Hominin Behaviour and Palaeoenvironments of Pleistocene West Africa

Dissertation

der Mathematisch-Naturwissenschaftlichen Fakultät
der Eberhard Karls Universität Tübingen
zur Enlangung des Grades eines
Doctor of Philosophy
(Dr. Phil.)

vorgelegt von

Jacopo Niccolò Cerasoni

aus Genzano di Roma, Italien

Tübingen
2022

Gedruckt mit Genehmigung der Mathematisch-Naturwissenschaftlichen Fakultät der Eberhard Karls Universität Tübingen.

Tag der müngdlichen Qualifikation:	12.07.2022
Dekan:	Prof. Dr. Thilo Stehle
1. Berichterstatter:	Prof. Dr. Christopher Miller
2. Berchiterstatter:	Prof. Nicholas J. Conard PhD

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SUMMARY

The African palaeoanthropological and archaeological record represents the earliest and richest collection of fossils, artefacts and environmental materials concerning the origin and development of our species. Whilst areas such as Eastern, Southern, and Northern Africa have been intensively explored and researched for centuries, other lesser-represented regions, such as West Africa, have not. To date, the currently known archaeological record in West Africa offers only a restricted view of past human presence and activity in the region. West Africa represents over 20% of the total area of the African continent and deserves greater consideration if behavioural dynamics and environmental patterns of African hominins are to be fully understood. To this end, this dissertation and its constituent studies set to provide a more complete understanding of the true extent of past hominin behaviour and palaeoenvironments within Pleistocene West Africa. Given the broad objective of this dissertation, the following explicitly defined studies were carried out: (1) review of the full extent of published literature on Pleistocene West African archaeological deposits and sites, (2) archaeological investigation of specific contexts within tropical and sub-tropical environments, and (3) the paleoenvironmental reconstruction of the ancient landscapes of Pleistocene West Africa. The employed methodology merged archaeological, palaeoenvironmental and digital methods, and was applied to a variety of contexts including published literature, archaeological surveys and excavations, lithic assemblages, vertebrate faunal assemblages, paleobotanical remains, and geospatial and paleoclimatic datasets. The results of this dissertation present evidence of a more complex human and environmental history than was previously thought. The re-investigation of published literature demonstrates a sporadic initial presence of hominins throughout the region with recurring occupations before 300,000 years ago during the Early Stone Age. With the establishment of Middle Stone Age traditions in West Africa during the Middle and Late Pleistocene, human populations became interconnected and demonstrated extensive capabilities to survive in tropical environments. The application of detailed and modern survey, excavation and laboratory-based techniques included in this dissertation also highlights the extremely complex cultural and environmental behaviour of hominins in the region. This dissertation serves as an initial framework to understand the true extent of Pleistocene human cultures and their relationship with the landscape in West Africa.

ZUSAMMENFASSUNG

Die paläoanthropologischen und archäologischen Aufzeichnungen Afrikas stellen die älteste und reichhaltigste Sammlung von Fossilien, Artefakten und Umweltmaterialien über den Ursprung und die Entwicklung unserer Spezies dar. Während Gebiete wie das östliche, südliche und nördliche Afrika seit Jahrhunderten intensiv erforscht und erforscht werden, ist dies bei anderen, weniger stark vertretenen Regionen wie Westafrika nicht der Fall. Bis heute bieten die derzeit bekannten archäologischen Aufzeichnungen in Westafrika nur einen begrenzten Einblick in die frühere menschliche Präsenz und Aktivität in der Region. Westafrika macht mehr als 20% der Gesamtfläche des afrikanischen Kontinents aus und verdient größere Beachtung, wenn man die Verhaltensdynamik und die Umweltmuster der afrikanischen Homininen vollständig verstehen will. Zu diesem Zweck sollen diese Dissertation und die darin enthaltenen Studien ein umfassenderes Verständnis des wahren Ausmaßes des Verhaltens der Homininen in der Vergangenheit und der Paläoumwelt im pleistozänen Westafrika vermitteln. Angesichts der weit gefassten Zielsetzung dieser Dissertation wurden die folgenden explizit definierten Studien durchgeführt: (1) Durchsicht der gesamten veröffentlichten Literatur über pleistozäne westafrikanische archäologische Ablagerungen und Stätten, (2) archäologische Untersuchung spezifischer Kontexte in tropischen und subtropischen Umgebungen und (3) die paläoökologische Rekonstruktion der alten Landschaften des pleistozänen Westafrika. Die angewandte Methodik kombinierte archäologische, paläoökologische und digitale Methoden und wurde auf eine Vielzahl von Kontexten angewandt, darunter veröffentlichte Literatur, archäologische Untersuchungen und Ausgrabungen, lithische Assemblagen, Wirbeltierfaunen, paläobotanische Überreste sowie georäumliche und paläoklimatische Datensätze. Die Ergebnisse dieser Dissertation zeigen, dass die Geschichte der Menschen und der Umwelt komplexer ist als bisher angenommen. Die erneute Untersuchung der veröffentlichten Literatur zeigt eine sporadische anfängliche Präsenz von Homininen in der gesamten Region mit wiederkehrenden Besiedlungen vor 300.000 Jahren während der frühen Steinzeit. Mit der Etablierung mittelsteinzeitlicher Traditionen in Westafrika während des mittleren und späten Pleistozäns wurden die menschlichen Populationen miteinander verbunden und bewiesen umfangreiche Fähigkeiten zum Überleben in tropischen Umgebungen. Die Anwendung detaillierter und moderner Vermessungs-, Ausgrabungs- und Labortechniken im Rahmen dieser Dissertation verdeutlicht auch das äußerst komplexe Kultur- und Umweltverhalten der Homininen in dieser Region. Diese Dissertation dient als Rahmen, um das Ausmaß der menschlichen Kulturen des Pleistozäns in Westafrika zu verstehen.

LIST OF PUBLICATIONS

*CORRESPONDING AUTHOR(S)

IN-TEXT INCLUSION OF THESE PUBLICATIONS WILL BE MARKED IN **BOLD**

I. Accepted Publications

(1) **Cerasoni*, J.N.**, Hallett, E.Y., Ben Arous, E., Beyer, R., Krapp, Manica, A., & Scerri, E.M.L. 'Archaeological sites and palaeoenvironments of Pleistocene West Africa'. In "PaleoMaps: representations of Quaternary paleoenvironments, human–environment interaction and human dispersal" special issue. Journal of Maps. DOI: 10.1080/17445647.2022.2052767 (appendix i.1)

(2) **Cerasoni*, J.N.**, Hallett, E.Y., Farr, L., Orijemie, E. A. & Scerri, E. M. L. (In Press). 'Iho Eleru'. In "Handbook of Pleistocene Archaeology of Africa: Hominin behavior, geography, and chronology" [Eds. A. Beyin, D.K. Wright, J. Wilkins, A. Bouzouggar & D.I. Olszewski]. Springer. (appendix i.2)

(3) Scerri*, E.M.L., Niang, K., Candy, I. Blinkhorn, J., Mills, W., **Cerasoni, J.N.**, Bateman, M.D., Crowther, A., & Groucutt, H.S. (2021). 'Continuity of the Middle Stone Age into the Holocene'. Scientific Reports 11, 70. DOI: 10.1038/s41598-020-79418-4 (appendix i.3)

(4) Hallett*, E.Y., Marean, C.W., Steele, T.E., Alvarez-Fernández, E., Jacobs, Z., **Cerasoni, J.N.,** … & Dibble, H.L. (2021). 'A worked bone assemblage from 120,000-90,000 year old deposits at Contrebandiers Cave, Atlantic Coast, Morocco'. iScience 24(9): 102988. DOI: 10.1016/j.isci.2021.102988 (appendix i.4)

(5) **Cerasoni*, J.N.**, Orijemie, E.A., Hallett, E.Y., Lucas, M., Ashastina, K., …, & Scerri, E. M. L. (2021). 'Late Pleistocene to Holocene paleoenvironmental reconstruction and human behaviour at Iho Eleru roch shelter, Nigeria.'. 11^{th} Annual Meeting of the European Society for the Study of Human Evolution, Abstracts. PaleoAnthropology, 2021(1), 161. DOI: 10.48738/2021.iss1.75 (appendix i.5)

(6) **Cerasoni*, J.N.**, do Nascimento Rodrigues, F., Tang, Y., & Hallett, E.Y. 'Do-It-Yourself Digital Archaeology: Introduction and Practical Applications of Photography and Photogrammetry for the 2D and 3D Representation of Small Objects and

Artefacts'. PLOS ONE, 17(4): e0267168. DOI: 10.1371/journal.pone.0267168 (appendix i.6)

(7) **Cerasoni*, J.N.** (2021). 'Vectorial application for the illustration of archaeological lithic artefacts using the "Stone Tools Illustrations with Vector Art" (STIVA) Method'. PLOS ONE, 16(5): e0251466. DOI: 10.1371/journal.pone.0251466 (appendix i.7)

II. Submitted (In Review) Manuscripts

(8) **Cerasoni*, J.N.,** Hallett, E.Y., Orijemie, E. A., Lucas, M., Ashastina, K., Farr, L., Höhn, A., Kiahtipes, Blinkhorn, J., C., Roberts, P., Manica, A., & Scerri, E.M.L. 'Human interactions with tropical environments over the last 14,000 years at Iho Eleru, Nigeria'. iScience. (appendix ii.1)

(9) **Cerasoni*, J.N**., N'Dah, D., Candy, I., Labiyi, N., Ayedoun, A., Hallett, E.Y., Blinkhorn, J., Armitage, S., & Scerri, E.M.L. Newly discovered Middle Stone sites in Tanongou Valley, Atakora Region, Benin. Submitted: Open Quaternary. (appendix ii.2)

(10) Hallett*, E.Y., Leonardi*, M., **Cerasoni, J.N.**, Will, M., Beyer, R., Krapp, M., Kandel, A.W., Manica*, A., & Scerri*, E.M.L. 'Major expansion in the human niche preceded out of Africa dispersal'. Nature.

III. Manuscripts in preparation

(11) **Cerasoni*, J.N.**, Hallett, E.Y., Roberts, Patrick, R., Manica, A., & Scerri, E.M.L. 'Refugium or not refugium? The role of refugia in African human evolution'. (appendix iii.1)

(12) **Cerasoni*, J.N.**, Neumann, K., & Bremond, L. 'Forest phytoliths for the identification of forest types in the African continent. A definition and description of new indices'.

PERSONAL CONTRIBUTION

DESCRIPTION OF THE EXTENT AND SIGNIFICANCE OF THE PERSONAL CONTRIBUTION ACCORDING TO § 6,2 PROMO², OF THE UNIVERSITY OF TÜBINGEN.

(1) Cerasoni et al. (2022). Journal of Maps. (appendix i.1)

I was first and corresponding author, responsible for the conceivement, development and supervision of the study design. I conducted most of the data collection, interpreted the data produced by co-authors, illustrated the maps and artwork, and was lead author of writing the manuscript. Co-authors participated in the data collection (E.B.A. and E.Y.H.), developed the paleoclimatic model used in the study (R.B., M.K., A.M. and E.Y.H.) and participating in the reviewing and editing of the manuscript (all co-authors).

(2) Cerasoni et al. (In Press). Springer (appendix i.2)

I was first and corresponding author, responsible for the development of the study design, archaeological data collection, writing of the manuscript, and illustration of the artwork. The co-authors aided in the interpretation of the archaeological stratigraphy (L.F.), palaeoanthropological research (E.Y.H.), and were principal project leaders of the studied site (E.M.L.S. and E.A.O.).

(3) Scerri et al. (2021). Scientific Reports (appendix i.3)

I was supporting co-author and assisted in the writing of the Supplementary Material and illustration of the the presented lithic materials.

(4) Hallett et al. (2021). iScience (appendix 1.4)

I was supporting co-author responsible for the creation of the illustrative figures, and participated in the writing, editing and reviewing of the manuscript.

(5) Cerasoni et al. (2021). PaleoAnthropology (appendix i.5)

I am first and corresponding author of this study, responsible for the conceivement and development of the study design. I lead the archaeological data collection, interpreted all the presented data, and created the poster. Co-authors assisted in the original data collection and fieldwork (L.F., E.A.O. and C.K.), were Principal Investigators for the funding project (E.M.L.S. and E.A.O.) and carried out paleoenvironmental and paleoclimatic analyses (E.Y.H., A.H., K.A., M.L., P.R., A.M.).

(6) Cerasoni et al. (2022). PLOS ONE (appendix i.6)

I was first and corresponding author responsible for the conceivement and development of the study design, main person responsible for the conducting of the reported research, interpretation of the data and writing of the manuscript. All co-authors participated in the development of the presented data, and helped with the writing and editing of the manuscript.

(7) Cerasoni (2021). PLOS ONE (appendix i.7)

I was sole author of this manuscript. I conceived and developed the study, and carried out every part of the research to publication.

(8) Cerasoni et al. (In Review). iScience (appendix ii.1)

I am first and corresponding author of this study, responsible for the conceivement and development of the study design. I lead the archaeological data collection, interpreted all the presented data, illustrated the figures, and wrote the initial manuscript. Co-authors assisted in the original data collection and fieldwork (L.F., E.A.O. and C.K.), were Principal Investigators for the funding project (E.M.L.S. and E.A.O.), carried out paleoenvironmental and paleoclimatic analyses (E.Y.H., A.H., K.A., M.L., P.R., A.M.), and participated in the reviewing and editing of the manuscript (all co-authors).

(9) Cerasoni et al. (In Review). Open Quaternary (appendix ii.2)

I am first and corresponding author responsible for the fieldwork excavation, data collection, interpretation, illustration of the figures, and writing of the manuscript. Co-authors participated in the fieldwork excavation (D.N., N.L., A.A., and I.C.) and the editing and reviewing of the manuscript (all co-authors).

(10) Hallett, Leonardi, Manica, Scerri et al. (In Review). Nature.

I am supporting co-author, assisting in the data collection, illustration of the figures, and writing of the manuscript. Due to strict copyright rules the manuscript cannot be included in this dissertation.

(11) Cerasoni et al. (in preparation). (appendix iii.1)

I am first and corresponding author of this study, responsible for the conceivement and development of the study design. I wrote the initial manuscript. Co-authors assisted by overseeing the study as supervisors (E.M.L.S.) and in the editing and reviewing of the manuscript (all co-authors).

(12) Cerasoni et al. (in preparation).

I am first and corresponding author of the study. I am responsible for data analysis, interpretation and writing of the manuscript. Co-authors carried out data collection and are assisting in supervisory roles in the analysis of the data and writing of the manuscript. Due to the current stage of production the manuscript cannot be included in this dissertation.

LIST OF MAPS, FIGURES AND TABLES

Figure 1. Map of West Africa, including: (1) modern ecoregional biomes, colored, (2) lithology, black pattern, (3) archaeological sites discussed in this study, red triangles, and (4) palaeoenvironmental sampling locations discussed in this study, black triangles.

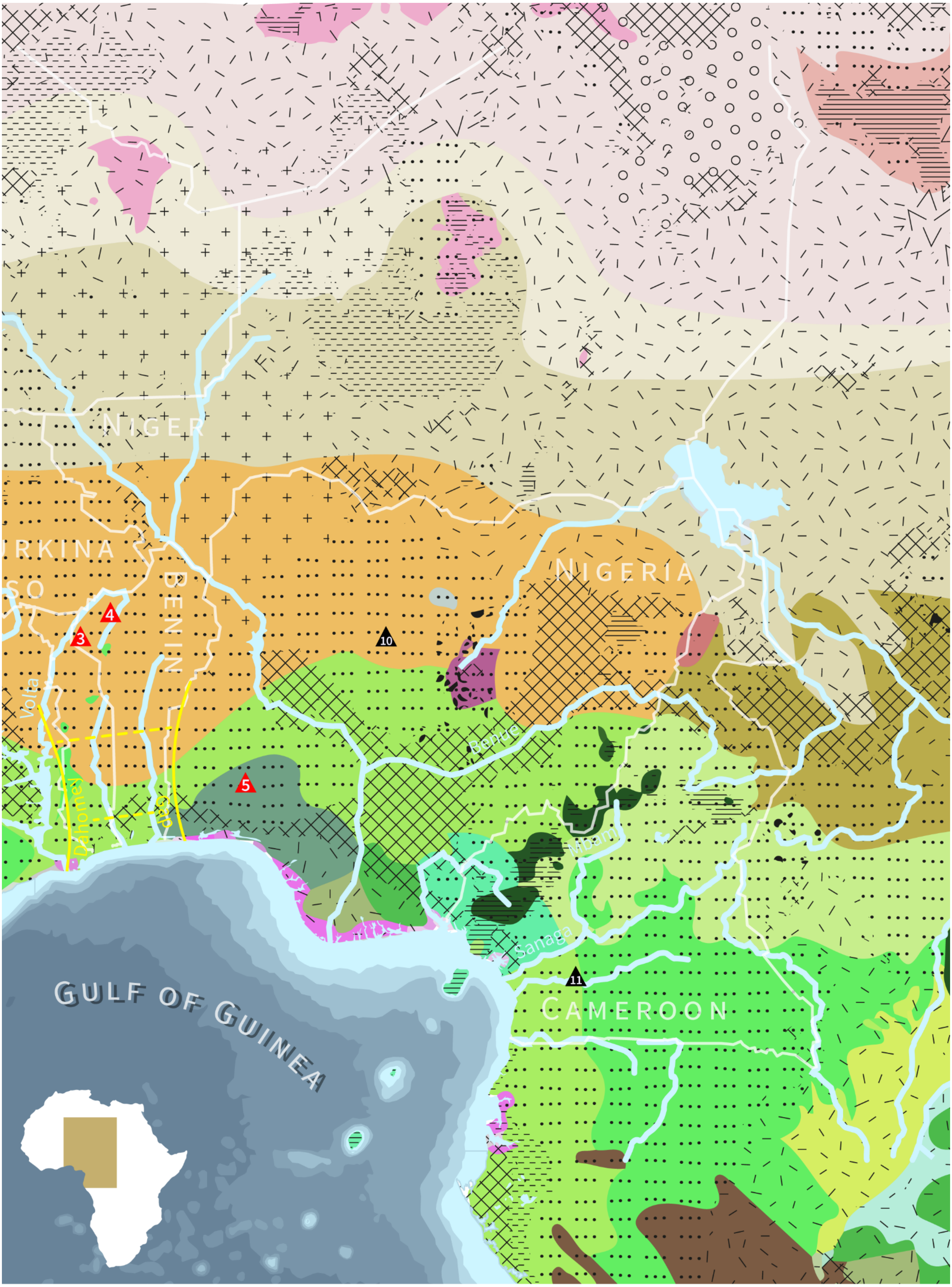

Figure 1. continued.

Figure 2. Topographic Map of West Africa showing: (1) major topographic features, (2) archaeological sites discussed in this study, red triangles, and (3) palaeoenvironmental sampling locations discussed in this study, black triangles.

CHAPTER 1. INTRODUCTION

Human evolutionary studies concentrate upon the discovery, analysis and interpretation of the past of our species. Palaeoanthropology, which is the field specialised in the study of extinct fossil hominids and extant species closely related to us, traces our origins well into the Miocene over 5.3 million years ago, when hominids such as Sahelanthropus tchadensis and Orrorin tugenensis lived (Brunet et al., 2005; Senut et al., 2001). Since that humble beginning, and following millions of years of evolution and developments, our ancient lineage branched into a multitude of different biological genera and species (for example, Australopithecus afarensis, A. africanus, A. anamensis, Homo erectus, H. floresiensis, H. habilis, H. luzonensis, among others) (Antón, 2003; Berger et al., 2015; Détroit et al., 2019; Falk et al., 2005; Johanson et al., 1987; Kimbel & Delezene, 2009; Ward et al., 1999; White et al., 1983). Among all of them, a single lineage survived to this day: Hominini.

Within this lineage resides our own genus, Homo, which was the first and only genus able to disperse beyond the African continent and thrive throughout Eurasia by ~1.5 million years ago (Lordkipanidze et al., 2007). The emergence, evolution and dispersal of Homo occurred during a geological epoch that lasted from about 2,580,000 to 11,700 years ago known as the Pleistocene. During this time period several Homo species existed, both within and out of Africa. Species such as Homo habilis, Homo erectus, Homo heidelbergensis and Homo neanderthalensis all lived during the Pleistocene epoch (Antón, 2003; de la Torre et al., 2021; Dennell et al., 2011; Johanson et al., 1987; Lordkipanidze et al., 2007; Stringer, 2012). Nevertheless, among all past Homo species, only one managed to survive and be present to this day: Homo sapiens. The underlying reasons and variables that caused such an outcome are still debated, but interdisciplinary studies including palaeoanthropological, archaeological, ecological and genetic input generally agree that the environmental and culturally flexible adaptability of Homo sapiens played a major role in its success as a species (Brooks et al., 2018; Brown et al., 2012; Grove, 2016; Marean et al., 2007; Roberts & Stewart, 2018; Tryon & Faith, 2013). Nevertheless, to truly and fully understand the underlying foundations that explain our ancestors' past and successes, major attention should be given to the environmental contexts within which they thrived. For this reason, the environmental backdrop to the African palaeoanthropological record is a fundamental piece of the puzzle that is Pleistocene hominin evolution.

As confirmed by palaeonthropological, archaeological and genetic data, our species, Homo sapiens, first originated and evolved within Africa (Bergström et al., 2021; Henn et al., 2012; Hublin et al., 2017; Scerri et al., 2018). The earliest palaeoanthropological fossil evidence of Homo sapiens appears in North Africa (Hublin et al., 2017), offering a terminus ante quem origin of our species to approximately 315,000 years ago (Richter et al., 2017). Culturally, this time period within the African archaeological record is characterised by a plethora of cultural innovations and technological changes. Developments in technology such as Middle and Later Stone Age lithic traditions (Barham, 2010; McBrearty & Brooks, 2000; Shipton et al., 2018; Villa et al., 2012), bone tool technology (Barham et al., 2002; Hallett et al., 2021; Henshilwood et al., 2001), production and use of ornaments (d'Errico & Backwell, 2016; d'Errico et al., 2009; d'Errico et al., 2012; Sehasseh et al., 2021; Steele et al., 2019; Villa et al., 2012), the creation of symbolic and artistic behaviour (Assefa et al., 2018; Brooks et al., 2018; Texier et al., 2010; Val et al., 2020), and anthropogenic modification of landscapes (Thompson et al., 2021) become common practice throughout the African continent only after the emergence of Homo sapiens, and can therefore be commonly attributed to them.

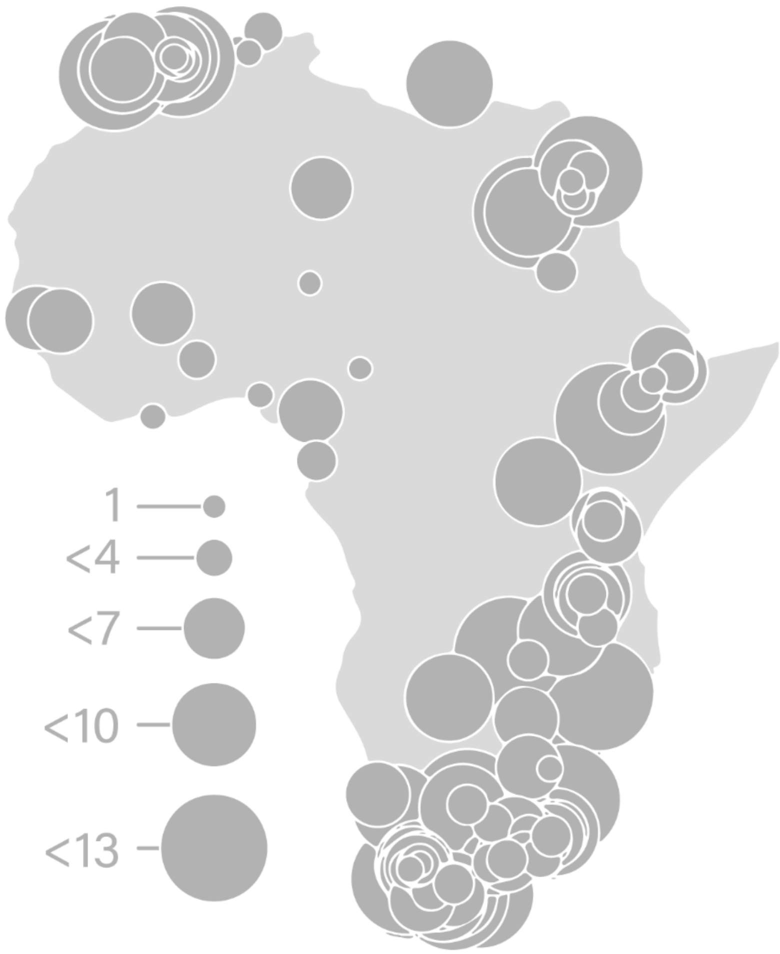

Figure 3. Density of Pleistocene archaeological sites per square kilometre in Africa (**Hallett et al., In Review**).

In geographic terms all these clear cultural and environmentally driven behaviors appeared throughout the African continent, with no single point of origin for all of them. This is well correlated with the modern consensus of Homo sapiens evolution in Africa being a product of a continent-wide, or pan-African, origin of our species. In other words, Homo sapiens developed its environmental and cultural adaptabilities and abilities as a product of highly structured populations located throughout Africa which were characterised by tight economic, migratory and cultural networks (Gunz et al., 2009; Scerri et al., 2018; Scerri et al., 2019). Hence, our species did not originate from a single region or population. The importance of this resides in the resulting interpretation that if palaeoanthropologists and archaeologists want to fully comprehend Homo sapiens evolution, both biologically, culturally and environmentally, the whole African continent and its derived record must be equally studied and evaluated.

Following this observation, it is clear that to better understand the complex technological and environmental behaviour of hominins in Africa during the Pleistocene a pan-African perspective is not only useful, but fundamental. Very often African palaeoanthropological studies focus on regions of the continent that have a rich multi-decennial history of archaeological research. These regions, such as Eastern and Southern Africa, hold extremely high concentrations and densities of Pleistocene archaeological sites (see Figure 3, Hallett et al., In Review; McBrearty & Brooks, 2000; Will et al., 2019). However, the density of sites should not necessarily be attributed to a definite higher concentration of Pleistocene hominin presence compared to the rest of the continent, but rather as a product of skewed misrepresentation of the regions that did not undergo nearly as much archaeological fieldwork and research (Cerasoni et al., 2022). The reasons underlying this difference are multiple and context-specific. When taking into consideration the climatic, environmental and political variables for each of the African regions, and sub-regions within them, it is clear that some areas will be more accessible to palaeoanthropologists and archaeologists than others. Furthermore, considering the same variables, some areas will naturally result in a lack of observable Pleistocene sites due to natural and anthropogenic causes; such as increased depositional rates, erosional processes or anthropogenic destruction of archaeological deposits. For example, regions such as the Great Rift Valley in Eastern Africa and the coastal areas of South Africa offer ideal conditions for the discovery and retrieval of Pleistocene deposits. In both cases, due to geological tectonic movements in the Rift Valley (Johanson, 2017) and good preservation of cave deposits in coastal South Africa (Hendey & Volman, 1986), Pleistocene deposits are easily identifiable and excavatable. To this day both of these regions are considered of primary importance within African palaeoanthropology as areas with extremely high concentrations of Pleistocene human presence and activity. The enourmous number of unique palaeoanthropological and archaeological discoveries made in these regions, such as a variety of Homo and Australopithecus fossils, and in-depth environmental reconstructions, could be explained by one, or a combination, of these reasons: (1) Both regional archaeological records demonstrate a true uniqueness during the Pleistocene causing a major attraction of human presence within them, or (2) There is a misrepresentation, as previously described, that has yet not been fully accepted. Consequently, the only way to shed light on the true demographic, cultural and environmental history of Pleistocene Africa is to increment our knowledge and research in the areas that have not been as heavily studied and represented. This in turn will either prove that in fact currently highly-represented regions were home to a higher concentration of Pleistocene populations, or that Pleistocene humans inhabited Africa at different rates and densities from what the current archaeological record shows.

Among all the less represented African regions lies West Africa, the focus of this dissertation. West Africa is one of the largest regions in the African continent, representing 20% of Africa's total landmass. Based on published literature and modern ecological observations, a series of considerations can be made towards Pleistocene West Africa in terms of climate, environments, and hydrography. The environmental footprint of the region follows a North-South gradient starting from Saharan desert environments to the North, shifting to temperate Sahelian and Sudanian grasslands, reaching tropical forest and rainforest environments to the South on the Guinean-Congolian Coast with the addition of mangrove-dominant coastal areas (Olson et al., 2001). These ecobiomes were present during the Pleistocene, albeit at different latitudes (Dupont, 2011). At a regional scale, it can be interpreted that West African ecobiomes moved on a North-South axis following climatic events and shifts (Dupont et al., 2000). Following alternating cycles such as stadial-interstadial cycles and ENSO climatic events (Lisiecki & Raymo, 2005) increased precipitation and humidity in the region would have caused tropical-dominant environments to expand Northwards, resulting in a decrease of temperate-dominant environments (**Cerasoni et al., 2022**; Dupont et al., 2000). Conversely, drier and less-humid periods would have caused the shrinking of tropical-dominant environments and the expansion of temperate-dominant environments (**Cerasoni et al., 2022**; Dupont et al., 2000). Topographically, West Africa tends to be an extremely uniform and accessible region (**Cerasoni et al., 2022**). The only areas with extreme topographic variability can be found in modern Guinea, with the Guinea Highlands, and at the intersection of Nigeria and Cameroon where the Shebshi and Mandara Mountain ranges are found. Overall, however, topography would not have caused any specific physical barrier to human migration. However, the hydrography of West Africa would have been a major barrier for Pleistocene migration. These hydrographic barriers to human migration were mostly due to major river basin systems, such as the Volta River and the Niger River systems, which were active and present throughout the Pleistocene. Although their wide river beds and extreme lengths would have made them surpassable with difficulty, these two rivers, together with their tributaries, were a continuous source of fresh water, which offered an array of lakes and distinct riverine environments. The correlation between their geographic locations, found within the central section of the Guinean-Congolian Coast, and the location of the Dahomey Gap (Salzmann & Hoelzmann, 2005, Demenou et al., 2016), visible between the two main river basins, shows the importance of water systems in investigating Pleistocene human presence in West Africa. The Dahomey Gap has been extensively studied from an environmental perspective (Salzmann & Hoelzmann, 2005, Demenou et al., 2016) as it has sustained extensive environmental remodelling during the Pleistocene and Holocene and has served as a major area for tropical fragmentation and expansion through time. All of this combined clearly shows the complex environmental picture that is West Africa, with continuous change through time caused by alternating temperate and tropical environments, responses to climatic variability, and complexity of hydrographic systems which caused intra-regional fragmentation and sub-divisions. Nevertheless, it is also clear that West Africa offered a large array of resources and ideal conditions for human inhabitation and survival during the Pleistocene.

The currently available archaeological record of West Africa impartially extends throughout the region, being mostly dependent on specific hotspots located along the Guinean-Congolian Coast, and higher altitude locations along the Sudanian Savanna belt. Currently, West Africa has evidence for human presence from the Early Stone Age until recent times. The earliest human presence in the region is shown to have occurred around 250,000 years ago at the site of Anyama, Ivory Coast, where a linear deposition of Early Stone Age to Iron Age (Holocene) assemblages have been excavated (Guédé, 1995; Lioubine & Guédé, 2000). The Early Stone Age (ESA), although present, is quite poorly represented in West Africa, with a handful of reliable sites present in hotspots, namely the Falémé Valley, coastal Guinean-Congolian Coast, and high altutitude regions of Nigeria

(**Cerasoni et al., 2022**). An increase in human presence in the region is observable starting from the Middle Stone Age (MSA), approximately 150,000 years ago, where an abudance of sites appears throughout the region from Saharan environments at the North, to densly forested tropical environments to the South and East of West Africa (**Cerasoni et al., 2022**).

1.1 Purpose of the study and research questions

West Africa has been under-represented in the African palaeoanthropological record for decades. This dissertation sets to aid in the further representation of this poorly-known region. By applying a three-sided framework, this dissertation, and the publications included within it, aim to start filling in some gaps which will, in time, amplify West Africa's role in the African palaeoanthropological record. To do so, these are the fundamental research questions that this study had set from its inception:

1. What is the true extent of the currently known West African Pleistocene record?

2. When and where did humans inhabit West Africa?

3. How did humans interact with their environments in Pleistocene West Africa, and was there a technological dependency on specific environments?

4. Did Pleistocene inhabitants of West Africa differ intra-regionally in terms of cultural and environmental behavior?

Clearly, these questions are extremely complex and broad, especially for a single doctoral dissertation. Given this, each question was narrowed down and approached taking into account either published and consutable data, or using specific sites, regions and case-studies as an initial testing ground for larger research projects in the future. Through a process of selection and narrowing of sub-regions and contexts, this study eventually included the following sub-regions, materials and assemblages:

1. All available literature on West African Pleistocene studies. This included all manuscripts available online, printed journals and books, site reports, and video documentaries and interviews. This data collection from avaialble literature included

several months of work, including the visiting and consideration of all available materials present at the libraries at the University of Ibadan (Nigeria), University of Cotonou (Benin), and University Aboumey-Calavi (Ivory Coast).

2. The site of Iho (Iwo) Eleru (Figure 4, site n.5) and its assemblages excavated in the 1960s, currently stored at the Department of Archaeology and Anthropology at the University of Ibadan, Nigeria.
3. The Atakora Region, in North Western Benin. This region comprised a total of three visited and excavated archaeological sites: Kumaaku (Figure 4, site n.3), Tanongou Cave (Figure 4, site n.4), and Paloli (Figure 4, site n.4). Kumaaku was investigated and visited, but no archaeological layers were identified. The latter two archaeological sites are both situated in the Tanongou Valley and were later selected for further sedimentary analysis, lithic analysis and general archaeological investigation for publication.
4. Coastal Ivory Coast, following re-evaluation and re-dating of the site of Anyama ((Figure 4, site n.2), including stratigraphical deposition of archaeological remains and previously identified lithic assemblages.
5. Phytolith assemblages from modern sampled forested environments (Figure 4, sites n.6-11). The regions included in this assemblage include a variety of West African forest biomes and regions (Sahelian, Sudanian, Cameroonian, Guinean-Congolian), as well as East African forest biomes and regions.

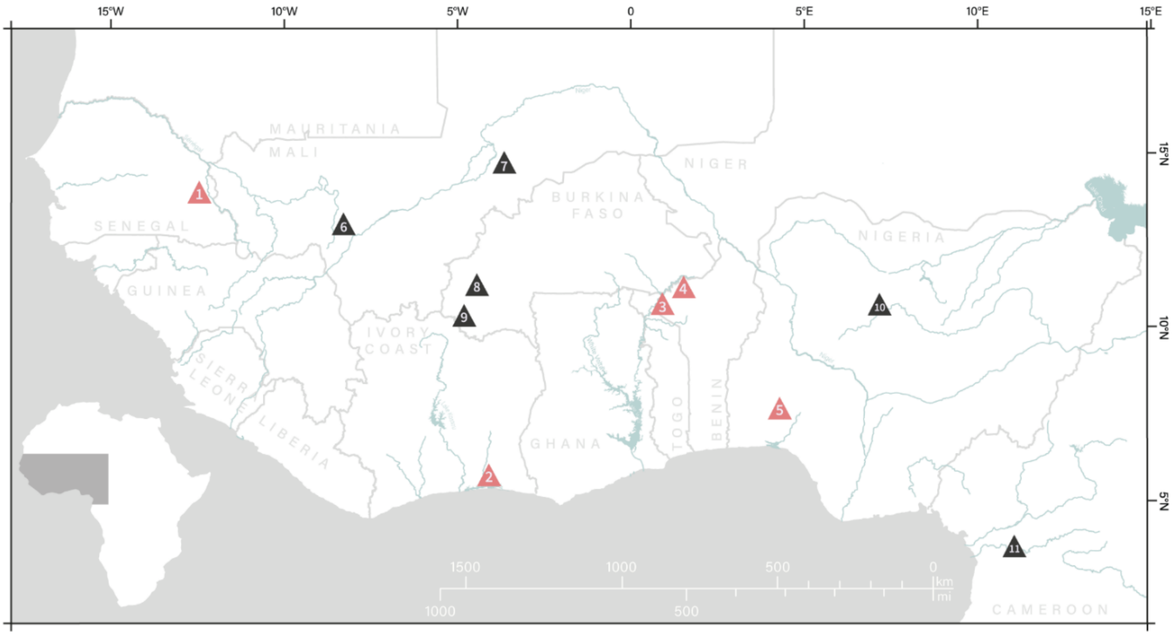

Figure 4. Map of West Africa and geolocalisation of sites included and studied in this dissertation. 1- Saxomunya (Senegal); 2-Anyama (Ivory Coast); 3-Kumaaku; 4- Tanongou Valley (Tanongou Cave, Paloli), Benin; 5- Iho Eleru, Nigeria; 6- Pays Dogon, Mali; 7- Kita, Mali; 8- Niangoloko, Burkina Faso; 9- Reserve Comoè-Leraba, Burkina Faso; Runse dei Bitini, Nigeria; 11- Ebyanemeyong and Nkongmeyos, Cameroon.

With the application and study of the aformentioned contexts and assemblages, this study sets to answer, albeit partially, the research questions presented. Nevertheless, this study sets to offer significant results for the advancement of palaeoanthropological and archaeological knowledge from West Africa. The expectations of this study are multiple, first of which is offering a single and easy-to-consult dissertation which will allow anyone interested in West African Pelistocene Archaeology to gather all of the most up-to-date information within a single source. This study will also hopefully present the richness of the archaeological record of West Africa, presenting new data and archaeological sites. Overall, this study will not only significantly change the common knowledge of Pleistocene West African archaeology, but will show the importance of this region and recognise its important role in the African and global palaeoanthropological record.

1.2 Definitions of acronyms and terms

Given the multidisciplinarity of this study and the archaeological, environmental and digitial methods employed, definitions for acronyms and terms used throughout this dissertation are presented below:

ka – *kilo annum*, time notation for 1,000 (one thousand) years. In this dissertation ka is also used as equivalent to "1,000 years ago".

ma – time notation for 1,000,000 (one million) years. In this dissertation ma is also used as equivalent to "1,000,000 years ago".

Pleistocene – Geological epoch ranging from 2.58 ma to 11.7 ka (Lisiecki & Raymo, 2005). Archaeological periods found within this epoch and discussed in this study are: Early Stone Age, Middle Stone Age, and Later Stone Age (as defined below).

Holocene – Geological epoch ranging from 11.7 ka to today (Walker et al., 2009). Archaeological periods found within this epoch and discussed in this study are: Later Stone Age, Iron Age, and modern times.

Paleoclimate – The study of past climates and climatic events. For the purpose of this dissertation, the main climatic variables considered when discussing paleoclimate are precipitation and humidity.

Paleoenvironment – The study of past environments and its inhabitants. This includes plants and animals.

Palaeoecology – The study of biomes and landscapes, taking into account plants and animals (palaeoenvironment), while considering also the effect that paleoclimate had on them.

Unifacial – Stone tool where flakes are removed solely from one side of the raw material. Commonly pebbles are used to produce unifacial tools.

Bifacial – Stone tool where flakes are removed from two sides of the raw material. This technique becomes commonly used starting from the Acheulean period (late ESA). Some examples of bifacial technology are handaxes and cleavers. The latter is generally a large scale stone tool with one single, straight, cutting edge perpendicular to the length of the stone tool (REF).

Early Stone Age (ESA) – African prehistoric period ranging from approximately 3.3 ma to 280 ka (REF). This time period is characterised by lithic industries dominated by Oldowan (unifacial stone tools) and Acheulean (bifacial handaxes and cleavers) technologies.

Middle Stone Age (MSA) – African prehistoric period ranging from approximately 280 ka to (generally) 50 ka. Exceptions in West Africa exist with younger ages of 13 ka (**Scerri et al., 2021**). This time period is characterised by lithic industries dominated by levallois (centripidal cores, preferential flakes removals) technology.

Later Stone Age (LSA) – African prehistoric period ranging from approximately 50 ka to (generally) 7 ka. This time period is characterised by lithic industries dominated by microlithic and ground stone technologies.

Phytolith – Opal silica structures found in plants. Generally produced for structural purposes, they can originate from any part of the plant. They can help in the identification of specific plants (with different degrees of certainty between taxa; family, genus, species) and can be extracted from a variety of contexts including, but not limited to, modern soil samples, archaeological sediment samples, residue from archaeological artefacts, dental calculus and lake/marine cored sediments. Given their silica-based molecular composition phytoliths are unaffected by changes in temperature, humidity or pressure, making them the most robust botanical microremain and potentially indestructible. Finally, phytoliths tend to be deposited at close range from the original location of production, as they are part of the plant that produces it, and are therefore generally deposited when the plant decays. Exception for this depositional process occurs when plants or sediments containing phytoliths get displaced due to erosional, wind or water activities, albeit usually never to great distances (as in the case of wind-driven pollen).

Niche – The combination of bioclimatic factors that determine where a species can survive and reproduce.

1.3 Limiations and assumptions of the study

After considerations of the purpose of the study, research questions, sites and sub-regions selected for this study, a series of limitations and assumptions naturally became an integral part of this study. First and foremost, although this study sets to answer questions that encompass a region as massive as West Africa, it will only be a generalisation based on the limited data collected and analysed for this study. Regarding the review of published literature on West African Pleistocene sites and contexts, the author comprehends that some sources and texts might have been missed or not found. Unfortunately, given the inadequately and inaccessibly published literature from decades prior to the age of online publishing, certainities will never exist on the possibility of collecting every single source of archaeological research carried out in West Africa since its beginnings. In turn, this limitation is approached by applying an assumption to this study which presumes that the literature collection included and reviewed for this study constitutes the great majority of the work carried in respect to the archaeology of Pleistocene West Africa.

Liminations also apply to the non-literature based research included in this study. Particularly applicable to the fieldwork-related projects, major delimitations on the amount of work carried out in each site or locality apply. With particular attention to Iho Eleru, Nigeria, and the Atakora Valley, Benin, both of these localities would require much more archaeological investigations given their extremely high potential for new data. Nevertheless, due to various reasons that include the scope of this study, time limitations, political instabilities and risks of warfare within these localities, further research projects will have to continue the work presented here.

Finally, one major delimitation that abruptly impacted this study is the emergence of the COVID-19 pandemic. As many other scholars and scholarly works, this study suffered a sudden and abrupt change in organization. While the original intent of this dissertation was to include several years of fieldwork with relevant data collection, the author of this study was able to collect original data only for the first eight months of their doctoral studies. To address this delimitation, a series of new projects were developed so to continue this work, while not needing new and original data which would have been accessible only with further fieldwork.

1.4 Organization of the study

Given the complexity and broadness of the topics and research questions of this study, a four-part organization was set so to ease both the research process and the understandability of the research itself. The fours part are the following: (1) Literature review of Pleistocene West

Africa, (2) Archaeological investigation of tropical and sub-tropical West Africa, (3) Environmental investigation of African forested biomes, and (4) Development of novel digital methods for the visualisation of archaeological materials. Each of four these parts was then broken down into three specific elements which include: (a) Purpose, (b) Data Collection, and (c) Resulting Publications. Among all four sections some theoretical and methodological overlaps will be present, however they all aim to answer the main research questions from different perspectives, offering novel approaches within the study of hominin behaviour and palaeoenvironments of Pleistocene West Africa. The four parts of this study are:

1.4.1 Literature review of Pleistocene West Africa

(a) **Purpose**: Offer an all-encompassing, single source of all published Pleistocene archaeological sites and deposits in West Africa. Given the current lack of understanding and knowledge of West Africa's role in African human evolutionary studies, this study aims to offer an accessible source for the future inclusion and accountability of West Africa.

(b) **Data Collection**: In-depth literature review from online and printed sources.

(c) Resulting Publications:

1. Cerasoni et al. (2022) 'Archaeological sites and palaeoenvironments of Pleistocene West Africa'. Journal of Maps. (appendix i.1)
2. Cerasoni et al. (In Press) 'Iho Eleru'. In "Handbook of Pleistocene Archaeology of Africa: Hominin behavior, geography, and chronology". Springer. (appendix i.2)

1.4.2 Archaeological investigation of tropical and sub-tropical West Africa

(a) **Purpose**: Further the archaeological record of Pleistocene West Africa. By applying modern excavation and material analyses methods this study aims to present new information on past hominin behaviour and environmental adaptability in tropical and sub-tropical enviornments of West Africa. Furthermore, the creation of a theoretical framework for the study of refugia in African tropical enviroments was formed.

(b) **Data Collection**: Archaeological excavation, material culture analysis (lithic assemblage analysis), palaeoenvironmental analysis (anthracological, phytoliths, isotopes), theoretical evaluation of the role of refugia for human-environment interaction in tropical and sub-tropical West Africa.

(c) **Resulting Publications**:

1. Cerasoni et al. (In Review). ‘Human interactions with tropical environments over the last 14,000 years at Iho Eleru, Nigeria’. iScience. (appendix ii.1)
2. Cerasoni et al. (2021). ‘Late Pleistocene to Holocene paleoenvironmental reconstruction and human behaviour at Iho Eleru roch shelter, Nigeria.’. PaleoAnthropology, 2021(1), 161. (appendix i.5)
3. Cerasoni et al. (In Review). ‘Newly discovered Middle Stone sites in Tanongou Valley, Atakora Region, Benin’. Open Quaternary. (appendix ii.2)
4. Cerasoni et al. (In Prep). ‘Refugium or not refugium? The role of refugia in African human evolution’. (appendix iii.1)

1.4.3 Environmental investigation of African forested biomes

(a) **Purpose**: Create an original comparative study and index for the identification of specific forested biomes from phytolith assemblages. With an index such as this, archaeologists and palaeoecologists will be able to process any sample containing phytoliths, and deduce the original type of forest the phytoliths were produced in.

(b) **Data Collection**: Phytolith extraction from modern soil samples, identification and counting of phytolith morphotypes, statistical analysis for the creation of indices.

(c) **Resulting Publications**:

1. Cerasoni et al. (In Prep). ‘Forest phytoliths for the identification of forest types in the African continent. A definition and description of new indices’.

1.4.4 Development of novel digital methods for the visualisation of archaeological materials

(a) **Purpose**: Create comprehensive and extensive digital methods for the development of accurate lithic illustration, artefact photography, and high-resolution 3D photogrammetric models.

(b) **Data Collection**: This study did not include the collection of raw data, rather it comprised experimentation, collaboration and development of novel methods.

(c) **Resulting Publications**:

1. Cerasoni et al. (2022). ‘Do-It-Yourself Digital Archaeology: Introduction and Practical Applications of Photography and

Photogrammetry for the 2D and 3D Representation of Small Objects and Artefacts'. PLOS ONE. (appendix i.6)

2. Cerasoni (2021). 'Vectorial application for the illustration of archaeological lithic artefacts using the "Stone Tools Illustrations with Vector Art" (STIVA) PLOS ONE. (appendix i.7)

Following the explanation of this study and its organization, the next chapter will explain in detail the methodologies which were employed within each research project. A summarised flow chart of the research questions, research projects and sites has been included below (Figure 5), showing how each of these separate parts is interconnected and how they are approached methodologically.

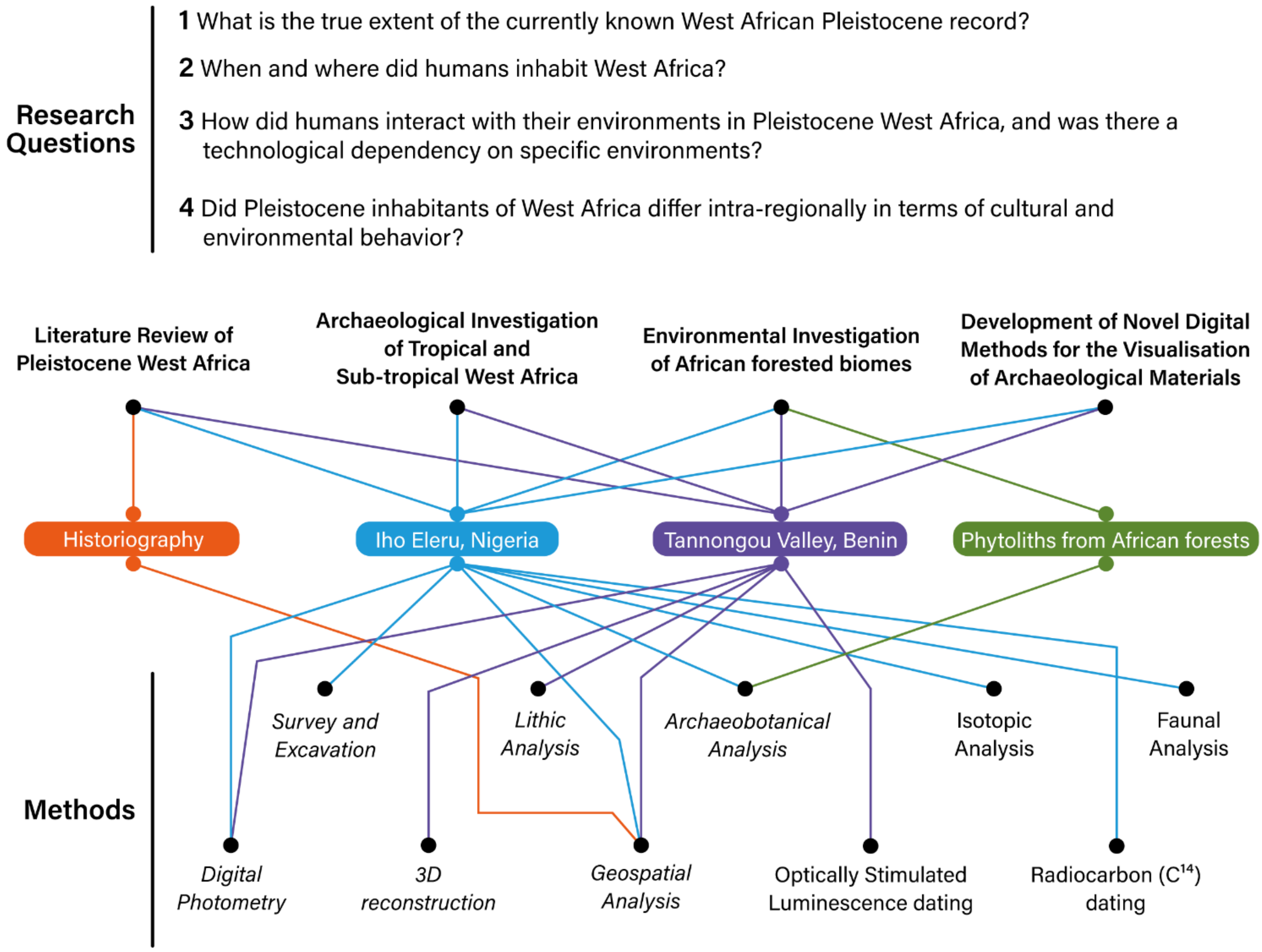

Figure 5. Synthesising workflow of the basic structure and organization of this dissertation. Above, the major research questions are shown. Below them the four main parts of this study are presented (Section 1.1), together with their relevantly connected research projects (Section 1.4). The research projects are then visually connected to the specific methods applied to each of them. Of the methods, the use of *italics* demonstrates the methods which were directly carried out by the author of this dissertation.

CHAPTER 2. MATERIALS AND METHODOLOGY

Following the extremely open-ended and wide range of research questions and topics that constitute this study, the resulting methodologies that are required are numerous and incredibly wide. This chapter intends to give a brief, yet detailed description of the methodologies employed within the theoretical, archaeological, palaeoenvironmental and digital frameworks of this dissertation.

As previously explained, the purpose of this study is to offer a novel and updated view of Pleistocene West African hominin behaviours and palaeoenvironments. This is achieved with the objectives to have a better understanding of Pleistocene demography, human-environment relationships and technological behaviour of past humans in this extremely underrepresented African region.

The materials and collections employed in this study include literature sources, geospatial data and databases, lithic assemblages, faunal remains, anthracological remains, botanical macroremains, and botanical microremains from various assemblages. For clarity purposes, each material type and collection is presented below within its research framework, explaining data collection methods and quality.

2.1. Archaeological and palaeoenvironmental materials and methods

Archaeological and palaeoenvironmental contexts and materials, originating from Iho Eleru (Nigeria), Tanongou Cave (Benin), Paloli (Benin) and the modern African forest phytolith collection provided the principal empirical basis for the archaeological and palaeoenvironmental sections of this dissertation.

In the case of Iho Eleru, the archaeological excavation was carried out in 1964 and 1965 by T. Shaw and S.G.H. Daniels (Shaw & Daniels, 1984). Within this study a complete re-evaluation of the original excavation and stratigraphical interpretations were brought forth following the investigation of original archival materials present at the University of Ibadan (Nigeria), and the University of Cambridge (UK). Digitalisation of the original excavation reports and archived materials generated the possibility to re-design and reinterpret the original in-situ materials at Iho Eleru and their depositional history. Through this, a new depositional history and archaeological framework of the site was developed. The entirety of the original excavated collection was also found, with the exception of excavated human remains. Through recording and digitalisation of the materials' location and type, a selection of the most interesting materials was carried out for further analyses. These analyses included taphonomic and taxonomic study of the faunal assemblage, taxonomic study of the anthracological and macroremains collection, radiometric analysis of macrobotanical and faunal remains, isotopic analyses of faunal dentition, digital photometry and imaging of the archaeological contexts and remains, and microbotanical extraction from soil sediments and residues from archaeological materials.

For Tanongou Valley (Tanongou Cave and Paloli), the majority of the archaeological methodology employed included the excavation of the sites, chronometric dating, and lithic assemblages analysis. Of the two sites only Tanongou Cave was previously recorded and partially excavated. Paloli was discovered during our first expedition to Tanongou Valley. Tanongou Cave was excavated by Petit et al. (2005), and the excavation concentrated upon the uppermost levels of the visible stratigraphy where the retrieval of Holocene deposits was the objective. In this study, both Paloli and Tanongou Cave were excavated within set 1x1 meter grid systems for each site. In addition, Paloli underwent surface lithic collection from the same grid system extended outside the excavation area. Finally, for the modern African forest phytolith collection, the entirety of the materials were collected from modern surface samples across West and East Africa (Figure 4). The samples were processed for phytolith extraction and morphotype analyses. For the completion of the presented projects, the following methods were applied to them:

Fieldwork survey and excavation (Cerasoni et al., In Review, appendix ii.2) - A targeted survey of the Tanongou Valley and neighbouring areas was organised, specifically along the border between the Atakora Chain Formation and the Pendjari National Park. GPS systems were used to record any surface finds or exposed Pleistocene deposits. Stratified archaeological deposits outside of the valley were scarce, however the survey resulted in the location of Tanongou Cave, and the discovery of the new site of Paloli. Both sites were excavated using hand tools (i.e. trowels, shovels), applying a single context excavation methodology, and subdivided into 5 cm spits in the case of Paloli-T1. In Tanongou Cave lithics were plotted using a standard (x, y, z) spatial grid at 1 cm resolution. All excavated sediments were sieved using a 5 mm mesh on site, and all finds were collected and labelled on site.

Lithic assemblage analysis (Cerasoni et al., In Review, appendix ii.2) - The finds were cleaned on site and imported to the Max Planck Institute for the Science of Human History, Jena, for analysis. The equipment used for analysis included a set of lamps and magnifying lenses, a scale, microscale, and a Mitutoyo caliper (150 mm, USB). The artefacts were recorded using the software E4 (https://www.oldstoneage.com/osa/tech/e4/). Recording was carried out using a .cfg file (Supplementary File 1) modified from the .cfg file published by Wilkins et al. (Wilkins et al., 2017).

Optically Stimulated Luminescence (OSL) dating (Cerasoni et al., In Review, appendix ii.2) – Sampling was carried out by I. Candy, dating was carried out by S. Armitage. Two OSL samples were collected at Tanongou Cave by collecting coherent blocks of sediment, which were subsequently wrapped in light-tight material for transport to the laboratory. Single-grain measurements on quartz (optically stimulated luminescence, OSL) and K-feldspar (post-infrared infrared stimulated luminescence at 275 °C, pIRIR275) were conducted using a Risø TL-DA-15 instrument following the procedures described in Supplementary Information C of Martinón-Torres et al. (2021). For each quartz sample, 2400 individual grains were measured, whereas 1200 grains of each K-feldspar sample were analysed. Data analysis was carried out using the calSARED() function in the R package numOSL (Peng et al., 2013) and the calc-CentralDose() and calc_FMM() functions in the Luminescence package (Kreutzer et al., 2012). Environmental dose rates were calculated using the Dose Rate and Age Calculator (Durcan, King and Duller, 2015) using alpha and beta counting data.

Radiocarbon dating (**Cerasoni et al., In Review, appendix ii.1**) – Sampling was carried out by J.N. Cerasoni and A. Höhn, dating was carried out by the Curt-Engelhorn-Center Archaeometry gGmbH. For the bone samples collagen was extracted (modified Longin method), purified by ultrafiltration (fraction >30kD) and freeze-dried. For the plant macroremains pre-treatment using ABA-Method (Acid/Base/Acid, HCl/NaOH/HCl) was used. The insoluble fraction was used for further treatment. Following pre-treatment, the sample material was combusted to CO2 in an Elemental Analyzer (EA). CO2 was then converted catalytically to graphite. 14C were analysed using a MICADAS-type AMS system in-house. The isotopic ratios 14C/12C and 13C/12C of samples, calibration standard (Oxalic Acid-II), blanks and control standards were measured simultaneously in the AMS. 14C-ages were normalized to 13C=-25‰ and calibrated using the dataset IntCal20 and software SwissCal (L. Wacker, ETH-Zürich). Calibration graphs are generated using the software OxCal.

Taphonomic and taxonomic identification of vertebrate faunal assemblage (**Cerasoni et al., In Review, appendix ii.1**) **-** Sampling was carried out by J.N. Cerasoni, analysis was carried out by E.Y. Hallett. The initial phase of taphonomic recording was completed using an Olympus 10-40X zoom binocular microscope with high incident light. For final verification of cut marked and percussion marked bones, SEM (Scanning Electron Microscope) imaging was completed using a JEOL InTouch Scope JSM-IT100LA compact

SEM. Each bone fragment was analysed for surface modification. This microscopic method of surface modification recording has shown 95% accuracy in blind tests (Blumenschine et al., 1996), and allows zooarchaeologists to distinguish between cut marks, percussion marks, and tooth marks. Trampling and biochemical marks (Domínguez-Rodrigo & Barba, 2006; Domínguez-Rodrigo et al., 2009), such as chemical, insect, and root etching (Andrews & Cook, 1985; Bunn, 1983; Dirks et al., 2015; Haynes, 1988), were also recorded. Burning severity was recorded as no burning, light, medium, heavy, or calcined. Burning extent was recorded as the proportion of a bone fragment displaying signs of burning. For each bone and tooth fragment that was not covered in an adhering carbonate matrix, the following variables were also recorded (see Supplementary Table 5): measurements (length, width, thickness, or height for tooth crown height), skeletal element, anatomical position, side (left of right), taxonomic identification to the lowest level, circumference of fragment (Bunn, 1983), surface visibility, exfoliation of bone surface, dendritic etching (Andrews & Cook, 1985; Haynes, 1988), pocking, sheen, smoothing, cut marks, percussion marks, percussion notches, tooth marks, tooth notches, rodent gnawing (Andrews & Cook, 1985), weathering (Behrensmeyer, 1978), fracture outline and angle (Villa & Mahieu, 1991), presence of fresh break(s) (Villa & Mahieu, 1991), and colour.

Archaeobotanical analysis (**Cerasoni et al., In Review, appendix ii.1**) **-** Sampling was carried out by J.N. Cerasoni, analysis was carried out by A. Höhn. Wherever possible wood charcoal was analysed using a reflected light microscope (Leica DM4000M) at different magnifications, 50x – 500x, in dark and bright field, after manually fracturing the charcoal fragments along the three planes: transverse, longitudinal tangential and longitudinal radial. The identification process follows the steps described in Höhn & Neumann (2018) and relies on the Inside Wood database (Wheeler, 2011), the wood reference collection of the Goethe University Frankfurt (JWGw), and wood anatomical atlases (Lebacq et al., 1955; Normand, 1960; Hubau, 2013). Carpological macro-remains were identified with a dissecting microscope (Leica S6D). Identification was achieved by comparison with specimens in the modern reference collection of the Laboratory of African Archaeobotany at Goethe University, Frankfurt am Main and with carbonized carpological material from Dibamba, Cameroon, identified by Stefanie Kahlheber (unpublished).

Phytolith analysis (**Cerasoni et al., In Review, appendix ii.1**) – Sampling, extraction and analysis was carried out by J.N. Cerasoni. The archaeobotanical samples containing sediment within their original storage bags were processed for sediment isolation using sieve meshes, with varying grid sizes between 1-0.25 cm. For the phytolith extraction, the samples were first deflocculated using a sodium hexametaphosphate and warm water solution. For every 10 ml of soil, 100 ml of solution was used (ratio 2:90, sodium hexametaphosphate:water). Any sample which did not correctly deflocculate after 72 hours within the solution was manually crushed with a mortar and pestle. Clays were then removed from the samples by gravity sedimentation, with a 1:10 ratio of solution to water, letting it stand for one hour and then removing supernatant liquids. The clay removal process was repeated 3 times. The resulting clay-free samples were then fractioned by wet sieving and dividing the samples into sands (mesh sieve with grid size of 250 μm) and silts (mesh sieve with grid size of 50 μm). A centrifuge (1500 rpm for 10 minutes) and distilled water were then used to repeatedly wash the silt samples. The sand samples were put aside and not used for the rest of the process. Given the high contraction of carbonates in the higher spits of the stratigraphy, HCl was used to remove any carbonate particles. This was done by carefully adding HCl to the samples until no reactions were visible. The samples were then rinsed three times with distilled water and a centrifuge at 1700 rpm for 10 minutes each. Organics were then removed using a 30% H2O2 solution and placing the samples within the solution in a hot water bath at 40 ºC. Given the low percentage of organic materials in the samples this step was concluded after 2 hours in the hot water bath, with the second hour reaching a temperature of 80 ºC. The samples were then rinsed five times with distilled water and a centrifuge at 1700 rpm for 10 minutes each. The resulting samples were then processed for any phytolith extraction by flotation using Sodium Polytungstate (SPT-1). A heavy liquid was created using a hygrometer at a specific density of 2.3 g/ml. The SPT-1 solution was then mixed with the samples, and centrifuged at 1700 rpm for 5 minutes. The materials which were floating at the top were then removed and then rinsed three times with distilled water and a centrifuge at 1700 rpm for 10 minutes each. Next, the samples were dried using acetone, which was mixed with the samples (approximately 10 ml for 1 ml of soil), stirred and centrifuged at 1500 rpm for 5 minutes. Supernatant acetone solution was removed, and the process repeated twice more. The final samples were then left to dry in a fume cupboard for 2 nights. Finally, the resulting materials were mounted on slides by mixing mounting oil with the samples, placing a few drops of the solution on each slide, and then covering with the slide cover and using clear nail polish to seal them. The slides were analysed with a Olympus BX53M microscope at 40-100x magnification.

Bulk stable isotope analysis (**Cerasoni et al., In Review, appendix ii.1**) – Selection and sampling was carried out by J.N. Cerasoni and E.Y. Hallett, mass spectrometry analysis was carried out by M. Lucas. Enamel sampling for δ13C and δ18O analysis was conducted at Max Planck Institute for the Science of Human History (MPI-SHH). Tooth samples were first cleaned by air abrasion to remove surface contaminants. Roughly 10 mg of enamel powder was then drilled from the buccal surface of the tooth to gain a sample representing the full growth period of the tooth. The drilled enamel powder was then pre-treated with a 1% NaOH solution for 1 hour. Samples were then rinsed, vortexed, and centrifuged three times with MilliQ water. A 0.1 M acetic acid solution was then added to the samples for 10 minutes followed by the rinsing process with MilliQ water. After pre-treatment, samples were frozen overnight before being freeze dried for 4 hours. Samples were analysed on a Thermo Gas Bench 2 connected to a Thermo Delta V Advantage Mass Spectrometer. Roughly 3 mg of each sample was weighed into borosilicate glass vials. The vials were then flushed with helium at 100 ml/min for 10-minutes. 20 ul of 100% phosphoric acid was then added to each sample and left to react for 1 hour. Samples were calibrated using a three point calibration with international standards IAEA NBS 18: δ13C -5.04‰, δ18O -23.2‰, IAEA 603: δ13C +2.46‰, δ18O -2.37‰, and IAEA CO8: δ13C -5.764‰, δ18O -22.7‰. Replicate precision of standards was used to measure machine error where δ13C ± 0.2‰ and δ18O ± 0.2‰. Overall measurement precision was studied through the measurement of repeat extracts from a bovid tooth enamel standard (n = 20, ± 0.2‰ for δ13C and ± 0.4‰ for δ18O).

Digital photometry (Hallett et al., 2021; Scerri et al. 2021; Cerasoni et al., In Review, appendix ii.1, ii.2) - Scanning Electron Microscopy (SEM) imaging was carried out by J.N. Cerasoni, K. Boxleitner and E.Y. Hallett. Morphological analysis of the specimens was carried out in a scanning electron microscope (SEM) Jeol JSM-IT100 at the Microscopy and Palaeobotany Laboratory of the Department of Archaeology at the Max Planck Institute for the Science of Human History, Jena. Samples were fixed on a 32 mm plain specimen holder with a conductive one-sided copper adhesive tape. For artefacts larger than 30 mm we used a specimen holder with a plain station; artefacts smaller than 30 mm were mounted on either aluminium cylinders or aluminium pin stubs. All samples were imaged uncoated. The SEM was operated in a high vacuum mode at an accelerating voltage of 10 kV. Specimens were visualized using an in-lens secondary electron detector (SED) at magnifications from 22x to 250x. Depending on the size of the artefact, we attuned working distance (WD) from 11 to 18 and probe current (P.C.) from 30 to 44. Brightness, contrast, stigma, and focus were adjusted manually for each sample in the InTouchScope program. Photographs of the faunal remains were taken following the protocol for photography of artefacts and small object (SOAP protocol) (**Cerasoni et al., 2022**). Archaeological figures were designed and composed using Adobe © Illustrator © 2021. For lithic illustrations, selected lithics were illustrated (fig. 5) following photography with a Sony Alpha II camera using a Sony macro lens. Photographs were then imported into Adobe Illustrator 2021©. Lithic illustrations were subsequently accomplished following the Stone Tool Illustrations with Vector Art (STIVA) Method (**Cerasoni, 2021**).

2.2. Geospatial methods (Hallett et al., 2021; Cerasoni et al., 2022; Cerasoni et al. In Press; Cerasoni et al., In Review, appendix ii.1, ii.2)

In addition to the archaeological and palaeoenvironmental methods, geospatial frameworks were employed throughout this study to offer a regional perspective of each project, and to offer cartographic contextualisation for the analyses, results and interpretations. Generally, geospatial analyses were carried out using QGIS, and further enhanced and processed for printing and publication using Adobe Illustrator. Most importantly, however, geospatial techniques formed the fundamental methods employed for the creation of a region-wide site review (**Cerasoni et al., 2022**). This study comprised a three-step method, as presented below:

Site selection and quality review (Cerasoni et al. 2022) - A database was constructed by reviewing previously published literature, including published articles, books and reports. A list of Pleistocene sites in West Africa was collated, recording the following variables for each site: (1) site name, (2) country, (3) type (open air, fluvial terrace, or rock shelter), (4) cultural attribution, (5) known or unknown stratigraphical origin, (6) number of recovered artefacts (<,=, or > than 10), (7) dating method used, (8) coordinates, and (9) original reference. By using the following variables, sites were selected for inclusion in this study, while partial, poorly understood, or questionable archaeological sites were excluded. The selection of archaeological sites was based on the following requirements: (1) a documented stratified archaeological origin, or not less than 10 characteristic artefacts, (2) published coordinates, and (3) published chronometric ages or relative dating (i.e. by cultural attribution such as lithic assemblage type, culture or tradition).

Geospatial distribution (Cerasoni et al. 2022) - The resulting dataset, collated and exported in a .csv file format, was imported on QGIS and was superimposed over an elevation map of the region developed from 1 km-resolution digital elevation models (DEMs, Jarvis et al. 2008). The elevation values from the original DEM dataset were categorised and colourised topographically and then further categorised into observable topographic bioregions, which are the following: coastal, flooded lowland, lowland, highland, sub-montane, and montane. Rivers and lakes were also included to offer modern distribution and location of major water sources (CGIAR, 2014; RCMRD, 2015).

Geospatial categorisation (Cerasoni et al. 2022) - The adopted elevation- and topography-based approach led to the evaluation of site location and type in direct comparison with modern ecoregional zones (lower left corner, Main Map; Olson et al., 2001) and modern political boundaries(OCHA ROWCA, 2021). The included archaeological sites were further sub-sampled and divided into categories based on their cultural attribution. Three of the six total categories represent archaeological sites that only show one single cultural attribution (i.e. a dated chronometric range for the site that fits within a single cultural attribution range, or the retrieval of artefacts that are categorised only within one single cultural attribution), and they are Early Stone Age (ESA), Middle Stone Age (MSA), and Later Stone Age (LSA). The other three categories include archaeological sites that have dated stratigraphies, by either chronometric or typological dating, and include more than one single attribution. These categories are: Early Stone Age to Middle Stone Age, Middle Stone Age to Later Stone Age, and Early Stone Age to Later Stone Age.

2.3. Scientific imaging methods (Cerasoni, 2021; Cerasoni et al., 2022)

Finally, scientific imaging methods employed in this study were utilised and developed throughout the presented projects. Within the archaeological and palaeoenvironmental methods a dedicated section for the photometric development of graphical elements used in the included publications was already presented (p. 22). Nevertheless, novel methods were developed for the visual representation of lithic artefacts (**Cerasoni, 2021**), photographic application and representation of material culture (**Cerasoni et al., 2022**), and three-dimensional visualisation of material culture (**Cerasoni et al., 2022**).

All of the described collection and analytical methods approach this study's research question from different perspectives. The inclusion of analytical methods for the production of archaeological and palaeoenvironmental data have the purpose of presenting new evidence for the better understanding of Pliestocene hominin behavior and human-environment interactions in West Africa. The application of geospatial analyses supports and helps the discovery of the true extent of past hominin demography and distribution in Pleistocene West Africa. Finally, modern digital and imaging methods were applied with the objective to share new types of data acquisition and analysis, which, are not only applicable to this study's research questions, but have a global and unlimited pertinence.

CHAPTER 3. RESULTS

This chapter summarises the principle findings of the articles that form this dissertation – as listed in LIST OF PUBLICATIONS and attached in the APPENDIX. The synoptic presentation of results is structured following the four main research areas presented in CHAPTERS 1.1 and 1.4:

3.1. Literature review of Pleistocene West Africa
3.2. Archaeological investigation of tropical and sub-tropical West Africa
3.3. Environmental investigation of African forested biomes
3.4. Development of novel digital methods for the visualisation of archaeological materials

For each presented section, the relevant published papers will be listed in connection to the APPENDIX, and will be followed by an exposition and contextualisation of their main findings. Further discussion and interpretation of the presented findings will be developed in CHAPTER 4. DISCUSSION AND CONCLUSIONS.

3.1. Literature review of Pleistocene West Africa

The following papers address the first of the research questions presented in this dissertation, and try to assess and present the true extent of the currently known West African Pleistocene record, both archaeologically and environmentally. The principle findings of these articles will constitute the fundamental framework from which all other presented articles will be based on, offering an in-depth literature review of all published and later-presented findings.

- Cerasoni et al. (2022) 'Archaeological sites and palaeoenvironments of Pleistocene West Africa'. Journal of Maps. DOI: 10.1080/17445647.2022.2052767 (appendix i.1)
- Cerasoni et al. (In Press) 'Iho Eleru'. In "Handbook of Pleistocene Archaeology of Africa: Hominin behavior, geography, and chronology". Springer. (appendix i.2)

In order to provide the first comprehensive literature review of Pliestocene West Africa, **Cerasoni et al. (2022)** presents a high-resolution map (Figure 6) and database (Table 1) that synthesises all well-contextualised Pleistocene archaeological sites present in West Africa. For the creation of our database, an in-depth literature review was carried out compiling all available sources from online, printed and media documentation. Initial data collection resulted in the identification of over 350 archaeological sites across West Africa. To achieve a database with the highest possible accuracy and reliability, quality review and selection was carried out, and the following variables were recorded for each site: (1) documented archaeological stratification or >10 characteristic artefacts, (2) published coordinates, and (3) published chronometric ages or relative dating. All sites that possessed valid data for all three variables were included in the final "quality-assured" database. This data collection was later geospatially processed to create a cartographic representation of their spatial and geographic distribution. Modern ecological biozones and paleoclimatic reconstructions were superimposed on the cartographic representation of archaeological sites. Following initial evaluation of the data, three sub-regions were selected for further investigation based on their high density of Pleistocene archaeological sites: (1) Falèmè Valley (Senegal), (2) Atakora Region (Benin), and (3) Jos Plateau (Nigeria). These sub-regions were then further analysed by modelling their paleoclimatic history during the last 120 ka.

This article, which collated bibliographical, geospatial, paleoenvironmental and paleoclimatic data, is the first representation of the true extent of past human presence in Pleistocene West Africa. The data collected and analysed allowed us to better consider Pleistocene archaeological and palaeoenvironmental sites in West Africa and display the extent and distribution of sites in the region from decades of published research. With a total of 61 highly reliable archaeological sites, **Cerasoni et al. (2022)** demostrated that past hominin presence in West Africa was not limited by geographic and topographic constraints, but rather it was extremely widespread since the Middle Stone Age. Pleistocene site presence was not wholly dependent on ecological contexts, as we show an equally wide distribution of sites in every modern biome (Figure 7), ranging from savanna dominated biomes in Northern Sahelian regions, to coastal and montane environments of Southern latitudes.

The sites included in this article, although originally sub-divided based on chronometric dates, were later assembled and published with their cultural attribution (i.e. ESA, MSA, LSA). The majority of sites in the collated database (Table 1) are MSA sites (N=52), with a much lower presence of ESA (N=4) and LSA sites (N=9). MSA sites are equally present through the region, with no apparent or distinct hominin preference for environmental or topographic locale. On the contrary, ESA sites have been identified solely in the northern latitudes of West Africa, within Sahelian grassland-dominated environments. In addition, LSA sites are found within specific ecoregional settings, most commonly within rock shelter sites and open-air settings in tropical and forested environments.

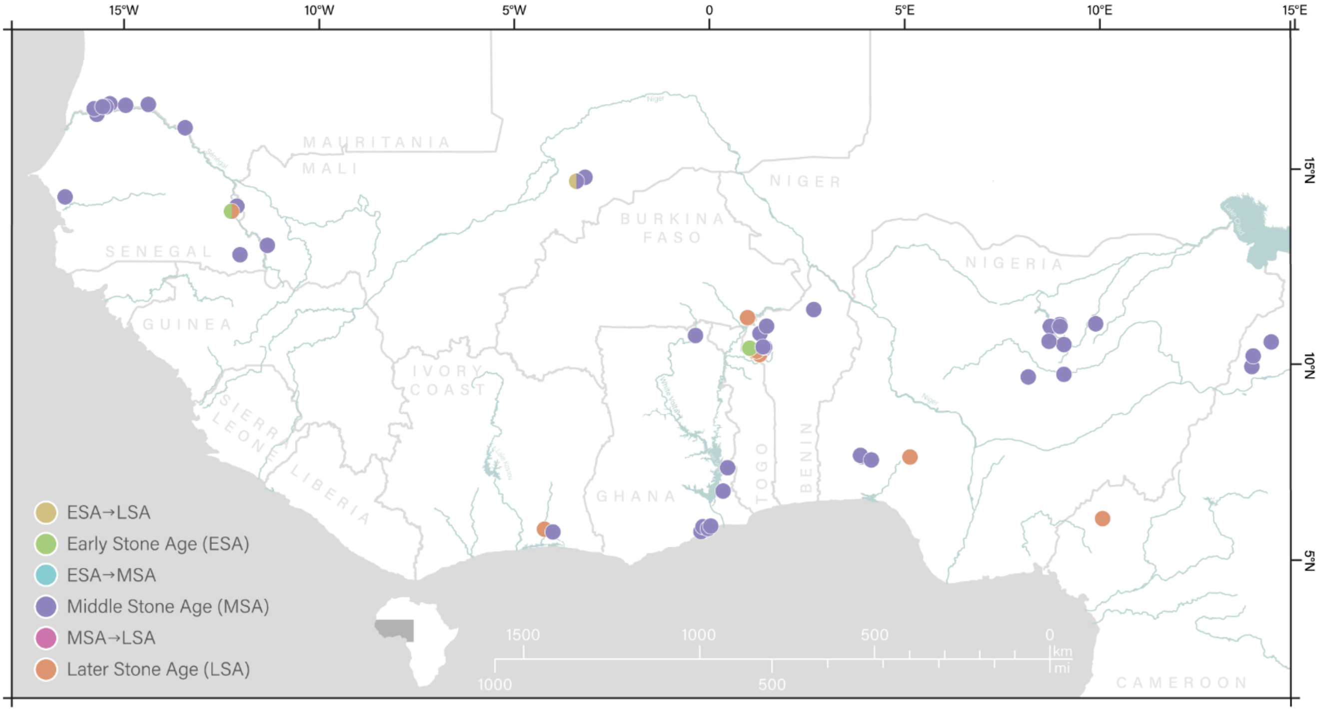

Figure 6. Distribution of culturally attributed Pleistocene sites from Cerasoni et al. (2022)

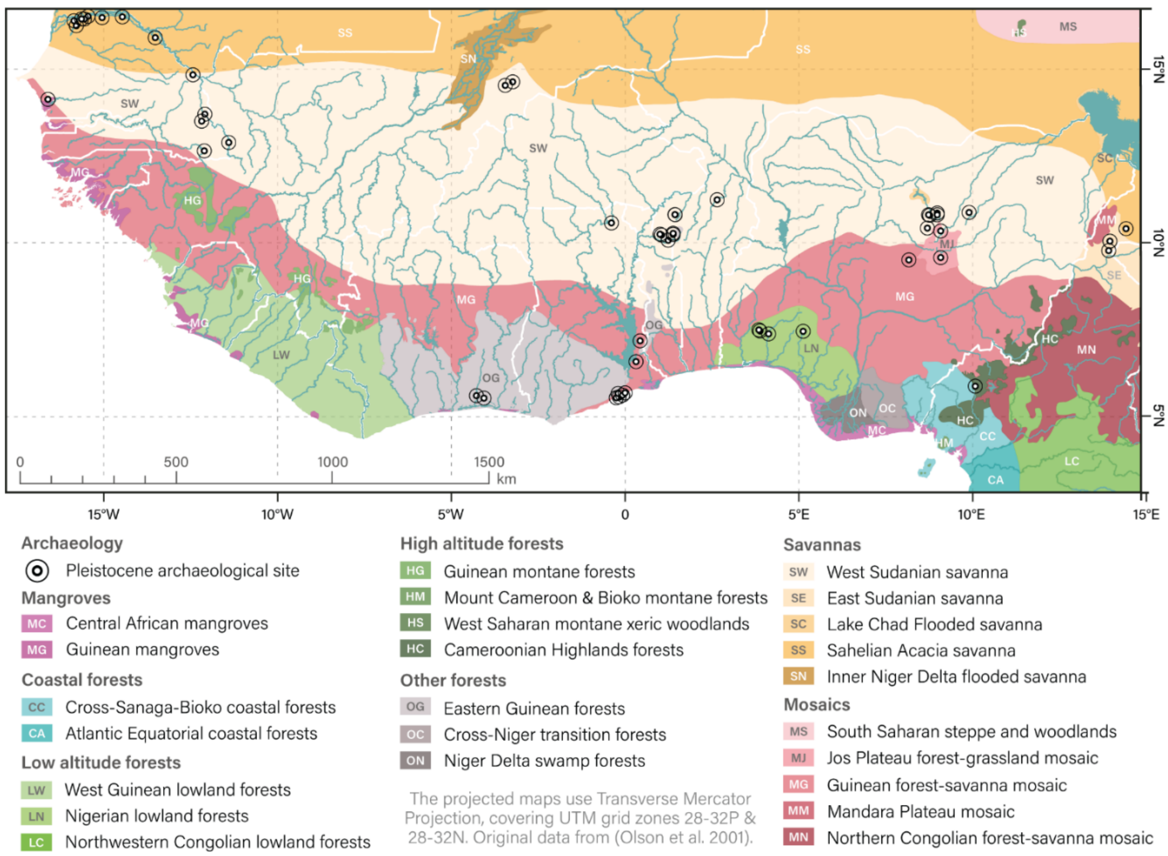

Figure 7. Modern ecoregional biomes of Sub-Saharan West Africa and location of Pleistocene archaeological sites. (Cerasoni et al. 2022).

N	Site	Country	Cultural Attribution	KSO?	>10 As?		Dating	Latitude	Longitude	References
1	Korontière-I	Benin	ESA	Yes	Yes		Typological (lithic)	10.23872	1.00201	Petit 2005
2	Djita	Senegal	ESA	Yes	Yes		Typological (lithic)	13.86600	-12.37100	Camara and Dubosq 1990
3	Kumaaku	Benin	ESA-MSA	Yes	Yes		Typological (lithic)	10.24111	1.00861	N'Dah 2009
4	Alibori (or Alibori Bridge)	Benin	MSA	Yes	Unknown		Typological (lithic)	11.23333	2.65000	Davies 1967
5	Bersingou	Benin	MSA	Yes	Unknown		Typological (lithic)	10.23333	1.38333	Davies 1967
6	Paloli	Benin	MSA	Yes	Yes		Typological (lithic)	10.80627	1.43523	Cerasoni 2020; Cerasoni et al. 2020
7	Sawètè	Benin	MSA	Yes	Unknown		Typological (lithic)	10.27202	1.34551	N'Dah 2009
8	Tanongou Cave	Benin	MSA	Yes	Yes		Typological (lithic)	10.80299	1.44272	Petit 2005; Cerasoni 2020; Cerasoni et al. 2020
9	Dent de Mindif	Cameroun	MSA	No	Yes		Typological (lithic)	10.40000	14.41667	Allsworth-Jones 2019
10	Figuil Louti	Cameroun	MSA	Yes	Yes		14C (radiocarbon) dating	10.04000	13.95200	Marliac 1973, 1987; Chevrier et al. 2018
11	Mayo Louti	Cameroun	MSA	Yes	Yes		Typological (lithic)	9.76667	13.91667	Allsworth-Jones 2019
12	Asokrochona	Ghana	MSA	Yes	Yes		Typological (lithic)	5.60279	-0.06892	Davies 1967; Nygaard and Talbot 1984; Chevrier et al. 2018
13	Birimi	Ghana	MSA	Yes	Yes		OSL (optically stimulated luminescence) dating	10.56547	-0.39219	Hawkins et al. 1996; Casey et al. 1997; Quickert et al. 2003; Lebrun et al. 2016
14	Chawenu	Ghana	MSA	Yes	Yes		Typological (lithic)	6.56667	0.31667	Allsworth-Jones 2019
15	Hohoe	Ghana	MSA	Yes	Yes		Typological (lithic)	7.16667	0.43333	Allsworth-Jones 2019
16	Labadi	Ghana	MSA	Yes	Yes		Typological (lithic)	5.55222	-0.16905	Allsworth-Jones 2019
17	Legon Botanical Garden	Ghana	MSA	Yes	Yes		Typological (lithic)	5.65000	-0.20000	Allsworth-Jones 2019
18	Manprobi	Ghana	MSA	Yes	Yes		Typological (lithic)	5.52435	-0.25161	Allsworth-Jones 2019
19	Tema II	Ghana	MSA	Yes	Yes		Typological (lithic)	5.66667	0.00000	Nygaard and Talbot 1984
20	Anyama	Ivory Coast	MSA	Yes	Yes		TL (thermoluminescence) dating	5.51500	-4.06000	Liubin & Guédé 2000
21	Dandoli 1	Mali	MSA	Yes	Yes		OSL (optically stimulated luminescence) dating	14.63330	-3.23330	Soriano et al. 2010; Tribolo et al. 2015
22	Dandoli 2	Mali	MSA	Yes	Yes		OSL (optically stimulated luminescence) dating	14.63330	-3.23330	Soriano et al. 2010; Tribolo et al. 2015
23	Kokolo 2	Mali	MSA	Yes	Yes		OSL (optically stimulated luminescence) dating	14.63330	-3.23330	Soriano et al. 2010; Tribolo et al. 2015
24	Kokolo 3 c.3	Mali	MSA	Yes	Yes		OSL (optically stimulated luminescence) dating	14.63330	-3.23330	Soriano et al. 2010; Tribolo et al. 2015
25	Oumounaama	Mali	MSA	Yes	Yes		OSL (optically stimulated luminescence) dating	14.63330	-3.23330	Robert et al. 2003; Rasse et al. 2004
26	Ajibode	Nigeria	MSA	Yes	Yes		Typological (lithic)	7.45000	3.88333	Allsworth-Jones 2019
27	Asejire	Nigeria	MSA	Yes	Yes		Typological (lithic)	7.36692	4.13002	Allsworth-Jones 2019
28	Mai Lumba	Nigeria	MSA	Yes	Yes		Typological (lithic)	10.80000	8.98333	Allsworth-Jones 2019
29	Nok	Nigeria	MSA	Yes	Yes		Typological (lithic)	9.50000	8.16667	Allsworth-Jones 2019
30	Olude-Araromi	Nigeria	MSA	Yes	Yes		Typological (lithic)	7.48333	3.85000	Allsworth-Jones 2019
31	Pingell	Nigeria	MSA	No	Yes		Typological (lithic)	10.33333	9.08333	Allsworth-Jones 2019
32	Saminaka	Nigeria	MSA	Yes	Yes		Typological (lithic)	10.41667	8.70000	Allsworth-Jones 2019
33	Tibchi	Nigeria	MSA	Yes	Yes		Typological (lithic)	10.85000	8.98333	Allsworth-Jones 2019
34	Yada Gungume	Nigeria	MSA	No	Yes		Typological (lithic)	10.86667	9.90000	Allsworth-Jones 2019
35	Yelwa	Nigeria	MSA	Yes	Yes		Typological (lithic)	10.80000	8.73333	Allsworth-Jones 2019
36	Zenabi	Nigeria	MSA	Yes	Yes		14C (radiocarbon) dating	10.78333	8.76667	Allsworth-Jones 2019
37	Rop	Nigeria	MSA	Yes	Yes		Typological (lithic)	9.50000	8.91667	Allsworth-Jones 2019
38	Dabià Quarry	Senegal	MSA	No	Yes		Typological (lithic)	15.90683	-13.52011	Scerri et al. 2016

39	Djiérigayè	Senegal	MSA	No	Yes		Typological (lithic)	16.52233	-15.45497	Scerri et al. 2016
40	Laminia	Senegal	MSA	Yes	Yes		OSL (optically stimulated luminescence) dating	12.64250	-12.10750	Scerri et al. 2021
41	Madina Cheikh Omar	Senegal	MSA	No	Yes		Typological (lithic)	16.44492	-15.55939	Scerri et al. 2016
42	Mbane	Senegal	MSA	No	Yes		Typological (lithic)	16.25155	-15.78998	Scerri et al. 2016
43	Ndiayéne Pendao	Senegal	MSA	Yes	Yes		Typological (lithic)	16.48433	-15.04844	Scerri et al. 2016
44	Ngnith	Senegal	MSA	No	Yes		Typological (lithic)	16.39592	-15.85736	Scerri et al. 2016
45	Njideri	Senegal	MSA	No	Yes		Typological (lithic)	16.44706	-15.64084	Duboscq 1986; Scerri et al. 2016
46	Ravin Blanc 1	Senegal	MSA	Yes	Yes		OSL (optically stimulated luminescence) dating	13.984733	-12.20647	Douze et al. 2021
47	Ravin des Guepiers	Senegal	MSA	Yes	Yes		OSL (optically stimulated luminescence) dating	13.86600	-12.37100	Huysecom et al. 2014, 2016; Chevrier et al. 2018
48	Saxomunya	Senegal	MSA	Yes	Yes		OSL (optically stimulated luminescence) dating	12.88360	-11.40510	Scerri et al. 2021
49	Tiemassas	Senegal	MSA	Yes	Yes		OSL (optically stimulated luminescence) dating	14.12800	-16.60700	Descamps 1979; Diop 2000; Niang and Ndiaye 2016; Niang et al. 2020
50	Toumboura II	Senegal	MSA	Yes	Yes		Typological (lithic)	13.86600	-12.37100	Chevrier et al. 2018
51	Toumboura III	Senegal	MSA	Yes	Yes		OSL (optically stimulated luminescence) dating	13.86600	-12.37100	Lebrun et al. 2016
52	Ravin de Missira	Senegal	MSA	Yes	Yes		OSL (optically stimulated luminescence) dating	13.86600	-12.37100	Lebrun et al. 2016
53	Ounjougou	Mali	ESA-LSA	Yes	Yes		OSL (optically stimulated luminescence) dating	14.53200	-3.44800	Soriano et al. 2010; De Weyer 2008; Huysecom 2014; Lebrun et al. 2016; Rasse et al. 2004
54	Koussokouangou	Benin	MSA-LSA	Yes	Unknown		Typological (lithic)	10.07522	1.25634	N'Dah 2009
55	Koukouan-I	Benin	LSA	Unknown	Yes		Typological (lithic)	10.21710	1.04967	Petit 2005
56	Pendjari-II	Benin	LSA	Yes	Yes		Typological (lithic)	11.02403	0.94628	Petit 2005
57	Shum Laka	Cameroun	LSA	Yes	Yes		14C (radiocarbon) dating	5.85861	10.07778	Lavachery and Cornelissen 2000
58	Bingerville Highway	Ivory Coast	LSA	Yes	Yes		14C (radiocarbon) dating	5.58500	-4.27700	Chenorkian 1983
59	Iho Eleru	Nigeria	LSA	Yes	Yes		14C (radiocarbon) dating	7.44138	5.12476	Shaw and Daniels 1984; Cerasoni et al. submitted
60	Fatandi V	Senegal	LSA	Yes	Yes		OSL (optically stimulated luminescence) dating	13.86600	-12.37100	Lebrun et al. 2016; Lebrun 2018; Chevrier et al. 2018
61	Toumboura I	Senegal	LSA	Yes	Yes		OSL (optically stimulated luminescence) dating	13.86600	-12.37100	Lebrun et al. 2016; Lebrun 2018

Table 1. Database of all Pleistocene sites in West Africa, as presented in Cerasoni et al. (2022).

As previously explained, the collated database shows a much greater density of MSA sites compared to ESA and LSA sites, explained in part by the extreme deposition of tropical and sub-tropical locales of West Africa. Nevertheless, interesting exceptions to the previously observation exist; although limited and explained as follows:

1. Ounjougou, among one of the most famous West African Pleistocene sites, has a depositional history extending from the ESA to the Holocene. This site has been excavated and researched for decades (Robert et al., 2003; Rasse et al., 2004; Soriano et al., 2010; Tribolo et al., 2015).

Extensive excavation at Ounjougou led to the discovery of some of the most important archaeological data in the African archaeological record, including the earliest evidence of pottery use (Rasse et al., 2004; Soriano et al., 2010; Allsworth-Jones, 2021). This site, however, has a distinct depositional history and excavation history compared to the rest of the region, as it is located in a fault area which resulted in the visible stratification of the site in its entirety (Rasse et al., 2004; Soriano et al., 2010; Allsworth-Jones, 2021) (similarly to the Great Rift Valley discussed in CHAPTER 1).

2. All other unusual ESA and LSA sites (Korontière-I, Djita, Kuumaku, Koussokouangou, Koukouan-I, Pendjari-II, Fatandi V and Toumboura I) that do not fit within the general observable trends are located within the three sub-regions presented above (Falémé Valley, Atakora Region, and Jos Plateau). The high density of archaeological research carried out in these sub-regions compared to the rest of West Africa is the only true differing variable that explains such ecological variation in archaeological site presences.

The article therefore shows the wide distribution of Pleistocene sites in West Africa, clearly demonstrating the variability in distribution dependent on chronology, cultural attribution, and ecological setting of the sites. While **Cerasoni et al. (2022)** present a generalised and regional perspective of past hominin presence and demography in Pleistocene West Africa, another article present in this dissertation presents a detailed review of one of the most important and well-known sites, Iho Eleru.

As presented in **Cerasoni et al. (In Press)**, Iho Eleru, also known as Iwo Eleru, is one of the sites that receives the most attention from archaeologists and palaeoanthropologists alike, as it is the only site in West Africa where a Pleistocene human fossil was recovered. This article (**Cerasoni et al., In Press**) presents a detailed and updated review of the original archaeological contexts excavated and published by Shaw and Daniels (1984), while offering new interpretations and data supporting the archaeological and palaeoanthropological history of the site. First and foremost, a renaming of the site was applied following a re-evaluation of the correct Yoruba name for the site, which is *Iho Elèeru*, meaning "Cave of Ashes", or "Iho Eleru". The original site name of "Iwo Eleru" is the anglicised form of *Iho Elèeru* . In this manuscript the authors carried out a detailed evaluation of the original interpretations of the site stratigraphy, material culture attribution, and palaeoanthropological history of the Iho Eleru human fossil remains. As a result, new evidence was presented in support of the difficult stratigraphical deposition of the site. This new stratigraphic interpretation of Iho Eleru suggests that the entirety of the site of Iho Eleru underwent stratigraphic disturbance, with the exception of the central platform area (Figure 8). The major observations and discoveries from the site, such as the human fossil, and chronometric ages of the human remains and the material culture, remain unchanged. Regarding these conflicting ideas between the original published interpretations of the site and the interpretations presented in our article, they were all considered and accounted for in a later article present in this dissertation (**Cerasoni *et al.*, In Review**, appendix ii.1).

3.2. Archaeological investigation of tropical and sub-tropical West Africa

This section presents all the articles reporting major findings from the archaeological projects and investigations carried out during this study. The findings assess the behavioural adaptations of Pleistocene hominins in tropical and sub-tropical West Africa, offering high-resolution windows into the human-environment interactions and processes in various West African localities, including tropical rainforests, seasonal wooded grasslands, and ecotonal environments. For ease of consultation and understanding, this section was divided into site, context and article specific subsections, as follows:

3.2.1. Iho Eleru (Tropical West Africa)

- Cerasoni et al. (In Review). 'Human interactions with tropical environments over the last 14,000 years at Iho Eleru, Nigeria'. iScience. (appendix ii.1)
- Cerasoni et al. (2021). 'Late Pleistocene to Holocene paleoenvironmental reconstruction and human behaviour at Iho Eleru roch shelter, Nigeria.'. PaleoAnthropology, 2021(1), 161. (appendix i.5)

3.2.2. Tanongou Valley (Sub-Tropical West Africa)

- Cerasoni et al. (In Review). 'Newly discovered Middle Stone sites in Tanongou Valley, Atakora Region, Benin'. Open Quaternary. (appendix ii.2)

Relevant to this section a series of publications included in this dissertation are not going to be discussed in terms of results (**Scerri et al., 2021**, appendix i.3; **Hallett et al., 2021**, appendix 1.4; **Hallett, et al., In Review**; **Cerasoni et al., In Preparation**). This is done following one of two reasons: (1) The presented publication was not carried out as a primary research project by the author of this dissertation, or (2) the results are yet under development and not conclusive. Following this, the listed publications which will not appear within this chapter will be further discussed in CHAPTER 4. DISCUSSION AND CONCLUSIONS.

3.2.1. Iho Eleru (Tropical West Africa)

- Cerasoni et al. (In Review). 'Human interactions with tropical environments over the last 14,000 years at Iho Eleru, Nigeria'. iScience. (appendix ii.1)
- Cerasoni et al. (2021). 'Late Pleistocene to Holocene paleoenvironmental reconstruction and human behaviour at Iho Eleru roch shelter, Nigeria.'. PaleoAnthropology, 2021(1), 161. (appendix i.5)

As presented in Section 3.1, Iho Eleru represents one of the most important archaeological and palaeoanthropological sites in West Africa. As part of this study, one published presentation (**Cerasoni et al., 2021**, appendix i.5), one handbook chapter (**Cerasoni et al., In Press**, appendix i.2) and one article (**Cerasoni et al., In Review**, appendix ii.1) set out to provide detailed characterisations of the archaeological, palaeoenvironmental and behavioural adaptations of the past inhabitants of the site. The Iho Eleru rock shelter, located in Southwest Nigeria, was visited in 2019 by the author of this study. The original intent of excavating the site was to re-investigate the stratigraphy and in situ archaeological materials. This ended abruptly due to political contension of the land within which the site was located. Therefore, following an attack and days-long difficulty of the author and team in the field, the team moved to the University of Ibadan where the original collection of excavated materials was evaluated and studied. From this material, a published refereed conference abstract was produced, and that later developed into the article present in this dissertation.

From the investigated collection stored at the University of Ibadan, new chronometric, archaeobotanical and paleoenvironmental findings were brought forth, and these are presented here (Figure 9 and 10). Firstly, our new ^{14}C dating results (Figure 9), sampled from charred plant macroremains and faunal remains originating from the plateau area of the rock shelter, confirm that Iho Eleru spans a wide timeframe, from approximately 13.2 ka to today. The earliest available radiometric age was obtained from sampled materials originating from the same deposit as the Iho Eleru fossil, confirming its Pliestocene chronology. The dating results obtained were remarkably close to the original dates published by Shaw and Daniels (1984), and complement the direct dating carried out by Harvati et al. (2011) which dated the Iho Eleru hominin reamins through U/TH dating to 11-16 ka. Furthermore, some of the samples that were dated originated from contexts outside of the central plateau area (see Section 3.1). These dated materials resulted in radiometric ages that were not stratigraphically compliant with the central plateau area, suggesting depositional inversion. This data supported once again the evidence of stratigraphical inversion within the areas outside the main central plateau.

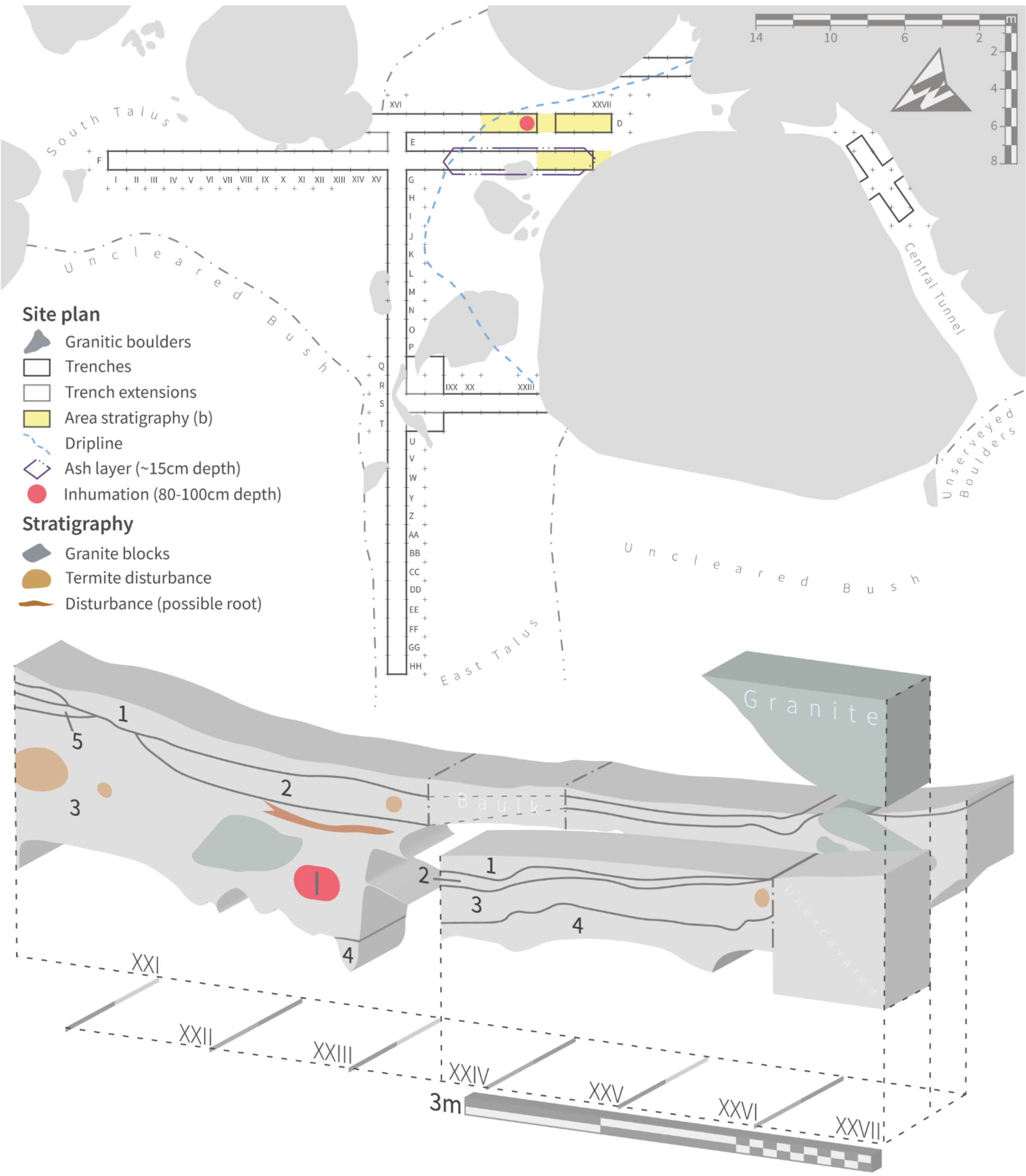

Figure 8. Site plan (a) of Iho Eleru and stratigraphic sections (b) of the upper plateau area (marked in yellow on the site plan), along the east faces of trench D XXI-XXVII, and trench F XXIV-XXVII. The plan and stratigraphical location of the inhumation has been shown with a red circle and with the letter "I". The stratigraphical layers are described as follows: 1 - superficial ash layer, 2 - red sandy layer, 3 - reddish brown soil, 4 - gravelly soil, 5 - browner and looser than 3, but redder and less sandy than 2. (Corrected and redrawn after Shaw and Daniels 1984, pp. 189 and 193).

Archaeobotanical analyses were also performed on the samples indentified from the Iho Eleru collection, and were comprised of twelve indentifiable wood charcoal fragments, fourteen endocarp fragments and twelve unidentifiable fragments of carbonized plant remains. Interestingly, the endocarps were identified as *Canarium schweinfurthii* (commonly known as African olive), and *Elaeis guineensis* (commonly known as oil palm) (Figure 9). Direct dating on the endocarps provides evidence for the earliest known exploitation of *Canarium* in West Africa, directly dating to ~11.3 ka, and an extremely early exploitation of *Eleais* before 10 ka. The wood charcoal analysis also shows the local use of wood species sich as *Gaurea* spp. and *Piptadeniastrum africanum*, both identifiable as forest environment species. Of the unidentified fragments, all fragments are probable forest and woodland taxa, with no clear representation of savanna- or grassland-originating taxa.

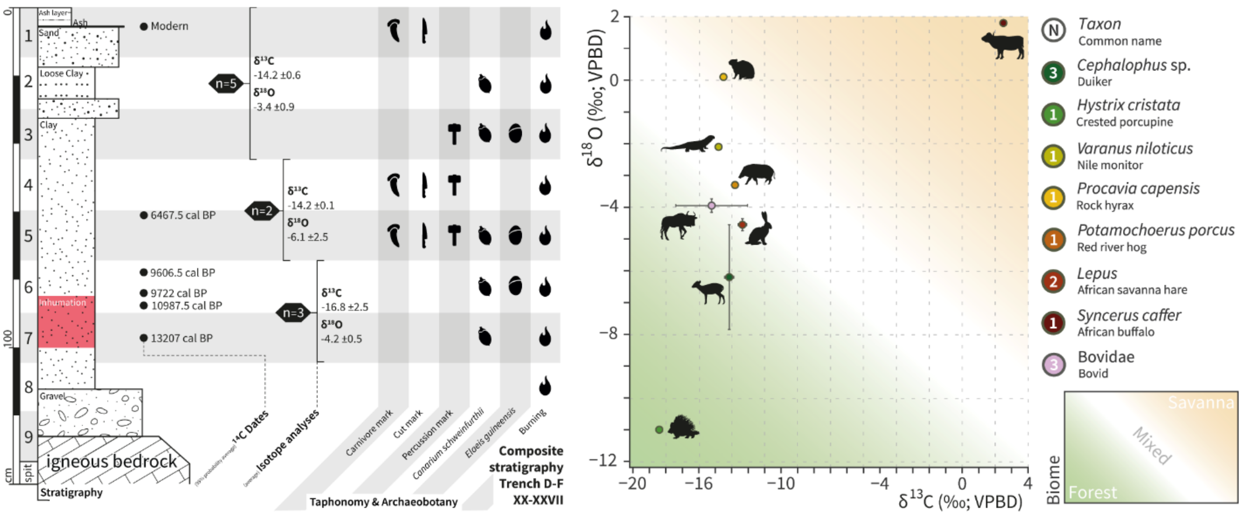

Figure 9. Left - Composite stratigraphy of Trenches D and F, spits XX-XXVII. Within it are presented the new 14C dates, the isotopic results averaged into three discrete groups, archaeobotanical identification of C. schweinfurthii and E. guineensis. **Right -** Stable carbon and oxygen isotope data for all faunal samples analysed (n=13). Mixed feeders both graze in grassland and browse in shrubland and forests (Hofmann and Stewart, 1972).

One of the surprises encountered during the evaluation of the excavated material collection was the identification of the previously reported lost faunal collection. This unique collection, representing the only Pleistocene faunal assemblage ever recovered in West Africa and previously reported lost (Shaw and Daniels, 1984, p. 30), was analysed by means of taphonomic, taxonomic and isotopic techniques. With a total of 207 bone fragments, 152 had intact bone surface and were able to be analysed for bone surface modification, burning and breakage patterns (Figure 9).

Although the faunal collection was highly fragmented, it was possible to assess that 28.9% of the assemblage was consistituted by burnt fragments, with the majority of them being carbonized, with far fewer being calcined. The differential rates of burning observed suiggested the use of open fires, and that most burnt bone fragments were heated post-depositionally beneath open fire. Furthermore, butchery marks were evident on the faunal collection, with evidence of percussion marks, percussion notches and cut marks present on 12.5% of the total assemblage. Nevertheless, other than the aforementioned anthropogenic activity visible on the faunal collection, evidence for carnivore accumulation was also present, albeit at a lower rate, with11.8% of bone surfaces displaying tooth marks or tooth notches, and 3.29% displaying gastric etching).

Taxonomic identification of the faunal collection led to a total of ten taxa diagnosed to the species level. The identified species range from forest to grassland inhabiting species. The assemblage includes taxa ranging in body size from large African buffalo (*Syncerus caffer*) to small West African black turtles (*Pelusios niger*). Forest-inhabiting species include yellow-backed duiker (*Cephalophus silvicultor*), bushpig (*Potamochoerus porcus)*, crested porcupine (*Hystrix cristata)*, giant pouched rat (*Cricetomys* sp.), and Nile monitor (*Varanus niloticus*). Identified vertebrates preferring savanna habitats include African buffalo (*Syncerus caffer*), African savanna hare (*Lepus microtis*), and ostrich (*Struthio camelus*). A single burnt ostrich eggshell fragment was identified. The relative frequency of forest vertebrates recovered from the Iho Eleru assemblage decreased over time, while the relative frequency of savanna vertebrates increased over time (Figure 10). Following the taxonomic indentification of the assemblage, no carnivore remains or coprolites were identified. Furthermore, a total of six Osteichthyes (bony fish) bone fragments and two marine shells were identified in modern deposits only, and no terrestrial gastropods were identified.

Finally, the isotopic analyses on the enamel of the faunal collection resulted in a total of thirteen sampled and analysed vertebrate teeth (Figure 9). Although the sample size is limited, the δ13C values covered a wide range (−18.6‰ to 2.5‰), exhibiting vertebrates that exploited a wide variety of habitats, including closed canopy C_3 forests and open C_4 dominated grasslands. The δ18O values covered a similarly wide range (−11.0‰ to 1.8‰), providing evidence for the exploitation of a variety of groundwater and fresh water sources for the animals present and consistent with access to a variety of environments, ranging from shaded forests to more open, arid settings.

Overall, considering the stratigraphical origin of the sampled vertebrate teeth, together with the taxonomically-identified faunal remains, the vertebrates suggest that a greater proportion of forest-dwelling species were dominant at the beginning of the recorded stratigraphy, with an increase of savanna-dwelling species over time.

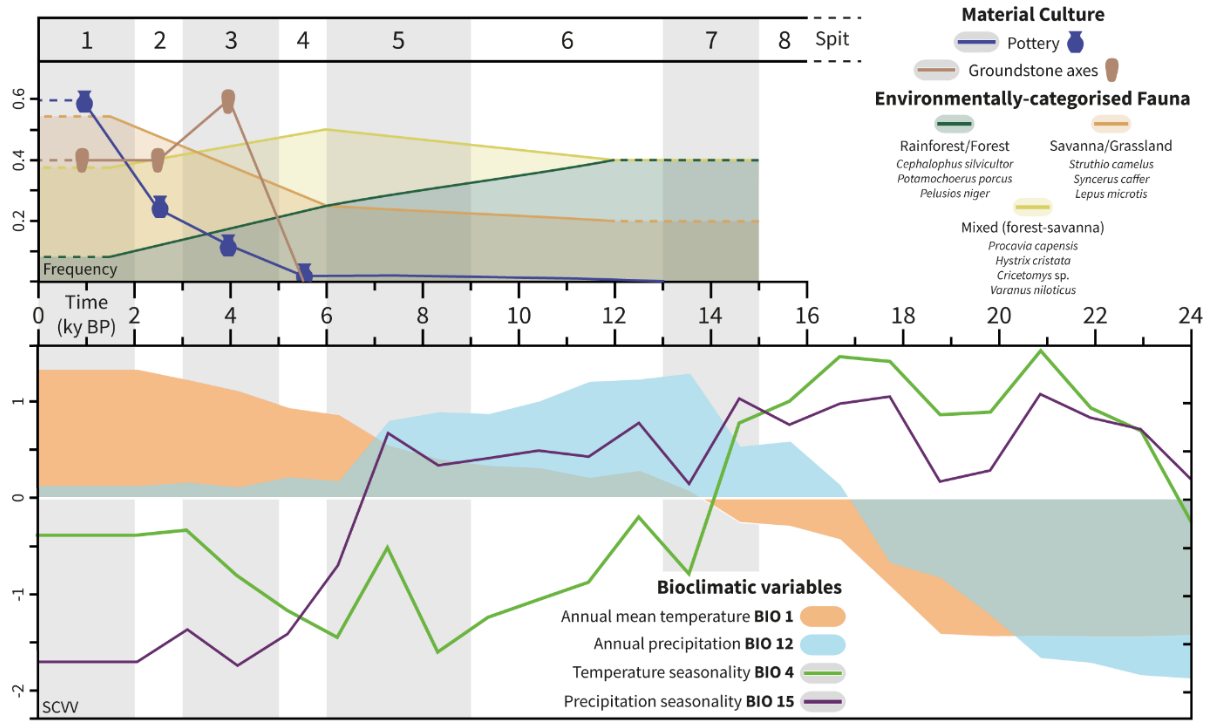

Figure 10. Synthesis of paleoclimatic variable curves, material culture frequency, and faunal remains frequency during the last 24 ka. At the bottom, scaled values of modelled annual mean temperature, annual precipitation, net primary productivity (vegetation biomass), and precipitation seasonality for each 1-thousand-year slice. At the top, frequency plots for the recovered material culture and identified fauna distinguished into environmentally categorised taxonomies.

In addition to the archaeological and palaeoenvironmental analyses carried out on the Iho Eleru assemblages, supporting paleoclimatic modelling was performed to have a modelled reconstruction of temperature and precipitation during the last 22 ka at the site. The purpose of this method was to test any correlation between faunal and floral trends and paleoclimatic shifts. As the paleoclimatic model shows, there was in fact an abrupt paleoecological change at Iho Eleru approximately 5-7 ka. During this period, the fauna at Iho Eleru changes from forest-dominant to savanna-dominant, and there is a visible increase in temperatures and decrease in precipitation rates. Interestingly, during this period the material culture also changes, with a sudden appearance of pottery and groundstone axes.

In sum, our data clearly demonstrates two archaeological periods at Iho Eleru, with an intersectional transition among them. Firstly, the Later Stone Age, or Late Pleistocene, chronology at Iho Eleru consisted of a local landscape characterised by a parchwork of forested-and savanna-dominant tropical environments. The site was most probably located within a small-scale forested island, surrounded by an ecotonal landscape. During this period, people inhabiting Iho Eleru used resources from both forest and savanna environments, with no distinct preference for forest or savanna vertebrate species, as supported by the taxonomic study. Finally, during the Late Pleistocene we found evidence for the use of *Canarium* (African olive) and *Eleais* (oil palm). So far, the data is not enough to prove a continuous use of these botanical species, but the data shows direct evidence of human use and probable consumption of them.

The second archaeological period within the rock shelter, which occurred following an approximately one thousand year long transitional period, was deposited during the Middle Holocene. During this period, a synchronous event occurred with an opening of the vegetation canopy, hence an increase and expansion of grassland environments, and a visible change in the material culture, with the appearance of relief/groove motifs pottery and ground stone axes). These correlated events could suggest an introduction of new cultural innovations triggered by the appearance of grassland corridors from the North. Following this, cultural borrowing processes or the arrival of a new cultural population at the site could have caused the visible drastic change in lithic, ceramic and ground stone material history.

3.2.2. Tanongou Valley (Sub-Tropical West Africa)

- Cerasoni et al. (In Review). 'Newly discovered Middle Stone Age sites in Tanongou Valley, Atakora Region, Benin'. Open Quaternary. (appendix ii.2)

Following the detailed environmental and archaeological studies carried out in the already well-known and published site of Iho Eleru, a different study carried out as part of this dissertation was in the Atakora Region of Benin. Following a field expedition to this region in February 2020, survey, excavation and material culture analysis was undertaken, resulting in the production of a manuscript currently in review (**Cerasoni et al.,** appendix ii.2).

As previously discussed in **Cerasoni et al. (2022)**, West Africa is a region that is poorly studied in terms of Pleistocene human evolution. Nevertheless, select sub-regions have been the focus of relatively intense survey and excavation programmes, resulting in the discovery of a higher concentration of sites compared to the rest of West Africa. Among these sub-regions, the Atakora Region is an interesting case, with a previously unidentified archaeological record spanning the ESA to the Iron Age. This area, although only becoming of interest to archaeologists in the recent decades, has been surveyed and studied extensively for the presence of preserved Pleistocene sites (Petit, 2005; N'Dah, 2009). Ecologically, it is located approximately 250 kilometers north of the current ecotonal boundary between Sahelian savannas and Guinean forests (Figure 1). This region is subject to extreme topographic and elevation variability, characterised by a mosaic-like environmental landscape with enclosed forested areas located within a dominant savanna environment. The ecological, topographic and archaeological uniqueness of this region led to the interest of its inclusion within this study in order to identify potentially important data to address the research questions in CHAPTER 1.

Consequently, an expedition was led by the Pan African Evolution Research Group in February 2020, in collaboration with the University of Abomey-Calavi in Benin. The major objective of this expedition was to visit and survey areas of high archaeological interest. During the surveying of the region, one area of particular interest was selected for further investigation and excavation within the Atakora Chain Formation (Figure 1, Figure 2): Tanongou Valley (Figure 11). This area is located within an ecotonal micro-landscape, consisting of an extremely small-scale densely forested area (identified as Eastern Guinean Forest biotype) within a quartzitic valley formed by water erosion from a waterfall and river. This valley features the MSA cave site of Tanongou Cave, partially excavated in the early 2000s (Petit, 2005; N'Dah, 2009), and the newly discovered open-air site of Paloli.

Tanongou Valley measures over two kilometres in length, with a width of approximately 450 meters at its widest point. The south-western portion of the valley originates at the location of the Tanongou Waterfall system, where its resulting plunge pool feeds a river which, following the length of the valley, reaches the town of Tanongou where the Valley ends. Previous excavations in this valley were carried out solely at Tanongou Cave (Figure 11), where partial excavations resulted in the recovery of Iron Age materials (Petit, 2005). Original reports of this excavation documented a lithic assemblage, although no detailed technological or cultural analyses were carried out. Following survey, excavation and chronometric dating of the discovered sites, we discovered extremely well preserved MSA layers and lithic assemblages.

Tanongou Cave, located approximately 15 meters from the plunge pool, is situated at an altitude of 8 meters above the water level (during dry season) on its western cliff. The formation origin of the cave is yet uncertain, but most probably it formed as a result of fracture-induced weaknesses within the quarzite bedrock, causing displacement and collapse of blocks and forming a cavity. The sedimentary stratigraphy of the site is extremely complex, due to the presence of collapsed quartzite blocks. However, a minimum of 3 meters of consolidated cave sediments was observed in situ, charactersied by loose, overlying sediments concealing any further depth of the primary deposits.

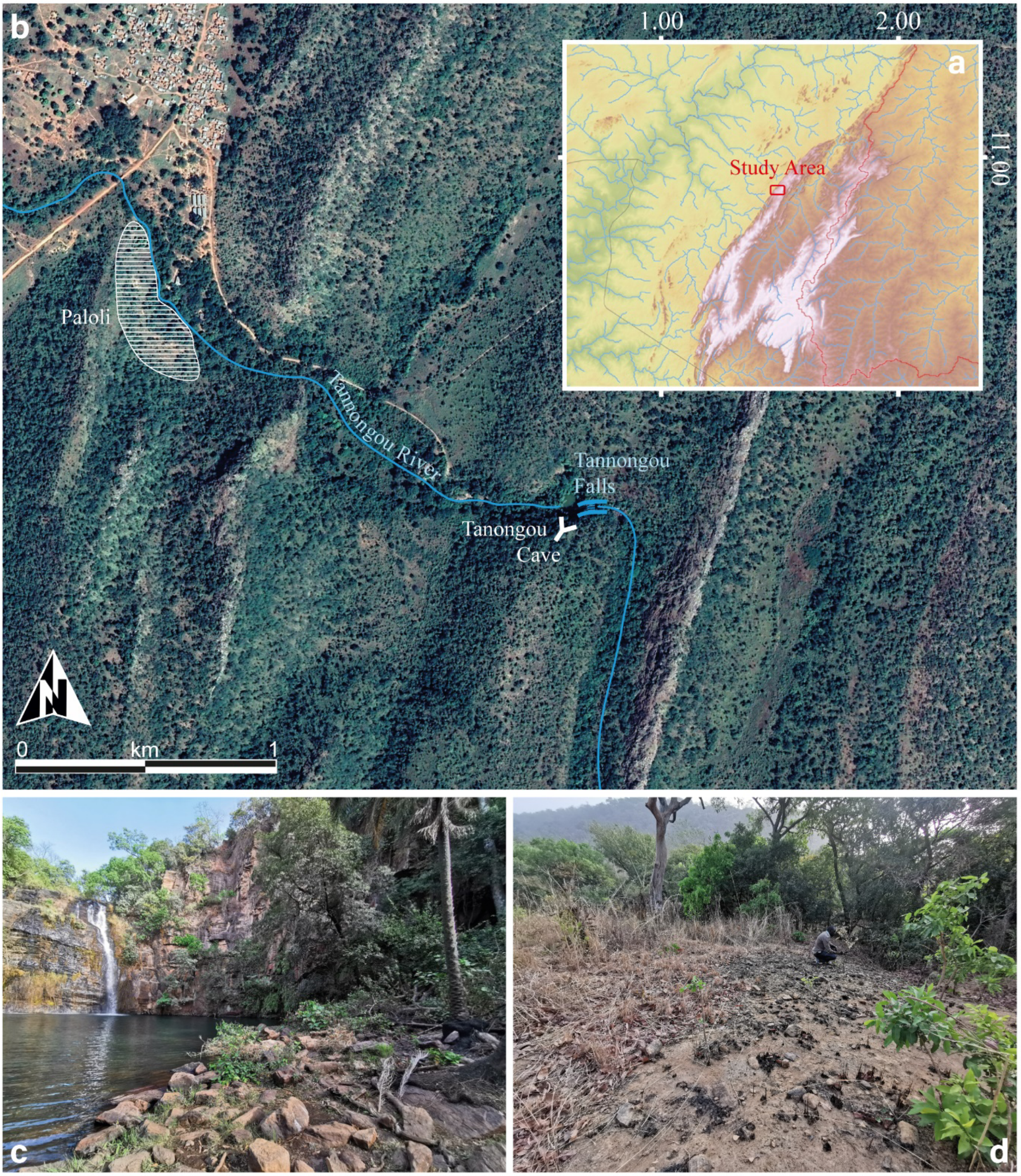

Figure 11. Upper section: study area location over altitude map of the Atakora Region (a) and site locations superimposed upon satellite imagery (Google Earth©) of the Tanongou Valley, with mapped fluvial systems (b). Lower section: Tanongou Falls, with plunge pool, and entrance of Tanongou Cave visible on the right (c); pre-cleaning area excavated during 2020 expedition (d).

Excavations at Tanongou Cave were carried out to test and evaluate the density, quality and character of material culture and sedimentary deposits. In view of previous investigations (Petit, 2005) a small 75x75 centimeter trench was set and excavated at a lower elevation from the original investigation (Figure 12). Following excavation, two sedimentary units were observed, one of primary (U1) and one of secondary (U2) deposition. Most of the lithic artefacts retrieved from the excavation were located within U2, with a total of 34 artefacts, and were mostly concentrated within a single pocket consisting of exclusively lithic artefacts and an absence of clasts and sedimentary matrix.

The site of Paloli was discovered during the survey of the valley, and is set in a narrow floodplain, with steep bedrock cliffs on its western and eastern sides (Figure 11). The site was first discovered following the observation of an extremely dense and extensive surface lithic scatter, with thousands of lithic artefacts visible from simple field walking. The site consists of a low slope sediment ramp occuring on the western side of the valley and stretching from the bedrock cliff to the modern river floodplain, with a 1.5 meters step separating the site from the floodplain. The surface of the identified sediment ramp is covered in quartzite boulders derived from the cliffs, with fine-grained particles forming the main matrix of the sediment. Similarly to Tanongou Cave, the close proximity environment is forested, albeit with a more sporadic wood coverage comparable to wooded savanna biomes.

During investigations the ramp was surveyed and a lithic-rich area of over three hectares was identified, with artefacts in primary (*in situ*) and secondary (superficial scatter) position. Among the whole area, four discrete locations were studied. Of these four, three were selected for surface lithic collection (with the intent of generating a teaching collection for the Department of Anthropology at University of Abomey-Calavi, Benin), and one was further excavated. The excavated trench (T1) was gridded into a 3x3 meter area. Surface lithics from T1 were recorded in their original position and collected, and the central square of the grid was excavated (Figure 12). A total of 134 lithic artefacts were retrieved in T1, with 44 being recovered in primary deposition within the excavated deposits. The stratigraphy of Paloli consisted of two separate sedimentary units. The upper unit (U1) was composed by a thin disturbed deposit, characterised by areas of heavy ferruginous encrustations at the surface level. This layer was formed by the deposition of secondary sediments which hardened and formed an extremely hard crust. The lower unit (U2) was characterised by homogeneous, unstructured red fine sand and silt mix. Most probably, U1 is an erosional product of U2 caused by the deflation of the latter, and a later hardening caused by climatic and environmental factors.

During the field expedition several sedimentary samples (see CHAPTER 2) were collected for OSL (optically stimulated luminescence) dating on quartz and K-feldspar grains. Unfortunately, due to contamination of the samples, the dose rates were relatively high. The values suggest that contamination occurred during transportation of the samples and that a possible disintegration in transit rendered them unreliable for dating. Nevertheless, the very limited data obtainable from the OSL samples supports a Pleistocene age of the dated sediments.

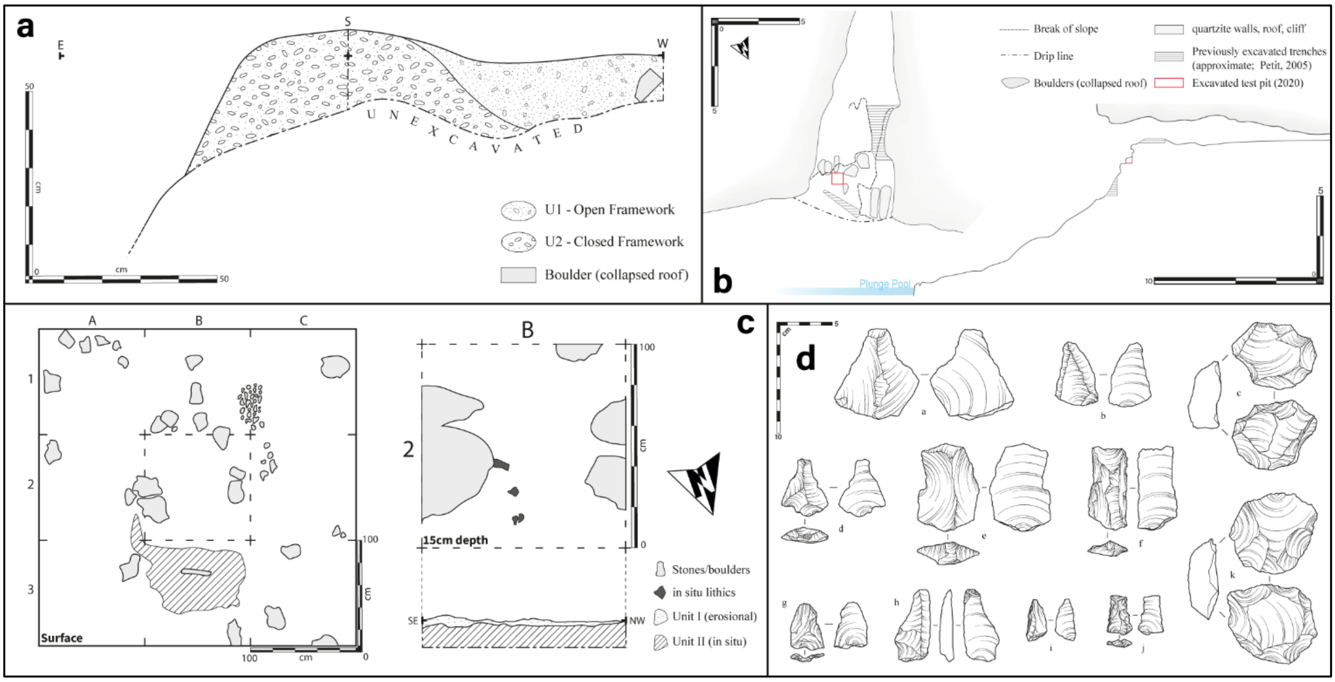

Figure 12. Composite figure showing plan of Tanongou Cave, excavated plans of Tanongou Cave and Paloli, and a selection of the retrieved lithic artefacts. (a) Stratigraphical section of Tanongou Cave, (b) Top and lateral plans of Tanongou Cave (modified from Petit, 2005), (c) Excavation at Paloli T1; on the right, top plan of T1 before excavation, and on the left, plan of the final surface reached after excavation of square B2 with its corresponding stratigraphical section, and (d) Selection of lithic objects excavated at Tanongou Cave (a-f) and Paloli (g-k). a, e, f, g, j: Levallois flakes; b, d: Levallois points; c, k: Levallois cores; h: end scraper; i: backed piece.

From the survey and excavations at Tanongou Valley, a total of 243 lithic objects were retrieved (Tanongou Cave, N=50; and Paloli, N=193). Both sites feature classic MSA technological characteristics. As an example, Levallois flake concentrations varied from an extremely high 40% in Tanongou Cave, to a relatively high average of 13% in Paloli. Core technology is poorly represented, with four Levallois cores retrieved at Paloli, of which only one was in situ, and none found at Tanongou Cave. Other technological features present in both assemblages are plain platforms, discoidal cores, and some core-on-flake morphologies (only at Tanongou Cave).

Raw material types at both sites are varied and different between the two sites (Figure 13). The majority of material types present are of metamorphic origin. The predominant raw material used was quartzite, which is available in the immediate vicinity of the sites and beyond, as it is the primary constituent of the Atakora Chain formation. Quartz is prevalent in the site of Paloli, yet is absent in Tanongou Cave. Siliceous raw materials such as jasper and chert are present in both sites (Figure 13). Cortex analysis of all lithic artefacts shows that local raw materials (quartzite and quartz) presented angular, sub-rounded and rounded cortex features, suggesting local raw material sources from outcrop and secondary formations. Siliceous materials, on the other hand, presented only angular cortex, suggesting surface outcrop collection. The observations made from the analysis of cortex features, and the lack of core technology at both sites, indicates that non-quartz and quartzite materials were collected from surface outcrops outside of Tanongou Valley. This suggests that completed and pre-formed artefacts were transported to the site from beyond the immediate landscape. Based on N'Dah (2009), the most probable origin of chert and jasper is within the northern region of the Pendjari park over 50 kilometers north, where outcrops of similar materials have been documented in association with Stone Age sites.

Statistical analyses were also carried out to assess and identify any possible correlation or relationship of interest that could offer further preliminary insights on the production strategies and technological characteristics of both sites. For this reason, correlation matrixes were plotted and categorised into three separated groups, and the correlation values between 36 different variables were calculated (Figure 13). A total of six matrix tables were plotted, with three tables for each of the two sites, and they were divided as follows: (1) only flakes and retouched pieces, (2) pieces made from local raw material, and (3) pieces from non-local raw material. These categories were selected with the intent to assess any possible relationship between the two assemblages based both on their technological charateristics of flakes and retouched pieces, and on the raw materials used throughout the assemblages. All the resulting correlation values were evaluated, and four discreet variables were selected for further testing based on their high correlation values: (1) technological length, (2) maximum technological width, (3) platform width, and (4) maximum platform thickness. The data presented in Figure 13 shows that these four discreet variables are strongly correlated. Based on the data, correlation values greater than 0.8 were selected, and the resulting relationships were further tested by plotting regression graphs (Figure 13c-f). The positive regressions, with extremely low p-values and mid-range r-squared values, suggest that toolmakers at Paloli and Tanongou Cave had similar lithic production strategies. Strong positive correlations between technological width and technological length indicate similarly shaped products, in both local and non-local raw materials for Paloli, and only in non-local materials in Tanongou Cave (Figure 13c and 13f). Furthermore, in Tanongou Cave both types of raw materials show a high correlation between platform width and thickness, indicating a production selection of lithic objects with very wide and thick platforms (Figure 13c). The last observed relationship was identified only in the assemblage from Paloli (Figure 13e), where platform width and technological width are highly correlated, suggesting a preferential selection for lithic objects with extremely wide and thin platforms. These stastical analyses offer an interesting overview of the possible selection patterns of their toolmakers. Although these findings are yet preliminary in nature and were applied on assemblages with low sample sizes, these observations should be considered in future studies of the lithic assemblages from Tanongou Valley.

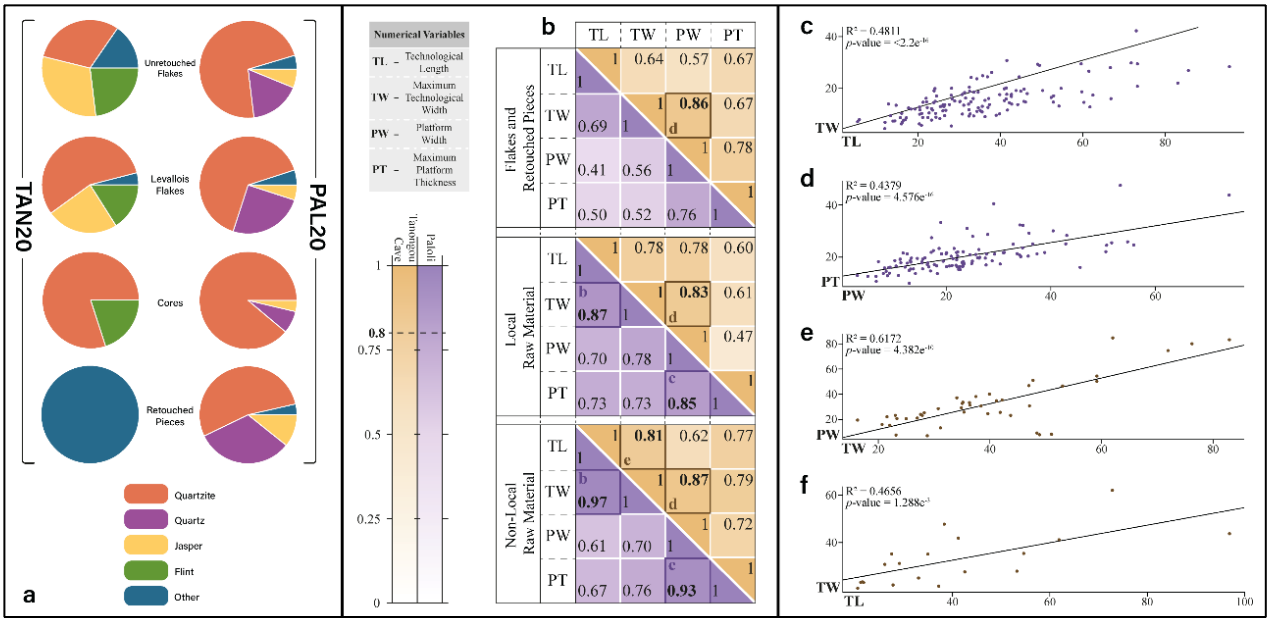

Figure 13. Plots of raw material types and statistical analyses of lithic assemblages at Tanongou Cave and Paloli. On the left, (a), Breakdown of major raw material classes by artefact class. In the center, (b), correlation matrix between the four selected variables (TL, TW, PW, and PT), for the sites of Tanongou Cave and Paloli. All values in bold are over 0.8 and were selected from further testing. On the right (c-f), regression plots illustration the relationships between the previously selected variables from the sites of Paloli (b-c), and Tanongou Cave (d-e).

The differences measured and calculated in technological character, material type, and cortex variability, together with a strong statistical correlation between both assemblages, suggest a similar MSA techno-complex was used at both sites. The collected and analysed data shows that both sites were inhabited by one or more populations using an MSA tool kit. Nevertheless, there are observable differences in the studied assemblages. This leads to the hypothesis that there was a difference in activity type and behavioural processes within the sites of Tanongou Cave and Paloli. To fully test this theory, more data will be necessary in the form of larger excavated assemblages, together with further analyses into the formation processes and possible post-depositional and erosional activities of both archaeological sites.

3.3. Environmental investigation of African forested biomes

This section presents a preliminary ongoing project. This study aims to better understand the microbotanical characters of different forest types in the African continent, geographically extending from West to East Africa. This project will be central to the creation of a comprehensive database and index that will offer a novel method for identifying specific African forest types from phytoliths extracted from a variety of sources, including sediment, lacustrine, riverine, biological and mineral samples.

- Cerasoni, J.N., Neumann, K., & Bremond, L. 'Forest phytoliths for the identification of forest types in the African continent. A definition and description of new indices'.

Within this study a series of modern surface samples were selected for phytolith analysis, all originating from different forest floristic regions spanning across West Africa (Figure 1, Figure 2, Figure 4, Table 3) and East Africa (Table 3). These regions are: Sudanian, Sahelian, Zambezian, Guinea-Congo, and Afromontane floristic zones. This study sets to carry out a morphological identification for each of these forested regions, followed by numeric and statistical analyses of phytolith morphotypes. The final objective is to identify any specific patterns or variations that can aid in the specific identification of forest types solely from their phytolith-production properties. To ensure the highest possible degree of reliability, a series of quantiative and qualitative variables will be considered and accounted for during the upcoming post-processing of the retrieved phytolith assemblages. The variables include: (1) Location (country, geographic coordinates), (2) Time (date, season), (3) Modern vegetation (type, water presence, landscape seasonality, ecotonal/savanna presence, unique identified taxon), (4) Morphological characters (will be denominated following ICPN 2.0; ICPT, 2019), (5) Morphometric character (size), (6) Presence of burning activity, and (7) D:P and Ic ratios (Bremond et al., 2005, 2008; Barboni et al., 2007; Neumann et al., 2009; Strömberg et al., 2018).

Currently, an initial morphotype identification from all included samples (Figure 1, Figure 2, Table 2, Table 3) has been completed. The identified morphotypes have been collected and categorised based on the ICPN 2.0 nomenclature (ICPT, 2019). The most interesting morphotypes that show variability in presence and density depending on forested floristic region are: spheroids, blockies, grass short cell phytoliths (GSSCP; bilobates, crosses, saddles, rondels), and sclereids (amoeboid, elongates, brachiates and polyhedrals). Initial observations suggest a distinct morphotype differentiation of phytolith assemblages between West and East African forests, hypothetically caused by differences in elevation and climatic variability. Furthermore, dense canopy environments show a distinct high presence of diagnostic phytolith morphotypes (i.e. spheroids, blockies, and sclereids), in contrast to the absence of any diagnostic phytolith morphotypes in open canopy environments such as ecotonal, gallery and transitional forests.

Identified Phytolith Morphotypes	**Spheroid**	**Sclereids**	**Tracheary**
	Psilate	Amoeboid baculate	annulate/helical
Acute bulbosus	Ornate	Amoeboid psilate	pitted
Blocky	Echinate	Elongate arcuate Type 1	**Special types**
Bulliform flabellate	Plicate	Elongate arcuate Type 2	Acute arcuate
Elongate	Nodular	Brachiate	Commelinaceae
Dentate Type 1	**GSSCP**	Geniculate	Cyperaceae
Dentate Type 2	Bilobate	Polyhedral	Perforated platelet
Dendritic	Crenate	Polyhedral elongate	
Entire Type 1	Cross	Dicot Epidermis	
Entire Type 2 (Runge A1)	Saddle	**Polygonal tabular**	
Sinuate	Sinarundinaria	**Polylobate tabular**	
Prismatic (Runge A3)	Rondel		

Table 2. Identified phytolith morphotypes. Named following ICPN 2.0. Morphotypes in bold represent major morphological groups.

Sample	Country	Location	Floristic zone
7	Mali	Pays Dogon, Ségué	Sahelian
16	Mali	Djiguibambo	Sahelian
17	Mali	Kani-Kombole	Sahelian
43	Cameroon	Nyabessan	Guinea-Congo
45	Cameroon	Parc Nat. Campo-Ma'an	Guinea-Congo
46	Cameroon	Parc Nat. Campo-Ma'an	Guinea-Congo
47	Cameroon	Nkongmeyos	Guinea-Congo
48	Cameroon	Nkongmeyos	Guinea-Congo
56	Cameroon	Aya'Aman	Guinea-Congo
57	Cameroon	Ebyanemeyong	Guinea-Congo
135	Mali	Djiguibambo	Sahelian
138	Mali	Pays Dogon, Ségué	Sahelian
282	Burkina Faso	Unknown	Sahelian
286	Burkina Faso	Foret classée de Niangoloko	Sudanian

287	Burkina Faso	Reserve Comoé-Leraba	Sudanian
288	Burkina Faso	Reserve Comoè-Leraba	Sudanian
289	Burkina Faso	Bala	Sudanian
317	Mali	Kita	Sahelian
318	Mali	Bamako	Sahelian
320	Mali	Unknown	Sahelian
321	Mali	Kita - Boulouli	Sahelian
324	Mali	Kita	Sahelian
326	Mali	Kita, Forêt Classée de Siguifiri	Sahelian
327	Mali	Kita	Sahelian
330	Mali	Kita	Sahelian
334	Mali	Pays Dogon, Teli	Sahelian
335	Mali	Kita	Sahelian
353	Nigeria	Runse bei Intini	Sudanian
384	Nigeria	Nahe Fundplatz Janruwa C	Sudanian
385	Nigeria	Piste Janruwa-Janjala	Sudanian
401	Tansania	Bei Kidayi	Zambezian
402	Tansania	Mikumi and Mbeya	Zambezian
403	Malawi	Wintukutu Forest Reserve	Zambezian
404	Kamerun	Nyabessan rive sud du Ntem	Guinea-Congo
405	Kamerun	Parc National Campo-Ma'an	Guinea-Congo
406	Kamerun	Parc National Campo-Ma'an	Guinea-Congo
407	Cameroon	Ebyanemeyong	Guinea-Congo
408	Cameroon	Nkongmeyos	Guinea-Congo
409	Cameroon	Meyos	Guinea-Congo
503	Kenya	Turkana Basin, Koobi For a	Afromontane
853	Ethiopia	Kure, SNNPR, South Omo Zone	Afromontane
854	Ethiopia	Kure, SNNPR, South Omo Zone	Afromontane
855	Ethiopia	Kure, SNNPR, South Omo Zone	Afromontane
856	Ethiopia	Kure, SNNPR, South Omo Zone	Afromontane
857	Ethiopia	Kure, SNNPR, South Omo Zone	Afromontane
858	Ethiopia	Zomba, SNNPR, South Omo Zone	Afromontane
859	Ethiopia	Busca, SNNPR, South Omo Zone	Afromontane
860	Ethiopia	Busca, SNNPR, South Omo Zone	Afromontane
861	Ethiopia	Kure, SNNPR, South Omo Zone	Afromontane
933	Cameroon	Unknown	Guinea-Congo
934	Cameroon	Essok	Guinea-Congo
935	Cameroon	Essok	Guinea-Congo
936	Cameroon	Bito	Guinea-Congo
937	Cameroon	Bito	Guinea-Congo
938	Cameroon	Bito	Guinea-Congo
939	Cameroon	Nie	Guinea-Congo
940	Cameroon	Zoe	Guinea-Congo
941b	Tanzania	Poroto	Afromontane
942b	Tanzania	Poroto	Zambezian
943b	Tanzania	Poroto	Zambezian
944b	Tanzania	Lake Kingeri	Zambezian

945b	Tanzania	Lake Kingeri	Zambezian
946b	Tanzania	Lake Masoko	Zambezian
947b	Tanzania	Lake Masoko	Zambezian
949	Tanzania	Mt. Kilimanjaro	Afromontane
950	Tanzania	Mt. Kilimanjaro	Afromontane
951	Tanzania	Mt. Kilimanjaro	Afromontane
951	Tanzania	Mt. Kilimanjaro	Afromontane
953	Tanzania	Mt. Kilimanjaro	Afromontane
954	Tanzania	Mt. Kilimanjaro	Afromontane
955	Tanzania	Mt. Kilimanjaro	Afromontane
956	Tanzania	Mt. Kilimanjaro	Afromontane

Table 2. List of locations where modern soil samples were exctracted for the purpose of this study. Samples were collected by K. Neumann, B. Eichorn, N. Garnier, L. Bremond, M. Schimdt, B. Tchiengué, V. Montade.

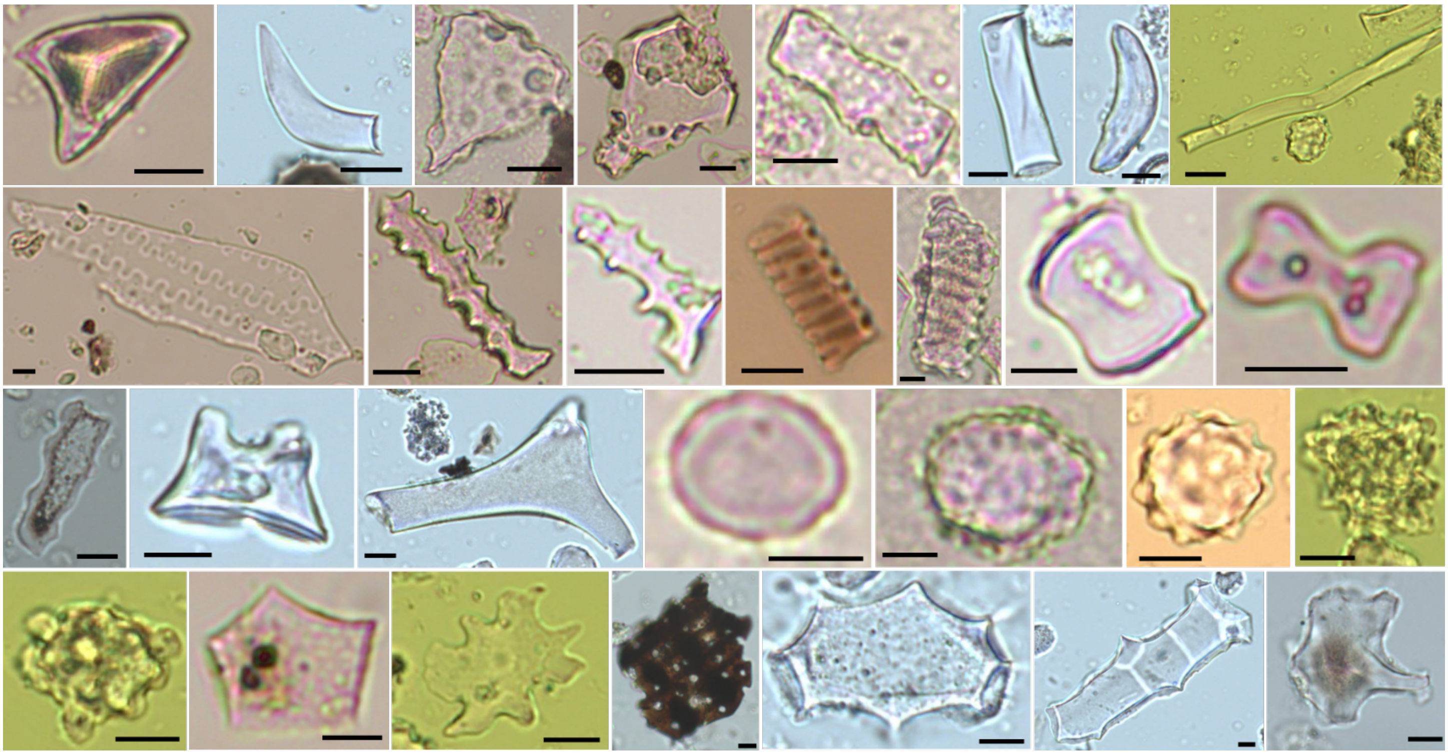

Figure 13. Micrographic selection of identified phytolith morphologies. All scale bars are 10µm. First row, left to right: acute bulbosus, acute arcuate, blocky, bulliform flabellate, elongate entire Type 1, Elongate entire type 2, elongate arcuate type 1, elongate arcuate type 2. Second row, left to right: elongate sinaute, elongate dentate type 1, elongate dentate type 2, tracheary annulate/helical, tracheary pitted, saddle, bilobate. Third row, left to right: crenate, rondel, geniculate, spheroid psilate, spheroid ornate, spheroid echinate, spheroid plicate. Fourth row, left to right: nodular, polygonal tabular, polylobate tabular, perforated platelet, sclereid polyhedral, sclereid polyhedral elongate, sclereid amoeboid psilate.

3.4. Development of novel digital methods for the visualisation of archaeological materials

The final major facet of the research projects included in this dissertation involves the utilisation of digital technologies for the production of data from archaeological material culture. This originally started with my involvement in **Scerri et al. (2021)**, and I then expanded on my work produced in said publication by developing three methods for the illustrative, photographic and volumetric representation of archaeological materials. The following publications were produced from this work:

- Cerasoni et al. (2022). 'Do-It-Yourself Digital Archaeology: Introduction and Practical Applications of Photography and Photogrammetry for the 2D and 3D Representation of Small Objects and Artefacts'. PLOS ONE. (appendix i.6)
- Cerasoni (2021). 'Vectorial application for the illustration of archaeological lithic artefacts using the "Stone Tools Illustrations with Vector Art" (STIVA). PLOS ONE. (appendix i.7)
- Scerri, E.M.L. et al. (2021). 'Continuity of the Middle Stone Age into the Holocene'. Scientific Reports 11, 70. DOI: 10.1038/s41598-020-79418-4 (appendix i.3)

To this day, the field of archaeology is heavily reliant on visual information. Whether it be visualisations of material culture or illustrations of artefacts that are difficult to discern in photographic form, figures and data gathered from visual- and graphic-reliant sources represent a fundamental part of any archaeological publication. Nevertheless, standardisation of the processes utilised to produce such visual representations is almost non-existent. Furthermore, modern techniques that produce the highest quality products tend to have limitations, including: (1) high cost of equipment and/or production time, (2) inaccessability caused by lack of method sharing, and (3) inaccessability caused by a lack sharing outside of a specific academic and laboratory environment. To address these issues, a series of protocols were developed, offering step-by-step methods with the lowest possible cost and production time. Said protocols were later peer-reviewed and published, offering background information on their applicabilities, limitations and potential outreach.

As a result of this work, three new methods were presented offering the possibility to:

1. Illustrate lithic artefacts using a tested and standardised method. This method sets to offer users of any level the opportunity to produce publishable and user-friendly illustration without being dependent on hand-drawing experience and skill. In addition, other than enabling users

to illustrate lithic artefacts, this method offers the possibility to use one single method for the illustration of any lithic assemblage, irrelevant of context and chronology. This can therefore aid with the standardisation of lithic artefact illustration, potentially becoming a very useful tool for comparative studies (**Cerasoni, 2021**, appendix i.7).

2. Photograph any small object or archaeological artefact using modern digital techniques. This method sets to share and illustate the theoretical and practical framework involving the correct photographic practices, particularly for users that are not already familiar with or experts in photography. In this regard, this work enables beginners and intermediate users to gather all the relevant information for the correct photographing of artefacts within one single source, and guides them from start to end to produce extremely high-quality and scientifically reliable photographs (**Cerasoni et al., 2022**, appendix i.6).

3. Produce extremely high-resolution three-dimensional models of any small object or archaeological artefact. By presenting a highly-optimised method developed from the merging of tools and practices among archaeological sciences, computer graphics and video-game development, this method is the first study of its kind that enables anyone to produce 3-D models with the lowest monetary and production cost possible. The applications of this study are varied, and can be applied to any academic, museum, and public context. These include, but are not limited to, 3-D representation of artefacts, morphometric and volumetric analyses, and outreach purposes. Furthermore, this study sets the opportunity to create reliable and accurate models at extremely high-resolution with minimal equipment and cost, making it the ideal tool for artefact recording anywhere in the world, whether it be a laboratory or in the field. The potential of this can include the scanning and 3-D modelling of archaeological artefacts within developing nations, which, applied in conjunction with the previously two presented models, could make the need of exporting archaeological materials for material culture analysis to wealthy nations avoidable.

CHAPTER 4. DISCUSSION AND CONCLUSIONS

CHAPTER 4 provides conclusions based on research findings from data included in CHAPTER 3, research background, questions and methods addressed in CHAPTER 1 and CHAPTER 2, as well as discussions and recommendations for future research. This chapter will review the purpose of the study, research questions, literature review, and findings of this study. It will then present conclusions, discussions of the conclusions, and recommendations for best practices and for further research.

This dissertation research was interested in describing hominin behaviour and environments in Pleistocene West Africa. The main goal was to add data from the understudied region of West Africa to form a more complete perspective on Pleistocene human evolution within Africa. This was seemingly simple but difficult to achieve. This conclusion provides a broad discussion of the major findings from this research within regional continental frameworks, presents the gaps in archaeological knowledge identified during the course of this dissertation, and provides concluding remarks and suggestions for future research.

4.1. Behaviour and environments of Pleistocene humans in West Africa

The previous chapters present the research background and results for each of the major findings of this dissertation. In terms of the known archaeological record of West Africa throughout the Pleistocene and Holocene, the presented data achieved a considerable enhancement of what we previously knew.

The earliest OSL ages retrieved from the site of Anyama in Ivory Coast indicate that past human populations have inhabited West Africa for at least 300 ka (Allsworth-Jones, 2021; Chenorkian, 1983). Nevertheless, sites where chronometric dating has never been carried out still constitute a fundamental part of the part human record in West Africa. As an example, for the whole modern country of Benin, no chronometric dating for Stone Age sites has ever been completed prior to our work (**Cerasoni et al., In Review**). Considering this, a great number of sites that have never been properly dated exist, and they have only been studied from a lithic typological perspective. As a matter of fact, several Early Stone Age sites have been excavated and studied in the past decades throughout West Africa (Chevrier et al., 2018; Lebrun et al., 2016; N'Dah, 2009). If we would consider the ESA techno-complexes discovered in West Africa complementary to similar assemblages discovered in the rest of Africa (Mcbrearty & Brooks, 2000), it would be safe to assume that human inhabitation of West Africa started before

300 ka. In view of these observations, an initial reconstruction of past human demography in West Africa can be hypothesised.

As early as the ESA, presumably prior to 300 ka, humans populated West Africa in a variety of contexts and environments. Extending from tropical forests to sub-tropical and ecotonal environments, human populations have been recorded to produce unifacial and bifacial ESA technologies in areas including the Sahelian savannas of Northern West Africa at Ounjougou, riverine environments of the Falèmè Valley, and tropical forests of Guinean Ivory Coast (Chenorkian, 1983; Chevrier et al., 2018; Huysecom, 2014). Following the ESA, a drastic increase in MSA technology use occurred throughout the region. The transition between these two cultural techno-complexes is undetermined, and the available data is far too sporadic to offer any clues. However, the ten-fold increase in ESA versus MSA sites leads to the hypothesis that a population turnover occurred. Such an increase in sites with no ecological or topographic preferential pattern could suggest arrival and inhabitation of the region by external populations. Of course, a case could be made for an internal evolution of lithic technology from ESA to MSA techno-complexes, as a result of convergent evolution with other African regions. However, the ESA record of West Africa so far is yet too sporadic and underrepresented to support the evidence of a complex and demographically-extensive inhabitation of the region prior to the Middle Stone Age.

MSA sites are the most prevalent and common in Pleistocene West Africa, and the technological tool kit seems to be uniform and lacking in sub-regional differentiations. Similarly to what was discovered in the Tannongou Valley (**Cerasoni et al., In Review**), most other MSA sites throughout West Africa are dominated by a Levallois technology composed of preferential core removal strategies and centripedal/discoidal core production (Allsworth-Jones, 2019; B. Chevrier et al., 2016; Dewar & Stewart, 2016; Lebrun et al., 2016; Niang et al., 2020; Niang & Ndiaye, 2016; Scerri, Blinkhorn, Groucutt, & Niang, 2016; Scerri, Drake, Jennings, & Groucutt, 2014; **Scerri et al., 2021**). It is important to note that statements could be made towards a separate and unique late ESA-early MSA techno-complex present only in select parts of West Africa, namely Sangoan technology. Sangoan technology is observable in only certain parts of Guinean West Africa, with the most notable case present at Anyama that is dated to approximately 200-250 ka (Chernokian, 1983). However, the technological identification and definition of Sangoan, particularly in West Africa, is extremely debated and uncertain (Davies, 1976; Mercader, 2002; Van Peer, Rots, & Vroomans, 2004). Given the very infrequent and complex nature of Sangoan assemblages in West Africa, no certainty can be given towards whether or not the described assemblages are effectively a different techno-complex, especially as they are generally defined as containing “heavy-duty tools” (McBrearty, 1988), but without displaying other typical features present in the East African record such as Sangoan picks (Davies, 1976). Given this, Sangoan should be considered as part of the standard MSA techno-complex present throughout the region, possibly containing infrequent presence of heavier tools compared to the typical Sangoan assemblage.

The MSA is generally considered the Stone Age period that marks the emergence of modern humans (Henshilwood et al., 2011; Hublin et al., 2017; Jacobs et al., 2008; Marean & Assefa, 2005)(Mcbrearty & Brooks, 2000). Within the African record there is an increasingly clear development over time of the transition, or replacement, from MSA to LSA traditions and technology starting from the Late Pleistocene (Bader et al., 2018; Barton et al., 2013; Clark, 1997; d'Errico et al., 2012; d’Errico et al., 2020; Hogue & Barton, 2016; Kusimba, 2001; Shipton et al., 2018; Tryon & Faith, 2016). This however cannot be applied as uniformly to West Africa. Published evidence present within this dissertation show that MSA techno-complexes persist in West Africa well after the emergence of LSA technology throughout the continent. With the presence of MSA layers in the Falémé Valley dated to approximately 11 ka (Scerri et al., 2021), it is clear that populations in West Africa maintained a MSA tradition into the Holocene.

The reasons behind the divergence in MSA traditions starting from the Late Pleistocene are yet debated and unsure. The leading theory supports an isolation of West Africa from the rest of the continent, caused by topographic and environmental barriers, in turn forming refugial environments for isolated populations to persist within for far longer than in non-isolated contexts. West Africa has been suggested by others (Iloh et al., 2017; Stewart & Stringer, 2012; Ziegler et al., 2013) to be a refugium from deteriorating habitats during Pleistocene glacial phases when rainfall and vegetation decreased on a continent-scale. If this were the case, then one would assume that archaeological sites dated to glacial phases would be numerous in West Africa. In archaeology, refugia are viewed as “melting pots” while in ecology, refugia are viewed as “isolates” (Hewitt, 1999; Mackay et al., 2014; **Cerasoni et al., In Preparation**). Although such theories could be valid given the available data, not enough evidence is present in support of it. Considering this, a continuation of MSA traditions could be a result of environmental necessity, where LSA technologies are not required for the successful survival of populations in areas such as the Falémé Valley. Furthermore, MSA deposits as young as the ones described in (**Scerri et al., 2021**) have yet not been discovered outside of the Falémé Valley, possibly hinting at a single region with a unique cultural footprint.

When evaluating sites of Late Pleistocene chronology with LSA deposits in West Africa, interesting observations can be made. As presented in (**Cerasoni et al., 2022**) only a total of nine highly reliable LSA sites have ever been discovered in West Africa. Among all of them, none are present within tropical open-air environments, but are instead found either in rock-shelter and cave contexts, or open-air environments in Sahelian and Sudanian savanna biomes. Similarly to the observations made on the ESA to MSA transition, the technological transition from MSA to LSA is sporadic and uncertain. Behavioural and environmental contexts for each of the studied LSA sites shows a wide variety of patterns, with a diversity of technological lithic assemblages and inhabitation occurrences. Sites such as Iho Eleru, Shum Laka, and Bosumpra Cave (Lavachery, 2001; Moeyersons, 1997; Oas, D'Andrea, & Watson, 2015; Watson, 2017; **Cerasoni et al., 2021, In Review**) appear to have been areas of human habitation within dense forested areas, with continuous occupation during their anthropogenic inhabitation and large scale tool production, and with populations using both their immediate forested environments, and farther ecotonal landscapes where savanna-dependent flora and fauna was available. On the contrary, sites such as Pendjari-II, Koukouan-I and Fatandi V (Chevrier et al., 2016; Chevrier et al., 2020; N'Dah, 2009) show non-recurrent uses of the sites with little evidence for large-scale tool production, and the utilisation of a single biome.

From the available data and these observations, it is clear that during the LSA diverse populations lived in West Africa, expressing two types of environmentally-dependant behavioural patterns: (1) Populations, or clusters of people, utilising ecotonal environments and based in forested and ecotonal biomes, taking advantage of local forested resources and farther grassland resources. This therefore implies a centralised pattern of habitation with recurrent visiting of neighbouring regions for resource gathering. (2) Populations, or clusters of people, moving throughout a landscape and utilising each locale for a limited amount of time, with no evidence of recurrent use of any single location.

Environmentally, MSA and LSA adaptability and behaviour within diverse biomes was distinctive for each technological tradition. The environmental variability throughout West Africa during the Pleistocene was diverse and complex. As presented in **Cerasoni et al. (2022)** both precipitation and temperature rates varied following stadial and interstadial cycles, affecting distinct regions at different rates. The presented data in this study shows how northern latitudes following the Sahelian biome belts (Figure 1) were less affected by climatic and environmental shifts, maintaing relatively consistent environmental conditions. On the contrary, areas in the southern latitudes such as the Guinean Coast and ecotonal regions at the south of the Sahelian belt were much more affected by climatic and environmental fluctuations.

These fluctuations would have caused a diversification and modification of landscapes throughout the Pleistocene, with expansions and contractions of forest biomes, and the associated increase and decrease of grassland environments. These observations match well with several paleoenvironmental records from the region (Dupont, Jahns, Marret, & Ning, 2000; Johns, Hüls, & Sarnthein, 1998; Maley, 1991; Miller & Gosling, 2014; Salzmann & Hoelzmann, 2005; Shanahan et al., 2015). The environmental flactuations that affected southern latitudes of West Africa can be observed in the environmental record of Iho Eleru (**Cerasoni et al., 2021, In Review**). From the Pleistocene to the the Mid-Holocene, climatic fluctuations caused the retraction of forested areas. Consequently, the expansion of grasslands created a theorised savanna belt connecting the northern Sahelian environments directly to the previously fully forested landscape surrounding Iho Eleru.

Overall, the Pleistocene behavioural and environmental history of West Africa is complex and characterised by numerous gaps in its archaeological record that lead to difficulty in interpretation. Nevertheless, published literature, together with the data and interpretations generated from this dissertation, offer a novel and unprecedented window to past hominin behaviour in Pleistocene West Africa. The lack of an extensive ESA record could be a true representation of the low population density of people in the region, but is it most probably a product of the lack of preservation and discovery rate of such ancient and poorly-preserved deposits (**Cerasoni et al., 2022**). Starting from the introduction, or emergence, of MSA traditions, West Africa was a widely-populated region. Populations were most probably inter-connected, with intra-population dynamics that led to a standardisation of technological traditions. During this period, humans were already well adjusted to living in every environment present in West Africa, suggesting an extremely developed capacity to gather resources and thrive even in the most complex enviroments of tropical latitudes such as rainforests and high-altitude montane regions (Figure 2). Finally, a clear population wide divergence occurred during the Late Pleistocene, supported by the evident decrease of MSA sites in all available biomes (**Cerasoni et al., 2022**), and a diversification of environmentally-dependent behavioural patterns.

West Africa clearly underwent complex demographic, environmental and cultural transitions throughout the Pleistocene. Although this dissertation presents major theories trying to reconstruct as much as possible of where humans lived, how they lived and what they did, they should all be considered as hypotheses developed on a very limited record compared to other African regional records. Nonetheless, the presented data, results, and interpretations could serve as a useful tool for the evaluation of West Africa's role in the dispersal and evolution of humans and traditions in Africa.

4.2 West Africa's role in the dispersal and evolution of humans in Africa

The overarching goal of this dissertation research was to understand the role of West Africa in the dispersal and evolution of humans within Africa. However, given the long and detailed history of archaeological research in Africa, notably in South, East, and North Africa, it is not yet possible to systematically compare West Africa to better-studied regions. South, East, and North Africa hold the highest densities of known Pleistocene archaeological sites (Breuil & Frobenius, 1931; Carrière, 1886; Clark, 1967; Clark et al., 1984; Dibble et al., 2013; Reygasse, 1921-1922; Thackeray, 2016; Will, Conard, et al., 2019; Will, Kandel, et al., 2019). The role of West Africa is therefore essential to reframing the debate on the origins of our species, and shifting it from a single origin point to a more complete, pan-African perspective (Bergström et al., 2021; Scerri et al., 2019). Despite the relative paucity of archaeological sites in Pleistocene West Africa, **Hallett et al. (In Review)** still found that there was a robust increase in the suitability of tropical forested habitats for humans roughly 70 ka. This predicts and suggests that humans would have already successfully inhabited West Africa by 70 ka. In addition, it provides a testable hypothesis for future research. That is, given the developed knowledge that habitats within tropical West Africa were suitable for humans 70 ka, then future archaeological field research should target deposits that are 70 ka.

It can thus be suggested that human population density within West Africa was at first sporadic, until at least 70 ka compared to the rest of the continent. This in turn offers the first chronological framework for the topics discussed previously, possibly suggesting the originally hypothesised large scale demographic and cultural expansion throughout the region, attributed to MSA traditions, occurred after 70 ka. Further ground testing will be necessary to fully test this hypothesis, as very few MSA sites have been chronometrically dated. More generally, however, this hypothesis can be used to evaluate West Africa within a continental African perspective.

ESA deposits are few and lacking of detailed chronometric descriptions, and therefore serve no direct evidence on the origin and movement of behavioural and environmental patterns within or out of West Africa. On the other hand, MSA deposits and sites in West Africa suggest a direct influx of cultural traditions from regions outside of West Africa. Until the Upper Pleistocene and the appearance of LSA traditions in West Africa approximately 20 ka, West Africa seems to have been a receiver of external populations and human traditions. Following this, after visible diversification becomes visible in the archaeological record as explained in regards to LSA traditions and behavioural patterns in West Africa, trends for the emergence and expansion of unique behaviours develop within and expand out of West Africa. Most notably, the earliest evidence of pottery production and use originates from Ounjougou (Huysecom et al., 2009) around 11 ka, with later emergence at the sites of Bosumpra Cave 9 ka (Watson, 2017), and Iho Eleru 5 ka (Shaw & Daniels, 1984; **Cerasoni et al., In Review**). Similarly, genetic studies have shown that West Africa was the origin for populations that contributed to a great extent the modern genetic makeup of the whole continent (Lipson et al., 2020). Arguably, evidence of this important contribution of West African ancestry is observable within the previously presented Iho Eleru mid-Holocene event (CHAPTER 3). The introduction of pottery and groundstone technology, coincident with an increase of grassland environments, could be evidence of an extremely early presence of a culture that expanded outside of West Africa to become recognised as Bantu (Lipson et al., 2020; Stager & Anfang-Sutter, 1999; **Cerasoni et al., 2021**).

In conclusion, West Africa represents a fundamental part of the record of our species. Although the available record is extremely poor compared to other better represented regions, the available data offers numerous fundamental observations to better understand past hominin behavioural and environmental dynamics. The aims of this dissertation are not only to further our understanding of the Pleistocene record of West Africa, but also, and most importantly, to highlight the importance of the region within its continental perspective.

4.3 Future directions and recommendations for best practice

This dissertation sets to offer a comprehensive and detailed account of the current knowledge of Pleistocene West Africa. It is important to note that this work is a general study based on limited time, constrained by various limitations and assumptions (CHAPTER 1.3). Nevertheless, future directions for archaeological research in West Africa are bright, and the following aspects and topics should be of primary importance and focus for the expansion of our knowledge in this complex and underrepresented region.

Firstly, a more detailed, field-based, environmental record is necessary. With further work such as more marine and lacustrine records for paleoenvironmental reconstructions, detailed microbotanical assemblages (**Cerasoni et al., In Preparation**), and more botanical and faunal records from sites excavated with modern techniques, we will have a better representation of true environmental diversity in the region. The previously discussed human-environment relationships were mostly based on region-wide, or modelled, datasets. With more detailed and local records archaeologists and palaeoecologists will be able to view the more minute variations which will in turn offer new perspectives and evidence on how past humans lived within their environments, and how the environments changed as a result of climatic and anthropogenic modifications.

The application of new and modern digital methods, such as Cerasoni (2021, 2022), will also offer invaluable new data for the better analysis of material culture. Without the necessity to export archaeological materials outside of West Africa, and offering the possibility to create standardised and extensive databases at low economic- and time-costs, assemblages will be able to be studied more efficiently. This will ideally, and hopefully, aid in the better study of single assemblages, and in unison aid in the study of regional behavioural and cultural dynamics through material culture analysis.

Of course, arguably the most important future direction for archaeological research in West Africa is fieldwork. Although extrapolation of data using novel technologies and methods from the currently published literature can offer interesting and new insights, it is clear that the number of known sites and contexts is extremely limited. Priority should be given to the organisation of survey expeditions, particularly in areas that are not as well represented as highly dense sub-regions such as the Falémé Valley, Atakora Region, and Jos Plateau. Based on topographic and environmental observations of modern environments (Figure 1, Figure 2), and required safe political and humanitarian conditions, areas including Northern and Guinean Ghana, Togo, and Guinean Ivory Coast seem to be areas with the highest potential of archaeological retrieval. Survey should also be necessarily followed by accurate and well-carried out excavations. The application of standard excavation methodologies (e.g. open-plan excavation by contexts and not spits, geospatial recording with a total station, sieving of all sediments for organic remains, etc.) should be absolute priorities, ensuring the highest possible degree of accuracy and standardisation for later comparison between excavations.

One final aspect of future research that should absolutely be carried out, but is currently not common, is the re-evaluation and re-studying of old collections. Among all locally-present universities and research centres in West Africa lie presumably millions of artefacts that have never been fully studied nor considered. Many of these artefacts still maintain high reliability and usefulness with original contexts and documentation preserved. If we wish to learn as much as we can about the West African archaeological record, the first places we should visit are the tens of storage rooms across the region that contain artefacts that will surely change the way we think of human evolution in West Africa and beyond.

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APPENDIX

The ensuing accepted publications (i.1-i.7), submitted manuscripts (ii.1-ii.2), and manuscripts in preparation (iii.1) are listed in the appendix following the order in the section LIST OF PUBLICATIONS (pages V-VI).

(1) Copyright and permissions

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The following manuscripts were not included in the APPENDIX due to (1) strict copyright regulations by Nature Publishing, and (2) current state of production of the manuscript:

(1) Hallett*, E.Y., Leonardi*, M., Cerasoni, J.N., Will, M., Beyer, R., Krapp, M., Kandel, A.W., Manica*, A., & Scerri*, E.M.L. 'Major expansion in the human niche preceded out of Africa dispersal'. Nature.

(2) Cerasoni*, J.N., Neumann, K., & Bremond, L. 'Forest phytoliths for the identification of forest types in the African continent. A definition and description of new indices'.

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Appendix i.1

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tjom20

Archaeological sites and palaeoenvironments of Pleistocene West Africa

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To cite this article: Jacopo Niccolò Cerasoni, Emily Y. Hallett, Eslem Ben Arous, Robert M. Beyer, Mario Krapp, Andrea Manica & Eleanor M. L. Scerri (2022): Archaeological sites and palaeoenvironments of Pleistocene West Africa, Journal of Maps, DOI: 10.1080/17445647.2022.2052767

To link to this article: https://doi.org/10.1080/17445647.2022.2052767

JOURNAL OF MAPS
https://doi.org/10.1080/17445647.2022.2052767

Archaeological sites and palaeoenvironments of Pleistocene West Africa

Jacopo Niccolò Cerasoni [a,b], Emily Y. Hallett [a], Eslem Ben Arous [a,c,d], Robert M. Beyer [e,f], Mario Krapp [g], Andrea Manica [e] and Eleanor M. L. Scerri [a,h,i]

[a]Pan-African Evolution Research Group, Max Planck Institute for the Science of Human History, Jena, Germany; [b]Institute of Archaeological Sciences, Eberhard Karls University Tubingen, Tubingen, Germany; [c]Geochronology and Geology programme, Centro Nacional de Investigación sobre la Evolución Human (CENIEH), Burgos, Spain; [d]Histoire Naturelle de l'Homme Préhistorique, Muséum national d'Historie naturelle, Sorbonne Universités, CNRS, UPVD, Paris, France; [e]Department of Zoology, University of Cambridge, Cambridge, UK; [f]Potsdam Institute for Climate Impact Research (PIK), Member of the Leibniz Association, Potsdam, Germany; [g]GNS Science | Te Pū Ao 30, Lower Hutt, New Zealand; [h]Department of Classics and Archaeology, University of Malta, Msida, Malta; [i]Institute of Prehistoric Archaeology, University of Cologne, Cologne, Germany

ABSTRACT
African paleoanthropological studies typically focus on regions of the continent such as Eastern, Southern and Northern Africa, which hold the highest density of Pleistocene archaeological sites. Nevertheless, lesser known areas such as West Africa also feature a high number of sites. Here, we present a high-resolution map synthesising all well contextualised Pleistocene archaeological sites present in Sub-Saharan West Africa. A detailed elevation and ecoregional map was developed and correlated with palaeoanthropological sites. This map is supplemented with 1,000- and 2000-year interval climate reconstructions over the last 120,000 years for three subregions of high archaeological interest. The presented archaeological sites were compiled by reviewing published literature, and selected based on: (1) documented archaeological stratification or >10 characteristic artefacts, (2) published coordinates, and (3) published chronometric ages or relative dating. The data presented here elucidates the current state of knowledge of Pleistocene West Africa, highlighting the regional potential for human evolutionary studies.

ARTICLE HISTORY
Received 1 November 2021
Revised 22 February 2022
Accepted 22 February 2022

KEYWORDS
Pleistocene archaeology; West Africa; paleoenvironmental reconstruction; paleoclimatic modelling

1. Introduction

African paleoanthropological studies have typically focused on regions of the continent such as Eastern, Southern and Northern Africa, which hold the highest concentration and density of Pleistocene archaeological sites. This notwithstanding, it is becoming clear that less well-researched regions, such as West Africa, also feature a high number of sites (e.g. Allsworth-Jones, 2019; Douze et al., 2021; Huysecom et al., 2014; Niang et al., 2018; Petit, 2005; Scerri et al., 2021).

Here, we present a series of high-resolution maps synthesising Pleistocene archaeological sites reported in Sub-Saharan West Africa (Supplementary File 1). A detailed elevation map of the region developed from 1 km-resolution digital elevation models (DEMs; Jarvis et al., 2008) was categorised based on elevation and correlated with topographic bioregion to show geolocated and culturally attributed hominin sites. This map is supplemented with 1,000- and 2,000-year interval climate reconstructions over the last 120 thousand years (ka) for three individually mapped subregions with a high concentration of archaeological sites. In addition, modern ecoregions are considered together with the modern ecological locations of Pleistocene archaeological sites. The locations of archaeological sites were compiled by reviewing published literature. Partial, poorly understood, or questionable archaeological sites were excluded. The selection of archaeological sites included in the map was based on the following requirements: (1) a documented stratified archaeological origin, or not less than 10 characteristic artefacts, (2) published coordinates, and (3) published chronometric ages or relative dating (i.e. by cultural attribution such as lithic assemblage type, culture or tradition). Too often Sub-Saharan West Africa is considered a marginal region in African palaeoanthropology, however this map illustrates the high concentration and density of archaeological sites in the region. As paleoenvironmental studies are sporadic, or even absent, in most areas of West Africa, the local climate reconstructions provided will

CONTACT Jacopo Niccolò Cerasoni cerasoni@shh.mpg.de Pan-African Evolution Research Group, Max Planck Institute for the Science of Human History, Kahlaische Straße 10, 07745, Jena, Germany; Institute of Archaeological Sciences, Eberhard Karls University Tubingen, Tubingen, Germany @JCerasoni

Supplemental data for this article can be accessed at https://doi.org/10.1080/17445647.2022.2052767.

contribute towards achieving a better understanding of human-environment interactions and past human activities in Pleistocene Sub-Saharan West Africa.

2. Data and methods

The construction of the map required the collation of a wide variety of data sources. These include previously published archaeological datasets, published ecological biome distribution ranges and newly developed paleoclimatic datasets for areas of interest. These sources were used and developed with the objective of offering a wide ranging archaeo-ecological framework for Pleistocene West Africa.

The base dataset (see legend in Main Map, and Supplementary File 1), upon which this study is based, was constructed by reviewing previously published literature, including published articles, books and reports. A list of Pleistocene sites in West Africa was collated, recording the following variables for each site: (1) site name, (2) country, (3) type (open air, fluvial terrace, or rock shelter), (4) cultural attribution, (5) known or unknown stratigraphical origin, (6) number of recovered artefacts (<, = , or > than 10), (7) dating method used, (8) coordinates, and (9) original reference. By using the following variables, sites were selected for inclusion in this study, while partial, poorly understood, or questionable archaeological sites were excluded. The selection of archaeological sites included in the Main Map was based on the following requirements: (1) a documented stratified archaeological origin, or not less than 10 characteristic artefacts, (2) published coordinates, and (3) published chronometric ages or relative dating (i.e. by cultural attribution such as lithic assemblage type, culture or tradition). Cultural attribution, or the classification of each site within Stone Age periods (Early, Middle, Later, or a combination of them), was designated based on either the original attribution given by the authors of the referenced studies, or based on the observable published material culture. In most cases, the sites included in this study were published with an already attributed cultural designation. In the rare cases where this did not happen, the authors of this study classified the sites to a cultural attribution. In both cases, cultural attribution was designated based on the models of lithic technology (Clark, 1969) and lithic groups for each Stone Age period (Barham & Mitchell, 2008). They are: (1) Early Stone Age (ESA; Mode 1 and 2), characterised by unifacial pebble tools and bifacially worked tools from large flakes and cores, e.g. handaxes and cleavers; (2) Middle Stone Age (MSA; Mode 3 and 4), characterised by prepared core technology, including the Levallois method, and typical MSA tools e.g. side and end scrapers, notched pieces denticulates; and (3) Later Stone Age (LSA; Mode 5), characterised by microlithic technology, including geometric microliths and segments. In the cases where sites displayed mixed or varied technological groups all divided into separate contexts, the site was attributed a range of Stone Age periods (e.g. Ounjougou contains different layers with materials ranging from the ESA to the LSA, therefore it was designated as ESA-LSA). Finally, regarding sites within the Falémé Valley, and building on the work of colleagues (e.g. Douze et al., 2021), we acknowledge the fact that while not all clear ESA/MSA/LSA assemblages are chronometrically dated, other chronometrically dated assemblages have an unclear cultural designation. Further study is yet needed to determine the local cultural character of such assemblages. We therefore note that all the sites within the Faleme Valley were culturally attributed solely on the published materials used for the database recording (full list of sites and references visible in Supplementary File 1).

The resulting dataset, collated and exported in a .csv file format, was imported on QGIS and was superimposed over an elevation map of the region developed from 1 km-resolution digital elevation models (DEMs, Jarvis et al., 2008). The elevation values from the original DEM dataset were categorised and colourised topographically and then further categorised into observable topographic bioregions, which are the following: coastal, flooded lowland, lowland, highland, sub-montane, and montane. Rivers and lakes were also included to offer modern distribution and location of major water sources (CGIAR, 2014; RCMRD, 2015). The adopted elevation- and topography-based approach led to the evaluation of site location and type in direct comparison with modern ecoregional zones (lower left corner, Main Map; Olson et al., 2001) and modern political boundaries (OCHA ROWCA, 2021). The included archaeological sites were further sub-sampled and divided into categories based on their cultural attribution. Three of the six total categories represent archaeological sites that only show one single cultural attribution (i.e. a dated chronometric range for the site that fits within a single cultural attribution range, or the retrieval of artefacts that are categorised only within one single cultural attribution), and they are Early Stone Age (ESA), Middle Stone Age (MSA), and Later Stone Age (LSA). The other three categories include archaeological sites that have dated stratigraphies, by either chronometric or typological dating, and include more than one single attribution. These categories are: Early Stone Age to Middle Stone Age, Middle Stone Age to Later Stone Age, and Early Stone Age to Later Stone Age.

From the evaluation of the Main Map and the geolocated archaeological sites, three subregions were selected for further analysis following their high concentration of archaeological sites. These subregions are: 1. Falémé Valley, Senegal, 2. Jos Plateau, Nigeria, and 3. Atakora Region, Benin. These subregions have been expanded and mapped individually (Main Map, left side). Furthermore, each of the three subregions are supplemented with 1,000-year interval climate model reconstructions over the last 21,000 years and 2000-year interval climate reconstructions over the last 22,000 to 120,000 years (lower right side). The paleoclimate models include plots of four climate variables, which include: annual mean temperature (BIO1), annual precipitation (BIO12), leaf area index (LAI), and net primary productivity (NPP). BIO1 and BIO12 model average annual mean temperature and precipitation in each subregion. Leaf area index represents the green leaf area per unit ground surface in broadleaf canopies, essentially offering a view of the density of forest canopies in each subregion, therefore modelling the presence of forest canopy coverages through time. Finally, net primary productivity was selected as it represents the amount of carbon dioxide metabolised by the vegetation in each subregion, therefore showing the density of faunal and floral biomass changes through time. The paleoclimate models are based on the combined HadAM3H and Hadley CM3 climate simulations published in Beyer et al. (2020) to model changes in climate for the selected subregions. We used the decimal coordinates of each of the subregion vertices to extract climate variable values at 0.5° resolution from the Beyer et al. (2020) dataset in 1000-year intervals (up to 21 ka) and 2000-year intervals (22-120 ka) (see Supplementary Data 2 for full script). All climate variable values were then scaled together (SCVV).

Data recording of the literature sources was carried out using Office Excel. For the Main Map (upper left corner) The exported data in .csv format was then imported on QGIS, where the DEM raster collation, averaging and visualisation was carried out. The same process was carried out for the ecoregional map (Main Map, lower left corner). The subregional maps (Main Map, centre left side) were extrapolated from the Main topographical map by using the crop function on QGIS. The paleoclimate data were processed and plotted using R. All the single maps and figures were exported from QGIS and R in a multi-layer .pdf format. The files were then imported on Adobe Illustrator 2021 where the Main Map was created adding final details, which included: 1. the assembling of all the single visualisations, 2. relabelling of visualised data, 3. standardisation of fonts, strokes and symbols, and 4. the addition of legends, labels, titles and logos.

3. Map description

The Main Map (upper left corner), exhibits all the archaeological sites of Pleistocene West Africa we were able to document, and shows a variety of trends and similarities, offering insights on the distribution, cultural characteristics and environmental footprints of past human activity in the region. The frequency of culturally attributed sites presents a skewing towards the presence of Middle Stone Age (MSA) sites (N = 52), representing the majority of recorded sites. Later Stone Age (LSA) sites (N = 9) are the second most frequent cultural sites in the region, and Early Stone Age (ESA) sites (N = 4) are the most sporadic with only four sites throughout West Africa. Firstly, the low frequency of ESA sites can be explained by the higher difficulty of identification and study, compared to its younger counterparts. This is probably a result of the deeper stratigraphy of ESA sites caused by a high sedimentation rate at tropical latitudes, including thick silt deposits caused by regular flooding in the river basins, and high possibilities of contamination from natural or anthropogenic processes at the oldest sites. The higher number of MSA sites, compared to LSA sites, may be explained either by: (1) a higher concentration of MSA human habitation of the region, or, most likely, (2) a research bias towards geographic, topographic and archaeological areas with a high occurrence of MSA sites.

The modern topographic distribution of the sites can offer clues towards the past human habitability of West Africa. Although topographic differences are to be expected between modern and Pleistocene landscapes, we consider major topographic features (coastal areas, major fluvial and lacustrine bodies, and montane environments) to have maintained their characters over the timeframe of the modelled biomes. Considering this, no distinct topographic preferences are observable, with the sites recorded in every context, spanning from coastal to montane habitats. Nevertheless, it is important to note that all the archaeological sites are situated within very close proximity to major water sources, and easily explained by the fundamental necessity of this prime resource for human survival and the habitability of a given location (Scerri et al., 2014). In particular, as visible in the Main Map, areas with a very high density of archaeological sites are all situated close to major fresh water sources, whether they be (1) coastal areas, such as the Guinean Coast in modern day Ivory Coast and Ghana, (2) river and floodplain areas, such as the Falémé Valley, or (3) high elevation areas with many fluvial terraces and stream systems such as the Atakora Region and Jos Plateau. The selection of the previously mentioned sub-regions was specifically based on these high archaeologically-dense areas, and have been complemented with their corresponding modern ecoregional boundaries (Olson et al., 2001).

The first presented subregion (bottom left of Main Map), the Falémé Valley, is an area which follows the

Falémé River. This is a region that has been of high archaeological interest for several decades (Chevrier et al., 2016; Descamps, 1979; Huysecom et al., 2014; Lebrun et al., 2016; Niang et al., 2018; Niang & Ndiaye, 2016; Rasse et al., 2004; Scerri et al., 2016; Scerri et al., 2021), displaying the presence of a multitude of sites spanning from the ESA (e.g. Djita), to the LSA (e.g. Fatandi V, Toumboura I). Most sites are situated within fluvial terraces, therefore representing past human activity taking place within riparian areas. Our paleoclimatic reconstruction for the region during the past 120 ka also shows that for most of its observed chronology it has undergone very little changes in temperature and humidity, mostly changing during the various stadial and interstadial stages. Also, the canopy coverage (LAI) and the environmental biomass (NPP) has been extremely stable for at least the last 100 ka. This paleoclimatic reconstruction possibly explains the suitability for human habitation in the region, and in turn the very high density of sites within it. This also shows how stable and suitable the Falémé Valley was for humans during the Pleistocene, a conclusion reinforced by previous studies (Scerri et al., 2016; Scerri et al., 2021). These results are consistent with other studies suggesting that West Africa has been relatively stable and broadly more humid than eastern Africa for the last 100 thousand years (Kaboth-Bahr et al., 2021).

The Jos Plateau, similarly to the Falémé Valley, is a region with a high density of archaeological sites. Nevertheless, the sites within this subregion are both culturally and environmentally different, as it contains solely MSA sites (Allsworth-Jones, 2019), and it is among the highest topographic subregions of the whole of West Africa. Climatically, a wider range of climatic shifts occurred in this region during the last 120 ka, with major changes in temperature and humidity occurring in concurrence with stadial and interstadial stages These changes were especially evident during Marine Isotope Stages (MIS) 5 (and its relative substages) and MIS 1, and less so during MIS 4 to MIS 2. These climatic variabilities fit well with the observed hominin presence within the region, as MSA sites documented in the Jos Plateau were inhabited during the less climatically variable period between MIS 4 and 2.

Finally, the last subregion, Atakora, was also selected for its high density of archaeological sites. In this region a variety of sites, from the ESA to the LSA, are visible (Cerasoni et al., 2020a, 2020b; Davies, 1967; N'Dah, 2009; Petit, 2005), suggesting continuous human habitation throughout the Pleistocene. Topographically, it is represented by a mixed geography, with both low altitude riparian valleys and high elevation areas resulting from the Atakora mountain chain. The Atakora Region is the subregion that underwent the most climatic variability, with extreme changes in every modelled variable during the last 120 ka. These climatic shifts occurred synchronously to stadial and interstadial stages and substages, seemingly having no direct effect on human habitability and distribution throughout the region. This is possibly attributable to all of the sites in the Atakora Region being situated within or near rivers and fluvial environments, with humans showing no preference for any topographic feature other than water during specific cultural periods.

4. Discussion

The combination of bibliographical, geospatial, paleoenvironmental and paleoclimatic data clearly shows an expected strong correlation between Pleistocene human activities and their environments. The various data collection and analyses performed here allow us to better consider Pleistocene archaeology and paleoenvironment in West Africa, displaying the arrangement and distribution of sites from decades of archaeological research.

Ecologically, an equally wide distribution can be noticed with archaeological sites being widely presented in every modern biome, ranging from savanna dominated biomes of the Northern Sahelian regions to sub-coastal and montane rainforests of Nigeria and Cameroon (Figure 1). The majority of sites are located within the Central and Northern regions which are today composed of Sahelian and Sudanian savannas, with much fewer sites in the lower latitudes of the region within tropical forested and mangrove environments. This difference, however, is not given by a portrayal of past human distribution in the region, but rather a bias towards preservation of archaeological sites which undergo more detrimental effects from the higher concentration of rainfall, humidity, temperature and increased soil depositional rates compared to non-tropical environments. Furthermore, our hypothesised climatic reconstructions for the three selected subregions shows a very complex environmental picture. Our observations, based on the modern biome distribution and modelled paleoenvironmental reconstructions, are a first tentative view of the Pleistocene environment history of West Africa. Given this, it should be noted that without detailed chronological frameworks for each of the considered sites we cannot assess direct human-environmental relationships at specific points in time. Therefore, although the modern ecological contexts of the displayed sites are a good starting point, in-depth chronological, climatic and environmental analyses will have to be carried out to better understand Pleistocene human-environment interaction in West Africa.

Although further fieldwork will be necessary to discover new West African Pleistocene sites, it is important to consider the reasons why there is a current

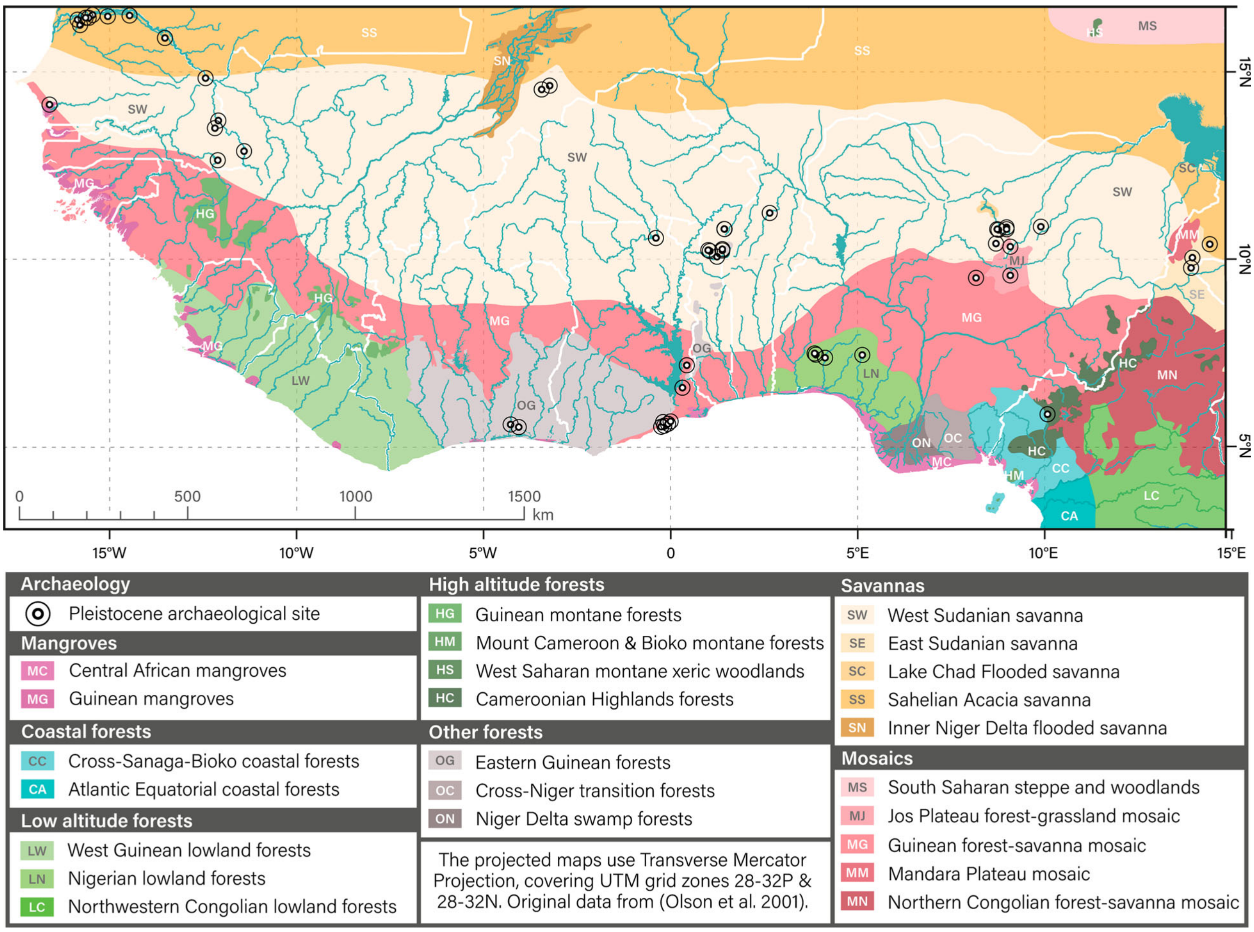

Figure 1. Modern ecoregional biomes of Sub-Saharan West Africa and location of Pleistocene archaeological sites. Original ecoregional data from Olson et al. (2001).

imbalance between regions with a high concentration of sites and regions with little to no identified sites. Major bias inherent to past fieldwork projects exist, where systematic surveys were carried out mostly in a select handful of West African subregions. Regions such as Falémé Valley, Atakora (Figure 2, g-i), and Jos Plateau contain a much higher concentration of identified archaeological sites not because of their higher Pleistocene human presence, but rather a modern archaeological bias caused by their environmental, sedimentary and political contexts. These areas are found within politically and environmentally stable areas, where Pleistocene deposits are easily accessible and visible. In contrast to these areas, other subregions such as Abidjan precinct (Ivory Coast) and Ondo State (Nigeria) contain a very low density of sites. As visible in Figure 2 (a-f), these subregions are characterised by very dense vegetation and increased sedimentation rates. Within them, the sites of Anyama and Iho Eleru are unique occurrences, where their Pleistocene deposits were identified as a consequence of mining, such as in the case of Anyama, and the preservation and protection of Pleistocene materials within a rock shelter, such as in the case of Iho Eleru.

It is therefore clear from our study and the map presented here, besides displaying the most reliable and accurately studied archaeological sites in West Africa, that a great extent of West Africa has yet not been effectively studied. Ideally systematic surveys will have to be carried out in the lesser known regions of West Africa to fill in the gaps, such as the central Sahelian plateaus between Guinea and Burkina Faso, and the Guinean coastal regions which are not in proximity of major metropolitan centres. However, the visibility of Pleistocene deposits will be a major issue for the identification of new site`s in regions where one or more of the following variables occur:

1. High depositional rates caused by increased humidity, rainfall, erosion and/or biomass exchange - causing Pleistocene deposits to be located below any visible surface or level.
2. Decreased erosional activity – causing any buried Pleistocene deposit to not be unveiled and found.
3. Lack of infrastructure and modern human presence – causing difficult access to any potential site containing Pleistocene deposits.

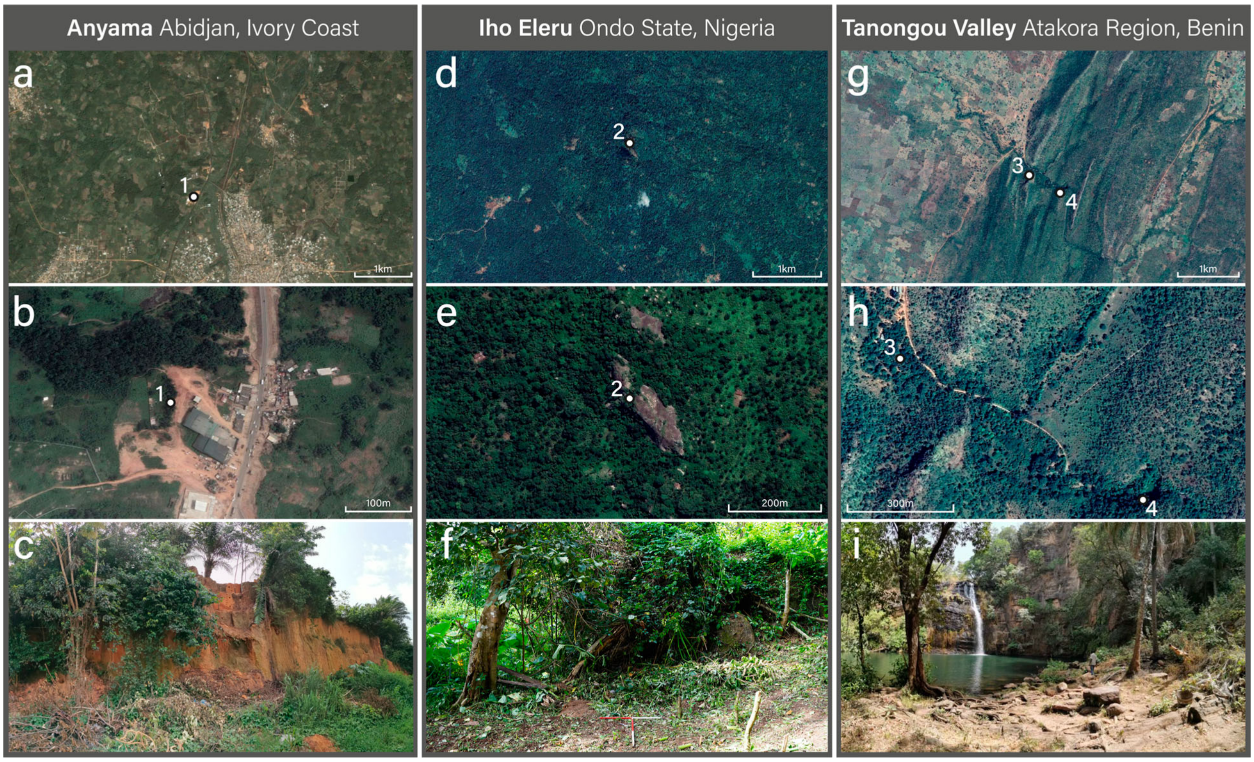

Figure 2. Satellite imagery of Anyama (1; a-b), Iho Eleru (2; d-e), Paloli (3; g-h) and Tanongou Valley (4; g-i) in Tanongou Valley. Below them are site photographs showing the mining activity which revealed Anyama (c), the dense forested environment which surrounds Iho Eleru (f), and the open forested environment of Tanongou Cave (i).

4. Inaccessibility caused by current political tensions and warfare – causing the impossibility to visit any potential site containing Pleistocene deposits.

The information presented in the Main Map, together with the observations that we can take from it, lead us to reasonably assume that future archaeological endeavours should concentrate on studying areas of West Africa which are currently underrepresented, while keeping in mind the issues stated above. Moreover, this map can be used as a reference for further archaeological studies not only in West Africa, but also the rest of the African continent, serving as an example and demonstration of the great density of archaeological sites, and the importance that West Africa had within the wider continental archaeological record.

Software

Bibliographical research and recording of the archaeological sites (visible in Supplementary File 1) was carried out on Office Excel. The exported .csv database, DEMs, ecoregional rasters, and other elements used in the map were created and modified on QGIS. For the subregion maps (Main Map, centre left side) QGIS was used to extrapolate and crop the final products from the Main topographical map. The paleoclimate model was performed using R version 3.6.2 and RStudio version 1.2.5033. All the single maps and figures were exported from QGIS and R in a multilayer .pdf format. The files were then important on Adobe Illustrator 2021 where the Main Map was created adding final details, which included: 1. the assembling of all the single visualisations, 2. relabelling of visualised data, 3. standardisation of fonts, strokes and symbols, and 4. the addition of legends, labels, titles and logos.

Data

The database of archaeological sites (S1) and script of the paleoclimate model (S2) can be found as Supplementary Material or can be found in the following repository – https://doi.org/10.6084/m9.figshare.16895959.v3. The digital elevation models used to create the topographic map are from Jarvis et al. (2008). Other shapefiles were used for the inclusion of water sources (CGIAR, 2014; RCMRD, 2015) and political boundaries (OCHA ROWCA, 2021).

Author contributions

This study was designed by J.N.C., and conceived with E.M.L.S. and E.Y.H. The database was compiled by J.N.C. with support by E.B.A. and E.Y.H. The paleoclimatic reconstruction models were developed by R.M.B., M.K., and A.M., and applied to this study by

E.Y.H. and A.M. The cartographic elements were developed by J.N.C. The initial draft was written by J.N.C., and all authors contributed to the revision of the paper.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by the Lise Meitner Pan-African Evolution Research Group, awarded by the Max-Planck-Gesellschaft, based at the Max Planck Institute for the Science of Human History, Jena. DE. E.B.A. was supported by the Fondacion Fyssen, based at the Max Planck Institute for the Science of Human History, Jena, DE. AM, RMB, and MK were supported by European Research Council Consolidator Grant 647797 'LocalAdaptation'.

ORCID

Jacopo Niccolò Cerasoni http://orcid.org/0000-0002-5546-1555
Emily Y. Hallett http://orcid.org/0000-0002-3074-7274
Eslem Ben Arous http://orcid.org/0000-0003-2489-825X
Robert M.Beyer http://orcid.org/0000-0003-2673-3096
Mario Krapp http://orcid.org/0000-0002-2599-0683
Andrea Manica http://orcid.org/0000-0003-1895-450X
Eleanor M. L.Scerri http://orcid.org/0000-0002-7468-9977

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Ihò Eléérú [Iwo Eleru], Nigeria

In "Handbook of Pleistocene Archaeology of Africa: Hominin behavior, geography, and chronology" [Eds. A. Beyin, D.K. Wright, J. Wilkins, A. Bouzouggar & D.I. Olszewski]. Springer.

Authors: Jacopo Niccolò Cerasoni[1]*, Emily Y. Hallett[1], Lucy Farr[2], Emuobosa Akpo Orijemie[3], Eleanor M.L. Scerri[1*]

[1]Pan-African Evolution Research Group, Max Planck Institute for the Science of Human History, Kahlaische Straße 10, D-07745 Jena, Germany

[2]Department of Archaeology, University of Cambridge, Cambridge CB2 3DZ, United Kingdom

[3]Department of Archaeology and Anthropology, University of Ibadan, Ibadan, Oyo State, Nigeria

*Corresponding authors: cerasoni@shh.mpg.de, scerri@shh.mpg.de

Main Text:

1.1 Location and Stratigraphy

The Ihò Eléérú rock shelter is located approximately 20 km NNW of Akure (Figure 1), near the Ondo State and Ekiti State border in Nigeria. The site, referred to here as 'Iho Eleru' to use common orthography, means "Cave of Ashes" in Yoruba, and is historically, if erroneously known as "Iwo Eleru". This latter name "Iwo Eleru" was an anglicised translation of the site's original Yoruba name, which was originally reported in 1961 by Chief officer J. Akeredolu of the Department of Antiquities in Benin, Nigeria (Shaw and Daniels 1984, pg. XI). In 1963, Thurstan Shaw led the exploration of caves and rock-shelters in the region (Figure 1), and was informed by another officer of the Department of Antiquities, G. Connah, of the existence of Iho Eleru. A first exploration of the site took place on 28 December 1963 (Shaw and Daniels 1984, pg. XI). Between 1964 and 1965, T. Shaw and S. Daniels conducted a series of excavations at the rock shelter, fully reporting their excavation findings in 1984 (Shaw and Daniels 1984).

The Iho Eleru rock shelter (7°26'28.83"N, 5° 7'29.16"E) is here described on the basis of the site's: (a) location, physiography and climate, (b) geology, and (c) ecology.

(a) The site sits at about 400m above sea level (a.s.l.) in the hilly landscapes that characterise the region between Ado Eketi and Akure. The area drains to the east towards the Ogbesse River, which flows south-southwest toward the Atlantic Ocean (Shaw and Daniels 1984). The climate of the region is characterized by distinct dry and wet seasons, with ~400mm rainfall falling during the dry season between October-February, and ~1500mm rainfall falling during the rainy season between March-September (NOAA, accessed 2019).

(b) The landscape features extensively eroded outcrops of ancient igneous deposits in lowlands characterised by river terraces and well oxidized sandy deposits underlain by sedimentary formations of laterite. Complex metamorphic formations also occur in the region as outcrops of crypto-crystalline silicates and siliceous stone formations. Shaw and Daniels (1984: pg. 190, figure 3) note veins of quartzite which occur along the igneous formations. Iho Eleru itself is located towards the base of an inselberg, on the western margin of the Ikere batholith. Veins of quartzite and crypto-crystalline silicates occur within 5 and 10 km of the site, respectively. Local river valleys are characterised by deposits of considerably eroded cobbles of quartz.

(c) The site sits at the edge of the modern boundary of the Guineo-Congolian rainforest phytogeographic region, just south of the Guinea Savanna zone which is characterised by forest islands and wooded savanna vegetation (White 1983). Currently, the region's vegetation is extensively modified by human activities including subsistence agriculture and agro-industry. Agricultural production in the region is focused on the cultivation of cocoa, yams, banana, and cola nuts. The area immediately surrounding Iho Eleru includes pioneer forest formations with low to medium canopy cover (5–10 m) and evidence of extensive anthropogenic modification.

The topography of the Iho Eleru rock shelter is characterised by an upper levelled platform area and steeply inclined talus slopes on the southern and eastern edges (Figure 2). Shaw and Daniels excavated four trenches in these areas (trenches D, F, S and trench XVI), aligning them approximately NE–SW and NW–SE. A fifth trench (central tunnel trench) was excavated in a narrow tunnel, at the rear of the rock shelter (Figure 2). The site was planned with a 1 metre resolution grid and the excavation units were identified by square numbers (e.g. t. D, sq. XXIII). The excavated area totalled $90m^2$. In the platform area of the site, Shaw and Daniels revealed a 0.5–1.4 m deep sequence and were able to identify 4 main stratigraphic units (Figure 3), although they note some localized differences which appear to relate to variation in depositional site formation processes (i.e. the drip line of the granite overhang, proximity to boulders and the rear wall of the rock shelter), and bioturbational disturbance (Shaw and Daniels 1984, pp. 3–7). The Shaw and Daniels excavation reached significant granite rock fall or 'granite bedrock' but it remains unclear if this deposit represents an erosional phase of the rock shelter or a bedrock surface.

Shaw and Daniels (1984) suggested that the sequence at Iho Eleru could be divided into 2 main cultural phases (A and B), split into 4 sub-phases: B1, B2, A1 and A2 (Table 1). The uppermost human occupation in the sequence is characterized by a combination of aceramic and ceramic levels (Phase B), interpreted from a mixture of different lithic technocomplexes (i.e. heavy-duty and ground stone lithics) and pottery types, which likely resulted from low-resolution spit excavation methods and the mixing of material of different ages. Below this phase, a Later Stone Age (LSA) industry was identified (Phase A). Human remains were found at a depth of c. 0.82–1.0 m although their position in the stratigraphy is not clear, due to the low-resolution spit excavation method which left no spatial referencing of finds and archaeological features.

The interpretation of the stratigraphic sequence was not based on direct evidence of distinct layers, due to the absence of clear partitioning of sedimentary units (Figure 3). The sequence proposed by Shaw and Daniels (1984) was largely developed from statistical analysis of the spatial distribution, material type, and concentration of lithic tools within the stratigraphy. A "time vector plane" was used, which accounted for 42.3% of the total variance of retrieved finds, and which subdivided the assemblage into 8 successive groups (Shaw and Daniels 1984, tables 7-9, figures 66-67; Allsworth-Jones et al. 2010). These groups were found to broadly agree with the stratigraphical observations of the material culture assemblages and radiocarbon dates. This system was developed from Shaw and Daniels' original idea of applying a "chalcedony index", advanced after initial observations of the concentration of chalcedony declining with depth within the platform area.

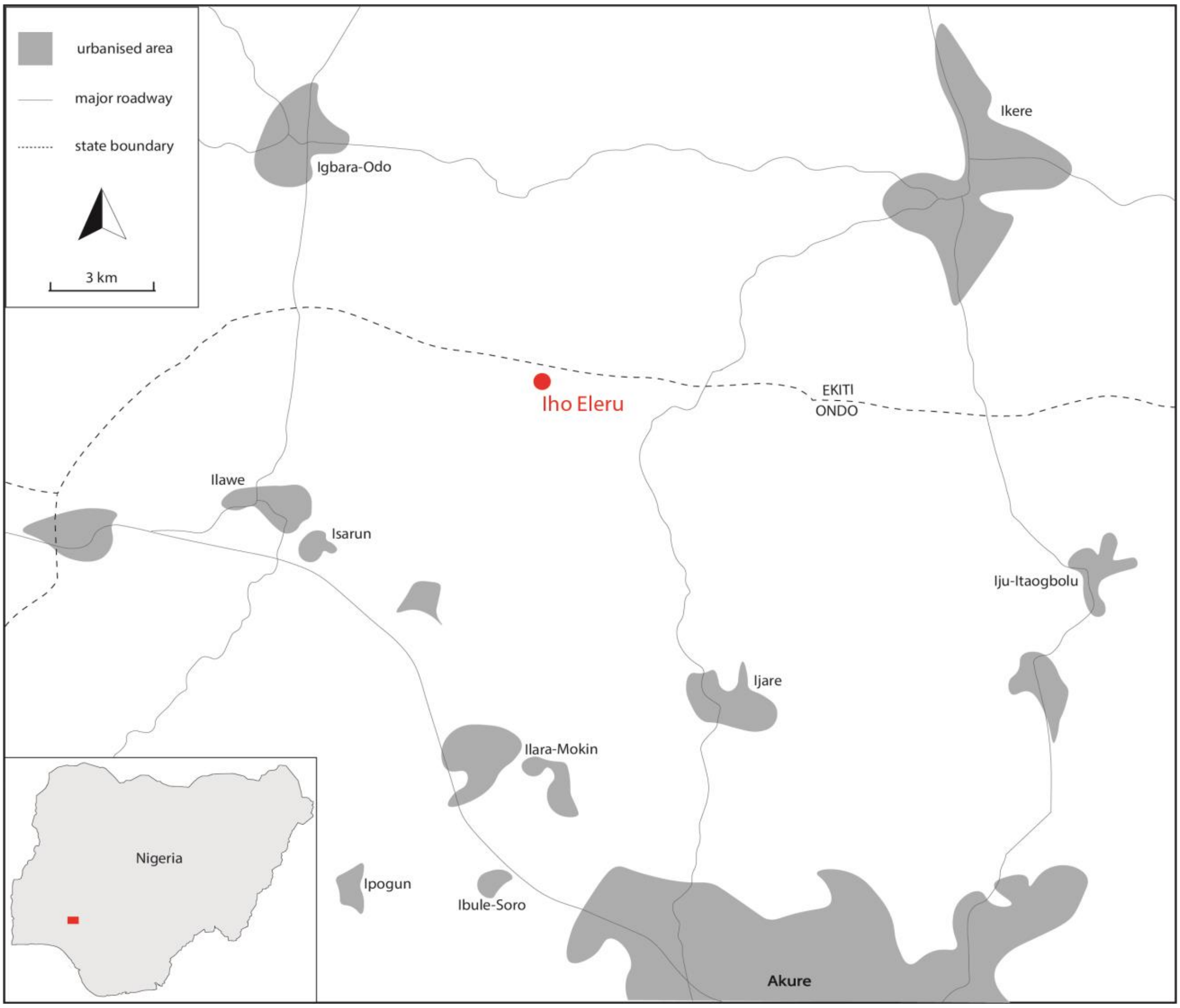

Figure 1: Regional map indicating the position of Iho Eleru, and showing the main modern urbanised areas (figure by J.N.C licensed under CC BY 4.0).

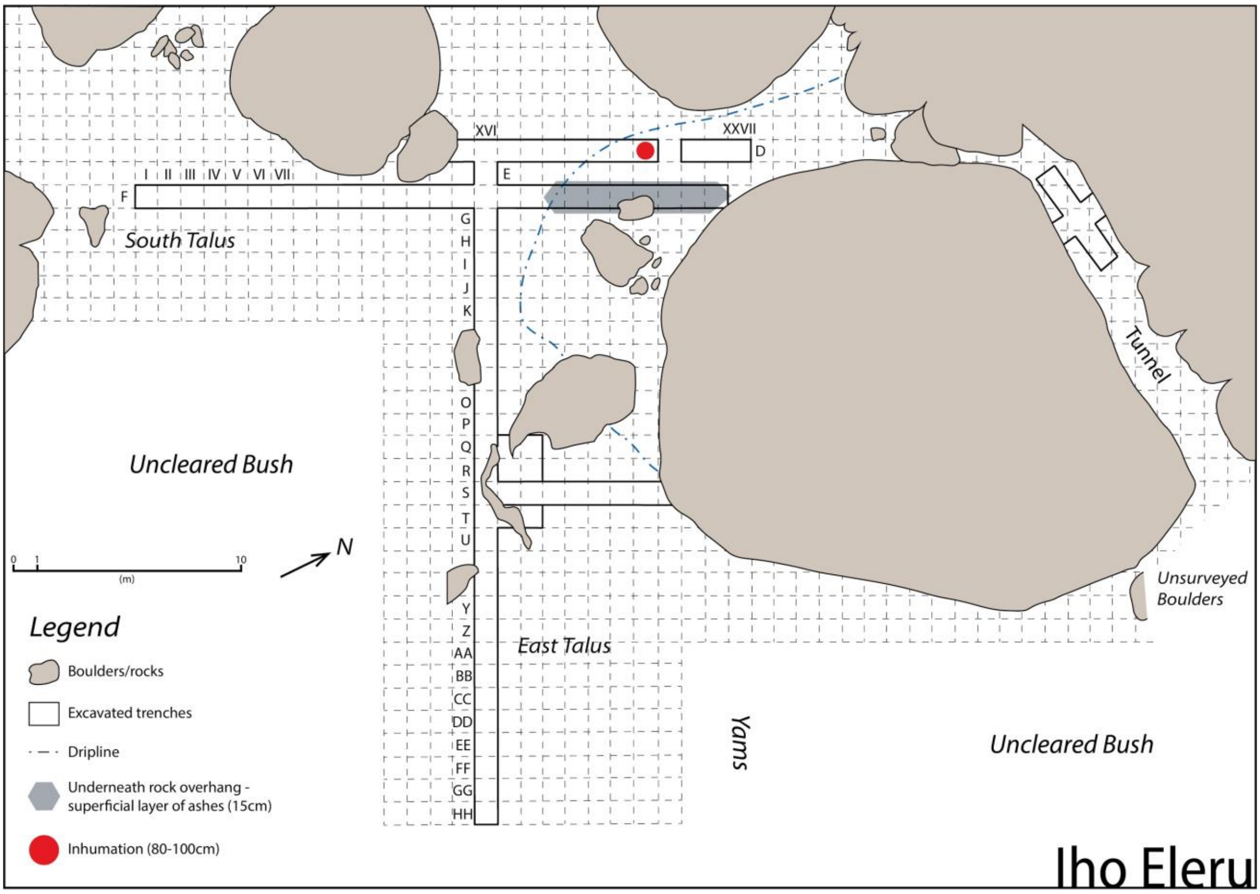

Figure 2: Plan of Iho Eleru (corrected and redrawn after Shaw and Daniels, 1984, fig 2, p. 189) (figure by J.N.C licensed under CC BY 4.0).

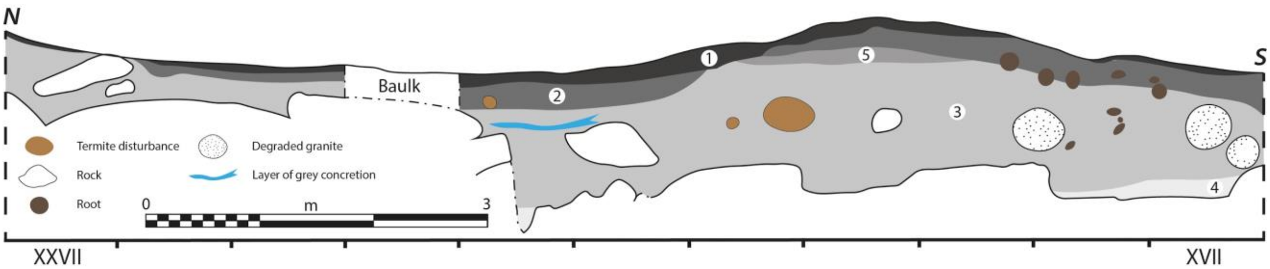

Figure 3: Stratigraphy of lower section along the east face of Trench D, XVII-XXVII. 1 - superficial ash layer, 2 - red sandy layer, 3 - reddish brown soil, 4 - gravelly soil, 5 - browner and looser than 3, but redder and less sandy than 2. (redrawn after Shaw and Daniels, 1984, fig 6, pg. 193) (figure by J.N.C licensed under CC BY 4.0).

Period	sub- period	Suggested dates (BC)	Material culture (in **bold** first appearance; in *italics* last appearance)
B	B2	After 2500	ground stone axes**, trapezoids**, microliths, querns, rubbed stones, grooved stones; **comb decorated pottery**
	B1	5000-2500	**ground stone axes, querns, rubbed stones and grooved stones,** core tools, choppers heavy duty chisels, heavy points and heavy duty scrapers; **pottery**
A	A2	7000-5000	**core tools, choppers, heavy duty chisels, heavy duty points, heavy duty scrapers,** *backed blades*
	A1	Before 7000	Triangles, backed blades, chisels, burins, microliths

Table 1: Cultural phases defined at Iho Eleru following Shaw and Daniels (1984).

1.2 Chronology

With deposits dated to the terminal Pleistocene to the middle Holocene, the material culture excavated at Iho Eleru documents a history of human occupation ranging from the LSA to the Neolithic. The stratigraphical sequence was dated using six non-calibrated radiocarbon age determinations on charcoal (Table 2) retrieved in trench D squares XX-XXIII, and between spits 2 to 8 (20-115 cm in depth). The only charcoal sample processed for radiocarbon dating that was retrieved in correlation with the human remains was also the only basal sample (I 1753) recovered. This sample produced the oldest radiocarbon date from the site, with an age estimate of 13,479-12,720 ca BP, and documents human activity at the site during the terminal Pleistocene. Recent direct dating of a "long bone cortical fragment" from the Iho Eleru human remains support a terminal Pleistocene age, with a Uranium-Series age of 16.3 ± 0.5–11.7 ± 1.7 kya (Harvati et al. 2011).

Lab No.	Provenance	Depth below surface (cm)	C^{14} age BP	Calibrated age BP
Hv 1512	Trench D XXII–XXI	20–35	3465 ± 65	3891–3575
Hv 1510	Trench D XIX–XX	50–65	5570 ± 60	6480–6280
Hv 1509	Trench D XX	65–80	7030 ± 85	7998–7688
Hv 1511	Trench D XVIII	95–110	8685 ± 120	10152–9489
I 1754	Trench D XVIII	100–115	9150 ± 150	10748–9888
I 1753	Trench D XXIII, "around burial"	70–100	11200 ± 200	13470–12720

Table 2: Radiocarbon dates determined by Shaw and Daniels (1984)

1.3 The Vertebrate Fauna of Iho Eleru

Shaw and Daniels (1984, pg. 30) reported that a very small quantity of non-human bone fragments were recovered during excavation. The non-human bone fragments were recovered from sieves with a 0.25 inch screen size. The non-human bone material was then taken to the University of Ibadan and given to a staff member of the Zoology Department. However, this staff member left the University of Ibadan, and "subsequent exhaustive search failed to reveal the whereabouts of this small quantity of bone material” (Shaw and Daniels 1984). Unfortunately the non-human bones were not described in detail, e.g. “…little in quantity and poor in preservation” (Shaw and Daniels 1984, pg. 30) - relative terms that can mean very different things depending on the point of comparison. Thankfully these issues can be resolved: in November 2019, J.N. Cerasoni searched the storage rooms of the Department of Archaeology and Anthropology at the University of Ibadan and found the entirety of the non-human bone fragments from Shaw and Daniels’ excavations. The original context identification tags were intact for each bag of bone fragments. A total of 59 bags of bone fragments were found in storage, and are currently under analysis by the Pan-African Evolution Research Group at the Max Planck Institute for the Science of Human History in Jena, Germany.

1.4 Human Remains

A human inhumation was discovered at Iho Eleru in 1965 (Shaw 1965a,b, 1968, 1972, 1978-1979) in trench D, square XXIII, at a depth of c. 0.82–1.0 m. The inhumation was described as being non-intrusive and between two large rocks, with no evidence of placement within a pit (Shaw and Daniels 1984).

The Iho Eleru human remains (Figure 4, Figure 5) were first described by Brothwell and Shaw in 1971 as “badly preserved remains of a tightly contracted skeleton” (Brothwell and Shaw 1971). The skeleton was encased in plaster at the time of discovery, but the skull was removed from the postcranial remains. The skull was sent to J. C. Trevor at the Duckworth Laboratory at the University of Cambridge, and D. Brothwell continued studying the skull following J. C. Trevor’s death. The postcranial remains (Figure 6) were also studied by D. Brothwell at the University of Cambridge, but they were only partially reconstructed as the state of preservation was too poor. Long bone epiphyses were not identified, and the shaft portions of the long bones were “severely shattered” (Brothwell and Shaw 1971). Cranial fragments were reconstructed to form the cranial vault, and teeth from the maxilla were studied in isolation. Much of the mandible was intact and described as “masculine in appearance” with several intact mandibular teeth and tooth roots. Brothwell and Shaw (1971) estimated that the individual was over thirty years in age based on the degree of wear on the molars. Brothwell and Shaw (1971) reconstructed the humeri, and noted that portions of the humeral shafts were incomplete following reconstruction. Shaft fragments were present from the individual’s clavicle, humeri, radii, ulnae, femorae, tibiae, fibulae, metacarpals, and metatarsals. Small fragments from the individual’s phalanges, vertebrae, and pelvis were also identified. The individual was estimated to have a stature of approximately 165 cm and a “medium height and build” (Brothwell and Shaw 1971).

Initial comparisons of the Iho Eleru calvaria with Neolithic, Mesolithic, and modern individuals revealed through Principal Components Analysis that the Iho Eleru individual was morphologically an outlier (Brothwell and Shaw 1971). C. Stringer (1974) then compared the Iho Eleru individual to Late Pleistocene human fossils from Africa and Eurasia, and found that while the Iho Eleru cranium was “modern” in some aspects, it was also “archaic” in others, and shared affinities with early *Homo sapiens* fossils from East Africa. Using a primary replica of the reconstructed cranium, Allsworth Jones et al. (2010) compared the Iho Eleru individual to 47 Pleistocene adult human individuals from Africa and Eurasia and 242 recent human individuals through geometric morphometric analyses and found that the Iho Eleru individual displayed archaic features in its long and low cranial shape. Harvati et al. (2011) likewise conducted 3D geometric morphometric analyses of the calvaria and found that its morphology was intermediate in shape, ranging between Neanderthals and *Homo erectus* (archaic hominins), and modern humans, and therefore suggestive of late-surviving archaic features and deep population substructure in Africa (see also Scerri et al. 2018).

Figure 4: Iho Eleru calvarium and mandible remains (figure by J.N.C licensed under CC BY 4.0).

Using a phenetic approach aimed at describing intra-specific patterns of variation, Stojanowski (2014) compared the Iho Eleru calvaria with terminal Pleistocene and Holocene contemporaries from the Maghreb, central and western Sahara, the Nile Valley, and East Africa, and found that the Iho Eleru individual demonstrated no affinities with its terminal Pleistocene contemporaries in the Maghreb and the Nile Valley. In addition, Stojanowski (2014) found that when compared with Holocene East African, Nile Valley, and west and central Saharan contemporaries, Iho Eleru was again an outlier in craniometric multivariate space. Stojanowski (2014) suggests that it was unlikely that terminal Pleistocene tropical West Africans contributed to the peopling of the Sahara during the African Humid Period.

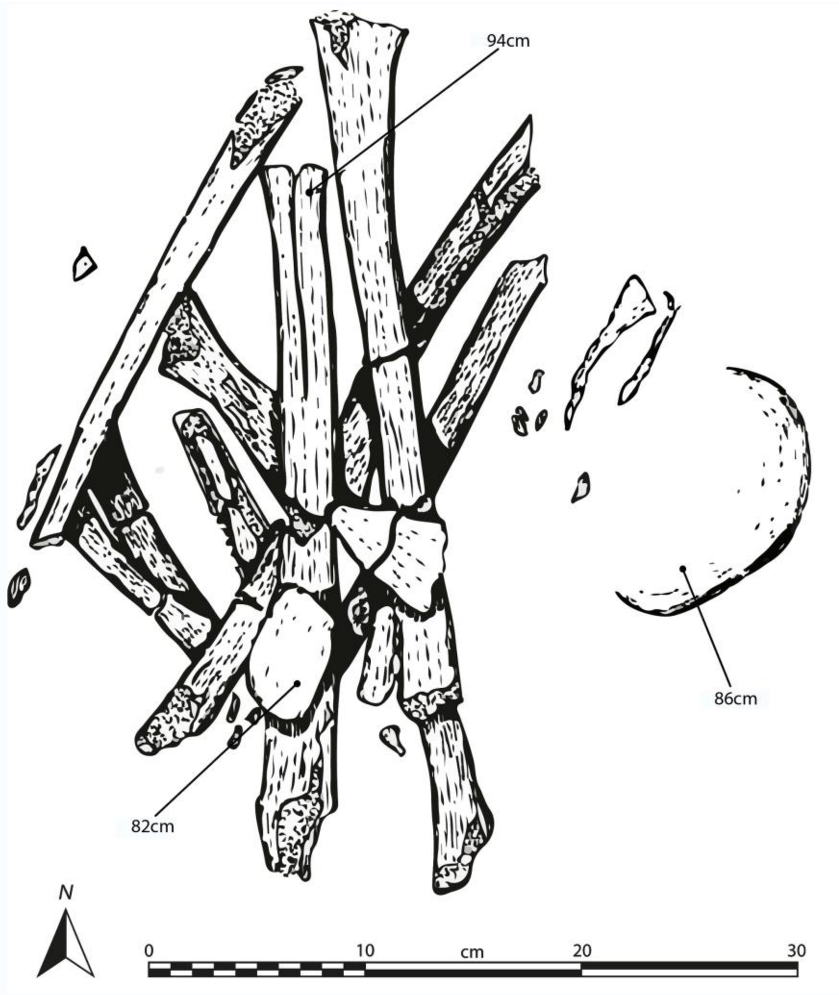

Figure 5: Plan of human remains in Trench D XXIII, where depths indicated are measured from the surface (redrawn after Shaw and Daniels 1984; figure 64, pg. 251) (figure by J.N.C licensed under CC BY 4.0).

1.5 Material Culture

Humans frequenting the Iho Eleru rock shelter used a wide variety of artefact types and methods of manufacture (Figure 6). Throughout West Africa the most common raw material type used in Pleistocene contexts is vein quartz, recognisable from its opaque white colour and highly fractured nature. Vein quartz is the most prevalent material type in the lower layers at Iho Eleru (A2 & A1), and was most likely sourced from local outcrops and nearby riverine areas where terrace deposits were exposed as a result of fluvial erosion. Chalcedony is also found, grey in colour and fine-grained, representing the majority of lithic artefacts in the upper layers (B2 & B1). The only lithic industry that was present throughout the stratigraphy were microliths, characterised by minor variations in microlithic types throughout the stratigraphy at Iho Eleru, such as the appearance of trapezoids and disappearance of triangles during phase B2 (Shaw and Daniels 1984).

The earliest layers at Iho Eleru (A1; 9000 – 12000 BP) were characterised by a typically LSA lithic industry, mostly in quartz, with backed blades, microliths, burins and chisels. With the onset of the subsequent cultural phase (A2; 7000-9000 BP) large cobbles, core tools and heavy duty tools (points and scrapers) appear. Chalcedony was the preferred material type during phase A2 for large scale and heavy duty tools, as it was the only sourceable material that permitted their knapping and working. Such tools continued to be used during the next phase (B1; 4500 – 7000 BP), with the introduction of ground stone technology using local granite and chalcedony. Querns also appear, together with the possible introduction of pottery, and the presence of rubbed haematite (ochre) fragments. With the onset of the youngest layer and cultural phase (B2; 4500 – 2000), heavy duty and larger lithics were abandoned, with the certain introduction of pottery, and a continuation of use of ground stone axes, querns, and microliths.

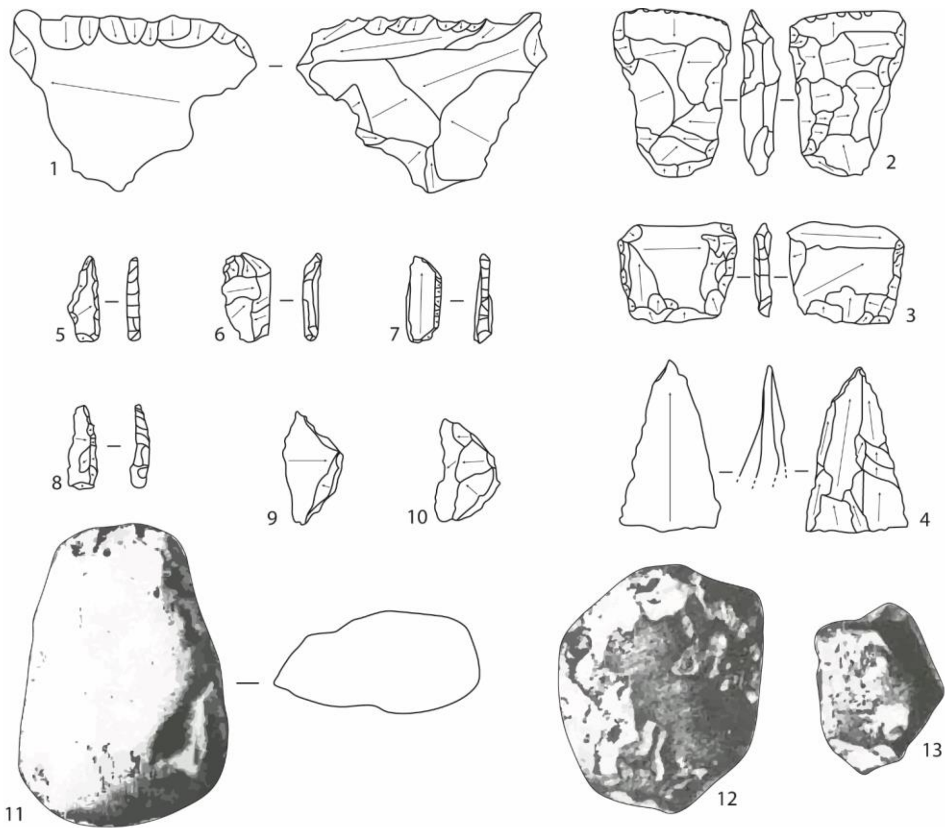

Figure 6: Representative artefacts from Iho Eleru (redrawn after Shaws and Daniels 1984). 1 - heavy chisel, chalcedony (fig. 37, 1, pg. 223); 2,3 - trapezoid microliths, chalcedony (fig. 38, n. 1-2, pg. 224); 4 - point (fig. 40, n. 1, pg. 227), chalcedony; 5,6,7,8 - backed blades, quartz (fig. 30, n. 1-4, pg. 216); 9 - segment microlith, chalcedony (fig. 28, n. 11, pg. 214); 10 - segment microlith, quartz (fig. 28, n. 12, pg. 214); 11 - ground stone axe, charnockitic granite (fig. 46, n. 1, pg. 223); 12, 13 - rubbed haematite (ochre) fragments (fig. 43, n. 10-11, pg. 230). (Scales omitted in original publication). (Figure by J. Cerasoni, licensed under CC BY 4.0).

1.6 Conclusions

The Iho Eleru rock shelter holds a unique position in Pleistocene African archaeology as it presents human remains that maintain some “archaic” morphological characteristics from deposits that are terminal Pleistocene in age, and associated with an LSA industry. The Iho Eleru human remains are morphologically dissimilar to hominin fossils from the Middle Pleistocene, and human fossils from the Late Pleistocene, early Holocene, and contemporary humans--and yet, the LSA material culture from Iho Eleru is widespread throughout Africa. The sedimentary sequence at the site spans at least 13,000 years. Terminal Pleistocene and Holocene deposits are divided into four distinct cultural phases, documenting a series of significant shifts in stone tool and ceramic material culture. The cultural sequence suggests that people at Iho Eleru lived in, or at least exploited, a tropical rainforest environment, with the local use of raw materials such as quartz, chalcedony, granite and rubbed ochre. Typical LSA technology (microliths, blades, burins), heavy duty and polished tools (choppers, chisels, points, scrapers, polished axes), and early pottery (comb decorated) dominate the material assemblages in the site. The newly rediscovered vertebrate faunal assemblage, together with future studies of the *in situ* stratigraphy and regional surveys will shed new light on past human activity at Iho Eleru.

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Appendix i.3

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Continuity of the Middle Stone Age into the Holocene

Eleanor M. L. Scerri[1,2,3✉], Khady Niang[4], Ian Candy[3], James Blinkhorn[1,5], William Mills[6], Jacopo N. Cerasoni[1], Mark D. Bateman[7], Alison Crowther[8,9] & Huw S. Groucutt[3,9,10]

The African Middle Stone Age (MSA, typically considered to span ca. 300–30 thousand years ago [ka]), represents our species' first and longest lasting cultural phase. Although the MSA to Later Stone Age (LSA) transition is known to have had a degree of spatial and temporal variability, recent studies have implied that in some regions, the MSA persisted well beyond 30 ka. Here we report two new sites in Senegal that date the end of the MSA to around 11 ka, the youngest yet documented MSA in Africa. This shows that this cultural phase persisted into the Holocene. These results highlight significant spatial and temporal cultural variability in the African Late Pleistocene, consistent with genomic and palaeoanthropological hypotheses that significant, long-standing inter-group cultural differences shaped the later stages of human evolution in Africa.

The African Middle Stone Age (MSA) is a cultural phase characterized by features such as a focus on prepared core lithic technology, hafting, and long-distance exchange, that emerged synchronously with the biological appearance of our species, *Homo sapiens*[1–5] (see Supplementary Materials [SM]). Together with these characteristics, the spatial and temporal distribution of the MSA across Africa between ca. 300–30 ka is seen as being relatively homogenous, and the term has also been used as a chronological marker (e.g.,[6]). While behavioural and cultural complexity is increasingly recognized in the MSA (e.g.,[1–5]), the transition to the Later Stone Age (LSA), with features such as miniaturized lithic technology and ostrich eggshell beads, is often seen as a seminal turning point in human history and the establishment of the first societies analogous to those characterizing recent humans[7–9]. To some, the transition was so dramatic as to suggest it was caused by a cognitive mutation that marks the appearance of truly 'modern humans'[9,10].

Recent research across Africa challenges this view of a simple, abrupt, continent-wide, transition from the MSA to the LSA (SM). The transition is gradual at some sites[11], and begins as early as ca. 67 ka in some cases[12]. At other sites the transition occurs much later[11,13], with late MSA assemblages often characterised by the same classic features documented in early MSA assemblages[2,3,14]. Growing evidence that human biological and cultural evolution was a Pan-African process[15,16] has also crystallized the regional spatial and temporal dynamics of the MSA and LSA as a key factor for understanding our species evolutionary history. In a continent where preserved Pleistocene biological remains are rare, material culture offers a rich record of human behaviour, which is both significant in itself and a crucial parameter in biologically focused models of human evolution.

Paleoanthropological research in West Africa highlights the distinct character of this poorly understood region. Although the only known Pleistocene *Homo sapiens* fossil from the area comes from an LSA context in Nigeria dating to ca. 16–12 ka, the Ihò Eleru (previously incorrectly labelled 'Iwo Eleru') calvaria displays morphological features typically found in much earlier human populations[17,18]. This shows that material culture 'stages' and skeletal morphology are not necessarily coupled, and critically, that there may have been a regional survival of a distinct and perhaps relatively isolated population until the end of the Pleistocene[19]. Likewise, genetic analyses highlight West Africa as a key wellspring of our species' genetic diversity[19], with some studies even suggesting contributions from past African archaic populations[20].

[1]Pan-African Evolution Research Group, Max Planck Institute for the Science of Human History, Kahlaische Straße 10, 07745 Jena, Germany. [2]Department of Classics and Archaeology, University of Malta, Msida, Malta. [3]Institute of Prehistoric Archaeology, University of Cologne, 50931 Cologne, Germany. [4]Département D'Histoire, Université Cheikh Anta Diop de Dakar, BP. 5005, Dakar-Fann, Senegal. [5]Centre for Quaternary Research, Department of Geography, Royal Holloway, University of London, London, UK. [6]School of Archaeology, University of Oxford, 1 South Parks Road, Oxford OX1 3TG, UK. [7]Department of Geography, Winter St., University of Sheffield, Sheffield S10 2TN, UK. [8]School of Social Science, The University of Queensland, St Lucia 4072, Australia. [9]Department of Archaeology, Max Planck Institute for the Science of Human History, Kahlaische Straße 10, 07745 Jena, Germany. [10]Extreme Events Research Group, Max Planck Institutes for Chemical Ecology, the Science of Human History, and Biogeochemistry, 07745 Jena, Germany. ✉email: scerri@shh.mpg.de

The archaeological record also indicates a distinctive character to human prehistory in this area. In West Africa, the argument for a young Middle Stone Age (MSA) has been made since at least the 1970s, typically on the basis of geomorphology and early radiocarbon dating (see[21–24] for summaries). Early studies of sites from across the region including those in Ghana[23], Senegal[24] and Niger[25] led to the prediction that the MSA in West Africa should date to between 35 and 15 ka[26], as indeed optically stimulated luminescence (OSL) dating at Birimi in Ghana demonstrated[26]. More recently, work on various localities at Ounjougou and in the Lower Falémé valley have identified lithic assemblages from Marine Isotope Stage (MIS) 6 to MIS 2 which feature varied technologies within an MSA umbrella (e.g.[22,27–29]). This work is further elaborated by work at Tiémassas, coastal Senegal, where three classic MSA assemblages span 62–25 ka[30,31] and in the Lower Senegal Valley[32,33] where MSA assemblages have been dated to 12 ka. These sites share a consistent focus on Levallois reduction approaches, sometimes complemented by discoidal methods, alongside the appearance of tools such as scrapers, denticulates and retouched points, which characterise the West African MSA. Critically, these assemblages lack technological features attributed to the earliest LSA assemblages in the region, including bipolar and blade reduction and backing, which do not appear until ca. 16–12 ka[17,21,22,27,34]. However, the majority of West African MSA sites offer limited chronological control (e.g.[23–25]), demanding clear demonstrations of the young timeframe of their occurrence to successfully integrate them into broader evolutionary models.

Results

Here we report late MSA assemblages from the sites of Laminia and Saxomununya, Senegal (Fig. 1), dating to ca. 22–21 ka and less than ca. 11 ka, respectively. These dates confirm the continuity of MSA technologies in West Africa thousands of years after they had been replaced by the LSA elsewhere on the continent. Both sites consist of river sediments that comprise the lowest terrace unit within the reach of each of their respective catchments; the Gambia River in the case of Laminia, and the Falémé river in the case of Saxomununya. The low rate of tectonic uplift that is found in this region means that unlike many large river systems, neither the Gambia nor the Falémé river valleys contain extensive sequences of terrace units. This observation is supported by the study of digital elevation models (DEMs) of the study sites, which show limited topographic evidence for multiple discrete terrace surfaces (Figs. S1; S2, see SM). Instead, in the study reaches, the near channel geomorphology consists of a single terrace surface, 5–7 m above the modern channel which is entrenched by gullies and tributary channels. The studied sediments at Laminia are found within exposures of this terrace feature whilst the site of Saxomununya is found on the terrace surface.

The site of Laminia is exposed in sections of a south bank terrace of the Gambia river. These exposures, approximately 3 m in height, consist of a lower unit of cobble/pebble dominated well-sorted gravels overlain by fine-grained sands and silts (Fig. 2, Figs. S3, S4, see SM). The sequence is interpreted as reflecting the downstream migration of a large bar-form under high flow conditions in the main channel followed by lower energy deposition, most likely in the overbank environment after the river has undergone lateral migration. The lithic artefacts at Laminia come from a very specific context, the upper 0.2 m of the gravel deposits (Unit 1B). No other units have yielded lithic artefacts. In the context of the geomorphology of the site the position of the lithic finds is key because they occur on top of the bar-form. The absence of these lithics from elsewhere within the gravels implies that the artefacts were not being reworked downstream as part of the bedload but are concentrated at the bar surface and accumulated after the bar had stabilized. We therefore interpret the presence of artefacts here as relating to exploitation of the stabilized bar as a raw material resource, the stone tools which were produced on site are therefore in situ.

The site of Saxomununya occurs on a river terrace surface on the west side of the Falémé river (Fig. 2, Figs. S5, S6, see SM). Much of the site consists of exposed bedrock, but to the south there is a shallow accumulation of sediments (SM). A 0.5-m deep trench was excavated into the terrace to examine the nature of the sediments that make up the land surface. The shallow sediments underlying the land surface consist of well-sorted coarse sands and pebbles with occasional cobbles. Generally, these deposits are structureless except for some weakly developed cross-bedding. The sediments are typical of deposition in an active fluvial environment. The terrace surface is rich in lithic artefacts, whilst five buried artefacts were recovered from excavation. The freshness, density, and size range of the artefacts implies that whilst the sediments are fluvial in origin the lithic assemblage itself is in situ, and has been left there by humans following the cessation of fluvial activity (SM). We interpret Saxomununya as a raw material source, where humans used the gravel deposit to produce stone tools.

We used optically OSL dating of quartz grains to date Laminia and Saxomununya. All samples were found to have good OSL characteristics, with fast OSL signal depletion with stimulation and high De replicate reproducibility taken to indicate good signal resetting prior to burial (Figs. 3, 4, Tables 1, 2). Three OSL samples were taken at Laminia (Fig. 2.1, Shfd16115-17, SM) which produced consistent ages of 24.6 ± 0.98 ka for Unit 1A and 22.0 ± 0.85 ka and 20.8 ± 0.83 ka Unit 1B. At Saxomununya, we dated the terrace deposits that were used as a raw material source to offer a *terminus post quem* of the human occupation. The OSL sample was taken from the base of the trench, which sits just above bedrock. The sample (Shfd18020) produced an age of 11.1 ± 0.58 ka. These chronometric age estimates are consistent with geomorphological interpretations of the sites, namely that they both represent the most recent stage of terrace formation.

Surprisingly, given the young ages of these sites, both Laminia and Saxomununya feature classic MSA technological characteristics. At Laminia, 30 lithics in a fresh condition were recovered directly from the upper part of Unit 1B (Figs. 2, 5, S4, S7) while a further 85 were found in the immediate vicinity in the downstream direction alongside evidence for the localized erosion of Unit 1B. Complete artefacts comprise 48 cores and 56 flakes (SM). The assemblage primarily consists of artefacts made from small cobbles/large pebbles of quartz, with only three cores made on quartzite, and displays a homogeneous technological character. Nodules with natural Levallois-like convexities were typically selected for flaking. Of the 48 cores, early stage cores, defined by their large size

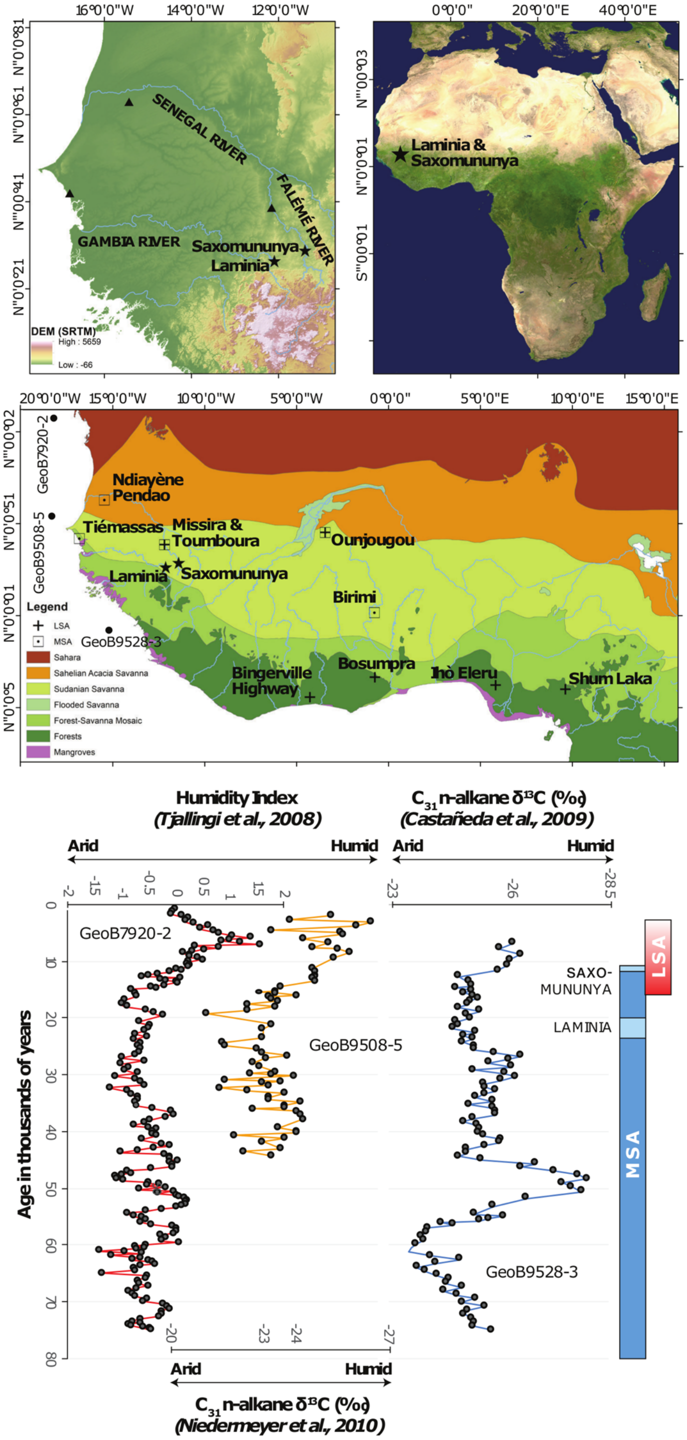

Figure 1. Site locations and chronological details. Maps illustrating the location of Laminia and Saxomununya in relation to the topography and major fluvial systems of Senegal (top left; SRTM DEM[63]), their position within Africa (top right; Image: NASA), and in respect to other key dated West African MSA and LSA sites, emphasizing the association of the MSA sites with Sudanian savannahs and the early LSA sites with tropical forest ecologies (centre yy[64]). (Bottom) The chronology of MSA (blue) and LSA (red) with the ages of Laminia and Saxomununya highlighted in light blue, against three Marine Core datasets indicating substantial directional change in humidity (left; *48*) and patterns of vegetation (centre (*49*); right (*50*)) at the MSA-LSA transition.

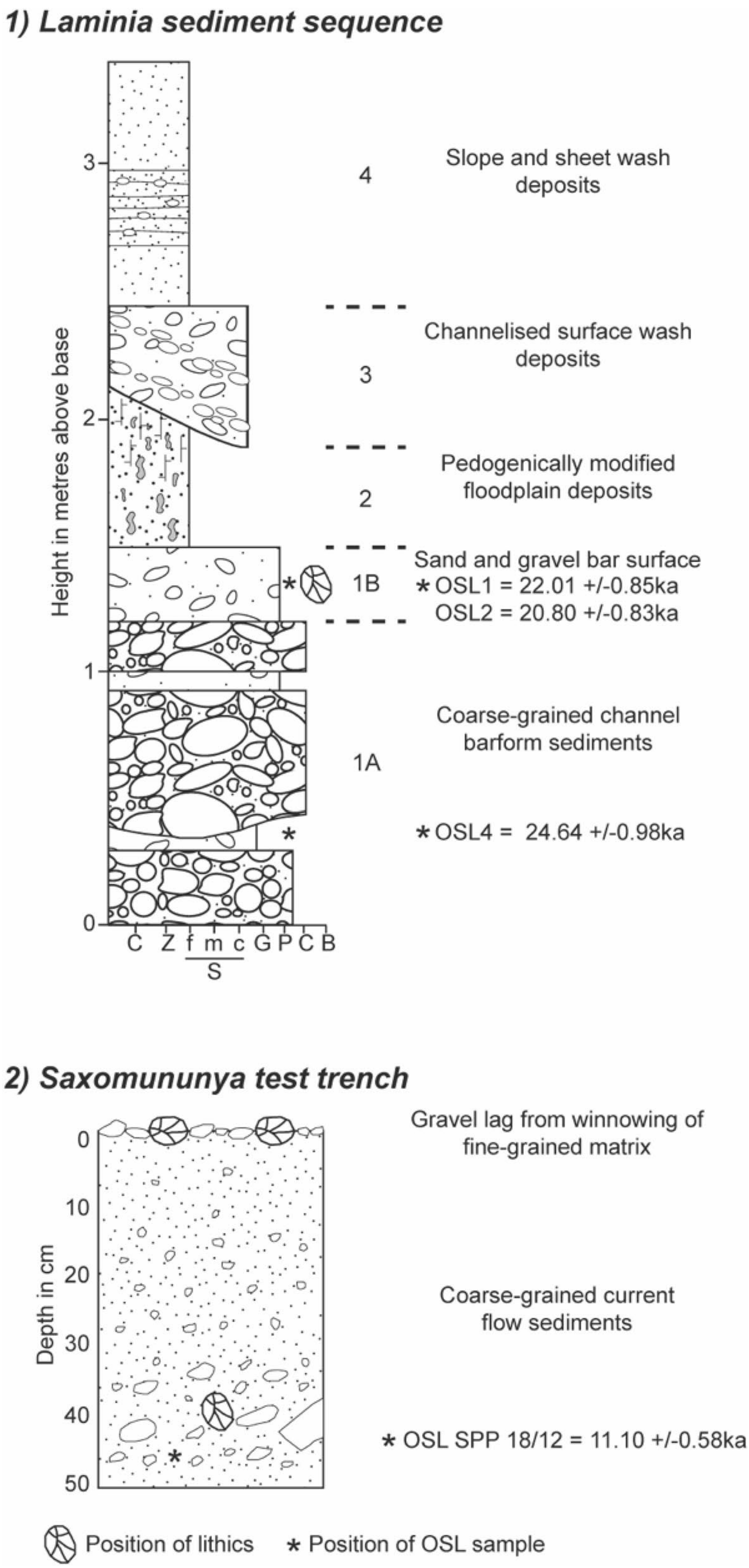

Figure 2. Sedimentary sequences from Laminia (1) and Saxomununya (2).

and the presence of few scars with high levels of cortex, are varied in their typology, as might be expected. This typology includes single platform (n = 7), multiplatform cores (n = 6) and tested pebbles (n = 5). These cores exhibit a high number of aberrant terminations (38%), and many appear to have flaws in them, such as natural

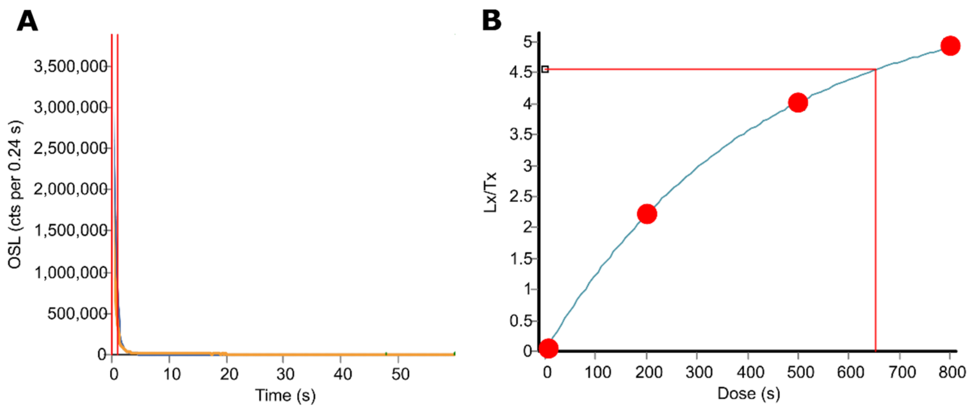

Figure 3. Examples of OSL measurements from Shfd16117. (**A**) A shine down curve showing rapid decay of the OSL signal with stimulation indicative of a signal dominated by the fast component. (**B**) A Single Aliquot Regenerative (SAR) growth curve showing low thermal transfer as the zero point is close to zero and good fit of growth to laboratory doses.

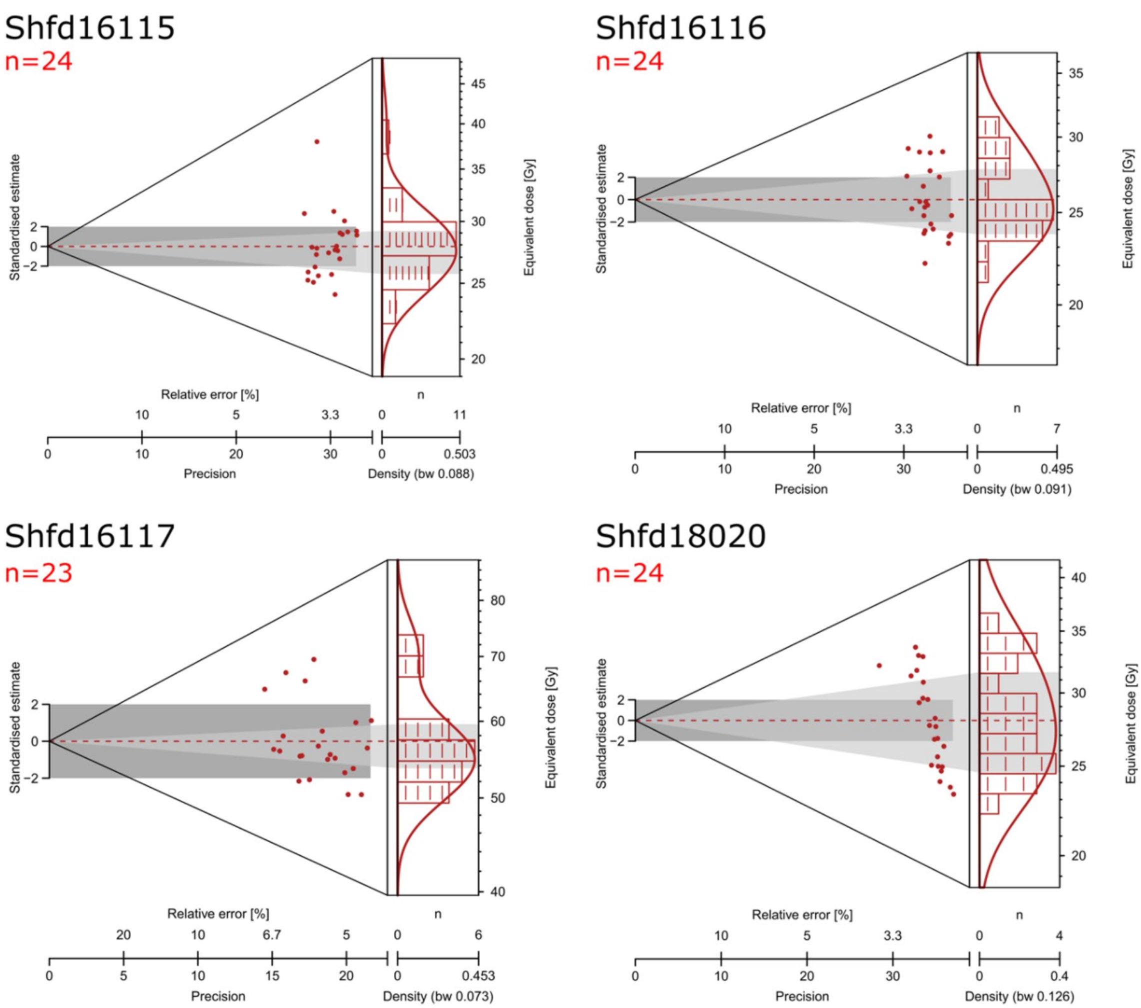

Figure 4. Abianco plots of OSL palaeodoses (De). These are shown for the three samples from Laminia (Shfd16115-17) and the sample from Saxomununya (Shfd18020).

Lab code	U (PPM)	Th (PPM)	Rb (PPM)	K (%)	D_{cosmic}^{+} (μGy/a^{-1})	Moisture (%)	Dose rate* (μGy/a^{-1})
Shfd16115	1.60	5.1	38.9	0.5	123 ± 6	3	1247 ± 44
Shfd16116	1.60	5.1	38.9	0.5	123 ± 6	3	1240 ± 43
Shfd16117	3.71	9.7	48.9	0.6	138 ± 7	5	2219 ± 82
Shfd18020	6.19	7.8	20	0.3	189 ± 9	4	2527 ± 112

Table 1. Summary of results for dosimetry data. + Cosmic dose is calculated as a linear decay curve at depths below 50 cm. Above this depth, errors in calculation may lead to an under-estimation of the cosmic dose contribution. * Total Dose is attenuated for grain size, density and moisture.

Lab Code	Field Ref	Depth (cm)	De (Gy)	OD (%)[a]	Dose rate (μGy/a^{-1})	Age (ka)
Shfd16115	OSL 1	370	27.44 ± 0.30	10	1247 ± 44	22.0 ± 0.85
Shfd16116	OSL 2	370	25.79 ± 0.50	9	1240 ± 43	20.8 ± 0.83
Shfd16117	OSL 4	280	54.68 ± 0.78	10	2219 ± 82	24.6 ± 0.98
Shfd18020	SPP18/12	45	28.00 ± 0.74	13	2527 ± 112	11.1 ± 0.58

Table 2. Summary of OSL results from Laminia (Shfd16115-17) and Saxomununya (Shfd18020), presented with one sigma confidence intervals which incorporate systematic uncertainties with the dosimetry data, uncertainties with the palaeomoisture content and errors associated with the De determination. [a] Overdispersation of De data.

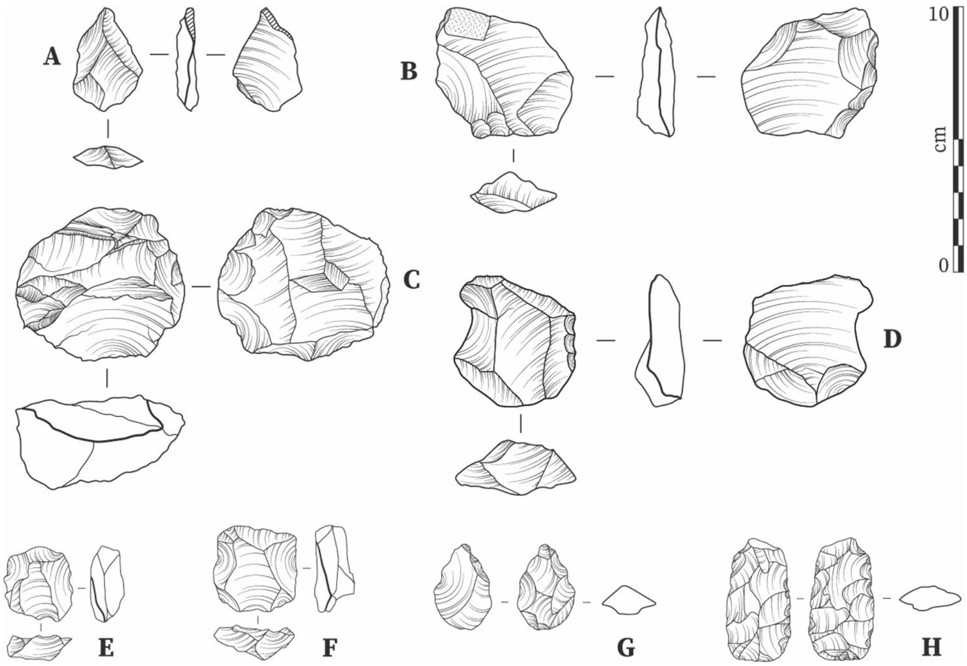

Figure 5. Lithics from Laminia (**A–D**) and Saxomununya (**E–H**). (**A**) unretouched flake; (**B**) bifacially retouched flake; (**C**) Levallois core evidencing a step fracture; (**D**) side retouched flake/scraper; (**E**, **F**) Levallois cores; (**G**) bifacial foliate point; (**H**) bifacial foliate. Figure licensed under CC-BY-4.0.

plains, which make knapping difficult. Four bidirectional cores seem to represent a slightly more advanced phase of reduction. Aside from two broken cores (one Levallois) the remaining 24 cores—making up 50% of the total number of cores – are Levallois cores, centripetally prepared for preferential removals. Where core reduction extends beyond preliminary nodule testing, Levallois reduction is clearly dominant.

The abundance of cores suggests that the site was targeted for raw material extraction, although removal of finer debitage from the site cannot be discounted. However, a notable proportion of the flakes (n = 44; ca. 66%) preserve cortex, extending over half the dorsal surface in 18% (n = 12) of cases, supporting the suggestion for a focus on primary reduction activities. The character of the debitage assemblage is consistent with the core technology, comprising facetted Levallois flakes alongside preparatory and débordant flakes, indicating that Levallois reduction schemes are the dominant technological feature of the assemblage. Retouched tools are rare, further supporting the focus on primary reduction activities at the site. The focus on preferential Levallois reduction, with centripetal preparation evident in both core and debitage assemblage is entirely consistent with an MSA attribution (Fig. 5, Fig. S7).

At Saxomununya, the lithic assemblage was collected in a spatially limited area of ca. 20 by 30 m, beyond which artefacts were very sparse. The total collected and excavated assemblage consisted of 231 cores, 336 flakes, 29 retouched flakes and 87 pieces of debitage and shatter. The predominant raw material consists of small quartz pebbles, while a few pieces of quartzite in the form of flakes are present. The small package size of the available raw material is reflected in the size of the lithics. These are small, but clearly not decoupled from raw material package size, a fact also reflected by the fact that no reduction techniques associated with the specific production of miniature lithics was observed. All the cores and retouched flakes, and just over half the flakes (192, randomly selected) were studied in detail (SM). Many of the cores (61 or 26.4%) are classic preferential Levallois cores with centripetal preparation. The three excavated cores belong to this category. A further 14 cores (6.1%) are Levallois core fragments or centripetally prepared but unstruck Levallois cores. Many of the 77 (33%) multiplatform or amorphous cores also display some evidence of previous Levallois-like exploitation (e.g. remnants of a central plane), suggesting discard once Levallois reduction schemes were no longer possible. A further 26 single platform cores (11.3%) display some evidence of core hierarchy, with the natural convexities of the pebbles used to detach relatively large flakes. Finally, eight cores (3.5%) are discoidal with a further 18 cores (7.8%) displaying a pattern of radial flaking but without evidence for platform preparation evident amongst the Levallois core sample.

The debitage is predominately comprised of small (mean = 32 mm length) complete flakes. Fifteen (7.8%) Levallois flakes with finely facetted platforms are present alongside eight (4.2%) débordant flakes, which maintain flaking surface convexities in Levallois reduction systems. A single pyramidal flake preserving an entire discoidal flake surface is present. The difficulty in knapping is well demonstrated by frequent aberrant terminations on flakes and cores (overshot flakes, step terminations) and siret fractures on the flakes. Twenty-nine flakes are retouched into classic MSA tool types, including denticulates, side and end scrapers, notches and retouched Levallois flakes that are well documented in MSA assemblages in West Africa and peripheral regions (e.g.,[2,21]). Three small foliate fragments, including two broken tips, were also recovered, as well as one whole foliate (Fig. 5, Fig. S8) and three possible foliate preforms. These tools resemble other Late Pleistocene examples recorded in the Lower Falémé. Although these are some distance away from Saxomununya, they are assemblages described as 'MSA-like', also featuring side-scrapers[28]. Overall, the core, debitage and tool assemblage, characterised by the presence of Levallois and discoidal reduction schemes and the absence of bipolar or laminar reduction, can best be ascribed to the MSA (S2, Fig. 5, Fig. S8), with the small size of artefact attributable to the limitations of available raw materials.

Discussion

The dates of ca. 11 ka from Saxonomunya and ca. 21–24 ka from Laminia sit at the end of a chronological arc of MSA assemblages in West Africa. These include ca. 11.6 ka at Ndiayène Pendao[33], ca. 20–50 ka at Birimi[26], ca. 33 ka at Toumboura III[28], and ca. 25–62 ka at Tiémassas[30,31]. This sequence demonstrates that MSA technologies persisted, rather than being reinvented, in the terminal Pleistocene. Our results mean that young MSA assemblages are now known from all of the major fluvial systems in the area; Laminia from the Gambia, Saxonomunya from the Falémé, Ndiayène Pendao from the Senegal, and Tiémassass from the Saloum. Although they represent the final phase of the MSA in the region, neither Laminia nor Saxonomunya yield any elements characteristic of the LSA. They are classically MSA in their composition, rather than indicative of a transitional phase between the MSA and LSA.

The record of a young MSA in West Africa builds on, consolidates and extends previously reported hints of a young MSA elsewhere in Africa, which have often been viewed as isolated or exceptional phenomena (e.g.[35,36]). Along with recent studies such as those as those extending the chronology of the LSA back in time (e.g.[12]), the young MSA of West Africa therefore adds to the evidence that the MSA to the LSA transition was highly variable in both chronology and character. West Africa presents particularly persuasive evidence of a late MSA: these assemblages comprise a suite of classic MSA characteristics that are absent in the earliest LSA in the region, which appears late with a discrete combination of stone tool technologies. This situation contrasts with some other regions of Africa, such as East Africa. Elements of stone tool technologies that are dominant features of LSA assemblages, such as the use of backing, blade production and bipolar reduction methods, are clearly apparent in MSA assemblages from MIS 5[37], whereas some 'MSA-like' elements may be reinvented in the Holocene[38]. At Panga ya Saidi in coastal Kenya, a major transition occurs from a classic late MIS 5 MSA to assemblages from ca. 67 ka characterized by small size and a focus on fine grained raw material[12]. Within the latter, various technologies (bipolar, blade etc.) alternate in frequency. Likewise, Levallois technologies re-appear. Such technological overlaps do not prohibit differentiation of the MSA and LSA in eastern Africa (e.g.[39]), but stand in stark contrast to West African records where late MSA assemblages lacking LSA-features clearly persist.

An interesting corollary to the demonstration of a young MSA in West Africa is the late onset of the LSA in the same region. LSA assemblages are present in the western part of Central Africa by ca. 30 ka[40]. LSA assemblages first appear in West Africa (i.e. west of Cameroon) ca. 16–12 ka in the forested regions of the modern countries of Nigeria, Côte d'Ivoire, and Ghana[17,18,21,22]. The LSA then appears further west and north in the Falémé Valley from around 11 ka[22]. The earliest LSA assemblages lack MSA features and emphasize the production of geometric microliths on small laminar blanks. The LSA does not seem to occur in West Africa until shortly before the use of ceramics and then the development of agriculture[41]. While much work remains to be carried out exploring the nuances of the spatial and temporal patterning in the transition from the MSA to the LSA, West Africa appears to follow an environmental dynamic, at least in some regards. The appearance of the LSA in the forested region of eastern and central West Africa correlates with an expansion of forests in the Terminal Pleistocene, around 15 ka[42–47]. On the basis of current data, transitions between glacial and interglacial peaks were unlikely to be smooth, leading to the formation of ecological bottlenecks that were non-synchronous between species[45]. Niang and colleagues[30] have suggested that occupation of ecotonal habitats, such as at Tiémassas where the MSA site is located in close proximity to Sudanian savannahs, Guinean mixed forest-savannahs and mangroves, may have played a role in fostering engagement with new ecological settings. Finally, time transgressive peaks in humidity also shed some light on the persistence of the MSA in the low latitudes and related temporally and spatially patchy cultural turnovers[42].

These findings suggest that a profound cultural turnover occurred in West Africa around the transition from the Pleistocene to the Holocene. In Senegal, at the westernmost point of the entire mainland Old World, the youngest known MSA at ca. 11 ka and the oldest LSA at ca. 11 ka occur within the same valley, with no technological overlap. This suggests the existence of strong cultural divisions in the Terminal Pleistocene and early Holocene of West Africa. The extent to which this division was biological versus cultural remains to be elucidated; but at a broad scale the end result is the same, that panmixia (random mating) is unlikely and that strong population subdivisions were present. The end of the MSA in West Africa occurs around a time of increasing humidity and forest growth (Fig. 1;[48–50]). This provides context for the spread of the LSA into areas which may have been relatively isolated by ecological barriers and bottlenecks[47] (SM). The relatively sudden increase in humidity from around 15 ka matches the age of the appearance of the LSA in West Africa, with the subsequent transition to the peak conditions of the African Humid Period from around 11 ka correlating with the end of the MSA and the spread of the LSA into Senegal[42].

Our results, along with other recent findings across Africa, demonstrate that the transition from the MSA to LSA is a spatially and chronologically heterogenous process of behavioural change. These findings do not fit a simple unilinear model of cultural change towards 'modernity', nor the use of these terms as specific, continent-wide chronological markers. Indeed, the continuity of a fairly generic MSA into the Holocene adds to a body of evidence showing that spatial and temporal expressions of complexity in the MSA are patchy (e.g.,[2]), indicating that motivations to invest in technological innovation related to factors other than simple behavioural capacity (e.g. [14].). Groups of hunter-gatherers embedded in radically different technological traditions occupied neighbouring, and sometimes perhaps shared, regions of Africa for thousands of years. This is at least consistent with the genetic signal for strong population structure seen in the last ca. 15 thousand years[18,51]. Elucidating the diverse relationships between populations is crucial for understanding the evolution of our species and offers an alternative to the extrapolation of the record from individual sites/regions to a continental scale.

Materials and methods

Fieldwork. Fieldwork in southeastern Senegal was undertaken between 2016 and 2018, as part of the Senegal Prehistory Project, which aimed to identify the presence of Stone Age occupations and understand their contexts. Previous survey work indicated that preservation of Late Pleistocene sediment archives was likely to be limited, resulting from considerable recycling of sediments within modern valleys, and limited topographic diversity across low altitude landscape. Additionally, thick, erosion resistant ferricrete profiles largely prohibit any substantial remodeling of the landscape. As a result, our survey aimed to target the margins of the modern valleys focusing on identifying older deposits that had not yet been eroded away. The focus of the survey was on the upper part of the Falémé in Senegal, and the Senegalese section of the Gambia River and its tributaries. Previous work on the fluvial geomorphology of the region is reported by Michel[52]. Although stratified archaeological deposits were scarce, where surface and isolated finds were recovered during the course of the survey, they typically fitted with technologies that are characteristic of the Middle Stone Age (MSA) in the region. We report here two key sites from this area. Laminia (12.6425 N, 12.1075 W) is a gravel deposit on the Gambia River, and was first identified in the 1960s[53,54]. Only a small number of lithics were previously collected, and no chronometric dating had been applied to the site. Saxomununya (field code SPP18-12) is a newly discovered site in the upper part of the Falémé Valley (12.8836 N, 11.4051 W) occurring on a terrace on the west side of the river.

OSL dating methodology. OSL samples were collected at Laminia and Saxomununya by hammering opaque metal tubes into freshly cleaned sediment sections. Three samples were collected at Laminia: Shfd16115 and Shfd16116 were located adjacent to each other at 370 cm depth from the modern surface, and Shfd16117 from 280 cm depth from the modern surface, with this variation in depth resulting from an uneven thickness of overlying, sloping deposits in Unit 4 (Fig. 2). At Saxomununya, the sample was taken from the trench at a depth of 45 cm. All samples were then transported to the Sheffield Luminescence Dating Laboratory, Department of Geography, University of Sheffield (UK) for analysis.

Quartz samples for OSL dating were prepared from the size range 125–180 µm as per Bateman and Catt[55]. OSL measurements were conducted in a Risø DA-20 luminescence reader fitted with blue/green LEDs for stimulation and signal detected was through Hoya U340 filters. Samples were mounted as a 2 mm diameter monolayer on 9.6 mm diameter aliquots with 24 replicates of palaeodoses (D_e) measured using the single aliquot regeneration (SAR) protocol[56]. A preheat of 260 °C for 10 s was used for the Laminia site and 200 °C for 10 s for the Saxomununya site. Both were derived experimentally using dose-recovery preheat plateau tests[56]. Overall, the samples showed rapid OSL decay curves, good recycling and low thermal transfer (Fig. 4). D_e distributions showed the samples to be normally distributed with low overdispersion (Fig. 5, Table 2). The final derived D_e values were therefore based on the Central Age Model[57]. Dose rates were based on concentrations of potassium, uranium and thorium as determined by ICP-MS and ICP-OES. All dose rates were appropriately attenuated for moisture (based on present-day values) and sediment size and incorporated a cosmic dose rate following the published algorithm of Prescott & Hutton[58].

Lithic analysis. Lithic analysis methods follow those previously reported by Scerri and colleagues[59,60] and Groucutt and colleagues[61,62]. We recorded detailed technological and metric features of the entire Laminia assemblage. For the larger Saxomununya assemblage, we studied cores and retouched flakes in more detail and a random sample of just over half (192) of the complete flakes.

The aim of the lithic analysis was to characterize the fundamental techo-typological features of the assemblage, as well as to assess characteristics such as weathering and breakage patterns. We therefore classified each studied lithic into raw material types, evaluated its weathering, and evaluated indications of knapping technique (e.g. percussor form), gave each piece a typological classification, and recorded technological features such as dorsal scar pattern, measured mass (grams) using digital scales, and recorded metric dimensions using digital calipers.

Received: 16 September 2020; Accepted: 8 December 2020
Published online: 11 January 2021

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Acknowledgments
All authors would like to thank the Institut Fondamental d'Afrique Noire in Dakar for their generous logistical support during fieldwork.

Author contributions
All authors contributed to the manuscript. Fieldwork was led by K.N. and E.M.L.S. Lithic analyses were conducted by E.M.L.S., K.N., H.S.G., J.B. and J.N.C. Chronological analyses were conducted by M.B., and J.N.C. produced the lithic illustrations. J.B., I.C. and W.M. conducted geoarchaeological assessments on the field.

Funding
Open Access funding enabled and organized by Projekt DEAL. E.M.L.S would like to thank the Oxford University Fell Fund and the British Academy/Leverhulme Small Grants for funding the field seasons leading to the results published in this paper.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-020-79418-4.

Correspondence and requests for materials should be addressed to E.M.L.S.

Supplementary Materials

Continuity of the Middle Stone Age into the Holocene

Eleanor M.L. Scerri[1,2,3*], Khady Niang[4], Ian Candy[3], James Blinkhorn[1,5], William Mills[6], Jacopo N. Cerasoni[1], Mark D. Bateman[7], Alison Crowther[8,9], Huw S. Groucutt[3,9,10]

[1]Pan-African Evolution Research Group, Max Planck Institute for the Science of Human History, Kahlaische Straße 10, 07745, Jena, Germany.

[2]Department of Classics and Archaeology, University of Malta, Msida, Malta

[3] Institute of Prehistoric Archaeology, University of Cologne, Cologne, 50931, Germany.

[4]Département d'Histoire, Université Cheikh Anta Diop de Dakar, BP. 5005 Dakar-Fann, Senegal.

[5]Centre for Quaternary Research, Department of Geography, Royal Holloway, University of London, U.K.

[6]School of Archaeology, University of Oxford, 1 South Parks Road, Oxford OX1 3TG, U.K.

[7]Department of Geography, Winter St., University of Sheffield Sheffield S10 2TN, U.K.

[8]School of Social Science, The University of Queensland, St Lucia 4072, Australia.

[9]Department of Archaeology, Max Planck Institute for the Science of Human History, Kahlaische Straße 10, 07745, Jena, Germany.

[10]Extreme Events Research Group, Max Planck Institutes for Chemical Ecology, the Science of Human History, and Biogeochemistry, Jena, 07745, Germany.

*Corresponding author: sceri@shh.mpg.de.

The Young MSA

In West Africa, the argument for a young Middle Stone Age (MSA) has been made since at least the 1970s, typically on the basis of geomorphology and early radiocarbon dating (see [*21- 24*] for summaries). However, many of these claims were made are based upon interpretations and age estimates which would no longer be considered reliable. For example, at Asokrochona and Tema II in Ghana, arguments for an MIS 2 date were made on the basis of geological interpretation [*23*]. In Senegal, artefacts described as 'Mousteroid' and 'Evolved Palaeolithic' (featuring small foliates) were considered to be as young as 13.5 ka [*24*]. Early radiocarbon dates seemed to corroborate this narrative. In Cameroon, a possible *terminus ante quem* of 15 kyr uncal BP was obtained in the 1970s by radiocarbon from the MSA assemblage of Figuil-Louti, which features Levallois and discoidal cores and Levallois flakes [*65*]. At the MSA site of Bilma, in Niger, a *terminus ante quem* of 33.4 ± 2.5 kyr uncal BP was also obtained in the 1970s by radiocarbon, from an assemblage in stratified but secondary position [*25*]. Summaries of these dates led to the prediction that the MSA in West Africa should date to between 35 and 15 ka [*26*], as indeed OSL dating at Birimi in Ghana demonstrated [*26*].

More recently, work on various localities at Ounjougou and in the Lower Falémé valley have identified lithic assemblages from MIS 6 to MIS 2 which feature varied technologies within an MSA umbrella (e.g. [*22; 27-29*]). While these assemblages often feature relatively simple flake production – in part potentially attributable to the frequent use of low-quality raw materials such as sandstone, they feature consistent core reduction methods and retouched tool forms characteristic of the MSA. Core reduction methods include Levallois methods, and retouched forms include denticulates, sidescrapers and bifacially retouched points. The site of Tiemassas has revealed excavated MSA lithic assemblages with a consistent presence of alternate modes of Levallois flake production and discoidal reduction alongside low frequencies of retouched tools, predominately side scrapers, dated using OSL between 62-25 ka [*30*-*31*]. Finally, work in the Senegal Valley identified the late MSA (ca. 12 ka) site of Ndiayène Pendao, which features Levallois cores and flakes, denticulates, basally thinned pieces and core axes, with no trace of LSA characteristics, such as microliths, microblade cores, splintered pieces and segments [*33*]. Other undated sites in the Senegal Valley, such as Njideri and Madina Cheikh Omar, feature similar characteristics to Ndiayène Pendao [*32*].

Laminia and Saxomununya site formation

We interpret both Laminia and Saxomununya as cobble or gravel deposits that were subsequently exploited by humans to produce stone tools. The OSL age estimates for these deposits therefore provide direct ages for human activity at Laminia and a maximum age at Saxomununya. As well as their stratigraphic position at Laminia, this is indicated by generally low weathering and edge and arris sharpness. In both cases very few examples showed the kind of chipped edges we would expect from fluvial transport of artefacts. Even in the large sample of artefacts from Saxomununya, most of which are small and with the flakes having edges vulnerable to chipping, few examples show signs of damage that would indicate redeposition. By comparison, in a study of fluvial deposition in a small Welsh river, Hosfield and Chambers [*66*] found that lithics which moved just a few meters to a few tens of meters featured relatively frequent breakage (4-20 %) and, crucially, very common micro-flaking of the edges, with several scatters having more than two-thirds of the flakes featuring small chipping. It therefore seems highly unlikely that the assemblage has been transported and redeposited without being damaged.

Spatial aspects are also consistent with the hypothesis that the lithics at Laminia and Saxomununya were knapped on site, rather than being fluvially redeposited. At Laminia this relates to the exclusive presence of lithics in the upper part of the gravels, and their horizontally limited extent (we did not find lithic artefacts in nearby gravel bars). As well as their limited spatial distribution, the artefacts show no significant weathering or edge rounding suggesting that they have not been substantially impacted by fluvial activity. Likewise, at Saxomununya the high-density of lithics at a particular locality, in contrast to very low artefact frequencies elsewhere in the area, are parsimoniously interpreted as suggesting that Saxomununya was a raw material source rather that representing the fluvial deposition of artefacts.

Our interpretation of Saxomununya is that the artefacts have suffered only slight deflation and spread, and there is no evidence that they were extensively fluvially redeposited. If the Saxomununya lithics had been redeposited we would expect to see more of a biased size profile, whereas in reality the size structure seems consistent with on-site knapping. The average weight of cores is 21.5 grams, for flakes 7.7 grams, while that of chips and chunks is 2.2 grams. The distribution of weights by category is shown graphically in Fig. S9. We could alternatively point out that while many chips and chunks weigh less than 1 gram, the larger cores weigh over 100 grams. A similar point could be made in terms of metric dimensions. The simplest explanation of this is that the lack of evidence for size sorting reflects on site knapping. If the lithics had simply become part of the gravel load, we do not imagine it likely that lithics with such varied masses would be densely deposited in a single spot.

Many experiments have been conducted by archaeologists in order to explore how fluvial redeposition can be inferred and understood (e.g., [*66-75*]). This is a complex area of research, as many variables are involved (e.g. the size of the river, the nature of the geology). For instance, several studies have been conducted in the small Afon Ystwyth in Wales. Here the movement of lithics was tracked over a short distance at several times. While providing a useful baseline, the probable difference between such rivers and rivers such as the Falémé, which has a very high-flow during the wet season should be emphasized. Likewise, most studies have focused on larger lithics (e.g. handaxes, large flakes) than the small-sized lithics from Saxomununya. Nevertheless, from these various studies a body of knowledge exists on the behavior of lithic assemblages in fluvial settings. What tends to emerge is that small lithics are preferentially removed (e.g., [*67-69, 73, 75]*). Some studies that have not agreed with this interpretation concern the movement of lithics in small rivers over a few meters to a few tens of meters (e.g., [*66*]).

While our collection at Saxomununya was in the form of a thorough walk over, it was not possible to collect every single small chip and chunk (as would be achieving by sieving, for instance). Nevertheless, it does appear that the small fraction of lithics at the site is under-represented. We interpret this as indicating the removal of smaller lithics from the site (see also [*69-70*]). This is not surprising, given the presence of sandy sediments overlying the gravel rich layers which are preserved in the southern part of the site, but seem to have been eroded to the north. The site therefore indicates winnowing leading to a removal of part of the smallest size component, but the presence of multiple size classes in a dense scatter of fresh artefacts is parsimoniously interpreted as indicating on site knapping. In perhaps the most comparable study, Schick [*70*] studied the impact of fluvial activity to dozens of test assemblages in different settings in East Africa. This study found that most experimental scatters were rapidly and significantly altered. Scatters located in active channels were quickly destroyed beyond recognition and the lithics scattered downstream.

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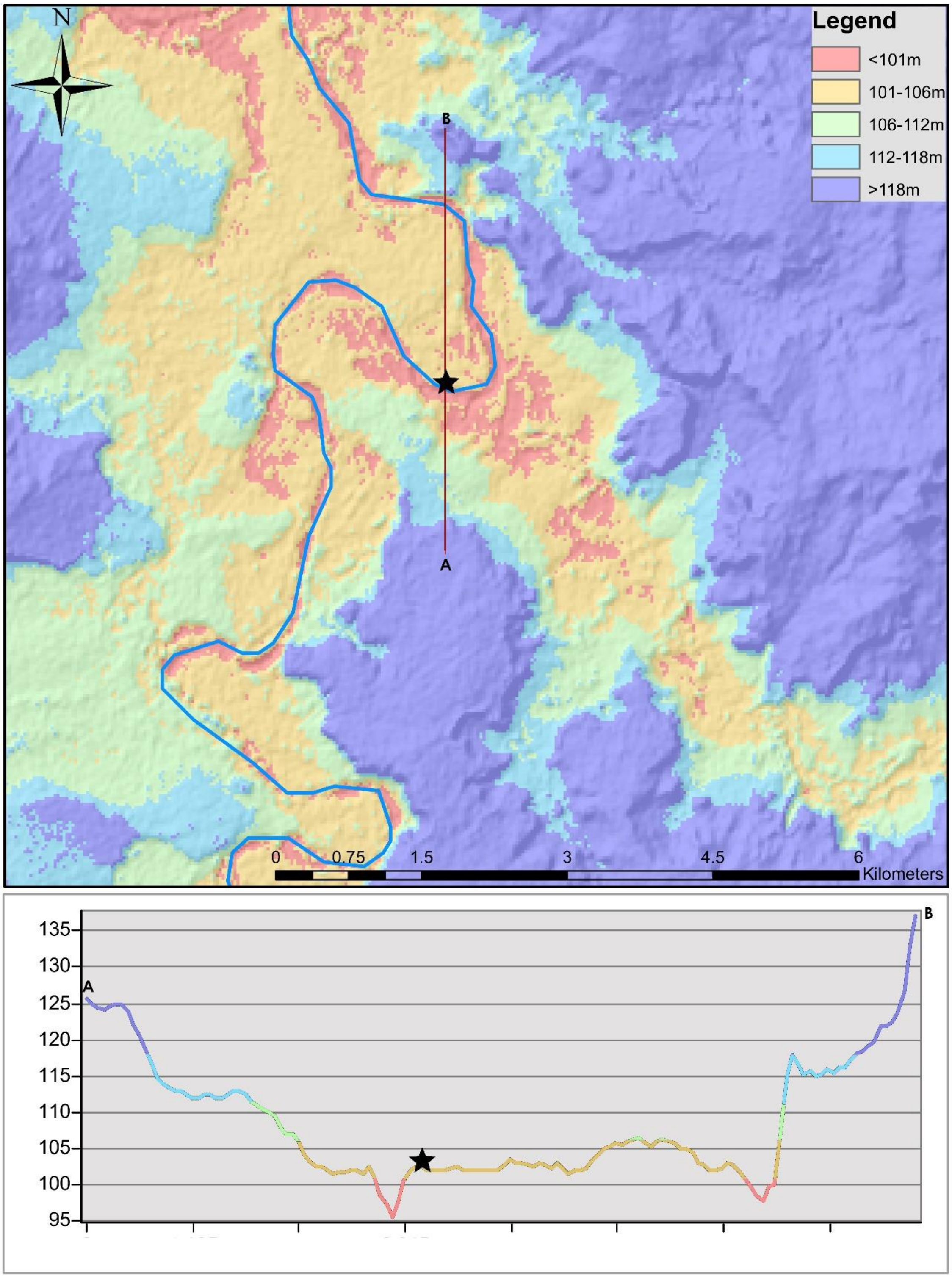

Fig. S1: (top) Digital terrain model (ALOS [JAXA]) illustrating the location of the archaeological site at Laminia (star) on a river terrace surface constrained in the immediate landscape to altitudes of 102-104m and a cross section across the Gambia Valley (red line); (bottom) elevation profile (generated from an ALOS DTM [JAXA] using ArcMap 10.5) across a section of the Gambia Valley (inidicated by the red line in top figure) illustrating the location of Laminia on a river terrace immediately adjacent to the modern, incised channel.

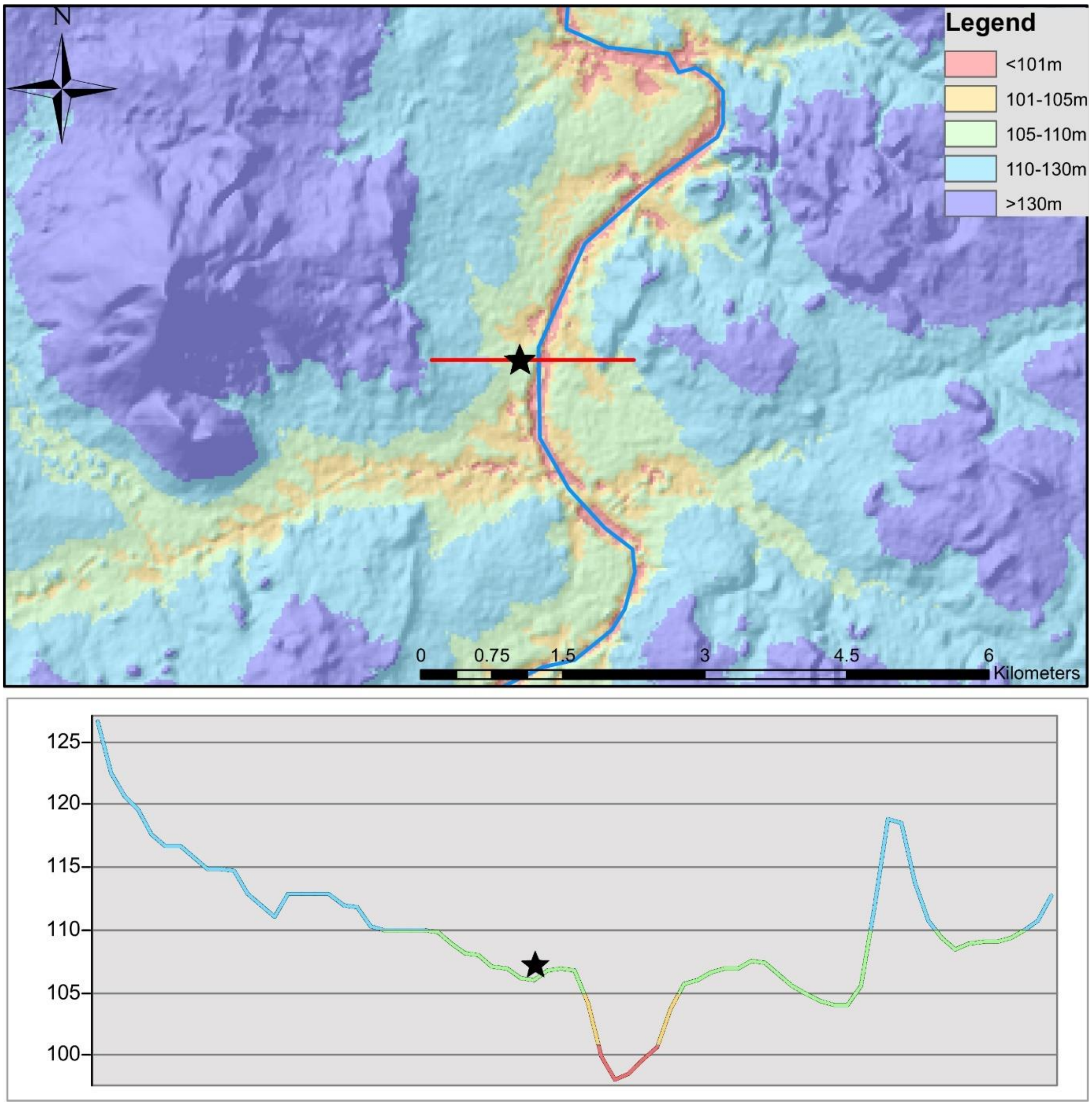

Fig. S2: (top) Digital terrain model (ALOS [JAXA]) illustrating the location of the archaeological site at Saxomununya (star) on a river terrace surface constrained in the immediate landscape to altitudes of 106-108m and a cross section across the Falémé Valley (red line); (bottom) elevation profile (generated from an ALOS DTM [JAXA] using ArcMap 10.5) across a section of the Falémé Valley (inidicated by the red line in top figure) illustrating the location of Saxomununya on a river terrace immediately adjacent to the modern, incised channel.

Fig. S3. Laminia section showing sediment type and gravel clasts.

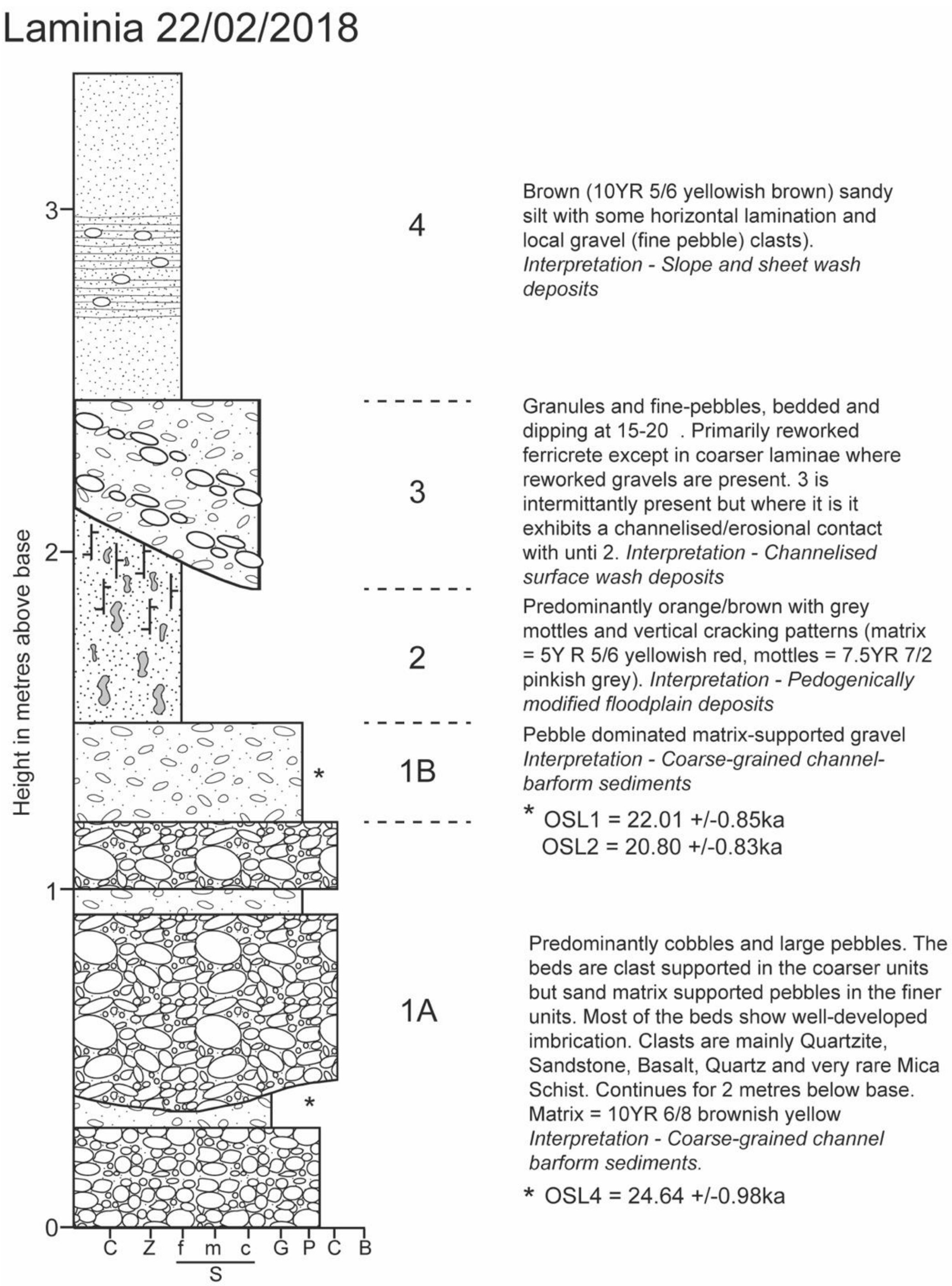

Fig. S4. Detailed sediment sequence from Laminia.

Fig. S5. Saxomununya**:** Surface of the site showing large numbers of lithics. The angular clasts are weathering from a bedrock exposure of very hard metamorphic rock. This slowed the waters of the ancestral Falémé River, leading to the deposition of a gravel deposit. This was then used by hominins as a raw material source. Lithics were found across the surface, and buried in sediments which have accumulated to the south (right on this image).

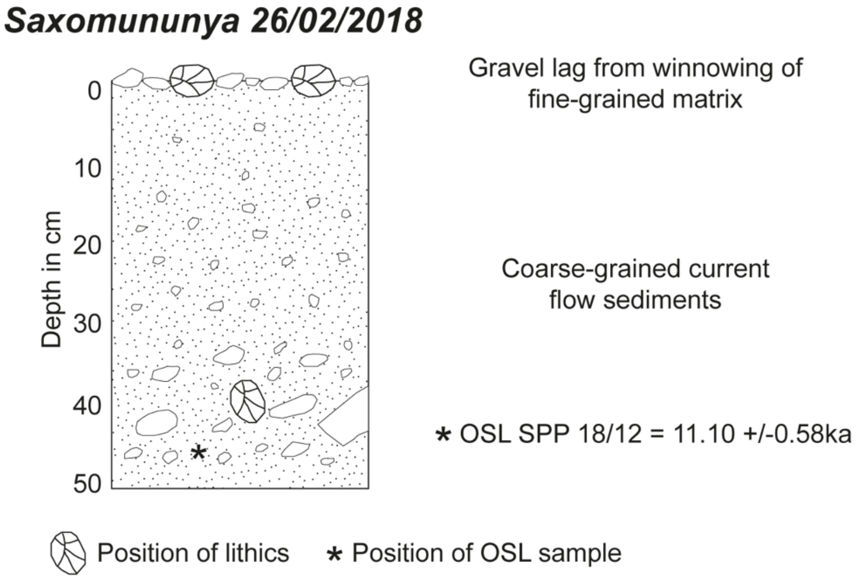

Fig. S6. Detailed sediment sequence from Saxomununya.

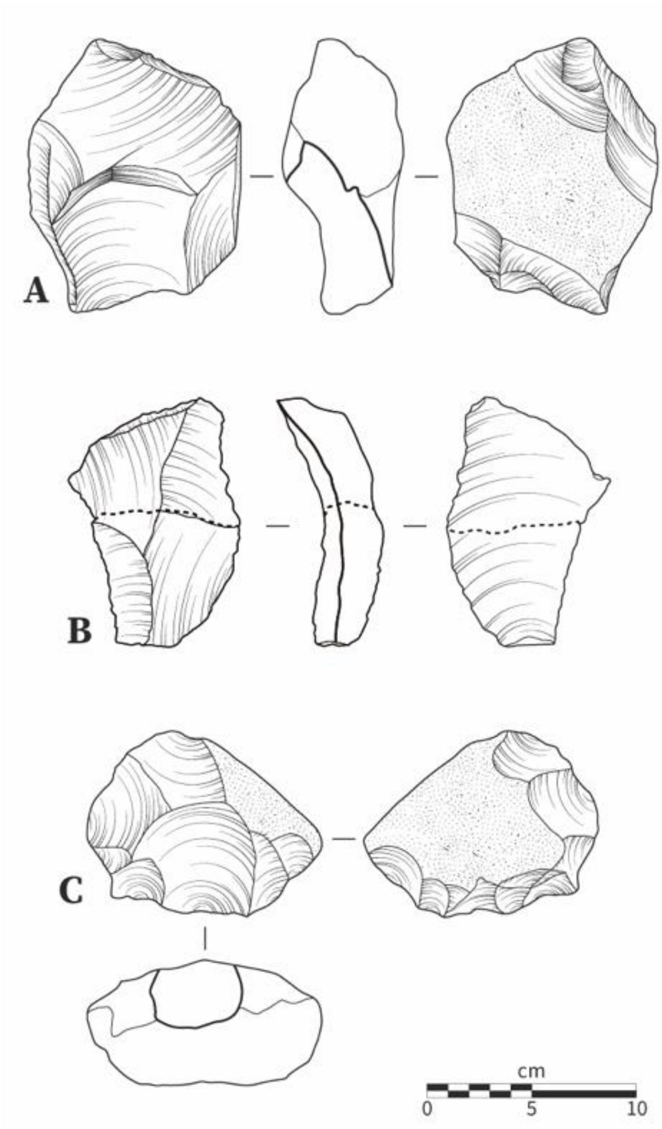

Fig. S7. Lithics from Laminia. A and C: Levallois Cores; B: Flake.

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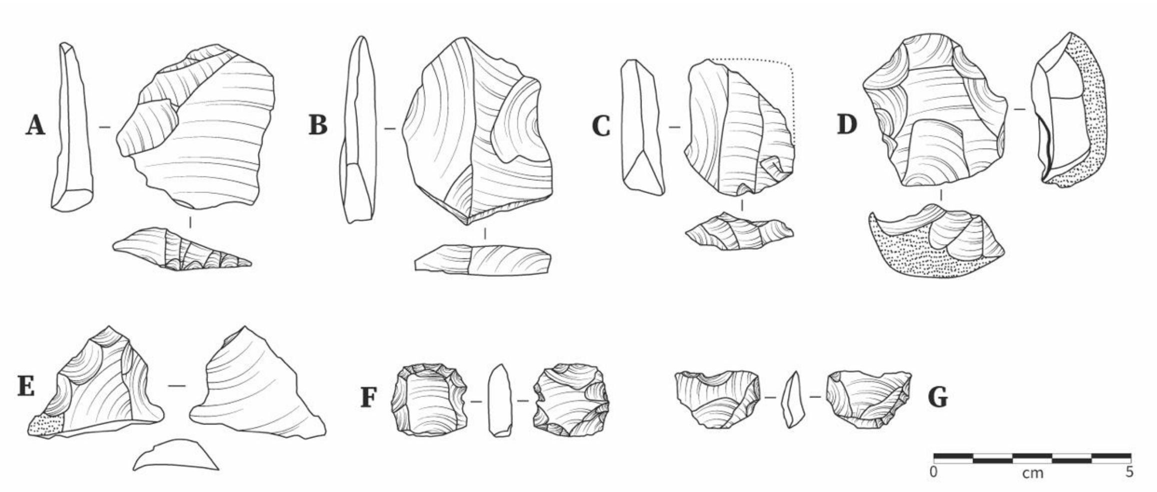

195 **Fig. S8.** Lithics from Saxomununya. A-C: Levallois flakes; D: Levallois Core; E: Broken

196 retouched point tip; F-G: Side and end retouched pieces/scrapers.

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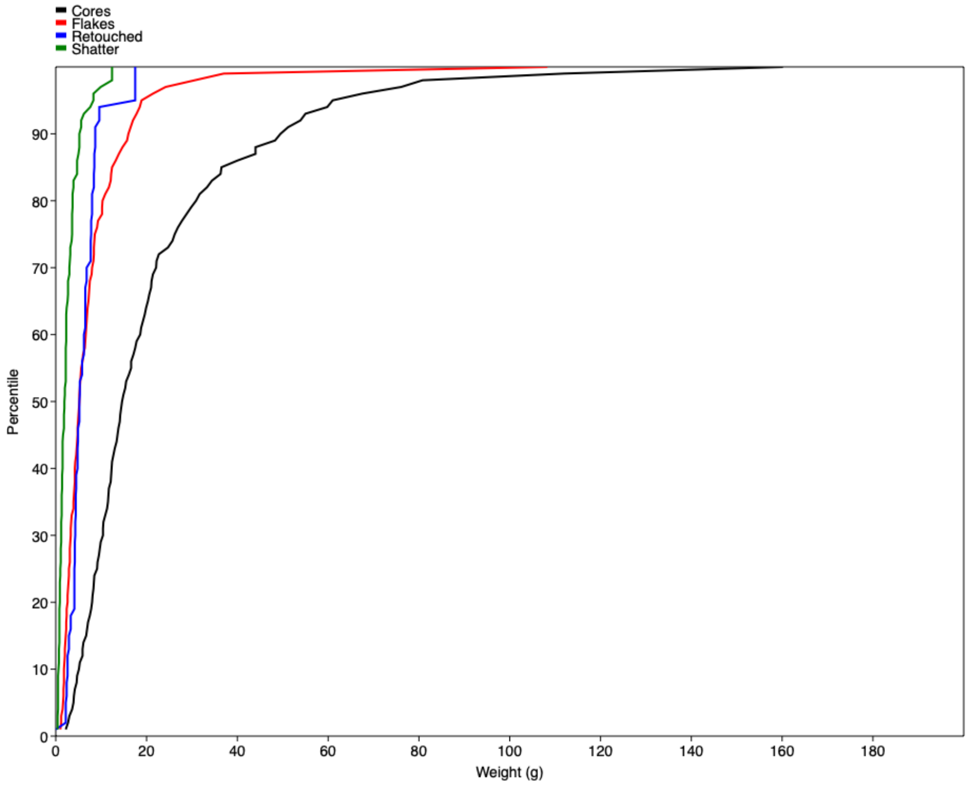

Fig. S9. Percentage **s**ize profile (grams) of Saxomununya lithics divided by categories.

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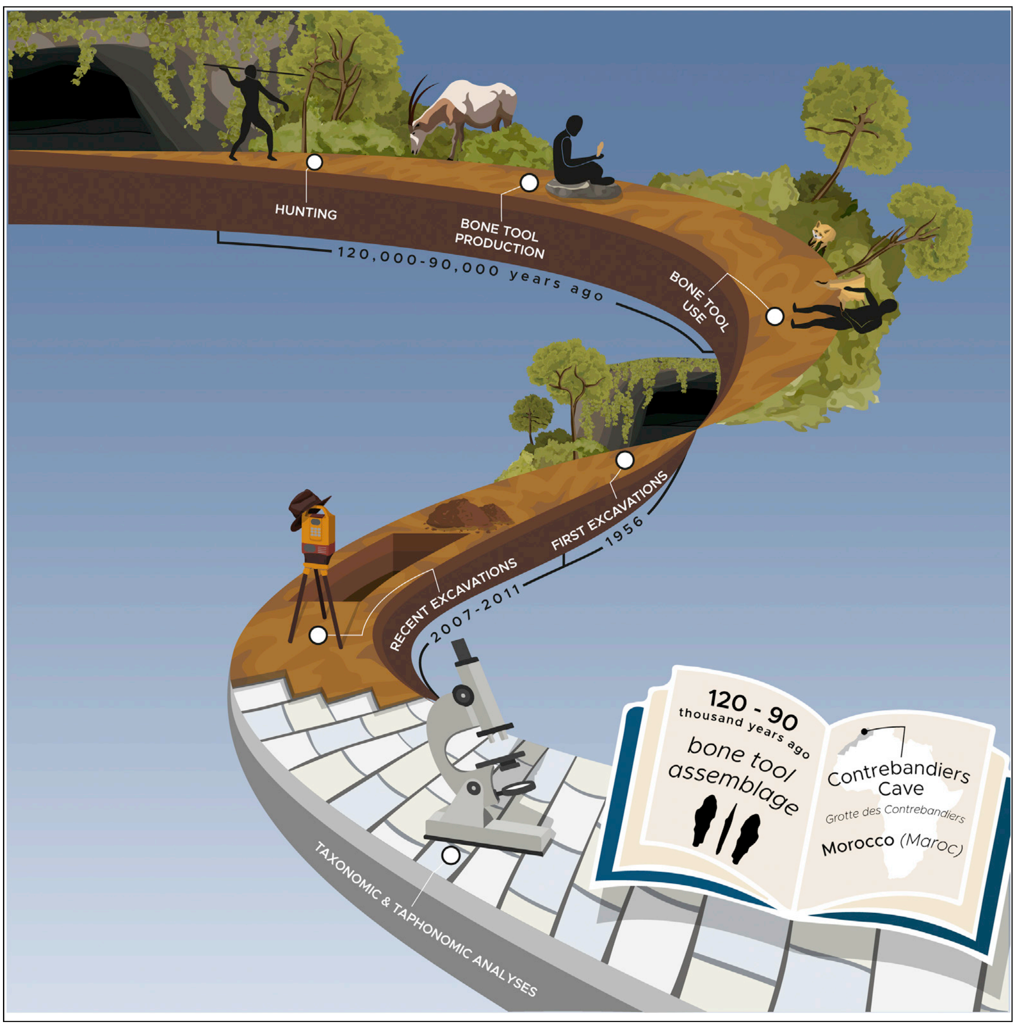
A worked bone assemblage from 120,000–90,000 year old deposits at Contrebandiers Cave, Atlantic Coast, Morocco



Emily Y. Hallett, Curtis W. Marean, Teresa E. Steele, ..., Deborah I. Olszewski, Mohamed Abdeljalil El Hajraoui, Harold L. Dibble

hallett@shh.mpg.de

Highlights

Bone tools from Contrebandiers Cave, Morocco, dated to 120,000 to 90,000 years ago

Bone tools likely used for leather and fur working, and other activities

Carnivore bones from cave show they were skinned for fur removal

Hallett et al., iScience *24*, 102988
September 24, 2021
https://doi.org/10.1016/j.isci.2021.102988

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Article

A worked bone assemblage from 120,000–90,000 year old deposits at Contrebandiers Cave, Atlantic Coast, Morocco

Emily Y. Hallett,[1,2,3,13,*] Curtis W. Marean,[2,3,4] Teresa E. Steele,[5,6] Esteban Álvarez-Fernández,[7] Zenobia Jacobs,[8] Jacopo Niccolò Cerasoni,[1] Vera Aldeias,[6,9] Eleanor M.L. Scerri,[1] Deborah I. Olszewski,[10] Mohamed Abdeljalil El Hajraoui,[11] and Harold L. Dibble[2,6,10,12]

SUMMARY

The emergence of *Homo sapiens* in Pleistocene Africa is associated with a profound reconfiguration of technology. Symbolic expression and personal ornamentation, new tool forms, and regional technological traditions are widely recognized as the earliest indicators of complex culture and cognition in humans. Here we describe a bone tool tradition from Contrebandiers Cave on the Atlantic coast of Morocco, dated between 120,000–90,000 years ago. The bone tools were produced for different activities, including likely leather and fur working, and were found in association with carnivore remains that were possibly skinned for fur. A cetacean tooth tip bears what is likely a combination of anthropogenic and non-anthropogenic modification and shows the use of a marine mammal tooth by early humans. The evidence from Contrebandiers Cave demonstrates that the pan-African emergence of complex culture included the use of multiple and diverse materials for specialized tool manufacture.

INTRODUCTION

Bones that were intentionally shaped and used as tools have been considered a hallmark of modern human behavior (d'Errico et al., 2012a) as they require substantial time and labor investments and elaborate production sequences (Henshilwood et al., 2001). Here we describe a bone tool assemblage likely used for leather and fur production from Contrebandiers Cave, dated to ~120–90 thousand years (ka) ago. Clothing and fur were likely necessary in the expansion of *Homo sapiens* into cold habitats during the Pleistocene. However, fur and other organic clothing materials are extremely unlikely to preserve in the fossil record. Genetic studies of clothing lice suggest an origin for clothing as early as 170 ka ago with *H. sapiens* in Africa (Toups et al., 2011). In this article, we present evidence for fur removal found on carnivore bones dated to as early as 120 ka ago at Contrebandiers Cave in Morocco. The combination of carnivore bones with skinning marks and bone tools likely used for fur processing provide highly suggestive proxy evidence for the earliest clothing in the archaeological record.

Bone tools vary regionally and are typically described as either formal or informal. This study follows d'Errico et al.'s concise definition of formal bone tools as ''functional artifacts shaped with techniques specifically conceived for bone, such as scraping, grinding, grooving, and polishing'' (d'Errico et al., 2012a), and therefore we add that formal bone tools can be identified as such because they are also shaped pieces of bone, antler, ivory, or tooth that bear manufacture marks. Following Tartar's definition of intermediate bone tools as ''not formally worked and only recognizable by the percussion marks at their ends'' (Tartar, 2012), we add that informal bone tools are pieces of bone that were used without prior shaping and therefore do not bear manufacture marks.

Informal and formal bone tools appear in several Pleistocene archaeological sites in Africa and Europe, with the earliest evidence of bones used as tools to dig termite mounds (Backwell and d'Errico, 2001) dating to ~2.0 million years (Ma) old (d'Errico and Backwell, 2003). At the site of Swartkrans, South Africa, four horn cores and one bone display grinding marks that suggest these digging tools were intentionally shaped and are therefore formal bone tools ranging in age from ~1.8 to 1.0 Ma ago (d'Errico and Backwell, 2003).

[1]Pan-African Evolution Research Group, Max Planck Institute for the Science of Human History, 07745 Jena, Germany

[2]Institute of Human Origins, Arizona State University, Tempe, AZ 85287, USA

[3]School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85287, USA

[4]African Centre for Coastal Palaeoscience, Nelson Mandela University, Gqeberha, Eastern Cape 6031, South Africa

[5]Department of Anthropology, University of California at Davis, Davis, CA 95616, USA

[6]Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany

[7]GIR PREHUSAL, Department of Prehistory, Ancient History and Archaeology, University of Salamanca, 37002 Salamanca, Spain

[8]Australian Research Council Centre of Excellence for Australian Biodiversity and Centre for Archaeological Science, School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, NSW 2522, Australia

[9]Interdisciplinary Center for Archaeology and the Evolution of Human Behaviour, University of Algarve, Campus de Gambelas, 8005-139 Faro, Portugal

[10]Department of Anthropology, University of Pennsylvania, Philadelphia, PA 19104, USA

[11]Institut National des Sciences de l'Archéologie et

Continued

However, the majority of bone tools from the Earlier Stone Age of southern Africa were not intentionally shaped, although they do appear to have been used for a variety of tasks (Stammers et al., 2018). In addition, bone tools shaped using methods often applied to stone—such as hammerstone percussion for flake removal—are found in Olduvai Beds I and II in Tanzania and are dated to ~2.0–1.8 Ma ago (Deino, 2012) and 1.338 ± 0.024 Ma ago (Domínguez-Rodrigo et al., 2013), respectively. An additional five bone tools from Olduvai Beds II-IV likewise exhibit shaping methods conceived for stone, and one bone tool from site WK East A, Olduvai Bed IV (0.93–0.8 Ma) is a preform of a barbed point that was likely shaped through scraping (Pante et al., 2020). A bifacially flaked handaxe made on the bone fragment of a large mammal was discovered in Acheulean contexts dated to 1.4 Ma from Konso, Ethiopia (Sano et al., 2020), and bone tools shaped through hammerstone percussion also appear in Acheulean contexts (Saccà, 2012) dated to ~327–260 ka ago (Michel et al., 2008) during the Middle Pleistocene in Italy. Bones used as tools have been documented in Marine Isotope Stage 9 Middle Pleistocene deposits from Schöningen 12 II in Germany (Julien et al., 2015). From the Middle Paleolithic of France, five formal bone tools manufactured by Neanderthals are known from two sites dated to ~50–45 ka (Soressi et al., 2013; Martisius et al., 2020). Soressi et al. describe *lissoir* formal bone tools made by Neanderthals in Europe and interpret these *lissoirs* as being used as leather working tools (Soressi et al., 2013).

Formal bone tools begin to appear occasionally in the Middle Stone Age archaeological records in Africa, but consistent bone tool manufacture and diverse bone and antler tool types are not typically found until ~48 ka ago, during the Upper Paleolithic of Eurasia (Hublin et al., 2020; Langley et al., 2020) and ~44 ka ago during the Later Stone Age of Africa (d'Errico et al., 2012b). Three formal bone tools were described from Broken Hill cave in Zambia and include two "gouges" and one bone point (Barham et al., 2002). The dating of deposits remains unresolved at Broken Hill, Zambia, but indirect dating in combination with problematic direct dating suggests that the Broken Hill formal bone tools are ~300–130 ka old (Barham et al., 2002). In Central Africa, formal bone tools from three MSA sites at Katanda, Democratic Republic of the Congo, include 12 barbed and unbarbed points and one "dagger-like" object from sites dated to 82 ± 8 ka ago (Feathers and Migliorini, 2001; Yellen et al., 1995), although the associations have been questioned (Klein, 2009). The oldest formal bone tools from Southern Africa are from Klasies River Main site in Cave 1A and include three notched artifacts that were most likely used for a range of activities, including animal skin and plant processing (Bradfield and Wurz, 2020). The Klasies River Main site notched bone tools have a likely minimum age of ~100 ka, as the dated overlain deposits have a U-series age from stalagmite of 85–101 ka (Bradfield and Wurz, 2020; Vogel, 2001). In addition, a bone point used as a hafted arrowhead was identified in Klasies River Main Cave 1 is from layer 19, directly below layers dated to 63.4 ± 2.6 ka (Bradfield et al., 2020; Jacobs and Roberts, 2008). The Blombos Cave assemblage in South Africa originally described in 2001 included 28 formal bone tools classified as "awls" and "points" from layers dated to ~71 ka ago (Henshilwood et al., 2001). Follow-up studies have revealed an additional nine pieces at Blombos (d'Errico and Henshilwood, 2007), and improved chronologies estimate the age of the bone tool-bearing layers to be ~80 ka (Jacobs et al., 2013). In addition, a bird bone that was shaped into an awl was recovered from the M3 archaeostratigraphic phase at Blombos, which has been dated to ~125 ka ago or older (d'Errico and Henshilwood, 2007). The Sibudu assemblage in South Africa contains two formal bone tools from layers dated to 72.5 ± 2 ka ago that include one wedge and one notched piece (d'Errico et al., 2012a). There are also 21 formal bone tools at Sibudu that are dated to ~64–57 ka ago (d'Errico et al., 2012a). Finally, in North Africa, a formal "bone knife" tool from Dar es-Soltan I cave was identified in Aterian deposits dated to ~90 ka ago (Bouzouggar et al., 2018) and "spatule" bone tools from Aterian deposits have been identified at El Mnasra (El Hajraoui, 1993, 1994; El Hajraoui and Debénath, 2012).

When comparing early formal and informal bone tool assemblages from Africa and Eurasia to those from the later African MSA ~100 ka, it is clear that the latter are: (1) geographically more widespread, (2) include greater numbers of them, and (3) reveal a higher diversity of types. However, it is not until the African Later Stone Age (~44 ka ago) (d'Errico et al., 2012b) and Eurasian Upper Palaeolithic (~48 ka ago) (Hublin et al., 2020; Langley et al., 2020) that there is an explosion of diverse and more elaborate bone tool forms.

Contrebandiers Cave (33°55′18.2″N, 6°57′42.4″W) is located on the Atlantic coast of Morocco (Figure 1), some 250 meters (m) from the current coast. Cut into Pleistocene calcarenites, it is 30 m deep with an entrance 28 m wide. Originally excavated in the 1950s and 1970s by Abbé Roche, a new Moroccan-American joint excavation began in 2007 directed by Harold Dibble and Mohamed Abdeljalil El Hajraoui

du Patrimoine, 10001 Rabat, Morocco

[12]Deceased June 10, 2018

[13]Lead contact

*Correspondence: hallett@shh.mpg.de

https://doi.org/10.1016/j.isci.2021.102988

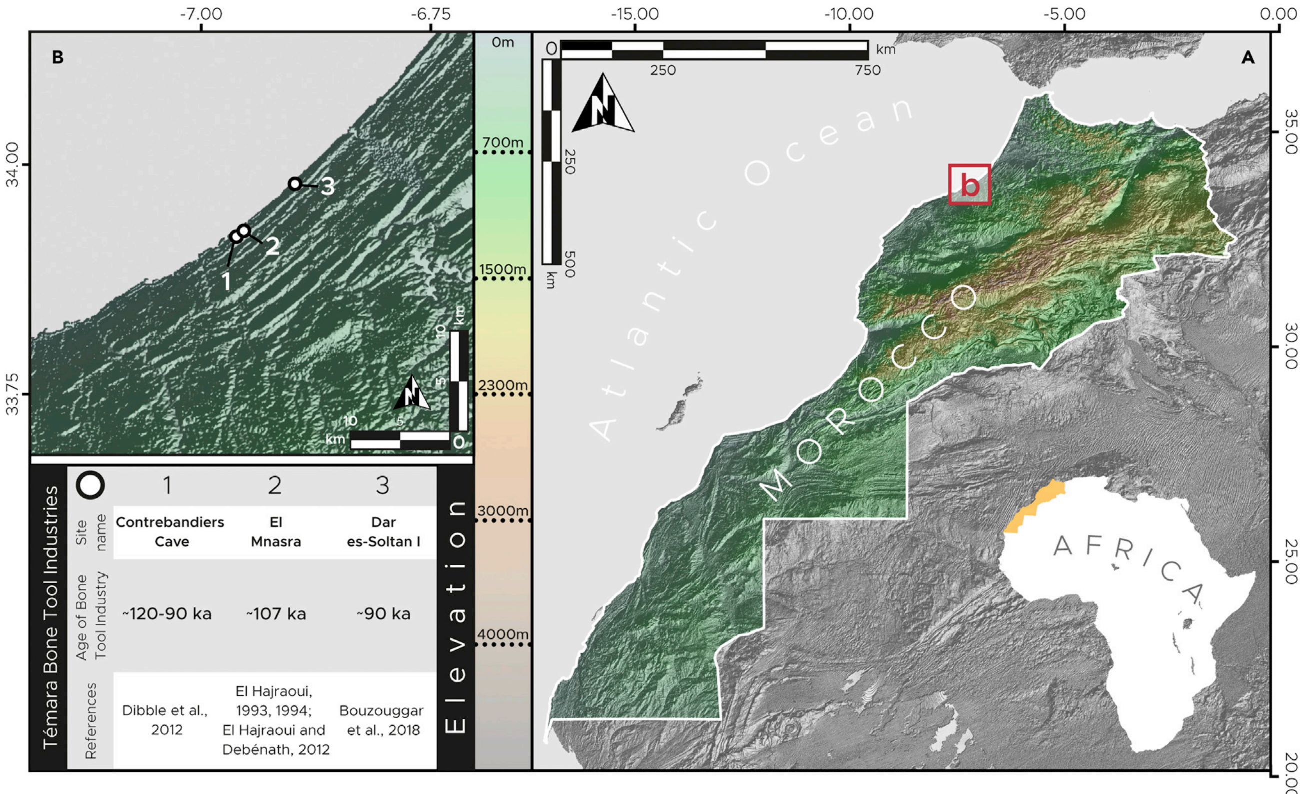

Figure 1. Contrebandiers Cave, El Mnasra, and Dar es-Soltan I are coastal caves with bone tools in stratified archaeological deposits in the Témara region of Morocco. Elevation map of Morocco, where km refers to kilometers, and ka refers to thousands of years

Map of (A) Morocco with (B) location of Contrebandiers Cave and archaeological sites mentioned in text.

(Dibble et al., 2012). The recent excavations used modern methods to ensure a high degree of contextual control, which included the point-proveniencing of all objects larger than 25 mm with a total station, and the screening of smaller objects from 7-L buckets with 1 cm and 2 mm mesh (Dibble et al., 2012).

Roche's previous excavations removed nearly all of the younger Iberomaurusian Later Stone Age (LSA) and Neolithic deposits (Dibble et al., 2012). A small amount of Iberomaurusian material remained in the front of the cave (Supplemental Information), and elsewhere in Morocco similar materials have been dated to 23,459–12,568 calibrated years before present (Staff et al., 2019). The bone tools described here come from the underlying so-called Maghrebian Mousterian and Aterian deposits (Figure S1), which are now assigned to the pan-African MSA (Dibble et al., 2013). Ages for the MSA layers have been estimated using three techniques (electron spin resonance, thermoluminescence, and optically stimulated luminescence dating) (Supplemental Information), all of which gave concordant results (Table S1) and indicate that the MSA bone tool-bearing layers began ~120 ka ago and ended ~90 ka ago (Dibble et al., 2012) (Supplemental Information).

RESULTS

At Contrebandiers Cave, 62 bone tools were identified in MSA deposits, and one bone tool was identified in LSA deposits. Here we describe the MSA bone tools from Layers IV-2, V-1a, V-1b, V-2, 4, 5A, 5B, 5C, 5D and 6B. These were shaped in diverse ways through: (1) scraping bone blanks with a lithic tool to create a regularized and desired shape; (2) polishing portions of bone during the manufacture phase to create smoothed and regular surfaces; (3) bone shaped by knapping with a stone; and/or (4) bone shaped from use by *H. sapiens*. Forms of bone tools include spatulates and other intentionally shaped pieces in a range of diverse types.

Spatulate tools made on rib bones (Figures 2–4 and S2) (N = 7) were identified in Contrebandiers Cave MSA Layer IV-2 (Table S2). A number of studies indicate that spatulates may have been used in hide preparation

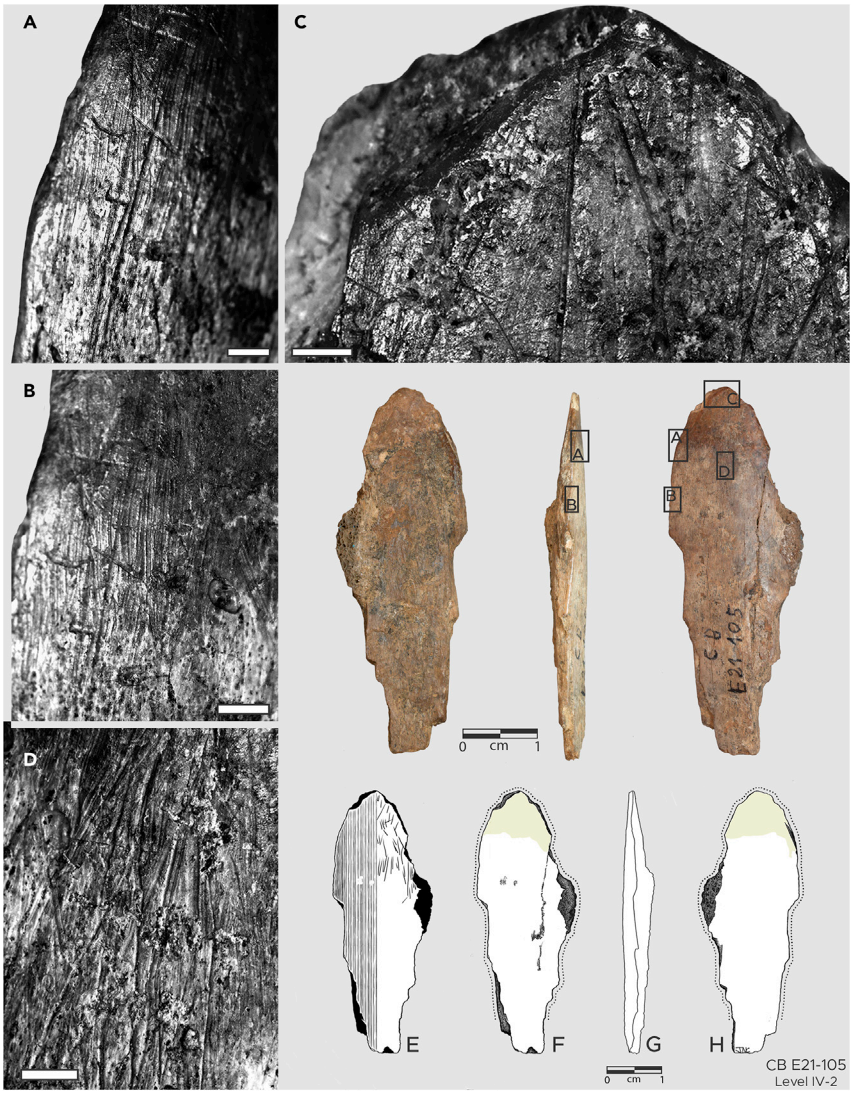

Figure 2. CB E21-105 spatulate bone tool photographs and illustration

(A, B, and D)Show somewhat wavy, rather than straight striations, due to the unevenness of retouched lithic edges and lateral movement of the lithic edge against the bone blank.

(C) Is an example of short, deep, non-parallel striations restricted to limited areas of a bone tool that were interpreted as resulting from use. (A and B) show examples of sheen and polish from use and restricted to the sides of the piece.

(D) Shows what are interpreted as manufacture marks on the body of the tool, and the lack of sheen and polish on the body away from the end and sides. (A–D) are microscope photographs with 1 cm scale.

(E–H) Illustrates both sub-parallel shaping marks covering the extent of the surface and short, irregular marks from use. Yellow areas on F and H represent the lightly burned and darkened area at the tip of this bone tool, where polish and sheen from use are frequent. Dotted outlines on (F and H) represent the extent of polish.(E–H) illustrated by J. N. Cerasoni.

during leather working activities (Soressi et al., 2013; Tartar, 2009). Ethnographic study of spatulate use in Africa is limited (Badenhorst, 2009), but in his 1796 publication, the explorer Le Vaillant described the Khoekhoe in South Africa using spatulate-shaped sheep rib bones as "a kind of chisel" to prepare hides for clothing ((Le Vaillant, 1790), p. 305). Our analyses of use-wear studies of archaeological spatulates and *lissoirs* also support their function as leather-working tools (Semenov, 1964; Soressi et al., 2013), as do experimental studies of manufacture and use (Tartar, 2009). Two bone "gouges" from MSA deposits at Broken Hill, Zambia, have been interpreted as resembling "spatulas" from younger Later Stone Age deposits in southern Africa (Barham et al., 2002). "Spatulas" are not unique to Contrebandiers Cave and the

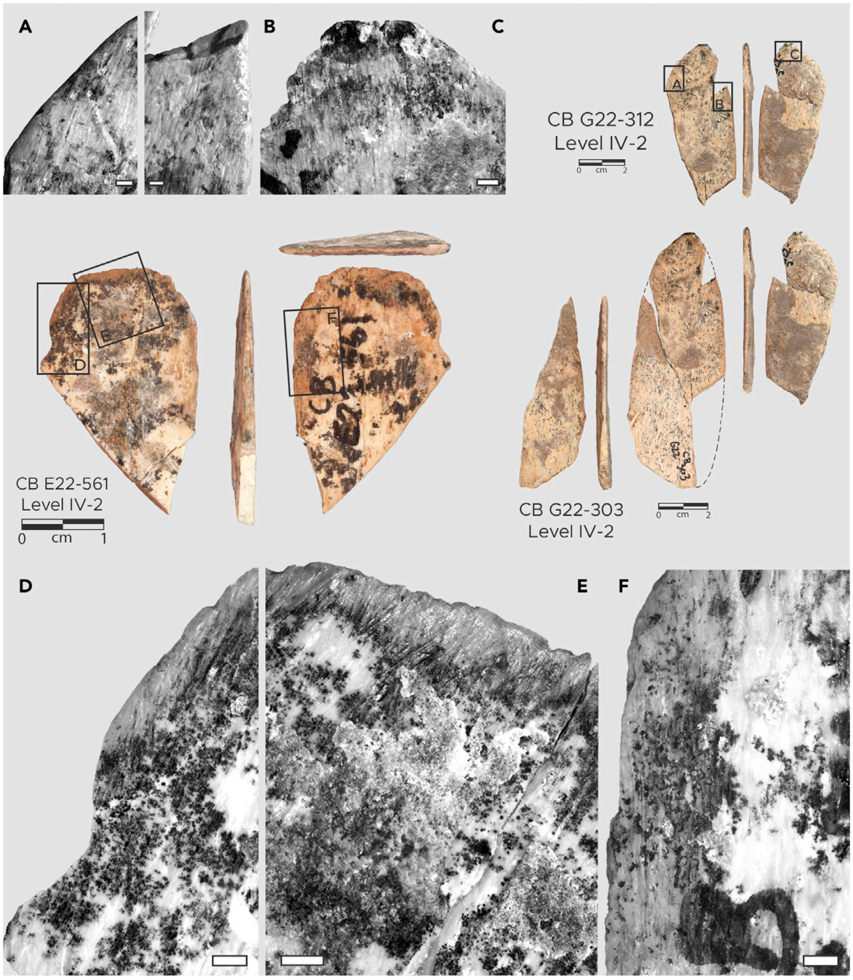

Figure 3. Spatulate tools made on rib bones from Contrebandiers Cave

(A–C) On specimen CB G22-312 are microscope photographs showing manufacture marks and smoothed edges from use, with post-depositional damage at the tip. CB G22-312 and CB G22-303 represent a spatulate bone tool refit, where the dashed lines represent an estimate of what the bone tool would look like complete.

(D–F) On specimen CB E22-561 show manufacture marks on the body and edges of the piece and polish restricted to the edges and tip. (A–F) are microscope photographs with 1 cm scale.

manufacturing processes and use-wear of Moroccan MSA spatulates have been described in detail for the neighboring MSA site of El Mnasra (El Hajraoui, 1993, 1994; El Hajraoui and Debénath, 2012). Spatulate-shaped tools are ideal for scraping and thus removing internal connective tissues from leathers and pelts during the hide or fur-working process, as they do not pierce the skin or pelt.

At Contrebandiers Cave, zooarchaeological analyses (Hallett, 2018) identified sand fox (*Vulpes rueppellii*), golden jackal (*Canis aureus*) and wildcat (*Felis silvestris*) skeletal remains bearing marks consistent with skinning for fur removals (Crezzini et al., 2014) that were found within the MSA deposits (Table S3). Cut marks were found on radius, ulna, tibia, and mandible fragments (Figures 5, and S5) for these three species of carnivores (*V. rueppellii* N = 12 bear cut marks, which is 9% of the total MSA sand fox remains, for *C. aureus* N = 2 bear cut marks, which is 7% of the total MSA golden jackal remains, and for *F. silvestris* N = 2 bear cut marks, which is 8% of the total MSA wildcat remains). This pattern of cut marks is consistent with modern fur removal techniques, where initial incisions are made on the forelimbs and the hind limbs to detach the skin from the paws. The skin is then pulled towards the head in one piece, and to finally detach the skin from the animal's head, incisions are made near the lips, resulting in cut marks on the mandible (Burch, 2002). In contrast, the bovids at Contrebandiers were processed for meat removal (Hallett, 2018),

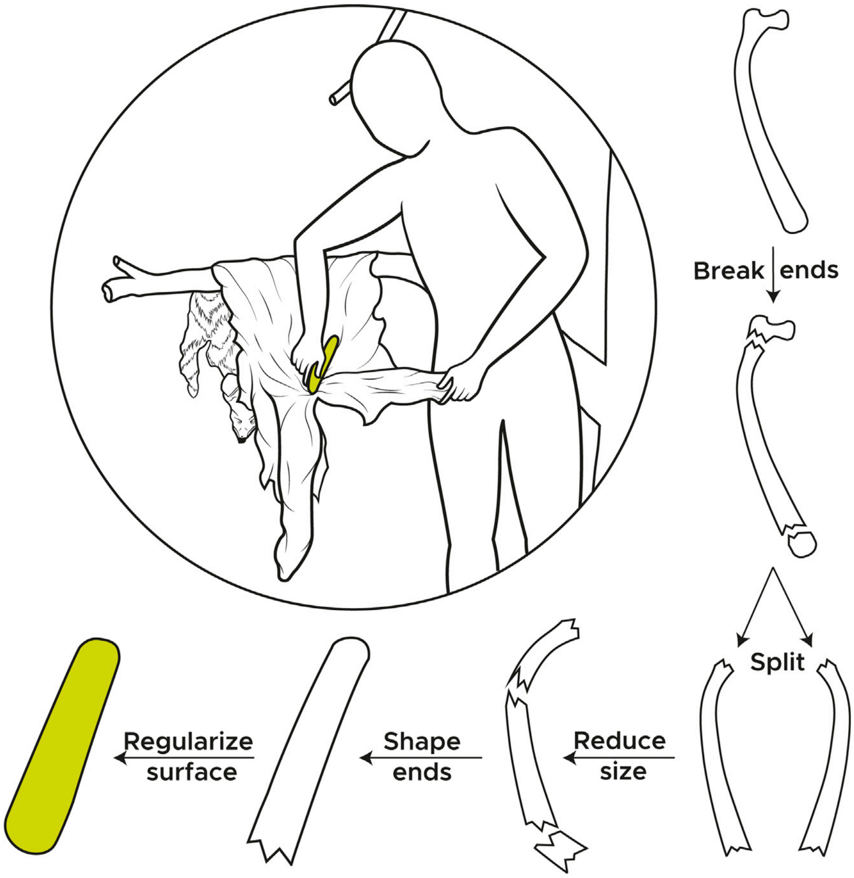

Figure 4. Spatulate bone tool manufacture stages

To manufacture a spatulate, a rib bone is broken at the ends, split lengthwise, reduced in size, and shaped then regularized with a lithic edge. Polish on the Contrebandiers Cave spatulates is interpreted as the result of use against the interior portion of skin to scrape hides for leather or fur preparation. Illustrated by J. N. Cerasoni.

as the distributions of cut marks are located on the middle and proximal shafts of all long bones, where muscle mass is concentrated (Figure S5). This shows that the distributions of cut marks on carnivores associated with fur processing are inconsistent with meat removal butchery patterns; the carnivores were only skinned and were not butchered for meat. No evidence for ornaments made on bone was found in the Contrebandiers Cave faunal assemblage.

The combination of carnivore bones bearing marks consistent with skinning and spatulates in MSA contexts at Contrebandiers Cave is a highly suggestive indicator that early humans were practicing fur removal. This shows that various animal resources were used for different purposes other than for food and that a diversity of tools were used for different activities.

Other Contrebandiers Cave MSA bone tools include three pieces that resemble hand-held pressure-flakers (Figure 6, and S3) produced in modern experimental studies (d'Errico et al., 2012a; Doyon et al., 2019). The earliest pressure flakers date to ~125–105 ka ago at Lingjing, China (Doyon et al., 2019). Pressure flaking technology was suggested by Mourre et al. (2010) with a date of ~75 ka ago at Blombos Cave, South Africa, and d'Errico et al. (2012a) described pressure flakers with a date of ~64–57 ka ago at Sibudu Cave, South Africa. Significantly in North Africa, small and finely flaked stone tool foliates found in association with Marine Isotope Stage (MIS) 5 classic Aterian tanged artifacts may also have been pressure flaked (Scerri, 2017). Stone tools shaped by hand-held pressure flaking are regularly documented by ~20 ka ago in Eurasia during the Upper Paleolithic (e.g. Bradley et al., 1995; Mourre et al., 2010).

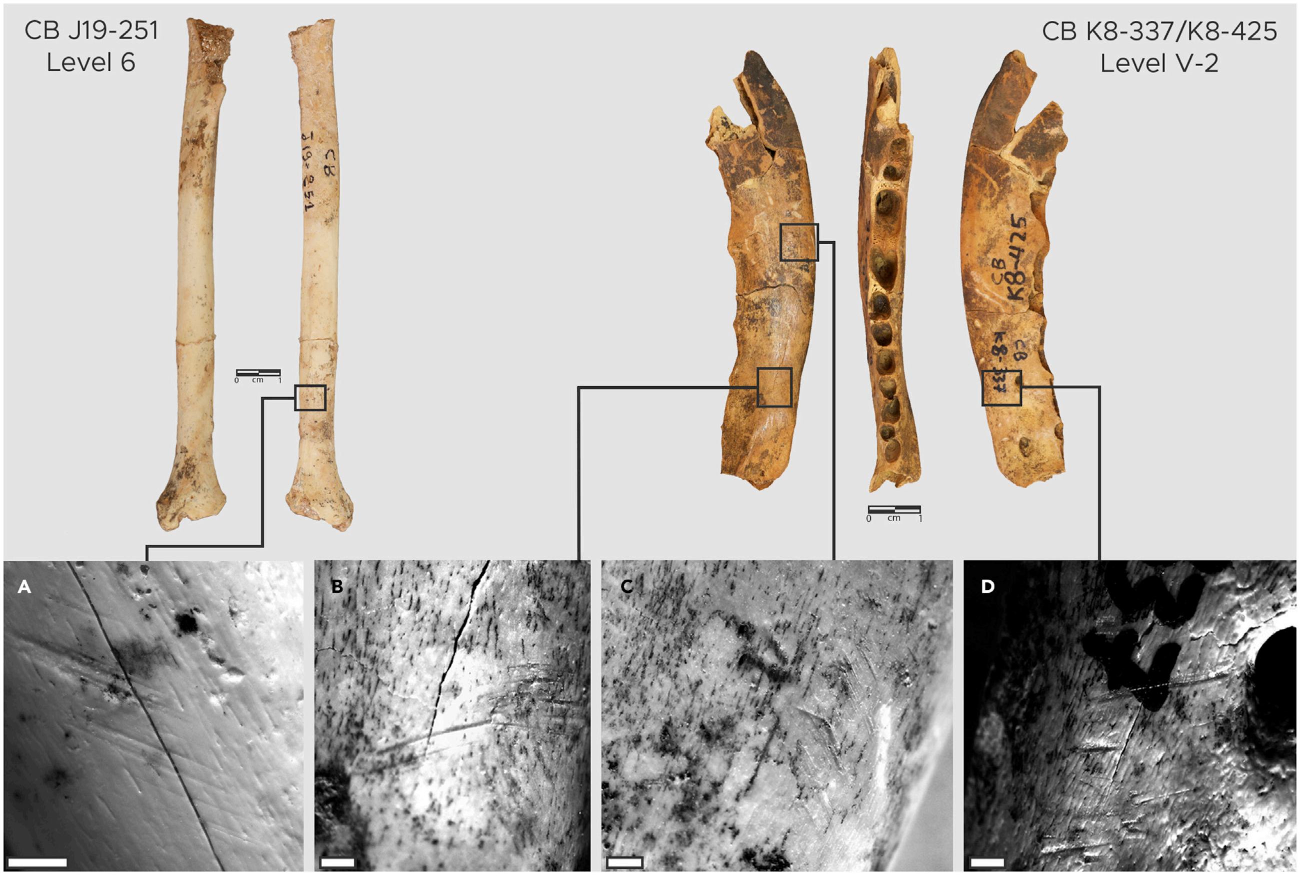

Figure 5. Skinned fox bones from Contrebandiers Cave

(A–D) CB J19-251 is a cut-marked fox tibia showing marks consistent with skinning, and CB K8-337/CB K8-425 is a cut-marked fox mandible showing marks consistent with skinning. (A–D) on specimens CB J19-251 and CB K8-337/CB K8-425 are microscope photographs with 1 cm scale.

At Contrebandiers Cave, in Layer V-1b (dated to 113 $\pm$ 7 ka, see Supplemental Information), a cetacean tooth tip (CB K8-1641) was discovered, bearing marks consistent with use as a hand-held pressure flaker (Figure 6). Whale, dolphin, and seal remains have been identified in MSA sediments in South Africa (Klein, 1976), yet none have been confirmed in Pleistocene North Africa (Steele and Álvarez-Fernández, 2011) except the piece we report here. In Lower and Middle Paleolithic contexts in Europe, elephant ivory fragments with striations on their surfaces were incorrectly identified as ivory points and later re-classified as pseudo-points (Villa and d'Errico, 2001). However, the striations and chipping on CB K8-1641 (Figure 6) are consistent with surface modification identified on hand-held pressure flakers as described in d'Errico et al. (2012a). No elephant remains were identified at Contrebandiers Cave, and the morphology of this piece indicates it is likely a cetacean tooth fragment and not elephant ivory (Espinoza et al., 1990). It is nonetheless possible that this marine mammal damaged its tooth tip from feeding on hard substances such as shellfish, bony fish, squid, or other marine vertebrates. Future use-wear analyses on this specimen could clarify whether the observed striations and chipping are anthropogenic or non-anthropogenic in nature. While species identification should be confirmed through molecular techniques, morphology and biogeography suggest that the tooth is likely from a sperm whale (*Physeter macrocephalus*) tooth. This specimen represents the use of a marine mammal tooth by humans ~113 ka.

Other formal and informal—as well as possible—bone tools include: (1) 13 "retouchers", (2) 28 shaped pieces that do not conform to a yet-known type (Figure S6), (3) two split-rib pieces that are likely the discarded byproducts from spatulate manufacture (see Tartar (Tartar, 2009) for the process of bone tools manufacture from split-ribs), and (4) three pieces with regular and smooth surfaces that appear to be the result of use rather than manufacturing (Figure S4, and Table S2). These bone tools will be analyzed for

Figure 6. Cetacean tooth pressure flaker

(A–D) On CB-1641 are microscope photographs showing marks interpreted as resulting from use as a hand-held pressure flaker, with 1 cm scale.

manufacturing traces and use-wear in future studies of the Contrebandiers Cave artifacts and are not described in detail here.

DISCUSSION

Excavations led by El Hajraoui at El Mnasra over twenty-five years ago uncovered spatulate bone tools in Aterian contexts (El Hajraoui, 1993) that were largely ignored in discussions of MSA bone tool technology and remained undated until recently. El Hajraoui continued to describe Aterian bone tools in subsequent studies (El Hajraoui, 1994; El Hajraoui and Debénath, 2012). Recently available chronologies at El Mnasra estimate the age of bone tool-bearing Aterian layers to be ~107 ka (Jacobs et al., 2012). Together, the Contrebandiers Cave, El Mnasra (El Hajraoui, 1993, 1994; El Hajraoui and Debénath, 2012) and Dar es-Soltan I (Bouzouggar et al., 2018) bone tool assemblages show that there is an archaeological tradition (El Hajraoui, 2019) of bone tool technology in the MSA of North Africa from 120 to 90 ka. Bone tools appear to be a pan-African phenomenon in the MSA well before they appear at similar levels of abundance in Europe.

By ~120 ka ago in North Africa, people occupied Contrebandiers Cave, hunting 67 species of vertebrate animals (Hallett, 2018) for food and hides. The Contrebandiers Cave bone tools demonstrate that by ~120 ka ago, *H. sapiens* began to intensify the use of bone to make formal tools, and bone was intentionally shaped for specific tasks that included leather and fur working. This versatility appears to be at the root of our species, and not a characteristic that emerged after *H. sapiens* expanded their range into Eurasia. The early, pan-African emergence of formal bone tool technology also highlights the role of the entire African continent in the development of modern human morphology and behavior (Hublin et al., 2017; Richter et al., 2017; Scerri et al., 2018). Given the level of specialization of the bone tool material culture at Contrebandiers Cave, it is likely that earlier examples will be found.

Limitations of the study

In the current study it was not possible to analyze the Contrebandiers Cave bone tools for residue identification. In addition, no experimental manufacture or use of bone tools was included in the current study. Published reference collections were consulted for the identification of tool types, manufacturing techniques, and interpretation of use-wear on the Contrebandiers Cave bone tools. While our study used 40X magnification to identify traces of use-wear on bone tools interpreted as being used for skinning, we did not use 100X-500X magnification to directly diagnose the contact material(s) each bone tool was used on.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2021.102988.

ACKNOWLEDGMENTS

The project at Contrebandiers Cave is a joint Moroccan-American project under the auspices of the Moroccan Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP). We thank A. Akerraz and A. Oujaa (INSAP) for their hospitality and access to collections. B. Bougariane (Université Moulay Ismail) provided access to personally collected comparative faunal skeletons. The Institute of Human Origins (IHO) at Arizona State University (ASU) provided access to photographic equipment and imaging software, and E. Fisher (IHO, ASU) aided with imaging methods and software. This research was funded by the National Science Foundation (grant BCS-1251354 to C.W.M. and E.Y.H.), the University of Salamanca (grant to E.A.F.), the Institute of Human Origins (fellowship and travel grant to E.Y.H.), a John Templeton Foundation grant to the Institute of Human Origins at Arizona State University, the School of Human Evolution and Social Change (travel grant, research award, Dean's Advanced Scholarship to E.Y.H. and Arizona State University (Graduate Fellowship to E.Y.H.). Funding for the excavation of the site came from the National Science Foundation (grant BCS-0935491 to H.L.D.), the Australian Research Council (Discovery Project grants DP0666084 to Z.J. and DP1092843 to Z.J. and H.L.D.), the Leakey Foundation (to D.I.O), the National Geographic Society (to H.L.D.), and the University Research Foundation of the University of Pennsylvania (to H.L.D.).

AUTHOR CONTRIBUTIONS

E.Y.H. conceived and performed the study and wrote initial drafts of the paper; T.E.S. provided comparative bone tool data and background research; Z.J. performed OSL dating and analyses of the site, and wrote the ages portion of this paper; E.Y.H., T.E.S., and E.A.F. identified, analyzed and interpreted the function of the bone tools; V.A. studied the stratigraphy and geology of the site; H.L.D. and M.E.H. are the project and excavation co-directors and permit holders; H.L.D. contributed to excavation methodology and stone tool studies; D.I.O. contributed to the stone tool studies; M.E.H. contributed to bone tool studies and Moroccan prehistory; E.Y.H., C.W.M., and E.M.L.S. took the lead in contextualizing results and writing the paper; J.N.C. and E.Y.H. created the figures and revised the main text. All authors contributed to the writing of this paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

One or more of the authors of this paper received support from a program designed to increase minority representation in science. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list. The author list of this paper includes contributors from the location where the research was conducted who participated in the data collection, design, analysis, and/or interpretation of the work.

Received: April 30, 2021
Revised: July 20, 2021
Accepted: August 12, 2021
Published: September 16, 2021

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Fossilized vertebrate archaeofaunal remains from Contrebandiers Cave, Morocco, raw and analyzed data	This paper	Table S3
Fossilized bone tools from Contrebandiers Cave, raw and analyzed data	This paper	Tables S2, and S4
Software and algorithms		
R Studio	RStudio Team https://www.rstudio.com/	RStudio version 1.2.5033
R	R Core Team https://www.r-project.org/	R version 3.6.2

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Emily Y. Hallett (hallett@shh.mpg.de).

Materials availability

All of the bone tools and vertebrate faunal remains from Contrebrandiers Cave that were analyzed in this study are curated in the Institut National des Sciences de l'Archéologie et du Patrimoine in Rabat, Morocco under the site code CB.

Data and code availability

- All data reported in this paper will be shared by the lead contact upon request.
- All data reported in the paper are available within the main text and Supplemental Information.
- All data necessary to interpret and replicate results are available in the main text and Supplemental Information, Supplemental Figures, and Supplemental Tables.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The fossilized non-human bone samples used in this study were recovered from archaeological excavations at the site of Contrebandiers Cave, Morocco. All necessary permits for archaeological excavation and analysis were obtained from the Institut National des Sciences de l'Archéologie et du Patrimoine in Rabat, Morocco. All archaeological samples were curated in Rabat, Morocco, in sterile plastic bags and given unique specimen identifiers.

METHOD DETAILS

Excavation methods

A total of 11,702 macrofaunal bone fragments were excavated between 2007 and 2010 following the methodology described in Dibble et al. (1995) and McPherron and Dibble (2002). All 11,702 macrofaunal bone fragments were analyzed in this study, as part of a complete zooarchaeological and taphonomic analysis of the Contrebandiers Cave bone assemblage (Hallett, 2018). Bones larger than 25 mm and all teeth were point-provenienced using a Total Station. Bones smaller than 25 mm were treated as aggregated data collected in 7-L buckets and screened with 1 cm and 2 mm mesh. All bone fragments were cleaned in a water bath to remove adhering sediment from bone surfaces, then allowed to dry completely before being placed in unused and new individual plastic specimen bags. Each bucket received a unique identifier and provenience at the center of the area from where the sediments were excavated. Aggregated bone from the 7-L buckets screened with 1 cm mesh was included in this study. Bones smaller than 1 cm that were screened using 2 mm mesh were not included in this study, as this division typically only includes microfaunal and macrofaunal bone fragments too small for confident identification. Each aggregate of bone from buckets was analyzed to remove bone fragments identifiable to skeletal element and/or taxonomic group, and fragments with signs of burning and/or surface modification were also removed, then assigned new unique identifiers, while retaining the original provenience information from the 7-L bucket. Also removed from the 1 cm division of aggregate bone and given unique identifiers were bone fragments displaying evidence of manufacture. Each bone tool analyzed in this study has a unique identifier.

Zooarchaeological methods

Surface modification and other taphonomic variables were recorded for all 11,702 macrofaunal bones (Hallett, 2018). Cut marks, carnivore tooth marks, and hammerstone percussion marks were identified using a 40-10X Olympus® zoom binocular microscope and bright incident light. This method of surface modification recording has shown 95% accuracy in a blind test (Blumenschine et al., 1996). Biochemical marks and trampling were also recorded, following the criteria outlined in Domínguez-Rodrigo and Barba (2006) and Domínguez-Rodrigo et al. (2009). Each layer at Contrebandiers Cave contains bones with evidence of cutmarks and hammerstone percussion marks. While the frequencies of human-accumulated large mammal bones vary according to layer, there are no layers where an absence of human accumulation was observed (Figure S7). Carnivore-accumulated bone is less frequent than human-accumulated bone at Contrebandiers Cave, in contrast to neighboring sites such as El Harhoura 2 and El Mnasra where carnivore accumulation dominates the assemblages (Campmas, 2012). In addition to each layer containing evidence for the predominantly human accumulation of bone, nearly all MSA layers at Contrebandiers Cave contain at least one bone tool.

Methods for identifying bone tools

Experimental and actualistic studies by others have established criteria for identifying bone tools. Natural processes can alter bones to the extent that their appearance resembles human modification and/or use. As such, a range of natural processes that can create "pseudo-bone tools" was considered in this study. Bone surface striations, sheen, polish, and breakage are criteria commonly used to identify human modification of bone. However, many non-human processes can produce similar modification. Striations can appear on bone surfaces as a result of rockfall (Fisher, 1995; Oliver, 1989), sedimentary abrasion (Andrews and Cook, 1985; Behrensmeyer et al., 1986; Fisher, 1995; Haynes, 1988; Olsen and Shipman, 1988; Shipman and Rose, 1983), trampling (Andrews and Cook, 1985; Behrensmeyer et al., 1986; Haynes, 1988; Olsen and Shipman, 1988), root etching (Andrews and Cook, 1985; Haynes, 1988), vascular grooves (Shipman and Rose, 1984), bone remodeling during the life of the animal (d'Errico, 1993), carnivore gnawing (Behrensmeyer, 1978; Binford, 1981; Blumenschine, 1988; Fisher, 1995; Shipman and Rose, 1983), herbivore gnawing (Sutcliffe, 1973), rodent gnawing (Andrews and Cook, 1985), insect burrowing (Shipman, 1981), and snail, beetle, and larvae damage (Dirks et al., 2015), among others. Sheen and polish can appear on bone surfaces through natural processing including water transport (Behrensmeyer, 1982; Jalvo and Andrews, 2003), sediment freezing/thawing or clay shrinking/swelling (Wood and Johnson, 1978), carnivore gnawing and repeated licking (Haynes, 1982; Sutcliffe, 1970), digestion by carnivores and raptors (Andrews, 1990; Fisher, 1981, 1995; Marean, 1991; Sutcliffe, 1970), and use as a juvenile carnivore play item (Haynes, 1982), among others.

In this study, criteria for identifying human modification and/or use of bone were based on experimental and archaeological studies that took natural processes into consideration, including striations on bone surfaces resulting from scraping with a lithic edge during manufacture (Campana, 1989; d'Errico, 1993; d'Errico and Backwell, 2003; Newcomer, 1974); striations from grinding bone against a fine or rough-grained surface during manufacture (Campana, 1989; d'Errico et al., 1984; Newcomer, 1974); striations from use (d'Errico and Backwell, 2003; d'Errico et al., 2012a; Tartar, 2012; Tartar, 2009); hammerstone percussion marks and notches from shaping during manufacture (d'Errico et al., 2012a; Henshilwood et al., 2001; Tartar, 2012; Tartar, 2009); and step-fractures from shaping and/or use (Henshilwood et al., 2001), and polish and sheen from use as a tool (Backwell and d'Errico, 2001; Campana, 1989; d'Errico et al., 2012a; Frison, 1982; Shipman and Rose, 1988; Tartar, 2009).

Following the methodology for bone tool recording presented in Henshilwood et al. (2001), a typological approach that incorporates manufacturing was used to analyze the Contrebandiers Cave bone tools. This approach was selected to allow for detailed descriptions of the steps taken in the manufacture and use of each piece. Each bone that displayed evidence of manufacture or use was recorded using the same criteria in order to reconstruct the sequences of actions taken. In addition, we recognize that similarly shaped bone tools might have been used for different tasks.

Identification of the raw material selected to manufacture or use each bone tool includes, when possible, taxonomic identification, size class, skeletal element, and skeletal element side (Table S4). Shaping techniques and use-wear were recorded for each piece using bright incident light coupled with an Olympus binocular 10x-40x zoom microscope, as well as a Leica EZ4 HD stereo 8x-35x zoom microscope with an integrated high-definition digital camera for photography. The manufacture of each piece was recorded using the following categories: Localization and extent of worked areas, manufacturing technique used, occurrence of wear, presence and location of breakage, burning, ochre or mineral staining, cut-marks, and post-depositional traces of damage. Shaping techniques were recorded according to the following categories: Scraping bone blank with stone tool, shaping by flake removal, holding the bone and abrading it against a fine-grained surface, and shaping by polishing. Length, width, and thickness were recorded for each bone, as well as width and thickness at 5 mm intervals from the tip. Possible reasons for discard were noted for each piece by analyzing breakage patterns, amount of retouch, and size.

Only adult bone was selected for manufacture. Adult long bones are distinguishable from juvenile long bones when epiphyseal fusion is visible, and cortical bone has a spongy, flaky appearance in juveniles. As most of the worked bones from Contrebandiers Cave were manufactured on long bone shafts where epiphyseal fusion is not visible, these bones were identified to age class with the aid of a comparative collection of bovid skeletons from individuals of known age class. A comparative collection was also used to identify the skeletal element that each worked bone was made from. Bone tools were made on long bone shafts, rib shafts, mandibular bodies, teeth, and unknown skeletal elements (Table S4). Bone tools that were made from unknown skeletal elements are heavily shaped through manufacture, making identification difficult, as diagnostic landmarks are not present. The skeletal elements most frequently used as blanks for manufacture are shafts from ribs, femora, humeri, radii, and metapodials. Adult long bone shafts were likely selected for bone tool manufacture because cortical bone provides a thick and strong material ideal for use. Taxonomic identifications were made when possible.

The majority of worked bones were made on shaft fragments from bovids belonging to size class 2 or 3 (Table S4). Brain's (Brain, 1981) bovid size class descriptions were modified for the study of the Contrebandiers Cave faunal assemblage, as the majority of bovid species from the Maghreb belong to size classes that border I and II, II and III, and III and IV. In addition, size classes were broken into subclasses, represented by a and b. For example, Brain's (Brain, 1981) bovid size class I (4.5–19 kilograms [kg]) is divided into class 1a (1–12 kg) and class 1b (12–23 kg). The remaining body size classes were subdivided as: 1b/2a (12–53 kg); 2a (23–53 kg); 2b (53–84 kg); 2b/3a (53–190 kg); 3a (84–190 kg); 3b (190–246 kg); 3b/4a (190–598 kg); 4a (296–598 kg); 4b (598–900 kg); 5 (900–1,500 kg); and 6 (1,500 + kg). Selection of long bone shafts from bovids belonging to either size class 1a/2a or size class 3 reflects the abundance of bone from these size classes and taxa within the site.

Four categories of manufacturing technique were identified: Shaping by scraping the bone blank with a stone tool (Figures 2 and 3) shaping by flake removal using percussion (Figure S4); shaping by direct abrasion against a fine-grained surface (Figure S6); and what is potentially shaping by polishing (Figure S4). Of these, shaping by polishing is the most difficult to distinguish from polish through use. In this study, intentional shaping by polish was distinguished from polish through use based on the extent of polish. If a bone tool had polish over the entire surface, then this was likely due to intentional polish. However, we are cautious in assigning bone tools with polish covering the entire surface as formal tools, as we are not yet able to confidently assign these to a known tool type. Polish restricted to tool tips, butts, edges, or elevated areas was likely the result of tool use (Figure 2).

Criteria for distinguishing striations left by scraping versus those left by abrasion are outlined in d'Errico and Backwell (2003), Newcomer (1974), and Campana (1989). Campana (1989) conducted experiments with fresh cattle bone, flint and sandstone to determine which manufacturing technique was used by the

Natufian and Zagros Proto-Neolithic cultures: scraping with a stone tool or abrasion. These experiments showed that it is possible to distinguish bone that was shaped by stone tool scraping (flint) from bone that was abraded against a sharp-grained surface (sandstone) (Campana, 1989). Both methods leave striations visible to the naked eye. However, when viewed with at least 24x magnification, differences are visible between the two techniques. When scraping a bone blank with a flint stone tool, in a manner similar to sharpening a pencil with a knife, striations are parallel to one another and often parallel to the long axis of the bone blank (Campana, 1989). Striations are also somewhat wavy, rather than straight, due to the unevenness of retouched lithic edges and lateral movement of the lithic edge against the bone blank, as shown in Figure 2. Striations produced with lithic scraping are also shallow and have curving cross sections, and striations overlap one another because of repeated shaving strokes, as shown in Figure 2. In contrast, shaping a bone blank with sandstone leaves striations that are straight (Campana, 1989). Striations from grinding are parallel to one another, overlapping, and v-shaped in cross section (Campana, 1989).

Spatules or "spatulas" (Figures 2, 3, and 4) are synonymous in form with the formally recognized tool type *lissoir*, following Tartar (2009). Tartar (2009) groups *spatules* or "spatulas" and *brunissoirs* (thicker than *lissoirs* and mostly made on deer antler) into sub-types within lissoirs. We agree with this sub-type designation and hope that comparison between MSA spatulates (also referred to as *spatules* in other literature) and Middle/Upper Paleolithic lissoirs can proceed in future studies with clarified terminology. As Tartar's (Tartar, 2009) study of bone tools from the Upper Paleolithic in France found that lissoirs are often made on split-rib shafts, the spatulates from Contrebandiers Cave are also often made on split-rib shafts (Figure 4).

Techniques for experimentally manufacturing split-rib shafts have been described elsewhere (Tartar, 2009). Generally, as shown in Figure 4, this process consists of first removing the head, neck and tubercle of the rib, then preparing the cranial (upper) and caudal (lower) edges with a lithic edge to create a flat surface for subsequent wedge insertion. After the edges have been prepared, a wedge is hammered into the length of the piece until the rib splits at the midline running between the cranial and caudal edges. This process produces two blanks (either the internal face of the rib or the external face) that can then be shaped using hammerstone percussion, scraping with a lithic edge, or abrasion against a sharp-grained surface. Tartar (2009) notes that the initial process of splitting the rib in half rarely leaves marks on lissoirs, as subsequent shaping and use modify the surface such that marks from blank production are not preserved. This was true for the Contrebandiers Cave spatulates. One piece (K7-707) more closely resembles the shape and use wear of a *lissoir*. K7-707 (Figure S6) is thicker at the end than the other Contrebandiers Cave *lissoirs*, and has sheen restricted to the tip. However, the tip curves away from the body, unlike other known *lissoirs*.

Burning extent and severity were also recorded for each bone tool. In sum, 6 pieces showed complete (100% coverage) burning, 8 pieces showed partial (10–75% coverage) burning, 6 pieces showed burning on the tip only, and 42 pieces were not burned (Table S2). It is possible that some pieces were heated to get a hardened tip. As Campana (1989) discusses, moderate heating of bone will harden it considerably. However, intense heating will result in the breakdown of the tensile strength of bone through the loss of its organic fraction.

Methods for recording use wear

Short, deep, non-parallel striations and polish restricted to limited areas of a bone tool were interpreted as resulting from use after manufacture (Figure 2). While specific uses of bone tools are difficult to determine, extensive experimental research on bone tool use and wear has been published by others (Backwell and d'Errico, 2001; Campana, 1989; d'Errico and Backwell, 2003; d'Errico et al., 1984; Henshilwood et al., 2001; Newcomer, 1974; Soressi et al., 2013; Tartar, 2009) and these studies were used as reference during analyses of the Contrebandiers Cave bone tools. The published reference collections and microscopic mark analyses from Backwell and d'Errico (2004), d'Errico and Backwell (2009) and Backwell et al.(2008) were also used in the Contrebandiers Cave bone tool analyses. The use wear recorded on the Contrebandiers Cave spatulates is consistent with experimental, ethnographic, and use-wear studies of leather-working tools (Semenov, 1964; Soressi et al., 2013; Tartar, 2009), as sheen and polish are restricted to the ends and sides but do not cover the entirety of the pieces. However, while our study used 40X magnification to identify use wear traces, others have used 100X-500X magnification to identify polish from use (see (Almeida Évora, 2015) for review and discussion of various magnification strengths). This is a possible limitation to our study, and future analyses of the Contrebandiers bone tool assemblage should use 100X-500X magnification to verify that the bone tools were used on skin, as has been suggested here.

Pressure flakers experimentally produced by d'Errico et al. (2012a) resemble three pieces at Contrebandiers Cave (Figures 6, and S3). When experimentally producing and using pressure flakers, d'Errico et al. (2012a) observed "crushing and flake removals originating from the tip [that] appeared when the broad aspect of the tool was applied perpendicular to the lithic edge and the tool was held almost upright during use." Mourre et al. (2010) identified stone tools at Blombos Cave, South Africa that suggest pressure flaking technology was used by ~75 ka in the final stages of Still Bay bifacial point manufacture, however, tools that were used as pressure flakers were not identified at Blombos Cave. d'Errico et al. (2012a) identified bone tools used as pressure flakers at Sibudu Cave, South Africa that support the presence of pressure flaking technology by ~64–57 ka in South Africa. While it is possible that hand-held pressure flaking was used in the manufacture of Aterian bifacial foliates—which have been identified at Contrebandiers Cave (Dibble et al., 2012)—further experimental studies must be completed to support this implication.

Bone tool imaging methods

Color photographs of bone tools and 5 cm scales were taken with a Canon EOS 10D Digital camera using a Canon Ultrasonic 100 mm macro lens. Photographs were then imported into Adobe Lightroom 5, where white balance was corrected for using the white portion of the scale in each photograph. Images were then imported into Adobe Photoshop CS6, where the same methods were used to remove the background in each image. These methods are: 1) open images in 6,000 x 8,000 pixels with 240 pixels per inch and in 16 bit color on 50% gray background, 2) use Magic Wand Tool at level 10 tolerance to select bone tool from background, then remove background, 3) refine edge with feather set at 1.5 pixels, and 4) draw rectangle over 1 cm portion of 5 cm scale to create 1 cm scale bar. Microscope photographs of bone tools were taken with a Leica EZ4 HD stereo 8x-35x zoom microscope with an integrated high definition digital camera. Microscope photographs were then imported into Adobe Photoshop CS6, where the same methods were used to convert each color to grey scale and remove the background in each photo. The methods are: 1) open images in 6,000 x 8,000 pixels with 240 pixels per inch and in 16 bit color on 10% or 50% grey background, 2) use Magic Wand Tool at level 10 tolerance to select bone tool from background, then remove background, 3) refine edge with feather set at 1.5 pixels, 4) convert each photo to grey scale and set auto contrast, and 5) scale each grey scale microscope photo to color photo taken with macro lens. The final microscope and bone tool photographs were composed and finaliz ed into Figures 2, 3, 5, and 6 using Adobe Photoshop 2021. Figure 2 illustrations G, H, I and J were drawn and composed using Adobe Photoshop CC 2019. The methods are: 1) import base layer with original bone tool photographs and scale set to 50% opacity, 2) use Jazza's Signature Photoshop Brushes (JSPB) Fineliners 0.3 and 0.5 to trace outline and major features of bone tool, 3) use JSPB Fineliner 0.1 to draw lateral breakage and irregular surfaces of bone tool, 4) draw dotted lines with Photoshop Hard Round Brush at 215% spacing, 5) draw bone tool shaping marks with ruler guides and JSPB Fineliner 0.1, 6) use JSPB Ink Brush to draw irregular marks, 7) trace darkened area of bone tool with Lasso Tool then fill with 50% grey, and 8) trace 1 cm scale bar then fill with black and white rectangles. Figure 4 illustrations were created using Adobe Illustrator CC 2020.

Stratigraphy methods

Contrebandiers Cave is carved into a Middle Pleistocene calcarenite (calcareous sandstone) formation and is located along the Atlantic Coast of Morocco in the town of Témara. The cave is currently ~250 m from the ocean with an entrance facing northwest. The top of the cave is ~14 m above current sea level. The basal deposits are archaeologically sterile beach sands (Aldeias et al., 2014) with a weighted mean OSL age of 126 $\pm$ 9 ka (Jacobs et al., 2011). This OSL age is concordant with widespread age estimates for Marine Isotope Stage (MIS) 5e high sea-level stand (Hearty et al., 2007). Anthropogenic inputs (in the form of stone tools, ash, charcoal and bones) are visible in deposits directly above the basal beach sands, indicating the onset of human occupation following the MIS 5e marine regression (Aldeias et al., 2014).

There are three stratigraphic sectors in the cave: the central excavation area (CEA), sector IV in the front of the cave, and sector V in the rear of the cave (Figure S1). Roche's previous excavations removed all of the uppermost Neolithic deposits and nearly all of the Iberomaurusian (Later Stone Age) deposits. As for the latter, Roche reported that the Iberomaurusian was spatially restricted within the site and never reached the back of the cave (Roche, 1976). A very small amount of sediment associated with Iberomaurusian occupations remains below the current dripline in sector IV, and unconformably overlies the uppermost MSA deposits of layer IV-2. Both field and micromorphological analyses attest to the lack of significant mixing between the Iberomaurusian layers and the underlying MSA deposits; the sedimentary contact between layer IV-2 and the overlying Iberomaurusian layers is sharp and clear. All of the stone tools associated with layer IV-2 are also consistent with MSA technocomplexes.

Sector V only contains Aterian MSA deposits; the base of the deposit was not reached in the rear of the cave. According to evidence from previous excavations, there were no Iberomaurusian occupations in this area of the cave. Presumably, the MSA deposits in sector V must, therefore, have been directly overlain by the distinct strong brown Neolithic sediments, which completely in-filled the cave at the time of its discovery (Roche, 1976). The MSA deposits in sector V (layers V-1a, V-1b and V-2) are composed of reddish brown silty sands, commonly incorporating combustion remains and discrete features (hearths).

The CEA contains Aterian and Maghrebian Mousterian MSA deposits, as well as MIS 5e beach sands at the base of the sequence. Within the ~3 m thick MSA sequence, the stratigraphical contacts between the different layers are clear and occasionally associated with calcium carbonate crusts (Aldeias et al., 2014). Within the CEA, 27 bone tools were identified in six MSA archaeological layers (Layers 4, 5A, 5B, 5C, 5D, and 6B). Fourteen bone tools were identified from one MSA archaeological layer in sector IV (Layer IV-2). Twenty-two bone tools were identified from three MSA archaeological layers in sector V (Layers V-1a, V-1b and V-2). Only one bone tool was identified in one archaeological layer associated with the Iberomaurusian in sector IV. In total, 62 MSA bone tools, and one Iberomaurusian bone tool were identified. Detailed descriptions of the geology (Aldeias et al., 2014; Dibble et al., 2012), stratigraphy (Aldeias et al., 2014; Dibble et al., 2012), and archaeological content (Dibble et al., 2012, 2013) of the Contrebandiers Cave sequence have previously been published.

Methods for dating the deposits

A large number of samples have been dated to construct a chronology for the MSA deposits at Contrebandiers Cave (Dibble et al., 2012). A multi-method dating approach was used, involving electron spin resonance (ESR), thermoluminescence (TL) and optically stimulated luminescence (OSL) techniques (Dibble et al., 2012). All three techniques are based on the same physical principles, but are applied to different minerals, namely hydroxyapatite in tooth enamel for ESR, microcrystalline quartz in flint or other rock types for TL, and sand-sized grains of quartz in sediment for OSL. Ages are obtained by measuring the cumulative effect of ionizing radiation on the crystal structure of these minerals. The greater the amount of energy stored in the crystal lattice, the longer the duration since first exposure to radiation and, consequently, the greater the age of the material being dated (Aitken, 1985). A series of OSL ages were first published in Schwenninger et al. (2010) for samples collected from a profile left by the Roche excavation. The OSL chronology associated with the latest excavations was first reported in Jacobs et al. (2011) and again in Dibble et al. (2012), and also together with the ESR and TL ages, in Dibble et al. (2012). No further dating of the MSA deposits has since been reported. Measurement and analytical details for all the samples are provided in these publications. In this article we will look more closely at the ages so far obtained for deposits that contain bone tools. Results relevant to the age of the bone tools presented in this article are summarized in Table S1 and the weighted mean ages for each of the Layers are shown in Figure S8.

Dating the central excavation area (CEA)

In Figure S1 the provenience of each of the bone tools is provided. Twenty-seven bone tools were discovered in deposits from the CEA, of which most (N = 20) come from Layer 5 (A, B and C) and are associated with the "Maghrebian Mousterian" of the MSA. The Maghrebian Mousterian is similar to the Aterian but without the diagnostic tanged artifacts, which are the *fossil directeur* of the Aterian Industry (Dibble et al., 2013). OSL ages for Layer 5 range between 124 $\pm$ 9 ka (SC19) and 112 $\pm$ 7 (SC13) (Table S1). Jacobs et al. (2011) calculated a weighted mean OSL age of 115.3 $\pm$ 3.4 ka for this layer. Preliminary TL ages for 4 individual burnt stone samples were reported in Dibble et al. (2012). These ages range between 116 $\pm$ 13 and 89 $\pm$ 14 ka. Preliminary ESR ages were also reported for 4 tooth samples. The ages range between 123 $\pm$ 10 ka and 90 $\pm$ 2 using the recent uptake (RU) model. The range of TL and ESR ages are almost identical and overlap with the OSL ages; all three sets of ages are statistically consistent at the 1σ level within the CEA and at the 2σ level for Layer 4 in the CEA, Layer V-1 in Sector V, and Layer IV-2 in Sector IV (Dibble et al., 2012). One bone tool was also collected from Layer 6B, which has a low artifact abundance and for which a weighted mean OSL age of 112.2 $\pm$ 4.2 ka was calculated. The youngest bone tools (N = 6) in the CEA were collected from Layer 4D which is associated with the Aterian with tanged pieces (Dibble et al., 2013). Three OSL ages of 104 $\pm$ 7 (SC20), 108 $\pm$ 9 (SC8) and 117 $\pm$ 9 ka (SC7) were calculated for Layer 4D and are similar to, and slightly younger than, those for Layer 5. The earliest occurrence of bone tools in the CEA can best be dated by the grand weighted mean OSL age for the archaeological units in Layers 5 and 6 of 116.1 ± 2.9 ka (see Table 3 in Jacobs et al. (2011)) and the mean TL age of 97 ± 7 and the mean ESR age of 111 ± 7 ka (weighted mean = 94 ± 8 ka), both for Layer 5.

Dating sector V

A large number of bone tools (N = 21) were also recovered from the MSA levels in Sector V (-1a, -1b and −2), all associated with the Aterian Industry. No TL ages were obtained from this Sector, but Dibble et al. (2012) reported ESR ages for 4 teeth collected from Layer V-1a and obtained ages that ranged between 109 ± 7 ka and 86 ± 2 using the linear uptake (LU) model or between 132 ± 9 ka and 108 ± 4 using the recent uptake (RU) model. Their respective weighted mean ages are 91.4 ± 7.7 and 110.5 ± 8.3 ka. A single OSL age was reported for each of Layer V-1b and V-2, and ages of 113 ± 7 (SC23) and 107 ± 9 ka (SC34) were calculated, respectively. Archaeologically, these deposits are similar to that of Layer 4D in the CEA for which comparable OSL ages were obtained.

Dating sector IV

A further 14 bone tools were also recovered from the Aterian deposits at the front of the Cave in Sector IV, in Layer IV-2. TL ages for 6 burnt stone samples were reported in Dibble et al. (2012) and 5 of the ages range between 115 ± 11 ka and 80 ± 11; there is a single outlier with an age of 179 ± 14 ka. No ESR ages have been reported for these deposits. Three OSL samples were collected from this Layer and these posed a number of issues. We were unable to obtain a reliable age for one of the samples (SC30) because of evidence for extensive sediment mixing (Jacobs et al., 2011); small-scale (mm-sized) bioturbation by wasps and other insects are pervasive in these sediments (Aldeias et al., 2014). We were able to obtain ages for the other two samples, but these two samples also showed evidence for mixing, both from the overlying Iberomaurusian deposits and incorporation of grains from the roof rock. The erosional boundary between the Aterian and Iberomaurusian deposits in this sector is sharp and easy to identify macroscopically in the field. The boundary, however, is not horizontal and undulates; this is probably due to erosion by water (see Aldeias et al. (Aldeias et al., 2014)). When we collected the OSL samples with ~15 cm long tubes, we likely cross-cut the boundary and sampled a mixture of both deposits. It is important to emphasize that the Aterian and Iberomaurusian deposits are not mixed here, rather the mixing is most likely the result of the sampling procedure. The best-estimate OSL ages for Layer IV-2 are 96 ± 8 (SC39) and 101 ± 9 ka (SC37). These ages are also supported by dating of 2 samples from the adjacent squares in the old excavation area of Roche that gave consistent ages of 92 ± 6 (SC31) and 97 ± 7 ka (SC32). Together, these samples gave a weighted mean OSL age of 95.9 ± 4.1 ka (Jacobs et al., 2011) that is statistically consistent with the range of TL ages for burnt stones collected from these sedimentary deposits, and provides an age for the youngest MSA bone tools at Contrebandiers Cave.

Checking the reliability of the OSL chronology

Most of the chronology is based on the large number of OSL ages provided in Jacobs et al. (2011). However, Guérin et al. (2013) recently critiqued the use of the beta dose correction procedure of Jacobs et al. (2008) to deal with scatter in equivalent dose (D_e) data sets for the samples from Contrebandiers Cave, among other sites. Quartz grains deposited at the same time but situated within a few mm or cm of each other can have experienced different beta dose rates, depending on their relative proximity to materials of high or low radioactivity, resulting in a range of different D_e values. Jacobs et al. (2011) explained in detail their reasons for applying this model at this site based on the heterogeneous distribution of organic and inorganic materials, and also described, with a worked-example, how it was implemented. To test the effect of the use of this model, we present in Figure S9, as filled circles, the individual ages reported in Jacobs et al. (2011) for samples from layers in which bone tools were recovered, together with ages (shown as open squares) for the same samples but for which we did not use the beta dose adjustment procedure (i.e., we used the central age model (CAM) of Galbraith et al. (1999) to obtain a weighted mean D_e, that is then divided by the bulk beta dose rate for the sample). From here it can be seen that the model, when applied to samples from this site, had a systematic effect and that ages are on average 5 ± 1% younger when the beta dose rate is not adjusted. The change in age, however, is well within the 1σ age uncertainty of the individual OSL samples (Figure S9), and also within the range of ages obtained from other independent methods that are statistically consistent with the OSL ages. Thus, the difference in age is insignificant and does not change the antiquity of the bone tools recovered from the MSA deposits at Contrebandiers Cave.

The weighted mean OSL age of 116.1 ± 2.9 ka, therefore, best constrains the age of the oldest bone tools found in Layers 5 and 6 in the CEA, and the weighted mean age of 95.9 ± 4.1 ka best constrain the age of the youngest MSA bone tools found in Layer IV-2 in Sector IV at the top of the MSA deposits. Bone tools are also found in layers between these oldest and youngest bone tool bearing deposits, so an age range of ∼120–90 ka obtained by all three dating techniques captures the ages of all MSA bone tools at Contrebandiers Cave.

Other Contrebandiers cave bone tools

Other bone tools from MSA layers at Contrebandiers Cave include scaled pieces (see Figure S4) and possible awls (see Figure S4), as well as other bone tools that do not conform to a yet-known type (see Figure S4). Future experimental studies are aimed at providing descriptions of the manufacturing stages for these bone tools, and at determining their function and typology.

MSA stone artifacts

As previously reported in Dibble et al. (Dibble et al., 2012, 2013), assemblages with MSA lithics at Contrebandiers were traditionally divided into two groups. The lower one (Layers 5A-5D and 6A-6C in the CEA), referred to as the Maghreb Mousterian, does not contain stemmed (tanged) implements, while the upper assemblage (Aterian) from Layers 4A-4E (CEA), Layer IV-2 (Sector IV near the front of the cave), and Layers V-Ia, V-Ib, and V-2 (Sector V near the back of the cave) does have stemmed pieces. Some stemmed pieces are pointed, but most are not, suggesting that these artifacts are not functional points but rather indicate the hafting of lithic artifacts, likely as scrapers and knives (Iovita, 2011). The Aterian occupation also produced one bifacial foliate. In other respects, these two MSA components are quite similar. Typologically, both have sidescrapers (primarily single sidescrapers) and notch/denticulates. All other tool types are rare, but include truncated-facetted, endscrapers, and various retouched pieces. A similar situation exists for the lithic technology, with Levallois technique present in low frequencies (ca. 3% overall) throughout, along with some examples of Kombewa cores and flakes (suggesting small flake production). Plain platforms are typical on flake debitage indicating that, with the exception of Levallois technique, no extensive core preparation or maintenance of cores was undertaken. Levallois cores are rare, while most other cores are single surface. Based on this combination of features, Dibble et al. (2013) suggested the possibility that the lower and upper occupations may not represent two distinct industries. Instead, they may reflect somewhat different activity profiles at the site over time, which might be supported by the fact that the identified spatulate bone tools are associated with the upper (Aterian) deposits (Table S1; but note that many bone tools have not been identified to type).

QUANTIFICATION AND STATISTICAL ANALYSIS

The ages are given as mean ± SEM (Table S1, Figures S8 and S9) as reported in Jacobs et al. (2011) and Dibble et al. (2012). Data were analyzed with RStudio version 1.2.5033 (RStudio Team, 2019) running R version 3.6.2 (R Core Team, 2020).

Poster Presentation Number 6, Session 1, Wednesday 2:45-3:45 pm

Late Pleistocene to Holocene palaeoenvironmental reconstruction and human behaviour at Iho Eleru rock shelter, Nigeria

Jacopo Niccolò Cerasoni[1,2], Emuobosa Akpo Orijemie[3], Emily Yuko Hallett[1], Mary Lucas[4], Kseniia Ashastina[4], Lucy Farr[5], Alexa Höhn[6], Christopher Kiahtipes[7], Patrick Roberts[4,8], Andrea Manica[9], James Blinkhorn[1,10], Eleanor Scerri[1,11,12]

1 - Pan-African Evolution Research Group, Max Planck Institute for the Science of Human History, Jena, Germany · 2 - Department of Early Prehistory and Quaternary Ecology, University of Tübingen, Tübingen, Germany · 3 - Department of Archaeology and Anthropology, University of Ibadan, Ibadan, Oyo State, Nigeria · 4 - Max Planck Institute for the Science of Human History, Department of Archaeology, Jena, Germany · 5 - Department of Archaeology, University of Cambridge, Cambridge, United Kingdom 6 - Institute of Archaeological Sciences, Goethe-Universität, Frankfurt am Main, Germany · 7 - Department of Anthropology, University of South Florida, Tampa, FL, USA · 8 - School of Social Science, The University of Queensland, Brisbane, Australia · 9 - Department of Zoology, University of Cambridge, Cambridge, United Kingdom · 10 - Centre for Quaternary Research, Department of Geography, Royal Holloway, University of London, Egham, UK · 11 - Department of Classics and Archaeology, University of Malta, Msida, Malta · 12 - Institute of Prehistoric Archaeology, University of Cologne, Cologne, Germany

The Ihò Eléérú (here named Iho Eleru in its anglicised rendition, and erroneously known as "Iwo Eleru") rock shelter (7°26'28.83"N, 5°7'29.16"E) is located within the hilly ancient igneous landscapes near Akure, Nigeria. It is widely known for the discovery of the only West African Pleistocene hominin fossil remains, identified as *Homo sapiens* associated with Later Stone Age (LSA) technology [1-2]. While the modern regional vegetation has been extensively modified by human activity, the environmental context of these fossils as associated with tropical rainforest has been debated [3]. Between 1964 and 1965, T. Shaw and S.G.H. Daniels conducted a series of excavations at the rock shelter [4], revealing a terminal Pleistocene to middle Holocene sequence documenting a history of recurring human occupations ranging from the LSA into the Holocene. Here, we present new findings following an expedition to the Iho Eleru rock shelter, and an inspection of the storage rooms of the Department of Archaeology and Anthropology at the University of Ibadan which took place in November 2019. During the re-analysis of the remaining assemblages excavated at Iho Eleru, J.N. Cerasoni and authors found: (1) the entirety of the excavated charcoal collection (65 bags), with samples ranging from the uppermost to the lowest excavated levels, and (2) the entirety of the vertebrate faunal assemblage (59 bags) which was originally thought to be lost and has never previously been described. The original context identification tags were intact for each bag of charcoal and faunal remains. We present new data from the analyses of these unique assemblages. Firstly, fourteen new ^{14}C dates from charcoal and faunal bone samples were obtained, originating from consecutive archaeological layers spanning two adjacent trenches and the entire depth of the stratigraphic section where the Iho Eleru human fossil was discovered. Secondly, we present anthracological identifications from the charcoal collection, and taxonomic identification and taphonomic analysis of the Iho Eleru vertebrate faunal assemblage, making it the first West African Pleistocene faunal assemblage ever discovered and described. Finally, isotopic analyses were carried out on the faunal assemblage. We synthesise these results with climate reconstructions spanning the last 22,000 years [5] for the area surrounding Iho Eleru to reveal the consistent human habitation of a mosaic forest-savannah ecotone.

References: [1] Harvati, K., Stringer, C., Grün, R. et al., 2011. The later stone age calvaria from Iwo Eleru, Nigeria: Morphology and chronology. PLoS ONE, 6(9). [2] Stojanowski, C.M., 2014. Iwo Eleru's place among Late Pleistocene and Early Holocene populations of North and East Africa. J. of Human Evo, 75, 80–89.[3] Allsworth-Jones, P., Harvati, K., & Stringer, C., 2010. The archaeological context of the Iwo Eleru cranium from Nigeria and preliminary results of new morphometric studies. In P. Allsworth-Jones (Ed.), West African Archaeology New developments, new perspectives. BAR international Series S2164 (pp. 29–42). Oxford: BAR Publishing. [4] Shaw, T., & Daniels, S.G.H., 1984. Excavations at Iwo Eleru, Ondo State, Nigeria. W African J of Archaeology, 14, 1–269. [5] Beyer, R.M., Krapp, M. & Manica, A., 2020. High-resolution terrestrial climate, bioclimate and vegetation for the last 120,000 years. Scientific Data 7, 236.

Late Pleistocene to Holocene palaeoenvironmental reconstruction and human behaviour at Iho Eleru rock shelter, Nigeria

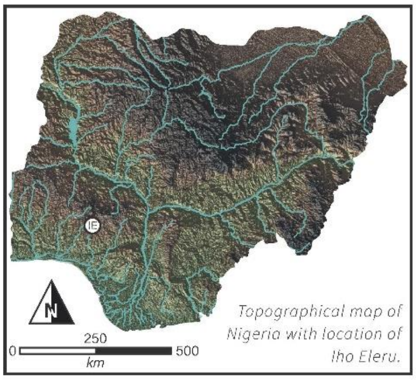
Max-Planck-Institut für Menschheitsgeschichte

Jacopo Niccolò Cerasoni[1,2*], Emuobosa Akpo Orijemie[3], Emily Yuko Hallett[1], Mary Lucas[4], Ksenia Ashastina[4], Lucy Farr[5], Alexa Höhn[6], Christopher Kiahtipes[7], Patrick Roberts[4,8], Andrea Manica[9], James Blinkhorn[1,10], Eleanor Scerri[1,11,12]

Introduction

The Ihò Eléérú (or Iho Eleru) rock shelter, located within the ancient igneous landscapes of South-West Nigeria, is widely known for the discovery of the only West African Pleistocene hominin fossil remains.

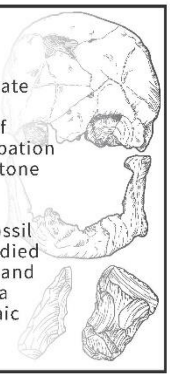
Here, we present new findings following the re-dating of the site, new anthracological results, and the taxonomic, taphonomic and isotopic analyses of the only Pleistocene faunal assemblage ever discovered in West Africa.



Topographical map of Nigeria with location of Iho Eleru.

Between 1964 and 1965 excavations revealed a terminal Pleistocene to late Holocene sequence documenting a history of continuous human occupation ranging from the Later Stone Age to present day [1,2].

The Iho Eleru hominin fossil has been extensively studied morphologically [3,4,5], and has been interpreted as a *Homo sapiens* with archaic features.



Methods and Results

In November 2019 J.N. Cerasoni and authors carried out an expedition to Iho Eleru and inspected the storage rooms of the Department of Archaeology and Anthropology, University of Ibadan. Examination of the original excavated material by T. Shaw and S.G.H Daniels in 1964-65 uncovered:

1. The entirity of the original **Archaeobotanical Assemblage**
2. The previously thought lost, only West African Pleistocene **Faunal Assemblage**

The following methods were carried out on the Iho Eleru assemblages:

^{14}C Dating
14C Dating was done on bone and charcoal samples from areas with a low degree of disturbance (D-F XX-XXVII)

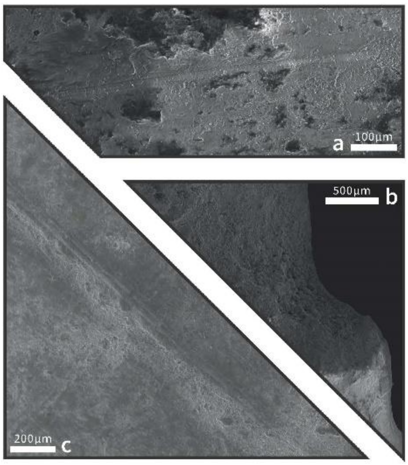
Taxonomy
Species identification and frequency was carried out on the faunal assemblage categorising species per environmental group

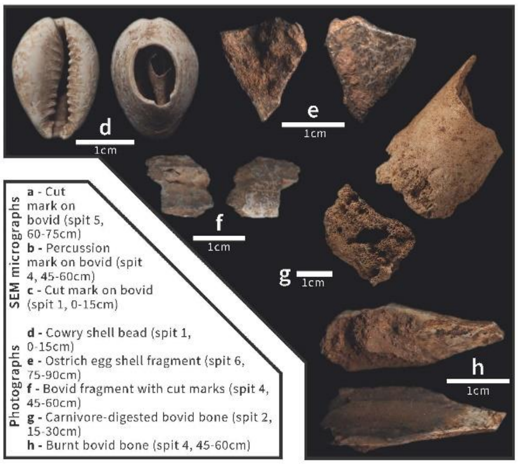
Archaeobotany
Archaeobotanical (wood and carpological) samples were analysed to determine species for identification to the lowest possible taxa

Taphonomy
The faunal assemblage was analysed for the identification of anthropogenic (cutting, percussion, burning) and carnivore (digestion, gnawing) activity

Paleoclimate
Bioclimatic variables [6] spanning the last 24,000 years were modelled for the landscape surrounding Iho Eleru

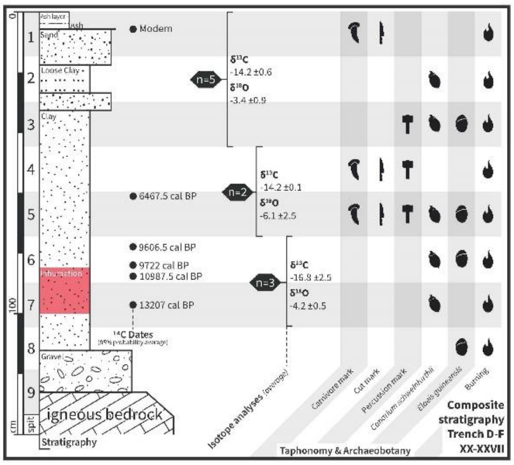
Isotopes
Faunal teeth were sampled and analysed for isotopic reconstruction of the species inhabiting the Iho Eleru landscape

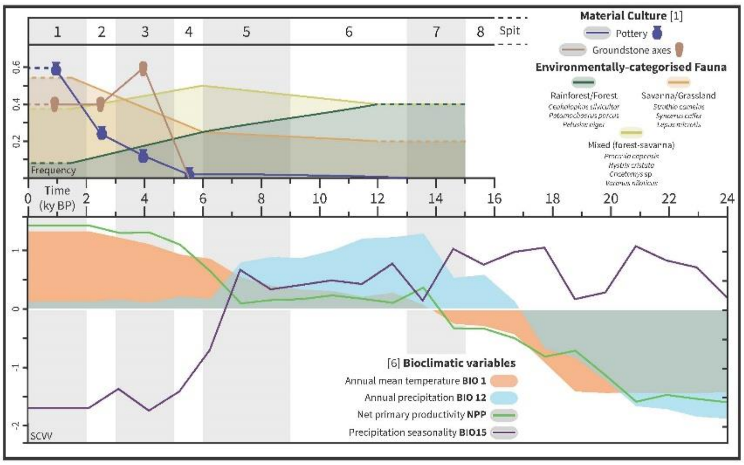




SEM micrographs
a - Cut mark on bovid (spit 5, 60-75cm)
b - Percussion mark on bovid (spit 4, 45-60cm)
c - Cut mark on bovid (spit 1, 0-15cm)

Photographs
d - Cowry shell bead (spit 1, 0-15cm)
e - Ostrich egg shell fragment (spit 6, 75-90cm)
f - Bovid fragment with cut marks (spit 4, 45-60cm)
g - Carnivore-digested bovid bone (spit 2, 15-30cm)
h - Burnt bovid bone (spit 4, 45-60cm)





Discussion

The results show that, whilst a **mixed tropical forest-savanna ecotonal landscape** persisted around Iho Eleru from the Late Pleistocene to the Late Holocene, its composition shifted from forest to savannah dominated at the onset of the **warm mid Holocene** (~6kya). Furthermore, Iho Eleru underwent **continuous human habitation** during the observable timeline, with focused use of resources from both forested and grassland environments.

Archaeologically, the observed warm mid Holocene event is represented with a change in material culture (appearance of relief motifs pottery and ground stone axes), showing a **strong correlation between material culture, fauna and environment**. Our data suggests that this subtle environmental shift was not caused by anthropogenic processes, such as forest clearing from the use of ground stone axes, but by **a change in precipitation rates and temperature** as shown by the paleoclimatic reconstruction.

The change in material culture was also likely a product of the 6 kya environmental transition, where people and/or material traditions moved in this area following an **expansion of the grassland and contraction of the forests**. This is further supported by the evident increase of available resources biomass (NPP) and the decrease in precipitation seasonality around Iho Eleru, which would have made a more liveable and stable environment for non hunter-gatherer communities.

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Contacts

*Corresponding author

cerasoni@shh.mpg.de

ORCID: 0000-0002-5546-1555

@JCerasoni

Affiliations

1 - Pan-African Evolution Research Group, Max Planck Institute for the Science of Human History, Kahlaische Straße 10, 07745, Jena, Germany; 2 - Institute for Archaeological Sciences, Universität Tübingen, 72070, Tübingen, Germany; 3 - Department of Archaeology and Anthropology, University of Ibadan, Ibadan, Oyo State, Nigeria; 4 - Department of Archaeology, Max Planck Institute for the Science of Human History, Jena, Germany; 5 - Department of Archaeology, University of Cambridge, Cambridge, United Kingdom; 6 - Goethe University, Institute of Archaeological Sciences, Grueneburgplatz 1, 60323, Frankfurt am Main, Germany; 7 - Department of Anthropology, University of South Florida, Tampa, FL, USA; 8 - School of Social Science, The University of Queensland, Brisbane, Australia; 9 - Department of Zoology, University of Cambridge, Cambridge, United Kingdom; 10 - Centre for Quaternary Research, Department of Geography, Royal Holloway, University of London, Egham, UK; 11 - Department of Classics and Archaeology, University of Malta, Msida, Malta; 12 - Institute of Prehistoric Archaeology, University of Cologne, Cologne, Germany

PLOS ONE

LAB PROTOCOL

Do-It-Yourself digital archaeology: Introduction and practical applications of photography and photogrammetry for the 2D and 3D representation of small objects and artefacts

Jacopo Niccolò Cerasoni[1,2]☯*, Felipe do Nascimento Rodrigues[3]☯, Yu Tang[4]☯, Emily Yuko Hallett[1]

1 Pan-African Evolution Research Group, Max Planck Institute for the Science of Human History, Jena, Germany, **2** Institute of Archaeological Sciences, Eberhard Karls University Tübingen, Tübingen, Germany, **3** Department of Archaeology, Centre for the Archaeology of the Americas, Material Lives -Transdisciplinary Research Group, University of Exeter, Exeter, United Kingdom, **4** Cygames, Inc., Shibuya-ku, Tokyo, Japan

☯ These authors contributed equally to this work.
* cerasoni@shh.mpg.de

OPEN ACCESS

Citation: Cerasoni JN, do Nascimento Rodrigues F, Tang Y, Hallett EY (2022) Do-It-Yourself digital archaeology: Introduction and practical applications of photography and photogrammetry for the 2D and 3D representation of small objects and artefacts. PLoS ONE 17(4): e0267168. https://doi.org/10.1371/journal.pone.0267168

Editor: Radu Iovita, New York University, UNITED STATES

Received: November 29, 2021

Accepted: April 3, 2022

Published: April 15, 2022

Peer Review History: PLOS recognizes the benefits of transparency in the peer review process; therefore, we enable the publication of all of the content of peer review and author responses alongside final, published articles. The editorial history of this article is available here: https://doi.org/10.1371/journal.pone.0267168

Data Availability Statement: The article does not contain data and the data availability policy is not applicable to the article.

Abstract

Photography and photogrammetry have recently become among the most widespread and preferred visualisation methods for the representation of small objects and artefacts. People want to see the past, not only know about it; and the ability to visualise objects into virtually realistic representations is fundamental for researchers, students and educators. Here, we present two new methods, the ‘Small Object and Artefact Photography’ (‘SOAP’) and the ‘High Resolution “DIY” Photogrammetry’ (‘HRP’) protocols. The ‘SOAP’ protocol involves the photographic application of modern digital techniques for the representation of any small object. The ‘HRP’ protocol involves the photographic capturing, digital reconstruction and three-dimensional representation of small objects. These protocols follow optimised step-by-step explanations for the production of high-resolution two- and three-dimensional object imaging, achievable with minimal practice and access to basic equipment and softwares. These methods were developed to allow anyone to easily and inexpensively produce high-quality images and models for any use, from simple graphic visualisations to complex analytical, statistical and spatial analyses.

Introduction

Archaeologists continuously apply novel approaches from complementary disciplines for the better understanding of archaeological contexts and past human activity and behaviour, both in the field and in the laboratory. For example, archaeological observations of stratigraphies (i.e. the study of accumulation of sediments and materials through time) first originated from geology in the 15th century [1], and modern archaeological scientific methods such as

Funding: J.N.C. and E.Y.H are funded by the Pan-African Evolution Research Group, based at the Max Planck Institute for the Science of Human History, Jena, Germany. F.N.R. is funded by the University of Exeter College of Humanities International PhD Studentship. Y.T. is funded by Cygames, Incorporated based in Tokyo, Japan. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

biomolecular and chemical archaeology apply theory and method from the disciplines of biology, genetics and chemistry. Similarly, the study of archaeological material culture and the methods used for the visual representation of artefacts has developed at an incredibly fast rate following the innovations in digital technology that have occurred during the past decades.

The ability to visually represent archaeological materials has always been a fundamental part of archaeological publications and dissemination, as the study of material culture (e.g. stone tools, pottery, metal objects, organic materials, etc.) is one of the principal factors of archaeological research. Traditional means of visual representation of material culture commonly include illustrations in physical or digital formats [2]. However, in the recent decades, and following an expansion of accessibility to digital equipment, photographic and three-dimensional (3D) representations of material culture have become dominant methods in the field.

Photography is undoubtedly the most common medium in use today to represent artefacts in archaeological research [3]. Its origins in this field can be traced back to the mid-nineteenth century [4], and the use of this photography for the recording archaeological artefacts is nearly as old as photographic technology [5]. Photography is generally used to record artefacts, archaeological sites, landscapes, and monuments [3,5,6].

A major improvement in the visual representation of archaeological artefacts has been the shift from an illustrative and artistic photographic style, to a more analytical and objective format. While artistic photographic styles are still employed in cases where public outreach and science communication are of primary interest, analytical and objective photography has become essential for the proper representation of archaeological materials and contexts following proper scientific methods. Examples of this are the increased use of satellite imagery as a primary data source for archaeological surveying [7] and high-resolution microscopic photography as an essential method for the identification and recording of past tool uses [8].

Thanks to its inherent value in the visual communication of past human behaviour, archaeological photography has been keenly scrutinised and ultimately improved over time. Major improvements to archaeological photography include methodological and technical improvements in the form of development of photographic equipment and digital control of photographic products and environments [4], the critical theoretical evaluation of the objective nature of photography [9], and the contemporary practical and theoretical reassessment of the relationship between archaeology and photography [10]. Overall, these advancements have raised photography to a status beyond that of an illustrative medium. Nevertheless, gaps remain in the practical teaching of archaeological photography, as can be seen in the lack of university-level Archaeology programmes offering photographic training [3]. Several valuable resources exist for archaeologists that discuss the practical aspects of photography, such as the BAJR guides introducing photography [11], and detailed site and artefact photography manuals [12,13].

Here we present the "Small Object and Artefact Photography", or 'SOAP', protocol as an addition to the field of archaeological photography. This new protocol combines a detailed, concise, and user-friendly workflow that covers the entire photographic acquisition and processing process, thereby contributing to the replicability and reproducibility of high-quality photographs. By clearly explaining every step of the process, and adding theoretical and practical notions to steps explaining camera technical functionalities, the 'SOAP' method shows users how to take high quality photographs and also described the reasons why photographs can be successful or unsuccessful.

Photogrammetry, like photography, has advanced as a method in archaeology over the last decade, resulting in a significant increase in use over the last six years [14,15]. Its growth in popularity among researchers, heritage professionals, and the public is mostly due to its exceptional ability to bring people even closer to objects and landscapes, in combination with its low cost in comparison to other 3D recording methods (e.g. structured light, laser, CT scanning, and terrestrial/aerial LiDAR) [2,14]. Photogrammetry has been used in a range of archaeological contexts, including faunal and paleontological studies [16], lithic use wear analysis [17], small artefact analysis [18], and site photogrammetric surveys [19].

Following the modern computational revolution in archaeology [20], photogrammetry finds itself at the spotlight of archaeological visual representation, with continuous technical and methodological developments [18,21]. While data visualisation methods are expanding at an exponential rate, the use of photogrammetric methods for new analytical techniques and analyses is yet to be fully explored; this issue has been raised by other researchers [15–20]. To address this, we present here the protocol for the High Resolution "DIY" Photogrammetry ('HRP') Method. This new protocol makes photogrammetry more accessible and less time consuming for beginners by providing a detailed workflow of each step and streamlining the entire photogrammetry process. Our protocol covers all stages of photogrammetry—from image acquisition to post processing—and allows more time for focusing on photogrammetry's analytical applications. Our aim in streamlining photogrammetry and making it widely accessible is to allow archaeologists to further integrate photogrammetry in archaeological research.

The 'SOAP' and 'HRP' protocols offer clear step-by-step processes that anyone can learn and put into practice. However, it is important to note that a good photograph or a good three-dimensional model will always be just a visual representation of the visualised artefact. For this reason, it is important to note that a good understanding of the artefact's morphology, technological characteristics and context will always be necessary for the correct interpretation of the visualised material culture. Furthermore, both methods will inevitably encounter limitations depending on the used equipment, workflow variations, and subjective evaluations during their application. Quantitative methods of image analysis [22–24] were not applied in our protocols as they fall outside the scope of the applied methods in archaeology that we present here. Both in terms of photographic and photogrammetric documentation, minor differences in image quality will occur depending on a range of variables that will be person- and case-specific. Improving equipment capabilities both in terms of hardware and software functionality will likely automatically result in better and more efficient final products. Increased time spent on practicing the presented methods will also exponentially improve their application and outcomes.

The 'SOAP' and 'HRP' protocols were developed using Adobe Camera Raw ©, Adobe Photoshop 2021 ©, RawDigger ©, DxO Photolab ©, and RealityCapture ©, as they have native functions and tools that make them easier and faster compared to other comparable softwares. Although most of the used softwares in the 'SOAP' and 'HRP' protocols are readily available in academic environments, these methods can be applied to any other non-subscription based softwares with similar features. In this regard, free and/or open-access softwares can be readily used, albeit with minor changes in the application of some of the presented steps depending on the used software's functionalities. For raster-based softwares used for both photography and photogrammetry, Adobe Photoshop © can be used, while free to access software such as GIMP © and Krita ©,or single-purchase products such as Affinity Photo © can be used. For 3D Reconstruction photogrammetric softwares, such as RealityCapture ©, a good free and open-source alternative is Meshroom ©.

Materials and methods

The protocols described in this peer-reviewed article are published on protocols.io, https://dx.doi.org/10.17504/protocols.io.b53zq8p6 ('SOAP' Protocol) and https://dx.doi.org/10.17504/protocols.io.b53xq8pn ('HRP' Protocol), and are included for printing supporting information file 1 and 2 with this article.

Expected results

While a variety of publications on artefact photography and small object photogrammetry already exist, with the application of the 'SOAP' and 'HRP' methods it is expected that users will be able to produce high-quality and publishable two- and three-dimensional visualisations of their archaeological artefacts independently and without the necessary dependency of other methodological sources. Furthermore, with enough practice over time and access to the softwares listed above, anyone who is interested in archaeological material culture, whether for personal, educational, or professional reasons, will be able to do so while keeping time and costs as efficient and low as possible.

Of particular importance, with the application of the 'HRP' Method, differentiations in skill or experience level will result in little to no difference in the application and comprehensibility of the method. Anyone will be able to produce high quality 3D scans at a fraction of the price of other scanning techniques, such as light structured scanning, laser scanning, or CT-scanning. The application of this method makes high-resolution models achievable using beginner or intermediate level equipment and at a much higher resolution compared to other expensive scanning methods.

Overall, whether for simple visualisation or more complex analytical purposes, the protocols presented here will offer the possibility to produce high quality visualisations of artefacts. It is therefore expected that any users of these protocols can produce photographs and photogrammetric models for: (1) academic and general audience publication, (2) quantitative and analytical purposes (e.g. geospatial, statistical, morphological, functional), or (3) public outreach (e.g. printable 3D models, museums, exhibitions, children's activities).

Supporting information

S1 Fig.
(PNG)

S1 File. Small Object and Artefact Photography—'SOAP' protocol. also available on protocols.io.
(PDF)

S2 File. High Resolution "DIY" Photogrammetry—'HRP' Protocol. also available on protocols.io.
(PDF)

Acknowledgments

We would like to thank the Pan-African Evolution Research Group and the Max Planck Institute for the Science of Human History for their support during the development of this study. We sincerely thank the reviewers of this study, particularly Dr. Samantha T. Porter (University of Minnesota) for her extremely detailed and in-depth review. E.Y.H. thanks Curtis W. Marean (Arizona State University) for assistance with best practices in macro photography. The following study was carried out as part of the Archaeological Creative Tank.

Author Contributions

Conceptualization: Jacopo Niccolò Cerasoni.

Investigation: Jacopo Niccolò Cerasoni, Felipe do Nascimento Rodrigues, Yu Tang, Emily Yuko Hallett.

Methodology: Jacopo Niccolò Cerasoni, Felipe do Nascimento Rodrigues, Yu Tang, Emily Yuko Hallett.

Project administration: Jacopo Niccolò Cerasoni.

Supervision: Jacopo Niccolò Cerasoni.

Validation: Jacopo Niccolò Cerasoni, Felipe do Nascimento Rodrigues, Yu Tang, Emily Yuko Hallett.

Writing – original draft: Jacopo Niccolò Cerasoni, Felipe do Nascimento Rodrigues.

Writing – review & editing: Jacopo Niccolò Cerasoni, Felipe do Nascimento Rodrigues, Yu Tang, Emily Yuko Hallett.

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PLOS ONE

LAB PROTOCOL

Vectorial application for the illustration of archaeological lithic artefacts using the "Stone Tools Illustrations with Vector Art" (STIVA) Method

Jacopo Niccolò Cerasoni *

Pan-African Evolution Research Group, Max Planck Institute for the Science of Human History, Jena, Germany

* cerasoni@shh.mpg.de

OPEN ACCESS

Citation: Cerasoni JN (2021) Vectorial application for the illustration of archaeological lithic artefacts using the "Stone Tools Illustrations with Vector Art" (STIVA) Method. PLoS ONE 16(5): e0251466. https://doi.org/10.1371/journal.pone.0251466

Editor: Peter F. Biehl, University at Buffalo - The State University of New York, UNITED STATES

Published: May 11, 2021

Peer Review History: PLOS recognizes the benefits of transparency in the peer review process; therefore, we enable the publication of all of the content of peer review and author responses alongside final, published articles. The editorial history of this article is available here: https://doi.org/10.1371/journal.pone.0251466

Data Availability Statement: All relevant data are within the manuscript and its Supporting Information files.

Funding: This study was funded by the Pan-African Evolution Research Group, based at the Max Planck Institute for the Science of Human History, Jena, Germany.

Abstract

Lithic illustrations are often used in scientific publications to efficiently communicate the technological and morphological characteristics of stone tools. They offer invaluable information and insights not only on how stone raw materials were transformed into their final form, but also on the individuals that made them. Here, the "Stone Tools Illustrations with Vector Art" (STIVA) Method is presented, which involves the illustration of lithic artefacts using vectorial graphics software (Adobe Illustrator ©). This protocol follows an optimised step-by-step method, presenting ten major sections that constitute the creation of a lithic illustration: photography, vectorial software configuration, scale, outline, scar borders, ripples, cortex, symbols, composition, and export. This method has been developed to allow researchers, students and educators to create clear and competent illustrations for any application, from scientific publications to public outreach.

Introduction

Archaeological research involves the study of past human activity, behaviour, and interaction with the environment. Although widely different approaches can be taken depending on geographic, cultural, and chronological contexts, one of the most important components of archaeological research is the study of material culture. Objects used and created in the past can offer invaluable information for the better understanding of who made them, why, and how they were used. These objects have to be represented and published to share the researchers' interpretations and hypotheses, and this is done using graphic, printable, representations.

One of the most ubiquitous types of materials retrieved in the archaeological record is stone. Due to its inorganic nature it can survive indefinitely both in open-air contexts and in below-surface deposits, and it is undoubtedly a type of raw material that has been used for the longest time in human prehistory [1]. Knapped stone objects are fundamental artefacts for the identification of human presence and behaviour, and are commonly used to identify the earliest tools produced by our ancestors. These important objects, whether for research or public engagement purposes, are therefore best represented by means of graphic representation.

Competing interests: The author declares no competing interests.

In the past decades the introduction of easy-to-use and fast imaging technologies has overtaken the world of archaeological imaging. Prior to the introduction of digital imaging technologies such as photography, photogrammetry and three-dimensional scanning, lithic illustrations were commonly drawn by artists and archaeologists. The fastest and most efficient of these modern imaging methods is certainly digital photography. Given the ease of access to digital photographic cameras and their affordability and wide-spread use, digital photographs have become the primary method for artefact depiction [2]. However, photography can be a challenging medium, as many variables must be considered when photographing lithic artefacts. Surface colour, patination, roughness, irregularities, raw material type, opacity, and background lighting are just a few of the variables that have to be reckoned with when photographing stone, and without a thorough understanding of photography it can be easy to misjudge the final product. When details and aspects of the artefacts have been obscured by improper photography, important observations and interpretations can be missed.

Photogrammetry uses digital photographs to create three-dimensional models of objects or locations. If poor quality or poorly processed digital photographs are used in photogrammetry, the problems described above are compounded and can result in unreliable digital models [3]. This method involves the modelling of three-dimensional objects that begins with the importing of two-dimensional photographs into specialised photogrammetry softwares [4]. This is followed by the processing of the photographs to create three-dimensional surfaces that are then merged into final volumetric models [5]. Furthermore, when photogrammetry is applied to small objects such as lithic artefacts, a series of issues can be encountered due to the minute nature of the topographic and textural details, often resulting in three-dimensional models lacking in high resolution.

3-D scanning can potentially suffer from different problems that are unlike those for photography and photogrammetry. 3-D scanning is a modern imaging method that includes several techniques that differ based on the specific technology used, and can highly differ in terms of cost, usability and scanned material limitations [6]. Structured light scanners are among the most commonly used 3-D scanners in archaeological contexts, and use patterns of light to identify any deformations or reflections on the surface of the scanned object. The application of structured light scanners for lithic artefacts is usually satisfactory, although it can be problematic when scanning translucent or transparent objects; these can be common features of lithic artefacts. This problem does not arise, however, when using laser scanners. These scanners create 3-D images by triangulating the positions of laser dots which are projected onto the object, in order to recreate three-dimensional surfaces. Both of these 3-D scanning techniques can be used to create high-quality lithic illustrations [7–9], both as three-dimensional objects and two-dimensional figures. Nevertheless, 3-D scanning is a costly and time-consuming method. The high cost of 3-D scanning equipment and post-processing machinery, together with the time required for the scanning process and subsequent post-processing, make this method rarely used.

In regards to lithic artefacts, the problems that might arise from inadequate photography, photogrammetry, or 3-D -scanning, can be easily resolved with a traditional lithic illustration. Such lithic illustrations offer the opportunity to select and emphasize areas or features of a lithic artefact, and there are little to no risks in obscuring what is important for developing interpretations and hypotheses. Unfortunately, traditional hand-drawn illustrations, which are still to this date the most common method for lithic illustration, can often be time consuming or expensive should an artist be hired. To resolve the issues of time and costs related to the hand illustration of lithics, the Stone Tools Illustrations with Vector Art 'STIVA' Method was developed. Although new, its application has already been tested and proved to be publishable in peer-reviewed manuscripts [10].

Taking inspiration from the traditional step-by-step processes used by archaeological illustrators [11, 12], the 'STIVA' Method transposes the depiction of lithics from pen and paper to any digital device. By using reference photographs for digital tracing, the 'STIVA' Method combines the ease of use and speed of digital photography with the representational power of hand illustrations.

The 'STIVA' protocol offers a clear step-by-step process that anyone can learn and put into practice. Nevertheless, to produce high-quality, publishable illustrations, it is important that the illustrator has a good understanding of lithic analysis. To produce objective figures, it is necessary to know what is being drawn, and to ensure that non-existent features or components are not fabricated. For this reason, it is highly advised to have a good understanding of stone tool morphology and production.

The 'STIVA' Method was developed using Adobe Illustrator ©, as it has native functions and tools that make the digital illustration of lithic artefacts easier and faster compared to other non subscription-based vectorial softwares. The 'STIVA' Method provides detailed explanations on how to navigate Adobe Illustrator ©, and offers a framework for archaeologists and others to illustrate any archaeological material.

Materials and methods

The protocol described in this peer-reviewed article is published on protocols.io, dx.doi.org/10.17504/protocols.io.bubqnsmw and is included for printing S1 File with this article.

Expected results

While a variety of methods for lithic illustration already exist, with the application of the 'STIVA' method it is expected that users will produce publishable and user-friendly illustrations without the dependency on hand-drawing experience and skill. With minimal practice and the access to graphic illustration softwares and hardware, anyone interested in lithics, whether for personal, educational, or professional reasons, can produce their own high-quality lithic illustrations.

Archaeological studies are at times incongruous when artefact comparisons from different sites and time periods are attempted. With the 'STIVA' protocol, one single method can be widely used when illustrating lithic artefacts from any context or chronology. This method can therefore aid with the standardisation of stone tools illustrations, offering the potential of new and invaluable comparative capabilities.

Supporting information

S1 File. Stone tools illustrations with vector art: The 'STIVA' method V.2 protocol. Also available on protocols.io.
(PDF)

Acknowledgments

I would like to thank the reviewer(s) for the invaluable comments. I also thank Emily Y. Hallett for the help with the editing of the manuscript and support on the protocol during development, and Eleanor M.L. Scerri and Huw S. Groucutt for offering me the opportunity to illustrate the lithic assemblages they studied.

Author Contributions

Conceptualization: Jacopo Niccolò Cerasoni.

Investigation: Jacopo Niccolò Cerasoni.

Writing – original draft: Jacopo Niccolò Cerasoni.

Writing – review & editing: Jacopo Niccolò Cerasoni.

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Title

Human interactions with tropical environments over the last 14,000 years at Iho Eleru, Nigeria

Authors:

Jacopo Niccolò Cerasoni[1,2]*, Emily Yuko Hallett[1]*, Emuobosa Akpo Orijemie[3]*, Kseniia Ashastina[4], Mary Lucas[4], Lucy Farr[5], Alexa Höhn[6], Christopher A. Kiahtipes[7], James Blinkhorn[1], Patrick Roberts[4,8], Andrea Manica[9], Eleanor M.L. Scerri[1,10,11]*

1 - Pan-African Evolution Research Group, Max Planck Institute for the Science of Human History, Jena, Germany

2 - Institute of Archaeological Sciences, Eberhard Karls University Tübingen, Tübingen, Germany

3 - Department of Archaeology and Anthropology, University of Ibadan, Ibadan, Oyo State, Nigeria

4 - Department of Archaeology, Max Planck Institute for the Science of Human History, Jena, Germany

5 - Department of Archaeology, University of Cambridge, Cambridge, United Kingdom

6 - Institute of Archaeological Sciences, Goethe-Universität, Frankfurt am Main, Germany

7 - Institute for the Advanced Study of Culture and the Environment, University of South Florida, Tampa, FL, USA

8 - School of Social Science, The University of Queensland, Brisbane, Australia

9 - Department of Zoology, University of Cambridge, Cambridge, United Kingdom

10 - Department of Classics and Archaeology, University of Malta, Msida, Malta

11 - Institute of Prehistoric Archaeology, University of Cologne, Cologne, Germany

*Corresponding authors

cerasoni@shh.mpg.de

hallett@shh.mpg.de

ae.orijemie@mail.ui.edu.ng

scerri@shh.mpg.de

Summary

The Ihò Eléérú (or Iho Eleru) rock shelter, located in Southwest Nigeria, is widely known for the discovery of the only West African Pleistocene hominin fossil. Excavations at Iho Eleru revealed regular human occupations ranging from the Later Stone Age (LSA) to the present day. Here, we present new chronometric, archaeobotanical and paleoenvironmental findings, which include the taxonomic, taphonomic and isotopic analyses of what is currently the only Pleistocene faunal assemblage documented in West Africa. Our results indicate that the local landscape surrounding Iho Eleru, although situated within a regional open-canopy biome, was heavily forested throughout the past human occupation of the site. At a regional scale, a shift from forest to savanna-dominated ecotonal environment occurred during a mid-Holocene warm event 6,000 years ago, with a subsequent modern reforestation of the landscape. Locally, no environmental shift was observable throughout the occupation of the site, placing Iho Eleru in a persistent forested 'island'.

Introduction

The Ihò Eléérú (or Iho Eleru, Supplementary Data 1) rock shelter (7.441378, 5.124756), is a unique site located within an inselberg area near the northern provincial boundary of Ondo State, Nigeria, approximately 25 kilometres North-West of the regional capital of Akure. First documented in the early 1960s by officers of the Nigerian Department of Antiquities, Iho Eleru was excavated by T. Shaw and S.G.H. Daniels between 1963 and 1964 (Shaw and Daniels, 1984). The excavations revealed a c.1.8m deep stratigraphic sequence containing very high densities of cultural material, spanning from the terminal Pleistocene 13.2 thousand years ago (ka) up to today. Approximately half a million stone tools were recovered, together with a variety of faunal remains, and the only Pleistocene hominin fossil ever discovered in West Africa (Shaw and Daniels, 1984). The latter has been extensively studied morphologically (Allsworth-Jones et al., 2010; Brothwell and Shaw, 1971; Harvati et al., 2011; Shaw, 1965a, 1965b; Stojanowski, 2014; Stringer, 1974), and has been interpreted as a *Homo sapiens* individual with archaic features. Only one publication (Allsworth-Jones et al., 2010) has documented the fossil's stratigraphic and chronological context since the original excavation report (Shaw and Daniels, 1984). Furthermore, the stratigraphic provenance of the remaining material, although well recorded by the original authors, has not been utilised to place the findings within their regional palaeoenvironmental and archaeological context.

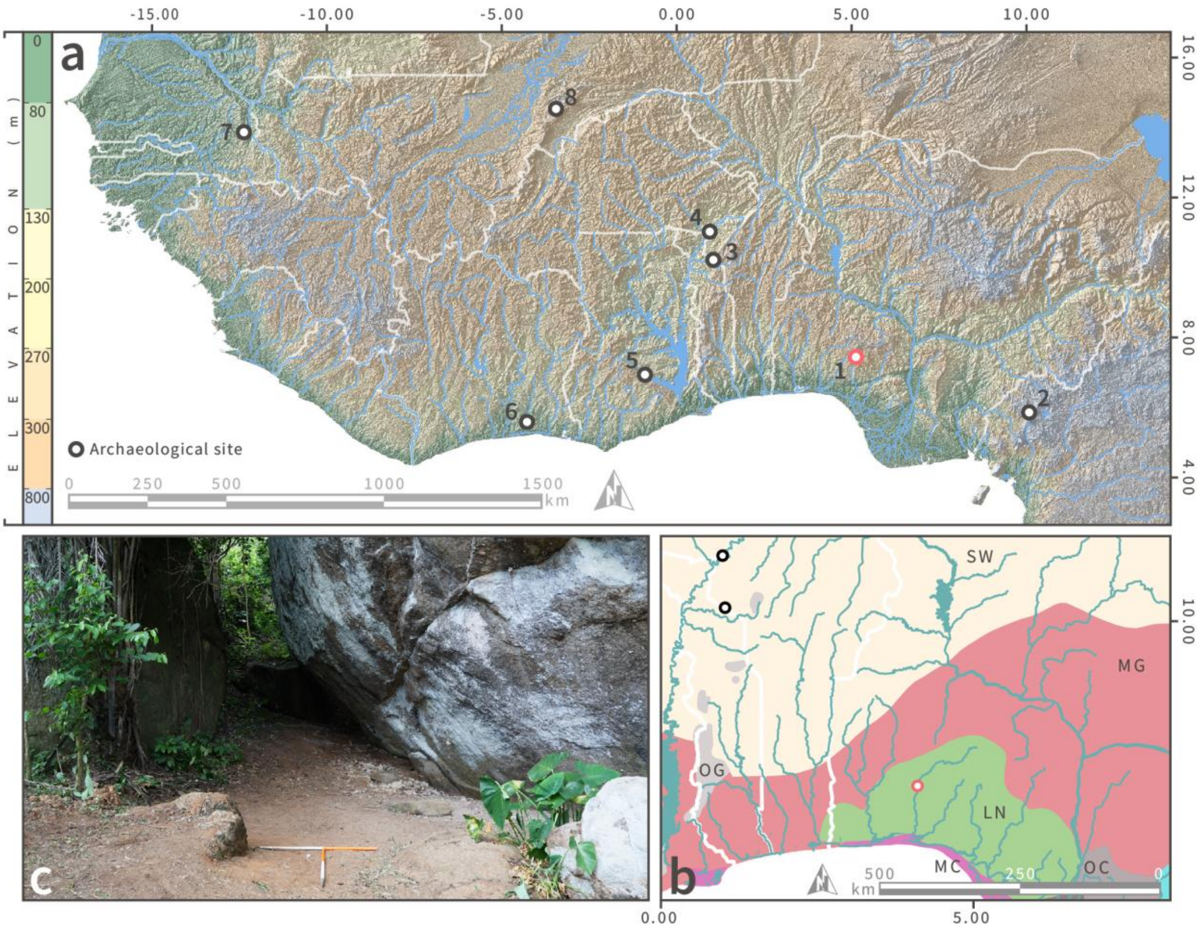

Figure 1. Geographical and Ecological context of Iho Eleru. a*, Map of West Africa showing river and lake systems (in blue), political boundaries (in white), geolocated position of Iho Eleru and other LSA and early ceramic sites (1- Iho Eleru, 2- Shum Laka, 3- Koukou-I, 4- Pendjari-II, 5- Bosumpra Cave, 6- Bingerville Highway, 7- Toumboura II and Fatandi V, 8- Ounjougou; Supplementary Table 1, Cerasoni et al., 2022),* ***b****, Map of Iho Eleru and neighbouring regions showing river and lake systems (in blue), political boundaries (in white), and modern ecoregions boundaries[9] (SW- West Sudanian savanna, MG- Guinean forest-savanna mosaic, OG- Eastern Guinean forest, LN- Nigerian Lowland Forest, OC- Cross-Niger transition forests, MC- Central African mangroves).* ***c****, North-facing view of the plateau area of Iho Eleru rock shelter.*

Various localities in West Africa and neighbouring regions report similar archaeological records, from the Western-most areas of the Falémé Valley in Senegal to the high-altitude plateaus of Northern Cameroon (Cerasoni et al., 2022; Figure 1). Most of these Later Stone Age (LSA) sites appear in open air contexts, such as Toumboura II, Fatandi V, Bingerville Highway, Koukou-I, Pendjari-II and Ounjougou (Supplementary Table 1). The only rock shelter sites which display LSA assemblages and have stratigraphies that cover the terminal Pleistocene-Holocene transitions are Iho Eleru, Bosumpra Cave and Shum Laka. All of the sites, in both open air and rock shelter settings, are characterised by a variety of LSA 'small tool' lithic types, such as microliths and foliates. Environmentally, from all the evaluated sites only Bingerville Highway, Shum Laka and Iho Eleru are not located in a pure savanna ecosystem, with Bingerville Highway being the only site found within modern rainforests. Tropical rainforests were widely inhabited during the Later Stone Age throughout Africa (Mercader, 2002; Roberts and Petraglia, 2015; Taylor, 2016) and sporadically during the Middle Stone Age in Anyama, Ivory Coast (Chenorkian, 1983). Uniquely, Iho Eleru is the only known site which is located near a border between savanna and forest ecoregions. Considering these differences, it is clear that Iho Eleru is a highly significant site both in terms of archaeological characterisation and environmental context. Furthermore, Iho Eleru is the only site in the West African region with a regularly intermittent human occupation from the terminal Pleistocene to recent times, and which is found within a modern biome with wide access to ecotonal resources.

A joint Max Planck Society - University of Ibadan expedition visited the site in 2019 and conducted a re-evaluation of the original collection of excavated materials, including re-analysis of materials at the Department of Anthropology and Archaeology, University of Ibadan, Nigeria. Access and exporting of the original archaeobotanical and faunal collections were granted by the University of Ibadan, and exported to the Max Planck Institute for the Science of Human History, Germany (Supplementary Data 4) for further analysis. In this study we applied a multidisciplinary approach to better understand behavioural and environmental changes at Iho Eleru at a local and regional scale and the broader relevance of the site to discussions of Pleistocene and Holocene tropical forest habitat occupation and utilisation of our species (see Mercader, 2002 and Roberts and Petraglia, 2015). The archaeobotanical collection was sub-sampled for chronometric and archaeobotanical analysis. The faunal collection, previously reported lost (Shaw and Daniels, 1984, p. 30), was analysed by means of taphonomic, taxonomic and isotopic techniques. Furthermore, paleoenvironmental reconstructions and paleoclimatic models were employed to gain a better understanding of regional environmental trends during the period of occupation. Similar multidisciplinary approaches to tropical caves and rock shelters have been applied successfully (Burney and Burney, 2007; Nelson, 2014; Roberts et al., 2021, 2017), improving our understanding of human-tropical environment interactions in the Pleistocene-Holocene timeframe.

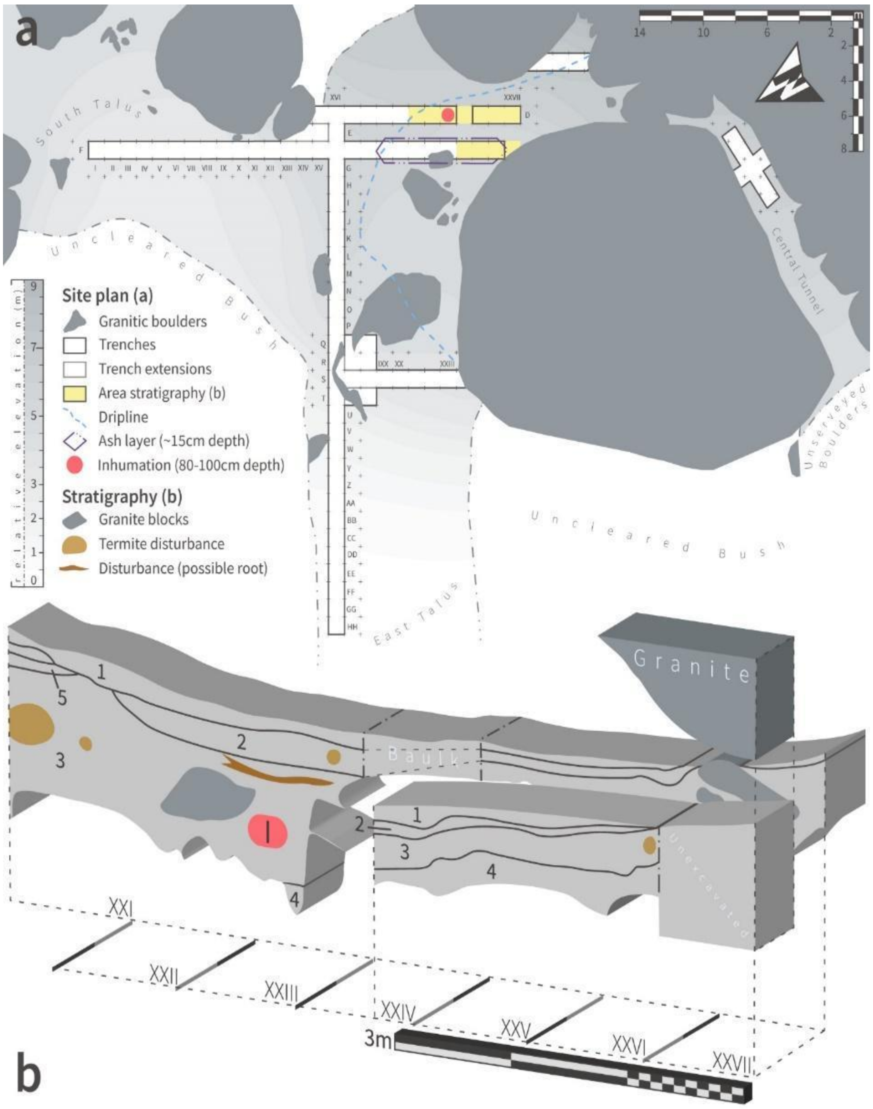

Figure 2*. *Site plan (a) of Iho Eleru and stratigraphic sections (b) of the upper plateau area (marked in yellow on the site plan), along the east faces of trench D XXI-XXVII, and trench F XXIV-XXVII. *The plan and stratigraphical location of the inhumation has been shown with a red circle (a) and with the letter "I" (b). The stratigraphical layers are described as follows: 1 - superficial ash layer, 2 - red sandy layer, 3 - reddish brown soil, 4 - gravelly soil, 5 - browner and looser than 3, but redder and less sandy than 2. (corrected and redrawn after Shaw and Daniels[1] pp. 189 and 193).*

Results

Chronometric Analysis

The summarised ^{14}C dating results for charred plant macroremains and faunal remains sampled from the plateau area of the rock shelter are shown in Figure 3 and Supplementary Table 2, and the full data and calibration curves can be found in Supplementary Data 3.

We applied modern radiocarbon dating methodologies to the recovered archival charred plant material to verify the original results of the Shaw and Daniels radiocarbon dating programme (Shaw and Daniels, 1984). The resulting dates (Supplementary Figure 1, Supplementary Table 2) span a wide timeframe, from c.13,200 cal. BP to recent. The dating results we obtained were remarkably close to the original dates offered by Shaw and Daniels and, similarly, they complement previously reported U/Th age estimates obtained directly from the Iho Eleru hominin skeletal material (Harvati et al., 2011). These results offer a reliable radiocarbon chronology for the sedimentary context of the remains. Due to partial stratigraphic inversion, several of the dates for this study are in disagreement with the original dates (Supplementary Table 2). Some of the sedimentary contexts at the site, specifically located within the taluses and external plateau areas of the rock shelter (Figure 2), are interpreted as sediments with post-erosional origins. To accommodate such inversion and erosional activities, we only considered the stratigraphy and dates from Trenches D and F, squares XX-XXVII, as reliably *in situ* (Supplementary Data 1).

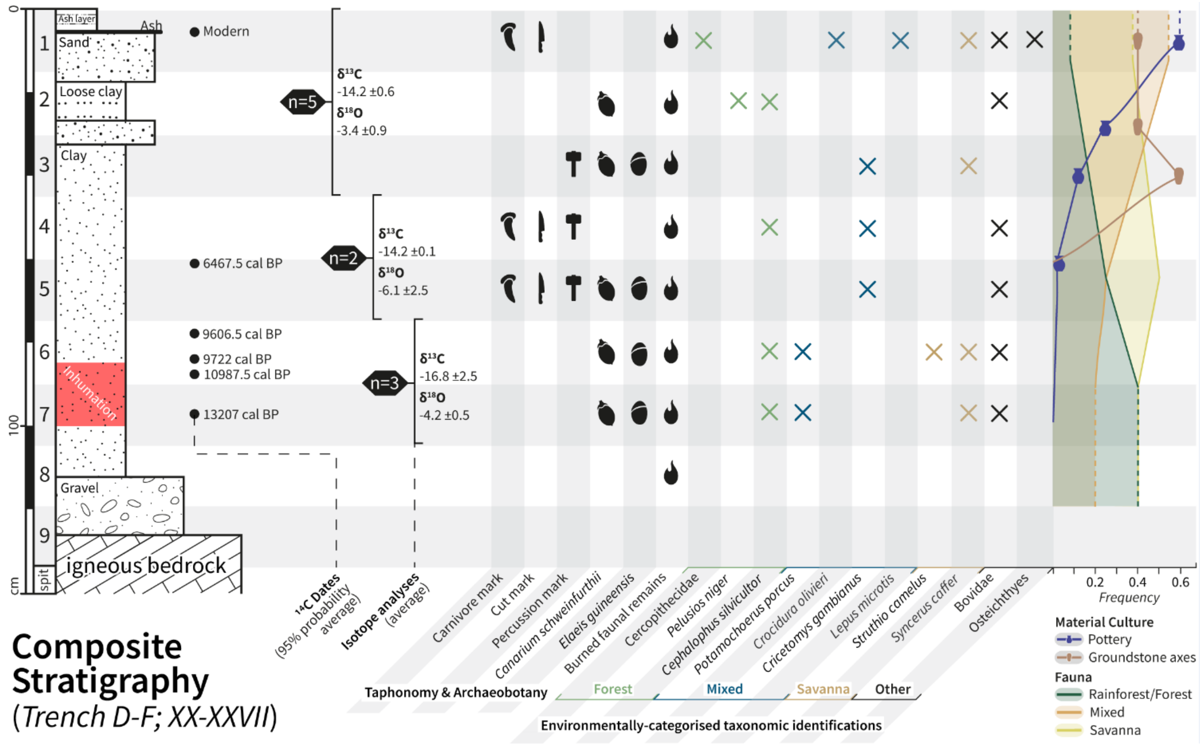

Figure 3. Composite stratigraphy of Trenches D and F, spits XX-XXVII. *Within it are presented the new ^{14}C dates, the isotopic results averaged into three discrete groups, archaeobotanical identification of C. schweinfurthii and E. guineensis, taphonomic identification of the faunal assemblage, environmentally-categorised taxonomic identifications, and frequency of major environmentally-categorised taxonomic groups and material culture (pottery and ground stone axes).*

Archaeobotany

Out of 21 analysed archaeobotanical samples (Supplementary Table 3), 12 contained identifiable wood charcoal fragments, six contained endocarp fragments of (cf.) *Canarium schweinfurthii*, eight contained (cf.) *Elaeis guineensis* and 12 contained other unidentifiable fragmented carbonized plant remains. Direct dating on the endocarps demonstrates early exploitation of canarium and probable oil palm from before 10 ka, with the earliest exploitation of *Canarium schweinfurthii* in West Africa, directly dated to ~11.3 cal. BP (sample IW2792, Supplementary Table 2). Fourteen different charcoal types were distinguished among the 82 analysable wood fragments. Due to preservation and fragment size, identification reached (probable) genus level in seven cases. Definite association of a charcoal type to forest trees is so far only possible for the sample dated to c. 400 years ago (STROMBOSIA spp./

STROMBOSIOPSIS spp.) and ZANTHOXYLUM spp. from spit 3. The cf. identification of charred GUAREA spp. and PIPTADEIASTRUM AFRICANUM (spit 5 and 6) also support the exploitation of forest vegetation. Other samples include possible forest and/or woodland taxa. No charcoal type clearly representing a savanna taxon was identified.

Several archaeobotanical samples contained trace amounts of sediment, with a varying amount between 1 to 10 grams each. These samples were processed for phytolith extraction and analysis (Supplementary Data 3). Unfortunately, no phytolith or other archaeobotanical microremains were identified based on the protocol used. The lack of microremains might reflect the taphonomic pathway of the sediment samples available to us, post-depositional degradation of these materials at the site, or degradation occurring post excavation while the samples were in storage over the last half a century. Further investigation of *in situ* deposits will be required to confirm whether or not phytoliths can be successfully retrieved from the sediments at Iho Eleru.

Fauna

The formation processes of the Iho Eleru vertebrate faunal assemblage were analysed through taphonomic investigation of all bone and tooth fragments. Our goal was to determine the extent of human-accumulated bone relative to carnivore-accumulated bone, and to reconstruct the foraging and butchery behaviour of humans over time. Of a total 207 retrieved bone fragments, only 152 had intact bone surfaces that could be analysed for bone surface modification, burning, and breakage patterns (Supplementary Table 5). The Iho Eleru faunal assemblage is highly fragmented, with the average analysed fragment length measuring 2.67 cm, width at 1.36 cm, and thickness at 0.88 cm. Burned bone fragments constitute 28.9% (N=44) of the assemblage, and the majority of these are carbonized, while few are calcined. Despite the small sample size of the assemblage, butchery marks in the form of percussion marks, percussion notches, and cut marks were present on 12.5% (N=19) of the bone fragments. The rate of carnivore accumulation was similar, with 11.8% (N=18) of the bone fragments bearing tooth marks or tooth notches, and 3.29% (N=5) displaying gastric etching from carnivore digestion. These rates of surface modification preservation are low in comparison to archaeological, experimental and actual assemblages (Marean and Kim, 1998, table 3) and are likely the result of significant post-depositional fragmentation (Marean, 1991) and poor preservation (i.e. acidity and soil moisture content) in a tropical context. No worked bone was identified.

Taxonomic identification of the Iho Eleru vertebrate faunal assemblage documented ten taxa to the species level. The identified species prefer habitats ranging from forests to savannas, and reveal the ecotonal nature of the exploited area surrounding the rock shelter. A complete list of identified taxa is shown in Supplementary Table 6. The Iho Eleru vertebrate faunal assemblage includes taxa ranging in body size from the large *Syncerus caffer* (African buffalo) to the small *Pelusios niger* (West African black turtle). Identified vertebrates that today prefer forest habitats include *Cephalophus silvicultor* (yellow-backed duiker) (Kingdon, 2015), *Potamochoerus porcus* (bushpig) (Groves and Harris, 2013; Kingdon, 2015), *Hystrix cristata* (crested porcupine) (Kingdon, 2015), *Cricetomys* sp. (giant pouched rat) (Kingdon, 2015), and *Varanus niloticus* (Nile monitor) (Angelici and Luiselli, 1999). The relative frequency of forest vertebrates recovered from the Iho Eleru assemblage decreased over time (Figure 3), while the relative frequency of savanna vertebrates increased over time (Figure 3). Identified vertebrates preferring savanna habitats include *Syncerus caffer* (African buffalo) (van Hoft and Prins, 2013), *Lepus microtis* (African savanna hare) (Kingdon, 2015), and *Struthio camelus* (ostrich) (Cooper et al., 2009). A single burned *S. camelus* (ostrich) eggshell fragment was identified in D27 spit 6, suggesting that either savanna was in close proximity to the site, as ostrich strictly occupy open grassland habitats, or that ostrich eggshell was transported to the site or exchanged either as a water canteen (Texier et al., 2010) or as an ornamental object (Stewart et al., 2020). No carnivore remains or coprolites were identified, although carnivores did apparently act as agents of bone accumulation. A total of six Osteichthyes (bony fish) bone fragments and two marine shells were identified in modern deposits only, and no terrestrial gastropods were identified.

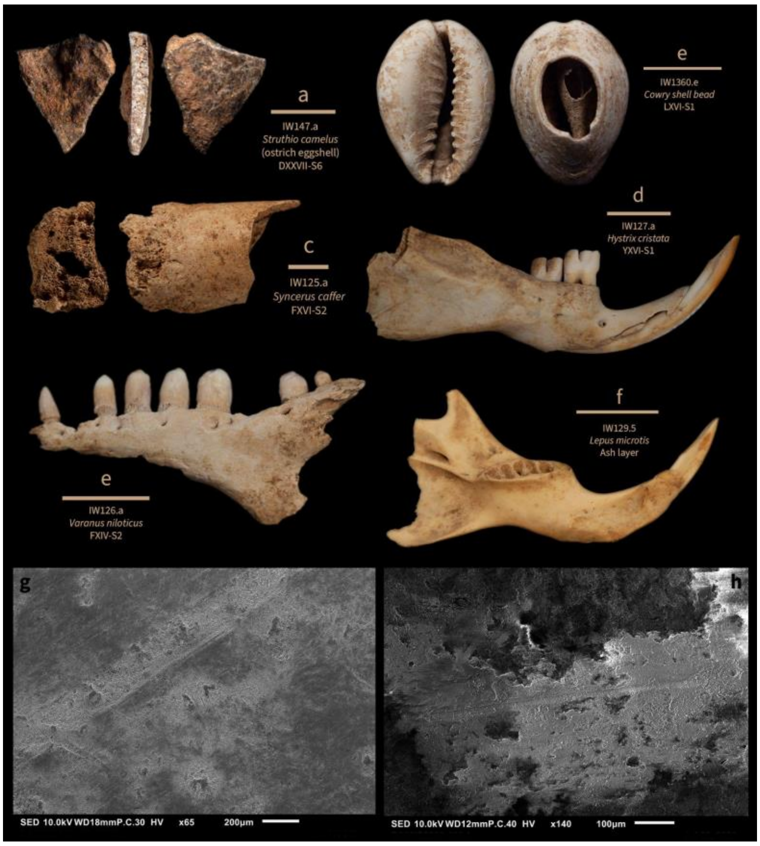

Figure 4*. *Selection of photographs of faunal remains and SEM of cut/percussion marks. *A selection of faunal remains (a-f) from taxa identifiable as either forest or savanna dwelling. One tooth sampled for isotope analysis is shown (f). Scales are 1 centimetre. SEM images of cut marks are presented on specimens from layers DXXVI-S1 (g) and FXXI-S5 (h).*

The δ^{13}C and δ^{18}O stable isotope results for all 13 analysed vertebrate teeth enamel samples from the site of Iho Eleru are shown in Fig. 5 and Supplementary Table 4, with photographed examples in Supplementary Figure 3. Although the sample size is limited, primarily by the number of teeth present in the assemblage, the δ^{13}C values cover a wide range (−18.6‰ to 2.5‰), suggesting that these animals exploited a variety of habitats, from closed canopy C_3 forests to open C_4 dominated grasslands. When we compare our isotopic data to documented modern habitat preferences for the sampled vertebrate species, the δ^{13}C values are consistent with ecological expectations, with *S. caffer* plotting as an outlier and signalling a preference for savanna (Figure 5). The δ^{18}O values covered a similarly wide range (−11.0‰ to 1.8‰), suggesting a variety of groundwater and food water sources for the animals present, consistent with access to a variety of environments ranging from shaded forests to more open, arid settings. Stratigraphically, both δ^{13}C and δ^{18}O values remain largely consistent throughout the stratigraphy, with elements of dense forest and ecotonal forest-savanna habitats (e.g. *P. porcus*, *H. cristata*, and *L. microtis*), and some sporadic elements of grassland habitat (e.g. *S. caffer*) exploited by animals procured by humans living at the site. Overall, the stable isotope results from vertebrate teeth sampled from Iho Eleru reveal greater proportions of forest habitats being utilised by humans at the site. Although the small sample size and taphonomic bias may contribute to this trend, this may be indicative of the human habitation of a forest island within a more mixed habitat landscape.

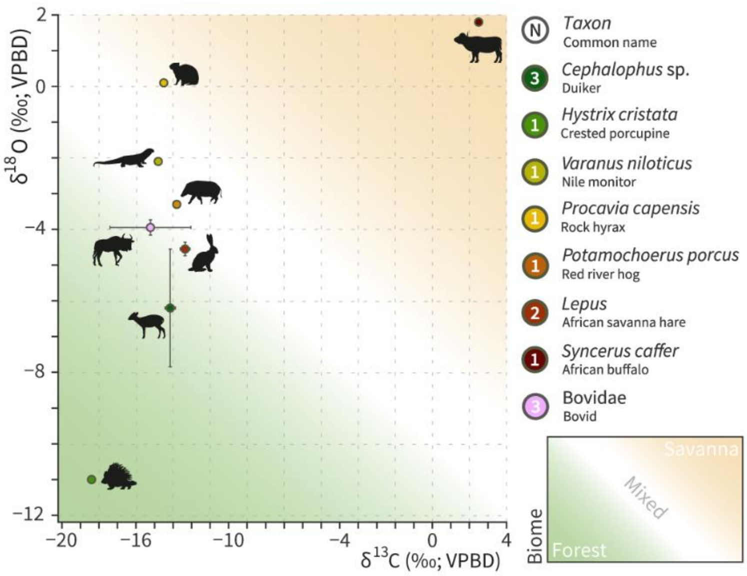

Figure 5. Stable carbon and oxygen isotope data for all faunal samples analysed (n=13). *Results table visible in Supplementary Table 4. Mixed feeders both graze in grassland and browse in shrubland and forests (Hofmann and Stewart, 1972).*

Discussion

Throughout the terminal Pleistocene and Holocene, West Africa was a complex region that was home to a variety of cultural-environmental processes, with synchronous presence of Middle Stone Age (Scerri et al., 2021), Later Stone Age, and ceramic cultures in different parts of the region. Our results show that Iho Eleru, characterised by Later Stone Age and some of the earliest West African ceramic culture, underwent regular occupation during the documented timeline, with focused use of resources from both forest and grassland environments. The archaeobotanical and isotopic data support a closed canopy environment in the close proximity of the site, as evidenced by the lack of retrieved savanna taxa charcoal remains (Supplementary Table 3) and the average isotopic results (figure 3). Further supporting this, studies (Parmentier, 2003; Richards, 1957) carried out on equatorial latitudes of West Africa show a correlation between inselberg areas, such as that where Iho Eleru is located, and forested environmental footprints within them compared to their surrounding environment. Indeed, it is clear that humans valued forest resources from their first arrival at the site. Nevertheless, our data also show a divergence in ecological and behavioural trends in regional and local scales.

The regional area around Iho Eleru seems to have persisted as a mixed tropical forest-savanna ecotonal landscape from the Late Pleistocene to the Late Holocene, where vegetation compositions varied in their proportion of forest and savanna, with the latter expanding at the onset of the warm mid Holocene (ca. 6 ka) as a result of changes in regional precipitation (Supplementary Data 2). The increase in identified non-arboreal pollen (NAP) producing species in a multitude of regional cores (Lezine et al., 2005; Salzmann et al., 2002; Salzmann and Hoelzmann, 2005; Sowunmi, 1981) around 5-6 ka suggests a similar increase in savanna-dominated environments across the region (Supplementary Data 2). The regional and local proxies compared in this study indicate three major environmental phases that occurred during the timeline of recorded human activity at Iho Eleru. The first, the terminal Pleistocene before 12 ka, was characterised by a wetter environment than today, with increased levels of precipitation and humidity. This aligns well with the African Humid Period (Shanahan et al., 2015) dated to 14.8-5.5 ka. The second, which occurred in the Middle Holocene, was characterised by an increase in temperature and a decrease in precipitation, as supported by a local increase in savanna-dwelling taxa and our modelled environmental and climatic proxies. This event occurred approximately 6 ka and can be interpreted as having caused an expansion of open-canopy environments.

Finally, the third event, which encompasses the present, is a yet unexplained phenomenon characterised by the contrasting results our proxies show in this study. The high concentration of savanna-dwelling faunal species in modern layers and paleoclimate models suggest that the environmental footprint of the modern landscape should be a mixed environment with open- and closed- canopy environments. Nevertheless, modern day observations of the local landscape around Iho Eleru show a densely forested environment (Chia and D’Andrea, 2017; Olson et al., 2001). This incongruence could be explained by one of two hypotheses: (1) Just as observed in the paleoenvironmental record, the modern landscape is composed by a dominant open-canopy landscape with micro-scale forested islands, within which Iho Eleru is situated, or (2) the modern local landscape is not a pure product of natural selection based on climatic conditions, but is undergoing landscape modification through agroforestry practices by local populations (e.g. planting useful tree species such as *Theobroma cacao* or cocoa tree, *Musa* spp. or plantain, and *Elaeis guineensis* or palm oil).

In terms of human behavioural trends, the observed 6 ka warm mid-Holocene period may have influenced human behaviour at the site. At ca. 6 ka a change in material culture is visible with the appearance of relief motif pottery and ground stone axes (Shaw and Daniels, 1984) (figure 3). This trend, also in concordance with the faunal and regional environmental information, suggests the arrival at Iho Eleru of new populations or material traditions, possibly aided by the increased presence of savannas and the relative contraction of forests. Our data also suggests that this subtle environmental shift was most likely not caused by anthropogenic processes (examples of anthropogenic processes in tropical environments (Maezumi et al., 2018a; Maezumi et al., 2018b; Roberts et al., 2021), such as forest clearing from the use of controlled fires or ground stone axes, but rather by a change in precipitation rates and temperature as shown by the paleoenvironmental reconstruction and paleoclimatic models. Furthermore, the appearance of comparable material cultures is also visible in other sites within close proximities. Similar to Iho Eleru, a shift in material culture has been identified at Shum Laka, Cameroon, between 6 and 7 ka (Lavachery, 2001), where a “less humid” period was identified (Moeyersons, 1997), and in which pottery and *Canarium schweinfurthii* first appeared. Other Holocene and LSA sites in West Africa with early ceramic traditions suggest an influx from the Western part of the region, with the earliest appearance of pottery around 11.9 ka in Ounjougou, Mali (Huysecom, 2020; Huysecom et al., 2009), and a slightly later appearance at Bosumpra, Ghana (Watson, 2017) (figure 1).

Despite these regional and behavioural changes, it is clear that both tropical forest and savanna environments remained important for humans at Iho Eleru, particularly for the available water sources and starchy plants (Headland, 1987; Yasuoka, 2013) in forests and protein- and fat-rich fauna resources in savannas (Hart and Hart, 1986; Marean, 1997). The uniqueness of this site, both in terms of the exceptional retrieval of bioarchaeological and material cultural finds and because of its location in tropical West Africa, offers a new look on past human activity and behaviour in tropical African environments. Nevertheless, further studies will be necessary to fully explain the dynamics of this environmental processes which affected, and were affected by past and modern people at Iho Eleru.

Methods

Radiocarbon dating. Sampling and dating were carried out by the Curt-Engelhorn-Center Archaeometry gGmbH. For the bone samples collagen was extracted (modified Longin method), purified by ultrafiltration (fraction >30kD) and freeze-dried. For the plant macroremains pre-treatment using ABA-Method (Acid/Base/Acid, HCl/NaOH/HCl) was used. The insoluble fraction was used for further treatment. Following pre-treatment, the sample material was combusted to CO2 in an Elemental Analyzer (EA). CO2 was then converted catalytically to graphite. ^{14}C were analysed using a MICADAS-type AMS system in-house. The isotopic ratios ^{14}C/^{12}C and ^{13}C/^{12}C of samples, calibration standard (Oxalic Acid-II), blanks and control standards were measured simultaneously in the AMS. ^{14}C-ages were normalised to ^{13}C=-25‰ and calibrated using the dataset IntCal20 and software SwissCal (L. Wacker, ETH-Zürich). Calibration graphs are generated using the software OxCal (small deviations between SwissCal and OxCal results are possible) (Supplementary Data 3).

Scanning Electron Microscopy. SEM creates a high-resolution image of a surface by scanning it with a focused beam of electrons. In order to closely evaluate characteristics of the cut marks and other surface features, morphological analysis of the specimens was carried out in a scanning electron microscope (SEM) Jeol JSM-IT100 at the Microscopy and Palaeobotany Laboratory of the Department of Archaeology at the Max Planck Institute for the Science of Human History, Jena. Samples were fixed on a 32 mm plain specimen holder with a conductive one-sided copper adhesive tape. For artefacts larger than 30 mm we used a specimen holder with a plain station; artefacts smaller than 30 mm were mounted on either aluminium cylinders or aluminium pin stubs. All samples were imaged uncoated. The SEM was operated in a high vacuum mode at an accelerating voltage of 10 kV. Specimens were visualised using an in-lens secondary electron detector (SED) at magnifications from 22x to 250x. Depending on the size of the artefact, we attuned working distance (WD) from 11 to 18 and probe current (P.C.) from 30 to 44. Brightness, contrast, stigma, and focus were adjusted manually for each sample in the InTouchScope program.

Stable Isotope Analysis. Enamel sampling for $\delta^{13}C$ and $\delta^{18}O$ analysis was conducted at the Max Planck Institute for the Science of Human History (MPI-SHH). Tooth samples were first cleaned by air abrasion to remove surface contaminants. Roughly 8mg of enamel powder was then drilled from the buccal surface of the tooth to gain a sample representing the full growth period of the tooth. The drilled enamel powder was then pre-treated with a 1% NaOH solution for 1 hour. Samples were then rinsed, vortexed, and centrifuged three times with MilliQ water. 0.1M acetic acid was then added to the samples for 10 minutes followed by the rinsing process with MilliQ water. After pre-treatment, samples were lyophilized overnight before being freeze dried for 4 hours. Samples were analysed on a Thermo Gas Bench 2 connected to a Thermo Delta V Advantage Mass Spectrometer. Roughly 3mg of each sample was weighed into borosilicate glass vials. The vials were then flushed with helium at 100ml/min for 10-minutes. 20ul of 100% phosphoric acid was then added to each sample and left to react for 1 hour. Samples were calibrated using a three-point calibration with international standards IAEA NBS 18: $\delta^{13}C$ -5.04‰, $\delta^{18}O$ -23.2‰, IAEA 603: $\delta^{13}C$ +2.46‰, $\delta^{18}O$ -2.37‰, and IAEA CO8: $\delta^{13}C$ -5.764‰, $\delta^{18}O$ -22.7‰. Replicate precision of standards was used to measure machine error where $\delta^{13}C \pm 0.2$‰ and $\delta^{18}O \pm 0.2$‰. Overall measurement precision was studied through the measurement of repeat extracts from a bovid tooth enamel standard (n = 20, ± 0.2‰ for $\delta^{13}C$ and ± 0.4‰ for $\delta^{18}O$). Generally, tropical environments are expected to produce relatively low $\delta^{18}O$ values due to the high intensity of rainfall (Gonfiantini et al., 2001), although values are heavily dependent on rainfall source.

Taphonomic and Taxonomic Identification of Vertebrate Faunal Assemblage. Shaw and Daniels (1984) (p. 2) report using ¼ inch sieves for excavated material, and sorting all vertebrate bone fragments according to context. To the best of our knowledge, all sieved material was preserved and no unidentifiable bone fragments were removed from the curated materials. The bone fragments were not cleaned in the present study, as no loose sediment adhered to bone surfaces. The initial phase of taphonomic recording was completed using an Olympus 10-40X zoom binocular microscope with high incident light. For final verification of cut marked and percussion marked bones, SEM (Scanning Electron Microscope) imaging was completed using a JEOL InTouch Scope JSM-IT100LA compact SEM. Each bone fragment was analysed for surface modification. This microscopic method of surface modification recording has shown 95% accuracy in blind tests (Blumenschine et al., 1996), and allows zooarchaeologists to distinguish between cut marks, percussion marks, and tooth marks. Trampling and biochemical marks (Dominguez-Rodrigo et al., 2009; Domínguez-Rodrigo and Barba, 2006), such as chemical, insect, and root etching (Andrews and Cook, 1985; Bunn, 1983; Dirks et al., 2015; Haynes, 1988), were also recorded. Burning severity was recorded using bone surface colours that indicate burning in either a reducing or oxidizing atmosphere as: no burning, light (dark brown to black color), medium (black to dark grey color), heavy (grey color with shallow cracks), or calcined (white color with deep cracks). Burning extent was recorded as the proportion of a bone fragment displaying signs of burning. For each bone and tooth fragment that was not covered in an adhering carbonate matrix, the following variables were also recorded (see Supplementary Table 5): measurements (length, width, thickness, or height for tooth crown height), skeletal element, element portion, side (left of right), taxonomic identification to the lowest level, circumference of fragment (Bunn, 1983), surface visibility, exfoliation of bone surface, dendritic etching (Andrews and Cook, 1985; Haynes, 1988), pocking, sheen, smoothing, cut marks, percussion marks, percussion notches, tooth marks, tooth notches, rodent gnawing (Andrews and Cook, 1985), weathering (Behrensmeyer, 1978), fracture outline and angle (Villa and Mahieu, 1991), presence of fresh break(s) from excavation or post-excavation (Villa and Mahieu, 1991), and colour.

Archaeobotanical Analysis. The archaeobotanical samples were taken during the original excavation from soil sieved with a mesh-size of 0,635 cm (0,25 inches) and mostly labelled as (wood) charcoal sample. The samples contain fragments of wood charcoal and/or other carbonised botanical macro-remains. Many wood charcoal fragments show breaks that have occurred during sieving and storing and are too small for anthracological analyses. Wherever possible wood charcoal was analysed using a reflected light microscope (Leica DM4000M) at different magnifications, 50x – 500x, in dark and bright field, after manually fracturing the charcoal fragments along the three planes: transverse, longitudinal tangential and longitudinal radial. The identification process follows the steps described in Höhn & Neumann (2018) and relies on the Inside Wood database (Wheeler, 2011), the wood reference collection of the Goethe University Frankfurt (JWGw), and wood anatomical atlases (Hubau, Wannes, 2013; Lebacq, 1955; Normand, 1960). The names of the charcoal types are given in small capitals to clearly discriminate the anatomical charcoal types from the botanical taxa with which they are not necessarily identical (Höhn and Neumann, 2018; Joosten and de Klerk, 2002). Most type descriptions are published and cf. *Piptadeniastrum africanum* resembles PARKIA spp. but has some septate fibres in addition (Höhn et al., 2021, 2018; Höhn and Neumann, 2018), ZANTHOXYLUM spp. is documented in Supplementary Figure 2. Carpological macro-remains were identified with a dissecting microscope (Leica S6D). Identification was achieved by comparison with specimens in the modern reference collection of the Laboratory of African Archaeobotany at Goethe University, Frankfurt am Main and with carbonized carpological material from Dibamba, Cameroon, identified by Stefanie Kahlheber (unpublished).

Material Culture Imaging and Figure Design. Photographs of the faunal remains were taken following the protocol for photography of artefacts and small object (SOAP protocol) (Cerasoni, 2021). Figures 1, 2, 3, 5 and 6 were designed and composed using Adobe © Illustrator © 2021. The maps on Figure 1 (a, b) were originally designed on QGis ©. For the maps a digital elevation map of the region was merged and developed (utilising WGS 84 projection) from 1 km-resolution digital elevation models (DEMs) (Jarvis et al., 2008), and then categorised based on elevation and correlated with topographic bioregions. Map b on Figure 1 was created by mapping the distribution of modern ecoregions (Olson et al. 2001) for the landscape surrounding Iho Eleru and geolocating the respective archaeological sites. Figure 4 was designed and created using Adobe © Photoshop © 2021.

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Acknowledgements

The project was funded by the Max Planck Society through the Pan-African Evolution Research Group. Collaboration between the Max Planck Society and the University of Ibadan was made possible by the support of Professor Abel Idowu Olayinka, the former Vice Chancellor of the University of Ibadan (2015-2020). We thank the Nigerian National Commission For Museums and Monuments for granting a permit (Number RL113109976NG) to excavate at Iho Eleru. We are grateful to Alayeluwa Oba (Dr) Francis Adefarakanmi Agbede, Olowa of Igbara-Oke Kingdom, for supporting our work at Iho Eleru and aiding in times of difficulty. We also thank the village of Isarun, without whom we could not have accessed the site. We are very grateful for the logistical, technical and collegial support offered to us by members of the Department of Archaeology and Anthropology University of Ibadan, and for granting our access to the archeological collections. Access to the collections was authorized by Professor D. A. Aremu (Head of Department), Professor C. A. Folorunso, Professor R. A. Alabi, and Dr O. A. Opadeji (Curator). Our fieldwork at Iho Eleru was greatly enhanced by the participation of the following students from the Department of Archaeology and Anthropology, University of Ibadan: Oluwadamilare Omigbai, Ezenwe Chinonso, and Nwosu Stanley Osinachi.

Author contributions

This study was designed by J.N.C., and conceived with E.A.O., C.A.K. and L.F. The fieldwork project was conceived and designed by E.M.L.S. and E.A.O. as part of the Pan-African Evolution Research Group's programme (MPI-SHH, Jena, DE). J.N.C., E.A.O., L.F. and C.A.K. carried out the fieldwork. E.A.O. procured local and export permits. E.Y.H. performed the taxonomic and taphonomic analysis on the faunal assemblage. P.R., M.L. and E.Y.H. carried out the isotopic analyses. K.A. performed the microscopic imaging of the faunal assemblage. A.H. performed the archaeobotanical analysis. J.N.C. performed the phytolith extraction and analysis. E.Y.H. and A.M. developed and performed the paleoclimatic reconstruction models. C.A.K. synthesised the palynological data. J.N.C. analysed and contextualised the data. E.Y.H. photographed the faunal remains, and J.N.C. produced the figures and illustrations. J.N.C. wrote the initial draft. All authors contributed to the writing of the paper.

Competing Interests statement

The authors declare no competing interest.

Supplementary Information

Human interactions with tropical environments over the last 14,000 years at Iho Eleru, Nigeria

Cerasoni et al.

Components present in this document:

- Supplementary Data 1 & 2
- Supplementary Figures 1, 2, 3, and 4
- Supplementary Tables 1, 2, 4, and 7

Supplementary Data 1

Iho Eleru historiography. The site name (Ihò Eléérú) means "Cave of Ashes" in Yoruba language. Throughout this article the Yoruba version of the name has been anglicised into "Iho Eleru" for ease of spelling. The site was first published by the name "Iwo Eleru", following an incorrect anglicised translation of the original Yoruba name.

The Iho Eleru rock shelter was first reported as part of a large-scale survey of the hilly landscapes around Akure, conducted by Chief officer J. Akeredolu of the Department of Antiquities from Benin, Nigeria, in 1961. Following this report, in 1963 Thurstan Shaw led an exploration of the rock shelters and caves previously reported by J. Akeredolu. During the exploration of the research area, the officer of the Department of Antiquities, G. Connah, informed T. Shaw of the existence of Iho Eleru. Following the initial exploration, T. Shaw and S. Daniels organised and conducted excavations at the rock shelter between 1964 and 1965. Following two decades of research, where the material culture was studied, a final report of the excavation findings was published in 1984. Since then, several studies have been published concerning the human remains retrieved from the original Shaw and Daniels excavation, with only one article discussing the archaeological context since the original report.

In 2019, a German-Nigerian-British team, as part of the Pan African Evolution Research Group Project (MPI-SHH, directed by Dr. Eleanor M.L. Scerri) conducted a survey of the rock shelter. Originally the team planned to excavate the site, re-opening the original Shaw and Daniels trenches, assessing the stratigraphical preservation, and recovering *in situ* material culture. Unfortunately, due to local political unrest, the excavation was prematurely terminated. Following this, the team redirected its time to the assessment of the original material collection from the Shaw and Daniels excavation, where the materials analysed in this study were re-discovered.

Iho Eleru ecology. Today, the Iho Eleru rock shelter is situated approximately 50km South of the modern boundary of the Guineo-Congolian rainforest phytogeographic region, with the local landscape being characterised by pioneer forest formations with a low to medium canopy cover (5-10m). Just North of this region is situated the Guinean Savanna zone, which is a large expanse of land extending West to East throughout West Africa and is characterised by forest islands and wooded savanna vegetation (White 1983). The modern landscape is extensively modified by human activity, with agroforestry production focused on the cultivation of yams, bananas, cocoa, and cola nuts.

Iho Eleru geology and site formation. The site is located within a lowland composed by eroded outcrops of ancient igneous deposits, with the presence of river terraces and well oxidised sandy deposits underlain by sedimentary formations of laterite. Within the region, various formations of complex metamorphic outcrops (crypto-crystalline silicates and siliceous stone formations) occur. Furthermore, Shaw and Daniels (1984: pg. 190, figure 3) show the presence of quartzite veins which appear approximately 5-10km West of Iho Eleru. Furthermore, various deposits of considerably eroded quartzite and vein quartz cobbles are present within local seasonal river valleys.

Iho Eleru is a rock shelter found towards the base of an igneous inselberg, found on the western margin of the Ikere Batholith. Topographically, the main human activity area would have been behind the drip line area of the shelter, within the main upper levelled platform area (trenches D & F, XVII-XXVII). On its southern and eastern edges, steep inclined taluses slope downwards. On its western edge, a very steep incline slopes upwards towards the upper levels of the inselberg, where other sheltered areas are found. On the northern edge of the platform area, the rock shelter closes following the two overhanging igneous outcrops, forming a small tunnel (Central Tunnel) with a SW-NE orientation. The stratigraphy at Iho Eleru shows very irregular igneous beds upon which the archaeological sediments sit. The depths of the stratigraphy vary from 0cm (subsurface outcrop) to over 2m in depth (Trench S). The sediments have post-erosional origin, where materials from the upper levels of the inselberg fall during particularly wet periods, depositing within the platform area and surrounding slopes. In turn, similar activities cause an erosion of the platform area sediments, causing the sloped areas to have inverted stratigraphies. For this reason, during our re-analysis of the chronometric dates of the site, only charcoal samples that were retrieved in the upper level area were selected. Nevertheless, the resulting ^{14}C dates still show discrepancies and inverted dates. This has been interpreted as being caused by heavy erosional processes, mostly during wet season periods, which cause Iho Eleru rock shelter to become a main channelling area for water moving downstream from the upper levels of the inselberg.

Also to note, Shaw and Daniels (1984, p.2) state that the stratigraphical excavation was conducted with an initial layer (spit 1) that was excavated with a total depth of 25cm, and subsequent spits of 15cm. However, later descriptions of the excavation show that each and every spit per square was considered to be 15cm in depth. This contradiction might be caused by a use of a 25cm deep spit only in specific areas of the rock shelter, however such information could not be found by the authors of this paper. For these reasons, a consistent depth of 15cm per spit was considered and applied for the upper plateau area which was evaluated in this study, and which is consistent with the original descriptions, interpretations and excavation diagrams by Shaw and Daniels (1984).

Stratigraphic Interpretation. In the platform area of the rock shelter, Shaw and Daniels describe 4 main sediment types:

Upper section along the west face of Trench D XXV-XXVI	Lower section along the east face of Trench D XVII-XXVII
1) Superficial ash layer	1) Superficial ash layer
2) Light red sandy layer	2) Red sandy layer
3) Reddish brown soil	3) Reddish brown soil
4) As in 3, but rather more clayey	4) Gravelly soil
5) Gravelly soil	5) Browner and looser than 3, but redder and less sandy than 2 (apparent in squares XIX–XXI only)
Summarised from Shaw and Daniels, 1984, pp.193, figure 6.	

These units appear to be very distinct in terms of their sedimentary properties and likely reflect changes in the local environment surrounding the rock shelter. We propose some thoughts regarding possible site formation factors operating at Iho Eleru and describe how these may relate to changes observed in our paleoclimatic modelling.

Gravelly soil

We Interpret the 'gravelly soil' at the base of the platform sequence to be colluvially deposited heavily weathered re-worked soils, eroded from the higher elevations of the Inselberg landform. Given that igneous bedrock and associated soils are apparently the only possible sources of colluvial sediment supply, there are limited options to explain the notable gravel component that Shaw and Daniels describe in this sedimentary horizon. We suggest that coarse components in the gravelly soil unit are likely crudely weathered elements of the igneous bedrock and/or pedogenic iron nodules re-worked from well-developed laterite soil deposits. It is also feasible that the coarse components in this unit may be derived from relict geological deposits of Quaternary, or pre-Quaternary age, situated at areas of high elevation on the inselberg, though we currently have no evidence to support this possibility.

Our oldest radiocarbon age estimate for the lower spits in the platform area is 13075–12840 cal. BP (IW2833, F21 Spit 10). According to our paleoclimatic modelling, environmental conditions at approximately this time are predicted to be characterised by increased precipitation and humidity. Our modelled environmental expectations support our preliminary interpretations of this stratigraphic unit, whereby increased precipitation and humidity would have likely increased geochemical weathering of any exposed bedrock and increased high-intensity, precipitation may have assisted in the periodic washing of re-worked materials into the rock shelter.

Reddish brown soil

This unit is annotated by Shaw and Daniels as varying in thickness (c.1.2m- 0.3m). We anticipate that where the deposit is thickest (i.e. square XX), it is likely formed of repeated depositions of re-worked soil, brought into the rock shelter by episodic pulses of in-washing. Discrete sedimentary hiatuses and stabilisation surfaces are thought to occur between pulses of in-wash. This intermittent sedimentary regime is deemed likely due to minor, in-situ, stratigraphic lensing that Shaw and Daniels describe, such as the layer of calcareous nodules (possibly biogenic ash) occurring at c. 0.45m below the ground surface. Well stratified horizons of rock spall clasts (Shaw and Daniels, Plt IX, pp. 182) also imply a repeated, episodic, mode of deposition.

Our new radiocarbon age estimates most probably associated with this layer span c. 11,000-6500 cal. BP. (earliest dated sample = IW2519, F21 Spit 8; youngest dated sample = IW2232, D27 Spit 6). According to our paleoclimatic models this stratigraphic unit was deposited during a modelled continuation of humid environmental conditions with high precipitation, which began approximately at c. 14,000 BP. We suggest that humid conditions are likely sustaining soil development in bedrock depressions located above the altitude of the Iho Eleru rock shelter and these soils are subject to intermittent erosion by high amplitude precipitation. The overall paucity of coarse components in this sedimentary unit might be attributed to the deposition of young, lesser developed, re-worked soil. A greater clay content in the lower portions of the 'reddish soil' could be attributed to phases of increased chemical weathering of the igneous bedrock, the input of a different sediment source, or sorting of the sediment's size fraction through water agency (i.e. pooling).

Light red sandy layer

Between c. 0.5-0.2m depth, Shaw and Daniels describe a light red sandy layer. This unit is observed to have a clear and abrupt lower contact to the underlying red soil deposits (Shaw and Daniels, 1984, Plt IX) which may indicate a rapid and drastic change in sedimentary regime, perhaps in association with a small-scale erosional event. A radiocarbon sample from this unit (IW1918, D27 Spit 3), returns an age estimate of 3365–3229 cal. BP. According to our paleoclimate models, the deposition of this unit occurs during a modelled phase of increased temperature, reduced precipitation, and overall reduced precipitation seasonality. We suggest that the overall change in sedimentary regime – from re-worked soil to sandy deposits – might be linked to reduced precipitation and the cessation of soil erosion at high elevations on the inselberg landform. It is possible that the sand component of this unit derives from continued chemical weathering of the Igneous bedrock, both at high elevations and within the rock shelter itself. Aeolian deposition of fine particle material from other proximal sources, such as seasonally dried soils or alluvial environments is also possible.

Superficial silt

The sedimentary sequence at Iho Eleru is capped by c.0.1-0.2m of mobile silts. This unit is described by Shaw and Daniels as ‘superficial ash’. This deposit is approximated to date to c. 460-314 cal. BP (IW1676, D25 Spit 1) to modern times. Two radiocarbon dates on faunal material from this unit have returned ‘modern’ ages. Recent fire making activities in the cave are likely to be the primary source of this fine-grained, mobile, ashy, material.

Further work in the field and laboratory are required to confirm the nature of the depositional sequence at Iho Eleru.

References

Shaw, T., & Daniels, S. G. H. (1984). Excavations at Iwo Eleru, Ondo State, Nigeria. West African Journal of Archaeology, 14, 1–269.

White, F. (1983). The vegetation of Africa. Natural Resources Research Volume XX. Paris: UNESCO.

Supplementary Data 2

In addition to the chronometric, archaeobotanical, and faunal studies, paleoclimatic model predictions and paleoenvironmental reconstructions were carried out for the regional area surrounding Iho Eleru over the last 22 ka at one-thousand-year intervals. We used bioclimatic variables from Beyer et al.[24] and based on Hadley CM3, downscaled and bias-corrected at 1.5° and 0.5° resolution (Supplementary Figure 4). The model predictions were then scaled with a summary of the influx of herbaceous pollen types (NAPs) in four pollen records[25–28]. Overall, the modelled paleoclimatic regional context is positively supported by the paleoenvironmental proxies, with a visible delayed correlation between the changes in NAPs and the modelled variation in temperature and precipitation means and seasonality.

Palaeoclimate Reconstruction Method (Script 1). We used the paleoclimate reconstructions based on the Hadley CM3 published in Beyer et al.24 to model changes in climate for the area surrounding Iho Eleru. We used the decimal coordinate location of Iho Eleru to extract climate variable values at 1.5° resolution from the Beyer et al.24 dataset in 1000-year intervals over the last 22,000 years (see Script 1). All climate variable values were then scaled together, and four climate variable values of interest were plotted in figure 6. These include BIO 1 (annual mean temperature), BIO4 (temperature seasonality), BIO 12 (annual precipitation), and BIO 15 (precipitation seasonality). Annual mean temperature and annual precipitation (BIO 1 and 12) were selected to have an average annual representation of the local climate and its effect on the local environment as precipitation and temperature are two main factors for vegetation growth and resilience. Temperature and precipitation seasonality were selected due to their effects on human resilience and agro-pastoral activities. Increased temperature and precipitation seasonality has a negative effect on agro-pastoral communities, as crop cultivation and livestock husbandry can be negatively impacted by drastic increases or decreases in temperature and precipitation.

Synthesised Regional Palynological (NAP) Record Modelling Method (Script 2). To provide additional context to the faunal, anthracological, and macrobotanical remains at Iho Eleru, multiple pollen records from Nigeria, Benin, and the Atlantic Ocean were summarized into indices tracking regional trends in vegetation cover. Pollen records were acquired from an archived version of the African Pollen Database64, harmonised, standardised, and plotted in the R statistical computing environment (R Core Team, 2021).

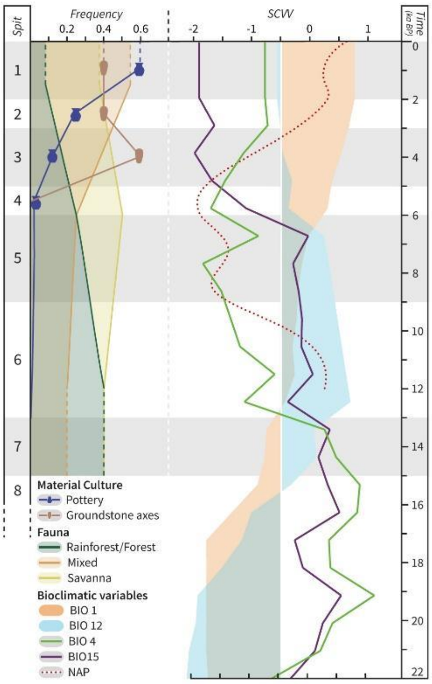

Figure 2a. Synthesis of non-arboreal pollen (NAP), climate variable curves, material culture frequency, and faunal remains frequency during the last 22 ka. On the left are the frequency plots for the recovered material culture and identified fauna divided into environmentally categorised taxonomies. On the right are the regional non-arboreal pollen (NAP) curve and predicted variables for each 1-thousand-year slice. Scaled climate variables are: annual mean temperature (BIO1), temperature seasonality (BIO4), annual precipitation (BIO12), and precipitation seasonality (BIO15).

Name	**Latitude**	**Longitude**	**Altitude (m)**	**Region**	**Reference**
KW31	3.5183	5.5668	1181	Gulf of Guinea	Lézine et al. 2005
Lake Sélé	5.00	2.43	NA	Southern Benin	Salzmann and Hoelzmann 2005
Lake Tilla	10.39	12.13	690	Sahel	Salzmann et al. 2002
Niger delta core (boring-22)	5.50	6.43	0	Atlantic Zone	Sowunmi 1981

Table 2a. List of palynological datasets used, APD database information, locations, and references.

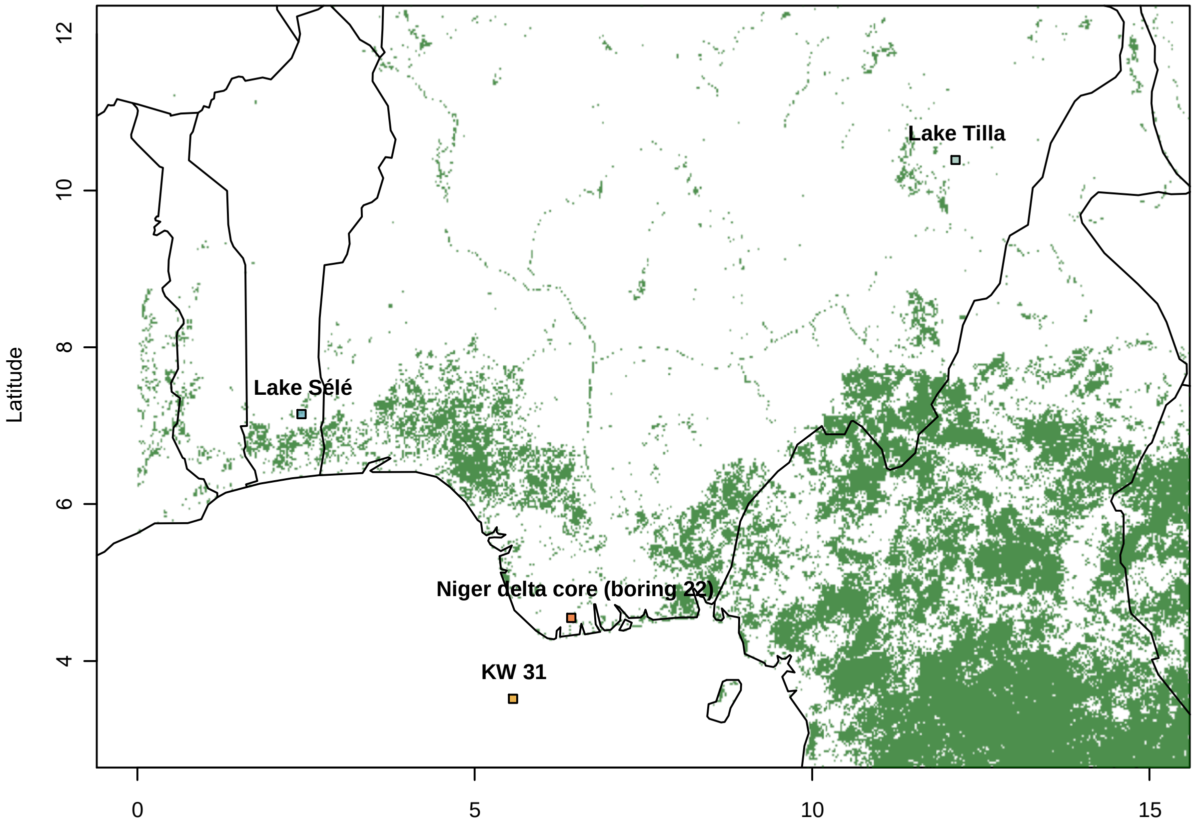

Figure 2b. Map of study region showing locations of paleovegetation. Green area is tropical rain forest summarized from the Global Land Cover Characterization dataset (doi: /10.5066/F7GB230D).

Harmonizing Datasets. Using a custom function, the datasets are harmonized with a master reference. This includes updating old taxonomic nomenclature as well as addressing spelling errors. Anne-Marie Lézine currently maintains the master list, which is a product of the African Pollen Database (Vincens et al. 2007). Below is the output from the harmonizer function.

```
## [1] "Taxa and Data files match, TILLA"
## [1] "TILLA"
## [1] "4 unmatched taxa"
## [1] "Umbelliferae" "Sample age" "Sample age" "Sample age"
## [1] "repairing Sample age variables"
## [1] "repairing Sample age variables"
## [1] "repairing Sample age variables"
## [1] "Taxa and Data files match, KW31"
## [1] "KW31"
## [1] "2 unmatched taxa"
## [1] "Sample age" "Sample age"
## [1] "repairing Sample age variables"
## [1] "repairing Sample age variables"
## [1] "Taxa and Data files match, NIGERDC2"
## [1] "NIGERDC2"
## [1] "2 unmatched taxa"
## [1] "Sample age" "Sample age"
## [1] "repairing Sample age variables"
## [1] "repairing Sample age variables"
## [1] "Taxa and Data files match, LACSELE_APD"
## [1] "LACSELE_APD"
## [1] "1 unmatched taxa"
```

```
## [1] "Labiatae"
## [1] "TILLA has doubles!"
## [1] "LACSELE_APD has doubles!"
```

Deriving Plant Functional Types and Percentages. Data harmonisation includes associating pollen taxa with known PFTs (Plant Functional Types) (Lézine et al. 2009). Plant functional types can be used to group pollen taxa by growth form (arboreal trees/shrubs, herbaceous vegetation, lianas, arboreal palms, etc.) and make comparisons of records from different regions. Pollen records were harmonized and percents of major plant functional types were calculated based on the total number of pollen identified (Figure S4-2). Our goal is to assess the relative proportion of forest and herbaceous vegetation cover (grasslands and savanna) and arboreal trees/shrubs and herbaceous PFTs are being used as proxies for these broad types of vegetation cover. Similar methods have been applied to regional assessments of vegetation change both for the African continent (Phelps et al. 2020).

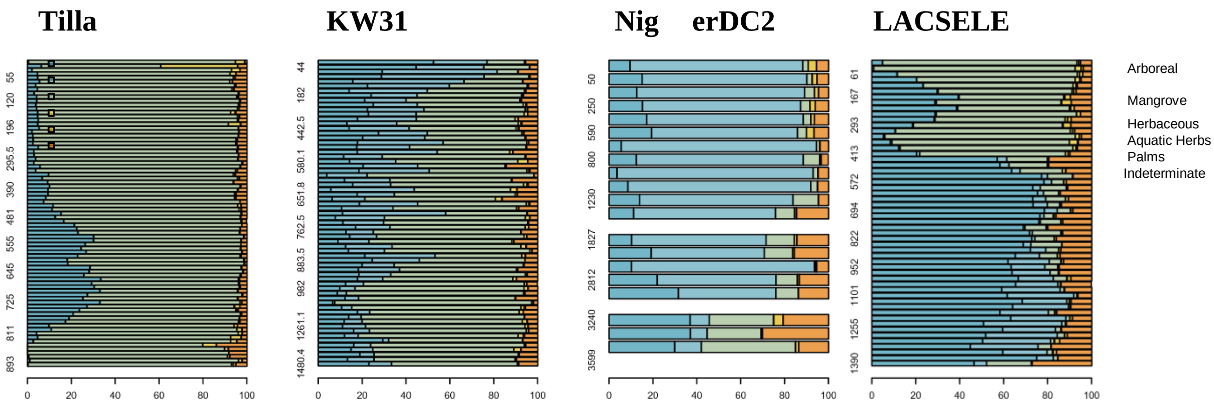

Figure. Barplots showing core results as percent of all pollen, grouped by PFT.

Summarizing PFT Results using Z-Scores. After summarizing these records by PFT and calculating the percent of each major group, we compare the datasets by setting them on an equal scale using Z-scores, which represent the results as the difference from the mean in standard deviation units. By doing so, we can compare fluctuations with small and large amplitudes on a uniform scale (Figure S4-3). The APD entry for Lac Sélé did not contain a radiocarbon chronology, so this code will either compute one using the Rbacon package or use an existing one.

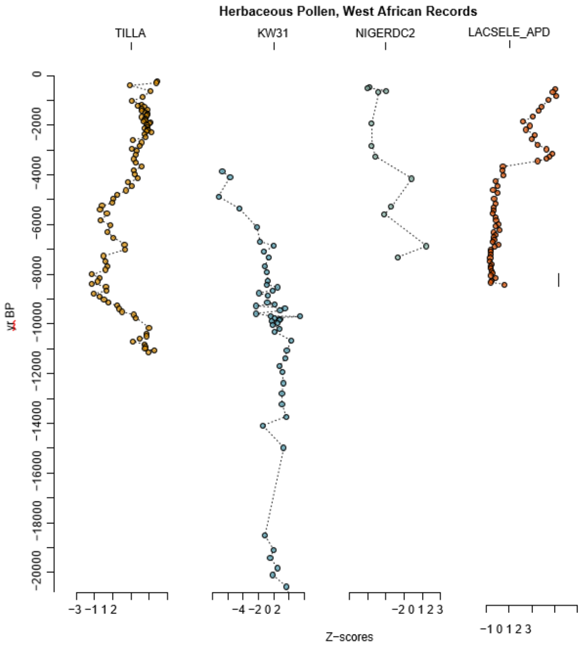

Figure. Z-scores of herbaceous pollen percent from selected regional pollen records.

Binning Data and Deriving Smoothed NAP Curve. In order to create a single index to compare with the finds at Iho Eleru, we aggregated the Z-scores of arboreal and herbaceous PFTs from all of the records and binned them by chronological intervals. In Figure S4-3, the sample density for chronological bins representing 500 and 100 years are compared. This shows that, using 500-year bins, the minimum number of samples in a bin (at 20000-19500 yr BP) is two. The maximum is 14 and all of the Holocene bins (11000 yr BP to present) are represented by a minimum of six data points.

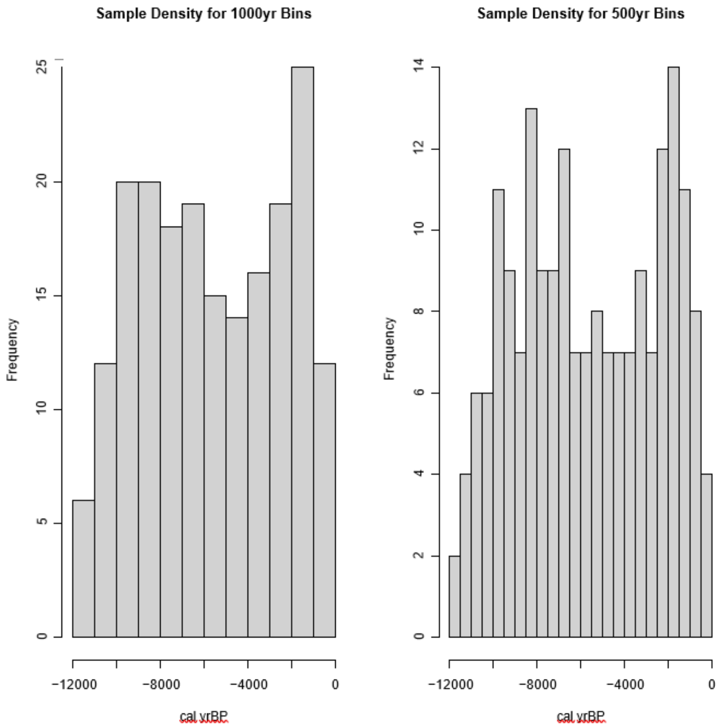

Figure. Histograms showing number of samples representing each chronological bin.

Samples were binned to 500-year intervals and the chronology was limited to the last 12,000 years. In order to evaluate whether our smoothing results were reasonable, multiple smoothing methods were applied to summarized results from both herbaceous and arboreal PFTs. All of the smoothing functions were calculated with 24 knots. Spline smoothing was calculated using R's smooth.spline function. Kernel-density smoothing was calculated using R's ksmooth function. Smoothed splines were also calculated with the ss function in the npreg package (https://CRAN.R-project.org/package=npreg). These methods produced consistent results (Figure S4-4) and produce a reasonable index of general patterns in vegetation cover as reflected in the representation of pollen in regional pollen records.

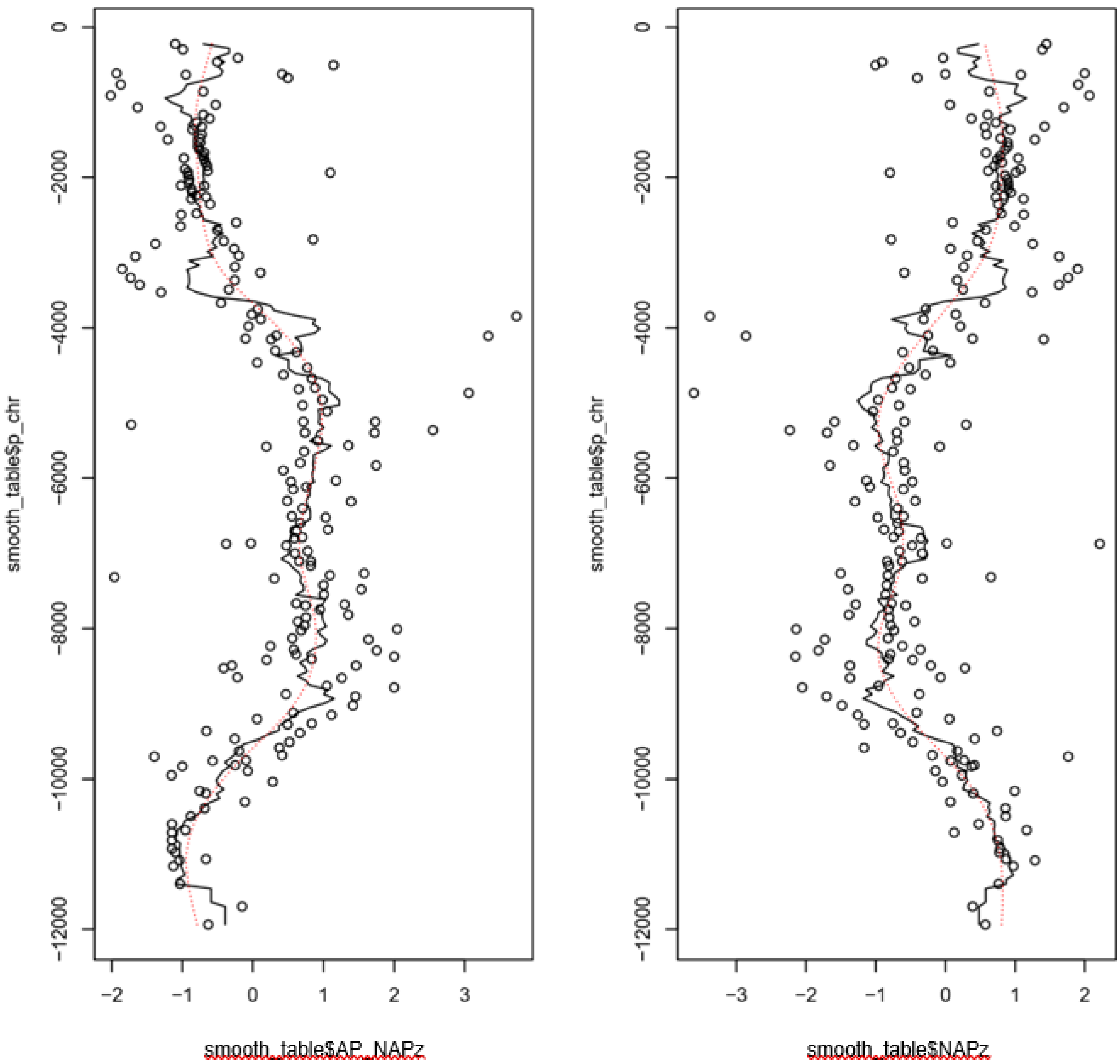

Figure. Plots showing all data points and results of different smoothing methods.

In order to visualize our uncertainty and as a final check on the smoothing methods, the smoothed results are presented below with box-and-whisker plots of the binned sample results (Figure S4-5). This visualization reveals where outliers may have an over-sized influence on the curve (at 7500-7000 yr BP and 5000-4000 yr BP) and in which direction.

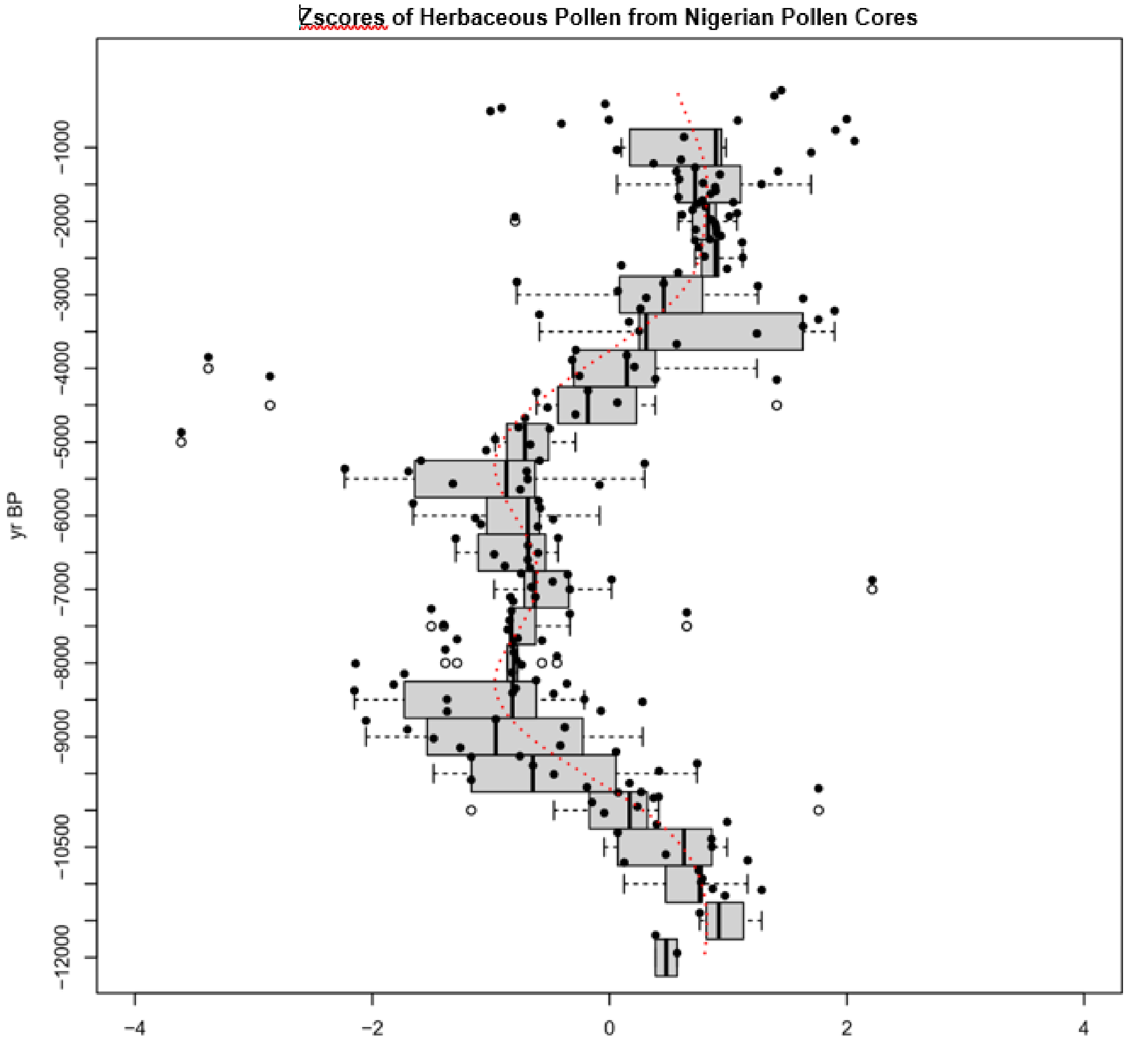

Figure. Box and whisker plot of data per chronological bin overlain with kernel-density smoothing result.

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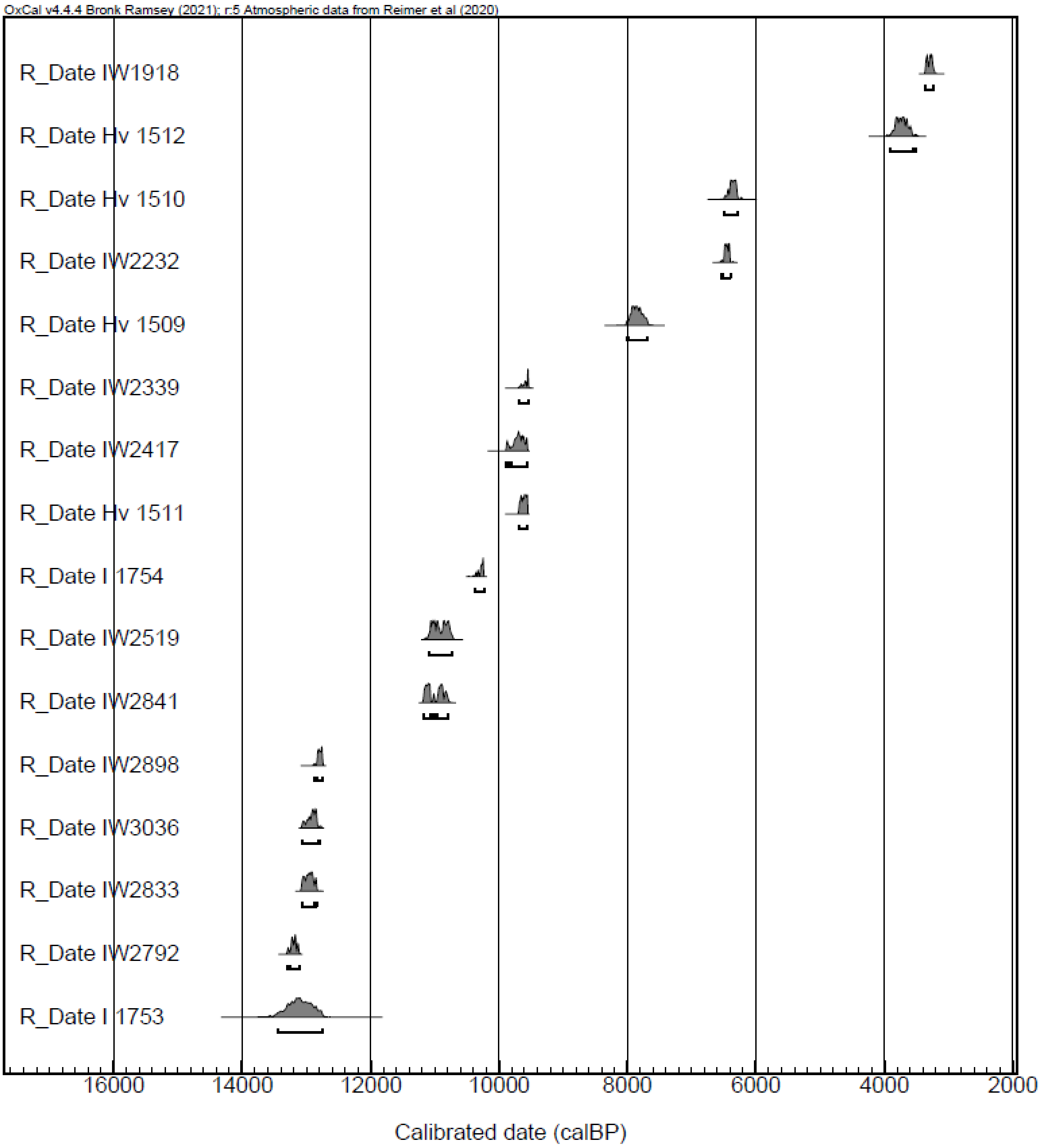
Vincens, A., Leźine, A. M., Buchet, G., Lewden, D., Le Thomas, A., Agwu, C. O. C., . . . Ybert, J. P. (2007). African pollen database inventory of tree and shrub pollen types. Review of Palaeobotany and Palynology, 145(1–2), 135–141. https://doi.org/10.1016/j.revpalbo.2006.09.004

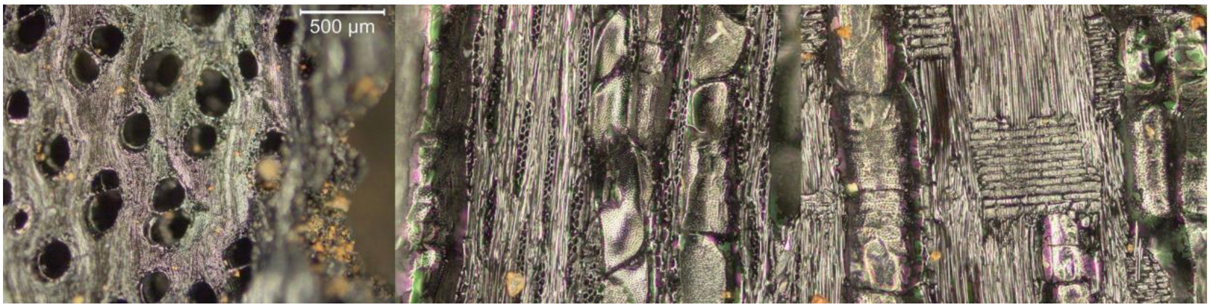
Supplementary Data 3

Phytolith Analysis Method. The archaeobotanical samples containing sediment within their original storage bags were processed for sediment isolation using sieve meshes, with varying grid sizes between 1-0.25cm. For the phytolith extraction, the samples were first deflocculated using a sodium hexametaphosphate and warm water solution. For every 10ml of soil, 100ml of solution was used (ratio 2:90, sodium hexametaphosphate:water). Any sample which did not correctly deflocculate after 72 hours within the solution was manually crushed with a mortar and pestle. Clays were then removed from the samples by gravity sedimentation, with a 1:10 ratio of solution to water, letting it stand for one hour and then removing supernatant liquids. The clay removal process was repeated 3 times. The resulting clay-free samples were then fractioned by wet sieving and dividing the samples into sands (mesh sieve with grid size of 250µm) and silts (mesh sieve with grid size of 50µm). A centrifuge (1500 rpm for 10 minutes) and distilled water were then used to repeatedly wash the silt samples. The sand samples were put aside and not used for the rest of the process. Given the high contraction of carbonates in the higher spits of the stratigraphy, HCl was used to remove any carbonate particles. This was done by carefully adding HCl to the samples until no reactions were visible. The samples were then rinsed three times with distilled water and a centrifuge at 1700 rpm for 10 minutes each. Organics were then removed using a 30% H2O2 solution and placing the samples within the solution in a hot water bath at 40oC. Given the low percentage of organic materials in the samples this step was concluded after 2 hours in the hot water bath, with the second hour reaching a temperature of 80oC. The samples were then rinsed five times with distilled water and a centrifuge at 1700 rpm for 10 minutes each. The resulting samples were then processed for any phytolith extraction by flotation using Sodium Polytungstate (SPT-1). A heavy liquid was created using a hygrometer at a specific density of 2.3g/ml. The SPT-1 solution was then mixed with the samples, and centrifuged at 1700 rpm for 5 minutes. The materials which were floating at the top were then removed and then rinsed three times with distilled water and a centrifuge at 1700 rpm for 10 minutes each. Next, the samples were dried using acetone, which was mixed with the samples (approximately 10ml for 1ml of soil), stirred and centrifuged at 1500 rpm for 5 minutes. Supernatant acetone solution was removed, and the process repeated twice more. The final samples were then left to dry in a fume cupboard for 2 nights. Finally, the resulting materials were mounted on slides by mixing silicon oil with the samples, placing a few drops of the solution on each slide, and then covering with the slide cover and using clear nail polish to seal them. The slides were analysed with a Olympus BX53M microscope at 40-100x magnification.

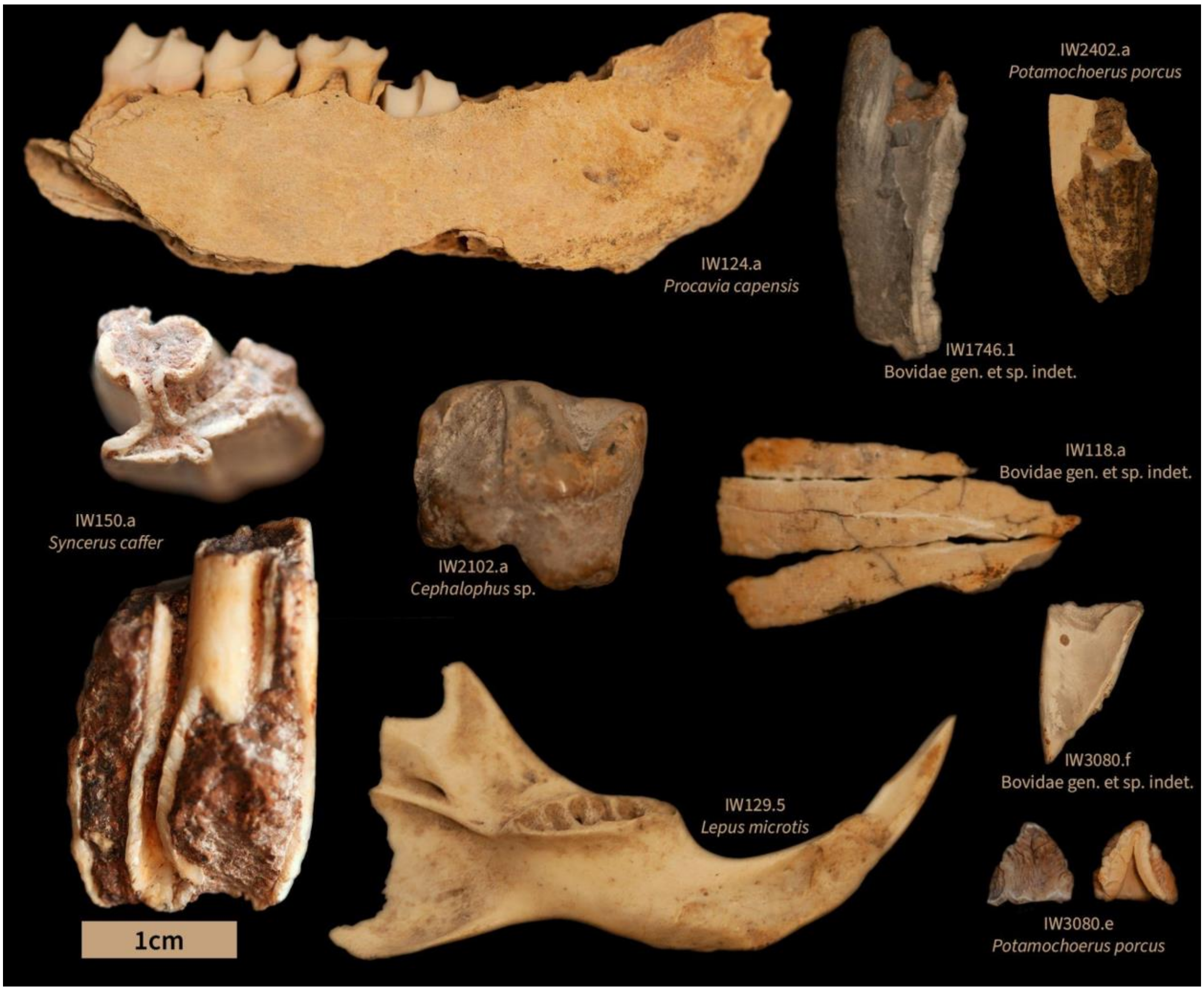
Supplementary Figure 1. Calibration of new chronometric ages and original chronometric ages (Shaw and Daniels 1984).



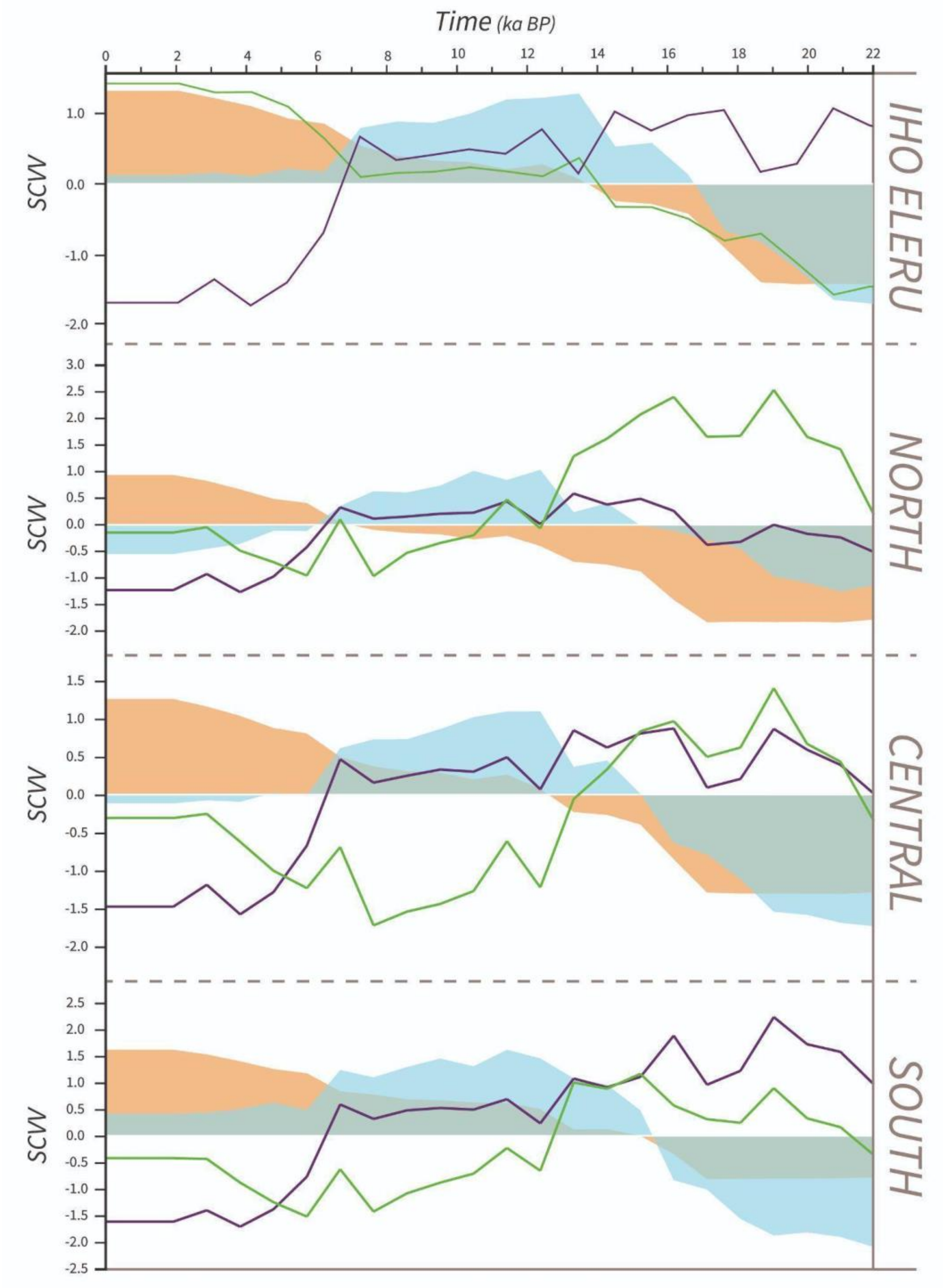
Supplementary Figure 2. ZANTHOXYLUM spp., transverse (left), tangential (centre) and radial (right) section of wood charcoal fragment (IW 1918).



Supplementary Figure 3. Selection of samples selected for isotope analysis.



Supplementary Figure 4. Modelled climate variables for each 1-thousand-year slice. Reconstructions were carried out on four separate areas. The first is at a 0.5° resolution around the site of Iho Eleru. The subsequent three are a division in longitude (0.5° each) of the total area analysed in the main study (see figure 1 and figure 6), divided as North, Central and South. Scaled climate variables are (see main text for legend): annual mean temperature (BIO1; orange), temperature seasonality (BIO4; green), annual precipitation (BIO12; blue), and precipitation seasonality (BIO15; purple).



Supplementary Table 1. Later Stone Age and early ceramic sites in West Africa. Shown on Figure 1 of Main Text.

N. on fig. 1	Context	Country	Type	Dating	Latitude	Longitude	Reference
1	Iho Eleru	Nigeria	Rock shelter	14C (radiocarbon) dating	7.44138	5.12476	(Shaw & Daniels, 1984)
2	Shum Laka	Cameroon	Rock shelter	14C (radiocarbon) dating	5.85861	10.07778	(Lavachery, 2001)
3	Koukouan-I	Benin	Open air	Typological (lithic)	10.21710	1.04967	(Petit, 2005)
4	Pendjari-II	Benin	Open air	Typological (lithic)	11.02403	0.94628	(Petit, 2005)
5	Bosumpra Cave	Ghana	Rock shelter	14C (radiocarbon) dating	6.683	-0.730	(Oas, D'Andrea, & Watson, 2015; Watson, 2017)
6	Bingerville Highway	Ivory Coast	River terrace	14C (radiocarbon) dating	5.58500	-4.277	(Chenorkian, 1983)
7	Fatandi V	Senegal	Open air	OSL (optically stimulated luminescence) dating	13.866	-12.371	(Chevrier et al., 2016; Lebrun et al., 2016)
7	Toumboura I	Senegal	River terrace	OSL (optically stimulated luminescence) dating	13.866	-12.371	(Lebrun et al., 2016)
8	Ounjougou	Mali	Open air	OSL (optically stimulated luminescence) dating	14.532	-3.448	(Huysecom et al., 2014; Lebrun et al., 2016; Rasse, Soriano, Tribolo, Stokes, & Huysecom, 2004)

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Supplementary Table 2. ^{14}C dating results - For further details on calibration calculations see Supplementary Information 2.

Sample Code	Context	Depth (cm)	Material	Uncalibrated ^{14}C ages (yr BP)	Calibrated ^{14}C ages (yr BP; 95% probability)
IW1676	D25 Spit 1	0-15	wood charcoal	334 ±16	387
IW3036	F19-21 Spit 2	15-30	canarium endocarp	10995 ±35	12934.5
IW1918	D27 Spit 3	30-45	oil palm endocarp (cf.)	3082 ±21	3297.5
IW2339	D23 Spit 5	60-75	unidentified botanical remain	8625 ±30	9606.5
IW2841	D23 Spit 6	75-90	oil palm endocarp (cf.)	9638 ±31	10987.5
IW2232	D27 Spit 6	75-90	canarium endocarp	5676 ±25	6467.5
IW2792	D23 Spit 7	90-105	canarium endocarp	11305 ±35	13207
IW2417	D20 Spit 8	105-120	oil palm endocarp (cf.)	8736 ±31	9722
IW2519	F21 Spit 8	105-120	canarium endocarp	9570 ±32	10917.5
IW2606	D20 Spit 9	120-135	unidentified botanical remain	2537 ±21	2621.5
IW2833	F21 Spit 10	135-150	canarium endocarp	11024 ±35	12958
IW2898	F21 Spit 11	150-165	canarium endocarp	10875 ±34	12809

IW1050	Ash surface	30-45 c.	faunal bone	(-)474 ±17	Modern
IW1050	Ash surface	30-45 c.	faunal bone	(-)617 ±18	Modern

Supplementary Table 4. Isotope analysis results

Sample Code	**Context**	**Taxon**	**$\delta^{13}C$**	**$\delta^{13}C$ st. dev.**	**$\delta^{18}O$**	**$\delta^{18}O$ st. dev.**
IW3080.e	D 23 spit 6-7	*Potamochoerus porcus*	-18.6	0.1	-4.6	0.1
IW3080F	D 23 spit 6-7	indeterminate bovid	-18.6	0.1	-4.6	0.1
IW118.a	D 23 spit 6	indeterminate bovid	-13.4	0.1	-3.6	0.1
IW1746.1	D 22 spit 5	indeterminate bovid	-14.2	0.1	-3.6	0.0
IW141A	D 27 spit 2	*Cephalophus* sp.	-14.1	0.1	-3.8	0.1
IW2102.a	D 27 spit 4	*Cephalophus* sp.	-14.2	0.2	-8.6	0.1
IW126A	F 14 spit 2	*Varanus niloticus*	-14.8	0.1	-2.1	0.0
IW124B	F 16 spit 1A	*Lepus microtis*	-13.1	0.2	-4.2	0.1
IW124.a	F 16 spit 1A	*Procavia capensis*	-14.5	0.1	0.1	0.1
IW129.5	Spit ash surface	*Lepus microtis*	-13.6	0.1	-4.9	0.1
IW2402.a	G 16 spit 4	*Potamochoerus porcus*	-13.8	0.2	-3.3	0.0
IW150.a	Tunnel 3 spit 7	*Syncerus caffer*	2.5	0.1	1.8	0.1

IW127.a	Y 16 spit 1	*Hystrix cristata*	-18.4	0.1	-11.0	0.2

Supplementary Table 7. Core locations used for NAP analysis (figure 1; Supplementary Text 1).

Core name	Latitude	Longitude	Altitude (m)	Country	Region	Reference
KW 31	3.5183	5.5668	-1181	Atlantic Ocean	Gulf of Guinea	Lézine A.-M., Duplessy J.-C., Cazet J.-P. (2005). West African monsoon variability during the last deglaciation and the Holocene: Evidence from fresh water algae, pollen and isotope data from core KW31, Gulf of Guinea. Palaeogeography, Palaeoclimatology, Palaeoecology 219, 225-237.
Lake Sélé	7.15	2.4333	0	Benin	West Africa	Salzmann U., P. Hoelzmann, 2005. The Dahomey Gap: an abrupt climatically induced rain forest fragmentation in West Africa during the late Holocene. The Holocene 15,2, 190-199.
Lake Tilla	10.3906667	12.1245	690	Nigeria	Sahel	Salzmann U., Hoelzmann P., Morczinek I. (2002). Late Quaternary climate and vegetation of the Sudanian zone of Northeast Nigeria. Quaternary Research 58, 73-83.
Niger delta core (boring 22)	4.55	6.4333	0	Nigeria	Atlantic Zone	Sowunmi M.A. (1981). Late Quaternary environmental changes in Nigeria. Pollen et Spores 23 ,1, 125-148.

Title: Newly discovered Middle Stone Age sites in the Tanongou Valley, Atakora Region, Benin

Authors: Jacopo Niccolò Cerasoni[1,2]*, Didier N'Dah[3], Ian Candy[4], Nestor Labiyi[3], Angelo Ayedoun[3], Emily Y. Hallett[1], James Blinkhorn[1,4], Simon Armitage[4,5], Eleanor M.L. Scerri[1,6,7]

Affiliations:

[1]Pan-African Evolution Research Group, Max Planck Institute for the Science of Human History, Jena, Germany.

[2]Institute of Archaeological Sciences, Eberhard Karls University Tübingen, Tübingen, Germany

[3]UAC, University of Abomey-Calavi, Cotonou, Benin.

[4]Centre for Quaternary Research, Department of Geography, Royal Holloway, University of London, London, UK.

[5]SFF Centre for Early Sapiens Behaviour (SapienCE<), University of Bergen, Bergen, Norway.

[6]Department of Classics and Archaeology, University of Malta, Msida, Malta.

[7]Institute of Prehistoric Archaeology, University of Cologne, Cologne, Germany.

*Corresponding author: J.N.C. - cerasoni@shh.mpg.de (ORCID: 0000-0002-5546-1555)

Abstract

West Africa is a region that has been poorly studied in terms of Pleistocene human evolution, especially when compared to other regions of the continent. Within West Africa, the Atakora Region in North-Western Benin is an area of high archaeological potential, containing a variety of Early, Middle and Later Stone Age sites. Nevertheless, chronometric dating has never been carried out in this area before, and no Pleistocene sites have ever been identified in *in-situ* cave contexts. Here, we report the results of fieldwork carried out in the Tanongou Valley, where Middle Stone Age (MSA) layers have been identified in the previously known Iron Age site of Tanongou Cave. We also report the newly discovered open-air site of Paloli, which consists of three hectares of lithic scatter found in close proximity to Tanongou Cave. These sites are situated within an ecotonal forested island. Chronometric dating of these newly discovered contexts, although partially unsuccessful, reliably establishes their *in-situ* context and Pleistocene age. Lithic assemblages at both sites are similar and of Middle Stone Age tradition with Levallois production, albeit with differences in terms of typology, raw material presence and debitage. This implies a possible contemporary use of both sites, with a difference in activity carried out within them. The Tanongou Valley represents the first MSA locale of its kind, with the only reported MSA cave site in West Africa. Both Tanongou Cave and Paloli are key sites for the re-evaluation of MSA cultural and environmental behaviours in West African human evolutionary studies.

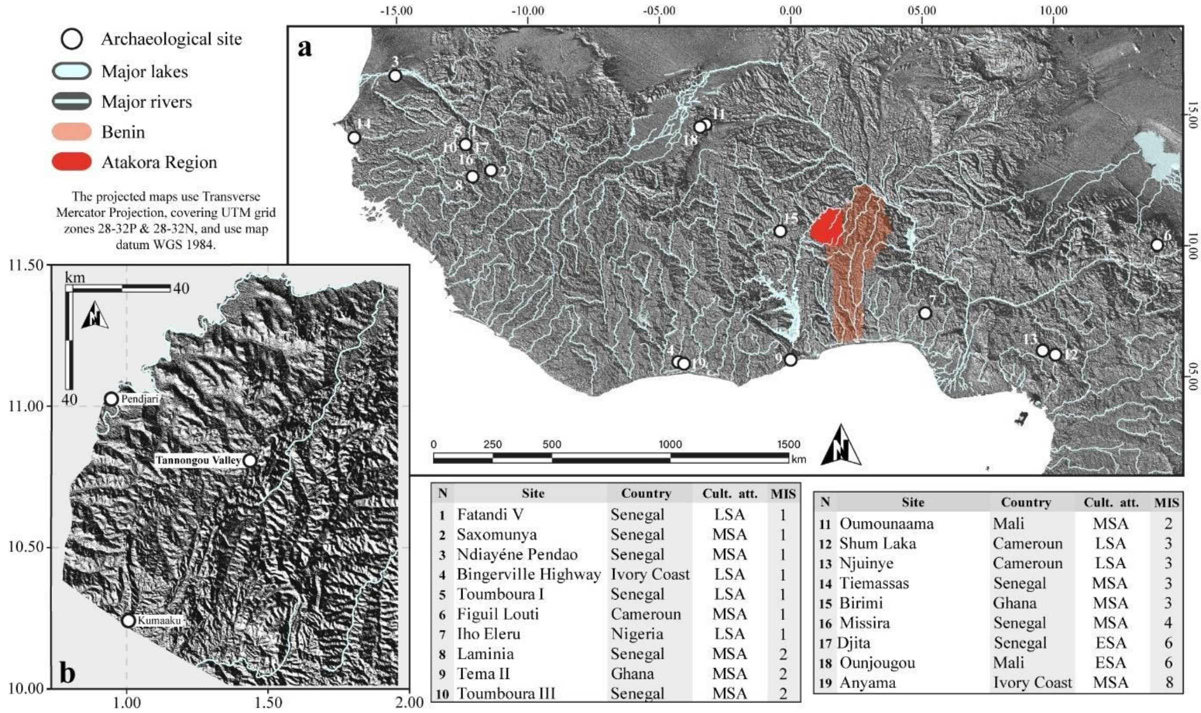
Keywords: West Africa; Pleistocene Africa; Middle Stone Age; Archaeological Excavation; Lithic Analysis.

Main Text

Introduction

West Africa remains one of the least well understood African regions for human evolution as the continent’s record is primarily constructed from sites in northern, eastern, and southern Africa. The historical lack of research investment in West Africa can be explained by the long-standing hypothesis that humans originated in the grasslands and savannahs of eastern Africa (Quintana-Murci *et al.*, 1999; Trinkaus, 2005; Rito *et al.*, 2013). However, recent work has since begun to unravel a rich Pleistocene archaeological record in West Africa. In particular, Middle Stone Age (MSA) sites in West Africa have been recorded across the entire region, in present-day Sahelian, savannah, and rainforest environments (e.g., (Paradis, 1980; Ljubin and Guédé, 2000; Huysecom *et al.*, 2014; Chevrier *et al.*, 2016; Allsworth-Jones, 2019; Niang *et al.*, 2020; Scerri *et al.*, 2021). Indeed, West Africa features a wide variety of environmental zones, which converge to form numerous ecotonal regions. These regions in particular, have been linked to early human demography (Butzer, 1982; Roberts and Stewart, 2018).

Currently, the 19 archaeological sites and assemblages that have been successfully dated and published (fig.1), suggest that MSA material culture is broadly comparable across the region, regardless of possible ecological differences in the past, However, as research expands, greater nuances of the archaeological record are being achieved (Schmid *et al*., 2021). Generally, while human activity dating to the terminal Middle Pleistocene has been identified, most sites have been reliably dated to the Late Pleistocene or MIS 3, through to the start of the Holocene. The most notable Late Pleistocene sites are located within or in close proximity to riparian environments of sub-sahelian Senegal (Saxomunya, Ndiayene Pendao, Tiemassas, Fatandi V), and in coastal Guinean regions of Ghana (Tema II) and Ivory Coast (Bingerville Highway). Sites older than MIS 3 are scarce, with only five reported sites so far, including Missira 1, Tiemassas S7, and Djita (riparian savannah, Senegal) Ounjougou (savannah, Mali), and Anyama (tropical rainforest, Ivory Coast) (Davies, 1967, 1976; Ljubin and Guédé, 2000; Huysecom *et al.*, 2014; Scerri *et al.*, 2021; Lebrun, Chantal, *et al.*, 2016; Niang and Ndiaye, 2016; Scerri *et al.*, 2016; Chevrier *et al.*, 2018, 2020; Niang, Blinkhorn and Ndiaye, 2018).



N	Site	Country	Cult. att.	MIS
1	Fatandi V	Senegal	LSA	1
2	Saxomunya	Senegal	MSA	1
3	Ndiayéne Pendao	Senegal	MSA	1
4	Bingerville Highway	Ivory Coast	LSA	1
5	Toumboura I	Senegal	LSA	1
6	Figuil Louti	Cameroun	MSA	1
7	Iho Eleru	Nigeria	LSA	1
8	Laminia	Senegal	MSA	2
9	Tema II	Ghana	MSA	2
10	Toumboura III	Senegal	MSA	2

N	Site	Country	Cult. att.	MIS
11	Oumounaama	Mali	MSA	2
12	Shum Laka	Cameroun	LSA	3
13	Njuinye	Cameroun	LSA	3
14	Tiemassas	Senegal	MSA	3
15	Birimi	Ghana	MSA	3
16	Missira	Senegal	MSA	4
17	Djita	Senegal	ESA	6
18	Ounjougou	Mali	ESA	6
19	Anyama	Ivory Coast	MSA	8

Figure 1. Location of dated Stone Age sites in West Africa with superimposed location of Benin (a), and map of the Atakora Region (b). The three Stone Age sites shown contain the three different stone age technological types present in the region: 1. Early Stone Age (Kumaaku), 2. Middle Stone Age (Tanongou Valley), and 3. Later Stone Age (Pendjari).

The West African MSA record is generally represented by similar observable characteristics within stone tool assemblages identified throughout chronological and spatial distributions within the region. Common focus on the use of bifacial, discoidal and Levallois reduction is present, with an emphasis on centripetal reduction regimes (Davies, 1967, 1976; Lebrun, Chantal, *et al.*, 2016). These production methods seem to be applied to a diverse raw material and are unconstrained by clast-size availability, in spite of varying topographic and geological contexts. Unfortunately, given the geographic and ecological focus of the existing record, it is unclear if the observable technological characteristics are a product of adaptation to particular environmental settings, or whether they are characteristic of the wider region.

In order to address these questions, an expedition was led by the Pan-African Evolution group in February 2020, in partnership with the University of Abomey-Calavi in Benin. The joint expedition focused on the northern Atakora Department of Benin. The major objective of this expedition was to visit, survey and excavate areas of high archaeological interest. As part of our expedition, investigations of Tanongou Valley were carried out. This ecotonal micro-landscape features the MSA cave site of Tanongou Cave, partially excavated in the early 2000s (Petit, 2005; N'Dah, 2009), and the newly discovered open-air site of Paloli, both of which we report here

Research Background

West Africa is home to a wide diversity of ecologies. They vary from open and arid savannahs, which host the best dated and known MSA sites, grading into more closed and humid forested habitats towards Southern Guinean regions. Between these different biomes a range of ecotonal mosaics exist. Spatial distribution of these mosaic habitats is highly dependent on environmental conditions and has been a main topic of discussion when trying to reconstruct past environmental conditions in West Africa (Jones, 1963; Hart and Hart, 1986; Cornelissen, 2002). Although past ecoregional boundaries are poorly understood, it can be hypothesised that boundaries primarily dividing savannah and forested areas were situated within a latitudinal axis parallel to the existing biome boundaries (Salzmann and Hoelzmann, 2005). For this reason, to explore and identify preserved Pleistocene archaeological sites, the southern margins of savannah environments are a good starting place. Of all the known and dated Pleistocene sites of West Africa, several gaps exist within interface areas between savannahs and forests. Of these, we identified Northern Benin as a location with high potential for the discovery of important new archaeological records, given its high density of undated Stone Age sites (Petit, 2005).

Northern Benin, more specifically the North-Western portion identified today as the Atakora Region, has sustained an increase in archaeological research in the past decades. This area has been surveyed and studied in the past for the presence of archaeological sites (N'Dah, 2009), uncovering a multitude of sites dated using material culture typology from the Early Stone Age to the Late Iron Age. Within its broader regional framework, this region can be identified as being located approximately 250 kilometres north of the current boundary between Sahelian savannas and Guinean forests. Furthermore, thanks to the extreme elevation differences (±450m) within the region caused by its topographic variations, the region includes patches of mosaic and forested areas located within the dominating savannah environment. Several of these environmentally-independent biome patches were identified and selected for further archaeological research. One of them, Tanongou Valley, produced the richest results.

The valley is located between the border of the Atakora Mountain Chain and the south-eastern margin of the Pendjari National Park, named after the Pendjari River that drains the region. The northern regions of Benin receive one season of rainfall, with peak precipitation between June-November, totalling 1100 mm annually, with Harmattan winds blowing from the north-east between December-March (Haggett, 2002). The altitude of the study area ranges between 200-650 m above sea level (Affaton, 1990). Geologically, this region falls within the Dahomeyide Orogen, located at the south-eastern margin of the West African Craton. The geology of north-western Benin comprises three major Neo-Proterozoic units with distinct boundaries from thrust faulting (from West to East): the Voltain Group, the Buem Group, and the Togo Group. The study sites are found within the metavolcanic and metasediment landscapes of the Togo group, which is predominately comprised of two units, a NE-SW aligned ridge formed of quartzite, sandstone and siltstone, within which the Tanongou Valley is found, and a basin comprising of quartzites, sandstones and conglomerates to the east of the ridge. Drainage within the basin comprises the headwaters of the Pendjari River which flows northwards (~350 m a.s.l.) before cutting through the ridge to the south of Compongou (~250 m a.s.l.), and flowing to the southwest, joined by the westward flowing channels that drain the ridge (150 m a.s.l.). The Pendjari River is a major tributary of the Volta River, draining the eastern region of the basin, and the boundary of the Togo Group geology marking the edge of this drainage from the Niger basin to the east.

Ecologically, today the region broadly falls within the West Sudanian Savannahs, dominated by grasslands and scrub, with isolated islands of Eastern Guinean Forest found at topographically high points within the landscape. These patches of Eastern Guinean Forests are what is found within the Tanongou Valley and other high-elevation valleys present within the ridges of the Atakora Chain. The Pendjari National Park was inscribed as a UNESCO World Heritage Site as part of the transnational W-Arly-Pendjari Complex, which provides an important international refuge for native fauna. A survey of large mammal species richness and abundance from April 2000 documented 20 species within Pendjari National Park in Benin, including *Papio anubis* (Olive baboon), *Syncerus caffer brachyceros* (West African savannah buffalo), *Alcelaphus buselaphus major* (western hartebeest), *Panthera leo leo* (West African lion), *Lycaon pictus manguensis* (West African wild dog), and *Loxodonta africana* (African bush elephant) (Sinsin *et al.*, 2002). Species richness and abundance of avifauna is high in Pendjari National Park, with 38 species of raptors identified in a 2004-2005 survey (Thiollay, 2007), and hundreds of small, medium, and large bird species (Borrow and Demey, 2002;

Dowsett-Lemaire and Dowsett, 2010) of scientific interest, as noted by Kassa et al. (2008).

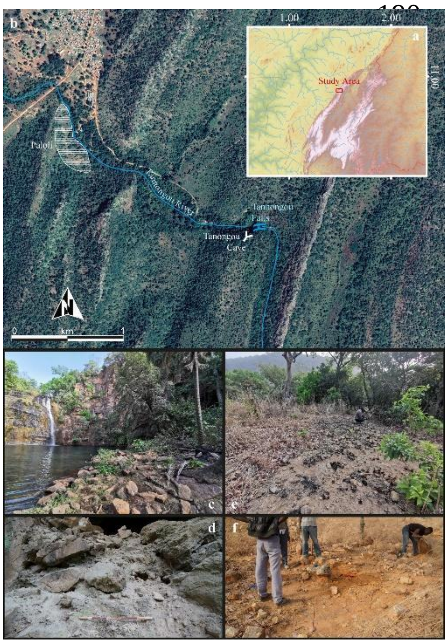


Figure 2. Upper section: study area location over altitude map of the Atakora Region (a) and site locations superimposed upon satellite imagery (Google Earth©) of the Tanongou Valley, with mapped fluvial systems (b). Lower section: Tanongou Falls, with plunge pool, and entrance of Tanongou Cave visible on the right (c); pre-cleaning area excavated during 2020 expedition (d); partial area of the Paloli sediment ramp, with opposing West-facing quartzite valley cliff (e); and T1 plotted grid, in the process of excavating square B2.

The Tanongou Valley measures approximately two kilometres in length, with a width of just over 450 metres at its widest point (figure 2). The valley starts on its western side with the Tanongou Falls, which drops into its plunge pool and feeds the Tanongou River. The plunge pool area consists of a circular cut into the quartzite cliff, and from which the Tanongou Cave is formed, with its entrance facing North-East towards the plunge pool. The valley ends at the entrance of the town of Tanongou, from which a road runs westwards in the valley reaching the Tanongou Falls. On the western side of the valley the cliff curves opening onto a series of flat terraces, within which the site of Paloli is located.

Although Paloli has not been documented before, the site of Tanongou Cave was previously excavated. L.P. Petit conducted excavations within the cave, as well as lower down the sediment slope behind the drip line in order to recover evidence of Iron Age occupations (Figure 3, Petit, 2005). Several hundred lithics were documented, of which 40 presented retouch (Petit, 2005). Although detailed analysis has not yet been carried out on the retrieved lithic assemblage, observations can be made based on the published illustrations and assemblage description. The majority of the previously excavated assemblage was described as containing flakes, discoids, and other tools. During our research no discoids were found, suggesting that Levallois materials were defined as discoids. Furthermore, the lithics that have been described as “other tools” seem to be comparable with our identification of retouched pieces retrieved at the site of Paloli, containing tools such as notched pieces and scrapers. Interestingly, the illustrated figures from Petit show the presence of a variety of débordant flakes , which together with retouched pieces were absent in the lithic assemblage from Tanongou Cave presented here. Petit mentioned a high percentage of flakes and debitage. His conclusion was that knapping activities were carried out in the cave, together with the use of the site as a shelter and living space.

Methods

The previously known sites of Kumaaku and Tanongou Cave indicated that the preservation of archaeological materials dating back to the Early Stone Age was limited yet present. For this reason, both sites were visited, although only Tanongou Cave still contained culturally -rich layers. As a result, a targeted survey of the Tanongou Valley and neighbouring areas was organised, specifically along the border between the Atakora Chain Formation and the Pendjari National Park. GPS systems were used to record any surface finds or exposed Pleistocene deposits. Stratified archaeological deposits outside of the valley were scarce, however the survey resulted in the location of Tanongou Cave, and the discovery of the new site of Paloli. Both sites were excavated using hand tools (i.e. trowels, shovels), applying a single context excavation methodology, and subdivided into 5 cm spits in the case of Paloli-T1. In Tanongou Cave lithics were plotted using a standard (x, y, z) spatial grid at 1 cm resolution. All excavated sediments were sieved using a 5mm mesh on site, and all finds were collected and labelled on site.

The finds were cleaned on site and imported to the Max Planck Institute for the Science of Human History, Jena, for analysis. The equipment used for analysis included a set of lamps and magnifying lenses, a scale, microscale, and a Mitutoyo caliper (150 mm, USB). The artefacts were recorded using the software E4 (https://www.oldstoneage.com/osa/tech/e4/). Recording was carried out using a .cfg file (Supplementary File 1) modified from the .cfg file published by Wilkins et al. (2017; Supplementary File 1). Selected lithics were illustrated (fig. 5) following photography with a Sony Alpha II camera using a Sony macro lens. Photographs were then imported into Adobe Illustrator 2021©. Lithic illustrations were subsequently accomplished following the Stone Tool Illustrations with Vector Art (STIVA) Method (Cerasoni, 2021). For other illustrations (fig 1-4): Plans drawn on-site (fig. 3-4), and other images such as satellite images (fig. 2), were imported onto Adobe Illustrator 2021© onto a base layer, and subsequently locked to use as reference. The figures were then drawn using vector objects. Once complete, the figures were exported in format .jpg at a resolution of

300dpi with RGB colour coding.

Two OSL samples were collected at Tanongou Cave by collecting coherent blocks of sediment, which were subsequently wrapped in light-tight material for transport to the laboratory. Both Tanongou Cave samples disintegrated in transit to Royal Holloway Luminescence Laboratory, meaning that light-exposed grains from the exterior of the sample block were mixed with material from towards the centre. In addition, the clast-rich nature of the sediments precluded the extraction of sufficiently large or regularly-shaped sample blocks to guarantee the presence of unexposed grains. Furthermore, since the samples were taken opportunistically from pockets of finer-grained material within a clast-rich sediment body, it is difficult to calculate an accurate environmental dose. Consequently, luminescence measurements were made to assess the potential for future geochronological work rather than with the expectation of producing absolute ages for the 2020 samples.

Single-grain measurements on quartz (optically stimulated luminescence, OSL) and K-feldspar (post-infrared infrared stimulated luminescence at 275 °C, $pIRIR_{275}$) were conducted using a Risø TL-DA-15 instrument following the procedures described in Supplementary Information C of Martinón-Torres *et al.* (2021). For each quartz sample, 2400 individual grains were measured, whereas 1200 grains of each K-feldspar sample were analysed. Data analysis was carried out using the calSARED() function in the R package *numOSL* (Peng *et al.*, 2013) and the calc-CentralDose() and calc_FMM() functions in the *Luminescence* package (Kreutzer *et al.*, 2012). Environmental dose rates were calculated using the Dose Rate and Age Calculator (Durcan, King and Duller, 2015) using alpha and beta counting data.

Results

Here we report the MSA layers and assemblages from the sites of Tanongou Cave and Paloli found within the Tanongou Valley, Atakora Region, Benin.

Tanongou Cave (10.802994, 1.442719)

Tanongou Cave is part of the western cliff line, overlooking the Tanongou Falls. In relation to the plunge pool, the cave is situated ~15 m South-East, with an altitude of 8 m from the water level during the dry season (fig. 3). The surrounding environment is consistent with most of the Tanongou Valley, and is identified as being typical Eastern Guinean Forest, with a medium canopy height of 10-15 m.

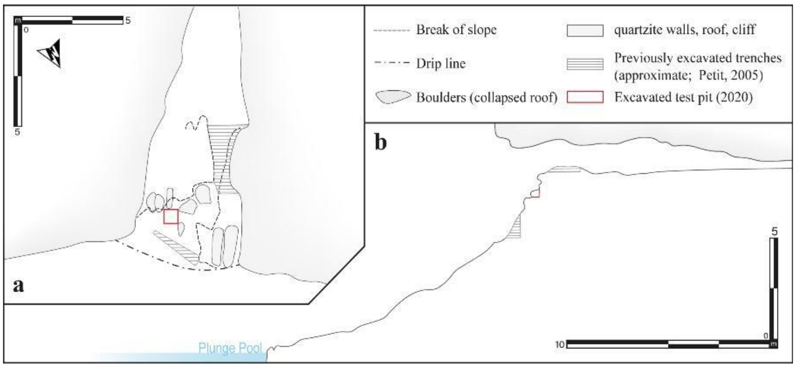


Figure 3. Top and lateral plans of Tanongou Cave (modified from Petit, 2005).

The cave appears to have formed as a result of fault/fracture induced weaknesses within the quartzite bedrock from which blocks have collapsed, generating a cavity. It is likely that the migration and retreat of the cliff line associated with the waterfall exposed these faults/fractures and initiated cave development. This mode of origin is supported by the block-like form of the cave, which consists of a flat and relatively regular roof form and relatively vertical walls. This implies an underlying structural control on its morphology.

The geometry and extent of the sediments that partially in-fill Tanongou Cave remains to be resolved, as the contact between the sediments and the cave floor was not observed and, as a result, the maximum thickness of the sediment sequence could not be estimated. However, a minimum of 3 m of consolidated cave sediments was observed *in situ*, with loose, overlying sediments concealing further depth to these deposits.

The sediment fill is very coarse in texture, consisting of a clast supported deposit which is either open framework (i.e. matrix poor) or closed framework (i.e. matrix rich) (fig. 4), with varying presence and concentration of a sand/silt matrix. The clasts range from small pebble to boulder in size, with the largest boulders being over a metre long. The clasts are uniformly angular in form, hence best identified as cemented breccias caused by intensified groundwater during the wet season. Although there is only poorly developed stratification with the sediments, some crude horizontal stratification does exist, produced primarily through the alternation of beds of open framework and closed framework breccias.

In view of previous investigations (Petit, 2005), a small trench of 75x75 cm was set up to examine the breccia deposits, close to the top break of slope (fig. 3). Preliminary cleaning of the trench surface recovered 16 lithic objects.

Excavations reached a depth of ~30 cm at its deepest point, with an average depth of 15 cm, revealing two sedimentary units. The first unit, Unit 1, was characterised by an open framework brecciated deposit with an observed depth of ~20 cm identified predominantly in the western portion of the trench with a loose, silty sand matrix. A sharp contact was observed with the underlying unit with a concave base. Low numbers of lithic objects were identified within Unit 1 (n=2). In contrast, Unit 2 was characterised by a closed framework brecciated deposit with an observed depth of ~30 cm, predominantly revealed in the eastern portion of the trench with highly concreted sediment and a gravel-sand matrix. A larger number of lithic objects were identified within Unit 2 (n=34), mostly concentrated within a single pocket consisting of almost exclusively lithic objects and an absence of clasts and matrix.

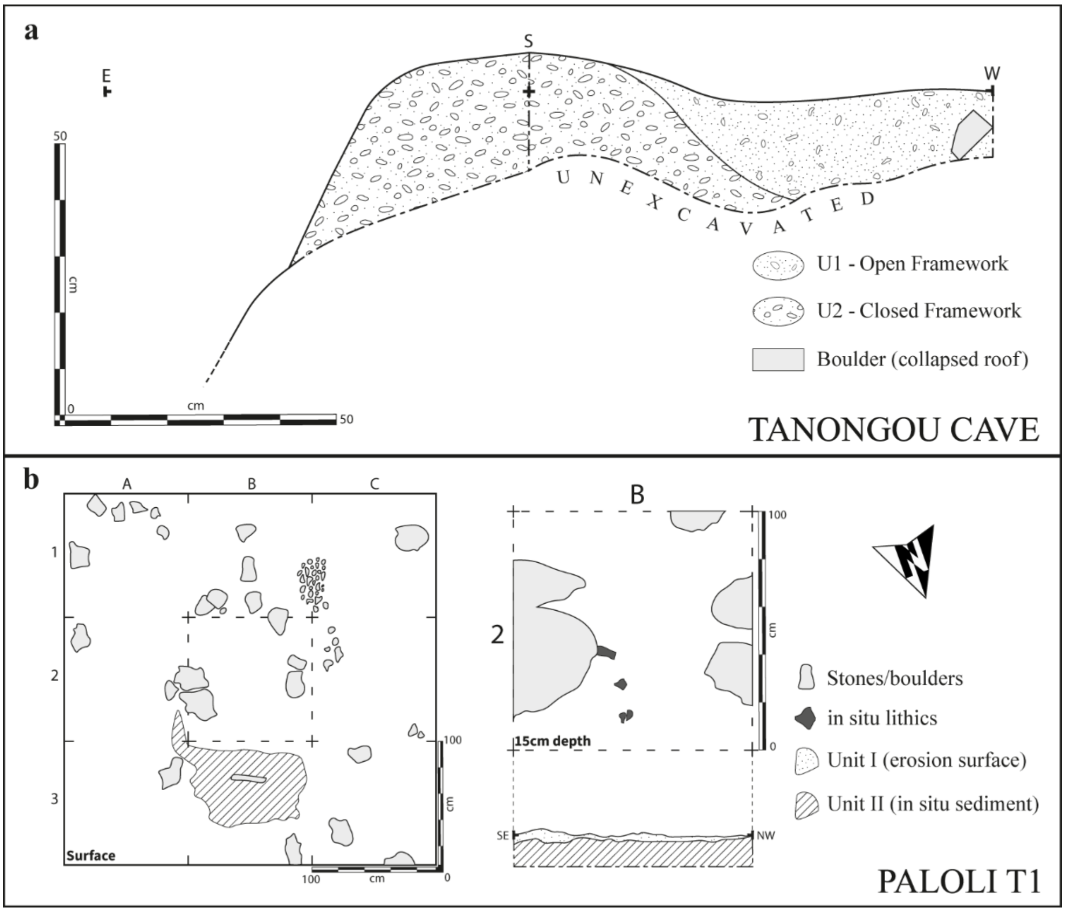


Figure 4: Upper section (a): Stratigraphical section of the 2020 excavation in Tanongou Cave (a). Lower section (b): 2020 excavation at Paloli T1; on the right, a top plan of T1 before excavation, and on the left, plan of the final surface reached after excavation of square B2 with its corresponding stratigraphical section.

Paloli (10.806272, 1.435230)

The newly discovered site of Paloli is an unfarmed and therefore undisturbed area, featuring an extensive surface lithic scatter, which extends for almost three hectares.

Paloli is set in a narrow floodplain surrounded on both sides by steep bedrock cliffs. A sediment ramp, very rich in lithic objects, occurs on the western side of the valley stretching down from the base of the cliff line to the edge of the floodplain, where a 1.5 metre step separates the surface of the ramp from the surface of the modern floodplain. The surface of the ramp is covered in boulders derived from bedrock cliffs, whilst surface walking shows that much of the ramp is made up of fine-grained sediments within which boulders and cobbles occur. The surrounding environment is different from the rest of the Tanongou Valley, with a more sporadic vegetation comparable in density to the Pendjari wooded savannah biome.

During the investigation of the floodplain site, four discrete areas were studied, and labelled T1-T4. T1 and T2 were arbitrary planned grids, respectively 3x3 m and 5x4 m in size, where surface lithics were collected from grid squares (1x1 m) and bagged for further study. The lithics collected from T2 were subsequently brought to the University of Abomey-Calavi, Cotonou, to generate a teaching collection. The surface collection of lithics from T1 resulted in a total of 134 lithic objects. Due to a high concentration of artefacts, the central grid square (B2) was selected for excavation.

The excavation reached a depth of ~15 cm, revealing two sedimentary units, and retrieving a total of 44 lithic objects. Unit 1 (spit 1) was composed by a thin disturbed deposit, with a maximum thickness of 4cm, and with disconformable contact with the underlying unit. Unit 2 (spit 2 and 3) was characterised by homogeneous, unstructured red fine sand and silt mix. Given the high number of lithics retrieved in spit 1 (N=33), together with its sedimentary characteristics, we hypothesise that Unit 1 is an erosional product of Unit 2 caused by deflation of the latter. The base of Unit 2 was not reached. Furthermore, the visible exposed sections of the surface ramp in other areas of Paloli have very similar colour and texture compared to Unit 2, suggesting a minimum depth of at least 1.5m.

The 1.5 m step between the sediment ramp of Paloli and the modern flood plain was investigated and facilitated the inspection of the sediment deposits. A section of the step was selected, labelled as T3, for further investigation of site geomorphology. The sediments exposed at the base of the ramp show that the landform was comprised of fine-grained sediments (silt/fine-sand in texture). The sediments were homogeneous and unstructured, characterised by a strong red colour, representing a high concentration of iron rich clay which decreased downward through the profile. The top of the unit was indurated because of the high clay concentration, indurations which were also present throughout the entire surface of Paloli. The base of the sediment was more friable, with the presence of clay restricted to root channels and pores.

Inspection of the sediment sequence of T3 identified the presence of *in situ* lithics. The artefacts appeared within discrete layers and are of significantly larger size than the host sediment, hence making it unlikely to have been transported into the site over any large distance. A cluster of eight *in situ* lithics were found between 80-100 cm below the land surface, and immediately above the dating sampling location for sample OSL1.

The final studied area, T4, consisted in a single find spot found on the Northern edge of the Paloli surface area. The location yielded seven lithic objects, and evidence of metal working by the retrieval of slag fragments. No further investigation of the area was conducted.

Chronometric Dating

Environmental dose rates calculated for the two Tanongou Cave samples were ~3.6 Gy/ka (quartz) and ~4.6 Gy/ka (K-feldspar). These dose rates are relatively high, and suggest that beyond ~30 ka (~100 Gy) K-feldspar could be the most reliable dosimeter for luminescence measurements. Using standard single-grain rejection criteria (~25% of grains measured for each of the Tanongou quartz samples displayed acceptable luminescence properties for age determination. For K-feldspar grains, the equivalent value is ~75% of grains measured. Both yields are at the higher end of the range reported in the literature, implying that luminescence dating approaches could successfully be applied at Tanongou Cave, and by extension in the surrounding area. However, in the case of the 2020 samples, equivalent dose distributions confirm the suspicion that block disintegration in transit rendered them undatable. Quartz samples yielded overdispersion values of 95% and 101% whereas equivalent values for K-feldspars are 103% and 105%. Analysis of the datasets using the Finite Mixture Model suggests that 5-6 populations are statistically supportable However, the age determined using the dominant component (~25 % of grains for K-feldspar and ~50 % for quartz) is not consistent between minerals, as might be expected if grains at the core of each sample retained a luminescence signal reflecting their true burial age. It is not possible to determine whether this results from some bleaching of all quartz grains during sampling and transport, or incomplete bleaching of the less-bleachable K-feldspar signal prior to deposition. Consequently, it is not appropriate to provide even tentative luminescence age estimates using the Tanongou Cave samples. Nonetheless, the data described above suggest that if coherent/or unexposed samples could be collected, e.g. by consolidation in the field or sampling under a light proof covering, luminescence dating should be successful at this site.

Lithic Analysis

Our 2020 field expedition recovered a total of 243 lithic objects from the sites of Tanongou Cave (N=50) and Paloli (N=193). Both sites feature classic MSA technological characteristics (table 1, figure 5). The percentage of Levallois flakes varies from an extremely high 40% in Tanongou, to an overall high average of 13% for Paloli (table 2). Levallois points (N=2) were excavated at Tanongou Cave and there is a low representation of Levallois cores in the Tanongou Valley generally (Table 4). Only four Levallois cores were retrieved at Paloli, of which only one was *in situ*, and none were found at Tanongou Cave. Paloli presents plain platform, discoidal and core-on-flake cores, while Tanongou presents only core-on-flake morphologies (table 4). This suggests on site production of non-diagnostic flakes. Furthermore, all lithics were subjected to visual analysis for the identification of heat exposure, however no indications of heat exposure were identified in either of the two assemblages.

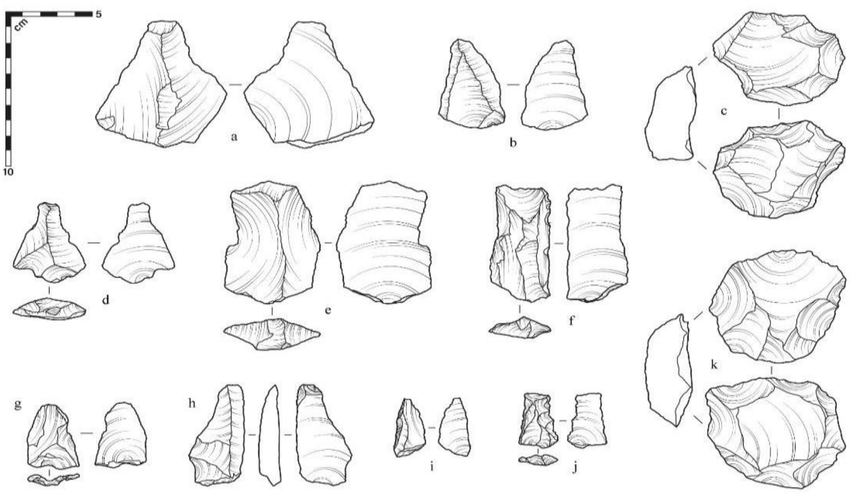


Figure 5: Examples of lithic objects excavated at Tannongou Cave (a-f) and Paloli (g-k). a,

e, f, g, j: Levallois flakes; b, d: Levallois points; c, k: Levallois cores; h: end scraper; i: backed piece.

A variety of raw material types were used, all of metamorphic origin. They include quartzite, quartz, jasper, chert and a series of metamorphic materials which are yet unidentified (figure 6). Cortex variability is high (table 3), indicating the use of materials from primary deposits (i.e. local quartzite outcrops) as a primary resource, and subsequently the use of alluvial materials identified as sub-rounded to rounded cobbles (Supplementary File 2). The predominant raw material used is quartzite, which is available in the immediate vicinity of the sites and beyond, as it is the primary constituent of the Atakora Chain formation. Quartz is also prevalent in the site of Paloli, while it is absent in Tanongou Cave. Cortex on quartz lithic objects suggests a primary collection of this raw material from alluvial deposits, supposedly originating from quartz vein formations present within the primary quartzite formation. Finally, siliceous raw materials such as jasper and chert, present in both sites, presented only angular cortex, suggesting surface outcrop collection. Our analysis of cortex presence (table 3) indicates that they were collected from surface outcrops although none were identified while surveying the Tanongou Valley. This may suggest that the artefacts were transported to the site from beyond the immediate landscape. It is possible that the raw material blocks or already worked lithic objects were transported from the northern region of Pendjari Park, where outcrops of chert and jasper have been documented in association with other Stone Age sites (N’Dah, 2009).

Raw Material Makeup (%)						
Site	**Context**	**Quartzite**	**Quartz**	**Jasper**	**Chert**	**Other**
PAL20	T1 surface	63	27	9	-	1
	T1-B2 spit 1	48	39	-	-	12
	T1-B2-spit 2	100	-	-	-	-
	T1-B2-spit 3	71	14	14	-	-
	T3	100	-	-	-	-
	T4 surface	86	14	-	-	-
TAN20	surface	38	-	-	56	6
	U1	50	-	50	-	-
	U2	53	-	38	-	9

Retouched Artefacts									
Site	**Retouch Type**	**Quartzite**		**Quartz**		**Jasper**		**Other**	
		%	N	%	N	%	N	%	N

PAL20	Scraper	47	8	29	5	18	3	6	1
	Notched	67	2	33	1	-	-	-	-
	Backed	-	-	100	1	-	-	-	-
	Minimal	71	5	29	2	-	-	-	-
TAN20	Minimal	-	-	-	-	-	-	100	1

Table 1: Breakdown of raw material input (count in percentage) and retouched lithics by raw material makeup as percentage of total site assemblage and count.

Site	Context	Outcrop	Cobble	Presence per layer (%)
PAL20	T1 surface	19	5	**21**
	T1-B2 spit 1	6	-	**2**
	T1-B2-spit 2	-	-	**-**
	T1-B2-spit 3	-	-	**1**
	T3	1	-	**1**
	T4 surface	-	1	**2**
	Total	**26**	**6**	**17**
TAN20	surface	-	-	**-**
	U1	-	-	**-**
	U2	-	2	**6**
	Total	**-**	**2**	**4**

Table 2: Count of lithic objects with identified cortex, and percentage of lithics with objects in relation to total count of layer and site. The type of cortex was determined based on cortex roundness: (1) angular-subangular for outcrops, and (2) subrounded-rounded for cobbles.

Retouched lithics are predominantly made from quartzite and quartz, suggesting that they were produced locally. Furthermore, several of the quartz scrapers recovered were made from debitage, suggesting a preference of the latter as blanks for scrapers. Paloli also contained other retouched types, including notched pieces, minimally retouched pieces, and a single backed quartz piece (figure 5). Interestingly, in Tanongou Cave we recovered only one single retouched piece, identified as a minimally retouched flake.

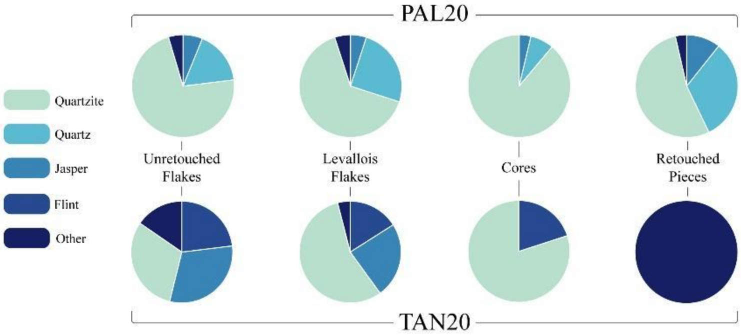


Figure 6: Breakdown of major raw material classes by artefact class.

Overall, the density of lithic artefacts varies depending on the site. Tanongou Cave presented a very high percentage of retrieved artefacts, with a total of 34 *in situ* artefacts, and an excavated volume of approximately 34 litres of sediment. Most lithics were recovered within Unit 1 (approximately 16 litres of sediment, N=32), where most lithic objects were concentrated within a single pocket. On the contrary, Paloli had a much lower retrieval rate, with a total of 44 *in situ* artefacts from 150 litres of excavated sediment. These differences raise the possibility of different activity types within the sites of Paloli and Tanongou Cave, although further analyses into the site's formation processes and possible post-depositional/erosional activities are necessary.

	Context	Unretouched Flakes	Levalloi s Flakes	Flake Fragments	Retouche d Pieces	Cores	Shatte r	Total Count
PAL20	T1 surface	47	11	16	18	21	21	**134**
	T1-B2 spit 1	9	5	3	6	2	8	**33**
	T1-B2-spit 2	3	-	-	1	-	-	**4**
	T1-B2-spit 3	3	1	1	1	1	-	**7**
	T3	2	1	2	1	1	1	**8**
	T4 surface	1	2	0	1	2	1	**7**
	Total Count	**65**	**20**	**22**	**28**	**27**	**31**	**193**
	%	34	10	11	15	14	16	-
TAN20	surface	7	7	1	-	1	-	**16**
	U1	1	1	-	-	-	-	**2**
	U2	5	17	3	1	4	2	**32**
	Total Count	**13**	**25**	**4**	**1**	**5**	**2**	**50**
	%	26	50	8	2	10	4	-

Table 3: Breakdown of lithic objects by major artefact class, site and layer, with total count per layer and percentage of artefact classes present for each site.

Levallois Technological Presence (%)				
Site	**Context**	**Levallois Flakes**	**Levallois Cores**	**Average**
PAL20	T1 surface	9	1	**5%**
	T1-B2 spit 1	15	3	**9%**
	T1-B2-spit 2	-	-	**0%**
	T1-B2-spit 3	14	-	**7%**
	T3	13	-	**6%**
	T4 surface	29	14	**21%**
	Average	**13%**	**3%**	**8%**
TAN20	surface	44	-	**22%**
	U1	50	-	**25%**
	U2	53	-	**27%**
	Site average	**40%**	**0%**	**20%**

Table 4: Levallois technological presence in percentages of Levallois flakes and cores, and respective averages for technological type and context.

Site	Context	Single Platform	Opposed Platform	Discoidal	Levallois	Core-on-flake	Total Count
PAL20	T1 surface	5	8	3	2	3	**21**
	T1-B2 spit 1	-	-	-	1	1	**2**
	T1-B2-spit 2	-	-	-	-	-	**-**
	T1-B2-spit 3	-	1	-	-	-	**1**
	T3	-	-	1	-	-	**1**
	T4 surface	-	-	-	1	1	**2**
	Total Count	**5**	**9**	**4**	**4**	**5**	**27**
TAN20	surface	-	-	-	-	1	**-**
	U1	-	-	-	-	-	**-**
	U2	-	-	-	-	4	**-**
	Total Count	**-**	**-**	**-**	**-**	**5**	**5**

Table 5: Breakdown of core types by removal strategy.

When comparing the lithic assemblages from Tanongou Cave and Paloli to other assemblages in the region, it should be noted that many excavated collections remain unpublished and poorly understood. Unfortunately, very few MSA assemblages published from West Africa come from *in situ*, stratigraphic excavations (Paradis, 1980; Ljubin and Guédé, 2000; Huysecom, 2014; Lebrun, Tribolo, *et al.*, 2016; Niang *et al.*, 2020; Scerri *et al.*, 2021). Nevertheless, our preliminary findings generally display the sites of Tanongou Cave and Paloli as typical West African Middle Stone Age sites. Notably, sites in similar savannah-dominated eco-regions, such as the Jos Plateau (Zenabi, Mai Lumba and Yada Gungume; Allsworth-Jones

2019), have very similar assemblages, both in terms of artefact classes and tools types.

Discussion

The sites of Tanongou Cave and Paloli both represent the first MSA sites of their kind. Both sites are situated with an environmental ecotone comprised by a forested island within a savanna-dominated environment, and are characterised by deep (>3.5m in Tanongou Cave and >2m in Paoli) stratigraphies with a high density of material culture. Furthermore, Tanongou Cave represents the first and only yet known MSA cave site in West Africa, showing the potential for more discoveries of this kind in the future. The location of this unique cave site in very close proximity to an extensive open-air site, Paloli, offers an invaluable picture into West African MSA hominin presence and behaviour. Furthermore, MSA caves and rock shelters sites are extremely common in other regions of the African continent, and the identification of the first site of this kind in West Africa represents an important new asset for comparability of MSA assemblages and hominin cultural and environmental behaviour in Africa.

The similarity of the lithics and production methods may suggest that past MSA activity at both sites was broadly contemporary. Although the lithic assemblages are similar enough to be considered as part of the same technological tradition, the typological and raw material differences in the two assemblages indicate Tanongou Cave and Paloli were perhaps dedicated to different activities. Furthermore, the seasonal variability between wet and dry seasons suggests that, while Paloli was accessible all year around, Tanongou Cave could only be reached during the dry season. This further supports the difference in material culture and on-site activity. The lack of lithic cores and waste material (debitage) of non-local raw material types indicates the transportation of completed pieces into the Tanongou Valley from neighbouring areas. Raw material outcrops which contain comparable non-local raw materials found in the Tanongou Valley have been identified over 50km away from our study area (N'Dah, 2009). This implies the wide movement range of MSA people in the Tanongou Valley, further supporting their possible seasonal movement throughout the landscape.

Although seasonality is an important factor in regards to the lithic assemblage, it should also be considered within the eco-regional perspective of the Tanongou Valley. The modern micro-refugial character of the site, characterised by a densely forested environment within a dominant Sudanian savannah, likely made it an attractive location for MSA populations.

Habitation in ecotonal environments has clear practical benefits, including a wider selection of resources and an increased resilience to climatic variability (Hart and Hart, 1986; Avery, 2001; Roberts and Stewart, 2018; Roberts *et al.*, 2020).

Further work to be carried out in the Tanongou Valley will lead to the clarification of complex human and environmental shifts which occurred at this site. Given the very high density of material culture and the unique ecological footprint of this area, Tanongou Cave and Paloli are expected to become key West African sites, further unravelling the unique and diverse evolutionary and cultural trajectories of this important African region.

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Supplementary Materials:

1. cfg file

2. recorded lithic data (database attached in Supplementary 3) measure variable list below:

List of variables recorded during lithic analysis		
SiteCode	FractureInitiationPoint	Face2TerminationFinalRemoval
Context	FissuringOnPlatform	Face3CortexArea
PlottedFindNumber	PlatAbrasion	Face3DorsalScarCount
LithicArtifactClass	PlatformDelineation	Face3ArisOrientation
RawMaterial	BulbLength (if present)	Face3CoreExploitation
Completeness	PlatformMorphology	Face3DorsalDirection
UnretouchedPoint	RetouchedPieceBlank	Face3LengthOfFinalRemoval
CortexArea	RetouchedPieceTypology	Face3WidthOfFinalRemoval
CortexLocation	RetouchType	Face3RemnantPlatformOfFinalRemoval
PlatformCortex	RetouchEdgeAngle	Face3TerminationFinalRemoval
CortexRoundness	DiameterOfLargestNotch	Face4CortexArea
CortexType	CoreHammerCompleteness	Face4DorsalScarCount
Mass	NumberCoreFaces	Face4ArisOrientation
MaxLength	Face1CortexArea	Face4CoreExploitation
MaxWidth	Face1DorsalScarCount	Face4DorsalDirection
TechLength	Face1ArisOrientation	Face4LengthOfFinalRemoval
MaxTechWidth	Face1CoreExploitation	Face4WidthOfFinalRemoval
MaxThickness	Face1DorsalDirection	Face4RemnantPlatformOfFinalRemoval
MidThickness	Face1LengthOfFinalRemoval	Face4TerminationFinalRemoval

PlatformWidth	Face1WidthOfFinalRemoval	CoreBlankSphericity
PlatformThickness	Face1RemnantPlatformOfFinalRemoval	IntendedProduct
DorsalDirection	Face1TerminationFinalRemoval	ConardUnifiedType
ArisOrientation	Face2CortexArea	VolmanTypeOne
DorsalScarCount	Face2DorsalScarCount	VolmanCoreForIntersectingScars
DorsalPrep	Face2ArisOrientation	VolmanCoreForParallelConvScars
ProfileShape	Face2CoreExploitation	CompletenessOfBackedPiece
FlakeTermination	Face2DorsalDirection	BackedPieceTypology
MarksVentralSurface	Face2LengthOfFinalRemoval	BackingDistribution
NumberPlatformScars	Face2WidthOfFinalRemoval	
PlatformPrep	Face2RemnantPlatformOfFinalRemoval	

"Refugium or not a refugium? Rainforest perspectives
On the role of African refugia in human evolution"

Refugium or not refugium? The role of refugia in African human evolution

1. Introduction

Refugia have been widely invoked in ecology, population biology, conservation biology and biogeography to explain aspects of evolution and demography. At its most general definition, a refugium is a geographically finite area which supports either an isolated, or a relict population of a once more widespread species, with biological, ecological and behavioural consequences. This isolation can be the result of topographic change, climatic change, or human activities.

Although largely used for understanding present ecosystem stability and change, the refugium-concept is also an important explanatory factor in models of past ecological change. In the 1950s, the term "refugia" was first used by palynologists studying observations of the contraction of plant ranges during the Late Glacial Maximum (LGM, ~25.5-19 kya) in North America (Heuesser 1955). Since then, refugium-driven changes in speciation, demography, distribution and behaviour of organisms have become a key focus in Quaternary Science. To date, this concept has been broadly applied in a variety of palaeoenvironmental and geographical research, temporally extending from Holocene to Pleistocene ecological studies all around the world (Fedorov and Stenseth 2002; Wüster et al. 2005; VanDerwal et al. 2009; Lowe et al. 2010; Williams et al. 2013). Palaeoanthropology is no exception, and refugia have been invoked to explain processes as diverse as speciation (Stewart and Stringer 2012), cultural efflorescence and collapse (Scholz et al. 2007, Wadley 2013, Ziegler et al. 2013) and hominin dispersal (Basell 2008, Lahr 2012).

These diverse palaeoanthropological studies have precipitated important advances. However, they have also catalysed the need to refine and test refugia-based models. In the paleoanthropological literature, a refugium is typically defined as an area where either a distinct hominin species or local population survived for an entire glacial-interglacial cycle (Hewitt 1996, Hewitt 2000, Harvati et al. 2009, Stewart and Stringer 2012, Cordova et al. 2013). This definition is helpful in that it is broad enough to encapsulate the diversity of possible examples. However, in terms of model testing, it arguably conflates a refugium with its consequences, leading to problems of inference. Despite this widespread use, explanatory models involving refugia are rarely presented with a set of contrasting expectations, including a null hypothesis. It is also unclear how such models are being operationalised. For example, a refugium can be conceptualized in terms of a few general processes, including changes in orbital parameters and anthropogenic actions (Sergin, 1980; Clement et al. 1999, Ruddiman 2001, Rosenzweig 2008). However, the properties affected by those processes are highly diverse. A given species may have biological, demographic and cultural trends that are positive, negative or neutral; they may also involve many different manifestations of such underlying processes, including for instance, morphology, physiology, behaviour, demography and culture.

Here, we offer a critical review of the various definitions of refugia used in palaeoanthropology, and create a novel theoretical framework for the study of refugial zones. We focus on how the refugium-concept can be used for the better understanding of past hominin behaviour and environments, evaluating to what extent existing archaeological and palaeoenvironmental records can demonstrate the presence of refugia in the past. We critically explore how past refugia can be identified and the degree to which refugia had an impact on populations in the past.

2. Deconstructing Refugia

As will be shown in this paper, the definition Refugia has undergone substantial interpretations and applications from its definition in ecological literature in the nineteenth century to present day. In order to develop an all-encompassing and over-arching meaning of refugia, it is important to understand both the ecological setting of a refugia as well as its specific parameters relevant to humans. Different types of refugia have been previously defined and described based on their ecology, and can be summarised into four major groups: relic, classic, cryptic and micro refugia (see figure & table 1). These major groups are categories summarised and extrapolated from all the discussions and theories that exist on the refugium-concept, both within the field of palaeoanthropology, and other ecological-based disciplines such as conservation biology, ecology, and palaeoecology (Bennett & Provan 2008, Mujica et al. 2010, Horsak et al. 2015, Tang et al. 2018, Hewitt 2000, Sommer & Nadachowski 2006, Bhagwat & Willis 2008, Haffer 1969, Cordova et al. 2013, Willis et al. 2000, Stewart and Lister 2001; Willis and van Andel 2004, Brochmann et al. 2003 Bennett, 1985, Magri 2008, Rull 2009, Rull 2010, Dobrowski 2011). Many sub-types and variations of these categories exist, although they fundamentally all fall within one of the four groups.

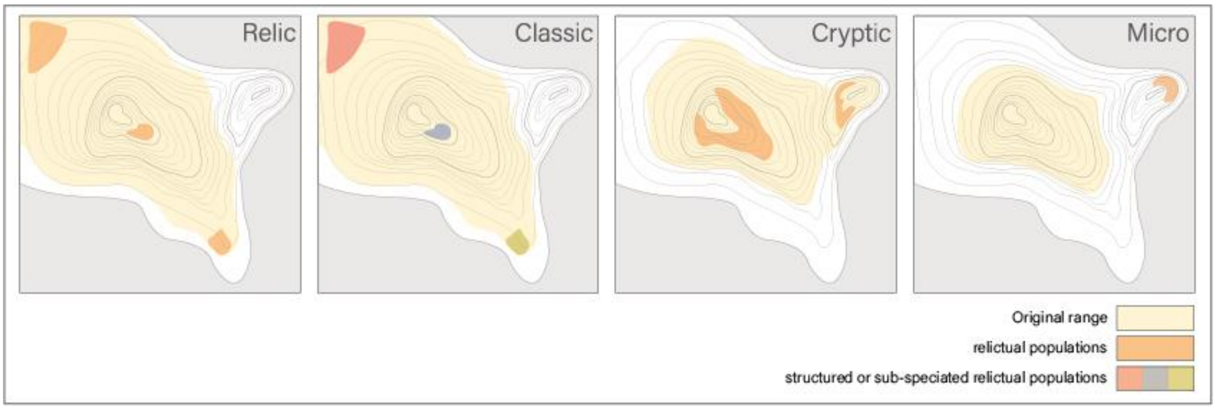

Figure 1 – Visual representations of the four main refugia concepts.

Concept	**Definition**	**To note**	**References**
Relic Refugia	Locations which support a *relict population,* i.e. of a once more widespread species.	Populations and taxons that occur in restricted areas (once refugial zones), whose original ranges were far wider are **relictual** populations and taxons.	Mujica et al. 2010 Horsak et al. 2015 Tang et al. 2018
Classic Refugia	A refugium is a geographical area where a population, species, or community has survived *environmental instabilities* over long periods of time.	Differentiated from Relic Refugia in that the populations may be widespread, but strongly structured or sub-speciated. Sub-types exist solely differentiated based on the environmental context within which the refugia is being identified, and they include: a. Glacial refugia b. Tropical refugia c. Desert glacial refugia	Glacial – Hewitt 2000, Sommer & Nadachowski 2006, Bhagwat & Willis 2008 Tropical – Haffer 1969 Desert glacial – Cordova et al. 2013
Cryptic Refugia	Populations in *'patches' of favourable microclimates* within areas at higher latitudes previously regarded as being inhospitable	Mostly used in the Southern hemisphere, especially in Amazonian ecology and the study of bird species in the Americas.	Willis et al. 2000 Stewart and Lister 2001 Willis and van Andel 2004
Micro Refugia	Small areas with local favourable environmental features, in which small populations can survive outside their main distribution area (macrorefugia), protected from the unfavourable regional environmental conditions	Three main types can be differentiated: 1. Distal or remote (Brochmann 2. Diffuse or widespread 3. Proximal or ecotonal	General – Rull 2009, Rull 2010, Dobrowski 2011 Distal or remote – Brochmann et al. 2003 Diffuse or widespread – Bennett, 1985 Proximal or ecotonal – Magri 2008

Table 1 – Main definitions and concepts of Refugia

Refugial concepts, and subsequently their definitions, are either based on a specific effect or a specific driver. The four types of refugia can therefore be explained as follows:

(a) Relic refugia is defined by the presence of relict populations, characterised by a limited distribution compared to the previous species' range (figure 2). The relictual nature of species' populations is the effect that illustrates this refugia type, and that can be caused by a multitude of undefined drivers, such ecological, climatic or anthropogenic. It is important, when talking about relic refugia, to not confuse relictual zones from relictual populations or bottleneck events, as they might seem the same from the paleoanthropological record, but they latter do not fit within the definition of refugia (figure 2).

(b) Cryptic refugia is also defined by an effect, identified as the survival of isolated populations within confined locations, or 'patches'. Also in this case no specific drivers are described, although the ecological setting is well-defined as being applied exclusively to high-altitude environments which were previously inhospitable. This ecological constraint is however dependent on drivers, which are identified as ecological and climatic changes that cause high-altitude environments to become hospitable.

Contrary to these refugia concepts, Classic refugia and Micro refugia are solely defined based on the drivers that generate refugial zones or populations.

(c) Classic refugia, as its name implies, was directly developed from the very first applications of paleoecological studies for the identification of refugial zones. This origin led to this refugia concept to be solely driver-dependant, being defined by a geographical location which has supported populations by being ecologically stable during phases of environmental instability over long periods of time.

(d) The definition of classic refugia is comparable to the final refugia concept, **micro refugia**, for which the same driver is applicable and where the concept is driver-dependant. The only difference lies in the scale of the geographical location, which must be smaller in size compared to the original distribution range, and in which specific populations must be protected from environmental instability in a refugial zone. Probably not applicable to humans (body size thresholds of some kind).

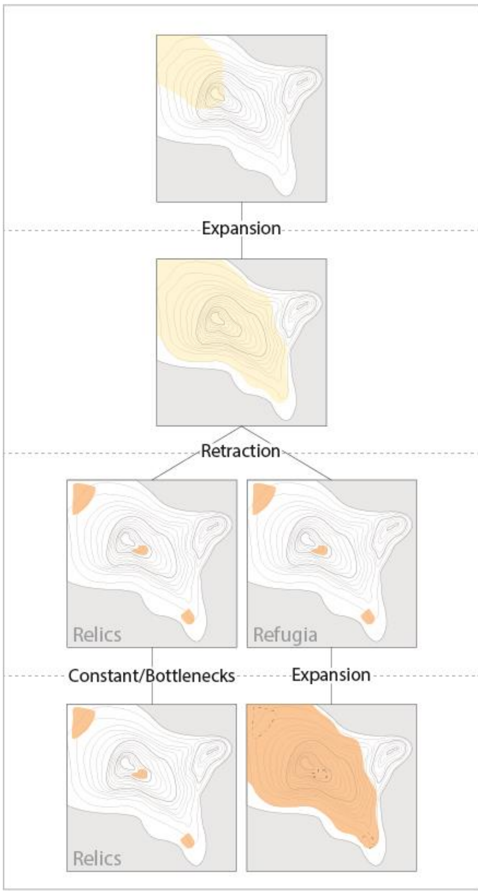

Figure 2 – Visual representation of the differentiation between relictual populations (relics) and refugial populations (refugia) based on their retraction and expansion in time.

From these descriptions of the various refugia concepts it is clear that problems exist as a consequence of the identification and definition inconsistencies between the various types. Better definitions should be developed, creating comparable and consistent concepts, through the application of a quantifiable approach, so to aid their identification no matter their ecological or chronological contexts.

3. Building a theoretical framework for human behaviour and environmental context

It is clear that the non-structuralisation of refugia theory is detrimental to its standardisation and operalisation. Nevertheless, by taking into account what has been already studied and applied, both from a methodological and theoretical perspective, a framework can be constructed as a first step towards the objective of this paper. First and foremost, a theoretical framework is fundamental to construct and determine the basic parameters for the identification and study of refugial zones and populations in the paleoanthropological record. As the objective of this work is to create an operationisable model for refugia in the past, the parameters that will be developed and explained are all based on proxies and measurable variables.

(a) Environmental gradient

Environmental variability is of course the fundamental parameter upon which the refugium-concept is based. In order to understand human behaviour within a specific landscape through time, a detailed understanding of the environmental gradient is necessary. This can be interpreted as being the variability, or shift, of any environment from a specific habitat to a different one. Environment gradients can be analysed and determined based on a variety of proxies that are commonly used in palaeoanthropology including, but not limited to, palaeobotanical, isotopic, paleoclimatic and geomorphological analyses.

(b) Time

Time has to be taken into account when developing an operationalisable model for refugia. Given the great variability in case studies and contexts that the refugium concept can be applied to, time will have to be totally dependent on specific geographic, archaeological and chronological contexts. For this study, a time sub-division into generational turns (30 years), with a time span of 30 to 300.000 years is considered.

(c) Resilience

Resilience theory has been a staple theoretical sub-field of archaeology for decades (REFS). The basic definition of resilience in archaeological terms is the continuity, development or disruption of population dynamics, material culture and settlements. The application of this already tested and accepted theoretical framework will help solve in advance problems and shortcomings of the palaeoanthropological and archaeological record, such as the lack of physical records and extensive data-driven interpretations.

(d) Size

Refugial zones and patches, although extensively referenced and included in many of the refugial concepts and literature presented in this paper, have never been thoroughly studied nor considered from a size-dependent standpoint. Although this parameter is highly variable upon geographic and chronological context, it is important to keep in mind how the size of the refugial zone could be important for the successful creation, stability and termination of refugial zones. Simple spatial expectations, in terms of topography and geography, have to be set before any further evaluation of refugia (figure 3).

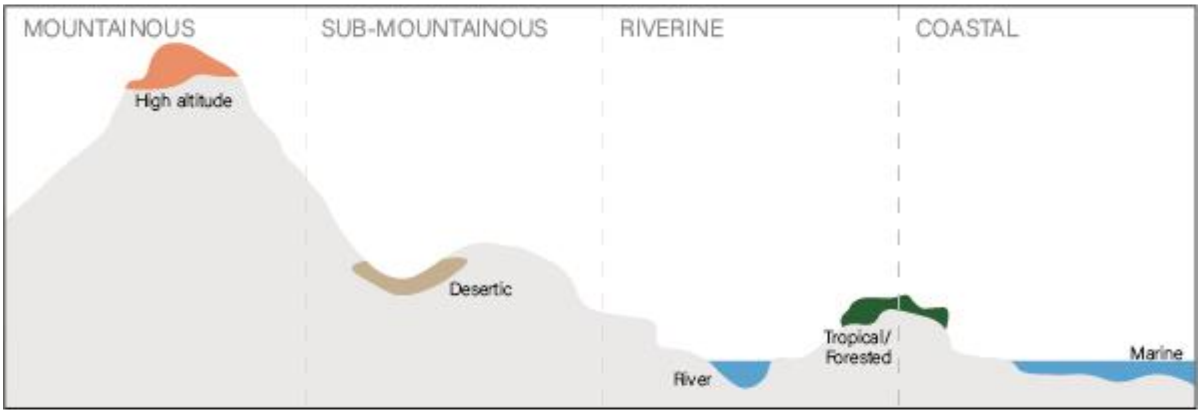

Figure 3 - Topographic and geographic features that should be considered when creating a simple spatial expectations of size as a parameter for the developed of a refugia prediction model.

(e) Application of the refugial explanatory model

Explanatory models can be hypothesised based on a purely theoretical framework constructed upon contrasting expectations developed on the observable relationship between the different parameters. Said expectations will not include size as a parameter, as it is yet a variable poorly understood and understudied. The use of size would make it too complicated and not applicable to most, if not all, case studies that were wished to be analysed using the proposed model. Furthermore, factors as dependency on regional context and available data make size not universally applicable and difficulty applicable.

To make the *following* model operationalisable, a single scale of magnitude was set, going from low to high, and the parameters were plot onto it based on the single parameters' gradients (figure 4). The relationship of the three scales will, ideally, offer insight on the expectations that should be constructed based on the individual case studies. Although the set values could be interpreted and applied in a variety of ways, these linear expectations are meant to be considered as guidelines for a novel way to view human activity in the past, and in particular the relationship between human behaviour and ecological shifts.

For a better visualisation of human resilience based on ecological gradient and time, or to better say speed of change, figure 4 has been constructed, presenting hypothetical relationships between the various parameters. Resilience is used as means of interpretation of human behaviour, as it encompasses its two major aspects: technological behaviour and mobility patterns. It was originally defined and used for the conceptualisation and operationalization of the Adaptive Cycle Model (Bradtmoller et al., 2012; Yustov & Martin, 2015; Bradtmoller et al., 2017). The expectations for human resilience based on ecological gradient and time are direct, yet simplistic, and based on the hypotheses that humans experience major behavioural changes when the ecological change is drastic or when the change is fast. These behavioural responses can be visualised three dimensionally (figure 5), showing how the pattern of human resilience can vary independently from the parameters it is based on.

The operationalisation of this model should therefore be applied following a step by step process, starting from: (1) the compiling of appropriate paleoecological and paleoanthropological literature for a theoretical groundwork of an area, population or context that is to be studied, (2) an outlining of the basic parameters (environmental gradient, …. And size if applicable), (3) the determination of magnitudes for each parameter, (4) the interpretation of relationships between the various parameters to theorise, and (5) establishment of a theoretical system within which datasets and direct observations can be visualised and interpreted.

Building on this, we evaluate the application of refugia theory in palaeoanthropology, and provide a case study from West Africa.

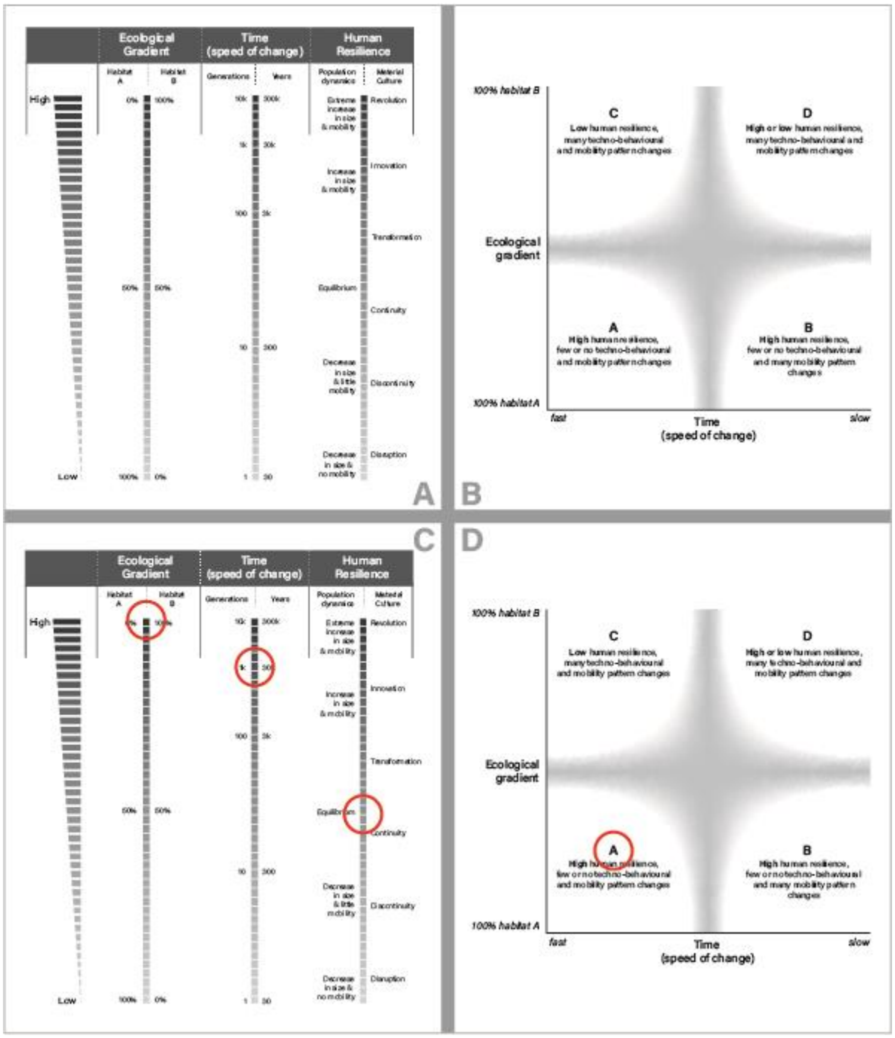

Figure 4 – (A) breakdown of the three parameters used for the predictive refugial model, (B) general predictions of the human resilience model based on ecological gradient variation and speed of change in time, (C and D) example of applied model A and B showing relationship between the parameters and the general predictive model for human resilience. (model B adapted from Dyson-Hudson and Smith, 1978, & Marean, 2016)

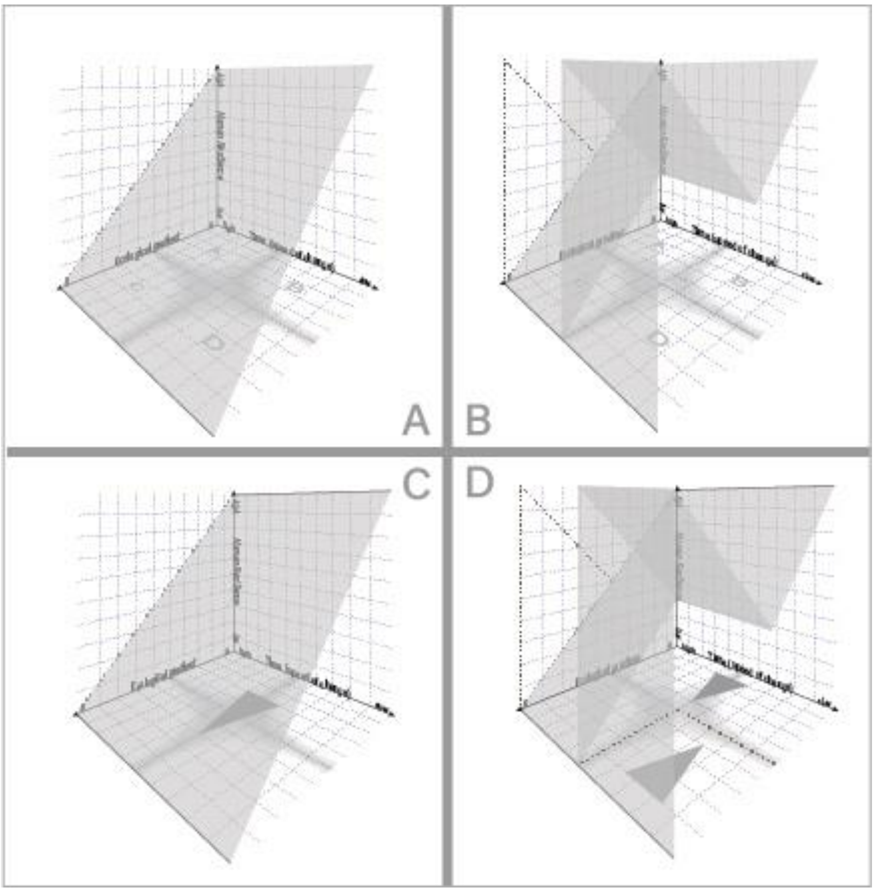

Figure 5 – Three dimensional representation of the refugial predictive model based on ecological gradient, speed of change in time, and human resilience. On the left (A, C) a spatial model where low human resilience was assumed when a high ecological change occurred slowly. On the right (B, D) a spatial model where high human resilience was assumed when a high ecological high occurred slowly.

4. Discussion – Current and novel perspectives of refugia in Africa and wider Palaeoanthropology

(a) Current significance and use of Refugia Theory

In palaeoanthropology there is no specific distinction between refugium-concepts, groups or types. This claim can be demonstrated with the way that paleoanthropologists use the concept of glacial refugia (see introduction, Hewitt 1996, Hewitt 2000, Harvati et al. 2009, Stewart and Stringer 2012, Cordova et al. 2013).

As an example, the concept of glacial refugia plays a major role in the interpretation of the paleoanthropological record of Ice Age Europe. In Pleistocene Europe, temperate-adapted taxa whose populations decreased during glacial periods, were shown to survive in small isolated regions of southern peninsulas and Eastern Europe (Sommer and Nadachowski 2006, Feliner 2011, Tzedakis 2013). As the climatic record indicates, during periods of glaciation, areas in the southern latitudes of Eurasia were subject to a lower degree of environmental change (Bradtmöller et al. 2012). Commonly it is believed that these areas became pockets of stable habitats that led to the occupancy of refugial populations (Dennell 2011). It can be argued, however, that what paleoanthropologists observed was not the presence of isolated population within a refugium due to glacial, hence restricting, conditions, but rather relictual populations (figure 2). Elsewhere, Dennell (2011), describes in detail the dynamics of the "sink and source" model, applying it to hominin demography from a refugial perspective. This model is arguably indistinguishable from Relic refugia, since it is dependent on observable and testable effects, such as population behaviour within the paleoanthropological record. Having the ability to empirically observe the expansion and retraction of people and material culture before, during and after habitat fragmentation and change, makes relic refugia a testable candidate for refugia identification. These effect-variables are not inherently testable within different concepts applied in palaeoanthropology, such as glacial refugia in Europe, as the idea of populations being in an area due to its habitability is lacking of testable variables. Furthermore, by considering relictual in character refugial zones or bottlenecks (Hawks et al. 2000) during their identification and evaluation, only processes and effects related to human evolution, observable through the paleoanthropological record, can be evaluated without the need to consider specific driver. This not only would simplify the work of paleoanthropologists, but it would also create a common ground, creating a comparable and consistent method for the further development of refugia theory in palaeoanthropology.

Other than the glacial refugia theory and "sink and source" model, which could both be considered valid representatives of relic refugia, there are no other examples of different types of refugia in the Old World Pleistocene. This lack of alternative models and theories is in part due to the limitations of the archaeological record, and its temporal dynamics in respect to the paleoenvironmental and paleoclimatic record.

While in Europe refugia theory has been a topic mostly discussed in terms of non-*sapiens* hominin speciation and demography, in Africa, refugia theory seems to be applied differently. Pleistocene Africa has always been paleoanthropologically interpreted very differently from Europe, both from a methodological and empirical perspective. Refugia theory has taken a primary role in discussions of *Homo sapiens* evolution in Africa, being used to define and explain records and interpretations that span from the biological speciation of hominin populations, to the cultural emergence of art and creative behaviour and range expansions across Eurasia. These paleoanthropological topics have in common how their explanatory models are all based on the idea of areas of 'survivability', sustaining overall metapopulation diversity and longevity of local populations.

The most common and widespread application of Refugia Theory in the African palaeoanthropological record is within the study of hominin speciation. The phylogenetic history of hominins in Africa is complex and still blurry, with most studies carried out in other continents, and then applied onto African contexts (Gandini et al. 2016, Jochim 1986, Stewart and Stringer, 2012). There is no history of speciation studies in Africa that are linked directly to refugia theory, and most refugial studies exist within paleoecological and archaeological contexts. (Anthony et al. 2007, Nicolas et al. 2011, Prendergast 2016). The relationship between speciation of *H. sapiens* and refugia is assumed in the examples offered. Based on observations of speciation, refugia are assumed on the bases that other organisms have been observed to speciate within the context of habitat fragmentation and change. The inference, however, is unavoidably indirect.

Culture and the efflorescence of creative behaviour is also a topic discussed when refugia theory is involved in African palaeoanthropology. While this paper does not explicitly deal with this topic, it is worth noting that the roles of refugia are implied when describing episodes of cultural efflorescence in Pleistocene Africa. Similarly to phylogeny, refugia are never explicitly involved when cultural efflorescence is involved, although implied when describing isolated or distant areas (Marean 2010, Jones 2016, Scerri 2017). The lack of detailed palaeoecological records, together with the lack of a single accepted interpretation of culture and creative efflorescence in Africa make studying refugia within this perspective very challenging.

Finally, many refugial studies in Africa have concentrated on the study of past human dispersal and mobility, assessing the role of refugial zones during human migration out of Africa, and more rarely within it (Lahr and Foley 2003, Basell 2008, Stewart and Stringer 2012). Refugial zones in Africa are used to try and explain how human adaptability and change of refugial environments increased human resilience, aiding the successful migration in Eurasia. However, given Africa's diverse ecologies, it seems likely that assumptions regarding the different effects should be context-dependent and not necessarily assumed to be universal. For example, demography group-size, land area and subsistence strategies.

(b) Why can't we study refugia in African Palaeoanthropology?

Although refugial populations have been and can be identified using a variety of proxies, such as genetics, population biology and ecology, identifying refugial zones in the deep human past is necessarily indirect, and therefore subject to various challenges. For paleoanthropologists, refugial theory should be directly related to landscapes, either meaning a geographically finite area or environmental zone (i.e. size and environmental character). In other words, the identification of refugial zones is primary a paleoenvironmental problem.

Studying the role of refugia in Pleistocene Africa is problematic because we do not have a detailed spatial and temporal record. This would be fundamental to identify the parameters necessary for testing the refugia model presented in this paper. While interpretations of refugial zones are justifiable, we do not have a record detailed enough to offer the information we need to securely interpret contexts as being refugial. As previously explained, refugia theory has formerly been applied to palaeoanthropology with no set of well-defined parameters. However, interpretations of refugial zones and populations could be justifiable if the parameters developed for this model are applied. Nevertheless, they may not stand to scrutiny when incorporated in an operationisable model. Furthermore, the palaeoenvironmental and archaeological records present today for the African continent do not always cover the same area I different regions, and there is considerable spatial bias in the archaeological record.

By acknowledging the basic parameters necessary, and reviewing the case studies of interest with the new observations and frameworks presented here, a case can be made for the identification and evaluation of refugial zones in the African Pleistocene record. Here, we use the case of tropical West Africa, a poorly understood region featuring for human evolution, to show how our theoretical framework can advance our understanding even in areas where the paleoanthropological data is extremely limited.

5. Constructing an ideal case – Tropics in Pleistocene West Africa

In order to understand if the tropics of Pleistocene West Africa included areas that could have supported refugial populations, a variety of environmental and human variables are considered. Theory can only be the groundwork for in-depth, data-driven, archaeological interpretation. If we wish to understand whether tropical environments of Pleistocene West Africa were in fact areas that could have supported refugial populations which survived within refugial zones, a variety of environmental and human variables have to be taken into account. Variables such as (1) human flexibility, (2) humidity and water availability, (3) ecological biodiversity, and (4) presence of human activity by means of recovered material culture, are all factors that have to be considered. Once all these variables are accounted for, they can then be applied to the theoretical framework to assess whether or not refugia in tropical West Africa supported human populations.

(a) Human flexibility

All of today's ecosystems are now in some way inhabited by our species (more REFS, Roberts and Stewart 2018). The ecological plasticity that is an inherent characteristic of *Homo sapiens* would have been a major advantage for its global expansions. Early *Homo sapiens* have been documented at the edges of deserts, ecotonal areas at the edges of rainforests, and cold, glacial environments of Europe and Asia (Breeze et al., 2017; Shipton et al., 2018; REFS). Evidence from Southeast Asia indicates that at least here, relatively newly arrived *H. sapiens* rapidly adapted to full rainforest environments too (Roberts et al. 2017; Westaway et al. 2018). Once specifically adapted to diverse ecological regions, it seems reasonable to assume that during periods of habitat fragmentation, hence where tropical environments retracted and expanded in time (Salzmann and Hoelzmann, 2005), humans could have easily adapted to the diverse range environments in West Africa, possibly supporting diverse types of refugia that may have an important role is sustaining population continuity and subdivisions.

(b) Humidity and water availability

Although very little is known about Pleistocene water systems, paleogeography and Pleistocene topography of West Africa, several observations can be made regarding water availability and presence in the region. West Africa supports three major river basin systems which are isolated from the rest of the continent. They are the Volta River, the Senegal River, and the Niger River systems, which were active and present throughout the Pleistocene (REFF). The Volta and Niger River, together with their lesser understood tributary rivers, were a continuous source of water, which offered an array of lakes and distinct fluvial environments. Additionally, the area within the southern branches of the Volta and Niger rivers form the so-called Dahomey Gap, which has been interpreted as being the location of environmental remodelling, as it is situated in an area of extensive tropical fragmentation and expansion through time (Oliver, 1989; Salzmann and Hoelzmann, 2005; and Allsworth-Jones, 2019). This therefore shows how water systems in West Africa acted as a major agent or alterer for environmental variability. Furthermore, humidity and rain water availability have to be considered. In modern day West Africa the average monthly rainfall in perennial rainforest environments is 1500mm, while savannah environment in the northern latitudes receive only one third of the average monthly rainfall (NOAS, accessed 25.10.20). The drastic difference in rainfall activity not only has an impact on available rain water, but it subsequently acts upon river systems in the region, meaning that lower-latitude rivers have a lower chance of draughts, and therefore a higher probability of maintaining a stable, water-rich environment. Finally, irregular climatic events could have played a role, as it has been noticed that variations like the ENSO (El Nino Southern Oscillations) could have had a considerable effect on environmental variability (REFF), compared to more commonly-known irregular period variations such as glacial-interglacial cycles.

(c) Biodiversity

The understanding of the speed and degree of environmental fragmentation is essential for both the application of an initial theoretical framework, and for the comprehension of the articulation and degree to which humans developed specialist adaptations to different ecotones. Partial reconstructions (Salzmann and Hoelzmann, 2005) of the fragmentation and dynamics of tropical rainforests in West Africa give a clear initial picture of what the environmental shifts would have been like. Formation of ecotonal regions, together with the disruption and modification of environments is key to understand what the human response to such changes would have been. Unfortunately, the resolution at which such changes occurred, together with its timeframe, is yet partial, and therefore not applicable for this case study.

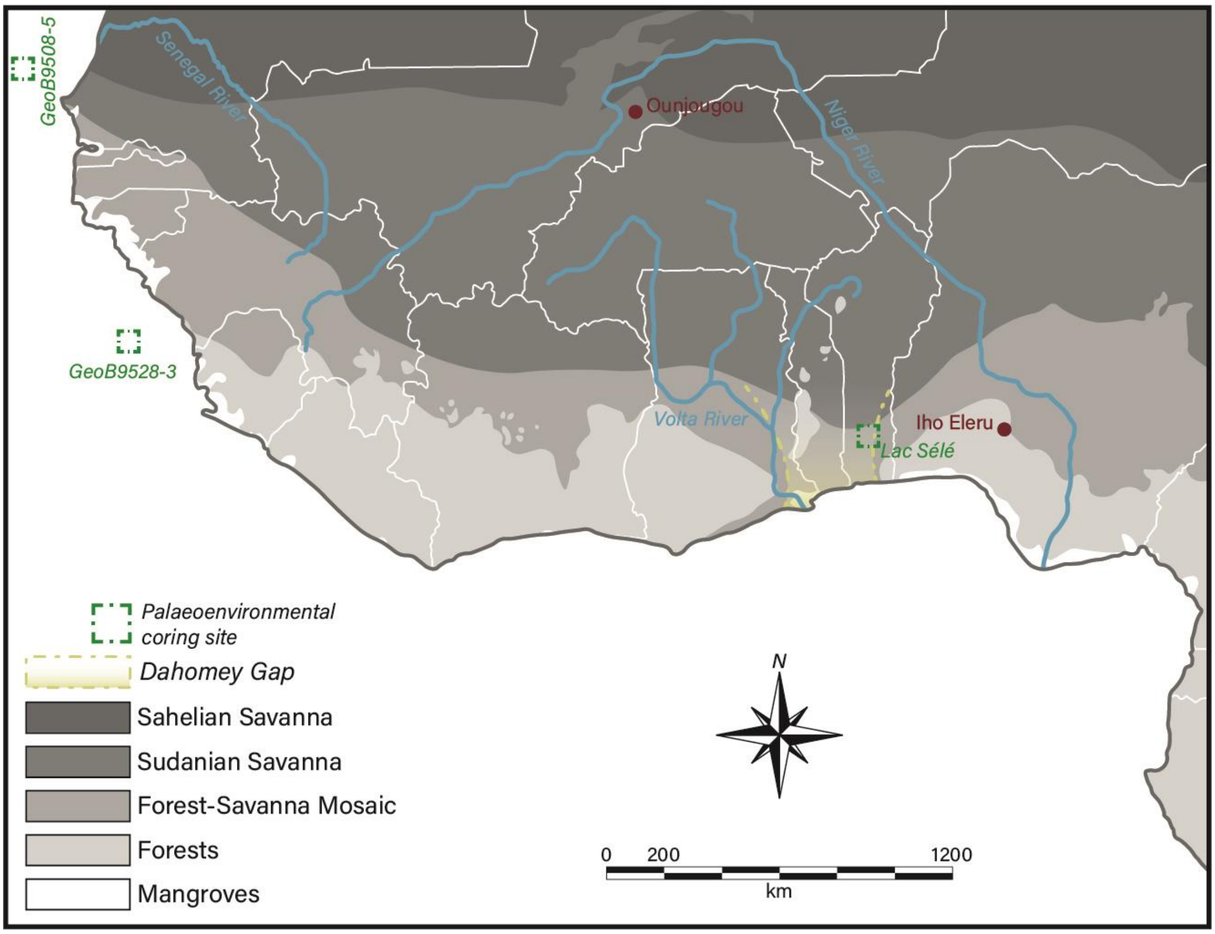

Figure 6 – Map illustration the location of paleoenvironmental coring sites (Salzmann and Hoelzmann, 2005, Castaneda et al., 2009, Niedermeyer et al., 2010) and archaeological sites mentioned in the text (Iho Eleru and Ounjougou) in relation to modern environmental ecoregions (adapted from WWF Global 200 ecoregions), major fluvial system of West Africa, and the estimated location of the Dahomey Gap (Salzmann and Hoelzmann, 2005).

(a) Archaeology

The available archaeological record of West Africa impartially extends throughout the region, being mostly dependent on specific hotspots located along the Guinean-Congolian Coast, and higher altitudes location along the Sudanian Savanna belt. For the application of this model, the archaeology record could be evaluated applying a variety of variables such as raw material uses and availability, mobility patterns following raw material use, and technological morphology and variability. For this specific case, however, such variables are not used as the partial record would offer an impartial interpretation. Nevertheless, archaeological records offer important information on whether people were present in a landscape, and showing when and in which environments they lived. The partial nature of the West African archaeological record cannot offer useful data, however when evaluated together with environmental and chronological analyses it is a great too. The site of Ounjougou in Mali, for example, was interpreted as being a recurrently exploited landscapes by different population turnovers, hence repeated incursions that were very brief by people with different cultural traditions (Robert, 2003; Huysecom, 2004).

(b) Application of model fits with West Africa

Finally, an evaluation of all the previously explained parameters, variables, and observations can be made. As already described the archaeological record for West Africa is present although often unclear and lacking of enough resolution. A similar case can be made for the palaeobotanical and palaeoclimatic records of the region, as very few environmental cores exist (Jahns et al., 1996; Jahns et al., 1998; Salzmann and Hoelzmann, 2005). Nevertheless, the data present would lead to a series of interpretation that could suggest the possible existence of patches of tropical rainforest in West Africa during the Pleistocene that could have supported populations. The existence of continuous rainforest environments in the southern latitudes of the region, together with the abundant presence of water and an observed continuity in technological behaviour and mobility patterns, leads to the interpretation of refugial, or relictual, populations existing within patches of tropical rainforests. These observations are clearly in line with the original theoretical framework. Still, the scattered nature of the base datasets present today for Pleistocene environments and archaeological sites of West Africa make these hypotheses in need of examination and verification, making this a limited, but extremely useful base for future analyses of the region.

The main problem that this interpretation arises, however, is not whether refugial zones could have existed, but whether refugial populations survived within them. As previously explained, it is very difficult to distinguish a refugial population from a relictual population. For example, the only fossil hominin ever found in West Africa is the Later Stone Age Iho Eleru fossil, dated at around 11.2 kya (Shaw and Daniels, 1984; Allsworth-Jones et al., 2010; Harvati et al. 2011; Stojanowski, 2014). As Stojanowski (2014) discusses, the unique morphology of the Iho Eleru crania, observed as being "archaic" and similar to much older specimen could be a hint towards the refugial and relictual nature of the landscape within which the individual lived in. The fossil was interpreted as being part of a relictual population, which arrived in the tropical rainforest environments of South-West Nigeria at an unknown time, and with the subsequent fragmentation and environmental change in the southern latitudes remained within a patch of tropical rainforest. The relictual nature of this population is currently certain, as we have no proof for a later expansion of this population outside their niche.

6. Conclusion

After 65 years from the first use in scientific publications, and over 20 years from its common use in paleoanthropological literature, the term refugia has become a widely spread and used concept in numerous fields and contexts all across the globe. Refugia, together with its associated terms such as refugial and relictual, has evolved and developed widely, resisting all attempts to get rid of it, and it is today widely used to refer to a geographically finite area which supports either an isolated, or a relict population of a once more widespread species.

This paper reviewed the cumulative knowledge of the original development and use of refugia in ecological research, up until our current understanding and use of the refugium-concept in palaeoanthropology, and how it played a fundamental role in our study and interpretation of past human-environment interactions. Although at present the refugium-concept is commonly applied and widely shared in paleoanthropological literature, a structuring of this concept has the potential to clarify and make future research of refugial zones and populations not only easier, but more reliable. For this reason, a destructuring of the past refugial definitions and concepts was carried out, to aid with the creation of a new theoretical framework for the prediction and analysis of refugia. Building this framework upon three fundamental parameters that take inspiration from both ecology and archaeology (ecological gradient, time and human resilience), gives paleoanthropologists the possibility to view paleoanthropological contexts under a new light, standardising and operationalising the processes that are currently unclear for the definition and interpretation of refugia. As a case study, this novel framework has been applied to tropical West Africa. With this example, we show how a standardisation of the theoretical framework helps with the better structuring of the data available, no matter how limited, presenting elucidation towards the possible degree of habitability of refugial zones. Thanks to this, we conclude that West Africa could have supported refugial or relictual populations during the Pleistocene, although more archaeological and paleoecological data is needed for confirmation.

Although at present a good broad picture of refugia-human interactions in the Pleistocene exists, a closer look at the specific underlying dynamics and variables reveals important gaps in terms of archaeological and paleoenvironmental records. Much more work is needed to clarify chronostratigraphic, palaeoenvironmental and paleoanthropological issues. To build solid contextual frameworks on the human-environment relationships which could or could not include refugia, the implementation of the theoretical perspective presented here could be fundamental for a more unbiased, reliable interpretation. Despite the challenges, refugia are still a mysterious part of our past. We hope that with the increasingly available pool of paleoanthropological data, and the fast pace of discoveries we see today, we will soon see how refugia were of vital importance for the evolution of Pleistocene hominins in the tropics and beyond.

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