such as Aduma in East Africa (Rightmire, 2009). However, as the Levantine sample either represents a rather variable population or two separate ones, it is perhaps not surprising that the few available fossils fall somewhere within that range of the sample. What does appear to be evident is that, across Africa, the overall character of variation amongst early *H. sapiens* is not consistent with a single origin and simple dispersal scenario (Howell, 1999; Hublin, 2000; Gunz et al, 2009, Stringer, 2016), complementing recent whole genome studies (Schiffels & Durbin, 2014).

STONE TOOLS

The NAMSA includes some of the earliest examples of stone tool technological regionalization and amongst the most distinctive lithic forms of the MSA. At present, the lithic record of the NAMSA is primarily described and understood in terms of localized industries and larger technocomplexes (Box 1), defined by Clarke (1968) as loose groupings of assemblages sharing a low degree of technological affinity. Specifically, the NAMSA is typically described as consisting of three major technocomplexes, the 'Aterian', 'Mousterian' and 'Nubian Complex', each of which appear to persist over vast chronological and spatial scales of the NAMSA (Box 1).

Industry Name	**Chronology**	**Distribution**	**Description**
Aterian	~145-30ka	North Africa as far east as the Western Desert. Absent from the Nile Valley.	Traditionally defined by tanged tools, sometimes with bifacial foliates, small Levallois cores and a 'Mousterian' substratum.
Denticulate Mousterian	MIS 5?	Western Desert	A classic 'Mousterian' industry including high frequencies of denticulates.
Generalised MSA	Largely undated	Across North Africa	Levallois or discoidal technology with few or no retouched tools.
Khargan	Unknown (post MIS 5?)	Egypt (Western Desert)	Small Levallois cores and discoidal cores and flakes with high levels of steep, marginal retouch, non-geometric, microlithic forms.
Khormusan	Uncertain, Late MIS 5-4 (~82-62ka)?	Egypt and Sudan	Various Levallois styles, denticulates, burins, use of diverse raw materials.
Levalloiso-	~73-65ka	Haua Fteah cave,	Specific to Haua Fteah. Thought to be a sampling

Mousterian		Cyrenaica	variant of the Pre-Aurignacian (see below).
Lupemban	Uncertain	Conservatively, only central Africa	Bifacially flaked lanceolate points, core axes, backed blades.
Mousterian	~250-30ka	North Africa-wide	Featuring classic Levallois and discoidal technology, side retouched pieces, retouched points, denticulates and notches.
Nubian Complex	From MIS 5	East and northeast Africa	Often defined by the prominent use of the Nubian Levallois reduction method, sometimes with thinned tip points, truncated facetted pieces and a 'Mousterian' substratum.
Nubian Middle Palaeolithic	Undated	Egypt and Sudan	Presence of Nubian Levallois cores, bifacial foliates, high Levallois index, bifaces, abundant side scrapers and low index of 'Upper Palaeolithic' types.
Nubian Mousterian (Type A and Type B)	Undated	Generally found close to the Nile.	Assemblages with low Levallois (incl. Nubian) and blade frequencies, discoidal cores, near equivalent proportions of 'Middle' and 'Upper Palaeolithic' types. Type A has no bifaces, Type B includes bifaces.
Pre-Aurignacian	Likely within MIS 5	Haua Fteah cave, Cyrenaica	Specific to Haua Fteah. Discoidal and classic Levallois cores. Side-scrapers and 'Mousterian points', with some notched forms and rarer blades from a small number of blade cores
Safahan	~62ka	Egypt	Flakes and blades from single platform cores and production of thin Levallois flakes using the 'Safahan' method.
Sangoan	Uncertain	Equatorial and southeastern Africa	Post-Acheulean industry featuring core axes, picks, flakes, and large planes.
Sbaikhian	Undated	Algeria	'Lupemban-like' with thick bifacial foliates, core axes
Taramsan	~55-45ka	Egypt	Blade production from an adapted Levallois system. Argued to represent a transitional industry.

Box 1: Historic *Dramatis Personae* of the NAMSA. As discussed in the text, these industrial names, many of which continue to be used, have obfuscated variability.

These technocomplexes are defined using different systems of categorization (Box 1). The much older Mousterian technocomplex, often described as indistinguishable from the European Mousterian, is widespread (e.g., in the Sahel, see Scerri et al., 2016) and can be reasonably considered as featuring the generic components of the Aterian and Nubian Complex. The localized industries described in Box 1 are variations on these themes and all continue to be perpetuated without statistical rigor and limited chronometric control. **While there is often some empirical basis for the use of these terms (e.g., tanged tools for the Aterian), the matter of defining variability has largely been addressed simply by lumping or splitting pre-existing classificatory systems.**

However, recent quantitative research indicates that similarities and differences do not correlate with named technocomplexes, supporting long-standing observations of technological overlap between them. Instead, quantitatively identified technological clusters correlate with geographic distances and hydrological networks, together mapping onto a patchwork of different ecological zones (Scerri et al., 2014a). For these reasons, this review focuses on the character of technological variability itself rather than descriptions of technological heuristics, with a summary of key technological features at chronometrically dated sites given in Table 2.

Table 2 hereabouts

Technological variability in the NAMSA can be broadly divided into three chronological stages. The first is an early MSA, which preceded MIS 5e, and which on technological terms displays similarities with other regions, such as the Sahel, sub-Saharan and East Africa. The second stage is a mid-MSA that correlates with MIS 5 and tails off into the beginning of MIS 3. This stage features an intense concern with hafting and the emergence of implements so distinctive that they cannot be confused with any other regions of Africa or southwest Asia during this time. In the late MSA, the near sub-continental distinctions observed west of the Nile seem to break down into a myriad of local variants and new technologies from the end of MIS 4. These technologies slowly shift towards an emphasis on the production of blades and microliths.

The earliest known NAMSA emerges at ~300ka at Jebel Irhoud in Morocco and ~250ka at Benzu rockshelter in Ceuta (Ramos et al., 2008; Richter et al., *in press*). At both sites, the lithic assemblages are characterized by side and end scrapers, retouched points, denticulates and Levallois technology. There may be some overlap between the earliest MSA and the latest Earlier Stone Age (ESA) in the region. The ESA at Cap Chatelier has an age in excess of ~200 ka and is characterized at a number of sites in the region by the production of small Levallois flakes alongside handaxes and cleavers (Raynal et al., 2010).

In northeast Africa the late ESA and early MSA converge at <230ka at Saï Island and Kharga Oasis (Hawkins et al., 2001; Van Peer et al., 2003). These dated sites evidence significant technological variability and some overlap with late ESA technology (Van Peer et al., 2003). At Kharga Oasis, preferential and recurrent Levallois cores have been documented (Hawkins et al., 2001). Other, similar sites, may also date to this period. This technology is markedly different to the contemporary site of Saï Island, in northern Sudan, where three MSA layers span from ~223 ± 19ka into MIS 6 (~191-131ka). These layers feature flakes from discoidal and globular cores, low numbers of Levallois cores, abundant core axes (thick bifaces, blunted on the distal end), rare foliates and blades (just two in each case), hammerstones and grinding stones (Van Peer et al., 2003). Broadly similar technology is found at other Middle Nile Valley sites such as Khor Abu Anga, Arkin 8, and Taramsa 1 (Van Peer et al., 2010).

The presence of core axes and foliates has linked Saï Island to the poorly understood 'Sangoan' and 'Lupemban' industries of equatorial Africa (see Box 1). However, core axes and foliates represent a huge taxonomic category over enormous territories of Africa. Such tools are also often heavily dependent on raw material type and package size and should not be assumed to represent cultural 'links' without significant comparative study (Schild, 1998). Elements thought to be indicative of the Lupemban, such as backed flakes and blades are absent, as are elements typical of the Sangoan, such as picks. Together with the observed technological variability and limited number of sites, characterization of the early NAMSA as either similar or different to the early MSA in other regions is premature.

In Morocco, MIS 6 assemblages are similar to the preceding MIS 7 assemblages from Benzu Cave, although no rigorous comparison has yet been published. They have been dated to ~171ka at Ifri n'Ammar. The clearest indication of technological change in the Maghreb region comes with the onset of MIS 5e and the early appearance of tanged tools at Ifri n'Ammar alongside a seemingly unchanged assemblage (Box 1) (Scerri, 2013a).

From MIS 5e, there is generally a marked change in the technology of the North African MSA in the form of new technologies and tool types (Figure 4) (Schwenninger et al., 2010). These new artifacts and the methods used to produce them continue alongside those found in pre-MIS 5 NAMSA assemblages. From MIS 5e, various tanged tools, including points, side and end retouched pieces and knives are found across the Sahara, from the Atlantic coast to the Western Desert of Egypt (e.g., Kharga Oasis, Dakhleh Oasis). Burins and diverse forms of foliate points also appear: in addition to the lanceolates found in northeast Africa at sites such as Saï Island and Kharga Oasis, finely made, elongated and seemingly pressure flaked diminutive forms appear in northwest Africa and southwards, to the central Sahara at Adrar Bous.

Other, more spatially restricted tool types include the so-called 'Y-shaped' tools, currently found only in the Maghreb, with one possible exception at Adrar Bous. Other forms that become common across North Africa include basally thinned tools and shouldered pieces, which together with tanged tools, emphasize a new focus on hafting from MIS 5 onwards (Rots et al., 2010; Scerri 2013b). The flexibility and reliability afforded by hafting may be associated with hunting and processing food in the newly available open grasslands, as well as other factors (discussed below) (Rots et al., 2011; Bouzouggar & Barton, 2012; Hawkins, 2012; Scerri, 2013a, 2013b). Tanged and other basally modified points as well as foliate points vary in size from those that could be considered as arrowheads to the tips of thrusting spears, matching a trend seen elsewhere in Africa during this time (Figure 4).

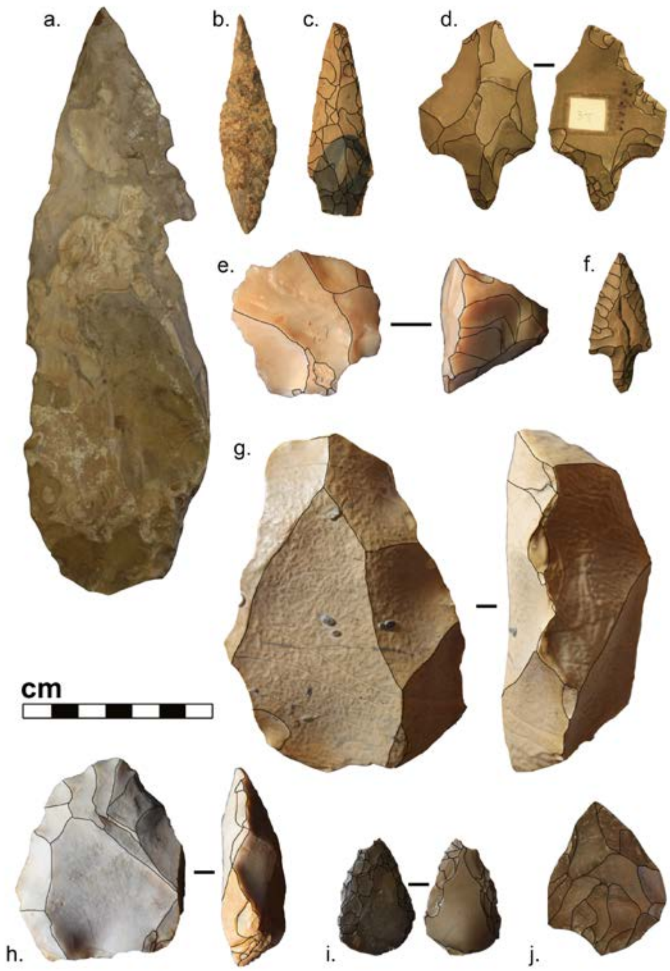

Figure 4: Cores and tools from MIS 5 assemblages. a: Bifacial lanceolate (Kharga Oasis, Egypt); b: bifacial foliate (Tabelbala, Algeria); c: shouldered bifacial foliate (Mugharet el Aliya, Morocco); d: tanged Levallois flake (Adrar Bous, Niger); e: recurrent centripetal Levallois core (Tabelbala); f: tanged, pressure flaked point (Adrar Bous); g: Nubian Levallois core (site 8751, Western Desert); h: centripetal preferential Levallois core (Kharga Oasis); i: bifacially retouched point (site 8708, Western Desert); j: basally thinned points (Kharga Oasis).

In terms of production methods, Levallois reduction generally appear to become more varied in North Africa from MIS 5, featuring centripetal preferential, unidirectional convergent, recurrent bidirectional and centripetal Levallois, and Nubian (or 'beaked') Levallois. Tanged tools were made using any of these techniques as well as non-Levallois and expedient production methods (Scerri 2013b). Although research on cores has been extremely limited, the suggestion that tanged tools are associated with 'small cores' in some areas (see e.g., Bouzouggar & Barton, 2012 for discussion) may be a function of recurrent centripetal reduction, which dominates at a number of NAMSA sites. In any case, similar 'micro Levallois' technology is characteristic of a number of MSA sites across Africa. Nubian Levallois core reduction is also found elsewhere, from at least MIS 5 to 3 in East Africa, South Africa and Asia (Blinkorn et al., 2013; Sahle et al., 2014; Will et al., 2015; Douze & Delagnes, 2016).

In late MIS 5 and early MIS 4, 'Khormusan' sites are present in the Nile Valley. 'Aterian' assemblages are present in the Maghreb at Taforalt and Rhafas Cave, and there are some indications of more humid conditions in this region (Bouzouggar et al., 2007; Mercier et al., 2007; Smith, 2012). However, other investigations elsewhere in the Maghreb have also indicated a lack of occupation during MIS 4 (Jacobs et al., 2012). It therefore seems that occupation in the Maghreb may have been patchier during this time, while allowing for OSL dating error-ranges and preservation.

Very few sites in the rest of North Africa have been dated to MIS 4/3. The current consensus view is that populations contracted back into refuge areas during MIS 4 or became extirpated. In support of this view, assemblages with tanged tools disappeared from most of North Africa. Research in the central Sahara suggests that MIS 4 populations bearing this technology contracted into the central Saharan mountains (see Figure 2) (Cancellieri and di Lernia, 2013). No convincingly dated younger 'Aterian' sites have yet been discovered in the Sahara desert.

The Late NAMSA in MIS 3 features the emergence of new technologies, the disappearance of older ones and the continuation of others established since the

beginning of the NAMSA. Young, MIS 3 dates for tanged tool assemblages come from the non-desert hinterlands of northwest Africa. These range between ~40-20ka, although there are problems with some of the contexts and dating techniques (Wrinn & Rink, 2003; Bouzouggar & Barton, 2012). By the end of MIS 3 (~29ka), tanged tools had disappeared from the NAMSA. No diachronic technological changes within tanged tool assemblages have yet been reported, despite the clear long duration of the use of these tools.

In northeast Africa, changes in lithic technology are documented at a small number of Nile Valley sites. At Taramsa 1 (Activity Phase IV, ~56ka, Activity Phase V, ~41ka), a new blade production system appears, based on a re-organization of the Levallois system (Van Peer et al., 2010). Contemporary assemblages from Nazlet Safaha 1 and 2, also in Egypt, feature a standardized method of Levallois core distal preparation as well as the presence of non-Levallois methods of reduction (see Box 1) (Vermeersch & Van Peer, 2002; Van Peer et al., 2010). Techniques similar to those at Taramsa and Nazlet Safaha have also been reported at Sodmein Cave, near the Red Sea Coast. Further technological entities described for the late MSA in northeast Africa, such as the 'Khargan' (Box 1) have poor chronological and stratigraphic resolution (Clark et al., 2008). Other sites in the region are argued to maintain an unchanged technological character from preceding MIS 5 assemblages (Vermeersch & Van Peer, 2002; Van Peer et al., 2010).

Towards the end of MIS 3, the MSA began to give way to the LSA or Upper Palaeolithic. The term LSA is used here for consistency, and in the context of North Africa is associated with technological changes in the form of blade production, which commence at Haua Fteah at ~40ka (Douka et al., 2014). Microlithic and blade-based industries also emerge elsewhere in northeast Africa. Although poorly dated, these appear to be later than the early examples, which are known only from Haua Fteah and Hagfet ed Dabba in Cyrenaica. At Adrar Bous in the Central Sahara, 'Aterian' MSA assemblages are followed by a hiatus and assemblages described as Epipalaeolithic, such as the 'Ounanian', an industry associated with the early Holocene wet phase (Clark et al., 2008). In the Maghreb, microlithic assemblages appear at ~20ka. A level dating to ~26ka at Sidi Saïd in Tunisia may represent a final 'Mousterian' and the end of the MSA across most of North Africa (Betrouni, 2001), although an even younger MSA (~12ka) has now been documented at the edges of the Sahara in northern Senegal (Scerri et al., 2017).

NON-LITHIC MATERIAL CULTURE

Among the earliest evidence of non-lithic material culture in the NAMSA is found at Saï Island, where it is bracketed to between ~223-182ka (MIS 7). Grindstones, lumps of red and yellow ochre and an apparently anthropogenically flattened limestone slab with pigment traces were found together with the lithic assemblage described in the previous section (Van Peer et al., 2003). Although the earliest such evidence in North Africa, ochre and grindstones are reported together in a number of other MSA contexts, which may suggest a functional association (Tryon & Faith, 2013).

From MIS 5, non-lithic material culture is more abundant. At Nile Valley sites described as 'Khormusan' (Box 1), which date from late MIS 5 to MIS 4, ground hematite pigment, bone tools, and hearths were found associated with the lithics (Marks, 1968). In Morocco, bone tools have been reported at a number of sites in the Temera region (e.g. El Harhoura 1 and 2, El Mnasra) in association with tanged tools (Nespoulet et al., 2008). At some sites, such as Ifri n'Ammar in the Moroccan Rif, bones were stained with hematite or ochre (Richter et al., 2010).

Perforated marine *Nassarius* shells have also been argued to represent personal ornamentation in the form of beads at a number of sites in the Maghreb (d'Errico et al., 2009). Such shells, whether intentionally perforated or not, were collected and transported. They have been found with tanged tool assemblages at five Moroccan and Algerian sites dating to MIS 5 (d'Errico et al., 2009). Three of the Moroccan sites are located 60-40km inland and the Algerian site is located 190km inland, suggesting the presence of networks linking the coastal areas to the non-desert hinterlands. Much further inland, two pierced and partially pierced stones were found at Seggedim in Niger made of quarzitic sandstone, the same raw material as the bulk of the associated 'Aterian' lithic assemblage (Tillet, 1978). Pigments, bone tools and shell 'beads' are argued to represent examples of complex or 'symbolic' behavior. Such behavioral aspects are discussed further in the following section.

Other non-lithic artifacts may represent more pragmatic factors of daily life. At Segeddim, a pile of stones and charcoal were interpreted as a hearth and a further feature described as a fence or palisade (Tillet, 1984). Clark has also argued for a "look out" at Adrar Bous, also in Niger (Clark, 1982). Hearths delimited with stones, as well as open hearths have been reported in Morocco at Taforalt, Dar es Soltane II, El Harhoura I, Chaperon Rouge and El Mnasra (Nespoulet et al., 2008). Ostrich eggshell fragments have been found as several sites, such as at Haua Fteah in Libya, Bir Tarfawi 14 in Egypt, Jebel Irhoud, Rhafas Cave and El Harhoura I and II in Morocco and Ain el Guettar in Tunisia (Clark, 1982; Aouadi-Abdeljaouad & Belhouchet, 2008). Such eggshells may have been used to store water (Steele, 2012). Like the ostrich eggshell, stone balls found associated with tanged tools at the nearby El Guettar spring, may have been used pragmatically. In the case of El Guettar, the stone balls are argued to have formed a platform that facilitated access to a spring. Some of these stone balls are spheroids, resembling others found at Dar es Soltane II (Débenath, 1994).

SUBSISTENCE, BEHAVIOUR AND DEMOGRAPHY

Hunter-gatherers in the NAMSA were extremely seasonally mobile, had a low overall population size and followed increasingly complex and diversified subsistence and social practices. In littoral regions, diverse subsistence strategies include the use of both large game (e.g., gazelles , equids, suids) and small fauna such as birds, tortoises and mollusks (barnacles, oysters, limpets and mussels). In mountainous regions (e.g. Haua Fteah and Ifri n'Ammar), humans preferentially consumed Barbary sheep, particularly during more arid periods. Inland, bovids such as *gazelle* sp. dominate assemblages.

Evidence for subsistence strategies other than animal consumption dates to the early NAMSA. At Saï Island, two limestone slabs associated with the Middle Pleistocene MSA layer were used, together with cobbles, to process siliceous and starchy plant materials (Van Peer et al., 2003). This evidence constitutes some of earliest documented for plant-processing behaviors and may represent a change in the foraging ecology of hominin populations.

From the Late Pleistocene, subsistence strategies become more diversified. Tortoises were consumed at least at El Mnasra and El Harhoura II in Morocco,[21] and there are reports of the probable consumption of birds at a number of sites, most notably at Haua Fteah (doves and partridges) (Steele, 2012; Stoetzel et al., 2014). Various limpets and mussels were found in levels associated with MSA lithics at Benzu Cave, and with tanged tools specifically at Grotte des Contrebandiers, Dar es-Soltane 1, El Harhoura 1, Mugharet el 'Aliya, El Harhoura 2 and Kebibat (Débenath, 1994; Ramos et al., 2008;

Steele, 2012; Stoetzel et al., 2014; Campmas et al., 2016). Marine mollusks were also mentioned as occurring in a similar context at sites along the coast of western Algeria and have been reported as forming dense masses, if not middens, at Haua Fteah in Libya (Steele, 2012). The limited presence of fish bones at some of these sites (i.e. Dar es-Soltane 1 and Mugharet el Aliya) is currently too sparse to determine whether people engaged with fishing practices. There is one report of Mediterranean monk seal bones at Mugharet el Aliya, now unfortunately lost (Steele, 2012).

Further inland, information is more sporadic due to preservation issues. At Bir Tarfawi 14 (BT-14) in the Western Desert of Egypt, animal fossils and stone tools were found together. Gazelles again dominate the assemblage, with complete skeletal parts. Rhinoceros and giraffe were also found, representing dry season deaths around a shrinking pool of water (Gautier, 1993). The association of stone tools and bone clusters may suggest that humans targeted the larger animals in their weakened state while regularly hunting gazelle.

Site-usage appears to reflect diverse activities and longer-term occupations may have been seasonal. Workshops (e.g. site 1033), hunting-stands (e.g. Mugharet el Aliya) and ephemeral occupations (e.g. Contrebandiers) have all been reported, along with 'residential' sites. There is also some faunal evidence for seasonally selective hunting behaviors (Steele, 2012). **Together with raw material transport distances of up to 200km, and shell 'bead' transport distances of 190km, these data show that, NAMSA populations were highly mobile (Clark et al., 2008; d'Errico et al., 2009). Significantly, these distances are comparable to those covered by ethnographically documented hunter-gatherers in arid regions (Kelly, 1995).** Like these modern groups, NAMSA populations may have practiced seasonal patterns of fragmentation and contraction to remaining water sources during the dry season (Clark et al., 2008; Hawkins, 2012). Patterns of mobility may have been more localized in regions of greater resource abundance (Campmas et al., 2016).

A number of different studies indicate that population sizes were low. Arid and semi-arid environments require the exploitation of much larger foraging areas than would be necessary in areas of higher net primary productivity, but the same factors also suppress population growth (Smith, 2013). Limited genetic studies in fact suggest that Late Pleistocene population sizes in North Africa were small (Atkinson et al., 2009). Despite the documentation of recurring, intensive occupations at particular sites, faunal studies also show that carnivores were the primary accumulators of bone (Stoetzel et al., 2014). It is likely that overall population size varied significantly with the arid-humid cycles of the Sahara, indirectly triggering social responses, such as long-distance social networks.

The organization and density of human populations in the landscape is more difficult to determine, but fossil and lithic evidence suggest both a strong degree of population structure within North Africa, and an overall population separation between North Africa west of the Nile and the rest of the continent (discussed further below). While the fossil data has already been discussed, faunal studies show that during MIS 5, the ecological patchwork of corridors and bottlenecks greatly impacted the degree to which some animals were able to disperse, particularly those requiring regular access to water (Drake et al., 2011; Scerri et al., 2014a). The correlation between multivariate technological clusters of MIS 5 stone tool assemblages with distinct North African ecological zones appears to reflect a comparable human patchwork (Scerri et al., 2014a). Specifically, differences between clusters increased with geographical distance in a pattern that would be expected in an isolation by distance model. The only exceptions to this pattern were the similarities observed between sites connected by palaeohydrological corridors. In these cases, sites connected by rivers displayed a greater degree of similarity than sites that were geographically closer, but not connected by rivers, showing how hunter-gatherer groups used the landscape and how they may have become subdivided.

DISCUSSION

The timing of many key behaviors observed in the NAMSA has close parallels with similar behaviors in eastern and southern Africa, as well as Southwest Asia (Table 1), including the emergence of the MSA itself, the use of pigments and long distance transport. The *H. sapiens* fossils from Jebel Irhoud are also the oldest yet known from the entire African continent, and contribute further detail to the morphological mosaic that characterizes the earliest populations of our species. **Evidence from the NAMSA therefore adds to a growing body of evidence suggesting that recent human evolutionary and demographic processes will be revealed in the relationships between diverse African regions**, **rather than within any one of them**. The independence of many parallel behaviors also points to the subdivision of at least cognitively modern populations.

Compared to some regions of sub-Saharan Africa, North Africa appears to have been never more than sparsely populated, although spatial and chronological variation in population density may have been significant (Atkinson et al., 2009; Kim et al., 2014). Such processes may have been critical to the divergence of our species (Richter et al., *in* press). The continuity of material culture in the form of tanged tools also attests to the possible isolation of much of North Africa, and significant population structure across the continent. Palaeoclimate data indicates that during MIS 5, both southern and northern Africa moved towards wetter conditions, in contrast to the areas separating them, which were both more arid and less stable (Blome et al., 2012; Groucutt et al., 2015; Lombard, 2012). The extent to which these features fit with genetic models of the split between African and non-African populations is yet to be tested. However, of note are recent genetic models recognizing the split as a protracted process beginning in Africa at ~150ka and peaking at ~100ka (Scally and Durbin, 2012), potentially via intermediate populations in northern Africa and/or the Middle East, where environmental conditions were synchronous during MIS 5e (Schiffels & Durbin, 2014; Groucutt et al., 2015).

The above genetic models provide lines of evidence that are independent to the archaeological data. As discussed above, quantitative comparisons of whole, non-tanged tool assemblages, controlled for raw material type, site type and ecozone have identified similarities between northeast African assemblages and other contemporary assemblages from northern Arabia (Scerri et al., 2014b). Similarities between these technological constellations and others in East Africa show that the Nile played an important role in dispersal out of Africa. However, the absence of tanged tool assemblages in the Nile Valley and eastwards suggests that at least culturally, the associated toolmakers did not play a role in dispersal out of Africa. The isolation by distance pattern observed for the overall MIS 5 technological structure of the NAMSA may also indicate that tanged tools may have been lost in processes of population fragmentation associated with dispersal. What seems clear is that the *genetic* contribution of these North African populations to those dispersing out of Africa cannot be determined on the basis of stone tools.

Evidence	**North Africa**	**Eastern Africa**	**Southern Africa**	**SW Asia**
Earliest MSA/MP technology	~250ka	~276ka	~279ka	~250ka

Use of pigments	~223-182ka	~284–500 ka	~164ka	~125ka
Plant processing	>182ka	~284–500 ka but not secure	~105ka	~60ka
Earliest *H. sapiens* fossils	~300ka	~195ka	~125ka	~125ka
Earliest MSA/MP unique stone tool regionalization	~145ka	High variability	110-72ka	High variability
Increased diet breadth (i.e. 'shellfishing')	~116ka	~125ka	~164ka	<MIS 5a
Personal ornamentation	~82ka	~40ka	~75ka	~125ka
Bone tools	MIS 5	~65ka	>77ka	None reported
Long distance transport of raw materials (~200km)	MIS 5	MIS 5	~65ka	~150ka

Table 3: Key data characterizing the North African MSA with corresponding dates for the same evidence (where applicable) in eastern and southern Africa and southwest Asia.

The emergence of complex 'symbolic' material culture in North Africa has been linked to the above demographic factors, as it has elsewhere in the continent (Table 3). The concurrent emergence of technological regionalization, extensive use of pigments, bone tools and personal ornamentation in North and southern Africa, as well as the later culture efflorescence in East Africa have been linked to possible isolation and increases in overall population size, triggered by environmental stability and amelioration (Chase, 2010; Blome et al., 2012). However, the 'population size hypothesis' has also been contested in all contexts. In North Africa, where populations appear to have been small, models have so far failed to support a population size increase for the emergence of complex culture (Powell et al., 2009). This is either because of an overall low population size or because population density, rather than overall size, is more relevant to the emergence of complex culture. Environmental risk, such as strong seasonality and prolonged drought, may have also provided the impetus for material culture diversification, as has been demonstrated in other studies (Collard et al., 2013). What the evidence from the NAMSA does contribute to the ongoing debate, is that a greater understanding of the relationship between population structure, density and ecological diversity is required to explain major demographic processes. The emergence of complex culture may correlate with multiple factors, not all of them identical to each other. The early efflorescence of culture in northwest Africa and southern Africa are also removed from the main stage of dispersal out of Africa, questioning the degree to which the two processes should be linked.

Future research must be concerned with plugging knowledge gaps and pursing new lines of inquiry. The former includes typical requirements for more chronometrically dated and spatially representative sites. Currently, 88% of the dated sites come from the coastal and hinterland regions and the Nile Valley, an ecological area currently representing just ~17% of North Africa. Material culture recovered from such new sites must be critically and quantitatively studied, thus avoiding fitting the data into problematic paradigms and systems of nomenclatures.

With respect to new lines of enquiry, major emerging questions concern the debates discussed above, namely: (1) The degree of population persistence versus turnover in the

NAMSA, with particular reference to Middle Pleistocene populations. What was the importance of 'backwaters' as well as refugia in different parts of North Africa for the divergence of our species? Did stable environments afford population isolation and relative sedentism, and did dispersal correlate with pushing mechanisms and major corridors, such as the Nile? (2) Understanding the causes of cultural efflorescence in North Africa from MIS 5. How did population isolation, growth, density and the environment contribute, if at all, to this? (3) The degree of separation between North Africa and the rest of the continent during MIS 5. Why are tanged tool assemblage so unique to North Africa and why do they never extend into the Nile Valley? How far can the unique features of the NAMSA be said to reflect the intra African population separation seen in the genetic data?

Finally, it is critical that the systems of lithic classification often used to described the NAMSA are recognized for what they are: heuristics which do not necessarily reflect the range of technological variability in the NAMSA, nor correlate with specific human populations. Their uncritical use may actively hinder the construction of valid research questions. As lithics are the most abundant source of data from this time period, the systematics and analytics used to describe them is not a niche concern. It is also imperative that explicit, interdisciplinary models are constructed to test the various hypotheses on human behavior in the NAMSA presented here. The range of different types of data makes the NAMSA a rich testing ground for different evolutionary scenarios, which can and must move beyond narrative approaches.

Acknowledgements

I wish to thank two anonymous reviewers, John Shea, Huw Groucutt, Nick Drake, Alex MacKay, Erella Hovers and Manuel Will for discussions and/or feedback on this manuscript. Their input has been invaluable to its development. I also thank the British Academy of Arts and Social Sciences, whose funding supported the production of this research.

Bibliography

Aouadi-Abdeljaouad, N., & Belhouchet, L. (2008). Recent Prehistoric Field Research in Central Tunisia: Prehistoric Occupations in the Meknassy Basin. *African Archaeological Review*, 25, 75-85.

Atkinson, Q., Gray, R.D., & Drummond, A.J. (2009). Bayesian coalescent inference of major human mitochondrial DNA haplogroup expansions in Africa. *Proceedings of the Royal Society B*, 276, 367-373.

Balter, M. (2011). Was North Africa the launch pad for modern human migrations? *Science*, 331, 20-23.

Betrouni, M. (2001). Le paleokarst de Sidi Saïd. Aspects chrono-culturels. In *L'Homme Maghrebin et son environment depuis 100,000 ans* (pp. 101-112). Alger: Centre national des recherches prehistoriques, anthropologiques et historiques.

Blinkhorn, J., Achyuthan, H., Petraglia, M.D., Ditchfield, P. (2013). Middle Palaeolithic occupation in the Thar Desert during the Upper Pleistocene: the signature of a modern human exit out of Africa? *Quaternary Science Reviews*, 77, 233-238.

Blome, M.W., Cohen, A.S., Tryon, C., Brooks, A.S. & Russell, J. (2012). The environmental context for the origins of modern human diversity: A synthesis of regional variability in African climate 150,000-30,000 years ago. *Journal of Human Evolution*, 62, 563-592.

Bouzouggar, A., Barton, R.N.E. & Igreja., A. (2007). A brief overview of recent research into the Aterian and Upper Palaeolithic of Northern and Eastern Morocco. In B. Barich (Ed.), *Tra il Sahara e il Mediterraneo: il Jebel Gharbi (Libia) e l'Archeologia del Maghreb* (pp. 473-488). Edizioni Quasar. Scienze dell'Antichità, Storia Archeologia Antopologia 12.

Bouzouggar, A. & Barton, R.N.E. (2012). The identity and timing of the Aterian in Morocco. In JJ. Hublin, S. McPherron (Eds.), *Modern Origins: A North African Perspective* (pp. 93-105). Dordtrecht: Springer.

Bräuer, G. (2012). Middle Pleistocene Diversity in Africa and the Origin of Modern Humans. In J.-J. Hublin & S. McPherron (Eds.), *Modern Origins: A North African Perspective* (pp 221-240). Springer: Dordrecht.

Breeze, P.S., Groucutt, H.S., Drake, N.A., White, T.S., Jennings, R.P. & Petraglia, M.D. (2016). Palaeohydrological corridors for hominin dispersals in the Middle East ~250-70,000 years ago. *Quaternary Science Reviews*, 144, 155–185.

Campmas, E., Amani, F., Morala, A., Debénath, A. el Hajraoui, M.A. & Nespoulet, R. (2016). Initial insights into Aterian hunter–gatherer settlements on coastal landscapes: The example of Unit 8 of El Mnasra Cave (Témara, Morocco). *Quaternary International*, 413, 5-20.

Cancellieri, E. & di Lernia S. (2013). Middle Stone Age human occupation and dispersals in the Messak plateau (SW Libya, central Sahara). *Quaternary International,* 300, 142-152.

Castañeda, I.S., Mulitza, S., Schefuss, E., Lopes dos Santos, R.A., Sinninghe Damasté, J.S & Schouten, S. (2009). Wet phases in the Sahara/Sahel region and human migration patterns in North Africa. *Proceedings of the National Academy of Sciences of the U.S.A,* 106: 20159–20163.

Caton-Thompson, G. (1952). *The Kharga Oasis in Prehistory*. London: Athlone Press.

Chase, B.M. (2010). South African palaeoenvironments during marine oxygen isotope stage 4: a context for the Howiesons Poort and Still Bay industries. *Journal of Archaeological Science*, 37, 1359-1366.

Clark, J.D., Schultz, D.U., Kroll, E.M., Freedman, E.E, Galloway, A., Batkin, J & Kurashina, K. (2008). The Aterian of Adrar Bous and the Central Sahara. In D. Gifford-Gonzalez (Ed.), *Adrar Bous, Archaeology of a Central Saharan Granitic Ring complex in Niger* (pp. 91-163). Tervuren: Royal Museum for Central Africa.

Clark, J.D. (1982). The cultures of the Middle Palaeolithic/Middle Stone Age. In J.D Clark (Ed.), *The Cambridge History of Africa, Volume I: From Earliest Times to c. 500 BC* (pp. 348-341). Cambridge: Cambridge University Press.

Clarke, D.L. (1968). *Analytical Archaeology*. Methuen, London.

Collard, M., Buchanan, B. & O'Brien, M.J. (2013). Population Size as an Explanation for Patterns in Paleolithic Archaeological Record: More Caution is Needed. *Current Anthropology*, 54, 388-396.

Crevecoeur, I. (2012). The Upper Paleolithic human remains of Nazlet Khater 2 (Egypt) and past modern human diversity. In J.-J. Hublin and S. McPherron (Eds.), *Modern Origins: A North African Perspective* (pp. 205-219). Dordrecht: Springer.

d'Errico, F., Vanhaeren, M., Barton, R.N.E., Bouzouggar, A., Mienis, H., Richter, D., Hublin, J.-J., McPherron, S.P, Louzouet, P. & Klein, R.G. (2009). Additional Evidence on the use of Personal Ornaments in the Middle Palaeolithic of North Africa. *Proceedings of the National Academy of Sciences U.S.A.*, 106, 16051-16056.

Débenath, A. (1980). Nouveaux restes humains ateriens du Maroc. *Comptes Rendus de l'Academie des Sciences de Paris* Series D, 290, 851-852.

Débenath, A. (1994). L'Aterien du nord de l'Afrique du Sahara. *Sahara*, 6, 21-30.

Douka, K., Jacobs, Z., Lane, C., Grün, R., Farr, L., Hunt, C., Inglis, R.H., Reynolds, T., Albert, P., Aubert, M., Cullen, V., Hill, E., Kinsley, L., Roberts, R.G., Tomlinson, E.L., Wulf, S. & Barker, G. (2014). The chronostratigraphy of the Haua Fteah cave (Cyrenaica, northeast Libya). *Journal of Human Evolution*, 66, 39-63.

Douze, K. & Delagnes, A. (2016). The pattern of emergence of a Middle Stone Age tradition at Gademotta and Kulkuletti (Ethiopia) through convergent tool and point technologies. *Journal of Human Evolution,* 91, 93–121.

Drake, N.A., Blench, R.M., Armitage, R., Bristow, C.S. & White, K.H. (2011). Ancient watercourses and biogeography of the Sahara explain the peopling of the desert. *Proceedings of the National Academy of Sciences U.S.A.*, 108, 358-462.
Drake, N.A., Breeze, P. & Parker, A. (2013). Palaeoclimate in the Saharan and Arabian Deserts during the Middle Palaeolithic and the potential for hominin dispersals. *Quaternary International*, 300, 48-61.

Ferembach, D. (1976). Les restes humains Aterien de Temera (Campagne 1975). *Bulletin Memoires de la Societe d'Anthropologie de Paris*, 13, 175-180.

Garcea, E.A.A. (2012). Successes and failures of human dispersals from North Africa. *Quaternary International*, 270, 119-128.

Gautier, A. (1993). The Middle Paleolithic archaeofaunas from Bir Tarfawi (Western Desert, Egypt). In F. Wendorf, R. Schild & A. Close (Eds.), *Egypt during the Last Interglacial* (pp. 121-143). Springer US.

Groucutt, H.S., Petraglia, M.D., Bailey, G., Scerri, E.M.L., Parton, A., Clark-Balzan, L., Jennings, R.P., Lewis, L., Blinkhorn, J., Drake, N.A., Breeze, P.S., Inglis, R.H., Devès, M.H., Meredith-Williams, M., Boivin, N., Thomas, M.G. & Scally, A. (2015). Rethinking the dispersal of Homo sapiens out of Africa. *Evolutionary Anthropology*, 24, 149-164.

Groucutt, H.S. & Blinkhorn, J. (2013). The Middle Palaeolithic in the desert and its implications for understanding hominin adaptation and dispersal. *Quaternary International*, 300, 1-12.

Gunz, P., Bookstein, F.L., Mitteroecker, P., Stadlmayr, A., Seidler, H., Weber, G.W. (2009). Early modern human diversity suggests subdivided population structure and a complex out-of-Africa scenario. *Proceedings of the National Academy of Sciences U.S.A.*, 106, 6094-6098.

Harvati, K. & Hublin J-J. (2012). Morphological continuity of the face in the late Middle and Upper Pleistocene hominins from northwestern Africa – A 3D geometric morphometric analysis. In J.-J. Hublin & S. McPherron (Eds.), *Modern Origins: A North African Perspective* (pp. 179-188). Dordrecht: Springer.

Hawkins, A., Smith, J.R., Giegengack, R., McDonald, M.M.A., Kleindienst, M.R., Schwarcz, H.P., Churcher, C.S., Wiseman, M.F. & Nicoll, K. (2001). New research on the prehistory of the escarpment in Kharga Oasis. *Nyame Akuma,* 55, 8-14.

Hawkins, A. (2012). The Aterian of the Western Desert of Egypt: adaptation to changing climatic conditions? In J.-J. Hublin & S. McPherron (Eds.), *Modern Origins: a North African Perspective* (pp. 157-175). Dordrecht: Springer.

Howell, F.C. (1999). Paleo-Demes, Species Clades, and Extinctions in the Pleistocene Hominin Record. *Journal of Anthropological Research*, 55, 191-243.

Hublin, J.-J., Verna, C., Bailey, T., Smith, T., Olejniczak, A., Sbihi-Alaoui, F.Z. & Zouak, M. (2012). Dental evidence from the Aterian populations of Morocco. In In J.-J. Hublin & S. McPherron (Eds.), *Modern Origins: A North African Perspective* (pp. 189-204). Dordrecht: Springer.

Hublin, J-J. (2000). Modern-nonmodern hominid interactions: a Mediterranean perspective. In O. Bar-Yosef, & D. Pilbeam (Eds.), *The geography of Neandertals and modern humans in Europe and the greater Mediterranean* (pp. 157-182). Peabody Museum: Harvard Univ. Press, Cambridge, MA.

Hublin, J.-J. (2001). Northwestern African Middle Pleistocene hominids and their bearing on the emergence of Homo sapiens. In L. Barham & K. Robson Brown (Eds.), *Human Roots: Africa and Asia in the Middle Pleistocene* (pp. 99-121). Bristol: Western Academic and Specialist Press.

Jacobs, Z., Roberts, R.G., Nespoulet, R., el Hajraoui, M.A. & Débenath, A. (2012). Single-grain OSL chronologies for Middle Palaeolithic deposits at El Mnasra and El Harhoura 2, Morocco: Implications for Late Pleistocene human-environment interactions along the Atlantic coast of northwest Africa. *Journal of Human Evolution*, 62, 377-394.

Kelly, R.L. (1995). *The Lifeways of Hunter-Gatherers: the foraging spectrum*. Cambridge: Cambridge University Press.

Kim, H.L., Ratan, A., Perry, G.H., Montenegro, A., Miller, M. & Schuster, S.C. (2014). Khoisan hunter-gatherers have been the largest population throughout most of modern-human demographic history. *Nature Communications,* 5, doi:10.1038/ncomms6692.

Lamb, H.F., Bates, C.R., Coombes, P.V., Marshall, M.H., Umer, M., Davies, S.J. & Dejen, E. (2007). Late Pleistocene desiccation of Lake Tana, source of the Blue Nile. *Quaternary Science Reviews*, 26, 287–299.

Lombard, M. (2012). Thinking through the Middle Stone Age of sub-Saharan Africa. *Quaternary International*, 270, 140-155.

Marks, A.E. (1968). The Khormusan: An Upper Pleistocene industry in Sudanese Nubia. In F. Wendorf (Ed.), *The prehistory of Nubia, vol. 1* (pp. 315-391). Dallas: Southern Methodist University Press.

Mbua, E. & Bräuer, G. (2012). 20 Patterns of Middle Pleistocene hominin evolution in Africa and the emergence of modern humans. In S.C. Reynolds & A. Gallagher (Eds.), *African Genesis: Perspectives on Hominin Evolution* (pp. 394–422). Cambridge: Cambridge University Press.

Richter, D., Grün, R., Joannes-Boyau, R., Steele, T.E., Amani, F., Rué, M., Fernandes, P., Raynal, J.-P., Geraads, D., Ben-Ncer, A., Hublin, J.-J., McPherron, S.P. (*In Press)*. The age of the hominin fossils from Jebel Irhoud,Morocco, and the origins of the Middle Stone Age. *Nature,* doi:10.1038/nature2233

Mercier, N., Wengler, L., Valladas, H., Joron, J.L., Froget, L. & Reyss, J.-L. (2007). The Rhafas Cave (Morocco): Chronology of the Mousterian and Aterian archaeological occupations and their implications for Quaternary geochronology based on luminescence (TL/OSL) age determinations. *Quaternary Geochronology*, 2, 309-313.

Nespoulet, R., El Hajraoui, M.A., Amani, F., Ben Ncer, A., Débenath, A., El Idrissi, A., Lacombe, J.-P., Michel, P., Oujaa, A. & Stoetzel, E. (2008). Palaeolithic and Neolithic Occupations in the Temara Region (Rabat, Morocco): Recent Data on Hominin Contexts and Behaviour. *African Archaeological Review*, 25, 21-39.

Powell, A., Shennan, S., Thomas, M.G. (2009). Late Pleistocene Demography and the Appearance of Modern Human Behaviour. *Science,* 324, 1298-1310.

Ramos, J., Bernal, D., Dominguez-Bella S, Calado, D., Ruiz, B., Gil, M.J., Clemente, I., Duran, J.J., Vijande, E. & Chamorro, S. (2008). The Benzu rockshelter: a Middle Palaeolithic site on the North African coast. *Quaternary Science Reviews*, 27, 2210-2218.

Raynal, J.-P., & Occhietti, S. (2012). Amino-chronology and an earlier age for the Aterian. In J.-J. Hublin & S. McPherron (Eds.), *Modern origins: A North African perspective* (pp. 79-92). Dordrecht: Springer.

Raynal, J.-P., Sbihi-Alaoui, F.-Z., Mohib, A., El Graoui, M., Lefevre, D., Texier, J.-P., Geraads, D., Hublin, J.-J., Smith, T., Tafforeau, P., Zouak., M., Grün, R., Rhodes, E., Eggins, S., Deaujard, C., Fernandes, P., Gallotti, R., Hossini, S. & Queffelec, A. (2010). Hominid Cave at Thomas Quarry I (Casablanca, Morocco): Recent findings and their context. *Quaternary International*, 223, 369-382.

Reade, H., O'Connell, T.C., Barker, G. & Stevens, R.H. (2016). Pleistocene and Holocene palaeoclimates in the Gebel Akhdar (Libya) estimated using herbivore tooth enamel oxygen isotope compositions. *Quaternary International*, 404, 150–162.

Richter, D., Moser, J., Nami, M., Eiwanger, J. & Mikdad, A. (2010). New chronometric data from Ifri n'Ammar (Morocco) and the chronostratigraphy of the Middle Palaeolithic in the Western Maghreb. *Journal of Human Evolution*, 59, 672-679.

Rightmire, P.G. (2009). Middle and later Pleistocene hominins in Africa and Southwest Asia. *Proceedings of the National Academy of Sciences U.S.A.*, 106, 16046-16050.

Roche, J. (1953). La grotte de Taforalt. *L'Anthropologie*, 57, 375–380.

Rots, V., Van Peer, P. & Vermeersch, P.M. (2011). Aspects of tool production, use, and hafting in Palaeolithic assemblages from Northeast Africa. *Journal of Human Evolution*, 60, 637-664.

Sahle, Y., Morgan, L.E., Braun, D.R., Atnafu, B. & Hutchings W.K. (2014). Chronological and behavioral contexts of the earliest Middle Stone Age in the Gademotta formation, main Ethiopian rift. *Quaternary International*, 331, 6-19.

Scally, A. and Durbin, R. (2012). Revising the human mutation rate: implications for understanding human evolution. *Nat. Rev. Genet.* 13, 745-753.

Scerri, E.M.L., Blinkhorn, J., Niang, K., Bateman, M., Groucutt, H.S. (2017). Persistence of Middle Stone Age technology to the Pleistocene/Holocene transition supports a complex hominin evolutionary scenario in West Africa. *Journal of Archaeological Science Reports* 11, 639-646.

Scerri, E.M.L., Blinkhorn, J., Groucutt, H.S. & Niang, K. (2016). The Middle Stone Age of the Senegal River Valley. *Quaternary International*, 408, 16-32.

Scerri, E.M.L., Drake, N., Jennings, R., Groucutt, H.S. (2014a). Earliest Evidence for the Structure of Homo sapiens Populations in Africa. *Quaternary Science Reviews*, 101, 207-216.

Scerri, E.M.L., Groucutt, H.S., Jennings, R., Petraglia, M.D. (2014b). Unexpected technological heterogeneity in northern Arabia indicates complex Late Pleistocene demography at the gateway to Asia. *Journal of Human Evolution*, 75, 125-142.

Scerri, E.M.L. (2013a). The Aterian and its place in the North African Middle Stone Age. *Quaternary International*, 300, 111-130.

Scerri, E.M.L. (2013b). On the spatial and technological organisation of hafting modifications in the North African Middle Stone Age. *Journal of Archaeological Science*, 40, 4234-4248.

Schiffels, S. & Durbin, R. (2014). Inferring human population size and separation history from multiple genome sequences. *Nature Genetics* 46, 919-925.

Schild, R. (1998). Comment to Van Peer, The Nile Corridor and the Out-of-Africa Model An Examination of the Archaeological Record. *Current Anthropology*, 39, S134-S135.

Schwenninger, J.-L., Collcutt, S.N., Barton, R.N.E., Bouzouggar, A., el Hajraoui, M.A., Nespoulet, R., Débenath, A. & Clark-Balzan, L. (2010). A new luminescence chronology for Aterian cave sites on the Atlantic Coast of Morocco. In E.A.A. Garcea (Ed.), *South-Eastern Mediterranean Peoples Between 130,000 and 10,000 Years Ago* (pp. 18-36). Oxford: Oxbow Books.

Senyurek, M.S. (1940). Fossil Man in Tangier. *Papers of the Peabody Museum of American Archaeology and Ethnology XVI*. Peabody Museum, Massachusetts.

Smith, J.R. (2012). Spatial and Temporal Variation in the Nature of Pleistocene Pluvial Phase Environments Across North Africa. In J.-J. Hublin & S. McPherron (Eds.), *Modern Origins: A North African Perspective*, (pp. 35-47). Dordrecht: Springer.

Smith, M. (2013). *The Archaeology of Australia's Deserts*. Cambridge: Cambridge University Press.

Steele, T. (2012). Late Pleistocene human subsistence in Northern Africa: the state of our knowledge and placement in a continental context. In J.-J. Hublin & S. McPherron (Eds.), *Modern Origins: A North African Perspective* (pp. 107-126). Dordtrecht: Springer.

Stoetzel, E., Campmas, E., Michel, P., Bougariane, B., Ouchaou, B., Amani, F., el Hajraoui, M.A. & Nespoulet, R. (2014). Context of modern human occupations in North Africa: Contribution of the Témara caves data. *Quaternary International* 320, 143-161.

Stringer, C. (2006). The origins of modern humans 1984-2004. In H. Soodyall (Ed.), *The Prehistory of Africa: Tracing the Lineage of Modern Man* (pp 10-20). Johannesburg & Cape Town: Jonathan Ball Publishers.

Stringer, C. (2016). The origin and evolution of *Homo sapiens*. *Philosophical Transactions of the Royal Society* B, 371, 20150237.

Tillet, T. (1978). Présence de pendeloques en milieu Atérien au Niger Orientale. *Bulletin de Société Préhistorique Française*, 75, 273-275.

Tillet, T. (1984). The Aterian Site of Seggedim. *Palaeoecology of Africa and the Surrounding Islands*, 16, 301-304.

Tryon, C. & Faith, J.T. (2013). Variability in the Middle Stone Age of East Africa. *Current Anthropology*, 54,234-254.

Vallois, H.V. & Roche, J. (1958). La mandibule acheuléenne de Temara. *Comptes-Rendus de l'Académie des Sciences de Paris*, 246, 3113–3116.

Van Peer, P., Fullagar, R., Stokes, S., Bailey, R.M., Moeyersons, J., Steenhoudt, F., Geerts, A., Vanderbeken, T., De Dapper, M. & Geus, F. (2003). The Early to Middle Stone Age Transition and the Emergence of Modern Human Behaviour at site 8-B-11, Saï Island, Sudan. *Journal of Human Evolution* 45, 197-193.

Van Peer, P., Rots, V. & Vroomans, J.-M. (2004). A story of colourful diggers and grinders: The Sangoan and Lupemban at the site 8-B-11, Saï Island, Northern Sudan. *Before Farming*, 3, 1-28.

Van Peer, P., Vermeersch, P.M. & Paulissen E. (2010). *Chert Quarrying, Lithic Technology, and a Modern Human Burial at the Palaeolithic Site of Taramsa 1, Upper Egypt* (Egyptian Prehistory Monographs, vol. 5.). Leuven: Leuven University Press.

Van Peer, P. (1998). The Nile Corridor and the Out-of-Africa Model An Examination of the Archaeological Record. *Current Anthropology*, 39, 115-140.

Vermeersch, P.M., Paulissen, E., Stokes, S., Charlier, C., Van Peer, P., Stringer, C. & Lindsay W. (1998). A Middle Palaeolithic Burial of a modern human at Taramsa Hill, Egypt. *Antiquity*, 72, 475-84.

Vermeersch, P. & Van Peer, P. (2002). Conclusions on the Palaeolithic chert extraction in Egypt. In P. Vermeersch P. (Ed.), *Palaeolithic Quarrying Sites in Upper and Middle Egypt* (pp. 353-360). Leuven: Leuven University Press.

Will, M., MacKay, A. & Philips, N. (2015). Implications of Nubian-Like Core Reduction Systems in Southern Africa for the Identification of Early Modern Human Dispersals. *PLoS One*, doi: 10.1371/journal.pone.0131824

Williams, M.A.J, USaï, D., Salvatori, S. & Williams, F.M. (2015). Late Quaternary environments and prehistoric occupation in the lower White Nile valley, central Sudan. *Quaternary Science Reviews*, 130, 72-88.

Wrinn, P.J. & Rink, W.J. (2003). ESR Dating of Tooth Enamel from Aterian Levels at Mugharet el 'Aliya (Tangier, Morocco). *Journal of Archaeological Science*, 30, 123-133.