Article:

Scerri, E.M.L., Blinkhorn, J., Niang, K. et al. (2 more authors) (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. pp. 639-646. ISSN 2352-409X

https://doi.org/10.1016/j.jasrep.2017.01.003

Persistence of Middle Stone Age technology to the Pleistocene/Holocene transition supports a complex hominin evolutionary scenario in West Africa

Eleanor M.L. Scerri[a*], James Blinkhorn[b], Khady Niang[c], Mark D. Bateman[d], Huw S. Groucutt[a]

[a] Research Laboratory for Archaeology and the History of Art, University of Oxford, Oxford, OX1 3QY, UK

[b] Department of Archaeology, Max Planck Institute for the Science of Human History, Kahlaische Strasse 10, 07745 Jena, Germany

[c] Department of History, Faculty of Arts and Humanities, Cheikh Anta Diop University, BP.5500 Fann/Dakar, Senegal

[d] Department of Geography, Winter St., University of Sheffield, Sheffield, S10 2TN, UK

* Corresponding author email address: eleanor.scerri@rlaha.ox.ac.uk

Abstract:

The evolutionary origins of *Homo sapiens* and associated behavioural changes are increasingly seen as complex processes, involving multiple regions of Africa. In West Africa, Terminal Pleistocene/Holocene aged human fossils, demonstrating the late continuity of archaic morphological features in the region have been linked to models of surprisingly recent admixture processes between late archaic hominins and *H. sapiens*. However, the limited chronological resolution of the archaeological record has prevented evaluation of how these biological records relate to patterns of behaviour. Here, we provide a preliminary report of the first excavated and dated Stone Age site in northern Senegal which features the youngest Middle Stone Age (MSA) technology yet documented in Africa. Ndiayène Pendao features classic MSA core axes, basally thinned flakes, Levallois points and denticulates mostly made from chert. Similar technological features characterise several, larger surface sites in the vicinity. From this, it is postulated that populations using 'anachronistic' technologies in the Lower Senegal Valley around the transition to the Holocene may have been widespread, in sharp contrast to other areas of Senegal and West Africa. The chronology and technology of Ndiayène Pendao provides the first cultural evidence to support a complex evolutionary history in West Africa. This is consistent with a persistently high degree of Pleistocene population substructure in Africa and the spatially and temporally complex character of behavioural and biological evolution.

Keywords: West Africa; Middle Stone Age archaeology; lithic technology; Pleistocene-Holocene transition; human evolution

1. Introduction

Evolutionary and palaeoenvironmental processes in the West African Pleistocene are extremely poorly understood, limiting assessments of the pan-African demographic complexity now invoked in models of the origin of *Homo sapiens* (Gunz et al., 2009; Scerri et al., 2014 ; Veeramah and Hammer, 2014; Groucutt et al., 2015). This notwithstanding, genetic patterns consistent with late *H. sapiens* and African archaic admixture in West Africa and the regional persistence of 'archaic' morphological features into the Holocene, indicate that the transition to 'anatomical modernity' was complex and long-lasting in West Africa (Hammer et al., 2011; Harvati et al., 2011; Mendez et al., 2013).

The potential for material culture to shed light on these complex evolutionary patterns in West African populations is significant. Material culture is both abundant and a product of learned traditions as well as other factors (e.g. environmental influences) and therefore subject to selective processes affected by the structure and evolutionary dynamics of the population producing it. However, little is known about the Pleistocene archaeology of West Africa. In view of this, a new programme of fieldwork was initiated to map patterns of cultural variability in the Senegal region of West Africa, commencing with the Lower Senegal region (Scerri et al., 2016).

The Lower Senegal River straddles the boundary between the present-day xeric Sahelian savannah to the north and more wooded western Sudanian savannah to the south and links today's arid northwest African coast to the tropical forest interior. Early research in the Lower Senegal Valley established a relative framework of geomorphological activity as well as the presence of Middle Stone Age (MSA) sites (Michel 1973). Here, we report the preliminary results of archaeological, geomorphological and chronometric analyses from Ndiayene Pendao, the first directly dated excavated Pleistocene archaeological site in the Lower Senegal Valley.

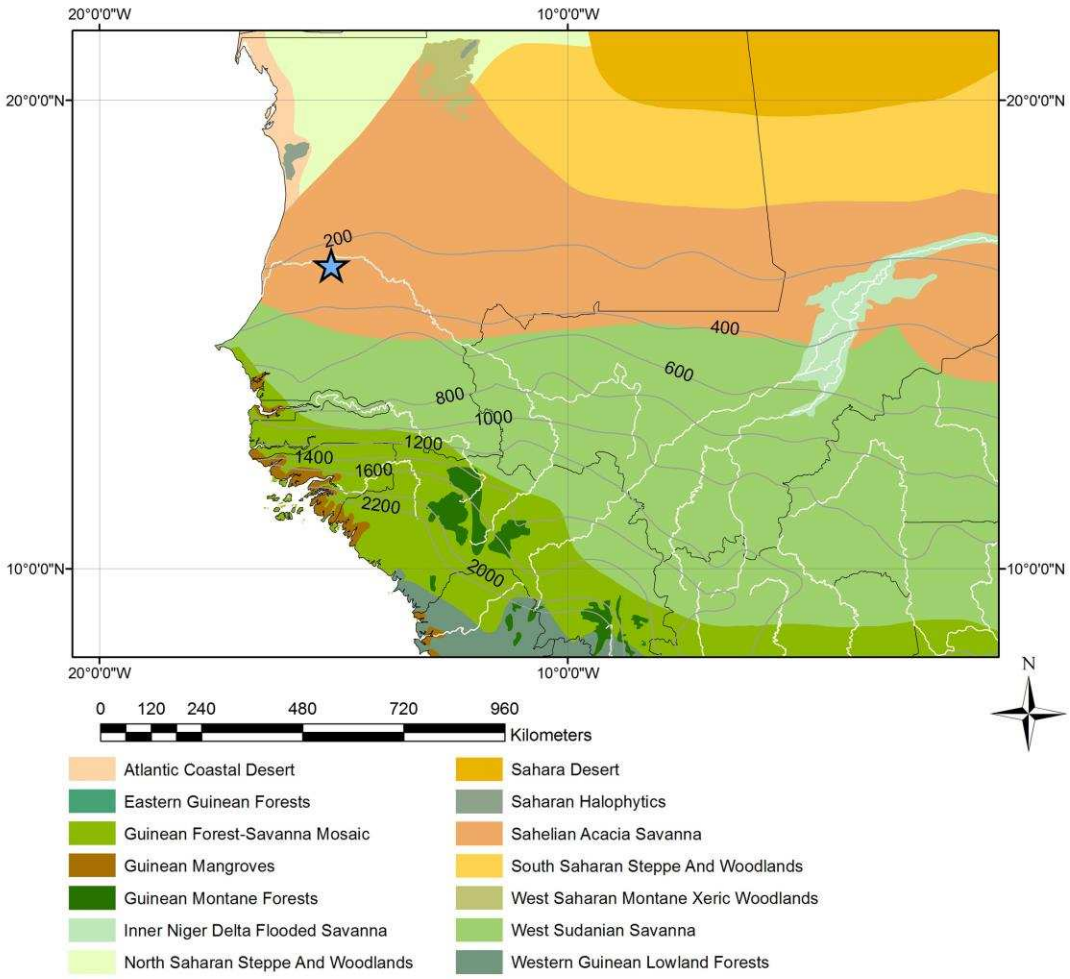
2. Ndiayène Pendao

The Ndiayène Pendao quarry (N16° 29’ 03.6”, W15° 02’ 54.4”) is located near Saint-Louis, northern Senegal, and is situated 10 km south of the modern course of the Senegal River, which forms the border with Mauritania (Figures 1 and 2) . The site is located at the edge of the Ferlo, the low-relief Neogene sandstone plateau (＞10 above mean sea level), not far from the Walo, which comprises the modern alluvial plains (＜10 m above mean sea level) (Figure 1b). Ferralitic alteration of the Neogene sandstones throughout the Senegal basin occurred during the Pliocene, leading to the widespread appearance of iron-crust formations in the Senegal Valley, structured as three discrete terrace formations (Michel 1973; Dubosc and Camara 1986; Conrad and Lappartient 1987; Lang et al. 1990). Following the cessation of weathering in the Early Quaternary, iron crust deposits began to be eroded, and dismantled iron crust deposits have become reworked as sediments (Michel 1973; Scerri et al. 2016) (Figure 2).

Terminal Pleistocene and Holocene alluvial and aeolian deposits cover much of the landscape in the lower course of the Senegal River, with the former including dismantled iron crust products mixed with fluvial sediments and quartz gravels. Ndiayène Pendao, however, marks a rare example of an outcrop of in situ iron crust in the lower Senegal valley, corresponding to the “basse terrace” identified by Michel (1973). This outcrop comprises pale reddish purple ferricrete deposit, displaying bleaching zones, that is eroding as gravels, boulders and large blocks. This is overlain by a further in situ indurated, dark purple iron crust horizon, set back slightly from the existing erosional front.

These in situ horizons are overlain by dismantled ferricrete nodules, which predominately appear cemented within an iron rich matrix as a result of Late Pleistocene pedogenic processes. Discrete pockets of calcareous clays are observed within the cemented horizon of ferricrete nodules closer to the course of the river at Ndiayene Pendao, suggesting that the iron crust outcrop may have supported pools of water away from the main channel during humid phases of the Late Pleistocene. Less cemented deposits of ferricrete nodules comprise the upper surface of the iron crust outcrop, formed of a thicker deposit of larger nodules (＜10mm) grading into the cemented deposits below, and an upper horizon of fine nodules (＜5mm). These deposits have been repeatedly associated with MSA artefacts both in the past (Bessac 1955; Michel 1973; Camara and Duboscq 1986) and through our own research (Scerri et al. 2016). A minimal aeolian sand caps the iron crust outcrop at Ndiayene Pendao, with more varied thickness evident along the ~4.5km iron crust outcrop.

Our study site occurs in a slightly raised position in the immediate landscape, accentuated when recent aeolian deposits are ignored. The site’s topographic position alongside the absence of mixing with other fluvial sediments and clasts, as observed elsewhere in the lower Senegal valley, makes the introduction of dismantled iron crust products at Ndiayene Pendao through fluvial processes an unlikely explanation of the formation history at the site. Rather, we suggest that the iron crust outcrop has been more gradually deflated through sheetwash episodes, resulting in the gradual creep of ferricrete nodules across the landscape.



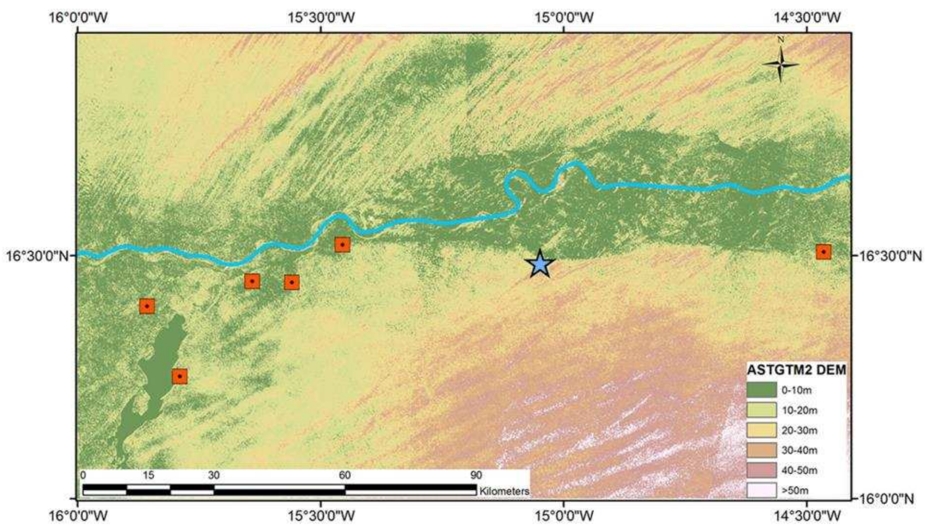


Figure 1: Top (a): Map illustrating the location of Ndiayène Pendao (blue star) in the Lower Senegal Valley in relation to the West African fluvial network, modern precipitation (isohyets in mm/year) and patterns of modern ecology (WWF Ecozones following Olson et al., 2001); Middle (b): Digital elevation map showing the position of Ndiayène Pendao in the Lower Senegal Valley and similar MSA –type sites (marked as red boxes, see Scerri et al., 2016).

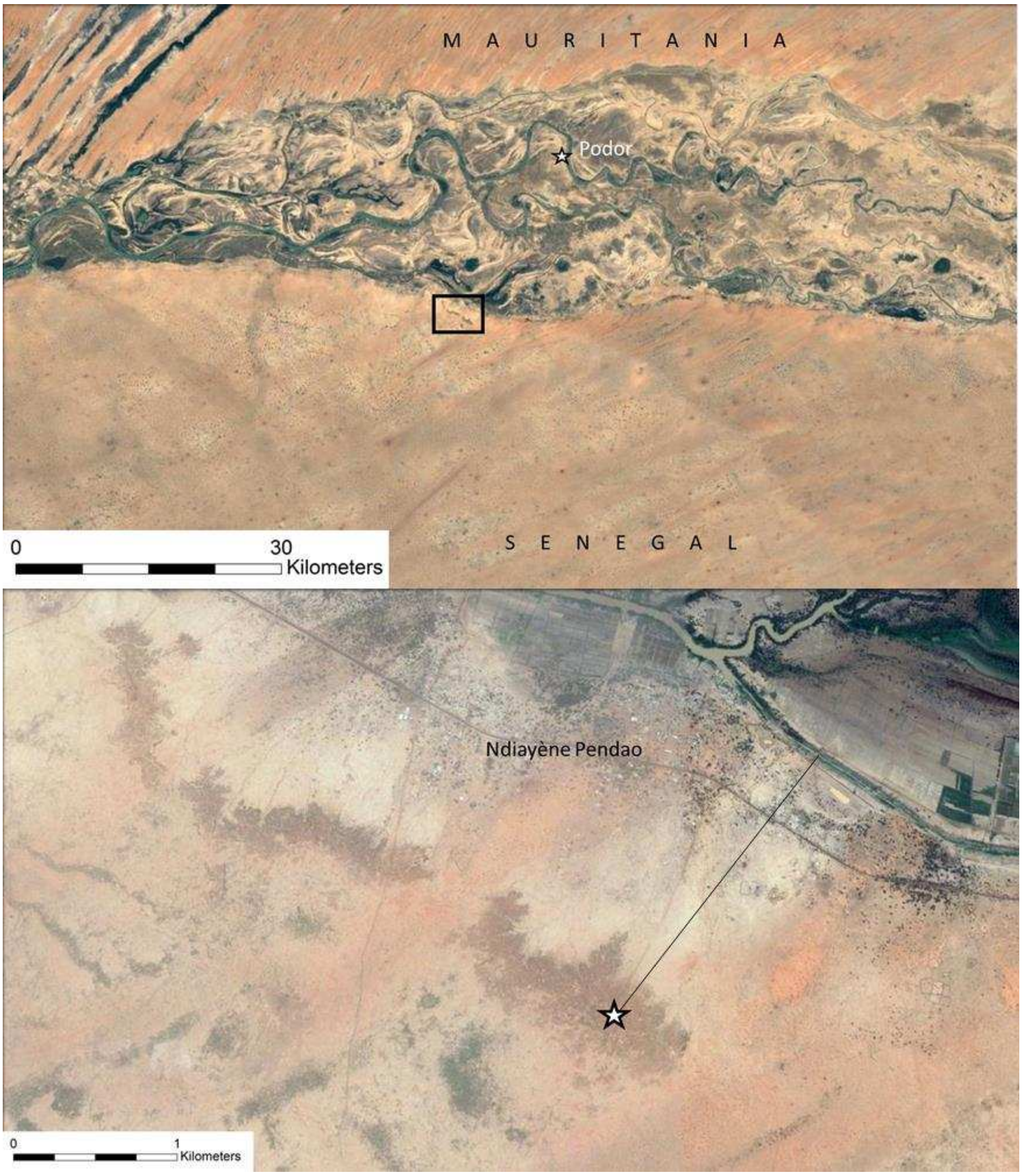


Figure 2: Satellite images of Ndiayene Pendao illustrating the presence of a distinct iron crust outcrop, visible as a NW-SE aligned dark reddish brown linear exposure, partially covered by SW-NE aligned linear dune systems (Photos © Google 2016). The study site is marked by the star in the lower picture, with a black line identifying the survey transect shown in the schematic stratigraphy shown in Figure 3.

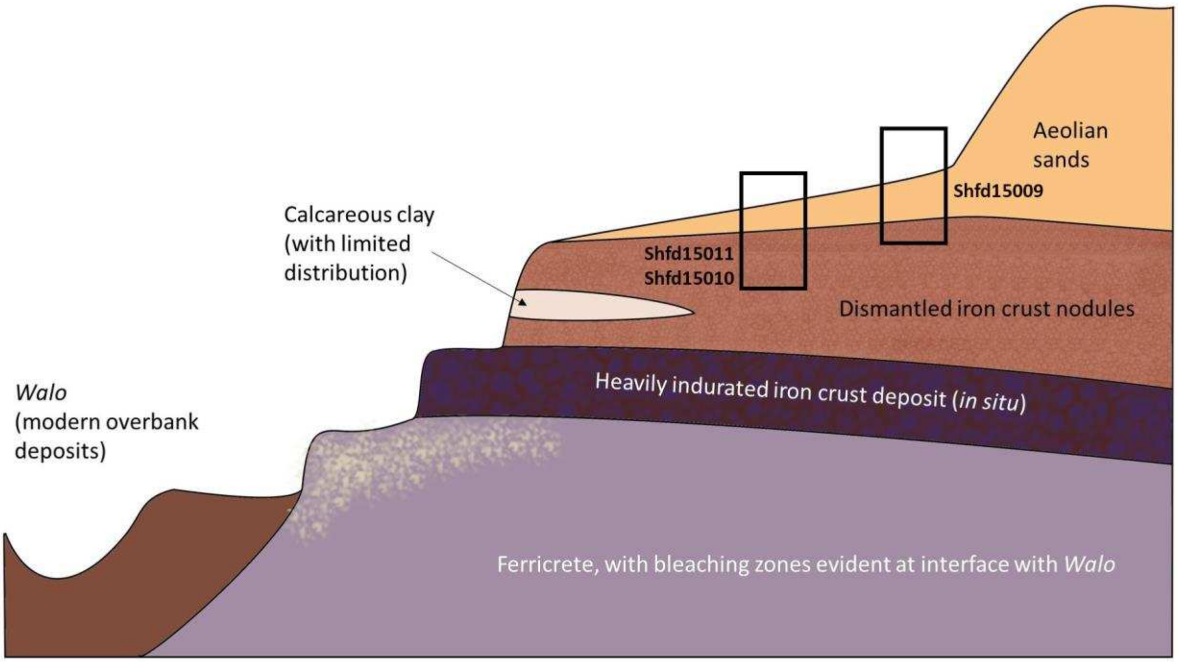


Figure 3: Schematic diagram of sediment deposits at Ndiayène Pendao identified on transects between the modern alluvial plains of the Senegal River and local topographic highpoint provided by sand dune cover, illustrating the relative location of dated sequences with respect to other sediment horizons (not to scale). Lateral scale ~5km, vertical scale ~50m. Black boxes represent excavated section samples for luminescence dating with luminescence sample codes shown.

Through systematic survey of exposed sediment sections and quarry spoil, spatially restricted concentrations of lithic artefacts were identified (see below). Survey across the rest of the quarry revealed no further artefacts and local workers maintained that only discrete concentrations of chert pieces occurred. We subsequently conducted shallow excavations (ca. 0.5m depth) at Ndiayène Pendao, targeting three concentrations of stone tool find spots (see below). The common sediment profile at the excavation sites comprised: (a) a pseudoconglomeratic ferricrete nodular facies, with decreasing nodular bridging upwards in the sediment profile; overlain by (b) a purple-brown pseudo-pisolitic deposit of indurated ferricrete nodules with concentric rinds, which are the reworked products of dismantled iron crust horizons, supporting a coarse sandy matrix with a thin upper horizon (~15cm) of small nodules (<5mm) overlying a thicker deposit (~30cm) of coarser nodules (<10 mm); capped with (c) friable aeolian sand deposits.

In all cases, excavations located lithic artefacts within the upper levels (0.05-0.2 m) of the pisolitic deposits, and no evidence for archaeological finds deflated on top of the iron crust surface were observed across the landscape, indicating that all artefacts recovered share a common stratigraphic provenance. All lithic artefacts recovered through excavation were significantly larger than the ferricrete nodules, most appearing in fresh condition with no indication of significant weathering or rolling. The lack of comparable size sorting between ferricrete nodules and lithic artefacts further supports interpretation that the dismantled iron crust products have not been introduced to the site by significant fluvial activity, favouring only limited mobility within the immediate landscape. Rather, we suggest that the lithic artefacts have undergone minimal disturbance from their place of discard, and became buried by ferricrete nodules through repeated, low energy sheetwash events that had limited capacity to mobilise the larger lithic artefacts but led to a gradual creeping of the smaller nodules. While this could have resulted in winnowing out of flaking debris of a similar size to the ferricrete nodules (i.e. <10mm), it is unlikely to have significantly mobilised larger artefacts that preserve more diagnostic technological traces. Such episodes of instability of the surface of dismanted iron crust deposits are likely to have occurred during periods of heightened climatic flux, when sand sheet or dune cover was unable to stabilise on the surface and highly seasonal precipitation enabled mobilisation of nodular deposits.

3. Lithic Technology

166 lithic artefacts were recovered from Ndiayene Pendao. All the artefacts came from a buried context. However, many artefacts had been recently dug out by quarrying activities, and were collected from fresh spoil heaps by the edges of shallow hand-dug quarry pits. Survey of the quarry area showed that artefacts were only present in a spatially restricted area of ~15m x ~12m in a topographic high point, most of which had been quarried. Excavation in three test trenches extending quarry pits at these locations led to the discovery of 32 buried lithic artefacts (see Tables 1 and 2). To evaluate whether artefacts whose excavation we supervised and those excavated through quarrying activities comprise part of the same technological system, we performed Multidimensional Scaling with the Gower metric using a suite of techno-morphological attributes (Table S1).The results, which can be seen in Figure 4, show that there are no differences between the groups across a range of techno-morphological attributes, supporting our analysis of them as a single assemblage recovered from the same buried deposits.

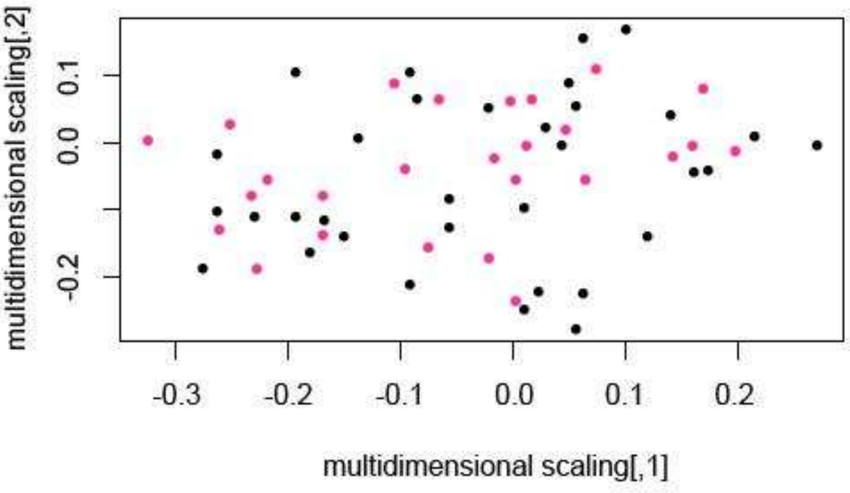


Figure 4: Multidimensional scaling using the Gower metric of whole surface (marked by black circles) and buried artefacts (marked by pink circles) showing no separation between the groups. See Table S1 for attributes measured.

The artefacts are mostly made from chert (54%), grading into silicified limestone (38%). A small number of artefacts were made from quartzite (8%). The source of the raw material was no identified. However, the typically small size of the artefacts and the presence of rounded cortex suggests that good quality chert river cobbles were being sourced for flaking. Of the lithics recovered, 9% were small debitage flakes (<2cm), including chips and chunks, and 34% of the assemblage was broken in some way (e.g., core fragments, distal flake fragments). Of the complete flakes, the average length was 4cm, with a median weight of 11g, reflecting the small and highly reduced nature of assemblage (Table 1 & 2).

Variable	**Mean**	**Standard deviation**
EPA (degrees)	68.6	13.8
Length (cm)	4.2	16.3
Width (cm)	3.3	12.1
Thickness (cm)	1.1	5.9
Weight (g)	23.4 (median)*	51
Platform Width (cm)	2.3	12.9
Platform Thickness (cm)	0.9	5.8
Cortex (%)	8	19.2

Table 1: Summary statistics of basic flake/tool variables.*Median weight given in text due to the highly skewed (right tailed) shape of the data and high standard deviation.

	Trench 1	Trench 2	Trench 3	Quarry Spoil
Core				24

Levallois Core		1		10
Core Tool				2
Flake	4	10	14	84
Levallois Flake			2	4
Retouched Flake				3
Retouched Levallois Flake			1	
Retouched Point				1
Chunk/Fragment				6

Table 2: Typological description of assemblage with counts and provenance information.

In terms of shape, the assemblage is dominated by small, largely oval shaped flakes with very little cortex (Figure 5). There is no significant difference in the amount of cortex on core management elements and flakes ($p = 0.001$), and the core management elements, although larger than the flakes, overlap in size (Figure 5). Together with the fact that larger flakes were re-used as cores, these features indicate that, while flaking occurred at the site, primary decortification took place elsewhere and the site represents a secondary and perhaps final stage of flaking. The location of the site at a topographic high point and the mixture of small elements, including chips and chunks, representing a post-decortification reduction sequence robustly indicates that the assemblage is broadly *in situ*.

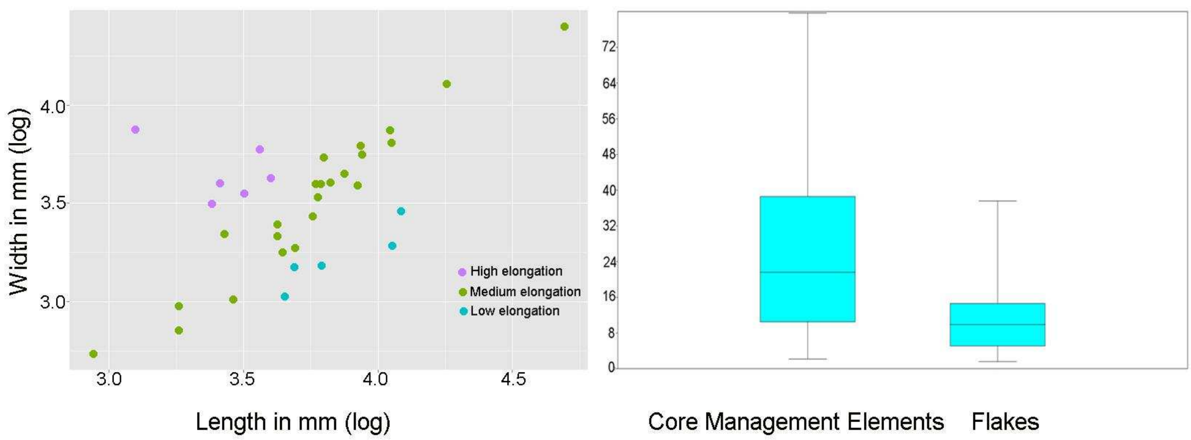


Figure 5: Flake elongation (left); Weight in grams by core management elements and flakes (right).

The Ndiayène Pendao assemblage displays a MSA (typically ~300-30 ka, see McBrearty and Brooks, 2000) technological structure. Technologically, Ndiayène Pendao primarily features Levallois reduction methods (Figure 6, d-e, Figure 7), alongside the production of simple blades from single and multiplatform cores. Levallois methods appear to be employed on chert for the production of points (unidirectional convergent methods) and flakes (centripetal preferential). Levallois products feature finely faceted platforms with an average of seven facets. Non-Levallois chert flakes were on average more laminar, with plain platforms and typically unidirectional scar patterns. A few large limestone and quartzite flakes also form part of the assemblage. These large flakes have all been subsequently used as cores. Together with the small size of the cores, these 'flaked flakes' indicate a high degree of reductionintensity. As discussed above, the presence of flake debitage, core management flakes (e.g., débordant flakes, core tablets) and a hammerstone indicates that flaking took place on site. The small number of unbroken Levallois products (n = 2) suggests that these artefacts were taken away from the site.

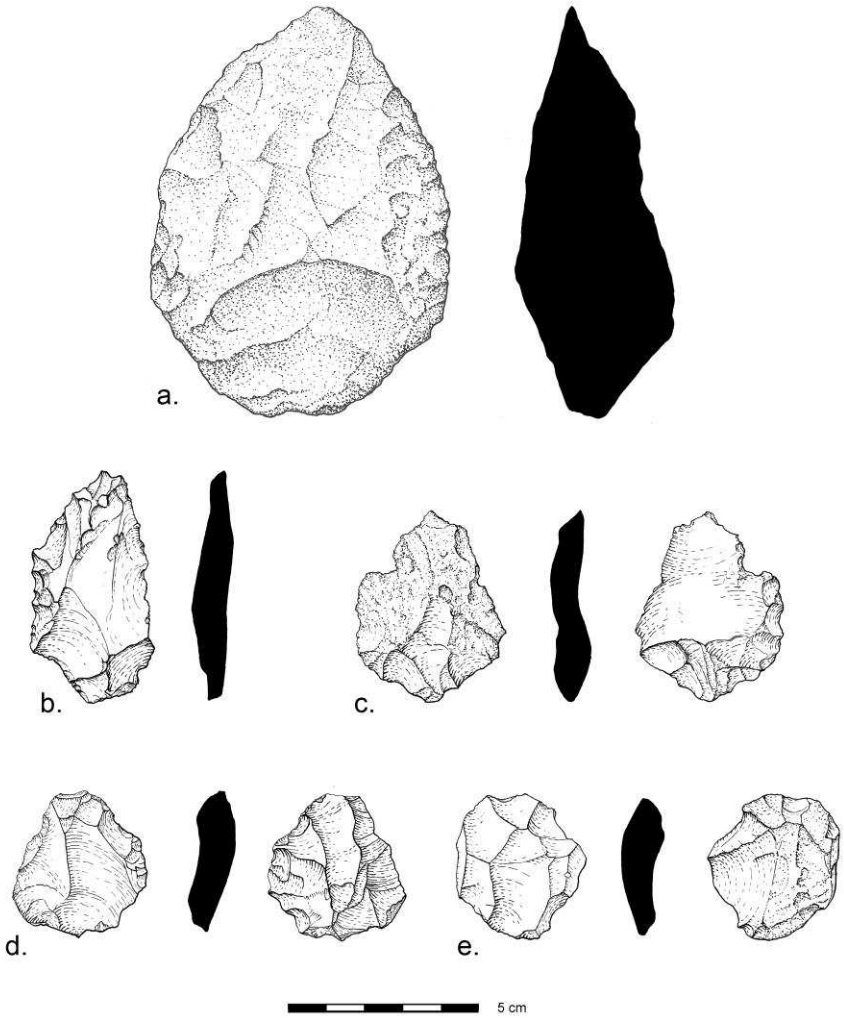


Figure 6. Selected lithics from Ndiayéne Pendao: a. Core axe; b. Denticulate; c. Basally thinned flake; d-e. Levallois cores.

Retouch was either regular or denticulated, and bases were sometimes modified through bifacial thinning (Figure 6, b, c). Two core axes (following the definition of Clark and Kleindienst, 2001) were also discovered (Figure 6, a), together with a thick bifacial thinning flake made out of the same cherty-limestone material. The assemblage was indistinguishable to other surface assemblages collected in northern Senegal during the same field season (Scerri et al., 2016).

Figure 7: Examples of excavated lithics from Ndiayéne Pendao. Left: denticulated Levallois flake found buried in Trench 3; Right: Recurrent centripetal Levallois core found buried in Trench 2.

4. Chronology

Optically stimulated luminescence (OSL) samples were recovered from the excavated sequence and measured using standard procedures (See SI for details). Shfd15009 was sampled from a thick sand sheet horizon at a location lacking artefacts, but which was better suited to OSL dating than the predominately thin aeolian deposits (< 10 cm) above the lithic-bearing layer located ~5 m away. Shfd15010 and Shfd15011 were both sampled from Trench 3 (Figure 8), which yielded the largest sample of artefacts. The majority of artefacts at this site were recovered from the lower, larger deposit of iron crust nodules (nodule diameter < 10 mm). Shfd 15010 was sampled from this horizon in direct association with a number of complete, fresh artefacts, and underlying the majority of artefacts at the site to provide a maximum age bracket. Shfd15011 was sampled from the interface between the lower deposit and a thin (8 cm) layer of finer iron crust nodules (nodule diameter < 5 mm), in direct association with the uppermost artefacts. The location of this sample at the interface between two units and less than 15 cm from the modern ground surface offer suboptimal conditions for reliable dose rate calculations for OSL dating, but offered an opportunity to provide a minimum age bracket for the artefact assemblages.

OSL measurement at the single aliquot level was applied to coarse quartz grains extracted from the three samples (Table 1). Dose rates are based on elemental concentrates determined by inductively coupled plasma - mass spectrometry and atomic emission spectroscopy (ICP-MS, ICPAES) both from sampled and adjacent sediments, which would have contributed dose. While the ratio or K, U and Th diverge from average crustal values there is no clear evidence that elemental mobility has taken place. The ratios diverge both in the unconsolidated sand sheet above and in the indurated sediment below the ferruginous nodules. It has therefore been assumed that present day values have remained constant during the time elapsed since burial. The presence of ferruginous nodules was considered in terms of dose rate homogeneity especially in the absence of field based gamma spectroscopy. Beta dose rates were based on ICP-MS and ICP-AES analysis of the sandy sediment contained within the OSL sample and therefore safely assumed to have provided the beta dose to the sample. Gamma dose rates were based on ICP-MS and ICP-AES analysis of bulk sediments surrounding the OSL samples (~ 1 kg) as well as from bulk sediment from adjacent stratigraphic units. In this way the full sediment content including nodules was analysed. Contributions of gamma dose rates from adjacent units were modelled as a function of distance to OSL sample and to unit boundaries using data from Aitken (1985). This reduced the dose-rates to samples Shfd15010 and Shfd15011 by 5% and 2% respectively.

The data show that all samples were reset prior to burial (See SI and figures and tables therein). The sand sheet covering at the site has an age of 1.34 ± 0.06 ka (Shfd15009), suggesting recent mobility of sand sheet deposits in the region. Shfd15011 returned an age of 22.7 ± 1.2 ka and Shfd15010 returned an age of 11.6 ± 0.51 ka (Shfd15010). There is therefore an apparent stratigraphic inversion of these two ages. We consider the age of Shfd15010 to be more consistent with the depositional setting and thus a more reliable representation of the age of the artifacts. This is because the sample was collected from a thicker single sediment unit, at greater depth, so should have been less susceptible to post-depositional disturbance or alteration of the dose rate. We interpret the results from Shfd15010 as being consistent with the burial of lithic artefacts around the Pleistocene/Holocene transition, at ~11.6 ka. The location of the site at a topographic high-point in sediments formed by low energy creeping of dismantled iron crust deposits alongside the assemblage size, composition and fresh appearance are consistent with contemporaneous deposition of artefacts and the dated sediments without significant reworking.

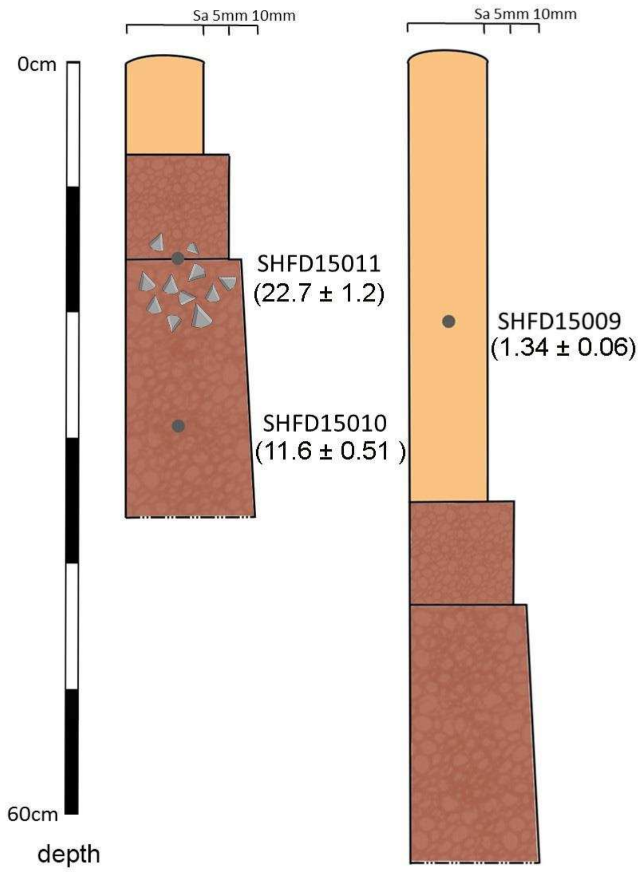


Figure 8: Stratigraphic log showing positions of the OSL samples Shfd5009, Shfd15010 and Shfd15011. The latter two samples were recovered from dismantled iron crust nodules directly associated with MSA artefacts in Trench 3. X axis (top) indicates sediment size, Sa = Sand. Ages are given in ka.

Table 1: Summary of OSL results. [a] Overdispersion of De replicate data. [b] reliability questioned see text. All OSL ages are presented in Ka from the time of measurement (2015) and include both systematic and unsystematic uncertainties.

Lab Code	**Depth (cm)**	**De (Gy)**	**OD (%)** [a]	**Dose rate ($\mu Gy/a^{-1}$)**	**Age (ka)**
Shfd15009	75	1.47 ± 0.04	17	1093 ± 36	1.34 ± 0.06
Shfd15011	15	57.8 ± 1.7	23	2544 ± 105	22.7 ± 1.2[b]
Shfd15010	28	30.1 ± 0.39	45	2590 ± 108	11.6 ± 0.51

5. Discussion

The young timeframe for artefact deposition reported in this paper fits neatly with broader schemes of geomorphological evolution throughout the Senegal Valley (e.g. Michel 1973). The dates associated with the artefacts also give the first benchmark for Pleistocene sediment sequences in the Lower Senegal Valley and constrain similar assemblages found elsewhere in similar stratigraphic contexts in the region. However, the greatest significance of the results lies in the fact that the timeframe and MSA character of Ndiayène Pendao indicates the late persistence of technology long replaced in every other studied region of Africa. Other, contemporary lithic assemblages from the Falémé (a major tributary of the Senegal River) Valley at the site of Fatandi V are Later Stone Age (LSA) in character, featuring backed pieces, including microliths and segments, and points (Lebrun et al., 2016). In Cameroon, minimum radiocarbon ages of 15.3ka were reported in association with centripetal preferential Levallois artefacts (MacDonald, 1997). Elsewhere in both the arid Sahelian and forested regions of West Africa, the few dated sites such as Ounjougou, Birimi and Bilma document the latest MSA at between ~40-30ka (Maley et al., 1971; Hawkins et al., 1996, Quickert et al., 2003; Soriano et al., 2010). However, since archaeological research in these regions is in its infancy further young MSA dates are anticipated. At the site of Goda Buticha in East Africa, a mid-Holocene (7.8–4.7 ka cal BP) assemblage is described as LSA, but with some MSA-like elements (primarily the use of the Levallois reduction method and the presence of retouched points) (Pleurdeau et al., 2014). While these MSA elements may reflect a degree of continuity, given the long hiatus at the site of ~24ka between the MSA and the LSA, it seems more likely that the more anachronistic elements were reinvented. In northeast Africa, a classic MSA assemblage documented at ~15ka in the Nile Valley most resembles the situation at Ndiayene Pendao (Osypiński & Osypińska, 2015), indicating that cultural diversity in Africa was complex, persistent and time-transgressive, perhaps particularly so in forested regions (Mercader, 2002).

The biological record presents parallels to the cultural record we document in West Africa. The Iwo Eleru calvaria (Harvati et al., 2011; Stojanowski, 2013), which is the only known West African human fossil contemporary to Ndiayène Pendao, preserves archaic features and demonstrates a distinct lack of similarities with contemporary Saharan, and indeed any other African populations at the Pleistocene/Holocene transition. The presence of such archaic features supports genetic models suggesting unexpectedly late admixture between *H. sapiens* and archaic hominins at ~35 ka in the region (Hammer et al., 2011; Mendez et al., 2013). These data have been argued to demonstrate a strong degree of population subdivision, in which West African groups may have remained relatively isolated from others living elsewhere in Africa (Stojanowski, 2013).

While the precise mechanisms of this apparent cultural and biological isolation are currently unclear, West and Central Africa form a discrete evolutionary realm, protected from the extreme aridity of North Africa and distinct from the grasslands and savannahs of southern and eastern Africa (Mercader, 2002). During the African Humid Period (~11-5ka), it is likely that Ndiayène Pendao was well within this forested ecozone (Drake et al., 2011; Shanahan et al., 2015). The Senegal and Gambia fluvial systems are also notably the westernmost and most remote river basins in Africa. Of the West African fluvial networks, only the Senegal and the Niger reach today's arid edges of the Sahara, allowing for a complex patchwork of biogeographic zones and cultural influences. It is possible that both ecological diversity and isolation by distance played a role in the persistence of 'anachronistic technology' in certain parts of Africa. However, such hypotheses have neither been explored nor tested and represent a future stage of research.

At present, the research presented here at least demonstrates for the first time that biological and cultural records in West Africa during the Pleistocene-Holocene transition are complementary, adding to a growing body of evidence demonstrating that Africa was until recently, more culturally and biologically diverse than has typically been considered (see also Crevecoeur et al., 2016). Future studies of behavioural diversity across this region will determine whether the patterns of spatial heterogeneity identified above were longstanding and the result of adaptation to distinct environmental circumstances or whether they reflect greater levels of behavioural flux than previously anticipated in West Africa. In the meantime, differences in the tempo of innovation and cultural change in West Africa, compared with the rest of the African continent at this time, in particular demonstrate the depth and complexity of population structure in this region. More broadly, the evidence affirms that the documentation of environmental, evolutionary and cultural processes across all regions of Africa, many of which remain very poorly understood, is critical for unravelling human origins.

Acknowledgements

The authors thank the Institut Fondamental Afrique Noire for support, assistance and permission to conduct fieldwork in Senegal. We also thank the British Academy of Arts and Social Sciences and the Leverhulme Trust for funding this research. We thank Alva

MacGowan for the lithic illustrations. JB thanks the Fondation Fyssen, the McDonald Institute for Archaeological Research (University of Cambridge) for their support.

Bibliography

Aitken, M.J. 1985. *Thermoluminescence dating*. London: Academic Press.

Bessac, H. 1955. Nouvelle découvertes du Paléolithique évolué au Moyen et Bas-Senegal. *Notes africain, Sénégal* 65, 1-5.

Camara, A., Duboscq, B. 1986. Evolution geomorphologique et peuplement prehistorique de la vallee du Senegal. In Livet-guide excursion No. 1: Nord Senegal. Symposium International INQUA-ASEQUA, Dakar. Pp. 55-59.

Clark, J.D., Kleindienst, M. 2001. The Stone Age cultural sequence: terminology, typology and raw material. In: J.D. Clark (Ed.), *Kalambo Falls Prehistoric Site, vol. 3. The Earlier Cultures: Middle and Earlier Stone Age*. Cambridge: Cambridge University Press, pp. 34-65.

Conrad, G, Lappartient, J-R. 1983. Le 'continental terminal', sa place dans l'evolution geodynamique du basin senegalo-mauritanien Durant le Cenozoique. *J Afr Earth Sci* 6, 45-60.

Drake, N. A, Blench, R. M, Armitage, S. J, Bristow, C. S, and White, K. H. Ancient watercourses and biogeography of the Sahara explain the peopling of the desert. *PNAS* 108, 358-462 (2011).

Gunz, P, Bookstein, F. L, Mitteroecker, P, Stadlmayr, A, Seidler, H, and Weber, G. W. 2009. Early modern human diversity suggests subdivided population structure and a complex out-of-Africa scenario. *PNAS* 106, 6094-6098.

Groucutt, H.S., Petraglia, M.D., Bailey, G., Parton, A., Clark-Balzan, L., Jennings, R.P., Lewis, L., Blinkhorn, J., Scerri, E.M.L., Drake, N.A., Breeze, P., 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.

Hammer, M.F., Woerner, A.E., Mendez, F.L., Watkins, J.C., Wall, J.D. 2011. Genetic evidence for archaic admixture in Africa. *PNAS* 108, 15123-15128.

Harvati K, Stringer C, Grün R, Aubert M, Allsworth-Jones P, et al. 2011. The Later Stone Age Calvaria from Iwo Eleru, Nigeria: Morphology and Chronology. *PLoS ONE* 6(9): e24024. doi: 10.1371/journal.pone.0024024

Hawkins, A., Casey, J., Godfrey-Smith, D., D'Andrea, A.C. 1996. A Middle Stone Age component at the Birimi site, Northern Region, Ghana. *Nyame Akuma* 46, 34-36.

Lang, J., Kogbe, C., Alidou, S., Alzouma, K.A., Bellion, G., Dubois, D., Durand, A., Guiraud, R., Houessou, A., De Klasz, I. and Romann, E., 1990. The continental terminal in West Africa. *J Afr Earth Sci* 10, 79-99.

Lebrun, B., Tribolo, C., Chevrier, B., Rasse, M., Lespez, L., Leplongeon, L., Hajdas, I., Camara, A., Mercier, N, Huysecom, E. 2016. Establishing a West African chrono-cultural framework: First luminescence dating of sedimentary formations from the Falémé Valley, Eastern Senegal. *J Archaeol Sci Reports* 7, 379–388.

MacDonald, K.C. 1997. Western African and Southern Saharan Advanced Foragers. In: Vogel, J, (Ed.) *Encylopaedia of Pre-Colonial Africa: Archaeology, History, Languages, Cultures and Environments*. Walnut Creek: Altamira, pp: 330-334.McBrearty, S. and Brooks, A. 2000. The Revolution that wasn't: a new interpretation of the origin of modern human behaviour. *J Hum Evol* 39, 453-563.

Maley, J., Roset, J.-P., Servant, M. 1971. Nouveaux gisements préhistoriques au Niger oriental, localisation stratigraphique. *Bulletin de liaison de l'A Se Qua.* 31, 9-18.

Mendez, F.L., Krahn, T., Schrack, B., Krahn, A.-M., Veeramah, K.R., Woerner, A.E., Fomine, F.L.M., Bradman, N., Thomas, M.G., Karafet, T.M., Hammer, M.F. 2013. An African American Paternal Lineage Adds an Extremely Ancient Root to the Human Y Chromosome Phylogenetic Tree. *Am J Hum Genet* 92 (3), 454-459.

Mercader, J. 2002. Forest people: The role of African rainforests in human evolution and dispersal. *Evol Anthropol* 11, 117–124.

Michel, P. 1973. *Les bassins des fleuves Sénégal et Gambie: étude géomorphologique*. Mémoires ORSTOM, no. 63, Editions de l'Office de la Recherche Scientifique et Technique Outre-mer.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., Kassem, K. R. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* 51, 933-938.

Osypiński, P., Osypińska, M. 2015. Optimal adjustment or cultural backwardness? New data on the latest Levallois industries in the Nile Valley. *Quatern Int* 408, 90–105.

Pleurdeau, D., Hovers, E., Assefa, Z., Asrat, A., Pearson, O., Bahrain, J.-J., Lam, Y.M. 2014. Cultural change or continuity in the late MSA/Early LSA of southeastern Ethiopia? The site of Goda Buticha, Dire Dawa area. *Quatern Int* 343, 117–135.

Quickert, N.A., Godfrey-Smith, D.I., Casey, J.L. 2003. Optical and thermoluminescence dating of Middle Stone Age and Kintampo bearing sedmients at Birimi, a multi-component archaeological site in Ghana. *Quatern Sci Rev* 22, 1291-1297.

Scerri, E.M.L., Blinhorn, J., Groucutt, H.S., Niang, K. 2016. The Middle Stone Age archaeology of the Senegal River Valley. *Quatern. Int* 408, 16-32.

Scerri, E. M. L., Drake, N., Jennings, R., Groucutt, H. S. 2014. Earliest Evidence for the Structure of Homo sapiens Populations in Africa. *Quatern Sci Rev* 101, 207-216

Shanahan, T.M., McKay, N.P., Hughen, K.A., Overpeck, J.T., Otto-Bliesner, B., Heil, C.W., King, J., Scholz, C.A., Peck, J. 2015. The time-transgressive termination of the African Humid Period. *Nat Geosci* 8, 140–144.

Soriano, S., Rasse, M., Tribolo, C. and Huysecom, E. 2010. Ounjougou: a long Middle Stone Age sequence in the Dogon country (Mali), in: P. Allsworth-Jones (ed.) *West African archaeology. New developments, new perspectives* (BAR International series 2164). Oxford: Archaeopress, pp. 1-14.

Stojanowski, C.M. 2014. Iwo Eleru's place among Late Pleistocene and Early Holocene populations of North and East Africa. *J Hum Evo* 75, 80-89.

Veeramah, K.R., Hammer, M.F. 2014. The impact of whole-genome sequencing on the reconstruction of human population history. *Nature Rev Genet* 15, 149-162.