Africa, the Cradle of Human Diversity

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Africa, the Cradle of Human Diversity

Cultural and Biological Approaches to Uncover African Diversity

Edited by

Cesar Fortes-Lima, Ezekia Mtetwa, and Carina Schlebusch

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Abbreviations

ACCME's	African Collaborative Center for Microbiome and Genomics Research's
AD	"Anno Domini" or after Christ
aDNA	Ancient DNA
AESA	The Alliance for Accelerating Excellence in Science in Africa
AIM(s)	Ancestry informative marker(s)
AMS	Accelerator Mass Spectrometry
APOL1	Apolipoprotein L1
AS-PCA	Ancestry-specific principal component analysis
ASS	African Academy of Sciences
AWI-Gen	Africa Wits-INDEPTH Partnership for Genomic Studies
BC	"Before Christ"
BCE	Before the Common Era
BMI	Body mass index
BP	Before present
CAfGEN	Collaborative African Genomics Network
CHAIR	Cardiovascular H3Africa Innovation Resource
CKD	Chronic kidney disease
CST	Costly Signalling Theory
CVD	Cardiovascular disease
DAC	Data Access Committee
DRC	Democratic Republic of the Congo
EIA	Early Iron Age
EMSA	Early Middle Stone Age
ESA	Earlier Stone Age
H3ABioNet	H3Africa Consortium Pan-African Bioinformatics Network
H3Africa	Human Heredity and Health in Africa Initiative/Consortium
HDL-C	High-density lipoprotein cholesterol
HLA	Human leukocyte antigens
HPC	High-performance computing clusters
IA	Iron Age
IAM	Ifri n'Amr ou Moussa site
ka	thousand years ago or old
KEB	Kehf el Baroud cave
LDL-C	Low-density lipoprotein cholesterol
LD	Linkage disequilibrium
LIA	Later Iron Age
LMIC	Low-middle-income country
LNP	Lactase Non-Persistence allele

LP	Lactase Persistence allele
LSA	Later Stone Age
MDS	Multidimensional scaling
MIS	Marine isotope stage
MSA	Middle Stone Age
mtDNA	Mitochondrial DNA
NCAA	Ngorongoro Conservation Area Authority
NIH	National Institutes of Health
PCA	Principal component analysis
PCR	Polymerase chain reaction
PIA	Pastoral Iron Age
PN	Pastoral Neolithic
RHG(s)	Rainforest hunter-gatherer(s)
SCD	Sickle cell disease
SEB	South-Eastern Bantu-speaking ethnolinguistic groups
SES	Socio-economic status
SIREN	Stroke Investigative Research and Education Network
SNP(s)	Single nucleotide polymorphism(s)
SRI	Sangha River Interval
TAST	Transatlantic slave trade
Tbg	Trypanosoma brucei gambiense
Tbr	Trypanosoma brucei rhodesiense
TB	Tuberculosis
YRI	Yoruba population from Nigeria
yrs B.P.	Years before present

INTRODUCTION

Engagement Cross-Disciplinary Research in Africa

Cesar Fortes-Lima, Ezekia Mtetwa, and Carina Schlebusch
(*editors of this book*)

Scientific articles included in this conference proceedings were all presented at the *"Africa, the cradle of human diversity"* international conference during May 22nd–25th 2019, held at Uppsala University, Sweden (https://africathecradleofhumandiversity.com). At this conference, leading researchers presented and discussed new results and multidisciplinary approaches to address long-standing questions about human evolutionary history and population dynamics in Africa and beyond. The conference covered an extensive time range in human evolution, starting with the evolution of early humans in Africa to the complex cultural and genetic diversity of ancient and modern African populations. In this international event, participants were from a wide range of academic backgrounds with 52% attendees and 48% invited speakers being female, and 31% from under-represented countries.

To present recent knowledge and ongoing research in Africa from a multidisciplinary perspective, ten articles on a range of topics and themes are presented in this conference proceedings, and they are structured around three main themes. In the first section, two papers are incorporated in the "Early Humans in Africa" theme. Both studies focus on paleoanthropological research in Africa to better understand the origins of our species, and human biological and behavioral evolution.

In Chapter 1 (entitled "A southern African perspective on human origins research between 500 000 and 50 000 years ago: Current dilemmas and questions for the future"), *Marlize Lombard* gives us an overview of the African fossil and archaeological record, spanning the Earlier to Middle Stone Age periods (500 kya to 50 kya). Although concentrating on southern Africa, the author put fossil discoveries across the continent in context and discuss the behaviors and cultural development of various *Homo* species across time and space. To weave together a composite story of the last 500 thousand years of our species' evolution, the author brings together recent findings from different disciplines: archaeology, paleoanthropology, genetics and cognitive anthropology.

In Chapter 2 (entitled "Further notes on the Ngaloba Industry, a Middle Stone Age Assemblage Directly associated with early Homo in the Greater Laetoli, northern Tanzania"), *Fidelis T. Masao* and *Jackson S. Kimambo* discuss

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new field data suggesting that the Ngaloban Middle Stone Age (MSA) lithic industry had considerable spatial diversity across the Greater Laetoli area of northern Tanzania than previously imagined. The authors reveal that previous research at the Ngaloba sites had overlooked the spatial distribution and occurrence of human activities during the MSA period in the Greater Laetoli and its surrounding areas. They also note that studies in the Laetoli locality, famous for its earliest hominid footprints and other materials indicating human cultural and biological evolution, had recurrently focused on artifacts identified as MSA, overlooking those suspected to be Later Stone Age (LSA). In this paper, the authors provide results of their recent fieldwork, aimed at understanding the cultural expressions of the early humans associated stratigraphically with the Ngaloba MSA assemblages. Their results, which included MSA materials, but also a sizeable amount of artifacts that could be described as LSA, open a new discussion in which the authors point out that the latter assemblage point to the possible existence of technological variation and diversity in the Greater Laetoli area, particularly between lowland and highland industries during the MSA period.

In the second section, four articles are incorporated in the "Cultural transitions in Africa" theme, to present a closer look at ancient communities from different locations, their lithic technologies, and cultural transitions from the Stone Age to the Iron Age in Africa.

In Chapter 3 (entitled "West-Central African diversity from the Stone Age to the Iron Age, continuities and transitions during the Late Pleistocene and the Holocene"), *Bernard Clist* presents a new comprehensive review of the archaeology of peoples who have inhabited Central Africa from the Middle Stone Age through the Iron Age to historical times. This chapter highlights high cultural diversity in Central Africa for the last 30,000 years. It also puts into perspective the available information related to ancient exchange networks, often over long distances, connecting various archaeological cultures. Further, the author reviews the social complexity found in the northwestern part of the region during the first half of the first millennium AD illustrated by small cemeteries in Cameroon, Equatorial Guinea, and Gabon. In addition, the author found sharp discontinuities in some cultural sequences, which are better interpreted as slow changes over several generations from the Neolithic to modern times indicating long-term traditions. Lastly, the author shows the need for local palaeoenvironmental sequences to complement the developing archaeological record.

In Chapter 4 (entitled "Ancient urban assemblages and complex spatial and socio-political organization in Iron Age archaeological sites from Southern Africa"), *Plan Shenjere-Nyabezi* and *Gilbert Pwiti* revisit the spatiotemporal development of drystone-walled urban settlements in southern Africa between the 11th and 19th centuries AD. Using a framework combining archaeological, architectural and spatial studies, as well as a combination of Costly Signalling, Assemblage and Actor Network Theories, the authors offer refreshed insights into the rise and fall of the Zimbabwe Culture. Moving away from function and use, the authors invite attention to the complex socio-political, ideological and economic processes as critical factors to consider for an account of the development of monumentality in southern Africa. Their broadened view in terms of time and space, as well as a strong component of interdisciplinary approaches, reinvigorates discussions and interpretations of the Zimbabwe Culture. Again, the authors' recent fieldwork in northwestern Zimbabwe further reveals a greater spatiotemporal complex and ambiguity into the stone-built settlements than previously defined.

In Chapter 5 (entitled "Diversity and variability in the preindustrial iron-smelting technologies of Great Zimbabwe, Southern Africa"), *Ezekia Mtetwa* draws attention to the iron industry of the famous site of Great Zimbabwe in southern Africa, overshadowed in research by the recurrent focus on the settlement's spectacular architecture. The author underscores the significance of iron in the socio-political and economic transformation of the agro-pastoral and trading societies of Great Zimbabwe. The author discusses the significance of the overlooked archaeological landscape surrounding Great Zimbabwe, revealing new archaeological data for the existence of a considerable iron industry that employed a diversity of innovative designs and processes for smelting iron. The author also discusses the spatial variability of iron production activities in Great Zimbabwe, some taking place within settlements. Using these new data sets, the author argues that the nature and social organisation of precolonial iron technology in Great Zimbabwe specifically, and sub-Saharan Africa as a whole, were more complex and ambiguous in time and space than previously thought.

In Chapter 6 (entitled "Grappling with diversity in livestock-related, non-agriculturist archaeology in the light of genetic research into the Lactase persistence allele, -14010*C, in southern Africa"), *Thembi Russell* and *Faye Lander* discuss the introduction of pastoralist practices to southern Africa and its connection with adaptation to milk drinking. The authors compare archaeological evidence of livestock on the southern African landscape with genetic evidence in the form of frequency distributions of the -14010C lactase persistence allele across southern African populations. They also integrate climatic factors and environmental influences (such as diseases) into their discussions and contribute ethnographic accounts of livestock herding histories. By combining evidence from these diverse fields, they highlight the importance and unsolved questions of milch pastoralism in the drier western half of southern Africa.

In the third section of the book, four articles are incorporated in the "Genomic research of ancient and modern populations in Africa" theme. In this section, ancient and modern-day DNA studies are reviewed and discussed, with regards to their contribution to inferences about population diversity and human history on the African continent, as well as the utility of genetics to health and disease-related research in Africa.

In Chapter 7 (entitled "Paleogenomics of the Neolithic transition in North Africa"), *Rosa Fregel* examines the so-called Neolithic revolution that started in the Fertile Crescent around 13,000 BCE and expanded from there to North Africa. The author shows how paleogenomics studies have proved to be a powerful source for providing new evidence to address long-standing questions about the Neolithic transition and migration dynamics. Although most of the paleogenomics research has been performed in European populations, the author highlights how recent paleogenomics studies in North Africa have started to shed light on the change from hunter-gatherer to farming societies. The author previously investigated ancient DNA data that evidenced how Early Neolithic people from Morocco are genetically similar to Upper Paleolithic individuals, while late Neolithic individuals from North Africa are admixed with a North African and a European component. In addition, in this review of paleogenomics studies in North Africa, the author also discusses the development of complex Epipaleolithic communities and the migration of farmers from Europe.

In Chapter 8 (entitled "Ancient DNA studies and African population history"), *Mário Vicente* and *Carina Schlebusch* present a review of the history and utility of ancient DNA studies in the framework of other disciplines that study human history. They furthermore discuss the African ancient DNA studies published to date and present a meta-analysis of ancient DNA data, in the context of modern-day genetic variation. They furthermore tie-in the genetic analyses and inferences with observations from the fields of archaeology, linguistics and palaeoanthropology. They also point to current caveats and discrepancies and suggest how future research can try to overcome current difficulties in the field. Through these discussions and interpretations, current African ancient DNA research is put into the perspective of cross-disciplinary research regarding human history inference.

In Chapter 9 (entitled "The H3Africa Consortium: Publication outputs of a pan-African genomics collaboration (2013 to 2020)"), *Ananyo Choudhury*, *Dhriti Sengupta*, *Shaun Aron* and *Michèle Ramsay* provide a comprehensive review of the scientific and academic activities at the Human Heredity and Health in Africa (H3Africa) Consortium. Over a 7-year period H3Africa has expanded its pan-African network to 30 countries. This outstanding African-led initiative is highly complex and includes a pan-African bioinformatics research network to investigate population genomics, non-communicable and infectious diseases, and the microbiome in several African regions, as well as ethics projects and community engagement. The authors show the strong focus of H3Africa on capacity strengthening and the genomics publications, and how they are currently steadily increasing, with outputs shifting from an emphasis on reviews and perspectives to original and groundbreaking research publications. To review the fruitful list of publications of the H3Africa Consortium, the authors analyse the core publications under specific themes that reflect the areas of activity. In addition to scientific knowledge, the H3Africa Consortium is making available for the international scientific community extensive genomic and phenotype data and the stored biospecimens of three Biorepositories. These resources would to notably increase our understanding of demographic processes that shaped the diversity of African populations, and health and disease in Africa and across the world.

In Chapter 10 (entitled "Disentangling the impact of the transatlantic slave trade in African Diaspora populations from a genomic perspective"), *Cesar Fortes-Lima* discusses the population history and admixture dynamics of African Diaspora populations that had undergone the transatlantic slave trade. The author focuses on recent genome-wide studies that use genomic information of ancient and modern-day African-descendant populations to complement and validate historical and archaeological resources. These studies have unravelled the ancestral origins of African-descendant populations from North America (in the USA), South America (in French Guiana and Suriname), and the Caribbean (in Cuba). The author also examines paleogenomics research that delves deeper into the living conditions and migration routes of enslaved Africans during the slave trade period by using aDNA generated with and without human skeletal remains. Overall, this chapter helps us to better understand one of the darkest chapters of human history shed new light on the demographic history of enslaved African-descendant populations, and by examining paleogenomics research brings forgotten histories of enslaved Africans back to life.

Together, chapters from the three main themes are a valuable source of information for the general audience and academic scholars interested to investigate African human diversity, and highly encourage a multidisciplinary perspective to understand the history of human populations in the African continent as well as the African Diaspora.

Editor's Acknowledgements

This edited volume is based on presentations and discussions at the *"Africa, the cradle of human diversity"* international conference held at Uppsala University, Sweden. The editors are extremely grateful to all the authors who contribute to this book, as well as to all the speakers and participants at the event. Our special thanks go to Cecile Jolly, Mário Vicente, Rickard Hammarén, and Imke Lankheet for organizational support during the conference. We are grateful to the European Research Council (ERC-2017-STG grant: AfricanNeo), the Swedish Research Council (grant reference number: 2018-06734), the Wenner-Gren Foundation, and the Riksbankens Jubileumsfond Foundation for supporting the conference.

Editorial Note

The contributions of this book were originally submitted in early 2020, and therefore do not incorporate subsequent developments in scientific research. For citations that were included as "in press" or "in preparation" at the time of submission and were later published during the review of the book, those citations were later updated accordingly with the date and journal of the publication.

PART 1

Early Humans in Africa

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CHAPTER 1

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

Marlize Lombard

1 Introduction

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

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

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

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

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

From an archaeological point of view, the tangible outflow of this development is our technologies and other forms of material culture. I argue that including technology, and therefore archaeology, in exploring human evolution is critical, because we have become the only species completely dependent on technology for our survival (Shea, 2017). The artefacts we excavate reflect past humans' knowledge about how the world works, how they thought about it, interacted with it, and to some extent can indicate how people thought about and interacted with each other. Human socio-technical contexts become extensions of ourselves, contributing to the shaping of our bodies, brains, neurological structures and our DNA (Malafouris, 2010; 1019; Bruner and Lozano, 2014; Pearce, 2018; Kuhlwilm and Boeckx, 2019; Lombard, 2019). They embody our identities, connect us with each other, and allow us to manipulate and control our socio-ecological contexts. All because sometime during our evolution on the African plains, our ancestors became reliant on what they learnt from each other socially and technically (see Högberg and Lombard (2020) for discussion on the socio-technical framework). It is therefore the interplay between, and co-evolution of, human ecology, biology, society and technology through time that resulted in the mind of *Homo sapiens* as we know it today (Lombard and Högberg, 2021).

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

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

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

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

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

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

Returning to southern Africa's first fossil, Robert Broom saw the Taung fossil a few weeks after Dart's publication, and was convinced that it was a hominin. A decade or so later, he was appointed at the then Transvaal Museum (now part of the Ditsong Museum amalgamation in Tshwane and Johannesburg), and went on to work in what is today the UNESCO World Heritage Site, known as the Cradle of Humankind on the Gauteng Highveld of South Africa. Here he discovered *Paranthropus robustus* and adult specimens of *Australopithecus africanus* such as Mrs Ples at Sterkfontein caves, validating the morphological affinities of the Taung Child as species-level morphology. Broom and Scheepers (1946) published the first synthesis of the then known hominins of South Africa, cementing the place of the subcontinent in the epic of human evolution. To date, the dolomitic palaeo-caves of the relatively small area (~51.5 thousand hectares) known as the 'Cradle of Humankind' have yielded one of the richest and most varied early hominin records worldwide with more than 3300 hominin fossil pieces including *Australopithecus africanus*, *Australopithecus sediba*, *Paranthropus robustus, Australopithecus prometheus,* early *Homo*, and *Homo erectus* (Table 1.1).

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

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

More than 150 additional pre-50 ka human fossils come from sites across South Africa such as Blind River, Blombos Cave, Border Cave, Cave of Hearths, Cornelia Uitzoek, Die Kelders, Diepkloof Rock Shelter, Elandsfontein, Equus Cave, Florisbad, Hoedjiespunt, Klasies River, Makapansgat, Pinnacle Point, Sea Harvest, Sibudu Cave, Taung, and Witkrans (e.g., Dusseldorp et al., 2013). The latest finds from the Cradle of Humankind continue in the region's tradition with the newly published *Paranthropus robustus* and *Homo erectus* fossil skulls from Drimolen, dating to between ~2.04 and 1.95 million years ago (Herries et al., 2020). Here an infant skull now represents the earliest known occurrence of a cranium with clear affinities to *Homo erectus* at ~2 million years (Figure 1.1), questioning the previous account of an exclusively eastern African origin for *Homo* (Herries et al., 2020; see Semaw et al., 2020 for the most recent on eastern African *Homo erectus*).

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

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

3 Becoming Human in Southern Africa

Here I do not aim to offer ultimate answers, but rather highlight some aspects in the various records, revealing the most pertinent gaps and questions for future multi-disciplinary research. To do so, I provide a brief overview of mainly the South African Pleistocene record between 500 and 50 thousand years ago – starting at the time just after the Neanderthal split from other populations and spanning the period during which *Homo sapiens* evolved in Africa (Figure 1.2). I use this record only as a window into what is known because, as an artefact of historical research focus, it is the most complete, and I am the most familiar with it. Geo-political boundaries are, however, meaningless in our evolutionary history, so that we may assume similar trends across southern Africa (roughly the region south of the Zambezi River), and possibly sub-Saharan Africa. For some global contextualisation, I also briefly touch on fossil and other records from elsewhere. Below are a few additional pointers for cross-disciplinary readers:

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

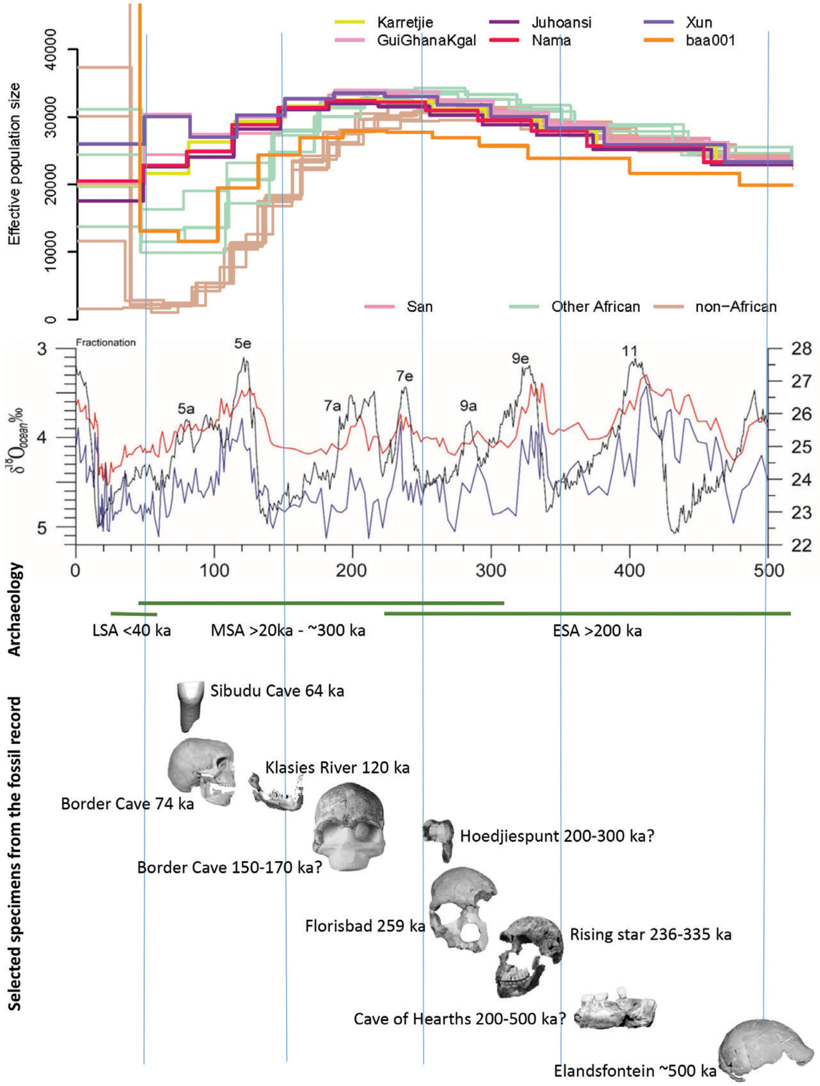

FIGURE 1.2 Top graph: Effective population sizes estimated for single individuals (i.e. two chromosomes) for the Khoe-San (average over the five individuals in each population), the HGDP individuals and the boy from Ballito (baa001) who lived 2000 years ago. Below the graph, the San group represents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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

One way to assess the age of *Homo naledi* and its affinity with other hominins would be to conduct DNA analyses on some of the well-preserved material. The risk is of course that such research may produce unexpected outcomes such as those obtained for Plovers Lake (Lombard et al., 2019), a site previously published as having human remains from an MSA context (de Ruiter et al., 2008). In this instance, we hoped to gain genetic insight about people who were supposed to live >60 ka in the Cradle of Humankind. Our cross-disciplinary work, however, provided at least four strands of independent evidence revealing that the deposits were not exclusive to the MSA. Our data included: *i*) Direct C14 dates that were only a few hundred years old; *ii*) bovid mtDNA profiles that were consistent with domestic cattle instead of buffalo; *iii*) human mtDNA profiles that were strongly associated with current-day Bantu-speakers, instead of hunter-gatherers from southern Africa; and d) isotope values that were consistent with a farming way of life (Lombard et al., 2019).

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

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

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

These relatively steady climatic conditions continue throughout the 250–150 ka window, but we do see a drop in population numbers associated with the lower temperatures of MIS 6 (Figure 1.2). The drop is especially pertinent in the non-African ancestry populations. The population ancestry representing the current southern African component remains the most stable, with its drop in numbers also less dramatic than that of other African populations. This raises the question of the southern tip of Africa potentially being a crucible or refuge for hominins and mammals during certain climatic conditions. Especially aridification of the landscape would have resulted in expansive deserts or semi-deserts void of enough fresh water to sustain some types of mammal populations or prevent them from crossing the continent (Shackley, 1985; Castañeda et al., 2009), limiting cross-continental gene flow. Additional records highlight fluctuating climates during the Quaternary in southern Africa that would have affected the distribution of both people and bio-ecologies (Tyson and Partridge, 2000; Dupont et al., 2005; Dupont, 2006; Scott and Neumann, 2018).

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

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

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

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

faunal assemblage, and stone points indicate the use of hunting weapons (Lombard, 2021). Yet, shifting subsistence practices towards including denser, more predictable and nutritious resources, such as starchy rhizomes and oily shellfish, has far-reaching evolutionary consequences – not only in terms of subsistence behaviour. Marean (2016), for example, explains the adaptation in terms of economic defendability, where maintaining access and control of such beneficial resources result in costly behaviours such as competition, aggression and territoriality amongst groups (also see Chabot-Hanowell and Smith 2012). Resulting pressure for conflict resolution within and amongst groups, may have stimulated selection towards cooperative networks of unrelated individuals, such as seen amongst recent hunter-gatherer groups (Wiessner, 1982), and suggested for Pleistocene *Homo sapiens* (Pearce, 2018), stimulating the evolution of higher order theory of mind (Barrett et al., 2010; Lombard and Gärdenfors, 2021).

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

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

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

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

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

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

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

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

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

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

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

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

Based on the genomes of living and ancient Khoe-San populations from southern Africa, Schlebusch and colleagues (2020) also found new variations in early *Homo sapiens* subsequent to their split from the Neanderthals, but before their split from other African populations at more than 300 ka. These findings include a brain-related region on chromosome 4, which plays an important role in determining the connectivity rates between the principal neurons of the cortex. Thus, based on the nature of brain-selective genetic distinctions, the notion that Neanderthals as a population were cognitively identical to *Homo sapiens* seems unlikely. Instead, they probably evolved their own unique way of thinking subsequent to the split that allowed them to be a very successful hominin population for several hundred thousand years in Eurasia (also see discussion in Lombard and Högberg, 2021).

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

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

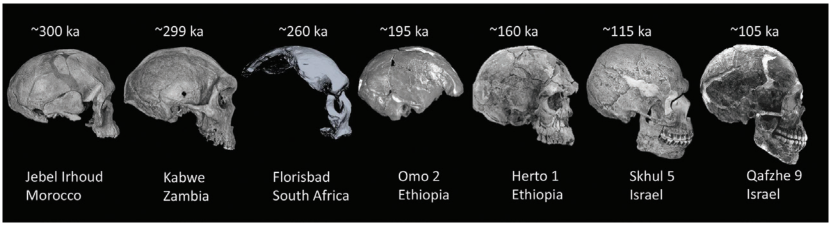

FIGURE 1.3 *Homo Sapiens* Fossil Crania >100 ka

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

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

8 Conclusions

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

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

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

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

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

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CHAPTER 2

Further Notes on the Ngaloba Industry, a Middle Stone Age Assemblage Directly Associated with Early Homo in the Greater Laetoli, Northern Tanzania

Fidelis T. Masao and Jackson S. Kimambo

1 Introduction

Laetoli is a well-known palaeontological locality in northern Tanzania whose outstanding record includes not only the earliest hominid footprints in the world, but also offers evidence of human cultural and biological evolution. The hominid footprint, discovered by the late Mary Leakey in the 1970s, subsequent to a recent discovery by one of the authors, is unique and the oldest evidence for early human bipedal locomotion dating to 3.6 Mya (Masao et al., 2016; Leakey, 1984, 1987a, 1987b, 1987c; Leakey and Hay, 1979; Leakey et al., 1978; Drake and Curtis, 1987). In addition to the hominin and animal footprints, the area has yielded several hominid fossil remains and stone tools (Harrison, 2011, 2002, 1997, 1981; Harris, 1985; Magori and Day, 1983; Su and White, 2015; White, 1980). The archeological significance of the Laetoli area was first recorded in 1938–39 by Kohl Larsen, who collected and reported bifacial implements and hominin fossil remains (Kohl-Larsen, 1943). In 1935, Louis and Marry Leakey visited Laetoli and collected some fossil vertebrates and terrestrial gastropods, which were sent to and housed at the Natural History Museum in London (Leakey, 1987a; Harrison, 2011; Leakey and Harris, 1987). The Leakeys being occupied with research at Olduvai, could not subject the area to the intensive investigation until 1974 when Mary Leakey was able to turn her attention to the area (Leakey, 1984, 1979, 1978).

Mary Leakey's 1974–75 field season was aimed at collecting fossil remains and to intensively search for stone tools (Leakey and Harris, 1987; Clarke, 1978). Given her knowledge of archeostratigraphy, she was of the opinion that because the Laetoli beds were older than Olduvai, the area might harbor stone tools predating the Early Stone Age deposit at Olduvai (Leakey and Harris, 1987; Harrison, 2011). Consequently, the Laetoli beds were investigated by Harris and Leakey (Harris, 1979), but they found no traces of tools or foreign materials predating the Oldowan. Instead, an abundance of scatters of artefacts associated with the Ngaloba beds was reported to exist in most of the site (Hay, 1987). Unfortunately, the reported stone tools assemblages were not fully studied.

In 1990, Ndesokia studied the archaeological composition of Olpiro and Ngaloba beds at Locality 16. Ndesokia's (1990) findings revealed lithic artefacts that were described as Developed Oldowan and Acheulean. In comparison with the assemblages from Olduvai, the aggregates from Olpiro beds were thought to be comparable to the Acheulean aggregates from the Olduvai sites of MNK, SHK, and FC west (Ndesokia, 1990). Despite the fact that the upper Ngaloba beds correspond with the MSA period, his study did not document Middle Stone Age (MSA) from the area. Though scattered artefacts from the surface were reported, their classification and categorization went unnoticed.

It was not until 2002 when Adelsberger and Mabulla briefly studied the provenience of MSA tools in Laetoli, and in 2011, the same authors analysed the geochemical and mineralogical attributes of these stone tools in order to identify a possible source of the raw materials (Adelsberger et al., 2002; 2011). The study stated that only materials identified as MSA were used for analysis, and materials suspected to be LSA were not included in their analysis. Results generated from Adelsberger et al., 2002; 2011 provide insightful information about the sourcing of raw material used for stone tool making at Laetoli. However, spatial distribution and occurrence of human activities during the MSA period at Greater Laetoli including the nearby Kakesio area has not been studied. Therefore, a short fieldwork was initiated in 2018 to document the distribution of archaeological remains, mostly MSA, across the Ngaloba beds landscape. The goal of this field trip was an effort to document the occurrences of the MSA for a better understanding of the cultural expression of Early *Homo sapiens* (EHS), stratigraphically associated with the Ngaloba MSA assemblages.

2 Synthesis of Middle Stone Age Industry

The MSA in Africa which is also described as the Middle Palaeolithic in Europe and the Middle East dates between 200kya and 30kya (Willoughby, 2006; d'Ericco and Banks, 2013). New dating techniques and more accurate climate correlations have placed the MSA beyond 100ka (Henshilwood et al., 2013; d' Errico et al., 2009; Marean et al., 2007), and now considered contemporaneous with Eurasia Middle Palaeolithic. Early MSA technologies could have been in place by ca 285ka and lasted until Ca. 40–30 ka (Henshilwood et al., 2013).

This Middle Pleistocene period represents the beginning of regional variation in technological and cultural adaptation as well as the period when modern humans appeared (Willoughby, 2006). During this time, Europe was occupied by *Homo neanderthalensis* (d'Ericco and Banks, 2013). In Africa, the MSA is associated with both anatomically modern man (*Homo sapiens*) as well as Archaic *Homo sapiens* (Rightmire, 2009). Early physical evidence comes from the Gademotta Formation in Ethiopia, the Kapthurian Formation in Kenya, and Kathu Pan in South Africa (Herries, 2011).

Other sub-Saharan African, localities that have yielded diagnostic fossils of EHS: include: Elandsfontein, Florisbad, and Cave of Hearths in South Africa; Kabwe in Zambia; Ndutu, Eyasi, and Ngaloba in Tanzania; Eliye Springs in Kenya; Omo-Kibishi and Bodo in Ethiopia; and Singa in Sudan (Godinho and O'Higgins, 2018; Drennan, 1937; Day and Magori, 1980). The individuals from these sites are not anatomically modern, but they all share closer morphological resemblances to modern *Homo sapiens sapiens* than *Homo ergaster* though not without dissenting views (Mehlman, 1989; Bauer, 1984a, 1984b; Rightmire, 2009, 1984, 1983; Howell, 1984; Clark, 1976). A more complete Middle Pleistocene skull and more relevant to the present study is the Ngaloba skull from the Ngaloba beds. Despite its robust appearance, the individual displays features that are derived compared with the anatomy of Bodo or Broken Hill. A cranium similar to LH 18 is known from Ileret Kenya KNM-ER 3884 dated to 27 ka (Rightmire, 2009). Other comparable hominins include Omo 1 and Omo 2 from the Omo Valley in Ethiopia associated with an MSA lithic assemblage of a Levallois technology with core and blades and ovate handaxes dated to 195,000 BP (Rightmire, 2009). These archaic *Homo sapiens* are assigned an antiquity which is at least early upper Pleistocene and associated with Acheulean, Sangoan or broadly MSA artefacts (Klindienst, 1967). While the fossil and gene records are important, it is however through archaeology that we gain glimpses into the cognitive behavioral and cultural evolution of our societies. The sub-Saharan MSA is considered the place and time where humans evolved into anatomically, genetically, and behaviourally modern humans. As such, the MSA has lately attracted a lot of studies.

The MSA in Tanzania includes a few localised industries or technocomplexes that are based on typology and technology, e.g., the ubiquitous occurrence of blades and blade cores, the employment of the Levallois technology, the sophistication of point technology, and the presence of geometric backed artefacts in some MSA assemblages. Typical MSA is represented by the Sanzako and Kisele industries overlain by LSA and subsequently Pastoral Neolithic (PN) and Iron Age (IA) industries in Lake Eyasi basin. As way back as the mid-1930s hominid remains were discovered in association with MSA by Koh-Larsen (Recks and Kohl Larsen, 1936) on the Eyasi Lake Shore in 1935 and 1936 and attributed to the subspecies *Homo sapiens rhodesiensis* (Rightimire, 1975; Wells, 1957).

The most complete early *H. sapiens* cranium was found at a place along the modern Lakeshore and designated Eyasi 1. The Eyasi beds hominins include archaic *H. sapiens* remains (Brauer, 1984) found in association with several extinct mammalian genera; *Theropithecus, Pelerovis, Hipparion*, a giraffid, a large carnivore, hippopotamus, and antelope (Mehlman, 1989). The Njarasa industry from these deposits has a combination of MSA technological features and Acheulean tool types (e.g., bifaces or core axes) that is usually called Sangoan (Mehlman, 1989). In the Serengeti, the MSA has been described from Loiyalangalani (Hc-JD-1) where the artefacts include scrapers, borers, bifaces, discs, and Levallois cores produced from quartzite and obsidian (Bower, 1977) At Kisese II, a local MSA variant exhibits features such as possession of tools which are generally smaller than those of Sanzako. Most frequent are retouched points, bifacially modified pieces, and a variety of unstandardized scrapers including a few small convex and end-nosed forms. Among the rarities are blades, dubious backed pieces, and burins (Mehlman, 1989). On the same level are the industries on the eastern side of Lake Natron which display MSA features such as Levallois technology, points, blade cores, and a high proportion of flakes (Masao, 2015).

3 Study Area

Our survey focused on an area located on the northern bank of the Garussi River valley and gently undulating hillocks exposing extensive outcrops of lower Ngaloba beds. The Ngaloba beds are the latest in series of the 7-layered Pleistocene sedimentary sequence beginning with the Laetoli beds at the base, and followed by the Upper Laetoli, Ndolanya, Naibadad, Olpiro, and finally the Ngaloba beds (Figure 2.1). The Laetoli beds are widely distributed across the Eyasi plateau on the northern side of Lake Eyasi and onto Laetoli covering an area of more than 1000km^2 (Harrison and Kwekason, 2011). The extinct volcanic centers of Lemagrut, Satiman, Oldeani, and Ngorongoro located to the east, represent the potential sources of tephra which forms part of the deposits in the area. The Middle Pleistocene Upper Ngaloba beds as already remarked are known to have yielded MSA tools in association with faunal remains including a relatively complete cranium of EHS, LH 18 (Magori and Day, 1983; Day et al., 1980) (Figure 2.2).

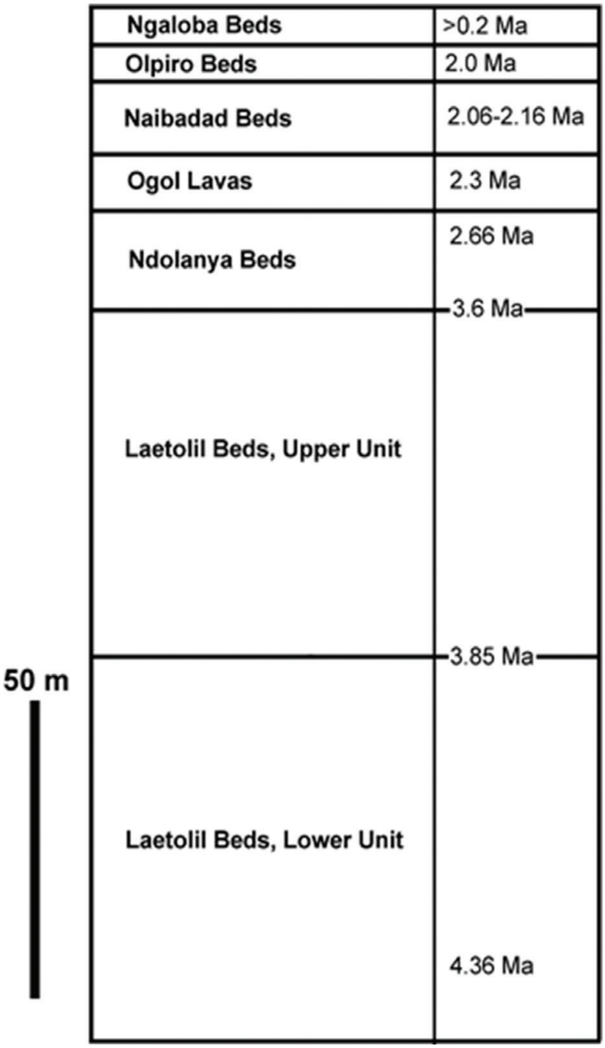

FIGURE 2.1
Simplified stratigraphy of Laetoli after Harrison 2011

The upper Ngaloba Beds deposits are known to contain assemblages that are technologically and chronologically considered to be mostly MSA while the Lower unit of the Ngaloba beds as at Locality 23, contains numerous fossil vertebrates and Acheulean artefacts. Since the MSA assemblages have not been comprehensively studied, this report should be seen as adding to the body of knowledge about the MSA in the area. Fieldwork started after obtaining the necessary permits to conduct fieldwork in the Greater Laetoli Area within the Ngorongoro Conservation Area Authority (NCAA). The fieldwork was dominated by a surface survey from which the assemblages reported here were recovered.

FIGURE 2.2 Early *homo sapiens* (LH 18) from Laetoli after Day and Magori (1980, 1983)

The fieldwork was concentrated in the Greater Laetoli area, particularly focusing on the deposits exposed on either side of the Garussi River lying between the main road to Kakesio and Loc 10W (Figure 2.3). These exposures are thought to consist of the upper unit of the Ngaloba beds which as remarked earlier, have been associated with MSA and LSA assemblages (Harrison and Kweka, 2011). Though there are many such exposed areas, the fieldwork team was able to survey and sample only four of the exposures, and the waypoint of the exposers for the later follow-up. Being devoid of vegetation cover, the exposures can be seen from a distance as extensive patches of brown sediments flanking the Garussi River flood plain. At or close to Locality 10W, the exposures have taken the form of deeply incised furrows leaving cliffs and pillars reminiscent of the Isimila Korongo residual pillars in southern Tanzania. The areas are littered with many artefacts. Several exposures were sampled for artefacts. Altogether a total of 710 artefacts were retrieved.

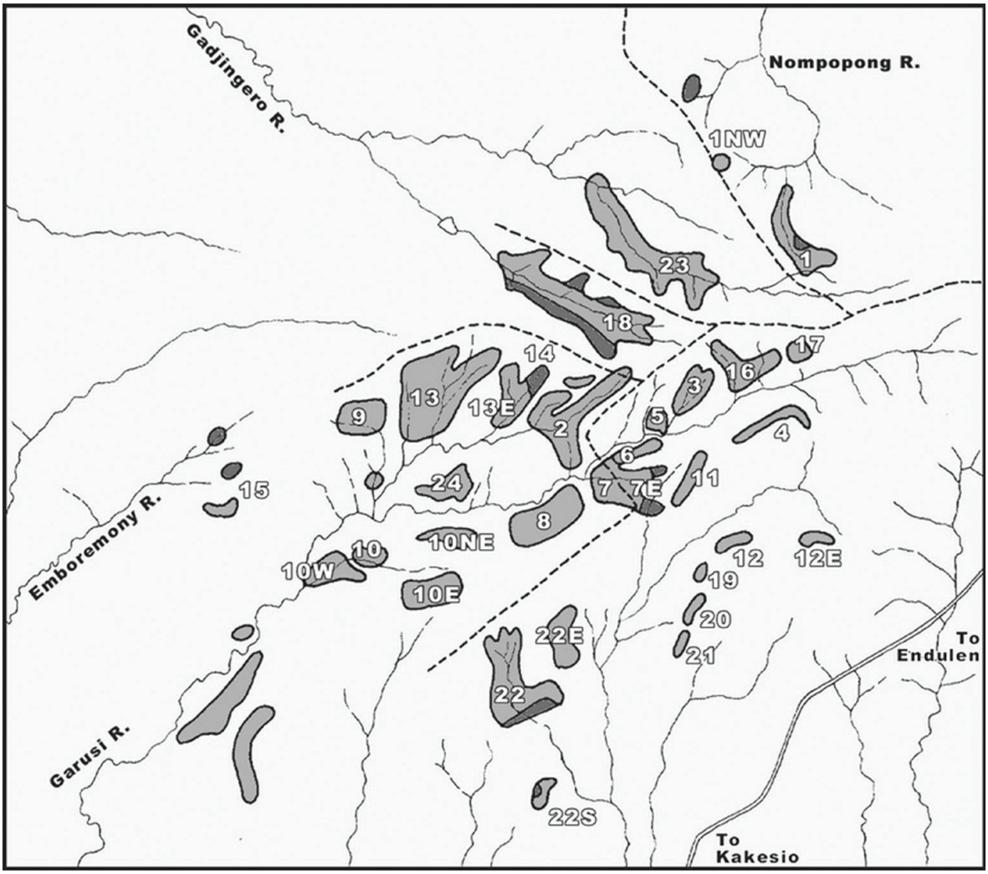

FIGURE 2.3 Map of Laetoli showing localities and area of fieldwork after Harrison *et al* 2011

4 Material and Methods

Both systematic and unsystematic surveys were used to recover the data described in this article. The former took two forms, transect and total collection in prescribed areas. As for the first one, a 70m long transect was laid in the N-S direction in one of the exposures (Exp A), and all artefacts 5m on either side were collected and bagged. Another transect was laid perpendicular to the first transect and as in the previous one, the artefacts and bones were collected. Two more transects, both 50m long were established one 10m from the edge of the exposure and the other 20 m from the edge of the flood plain and artefacts retrieved.

Total Collection from circles: Another systematic sampling strategy adopted was to inscribe circles and collect all artefacts and bones. Two such circles of 10m and 5m radii were inscribed at different places in the exposure and artefacts collected. The table summarises the number of artefacts thus collected.

Test pits. Four test pits of varying sizes were dug in order to assess the vertical distribution of the artefacts, to see if the surface material is a mirror image of the subsurface material. Unfortunately, the test pits did not reveal much material. Based on the few artefacts that were found, one can say the surface and stratified material belong to the same component. This point will be taken up later when the analysis has been completed.

In addition to the above strategies, unsystematic pedestrian survey was employed to cover as much area of the three exposures as possible, two on the western and one on the eastern side of the Garussi River. The team members having been instructed on what to look for, i.e., artefacts and identifiable fossilized bone, walked over the terrain. Many artefacts and bones were collected in the process as reported in the tables below (Tables 2.1 and 2.2).

5 Results

The fieldwork recovered a total of 710 lithic items and 78 faunal remains (Table 2.1 and 2.2). The majority of these artefacts were from the surface collection and only a few were recovered from test pits excavation. Most of the lithic artifacts are made from the Ogol lava which is locally obtained in the area. Artefacts made from chert quartzite, obsidian, and Iron-banded rocks are present in the assemblage but only in negligible percentages.

The lithic assemblage is made up of a variety of unifacially and bifacially trimmed forms which are traditionally associated with MSA, as shown in the Table 2.1. Utilized flakes, flakes, and blades (26.5 and 15.4 %) outnumber the rest of the tool category on the assemblage. Scrapers contribute a significant amount of the assemblage while cores, cleavers, choppers, and burin are less common (Figure 2.4 and 2.5). A sizeable component of the assemblage is made up of tools types that would be scored as LSA on account of their small sizes, i.e. microlithic. These include geometrics, backed pieces, scrapers, and unmodified flakes.

A total of 78 faunal remains representing different genera were recovered from the surface. Bovids are most common in the assemblage (Table 2.2). Other genera are also represented but in a small percentage. Most of the bones

TABLE 2.1 Summary of artefacts recovered from the survey

Artifact type	Transect A	Transect B	Circle A &B	Unsystematic Survey	Testpit	Total	Percentage (%)
Flakes/Blade	55	41	22	67	3	188	26.5
Utilized flakes	32	29	16	30	2	109	15.4
Backed pieces	35	12	11	33	1	92	13
Scrapers	28	10	8	21	2	69	9.7
Unifacial point	14	5	5	19	0	43	6.1
Bifacial point	9	7	3	7	0	26	3.7
Burin	5	2	2	5	0	14	2.0
Biface dimunitive	5	6	1	7	0	18	2.5
Biface large	2	3	1	3	0	9	1.3
Cleaver	1	0	0	2	1	4	0.6
Core axe	2	1	3	3	1	11	1.5
Chopper	2	2	2	3	0	9	1.3
Core peripheral	11	12	8	13	3	47	6.6
Core bipolar	5	6	4	3	2	20	2.8
Core irregular	16	I3	8	11	3	51	7.2
Total	222	149	94	227	18	710	

display medium weathering stage 1 (Behrensmeyer, 1978). Despite the small sample, it nevertheless represents the expected Middle Pleistocene fauna which is as shown from the nearby Lake Eyasi basin and southern Serengeti is mostly modern with the exception of five extinct taxa: *Theropithecus oswaldi, Pelerovis sp, Hipparion sp., Sivatherium sp.*, and *Hippopotamus* (Dominguez et al., 2007). As of today, *bovid*s followed by *equids* are the most frequent genera. Cursory examination for surface modification revealed that the majority of the bovid and *equid* specimens displayed bone surface modification in form of cut marks and percussion though some of the marks could have been concealed by the weathering. The bones displayed no evidence of carnivore modification such as tooth marks.

TABLE 2.2 Summary of fossil bones recovered according to genera

Genus	Number	Percentage (%)
Bovid	40	51.9
Equid	14	17.9
Rodents	5	6.4
Ostrich	4	5.1
Suid	2	2.56
Canid	2	2.56
Giraffe	1	1.28
Hippo	1	1.28
Non-Identified	9	11.5

6 Discussion and Conclusions

Unlike the nearby Lake Eyasi basin sites which are sealed and hence yield undisturbed association of lithic and faunal remains, the Ngaloba remains lack this context. Most artefacts and ecofacts reported here are surface collection. These were found littering on the surface following erosion of the upper Ngaloba beds. Suffice it to point out that comparable assemblages have been recovered from Ngaloba stratified contexts and described as MSA (Mabulla, 2015). On the other hand, the surface finds may bespeak a persistent place. As Camilli and Ebert (1992) point out, the argument that post-deposition processes and disturbance render surface distribution of artefacts of little use for analysis has also been countered with the assertion that almost all assemblages presently buried or on the surface have been subjected to these disarranging processes because all assemblages are originally surface assemblages. Along this vein, the spatial integrity of sealed deposits has recently been likened to no more than that of surface deposits (Ebert, 1992).

Our short fieldwork did not investigate how far the contact with the lower Ngaloba beds would be from the exposures. As such, we did not establish the relationship with any underlying deposits such as Acheulean or any pre MSA assemblages. One thing seems certain though, the underlying deposits, seem, on account of what the test pits revealed, to be almost devoid of artefacts. There are several possible explanations for this. First, it is possible that the Kakesio and the greater Laetoli area may contain a very thin layer of MSA assemblage that has been exposed by erosion. This would imply that hominins

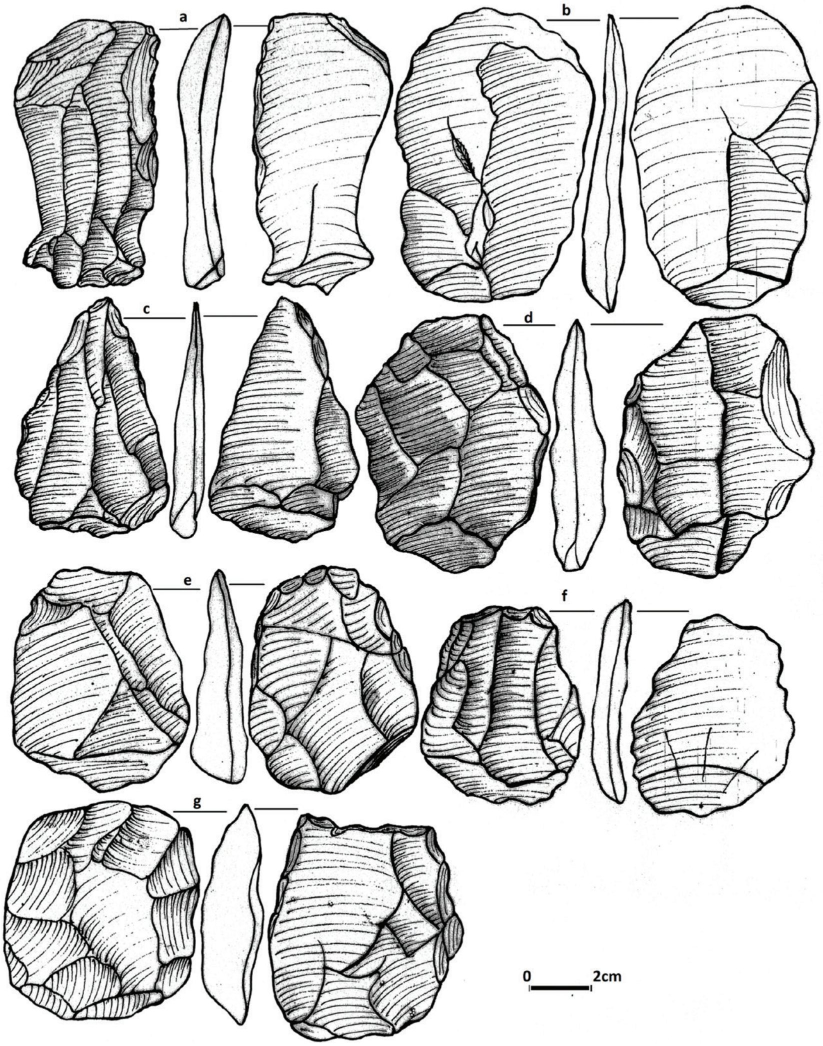

FIGURE 2.4 Some of the artefacts retrieved from the Ngaloba Beds: (A) Levallois Flake, (B-D) Diminutive Bifaces (C) Bifacial Point (E-F) Scarpers (G) Diminutive Cleaver Scraper

occupied this area for during a very short period. Second, we cannot rule out the possibility that our test pits were dug on a non-stratified spot. The nearest well investigated locality to the study area is the Lake Eyasi basin including Mumba Hohle where following Kohl-Larsen studies, Mehlman has conducted a detailed investigation of the Quaternary archaeology revealing a long sequence documenting the Acheulean-MSA and MSA-LSA transitions up to Pastoral Neolithic (PN) industries (Kohl-Larsen, 1943; Mehlman, 1989). In addition to

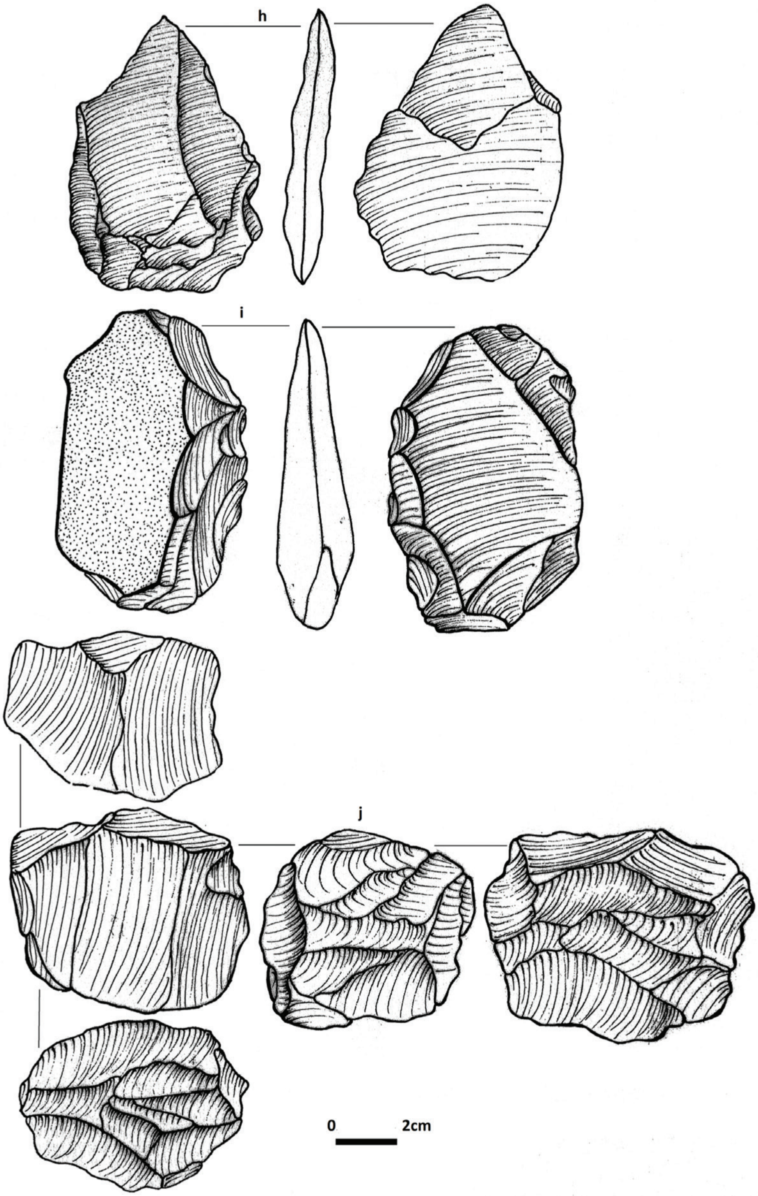

FIGURE 2.5 MSA artefacts retrieved from the Ngaloba Beds: (H) Point (I) Scraper (J) Core

MSA, LSA, and PN sequence, the Lake Eyasi basin has revealed important early *Homo* specimens associated with an early MSA industry described as the Njarassa. These include three individuals discovered by Kohl-Larsen's expedition (Reck and Kohl-Larsen, 1936) and another discovery of a skull fragment in 1993

(Brauer and Mabulla, 1996). The Eyasi hominin remains have now been dated to at least 100 ka and most likely older than 130 ka. (Mehlman, 1984) and hence contemporary with the Ngaloba hominin.

The majority of the lithic artefacts are manufactured from basalt obtained from nearby exposures of basaltic lava, the Ogol lava. This observation is interesting because as Mabulla 2015 and Adelsberger et al., 2002 and 2011 observed, the raw material from which the Middle Pleistocene MSA artefacts from Upper Ngaloba beds include local and non-local materials. The local materials would be dominated by the Ogol lava while non-local material consists of other forms of lava such as trachyandesite, and phonolite as well as non-volcanic material such as quartzite, gneiss, chert, etc. For reasons presently not clear, the hominins in the Greater Laetoli area seem to have been satisfied with the use of the Ogol lava which as was seen from the surface easily obtained. The artefacts have a mixture of light duty implements, sometimes becoming microscopic, in addition to large duty forms. While the former component suggests LSA affinity, the latter would suggest MSA belongingness. This mixture has led Mabulla (2015), Tyron et al. (2014) to refer to the industry as Early Middle Stone Age (EMSA) or Ngaloba industry. However, the recent fieldwork has observed very few light-duty or microlithic implements. This result can be interpreted as spatial variability within the assemblages associated with the upper Ngalobal beds, an indication of site use variability or intersite variability.

The above observation is supported by the fact that the artifact assemblage discussed here unlike the ones that have been reported by Mabulla 2015 are dominated by heavy duty tools. Alternatively, it must be underscored that since the assemblages discussed here are as remarked earlier surface, natural post depositional factors may have washed away the less bulky artefacts leaving the heavy-duty artefacts behind. It is tempting to surmise if the Ngaloba industry described here could be a variant of the Njarassa industry described from the nearby Lake Eyasi basin by Mehlman (1989). Some of the bifaces such as the ovate handaxes and core axes could pass as belonging to Sangoan and hence Mabullla's description of the Ngaloba MSA as early MSA (Mabulla, 2015). Alternatively, the industry is possibly a highland expression of the Njarassa, but this needs a larger sample. Another variant of the MSA not too far away from Ngaloba has been recognised at Nasera in southern Serengeti where the industry displays a mixture of MSA and LSA technocomplex. Most of the artefacts are made from quartzite, though there is a low frequency of obsidian and chert described by Mehlman (1989) as the Naseran industry. Employment of comparable raw materials has also been observed in the MSA/LSA industries in the eastern Lake Natron (Masao, 2015; Mehlmam, 1989; Isaac, 1966). The lowest MSA/LSA Naseran industry levels seem to have dates that are appreciably younger than those of Kisele and Sanzako being 55,960 ±2,675 - 18,475 ±860. Moreover, the Upper Ngaloba trachytic tuff has been correlated to the lower Ndutu marker tuff at Olduvai (Day et al., 1980). A uranium series date of ca 129,000 ±4,000 B.P. associated with early *H. sapiens* (LH 18) immediately postdates the trachytic tuff at Laetoli (Hay, 1987).

As remarked earlier, few bones were collected. We are not sure that they are from MSA horizon despite finding them with the MSA assemblages. Although fossil remains from the Laetoli beds are dispersed and fragmented (e.g., Leakey et al., 1979: 164), our faunal sample exhibit a medium weathering stage as they were relatively from a recent ongoing erosion (Behrensmeyer, 1978). This has contributed to the preservation of surface modification in form of cut marks and percussion marks. These modifications have broader implication of MSA tools uses and feeding behaviour. Documentation of surface modification analysed together with the artefacts shed light on food procurement strategies of the Ngaloba LH 18 folks, but one would require a larger sample in order to make more meaningful statements about EHs' food procurement hypotheses. Archaeological remains such as bone tools, points projectile and cut marked bones suggest that humans started active hunting during the MSA period (Badenhorst et al., 2016; Stiner et al., 2009; Wadley et al., 2009; Clark and Plug, 2008; Brooks, 2006; Lombard, 2012; McCall, 2015). Some of the artefacts e.g., the points and projectiles as reported by Mabulla (2015) could have been used for hunting, it is not unimaginable, that the faunal remains and modification thereof are associated with the assemblage and that LH 18 was capable of hunting. Hunting during the MSA is well studied in southern Africa archaeological sites (e.g., Faith, 2013; Dusseldorp, 2012; Brooks, 2006; Marean, 2005). However, this topic is poorly investigated in eastern Africa due to the lack of zooarchaeological studies on fauna assemblage recovered from MSA (Prendergast et al., 2007). As a result, this limits our knowledge and understanding about butchering and foraging behaviour during MSA period (Prendergast et al., 2007). Therefore, we recommend that future study should focus on locating *insitu* faunal and lithic remains. Second, a systematic investigation of faunal remains should be undertaken to investigate carcass acquisition and butchering behaviour during the MSA period. Only then we can properly use the assemblage to address questions of LH 18 and related hominins behaviour and cognition.

Acknowledgements

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PART 2

Cultural Transitions in Africa

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CHAPTER 3

West-Central African Diversity from the Stone Age to the Iron Age, Continuities and Transitions during the Late Pleistocene and the Holocene

Bernard Clist

1 Introduction

> No matter which site is studied and regardless of its age, archaeology should be concerned only with the search for man and his behavior. This will demand careful excavations of living sites, which should be well chosen. Excavation techniques should be such as to record maximum observation in the field, and in the laboratory the most recent techniques should be used. VAN NOTEN 1982: 13

Nearly forty years later, sadly we are still lacking the most basic chrono-cultural sequences in most parts of Central Africa, and '*the search of man and his behavior*' is still wishful thinking. Of course, one of the important explanations (though not the only one) is the fragile political and social situation inhibiting research.

Nevertheless, archaeological research shows evidence for multiple, complex material cultures, suggesting various levels of human admixtures before the start of the Holocene (about 12,000 years ago). Though the picture we present here is based on research of heterogeneous quality and irregular geographical coverage in a vast area (roughly equivalent to the 27 countries of the European Union), a general pattern can still be outlined and of use as a benchmark for modern genetic research. Figure 3.1 locates the sectors with better Neolithic and Iron Age pottery sequences, and the four circled in black have a full sequence, starting from the Neolithic: 1), Corisco Island in Equatorial Guinea (Figure 3.1, n°3); 2), northwest Gabon (n°4); 3), the Inner Congo Basin (n°9); and 4), the Upemba depression in the DRC (n°10).

Unfortunately, the archaeological cultures cannot be easily associated with languages or human groups:

> … from a methodological standpoint, Bantu is a linguistic term, while a mute archaeological artefact is not Bantu. DE MARET 1989: 129

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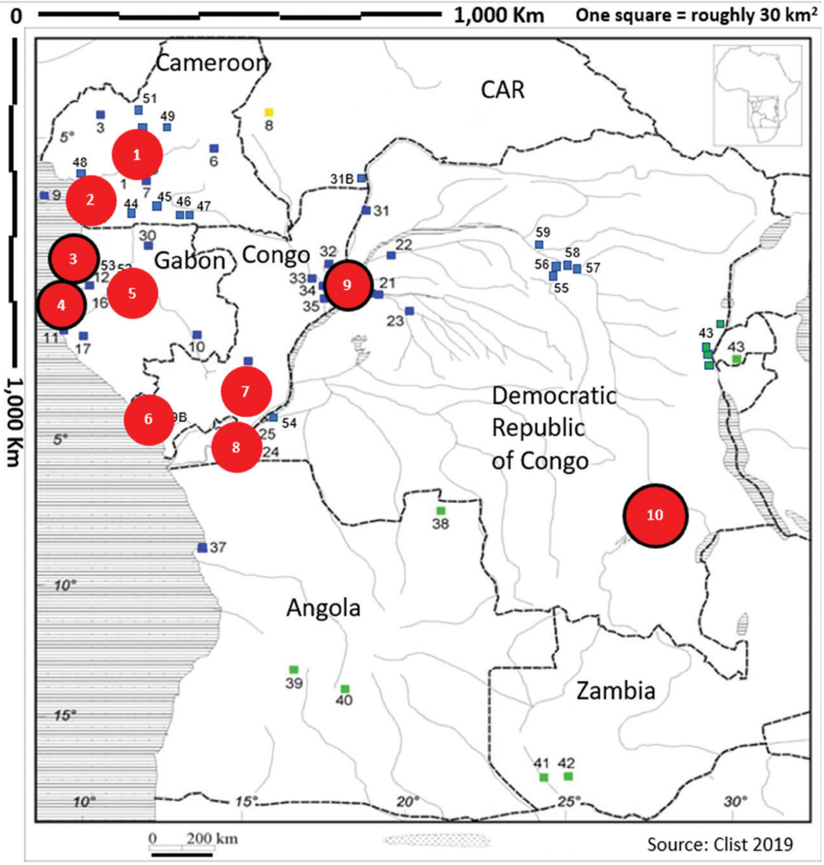


Source: Clist 2019

FIGURE 3.1 The better Iron Age cultural sequences in Central Africa. 1: Yaoundé area, Cameroon, 2: Coastal area, Cameroon, 3: Corisco island, Equatorial Guinea, 4: Libreville area, Gabon, 5: Middle Ogooué area, Gabon, 6: Coastal area, Congo, 7: Bateke plateaux, Congo, 8: Kongo Central province, DRC, 9: Inner Congo Basin, DRC, 10: Upemba depression, DRC. Circled in black, the only 4 complete sequences known today. Blue squares are some of the villages dated before and around 2,000 BP

FIGURE BY B. CLIST

Central Africa includes eight countries: Cameroon; Central African Republic (CAR); Sao Tomé and Principe; Equatorial Guinea; Gabon; Congo; Democratic Republic of Congo (DRC); and Angola (Figure 3.1). If we consider only the major fluvial basins in between plateaus and high ranges to the north, east and south (Lanfranchi & Schwartz 1990: 5-67; Lanfranchi & Clist 1991: 5-54), we can exclude northern Cameroon and northern CAR (associated with the Sahel region), southern Angola south of Lobito, and Zambia (oriented towards southern Africa). Different types of forests cover the landscape, with wooded

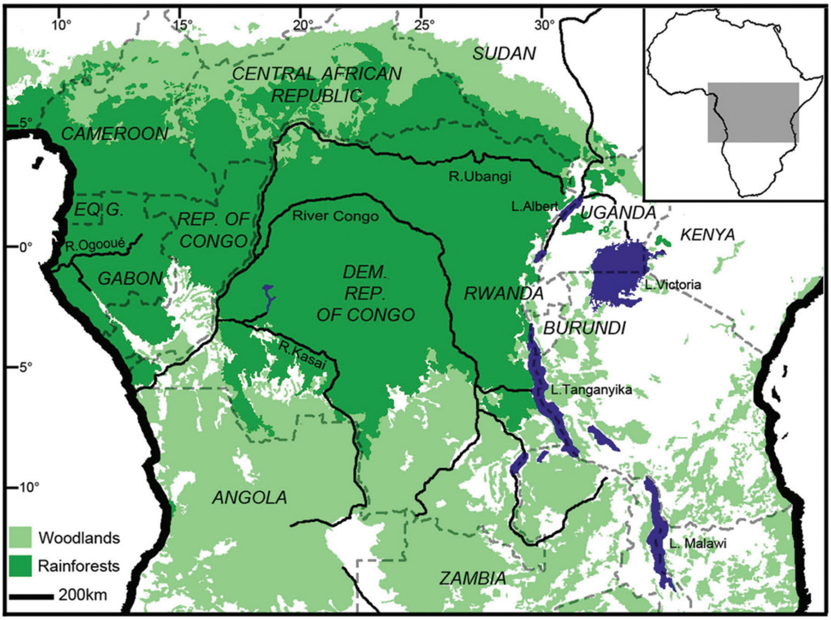
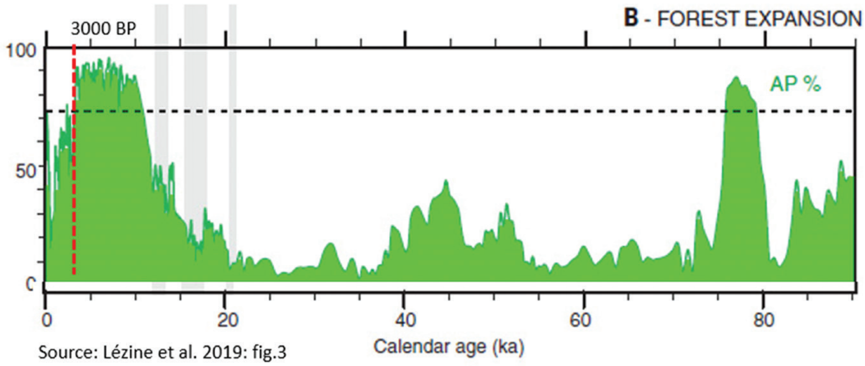


FIGURE 3.2 Rainforests and woodlands modern extension in Central Africa, white areas are savannas
FIGURE FROM TAYLOR 2016, FIG.15.1

savannas and woodlands extending to the north and south around the Congo and Ogooué River basins (Figure 3.2).

2 Climatic Changes

According to paleo-environmental data, dry climate periods with open savanna-like vegetation alternated with a warmer, humid climate and more forested vegetation during the Late Pleistocene and the following Holocene. Research at Bambili Lake in Cameroon (Lézine et al., 2019), supported by long-term pollen profiles onshore and offshore in Cameroon and offshore in Angola (Dupont et al., 2008, Lébamba et al., 2012, Lézine & Cazet 2005, Maley & Brenac 1998), document these changes. The Bambili evidence shows the expansion of forests before 82,000 BP, then between 80,000-75,000 BP, 53,000-38,000 BP, and 20,000-5,000 BP (Figure 3.3). The 80,000-75,000 BP period was of similar amplitude as at the Pleistocene-Holocene boundary (*c.* 12,000 BP), both with higher tree-pollen counts than today. The well-known 'Stone Lines' were formed during the transition from dry to humid periods: increasing rainfall on savanna or wooded savanna let heavier components ('stone') move down-slope to form concentrations ('lines'). Sangoan and Lupemban tools are



Source: Lézine et al. 2019: fig.3

FIGURE 3.3 Palaeoenvironmental sequence of 90,000 years from Bambili lake, Cameroon. The tree pollen is illustrated in green, the other pollen in white. The black horizontal dotted line represents the modern level of the tree pollen. The vertical dotted red line marks the arrival of the first pottery using villages in the Cameroon/Gabon area circa 3,000 BP

FIGURE FROM LÉZINE ET AL., 2019, FIG.3, ADAPTATION BY B. CLIST

found in or on the stone-lines (e.g. Bayle des Hermens et al., 1987; Mercader et al., 2002).

A severe transition separates the Pleistocene from the Holocene, characterized by mountain forests expanding (starting around 20,000 BP, Figure 3.3), and the Atlantic Ocean rising enough to submerge coastal Stone Age sites. This humid climate persisted until *c.* 3,000 BP when savannas spread due to a severe dry period, known as the Late Holocene Forest Crisis (LHFC), ending around 2,000 BP (Maley et al., 2018). The mechanism of this major vegetation change is felt earlier, c. 5,000 BP, with the slow lowering of the Sinnda and Kitina lakes in Congo (Schwartz et al., 2000). It is around the start of the LHFC that several waves of low-density stone and pottery using villagers inhabited the west, but the first movements southwards from Cameroon happened before the forest regression. Other groups of people, this time iron-using and/or metallurgists (de Maret 2013), followed several centuries later.

We need more local studies to establish the way local climate and vegetation changed following the trend we have outlined. From the available data about the LHFC, vast expanses of savanna developed (Maley 1987; Schwartz 1991), creating a 400 km wide Sangha River Interval (SRI), a corridor that enabled Early Iron Age (EIA) peoples and Bantu-speakers (Bostoen et al., 2015, Grollemund et al., 2015) to expand more easily through the region's dense vegetation (Schwartz 1992). Other data, however, show that forests persisted in this corridor (Brncic et al., 2007, 2009, Kiahtipes 2016; Brémond et al., 2017; Tovar et al., 2019). A recent reassessment concluded the SRI was covered by forests (Giresse et al., 2020). Archaeological evidence does not show any settlement in the SRI before 2,020 BP for the Pikunda-Munda Group (Seidensticker 2016) or before 2,130 BP to the north (Morin-Rivat et al., 2014), while on the western fringe of the SRI no settlement existed before c. 2,260 BP (Morin-Rivat et al., 2014, 2016). This re-evaluation strengthens our modelling of the EIA and illustrates a large-scale movement of various peoples between about 2,200 and 2,000 BP from Cameroon to the DRC, mainly through the forests, and without using the SRI as it was stated a few years ago (see below).

Figure 3.3 illustrates the speed of vegetation changes for humans who had to adapt accordingly to the new climatic conditions, the changing position and availability of the animals they were hunting, and the fruit trees and tubers they were collecting. We can suggest that climate-induced movements of hunter-gatherer groups sometimes led to their physical interaction.

Local palaeoenvironemental sequences must also reach into the EIA and the Late Iron Age (LIA). Several short-term studies with a high resolution already exist (e.g. Ngomanda et al., 2005, 2007; Brnic et al., 2009). We have to determine if the 'Medieval Warm Period' (or 'Medieval Climate Optimum') of AD 950 to 1250 and the colder 'Little Ice Age' of AD 1270 to 1850 impacted human societies through increasing or decreasing food production yields. Perhaps the 'Little Ice Age' contributed to the rise of kingdoms on the southern edge of the rainforests as a response to agricultural stress, as illustrated by the drop in rainfall between AD 1400 and 1700 recorded at Kamalete Lake in Gabon (Ngomanda et al., 2005). Potential reactions of a society facing an ecological or economic crisis are, amongst several, changes in social organization.

3 Hunter-Gatherers

The succession of an Early, Middle, and Later Stone Age was long considered as being chronological markers through the Pleistocene and Holocene, following a simple evolutionist perspective. Chronology went hand in hand with technological development, from the pre-Acheulean to the Later Stone Age (LSA). Since the 1980s, we acknowledge the complex reality and differences in stone industries.

The Middle Stone Age (MSA) is characterized by tools struck from carefully prepared Levallois cores, dated from 300,000 BP (Taylor 2014). It witnessed the co-occurrence of diverse lithic reduction strategies, including bifacial prepared core technique, blade and backed blade technologies (Cornelissen 2016; Taylor 2016; Lanfranchi and Clist 1991: 55-95), and ending with a major size reduction to microlithic assemblages in the Holocene (see Lanfranchi and Clist 1991: 97-132). We now know that LSA assemblages co-existed alongside

MSA assemblages before 30,000 BP (e.g. Matupi cave in the DRC and Shum Laka rock shelter in Cameroon; Cornelissen 2016 and our Figure 3.4).

While in some parts of Central Africa, it is only with the Pleistocene/Holocene climate transition we witness a transformation of tool kits, from bifacial to microlithic components, in other areas microlithic industries existed throughout the MSA (Cornelissen 1997). People used several "*chaînes opératoires*", or production sequences, to create various tool-kits, suggesting

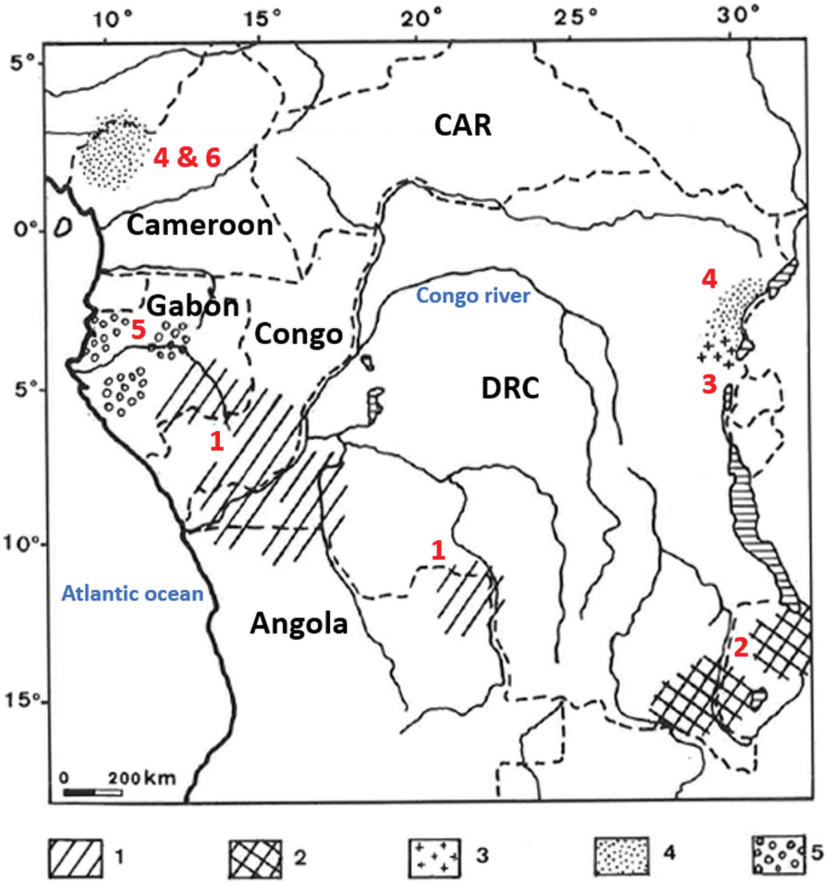


FIGURE 3.4 Spatial extension of the known stone industries from West-Central Africa. 1: Bifacial tradition of the Sangoan, Lupemban, and Tshitolean industries, 2: Middle Stone Age occupations with, and Holocene microlithic industries without bifacially flaked implements, 3: Middle Stone Age occupations without bifacially flaked implements, 4: Pre-Holocene microlithic industries, 5: Holocene microlithic industries without a bifacial component, 6: Holocene microlithic industries

FIGURE BASED ON CORNELISSEN 1997, FIG. 30, ADAPTED BY B. CLIST

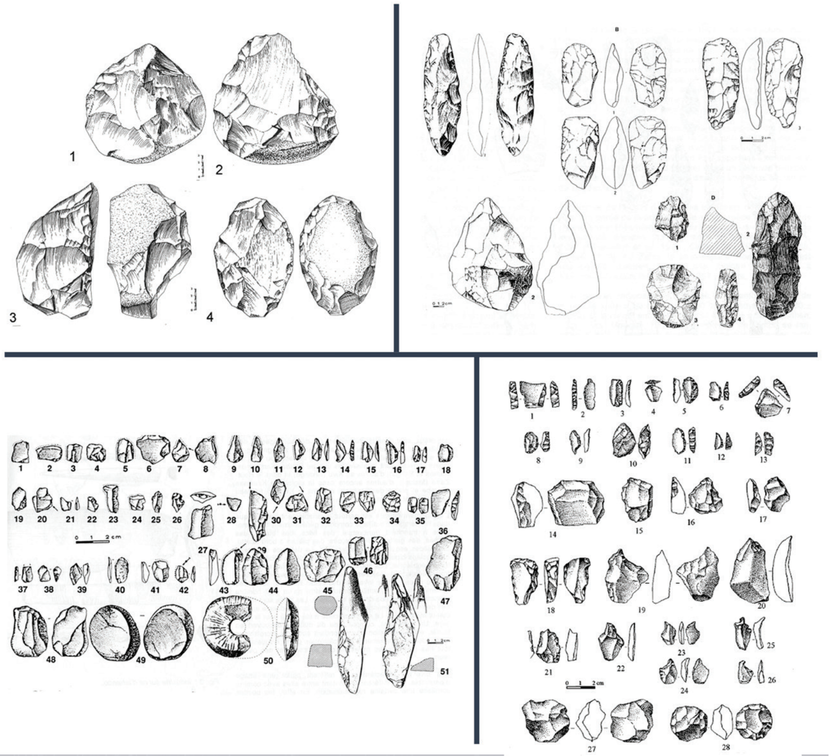


FIGURE 3.5 Pleistocene stone industries of Central Africa. Pleistocene stone industries of Central Africa: upper left, Sangoan from Gabon (Locko 1991a: 68-69); upper right, Lupemban from the DRC (Muya 1991a: 79); lower left, microlithic from Matupi cave, DRC (Muya 1991b: 119); lower right, microlithic from Shum Laka rockshelter, Cameroon (Cornelissen 2003: 15, fig. 8)

several historical trajectories and therefore several co-existing human groups. They appear not to be in close proximity to one another, but this observation is probably due to uneven archaeological fieldwork.

During pre-Holocene times, while hunter-gatherers had microlithic techniques in the northwest and eastern parts of the region (Figure 3.4, n°4 and Figure 3.5), others used macrolithic bifacial techniques in Gabon and the DRC (Figure 3.4, n°1-2 and Figure 3.5). Later in the Holocene, the other communities turned to microlithic production techniques. Diversity was maintained with specific innovations entering the toolkits, for example in the Grassfields of Cameroon, such as polished stone tools from c. 7,000-6,000 BP, and pottery from 5,000-4,000 BP (Figure 3.6). Serious climatic deterioration around 7,100–6,900 BP in the Sahara and the Sahel appears to have caused new communities

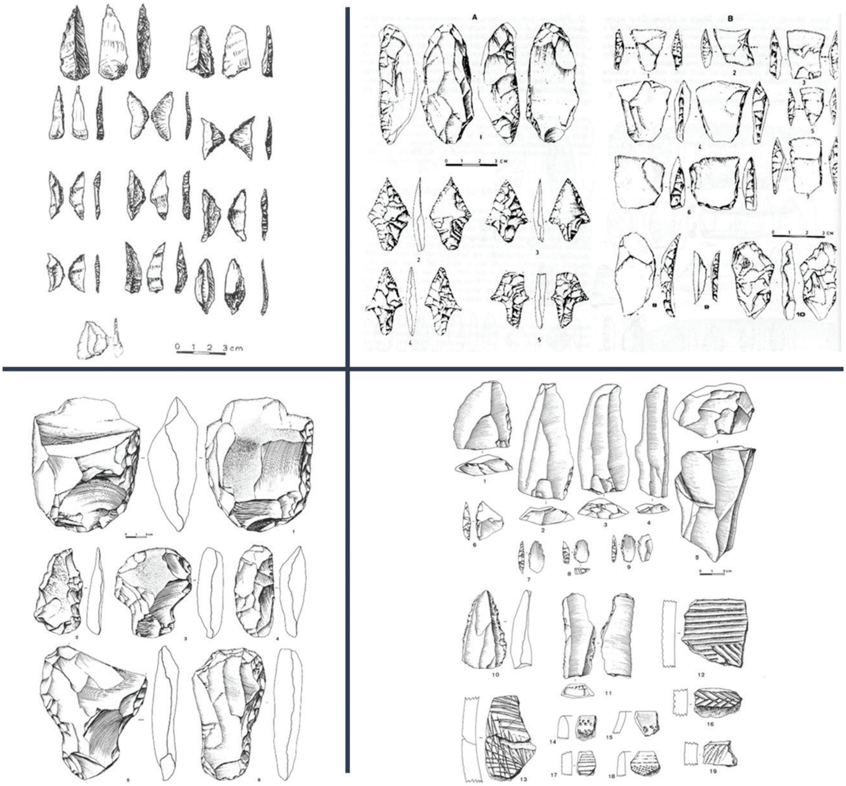


FIGURE 3.6 Holocene stone industries of Central Africa. Upper left, north-west Gabon (Locko 1991b: 110); upper right, plateau Bateke, DRC (Muya 1991b: 120); lower left and right, Shum Laka, Cameroon (Lavachery 1996, 1998 & adapted in Clist 2006)

to slowly settle the Grassfields and introduce these new technologies (Bostoen et al., 2015: 362).

4 Genetic Background of Hunter-Gatherers

Generally, other than caves and rock shelters, environmental conditions are not conducive to the preservation of animal and human bones. The acidic soils of open-air sites often do not permit preservation beyond 400 years (e.g. Linseele 2018 for the Kongo Central province of western DRC), unless exceptional chemical peculiarities exist in places such as pits (e.g. Nkang in Cameroon and Toubé in Gabon, Van Neer 2000) or decomposing iron objects preserving pieces of bone or teeth in burials (e.g. Corisco Island, Gonzalez-Ruibal et al., 2013). Because of the paucity of research relating to the Stone Ages, few sites have yielded human remains, and even fewer have been genetically analyzed (animals: see Van Neer 1990, 1991, 2000; humans: see Asombang 1988, Van Neer & Lanfranchi 1985: 354, Mercader et al., 2001, Ribot et al., 2001, Crevecoeur et al., 2016; genetics: see Lipson et al., 2020, Wang et al., 2020).

This is why genetic studies turn to modern populations, especially rainforest hunter-gatherers (RHG), likely descendants of MSA and LSA communities of Central Africa. These studies suggest that the RHG split off from the main *Homo sapiens* lineage over 100,000 years ago (Lopez et al., 2019), diverging into the modern western and eastern Batwa some 20,000 years ago, with further internal differentiation amongst the western groups from 3,000 BP (Verdu et al., 2009). Some evidence indicates a lack of interaction between villagers and hunter-gatherers before 1,000 years ago (Verdu et al., 2014), and internal differentiation would then not be related to villager/hunter-gatherer contact. Significantly, the location of modern RHG groups correlates with some LSA cultures (Figure 3.7). The western groups north of the Congo River (Bezan, Kola / Gyeli, Baka, Aka, Koya / Kola, Bongo, and Barimba) are in the same area as the ancient Atlantic coastal and Tshitolean LSA industries; the central groups (Twa and Cwa) south of the Congo River correlate with other Tshitolean sites; and the eastern groups (Asua, Sua, Efe, and Twa), located in eastern DRC and East Africa, have a stronger spatial relationship with LSA industries typologically

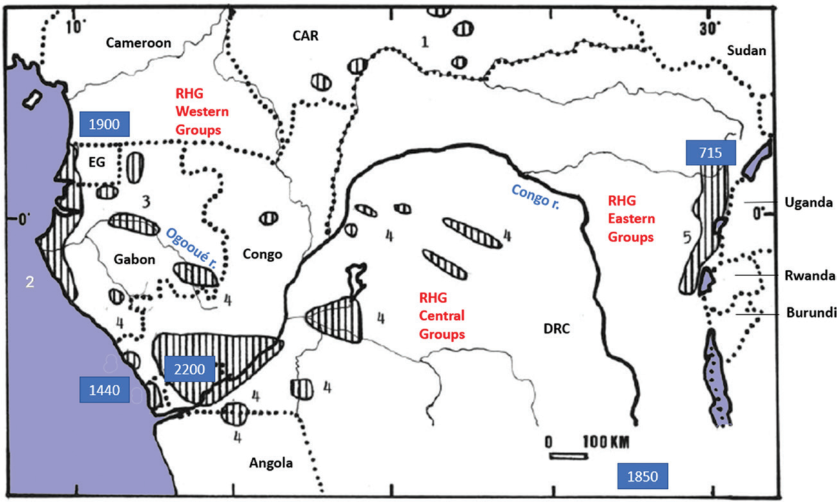


FIGURE 3.7 Holocene Late Stone Age cultures and latest stone-using hunter-gatherers (blue rectangles with BP dates). 1: CAR sites, 2: Coastal sites of Equatorial Guinea and Gabon, 3: Dual influence sites in Gabon (coastal & Tshitolean), 4: Tshitolean, Congo and the DRC, 5: East Africa related sites, 6: Grassfields of Cameroon
FIGURE ADAPTED FROM CLIST 1995: 218, FIG. 73

related to East Africa (Lanfranchi 1991a; Muya Wa Bitanko Kamuanga 1991b). In this context, the aDNA analysis of a 750 year-old hunter-gatherer from the Matangai Turu rock shelter in the north-eastern part of the DRC (Mercader et al., 2001) indicates a possible relationship with Pastoral Neolithic peoples from East Africa (Wang et al., 2020).

5 Probable Interaction between Late Hunter-Gatherers and the Earliest Villagers

Excavations in Central Africa have revealed stone-using peoples with stone-knapping techniques identical to LSA industries living near early villages and dated in the same time range (i.e. after 3,000 BP). Sometimes, Iron Age potsherds and/or iron tools are also associated with lithics. The youngest of such interactions may be dated to around 700 BP in the Ituri forest of north-eastern DRC (Mercader et al., 2000). But a few others exist (Figure 3.7): Ndtoua rockshelter at c. 1,900 BP (Lavachery et al., 2005: 182) and Mbol at c. 1,870 BP (Morin-Rivat et al., 2014), both in southern Cameroon, the Moulandou-Fouala site in Gabon at c. 1672 BP (Livingstone Smith et al., 2007: 27), Kouilou River area in Congo at c. 1,240 BP (Lanfranchi 1991b: 172), eastern Mayumbe range in the DRC at c. 2,200 BP (Clist, Bigohe et al., 2018: 16-17), Upemba depression in the Katanga province in the DRC c. 1,850 BP (Cahen 1975), and several others in Gabon (Clist 2006a: 300). The overall picture seems to be a gradual disappearance of stone working after contact with the first villagers, with differing scenarios as southwards moving villagers entered new territories. Two sites strengthen our observation, with continuous use of stone knapping since thousands of years ago and into the Iron Age: the Nangara-Komba and Shum Laka rockshelters, respectively in the CAR and in Cameroon.

At Nangara-Komba, the earliest Stone Age layers are dated to c. 6,100 BP and the quartz components are followed up to c. 200 BP (Lupo et al., 2021). They are coming mostly from small quartz and quartzite cobbles, producing microlithic assemblages under 4 cm size with rare tools. There is no significant change in the knapping technology throughout the deposit, from c. 6,100 BP to historical times (*Ibid.*). Pottery was probably imported from neighboring villages to the hunter-gatherer groups occupying the rock shelter during the later stages of its use, certainly since c. 2,400 BP, perhaps since c. 2,800 BP (*Ibid.*); some potsherds are decorated with rocking comb impressions, a technique similar to contemporaneous pre-metallurgical villages known in southern Cameroon.

The Shum Laka rockshelter in the Cameroon Grassfields (Figure 3.7, n°6) provides evidence of hunter-gatherers with polished stone tools since 7,000-6,000

BP and pottery from around 5,000-4,000 BP (Lavachery 1996, 1998, 2001, 2003; Lavachery and Cornelissen 2000; Lavachery et al., 1996). On the basis of reconstructed vocabulary, proto-Bantu speakers knew pottery (Bostoen 2007), and researchers have considered the Shum Laka artifacts as representative of the original proto-Bantu toolkit (de Maret et al., 1987; see also Bostoen et al., 2015 for the latest). A recent genetic study on four individuals from burials dated to around 7,000 and 3,000 BP, however, concludes that "these individuals are not representative of the primary source population(s) that were ancestral to present-day Bantu-speakers" (Lipson et al., 2020). These people were therefore stone-using hunter-gatherers, and up to 3,000 BP, did not have any physical interaction with villagers using pottery. Later, after 2,150 BP, iron tools and roulette decorated pottery were used together with the same LSA lithics. Neighboring Iron Age villages probably supplied these hunter-gatherers with a few pots, as elsewhere in the region. This explains why some researchers have noted a discrepancy between the developed LSA lithics of the Grassfields sites and the poor stone tools in the first villages in southern Cameroon:

> il est impossible de comprendre, dans l'état actuel de notre ignorance, comment les préhistoriques sont passés de la confection d'une industrie lithique assez élaborée dans les Grassfields à celle d'une industrie très simple autour de Yaoundé. CLIST 2006B: 380

The re-evaluation of the late Grassfields LSA sites brings into focus an important research question: did people really establish villages in the Grassfields area, as a pit with pottery similar to the Obobogo Group of the Yaoundé area (Schmidt and Asombang 1990: 14-15) and the few potsherds at Shum Laka and Fiye Nkwi rockshelters suggest (Lavachery 2001; Asombang 1988)? The alternative would be the pottery are imports from outlying villages to LSA communities, using long distance exchange networks, or the RHG themselves developed pottery making. Renewed research is needed in the Grassfields, and to the south, to look for these early villages (though for the time being, due to social unrest, this is not possible).

6 Rock art

Rock art is known throughout the region, although it has been studied in a very uneven way. Several styles, with differing techniques, are located on different surfaces, such as caves and rock-shelters walls and open air slabs and boulders (de Maret 1982; Loumpet Galitzine 1992). Possibly, open-air rock engravings were also painted, like the better preserved images in rock shelters in Congo and Angola (Ervedosa 1980: 233-391; Lanfranchi 1985; Gutierrez 1996). Since the mid-1990s, research has led to new discoveries, re-interpretations of old data, and Accelerator Mass Spectrometry (AMS) dating. The latter has been put to use in the CAR at the Nangara-Komba site with a date to circa 500 BP (Lupo et al., 2021: 10, table 1), in the western DRC where paintings are dated to the LIA and the time of the Kongo kingdom (Heimlich 2017), at the Ndalambiri site of west-central Angola dated to circa 80 BP (Rosina et al., 2018) and at the Tchitundo-Hulo Opeleva site in southwest Angola dated to circa 1980 BP (Gutierrez 1996: 190) where it relates to the LSA or possibly to the EIA.

The various rock art styles probably belong to at least two periods, as they do in Gabon (Clist 1995a: 184-197, 2005: 533-540), or in Angola (Martins 2014). They are thus also a marker of regional social diversity. We must reinterpret them and test their fit with the pottery sequences we now have, after having untangled their chronology and styles based on updated national catalogues (Angola—Ervedosa 1980: 233-391 and Gutierrez 1996; Cameroon—Loumpet-Galitzine 1998 and Tchandeu 2016; CAR—Bayle des Hermens 1975: 265-277, 1984 and Clist 1991: 199-201; Congo—Lanfranchi 1985 and Mongolo Mololi 2012, 2013; DRC—Mortelmans 1952 and Heimlich 2017; Gabon—Oslisly and Peyrot 1993, Clist 1995: 184-197 and Oslisly 2016; Equatorial Guinea—Perramon Marti 1968 and Clist 2020).

7 Interaction among Early Villagers

Since the late 1950s, archaeology has been linked with linguistics to study the southwards expansion of Bantu-speakers whose homeland was located astride the Cross River in Nigeria and the Grassfields of Cameroon (Bostoen 2018). At present, it is only from southern Cameroon that one can document two movements of villagers, not yet using iron tools, between about 3,000 and 2,300 BP (Figure 3.8). These movements connect southern Cameroon to the Congo River along some 1,000 km of mainly forest with some interspersed savannas (Clist 2006a, 2006b).

The first and earlier movement seems to have followed the Atlantic Coast between 3,000 and 2,500 BP, linking the Obobogo (Cameroon), Okala (Gabon), and early Tchissanga (Congo) Traditions, or Groups (Figure 3.8, group A) (Nlend Nlend 2014; Clist 2005; Denbow 2014). Later, around 2,500-2,300 BP, a second movement with different pottery links the late Tchissanga (Congo) and the Ngovo (DRC) Traditions (Denbow 2014; de Maret 1986). We do not yet understand the connection, if any, with the first incomers and between

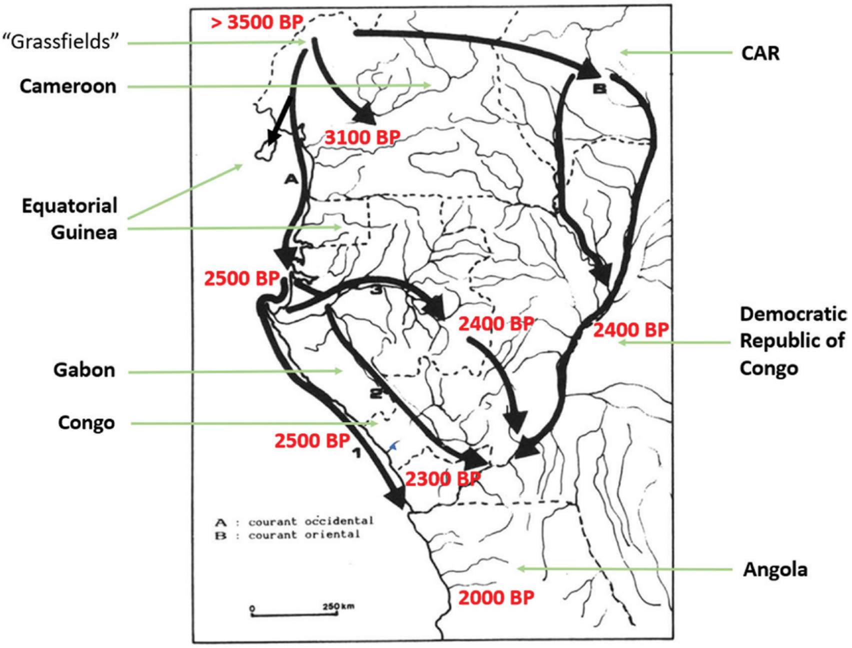


FIGURE 3.8 Probable axes of expansion of the first villagers in West-Central Africa. General timeline, the "A group" following the Atlantic Ocean coastline. The "B group" probably went through the forest and not along rivers as shown
MARCHAL-NASSE 1991: 142, FIG.4, A MAP MADE BY B. CLIST – ADAPTED 2019 BY B. CLIST

them. Based on the distribution of the Okala Group, people probably travelled up the Ogooué River from the Atlantic coastline to reach Franceville and the savannas astride the Gabon-Congo border about 550 km to the southeast (Figure 3.8). The Okala evidence consists of a pit at Franceville dated to 2,440 BP, an undated archaeological layer at Massango with pottery and polished stone tools, and surface finds of dozens of polished stone adzes and axes in the province (Clist 1995: 147–149).

We still do not understand what happened there later, when iron smelting started in Moanda about 2,350 BP associated with a pottery still unpublished (Jézégou and Clist 1991), and with a pit at Djambala 200 km to the southeast on the Bateke Plateaux in Congo dated to 2,300 BP, containing pottery but without evidence of iron working (Lanfranchi 1991b: 172-173). Given that the Bateke Plateaux was not settled by iron-using villagers until 1,900 BP (Dupré and Pinçon 1997: 37-59), this data may represent a third axis of movement, from the north through the forests. Such a third axis is also suggested by the sites of Oyem (2,280-2,220 BP) and Koualessis (2,100-1900 BP) in northern Gabon, and Okanda near the Ogooué River (c. 2,110 BP) where iron smelting was practiced

(Clist 1989a: 81-83, 2005: 773-777). While iron metallurgy developed at Moanda and then slightly later in Oyem and central Gabon, the Okala Group material culture continued on the coast and in the middle reaches of the Ogooué River without evidence of iron production, though it probably imported iron tools from the inland production centers c. 2,370-2,200 BP (Clist 2005). Iron-working expanded on later with the establishment along the coast of Gabon and Equatorial Guinea of the Oveng Group from about 2,000 BP (Sánchez-Elipe Lorente et al., 2016, and see below).

Far to the east, iron-producing Urewe Tradition sites are known in Kivu (DRC) (Hiernaux & Maquet 1960), possibly dating to 2,800-2,500 BP and the highlands of the Interlacustrine area in Rwanda, Burundi, and Tanzania (Clist 1987, 2013: 26) (Figure 3.9). The geographical isolation at 2,300 BP of

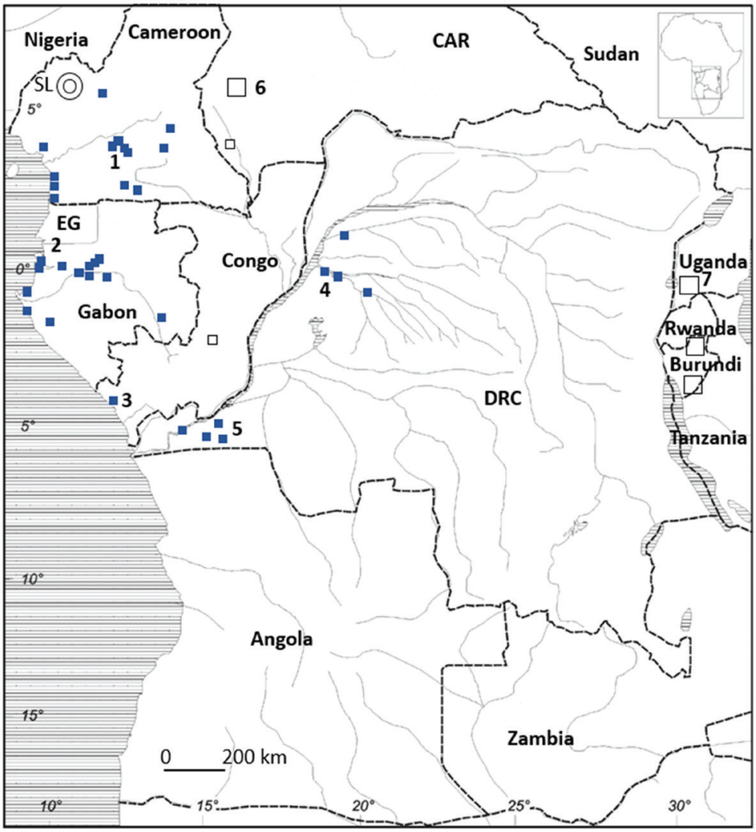


FIGURE 3.9 Pre-metallurgical villages maximum extension around 2,300 BP (blue squares). SL: Shum Laka rockshelter and Grassfields. 1: Obobogo Group. 2: Okala Group. 3: Tchissanga Group. 4: Imbonga Group. 5: Ngovo Group. 6: Bouar area Neolithic and megaliths. 7: Early Iron Age Urewe Group
ADAPTED FROM CLIST 2005: 722, FIG.8-11

the ‘neolithic’ villages in Cameroon, Gabon, and Congo, slowly expanding to the east and south, from the Urewe Tradition iron-producing settlements, is enough evidence to underline they are quite probably the result of two contemporaneous and separate social developments (Figure 3.9 and Ehret 2015).

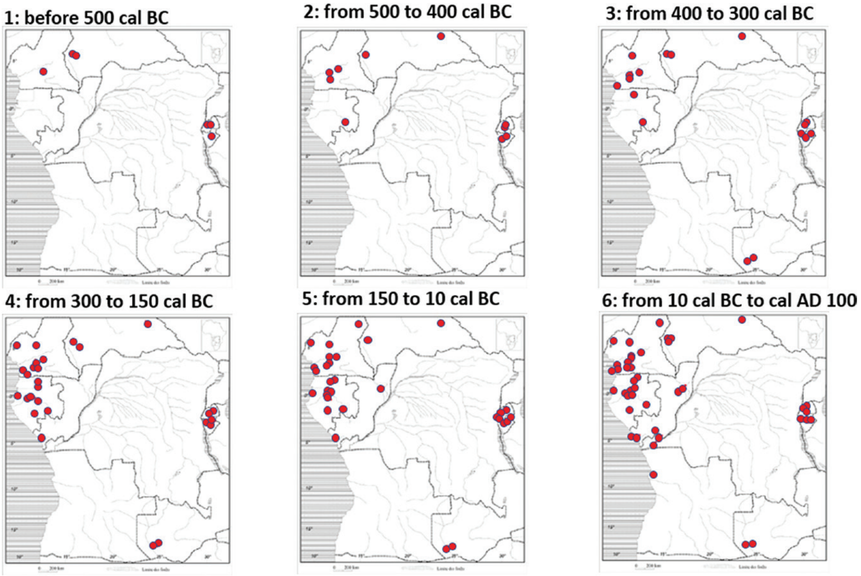
We now know of another and distinct group of pottery-using villagers who maybe moved upstream through the forest along the Congo River, reaching east to the Kisangani area by 2,100 BP (Livingstone Smith et al., 2017). If so, they may be related to the Imbonga Group located near Mbandaka on the Congo River, first dated to around 2,400 BP (Figure 3.8. Eggert 1987, 1994-1995; Wotzka 1995; Seidensticker 2016). The only possible origin for Imbonga communities is southeastern Cameroon, even though preliminary research there and neighboring Congo has not found any connections (Seidensticker 2016). But we cannot exclude the sites found around Kisangani relate to people arriving to the Congo river through the forests of its north bank. Ongoing research will certainly make the situation clearer in the years to come.

8 Iron Working

Two sets of facts from archaeology and historical linguistics must be considered to ascertain if the diffusion of iron working can be explained as an independent factor parallel to the expansion of the various EIA peoples. Historical linguistics told us long ago that metallurgy was not known to proto-Bantu speakers when they resided in the Cross River of Nigeria and the Grassfields of Cameroon (de Maret & Nsukka 1977, Nsuka-Nkutsi & de Maret 1982). Iron was a later introduction to Central Africa from the northwest, from Nigeria and Cameroon (Vansina 2006), which spread southwards (Clist 2012, 2013; Eggert 2014).

The earliest iron smelting centers developed in the north before 2,600 BP in the western CAR (Figure 3.10, n°1: Gbabiri in western CAR – 2,640 BP), before being attested in southern Cameroon (Zili – 2,630 BP, Figure 3.10, n°2), and around 2,300 BP in southeastern Gabon (Moanda – 2,350 BP, Figure 3.10, n°3). Iron smelting then spread south and eastwards (Figure 3.10, n°4 and 5) before ultimately reaching the Congo River and the Luanda area of Angola around 1,900 BP (Figure 3.10, n°6). Once again, now using the respective chronology of west-central Africa’s early iron-working centers and of the iron-producing Urewe Tradition of the Great Lakes area of eastern Africa (Clist 1987), we are left with the absence of any possible relationship between the two regions (Figure 3.10, n°1).

No metallurgical analyses have been published from metallurgical sites. Such research is needed to verify the types of production sequence in the



1: before 500 cal BC

2: from 500 to 400 cal BC

3: from 400 to 300 cal BC

4: from 300 to 150 cal BC

5: from 150 to 10 cal BC

6: from 10 cal BC to cal AD 100

FIGURE 3.10 Geographical location and chronology of archaeological sites with iron-working evidence
ADAPTED FROM CLIST 2013, FIGS. 1–6

smelting process. We should also establish the ceramic links to clarify several peculiarities in the data at hand. For example, it is known the Oveng Group, extending from Equatorial Guinea (Sánchez-Elipe Lorente et al., 2016) to the south of the Ogooué River in Gabon (Livinstone Smith et al., 2007: 31-34), starts slightly before the Kay Ladio Group of the Kongo Central Province in the DRC (Clist et al., 2019). Their respective pottery are strikingly similar in several ways (Figure 3.11). Further investigation is needed in the context of the cultural transitions found between 2,200 BP and 1,900 BP from southern Cameroon to the western DRC and to the Inner Congo Basin (Wotzka 1995; Clist 2005; Seidensticker 2016).

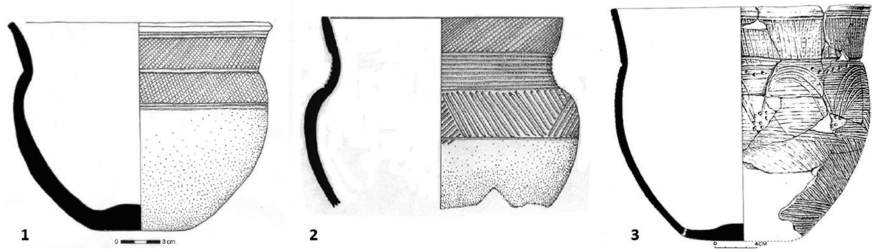


FIGURE 3.11 Pottery from the Oveng and Kay Ladio Groups. 1 & 2 (from Clist 2005): Pottery from the Oveng Group, c. 2,000-1,300 BP (Gabon), 3 (from Gosselain 1988): Pottery from the Kay Ladio Group, c. 1,950- 1,650 BP (DRC)

9 Cultural Transitions

Probably the most fascinating research outcome during the last 40 years is the identification of cultural transitions (Figure 3.1). This research is often based on PhD projects, most of which unfortunately remain unpublished.

As previously mentioned, we easily follow Neolithic transitions which are in stark contrast to LSA traditions. The earliest such transition is slightly older than 3,000 BP in southern Cameroon, around 2,300 BP on the Congo River in the western DRC, and around 2,400 BP in the Inner Congo Basin (Figure 3.8). In the latter area, the earliest settlers may have been already connected to iron-producing centers as they did not use polished stone adzes and axes.

Though stone-using hunter-gatherers coexisted with villagers from then until modern times, losing along the way their stone toolkit (Figure 3.7), the Iron Age brought different pottery traditions. Such Neolithic/Iron Age transitions are situated between 2,200 and 1,900 BP. They follow an irregular north to south chronological gradient, probably associated with the diffusion of iron smelting, but also with new waves of people moving towards the Atlantic coast. The spatial extension of their material culture is more restricted than during the preceding Neolithic, and shows marked stylistic differences along shorter distances.

These breaks are likely caused by a new human influx, replacing the previous production sequences, and changing the visual labels for group identification. Research on small cemeteries in southern Cameroon, southern Equatorial Guinea and northern Gabon revealed important differences in burial practice together with major changes in pottery production (Cameroon—Meister 2008, 2010; Meister and Eggert 2008; Eggert et al., 2006; Eggert and Seidensticker 2016. Equatorial Guinea— Gonzalez-Ruibal et al., 2011, 2013; Sánchez-Elipe Lorente 2015; Gabon—Peyrot et al., 1990, Clist 1995, 2005; and see below).

In this respect, four examples stand out illustrating similar scenarios: 1) southern Equatorial Guinea and northern Gabon; 2) the center of Gabon along the Ogooué River; 3) the coast of the Congo Republic; and 4) the DRC between Kinshasa and the Atlantic Ocean. We focus here on the first area, encompassing the Okala, Oveng. Nandá and Angondjé groups.

Throughout our review, we consider if one component is found on one site of a given cultural group, e.g. within the Okala Group, millet horticulture or stock raising, then it is probable all the villages of the group knew about it. Most excavations did not use flotation techniques to register millet seeds, and the soils are too acid to preserve animal bones.

10 The Okala Group

It was described early (Clist 1988, 1997) and is now bracketed by 44 radiocarbon dates from 2,460 to 1,870 BP. Okala communities are distributed over about 500 km, from the Gabon Estuary to Franceville near the Congo border, and southward for about 300 km to the lagoons and forests south of Port-Gentil (Figure 3.12. See Clist and Jézégou 1991; Clist 1995: 151–153, 2005: 490; Assoko Ndong 2001, 2003). The sites appear to be true villages with a cluster of contemporaneous houses spatially organized. Ubiquitous pits of varying volume (from 0.5m^3 to 9m^3) yielded fragments of burnt clay walls with pole impressions of the wooden framework. Some excavations revealed post holes near the pits. These villages seem to extend over large areas: Kango 5 was 6 ha, while Okala 1 was at least 3.4 ha. Contemporaneous sites in Cameroon varied from 0.5 ha at Okolo and Ndindan to 1.5 ha at Nkang, 2 ha at Obobogo and 5 ha at

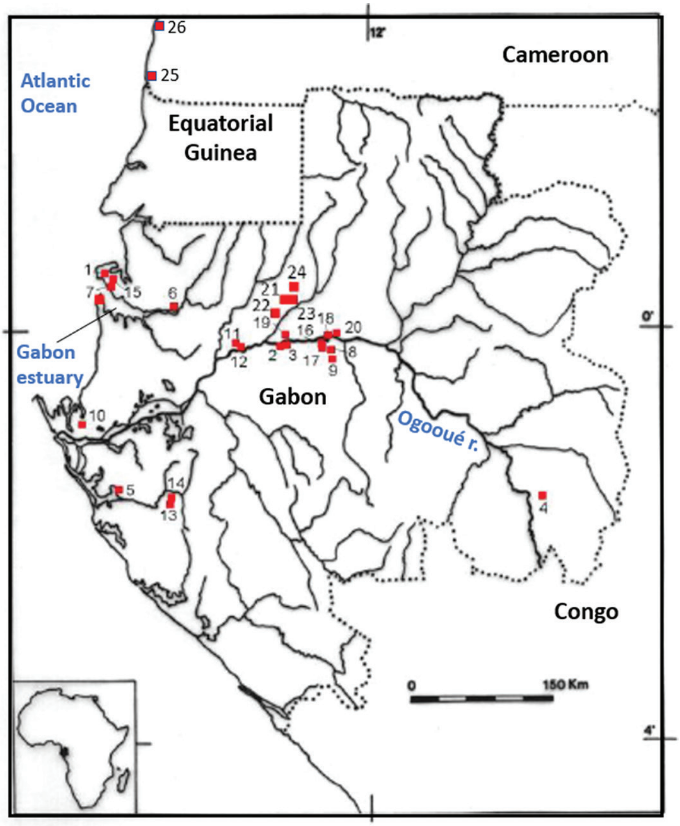


FIGURE 3.12 Map of the Okala Group sites in Gabon and Cameroon
MAP BY B. CLIST

Nkométou (Clist, 1990, p.466; Mbida, 1996, p.643; 2003, p.105). Pit fillings contained several artefact types, including pottery (sometimes in large numbers), a limited amount of stone tools, and polished stone adzes and axes, but no evidence of local iron working.

Within the characteristic Okala Group style, one decorative element stands out, the rocking comb, or spatula impressions, often covering the entire pot surface and at least 50% of the pots flat bottoms (Figure 3.13, lower four). One characteristic shape is the double-curve pot (Figure 3.13, right, upper two), which is also found in southern Cameroon 180 and 230 km to the north, at Campo Eglise and Bwambé, respectively. Villages using similar pottery both on the southern coast of Cameroon and in northwestern Gabon allows us to infer their concomitant presence on the Equatorial Guinean coast. Indeed, several sites with polished axes and grindstones have already been documented there (Clist 1998: 215–216). Forthcoming excavations will provide a clearer picture of

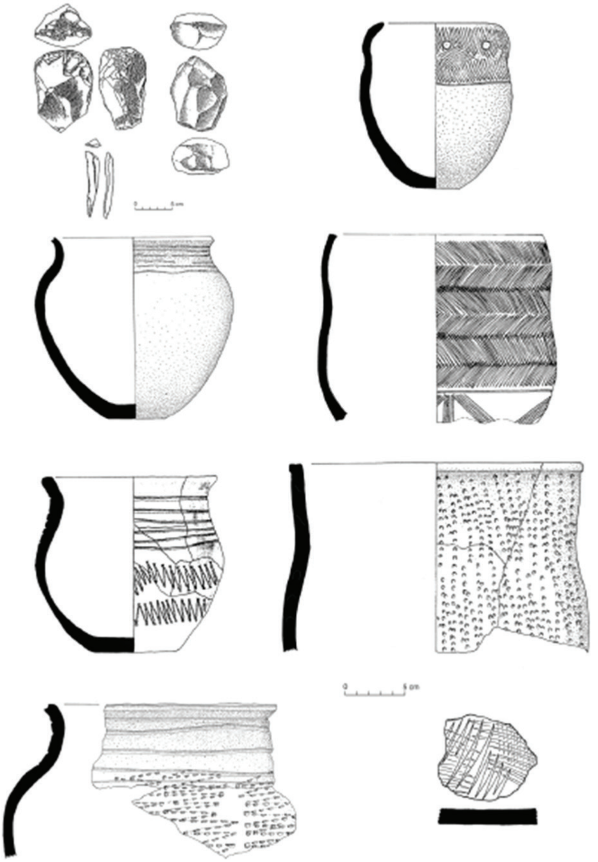


FIGURE 3.13
Okala Group pottery and stone tools (2,460–1,870 BP), Gabon
CLIST 2006A, 297, FIG.4

the socio-economic connections and exchange strategies that probably existed prior to 2,200 BP along 300 km of the Atlantic coastline. A close relationship between Okala and Obobogo pottery is already known (Clist 2005: 489-533 for Okala, 721-740 and appendix 5 for Obobogo/Okala). Another study, using material from more recent excavations along the Cameroon coast, showed all the sites before 2,200 BP were linked to the Gabonese Okala Group and formed a larger tradition (Nlend Nlend 2014: 230-273).

While feature 07/11 of Campo Eglise with typical double curve pots is late for the Okala Group 2,185-2,150 BP (Eggert & Seidensticker 2016: 187), the four pits at Bwambé (pits n°12, 16, 19, 33) correspond to an earlier phase, 2,360-2,240 BP (Nlend Nlend 2014). Pit n°33 at Bwambé is very interesting. It is dated three times on millet seeds, palm nuts and charcoal extracted from the same layer in the pit (*cf.* Nlend Nlend 2014: 147, 167, Table 39 and fig 65; Kahlheber et al., 2014: 115: Erl-9176: 2326±86 BP, Erl-9177: 2305±44 BP, Erl-9177: 2305±44 BP). The fill contained as many shards from the so-called 'Malongo Tradition' as of the 'Bwambé Tradition', which are quite distinct (Nlend Nlend 2014: 148, 250 and Table 34). The 'Malongo Tradition' is equivalent to both the Obobogo and Okala Groups, a different label for the same material. Only a close examination of the pottery assemblages can distinguish these two Groups. As the double curve pots are unknown in the Obobogo Group, we can associate the Campo Eglise and Bwambé sites to an Okala cultural context. Millet is also found at Abang Minko'o dated around 2300-2100 BP, some 200 km to the east, with pottery similar to the Obobogo Group (Eggert et al., 2006: 290 and Table 4: 283, pottery see their fig. 7). Millet seeds in Obobogo (Abang Minko'o) and Okala (Bwambé) contexts support the earlier identification of "two charred seeds of Monocotyledone, a grass of the genus Pennisetum sp" (Claes 1985: 137) found in two sherds from pits II (*c.* 3,055-3,070 BP) and VII (*c.* 2,120 BP) at the eponymous Obobogo site and identified by H. Doutrelepont (*Ibid.*), though the seeds could also have been from the wild variety. The doubts about these identifications (e.g.Wotzka 2019: 411) underline the need to publish these excavations. Of course, renewed fieldwork, this time with systematic flotation, would be better. Unfortunately, the Obobogo potsherds studied by H. Doutrelepont could not be relocated (P. de Maret personal communication).

Domesticated millet at *c.* 3,000 BP contradicts the assumption that millet cultivation was difficult or impossible under rainforest conditions, and was only possible during the LHFC, i.e. after 2,500 BP (Neumann et al., 2012, and see historical development in Wotzka 2019). Wotzka has shown this is not true: millet could be, and has been grown at least until the 14th-16th centuries AD in the humid conditions of the forests (Wotzka 2019: 408 and his location map: 423, fig.7).

> It clearly contradict[s] some of the major ideas held in the literature about a supposed general unsuitability of rainforest and climatically similar settings for pearl millet cultivation. WOTZKA 2019: 424

The use of millet may have been more widespread in this cultural context than is currently recognized due to the lack of the use of systematic flotation (*cf.* Fuller et al., 2014). We can conclude millet cultivation was practiced in the Obobogo and Okala Groups, at least from southern Cameroon to northern Gabon. Its presence suggests former contacts between northwest Central Africa and the Sahel zone where it was domesticated (Neumann 2018: 8) and cultivated alongside cowpeas (*Vigna unguiculata*) in the Gajiganna Tradition and in the Nok culture of Nigeria (Neumann 2018: 13-14).

The use of the word *-cángú', designating finger millet in west Bantu languages, can be reconstructed for proto-Bantu. But it was probably associated with millet slightly later, after the start of the Bantu expansion (Bostoen 2006-207). Polished stone axes and adzes, grinding stones and grinders of the Obobogo and Okala Groups are indirect evidence for horticulture.

We tested the probability that early villagers chose specific soil types to settle and develop horticulture and fishing. We used soil maps of the French '*Bureau de Recherches Géologiques et Minières*, and mapped a 5 km radius around 18 sites of the Okala Group. Six are along the Gabon estuary, ten along the Ogooué River, and two are the Ofoubou River sites (Figure 3.12, n°13-14). Although not conclusive, five sites have 80-90% cultivable land, five have 40-60%, seven have 10-30% and one has none (Otoumbi 13, Ogooué sector) (Clist 2005: 512-516). Fishing was certainly practised: fifteen sites are situated near the ocean or rivers. Even if communication between communities played an important role, this proximity to water implies the use of dugout canoes. Further, an iron fish hook was found in pit n°1 of the Bwambé site in Cameroon, dated to *c.* 2,200 BP (Nlend Nlend 2014: 258). Prehistoric visits to nearby mangroves is attested by *Anadara senilis* shells (adapted to muddy river bottoms and mud flats in mangrove). They were found in pit n°1 of Okala, and were probably collected around 2,230 BP (Clist 2005: 256). Okala Group villagers also exploited oil-containing tree fruits, such as the oil palm (*Elaeis guineensis*) and the incense tree (*Canarium schweinfurthii*). While *Elaeis* carbonized endocarps are found in most of the excavated pits, sometimes by the hundreds as at Okala, *Canarium* was only found at Toubé on the Ogooué River. The latter site also yielded carbonized endocarps from *Anthrocaryon klaineanum* and *Coula edulis*, while *Panda oleosa* was found at Okala and Toubé, and *Maranthes polyandra* at Kango. This is evidence for early agroforestry practices. On the Ogooué River, small stock raising is documented at Toubé 1 (*Capra aegagrus* *f.Hircus*), hunting at Otoumbi 13 (*Tragelaphus scriptus* and *Cephalophus sylvicultor*, Assoko Ndong 2002: 141), and at Toubé 1 (*Tragelaphus scriptus* and *Atilax paludinosus*, Assoko Ndong 2001: 230).

Long-distance exchanges existed. The Okala Group had come from the north and they must have had some knowledge of the lands crossed and kept social relationships with parent communities. Iron working is not attested on these sites. The two iron artefacts found at Okala and Lopé are evidence of long-distance contact with iron producing centres, maybe the one at Moanda some 550 km away. Raw material for the polished stone tools in estuary communities could have come from 80 km (Kango 5) to 70 km away (Okala 1), while 40 km was needed on the Ogooué River to reach the stone sources (Ndjolé Pk5). Lastly, the potting clay and temper used on the coast and along the Ogooué River are different. Several potsherds at the coastal Okala site may have been imports from inland, 300 km away:

> La recette « minérale » quant à elle rappelle étrangement les productions du centre du Gabon. Là, les sites de la Tradition d'Okala fabriquent une poterie oxydée, claire, rougeâtre, probablement due à l'importance des oxydes de fer dans les argiles natives, dont la charge non plastique est composée du cortège minéral local, c'est-à-dire par ordre décroissant le quartz, le feldspath, le mica et l'amphibolite. CLIST 2005: 422

11 The Oveng Group

Research around the Gabon estuary (Clist 1989a) identified the Oveng Group. This Group extends from Corisco Island in Equatorial Guinea southwards to the Lambaréné area on the Ogooué River, 230 km away (Clist 1995: 164–167; Livingstone-Smith et al., 2007; Clist 2005: 541–599; Sánchez-Elipe Lorente 2015: 267–298). Eastwards, its inland extension is unknown, though the contemporaneous Otoumbi and Okala villages along the Ogooué River (Assoko Ndong 2002, Oslisly 1986, 1992) and in the forest to the north (Clist 1989a; Oslisly and Assoko Ndong 2006) using their own pottery show the 'border' was somewhere to their west (Figure 3.14). The Oveng Group is well bracketed by 25 radiocarbon dates between 1,970 and 1,296 BP (an older date, Gif-8151 2,210 BP, from mangrove *Anadara senilis* shells is probably too old).

Local iron production started with the Oveng Group around the Gabon estuary, as is the case inland with the Otoumbi (c. 2,060 BP) and Okanda groups (c. 2,210 BP); all three appear at the same time, between 2,200 and 2,000 BP. The metallurgical residues and iron implements have not yet been studied.

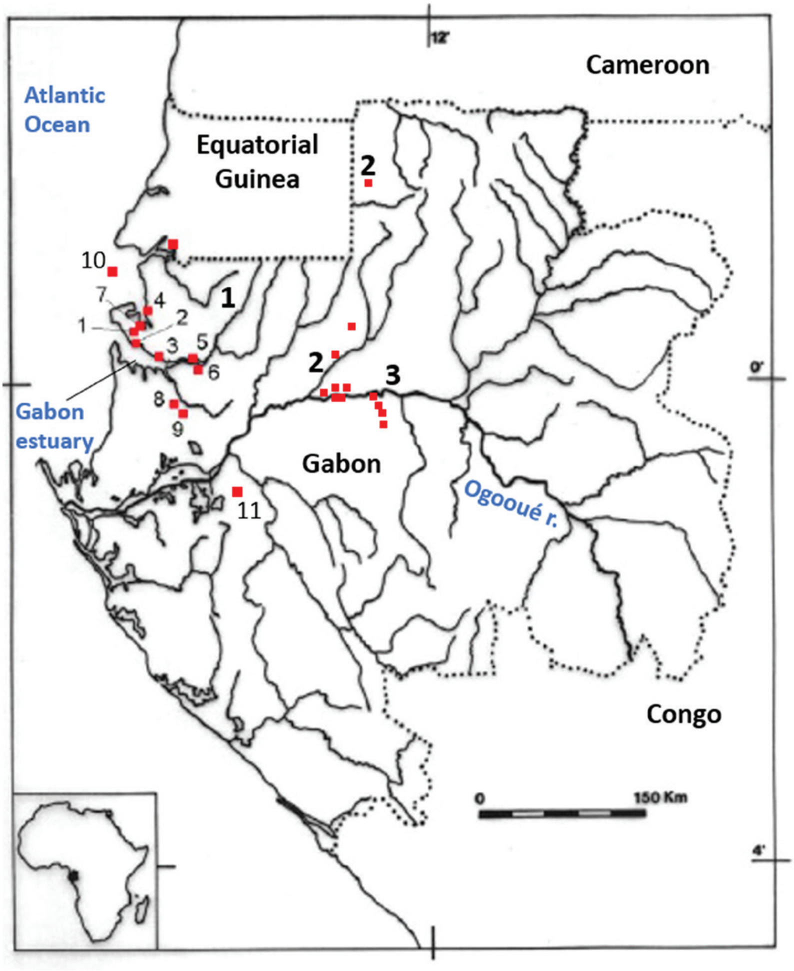


FIGURE 3.14 Location map of the Oveng (1, from n°1-11), Otoumbi (2), and Okanda Groups (3)

Based on the ^{14}C dates, Neolithic and EIA settlements probably coexisted for some time (DIBAC database).[1] Furthermore, on the coast the Okala (youngest date *c.* 1,870 BP) and Oveng Groups (oldest accepted date *c.* 1,970 BP) overlap,

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[1] DIBAC: *Datations absolues, Inventaires archéologiques et Bibliographies en Afrique Centrale*. Absolute dates database created by B. Clist et R. Lanfranchi in 1987 (*Cibadate* project: *cf.* Sarrazin 1987), extended to cultural resources management and national archaeological bibliographies of Central Africa (Cultural resources management: Clist 1995, 238–244; absolute dates database: Clist 1995, 259–280; bibliographies: http://www.african-archaeology.net/biblio/index.html). All the ^{14}C data in this paper is taken from DIBAC.

while inland, the Okala Group (youngest date *c.* 1,935 BP) seem to have coexisted with the Okanda Group (earliest date *c.* 2,260 BP).

Vessel shapes are completely different from the preceding Okala tradition, though the bottoms are still flat. Decoration is limited to the upper parts, from the lip to the upper body, and new decorative techniques are in use (Figure 3.15, 1). Out of a minimum of 149 vessels at the Oveng site, only 25% are left undecorated. Of specific visual significance, the impressed comb is present on 37% of the pots, forming simple oblique or horizontal alignments, sometimes forming simple or multiple herringbone units (7% and 4% respectively). Rare (n=3 pots), but visually significant, are the appliqués buttons—small conically shaped pieces of clay forming a single horizontal line (Figure 3.15, 1). Lips were sometimes decorated by small incisions (Figure 3.15, 1), as in the Otoumbi and Okanda assemblages. Lastly, another and very characteristic tool is the half-circular stylus (Figure 3.15, 1). It appears at the start of the EIA in all the cultural groups known in Gabon and used the same way: horizontal single or double lines bordering other decorative bands (*cf.* Okanda and Otoumbi groups). In the Oveng Group it is present on 40%-56% of four of the six known shapes. This tool was used in the contemporaneous "Herringbone" pottery in Congo (Denbow 2014: 106-135), the Kay Ladio Group in the DRC (Clist et al., 2019) and in the Campo and Akonétyé groups of Cameroon (Meister and Eggert 2008; Nlend Nlend 2014; de Saulieu et al., 2015; Eggert and Seidensticker 2016). Some pots were also decorated with it within the Kribi Group of southern Cameroon (Nlend Nlend 2014).

Evidence for contacts between the Okanda and Oveng groups can be found in a pot uncovered at Oveng (Clist 2005: 566, fig.7-22, n°8) which is identical in shape and decoration to another from the Okanda 5 site over 200 km away (Assoko Ndong 2001: 375, pl.38, R23), both dated to the same period (Figure 3.15, 2A and 2B).

Carbonized endocarps of some fruits were found. As usual, *Elaeis guineensis* occurs in higher numbers, but the Oveng site also contained some *Antrocaryon klaineanum*, *Coula edulis* and *Panda oleosa* carbonized endocarps. Fruit trees as part of the subsistence system may have been inherited from earlier communities.

Excavation of the Oveng site added greatly to our knowledge of EIA ecological adaptations 2,000 years ago. For the first time in Central Africa, we had proof of adaptations to mangrove and ocean ecosystems: villagers fished (a lot), hunted (minimal), collected gastropods and bivalves in the mangroves, and fruits in the forest (a lot). Within their settlements set up in the forest they processed iron (Clist 1989a, 2005: 541-588, 2006c; Van Neer and Clist 1991; Van Neer 2000: 168 and 170). African manatee (*Trichechus senegalensis*) alongside

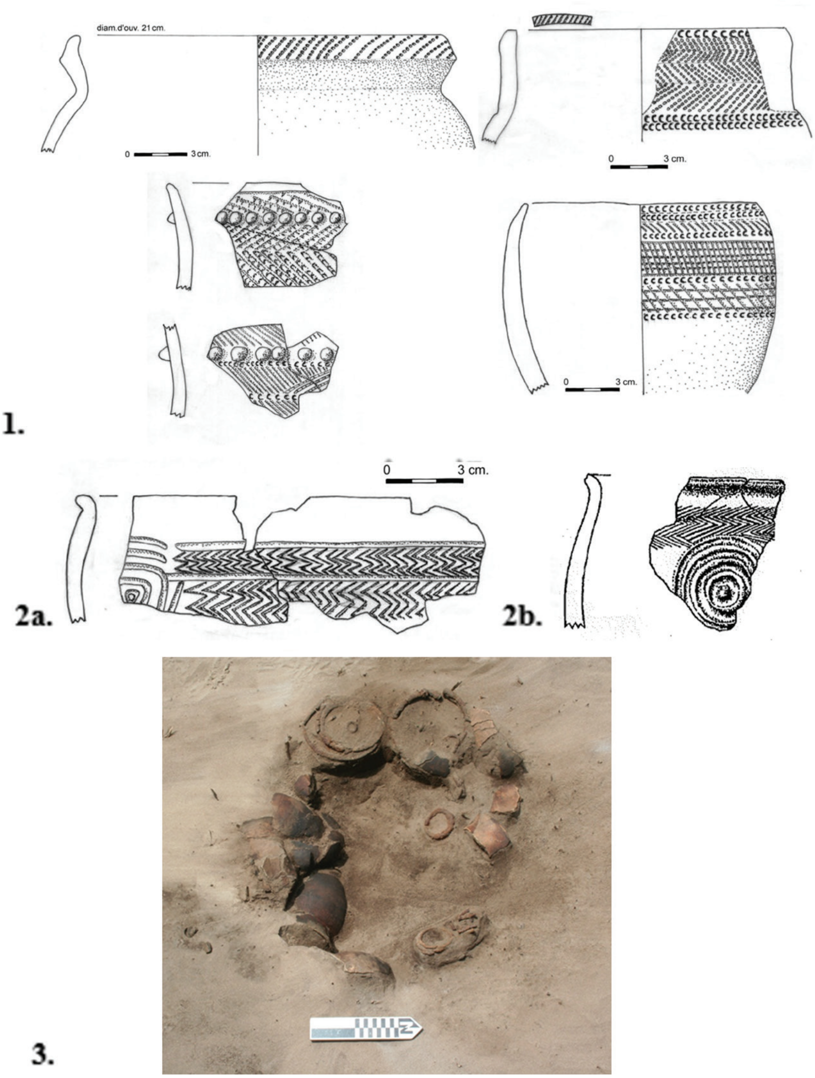

FIGURE 3.15 Oveng Group pottery and burial. Oveng Group, c. 1,970-1,296 BP. (1) pottery, Oveng and Kaféle sites, Gabon. (2a) Pottery from Oveng, (2b) Pottery from Okanda 5, (3) Burial of the Oveng Group. (fig. 1, 2a & 5: Clist 2005, 2b: Assoko Ndong 2001, 3: Sánchez-Elipe Lorente 2015)

fifteen other fish species were fished in the mangrove rivers and in a nearby estuary, while the python was hunted on land (*Python* sp.). Although we systematically water sieved the deposits, we found no evidence of domestic seeds. Ten circular disc beads were made from shells, probably of *Anadara senilis* (2.5 to 3.6 mm in diameter, with a thickness from 0.4 to 1.5 mm). The shell beads are similar to others found at the EIA midden of Cabolombo (ex-Benfica) near

Luanda (Angola) dated to *c.* 1,800 BP (Santos and Ervedosa 1970; Valdeyron and Domingos 2009, 2012), and to more recent shell beads at Muanda 6 on the DRC coast dated to *c.* 1,600 BP (Clist, Bigohe et al., 2018; Clist and Béarez *et al.* Forthcoming). Together with the Muanko Lobethal site in Cameroon, dated to between 1950 and 1750 BP which yielded oyster shells (Williams-Schmid 2001; Eggert 2002: 513-521), the shells attest to a better EIA adaptation to coastal ecosystems compared to Neolithic times.

In 2009, a survey on Corisco Island (Equatorial Guinea) identified important features impacted by the construction of an airstrip. Several of them were radiocarbon-dated (Gonzalez-Ruibal et al., 2011). Analysis of the 2011 excavations (Gonzalez-Ruibal et al., 2013; Sánchez-Elipe Lorente 2015) revealed interesting burial practices of the Oveng (Figure 3.15, n°3) and Nandá groups that are similar, but different from contemporaneous burials in southern Cameroon (Meister 2008, 2010; Meister and Eggert 2008; Eggert and Seidensticker 2016). The iron artefacts from 22 Oveng burials comprise axes, *bikuele* (traditional iron currency used in the LIA with exactly the same shape), bracelets, knives, necklaces, rings and spoons. They number from zero (4 burials) to nine per feature; exceptionally one had 14 and another 27. One iron necklace from burial n°20 had a bone fragment preserved by the decomposed metal; other pieces of human bone were also found in another three deposits (Gonzalez-Ruibal et al., 2013; Sánchez-Elipe Lorente 2015). Whole pots occurred in burials without iron implements, while 15 burials with metal lacked pots. In the remaining seven burials, the pots number from one to five (Gonzalez-Ruibal et al., 2013; Sánchez-Elipe Lorente 2015, and our Figure 3.15, n°3). The cemeteries in Cameroon consisted of primary burials in oval-shaped pits, while on Corisco there were secondary burials in circular pits, though two elongated pits were also documented. Further, some types of iron artefacts were found in Cameroon but absent in Equatorial Guinea. The associated pottery was inverted in Cameroon, while they were upright on Corisco Island. The pottery found in the burials helped to identify the Akonétyé, Campo, and Oveng stylistic zones. Significant similarities between the three zones over about 300 km include iron artefacts, such as spoons, anklets, axes with widened cutting edge, and bundled iron pieces interpreted as special purpose currency. But comparisons between the Akonetye, Campo and Mouanko Lobethal sites in Cameroon (Figure 3.16) show they form a group quite distinct from Oveng in Equatorial Guinea (Meister 2010). A previous find in the suburbs of Yaoundé, at Obobogo, was probably part of a cemetery similar to the other sites in Cameroon (Meister 2010: 239-240).

The emergence of inequalities and the development of inegalitarian polities in sub-Saharan Africa will eventually be found in the northwestern part of

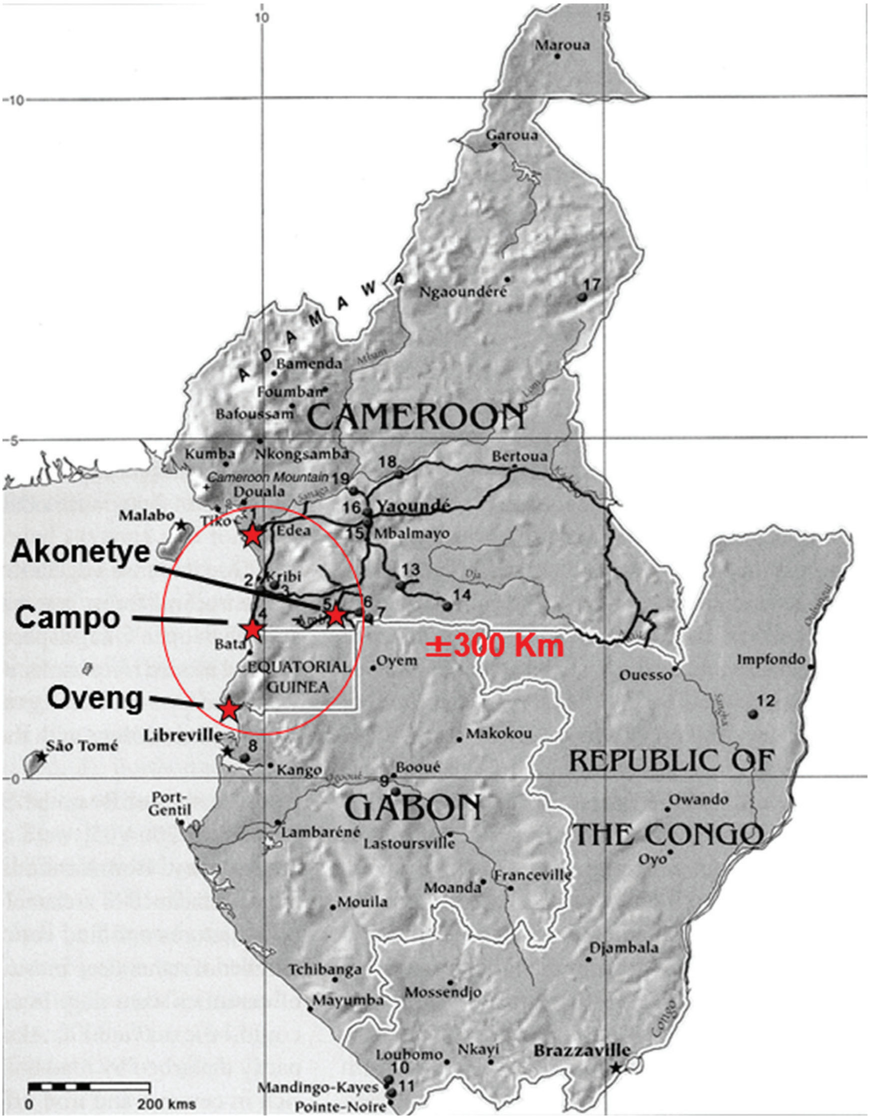

FIGURE 3.16 Position of the four cemeteries associated with the Oveng, Campo, and Akonetye Groups
ADAPTED FROM EGGERT ET AL 2006: 280, FIG. 2

Central Africa, from Cameroon to Gabon. Indeed, the political and symbolic relevance of iron to wives and wealth is probably much older than previously thought (Gonzalez-Ruibal et al., 2013; Eggert and Seidensticker 2016). Taking into account the oldest Oveng burials, we can push back to the 1st century AD the development of prestige goods to enhance political formations (Vansina 1990, 1999; McIntosh 1999; de Maret 2012). The possible historical relationship between the EIA Groups of southern Cameroon, Equatorial Guinea and Gabon with peoples south of the rainforests suggests these emerging traditions could have been implicated in the later rise of the Kongo kingdom (de Maret 1999, 2018; de Maret et al., 2018; Clist, de Maret et al., 2018a, 2018b).

We must now consider the Otoumbi Group in central Gabon dated from *c.* 2,000 BP. Though identified some time ago (Oslisly 1992), we can only call attention to the similarity between Otoumbi and Oveng pottery, in contrast to Okanda ware. Its corpus of 11 ^{14}C dates, together with 18 from the Okanda Group, and the respective distribution maps, show that Okanda preceded Otoumbi. Later, Okanda settlements moved further east, while Otoumbi communities expanded in their sector. The Oyem EIA site located 180 km north, dates to 2,200 BP, has pottery similar to Otoumbi and suggest this Group may have come from the forests at the Cameroon-Gabon border (Figure 3.14; Oslisly and Assoko Ndong 2006).

12 The Nandá and Angondjé Groups

These two groups in northwest Gabon were originally called 'Groupe II' and Angondjé Group (Figure 3.17) (Clist 1995: 167–168 and 168–169, 1995b: 18–20; Sánchez-Elipe Lorente 2015; Sánchez-Elipe Lorente et al., 2016). The Nandá Group (formerly Groupe II) is dated by ten ^{14}C results from 1,360 to 907 BP and the Angondjé Group by eight dates from 985 to 440 BP. However, it has been suggested the two cultural groups may be two sides of the same coin. After having stated

> the small number of radiocarbon dates from Gabon associated with the Nandá tradition and the larger assemblage of dates from Corisco suggest that the traditions coexisted, at least in Corisco", SÁNCHEZ-ELIPE LORENTE ET AL., 2016: 364

he further suggested

> the pottery traditions Nandá and Angondjé do not represent two different human groups; rather, they belong to the same tradition but relate to two different communities of practice – everyday life and burial. 2016: 364–365

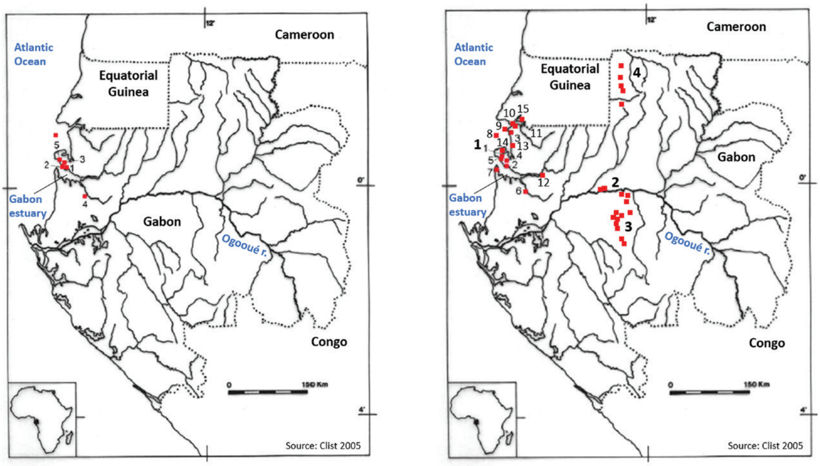

FIGURE 3.17 Location map of Late Iron Age Groups in Gabon. Sites from the Nandá Group, c. 1,360–907 BP (left) and from the Angondjé Group, c. 985–440 BP (right, n°1). Also illustrated, the Lopé Group (n°2), the Leledi Group (n°3), and LIA dated sites near Oyem (n°4)

13 The Nandá Group

The 16 Nandá burials on Corisco Island yielded iron artefacts and pottery (Figure 3.18, n°1-3). They contained from zero (5 features) to 12 iron objects. All of them had pottery, mostly from one to eight vessels, while one with 18 pots also contained six iron objects. The iron artefacts consisted of anklets, axes, small bell (1), bracelets, necklaces, and knives (Figure 3.18, n°3). The number of iron artefacts is less and the pottery more abundant than during Oveng times. Pottery assemblages are limited to a few jars (Figure 3.18, n°1, 2 and 4) and many bottles (Figure 3.18, n°3 and 5). The types of metal and pottery offerings are different from the Oveng Group, and we have no evidence for the exploitation of local mangroves. The corpses were set the head to the southwest, feet to the northeast, with bent arms and hands placed on the chest and belly (Gonzalez-Ruibal et al., 2013: 136). The pottery, especially the bottles, may have been produced specifically for funerary purposes because

> the pots were barely fired and they crumble easily when they are removed from their original position; on the other hand, it seems that they were made quickly, as proved by the deficiencies in the modeling (using coils) and, especially, the often clumsy decoration. GONZALEZ-RUIBAL ET AL., 2013: 138

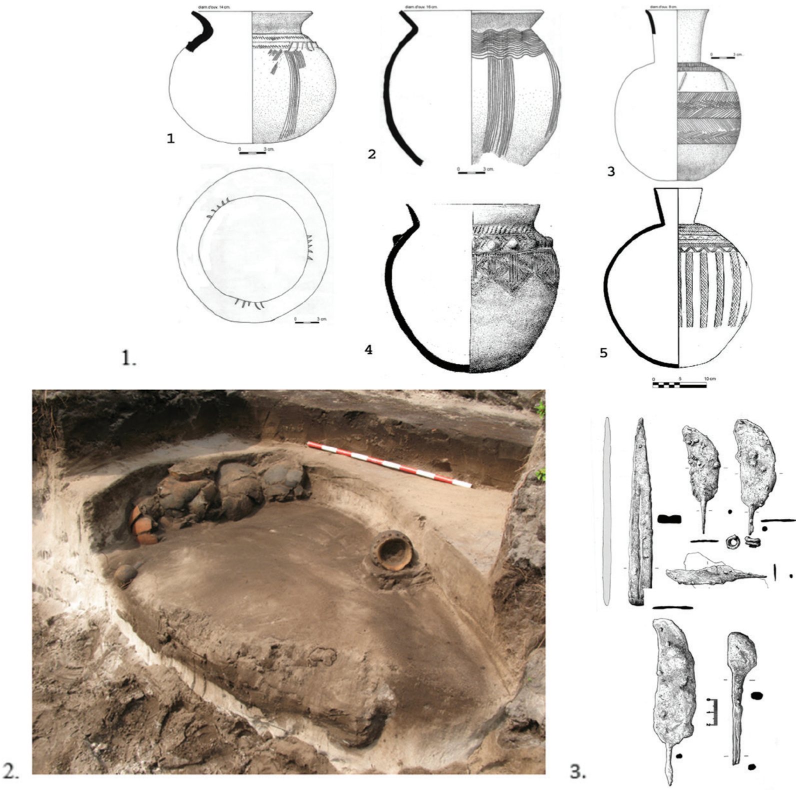

FIGURE 3.18 Nandá Group pottery and iron artefacts from burials. Nandá Group, c. 1,360–907 BP. (1) Pottery from the 'Sablières', Gabon (n°1-3) and from Corisco Island, Equatorial Guinea (n°4-5) (Clist 2005, Sánchez-Elipe Lorente 2015). (2) Burial n°9 from Corisco Island (Gonzalez-Ruibal et al., 2013, 137, fig.17). (3) Iron artefacts from burials n°26, Corisco Island (Sánchez-Elipe Lorente 2015)

At the 'Sablières' site in Gabon, however, all pottery was well made and finely decorated (Peyrot et al., 1990; Clist 2005: 600-614). One of these pots was found on the northern part of Bioko Island (Peyrot et al., 1990: 496). When it was published, a connection to Nigeria was suggested (Martin del Molino 1965: 26 and fig. 10B). Instead, this is evidence for long-distance contact between Bioko and Nandá coastal villages, probably located around the Rio Muni or the Gabon estuary. This find strengthens cultural links over some 300 km between southern Cameroon and the Equatorial Guinea-Gabon border (Figure 3.16), and, notably, highlights long-distance contacts since the Neolithic, 1,000 years previously.

14 The Angondjé Group

The Angondjé Group still had settlements around the Gabon estuary (Clist 2005) when the Portuguese sailed along the coast between AD 1471 and 1475 (Merlet 1990: 18). The occupation at Okala, north of Libreville, is dated to AD 1406-1631 (Gif-8152: 440 BP). A pit at Bisségué 1 contained Angondjé ware and European glazed pottery from the 16th century (Clist 2005: 681). The earliest date for this Group dates back to calAD 991-1153 (CAN-1564: 985 BP on Corisco Island). Since then, the peoples living on the coast from at least the Gabon to the Muni estuaries and its adjoining islands shared a common material culture. Its most characteristic artefacts were carinated cooking pots with convex bottoms, clay beads, clay lid knobs with appliqués or incised decorations and iron swords (Figure 3.19). As no cemeteries have yet been excavated, we do not know the range of iron implements produced. But the Angondjé site has shown evidence of post holes, some organized to form the corner of a possible quadrangular house, and the use of deep pits (Clist 2005: 632–652).

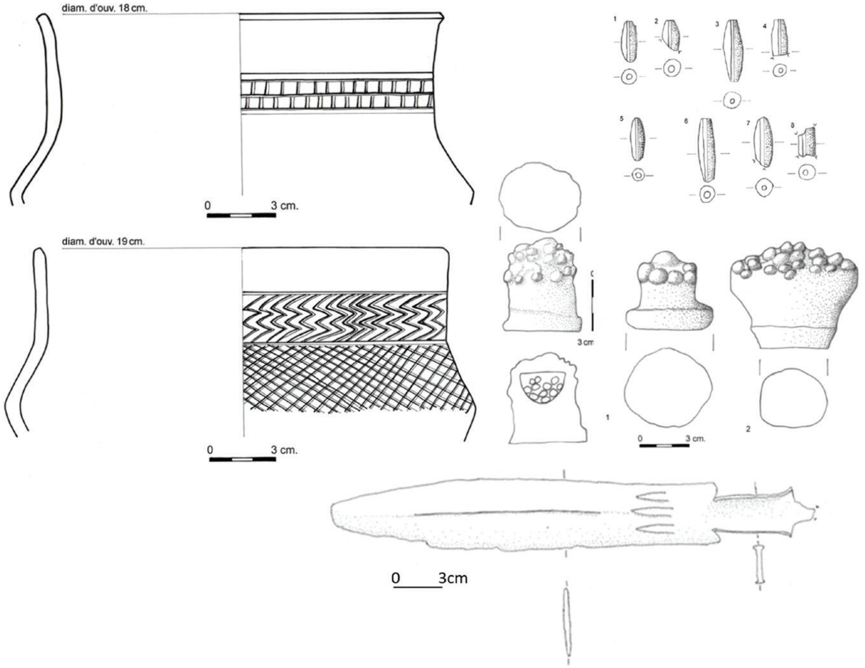

FIGURE 3.19 Angondjé Group pottery and other artefacts. Angondjé Group pottery, clay beads, decorated clay lid knobs, and iron sword (985–440 BP)
CLIST 2005

Wood carved roulettes were used to decorate Angondjé Group pottery on the Muni estuary near Corisco Island (Clist 1989a: 87, fig.14 and our Figure 3.20, n°1-2). This is a southern extension of their geographical distribution from West to East Africa (Livingstone Smith 2007).

Looking to the east, towards the Ogooué River and central Gabon, we have a strikingly different archaeological picture (Assoko Ndong 2002, 2003). As is often the case regarding the LIA, it has not been as thoroughly studied as older periods. Nevertheless, the Lopé and Lélédi groups have been identified (Figure 3.17, right, n°2 and 3). It is noteworthy that LIA settlements along the Ogooué and adjoining forests lack pits (Assoko Ndong 2002: 151, 2003: 121). This helps to explain the paucity of ^{14}C dates because archaeologists often miss sites without these dark filled pits (Assoko Ndong 2001: 473). In terms of ceramics, fiber-roulette decoration characterizes Lopé ware (Figure 3.20, n°3, and Assoko Ndong 2002: 152-154). Eight ^{14}C dates put Lopé material culture at. 820-250 BP. Sometime within this sequence, tobacco pipes (at least post *c.* AD 1600, see Clist 2018) and European pottery appear. On the other hand, the Lélédi Group further south in the forest (our Figure 3.17, right, n°3, and Assoko Ndong 2002: 154-155) is more similar to the Otoumbi ware than to the Lopé ware (see Assoko Ndong 2002: 153, fig.12, n°2). Ten radiocarbon dates place it at 860-80 BP. This means the peoples who produced the Angondjé, Lopé and Lélédi material culture were contemporaneous and probably like their ancestors had long-distance contacts with each other. Further and more exhaustive publications are needed to evaluate the diversity of central Gabon's LIA. It must be noted that wooden-roulette and fiber-roulette decoration have been found at the Mayoko iron mine in Congo a few kilometers from the Gabonese border, dated from 500 BP (Ndanga et al., 2013a, 2013b), and significantly extends the known distribution of such pottery.

To be exhaustive, we note several LIA sites in the Woleu Ntem Province in northern Gabon (Figure 3.17, right, n°4). Since their excavations in the late 1980s, no other fieldwork has developed the local sequence (Assoko Ndong 1988; Clist 1987b, 1987c, 1989b, 1989c, 1993; Meye Medou 1990). At present, both settlements and iron smelting sites are recorded, dated to between 360-140 BP by five radiocarbon results. These sites must be associated with the Fang before they moved towards the coast to trade with European merchants (Merlet 1990: 91-134). The archaeological furnaces, it is worth noting, are identical to ethnographic descriptions in Fang territory by G. Tessman (1923) and C. Von Morgen (1893). The oldest ^{14}C date comes from the Mbam furnace which calibrates to AD 1433-1664 (Clist 1993).

FIGURE 3.20 Roulette decorated potsherds from Angondjé and Lopé Groups context. Carved wooden roulettes decorated potsherds from Angondjé Group, and fibre roulette from Lopé Group
ILLUSTRATION FROM CLIST 1989A: 87, FIG. 14

15 Conclusions

We have shown the complexity of the material-culture sequence over the last 30,000 years. This long period saw successive waves of people, stone and pottery using, occupying and re-occupying large tracts of land from the northern to the southern savannas of Central Africa. Such diversity probably parallels genetic and linguistic diversity in this vast region.

Following the Stone Ages, Neolithic villagers first settled along the coast from Cameroon to Congo and inland along the Ogooué River in Gabon from 3,000 to 2,400 BP. Probably from southern Cameroon, another group made its way through the forests to enter the Inner Congo Basin around 2,400 BP. Some rare early sites in southeast Cameroon and southwest CAR may connect Cameroon to the Congo River. The LHFC of 3000-2000 BP only helped this dispersal, rather than caused it, as evidence exists of pre-metallurgical peoples inhabiting the forests before then. Furthermore, the often cited Sangha River Interval savannas seems not to have existed. It would explain why the first villages did not appear there in the forest before 2,200 BP.

Iron smelting is not older than 2,400 BP in the northwestern rainforest, and it was probably transmitted via an already pre-existing network of long-distance exchanges. It is not clear yet if iron-working techniques diffused independently, or were also associated with the expansion of peoples seen in the archaeological record from 2,200 BP. This EIA expansion through equatorial forests between 2,200 and 1,900 BP created major discontinuities in material culture from Cameroon to the DRC, resulting in smaller territories than during the preceding Neolithic.

The social mechanism responsible for the succeeding waves of expansion must have been complex, diverse and irregular. Social complexity is evident in the small cemeteries in the northwest (Cameroon, Equatorial Guinea and Gabon). It predates by several centuries what was to become the Kongo kingdom to the south and the Luba kingdom in the southeast (de Maret 1991, 1999, 2018). The emergence of inequalities in the northwest is worthy of further archaeological research. We suggest the smaller territories identified by the mapping of the various material cultures is linked to the development of local iron working, leading to the possibility of producing excess iron objects, some of them probably invested in symbolic value and deposited in the EIA cemeteries of Cameroon and Equatorial Guinea. The pottery groups regionalization must have been a side effect of the rise of social inequalities.

Overall, the pottery sequence from the earliest Neolithic villages to the Late Iron Age shows continuity of occupation at least for parts of Equatorial Guinea and Gabon. This continuity created a high degree of interaction between the cultural entities, leading to a high level of regional diversity. Within this continuity, we identify transitions in the material culture occurring after several centuries of stability; these radical changes in the production sequences are, we believe, evidence of new incoming people. The radiocarbon dates series for the transition from Neolithic to the Early Iron Age and later within the Iron Age show the new communities probably coexisted for some time with the preceding inhabitants before the former material culture disappeared. This is a picture we have seen for Gabon, but it is also known in Congo and in the western DRC.

Some 40 years ago, Jan Vansina correctly stated "new beginnings on limited portions of the Bantu question are required, rather than new paragdigms" (Vansina 1980: 313), a statement regrettably still true. More recently, it has been proposed the combination of historical Bantu linguistics, archaeology and molecular genetics had not significantly changed the overall preliminary picture of the past 3,000 years of history of Central Africa (Eggert 2016: 88). Maybe this Uppsala International Conference will become another starting point for this renewed research. But we are convinced, as Eggert before us (Eggert 2005: 322), that archaeology must develop its own set of transdisciplinary research, closely associating archaeology, paleo-ethnobotany, archaeozoology, geography, and ecology—amongst others—united within programs of intensive and systematic fieldwork and using its own agenda.

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CHAPTER 4

Ancient Urban Assemblages and Complex Spatial and Socio-Political Organization in Iron Age Archaeological Sites from Southern Africa

Plan Shenjere-Nyabezi and Gilbert Pwiti

1 Introduction

The Iron Age of southern Africa is dated from around the 1st Century AD and archaeologically understood as the result of population movements from further north and generally associated with the advent of settled agro-pastoral communities in the region. Although areas of uncertainty and disagreement still remain in the scholarly community, it is generally accepted that until sometime towards the end of the 1st millennium AD, these communities were basically non-stratified village-based societies that lacked significant differentiation in political, social and economic terms. Economically, they were subsistence agro-pastoral people who relied on the cultivation of crops such as millet and sorghum and the rearing of sheep/goat and cattle. The archaeological evidence indicates that they lived in villages of varying sizes from as small as 1 hectare to as large as 10 hectares which were made up of simple houses of the cone-on-cylinder type (Pwiti, 1996) (Figure 4.1).

There is very little evidence of differentiation of people within and between villages and somewhat limited evidence of occupational specialisation, except perhaps in the context of the manufacture of pottery and the processing of iron ore into utilitarian products such as arrow or spear heads, axes and hoes which were used for hunting and for agricultural engagements, respectively. Essentially therefore, in terms of socio-political and economic organisation, the early farming communities represented what anthropologists have traditionally classified as “tribal” societies or what in other circles, are now also referred to as non-stratified peasant village societies (Maggs, 1984; Pwiti, 1996a; Friedman and Rowlands, 1978).

Towards the end of the 1st millennium AD into the early part of the 2nd millennium AD, however, the farming communities of southern Africa underwent a number of important changes which among other things saw the development of socio-political and economic stratification as well as changes in settlement organisation and settlement types. This is the background against

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FIGURE 4.1 Cone-on-cylinder type houses

which the archaeology of farming communities of southern Africa has traditionally been divided into two main periods, an Early Iron Age (EIA) and a Later Iron Age (LIA) with the change over placed at around 1000 AD. In the past, the two periods were seen as bracketing separate cultural phenomenon, with the LIA communities being seen as new migrants into the region who replaced the EIA (Phillipson, 1977). However, new field research accompanied by the application of, and development of new theoretical frameworks over the years has persuaded the view that while the changes in the region were notable and seemingly dramatic, they were not the result of new population arrivals but rather the result of gradual changes among the EIA, thus representing a clear case of continuity and change (Hall, 1987; Maggs, 1992; Pwiti, 1996). Apart from the changes in socio-political organization briefly alluded to above, other notable changes that are observable during the late 1st millennium AD into the 2nd millennium AD included changes in ceramic style, which itself was a major premise for the population replacement thinking and a basis for the division of the Iron Age into two cultural periods. Ceramics of the EIA communities reflected fairly widespread homogeneity in space and time and was characterized by the manufacture of pots with thickened rims and lavish comb stamping decoration on the rim, neck and neck-shoulder area. In contrast, ceramics of the later period reflected considerable heterogeneity and somewhat poorer finish and less elaborate style. As noted above, settlement types and patterns also changed from the widespread location of settlement sites along river and stream valleys during the EIA to the location of settlements on higher ground, including hilltops (Maggs, 1984). It is archaeologically observable that the settlement structures also became more substantial, compared to the flimsier structures of the EIA and with time, one of the major changes was the appearance of stone buildings as part of the settlement systems. Over and above these many changes, there is also evidence of population increase, as more settlement sites of the later period have been recorded across the region.

Perhaps the most outstanding changes were seen in economic organization, a factor which becomes important in relation to the development of complex societies and the origins and growth of the urban assemblages that are the concern and subject of this paper. Here, the evidence indicates that towards the end of the 1st millennium AD, a notable change is seen in the domestic animal economies where cattle herds increased substantially compared to small stock (Table 4.1).

TABLE 4.1 Increased cattle herds against decreased small stock at nine Iron Age sites using both NISP and MNI

Sample	**Cattle NISP**	**Sheep/goat NISP**	**Cattle index**	**Cattle MNI**	**Sheep/goat MNI**	**Cattle index**	**References**
Nanda (AD 6th–7th)	112	553	0.17	14	55	0.20	Plug 1993
Bosutwe Taukome (AD 700–800)	101	76	0.57	10	13	0.43	Plug 1996
Bosutswe Toutswe (AD 800–1200)	1125	698	0.62	52	46	0.53	Plug 1996
Bosutswe Mapungubwe (AD 1200–1300)	1197	554	0.68	47	36	0.57	Plug 1996
Bosutswe Zimbabwe (AD 1450)	227	106	0.68	9	12	0.43	Plug 1996
Boitsemagano (AD 17th century)	569	188	0.75	34	20	0.62	Plug & Badenhorst 2006
Mabjanamatshwana (AD 17th century)	449	118	0.79	79	41	0.66	Plug & Badenhorst 2006
Molokwane (AD 17th century)	1702	426	0.8	90	49	0.65	Plug & Badenhorst 2006
uMgungundlovu (AD 1829–1839)	2576	8	1	124	6	0.95	Plug & Roodt 1990

AFTER BADENHORST, 2011

In the broader framework and beyond purely economic considerations, this development laid the foundations of the political, social and ideological importance of cattle that became one of the mainstays of the socio-political fabric of southern Bantu societies during the Iron Age which has continued into modern times (Shenjere-Nyabezi, 2016). Another major economic change was the development of external trade relations between the southern African interior and the outside world via the Indian Ocean Coast and mainly with the Oriental world (Pwiti, 2005). As expanded on below, this economic development had major repercussions on socio-political developments in the region that relate closely to the concerns of this paper.

2 Socio-Political and Economic Transformations

The reasons for the transformations that took place in the region around 1000 AD have been a matter of scholarly debate for many decades. As noted above, the transformations were originally explained as resulting from the arrival of new populations into the region, populations who were equipped with higher forms of socio-political and economic organization who then replaced the earlier farming communities. This explanation was rooted within migrationist theoretical frameworks that were in vogue at the time. Since then, with the growing global wave against migrationist thinking and the adoption of popular theoretical operational frameworks such as systems thinking in archaeology archaeologists began to think in terms of internally driven systems growth rather than externally stimulated socio-economic and political development (Renfrew, 1984). Re-examinations of some of the ceramic breaks also began to argue against migrations while some archaeologists argued for ideological change although from different directions and on different platforms (Pwiti, 1996; Pwiti, 2004; Garlake, 1982). For example, Garlake argued that the ceramic and other changes were explainable in terms of a change from matrilineal social systems in the EIA to patrilineal societies in the latter period (Garlake, 1982). For Garlake, this explained the change from the better quality and more elaborately decorated ceramics of the EIA to the less stylistic ceramics of the LIA. He argued that the ceramics of the EIA were manufactured by specialist male potters while LIA pots were made by women for household consumption, hence the poorer finish. Apart from the sexist connotations of Garlake's argument, this does not seem to have provided an explanation for all the other observable changes. Pwiti on the other hand argued that the changes were the result of ideological change from an ideology of equality and the ethic of sharing during the EIA to an ideology of accumulation which in due course saw the emergence of social, economic and political inequalities that were to characterise the LIA communities in prehistory through to historical times, as complex societies developed, grew and declined in the region (Pwiti, 1996c, 2004).

While the debate on explaining the changes continues, what is important to note here in the context of this paper is that during the 2nd millennium AD, the farming communities went through major changes which were accompanied by important political developments in the form of complex societies, initially at the chiefdom level and in the course of time, the development of state societies particularly from the 11th Century AD (Pwiti, 1996c). Away from explaining the various changes that took place at the turn of the millennium, archaeologists have also expended considerable intellectual energy in trying to explain the development of complex societies in the region. Traditionally, the most popular explanation was external in outlook where the introduction of external trade towards the end of the 1st millennium AD is argued to have introduced a new form of wealth that was monopolised by a few individuals who grew wealthy and powerful and used their newly found wealth as a base for building political power (Huffman, 1984b; Pikirayi, 2013; Kusimba and Kusimba, 2017). Ultimately, this was to see the emergence of the region's earliest complex systems which eventually grew into major systems such as the Zimbabwe state based at Great Zimbabwe. Popularly known as the "trade hypothesis", this explanation was grounded in global theoretical frameworks of the day which were to be subjected to considerable criticism from the late 1970s with the development of inward rather than outward looking explanations that came in the wake of the growth of post-processual archaeology.

Others have also advanced religion as a causative factor where it has been argued that complexity developed as a result of some individuals acquiring religious influence where they used the power and mystery of their relationship with the supernatural to build social, economic and political power (Garlake, 1973). This is thought to have been particularly effective in the context of important branches of production such as agriculture where the power of such individuals to intervene with the supernatural to give or withhold rainfall for example would have made for social and political allegiances among ordinary people, with such allegiances having economic or material as well as political benefits. In as far as religion has always been part of statecraft, and from what is known about the relationship between religion and politics among historical southern African societies, it is undeniable that religion would have been important in the life of these complex systems. What is at issue however, is how religion would have originated the systems (Wenke, 1989; Pwiti, 1996c; Garbett, 1966; Bourdillon, 1987). Yet others have argued for and appealed to the warfare/conflict theory (Carneiro, 1981). In the southern African context, such thinking has also been advanced as part of the explanation of rising of Great Zimbabwe and other systems (Kusimba and Keeley, 2015). Here again, we do have historical evidence that warfare did take place in southern Africa. Portuguese records and oral traditions have shown, for example, that during the 17th Century, there was an armed conflict between the Mutapa state of northern Zimbabwe and the Changamire state based in the south west (Pikirayi, 2013). By extrapolation, we can expect that systems such as the Mapela, Mapungubwe and Zimbabwe states would have raised armies for defensive or offensive purposes. What remains problematic is accepting warfare as a causative factor, apart from the fact that warfare can be notoriously difficult to identify in the archaeological record, especially in the southern African context.

As an alternative to the external trade, warfare and religion hypotheses in the context of the development of complexity and more specifically Great Zimbabwe, Garlake argued that socio-political growth was best explainable in terms of the growth in the indigenous branches of production especially cattle herding, and others such as agricultural production and mining (Garlake, 1978; 1982). To this end, Garlake went so far as to dismiss the economic proceeds from external trade as peripheral to the growth of complex socio-political formations in the southern African past (Garlake, 1982). This position found support amongst historians such as Mudenge for the Rozvi state, a major but later complex state system in Zimbabwe as well as the Mutapa state (Mudenge, 1974; 1988). Around the same time and in later years, archaeologists such as Sinclair and Pwiti were to argue for a combination of factors (Sinclair, 1987; Pwiti, 1996). Using a systems thinking approach (while acknowledging some of its weaknesses), for example, (Pwiti, 1996) argues that external trade impacted on systems that were already in a state of growth in southern Africa and thus only accelerated a process that was already under way, rather than originating it (Pwiti, 2005; Chirikure et al., 2013; Cobbing, 1976). In this framework, it is argued that at the heart of the growth in the indigenous branches of production was cattle herding. As observed above, the archaeological evidence does show that cattle herds did increase among societies in different parts of the region. In time, cattle became an important source of social and political power. As evident from Portuguese documents on the Mutapa state as well as the historical complex systems such as the Zulu and Ndebele states and indirectly from the archaeological record, cattle were used as an avenue to political power and a base for holding on to such power (Cobbing, 1976; Kuper, 1982). For the formative stages, the more cattle an individual possessed, the more such individuals became powerful and influential economically, socially and politically (Garlake, 1978; Sinclair, 1987; Pwiti, 1996c; Shenjere-Nyabezi, 2016, 2018). It is then arguable that these are the local circumstances under which complex socio-political systems originated and developed. It is also then arguable that external trade brought in an additional form of wealth to systems that had grown wealthy as a result of local factors. In the final analysis however, we take the integrationist view that the development of complexity was the result of a network of economic, social and political actions. This is in the sense that the different economic activities relating to the complex systems that developed in southern Africa took place in social and political contexts at different levels from the household all the way up to the apex of the power structures. In these contexts and processes, people, cattle, exotic and local goods as well as services moved up and down in the networks to create, promote and cement relationships. Stated differently, centers of power relied on the local and wider regional networks and vice versa, thus bringing in the concept of Actor Network Theory as applied in Chirikure and more recently very ably articulated by Scholfield in examination and discussion of socio-political developments relating to the Zimbabwe Culture in the Shashi-Limpopo basin between the 10th and the 14th Centuries AD (Scholfield, 2019; Chirikure et al., 2014).

3 The Development of Complexity: Urbanism, Monumentality and the Zimbabwe Culture

> It has long been recognised that politically and economically powerful persons often sponsored monumental architecture as an expression of their power. COWGILL, 2004

The development of urbanism and complex socio-political formations in southern Africa is archaeologically best known from and associated with what has been defined and termed the Zimbabwe Culture. Archaeologically, the Zimbabwe Culture of southern Africa was the most successful of the several Later Iron Age cultures that developed during the 2nd millennium AD (Figure 4.2).

It is dated to the period between the 11th and the 19th Centuries AD and apart from its distinctive graphite burnished pottery, it has largely been defined by its monumental stone walls that come in a variety of styles and constitute its most striking and immediately visible attribute. Traditionally, this archaeological culture was conventionally divided into 3 phases, a Mapungubwe phase (AD1220–1290), a Zimbabwe phase (AD1250–1450) and finally the Khami phase (AD1450–1650). In the absence of clear chronological data, these phases were derived from the major sites of Mapungubwe, Great Zimbabwe and Khami whose rise and collapse were assumed to have been in tandem. However,

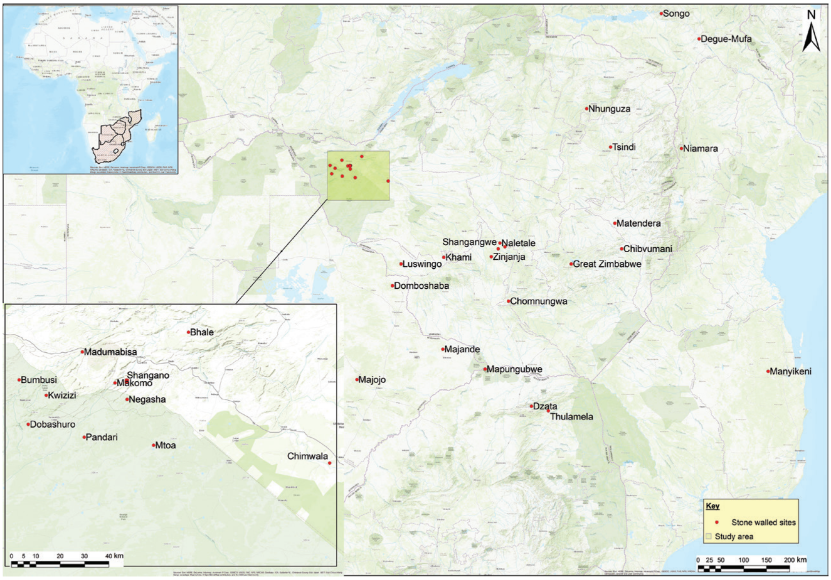


FIGURE 4.2 Map of Southern Africa showing Zimbabwe Culture sites

recent research has shown that some of these sites chronologically overlap thereby challenging the linear evolutionary framework (Chirikure et al., 2016; Shenjere-Nyabezi et al., 2020). The definition of the different phases has been based on variation in architectural style as well as other archaeological considerations such as changes in ceramic style. The stone wall stylistic classification was defined by Anthony Whitty, an architect, back in the 1950s (Whitty, 1961, 1959). The classifications were largely based on architectural considerations, including the refinement of walling. Building on earlier observations by Schofield and others at Great Zimbabwe, Whitty defined four architectural styles for the Zimbabwe Culture, namely, P (Poor), PQ (Poor/Quality) Q (Quality) and R (Rough) (Figure 4.3) (Whitty, 1961).

This classification was then translated into an evolutionary sequence where there was thought to be a refinement and progressive development in building and construction skills from the original poor walling in P style, a transition towards better construction skills represented by PQ style (a combination of P and Q) and culminating in the perfection of walling with Q style, which the British antiquarian Bent described as “The best of what we call the Zimbabwe culture” (Bent, 1896). R walling was thought to represent degeneration in building and construction skills and associated with culture decline.

Influenced by their western home backgrounds and experience, many early European observers interpreted the Zimbabwe Culture stone walling as defensive and described the ancient city of Great Zimbabwe as a fortress (Bent, 1896; Hall, 1905). This was an unsurprising view, given that many monumental or

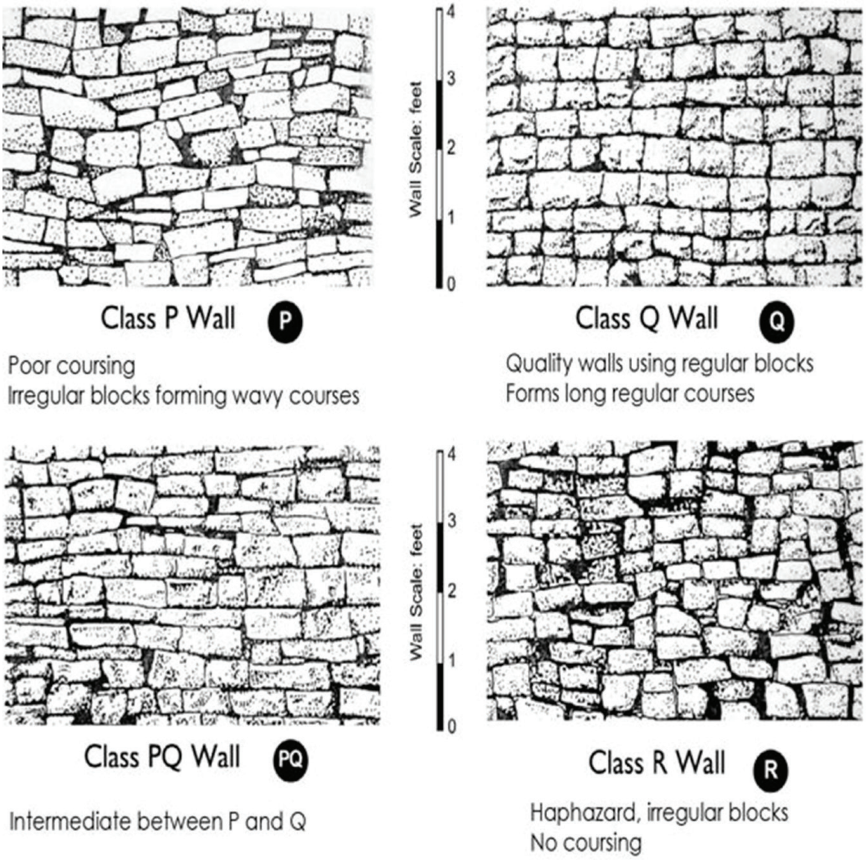


FIGURE 4.3 P PQ Q R wall construction styles after WHITTY, 1961

stone-built constructions known in Europe and Asia were generally assigned a defensive fortification function without consideration of any other possibilities, an interpretation which is no longer wholly acceptable as recently discussed by Ashkenazi (Ashkenazi, 2020).

Others, who were awed by the grand and visually impressive parts of the settlement such as the Great Enclosure and the Conical Tower therein, preferred to interpret such parts of the site as the result of religious inspiration and therefore representing a temple (Hall and Neal, 1902). This was in the context of the exotic origin hypothesis for the Zimbabwe Culture and its architecture where the whole complex was attributed to Phoenicians and Arabs, among a host of other foreign candidates (Hall and Neal, 1902; Mahachi and Ndoro 1997). It is of some interest to note here that the exotic identity has not altogether died as reflected in recent publications such as Nyamutswa (Nyamutswa, 2017). Nyamutswa has argued that Great Zimbabwe was the product of the Remba people, a Shona speaking group who claim a Jewish origin. Drawing on his Remba identity and Jewish origin thereof, Nyamutswa has specifically argued that the Great Enclosure was constructed to function as a male circumcision centre (circumcision being a central part of being Jewish). He cites several lines of evidence, including what he sees as the dominance of phallic symbolic objects recovered from the Great Enclosure and used in circumcision ceremonies. Equally important, he has resurrected the 19th Century interpretation of the Conical Tower in the Great enclosure as a colossal phallic symbol. The interpretation is however fraught with chronological and many other archaeological problems. Chief of these is the fact that Nyamutswa only provides an interpretation of the Great Enclosure and virtually ignores all other parts of the ancient city of Great Zimbabwe. He further fails to offer any interpretation of the hundreds of other similar stone-built sites across southern Africa and offers no supporting evidence for his argument and interpretation that Great Zimbabwe was constructed much further back in antiquity (to correspond with a Jewish origin) than what the currently available scientific dating has shown.

The religious interpretation of Great Zimbabwe and similar sites has not been the preserve of foreigners however. Among many indigenous people of southern Africa, Great Zimbabwe and related sites are indeed held as sacred and for Great Zimbabwe itself there have always been very strong local claims and sentiments that it was constructed as a religious centre (Pwiti, 1996b). That the stone buildings may have had cosmogramic associations and significance cannot be in doubt. What is doubtful however, is the claim that such edifices were erected for, and to fulfill religious functions. This is because it is well known that Shona traditional religion or indeed any other indigenous religion in southern Africa did not and has never required such monumental buildings (Bourdillon, 1987).

Following the discard of the exotic origin hypothesis over the years, there is now general agreement that Zimbabwe culture stonewalling was constructed for prestige, standing as symbols in action and a highly visible outward expression of the wealth, power and prestige of the ruling classes (Pikirayi, 2001; 2013).

4 Defining Urbanism

The relationship between geography and archaeology has a long history in as far as both disciplines trade in and deal with space and the cultural manifestations across it (Hodder and Orton, 1976). In this regard, archaeological concerns with spatial analysis going back many decades and conceptual issues and definitions of past human imprints of such phenomenon as urban centres or cities have taken their lead from geography (Fox, 1943). In this context, an urban centre, considered at the simplest level, is geographically understood as a built up area in which there resides a large population characterised by high population density, with such populations engaged in a variety of activities beyond basic subsistence. Such centres will normally be run by a bureaucracy and may entail the existence of craft specialists and land use is intensive. From an archaeological perspective, perhaps one of the best surveys on urbanism in recent years is that of Cowgill (Cowgill, 2004). In a wide ranging theoretical expose of the concept of urbanism as archaeologically understood, accompanied by a global survey of major sites, Cogwill provides a number of useful platforms against which the stone walled buildings of the Zimbabwe Culture can be examined and understood as urban formations (Cowgill, 2004). One such is the observation that urban centres or cities are typically political, economic and religious centres for a surrounding territory and loci for wider ranges of specialised production and sources than are found elsewhere in the region (Cowgill, 2004). As already noted above, and elaborated below, there is now general agreement that sites such as Great Zimbabwe, Khami and the Shangano cluster were capitals of different Zimbabwe Culture political systems that flourished across southern Africa between the 11th and the 19th centuries AD. At Great Zimbabwe and elsewhere, there is abundant obvious evidence that commercial transactions involving exotic and local goods were the order of the day while specialised production of goods such as pottery and iron implements is clearly evident (Chirikure, Nyamushosho et al., 2018; Mtetwa, 2017). To this end therefore, there can be little doubt that in terms of the functional attributes of urban centres, whether political or economic, major sites of the Zimbabwe Culture were clearly urban in character and form. To this may be added the demographic aspect where excavations at different sites of the culture across the region have revealed that the monumental stone walled enclosures screened houses of the ruling elites while unwalled areas accommodated houses of sizeable populations of commoner people. In other contexts such as Khami, elite houses were built on platforms that were also surrounded by commoner settlement (Robinson, 1959; Mukwende, 2018). While the population estimates for Great Zimbabwe and other large sites have been problematic and controversial, the density of houses outside enclosures indicates that there would have been several thousands of people living there at any one given time. Past estimates by archaeologists such as Garlake and Huffman for Great Zimbabwe (which are now seen as unrealistic) argued for populations running up to between 10 000 and 18 000 (Garlake, 1973). More recent estimates based on the use of new techniques and extrapolation of historical population estimates for the Zimbabwe plateau as well as archaeological data by Chirikure and his associates now argue for more conservative figures of around 8000 (Chirikure et al., 2017). Whatever the case may be, what remains clear is the fact that the larger of the Zimbabwe Culture sites were major population centres, thus conforming to Cowgill's qualification that "Populations of at least a few thousand seem necessary if not a sufficient requirement for a settlement or society to be urban" (Chirikure et al., 2017; Cowgill, 2004).

Other important geographical and archaeological definitions and criteria for urbanism have highlighted that urban centres are constituted of built up areas accompanied by or made up of monumental structures. In addition, the existence of public buildings has also been added as important, though not necessarily regarded as a major defining attribute. Global surveys of complex societies and related centres from the Americas, Europe and through Africa to Asia have indeed shown that there is a degree of correspondence and relationship between monumental constructions and the development and manifestations of urbanism. As far as this goes, the monumental stone buildings of the Zimbabwe Culture and their spatial extent and layout clearly stand as physical evidence of their being urban. Here, we may however note that the Zimbabwe culture exhibits two types of urban patterning, the concentrated and discrete pattern and the dispersed urban pattern. Centres such as Mapungubwe, Great Zimbabwe and Khami are good examples of the first type while the Zvongombe cluster in northern Zimbabwe and the Shangano cluster in north-western Zimbabwe represent examples of the latter (Sinclair et al., 1993; Shenjere-Nyabezi et al., 2020).

However, while we embrace the concept of monumentality and other attributes in defining and understanding urbanism, we acknowledge that elsewhere in Africa and possibly beyond, it has been archaeologically argued and demonstrated that the absence of visible monumental structures is not a demonstration of the absence of urban centres in the past (McIntosh, 1999). Indeed, as McIntosh and McIntosh (McIntosh and McIntosh, 1984; McIntosh, 1999) have shown, cities without citadels did exist and did flourish in parts of West Africa. Elsewhere, in East Africa, historically observed urban capital sites of the interlacustrine states of Buganda, Bunyoro, Nkore and Rwanda, for example, have left no immediately visible traces of the expansive royal capitals that were constructed from perishable organic materials (Connah, 2015). In the final analysis therefore, it seems clear to us that whether it is being considered in the southern African or the Medieval England or the Mesoamerica past, urbanism was a complex phenomenon and development where there is a clear need to take into account variability in terms of process, development, form and character. This is a contention that is well articulated in Jervis (2016) that "…not only do different forms of urbanism exist, but that if urbanism emerges at the intersections between assemblages…towns emerge through various forms of discourse", hence his and our adoption of the concept of "multiple urbanisms" (Jervis, 2016; Kapumha, 2019).

5 Urbanism and the Zimbabwe Culture Architecture

The Zimbabwe Culture architecture has been the subject of archaeological and architectural inquiry for some time since the original exploratory studies by Schofield and the more comprehensive studies carried out by the architect Antony Whitty. Essentially, the architecture that resulted in the monumental buildings belongs to the class of dry stone walling which consisted of the production of walls of varying heights, terraces and platforms. These were constructed without the use of mortar using dressed as well as undressed blocks of stones that were quarried from the surrounding landscapes. The raw materials used were greatly influenced, though not always, by the local geology (Kapumha, 2019). The majority of the raw material for the buildings was quarried from granite, which is perhaps the most widely available rock type across the Zimbabwe plateau where most of the buildings are found (Garlake, 1970). Elsewhere, such as in north-western Zimbabwe, sandstone was exploited while in the mid-Zambezi Valley in northern Zimbabwe, iron stone was used (Shenjere-Nyabezi et al., 2020; Pwiti, 1996). In Eastern Botswana, quartz was quarried for sites such as Majojo while in central Mozambique the major site of Manyikeni was constructed out of limestone (Sinclair et al., 1993). To this end, it is fairly clear that local geology and other factors played a role in the development of the Zimbabwe Culture architecture. This had certain implications for the types and styles of the assemblages that were produced as architectural artefacts.

In summary, the construction of Zimbabwe culture stone buildings started with the quarrying of the raw materials. This took the laborious processes of subjecting rock outcrops to extreme heat, which would crack the rock into slabs, followed by shaping the resultant slabs into building blocks. It is thought that the process of transforming the raw materials into usable building blocks made use of stone and iron tools. Considering the number of blocks required to construct an edifice of the magnitude of the Great Enclosure at Great Zimbabwe, this must have required substantial inputs in work hours. This was followed by transportation of the building blocks to the construction site, which itself would have been a major feat. Finally, would come the process of construction of the dry stone walls, platforms and the other associated architectural features. Experimental work at Great Zimbabwe, accompanied by observations during the wall conservation work involving restorations have shown that substantial numbers of people and many days would have been required to construct even the shortest and smallest of Zimbabwe Culture structures (Dube, 1990; Matenga, 1996).

6 Power, Status and Architecture: Costly Signalling and the Zimbabwe Culture

As noted above, the most outstanding attribute of the Zimbabwe Culture was the monumental stone buildings that came in a variety of forms and styles. While it has been generally acknowledged that the stone walls were constructed as an expression and symbol of the power of the ruling classes, this interpretation has not previously been subjected to in-depth analysis and has more or less been taken for granted. In this section, we use two recent theoretical approaches and frameworks of Costly Signalling and Assemblage theory to further explore these stone built urban architectural remains.

7 Costly Signalling Theory

As a theoretical construct, Costly Signalling Theory (CST) originated from evolutionary biology and its recent adaptation to archaeological thought and practice has been developed following a number of concepts and understandings (Conolly, 2017). This has involved examination of, thinking about and interpretation of different archaeological phenomenon, including art, faunal assemblages and monumental constructions (Conolly, 2017). Such archaeological phenomena are viewed as reflections of actions and activities of past societies that carried or involved heavy investment and therefore were very costly from different perspectives, dimensions and directions. This includes considerations of heavy and costly investment in material, social, political and emotional terms. In traditional anthropological theory, which has also been applied in archaeology and other social sciences, such investment, actions and activities were embraced under the Conspicuous Consumption Theory. In the same vein and along similar lines, such behaviours have also been examined under the "Wasteful Advertising" theory. While embracing much of the thinking and premises of Conspicuous Consumption Theory, and to a degree, Wasteful Advertising Theory, the development of CST over the past two decades or so and more recently has sought to examine and interrogate the archaeological record beyond the immediately visible. This has included seeking to understand how and why individuals or groups of people engaged in costly signalling.

8 Understandings of Costly Signalling

The concept of costly signalling has been understood in several but related senses. In one sense, it is read as a form of signalling strength and power in which the costs of the signal are unaffordable for the less wealthy and less powerful to attempt. In another sense, it is seen as engaging in investment in the production of non-functional objects and highly visible monuments that have no immediate material reward or benefit. This extends to overinvestment in signalling one's or a group's power and prestige through non-utilitarian material culture such as objects and monuments which translates to costly behaviours that have long term but non-material benefits to the participating individuals (Conolly, 2017).

Beyond the immediately visible from an archaeological point of view, such signalling is deduced from reflections of costly acts and belief, commitment and investment in lavish gift giving. Along the same lines, this also includes engagement in acts of substantial generosity. Here, it is noted from cultural and social anthropological studies that such costly signalling is not the preserve of complex societies, but rather cuts across different forms and expressions of socio-political organisation. This includes what anthropologists have called non-ranked societies or systems that do not have institutionalised or hereditary leadership structures such as the Big Man societies, systems that scholars do not consider complex societies in the structural and conventional sense (Harris, 1977).

In the context of the Zimbabwe Culture monumental stone built centres under discussion, costly signalling is reflected in a number of ways, areas and contexts. At Great Zimbabwe and related sites across southern Africa, substantial labour and other inputs were invested in the production of the monumental architecture. The final products were in the form of the different stone structures that were non-functional and did not fulfil residential or other practical purposes. Rather, they were constructed to make a statement about social, political and economic power and by definition a statement about status. In this sense, southern Africa reflected developments comparable to many other parts of the globe such as South America and Asia in the sense of the production of monumental architecture as part of the development of complex socio-political systems sometimes referred to as civilisations.

9 Costly Signalling at Great Zimbabwe

The larger part of the architectural remains at Great Zimbabwe is in the form of enclosures. The Great Enclosure, situated in the valley, is the most impressive structure at Great Zimbabwe. (Figure 4.4).

Its outer wall, measuring some 178 metres in length and standing at a height of 10 metres is the largest single prehistoric construction in sub-Saharan Africa (Ndoro, 2001). Estimates of the number of blocks required to erect this edifice have varied between half a million and a million blocks. The interior contains a number of smaller stone enclosures and several solid mud platforms. At the back of the Great Enclosure is perhaps one of the most intriguing structures in the ancient city, the Conical Tower (Figure 4.5).

This is now regarded as a symbol of power rather than a phallic symbol, as early observers and more recently Nyamutswa believed (Nyamutswa, 2017). Its shape is similar to that of the clay granaries used in recent historical times and which continue to be used today and thus some scholars have theorised that it may have symbolically represented the rulers' ability to collect and store food grain tribute from among their subjects and also to care for them in times of drought and food shortage (Garlake, 2003). One other impressive part of the Great Enclosure is the parallel passage where an earlier wall is enclosed by the outer wall forming a long narrow corridor (Figure 4.6).

FIGURE 4.4 The Great Enclosure

FIGURE 4.5 The Conical Tower
IMAGE BY MUNYARADZI ELTON SAGIYA

FIGURE 4.6 The Parallel Passage
IMAGE BY MUNYARADZI ELTON SAGIYA

The outer wall demonstrates perhaps the highest level of masonry craftsmanship ever achieved at Great Zimbabwe. The top of the eastern outer-facing surface is decorated with a double chevron pattern and stone monoliths (Figure 4.7).

FIGURE 4.7 Double chevron and monoliths
IMAGE BY MUNYARADZI ELTON SAGIYA

10 Khami and Other Zimbabwe Culture Sites

While the stone enclosures at Great Zimbabwe were the dominant architectural features used for defining status and dividing space, away from there, at Khami the second largest Zimbabwe Culture site in southern Africa, as well as at Naletale and Danangombe, for example, the builders emphasised the construction of elaborate platforms on which thick solid walled mud houses were built. The platforms were connected by a system of passages, covered entrances and thick mud walls. Thus, while the elite people at Great Zimbabwe and related sites were screened within stone wall enclosures, the elite at Khami and the other sites mostly in central, south-western and north-western Zimbabwe exposed themselves on prominent artificial stone platforms (Figures 4.8A and 4.8B).

11 Zimbabwe Culture Stone Buildings Decoration as Costly Signalling

One of the characteristic features of Zimbabwe culture stone buildings across space and time is the presence of decoration ranging from nominal to very lavish (Figs 4.9A and 4.9B).

Over the years, the decoration has been the subject of some debate. There has however been a general understanding that while it was artistic, it was certainly not art or style in the conventional Western sense, but rather fitted within the symbolic realm of things much in the same way the stone buildings

FIGURE 4.8 (A) Artificial House Platform at Khami, western Zimbabwe; (B) Artificial House Platform at Shangano site, north-western Zimbabwe

themselves were symbols in action. In this sense, there is general acknowledgement that the decorative motifs on Zimbabwe Culture sites were part of a symbolic code and a cultural grammar. It is against this background that Huffman (1981, 2007), has offered very comprehensive interpretations of the

FIGURE 4.9 (A) Nominal decoration at Mtoa, north-western Zimbabwe; (B) Lavish decoration at Naletale, central Zimbabwe

meanings and significance of the many decorative motifs found on the walls and platform at Great Zimbabwe and elsewhere, mainly using Shona ethnography (Huffman, 1981; 2007). Although Huffman's work has been questioned and widely debated, its value has lain in the fact that it has provided for recognition and acknowledgement of the fact that the decorations were part of an urban cultural code of its times. Regardless of the debated meanings and symbolism of the decorations, what is important in the current consideration of costly investment is the observation that the decorations represented a substantial investment in terms of construction skills, labour and artistic creativity. To this extent therefore, they represented another level of costly signalling within the Zimbabwe Culture. What is also of interest in this regard is that at most of the sites where it occurs, the decoration is almost always found on places where it is highly visible, as if meant to be immediately readable (see Fig. 4.10A and 4.10B). Rare exceptions have however been noted at some sites where decoration is in the interior and therefore not immediately visible as at the sites of Nsalansala and Shangagwe in central Zimbabwe (Figure 4.10A and 4.10B).

FIGURE 4.10 (A) Interior and less visible decoration at Nsalansala, central Zimbabwe; (B) Interior and less visible decoration at Shangagwe, central Zimbabwe

12 Elite Domestic Architecture as Costly Signalling

Excavations at various Zimbabwe culture sites have shown that there was some differentiation in the production of residential structures between stone walls and on platforms and outside stone walls. Houses within stone walls and on platforms were all invariably constructed with thick solid *dhaka* (adobe) walls (Figure 4.11) and on substantial stone foundations with compact thick plastered floors.

These contrasted with the flimsier houses outside stone walls which were the pole and dhaka cone-on-cylinder type observed in historical times among Shona people. In as far the solid houses required considerable investment and input in their construction, they must have represented a structurally and visually more impressive product well beyond the normal requirements for accommodation purposes. It is against this background that it becomes observable that the elite domestic architecture of the Zimbabwe Culture urban centers constituted yet another level of costly signalling in relation to the costs invested.

In the final analysis, what emerges is that the various aspects of the material expressions of the Zimbabwe Culture represented a classic case of costly signalling where substantial labour and other inputs were invested in non-functional monumental production to make a statement about political power and status (Conolly, 2017; O'Driscoll, 2017; Wright, 2017).

FIGURE 4.11 Solid dhaka (adobe) walls at Khami site, western Zimbabwe

13 Participation in Costly Signalling and the Zimbabwe Culture

> Throughout history, people have been duped again and again into believing that enormous inequalities in the distribution of wealth are necessary for their own welfare. HARRIS, 1977

From our presentation of the various forms of costly signalling above, one of the obvious observations would be that the stone edifices were not constructed by members of the elite, seeing as a major investment in labour and other arduous work was called for. Powerful elites would not normally engage in such exacting undertakings. There is therefore a commonly held and largely accepted (and acceptable) assumption that the buildings were the result of the sweat and blood of commoner people that was voluntarily offered to enable those in power to make statements about themselves. This assumption is particularly accepted in the absence of any direct evidence of the use of slave labour or compelling evidence of the use of some such other coercive measures. The question that presents itself which remains to be addressed is why people would have voluntarily participated in costly signalling of power and prestige which they themselves were not directly a part of or direct beneficiaries. Answers to such questions have been asked of many such highly demanding undertakings across the globe in prehistory and even in contemporary times. Today for example, people engage in costly and risky behaviors on behalf of political leaders or political parties where in the end, they do not really derive any direct personal benefit. In attempting to answer these questions, we appeal to theoretical constructs linked to the ideology of control, including the role of religion in making populations engage in acts and processes of costly signalling for no clear immediate benefit but rather a belief that participation in public works for the elite or the politically and economically powerful is good for them, as summarized by Harris' contention above. We here argue that the participation in costly signalling to produce the Zimbabwe Culture monumental architectural assemblages was situated within an ideology that made people to believe that such undertakings were good for them, rooted in a belief that what is good for the leader(s) is good for the common good. Costly signalling then becomes an instrument of ideological control where inequalities and outright exploitation are masked. This does not however, discount the ever present possibility that on the part of the commoners, there may have been a sense of pride and satisfaction to be gained or derived from participating or having participated in the production of something grand and lasting, and acting as a lasting reminder of a sense of belonging to and sharing in the greatness of a socio-economic and political system which they belonged to and identified with. In the end, the production of the monumental structures would have been part of the construction and production of identity and belonging as a long-term gain but not in the immediate material sense. Ultimately, this becomes hinged on the two theoretical concepts of belonging and identity (Cooper and Brubaker, 2005; Mujere, 2019; Hodder et al., 1982). In this case, this is in a context where material cultures such as architecture are deployed by sections of a given socio-political formation to reinforce and reflect a strong sense of being and belonging. This is regardless of the fact that some such sections of the society are the active and direct producers of the material manifestations of belonging while a small section is consumers and the larger beneficiaries.

14 The Spatial and Socio-Political Organization of the Zimbabwe Culture Centres

Intra-site spatial analysis in archaeology beyond functionalist approaches towards the quest to understand the significance and meanings of the organization of space came into vogue in the discipline during the early years of the post-processual archaeology era from the late 1970s into the early 1980s (Hodder et al., 1982; Hodder and Hutson, 2003). Much of the theoretical frameworks and methodological approaches took their lead in cultural anthropology based on work by Edmund Leach, among others. From this perspective in the context of this paper was the development of structuralist and cognitive models and thinking in anthropology. In southern African archaeology, the lead in the examination and analysis of the significance and meanings of spatial organization was taken up by Huffman in the seminal paper entitled *Snakes and Crocodiles: Expressive space at Great Zimbabwe* (*Huffman, 1981*). Much of Huffman's thinking and applications of structuralism were themselves heavily influenced, if not guided by South African anthropologist Adam Kuper's work on aspects of Zulu marriage as well as cosmology and its relationship to spatial organization (Kuper, 1980; 1982). In some of the applications that took their inspiration from Kuper's work, Huffman developed the archaeological settlement model for southern African EIA communities that was labelled the Central Cattle Pattern (CCP). Based on excavation work at sites such as Broederstroom in South Africa, it was argued that settlement sites of archaeological Bantu communities followed a fixed or standard spatial layout and pattern that was informed by the ideological and economic importance of cattle in the male world as well as by the higher status of men in society in relation to women (Figure 4.12) (Huffman, 2001; 1986; 1993).

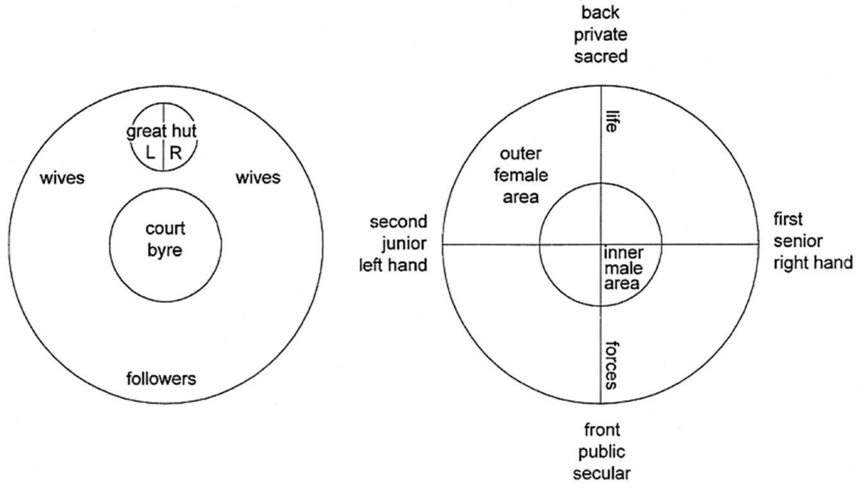


FIGURE 4.12 Structural arrangement of the Central Cattle Pattern
AFTER HUFFMAN, 2001

The model has however been widely questioned on archaeological and other grounds (Hall, 1984; Lane, 1994; Shenjere-Nyabezi, 2016). It was also from and within the same intellectual background that Huffman also developed what he termed the Zimbabwe Culture Pattern which he argued was the product of transformations that took place among the farming communities of southern Africa during the 2nd millennium AD.

15 Socio-Political Organization and the Zimbabwe Culture Settlement Pattern

In a series of papers and two major monographs since the seminal paper in 1981, Huffman has argued that the Zimbabwe Culture spatial pattern developed and was maintained almost unchanged over the several centuries of its lifespan, and was informed and dictated by a system of cultural codes and rules (Huffman, 1984a; Huffman et al., 1986; Huffman, 1996; 2007). In summary, it has been argued that the major sites of the Zimbabwe Culture, such as Mapungubwe, Great Zimbabwe, Khami, Danangombe (Dhlohlo), Zvongombe and Tsindi conformed to a spatial and symbol laden pattern that signified and was guided by the socio-economic and political relations between people within the culture. Based on structuralist theory, it was argued that in the same way society consisted of a series of dichotomies (inside/outside, rich/poor, elite/commoner, male/female, high/low, old/young) so was the organization of space. Among other such dichotomies and symbolic spatial representations and signifiers of different status was the walls themselves which divided elite and commoner people based on the inside/outside principle. By the same logic, Great Zimbabwe and similar ancient towns were argued to reflect a high/low, ruler/ruled, elite/commoner and male/female dichotomy physically represented by the location of rulers on hilltops and all others on the lower landscape overlooked by the ruler's hilltop residence.

This pattern was argued to represent the symbolic manifestation of political and social status which is thought to have remained an important part of the people's "town planning" and cultural geography through space and time.

The presentation and subsequent elaboration of the structuralist and cognitive theory-based Zimbabwe Culture Settlement Pattern model has been one of the most debated topics in southern African archaeology in the past three decades or so (Beach, 1998; Beach et al., 2013; Chirikure et al., 2014). One of the major critiques has been that the interpretive model adopted a static view of culture and failed to take cultural dynamism and other issues into account (Pwiti, 1996). In this paper, we use two theoretical constructs of recent years to further question and place this debate in context. Using assemblage theory from its various perspectives, we here argue that it is perhaps more useful and more rewarding to view the Zimbabwe Culture settlements as assemblages at two levels (Jervis, 2016; Kertai, 2019; Hamilakis and Jones, 2017). At the wider regional level we see the architectural remains as cultural assemblages that were produced through space and time and as dynamic rather than a constant. We further see them as representing cultural expressions that need to be viewed as a changing assemblage in form and composition. In this regard, we note for example that the original Whitty stylistic classification of the walling styles into P, Q and R with the generally accepted chronological significance and association with the development of different complex state systems of the Zimbabwe Culture is problematic (Shenjere-Nyabezi et al., 2020; Kertai, 2019). Based on detailed architectural observations in north-western Zimbabwe and elsewhere, we have noted that in terms of wall styles, the different styles, previously seen as signifiers of architectural evolutionary development do in fact occur within the same walls at some sites and also occur in combination within and between sites. To this extent, the architecture was not a constant. Similarly, within and between the different socio-political systems, the architecture was a changing cultural phenomenon. This is to the extent that while it is acknowledged that cognitive cultural maps did and do exist, such maps and their production as artifacts would have been subject to and the result of various factors. As such, while the organization of space is culturally meaningful, understanding of it need not be situated within static spatial models.

Rather, the assemblages that represent the cultural meanings of space would have been constantly shifting and changing. At the site level, the construction of cultural space and the production of an assemblage at this level would also have been subject to change as a result of various factors, geographical, environmental, social, political and economic. This is in the sense that the architectural assemblages that characterize and constitute the Zimbabwe Culture should be regarded not only as architectural arrangements, but things that highlight the processes of arranging (Kertai, 2019). In this sense, the assemblages then become products of various processes operating among people working individually and collectively. As such, in the context of agency theory, we would argue that the production of the stone walls and the wall styles they exhibit, and how the walls define and divide space would have been the outcome of many different and perhaps even conflicting processes that bring in agency as a part of the overall production processes. In terms of the complex spatial arrangements of the Zimbabwe Culture urban configurations therefore, we see them as assemblages that did carry, contain and signify cultural messages but in a changing world rather than conforming to a pre-conceived cultural geography and town plan.

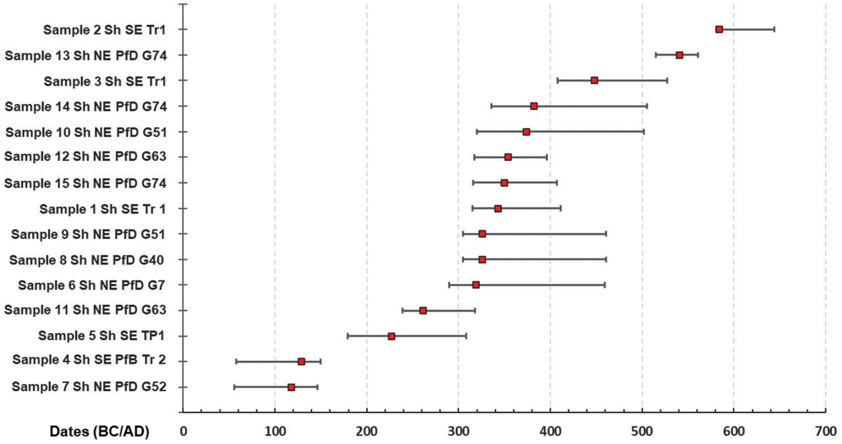
16 Zimbabwe Culture Urban Complexes in the Political Context

As noted in the introduction, the traditional model for the development of the Zimbabwe Culture complex state systems was influenced by Eurocentric frameworks where state systems rose, declined and collapsed with the collapse of one leading to the rise of another in linear successive fashion. This framework assumed a causative relationship between the decline of one state and the rise of another and correspondingly, the development and collapse and abandonment of their associated capitals. Thus, according to this historical analytical trajectory, the Mapungubwe state developed with its capital at the stone built hilltop site of Mapungubwe in the Shashi-Limpopo basin. The rise of the system during the 11th Century AD was attributed to the accumulation of wealth from external trade based on the export of ivory to the Oriental world via the Indian Ocean coast. It was then argued that when ivory lost its value on the trade market sometime during the 12th Century AD, to be replaced by gold, economic and political power then shifted to Great Zimbabwe, leading to the development of the Zimbabwe state. Great Zimbabwe then developed to become the largest stone built complex in southern Africa between the 13th and the middle of the 15th Century AD. Its size and extent of the monumentality reflected the success of the engagement of the state in the production of gold and its export, in exchange for exotic goods such as glass beads, ceramics and cloth. The Zimbabwe state itself was argued to have collapsed during the middle of the 15th Century AD as a result of the loss of the gold trade to the Mutapa state in northern Zimbabwe and the Torwa state based at Khami, the second largest of the Zimbabwe Culture urban capitals. The Torwa and the Mutapa states both came into being as successors to and therefore in a sense off springs of the Zimbabwe state following its collapse. By the same token, the Nambya state based in north-western Zimbabwe with its stone built capitals at the sites of Shangano, Bumbusi and Matoa were also seen as off shoots of Great Zimbabwe. In all cases, it was previously thought that the architecture of the assemblages of the stone built capitals reflected successive and progressive development from Great Zimbabwe. Recent research at the site of Mapela in the Shashi Limpopo Valley, previously thought to have been an offshoot or provincial centre of the Mapungubwe state has shown that it was in fact earlier and overlapped with Mapungubwe and is now thought to have represented a state system that developed at the same time as Mapungubwe (Chirikure et al., 2014). Using such empirical evidence as well as new theoretical frameworks, Chirikure and his associates have demonstrated that views of Mapungubwe having been the place of origin of the Zimbabwe Culture and southern Africa's earliest city and the centre of the region's earliest state system can no longer be acceptable. It is now thought that the stone building culture and its associated political developments may in fact have had multiple centres of origin rather than one centre, a way of thinking which is reminiscent of the abandonment of the arguments for a primary centre for the origins of agriculture and the search for the earliest maize cob! Further problems with the Zimbabwe state and Great Zimbabwe offshoot model have surfaced in north-western Zimbabwe for the origins and development of the Zimbabwe Culture Nambya state. Here, new dating evidence now shows that the state was contemporary with Great Zimbabwe and Khami, rather than an offshoot from one of them as previously thought (Ncube, 2004). Dating evidence recently obtained from one of the capital sites, Shangano, has placed the site occupation and the construction of the stone buildings from as early as the 14th Century AD (Shenjere-Nyabezi et al., 2020) (Table 4.2).

Elsewhere, for the Mutapa state based in northern Zimbabwe, Pwiti also showed a similar picture where rather than being a direct political successor to the Zimbabwe state as previously and popularly believed, the Mutapa state developed well before the Zimbabwe state had collapsed (Pwiti, 1996). When all this is combined and considered within the context of other new chronological data (see Chirukure et al., (2017) and Table 4.2), the picture that is now emerging is one of very complex multiple faceted socio-political developments

TABLE 4.2 Shangano site radiocarbon dates

Sample label	**14C Alter [yr BP]**	**± SD**	**Max. (% probability) Min. CI values [calBP]**	**Cal 1-sigma**	**C [%]**
Sample 2 Sh SE Tr1	584	21	644 (67.1%) 587	cal AD 1319–1403	595
Sample 13 Sh NE PfD G74	541	28	561 (66.3%) 515	cal AD 1330–1425	76
Sample 3 Sh SE Tr1	448	21	527 (95.4%) 488	cal AD 1435–1449	541
Sample 14 Sh NE PfD G74	382	20	505 (73.9%) 428	cal AD 1453–1613	568
Sample 10 Sh NE PfD G51	374	21	502 (65.7%) 428	cal AD 1456–1615	559
Sample 12 Sh NE PfD G63	354	21	396 (49.2%) 317	cal AD 1476–1623	567
Sample 15 Sh NE PfD G74	350	21	407 (53.3%) 316	cal AD 1485–1625	543
Sample 1 Sh SE Tr 1	343	21	411 (59.2%) 315	cal AD 1491–1630	539
Sample 9 Sh NE PfD G51	326	21	461 (75.8%) 347	cal AD 1516–1634	545
Sample 8 Sh NE PfD G40	326	21	461 (75.8%) 347	cal AD 1515–1634	479
Sample 6 Sh NE PfD G7	319	21	459 (75.5%) 348	cal AD 1521–1636	486
Sample 11 Sh NE PfD G63	261	21	318 (74.2%) 283	cal AD 1640–1662	561
Sample 5 Sh SE TP1	227	21	308 (48.9%) 275	cal AD 1651–1795	573
Sample 4 Sh SE PfB Tr 2	129	21	150 (46.7%) 58	cal AD 1683–1935	579
Sample 7 Sh NE PfD G52	118	21	146 (53.5%) 56	cal AD 1690–1925	458



in southern Africa whose understanding must be considered as equally complex (Chirikure et al., 2018). In particular, the production and development of the architectural monumental urban assemblages as centres of political and economic power can no longer be viewed in linear evolutionary terms, using rigid spatial models. Rather, as assemblages at the regional and local level, they were subject to processes of change and adaptation to a variety of circumstances (Chirikure et al., 2016).

17 Conclusions

The Zimbabwe Culture dominated the social, economic and political landscape of southern Africa for at least six centuries from the 11th Century AD onwards, during which time the region witnessed the origins, growth and prosperity of major political entities commonly referred to as states. Supported by successful economies based on indigenous branches of production and the proceeds from participation in global trading networks, these polities were able to use their wealth, power and social systems to transform many different parts of the regional landscapes into built environments using local resources to develop large stone built population centres that flourished as multi-scale settlements that exhibited many of the attributes of urban assemblages, however defined. While these monumental stone buildings that made up the urban centres have been examined from various perspectives in the past, in this paper, we have employed theoretical constructs such as Costly Signalling Theory and Assemblage Theory to think on why they were erected and how the processes involved in their construction, production and spatial organization are likely to have been the results of a complex combination of factors. In the final analysis, we argue that the Zimbabwe Culture stone buildings reflect engagement in costly signalling and conspicuous consumption in as far as the monumental architectural edifices did not meet any defensive of other functional needs. Engagement in such heavy investment on the part of those who directly participated in the construction activities but did not directly or immediately benefit from the final products might have been motivated by, and situated within the framework of a sense of being part of, belonging and identifying with the power and success of those for whom the buildings were being constructed. Using Assemblage and Agency Theory, we further argue that the buildings themselves, and their spatial and other arrangements as urban centres, were not products of or the result of fixed or standard cultural town planning. Rather, they are best seen as assemblages whose composition, form, meanings and significance are likely to have been subject to change as the centres grew or even shrunk and as new structures were built or added to existing ones. In the end, following the results of new research at the regional level and at the local scale in north-western Zimbabwe, we suggest that the past straight jacketed Western derived interpretations of the political history of the Zimbabwe Culture state systems and their capitals as being characterized by successive rises and falls following cause and effect models are no longer supportable, including previous perceptions of the different centres of the state systems as exhibiting progressive refinement in their architectural styles (Chirikure et al., 2016; Shenjere-Nyabezi et al., 2020).

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CHAPTER 5

Diversity and Variability in the Preindustrial Iron-Smelting Technologies of Great Zimbabwe, Southern Africa

Ezekia Mtetwa

1 Introduction

The earliest Europeans to think and write about Africa, particularly sub-Saharan Africa, developed a narrative of uniformity, stagnancy and lack of sophistication in the social and material practices of its extinct and extant populations. Those were views that claimed that there were *"… no ingenious manufactures among them, no arts, no sciences"* (Hume, 1758:125). George Hegel wrote, echoing the same views later: "*They have no arts, no sciences — as we see them now, so have they always been …"* (Hegel, 1840:116). James Theodore Bent, an English explorer and antiquarian who toured southern Africa at the turn of the 19 century, concluded that the iron-smelting technology of the Shona people of Zimbabwe, the primary focus of this chapter, was clumsy and replete with barbaric rituals (Bent, 1892). Again, as late as the 20th century, some writers still doubted the very possibility and existence of African history (Roper, 1966). In general, Zimbabwe's precolonial indigenous iron-smelting technologies were dismissed as in deep and perpetual slumber, and 19th-century master smelters were scorned as turning out the same product that their ancestors had produced over the past millennia (Brown, 1973). Clearly, these views painted a picture of technological naivety and backwardness in the Zimbabwean past specifically and sub-Saharan Africa as a whole in general. Sadly, as noted by Killick (2015) and Farrar (2020), among others, such scientific racism continues today in some scholarly and popular opinions, including global political figures[1] and at times, it is re-echoed by Africans themselves.[2]

An effect of these misconceptions on African technology was that the archaeological record of preindustrial iron metallurgy was perceived as non-existent or less diversified, particularly in areas south of the Zambezi River. The earliest bibliographical study of African metallurgy stopped at the Zambezi River, claiming a lack of relevant literature further south (Cline, 1937). The initial speculative understanding was that the classic type of iron smelting furnace south of the Zambezi was the low shaft type fired by forced draft, in contrast to the multiplicity of types in South and Central Africa (Friede, 1972; Cline, 1937; Chirikure and Bandama, 2014). The low shaft furnace has been found at iron-smelting sites dated to both the Early and Late Iron Age, and was present during colonial times, giving it a record of more than 1500 years of use between the Zambezi and Limpopo Rivers without much variation. The other type, the tall shaft furnace fired by natural draft, was thought to be confined to regions further north of the Zambezi, where they were said to be well adapted to large-scale trade in iron by their capacity and quality of smelt (Fagan, 1961). Several archaeological researchers have indeed attested their widespread existence in Zambia, Malawi and Tanzania (Mapunda, 1995; Killick, 1990).

However, mounting evidence from archaeological research across Zimbabwe reveals that the lack of technological variability and diversity claimed by earlier scholars reflect an incomplete knowledge of the archaeology of southern Africa as a whole and Zimbabwe in particular. Martin Prendergast (1975; 1979), for instance, discovered a new type of furnace suggestive of natural draft technology in the Darwendale area, northern Zimbabwe, which he dated to the 14th century AD. Here, Prendergast posits that this type of furnace was used to smelt an unusually high-grade asbestiform magnetite ore found only in the Great Dyke (Prendergast, 1979). However, the existence of this new

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[1] During his first visit to sub-Saharan Africa after winning power, former French President Nicolas Sarkozy made the following remarks in Senegal typical of 19th-century stereotypes: "The tragedy of Africa is that the African has not fully entered into history... They have never really launched themselves into the future... The African peasant only knew the eternal renewal of time, marked by the endless repetition of the same gestures and the same words... In this realm of fancy... there is neither room for human endeavour nor the idea of progress." https://uk.reuters.com/article/uk-africa-sarkozy/africans-still-seething-over-sarkozy-speech-idUKL0513034620070905.

[2] See Humphris et al., (2009) for an example of a science teacher in Uganda overhead by a team of archaeometallurgists researching precolonial iron-smelting claiming that Africa had no science and technology before colonialism despite living close to large iron-smelting sites in his area.

type of furnace in northern Zimbabwe was simply dismissed as an overspill of the Zambian Iron Age, rather than an artifact of broader socio-economic and technological transformations in southern Zambezia. Subsequent archaeological researches in northern Zimbabwe have illustrated that contrary to these stereotypes, pre-industrial iron technology in Zimbabwe was indeed diverse and extensive. Examples of technological variability and change in other sections of northern Zimbabwe have been recorded at such sites as Swartkrans and Baranda, showing evidence of slag tapping techniques in form of flow slag (Chirikure, 2005; Chirikure and Rehren, 2006).

This chapter uses increasing evidence from archaeological research around Great Zimbabwe to demonstrate that the record of preindustrial iron metallurgy in the area has greater technological diversity and variability than previously thought. Great Zimbabwe was at its peak as the most important political, religious and trade centre in southern Africa during the mid-second millennium AD. Despite its fame in global archaeology (Trigger, 2003; Smith, 2004), the extent of Great Zimbabwe's iron industry remained unknown and undocumented for a long time. Large areas of its wider archaeological landscape are still relatively poorly surveyed, despite more than a century of research at and around the drystone built capital. Research recurrently focused on the more archaeologically visible monumental walls and material culture within the constituent enclosures making up the urban centre of the medieval settlement (Chirikure and Pikirayi, 2008). Again, Great Zimbabwe's postcolonial era became predominated by the preservation and presentation concerns of the site, and rightly so (Ndoro, 2001). During the early phases of colonial rule in Zimbabwe, excavation activities by antiquarians left large areas of the site extensively desiccated and so other aspects of Great Zimbabwe's archaeological record are beyond reconstruction (Hall, 1909). Thus, postcolonial conservation interventions at Great Zimbabwe, which included a moratorium on further excavations within the site, made it rather difficult to explore satisfactorily the numerous angles of the site using standard archaeological methods. For instance, key aspects of the population of Great Zimbabwe have not been possible to explain in satisfactory ways, including its size (Chirikure et al., 2017), genetic composition and the whereabouts of the burial grounds of its inhabitants (Mtetwa et al, in preparation)[3]

In light of the research restrictions on the main site of Great Zimbabwe and the knowledge gaps of the settlement, I employed a lateral thinking

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[3] In 2018, the author initiated an ongoing project on the whereabouts of Great Zimbabwe burial grounds, and a report publishing results and radiocarbon dates of a much richer mortuary record is forthcoming.

methodology between 2012 and 2017, during which I looked away from the impressive drystone walls to the iron-smelting debris in the wider landscape. Archaeometallurgy, the study of metal production in the past, has come of age as a sub-discipline of archaeology in exploring not just material properties and chemical reactions, but also the social history of our human past (Herbert, 1984; Chirikure, 2015). Within Great Zimbabwe's political and economic system, and an estimated population of around 10 000 inhabitants (Chirikure et al., 2017), the demand for iron would have been very high and the metal consumed in a wide range of social contexts. Like in many societies of sub-Saharan Africa, iron in Great Zimbabwe was critical for its use in daily utilitarian activities such as cultivation and clearance of agricultural fields, but also in ritual and power negotiation relations (Childs and Killick, 1993; Chirikure, 2007; Herbert, 1996).

Agro-pastoral and metalworking populations were present in the Great Zimbabwe cultural landscape by the mid-first millennium AD (Chirikure, Pollard et al., 2013) a phenomenon attested in many parts of southern Africa (Mitchell, 2002). From the end of the first to the mid-second millennium AD, the rest of southern Africa experienced major technological and sociopolitical transformations generally associated with the origins of social complexity, urbanism and early state systems (Manyanga et al., 2013). These changes included an exclusive lifestyle of building monumental capitals in drystone architecture and specialised production of materials and artifacts for local consumption and trade, intensifying links with distant parts of the world (Chipunza, 1994; Pikirayi, 2013). Local metals such as gold and iron, as well as wildlife resources in the form of ivory and, possibly, skins of royal animals were exchanged with imported ceramics, beads, clothes and other trinkets in the Indian Ocean and central African trade systems (Chirikure, 2014; Wood, 2012; Swan, 2008). There is revived discussion regarding the impact of such connections and disconnections on the rise and collapse of social complexity in southern Africa as a whole and Great Zimbabwe specifically (Pwiti, 1991; Moffett and Chirikure, 2016; Pikirayi, 2017).

So far, only the iron production debris within the dry-stone-built capital has received enviable research attention (Herbert, 1996; Miller, 2002; Chirikure, 2007; Foreman et al., 2017; Bandama et al., 2016). However, until the nature and organisation of iron metallurgy in the hinterland of the Great Zimbabwe settlement is known, the archaeological meaning of remains within the urban centre itself remains largely diminished and incomplete. Thus, this paper uses results of previous and recent archaeological surveys and excavations conducted in areas surrounding the medieval urban centre to draw a richer account of its iron-smelting technologies. I have chosen to focus on macroscopic attributes of such archaeometallurgical data sets as multiple-fused tuyeres, tap slag and clusters of large circular furnace bases, including one with a unique rectangular morphology. Clearly, the growing corpus of data underpinning greater technological variability and diversity raise critical questions regarding how social changes shaped and were reshaped by iron-related practices in the history of Great Zimbabwe. In other words, exploring the nature and organisation of iron technology in the Great Zimbabwe area offers another way of looking into the everyday social life of its inhabitants, overshadowed by a focus on its spectacular monumental architecture. Aspects of these questions are addressed in detail in several papers that explore the multifaceted archaeologies of iron in Great Zimbabwe (Mtetwa, 2017). Detailed technological analyses of the recovered slags and metallurgical tuyeres are also published elsewhere (Mtetwa, in preparation; Mtetwa and Lindahl, in preparation).

1.1 *The Physical Landscape of Iron Production in Great Zimbabwe*

Great Zimbabwe (Figure 5.1), which is situated on the southern margin of the Zimbabwe Plateau, is surrounded by mountain ranges such as Nyanda and

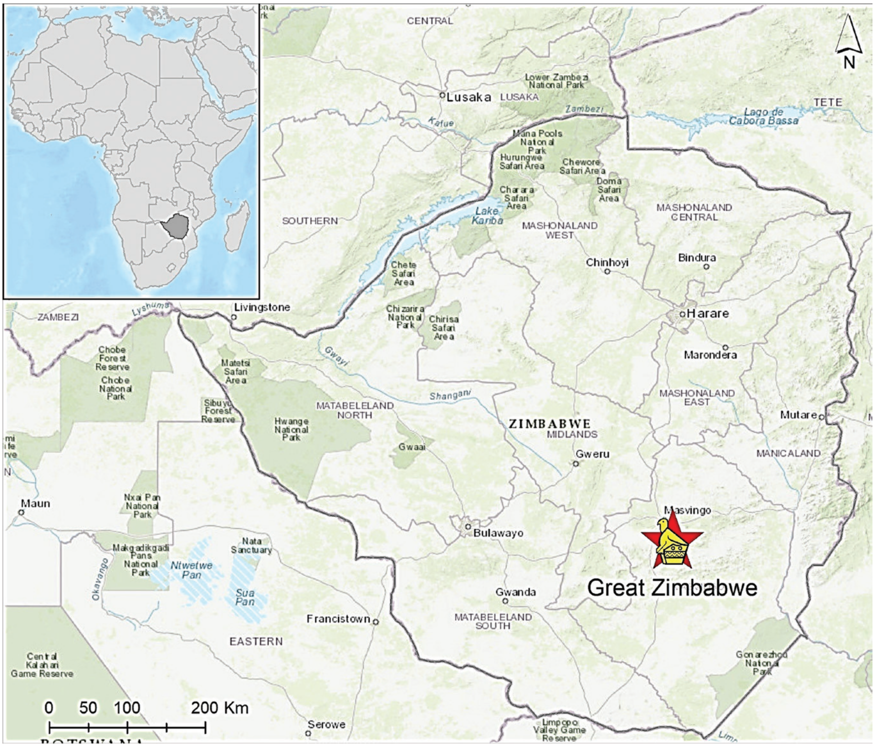

FIGURE 5.1 Map of Zimbabwe showing the location of Great Zimbabwe in Southern Africa

Ruvhuri to the west, Beza and Nyuni to the north, as well as Chigaramboni to the southwest. These mountain ranges are rich in banded ironstones (Lister, 1987). Presumably, these iron-rich ores sustained pre-industrial iron metallurgy in the area (Mtetwa, 2011; Ndoro, 1994), as evidenced by modern iron ore mining in the Nyuni Hills (Mapira, 2012). In addition, areas near the Bondolfi Mission 15km northwest of the Great Zimbabwe centre have rich gold deposits, which supported precolonial gold mining (Phimister, 1976; 1974) and continue to be exploited today. Great Zimbabwe's whalebacked granite outcrops provided natural platforms for crushing iron ore, a practice observed by Carl Mauch, a German explorer who visited Great Zimbabwe in the 1870s (Burke and Mauch, 1969). There are numerous dolly holes around the Great Zimbabwe area attesting to such symbiotic relations between the physical environment and the processing of mineral ores, among other functions.

In addition, the Great Zimbabwe area is relatively well favoured by Zimbabwe's savanna climate rainfall, which is often unpredictable. Much of the rain comes in the form of mist, locally known as *guti,* which, together with its numerous natural springs, make the Great Zimbabwe area a water-rich landscape that supports the production of grain and other crops (Bannerman, 1982; Pikirayi et al., 2016). This microclimate sustains deciduous *miombo* savanna woodlands, which would have been exploited by its populations for timber, medicines, domestic fuel and, importantly, charcoal for metallurgical activities (Ndoro, 2001). Anthracological analysis of charcoals recovered from furnace pits in the Chigaramboni iron-smelting sites indicate that such tree species as *Acacia robusta, Acacia sieberiana, Acacia xanthophloea, Acacia polyacantha, Acacia burkei, Faurea saligna, Schotia brachypetala, Kigelia africana* and *Parinari curatellifolia* were exploited in the iron industry (Chikumbirike, 2014). The narrow valleys between the numerous bornhardts and whalebacked hills common in the area have cultivable and very fertile loamy soils, adding to the natural resources that would have attracted agro-pastoral populations to flourish in this area over time.

1.2 *Archaeological Surveys and Excavations: A Brief Note*

Earlier investigations, particularly between the 1970s and 1990s, sought to examine state formation processes and settlement patterns around the Great Zimbabwe centre (Ndoro, 1994; Sinclair, 1987; Sinclair, 1984). In the process, these researches encountered and made reports of considerable iron production debris, which have received very little archaeological attention. The most recent investigations, undertaken as components of my Masters and Doctoral projects between 2010 and 2016, aimed to achieve three specific objectives. First, the fieldwork in 2010 sought to establish technological parameters of an

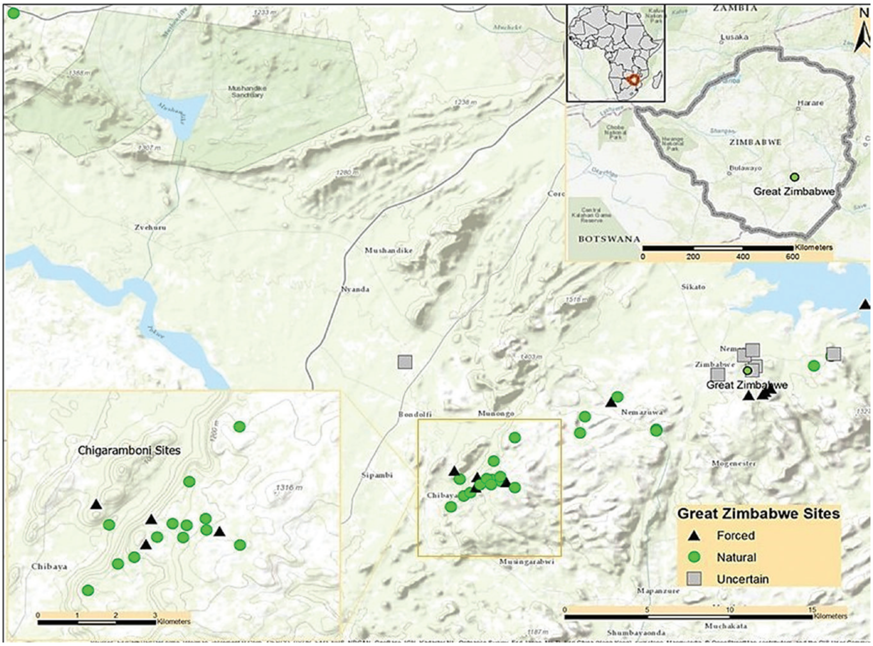

FIGURE 5.2 The distribution of iron production sites in the wider Great Zimbabwe landscape

iron production site threatened by the Gaths Mine chrome prospecting activities in Mashava (Mtetwa, 2011). The second fieldwork, between 2013 and 2016, aimed to identify previously undocumented iron-working sites and confirm others reported by previous researchers; examining their wider implications in the archaeology of Great Zimbabwe (see the distribution and concentrations of sites recorded sites in Figure 5.2). Finally, the investigations aimed to recover high quality remains of iron production from the best-preserved and technologically most representative sites for subsequent reconstructions of the iron technology itself, but also aspects of the environment and radiometric dating.

2 Results

Forty-two iron production sites were recorded during the recent field surveys (see Figure 5.2 and Table 5.1). Four of the sites were excavated during the course of my PhD study, bringing the total number of excavated sites around Great Zimbabwe to six after the respective works of David Collett at Goose Bay in 1986 and Webber Ndoro at Chigaramboni in 1991. This section presents examples of the recovered materials from these excavations, including samples from surface collections at two other sites that could not be excavated due to limited time and funding. Results of the detailed laboratory analyses conducted on the recovered materials, as pointed out before, are published elsewhere. Only the macroscopic attributes of remains from eight sites are dealt with in this paper to draw an initial picture of yet another category of technology associated with Great Zimbabwe, apart from the famous drystone architecture.

2.1 *Chigaramboni*

The Chigaramboni cluster of iron production sites is located 15 km southwest of the medieval Great Zimbabwe urban centre. Initially investigated in 1991 by Webber Ndoro (1994) and this author recently, the majority out of a total of 15 recorded sites are characterized by concentrations of large furnace bases, heaps of multiple fused tuyeres and slags (Figure 5.3). Ndoro's excavations uncovered furnace pits measuring about 1.4m in internal diameter, which were also lined inside. These furnaces occur in clusters at the various recorded sites around Chigaramboni hills as evidenced by the visible circular furnace bases showing on the ground in association with large heaps of tuyeres. He noted that the biggest site, for instance, carried at least ten large heaps of tuyeres in association with at least five visible furnace bases (Ndoro, 1994), suggestive of large-scale iron production.

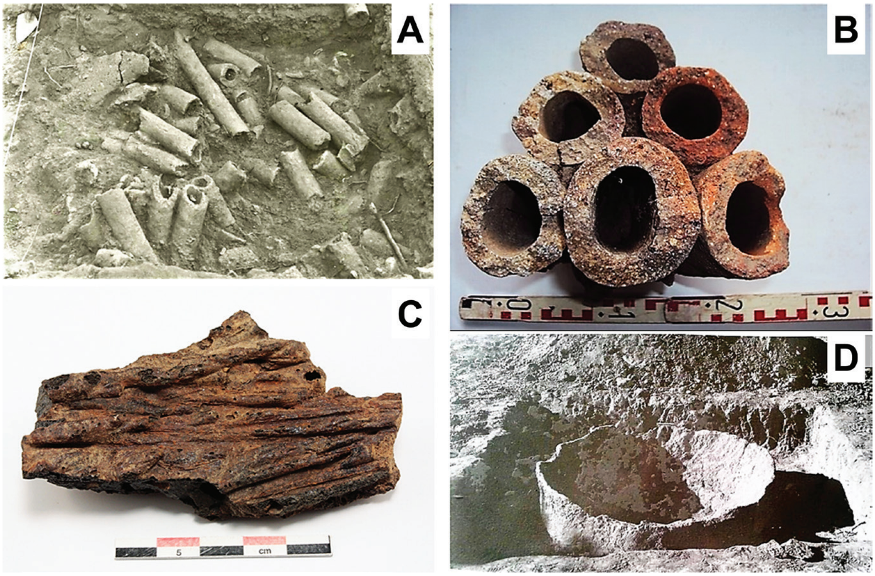

FIGURE 5.3 Archaeometallurgical materials from Chigaramboni site: (A) A heap of excavated tuyeres; (B) Tuyeres fused in multiples; (C) Furnace slag with plant impressions; (D) A furnace pit with lining

Many of the tuyeres at the Chigaramboni sites are fused together, ranging from two up to ten pipes (Figure 5.3B), a feature known elsewhere which underpin the use of natural draft air-supply mechanisms (Prendergast, 1975; Killick, 1991). The tuyeres average about eight centimetres in external diameter and five centimetres internal diameter on both ends, allowing much air to be blown into the furnace for intense heating (Rehder, 2000). They also show signs of vitrification and sintering, causing the tuyere pipes to fuse together. There is no evidence of a settlement in the immediate vicinities of the smelting sites, possibly highlighting the influence of mineral and wood fuel resources in the location of smelting activities. Owing to its absence in the ethnographic and written accounts of Zimbabwean iron metallurgy, the natural draft technology from Chigaramboni sites is dated relatively to before 1800 AD (Ndoro, 1994).

2.2 *Mashava*

Mashava site lies about 40 km west of the Great Zimbabwe urban centre. The area falls under Gaths Mine, which currently extracts chrome and asbestos from the southern ends of the Great Dyke. The high concentration of iron production debris at the site, divided into two clusters by a seasonal stream (Figure 5.4A), suggests large-scale iron production beyond subsistence consumption. These metallurgical remains are in the form of at least twenty visible furnace features, massive and dense slag, heaps of tuyeres and possible quarries of magnetite iron ore. Some of the slag pieces at the site are tuyere-moulded (Figure 5.4B), showing the cylindrical shape of the tuyeres into which the molten slag flowed and solidified. Other slag pieces show a clear flow texture

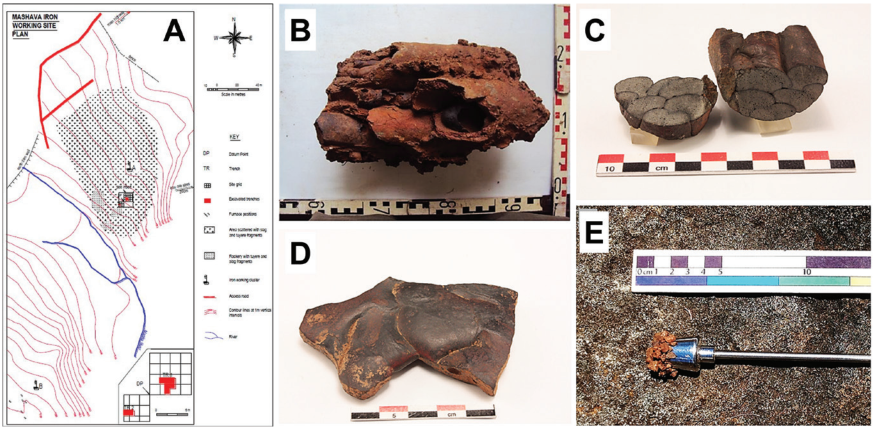

FIGURE 5.4 Archaeometallurgical materials from Mashava site: (A) Mashava site plan (B) Tuyeres fused in multiples; (C) Tuyere-moulded slag; (D) Tap or flow slag; (E) Magnetite iron ore

in the form of wrinkled red-brown surfaces and sand impression underneath (Figure 5.4C), which typically indicates slag tapping practices (Killick, 1990; Chirikure and Rehren, 2006; Miller et al., 2001). Five tuyere pieces were found fused together, clogged inside and coated on external surfaces with slag, while others were completely collapsed, vitrified and eroded away around the mouth due to intense heat inside the furnace. Macroscopically, the tuyeres and furnace blocks have visible coarse quartz sand, which raises questions regarding the nature of soils selected for the manufacture of metallurgical ceramics and fluxing techniques adopted at Mashava site (Mtetwa and Lindahl, manuscript).

About 200 m east of the smelting site, there are shallow depressions in which are found scatters of a highly magnetic magnetite iron ore, which presumably supported iron production activities at Mashava site. Detailed laboratory analyses of the presumed iron ore, slags, and crown materials will shed more light on this possibility as well as illuminating the complexity and sophistication of the designs and processes of iron production at Mashava site (Mtetwa, in preparation). Owing to a dearth of diagnostic material culture, the period of the site could not be established by relative dating and further excavations are expected to recover charcoal samples for radiocarbon dating.

2.3 *Mutevedzi*

Mutevedzi site (also known as Nezvigaro) is located 6 km south-west of Great Zimbabwe World Heritage Site. It is located on a pass some 200 m away from Shambinyara, a perennial stream that would have supplied water for metallurgical purposes at the site. The site consists of a dense scatter of slag, tuyere fragments and furnace rubble spread across an area covering 3 hectares. Excavations of a less disturbed section of the site revealed a rectangular furnace base measuring about 2x1 m (Figure 5.5). The blocks of the broken furnace wall, which measure about 10 cm thick on average, have visible finger impressions and evidence of vitrification. As mentioned before, the furnace blocks lack the typical curvilinear shape common with most iron smelting furnaces in African iron metallurgy, further confirming that the sides of the superstructure, like the base, were rectilinear. The floor of the furnace slopes gently northwards and its southern end was destroyed.

At least twenty near-complete tuyeres pieces were found in association with the rectangular furnace, averaging 25 cm in length, about 4 cm in internal diameter and 6 cm external diameter, showing signs of vitrification at the distal end. At least three tuyeres were found fused together, suggesting the possible use of natural draft air-supply mechanisms to drive the furnace. The slag recovered from the excavation had very high porosity and plant impressions, with some of them exhibiting near-straight edges from the linear shape of the

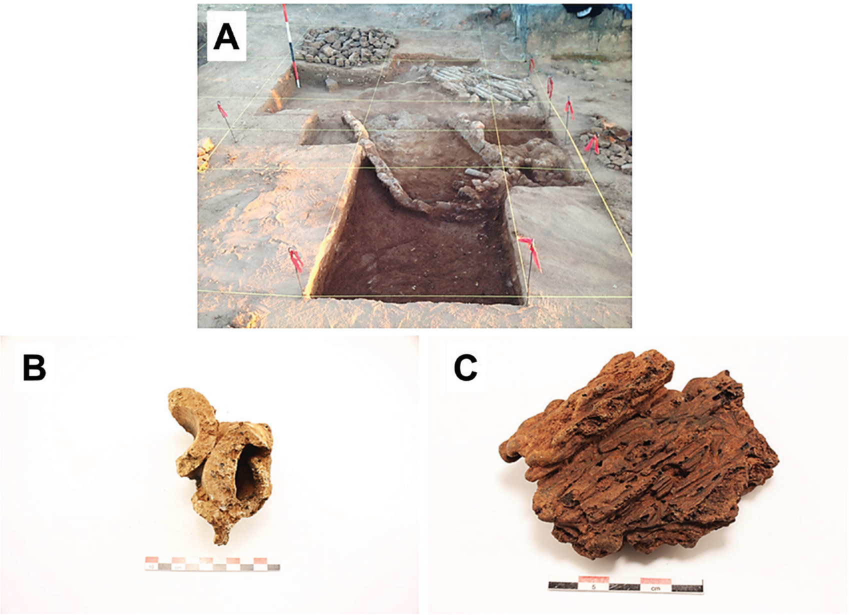

FIGURE 5.5 A rectangular furnace base from Mutevedzi site (A). Tuyeres fused in multiples (B). Furnace slag with plant impressions (C)

furnace. The slag had very low magnetism. There were no iron ore and finished metal objects found at the site, suggesting that smelting and secondary iron processing were spatially and socially differentiated, a point that will be dealt with in the discussion section later. No charcoals were recovered from this site for the production of radiocarbon dates of the rectangular furnace technology, but also to determine the tree species selected for wood charcoal fuel. Efforts to date the metallurgical tuyeres using thermoluminescence were dismissed as unfruitful due to the usual wide error margins produced by such methods (Lindahl, *personal communication*). More excavations at the site will most likely yield materials datable by radiocarbon methods.

2.4 *Boroma*

Boroma site lies approximately 4 km northeast of the Great Zimbabwe centre, making it one of the iron working sites closest to the urban centre. It is located on the west site of a huge granite boulder about eighty metres from Chebopopo stream. There are also a couple of perennial natural springs in the vicinities of the site (Pikirayi et al., 2016), which would have been critical for agricultural and domestic consumption, but also iron production activities in the past. Intra-site surveys at Boroma site identified two distinct activity areas –iron smelting and smithing locations, the latter in association with house foundations.

Archaeological excavations at Boroma Site recovered iron smelting slag, broken tuyere pieces, blocks of furnace rubble, and charcoals. The bulk of the slag was made up of large cake-like blocks, the largest one measured about 15 x 13 cm with a thickness of about 7 cm. Some of the recovered slag blocks had plant impressions and bone inclusions, which would have been significant components of the bloomery recipes, as observed elsewhere (De Caro, et al., 2013; Prendergast, 1974). At least 30 broken tuyere pieces measuring at most 15 cm in length were recovered from one of the excavated trenches. Four broken tuyere pieces were fused together, suggesting that the smelting process used natural draft technology to drive the furnaces. Both single and multiple-fused tuyeres exhibited evidence of vitrification and collapse at the mouth (Figure 5.6), indicating the intense heat generated during the smelting process.

FIGURE 5.6 Multiple fused tuyeres (A). Single tuyere (B)

The internal diameter of the different tuyeres recovered at Boroma site ranged between 30 and 40 cm, while their external diameters measured between 50 and 60 cm, showing a very fine brick-red fabric.

The site also consists of remains of iron smithing activities in the form of a possible smithing hearth, slags, and flat surfaced granite block located less than 200 m further west of the smelting area. Isolated domestic artifacts such as a piece of green and white chinaware, a potsherd with cross hatched lines and an iron hoe blade were collected from the cultivated land between the smelting and smithing areas. These were too few to shed adequate light towards our understanding of the period of occupation and the contemporaneity of the settlement and ironworking activities.

Boroma iron production site has been radiocarbon dated to 1058 ± 28 BP (Ua- Ua-54052) using charcoals recovered from the furnace pit (Table 5.1), making the site possibly one of the earliest sites associated with natural draft technology in southern Africa. More research at the site is required to verify this date, which has the potential to refine our understanding of the chronology and distribution of natural draft technology in African iron metallurgy.

2.5 *Veza A*

The Veza A iron-working site is located about 8 km south-west of Great Zimbabwe. It is situated at the foot of the western slope of a large granite inselberg and is bounded on the south by the Veza River about 100 metres away, which would have supplied water for the iron production activities at the site. Right within the site is an abandoned modern homestead whose flowerbeds and courtyard were demarcated using finger-impressed and vitrified blocks of broken furnace walls. Other furnace blocks and dense pieces of slag (measuring approximately 20 x 15 cm) were used to stabilize soil on top of the graves belonging to members of the family that settled within the site in recent times. Many more blocks of slags, furnace rubble and pieces of tuyere were cleared from the land surrounding the homestead in preparation for maize cultivation and made into large heaps on the edges of the fields. Pedestrian surveys around the site identified more iron production debris towards the top of the granite inselberg about 800m east of the main site. The site has a dense scatter of iron slag over an area of about 3 hectares.

Excavations at the site uncovered a possible semi-circular furnace wall measuring 100 cm in diameter, with a plastered base tilting westward gently (Figure 5.7). The western section of the furnace wall had been totally removed, most probably, by the ancient metallurgists themselves as a way of harvesting the bloom from the furnace chamber. A possible rake channel was also exposed sloping down to the west from the furnace measuring another one metre,

FIGURE 5.7 A circular furnace base (A) and double-fused tuyeres (B) from Veza site

making it likely that this could have been the floor of yet another linear furnace similar to the one uncovered at Mutevedzi site. Charcoal samples collected from a cluster of tuyeres on the floor of the furnace have been radiocarbon dated to 917 ± 28 BP (Ua-54055). The charcoal samples have been submitted also for trees species identification at the Witwatersrand University laboratories, to illuminate aspects of the exploitation and management of environmental resources in Great Zimbabwe's preindustrial iron metallurgy.

Many of the tuyeres recovered from Veza A site were fused together in doubles, measuring about 3.5 cm internal diameter, 1.5. cm wall thickness and 20 cm length. The tuyeres show evidence of vitrification and melting at the distal end, which indicate that they were exposed to very high temperatures deep inside the furnace. The excavations also yielded very magnetic and heavily corroded slags with a curvilinear shape, which usually indicates smithing slag (Serneels and Perret, 2003; Miller et al., 2001). The occurrence of both smelting and smithing slags at the same location is a common encounter in African iron metallurgy, which makes it possible to reconstruct a fuller picture of the iron production and metal fabrication techniques.

2.6 *Veza B*

This smelting site lies about one kilometre up the Veza stream, southeast of Veza A site. It is located on the west side of a cluster of granite boulders about 200m away from the stream. The site consists of large blocks of broken furnace walls measuring about 12 cm thick bearing visible finger impressions of the ironworkers who constructed the furnaces. Some of the furnace blocks show evidence of vitrification, indicative of the slag attacks on the fabric of the furnace wall. The site also has large heaps of tuyere pieces many of which are fused together in doubles (Figure 5.8). The tuyeres at the site show extensive evidence of melting at the mouth backwards due to intense heat in the furnace

FIGURE 5.8 A double fused tuyeres from Veza B site

where they were deeply inserted, leaving them significantly eroded and coated by slag on their external surfaces.

Many slag blocks at the site, alongside tuyeres and furnace blocks, were cleared away for agricultural purposes yearly ahead of the farming season since 1983 when the current landowner settled in the area, a possible indication of the large volumes of metallurgical wastes deposited at the site. The slags at the site have a grey streak and metallic lustre, showing low magnetism, porosity and no evidence of weathering, which suggests efficient slag-metal separation conditions in the furnace.

2.7 *Goose Bay*

David Collett was the first to investigate this site in 1986. It lies about 5 kilometers north of the Great Zimbabwe site. It is located on the western side of one of the numerous granite hills that are usually inundated by the waters of Lake Mutirikwi, which was built in the mid-20th century. The site consists of broken furnace walls, dense slag and broken tuyere pieces. The tuyeres are flared on one end, indicating the use of forced-draft technology for iron-smelting at the site. Located in between the boulders that make up the granite hill are remains of a hut floor and pole impressed *dhaka*. Intra-site pedestrian surveys in 2013 around Goose Bay site, when Lake Mutirikwi was almost dry, recovered a clay phallic object, a possible crucible, potsherds and lower grinding stones, suggesting that the iron production activities at this site took place within a domestic context. The site was radiocarbon dated to 121 ± 27 (Ua-54053) using charcoal stored in the Great Zimbabwe Conservation Centre from Collett's 1986 excavations, which places it in the terminal or post-Great Zimbabwe period (Chirikure et al., 2013).

2.8 *Sviba*

Sviba site lies about 5km northeast of Great Zimbabwe and is located at the bottom of the western slope of Sviba hill. The site covers an area of about two hectares in which such iron production remains as furnace rubble, slag blocks and tuyere fragments are dispersed in small quantities. The largest slag block recovered at the site measures about 40 cm in diameter and is about 15 cm thick, and has a circular shape, suggestive of the use of low shaft furnaces at the site (Figure 5.9A). All the slag blocks at the site bear charcoal impressions, confirming the materials to be furnace slag. One of the tuyeres recovered at the site has a flared proximal, which is typically indicative of forced-draft air supply mechanisms at the site (Figure 5.9B). Surface slag and tuyere samples were collected for laboratory investigation meant to shed more light on the nature of the iron smelting processes practiced at the site. A second phase of

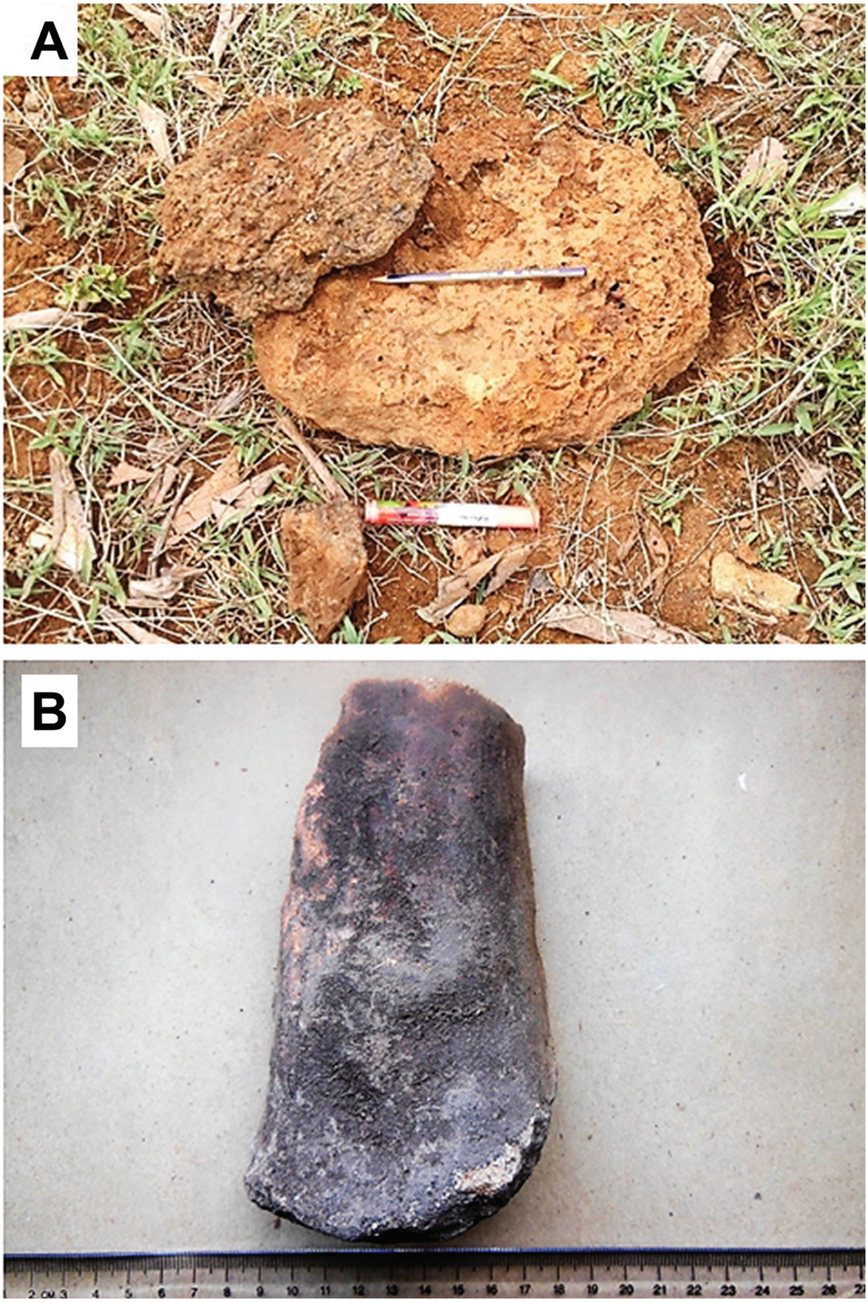

FIGURE 5.9 Archaeometallurgical materials from Sviba site: Dense furnace slag with plant impressions (A); Funnel shaped tuyere (B)

archaeological investigations involving the excavation of the best-preserved sections of the site is necessary, which will most likely recover high quality material for chronometric dating and further archaeometallurgical analyses.

2.9 *Chronology*

Table 5.1 below presents a set of old and new radiocarbon dates reflecting a broad view of the chronology of the iron production sites around Great Zimbabwe. The circular and smaller furnace that Sinclair (1984) uncovered at Gokomere Mission was unequivocally driven by forced draft and is radiocarbon dated to 1800–1940 cal.AD (Pta-1975). According to Prendergast (1979: 118), this type of furnace was the most popular among 19th century Shona metallurgists. Earliest visitors to Great Zimbabwe in particular and southern Africa in general have provided detailed descriptions of this type of furnace, including its anthropomorphic features (Bent, 1893; Burke and Mauch, 1969; also Chirikure (2006) on the Njanja iron production).

TABLE 5.1 Radiocarbon dates of charcoal samples from furnace pits around Great Zimbabwe calibrated using OxCal 4.2 (Ramsey, 2009) and the SHCal13 curve (Hogg et al., 2013)

Site name	**Lab number**	**^{14}C age BP**	**δ^{13}C ‰**	**Calibrated date range (95% confidence)**	**Reference**
Gokomere Mission	Pta-1975	90 ± 50	-	1800–1940 cal. AD	Sinclair 1984
Goose Bay	Ua-54053	121 ± 27	-24.7	1696–1807 cal. AD	Mtetwa 2017
Veza 1	Ua-54055	917 ± 28	-25.7	1047–1227 cal. AD	Mtetwa 2017
Boroma	Ua-54052	1058 ± 28	-26.3	986–1141 cal. AD	Mtetwa 2017

3 Discussion

As highlighted in the introduction, the key question of this paper concerns the possibility of illuminating the presence of remarkable technological diversity and variability in the iron industry of Great Zimbabwe during precolonial times. The foregoing section presented a growing corpus of various furnace designs, different slag types and tuyeres, some fused in multiples.

3.1 Furnaces

The fieldwork results presented above, in conjunction with written sources (Bent, 1892; Burke and Mauch, 1969), indicate the use of low forced draft and high natural draft furnaces in the area. The internal diameters of furnaces discovered in the Chigaramboni hills, Mashava and Boroma, which measured between 1.0 and 1.4m, fall within a range usually associated elsewhere with high natural draft furnaces (Halaand and Shinnie, 1985; Killick, 1990; Mapunda, 1995). The growing evidence of natural draft iron smelting furnaces in large clusters around the Great Zimbabwe area is particularly noteworthy. Their occurrence in large clusters, as observed at Chigaramboni and Mashava sites, offers a critical opportunity to rethink the scales of iron production and the size of the market that would have consumed such quantities of iron.

Due to insufficient knowledge of African technology, it was generally assumed that the high natural draft furnaces were largely limited to west, east and central Africa and were not popular in regions that lie south of the Zambezi River (Van der Merwe, 1980; Kense, 1985; Halaand and Shinnie, 1985). Cline (1937), for instance, thinks that this geographical distribution of natural draft furnaces north of the Zambezi River coincided with areas known to have been hubs of extensive trade networks from around AD 1600. Fagan (1961) also thinks that natural draft furnaces were well adapted to the northerly regions' large-scale trade in iron by their capacity and, presumably, the quality of the resultant metal. Curiously, Cline and Fagan were undoubtedly aware of the place of Great Zimbabwe in the Indian Ocean and central African trade systems, which should naturally have stimulated their attention towards proper consideration of its archaeometallurgy. Nevertheless, they maintained that the low shaft furnaces, driven by forced-draft, was the 'classic Rhodesian type', which was regarded as lagging behind technologies further north.

Importantly, new radiocarbon dates of 1058 ± 28 BP (Ua-54052) and 917 ±28 BP (Ua-54055) from the respective sites of Boroma and Veza 1 suggest that the Great Zimbabwe area carried perhaps some of the earliest natural draft iron smelting sites than areas north of the Zambezi River. So far, the earliest known natural draft iron smelting furnaces were discovered in northern Zimbabwe by Prendergast (1979, 1975) and fall in the 14th century AD calibrated radiocarbon dates. As pointed out by Ndoro (1994), there is no ethnographic and written evidence for natural draft technology in the Great Zimbabwe area, or elsewhere in southern Africa as is the case north of the Zambezi River (see Killick, 1990; Mapunda, 1995). On the basis of these two recent dates and the criterion of tuyeres fused in multiples from Boroma and Veza 1 sites, this paper proposes that natural draft furnaces were possibly earlier in southern Africa where they developed as a component of the technological transformations related to the Great Zimbabwe Culture. More radiometric dates from such sites as Chigaramboni and Mashava with tuyeres fused in as many as ten pieces will shed more light on the early history of this technique in African metallurgy.

Another important example of furnace type from Great Zimbabwe is the rectangular furnace base uncovered at Mutevedzi. So far, there are few reports of a similar design in the archaeometallurgical record of sub-Saharan Africa (Thebe et al., 2016). Its dimensions of about 2x1 metres suggest that the furnace would have been well adapted for large-scale iron smelting processes. Once again, the presence of tuyeres fused in multiples of three at the site suggests that this was yet another variant of natural draft technology. Well-researched examples of metallurgical furnaces of a rectangular or linear design have been reported from Sri Lanka, Burma, Cambodia and Japan (Juleff, 2009; 1996), but also in Egypt (Scheel, 1989). The Sri Lankan rectangular furnaces, dated to the end of the first millennium AD, were driven by strong monsoon winds to produce high quality steel (Juleff, 1996; Tabor, Molinari, and Juleff, 2005). A more similar example to the Great Zimbabwe case is the Burmese furnaces, which operated by natural draft using as many as twenty tuyeres on one of the long sides of the rectangular furnace. The Burmese furnaces have been dated to the second half of the second millennium AD. There is also the Cambodian linear furnace technology, which is operated by forced-draft, with as many as twenty-three tuyeres on each of the two long sides (Juleff, 2009).

Unfortunately, the Great Zimbabwe furnace was demolished to ground level where the remaining rectangular wall stands barely 10cm high, showing no visible tuyere holes. Juleff has suggested that elements of the Sri Lankan linear furnace technology were possibly transmitted to other regions of southern Asia such as Burma, Cambodia and Japan within trade contexts (Juleff, 2009). Likewise, it is reasonable to ask whether elements of the Southern Asian linear furnace technology were transmitted to southern Africa within contexts of the Indian Ocean trade connections. Already, the introduction of tin, gold and bronze in southern Africa in the early second millennium AD, and the use of such infrastructure as flat-based crucibles at Great Zimbabwe is regarded as indicative of cross-borrowing of technology (Summers, 1969). Increased archaeological fieldwork in southern Africa including the adjacent island of Madagascar, where local histories of iron metallurgy remain poorly illuminated, will shed more light on the origins or spread of technologies that were present in Zimbabwe by the mid-second millennium AD. Investigations are underway to obtain radiometric dates for the Great Zimbabwe linear furnace technology and more research, which may include experimental archaeology, is required to understand the mechanics of smelting iron in a rectangular furnace.

3.2 *Tuyeres*

Archaeological fieldwork in the Great Zimbabwe landscape encountered two types of tuyeres, commonly known to have penetrated the furnace from around the base. Clearly, the two types of tuyeres indicate significant technological variation in Great Zimbabwe synchronically and diachronically. Flared tuyeres typically functioned with bowl and low shaft furnaces, which are generally viewed as the earliest smelting techniques (Chirikure et al., 2009; Friede, 1979; Miller and Van Der Merwe, 1994). The technique was evidently the only one in use, at least in southern Africa during the 19th and early 20th centuries as attested by written accounts, archaeological research as well as local tradition (Chirikure, 2006; Prendergast, 1979; Sinclair, 1984).

The advent of a smelting technique, which used multiple tuyeres to drive high natural draft furnaces, represents a significant turning point in the history of not just iron metallurgy in southern Africa as a region, and Great Zimbabwe specifically, but in the broader society. The calibrated radiocarbon dates for two of the sites with multiple fused tuyeres fall between the 10th and 12th centuries AD. The new dates suggest that the advent of high natural draft furnaces would have been one component of a much broader socio-economic, political and technological transformation observed in the archaeological record of southern Africa from the late first millennium AD. Phillipson (2005) posits that from around the first and second millennium AD changeover, there was a sudden restructuring of the entire range of daily activities associated with the specialised production of artifacts and materials. In architecture, which has received relatively more research attention, these changes were characterized by so much experimentation and change in the organization of space as well as new materials and techniques. In the archaeology of Great Zimbabwe, archaeologists have robustly pursued these major technological transformations more in the area of architectural innovations (see, for example Chipunza, 1994), overlooking possible developments in, for instance, metallurgical ingenuity. The new evidence presented in this paper provides perhaps the first detailed picture of other technological innovations associated with Great Zimbabwe outside drystone architecture, a well-known example in southern African archaeology. The archaeometallurgical data provides more evidence useful for further deconstruction of earlier stereotypes of uniformity, stagnation and lack of sophistication in African technology as has been demonstrated in other regions of sub-Saharan Africa (Killick and Fenn, 2012; Killick, 2015).

3.3 *Slags*

Initially, the absence of ethnographic and written evidence for the tapping of slag in Zimbabwe was taken as evidence for the absence of the slag tapping technique between the Zambezi and Limpopo Rivers (see for example Miller and Van der Merwe 1994). Nevertheless, archaeological research has attested the use of the technique at Baranda, a Zimbabwe Culture capital of the Mutapa State in northern Zimbabwe (Chirikure and Rehren, 2006). The tuyere-moulded slags and some with flat bottoms bearing sand impressions excavated at Mashava site clearly demonstrate that the technique of tapping out of the furnace, to allow for longer hours of smelting iron and improving its quality, was perhaps more widespread in Zimbabwe. It was certainly not limited to northern areas of Zimbabwe, where it was first recorded (Prendergast, 1979). Archaeological iron smelting slags further south of Zimbabwe were assumed to have always originated in non-tapping bloomery furnaces. Miller and Van der Merwe (1994), for instance, argue that there was no record of liquid slags having been deliberately drained from the operational chamber of the furnace during smelting. On the contrary, the tuyere-moulded slags from Mashava site even suggest that some tuyeres may have been specially positioned to function as air inlets first and slag outlets later on during the smelting process. Slag tapping using tuyeres at the rake hole is ethnographically confirmed among the Fipa of southwestern Tanzania (Mapunda, 2010), and may actually have been practiced more widely and much earlier in Africa.

Other macroscopic attributes of slags from the Great Zimbabwe landscape give interesting hints about the raw materials, fluxing practices, as well as slag-metal separation, reflecting the varied decisions and choices made by the iron smelters (Rehren et al., 2007). For instance, many of the recovered furnace slag samples had evidence of plant impressions (see Table 5.2), indicative of the different types of plant materials charged in the furnace as part of the smelting recipes.

Most of the recovered slag samples had very low magnetism, which typically reflects efficient slag-metal separation (Miller et al., 2001). However, there were other slag samples from within the same sites, which had high magnetism, exhibiting a metallic lustre and grey streak. Some of these highly magnetic samples are possibly smithing slags, which would imply that both primary metal extraction and secondary processing took place at the same location such as Boroma.

4 Conclusions

The evidence of preindustrial iron metallurgy in the wider archaeological landscape of Great Zimbabwe presented in this paper suggest that the area carried a remarkable variety of iron production technologies over time. Instead of a

TABLE 5.2 A summary of macroscopic attributes of slag samples and bloom analyzed with the aid of optical and electron microscopy on polished thin sections

Sample	Material	Morphology	Lustre	Porosity	Magnetism	Inclusions/ Impressions	Streak/ Color
Mas1	Smelting slag	Cylindrical	Metallic section	Low	Nil	None	dark-brown
Mas2	Smelting slag	Flat	Metallic section	Low	Nil	ground floor	red-brown
Mas3	Bloom	Amorphous	glass section	Low	Very high	None	Brown cortex
Mut1	Smelting slag	Quadrilateral	ceramic	High	Low	plant impressions	Brown
Bor1	Smelting slag	Amorphous	ceramic	Medium	Low	plant impressions	Brown
Bor2	Smelting slag	Elongated	ceramic	Medium	Low	plant impressions	Brown
Bor3	Smelting slag	Amorphous	ceramic	Medium	Low	Nil	Brown
Svi1	Smelting slag	Amorphous	ceramic	Medium	Low	plant impressions	Brown
VezA1	Smithing slag	Amorphous	Metallic section	Low	High	Vitrified ceramic	Brown
VezA2	Smithing slag	Concave/ Convex	Greasy	Low	Very high	None	Brown
VezB1	Smelting slag	Amorphous	Greasy	High	Low	Plant impressions	Brown
Chi1	Smelting slag	Plano-convex	Greasy	Medium	Low	Floor, plant impressions	Brown
Chi2	Smithing slag?	Amorphous	Metallic	Low/	Very magnetic	None	Grey
Goo1	Smithing slag?	Amorphous	Metallic section	High	High	None	Brown

dearth of archaeometallurgical debris as previously assumed, the area has concentrations of iron production sites intimately correlated with the mountain ranges surrounding the urban centre, whose banded ironstones would have provided quality iron ores. These remains of iron production reflect a wide range of novel designs and processes of metal extraction in the form of natural draft furnaces, tap slags and a rectangular furnace design previously unknown in the iron metallurgy of southern Africa. The presence of huge natural draft furnaces in the Chigaramboni hills, Mashava, Boroma, Mutevedzi and Veza sites represents a significant change not just in the technology of Great Zimbabwe, but its social, economic, as well as environmental systems and processes as a whole.

The radiocarbon dates obtained for two of the recorded iron production sites associated with multiple fused tuyeres suggest that the Great Zimbabwe area has the earliest evidence of natural draft technologies in southern Africa. The dates, which fall in the beginning of the second millennium AD, offer a new chronological frame to rethink the distribution and circumstances surrounding the development of natural draft furnaces. Because of their contemporaneity and proximity to the urban centre, it is not unreasonable to associate the newly dated iron production sites with the metal extraction strategies of Great Zimbabwe, which was at its peak between the 12th and 16th centuries AD. This new picture of contemporaneity, however, requires more refinement using high quality material for chronometric dating and archaeometallurgical analyses. Lead isotope and elemental analyses of metal objects and the geochemistry of the exploited iron ores (Ling et al., 2014), for instance, have the potential to yield insights into the connections and disconnections between the Great Zimbabwe urban centre and the metallurgical resources and technologies across its wider archaeological landscape.

Acknowledgements

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CHAPTER 6

Grappling with Diversity in Livestock-Related, Non-Agriculturist Archaeology in the Light of Genetic Research into the Lactase Persistence Allele, -14010*C, in Southern Africa

Thembi Russell and Faye Lander

1 Introduction

The paper by Breton *et al.* (2014) demonstrating a shared ancestry between an eastern Africa population and the Khoe-speaking Nama of southern Africa has freed archaeologists to consider once again the place of demic diffusion in the spread of the first domestic animals without agriculture, to southern Africa. This follows its unpopularity as an explanation for change amongst the southern Africanist archaeological community in the 1990s and early 2000s (Kinahan, 1991; Sadr, 1998, 2003, 2008; Orton, 2015). It is difficult to separate demic diffusion from cultural diffusion using archaeology, as evidenced in debates worldwide.

This paper looks at the livestock-related, non-agriculturist archaeology in southern Africa in the light of the new genetic insights into the distribution of the lactase persistence allele in southern Africa. We focus on the spread of livestock without agriculture, a process that is connected to Khoe-language speakers. Agro-pastoralism, the spread of farming with speakers of Bantu-languages, is occasionally mentioned for comparative purposes. We briefly review the archaeological evidence for the last 3000 years BP in southern Africa. We then present the modern day southern African distribution of lactose persistence and compare this with the archaeological evidence for livestock-keeping. Finally we consider ethnographic and historic sources for milk-drinking in southern Africa.

2 Review of the Archaeological Evidence from Approximately 3000 BP, Southern Africa

Southern Africa is here defined as countries to the south of Congo, the Democratic Republic of Congo and Tanzania. From about 2100 years ago, the

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first, very slight evidence for pottery and domestic stock appears at sites that are conventionally associated with the spread of livestock-keeping without agriculture (referred to as Later Stone Age (LSA) sites in this chapter) (see Lander and Russell (2018) for a detailed review of the data from 551 BC to AD 1056). The most securely identified and directly dated sheep specimen derives from the site Spoegrivier on the western half of southern Africa and dates to around 2100 years ago (Coutu et al., 2021). The earliest appearance of domestic cattle at sites conventionally associated with the spread of farmers speaking Bantu-languages occurs from about 1750 BP onwards (referred to as farmer sites in this chapter). At around 1500 years BP livestock counts reach a peak at Later Stone Age sites, with evidence of caprines outweighing cattle, whilst in the summer rainfall area, on the eastern side of southern Africa, many farmer sites have evidence of livestock-keeping in the form of cattle bones (Figure 6.1). From 1300 years BP, the number and distribution of farmer-related sites steadily increase, whilst the number of Later Stone Age livestock-related sites remain constant from this period onwards. Notably LSA sites have consistently low numbers of domestic livestock (Russell and Lander, 2015). Cattle are rare. The total cattle count (MNI) at all LSA sites is just 21, whilst that for caprines (mainly sheep) is 365 (Russell and Lander, 2015).

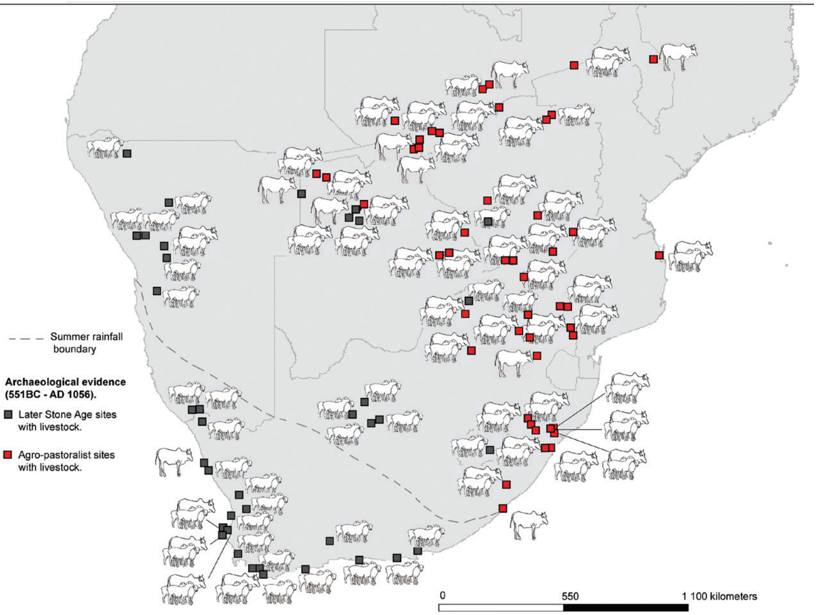

FIGURE 6.1 Archaeological evidence for livestock in Southern Africa, 551 BC to AD 1058

Contemporary with the first appearance of livestock is pottery. However, attempts to link it with the spread of livestock at Later Stone Age sites based on stylistic analysis have been unfruitful (Sadr and Sampson, 2006; Sadr, 2008; see also Smith, 2008, 2017). Lander and Russell (2020) suggest that pottery spread rapidly amongst hunter-gatherers from its first appearance in a process of cultural diffusion, which might also have carried domestic livestock, particularly sheep, across South Africa along already established exchange networks (see also Sadr, 2004; Russell, 2017).

3 Distribution of the Southern African Lactase Persistence Allele, -14010*C Compared to the Archaeological Evidence for Livestock

The presence of the east African lactase persistence allele, -14010*C, amongst present-day southern African populations is important because it signifies the presence of a proto-historic, fresh-milk-drinking pastoral population in southern Africa, and in the case of the Nama, a degree of relatedness to an East African source population (Breton et al., 2014; Macholdt et al., 2014). In southern Africa, 59 ethnic population groups have been screened for the LP allele (Table 6.1 and Figure 6.2) (Coelho et al., 2009; Tornianen et al., 2009; Breton et al., 2014; Macholdt et al., 2014; Jones et al., 2015; Pinto et al., 2016). These include Afrikaans-, Khoesan- and Bantu- language-speakers from agro-pastoralist, hunter-gatherer and agriculturist communities. The geographical coverage includes parts of Angola, Namibia, Botswana, Zambia, Kingdom of Eswatini, Mozambique and South Africa (Figure 6.3).

The lactase persistence allele reflects the continuous consumption of fresh milk from one generation to the next (Tishkoff et al., 2007; Breton et al., 2014; Ranciaro et al., 2014). Its presence is thus indicative of a group that either keeps livestock and drinks fresh milk or gets fresh milk regularly from a continuous relationship with livestock-keepers.

In the review of LP -14010*C allele amongst extant southern African population groups, twelve have the allele at frequencies of 10% or above (Table 6.1). The highest incidence is found amongst the Namibian Nama Khoe-speaking pastoralists (35.7%) (Breton et al., 2014; Macholdt et al., 2014). Nine of these groups are found in northern/north-western parts of southern Africa. The remaining three are distinctive. Two are eastern Bantu-language speaking groups (Map Code 15 and 35, Figure 6.4). The third is an Afrikaans-speaking community of mixed Khoesan ancestry, sampled in the western Cape, South Africa (Breton et al., 2014) (map code 3, Figure 6.4).

TABLE 6.1 The frequency of the East African - lactase persistence allele in Southern Africa

Map code	Ethnic group	Subsistence base, language group, ref.	N of individuals
1	Nama	Pastoralist Khoe Breton *et al.* 2014	22
2	Askham Coloured	Not provided Khoe – North Breton *et al.* 2014	20
3	Wellington Coloured	Not provided Afrikaans Breton *et al.* 2014	20
4	Colesberg Coloured	Not provided Afrikaans Breton *et al.* 2014	20
5	/Gui and //Gana	Hunter-gatherer Khoe Breton *et al.* 2014	20
5	//Gana	Hunter-gatherer Khoe Macholdt *et al.* 2014	10
5	/Gui	Hunter-gatherer Khoe Macholdt *et al.* 2014	17
6	Khwe	Hunter-gatherer Khoe Breton *et al.* 2014	19
6	Khwe	Hunter-gatherer Khoe Breton *et al.* 2014	19
7	Ju/'hoansi	Hunter-gatherer Ju - Northeast - Ju/'hoan Breton *et al.* 2014	20
8	Ju|hoan_North	Hunter-gatherer Kx'a Macholdt *et al.* 2014	21

Sample region	**Decimal latitude**	**Decimal longitude**	**-14010*C freq.**	**Ref.**
Windhoek, Namibia	−22,5624	17,06599	0,357	Breton *et al.* (2014) Macholdt *et al.* (2014)
Askham, Northern Cape, South Africa	−26,9834	20,78333	0,225	Breton *et al.* (2014)
Wellington, Western Cape, South Africa	−33,6818	19,01023	0,1	Breton *et al.* (2014)
Colesberg, Northern Cape, South Africa	−30,8388	25,07629	0,025	Breton *et al.*(2014)
Kutse Game Reserve, Kalahari, Botswana	−23,4223	24,04879	0,071	Breton *et al.* (2014)
Kutse Game Reserve, Kalahari, Botswana	−23,4223	24,04879	0,2	Macholdt *et al.* (2014)
Kutse Game Reserve, Kalahari, Botswana	−23,4223	24,04879	0,088	Macholdt *et al.* (2014)
Schmidtsdrif Northern Cape, South Africa	−28,8134	24,10132	0,029	Breton *et al.* (2014)
Rootfontein, Namibia	−19,6113	18,10939	0,029	Breton *et al.* (2014)
Tsumkwe, Namibia	−19,6009	20,50384	0,029	Breton *et al.* (2014)
North West, Botswana	−20,5814	21,67013	0,024	Macholdt *et al.* (2014)

TABLE 6.1 The Frequency of the East African - lactase persistence allele in Southern Africa (*cont.*)

Map code	Ethnic group	Subsistence base, language group, ref.	N of individuals
9	Ju|hoan South	Hunter-gatherer Kx'a Macholdt *et al.* 2014	26
10	!Xun	Hunter-gatherer Ju - Northwest - /Xũu Breton *et al.* 2014	20
10	!Xun	Hunter-gatherer Ju - Northwest - /Xũu Breton *et al.* 2014	-
20	!Xuun	Hunter-gatherer Kx'a Macholdt *et al.* 2014	19
47	!Xuun	Hunter-gatherer Kx'a Pinto *et al.* 2016	-
11	Karretjie People	Hunter-gatherer and herder /Xam descendants Breton *et al.* 2014	20
12	≠Khomani	Hunter-gatherer herders Germanic Tuu Breton *et al.* 2014	20
13	Herero	Farmer and herder western Bantu Breton *et al.* 2014	14
14	Herero	Pastoralist western Bantu Macholdt *et al.* 2014	21
38	Kuvale/ Herero	Pastoralist west Savanna Bantu Coelho *et al.* 2009	
42	Kuvale	Farming with some pastoralism west Savanna Bantu Pinto *et al.* 2016	-

Sample region	Decimal latitude	Decimal longitude	-14010*C freq.	Ref.
Ghanzi, Botswana border with Namibia	−21,1943	21,06119	0,058	Macholdt *et al.* (2014)
Schmidtsdrif, Northern Cape, South Africa	−28,8134	24,10119	0,038	Breton *et al.* (2014)
Grootfontein, Namibia	−19,6113	18,10939	0,038	Breton *et al.* (2014)
Nyae Nyae, Namibia	−19,7057	20,49703	0,053	Macholdt *et al.* (2014)
Mupa, Angola	−16,1831	15,76708	0,014	Pinto *et al.* (2016)
Colesberg, Northern Cape, South Africa	−30,8388	25,07629	0,083	Breton *et al.* (2014)
Askham, Northern Cape, South Africa	−26,9834	20,78333	0,11	Breton *et al.* (2014)
Windhoek, Namibia	−17,0624	17,06599	0	Breton *et al.* (2014)
Windhoek, Namibia	−22,5624	17,06599	0,071	Macholdt *et al.* (2014) (see Torniainen *et al.* 2009 and Breton *et al.* 2014)
Namibe, Angola	−16,0277	12,43632	0,06	Coelho *et al.* (2009) (see Alves *et al.* 2011)
Namibe, Angola [1 sample location]	−14,5436	13,10684	0,037	Pinto *et al.* (2016) (see Coelho *et al.* 2009)

TABLE 6.1 The Frequency of the East African - lactase persistence allele in Southern Africa (*cont.*)

Map code	Ethnic group	Subsistence base, language group, ref.	N of individuals
42	Kuvale	Farming with some pastoralism west Savanna Bantu Pinto *et al.* 2016	-
42	Kuvale	Farming with some pastoralism west Savanna Bantu Pinto *et al.* 2016	-
15	Sotho-Tswana and Zulu	Agropastoralist farmer southeastern Bantu Breton *et al.* 2014	16 (Sotho-Tswana) 25 (Zulu)
16	Taa-East	Hunter-gatherer Tuu Macholdt *et al.* 2014	11
17	Taa-North	Hunter-gatherer Tuu Macholdt *et al.* 2014	11
18	Taa-West	Hunter-gatherer Tuu Macholdt *et al.* 2014	20
19	ǂHoan	Hunter-gatherer Kx'a Macholdt *et al.* 2014	7
21	||Ani	Hunter-gatherer Khoe Macholdt *et al.* 2014	11
22	Buga	Hunter-gatherer Khoe Macholdt *et al.* 2014	9
23	||Xo	Hunter-gatherer Khoe Macholdt *et al.* 2014	19

Sample region	**Decimal latitude**	**Decimal longitude**	**-14010*C freq.**	**Ref.**
Namibe, Angola [2 sample location]	–15,3969	12,83899	0,037	Pinto *et al.*(2016) (see Coelho *et al.* 2009)
Namibe, Angola [3 sample location]	–15,5753	12,76128	0,037	Pinto *et al.* (2016) (see Coelho *et al.* 2009)
Various regions, South Africa	–27,9865	29,86269	0,1	Breton *et al.* (2014)
Kgalagadi, Botswana	–24,3548	22,81767	0,045	Macholdt *et al.* (2014)
Kgalagadi, Botswana	–23,59	21,61049	0	Macholdt *et al.* (2014)
Kgalagadi, Botswana	–24,7803	20,10442	0,025	Macholdt *et al.* (2014)
Kgalagadi, Botswana	–24,3368	22,34	0	Macholdt *et al.* (2014)
North West, Botswana	–18,5167	21,94934	0,091	Macholdt *et al.* (2014)
North West, Botswana	–18,3716	21,85806	0	Macholdt *et al.* (2014)
Caprivi Strip	–17,9231	22,72381	0,079	Macholdt *et al.* (2014)

TABLE 6.1 The Frequency of the East African - lactase persistence allele in Southern Africa (*cont.*)

Map code	Ethnic group	Subsistence base, language group, ref.	N of individuals
24	Damara	Hunter-gatherer and pastoralist Khoe Macholdt *et al.* 2014	34
25	Haiǁom	Hunter-gatherer Khoe Macholdt *et al.* 2014	40
26	Naro	Hunter-gatherer Khoe Macholdt *et al.* 2014	19
27	Shua	Hunter-gatherer Khoe Macholdt *et al.* 2014	27
28	Tshwa	Hunter-gatherer Khoe Macholdt *et al.* 2014	15
29	Himba	Pastoralist west Savanna Bantu Macholdt *et al.* 2014	16
41	Himba	Pastoralist west Savanna Bantu Pinto *et al.* 2016; Macholdt *et al.* 2014	-
41	Himba	Pastoralist west Savanna Bantu Pinto *et al.* 2016; Macholdt *et al.* 2014	-
30	Kgalagadi	Agropastoralist southeastern Bantu Macholdt *et al.* 2014	20
31	Tonga	Agriculturist southeastern Bantu Macholdt *et al.* 2014	17

Sample region	**Decimal latitude**	**Decimal longitude**	**-14010*C freq.**	**Ref.**
Kunene Region, Namibia	–20,4608	14,01402	0,044	Macholdt *et al.* (2014)
Kunene Region, Namibia	–19,6687	14,70835	0,088	Macholdt *et al.* (2014)
Ghanzi, Botswana	–22,01	21,23226	0,053	Macholdt *et al.* (2014)
Makgadikgadi, Botswana	–20,5509	25,81031	0,074	Macholdt *et al.* (2014)
Makgadikgadi, Botswana	–21,3433	26,04308	0,167	Macholdt *et al.* (2014)
Skeleton Coast, Namibia	–19,5689	13,67961	0,125	Macholdt *et al.* (2014)
Namibe, Angola [1 sample location]	–17,0017	12,43598	0,087	Pinto *et al.* (2016) (see Macholdt *et al.* 2014)
Namibe, Angola [2 sample location]	–16,8911	12,43598	0,087	Pinto *et al.* (2016) (see Macholdt *et al.* 2014)
Kgalagadi, Botswana	–24,7289	22,70295	0	Macholdt *et al.* (2014)
southern Zambia	–17,7183	26,82519	0	Macholdt *et al.* (2014)

TABLE 6.1 The Frequency of the East African - lactase persistence allele in Southern Africa (*cont.*)

Map code	Ethnic group	Subsistence base, language group, ref.	N of individuals
32	Tswana	Agropastoralist southeastern Bantu Macholdt *et al.* 2014	18
33	Nkoya	Agropastoralist eastern Bantu Macholdt *et al.* 2014	16
34	Wambo	Agriculturist western Bantu Macholdt *et al.* 2014	8
35	!Xhosa	Agropastoralist southeastern Bantu Torniainen *et al.* 2009	109
35	!Xhosa	Agropastoralist southeastern Bantu Ranciaro *et al.* 2014	16
36	Venda	Agropastoralist southeastern Bantu Ranciaro *et al.* 2014	18
37	Ovim-bundu	Mostly agriculturists (cattle raising not crucial for subsistence) west Savanna Bantu Coelho *et al.* 2009	-
39	Nyaneka-Nkhumbi	Agropastoralist (predominantly cattle raisers) west Savanna Bantu Coelho *et al.* 2009	-
40	Guang-uela	Agropastoralist west Savanna Bantu Coelho *et al.* 2009	-

Sample region	**Decimal latitude**	**Decimal longitude**	**-14010*C freq.**	**Ref.**
Kweneng, southern Botswana	−24,3324	25,6049	0,028	Macholdt *et al.* (2014) (see Breton *et al.* 2014)
Zambia	−14,6633	25,50005	0,031	Macholdt *et al.* (2014)
Northern Nambia	−17,7569	16,63925	0	Macholdt *et al.* (2014)
Eastern Cape and western Cape, South Africa	−33,1477	26,54454	0,128	Torniainen *et al.* (2009)
Western Cape, South Africa	−34,079	19,10157	0,1429	Ranciaro *et al.* (2014)
Thohoyandou, South Africa	−23,1016	30,59716	0	Ranciaro *et al.* (2014)
Namibe, Angola	−14,733	13,24521	0,01	Coelho *et al.* (2009)
Namibe, Angola	−15,1194	12,71634	0,03	Coelho *et al.* (2009)
Namibe, Angola	−15,44	12,92882	0	Coelho *et al.* (2009)

TABLE 6.1 The Frequency of the East African - lactase persistence allele in Southern Africa (*cont.*)

Map code	Ethnic group	Subsistence base, language group, ref.	N of individuals
43	Kwepe	Shepherd/livestock-keeper Khoe-Kwadi (recently replaced by Kuvale) Pinto *et al.* 2016	-
43	Kwepe	Shepherd/livestock-keeper Khoe-Kwadi (recently replaced by Kuvale) Pinto *et al.* 2016	-
44	Kwisi	Hunter-gatherer (recently cattle-keepers) west Savanna Bantu Pinto *et al.* 2016	-
44	Kwisi	Hunter-gatherer (recently cattle-keepers) west Savanna Bantu Pinto *et al.* 2016	-
45	Twa	Hunter-gatherer (recently cattle-keepers) west Savanna Bantu Pinto *et al.* 2016	-
45	Twa	Hunter-gatherer (recently cattle-keepers) west Savanna Bantu Pinto *et al.* 2016	-
46	Tjimba	Hunter-gatherer (cattle-less pastoralists) west Savanna Bantu Pinto *et al.* 2016	-
48	Yao	Agriculturist Kaskazi–speaking Pinto *et al.* 2016	-
49	Nyanja	Agriculturist southeastern Bantu Pinto *et al.* 2016	-

Sample region	Decimal latitude	Decimal longitude	-14010*C freq.	Ref.
Namibe, Angola [1 sample location]	–15,8062	12,1081	0,044	Pinto *et al.* (2016)
Namibe, Angola [2 sample location]	–15,8274	12,45268	0,044	Pinto *et al.* (2016)
Namibe, Angola [1 sample location]	–15,7196	12,45046	0,175	Pinto *et al.* (2016)
Namibe, Angola [2 sample location]	–15,5978	12,73733	0,175	Pinto *et al.* (2016)
Namibe, Angola [1 sample location]	–15,8536	12,12054	0,194	Pinto *et al.* (2016)
Namibe, Angola [2 sample location]	–16,8092	12,50899	0,194	Pinto *et al.* (2016)
Namibe, Angola	–17,1096	12,69041	0,233	Pinto *et al.* (2016)
Northern Mozambique	–12,9998	35,30324	0	Pinto *et al.* (2016) (see Alves *et al.* 2011)
Mozambique	–14,9577	34,16792	0	Pinto *et al.* (2016) (see Alves *et al.* 2011)

TABLE 6.1 The Frequency of the East African - lactase persistence allele in Southern Africa (*cont.*)

Map code	Ethnic group	Subsistence base, language group, ref.	N of individuals
50	Makua	Agriculturist southeastern Bantu Pinto *et al.* 2016	-
51	Tswa	Mixed agriculturist southeastern Bantu Pinto *et al.* 2016	-
52	Shangaan	Mixed agriculturist southeastern Bantu Pinto *et al.* 2016	-
53	Chopi	Agriculturist southeastern Bantu Coelho *et al.* 2009	3
54	Ronga	Agriculturist southeastern Bantu Coelho *et al.* 2009	15
55	Sena	Agriculturist southeastern Bantu Coelho *et al.* 2009	2
56	Ndau	Mixed agriculturist southeastern Bantu Coelho *et al.* 2009	15
57	Chwabo	Agriculturist southeastern Bantu Coelho *et al.* 2009	4
58	Shona	Mixed agriculturist southeastern Bantu Coelho *et al.* 2009	1
59	Swazi	Agropastoralist southeastern Bantu Segal *et al.* 1987	12

Sample region	Decimal latitude	Decimal longitude	-14010*C freq.	Ref.
Mozambique	−15,2267	39,23246	0	Pinto *et al.* (2016) (see Alves *et al.* 2011)
Mozambique	−21,4492	35,00139	0	Pinto *et al.* (2016) (see Alves *et al.* 2011)
Mozambique	−24,8958	32,98332	0,022	Pinto *et al.* (2016) (see Alves *et al.* 2011)
Mozambique	−24,792	34,37146	0	Coehlo *et al.* (2009) (see Alves *et al.* 2011; Pinto *et al.* 2016)
Southern Mozambique	−26,345	32,50994	0	Coehlo *et al.* (2009) (see Alves *et al.* 2011; Pinto *et al.* 2016)
Mozambique	−17,7261	34,95491	0	Coehlo *et al.* (2009) (see Alves *et al.* 2011; Pinto *et al.* 2016)
Mozambique	−19,3029	34,55766	0	Coehlo *et al.* (2009) (see Alves *et al.* 2011; Pinto *et al.* 2016)
Mozambique	−17,1928	36,45974	0	Coehlo *et al.* (2009) (see Alves *et al.*2011; Pinto *et al.* 2016)
Harare, Zimbabwe	−17,9233	30,95064	0	Coelho *et al.* (2009)
Mbabane, Eswatini	−26,3323	31,15249	0	Segal *et al.* (1987) (see Holden and Mace 2009).

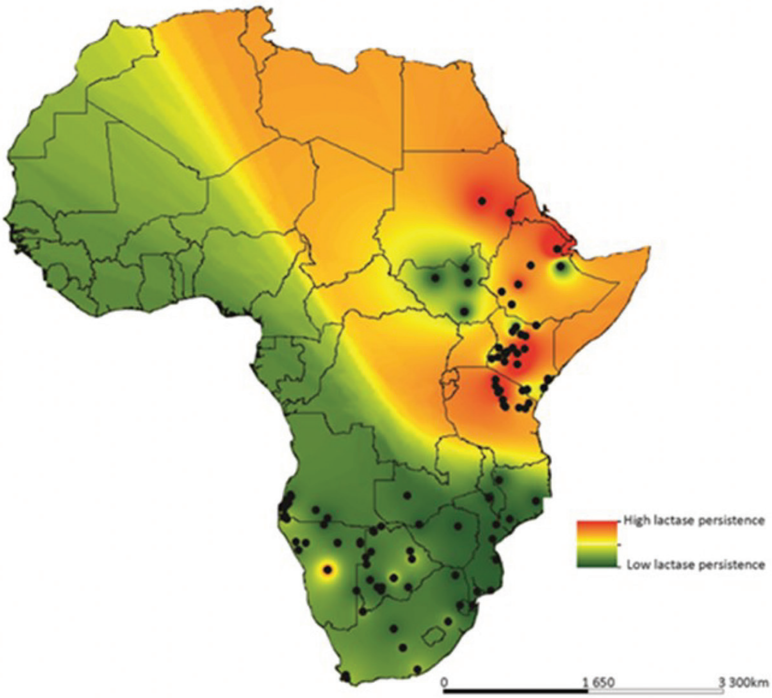

FIGURE 6.2 Map showing the distribution of modern East and Southern African populations screened for the East African LP allele -14010*C

Three patterns in the distribution of the LP allele stand out. These are considered in relation to the archaeological evidence for livestock-keeping.

1. The lactase persistence allele occurs in its highest frequencies amongst livestock-keepers without agriculture or recent livestock-keepers without agriculture, irrespective of the language group.

   People have retained the ability to digest milk in the western, drier half of southern Africa for at least the last 1300 years (Breton et al., 2014). This area is unsuitable for the cultivation of the indigenous summer rainfall crops, sorghum and millet, due to the low rainfall. This confirms Simoons (1970, 695) argument that the "Low incidence of intolerance, it is held, would develop over time in a group that has an abundant milk supply, that has alternate foodstuffs inadequate in amount and quality, and that consumes milk in lactose-rich forms." The contemporary distribution of groups with lactase persistence matches the distribution of Later Stone Age sites with evidence of livestock (Figure 6.5) – confirming the strong

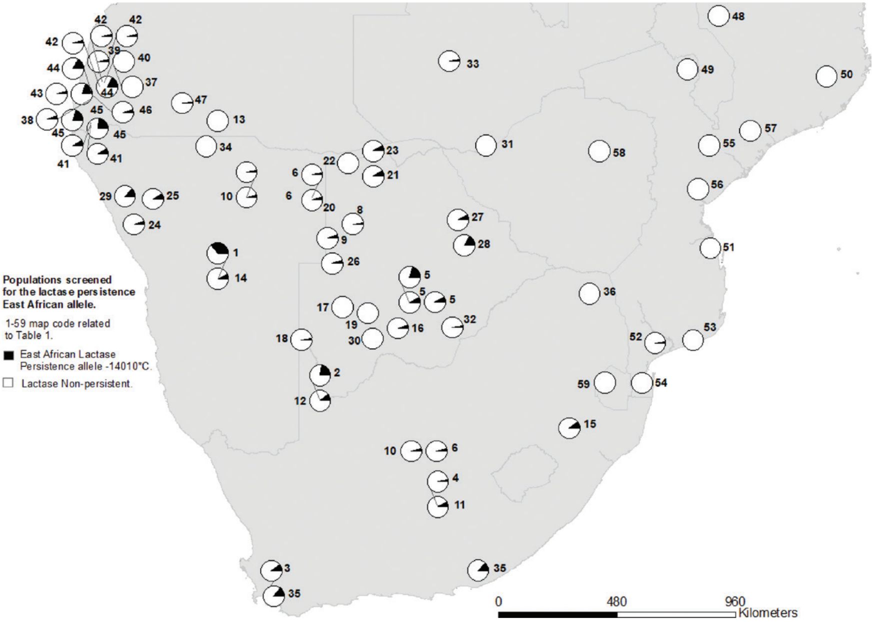

FIGURE 6.3 Map showing the distribution of the East African lactase persistence allele in Southern African

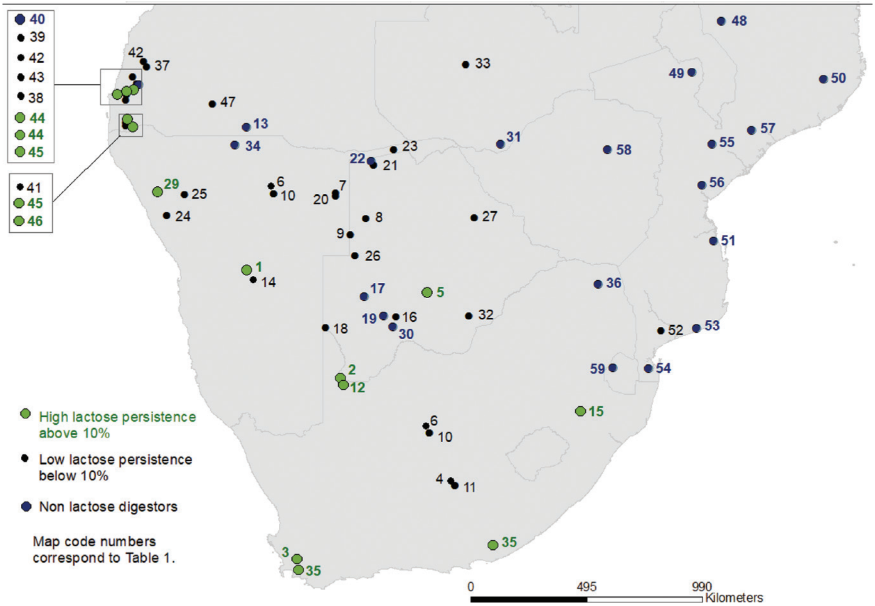

FIGURE 6.4 Map showing Southern African populations with the highest prevalence of LP Allele -14010*C

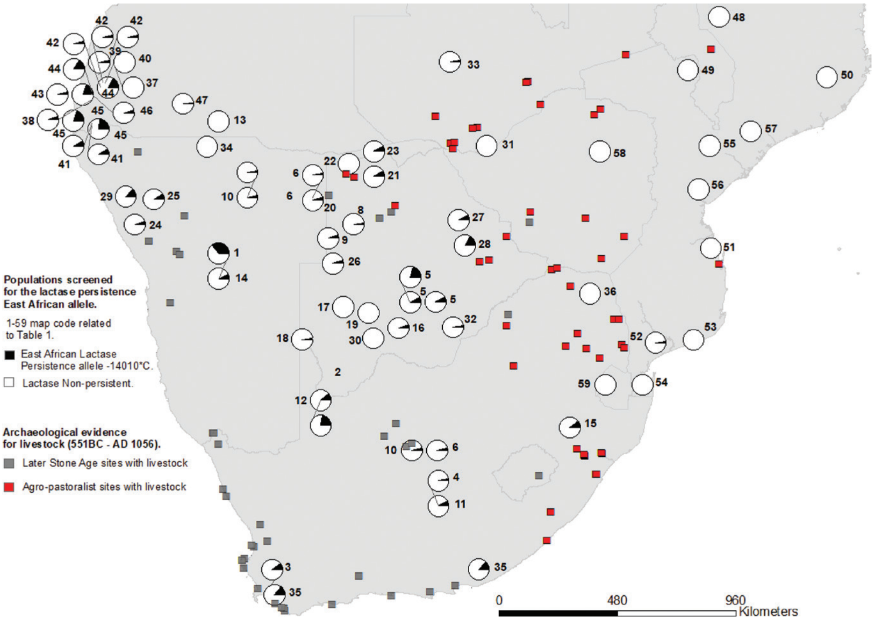

FIGURE 6.5 Archaeological evidence for livestock-keeping with and without agriculture compared to the distribution of the lactase persistence allele

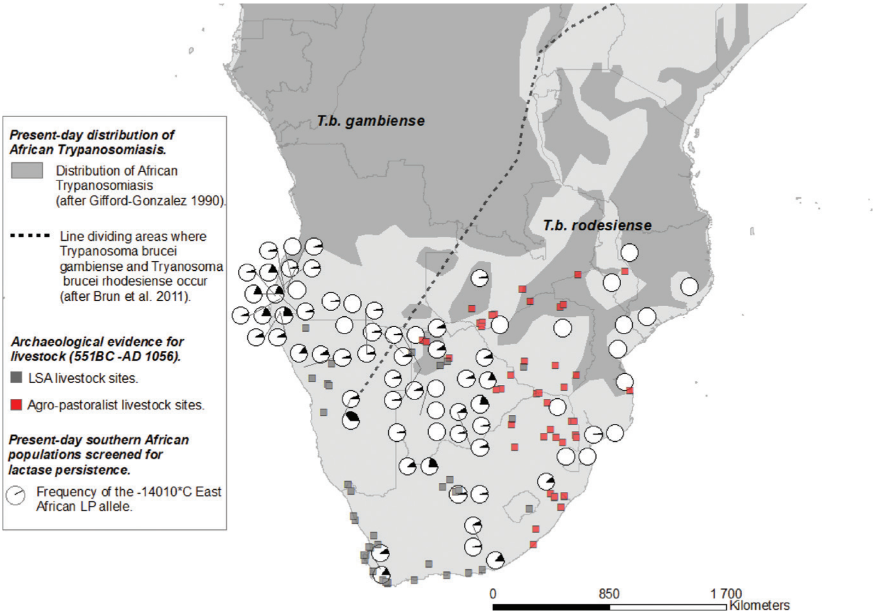

FIGURE 6.6 Archaeological evidence for livestock-keeping at approximately 1000 – 1200 BP and the lactase persistence allele overlaid on the present-day distribution of African trypanosomiasis

association of the ability to digest lactose with pastoralism (Holden and Mace, 1997). The ethnographic and historic record of milk consumption – in its fresh lactose-rich form - amongst the Khoe supports this association (Lombard and Parson, 2015).

Unique to the southernmost part of southern Africa is a winter rainfall zone that stretches from the Cape northwards into Namibia (Figure 6.1). Seasonal movement across its boundaries to the summer rainfall zone would have provided pastoralists with all year round rainfall that would be necessary for specialized milch pastoralism to flourish, mimicking the bimodal rainfall that is seen as central to the rise of pure milch pastoralism in East Africa 3000 years ago (Marshall, 1990; Marchant et al., 2018; Russell, 2020).

2. Southern Africa's Bantu-language speaking groups have a low incidence of the allele as compared to Khoe-speaking groups.

   This low incidence might reflect (1) the absence of a history of livestock-keeping. The trypanosomiasis belt excludes much of tropical Africa as a cattle-keeping area (Simoons, 1974). Where it is endemic in southern Africa we find Bantu-language speaking matrilineal farmers without livestock (Holden and Mace, 2003) (Figure 6.6), or (2) the absence of *fresh* milk consumption rather than the absence of livestock. The cultural practice of drinking sour milk products is well documented amongst southern African Bantu-speaking peoples (Table 6.2). It is hard to find any record of the consumption of fresh milk by southern Bantu-language speakers with the exception of herd boys, who may drink milk directly from cows when out herding, and fresh milk sometimes given to children. Fermented, sour milk products have a reduced lactose content making them more digestible to lactase deficient groups (Holden and Mace, 1997). Segal et al. (1983), in their study of lactase persistence in southern African population groups show that raw milk, fermented in a gourd in the traditional way, contains 2.6% lactose, compared to the 4.7% lactose of full cream fresh milk. Thirdly, (3) those southern African Bantu-language speakers without the LP allele might represent a demic migration from the area of northern Angola, Gabon, and Congo in a southeastward direction towards South Africa, rather than from an origin in East Africa. The archaeological evidence, whilst fairly robust for the connection between East Africa and South Africa (Parkington and Hall, 2012), is unhelpful for tracing connections to western-central Africa. Such evidence for a western stream of demic migration from Angola to South Africa, as suggested by Huffman (2007) on the basis of pottery styles is weak and must be revisited (Parkington and Hall, 2012; Lander

TABLE 6.2 List of ethnographic and historic accounts of the consumption of milk amongst Southern African groups

Group	Country	Sour cows's milk	Fresh cows's milk	Reference
Swazi	*Eswatini*	*Emasi* (mainly drunk by children)	Herdboys in the veld milk directly into their mouths (Jones 1963: 75)	Simatende *et al.* 2015; Kuper 1986: 44; Jones 1963
Xhosa	Eastern Cape, South Africa	Amasi	Milk 'always used sour' (Hunter 1961:105)	Beukes *et al.* 2001; Hunter 1961; Shaw and van Wermelo 1974: 247, 250
Zulu	South Africa	Amasi	Hardly ever drank "green milk"	
Southern Sotho	South Africa	Mafi		Beukes *et al.* 2001
	Botswana	Madila		Ohiokpehai and Jagow 1998
	South Africa	Sethemi		Kebede *et al.* 2007
	Zambia	Mabisi		Jans *et al.* 2017
Nharo	Ghanzi, Botswana		Fresh goats' milk	Guenther 1986
Gwi	Kutse, Botswana		Fresh goats' milk	Ikeya 1993, Sugwara 1991
Gana	Kutse, Botswana		Fresh goats' milk	Ikeya 1993, Sugwara 1991
Hunter-gatherer stock-keepers	Nyae Nyae, Nambia	Sour milk products		Marshall and Ritchie, 1984
Nama	Richtersveld, Northern Cape, South Africa	Soured milk		Schapera 1930

and Russell, 2018). The Kalundu pottery tradition of the western stream, purporting to link pottery found at the coastal midden site of Benfica, in Angola to sites in the eastern half of South Africa, includes very few sites and the basis of the argument is unclear (cf. Huffman, 2007) (Table 6.3).

And lastly, (4) it might reflect interaction and proximity with a milch pastoralist group. The high incidence of the LP allele among the Xhosa, Sotho-Tswana and Zulu agro-pastoralists is suggestive of a long history of interaction between their ancestral groups and Khoe pastoralists. These Bantu-language speaking agro-pastoralists lived close to the historically known territory of Khoe pastoralists along the natural boundary to farmer expansion, the summer rainfall boundary. This boundary is also seen in the archaeological distribution of LSA sites as compared to farmer sites (Figure 6.1) (Parking and Hall, 2012). Genetic and linguistic studies reflect a similar pattern of the long interaction of Khoisan and Bantu-speaking groups (Pakendorf et al., 2017).

3. Non-Khoe-speaking hunter-gatherers have low levels of the allele. This is not unexpected as this is one of the few examples of foragers who resisted and rejected the more labour intensive economies of animal domestication and crop production (Russell and Lander, 2015). More interesting and requiring further investigation is why *Khoe-speaking* hunter-gatherers, in particular, have the LP allele. Examples of hunter-gatherers with the LP allele, in frequencies of up to 20%, are the Khoe-speaking Gui and Gana of the Kutse Game Reserve, in central Botswana (Table 6.1). Although they live by hunting and gathering, their livestock keeping is well-documented (Ikeya, 1993; Osaki, 1984; 1990; Sugawara, 1991; Tanaka, 1969, 1976). Livestock, predominately goats, are never slaughtered but are kept as a social rather than a subsistence strategy, to build alliances and to use in economic exchanges (Russell, 2017). The low levels of livestock at LSA sites might reflect such a livestock-keeping and circulating system. Milking would fit easily within such a system, although little milking was recorded amongst these ethnographically observed hunter-gatherer groups (Ikeya (1993) records 200 ml of milk being collected on a particular day), there is evidence of them following milking practices. For example, young animals are separated from their mothers during the day and dung is applied to their udders to deter feeding. Goat-keeping within a similar system is also mentioned by Guenther (1986), who notes the drinking of fresh goats' milk among the Nharo of Ghanzi, Botswana.

TABLE 6.3 Sites with pottery which fit Huffman's (2007) western stream of demic diffusion among Bantu-language speaking farmers

Site, Country, site type	Radiocarbon date	Calibrated Date	Western stream, kalundu tradition, pottery type	Reference
Benfica, Angola Coastal shell midden	1810±50 Pta-212	AD 212–322	Kalundu	Dos Santos and Ervedosa 1970; Vogel and Marais 1971; Huffman 2005, 2007
Gundu, Zambia Inland open-air	1510±85 GX-1114	AD 480–658	Kamangoza type pottery showing affiliation to Kalundu, Dambwa and Kumadzulo ware and has origins with Naviundu pottery in the Congo.	Huffman 1989, 2007
Wosi, South Africa Inland open-air riverside	1460±50 Pta-4100	AD 592–662	Msuluzi	Van Schalkwyk 1994
Lydenburg Head site, South Africa Inland open-air	1460±50 Pta-328	AD 592–662	Kalundu or Matola	Maggs 1980, Evers *et al.* 1982, Whitelaw 1996
Zambezi Farm, Zambia Inland open-air	1410±130 N-1140	AD 544–856	Pottery similar to Kalundu, Dambwa and Kumadzulo ware.	Vogel 1973
Mhlopeni, South Africa Inland open-air riverside	1400±50 Pta-2878	AD 636–765	Msuluzi	Maggs and Ward 1984

TABLE 6.3 Sites with pottery which fit Huffman's (2007) western stream of demic diffusion among Bantu-language speaking farmers (*cont.*)

Site, Country, site type	**Radiocarbon date**	**Calibrated Date**	**Western stream, kalundu tradition, pottery type**	**Reference**
Divuyu, Botswana Inland open-air	1400±70 Beta-13260	AD 635–766	Divuyu	Turner 1987; Denbow 2011
KwaGandaganda, South Africa Inland open-air riverside	1395±60 Wits-1918	AD 639–765	Msuluzi	Whitelaw 1994 a,b.
Mamba, South Africa Inland open-air riverside	1390±50 Pta-4093	AD 643–765	Msuluzi	Van Schalkwyk 1994
Msuluzi Confluence, South Africa Inland open-air riverside	1370±30 Pta-2193	AD 654–763	Msuluzi	Maggs 1980
Magogo, South Africa Inland open-air riverside	1360±50 Pta-2874	AD 659–765	Msuluzi	Maggs 1984
Magarape, Botswana Inland open-air riverside	1350±80 KN-2641	AD 648–841	Mzonjani type pottery or Kalundu type pottery.	Cambpell *et al.* 1996; Huffman 2009
Mpame, South Africa Coastal open-air	1340±60 Pta-2019	AD 657–830	Msuluzi	Vogel and Fuls 1999
Bisoli, Botswana Inland open-air	1340±60 Wits-1099	AD 657–830	Bisoli	Denbow and Wilmsen 1986; Campbell *et al.* 1996; Huffman 2007

TABLE 6.3 Sites with pottery which fit Huffman's (2007) western stream of demic diffusion among Bantu-language speaking farmers (*cont.*)

Site, Country, site type	**Radiocarbon date**	**Calibrated Date**	**Western stream, kalundu tradition, pottery type**	**Reference**
Nqoma, Botswana Inland open-air	1290±60 Beta-13257	AD 685–860	Divuyu and Xaro	Wilmsen 1989, 2011; Denbow 2011
Ntsitsana, South Africa Inland open-air riverside	1290±50 Pta-4684	AD 685–858	Mzuluzi and Ndondondwane	Prins and Granger 1993
Nanda, South Africa Inland open-air riverside	1275±60 Wits-1917	AD 690–880	Msuluzi	Whitelaw 1993
Kulubele , South Africa Inland open-air riverside	1250±40 Pta-5865	AD 773–881	Mzuluzi pottery and/or Ndondondwane	Binneman *et al.* 1992
Kanono Mulapo, Namibia shell midden site	1230±50 Pta-8656	AD 770–960	Kalomo pottery showing similarities to Kalundu and Gundu	Kinahan 2013; Huffman 1989
Ndondondwane , South Africa Inland open-air riverside	1220±50 Pta-238	AD 774–819	Ndondondwane	Maggs 1984, Van Schalkwyk *et al.* 1997
SK17, South Africa Inland open-air	1210±50 Pta-3507	AD 777–967	Garonga pottery or Kalundu (Ndondondwane/ Lydenburg) pottery	Meyer 1984; Plug 1989; Huffman 2007
Kalundu Mound , Zambia Inland open-air	1160±90 SR-41	AD 780–1020	Kalundu	Fagan 1967

TABLE 6.3 Sites with pottery which fit Huffman's (2007) western stream of demic diffusion among Bantu-language speaking farmers (*cont.*)

Site, Country, site type	Radiocarbon date	Calibrated Date	Western stream, kalundu tradition, pottery type	Reference
Dombashaba, Botswana Inland hilltop	1150±80 I-13746	AD 859–1024	Bisoli	Huffman 2005, 2007
Ntshekane, South Africa Inland open-air riverside	1150±45 Pta-1058	AD 893–989	Ntshekane	Maggs and Michael 1976
Kamangoza, Zambia Inland open-air	1015±105 N-419	AD 987–1185	Kamangoza pottery showing affiliation to Kalundu, Dambwa and Kumadzulo ware.	Vogel 1971
Isamu Pati, Zambia Inland open-air	910±90 SR-31	AD 1046–1265	Kalomo pottery showing similarities to Kalundu and Gundu (Naviundu from Congo (western origin) is an ancestor to Gundu pottery)	Huffman 1989, 2005

4 Conclusions

The archaeological distribution for livestock remains over the last 2100 years shows the predominance of cattle-keeping among farmers in the eastern half of the sub-continent and sparser, yet continuous, caprine-keeping among Later Stone Age livestock-keepers in the low rainfall areas to the west. We might at a first glance expect that lactase persistence might dominate on the eastern side of southern Africa. Genetic research shows that the reverse is true. The east African lactase persistence allele, -14010*C, is overwhelmingly found among pastoralist people in the western parts, irrespective of their language group. To explain this pattern, we turn to the ethnographic and historic record, which show the cultural practice among Bantu-speakers of drinking milk only in its fermented, lactose- reduced form. This is sometimes through its spontaneous fermentation in a gourd, at room temperature over a number of days, or through the addition of certain plants. Ethnography helps to explain why some hunter-gatherers have a high incidence of lactase persistence: they are those who have seen the social value of livestock in exchange networks, with small quantities of milk drinking. They remain overwhelmingly foragers for subsistence.

Archaeological evidence for the large herds of Khoe-owned cattle, observed historically, from the late 16th century onwards in the western and eastern Cape, which drew sailors and then settlers to southern Africa, has not been found. The archaeological picture is incomplete. For example, from 1652 to 1699, careful mercantile records show that 20 000 cattle and 40 000 sheep were traded with the Cape Khoe by the passing ships of the Dutch East India Company (VOC) (Ross, 2012). The contrast with the total 21 cattle and 365 caprine bones found across the entire 2100 year period of the archaeology of the Later Stone Age livestock-keepers, is useful as an example of just how fragmentary the archaeological record can be (Russell and Lander 2015).

There are unresolved differences between and within the genetic and the archaeological findings. For example, the timing of the arrival of the LP allele, -14010*C, is estimated to be at 1300 years BP by geneticists (Breton et al., 2014). This is 800 years later than the earliest archaeological discovery of remains of livestock in this region. On the basis of Y chromosomal evidence, Henn *et al.* (2009) estimate that pastoralism arrived in southern Africa from eastern Africa at around 2000 years ago. How accurate are the genetic clock estimations? Why do they differ? The ethnic identities of modern day southern African populations are complicated and complex: it would be useful to attempt to re-trace the histories of those groups sampled by geneticists.

Yet it is only by boldly confronting and challenging discrepancies between and within different disciplines that a fuller understanding of the complex history of Africa's past will be achieved. And what satisfaction when, as in the recognition of the importance of milch pastoralism in the drier western half of southern Africa for over a millennium by scholars from genetics, ethnography and archaeology, they concur.

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PART 3

Genomic Research of Ancient and Modern Populations in Africa

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CHAPTER 7

Paleogenomics of the Neolithic Transition in North Africa

Rosa Fregel

1 Introduction

The Neolithic revolution, which is the transition from hunting and gathering to farming, started in the Near East around 13,000 BCE. How human populations acquired agricultural and herding technologies has historically been the focus of a heated debate. Two opposing models can be applied to explain the Neolithic transition: the demic diffusion model and the cultural diffusion model. The first one argues that the Neolithic revolution involved the movement of people, in such a way that the arrival of agricultural and herding techniques was the result of the migration of farmers, who would admix with or replace previous hunter-gatherer populations. The other model proposes that the Neolithic transition was the result of the movement of ideas. In this scenario, local hunter-gatherer populations would acquire agricultural and herding technologies from neighbouring populations, without genetic admixture.

Prehistoric research in North Africa has largely focused on the Lower and Middle Paleolithic periods as exemplified by the discovery of the oldest early modern human in Morocco (Richter et al., 2017) and the older stone artifacts and cut-marked bones in Algeria (Sahnouni et al., 2018). On the other hand, how populations transitioned to farming in North Africa has received less attention. Paleolithic North Africa is characterized by the Aterian culture that flourished about 30,000 BCE, and was later replaced by the Upper Paleolithic Iberomaurusian industry (~15,000 BCE). By ~12,000 BCE the Mesolithic Capsian culture appeared in the Maghreb, transitioning to farming communities in the 6th millennia BCE (Naylor 2015).

Based on archaeological data, it is thought that the Neolithic transition occurred simultaneously at both shores of the Western Mediterranean through a coastal diffusion (Zilhao 2001, Linstädter 2008). Two main diffusion waves have been evidenced in the Mediterranean basin: *i*) a first one defined by the spread of a specific lithic industry characterized by pressure and indirect percussion reduction *ii*) a later one related to the spread of Cardial pottery and domesticated plants and animals (Mulazzani et al., 2016). However, some evidence points to the Neolithic revolution in North Africa as an *in situ* development from Iberomaurusian communities. For example, the Hattab II cave in Morocco produced a Late Paleolithic Iberomaurusian human burial dated 6,900 years BCE. This find questions the complete replacement of local hunter-gatherer communities in the Maghreb and evidences certain continuity in burial practices through the early Neolithic period (Barton et al., 2008). Also, elements usually associated with Neolithic economies, such as pottery fragments and an adze, have been found at two hunter-gatherer contexts dated 6,000 BCE in Tunisia (Mulazzani et al., 2016). These results point to a complex Neolithic transition scenario with both demic and cultural diffusion. Upon those layers, successive prehistoric and historical migrations reached North Africa. It is known that Bell-Beaker pottery, associated with the expansion of Bronze Age populations in Eurasia, is present in the North African region (Bokbot and Ben-Ncer 2008). In historical times, North Africa was settled by different populations including Romans, Phoenicians, Vandals, Byzantines and Arabs (Naylor 2015), leading to the complex genetic structure observed today.

2 What We Knew before Paleogenomics: Modern DNA Evidence on the Neolithic Transition in North Africa

Well before the emergence of the paleogenomics field, the analysis of classical markers on modern populations (e.g. blood groups, red cell enzymes and human leukocyte antigens (HLA)) produced the first genetic evidence of the impact of the Neolithic transition in human populations (Sokal, Oden, and Wilson 1991, Ammermann and Cavalli Sforza 1984, Cavalli-Sforza, Menozzi, and Piazza 1994). A major southeast to northwest cline was observed in Europe, coinciding with the advance of Neolithic farmers from the Fertile Crescent and supporting the demic diffusion model. As archaeological evidence indicates that North Africa and Western Mediterranean Europe mirrored each other during Neolithic times, it would be reasonable to expect a similar scenario in both regions. When analyzing classical markers data in North Africa, Bosch et al. (1997) observed a clear east-west pattern of variation, separating Berber and Arab populations in the Maghreb from the northeastern populations of Libya and Egypt. However, instead of the smooth cline found in Europe, the separation between East and West was rather abrupt. The authors concluded that, although a demic diffusion model for the Neolithic transition was possible for explaining differences between eastern and western North Africa, the presence of an older component was needed to account for the high level of differentiation of northwestern populations.

Additional evidence on the Neolithic transition in North Africa was obtained with the use of the two haploid, uniparental markers: the mitochondrial DNA (mtDNA) and the non-recombinant portion of the Y-chromosome. Many human population studies have been focused on these highly informative genetic markers, whose direct inheritance and absence of recombination allow the reconstruction of female and male genealogies. During the 90s and the 2000s, an increasing amount of mitochondrial DNA and Y-chromosome data was gathered from modern human populations worldwide and exhaustive phylogeographic analyses were performed both at global and regional levels. This allowed the building of more detailed phylogenetic trees for both genetic markers and led to a deeper knowledge of the times and routes of expansion of major maternal and paternal lineages around the globe. For example, Richards et al. (1996) reported that most of the mitochondrial DNA diversity in Europe had a Paleolithic origin. Contrary to conclusions drawn from classical markers, the European Neolithic transition from the mitochondrial DNA perspective was outlined as a cultural diffusion rather than the result of the migration of people. Accordingly, only a small set of modern European linages was considered to have arrived from the Near East in Neolithic times, represented mainly by haplogroups J, K and T. Regarding North Africa's mitochondrial DNA composition, the most striking feature was the presence of two African-specific sub-lineages related to a back migration to Africa from Eurasia in Paleolithic times (Maca-Meyer et al., 2003, Olivieri et al., 2006, Gonzalez et al., 2007, Pereira et al., 2010): haplogroups U6 and M1. Both lineages are relatively frequent in modern-day North Africans indicating maternal continuity in the region since the Paleolithic (Secher et al., 2014, Pennarun et al., 2012). However, the presence in North Africa of mitochondrial DNA haplogroups linked to Neolithic expansions in Eurasia supported the existence of a farmer's migration into the area from the Middle East (Macaulay et al., 1999, Rando et al., 1998). Regarding the Y chromosome, current North Africans are characterized by the high frequency of haplogroup E-M81, a lineage considered to be autochthonous of this region. Interestingly, the frequency of E-M81 follows an east to west cline, with the highest frequencies in Morocco and the lowest in Egypt, similar to the results obtained for classical markers. Based on that evidence and contrary to the conclusions drawn from mitochondrial DNA, Arredi et al. (2004) proposed that North African paternal diversity was compatible with a demic expansion from the Middle East. Because the age of E-M81 and other common lineages in North Africa (E-M78 and J-304) were relatively recent, they proposed that the North African pattern of Y-chromosome variation was mostly of Neolithic origin.

With the contradictory evidence gathered from classical markers and the Y chromosome on one side and mitochondrial DNA on the other side, the advent of genome-wide technologies has been fundamental for obtaining a more nuanced picture of the complex genetic history of North Africa (Henn et al., 2012, Arauna et al., 2017, Fadhlaoui-Zid et al., 2013). Based on both genome-wide SNP data and whole-genome sequencing, it has been suggested that North Africans' ancestry can be explained as the result of four migration events. First, present-day ancestry in North Africans is characterized by an autochthonous Maghrebi component related to a Paleolithic back migration to Africa from Eurasia. Second, there is a recent admixture event with a Middle Eastern component, which can be the result of the Arab expansion in North Africa in the seventh century. Third, historical trans-Saharan migrations produced gene flow from sub-Saharan Africa. Finally, North Africans carry a European component that can be linked to historic movements, such as the Roman occupation.

Although useful to get a glimpse of the genetic history of a certain population, studies based on modern DNA variation are usually not suited for disentangling complex migration patterns. As several layers of migration have affected North Africa at different periods, recent human movements can erase or distort more ancient admixture signals. In these cases, obtaining ancient DNA from archaeological remains is more appropriate because it allows us to directly examining how the population changed through time. Because the two competing models proposed to explain the acquisition of farming technologies are based on either the existence or the absence of genetic admixture, ancient DNA analysis is a powerful tool to study the Neolithic transition. The reasoning behind this approach is quite simple: if the genetic composition of human remains from hunter-gatherers and farmers is similar, then the Neolithic transition happened through the movement of ideas rather than genes; on the other hand, if hunter-gatherers and early farmers are genetically different, then the spread of farming required the movement of people.

3 The Ancient DNA and Paleogenomics Revolutions

In 1986, the development of the polymerase chain reaction (PCR) technique allowed for the first time the amplification and analysis of trace amounts of DNA (Mullis et al., 1986). This methodology was immediately applied to obtaining DNA from archaeological and paleontological materials (Paabo, Gifford, and Wilson 1988) initiating the ancient DNA revolution. Between the late 80s and the early 2000s, researchers retrieved DNA from all sorts of ancient materials and provided valuable information from the past of several species, including our own (Paabo et al., 2004). However, classic ancient DNA methodologies based on PCR amplification have important limitations. DNA extracted from archaeological remains is usually in very low concentration and highly degraded. For that reason, the vast majority of ancient DNA analyses had to be limited to specific regions such as the mitochondrial DNA. Each cell contains only one nucleus with one copy of the nuclear diploid genome. On the other hand, every cell has multiple mitochondria, with each one containing several copies of its mitochondrial DNA. For that reason, mitochondrial DNA is more abundant in ancient DNA extractions, and it is better suited to paleogenetic analyses based on PCR amplification. The limitation of using mitochondrial DNA is that this genetic material is maternally inherited and only carries information from the maternal side, thus it does not inform on the global ancestry of a population. Additionally, uniparental markers such as the mitochondrial DNA are more prone to suffer from the effects of genetic drift and the loss of genetic variants due to stochastic processes, complicating the interpretation of the genetic data. But maybe the biggest limitation of the classical techniques is the risk of contamination with modern DNA.

PCR was a revolution for ancient DNA studies because it can obtain amplified DNA from just a few molecules. But that same advantageous characteristic of PCR also represents its Achilles' heel: because PCR is extremely sensitive, any trace of modern DNA contamination can be potentially amplified, especially in highly degraded samples. The contamination problem is more dangerous when analyzing ancient human remains, as the sole manipulation of the samples by researchers is a potential source of modern DNA from the same species. To avoid and monitor contamination, several criteria were established to assure the authenticity of the ancient DNA results (Cooper and Poinar 2000). However, paleogenetic studies based on PCR have always been hindered by the risk of sample contamination, especially those involving extremely ancient human remains (Paabo et al., 2004).

As it occurred with the development of the PCR in the 80s, the implementation of next-generation sequencing techniques produced a huge revolution in the ancient DNA field. Instead of being limited to just one locus, this new methodology allows the recovery of complete genomes from archaeological materials. By providing information at the genomic level, ancient DNA analyses using next-generation sequencing are more appropriate to elucidate the demographic structure and history of ancient populations. Moreover, next-generation sequencing techniques overcome the problem of ancient DNA data authentication, solving the contamination conundrum. Due to post-mortem damage, two features characterize DNA recovered from ancient samples: high fragmentation and chemical modification of the molecule's ends. Next-generation sequencing allows the identification of both damage patterns that are unique to old DNA and provides empirical verification of the authenticity of the results. The paleogenomics field has proved its value by illuminating the Prehistory of Eurasia (Haak et al., 2015, Lazaridis et al., 2016, Allentoft et al., 2015, Mathieson et al., 2015, Olalde et al., 2018, Mathieson et al., 2018, Olalde et al., 2019). For example, ancient DNA studies have provided a clear picture of the Neolithic transition in West Europe, establishing that early European farmers migrated from Anatolian and replaced previous hunter-gatherer populations with little genetic admixture. However, although this is the general picture, some West European Neolithic individuals exhibit considerable amounts of hunter-gatherer ancestry demonstrating the admixture of farmers with local populations. This evidence suggests a diverse genetic impact of the Neolithic transition in different regions of Europe, contradicting the more simplistic total acculturation or total replacement models.

4 Ancient Genomes from North Africa and What They Tell Us about the Neolithic Transition

The amount of detailed ancient DNA information obtained from Europe is not comparable to any other region worldwide, especially in the case of the African continent. One of the problems for developing ancient DNA studies in North Africa is the availability of well-conserved samples. Next-generation sequencing methodologies by themselves can obtain whole-genome information from ancient samples but only for archaeological remains with enough human endogenous DNA content. Human remains from warm areas such as North Africa usually contain low quantities of endogenous genetic material. As a consequence of their greater level of degradation, there is also a higher relative content of bacterial and fungal DNA from the soil. This limitation has hindered ancient DNA studies in the African continent, but recently it has been overcome with the development of enrichment techniques. For those samples with low human endogenous DNA, there are two methodologies available. One is directed to capture the whole human genome by using genomic DNA or RNA as baits (see Carpenter et al. (2013)). The other approach is directed at enriching ancient samples in DNA molecules covering sites that are known to be variable in human populations (see Lazaridis et al. (2016) or Fregel et al. (2018)). Both methodologies have been applied to the study of ancient populations in North Africa, producing valuable evidence on the Neolithic transition in the Maghreb.

4.1 *Taforalt (Morocco): A Eurasian Origin for North African Upper Paleolithic Populations*

The site of Taforalt, also known as Grotte des Pigeons, is located in eastern Morocco (Figure 7.1), in the Beni-Snassen Mountains. Taforalt's stratigraphic sequence evidences human occupation ranging from the Aterian to the Iberomaurusian period. The Iberomaurusian sequence contained the human remains of fourteen individuals, including eight adults and six children. Human remains were radiocarbon dated, yielding age estimates between 13,000 and 11,900 years BCE. Nine individuals were analyzed using paleogenomics techniques by van de Loosdrecht et al. (2018), but only seven produced enough endogenous DNA. Because human DNA content was low, the authors used two enrichment techniques: one directed to variants present in the Human Origins panel (Lazaridis et al., 2014) and the other aimed to capture the complete mitochondrial DNA sequence.

Mitochondrial DNA sequences from Taforalt individuals were all classified within the two autochthonous North African lineages associated with the back migration to Africa in Paleolithic times: haplogroups U6 and M1 (van de Loosdrecht et al., 2018). Phylogenetic analyses of the sequences indicated that the six individuals belong to different sub-lineages of haplogroup U6a, while the remaining one was classified as M1b (Fregel et al., 2018) (Figure 7.2). Congruently, all these lineages are believed to have originated in the Maghreb around the Upper Paleolithic period (Secher et al., 2014). The presence of U6a and M1b lineages in both Iberomaurusian and present-day populations confirmed temporal continuity in the Maghreb from Paleolithic times to the present, coinciding with results obtained using classical markers (Bosch et al., 1997) and genome-wide data (Henn et al., 2012). Interestingly, the mitochondrial DNA of

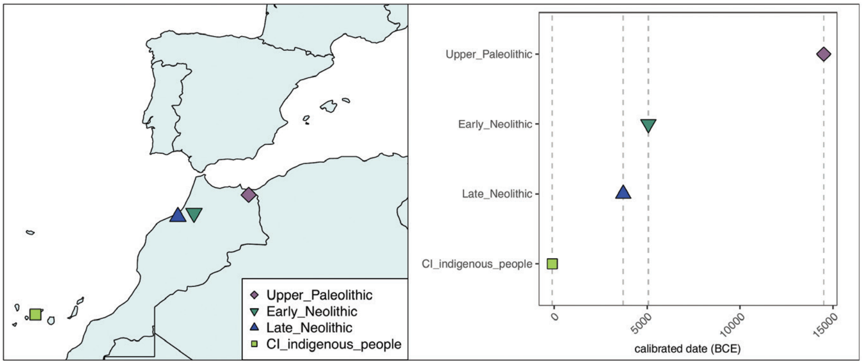

FIGURE 7.1 Locations (left panel) and radiocarbon dates (right panel) of the North African archaeological sites analyzed using paleogenomics techniques

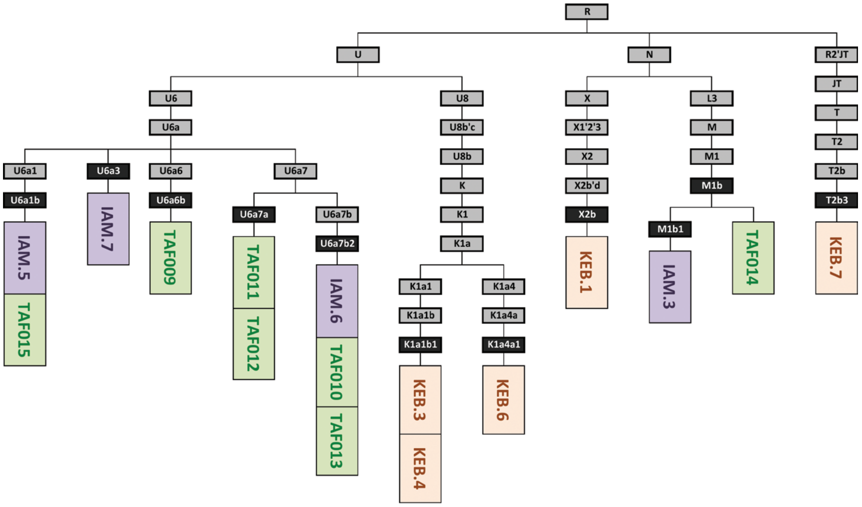

FIGURE 7.2 Mitochondrial DNA phylogenetic tree including ancient samples from North Africa. In this phylogenetic tree, modified from Fregel et al. (2018), it is shown the different mitochondrial DNA composition of Early and Late Neolithic populations from North Africa. Upper Paleolithic (green) and Early Neolithic (violet) samples from North Africa belong to the North African autochthonous haplogroups U6 and M1. On the other hand, Moroccan Early Neolithic samples (orange) belong to haplogroups K1, T2 and X2, which are common in Anatolian and European Neolithic populations

additional Iberomaurusian remains from the Taforalt region had been previously studied using classical ancient DNA techniques (Kefi et al., 2005, Kefi et al., 2018). Some samples were assigned to the North African U6 mtDNA-haplogroup, but most of them were classified within Eurasian lineages such as H, U and R0. Authenticating these results is challenging due to the high contamination risk associated with the PCR amplification of extremely degraded human samples. Future reanalysis of these individuals using paleogenomics techniques would be needed to confirm the presence of lineages different from U6 and M1 in Upper Paleolithic North Africa.

The obtaining of nuclear DNA from the seven Taforalt samples allowed the authors to identify their molecular sex. Six individuals were classified as males and one as a female, offering an excellent opportunity for understanding the Y-chromosome composition of Upper Paleolithic communities in the Maghreb. All male samples from Taforalt were classified within haplogroup E-M35 (van de Loosdrecht et al., 2018), a clade that is characterized by a broad geographic distribution, from northern and eastern Africa to Europe and western Asia (Trombetta et al., 2015). More concretely, Taforalt samples belong to haplogroup E-M78, a lineage that is also widely distributed. E-M78 most probably originated in northeastern Africa (Cruciani et al., 2007, Trombetta et al., 2015, Sole-Morata et al., 2017) and dispersed from there approximately 20,300 - 14,800 years ago. As E-M78 is still frequent in North Africa (Arredi et al., 2004), this result also indicates a temporal continuity between Upper Paleolithic and current populations in the Maghreb.

Lazaridis et al. (2016) observed that Eurasian populations could be explained as a mixture of four sources of ancestry: Iranian Neolithic, Levantine Neolithic, East European Paleolithic and West European Paleolithic. When Taforalt people were compared to previously published ancient and modern DNA data, Upper Paleolithic North Africans can be modeled as a mixture of Natufians (Epipaleolithic populations from the Levant) and West Africans, without the contribution of Paleolithic Europe (van de Loosdrecht et al., 2018). This result suggests that Iberomaurusian populations in North Africa were related to Paleolithic people in the Levant, but also that migrations of sub-Saharan African origin reached the Maghreb during the Pleistocene. However, a preprint from Lazaridis et al. (2018) has contested this conclusion based on new evidence from Paleolithic samples from the Dzudzuana site in Georgia (25,000 years BCE). When these samples are considered in the analysis, Taforalt can be better modeled as a mixture of a Dzudzuana component and a sub-Saharan African component. They also argue that it is the Taforalt people who contributed to the genetic composition of Natufians and not the other way around. More evidence will be needed to determine the specific origin of the North African Upper Paleolithic populations, but the presence of an ancestral U6 lineage in the Dzudzuana people is consistent with this population being related to the back migration to Africa.

4.2 *Ifri n'Amr o'Moussa (Morocco): Cultural Diffusion or in situ Development Explains the Early Phase of the Neolithic Transition in North Africa*

The Ifri n'Amr ou Moussa (IAM) site is located in central Morocco, on the banks of the river Beht. This cave has produced a wide stratigraphic sequence ranging from the Iberomaurusian to the Chalcolithic period (Martínez-Sánchez et al., 2017, Ben-Ncer et al., 2011, 2015, Laviano 2015). Human remains have been recovered from a sequence with archaeological evidence belonging to the Early Neolithic period, including the presence of cereal grains, Cardial pottery and possible domestic fauna (Martínez-Sánchez et al., 2017). In total, seven different individuals were excavated in anatomical connection. Direct radiocarbon dating of the human remains yielded dates pointing to the late 6th and early 5th millennia BCE (Figure 7.1). This result coincides with the date obtained from a barley grain from the same stratigraphic level (Martínez-Sánchez et al., 2017). All individuals were sampled for obtaining ancient DNA by Fregel et al. (2018). Because of the low endogenous DNA content, Ifri n'Amr o'Moussa samples had to be subjected to enrichment methodologies directed both at the whole genome and to specific variants. Despite the application of capture methodologies, only five Ifri n'Amr o'Moussa samples produced enough DNA. Nuclear DNA analyses revealed that IAM.4 and IAM.5 shared a high proportion of relatedness and IAM.4 had to be excluded from analysis (Fregel et al., 2018).[1]

Mitochondrial DNA analysis indicated that Early Neolithic samples in North Africa belong to the same haplogroups observed in Taforalt: individual 3 is classified within haplogroup M1b, while the remaining belong to U6a. In fact, Ifri n'Amr o'Moussa samples are classified within some of the same haplogroup sub-lineages present in Taforalt (Figure 7.2), which proves temporal continuity in North Africa from 13,000 to 5,000 years BCE. This first result is of great importance for addressing the Neolithic question in North Africa as it evidences that the first stages of this transition occurred through the movement of ideas rather than people.

From the four Ifri n'Amr o'Moussa samples that yielded DNA, two were classified as males but only one produced enough DNA to perform Y-chromosome phylogenetic analysis. This sample belongs to the E-M35 haplogroup, the same clade found in the Taforalt individuals. However, in this case, the sample clusters with the E-L19 clade, a lineage that is ancestral to the autochthonous North African E-M81 haplogroup. This result is expected because E-M81 is younger than Ifri n'Amr o'Moussa samples (2,000–3,000 years ago) (Fadhlaoui-Zid et al., 2015, Sole-Morata et al., 2017). As explained before, E-M81 is the most frequent Y-chromosome lineage within North Africa, with its frequency varying in a latitudinal fashion, with the highest frequencies in Morocco and the lowest in Egypt (Arredi et al., 2004). The observation of an ancestor of E-M81 in an Early Neolithic site in Morocco reinforces the idea of temporal continuity in the area from prehistoric to current times.

When analyzing genome-wide data, Fregel et al. (2018) reported that Early Neolithic samples from Morocco are similar to those from the Upper Paleolithic period in Taforalt (Figure 7.3). When compared using genetic ancestry inference, Early Neolithic and Upper Paleolithic samples from North Africa share the same ancestral components. In fact, both Taforalt and Ifri n'Amr o'Moussa share a component that is still retained in modern populations. This

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[1] Later data analyses have proved that both samples belonged to the same individual.

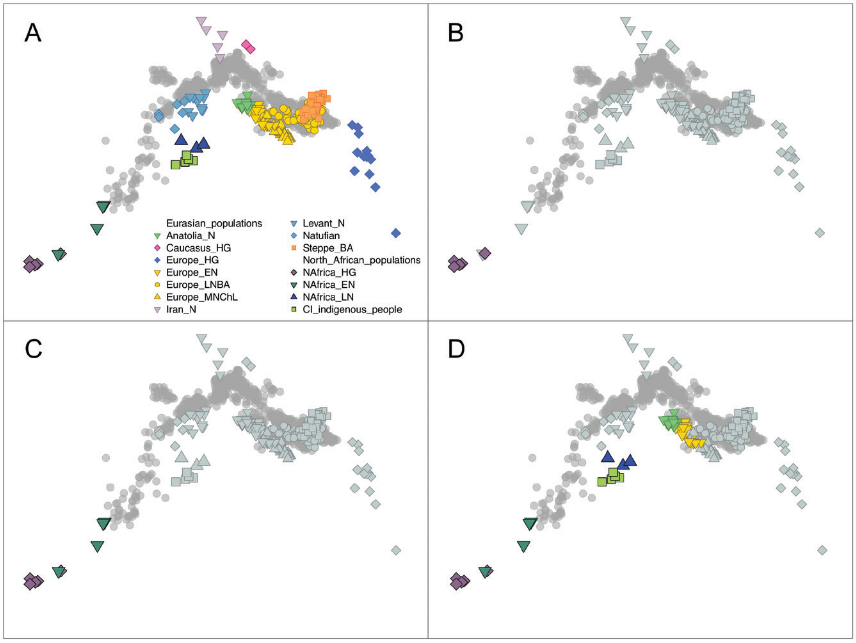

FIGURE 7.3 Ancestry inference of ancient North African samples using principal component analysis (PCA). PCA is a statistical tool that can be used for exploring the relationship between individuals of different populations based on genome-wide data. (A) PCA including North African and other previously published ancient samples projected onto modern Eurasian populations (grey circles). (B) Upper Paleolithic samples from Taforalt (violet diamonds) are clustered close to North African populations. (C) Early Neolithic samples from Ifri n'Amr o'Moussa (dark green inverted triangles) are positioned close to Taforalt samples (violet diamonds), indicating temporal continuity during the early phases of Neolithic transition. (D) Late Neolithic samples from Kef el Baroud (blue triangles) are clustered between ancient samples from North Africa (violet diamonds and dark green inverted triangles) and early farmers from Anatolia and Europe (light green and yellow inverted triangles), and close to samples from the indigenous population of the Canary Islands (light green squares)

is the same ancestral Maghrebi component reported by Henn et al. (2012) that follows an east to west cline in the North African region. Genetic distances also indicate that Early Neolithic from Ifri n'Amr o'Moussa and Upper Paleolithic samples from Taforalt are close between them and far from the rest, suggesting long-term isolation of North African between 13,000 - 5,000 years BCE. The similitude between Taforalt and Ifri n'Amr o'Moussa implies that early farming and herding acquisition in North Africa did not involve the migration of people and can be better explained either by the transmission of ideas or an *in situ* development of local populations.

5 Kef el Baround (Morocco): Late Neolithic in North Africa is Explained by a Demic Diffusion Model

The Kehf el Baroud (KEB) cave is located in central-western Morocco, close to the city of Casablanca (Figure 7.1). The stratigraphic sequence at Kef el Baround shows human occupation ranging from the Epipaleolithic to the Bronze Age (Banerjee et al., 2011). Human remains were excavated in the Neolithic phase, which is characterized by undecorated ceramic fragments, flint tools and domestic fauna. Direct radiocarbon dating from the human material (Fregel et al., 2018) indicates the samples belonged to the Middle-Late Neolithic at the beginning of the 4th millennium BCE (Figure 7.1). Eight different teeth and phalanx samples were taken from Kef el Baround to perform ancient DNA analyses (Fregel et al., 2018). Because the human remains were not in anatomical connection, it was possible that different samples could belong to the same individual. In fact, samples KEB.1 and KEB.8 were identified as being duplicates of the same individual. Due to low endogenous DNA content, samples were also captured using the same methodologies as in the Early Neolithic remains.

From the eight samples analyzed, only five produced complete mitochondrial DNA genomes. In sharp contrast to lineages observed in North African Upper Paleolithic and Early Neolithic samples, the mitochondrial DNA sequences obtained in Kef el Baround belonged to typically Anatolian and European Neolithic haplogroups (Fregel et al., 2018). The five Kef el Baround samples were classified within K1a1b1, K1a4a1, T2b3 and X2b (Figure 7.2). These haplogroups have been observed in Early and Middle Neolithic sites in the Near East and Europe. For example, an X2b sample was found in the Early Neolithic site of Garadna in Hungary (Gamba et al., 2014) and a K1a1b1 individual in the Middle Neolithic site of La Mina in Spain (Mathieson et al., 2015). The presence of these mitochondrial DNA lineages in Kef el Baround suggests the migration of Near Eastern or European early farmers in North Africa ~3,000 years BCE and rules out the exclusive introduction of European ancestry from the Mediterranean during historical times.

Lineages associated with the Neolithic transition in the Near East and Europe have also been observed for the indigenous people of the Canary Islands (Maca-Meyer et al., 2004, Fregel et al., 2019), a population that can be considered an ancient North African isolate. The Canarian archipelago is located off the coast of Morocco (Figure 7.1) and its indigenous population is considered to be of North African origin based on multidisciplinary evidence. Radiocarbon dating indicates that the indigenous colonization of the islands happened around 100 years CE (Fregel et al., 2019). The conquest and colonization of the islands by the Spanish Crown in the 15th century led to the complete admixture of the natives with the European population. However, ancient DNA analyses have allowed reconstructing the genetic composition of the Canarian indigenous people (Fregel et al., 2009, Maca-Meyer et al., 2004, Rodriguez-Varela et al., 2017). In line with the results observed in Kef el Baround, most of the lineages observed in the ancient population of the Canary Islands are related to Neolithic expansion in the Mediterranean (e.g. T2c1d, J1c3 or J2a2d) and attest the impact of this migration in North Africa (Fregel et al., 2019).

Three Late Neolithic samples from Morocco produced nuclear DNA and two were classified as males, with only one generating enough DNA to be assigned to a Y-chromosome haplogroup. Sample KEB.6 was classified within haplogroup T-M70, a result that is in agreement with the results observed for the mitochondrial DNA (Fregel et al., 2018). The presence of haplogroup T-M70 in Kef el Baround indicates a tight relationship of Late Neolithic North Africa with Near Eastern and European Neolithic populations. Haplogroup T-M70 has been found in Neolithic samples from Germany (Haak et al., 2015) and from Jordan (Lazaridis et al., 2016). In agreement again with the mitochondrial DNA, haplogroup T-M70 has also been observed in the indigenous population of the Canary Islands (Fregel et al., 2009). Interestingly, present-day haplogroup T-M70 frequencies in North Africa are higher in Egypt than in Morocco (Bekada et al., 2013), following an opposite distribution than E-M81 (Arredi et al., 2004). Although it is an exceedingly simplistic model that ignores later migrations, this result could be explained by a larger Paleolithic persistence in the western region and a larger Neolithic impact in eastern North Africa.

Uniparental markers show that Late Neolithic populations in North Africa had a genetic composition consistent with a demic diffusion from Europe or the Near East. This result was corroborated at a genome-wide level when Kef el Baround samples were found to be composed of both the same ancestral Maghrebi component observed in Ifri n'Amr o'Moussa and Taforalt, and an early Anatolian/European farmer's component (Figure 7.3). This is consistent with Late Neolithic Moroccans being a mixture of the local population and farmers coming from Europe or the Near East. Genetic distance estimates point to Kef el Baround people being closer to Early Neolithic populations in Iberia. In fact, Kef el Baround people can be modeled as a simple mixture of an Ifri n'Amr o'Moussa and an Early Iberian component. The existence of migrations through the Strait of Gibraltar has been already proposed based on archaeological evidence. Also, Olalde et al. (2019) have analyzed two Iberian sites from the Cooper and the Bronze Age periods that show evidence of admixture with a component of North African origin, pointing to the existence of prehistoric exchanges between both sides of the strait.

A similar result is observed for the indigenous population of the Canary Islands (Fregel et al., 2018, Rodriguez-Varela et al., 2017). This North African isolate is similar to Kef el Baround samples (Figure 7.3), but with additional evidence of Middle Neolithic/Chalcolithic Europe and sub-Saharan African gene flow. These two components could be the result of later migrations in North Africa, probably related to the Bell-Beaker expansion in the Mediterranean and trans-Saharan migrations. Also, the proportion of the Maghrebi component present in the indigenous population of the Canary Islands is higher than that observed in Late Neolithic Moroccans. This result is interesting as it indicates that the impact of the migration of early farmers from Europe in North Africa could have been heterogeneous, with some areas retaining a higher Paleolithic component.

6 Conclusions

Ancient DNA obtained directly from hunter-gatherer and early farmer human remains from Morocco has provided the first paleogenomic evidence on the Neolithic transition in North Africa (Fregel et al., 2018, van de Loosdrecht et al., 2018). The picture drew from these studies points to a complex scenario where both cultural and demic diffusion led to the acquisition of farming and herding technologies. Upper Paleolithic and Early Neolithic populations in North Africa share the same genetic makeup, related to a back migration from Eurasia in Paleolithic times. This component is characterized by African autochthonous lineages U6 and M1 from the mitochondrial DNA and sublineages of E-M35 from the Y-chromosome. From a genome-wide perspective, Moroccan Upper Paleolithic and Early Neolithic populations are characterized by an autochthonous Maghrebi component still retained in present-day North Africans, following an east-to-west cline. Altogether, these results evidence that the early steps of farming and herding acquisition in North Africa happened through an *in situ* development process or mediated by the acculturation of local hunter-gatherer populations.

Late Neolithic individuals from Morocco are characterized by a mixture of both the autochthonous Maghrebi component and gene flow from early farmers in Europe. Mitochondrial DNA and Y-chromosome lineages in North African Late Neolithic are different from those in previous periods and have a clear affiliation to early farmers in the Near East and Europe. Genome-wide data indicate that Late Neolithic communities in Morocco had a Neolithic European component, most probably related to the migration of early farmers from

Iberia. Genetic evidence from the indigenous people of the Canary Islands suggests that the impact of the European Neolithic gene flow could have been heterogeneous and that additional European ancestry could have reached North Africa between the 4th millennium BCE and the 1st century CE, probably related to the expansion of the Bell-Beaker culture in the Mediterranean.

Compared to ancient DNA evidence in Europe, our understanding of the genetic composition of prehistoric populations of North Africa is just a crude draft. Our present knowledge is only based on two specific archaeological sites from Morocco that are not representative of the whole North African region. Additional paleogenomics evidence from different archaeological sites from both western and eastern North Africa will be needed to comprehend the nuances of Neolithic transition on this region and the human movements that shaped Berber populations.

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CHAPTER 8

Ancient DNA Studies and African Population History

Mário Vicente and Carina Schlebusch

1 Introduction

In the last three decades, genetics played an increasingly important role in the inference of human history. Genetic studies provided conclusive information that helped to answer challenging questions, such as the "Out of Africa" migration of modern humans. Moreover, genetics helped to establish Africa as the birthplace of anatomically modern humans. The history of human populations in Africa is complex and includes various demographic events that influenced patterns of genetic variation across the continent. Several studies based on mitochondrial DNA, Y-chromosomes, autosomal markers, whole genomes and ancient DNA, contributed to unraveling the genetic sub-structure of African populations. Through these genetic studies of modern-day, and most recently, ancient African genetic variation, it became evident the deepest population split among modern humans was between southern African Khoe-San populations and other African groups, while the central African rainforest hunter-gatherer groups diverged subsequently from the common human lineage. Furthermore, it was shown that agriculture had a large influence on the distribution of current-day Africans and that West African agriculturist populations populated the whole of sub-Saharan Africa, replacing and/or assimilating former groups. Other farming groups from Northeast Africa, speaking Nilo-Saharan and Afro-Asiatic languages, admixed with Eurasian groups and also expanded southwards. They settled in East Africa and migrated as far as southern Africa where they admixed with San hunter-gatherer ancestors to form the Khoekhoe herding groups. These later population movements disrupted pre-existing population distributions and complicate inferences regarding deep human history. With the increased availability of full genomic data from diverse modern-day African populations and prehistoric Africans, we will have more power to infer human demography. The first successful ancient DNA studies in Africa and the promise of many more African ancient DNA studies to come, will enable direct temporal comparisons – which will further contribute to unraveling deep human history on the African continent.

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With improvements in laboratory techniques and the strengthening of bioinformatics analysis, we are constantly increasing our ability to analyze ancient DNA more effectively and the next few years will be exciting for investigating human history on the African continent.

2 Investigating Human History

The study of human history is a subject where many disciplines converge with a common goal – deciphering the human past. Disciplines such as history, archaeology, paleoanthropology, evolutionary linguistics, and more recently, genetics, analyse different types of data to help unravel human history and the story of our origin. Each field has their own valuable contributions, but they are also subject to their own sets of limitations (Jobling et al., 2014). It is thus important to keep in mind that none of these fields provide an unbiased description of human evolution. Findings from different disciplines should try to complement each other and therefore genetics is often combined with other research fields to help understand the history and evolution of humankind. Rapid developments in the ancient DNA (aDNA) field, extended the power of genetics to make inferences about the history of our species (Nielsen et al., 2017). aDNA offers a unique opportunity to access the genetic variation of past populations and enables us to put past populations in context of present-day genetic variation.

Human population groups from all regions of the world, have unique histories of migration, admixture, and adaptation which have shaped their past. For a long time, human prehistory on the African continent has been actively investigated by the disciplines of archaeology, paleoanthropology and linguistics (Greenberg 1963, Mitchell and Lane 2013, Güldemann 2018, Stringer 2002). Although these fields have greatly contributed to the understanding of our species deep history on the African continent, as well as later population migrations in Africa, key questions regarding African history remain unanswered. Integral to the above, is the question of whether changes in material culture, observed in the archeological record, can be ascribed to 'Pots', or 'People'. In other words, are observed cultural changes a result of the physical migration of people, or alternatively, due to the spread of ideas? Similarly, the spread of a language or change in morphological characteristics are not necessarily always correlated to migration and gene-flow between groups of people. The field of genetics offers a unique possibility to investigate human history with regards to population migration and cultural change. However, complex migration patterns are difficult to disentangle in modern-day genomes and ancient DNA studies are ideal to study migration history by directly accessing the genetic variation of pre-historic individuals and comparing this variation to other pre-historic individuals from different temporal and geographic contexts and also to modern-day populations. Furthermore, current-day people who live in certain places may not be representative of the populations who inhabited these areas in the past. With support from aDNA, genetics has started to directly access the genetic variation of human prehistory by comparing it to different temporal and geographic comparative data points, including the populations of today. Perhaps one of the greatest benefits of aDNA will be in understanding how population migration and/or population continuity has impacted the genetic landscape of our species through time. Therefore, while contributions from other disciplines have suggested a complex, multifaceted past, genetic studies on modern populations improved inferences, and now aDNA are helping to clarify even further, the questions surrounding African prehistory.

3 Ancient DNA in Africa

Due to the difficulty of extracting DNA from samples from warm climates and the initial focus on European aDNA studies, genome-wide aDNA studies in Africa presently number only few (Table 8.1) (Gallego Llorente et al., 2015, Skoglund et al., 2017, Prendergast et al., 2019, Lipson et al., 2020, Schlebusch et al., 2017, van de Loosdrecht et al., 2018, Fregel et al., 2018, Schuenemann et al., 2017, Rodriguez-Varela et al., 2017). However, with the development of new and improved molecular genetic methods and bioinformatic tools, it is becoming easier to not only extract DNA from samples found in warm climates, but more ancient samples too. At the time of writing this review, only nine studies in total have published ancient genome-wide results from Africa, four studies for North African aDNA and five for sub-Saharan African aDNA (Table 8.1). We analyzed the results of aDNA studies from continental Africa, published to date, in context of modern day African genetic variation (Figure 8.1 and 8.2).

3.1 *North Africa*

In North Africa, human population history has a unique standing, with modern-day groups largely related to Eurasian and Middle Eastern populations, with very low levels of genetic contributions from sub-Saharan Africa (blue dots, Figure 8.1 and heat-map in Figure 8.2C) (Henn et al., 2012, Arauna et al., 2016). A debate existed whether this was the result of Paleolithic back-to-Africa migrations, or migrations connected to the Neolithic period and the

TABLE 8.1 Summary of genome-wide African ancient DNA studies published to date. Context: LSA – Later Stone Age; PN – Pastoral Neolithic; PIA – Pastoral Iron Age; and IA – Iron Age

Study	Region	Current day African counties	Date range Cal BP / BP	Context*	N Capture / Full genomes	Coverage
Schuenemann et al. 2017	Northeast Africa	Egypt	2726–1952 calBP	Pre-Ptolemaic Period, Ptolemaic Period	3 Capture	132,084 to 508,360 SNPs
Rodriguez-Varela et al. 2017	Northwest Africa	Canary Islands	951–1421 BP	-	5 Full genomes	0.21 to 3.93x
van de Loosdrecht et al. 2018	Northwest Africa	Morocco	15,100–13,900 calBP	LSA/ Paleolithic	5 Capture	343,764 to 1,013,869 SNPs
Fregel et al. 2018	Northwest Africa	Morocco	7,275–5,600 calBP	Early Neolithic Late Neolithic	13 Full genomes and capture	Full gen: 0.01 to 0.74x Capt: 0.04 to 1.72x
Gallego Llorente et al. 2015	East Africa	Ethiopia	4500 calBP	LSA	1 Full genome	12.5x
Skoglund et al. 2017	East and southern Africa	South Africa, Tanzania, Malawi	8173–322 calBP	LSA PN IA	12 Capture 3 Full genomes	Full gen: 0.7 to 2.0x Capt: 9,355 to 845,016 SNPs
Schlebusch et al. 2017	Southern Africa	South Africa	2296–282 calBP	LSA IA	7 Full genomes	0.01 to 13.2x
Prendergast et al. 2019	East Africa	Kenya, Tanzania	4080–160 calBP	LSA PN PIA IA	41 Capture	0.01 to 3.9x
Lipson et al. 2020	West Africa	Cameroon	7,920–2,970 BP	Stone to Metal Age	4 Capture 2 Full genomes	Capt: 0.7 to 7.7x Full gen: 3.9 to 18.5x

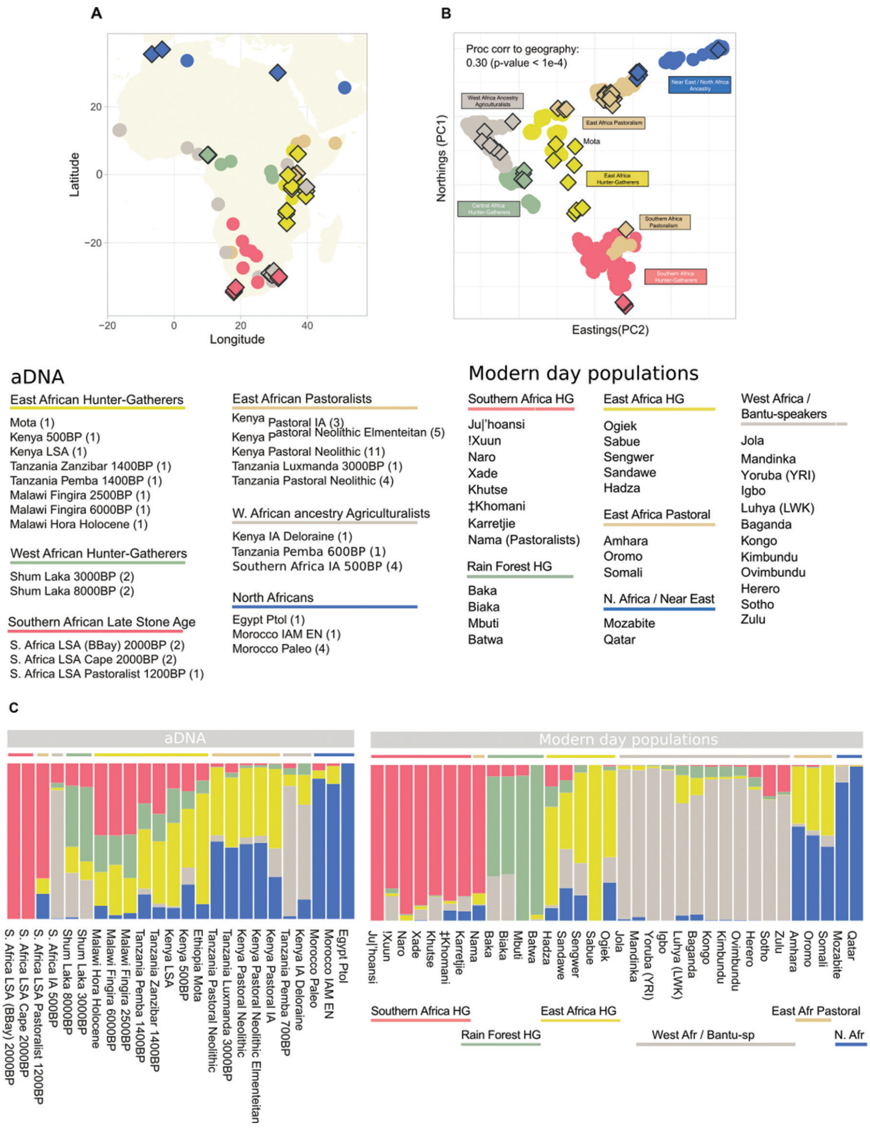

FIGURE 8.1 Modern-day and ancient genetic structure in Africa. A. Geographic locations of modern-day populations (colored circles) and remains of ancient individuals for whom DNA could be extracted and analyzed (diamonds with border). B. PCA rotated to geography PC1 vs. PC2. (rotation to geography were done using Procrustes analysis). C. Averaged per population admixture clustering analysis for K=5. PCA analysis and Admixture were performed on overlapping SNP positions from: Li et al., 2008, Schlebusch et al., 2012, Perry et al., 2014, Auton et al., 2015, Gurdasani et al., 2015, Rodriguez-Flores et al., 2016, Patin et al., 2017, Scheinfeldt et al., 2019, Vicente et al., 2019, Skoglund et al., 2017. Positions with more than 0.15 missingness were discarded, in the end 182,977 LD-pruned SNPs were analyzed. Only aDNA samples with at least 15,000 overlapping SNPs were considered in the analyses

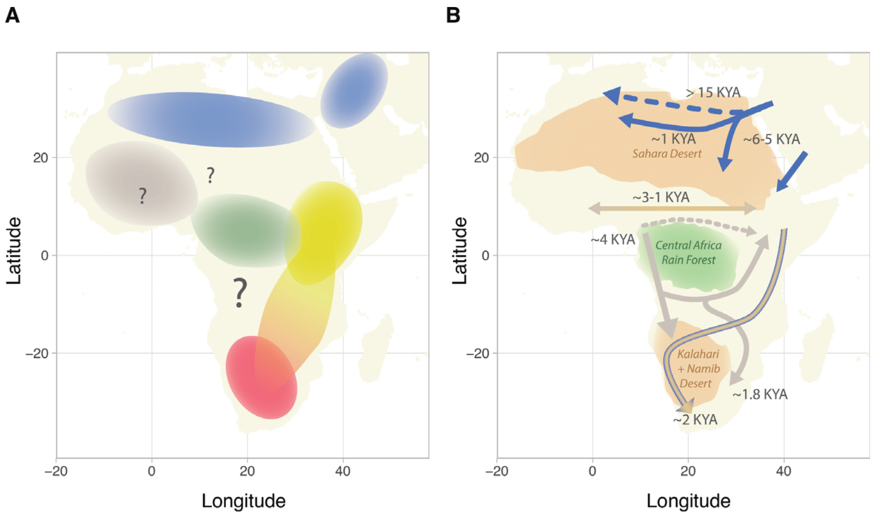

FIGURE 8.2 A. Map of pre-farming population stratification across the African continent, showing non-Africans (blue), East Africans (yellow), West Africans (gray), central African hunter–gatherers (green), and Khoe-San (red). B. Migration routes related to the expansion of herders and crop farmers during Holocene times. The gray arrows represent the Bantu expansion, the blue arrows represent the Eurasian back-migration, the brown/blue arrow represents the southward migration of mixed East African/Eurasian pastoralists, and the gray/brown arrow represents bidirectional migration across the Sahel belt. Abbreviation: KYA, thousand years ago

introduction of farming practices to North Africa (Barbujani et al., 1994, Henn et al., 2012). Ancient DNA studies in early Neolithic (~7 kya – thousand years ago) Moroccan remains (blue diamonds, Figure 8.1) (Fregel et al., 2018) indeed found the individuals to be genetically most similar to Anatolian farmers and Natufians from the Middle East, suggesting a potential early migration of these groups westward (Fregel et al., 2018). However, a study on 15 kya old remains from Morocco conclusively demonstrated that northern Africa received significant amounts of gene-flow from Eurasia predating the start of the Holocene and the development of farming practices (van de Loosdrecht et al., 2018). aDNA studies further found that the Early Neolithic North Africans (~7 kya) trace their ancestry to these Paleolithic north African groups (Fregel et al., 2018), while Late Neolithic groups (~5 kya) contains an Iberian component, indicating trans-Gibraltar gene-flow. These two different signals in the Early and Late Neolithic indicate that the spread of farming practices in North Africa involved both the movement of ideas and people [See further information in Chapter 7].

The Sahara isolates North Africa from the rest of Africa and poses a barrier to human migration, aside from intermittent greening periods (Drake et al., 2011). Gene flow from the south, across the Sahara into modern-day North Africans, seemed to have been low and appeared in relatively recent times (Henn et al., 2012). In the easternmost part of North Africa, ancient DNA studies of mummies also indicated that gene flow from sub-Saharan was recent and that people in classical Egypt displayed less sub-Saharan admixture compared to present-day Egyptians (Schuenemann et al., 2017). More ancient individuals from Morocco however seem to have had higher affinities to sub-Saharan Africans (van de Loosdrecht et al., 2018, Fregel et al., 2018) (Figure 8.1B) and the 15 kya Paleolithic individuals (van de Loosdrecht et al., 2018) derived one-third of their ancestry from sub-Saharan Africans. This sub-Saharan ancestry was best represented by an equal mixture of present-day East African hunter-gatherers and West Africans (van de Loosdrecht et al., 2018).

The Paleolithic (15 kya) and Early Neolithic (7 kya) individuals lived before and during the most recent green Sahara period (stretching from 12 kya to 5 kya) and yet they have similar genetic compositions with similar affinities to sub-Sahara Africa, while modern-day North Africans have very little sub-Sahara African contribution. Little is known about the peopling of the Sahara during the last humid period, when the desert was replaced by a fertile Savanna grassland. An aDNA study generated two mitochondrial genomes from ~7 kya individuals associated to a Middle Pastoral (Neolithic) context from the central Sahara region (Vai et al., 2018). These individuals carried a lineage basal to the Eurasian haplogroup N. While the result demonstrated the presence of an ancestral lineage of the N haplogroup in the Holocene green Sahara it is unclear whether the haplogroup originated in Africa and subsequently was lost due to drift or population replacement, or whether the haplogroup was introduced by a back migration into Africa. Consequently, the cycling of the Sahara through its wet and dry phases seems to have had an influence on the amount of gene-flow between North and Sub-Sahara Africa, although the exact dynamics of those migrations need to be further investigated, ideally through genome-wide ancient DNA studies.

3.2 *Sub-Sahara Africa*

Modern and ancient DNA studies for sub-Saharan Africa indicated that this part of the continent had two very different phases in its history (Figure 8.3) (reviewed in (Schlebusch and Jakobsson 2018)). During the deep history of sub-Saharan Africa, before the invention and spread of farming practices, hunter-gather groups seemed to have been related in an “isolation-by-distance” pattern where geography played an important role. This pattern entails that groups are closest related to their neighboring groups and less related to groups that are geographically further away in a step-wise manner. This isolation-by-distance pattern was shown to drive genetic structure among southern

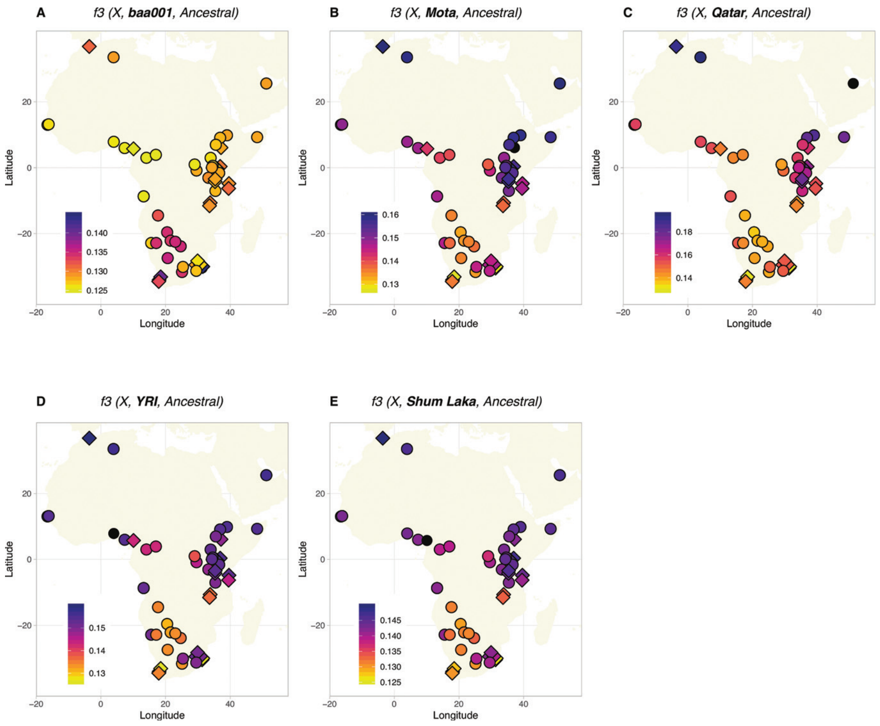

FIGURE 8.3 Genetic affinities among sub-Saharan current-day (coloured dots) and ancient individuals (diamonds with borders) as represented by heat maps of *f3*-outgroup analyses. A. Affinities to “Ballito Bay A” (baa001) representing the southern African aboriginal component. B. Affinities to “Mota” representing the East African aboriginal component. C. Affinities to Qatar representing the back migration of non-Africans into Africa. D. Affinities to Yoruba from Nigeria (YRI) representing a West African component and illustrating the Bantu expansion. E. Affinities to Shum Laka representing the Central African aboriginal component. For all *f3*-analyses the Ancestral outgroup was generated from the identified allele present in at least two reference genomes of Chimpanzee, Gorilla and Orangutan. *f3*-outgroup analyses were performed only within samples with at least 10,000 pairwise overlapping SNPs

African hunter-gathers (Vicente et al., 2019) and a simple Procrustes analysis suggest that this pattern also might apply on a continental scale (see procrustes correlation factor in Figure 8.4). Thus the geographic distance across the continent is highly correlated with the genetic relatedness of groups.

The early history of the African continent (captured by genetic relatedness among hunter-gatherer groups) is in stark contrast with the large population movements that followed the invention of farming practices in Africa. The development of food-producing lifeways caused dramatic population increases followed by migrations, which is visible in the genetic signatures of expanding farming populations who spread across the whole continent within a relatively short time period (Figure 8.3) (Schlebusch 2019, Schlebusch and Jakobsson 2018). African farming societies outcompeted the autochthonous hunter-gatherer groups who, to a large extent, were replaced and/or assimilated by the farming groups. The origins of food-producing practices in Africa are still unclear but it is believed that crop cultivation was developed independently, in at least three regions in Africa: the Sahara/Sahel (around 7 kya), the Ethiopian highlands (~7–4 kya), and western Africa (~5–3 kya). The Nile River Valley is thought to have adopted agriculture (~7–8 kya) from the Neolithic transition in the Middle East (~10–11 kya) (Jobling et al., 2014, Mitchell and Lane 2013). From these centers of origin, farming practices spread to the rest of Africa, with domesticated animals reaching the southern tip of Africa around 2 kya and crop farming around 1.8 kya (Mitchell and Lane 2013). Genomic investigations of both present-day and past humans contributed to hypotheses regarding the spread of farming groups in Africa.

3.3 *Migrations of Food Producers in Sub-Sahara Africa*

The first African ancient DNA nuclear genome to be sequenced was that of a 4.5 thousand year old Ethiopian individual (from Mota, Figure 8.1) (Gallego Llorente et al., 2015). This genome revealed that East African populations, more recent in time than 4.5 kya (beige dots and diamonds, Figure 8.1), have been influenced by a back to Africa migration(s) from a population(s) genetically similar to early Neolithic farmers from Western Eurasia (heat map in Figure 8.2C). On the principal component analysis (PCA) (Figure 8.1) this can be seen through the current day East African populations (beige dots) and ancient East African individuals from farming contexts (beige diamonds) who are intermediate between the Mota individual (yellow diamond – Mota is a representative non-admixed East African hunter-gatherer) and non-Africans (blue dots). This study clearly indicated a Eurasian back migration into East Africa that caused many current-day East African groups to display genetic variation that link them to both groups with a deep East African history (as represented by Mota) as well as Eurasian groups that migrated back into Africa. However, subsequent genetic studies showed that certain Northeast and East African groups, such as the Nilotic speaking Dinka and Nuer groups from Sudan (Hollfelder et al., 2017) and East African hunter gatherers such as the Sabue (Scheinfeldt et al., 2019) (Figure 8.1C and Figure 8.2B and 8.2C), until today had little to no Eurasian admixture.

A study that sequenced 15 ancient Africans across eastern and southern Africa dating as far back as 8.1 kya (Skoglund et al., 2017), also found evidence of this Eurasian back migration into East Africa. The study furthermore found that ancient herders carrying this East African-Eurasian mixed ancestry migrated all the way down into southern Africa to introduce herding practices to the south of the continent (beige diamonds and dots in Eastern and Southern Africa, Figure 8.1B). The individual from Kasteelberg in South Africa, found in a pastoralist context (S. Africa LSA Pastoralist 1200 before present (BP) on Figure 8.1C) was found to have received 40% of her ancestry from the pastoralist individual from Luxmanda (Tanzania Luxmanda 3000 BP on Figure 8.1C) and the rest of her ancestry from southern African hunter-gatherers (South Africa LSA Cape 2000 BP) (Skoglund et al., 2017). This finding confirmed previous results based on modern-day autosomal (Schlebusch et al., 2012, Pickrell et al., 2012, Pickrell et al., 2014), Y-chromosome (Henn et al., 2008) and Lactase Persistence (LP) (Breton et al., 2014, Macholdt et al., 2014) variants, which detected the presence of an East African component in Southern African herders (see the East African component in the southern African herding population "Nama" in Figure 8.1C).

The introduction of farming in East Africa was further refined by a study of 41 individuals associated with Later Stone Age (LSA), Pastoral Neolithic (PN), and Iron Age (IA) contexts in current day Kenya and Tanzania (Prendergast et al., 2019). The study inferred two phases of admixture associated with the spread of pastoralists in the region: the first admixture event likely occurred ~6–5 kya in northeastern Africa between a group carrying non-African genetic ancestry (related to the groups from the Levant or North Africa) and a local northeast African group (related to present day Dinka/Nuer), and the second admixture event occurred ~4 kya between this admixed group and eastern African foragers (related to Mota and Kenyan LSA individuals). The route of this non-African component into East Africa is as yet unclear and was proposed to be either through the Nile valley or through the horn of Africa. Results in the study also pointed to at least two chronologically distinct southwards movements of herders into eastern Africa, an initial limited spread and a later more successful spread giving rise to the PN culture. Interestingly genetic analyses failed to find any differentiation between two archeologically distinct PN cultures, Elmenteitan and Savanna Pastoral Neolithic cultures (Figure 8.1C) (Prendergast et al., 2019). The Savanna Pastoral Neolithic was previously hypothesized to be affiliated with Afro-Asiatic speakers and the Elmenteitan with an expansion of pastoralists speaking Nilo-Saharan languages (Ambrose 2001). This observation suggests that cultures that are archeologically very distinct, do not necessarily imply genetically distinct groups. The subsequent arrival of the Iron Age in East Africa was a similarly complex process. An additional Sudan related gene flow event contributed to the Pastoral Iron Age (PIA) in the region (Kenya Pastoral IA in Figure 8.1). This was closely followed by the introduction of western African-origin ancestry related to present-day Bantu-speakers into the area that also marks the onset of the Iron Age in the region and the introduction of crop farming (Kenya IA Deloraine and Tanzania Pemba 700 BP) (Prendergast et al., 2019, Skoglund et al., 2017).

The Bantu Expansion is one of the largest Holocene expansion events globally and began around ~5–3 kya in western Africa (in the region of current eastern Nigeria and western Cameroon) (de Filippo et al., 2012, Bostoen 2018, Li, Schlebusch, and Jakobsson 2014). It is visible in the archaeological record via increased sedentism, followed by the spread of agricultural practices and the use of iron (Bostoen 2018, Mitchell and Lane 2013). Today, the majority of sub-Saharan Africans speak one of the ~500 closely related Bantu languages even though they are distributed over an area of ~500,000 km^2. Earlier genetic studies on autosomal data have indicated that the current distribution of Bantu-speaking populations is largely a consequence of the movement of people (demic diffusion) rather than a diffusion of only language (Tishkoff et al., 2009, Li, Schlebusch, and Jakobsson 2014, Schlebusch et al., 2012, de Filippo et al., 2012). This has been confirmed by ancient DNA studies; i.e. ancient remains found in Iron Age contexts (gray diamonds on Figure 8.1), in Eastern Africa (Prendergast et al., 2019, Skoglund et al., 2017) and Southern Africa (Schlebusch et al., 2017) group genetically with current-day West African groups on the PCA (Figure 8.1 A-C). This testifies to the relatively recent, large scale movement of people of West African descent to the rest of the continent, coupled with the spread of agriculture and the use of iron (illustrated by the heat map of Figure 8.2D).

A study that sequenced the nuclear genomes of 7 ancient southern African individuals, three dating to the LSA (2 kya – red diamonds in southern Africa – Figure 8.1), and 4 dating to the Iron Age (300 to 400 years ago – gray diamonds in Southern Africa – Figure 8.1) found that the LSA individuals were related to current day Khoe-San hunter-gatherer individuals (red dots) and the Iron Age individuals to current day West Africans (gray dots). This study confirmed a large-scale population replacement in southern Africa, where LSA ancestors of the Khoe-San hunter-gatherers were replaced by incoming Bantu-speaking farmer groups of West African genetic ancestry. In southern Africa, Bantu-speakers received substantial amounts of gene-flow from local Khoe-San hunter-gatherers (e.g. see in S. Africa IA 500 BP ancient individuals and Zulu and Sotho modern day populations, Figure 8.1C). Interestingly, further north, the Bantu-expansion seemed to have had different demographic dynamics in terms of interaction between hunter-gatherers and incoming farmers. Current day populations from Malawi (Skoglund et al., 2017) and Mozambique (Semo et al., 2019) show little to no admixture with hunter-gather groups that occupied the area before the Bantu-expansion. These findings indicate that the diffusion of Bantu languages and culture throughout sub-equatorial Africa was a complex process and the admixture dynamics between farmers and hunter-gatherers played an important role in creating patterns of genetic diversity. Further ancient DNA studies and better coverage of sub-equatorial Africa in terms of modern-day populations are needed to further clarify the demographic dynamics, migration routes and interactions during the Bantu-expansion.

3.4 *Sub-Sahara Africa before Farming*

Before the large-scale migrations of farming groups across the continent, hunter-gatherer groups seemed to have been related in clinal patterns with geographic distance between groups and the landscape determining relationships. This isolation-by-distance pattern is still reflected in the relatedness between present day hunter-gatherer groups. Southern Africa Khoe-San hunter-gatherers follow an isolation-by-distance pattern of relationship when all admixed parts of their genomes (contributed by West African Bantu-speaking farmers and herders of East African origin) are removed (Vicente et al., 2019). Likewise, the ancient DNA study by Skoglund et al (Skoglund et al., 2017) also found that before farming, a genetic cline between hunter-gatherer populations of East and southern African existed (yellow to red cline on PCA – Figure 8.1). The cline showed a gradient of decrease for a Southern African genetic component towards Eastern Africa (Figures 8.2A and 8.4D) and, similarly, a gradient of decrease in Eastern African ancestry towards southern Africa (Figures 8.2B and 8.4E). As a result, LSA Malawi hunter-gatherers had intermediate amounts of genetic contribution from both Eastern and Southern Africa. This cline might also have extended to West Africa and ancient hunter-gatherers from Shum Laka in West-central Africa (current day Cameroon) (Lipson et al., 2020), related to current day West-central African rainforest hunter-gatherers (RHGs) (green dots, Figure 8.1) fall intermediate between southern African hunter-gathers and West African Niger Congo speakers on PC 1 (Figure 8.1B). A PCA that included only ancient and modern-day hunter-gatherers and excluded farming groups (Figure 8.4) show a Procrustes correlation factor with geography of 77%. While, when farmers are included in the analyses, the correlation coefficient is reduced to 30% (Figure 8.1).

A two-dimensional reduction of the genetic components of hunter-gatherers (e.g. Figure 8.4), might thus suggest long term clinal relationships between groups driven by geographic distance across the African landscape, with few large scale migrations (characteristic of the farming period). This hypothesis however needs to be thoroughly tested with data from more aDNA studies.

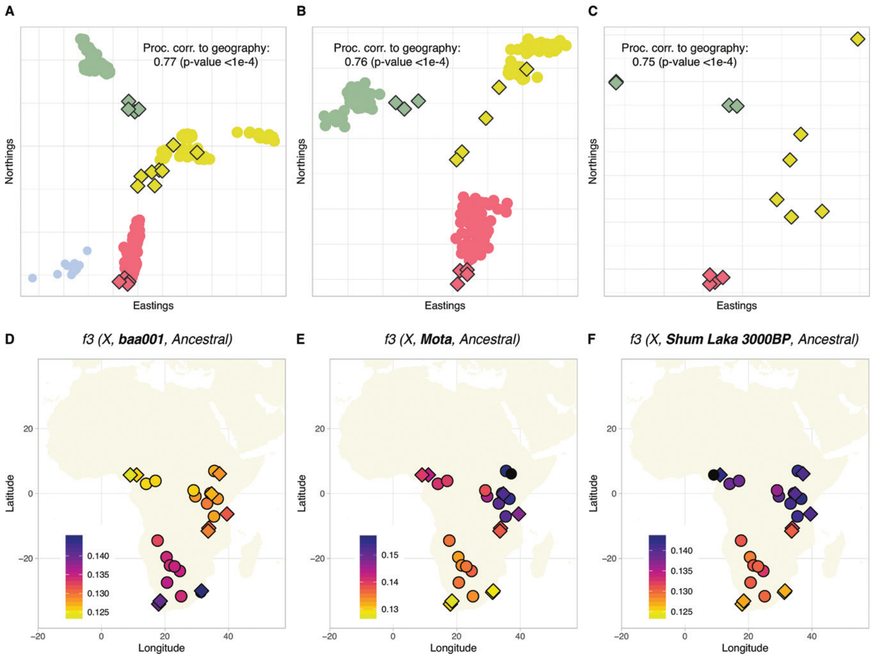

FIGURE 8.4 Genetic affinities among sub-Saharan current-day (coloured dots) and ancient hunter-gatherers (diamonds with borders), attempting to represent pre-farming population structure. (A) PCA including only sub-Saharan modern-day and ancient hunter-gatherers. Yellow – East African, Green – West/Central African, Pink – Southern Africa. The Qatari population (light blue) was used to extract Eurasian admixture on PC1 (not shown). PC 2 and 3 were rotated to geography. The Procrustes correlation factor with geography is 77%. (B) Multidimensional scaling (MDS) analysis of pairwise (1 minus *f3*-outgroup) including current-day and ancient hunter-gatherers. The Procrustes correlation factor with geography is 76%. (C) MDS analysis of pairwise (1 minus *f3*-outgroup) including only ancient hunter-gatherers. The Procrustes correlation factor with geography is 75%. The Procrustes correlation factor with geography of A-C is 75–77%, compared to 30% when farmers are included - Figure 8.1. (D-F) Heat maps of *f3*-outgroup analyses including current-day and ancient hunter-gatherers. D. Affinities to Ballito Bay A (baa001) representing the southern African aboriginal component. E. Affinities to Mota and the East African aboriginal component. F. Affinities to Shum Laka representing the Central African aboriginal component. In B-F, the Ancestral outgroup was generated from the identified allele present in at least two reference genomes of Chimpanzee, Gorilla and Orangutan. *f3*-outgroup analyses were performed only within samples with at least 10,000 pairwise overlapping SNPs

From European modern-day (Novembre et al., 2008) and subsequent aDNA studies (Gunther and Jakobsson 2016), we have learnt that isolation-by-distance patterns can also mask several large scale movements and replacements in the distant past, especially if no un-admixed present day groups are remaining. In contrast to Europe, Africa still had current-day hunter-gatherer groups left, connected to deep histories in their regions, which simplified and supported inferences based on modern-day genetic variation. Nonetheless, the deep history of Africa remains to be clarified further and aDNA studies already started to contribute to inferences.

In the study by Schlebusch et al (Schlebusch et al., 2017), one of the 2 kya individuals, related to present-day Khoe-San groups, yielded particularly good ancient DNA and was sequenced to 13x genome coverage. This high coverage ancient genome was used as a reference ancient genome for subsequent analyses. It revealed that all modern Khoe-San groups, have 9–22% admixture from the admixed group of Eurasian-East African ancestry that introduced herding into southern Africa. This can be seen on the PCA (Figure 8.1B) as a shift in modern day Khoe-San groups (red dots) towards the East African side of the PCA. This result will have an effect on past genomic research as one of the Khoe-San groups, the Ju|'hoansi was considered as a group with very little admixture from neighbouring groups, and was used previously to date the first divergence event between modern human population groups (Schlebusch et al., 2012, Gronau et al., 2011, Veeramah et al., 2011). When the high coverage ancient individual, as a non-admixed San ancestral group, was compared to other Africans to re-estimate the earliest divergence time between modern human groups, a deeper divergence time was obtained (Schlebusch et al., 2017). Whereas past research estimated a divergence time of around 100 thousand years, (200 thousand, using the updated human mutation rate) (Schlebusch et al., 2012, Gronau et al., 2011, Veeramah et al., 2011), using the non-admixed Stone Age individual pushed back the divergence time to between 260–350 thousand years, towards the genesis of the Middle Stone Age when humans became morphologically and behaviourally modern. Using a coalescent-based tree model, the study found hierarchical divergence times, first between, Khoe-San and all other populations (mean of 322 kya), followed by the split of RHGs and all other populations (221 kya) followed by a split between West and East Africans (137 kya) (Schlebusch et al., 2017).

While hierarchical bifurcating tree models provide a good estimation of general relatedness between groups, it certainly is a simplified representation of human history and more complex models incorporating gene-flow, migration and deep population structure (sometimes referred to as ghost archaic admixture in the African context) need to be considered in future research (Henn, Steele, and Weaver 2018). Several studies have already reported evidence of deep coalescencing lineages in west Africa suggesting possible deep rooting admixture by a "ghost" population – a population distantly related to modern humans that do not exist as a separate population today (Schlebusch et al., 2017, Skoglund et al., 2017, Lachance et al., 2012, Hsieh et al., 2016, Durvasula and Sankararaman 2020). Furthermore, a recent study (Chen et al., 2020) also suggested extensive Neanderthal admixture in African populations, adding additional deep structure to the African demographic picture. These additional deep rooting gene-flow events thus need to be incorporated in models of deep human history in Africa. A study by Lipson et al (Lipson et al., 2020), suggested radiations between four ancestral groups rather than a bifurcating split model. This four-fold radiation involved; a lineage leading to Khoe-San hunter-gatherers, a lineage leading to RHGs, a lineage leading to East and West Africans and a fourth "ghost modern" lineage of a population that does not exist anymore today. In this model a "ghost-archaic" source was also added and West African groups contained low amounts of ghost-archaic admixture, together with a larger amount of ghost-modern admixture. There were however other models that also fitted their data, for example a model where only one ghost population, with an intermediate divergence time between the ghost-modern and ghost-archaic source, admixed into West Africans.

With more and more evidence from the paleoanthropology and genetics fields, adding support for a possible multiregional origin of modern humans on the African continent (Scerri et al., 2018, Stringer 2016, Schlebusch and Jakobsson 2018, Henn, Steele, and Weaver 2018), future generic studies on deep African history need more rigorous testing. This will require hypothesis testing through the simulation of representative models and thorough testing of these models employing appropriate summary statistics that are sensitive to distinguish between models. Furthermore, geographic and climatic modelling need to be incorporated in these models, together with time-serial data obtained from aDNA studies (Fenderson, Kovach, and Llamas 2020). Although this represents a demanding task, some frameworks have already been laid regarding proposed models (Henn, Steele, and Weaver 2018) and methods to incorporate spatiotemporal components (Fenderson, Kovach, and Llamas 2020). As more data becomes available in the form of aDNA together with genomic data from modern-day African populations, research will continue to clarify the picture of our deep genetic history in Africa and bring us closer to answering the questions of human origins.

4 Future of Ancient DNA research

Ancient DNA methods are continually evolving, and we see evidence of this in how research has advanced in the last decade. Improvements in laboratory techniques allowed for sequencing of DNA samples from areas prone to bad

DNA preservation, such as southern Europe, the Middle East, Southeast Asia and Africa. In areas where DNA preservation is favourable, such as Europe, there are now data from hundreds of ancient individuals to strengthen bioinformatics analysis and increase the amount of reliable information on the ancient populations analyzed. As ancient DNA is becoming more common as means of interpreting human history, researchers are improving bioinformatics pipelines to specifically handle ancient DNA sequence data and population genetic analysis techniques are also tailored to incorporate time-serial data. In the future, ancient DNA research will continue to reveal more nuanced stories of human prehistory, and these stories might help us to understand the present, and better predict how we may react in the future in an ever-changing environment.

Acknowledgements

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CHAPTER 9

The H3Africa Consortium: Publication Outputs of a Pan-African Genomics Collaboration (2013 to 2020)

Ananyo Choudhury, Dhriti Sengupta, Shaun Aron, and Michèle Ramsay

1 Introduction

Developing a complex collaborative program across multiple African countries, characterized by a diversity of government models, laws, cultures and norms, resources and skills, climatic conditions and health challenges is a daunting task. In 2010, discussions began to work toward developing a model to support a pan-African genomics initiative to ensure that Africa was not left behind in the post-genomics era with the possibility of precision medicine on the horizon. By examining the opportunities and challenges, a white paper was drafted titled: Harnessing Genomic Technologies Toward Improving Health in Africa: Recommendations for the Human Heredity and Health in Africa (H3Africa) Initiative (https://h3africa.org/index.php/about/white-paper). This was prepsented to the leadership of the Wellcome Trust and the National Institutes of Health, resulting in committed funding and calls for funding applications.

The H3Africa Consortium had its first meeting in August 2012 in Addis Ababa with just 7 supported projects. As of March 2020, the H3Africa Consortium has grown to over 50 funded projects (1 central coordinating center; 14 collaborative centers and 16 research projects; 2 ethics collaborative centers and 8 ethics projects; 4 pilot biorepositories and 1 bioinformatics collaborative center and 4 bioinformatics training grants), with over 500 consortium members and the equivalent of 170M USD in investment. Figure 9.1 shows the geographic location of the different projects on the continent. The African Academy of Science has become a key partner taking on specific governance roles, including managing access to the resources developed by the Consortium.

It is a challenging task to assess and quantify the impact and outputs of such a complex and multi-faceted Consortium. These include data generation, discovery and new knowledge generation, resource development (research and ethics guidelines, infrastructure, capacity strengthening through skills development and biobanks with biospecimens, development of bioinformatics tools and pipelines), information for health policy development and targeted interventions, patents and peer-reviewed publications. Importantly, the

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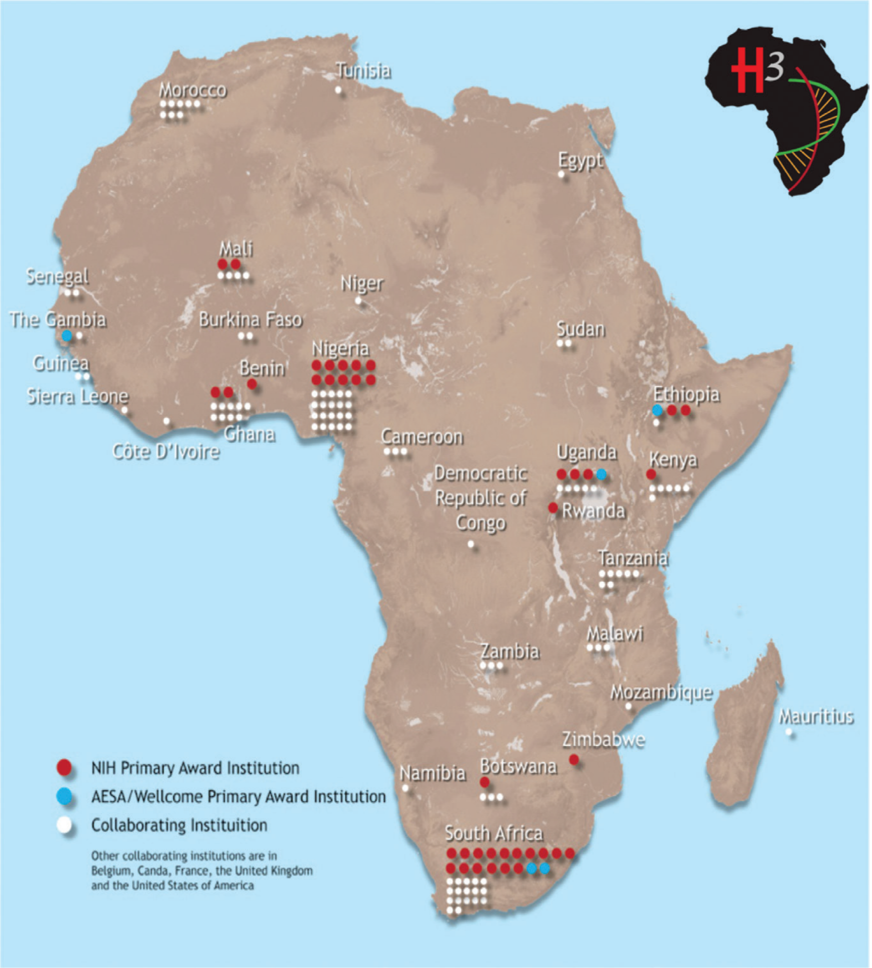


FIGURE 9.1 Map of Africa showing the distribution of H3Africa projects. Each circle represents a group working on an H3Africa project. The location of the primary award institutions are shown in red (NIH funded projects) and Blue (Wellcome funded projects, managed through The Alliance for Accelerating Excellence in Science in Africa (AESA), under the umbrella of the African Academy of Sciences (AAS)). The location of institutions collaborating with the primary award institutions are shown by white dots.
THE MAP IS USED WITH PERMISSION FROM THE H3AFRICA COORDINATING CENTRE (HTTPS://H3AFRICA.ORG)

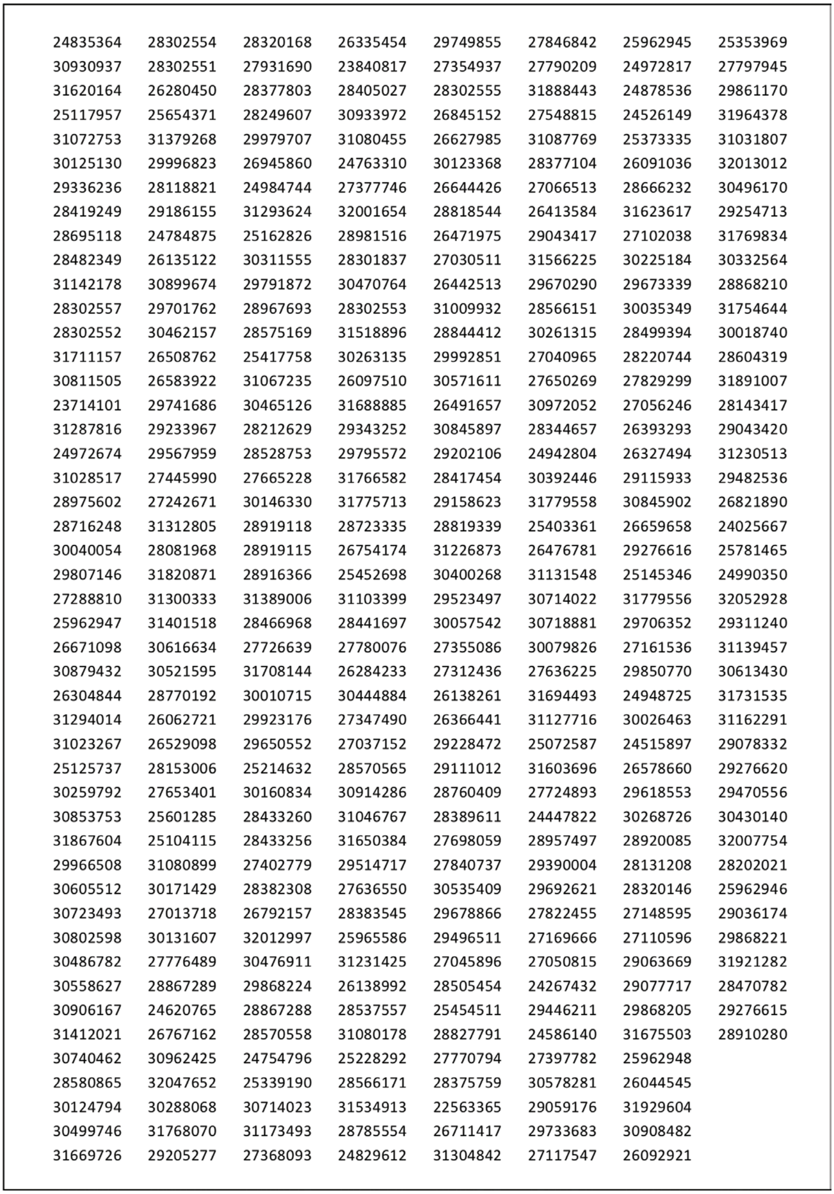
H3Africa Consortium contributes large African genome datasets from populations across the continent to explore insights into demographic histories of migration and admixture across Africa. These data are available to the global scientific community for further analysis.

In this chapter, we have limited ourselves to assessing the publications oeuvre of the H3Africa Consortium (January 2013 to February 2020) under specific themes that reflect the areas of substantive activity. Each paper was assessed and the acknowledgements and funding attribution scrutinized to identify publications by H3Africa-associated researchers. We divided the papers into three broad categories: *i*) H3Africa Core Publications, including the marker paper and H3Africa workshop meeting reports, *ii*) Perspectives, editorials and reviews about the H3Africa Consortium more generally, and *iii*) the extended reach of H3Africa. The core publications are cited in the reference list, whereas the complete list of PubMed IDs is provided in Figure 9.2. The authors take full responsibility for the potential misclassification of publications, but have attempted to be objective and fair. We apologize in advance for any omissions or distress caused in this regard.

2 Identification of Publications and Categorization

We performed a PubMed database (https://www.ncbi.nlm.nih.gov/pubmed) search for publications potentially originating out of the H3Africa Consortium. We used “H3Africa” as a search term along with a list of NIH grant IDs associated with NIH funded H3Africa projects. The grant IDs searched were - HG006938, DK116913, AI110398, HG007479, HG006947, HG007480, HG009826, HL141011, HG009824, MH096754, AI136677, MH115484, HG009784, HD094658, HG007044, MH115485, HG008226, HG008222, HG008224, HG009810, HG009790, HG007008, HG007438, HG007051, HG006941, HG009780, TW010677, TW010672, TW010673, TW010679, HG006939, AI110398, HG007480, AI110422, HG007465, AI110466, HG007472, HG007459, HG007628, HG007654, HG007092, HG006941, HG010273, HG010275 and HG009822. The search was conducted on the 20th of February 2020. In addition to the 371 unique publications identified by the search, two additional key papers (in press at the time of writing) were reviewed (Figure 9.3). Based on a manual scrutiny of the research subject matter, funding and acknowledgements these 373 publications were categorized into the following groups:

H3Africa Core Publications: Publications that are the direct outcome of original research from an H3Africa funded project, with acknowledgement of the specific grant. In this category, the papers have been divided into eight different subject-related categories as follows: marker papers and cohort descriptions; governance, ethics, community engagement and biobanking; epidemiological studies on diseases, traits and risk factors; disease-associated behaviour and awareness studies; genetics and genomics studies; bioinformatics and



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24942804
30392446
31779558
25403361
26476781
31131548
30714022
30718881
30079826
27636225
31694493
31127716
25072587
31603696
27724893
24447822
28957497
29390004
29692621
27822455
27169666
27050815
24267432
29446211
24586140
27397782
30578281
29059176
29733683
27117547
25962945
24972817
24878536
24526149
25373335
26091036
28666232
31623617
27102038
30225184
29673339
30035349
28499394
28220744
27829299
27056246
26393293
26327494
29115933
30845902
26659658
29276616
25145346
31779556
29706352
27161536
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24948725
30026463
24515897
26578660
29618553
30268726
28920085
28131208
28320146
27148595
27110596
29063669
29077717
29868205
31675503
25962948
26044545
31929604
30908482
26092921
25353969
27797945
29861170
31964378
31031807
32013012
30496170
29254713
31769834
30332564
28868210
31754644
30018740
28604319
31891007
28143417
29043420
31230513
29482536
26821890
24025667
25781465
24990350
32052928
29311240
31139457
30613430
31731535
31162291
29078332
29276620
29470556
30430140
32007754
28202021
25962946
29036174
29868221
31921282
28470782
29276615
28910280

FIGURE 9.2 PMIDs of 371 publications associated with H3Africa

genomics capacity development; and microbiome and pathogen studies (Figure 9.4).

H3Africa Perspectives, Editorials and Reviews: Publications written by H3Africa members about the H3Africa Consortium and its role in enhancing genomics research in Africa.

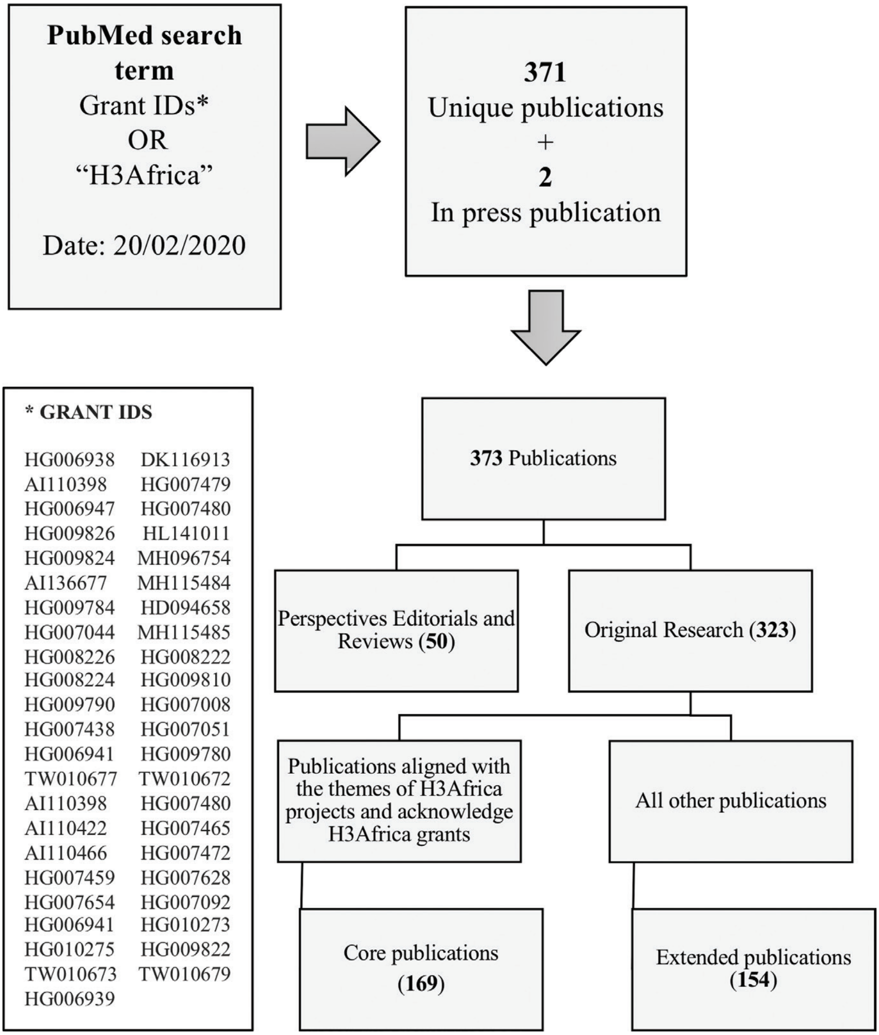

FIGURE 9.3 Summary of PubMed search and classification of H3Africa publications. Two key H3Africa genomics papers currently in press were added to the list. The publications were manually sorted into three categories- core, perspectives and reviews and extended publications

Extended Reach H3Africa Publications: Publications with one or more author(s) who are fully or partly supported by H3Africa funds, whose contributing research for the paper may be partly funded by H3Africa, and who have contributed to large multi-authored papers not directly related to a project that was funded under the H3Africa Consortium, and acknowledging funding under the H3Africa Consortium umbrella.

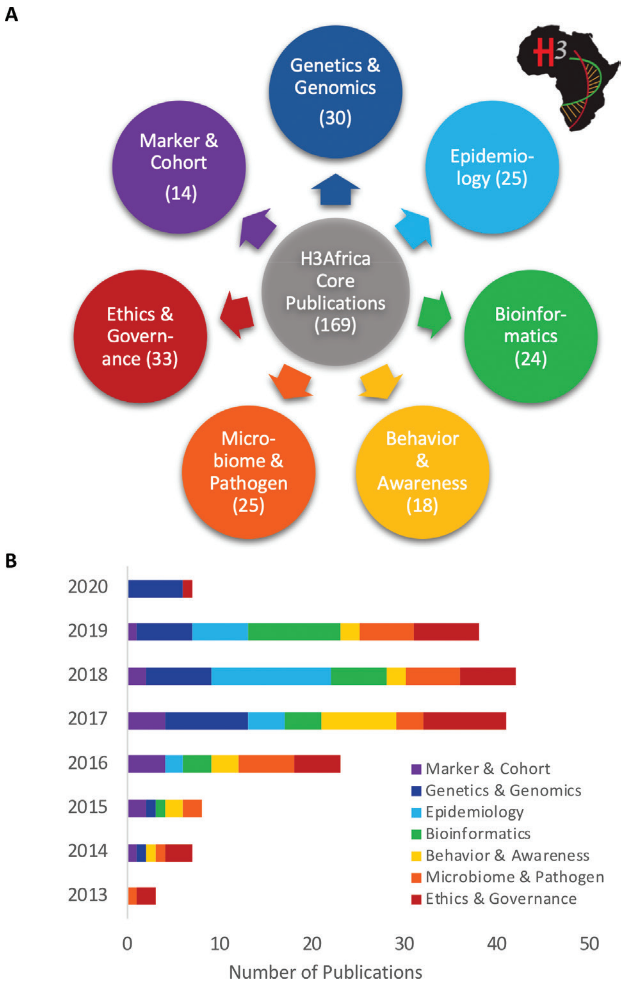

FIGURE 9.4 Allocation of 169 core H3Africa publications to different subject areas (January 2013 to 20 February 2020) (A) Classification of publications by major research area/category: Marker Paper and Cohort Descriptions (Marker and Cohort); Governance, Ethics, Community Engagement, and Biobanking (Ethics and Governance); Epidemiological studies on diseases, traits and risk factors (Epidemiology); Disease-associated behavior and awareness studies (Behavior and Awareness); Bioinformatics and Genomics Capacity Development (Bioinformatics); Genetics and Genomics Studies; Microbiome and Pathogen Studies. (B) Yearly breakdown of publications in each category. A few of these publications were aligned to more than one of the above-mentioned categories. Although we have cited these papers in each respective section, they have only been included in the category they best aligned to

3 Marker Paper and Cohort Descriptions

The H3Africa marker paper, published in 2014 with 122 citations in PubMed Central articles, described the vision and anticipated trajectory of the Consortium emphasizing the need to develop capacity for health-related genomics research in Africa (Rotimi et al., 2014). In terms of the proposed measures of success, H3Africa has fully achieved success in 4 areas (high impact publications; establishing a pan-African bioinformatics network; establishing biorepositories; obtaining extended funding for another 5 years) and partially succeeded in the remaining 4 areas (increased availability of funding for African research; contributing to reversing the African brain-drain; regular and effective release of data; and the storage and release of samples). Several H3Africa Collaborative Centres, networks and projects have published their own marker papers or resource papers.

The H3Africa Consortium Pan-African Bioinformatics Network (H3ABioNet) has published two landmark papers on sustainability and on the model for developing bioinformatics infrastructure and genomics research on the African continent (Mulder et al., 2016; 2017). The Collaborative African Genomics Network (CAfGEN) published a paper describing their network and explaining its objective of applying genomic technologies to probe host factors important in the progression of HIV and HIV-tuberculosis (TB) infection in sub-Saharan Africa (Mboowa et al., 2018).

Several of the projects involved in developing substantive African cohorts have published study-related marker/protocol papers and/or cohort descriptions, including the Stroke Investigative Research and Education Network (SIREN) (Akpalu et al., 2015; Owolabi et al., 2017; Adeoye, Ovbiagele et al., 2017); the Africa Wits-INDEPTH Partnership for Genomic Studies (AWI-Gen) which is investigating the genetic and environmental contributions to cardiometabolic diseases in Africans (Ramsay et al., 2016; Ali et al., 2018); the African Collaborative Center for Microbiome and Genomics Research's (ACCME's) Human Papillomavirus (HPV) and Cervical Cancer Study (Adebamowo, Dareng et al., 2017); Kidney Disease Research Network (Osafo et al., 2016; 2015) and the H3Africa multi-center study on the prevalence and environmental and genetic determinants of type 2 diabetes in sub-Saharan Africa (Ekoru et al., 2016). These 5 studies, together with the rheumatic heart study, RHDGen, have harmonized and combined overlapping aspects of their data to develop the Cardiovascular H3Africa Innovation Resource (CHAIR) (Owolabi et al., 2019). CHAIR is expected to have >50,000 African participants from 13 different African countries, and a harmonized dataset with key cardiovascular disease (CVD)-related variables. In developing this collaborative resource, one of the main goals of the Consortium has been realized, which is to strengthen the potential for novel discovery, to increase the power of analyses by combining resources, and to address research questions related to the health of Africans across the continent.

4 Governance, Ethics, Community Engagement and Biobanking

The success of any large and complex consortium rests on good governance and the development of sound and feasible policies and guidelines that support its research endeavour. One of the first challenges for the H3Africa Consortium was to develop policies and processes for genomic research and large data projects, with the long-term objective of sharing data and biospecimens with the global scientific community, for the purpose of improving the health of African and other global communities. This involves storing data in international repositories, in the case of H3Africa it is the European Genome-Phenome Archive, and developing biorepositories on the African continent. A series of workshops were held with ethics review committee members from many African institutions to examine the acceptance of a broad consent model for African Genomic Research; the equitable and fair sharing of data and samples; and the notion of benefit sharing (Ramsay et al., 2014; de Vries et al., 2016; Munung, Mayosi, and de Vries 2017; Tindana et al., 2019). Governance of digital health data in low and middle-income countries, biobank governance and potential exploitation of African biospecimens were considered in several publications (Staunton and Moodley 2013; Staunton and Moodley 2016; Tiffin, George, and Lefevre 2019). To better understand the African research landscape, there was an analysis on ethical guidelines, policies and procedures for research in 22 African countries (de Vries et al., 2017) and a governance framework was proposed for genomic research and biobanking in Africa (Yakubu et al., 2018).

Since African countries have different cultural norms and languages and their populations are mostly naïve to genomic research, much has been written by H3Africa research groups on appropriate African models or approaches for community engagement in the context of genomic research (Jenkins, Arulogun et al., 2016; Tindana et al., 2017; Pratt and de Vries 2018; Moodley and Beyer 2019; Singh et al., 2017; Staunton et al., 2019) the appropriate use of analogies and nomenclature, religious perspectives (Dennis-Antwi et al., 2019), return of incidental findings (Wonkam and de Vries 2020), the diagnostic/therapeutic misconceptions (Masiye, Mayosi, and de Vries 2017) and ethical and consent issues related to immortalized cell lines (de Vries et al., 2014; Campbell et al., 2018).

Consent models have been the topic of dedicated workshops, much discussion and publications since the H3Africa Consortium started its work with the intention of maximizing its resources by sharing data and biospecimens with the international research community. To enable future research through the use and re-use of data and biospecimens, it has been important to obtain broad consent from participants, either through a single consent or tiered consent model (Wright, Adeyemo, and Tiffin 2014; de Vries et al., 2016; Munung et al., 2016; Campbell, Susser et al., 2017; Tiffin 2018; Bukini et al., 2019). To ensure good governance, access to H3Africa resources is provided to the scientific community through a process of application to the H3Africa Data and Biospecimen Access Committee, and several research ethics committees have further stipulated that ethics approval is required for any new studies performed on these resources.

These activities have led to the development of three H3Africa guideline documents that are available from the H3Africa website and can be used by researchers who work in African communities when developing their own information sheets and informed consent documents: (1) H3Africa Guidelines for Community Engagement (2) H3Africa Guidelines for Informed Consent (3) H3Africa Guidelines for the Return of Individual Genetic Research Findings (https://h3africa.org).

H3Africa currently supports three African Biobanks, one each in Nigeria, Uganda and South Africa. Publications have addressed consent and stakeholder engagement for biobanking in Africa (de Vries et al., 2016; Moodley and Singh 2016; Staunton et al., 2018). Since building biobanks in resource limited environments is challenging, several papers have provided insights on building cost-effective biobanks and laboratory information management systems that align with international good practice (Abayomi et al., 2013; Matimba et al., 2016; Soo et al., 2017; Bendou et al., 2017; Ilboudo et al., 2017; Akinyemi et al., 2018; Abimiku et al., 2019). These publications have many practical suggestions on achieving ethically sound biobanking practices in resource-limited environments, with appropriate informed consent for the future use of samples.

5 Epidemiological Studies on Diseases, Traits and Risk Factors

An important outcome of the H3Africa Consortium is the development of large patient-control cohorts and population cross-sectional cohorts that provide an opportunity to assess the prevalence and distribution of cardiovascular and metabolic diseases and associated traits across the continent. In this section we describe 25 publications that examined and compared the distributions of several traits and associated risk factors, including body mass index (BMI), obesity, stroke, carotid intima-media thickness (cIMT) and hypertension.

A series of publications described the BMI distribution and obesity in older adults in a population cross-sectional study by the AWI-Gen group, and included data from over 10,000 individuals sampled from six centres, both rural and urban, across four African countries, (Ramsay et al., 2016; Ramsay et al., 2018; Asiki et al., 2018; Haregu et al., 2018; Micklesfield et al., 2018; Wagner et al., 2018; Boua et al., 2018; Nonterah et al., 2018; Mohamed et al., 2019; Mashinya et al., 2018). These studies emphasised differences in the BMI distribution among East, West and South African populations, with higher BMI in the South and East, compared to the West (Ramsay et al., 2018). Differences in obesity were observed between men and women in the South and East, with women disproportionately affected, and over 65% of women from Soweto, South Africa, having a BMI >30. Dual-energy X-ray absorptiometry (DXA)-derived measures of fat distribution in Soweto further showed that women not only had higher BMI but also higher waist circumference (WC), fat mass (FM), subcutaneous adipose tissue (SAT), visceral adipose tissue (VAT), FM/fat free soft tissue mass (FFSTM) ratio and body fat percentage, in comparison to men (Pisa et al., 2018). Statistical models simultaneously compared the impact of various risk factors and demonstrated regional differences across Africa and between men and women. An in-depth characterization of several known BMI-associated risk factors, such as socio-economic status, diet and tobacco and alcohol use, highlighted potential explanations for the observed differences. For instance, while higher estimated socio-economic status (SES) was strongly associated with higher BMI across several of the African study sites, as reported for other low- and middle-income countries, this association was much stronger among women (Ramsay et al., 2018; Haregu et al., 2018). The association of BMI to partnership status, and level of education was also found to differ between the sexes and according to geographic region. Factors that were detected to contribute to lower BMI included smoking, drinking and infectious diseases such as TB and HIV (Ramsay et al., 2018). A key insight from these studies was the identification of specific associations between BMI and ethnicity, even among geographically and genetically proximal ethnic groups such as the Zulu and Tswana from South Africa (Micklesfield et al., 2018) and Kassena and Nankana from Ghana (Nonterah et al., 2018). These differences point to potential partitioning of genetic risk based on the characterization of fine-scale differences in genetic background.

Other CVD-associated traits that were investigated in the pan-African AWI-Gen cohort included cIMT, hypertension and chronic kidney disease. The distribution of cIMT, an early marker of atherosclerosis measured using ultrasound, also showed strong regional variation, with the highest measurements in West African individuals, despite lower BMI levels (Nonterah et al., 2019). cIMT measurements were also found to demonstrate considerable sex differences, however, this was not uniform across the study sites. For example, women from Kenya were observed to have higher cIMT measurements compared to men whereas men in Burkina Faso demonstrated statistically significantly higher cIMT measurements compared to women. The major risk factors for higher cIMT identified in this study included increased age, BMI, systolic blood pressure, low-density lipoprotein cholesterol and smoking. High-density lipoprotein cholesterol (HDL-C), alcohol consumption and HIV were associated with lower cIMT.

The distribution of hypertension (defined as systolic blood pressure ≥140 mmHg and/or diastolic blood pressure ≥90 mmHg or taking anti-hypertensive medication) among older adult participants from the six study sites of the AWI-Gen study also showed striking regional differences in prevalence, awareness and control (Gómez-Olivé et al., 2017). The highest prevalence of hypertension was observed in Soweto (>50%) with several sites having significant differences between men and women. Sex-based comparisons detected a significantly higher prevalence of hypertension in women from Agincourt (South Africa), Dikgale (South Africa) and Nairobi (Kenya), while a reverse trend was observed for Nanoro (Burkina Faso). In a study on hypertension in a cohort of over 1000 adolescent sickle cell anaemia (SCA) patients from Tanzania, 8% had hypertension and risk factors that were independently associated with hypertension in SCA included age, BMI, pulse pressure and haemoglobin levels (Makubi et al., 2017).

Regional and sex differences were also observed for indices of kidney damage, including Estimated Glomerular Filtration Rate (eGFR) and albumin creatinine ratio (ACR), a measure of albuminuria. Chronic kidney disease (CKD), defined as eGFR<60 and ACR>3, had the highest prevalence in the South African study sites of AWI-Gen, being two-fold higher than in the West African study sites (George et al., 2019). Women were observed to have significantly higher prevalence compared to men. Major risk factors identified for kidney damage in this study included, age, hypertension, diabetes and HIV. Interestingly, about a third of the participants with CKD did not have diabetes, HIV infection or hypertension, suggesting the possible involvement of unidentified risk factors in African populations. An independent explorative study by the H3Africa Kidney Disease Research Network on the impact of perflouroalkyl substances (PFASS) (a class of compound used in household products that are associated with kidney dysfunction), demonstrated overall lower exposure to these compounds in African populations compared to American populations

(Sood et al., 2019). This study was based on 89 children and adolescents and showed that, in contrast to the American population-based National Health and Nutrition Examination Survey (NHANES) cohort that did not show any sex bias in the impact of PFASs, males in the African cohort were more strongly affected by the exposure compared to females.

A study aimed at characterising dyslipidaemia (hypercholesterolaemia, hypertriglyceridemia, elevated Low-density lipoprotein cholesterol (LDL-C) and low HDL-C) in 1839 individuals from the rural Ghana AWI-Gen study site (Novrongo) detected low HDL-C levels in about 60% of individuals (Agongo et al., 2018). Risk factors such as BMI, waist circumference and sub-cutaneous abdominal fat were found to be associated with different measures of dyslipidaemia in a sex-dependent manner. Notably, two of the well-known risk factors, age and diet, did not show any association with any form of dyslipidaemia, and SES was only found to be associated with HDL-C. As observed for BMI, the role of fine-scale ethnic differences (between Kassena and Nankana) was also observed for dyslipidaemia.

Phenotype data from the SIREN study, including 4200 individuals sampled across 15 study sites in Nigeria and Ghana, provided valuable estimates of the distribution of stroke and related risk factors in Central-West Africa (Owolabi et al., 2018). The primary risk factors associated with stroke included CVDs (hypertension, dyslipidaemia, diabetes and cardiac disease), diet (regular meat consumption, low green leafy vegetable consumption and added salt at the table), anthropometric indicators (elevated waist-to-hip ratio) and behavioural factors (stress, physical inactivity and current cigarette smoking) (Owolabi et al., 2018). Although some of these risk factors were also observed in a previous study (Feigin et al., 2016), the ranking of the contributions was found to be different in the SIREN cohort.

In attempts to identify biological parameters that could estimate the risk of stroke, the SIREN study investigated the role of cIMT as a risk factor using data from 555 participants from Nigeria. The results not only showed a strong association of cIMT with stroke but also demonstrated that it outperformed multivariable risk prediction schemes such as the Framingham's Risk Score (FRS) and the Omnibus Risk Score (ORS) in estimating the overall risk of stroke (Owolabi, Akpa, and Agunloye 2016). Electrocardiographic profiles among 1020 acute stroke patients identified 90% with abnormal left ventricular (LV) geometry and 30% with systolic dysfunction, and showed that severe LV systolic dysfunction was significantly associated with one-month mortality (Adeoye et al., 2019). The high predictive value and regional variations in cIMT (Nonterah et al., 2019) call for more large-scale pan-African studies to introduce risk screening and timeous interventions.

A more nuanced analysis based on the classification of stroke by type, demonstrated a clear age stratification (Sarfo, Ovbiagele et al., 2018). In patients 50 years or younger, haemorrhagic and ischemic stroke were observed to be almost equally common, while ischemic stroke was three-fold higher in patients over 50 years (Sarfo, Ovbiagele et al., 2018). Further, classification of the type of stroke by sex detected that haemorrhagic stroke was more common among men, but with increased severity in women (Akpalu et al., 2019). Most risk factors, with the exception of salt intake and income, were shared by both men and women. Finally, ECG abnormalities also varied between stroke type and sex with atrial fibrillation being more common in women and ischemic stroke patients (Adeoye, Ogah et al., 2017).

Infectious diseases and specific monogenic traits related to malaria and HIV, both of which are common in Central-West Africa, have the potential to affect stroke outcome. A preliminary investigation of the impact of SCA and HIV on stroke outcome in a set of 35 patients from Nigeria demonstrated a worse 30-day mortality in patients with sickle cell trait (HbAS) compared to patients with normal adult haemoglobin (HbAA) (Olowoyo et al., 2016). In contrast, the impact of HIV, based on a study of 540 stroke cases and 540 controls from Ghana, showed that HIV infection was not associated with stroke outcome (Sarfo, Opare-Sem et al., 2018). However, due to the low incidence of HIV in West Africa (~2% in the study site), as well as the limited number of sickle cell patients in the cohort (n=35), these results need to be validated in larger cohorts. A study in Mali examined neurological complications in patients with sickle cell disease or trait, and showed that six out of eight patients with neurological symptoms had a diagnosis of stroke (Landouré et al., 2017). These studies highlight the need for further in-depth investigation of multi-morbidity in African populations.

6 Disease-Associated Behaviour and Awareness Studies

Planning and implementing approaches to address diseases at a population-scale requires careful assessment of the overall awareness of the diseases and the factors that increase risk. Although a plethora of studies have reported on these aspects in non-African populations, the varied socio-cultural settings in Africa have the potential to result in unique behavioural patterns that require careful investigation across countries and communities. In parallel to collecting phenotype information related to diseases, some of the H3Africa groups, based on questionnaires and interviews, have also collected valuable data on awareness, psychological and behavioural attitudes of individuals, families and communities towards various diseases. This is well described in the reports from the SIREN group that provide key insights into awareness levels and attitudes towards stroke and stroke-associated risk factors (Ojagbemi et al., 2017; Sarfo, Nichols et al., 2017; Jenkins et al., 2018; Akinyemi et al., 2019). For example, independent surveys and interviews of stroke survivors from communities across Nigeria and Ghana show anxiety and stigma to be two major issues encountered by these patients (Jenkins, Arulogun, and Sarfo 2017; Ojagbemi et al., 2017; Akinyemi et al., 2019). The experience of stigma was found to be common among the stroke survivors interviewed, with 80% in a survey of 200 stroke survivors in Ghana reporting experiencing some form of stigma (Sarfo, Nichols et al., 2017). Interestingly, this was found to be more common among urban dwellers compared to rural, suggesting an important role of socio-cultural settings in this process. Similar investigations demonstrated about 20% of stroke survivors interviewed suffered from clinical anxiety and 70% of them were also found to suffer from depression (Ojagbemi et al., 2017). To investigate the source of the observed behavioural patterns, patient families and communities were interviewed, which showed clear gaps in awareness of the causes of stroke (Jenkins et al., 2018). Similarly, there was a major lack of understanding of the role of genetic susceptibility in stroke even among stroke survivors (57%) (Akinyemi et al., 2019). The studies strongly emphasize the need for developing comprehensive counselling approaches for patients and improving awareness at the community level for addressing these challenges.

A survey from the SIREN study also investigated the medication profile and adherence patterns in a set of stroke survivors in Ghana (Sarfo, Ovbiagele et al., 2017). The study showed the majority of patients to be on antihypertensive (94.5%), lipid-modifying (72.5%) and anti-platelet (65.6%) medication for the first twelve months following a stroke, and despite limited resources, 92% in this cohort remained on secondary prevention medications beyond a year. Other studies focused on the development of resources to enable efficient screening and intervention strategies, such as screening tools for stroke-associated depression (Ojagbemi et al., 2017b; 2017a), a monitoring tool for medication adherence (Jenkins, Burkett et al., 2016) and specialized training for healthcare professionals (Akinyemi et al., 2015). A major factor in the success of cohort surveys is the efficiencies with which the questionnaires capture data in a cohort. Three reports from the SIREN study describe the performance of different types of questionnaires in screening stroke/stroke free status among participants (Sarfo et al., 2016; Sarfo et al., 2016; 2017).

Publications involving the study of behavioural patterns included three studies from the ACCME group reporting on nuances and considerations in data collection. Dareng et al. (2015) investigated the cultural barriers preventing women from going for cancer screenings and found that there were several misconceptions about the cause of cervical cancer as well as various cultural, religious and social factors that prevented women from going for cervical cancer screening (Dareng et al., 2015). Given the importance of particular patterns of sexual behaviour in the transmission of diseases, the ACCME group also examined the reliability of self-reporting of sexual behaviour history in a group of 725 urbanized women from Nigeria (Dareng et al., 2017). The study demonstrated overall high reliability in self-reporting of sexual behaviour and also emphasized the importance of interviewing skills and questionnaires, in capturing self-reported sexual history data reliably. Visual inspection with acetic acid (VIA) by health workers has been suggested as a low-cost solution for cervical cancer screening. However, a high element of subjectivity has been a major concern about this approach. The third study from the ACCME group, compared the outcomes from the VIA-based diagnosis to that from specialists, and highlighted the lack of interobserver concordance and objectivity in diagnosing cervical cancer using nurse-based VIA (Dareng et al., 2018).

Publications addressing attitudes and awareness towards diseases also included studies on hearing loss (Gardiner et al., 2019) and sickle-cell disease (Wonkam and Hurst 2014). An interview-based investigation of the content of delusion in 200 Xhosa-speaking individuals with schizophrenia, demonstrated a strong impact of cultural influence with a majority of participants believing bewitchment as the cause of their mental illness (Campbell, Sibeko et al., 2017). A questionnaire-based evaluation of the awareness of hypertension in the AWI-Gen cohort, found a generally low awareness of high blood pressure in rural and urban communities (Gómez-Olivé et al., 2017). Moreover, even among those who had been diagnosed, control was observed to be poor. The study also reported a considerable amount of sex-specific and regional variation in the awareness of hypertension. Although, some of these studies are relatively small in scale, as a whole they provide critical base-line data for further investigations and demonstrate the significance of cohort surveys in informing interventions, both at the level of the clinics and in informing public health policies.

7 Genetics and Genomics Studies

The genetics and genomics studies reported by the H3Africa Consortium can be broadly categorized into studies of monogenic diseases, and complex diseases and traits. The latter included candidate gene studies and genome-wide association studies. In addition, there were population genetic studies. The monogenic disease studies predominantly addressed hearing impairment, neurological disorders and sickle cell anaemia.

Several studies, based on samples from Cameroon, South Africa and Ghana, examined the distribution of genetic variants for various forms of hearing impairment/deafness (HI) (Bosch et al., 2014; Wonkam et al., 2019; Adadey et al., 2019). These studies showed that while *GJB2* gene variants are largely responsible for HI in European populations, the contribution of variants in this gene to HI in African populations is limited, highlighting the necessity of next-generation sequencing and functional genomics-based studies to identify genes and mutations responsible for HI in Africans (Bosch et al., 2014; Wonkam et al., 2019; Adadey et al., 2019). In addition, two recent publications reported on a large family with fragile-X syndrome (FXS) (Kamga et al., 2020) and *MECP2* duplication syndrome (Tekendo-Ngongang et al., 2020) in families from Cameroon. The researchers also explored attitudes and understanding of genetic diseases in these settings. Another set of studies on neurological disorders reported cases of variation in the *FA2H* (Landouré et al., 2019), *KIF5A* (Guinto et al., 2017) and *SPG11* (Landouré et al., 2020) genes causing hereditary spastic paraplegias (HSPs) in three independent families from Mali. Another study from this group reported a case study of a *GARS* mutation causing autosomal dominant Charcot-Marie-Tooth (CMT) syndrome in a consanguineous family from Mali (Yalcouyé et al., 2019).

Despite being a monogenic trait, the severity of sickle cell disease (SCD) and drug responses have been found to be modulated by a number of factors. This motivated studies to identify genetic variants underpinning various SCD related phenotypes (Gabriel and Przybylski 2010). Three candidate gene studies reported investigations into the genetic associations of SCD-related phenotypes in a cohort from Cameroon. The phenotypes analyzed in these studies included fetal hemoglobin levels (Pule et al., 2015; Pule, Bitoungui et al., 2017; Pule, Mnika et al., 2017), renal dysfunction (Geard et al., 2017), vaso-occlusive crises and the frequency of hospitalization (Wonkam et al., 2018). Genetic investigations into SCD also included a study on the impact of the drug hydroxyurea (HU) on miRNA expression in peripheral blood isolates of SCD patients (Mnika et al., 2019). Among the miRNAs detected to be differentially expressed following HU treatment, more than half were found to be associated with HbF regulatory genes (*BCL11A*, *MYB*, *KLF-3*, and *SP1*), indicating the possible significance of these genes in deciphering the mechanism of action of the drug and its therapeutic targets (Mnika et al., 2019).

The candidate gene studies for disease susceptibility included 7 publications related to trypanosomiasis, based on cohorts from Malawi, Cameroon, Uganda, Guinea and Ivory Coast (Cooper et al., 2017; Ofon et al., 2017; Ahouty et al., 2017; Kaboré et al., 2017; Ofon et al., 2018; Kimuda et al., 2018; Kamoto et al., 2019). In addition to the apolipoprotein L1 (*APOL1*) trypanosomiasis protective variants, these studies also investigated the association of other genes with trypanosomiasis including *IL10, IL8, IL4, HLAG, TNFA, TNX4LB, IL6, IFNG, MIF, APOL1, HLAA, IL1B, IL4R, IL12B, IL12R, HP, HPR*, and *CFH*. However, the studies were not uniform in design, with one focusing only on *APOL1* variants (Cooper et al., 2017), while others included variants from 7 (Ofon et al., 2018), 8 (Kaboré et al., 2017), 16 (Ahouty et al., 2017), 17 (Ofon et al., 2017; Kamoto et al., 2019) and 18 genes (Kimuda et al., 2018). A key insight from these studies was the characterization of the complex and geographically dependent interaction of the *APOL1* G1 and G2 variants with the two major *Trypanosom*a subtypes. For example, while neither of the *APOL1* variants were protective against infection with the West African parasite, *Trypanosoma brucei gambiense* (Tbg), the *APOL1* G2 variant was found to provide more than five-fold greater protection against the East African parasite, *Trypanosoma brucei rhodesiense* (Tbr) (Cooper et al., 2017). Moreover, while the G1 variant was associated with a reduced number of parasites in the blood, thereby decreasing severity, the G2 variant increased the severity of the infection by Tbg (Cooper et al., 2017). Therefore, from an evolutionary perspective, populations from East Africa that are exposed to both Tbg and Tbr, would have needed to develop a balance between the protective and potentially negative impacts of the G2 allele. Perhaps due to these complexities and despite its highly protective role and association to trypanosomiasis in populations from Uganda (Cooper et al., 2017) and Malawi (Kamoto et al., 2019), Kimuda *et al.* failed to detect any association of G2 with Tbr in an independent Ugandan population (Kimuda et al., 2018). The candidate gene studies also identified trypanosomiasis-associated variants in *IL1A*, (Ofon et al., 2018), *IL1RN* (Ofon et al., 2018) and *IL6* (Kaboré et al., 2017) in different African populations. In addition, suggestive associations were detected for variants in *IL6* and *TFNA* (Ahouty et al., 2017). Interestingly, two independent candidate gene studies for ischemic stroke in West Africans also converged on variants in *APOL1* (Akinyemi et al., 2018) and *IL6* (Voight et al., 2012), underlining the significance of these genes in both infectious and cardiovascular diseases.

Based on data generated on the Metabochip genotyping array, a specialized tool for replicating and fine-mapping variants associated with diseases and traits (including type 2 diabetes, coronary artery disease and myocardial infarction, body mass index, glucose and insulin levels, blood lipid levels, and blood pressure) (Voight et al., 2012), Sahibdeen *et al.* investigated the genetics of body composition in a South African cohort of 2000 participants (Sahibdeen et al., 2018). In addition to common anthropometric measurements such as height, weight, hip and waist circumference, the study also tested the associations of quantitative traits based on DXA-derived measurements such as body fat percentage, fat mass, lean mass, visceral fat and subcutaneous fat. The study replicated signals around well-known loci such as *FTO* (for waist to hip ratio), *SEC16B* (for fat mass) and *WARS2* (for waist to hip ratio) in the South African cohort (Sahibdeen et al., 2018). Another study conducted on the same cohort identified associations of variants in/around the *NOS1AP, MYRF, POC1B, DACH1* and *LPL* genes with blood pressure in South Africans (Hendry et al., 2018).

During the initial planning and design of projects under the H3Africa Consortium, the necessity for a cost-effective, Africa-centric genotyping array to enable efficient discovery of complex-trait associations, was recognized. To address this, the Consortium, in association with Illumina Inc, designed a custom ~2.3 million single nucleotide variant genotyping-array (Mulder et al., 2018). This array was optimized to capture common African variants, based on more than 3000 African whole genome sequences, and was enriched with genetic variants previously reported to be associated with various phenotypes. Moreover, to enable efficient genotype imputation for this array, the Consortium developed a reference panel and core imputation facility (Mulder et al., 2018). As the H3Africa genotyping array only became available in early 2018, most of the GWAS studies were delayed, explaining the scarcity of full-scale genome-wide associations studies in the current H3Africa publication list.

A survey of abstracts presented by groups at H3Africa Consortium and other international meetings/conferences suggests that genome-wide data analysis for many H3Africa studies are approaching completion, and two were recently published. The first was published in early 2020, reporting on an exome sequencing-based case-control study of schizophrenia in 1800 South Africans, which identified novel damaging variants in key synaptic function associated genes to be enriched in the cases (Gulsuner et al., 2020). The second was a study on the interaction of genetic variants and smoking on cIMT in 1776 West-African male participants, and also was the first H3Africa study based on genotype data generated on the H3Africa array (Boua et al., 2020). These developments predict major insights into the genetics of complex traits in African populations, from GWASs conducted by individual H3Africa groups as well as cross-Consortium studies such as CHAIR.

The characterization of intrinsic population structure and major demographic features, such as admixture and relatedness, are key to the effective design of genetic association studies in African populations. The high genetic diversity and unique linkage-disequilibrium (LD) architecture along with the scarcity of genome-scale data from some parts of the continent raised particular challenges for studying African populations. Although many of the candidate gene studies have demonstrated extreme differences in the distribution of disease-associated alleles, based on only a limited number of variants, these studies did not provide suitable data for population-genetic research. The first study to investigate population structure at a genome-wide scale was a whole exome sequencing study of 314 children from Botswana and Uganda (Retshabile et al., 2018). In addition to demonstrating genomic distinctiveness of the Batswana population in comparison to 1000 Genomes Project populations, the study also identified a higher level of relatedness among the participants (Retshabile et al., 2018).

8 Bioinformatics and Genomics Capacity Development

Prior to the formation of the H3Africa Consortium, limited large scale genomic studies were being conducted on the African continent. As a result, there were few African-based researchers with the skills required to efficiently organize, store and analyse the large-scale biological datasets anticipated from the various H3Africa projects. With this in mind, the H3Africa Bioinformatics Network (H3ABioNet) was established to support H3Africa researchers through the development of bioinformatics capacity. H3ABioNet was established with over 30 nodes across 15 African countries with bioinformatics capacity ranging from established to intermediate, to little or no bioinformatics capacity. The initial overarching aim was to work towards building a network of nodes across Africa that would have the necessary skilled personnel and computational infrastructure to analyse the large H3Africa datasets. A major focus area of the initial activity for the network was core capacity development through the provision of teaching and training events, coupled with building core computational infrastructure at developing nodes (Table 9.1). This involved addressing some low-middle-income country (LMIC) specific challenges, such as limited/unstable network connectivity. Another major challenge was to monitor, follow up and advance the training imparted both at the participant and the node level, which was done through node accreditation in specific skills areas (e.g. GWAS and NGS workflows), internships and webinars. In addition, tools and resources were developed to facilitate communication between H3Africa projects and to ensure that a framework and policy guidelines were developed and implemented for the efficient organization, storage and analysis of the various datasets being generated (Table 9.1).

Building on this foundation, the emphasis of the network gradually shifted from capacity building to developing sustainable applied informatics solutions to continue to support the emerging requirements of the H3Africa Consortium.

TABLE 9.1 Approaches and tools employed by H3ABioNet to address the challenges in genomics capacity development across the H3Africa Consortium

Challenge	**Approach**
Core infrastructure development	– Computational resources: 15 servers equipped with a total of 512 cores, 2384GB RAM and 120TB were installed – Training: hands on practical experience was provided with setting up and managing computing resources (Mulder et al. 2016)
Unstable internet connectivity	– Regular monitoring and troubleshooting of problematic network connections at each of the nodes – Globus Online service was used to facilitate the efficient transfer of large datasets over the internet – At sites identified to have limited internet connectivity, eBioKits (stand-alone devices containing pre-installed tools and databases) were set up (Mulder et al. 2016; Hernández-de-Diego et al. 2017)
Core capacity development	– Extensive training: Over 30 face-to-face workshops were held from 2012 to 2019 on data management, system administration, genome-wide association studies (GWAS), next generation sequencing (NGS) data analysis, metagenomics, grant writing and professional development (Aron et al. 2017)
Follow up on capacity development	– An internship program was initiated to provide individuals with the opportunity to spend an extended period of time at a partner institute in order to develop specialized skills (Aron et al. 2017) – A webinar series was initiated to further encourage communication and collaboration between nodes (Fadlelmola et al. 2019)
Sustainable capacity development	– Bioinformatics course: a 3-month Introduction to Bioinformatics Training (IBT) online course, which has successfully run annually since 2016 (In 2016 alone, there were 364 participants across 20 classrooms in 10 African countries) (Gurwitz et al. 2017). – Curriculum development: The African Genomic Medicine Training (AGMT) course was developed that initially focused on a needs-assessment-based comprehensive genomics medicine curriculum, aimed, in the first instance, at nurses. The first course in 2017 included 225 participants in 19 classrooms across 11 countries, and it has been held annually since then (Nembaware and Mulder 2019). – Formation of an African Bioinformatics Education Committee tasked with developing a curriculum for setting up a bioinformatics degree program at African institutions (Mulder et al. 2016; Shaffer et al. 2019)

TABLE 9.1 Approaches and tools employed by H3ABioNet to address the challenges in genomics capacity development across the H3Africa Consortium (*cont.*)

Challenge	**Approach**
Evaluation of capacity development	– Node accreditation exercises were designed to assess the capacity of H3ABioNet nodes to properly process and analyse a variety of datasets (Jongeneel et al. 2017). – NetCapDB, a database for automated capture of quantitative metrics for bioinformatics capacity at each of the nodes, was established (Bendou et al. 2016) – HtrainDB, a database to track the career progression of individuals who have attended training events, was developed (Mulder et al. 2018)
Development of computational resources and research support	– Pipelines and workflows: skilled individuals were tasked with using the latest workflow languages to develop workflows for variant calling from NGS data, 16s rRNA sequence analysis for metagenomics, GWAS genotype calling and data analysis and imputation for SNP genotyping arrays (Baichoo et al. 2018) – Tools were developed for genomic analyses (Please see text for details) – Hackathons were developed and run to promote skills and tool development (Ghouila et al. 2018). – The H3Africa Catalogue was developed as a public resource to list H3Africa metadata and samples for potential external users (Mulder et al. 2018). – The H3Africa data archive was developed to store genomic and phenotype data generated by H3Africa projects (Mulder et al. 2016; Mulder et al. 2018). – An online helpdesk was developed and is backed by a team with a diverse range of expertise to address general and specialised questions (Kumuthini et al. 2019).

This was achieved through advanced capacity development across the established network, setting up a data coordinating centre, providing high-quality informatics support, enabling and enhancing innovative translational research and continuing to build and promote the network beyond the Consortium to foster and promote external collaboration. To ensure that training activities are aligned with international standards and best practices in bioinformatics, H3ABioNet worked closely with international training organisations such as the Global Organisation for Bioinformatics Learning, Education and Training (GOBLET), the European life-sciences Infrastructure for biological Information (ELIXIR) and the International Society for Computational Biology (ISCB). An Education Summit was held in May 2019 to bring together bioinformatics educators and trainers to refine core competencies and define guidelines on their application, and to develop additional bioinformatics training resources for the community. H3ABioNet has adopted and applied these competencies in the development of core training courses (Mulder et al., 2016; Mulder et al., 2018). Although still a challenging area, H3ABioNet has made great strides in building large-scale data analysis capacity on the continent.

Against the backdrop of a critical lack of bioinformatics expertise in Africa, a major accomplishment for the network was the development of a large number of resources and tools to support the analysis and exploration of data being generated by the larger H3Africa Consortium (Table 9.1). The tools include a novel post-GWAS approach called *ancGWAS* that was developed to improve the detection of disease variants with small effects by integrating the signals from a GWAS dataset, the local ancestry information and the SNP pairwise linkage disequilibrium in admixed populations (4-way complex admixture) into a protein-protein interaction network (Chimusa et al., 2016). Further exploration of the limitations of the current methods available in this area of post-GWAS analysis in admixed populations has been conducted (Chimusa et al., 2018; Geza et al., 2019; Awany, Allali, and Chimusa 2019; Chimusa et al., 2019) to identify the caveats and develop better suited methods to identify variants with small to moderate effects. The inability to access and use high-performance computing (HPC) clusters via a command line terminal is usually a limiting factor for most researchers wanting to analyse large datasets. Job Management System (JMS) was developed as a web-based front-end to an HPC cluster that allows users to create workflows based on different tools and to run, manage and monitor jobs on an HPC via an intuitive web-based graphical user interface (Brown et al., 2015). Several projects within the Consortium are centred around the identification and functional impact of African-specific genetic variants. The network also contributed to the development of specialized ontologies for sickle cell disease (Mulder et al., 2016; Adekile et al., 2019) and hearing impairment (Hotchkiss et al., 2019). A Human Mutation Analysis (HUMA) web server and database was designed to integrate sequence data, protein structure variation and disease data into a single connected database (Brown and Tastan Bishop 2018). HUMA allows for the uploading and interrogation of genetic variant data and the prediction of the impact at the protein structural level. A number of additional tools have been developed examining novel methods for modelling the molecular dynamics of a protein including MD-TASK and MODE-TASK (Brown et al., 2017; Ross et al., 2018). On the pathogen front, Genome Detective is a web-based application that allows for the rapid assembly and identification of viral genomes from high throughput sequencing data and this tool has been used to accurately classify Dengue, Chikungunya and Zika viruses down to their species and sub-species levels (Vilsker et al., 2019; Fonseca et al., 2019).

9 Microbiome and Pathogen Studies

Several H3Africa projects are focusing on the contribution of the microbiome to disease susceptibility and progression in African settings. While a healthy microbiome promotes good health, changes in the microbiome can lead to severe disease, especially in younger children and immune-compromised individuals. In addition, outbreaks such as Ebola, Lassa Fever, Malaria and TB contribute significantly to the disease burden on the continent, especially in West Africa, and it is important to efficiently characterise circulating and novel viral pathogens using current and affordable technologies to reduce the impact of viral outbreaks (Folarin et al., 2016). Furthermore, understanding the host-pathogen interactions could lead to advancements in clinical care and treatment.

The Respiratory Microbiota of African Children (ReMac) Center has three projects aimed at describing the nasopharyngeal (NP) and upper airways microbiota and understanding the impact of lower respiratory tract infection and environmental exposures on the nasal microbiota in African children. *Streptoccocus pneumoniae* is the major bacterial cause of upper respiratory infections such as pneumonia in children under the age of 5 with a particularly high incidence in Africa (Rudan et al., 2013). Two independent longitudinal studies report on aspects of antimicrobial resistance to pneumococcal immunization with the pneumococcal conjugate vaccine (PCV13) aimed at reducing the colonization of the NP airways by 13 pneumococcal serotypes in children (Dube et al., 2018; Manenzhe et al., 2019). Similar investigations into carriage patterns of *Staphylococcus aureus,* also known to colonise the NP epithelial surfaces, showed that it is a risk factor for a variety of other infections (Abdulgader et al., 2019). The nasal microbiome of children with pulmonary TB was also studied (Dube et al., 2016). The NP microbiome was shown to be influenced by environmental factors such as air pollution and tobacco smoke, and perturbation of the diversity of NP bacteria could lead to the development of lower respiratory tract infections. Similarly, another study aimed at examining the effect of indoor air pollution and environmental tobacco smoke on the NP microbiome (in a cohort of mother-infant pairs during the first 12 months of life) showed exposure to antenatal environmental tobacco smoke to be associated with *Streptococcus pneumoniae* carriage in mothers, while postnatal tobacco smoke exposure was associated with carriage in infants (Vanker et al., 2019). Moreover, postnatal air pollution exposure was also associated with NP carriage of *Haemophilus influenzae* or *Moraxella catarrhalis* in infants. Therefore, exposure to environmental factors of both the mother and infant could result in an increased risk of lower respiratory tract infections.

The African Collaborative Center for Microbiome and Genomics Research (ACCME) aims to study the relationship between human papillomavirus (HPV), the vaginal microbiome and cervical cancer (Adebamowo, Dareng et al., 2017). Initial publications from this group assessed the incidence of cancer and cancer-associated infections in two Nigerian cancer registries, based on information collected between 2012 and 2014. A study examining the incidence of cancers attributed to infections revealed that 24% of cancers were associated to infections, while 22% were attributable to infections with the most common infectious agents being EBV, HPV, Hepatitis B and C, HIV and HHV8 (Odutola et al., 2016). A subsequent ACCME study confirmed that HPV infection was associated with a significant proportion of cancer cases in Nigerian women (Jedy-Agba et al., 2016). To further explore the prevalence of HPV, the age prevalence of HPV infection was determined in a sample of 278 women who presented for cervical cancer screening in Abuja, Nigeria. Based on questionnaire data, demographic characteristics, risk factors for cervical cancer and HPV genotyping using DNA extracted from cervical cells, the prevalence of HPV was detected to be 37% with the most prevalent type being HPV 35. HPV infection in women under 30 years was higher (52%) than those women over the age of 45 years (23%), showing a linear association between age and the prevalence of HPV infection (Akarolo-Anthony et al., 2014).

The persistence of high-risk HPV (hrHPV) infection plays a major role in the incidence and progression of cervical cancer and it is proposed that the vaginal microbiota play an important role in the persistence of hrHPV infection. Studies examining the vaginal microbiota and prevalent hrHPV infection in women in Nigeria found a suggestive association between prevalent hrHPV infection and a reduced abundance of *Lactobacillus sp.* and an increased abundance of the genera *Prevotella* and *Leptotrichia* in HIV-negative women (Dareng et al., 2016). Possible association between *Mycoplasma hominis* and persistent hrHPV in the vaginal microbiota was also reported (Adebamowo, Ma et al., 2017). In addition, significant associations between prevalent and persistent hrHPV infections and specific HLA haplotypes were detected, suggesting a possible genetic risk factor for hrHPV infection in African women

(Adebamowo and Adeyemo 2019). Analysis of the role of HIV infection in cervical cancer in women indicates possible interactions between HIV and hrHPV (Adebamowo, Olawande et al., 2017; Adebamowo et al., 2018). Furthermore, association between cervical HPV11, HIV and genital warts was also observed in women in Nigeria (Dareng et al., 2019). These studies highlight the burden of HPV infection in cervical cancer and the role of potential screening and other intervention strategies such as vaccines to reduce the incidence of cervical cancer in African women.

Infectious diseases contribute significantly to the disease burden in Africa. In particular, West African countries are exposed to periodic outbreaks of viral diseases such as Ebola and Lassa Fever. A number of H3Africa studies have focused on sequencing-based in-depth analysis of these pathogens to generate insights into infection outbreaks. These include studies of Ebola pathogens (Folarin et al., 2016), RNA viruses (Stremlau et al., 2015) and Lassa virus genomes (Siddle et al., 2018). A study of RNA viruses in unexplained acute febrile disease (UAFI) patients and healthy individuals in a Nigerian community revealed the presence of many well characterized viruses in the blood of the UAFI patients (Stremlau et al., 2015). These included HIV-1, hepatitis B and C and Lassa virus. The study also identified two novel rhabdoviruses, Ekpoma virus 1 (EKV-1) and Ekpoma virus 2 (EKV-2), isolated from two healthy female individuals, which are similar to the Bas-Congo virus identified in a patient with viral haemorrhagic fever. Further analysis revealed exposure to EKV-1 and EKV-2 in a larger healthier cohort at 10% and 50% respectively (Stremlau et al., 2015).

While the incidence of malaria infection and the mortality rate has declined in most African countries, it is still a major health threat, especially in certain parts of the continent where malaria is endemic. The identification and understanding of the genomic diversity of *Plasmodium falciparum* have been explored using various approaches, however, a standardized method is still needed to monitor population dynamics, transmission and drug resistance between closely related parasites. A study utilizing the malaria barcode, which is a 24 single nucleotide polymorphism based molecular barcode assay, was able to differentiate between closely related *P. falciparum* infections in two urban cities in Nigeria. The results showed a low level of intra-population diversity in *P. falciparum* and a low degree of polygenomic infections across the two groups that had not been observed before. This indicates that the 24-SNP barcode method is efficient at monitoring changes in parasite population diversity and divergence over time and can be extended to explore transmission patterns and drug resistance in future studies (Bankole et al., 2018).

Tuberculosis is another major illness that impacts millions of people in Africa. A number of studies based on an Ethiopian cohort, generated insights into aspects of tuberculosis infection, diagnosis and treatment. Studies on *Mycobacterium tuberculosis* complex (MBTC) diversity (Nuru et al., 2015; Bedewi et al., 2017) showed significant geographic diversity of bacterial strains within a country and reported several strains that were not present in the molecular genotyping databases of MTBC. As the accurate diagnosis of TB and latent TB infection (LTBI) play an integral role in administering the correct treatment regime to tackle the infection, the detection of LTBI plays a key role in addressing the disease. Culture-based methods are routinely used to diagnose of active TB, but have limited sensitivity and efficiency. A study reporting an antibody microarray-based approach for studying abundance of cytokine and chemokine showed an increase in IFN-γ and interleukin 17 levels that might serve as good indicators of LTBI (Teklu et al., 2018). Moreover, the chemokines RANTES and MIP-1β showed the potential for use in differentiating between combined active TB and LTBI groups, and the unaffected control group (Teklu et al., 2018). Similarly, analysis of the performance of the GenoType MTBDRplus assay, an assay aimed at investigating the development of multidrug-resistant strains (MDR-TB) also demonstrated the possibility of improving both efficiency and reducing the time needed to diagnose MDR-TB (Bedewi et al., 2016). Two studies that aimed to estimate the distribution of MDR-TB in Ethiopia showed a relatively lower number of MDR isolates in new TB cases, compared to previous studies hinting at a positive impact of current intervention measures (Bedewi et al., 2017; Wondale et al., 2018; Alelign et al., 2019).

10 Epilogue - H3Africa Data in Population-Genetics Research

Although the H3Africa Consortium's main objective is to identify genetic underpinnings of communicable and non-communicable diseases in Africa, the data generated for these studies are playing an instrumental role in generating insights into the population structure and demographic history of African populations. Two key studies pertinent to African population genetics were published just after the period under review, and are briefly discussed because of their relevance to the theme of this book.

The first is a South African study based on data from the AWI-Gen project (Sengupta et al., 2021). It demonstrates the valuable role of consortium data in enhancing our understanding of the genetics of a particular country or geographic region. This population-cross sectional dataset, generated primarily for studying cardio-metabolic diseases (Ramsay et al., 2016), included most of the major South African Bantu-speaking groups, was used to investigate population structure. The analyses of genome-wide genetic data demonstrated a clear population structure within the South-Eastern Bantu-speaking (SEB) ethnolinguistic groups in the country. The structure showed correspondence with geographic location and languages and provided insights into the migration and admixture events that may have contributed to the current distribution of SEB groups across the country. Moreover, by recording parental and grandparental ethnicity it became apparent that recent inter-group admixture has made the study of population structure more complex and that this would need to be considered when performing disease-association studies.

The second study is based on whole-genome sequence data that was generated primarily for the design of a genotyping array for the Consortium, and resulted in a landmark population genetics paper for H3Africa. This pan-African study included participants from 50 ethnolinguistic groups sampled across 13 countries and provided the most comprehensive description of genetic diversity and population structure across African populations (Choudhury et al., 2020). Despite the recent inclusion of variants from thousands of African genomes in current databases, the study identified over 3 million novel variants from only 300 genomes. Some of the novel findings included the detection of gene flow events that identified East African gene flow into a population in Nigeria, and rain-forest forager gene flow into a population from Uganda. This highlights the potential of genetic studies to detect major differences in genetic and demographic histories of geographically neighbouring populations. These differences are also pertinent to the distribution of disease-causing variants such as the sickle cell mutation (HbS). While supporting the overlap in the distribution of HbS and malaria in Africa, this study noted marked differences in HbS allele frequency in two presently neighbouring but historically distant populations from Uganda. A study based on a subset of the data further explored the genetic diversity of the Nilo-Saharan populations and their genetic contributions to the Niger-Congo populations from neighbouring regions (Mulindwa et al., 2020).

These studies underline the promise of novel population genetic insights from genomic data generated by the H3Africa Consortium projects, and emphasise the need for including previously understudied geographic regions and ethnic groups. The aggregation and in-depth analysis of the genotype-array and whole-genome sequence data being generated by H3Africa studies promise to provide robust insights into genetic diversity and demographic history of African ethnolinguistic groups. Moreover, African-centric resources such as a genotyping array, imputation panel, local ancestry reference panels and variation databases are being developed by the Consortium and are expected to help researchers to capture and analyse African genetic data at a greater depth.

11 Conclusions

Over a period of seven years the publications from the H3Africa Consortium have shown a significant shift from reviews and perspectives to original research papers that contribute new knowledge to understanding health and disease in Africa (Figure 9.4B). Although presently skewed toward phenotype and behavioural studies, many genetics and genomics papers have been published and are expected to increase as several projects analyse and interpret their genomic data. Key words from the titles of the 169 core H3Africa papers have been assessed and quantified to highlight the most active themes under six domain categories (Figure 9.5). Once H3Africa Consortium project data are submitted to the European Genome-Phenome archive and access is provided by the H3Africa Data and Biospecimens Access Committee the number of publications that use these resources for discovery, validation and comparative purposes will increase. We anticipate that the next three years will be characterized by more complex epidemiological models to tease out disease mechanisms, and by genomic studies to identify genetic variants associated with disease risk. The genome-wide genotype data and whole-genome sequence data will be available to the research community to further explore population genetics studies to reveal hidden population demographic histories and to compare these findings to hypotheses put forward by linguistic and anthropological research. In addition, the Consortium will contribute to developing African-appropriate approaches to data analysis and to a better understanding of the value that African genetic diversity, together with rich phenotype, behavioural and infection data, can bring to a global understanding of health and disease.

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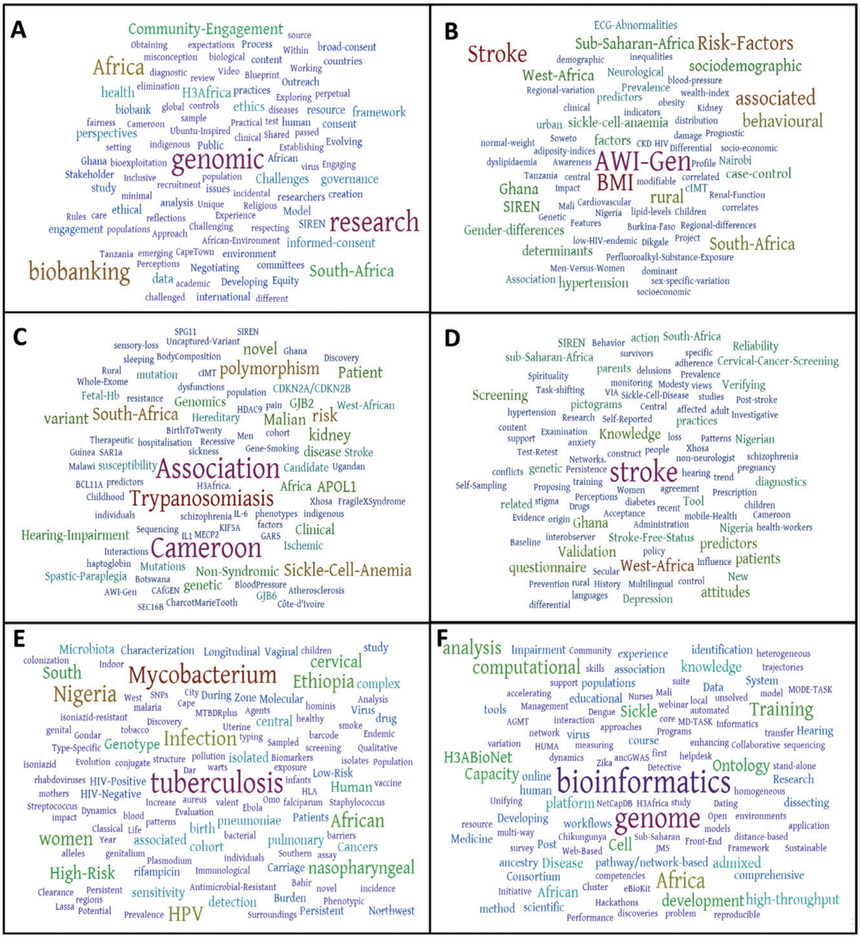

FIGURE 9.5 Wordgrams constructed using the text of the titles of the papers in six research categories: (A) Governance, Ethics, Community Engagement, and Biobanking studies (B) Epidemiological studies on diseases, traits and risk factors (C) Genetics and Genomics Studies (D) Disease-associated behaviour and awareness studies (E) Microbiome and Pathogen Studies (F) Bioinformatics and Genomics Capacity Development. Common English words (e.g. and, the, as) were filtered out of the text from the titles, as well as qualifiers that are only meaningful in a particular context (e.g. summary, collection)
SOFTWARE SOURCE HTTPS://WORDITOUT.COM/WORD-CLOUD

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CHAPTER 10

Disentangling the Impact of the Transatlantic Slave Trade in African Diaspora Populations from a Genomic Perspective

Cesar A. Fortes-Lima

1 Introduction

The transatlantic slave trade (TAST) was the largest forced migration in human history. Between the 15th and the 19th century, around twelve million Africans were forcibly displaced from their countries to be enslaved (that means around 30,000 captives a year over three and a half centuries). Enslaved Africans were taken from African slaving coasts that stretched thousands of miles, from Senegal to Angola, and even round the Cape and on to Mozambique (Eltis 2013). The largest number (around 95%) of slaves arrived in Latin America, with ~43% disembarked in South America, ~52% in the Caribbean, while the remaining 5% arrived in what has become today the United States (Eltis and Richardson 2015). This forced and massive migration of people radically changed the genetic landscape of present-day populations in the Americas (Adhikari et al., 2017). Today African-descendant populations in the Americas seek to clarify their genetic ancestry and to better understand their genetic identity and ancestral origins (Nelson 2016).

According to historical resources, from 1501 to 1867 enslaved Africans were embarked from eight major historical coastal regions in sub-Saharan Africa: 5.7% of the captives were from Senegambia, 3.2% from Sierra Leone, 2.7% from Windward Coast, 9.6% from Gold Coast, 16.1% from Bight of Benin, 12.3% from the Bight of Biafra, 46.3% from West Central Africa, and 4.1% from Southeast Africa (Figure 10.1). West Central Africa region (coastal region from present-day Gabon to Angola) was always the largest regional point for captives throughout most of the TAST period, and much of the trade there was focused in present-day Angola. As the TAST expanded after 1641, slaving regions such as Gold Coast, the Bights of Benin and Biafra, and West Central Africa became more prominent than they had been before (Figure 10.1). However, there are important gaps in historical sources regarding the ancestral origin of the captives in mainland Africa. In addition, the proportions of African captives disembarked in the Americas differed remarkably among North, Central and

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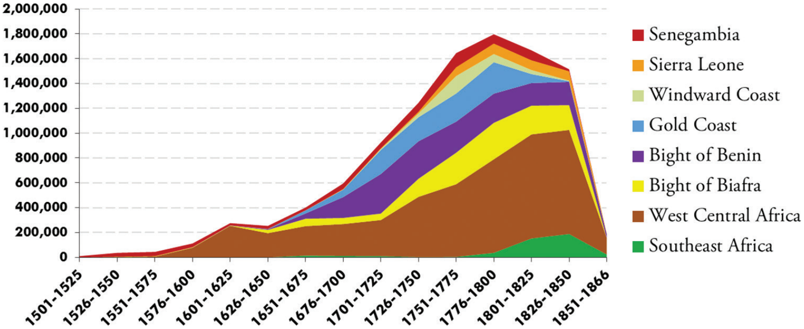

FIGURE 10.1 Estimated number of enslaved Africans disembarked in the Americas from 1501 to 1866 leaving African coastal regions
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especially in South America (Eltis 2013). To fill those gaps and shed new light on one of the darkest chapters in human history, recent genomic studies provide crucial information about the ancestors of African-descendant populations and their current genetic makeup.

Genome-wide studies analysing millions of genetic markers (single nucleotide polymorphisms, or SNPs) increased our understanding of the genetic heritage in African descendants, and more in particular communities established by runaway enslaved Africans during the slave trade in the Americas. One of the first genome-wide studies, authors focused on the genetic admixture of African-American groups in the United States (Bryc et al., 2010; Zakharia et al., 2009), and tried to ping-point their African ancestral origins. However, they used a limited number of African populations in their analyses, especially from western Africa. In this last decade, the development of new genome-wide methods for the production of dense genome-wide SNP data of more and more African populations, including whole-genome sequencing, have allowed us to address more complex questions about the genetic diversity in the Americas and the African Diaspora (Adhikari et al., 2017; Fortes-Lima and Dugoujon 2018). Therefore, recent studies that generated and analysed new genomic data of reference African, European and Native American populations help to gain a better understanding of the admixture history of African-descendant populations and to reconstruct trans-continental migrations.

To highlight important contributions from recent genome-wide studies, this chapter will review new insights about events that took place during and after the TAST period, the impact of this forced mass migration in the genomic diversity of African Diaspora populations, the formation of run-away communities from South America, and how genomics and paleogenomics research can unravel the history of the slave trade.

2 Brief Introduction about the Transatlantic Slave Trade and the Abolitionist Movement

The TAST era is generally considered to have begun uninterrupted human traffic in 1501, when vessels crossing the Atlantic from Spain begun to carry African captives for sale in the Greater Antilles (the largest islands of the West Indies); and ended in 1867, when the last slave vessel from Africa thought to have disembarked its captives in Cuba (Eltis and Richardson 2015). Most historians break down the slave-trade era into three main time periods that reflect the principal slave-trading nations' entry into and departure from the slave trade (Eltis et al., 2017). In the first period, the Spanish and the Portuguese established the first European empires in the Americas, with large assists from northern Italian capital and maritime expertise, they were pioneered the early slave trade. The Iberian powers dominated the trade, with Portugal and Spain being united in 1580-1640 and, in commercial terms, their separation took place in 1641 (Eltis and Richardson, 2015).

A second phase of the trade started around 1642, when the northern European nations established their own colonies in the Americas, and almost immediately began to engage in the slave trade, joined by traders from mainland North America. Before 1700, the Dutch, French, English, Danish, and Swedes systematically sent vessels to Africa to obtain captives. By the early 18th century, the slave trade systems in North and South America were firmly established. At that period, the Portuguese flag no longer had much of a presence in the slave traffic to Spanish America and the Caribbean but had the major control of the slave trade in South America, which was conducted not from Portugal but from Brazil (Eltis and Richardson, 2015). The second phase ended in 1808, when the British and the U.S. anti-slave-trade laws of 1807-1808 took effect, and other northern European nations began disengaging from the slave trade.

Anti-slavery movements ushered in the third period, which lasted through 1867 and during which abolition and suppression movements dramatically altered the pattern of participation in the slave trade. With the gradual withdrawal of the northern European powers, the TAST came to be dominated once again by the Portuguese and the Spanish, operating largely from their bases in Brazil and Cuba respectively, and against a background of growing abolitionist and suppression activities (Eltis and Richardson, 2015). Besides, the abolition of slavery in the Atlantic world occurred during the 19th century, its origins are generally recognized to be intellectual grown during the 18th century, the age of Enlightenment, with the political turmoil of the "Age of Revolution" and the economic transformations associated with the development of modern industrial capitalism (Inikori and Engerman 1992). The abolitionist movement started with small groups of Europeans and North Americans, who began to turn against the entrenched and lucrative business of slave trading. Later, maritime nations in Europe and North America, led by Danish and British governments, finally began legislating to ban the slave trade throughout the Atlantic world (Walvin 2013).

Although antislavery ideas circulated much more widely beginning in the 1760s, the first sustained effort to do something about slavery began in the 1780s, particularly with slave rebellions and the British campaign to end the slave trade (Walvin 2013). The Saint Domingue Revolution was a well-known slave rebellion in the French colony that broke out in 1791 and soon turned into a revolution that led to the freedom of 500,000 enslaved Africans, and ultimately to the creation of the Republic of Haiti in 1804 (Eltis et al., 2017). Consequently, the Saint Domingue Revolution closed down the biggest slave market in the Caribbean, and added a new sense of urgency to the issue in European countries and the United States. In the first decade of the 19th century, the British and the US governments abolished the slave trade in 1807. Although, the institution of slavery itself lived in the British colonies until 1838 and in the United States until 1865. Despite their efforts, over 2.5 million Africans were further transported across the Atlantic as slaves in the decades of the mid-19th century (Eltis et al., 2017). During the slave trade periods, European colonies captured African people from different regions and at different periods (Figure 10.1). Therefore, present-day African Diaspora populations have complex population history and African origins due to their different European colonial past. As a result, the genomic landscape of present-day African-descendant populations in the Americas was shaped by centuries of migration, isolation, growth, selection, and admixture between recent migrants and indigenous populations.

3 Genetic History of African-Descendants in North America

In the USA, a former British colony, African-Americans have a complex demographic history of admixture and migration during and after the slave trade, due to mass migrations during the TAST and after during the great African-American migration that shaped the current genetic background in the USA (Baharian et al., 2016; Dai et al., 2020). In this context, recent genome-wide studies have shown that African-Americans have chromosomal segments with predominantly African and European ancestries and, over the past 400 years, their admixture patterns have also changed between different

African-American groups across the country (Baharian et al., 2016; Bryc et al., 2015; Dai et al., 2020; Han et al., 2017).

An outstanding genomic study was performed by the CAAPA Consortium,[1] which analysed whole-genome sequencing data of a large number of African-descendant populations selected from North America, South America, and the Caribbean (Mathias et al., 2016). In total, 642 African descendants from fifteen American populations were sequenced to investigate admixture patterns across the Americas. Among the 328 African Americans in the United States, the authors detected a high proportion of African ancestry (on average 80%). Due to their complex history of admixture, participants from selected populations across the Americas have a large variation in their admixture patterns (ranging from 27% among Puerto Ricans to 89% among Jamaicans) (Figure 10.2), including among people who self-identify as African-descendants. In addition, sex-biased admixture patterns were also different between groups (Mathias et al., 2016). Altogether, these results underline the erroneous vision of a homogeneous pattern of African genetic ancestry among African Diaspora populations in the Americas.

In a large-scale genome-wide study, Patin et al. (2017) estimated the demographic history and African ancestral origins of African-American populations by analysing 5,244 individuals from three large cohorts in the USA. The authors analysed the genetic diversity (around one million SNPs) of 1,033 participants from the *"eMERGE"* cohort from Chicago and Nashville, 1,052 participants from the *"Health ABC"* cohort from Memphis and Pittsburgh, and 3,159 participants from the *"Multiethnic"* cohort in Los Angeles. These cohorts have between 73% and 78% of African genetic ancestry (Patin et al., 2017). To more precisely trace their African genetic origin, the authors compared their African chromosomal segments with a background of 1,955 individuals from West and West-Central African populations currently living in the major historical regions of slavery. Almost 50% of their genome was estimated to come from the former region of Bight of Benin (present-day Togo, Benin and western Nigeria), 30% from West and Central Africa (present-day Angola), 13% from Senegambia, and 7% from the Windward Coast (Patin et al., 2017). It is interesting to note that a small amount (4.8%) of the genetic diversity of enslaved Africans who were forced to move to the USA comes from Bantu-speaking populations from western Africa that had about 16% of rainforest hunter-gatherer (RHG) ancestry before they

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[1] The CAAPA Consortium studies the genomic diversity of a large number of African descendants with asthma and non-asthma selected from North America, South America, the Caribbean, and continental Africa, to represent a wide range of African ancestry. More detailed information can be found on the site (https://www.caapa-project.org).

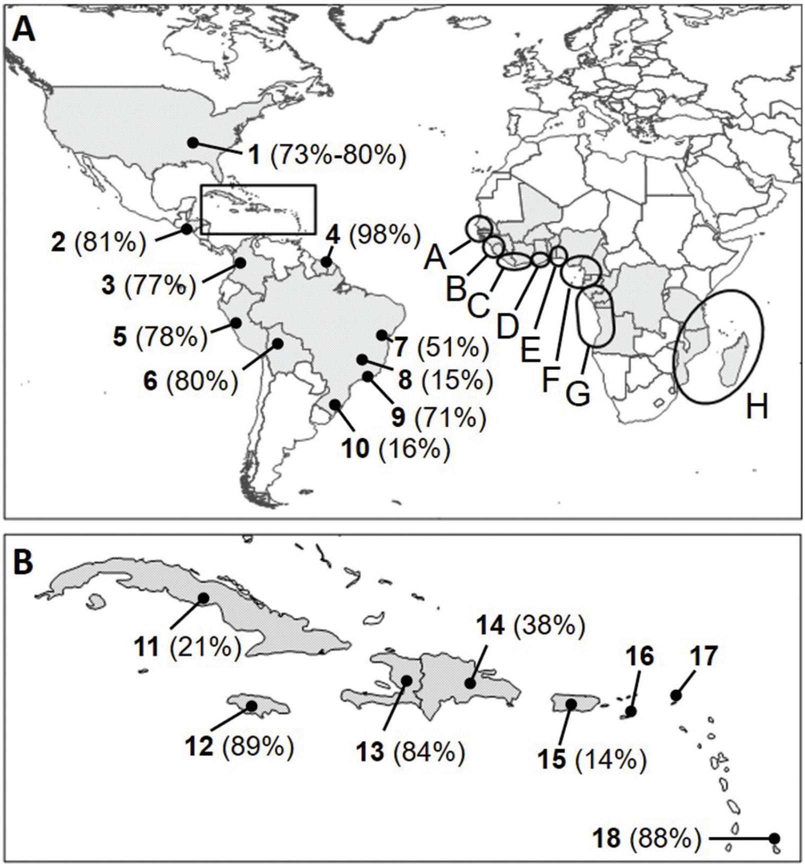

FIGURE 10.2 Geographical location of the African-descendant populations described in this chapter (and their estimated average of African ancestry in parenthesis). (A) African-descendant populations from North, Central and South America: 1- African-Americans from the United States; 2- Garifunas from Honduras; 3- African-Colombians from Chòco in Colombia; 4- Noir Marron from French Guiana and Suriname; 5- African-Peruvians from Peru; 6- African-Bolivians from the Yungas Valley in Bolivia; 7–10 African-Brazilians in Brazil. (B) In detail, figure showing populations in the Caribbean: 11 Cuba; 12 Jamaica; 13 Haiti; 14 Dominican Republic; 15 Puerto Rico; 16 Sainte-Croix; 17 Saint-Martin; and 18 Barbados. Figure also shows the eight historical African regions at the time of the slave trade in Africa: A- Senegambia; B- Sierra Leone; C- Windward Coast; D- Gold Coast; E- Bight of Benin; F- Bight of Biafra; G- Central West African; and H- South-East African slave region

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migrationed to the New World (Patin et al., 2017). Therefore, the genetic background and admixture dynamics of African-American groups in the United

States are more complex than previously thought, due to the complexity of their African ancestral origins and the history of African populations before the slave trade period (Schlebusch and Jakobsson 2018). In order to better understand the genetic diversity of African Diaspora populations, it is very important to first understand the population history in the African continent.

4 Genetic Heritage of African-Descendants in South America

Between 1526 and 1875, about seven million Africans were forcibly moved to South America (Eltis and Richardson 2015). During this period, enslaved Africans actively mobilized with the creation of systems of resistance against the inhuman repression that accompanied slavery. To escape captivity, a large number of slaves strongly fought against European slave systems. Between the end of 1680 and the beginning of 1712 began the phenomenon known as *marronnage*, characterized by massive escapes of enslaved Africans who then grouped in small and independent communities of free people, known as Maroon[2] communities (Price 2013b). Currently, the cultural originality of Maroon societies is based on the preservation of their African heritage (linguistic, political, religious, or domestic traditions). Having developed their African cultures outside of European or Native American influences, and adapted them to the circumstances. Therefore, only among Maroon communities is more likely to find the most remarkable African cultural and linguistic legacies in the Americas (Price and Price 2003).

During the TAST, the system of slave resistance disrupts the functioning of slave plantations but without destabilizing them, e.g. in Honduras, Mexico, and Panama. In some cases, European settlers had resolved to approach their fugitive slaves to demand peace. They proposed treaties that granted their freedom and recognized their territorial integrity, in exchange for which they should cease all hostile acts against the plantations and refuse to help other slaves to escape. In particular regions, European colonial authorities conceded to Maroon communities the establishment of spaces enjoying official autonomy, like in Jamaica, Colombia, Surinam, and French Guiana. In a few regions,

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[2] The word Marron indicates fugitive slaves during the slave trade. The term, generalized in the French-speaking (*"Marron"*) and English-speaking (*"Maroon"*) areas, comes from the Spanish word *"Cimarrón"*. A word borrowed from the first Amerindian inhabitants Arawak of Haiti. This word was used to designate a wild animal, or more precisely a domestic animal that has returned to wild life. While in the Spanish-Portuguese areas the common terms are *"Quilombos"* in Brazil, *"Garifuna"* in Honduras, and *"Palenques"* in Cuba and Colombia.

the rebellions ended up integrating into the war of national independence, for example in Cuba and Haiti (Price 2013b).

Particularly, in Suriname (former Dutch Guiana) and French Guiana marronnage reached its peak in South America, due to in these regions the slave system experienced its major development and its maximum severity (Dupuy 2002). The punishments for fugitive slaves that were captured in Suriname were among the most brutal in the hemisphere, and included murder if they were captured for the third time (Price and Price 2003). Besides the hostility, numerous fugitive slaves from French and Dutch colonies successfully managed to escape captivity, and they were known under the names of Noir Marron or *"Bushinengués"* (that means "Black people in the forest", or "Bush Negroes") (Price 2013b). With an immense hinterland with this Amazon rainforest that offered a protective refuge, Noir Marron groups had the possibility to escape, to resist the repression of the European colonial masters, and some of them are still present today in isolated regions of the Amazon rainforest since the foundation of those communities (Dupuy 2002). Currently, the Noir Marron population is one of the largest and the most autonomous Maroon in the Americas (Price and Price 2003). These groups of run-away slaves organized themselves into six scattered Noir Marron communities (known as Alukus, Ndjukas, Saramakas, Paramakas, Matawai and Kwinti). Each community has their own political autonomy, cultural identity, and unique Creole languages deeply rooted in its African heritage (Price and Price 2003). As early as the 1760s, certain groups signed peace treaties with the Dutch government, in particular the Ndjukas and the Saramakas, and years later with the Alukus and the Paramakas (Price 2013a). These are the four major communities of the Noir Marron population that now inhabit this region of Suriname and western French Guiana. The remaining two communities, the Matawai and the Kwinti, settled west of the Saramakas but never had a significant presence or large population sizes.

The first genetic studies that investigated the genetic history of Noir Marron communities used uniparental markers and a very limited number of autosomal markers (GM allotypes of the immunoglobulin system) (Brucato et al., 2009, 2010). Recently, within the framework of the EUROTAST European Research Network[3], Fortes-Lima et al. (2017) presented the first genome-wide

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[3] The EUROTAST Research Network is a European Marie Curie Actions network for the multidisciplinary study of the transatlantic slave trade using new historical, anthropological, archaeological, and genetic approaches. In this international training network, thirteen doctoral students from different European universities and their supervisors worked in close collaboration to improve our knowledge on this subject, by including different scientific and historical perspectives. More detailed information can be found on the site (https://cordis.europa.eu/project/id/290344/reporting).

study of the four major Noir Marron communities. The authors analysed genome-wide SNP data (around five million SNPs) of 107 African-descendants (71 Noir Marron from French Guiana and Suriname: 23 Alukus, 23 Ndjukas, 19 Saramakas, and 6 Paramakas; 16 African-Brazilians from Rio de Janeiro; and 20 African-Colombians the Chòco and Antioquia departments in Colombia). The authors compared their African genomic diversity with genome-wide SNP data of 124 individuals from West Africa (Benin, Ivory Coast, and Mali) analysed for the first time in that study, and genomic data of 2,054 African individuals obtained from previous studies.

Fortes-Lima et al. (2017) estimated a high (~98%) African genetic ancestry among Noir Marron communities, despite 400 years of separation from their African ancestors. In addition, these communities have high values of inbreeding coefficients, which suggest strong genetic isolation in these communities since their foundation. This exceptional African genetic heritage is one of the highest observed to date in the African Diaspora, and notably different than other African-descendants analysed in other genomic studies (Figure 10.2), e.g. Jamaicans of the CAAPA Consortium have 89% of African ancestry (Mathias et al., 2016), African-descendants from Barbados have 88% (Martin et al., 2017), Garifuna in Saint Vincent has 70% (Benn Torres et al., 2019), African-Bolivians in the Yungas Valley in Bolivia have 80% (Pardo-Seco et al., 2016), and African-Peruvians have 78% (Harris et al., 2018).

Comparisons between the genetic diversity between the Noir Marron and African-descendant populations from Colombia and Brazil highlights notable differences in their admixture patterns (Figure 10.3), likely associated with their different European colonial past. While individuals of Noir Marron communities maintained a remarkably high African genetic ancestry, other African-descendant populations have a mosaic genome with chromosomal regions of different continental ancestries with different proportions and length across the genome of individuals in each population (Figure 10.3). Besides, the African ancestry is the major ancestry in both populations (on average 70.8% in African-Brazilians and 76.8% in African-Colombians), the admixture patterns are different between these two African-descendant populations, characterized by a high percentage of European and low Native American admixture among African-Brazilians in Rio de Janeiro (24.0% and 5.0%, respectively). In contrast, African-Colombians have a similar percentage of European and Native American admixture (10.7% and 11.9%, respectively).

The TAST broke familiar links between African-descendant populations and their putative African ancestors, however genomic tools can bring new information about those links (Fortes-Lima and Dugoujon 2018). Fortes-Lima et al. (2017) analyzed genome-wide SNP data to reconstruct genetic links between

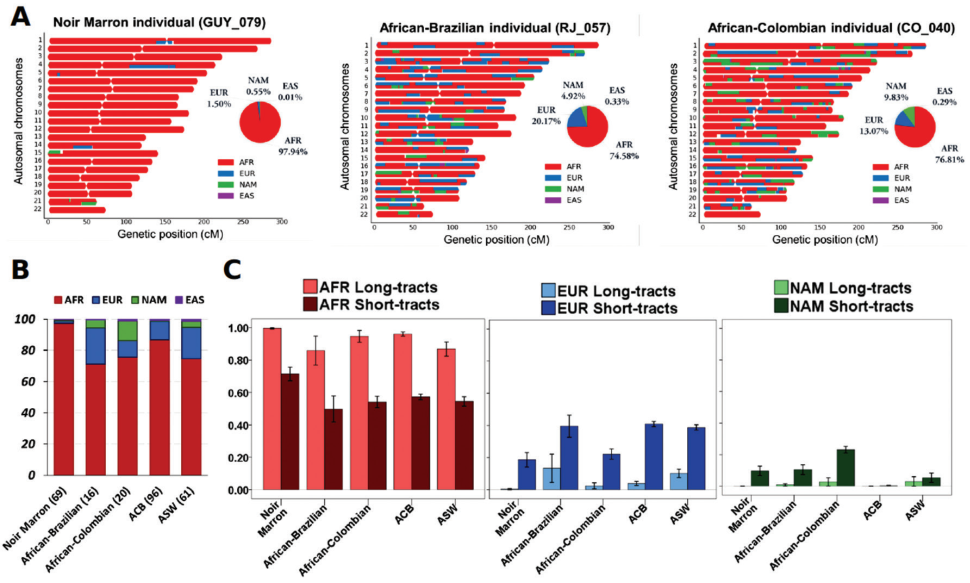

FIGURE 10.3 (A) Continental ancestries in chromosomal regions of haploid genomes in individuals from the Noir Marron, African-Brazilian and African-Colombian population. Figure showing continental ancestries estimated using a four-way admixture inference method for each individual (AFR: African ancestry represented in red; EUR: European ancestry in blue; NAM: Native American ancestry in green; and EAS: East Asian ancestry in purple). (B) Figure showing different admixture patterns estimated in those populations, as well as African-descendant populations from Barbados and the USA (ACB and ASW, respectively). (C) Except for Noir Marron individuals, African descendants in the Americas have a mosaic genome with chromosomal regions (or ancestry tracts) of different continental ancestries and different lengths (short- and long-tracts). In particular, they have a high average of short European tracts, suggesting strong and recent European admixture
FIGURE MODIFIED WITH PERMISSION FROM FORTES-LIMA ET AL., 2017

the Noir Marron communities and present-day populations from the Bight of Benin. In the ancestry-specific principal component analysis (AS-PCA), the results evidence strong genetic similarities between African haplotypes of Noir Marron individuals and populations in present-day Benin (Figure 10.4). The results were also consistent with linguistic studies based on hundreds of African words and linguistic characteristics that are commonly used by Noir Marron communities today (Essegbey et al., 2013a; Essegbey et al., 2013b; Muysken and Smith 2014). These studies revealed functional similarities with the sub-family of the Gbe linguistic family, which is spoken today by African populations from Benin (such as Fon). Therefore, genetic and linguistic studies indicate that the Bight of Benin is the most likely origin of the source population of the Noir Marron communities.

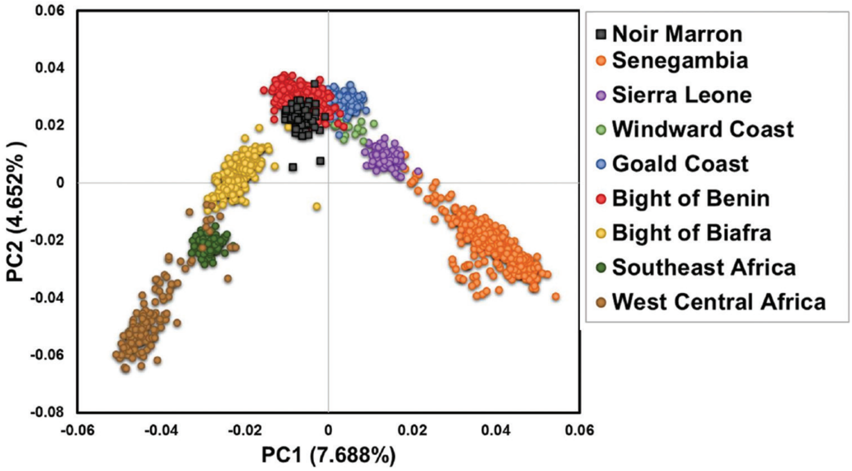

FIGURE 10.4 Ancestry-specific principal component analysis (AS-PCA) for African haplotypes of Noir Marron communities projected in a background of sub-Saharan African populations representative of the eight historical slave trade regions in Africa (described in Figure 10.2A). Figure showing strong genetic affinities between Noir Marron individuals (black squares) and African populations residing in the Bight of Benin (red dots)

FIGURE MODIFIED WITH PERMISSION FROM FORTES-LIMA ET AL., 2017

5 Admixture Histories of African-Descendants in the Caribbean

During the slave trade in the Caribbean colonies, some Maroon communities opposed the European colonial system and ended up into a war of national independence, like in Cuba and Haiti. Most of the genomic studies have been mainly concentrated in African-descendant populations from islands in the Greater Antilles, such as Puerto Rico (Belbin et al., 2017), Dominican Republic (Mathias et al., 2016) and Cuba (Moreno-Estrada et al., 2013). Cuba is the largest island in the Greater Antilles, and also the most populous country in the Caribbean with around 12 million inhabitants. During the TAST, around 853,000 enslaved Africans arrived in Cuba from 1526 to 1875 (Eltis and Richardson 2015). The vast majority (92%) arrived during the last period of slavery, from 1801 to 1875 (Guanche 2011). Previous genetic studies in Cuba have provided relevant information on population history, disease resistance, and admixture dynamics (Browning et al., 2016; Moreno-Estrada et al., 2013). However, these studies analysed Cuban participants residing in the USA for a few generations.

By analysing over 1,000 individuals born and living today in the fifteen provinces of Cuba, Marcheco-Teruel et al. (2014) carried out a comprehensive study of this large sample size by using uniparental markers and 128 ancestry informative markers (AIMs). This large number of individuals born in Cuba is a very good representation of the current distribution of the population in terms of sex, age, and population density (Roblejo and Marcheco-Teruel 2017). To investigate the population structure and the demographic history in Cuba, more recently Fortes-Lima et al. (2018) analysed genome-wide SNP data (around 600,000 SNPs) of 860 participants sampled previously by Marcheco-Teruel et al. (2014). The results showed a fine-scale population structure within Cuba and variable admixture profiles between the Cuban provinces. On average, the proportion of European ancestry estimated in all of the studied Cuban samples was notably high (71%), with the highest values among western Cuban provinces, such as Mayabeque (87.7%). On the other hand, the results showed high levels of African ancestry among participants from eastern Cuban provinces, such as Santiago de Cuba (38.8%) and Guantanamo (40.1%). Interestingly, western Cuban participants in Havana have also important proportions of African genetic ancestry (~27.9%). In the eastern Cuban provinces, individuals have also relatively high Native American ancestry (like in Holguin with 10.6%, Granma with 12.4%, and Las Tunas with 13.9% on average). In agreement, in those provinces is where there is the highest concentration of Taíno archaeological sites (Dominguez 2014).

To study the African ancestral origin in the Cuban population, the authors used an African reference panel of 45 sub-Saharan African populations. Using haplotype-based analyses, the authors estimated strong genetic affinities between the haplotypes of the Cuban population with African ancestry and the haplotypes of African populations originally from the historical slave regions of Bight of Benin, Bight of Biafra, and West Central Africa (Fortes-Lima et al., 2018). Interestingly, the genomic results were in accordance with historical sources that highlight these regions were the three main sources of enslaved Africans who arrived in Cuba (representing 70% of the slave population) (Guanche 2011, Eltis and Richardson 2015). Further, the highest proportions of African admixture were observed in the municipalities of the provinces of Havana and Santiago de Cuba. These provinces were respectively the first- and second-largest ports of slaves during the slave trade in Cuba. From 1551 to 1875, more than 350,000 enslaved Africans arrived in Havana (41% of the total slave population) (Eltis and Richardson 2015). In the rest of the island, especially in the eastern region, the slave trade was less intensive and later, e.g. in Santiago de Cuba more than 55,000 enslaved Africans arrived from 1701 to 1875 (6.5% of the total slave population) (Eltis and Richardson 2015).

To reconstruct recent histories of admixture, different scenarios of admixture events were modelled in the three main historical regions in Cuba (western, central, and eastern Cuba). In agreement with Marcheco-Teruel et al. (2014), the models of the geographic admixture observed comply with archaeological and historical sources (Guanche 2011). In the western and central regions, the results show dates of early admixture for the first African and Native American admixture event (14-15 generations ago in both regions), while a second African and Native American admixture event was estimated much later (3-4 and 7-8 generations ago, respectively). The inferred model (the tested model with the "best" fitting parameters) showed stronger African ancestry in the eastern provinces of Cuba, which is consistent with the admixture proportions estimated in Santiago de Cuba and Guantanamo using different genome-wide methods (39% and 40%, respectively). Interestingly, these eastern provinces have a higher frequency of long chromosomal segments of African ancestry (on average 41%) than the other provinces (on average 14%), suggesting a more recent and strong African gene-flow in the eastern Cuba region that post-date the TAST (after the abolition of the slave trade) (Fortes-Lima et al., 2018).

The results were in line with intra-continental migrations within the Caribbean rather than with trans-continental migrations from Africa to the Americas. In agreement, a significant mass migration took place from Haiti to Cuba. Between 1913 and 1931, legal migration from Haiti to Cuba was estimated at more than 189,000 migrants, while illegal migration was estimated from 450,000 to 600,000 (Guanche 2011). The Haitian population has one of the highest of African ancestry in the Caribbean (84% on average) (Moreno-Estrada et al., 2013), in contrast with the Garifuna community in Saint Vincent that is a well-known Maroon community in the Caribbean, which has 70% of African ancestry (Benn Torres et al., 2019). The estimated admixture dates likely reflect recent events of African migration (3-4 generations ago) that are particularly high in the eastern Cuban region. Therefore, Cuba has experienced major mass migrations involving multiple indigenous and European groups, as well as African migrants due to trans-continental forced migration in the Atlantic world during the TAST, and more recently large-scale intra-continental movements in the Caribbean after the abolition of the slave trade likely from Haitian labour workers. For that reason it is important that researchers ensure an appropriate representation of individuals from different Cuban regions in future biomedical and genomic studies (Roblejo and Marcheco-Teruel 2017).

6 Paleogenomics Studies in the Context of the Transatlantic Slave Trade

Due to the high temperature and humidity, one would expect not to find traces of ancient DNA (aDNA) in the Caribbean. Nonetheless, Schroeder et al. (2015) successfully generated genomic data of three enslaved Africans from the 17th century to study their individual genetic histories, as part of the EUROTAST research network. Those human remains about 400 years old were accidentally found in 2010 in a cemetery, in the Zoutsteeg region of Philipsburg, on the Antillean Island of Saint Martin (Figure 10.2B), in the area which was colonized by the Dutch government. They are known as the "Zoutsteeg Three" and were identified two as men and one as a woman. They were found together with artifacts dating from the 17th century, osteo-archaeological analysis indicated that they were between 25 and 40 years old when they died. Radiocarbon dating indicated they were buried between 1660 and 1688 (Schroeder et al., 2015). Interestingly, their teeth had been deliberately chipped and cut into points and other shapes, suggesting that they were apparently not born in Saint-Martin, because that is a foreign cultural practice in the Caribbean more commonly practised in sub-Saharan Africa (Jones 1992). Together, their dental modifications and isotopes analysis strongly suggested that they were born somewhere in Africa and most likely brought by force to Saint Martin to work as slaves on sugar plantations (Schroeder, Haviser, and Price 2014).

From small bits in the dental roots of three enslaved Africans, the Zoutsteeg Three, Schroeder et al. (2015) successfully generated human nuclear and mitochondrial DNA data using whole-genome capture methods to enrich human DNA content in sets of aDNA libraries (Carpenter et al., 2013). In addition, the estimated modern DNA contamination was very low (<1%). To trace their African origins, the authors compared ancient genomes with those of eleven modern populations in West Africa, and found genetic affinities with at least two distinct linguistic groups. Thus, besides these three individuals were buried together, they may not have had a language in common. One of the men probably belonged to Bantu-speaking populations residing in Congo and Cameroon, while the other man and the woman most probably belonged to non-Bantu-speaking populations from present-day Nigeria or Ghana (Schroeder et al., 2015). Their different African ancestral origin underlines that enslaved Africans from the same plantations likely lived together with other captives speaking different languages and belonging to different ethno-linguistic groups. Nonetheless, it is possible that the genomes of the closest genetic ancestors of to the Zoutsteeg Three have not been analysed yet, and future analyses would require to increase the number of reference African populations to have more comprehensive information.

In another outstanding paleogenomics study, Barquera et al. (2020) analysed human remains of enslaved Africans buried in a mass burial in Mexico City. To better understand the lives and health status of enslaved Africans in Mexico colonial, the authors performed comprehensive analyses of those remains using a multi-disciplinary approach that combined bioarchaeological, osteological, isotopic, and genome-wide analysis of three individuals (named as SJN001, SJN002 and SJN003). Bioarchaeological analysis of their remains evidenced dental modification patterns that are culturally associated with a sub-Saharan African origin. Those three individuals were genetically identified as males, and radiocarbon dating analysis suggested that the individuals died shortly after the beginning of the colonial period in Mexico City (^{14}C dating: AD 1436-1626). Together, the results highlighted these individuals were likely the first-generation enslaved Africans who died very early during the colonial period in Mexico (Barquera et al., 2020).

However, the lives of the first-generation enslaved Africans in Mexico were remarkably hurtful. Osteological analyses revealed a life experience of conflict and hardship in the three individuals. Individual SJN001 was found with two healing needles in the thoracic cavity and gunshot wounds. In addition, both SJN001 and SJN003 presented pathological changes such as "*cribra orbitalia*" (Barquera et al., 2020), which is generally associated with a skeletal response to nutritionally inadequate diets, anaemia, parasitic infectious diseases, and blood loss (Walker et al., 2009). Individual SJN002 displayed several skeletal changes associated with intense labour and heavy manual activity, including deformations on the clavicle and scapula. Additionally, he suffered from a poorly aligned complete fracture in the right fibula and tibia, resulting in associated joint changes of the knee and deformation (Barquera et al., 2020).

The dental modification patterns by mechanical modifications are consistent with cultural practices previously reported for enslaved Africans from different contexts (Wasterlain, Neves, and Ferreira 2016), but also observed in groups living in coastal Western African regions today (Jones 1992). Both uniparental markers of these individuals were associated with sub-Saharan African mitochondrial haplogroups (L1b, L3d and L3e1) and Y-chromosome haplogroups (E3b1a and E-M2 for the three individuals). In addition, *HLA* allelic variation of the three individuals is highlighting a sub-Saharan African origin (Barquera et al., 2020). They have similar *HLA* haplotypes that the haplotypes previously reported in sub-Saharan African populations (Arlehamn et al., 2017). To further assess the origin of these ancient individuals, the authors carried out strontium analysis on the molars of each individual, which forms early during childhood and thus is a good proxy for place of birth. The strontium ratio values are above 0.7107 for or the three studied individuals (Barquera et al., 2020), which are the highest values recorded in the central part of Mexico (range: 0.7045-0.7052) and Mexico City (range: 0.7062–0.7064) (Price et al., 2012; Juarez 2008). In fact, those values are consistent with a West African origin estimated for enslaved Africans in Barbados (range: 0.7060–0.7414) (Schroeder et al., 2009).

The three individuals were buried in a mass grave in the grounds located just outside of the hospital that contained skeletal remains of several individuals disposed in layers, which is consistent with burials made during epidemics. By using genetic tools, researchers can screen ancient individuals to look for potential pathogenic agents using novel bioinformatic approaches to search and filter reads from the genomic libraries (Hübler et al., 2019). Barquera et al. (2020) used this approach to sequence reads from ancient remains (tooth dentine powder) that were mapped to bacteria genomes, which could either be part of the oral microbiota or implicated in taphonomic processes. Apart from environmental bacteria, interestingly over 50 reads were mapped specifically to *Treponema pallidum* genomes in individual SJN003, which is a positive evidence of treponemal infection (Barquera et al., 2020). Further, eight sequenced reads mapped specifically to hepatitis B virus (HBV) DNA in individual SJN001. Phylogenetic analysis confirmed that SJN001 HBV belonged to sub-genotype A3, which is typically found in West Africa (Pourkarim et al., 2014; Andernach et al., 2009). A maximum-likelihood tree of *Treponema* strains showed the SJN003 genome clustered within the *Treponema pallidum subsp. pertenue* (TPE), which is the causative agent of yaws, and phylogenetically associated with strains isolated from patients in Western Africa (Barquera et al., 2020). Overall, paleogenomics analyses of enslaved Africans in the Americas further increase our understanding of the genetic history of these enslaved Africans and their ancestral African origins. These findings demonstrate that aDNA methods together with other approaches can successfully be used to trace the putative ancestors, infer the living conditions of populations in the Americas from the first-generation of enslaved African until present-day African descendants, and provide new findings that have important implications in archaeology and biological anthropology, especially in cases where historical information about the TAST is missing.

Since written histories about the lives and enslavement of the ancestors of African descendants are scant, archaeological data becomes invaluable. However, archaeologists often struggle with the challenge of linking historic-period artifact assemblages with specific communities. By using another interesting approach, Jagadeesan et al. (2018) carried out a virtual reconstruction of aDNA of the African genome of one enslaved African born in the 18th century (1784) on Saint Croix island (one of the U.S. Virgin islands) (Figure 10.2B). Within the framework of the EUROTAST research network, the authors carried out a "virtual" aDNA study without using (or destroying) this person's biological material (such as bones or hair), whose name was Hans Jonatan (Palsson 2016). The genetic information obtained from current descendants of this man (who are part of the Islandic population) was used to reconstruct chromosomal fragments of his African genetic ancestry. This information was used to first reconstruct the maternal part of the genome of Hans Jonatan, and then to determine that his mother was originally from the historic regions of the Bights of Benin and Biafra (Jagadeesan et al., 2018). This study therefore shows that the use of genealogical and genomic data can largely reconstruct, in certain specific populations, the genome of the putative ancestors of enslaved Africans, without having direct access to ancient remains for the study.

Today, through aDNA analysis is also possible to recover aspects of people's lives that were once thought unknowable, and hold the potential to connect living descendants with their putative ancestors. Future paleogenomics studies will retrieve aDNA from human remains as well as personal artifacts of enslaved Africans found in historic plantations, like tobacco pipes. The study presented by Schablitsky et al. (2019) is a great example of this cross-disciplinary research. First, the authors successfully extracted aDNA from a clay tobacco pipe stem collected from an African-American slave quarter in Maryland (USA), where generations of enslaved Africans lived and worked on tobacco plantations between 1736 and 1864. The owner of that tobacco pipe was genetically identified as a woman. Then, genome-wide analyses revealed she was closely related to Mende-speaking people living in present-day Sierra Leone (former Sierra Leone slave coastal region). Therefore, paleogenomics research provides archaeologists with novel tools to address questions about African-American communities and their African ancestral origins.

7 Conclusions and Future Directions

These stories of complex admixture in America, during and after the slave trade, had a great influence on genetic diversity. In this chapter, through a few examples, I seek to review the latest studies that combine historical factors and genetic history. With the new genomic data available today, it is possible to more accurately determine ancestral origins and also to better specify the influence of triangular trade on the various histories of interbreeding in African-descendant populations in the Americas. In this context, recent genomic research unravels the impact of demographic events associated with complex admixture events, as well as ancestral origins with unprecedented geographic resolution. In future studies, researchers will apply new statistical methods to further test complex events of admixture in African-descendant populations and reconstruct demographic histories across the Americas of populations that had undergone the TAST (Fortes-Lima et al., 2021).

Ancient DNA studies of human remains have painted a more complete picture of the living conditions of enslaved Africans during the transatlantic slave trade, e.g. for the Zoutsteeg Three in Saint Martin and the first-generation enslaved Africans in Mexico. Furthermore, aDNA studies have shown that ancient and modern DNA can help us to reconstruct family histories and historical movements of populations by retrieving aDNA from human remains, present-day African descendants or personal artifacts of enslaved Africans found in historic plantations.

Altogether, genome-wide studies of both ancient and present-day populations in Africa and the Americas present valuable information about the slave trade that can complement fragmented historical sources (Fortes-Lima et al., 2017; Patin et al., 2017). In this context, recent findings presented in genomic studies have made possible to draw conclusions on the continental and sub-continental ancestral origins and genetic history of African and African-descendant populations at each side of the Atlantic.

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