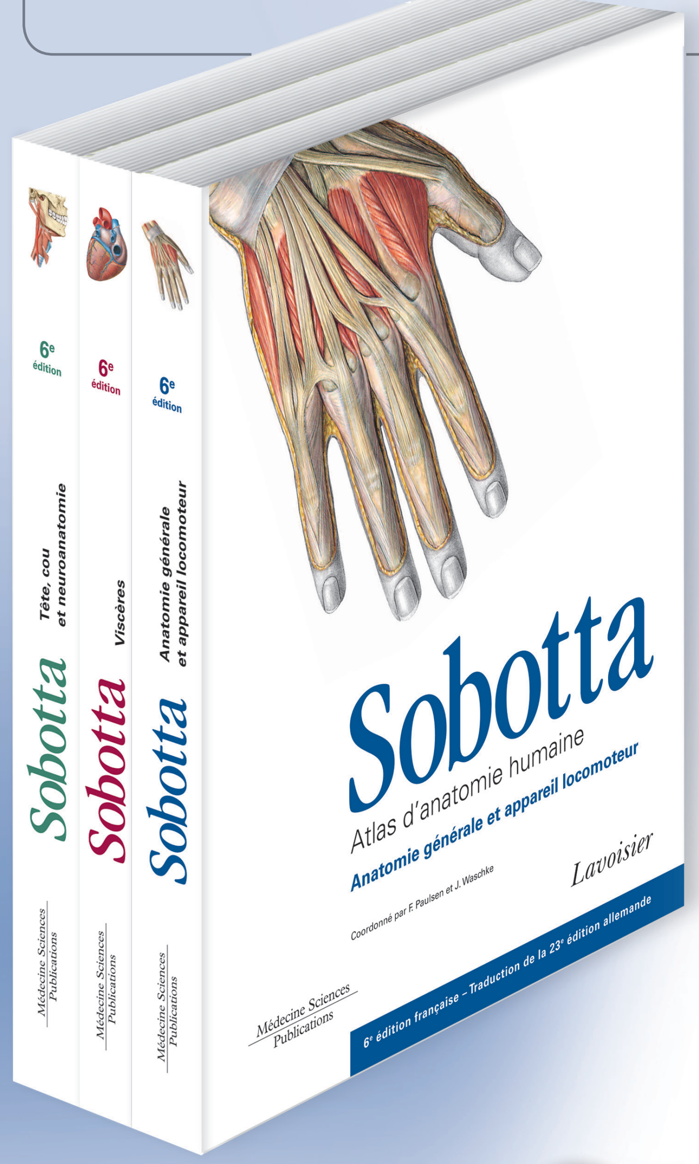
Pack 3 tomes brochés + fascicule

Atlas d'anatomie humaine - 6e édition

Johannes SOBOTTA



Sobotta – Depuis plus d'un siècle, la référence mondiale en anatomie humaine.

Le Sobotta, reconnu pour la précision et la qualité de ses illustrations, s'est enrichi, dans cette nouvelle édition, de nombreuses figures ainsi que de textes explicatifs et cliniques complémentaires aux structures anatomiques présentées :

- Plus de 2 000 illustrations de qualité exceptionnelle, représentant avec exactitude des pièces de dissection.
- Accès facilité aux figures complexes à l'aide de croquis d'orientation et mise en évidence des structures importantes.
- Variantes anatomiques et schémas didactiques alimentant la grande richesse iconographique.
- Approche pédagogique des illustrations s'appuyant sur des explicitations synthétiques.
- Lien constant entre l'anatomie et la clinique reposant sur l'imagerie médicale et des descriptions des maladies en relation avec les structures anatomiques.
- Étude exhaustive des muscles, articulations et nerfs dans un livret mobile en parallèle des régions étudiées.

Date de parution : 04-2015
1121 pages · 24 x 31 cm · Broché · Quadrichromie
ISBN : 978-2-257-20566-7

99 €
Prix public TTC

◀ **Retrouvez plus d'informations sur ce pack.**

www.lavoisier.fr

Lavoisier
Médecine
SCIENCES

Bulletins et Mémoires de la Société d'Anthropologie de Paris

Volume 30 • Numéro 1-2 • Avril 2018 • pp. 1 – 108

BMSAP

VOLUME 30 . NUMÉRO 1-2
Avril 2018
ISSN : 0037-8984

BULLETINS ET MÉMOIRES DE LA SOCIÉTÉ D'ANTHROPOLOGIE DE PARIS

PUBLICATION FONDÉE EN 1859

Anthropologie biologique du continent africain : des premiers hominines aux populations actuelles

Lavoisier

couv-sprsap-30-1-2.indd 1
16/04/2018 12:31:08

BMSAP

BULLETINS ET MÉMOIRES DE LA SOCIÉTÉ D'ANTHROPOLOGIE DE PARIS

Lavoisier

BMSAP

BULLETINS ET MÉMOIRES DE LA SOCIÉTÉ D'ANTHROPOLOGIE DE PARIS

Les *Bulletins et Mémoires de la Société d'Anthropologie de Paris* (BMSAP) ont été créés en même temps que cette Société, en 1859. C'est la plus ancienne publication du monde en anthropologie biologique et la principale revue (majoritairement) francophone dans ce domaine.

Les *BMSAP* ont pour objectif de rendre compte de l'activité scientifique internationale dans le domaine de l'« histoire naturelle de l'homme » comprise comme l'étude de l'origine et de la diversité biologique de l'espèce humaine. Ils couvrent de manière pluridisciplinaire le champ de l'anthropologie biologique, depuis la paléoanthropologie jusqu'à l'écologie humaine, en passant par la génétique des populations. Ils publient en français ou en anglais des articles originaux, des revues de synthèse, des comptes rendus de lecture ou de congrès et possèdent une rubrique consacrée à l'histoire de la discipline.

Éditions
Lavoisier
BMSAP
14, rue de Provigny
94236 Cachan cedex
France
Tél : +33 (0)1 47 40 67 00
Fax : +33 (0)1 47 40 67 02

Directeur de publication
Patrick Fenouil

Édition
Méline Berthelot
Tél : +33 (0)1 47 40 67 24
Fax : +33 (0)1 47 40 67 02
Email : meline.berthelot@lavoisier.fr

Secrétariat de rédaction
Alice Rouquie
Tél : +33 (0)1 47 40 67 30
Fax : +33 (0)1 47 40 67 02
Email : rouquie@lavoisier.fr

Abonnements
Le volume 30 (2 numéros doubles) paraît en 2018.

Abonnement Membre (SAP)
Contactez la Société d'Anthropologie de
Paris (www.sapweb.fr)

Frais de port inclus. *Pour les tarifs TTC, merci de contacter votre service abonnement.

Abonnements
Lavoisier
Abonnement BMSAP
14, rue de Provigny
94236 Cachan cedex
France
Tél : +33 (0)1 47 40 67 68
Fax : +33 (0)1 47 40 67 02
Email :abonne.bmsap@lavoisier.fr

Institutions et agences d'abonnement :
Email :pascal.pinard@lavoisier.fr

Changements d'adresses
En cas de changement d'adresse de l'abonné, la livraison du numéro suivant sera retardée d'environ six semaines.
En informant le service d'abonnement concerné de ce changement, l'abonné est prié d'indiquer à la fois son ancienne et sa nouvelle adresse (avec le code postal).

Impression
Jouve (Mayenne, France)
Imprimé sur papier garanti sans acide

ISSN version papier : 0037-8984
ISSN version électronique : 1777-5469

Copyright

BMSAP

BULLETINS ET MÉMOIRES
DE LA SOCIÉTÉ D'ANTHROPOLOGIE DE PARIS

Indexée dans SCOPUS, Google Scholar, Academic OneFile, Anthropolocial Index Online, Anthropological Literature, Biological Abstracts, BIOSIS, ERIH PLUS, GeoRef, OCLC, SCImago, Summon by ProQuest.

Chaque auteur recevra la version électronique définitive de son article pour usage privé uniquement.

Lavoisier

Sommaire

Volume 30 · Numéro 1-2 · Avril 2018

DOSSIER
ANTHROPOLOGIE BIOLOGIQUE DU CONTINENT AFRICAIN : DES PREMIERS HOMININES AUX POPULATIONS ACTUELLES

NOTE

INTRODUCTION

~~NOTES~~

~~ARTICLES~~

~~NOTE~~

THÈSES

Composé et imprimé par Jouve, 1, rue du Docteur Sauvé, 53100 Mayenne
Vol. 30 - N° 1-2 - Dépôt légal : Avril 2018

BMSAP
BULLETINS ET MÉMOIRES
DE LA SOCIÉTÉ D'ANTHROPOLOGIE DE PARIS

Indexed in SCOPUS, Google Scholar, Academic OneFile, Anthropolocial Index Online, Anthropological Literature, Biological Abstracts, BIOSIS, ERIH PLUS, GeoRef, OCLC, SCImago, Summon by ProQuest.

Lavoisier

Table of contents

THEMATIC FILE
BIOLOGICAL ANTHROPOLOGY OF THE AFRICAN CONTINENT: FROM THE FIRST HOMININS TO EXTANT POPULATIONS

NOTE

INTRODUCTION

NOTES

ARTICLES

NOTE

BMSAP (2018) 30:1-13
DOI 10.1007/s13219-017-0187-8

NOTE / *NOTE*

Prehistory of the British Isles: A Tale of Coming and Going*

La préhistoire des îles britanniques : une histoire de va-et-vient

I. De Groote · M. Lewis · C. Stringer

Received: 8 May 2017; Accepted: 11 July 2017

Abstract It is now recognised that Britain has not always been geographically isolated from Europe and, for most of the last one million years, formed an extension of the northwest European landmass. During most of this time, Britain was accessible to migrating humans and animals, although climatic conditions varied greatly from Mediterranean-like through to glaciations and extreme cold, making Britain a difficult place to settle for any length of time. The oldest evidence for humans in Britain dates to between about 850,000 and 1 million years ago. Recovered lithic artefacts suggest that hominin species occupied and deserted the British Isles at least nine times. This article reviews the prehistory of the British Isles and presents the main sites and time periods.

Keywords Pleistocene · Palaeolithic · Migration · *Homo sapiens* · *Homo neanderthalensis* · *Homo heidelbergensis* · *Homo antecessor*

Résumé Il est bien connu que les îles britanniques n'ont pas toujours été des îles et que pendant la plus grande partie du dernier million d'années, elles faisaient partie d'une péninsule s'étendant à partir (ou à l'extrémité) du Nord-Ouest de l'Europe. Cette région était alors accessible aux Hommes et aux animaux venant du continent. Les conditions climatiques ont varié entre celles trouvées aujourd'hui en Méditerranée et les conditions désertiques des régions polaires, rendant la Grande-Bretagne un endroit difficile à habiter. La plus ancienne preuve de présence humaine en Grande-Bretagne date entre 850 000 et 1 million d'années. Les industries lithiques suggèrent que les espèces d'homininés se sont depuis installées puis ont déserté les îles britanniques au moins neuf fois. Dans cet article, nous proposons une revue des connaissances sur la préhistoire des îles britanniques, à partir des principaux sites et périodes correspondantes.

Mots clés Pléistocène · Paléolithique · Migration · *Homo sapiens* · *Homo neanderthalensis* · *Homo heidelbergensis* · *Homo antecessor*

Introduction

When did the first humans arrive in what is now known as the British Isles? It is well known that the British Isles were not always islands and for most of the last one million years, they formed part of a peninsula extending from northwest Europe, potentially accessible by migrating humans and animals. Britain was not a straightforward place to settle, however, with the local climate oscillating between temperatures similar to those found in the modern Mediterranean through to polar desert conditions. Humans were able to migrate temporarily into the territory but were repeatedly pushed out by successive ice ages. The process of colonisation was repeated at least nine times, but when the last British ice sheets began to melt around 12,000 years ago, a new wave of migrants was able to settle more permanently. The main Palaeolithic sites in Britain presented in this review are shown in Table 1. Lithic artefacts of varying industries and ages have been found across most of Britain from its one-million-year-long human history, but human fossil remains are few. This article provides an overview of the presence of humans in the British Isles and their tale of coming and going.

I. De Groote (✉)
Research Centre in Evolutionary Anthropology and Palaeoecology, School of Natural Sciences and Psychology, John Moores University, Liverpool, UK
e-mail : I.E.DeGroote@ljmu.ac.uk

M. Lewis · C. Stringer
Earth Sciences Department, Natural History Museum, London, UK

* This is an invited contribution following the Annual Meeting of the SAP

Table 1 Simplified table of the main Pleistocene sites in the text; dates given in most cases are approximate; at many sites, only the relevant horizons and dates mentioned in the text are provided / *Tableau récapitulatif des principaux sites Pléistocènes cités dans le texte. Les dates sont pour la plupart approximatives, pour la majorité des sites seuls les niveaux et dates mentionnés dans le texte sont indiqués*

Site	Industry	Age	Dating method
Happisburgh 3	Lower Palaeolithic	950,000–850,000 BP Early Pleistocene; MIS 25 or 21	Palaeomagnetism, biostratigraphy
Pakefield	Lower Palaeolithic	750,000–680,000 BP; MIS 19 or 17	Lithostratigraphy, biostratigraphy, AAR, palaeomagnetism
West Runton	None	~700,000 BP; MIS 17	AAR, biostratigraphy
Boxgrove	Lower Palaeolithic	~500,000 BP; MIS 13	Lithostratigraphy, biostratigraphy
Swanscombe	Lower Palaeolithic	~400,000 BP; MIS 11	Lithostratigraphy, biostratigraphy AAR
Baker's Hole	Levallois	MIS 8/7	AAR, biostratigraphy
Pontnewydd Cave	Levallois	~225,000 BP; MIS 7a	U-series, ESR, TL, biostratigraphy
Crayford	Levallois	MIS 7a	AAR, biostratigraphy
La Cotte	Levallois	MIS 7 to 2	OSL, 14C, TL, biostratigraphy
Lynford Quarry	Middle Palaeolithic	~60,000 BP; MIS 4/3	OSL (+14C)
Kent's Cavern	Middle & Upper Palaeolithic	Maxilla ~40,000 BP; MIS 3	14C, biostratigraphy
Paviland	Upper Palaeolithic	Burial ~ 34,000 BP; MIS 3	14C
Church Hole	Middle & Upper Palaeolithic	MIS 3 to 1	U-series, 14C
Gough's Cave	Late Upper Palaeolithic	14,700 BP; MIS 2	14C

BP: before present; AAR: amino acid racemisation; OSL: optically stimulated luminescence; TL: thermoluminescence; U-series: Uranium series; 14C: Ultra filtered radiocarbon; MIS: Marine Isotope Stage / *BP : avant le présent ; AAR : racémisation des acides aminés ; OSL : luminescence stipulée optiquement ; U-series : séries de l'uranium ; 14C : radiocarbone avec ultrafiltration ; MIS : stades isotopiques marins*

References: HSB 3 [4]; Pakefield [7,51]; West Runton [10,51]; Boxgrove [11]; Swanscombe [23,51]; Baker's Hole [24,51]; Pontnewydd [52]; La Cotte [31,32]; Lynford [36,37]; Kent's Cavern [39]; Paviland [40]; Church Hole [46,53]; Gough's Cave [43]

The first explorers (1 million – 475,000 years ago)

Connected lands

From the early Pleistocene, Britain was connected to mainland Europe by a land-bridge that enabled humans and fauna to migrate in and out (Fig. 1A). Until about 130,000 years ago, this narrow chalk isthmus, separating the north (North Sea) and southwest (English Channel) marine embayments, kept Britain connected to varying extents even when sea-levels were high during the warm interglacial periods [2]; the eventual complete breaching of this chalk barrier was crucial in forming the island and the Dover Strait. During glacial periods, much of the earth's water would have been trapped in the ice caps and when, during the later Pleistocene, the bed of the North Sea was exposed, a large land area known as Doggerland, created by geological uplift and sedimentation from rivers, also provided a route into the British Isles and fauna, including hominins, would have entered this way. The flooding of the shallow shelf areas of the English Channel and the North Sea are the consequence of the current high interglacial sea levels.

The main sites and their evidence

The site with the oldest evidence for humans in the British Isles is at *Happisburgh*, Norfolk, now located on the eastern English coast (Figs. 2, 3) [3,4]. During the late Early Pleistocene (between about 1 and 0.78 million years ago), Happisburgh formed part of a large river estuary, close to the confluence of the now extinct Bytham and the palaeo-Thames (currently flowing further south through London) [5]. The Happisburgh sites, now numbering more than five localities, are situated on and near the present-day beach. The cliffs are composed of till deposited by glaciers with laminae of undisturbed bedding surfaces beneath. The sediments at the base of the cliffs (Happisburgh site 3) were excavated between 2005 and 2010, and around 80 lithic artefacts were discovered dating broadly to between 850,000 and 950,000 years ago, the oldest known stone tools in northwest Europe [4]. A borehole through the cliffs to the underlying estuarine sediments was taken in May 2013.

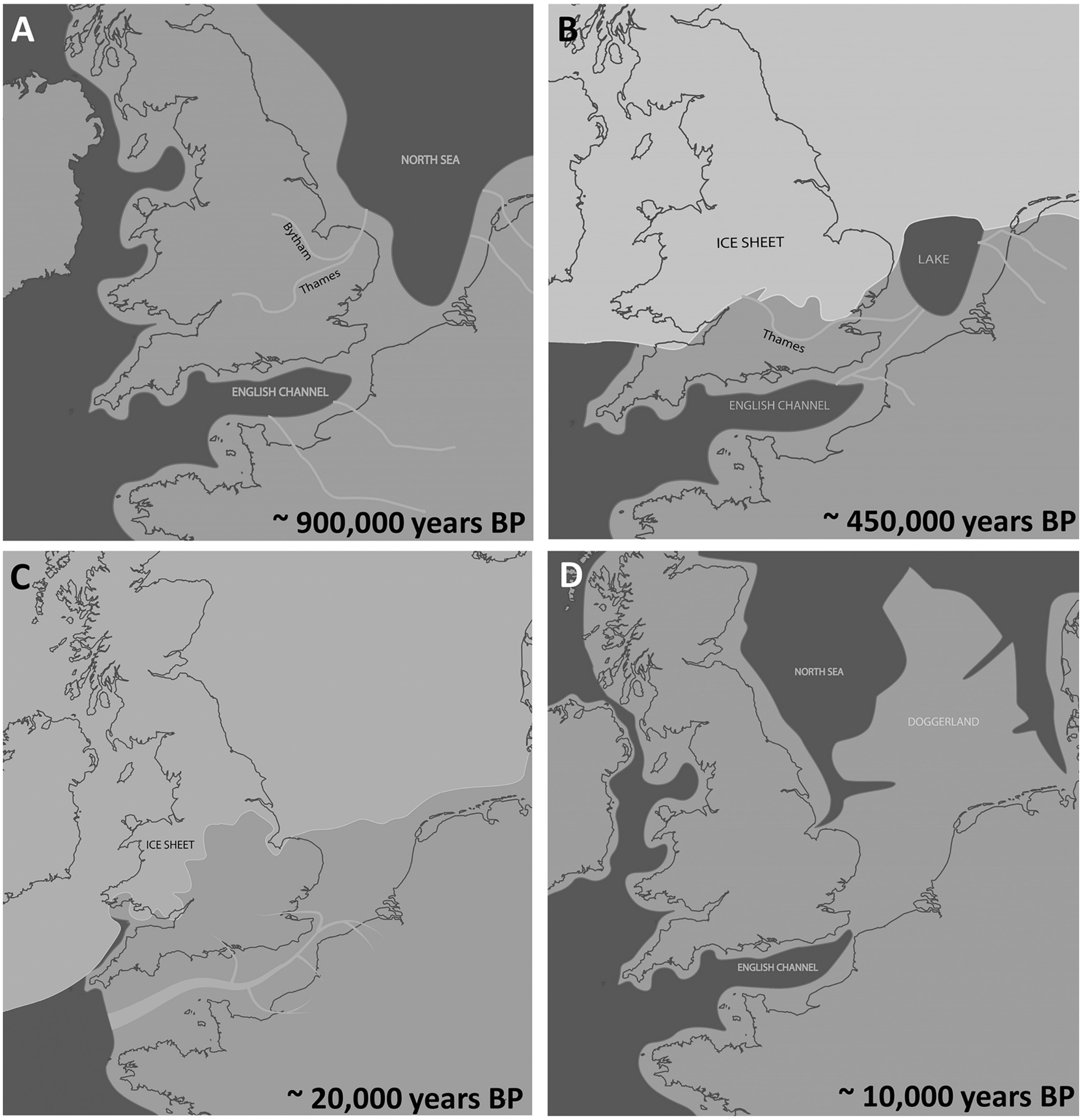


Fig. 1 Generalised reconstruction of the land surface and the extent of ice sheets of the British Isles. A. ~900,000 years BP. B. ~450,000 BP (MIS 12 – Elsterian Glaciation). C. ~20,000 years BP (MIS 2 – Last Glacial Maximum). D. ~10,000 years BP (MIS 1 – Early Holocene) (after Stringer [1]) / *Reconstitution des surfaces émergées et de l'étendue des glaciers sur les îles Britanniques. A. ~900 000 ans BP. B. ~450 000 BP (SIM 12 – Glaciation Elsterienne). C. ~20 000 ans BP (SIM 2 – Dernier Maximum Glaciaire). D. ~10 000 ans BP (SIM 1 – Holocène ancien) (d'après Stringer [1])*

Results show that these sediments are predominantly estuarine sands and silts forming the infill of channels with intermittent gravel deposits. The gravel deposits, up to 20 cm in thickness, within these sands and silts have yielded flint flakes and cores. In addition, a rich assemblage of flora and fauna has allowed their attribution to the latter part of an interglacial during the late Early Pleistocene, perhaps Marine Isotope Stage (MIS) 21 or 25.

In May 2013, a footprint surface was discovered near Happisburgh site 3 and was found to be in the same complex

Fig. 2 Current distribution of the main Palaeolithic archaeological sites of the British Isles / *Distribution actuelle des principaux sites archéologiques du Paléolithique des îles Britanniques*

of channel fills as the archaeological layers [3]. The exposure of the laminated silts through coastal erosion is frequent at Happisburgh and usually takes the form of flat or gently undulating surfaces. The exposed surface, approximately 12 m^2, showed very different characteristics with a series of hollows from circular to elongate, and the visual similarity to other coastal footprint surfaces in Britain (e.g. Formby, Sefton Coast [6]) prompted analyses of these hollows. The surface was located in the intertidal zone and subsequently eroded by tidal action over a period of two weeks, until the footprints were completely destroyed. The footprints may well have been left by *Homo antecessor*, the only hominin species so far known in Europe at that time [3].

Although no human fossils have been found at *Pakefield* (Suffolk), flint artefacts dating back approximately 700,000 years were, until the more recent Happisburgh discoveries, the earliest evidence for human presence in Britain (Fig. 4) [7]. The presence of hippopotamus, elephant, lion

Fig. 3 Happisburgh, Norfolk. A. Site 3 excavation (courtesy of NHM, London). B. Artist's reconstruction of the environment at Happisburgh ~900,000 years BP (courtesy of John Sibbick and the AHOB Project) / *Happisburgh, Norfolk. A. Fouilles du site 3 (NHM, London). B. Vue d'artiste de l'environnement à Happisburgh il y a ~900 000 ans BP (John Sibbick et le projet AHOB)*

and deer remains, as well as analyses of sediments and pollen, suggest the climate of the British Isles was warmer than at the earlier Happisburgh 3 site, with summers as warm as those in the Mediterranean today [7–9]. At *West Runton*, on the North Norfolk coast, an almost complete skeleton of a mammoth was found in 1990, the largest and oldest steppe mammoth skeleton found in Britain, dating to about 700,000 years ago, but no evidence of human occupation was found at the site [10]. Climatic conditions at West Runton were similar to those today. However, from soon after this time climatic oscillations became more extreme and Britain was regularly plunged into severe 'Ice Ages', experiencing the effects of ice sheets reaching the lower latitudes and the chilling of the North Atlantic.

Archaeological excavations at *Boxgrove*, in Sussex, England, uncovered a land surface with freshwater pools where animals gathered, dating from about 500,000 years ago (Fig. 5). As well as the butchered bones of a range of

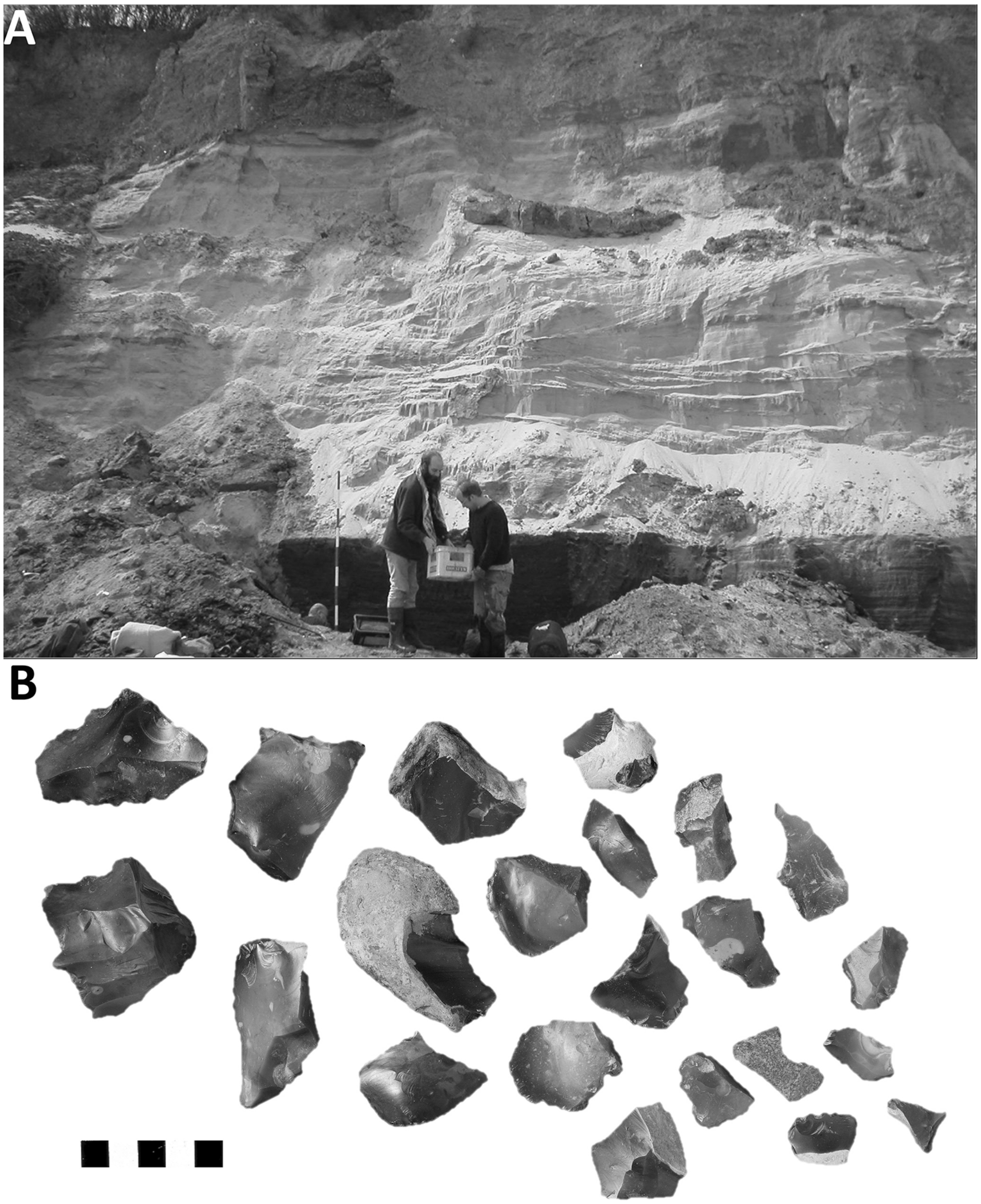


Fig. 4 Pakefield, Norfolk. A. Excavation at Pakefield with the Cromer Forest-bed deposits clearly visible at base of cliff. B. Flint artefacts recovered from the site (courtesy of NHM, London) / *Pakefield, Norfolk. A. Fouilles à Pakefield avec le niveau sédimentaire de forêt du Cromérien clairement visible à la base du remplissage. B. Artefacts en silex découverts dans le site (NHM, London)*

herbivores such as rhinoceros, horse and deer, large numbers of Acheulian handaxes were discovered [11,12]. These tools are more sophisticated than those found at Happisburgh and Pakefield, and the earliest British human fossils, a tibia and two teeth, were uncovered here in association with the cutmarked animal bones and handaxes [13]. Around 475,000 years ago we see the onset of the most severe cold stage of the Middle and Late Pleistocene, known as the Anglian (or Elsterian), with ice sheets extending far into southern Britain, making it uninhabitable.

Hominins

There are no *Homo antecessor* fossils currently known from Britain, but the footprint surface associated with Happisburgh 3, with a range of juvenile to adult hominin foot sizes, may be evidence of that species. Using foot length to stature ratios, the hominins who left the prints were estimated to have been between 0.93 m and 1.73 m in height, which suggests that the group consisted of individuals of different ages [3]. The estimated adult statures of the

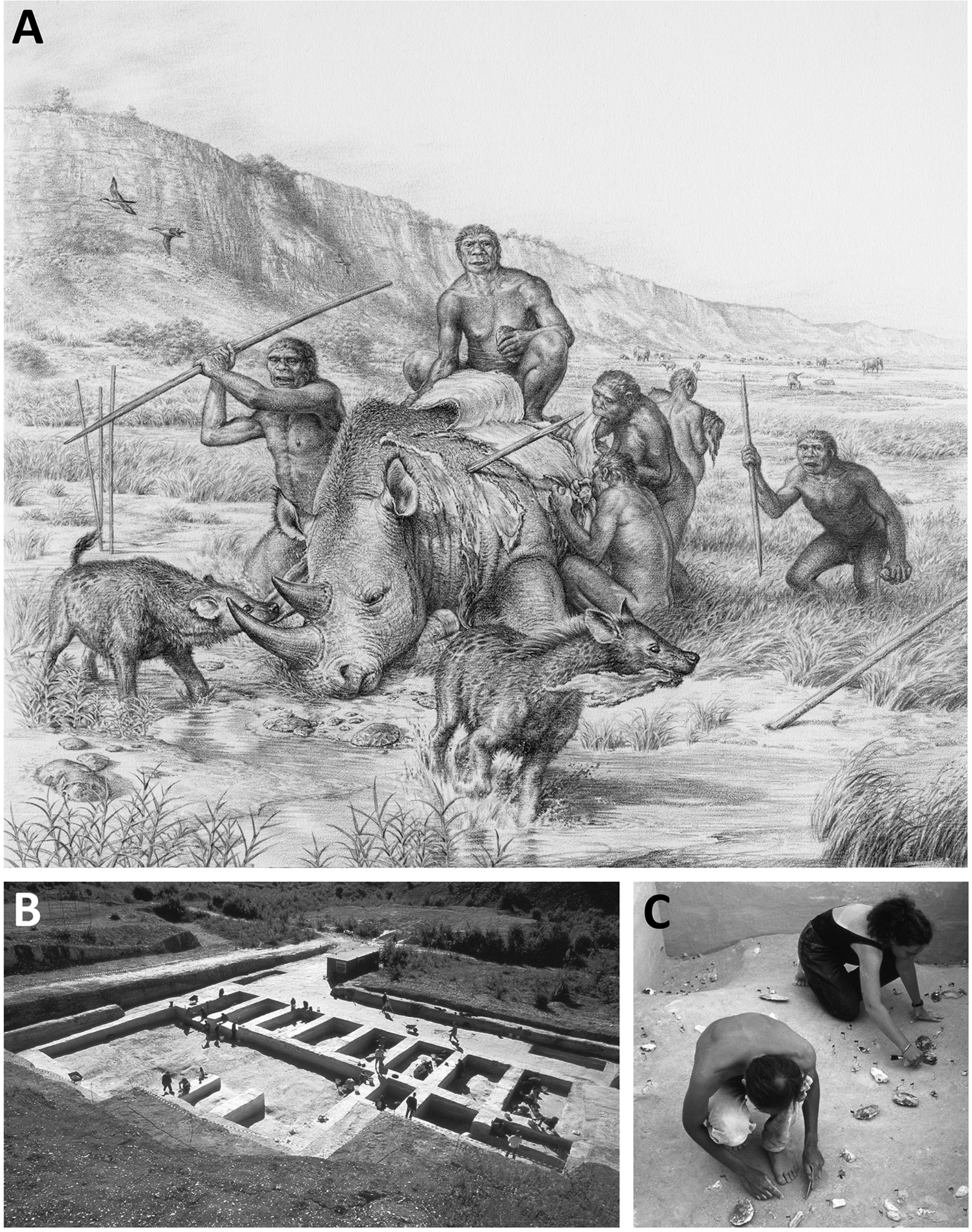


Fig. 5 Boxgrove, West Sussex. A. Reconstruction of butchering of a rhinoceros at the Boxgrove site (courtesy of John Sibbick). B. Excavations at Boxgrove. C. A rich assemblage of handaxes being excavated / *Boxgrove, West Sussex. A. Reconstruction du découpage d'un rhinocéros sur le site de Boxgrove (John Sibbick). B. Fouilles à Boxgrove. C. Un riche assemblage de bifaces a été découvert*

hominins from Happisburgh fall within the range derived from the fossil evidence of *Homo antecessor*, the only known species in western Europe of a similar age and known only from fossils found at the site of Gran Dolina, Atapuerca, Spain and dated to about 860,000–780,000 years ago. The species is believed to have evolved from *Homo erectus*, but had unique features that distinguish it from other *Homo* species [14–17]. A number of lithic artefacts similar in typology to those found at Gran Dolina were found at Happisburgh.

Animal remains at these early Pleistocene sites suggest that the climate was largely warm but this changed after about 650,000 years ago. At times, conditions throughout Europe became harsh and cold and Britain became uninhabitable. It is unclear whether *Homo antecessor* gave rise to *Homo heidelbergensis*, and subsequently to Neanderthals, or whether they were an evolutionary dead-end.

Homo heidelbergensis is the earliest human species for which we have fossil evidence in Britain, from around 500,000 years ago at Boxgrove. Two lower incisors were found close to one another and probably belong to the same adult individual. The morphology of the teeth is similar to that of other middle Pleistocene hominins making their assignment to *Homo heidelbergensis* possible. The tibia most likely originated from a different individual because it was discovered in a different stratigraphic context from the two teeth [18]. The tibia reveals a mosaic morphology relative to other archaic *Homo* tibiae. The external diaphyseal robusticity and mediolaterally thickened cortical bone distribution are characteristic of Late Pliocene to Late Pleistocene archaic *Homo*. The estimated cold-adapted body proportions would have promoted body heat conservation in a hominin practicing minimal cultural buffering during the late interglacial cool temperate climate [19]. From the Boxgrove tibia, it has been shown that *Homo heidelbergensis* was taller than the later, cold-adapted, Neanderthals [20]. Although no other British sites have yielded *Homo heidelbergensis* fossils, some have yielded similar lithic artefacts to those found at Boxgrove, Brandon and Waverley Wood, for example [11,21]. The tools associated with *Homo heidelbergensis* were more varied than those of *Homo antecessor* and included bifacial handaxes, cleavers and scrapers; they were probably skilled hunters of large animals, such as rhinoceros, bear, horse and deer [11].

The colonisers (425,000 – 40,000 years ago)

Connected or disconnected?

Britain's history of connectivity to mainland Europe is complex. However, in broad terms around 450,000 years ago (MIS 12), ice stretched across the North Sea, from Britain to Scandinavia, and at the end of this glacial stage there was an initial breaching of the chalk ridge (Fig. 1B). This initial erosion of the land bridge was probably characterised by waterfalls and channels that would have emptied proglacial lakes in the southern North Sea basin [2]. During the following glacial periods, Britain would have been too cold to inhabit and Neanderthals would have been pushed out of the British Isles to return during the interglacials. From around 180,000 years ago, there was a steady decline in global temperature which must have forced the Neanderthals out of Britain, and at about 160,000 years ago (MIS 6) it is unlikely that any humans were still present; however, the climate then recovered rapidly at around 130,000 years ago. This led to the rise of sea levels and the submerging of the land surface between Britain and the continent, making Britain an island. Some mammals, depending on the distances of their glacial refugia, were fast to migrate and managed to reach Britain before it became an island. Others, such as elephants and hippopotamus, may have swum across, but Neanderthals (without boats) are not thought to have returned until around 60,000 years ago [22].

Coming and going: Ice ages and deserted lands

Just over 400,000 years ago a rapid improvement of the climate after the Anglian glaciation made Britain habitable again. *Swanscombe* is the only British site, to date, where a very early Neanderthal fossil [23] has been discovered and it is possible that Neanderthals evolved from *Homo heidelbergensis* around this time (Fig. 6). The climate worsened again by about 375,000 years ago, driving these early Neanderthals out again. Neanderthals returned to Britain after the ice had retreated around 330,000 years ago, bringing with them new technologies. The Neanderthals are mostly known from sites across Britain with Mousterian artefacts, an industry which incorporates Levallois technique[1]. *Baker's Hole* (Ebbsfleet, Kent) is one of the foremost sites that shows the Levallois industry [24].

The oldest human fossils in Wales found until now came from *Pontnewydd Cave*, which has been dated to about 225,000 years ago [25,26], and comprise teeth of early Neanderthal adults and children (Fig. 7). The Mousterian industry was also found at *Crayford*, Kent [27,28]. Additionally, more than 250,000 lithic artefacts were found on the other side of the channel at the site of *La Cotte* and although this site is now on the island of Jersey, the island was connected to mainland France during periods of Neanderthal occupation. Generations of Neanderthals most likely returned to the site over a period totalling more than 150,000 years [29–32]. Although for a long time it was believed Neanderthals did not return to Britain until about 60,000 years ago, a recent discovery from Dartford (Kent), dated at about 100,000 years ago, may hint that small Neanderthal groups possibly made rare visits into Britain from their more permanent camps in France or Belgium [33,34]. It is possible that they followed herds of mammoths, rhinoceros, horse and deer into Britain, but further analyses and evidence are needed to support this claim.

Neanderthals were back in full force around 60,000 years ago. The site of *Lynford Quarry*, Norfolk has extensive evidence for classic Neanderthal Mousterian tools associated with the remains of at least eleven woolly mammoths [35–37]. Although no butchery marks were found on the recovered mammal bones, none of the large meat-bearing bones were found, indicating they may have been transported away from the kill site.

---

[1] A method of stone reduction, involving the striking of flakes from a prepared core that provided much greater control over the size and shape of the final flakes which would then be employed as scrapers, knives and points.

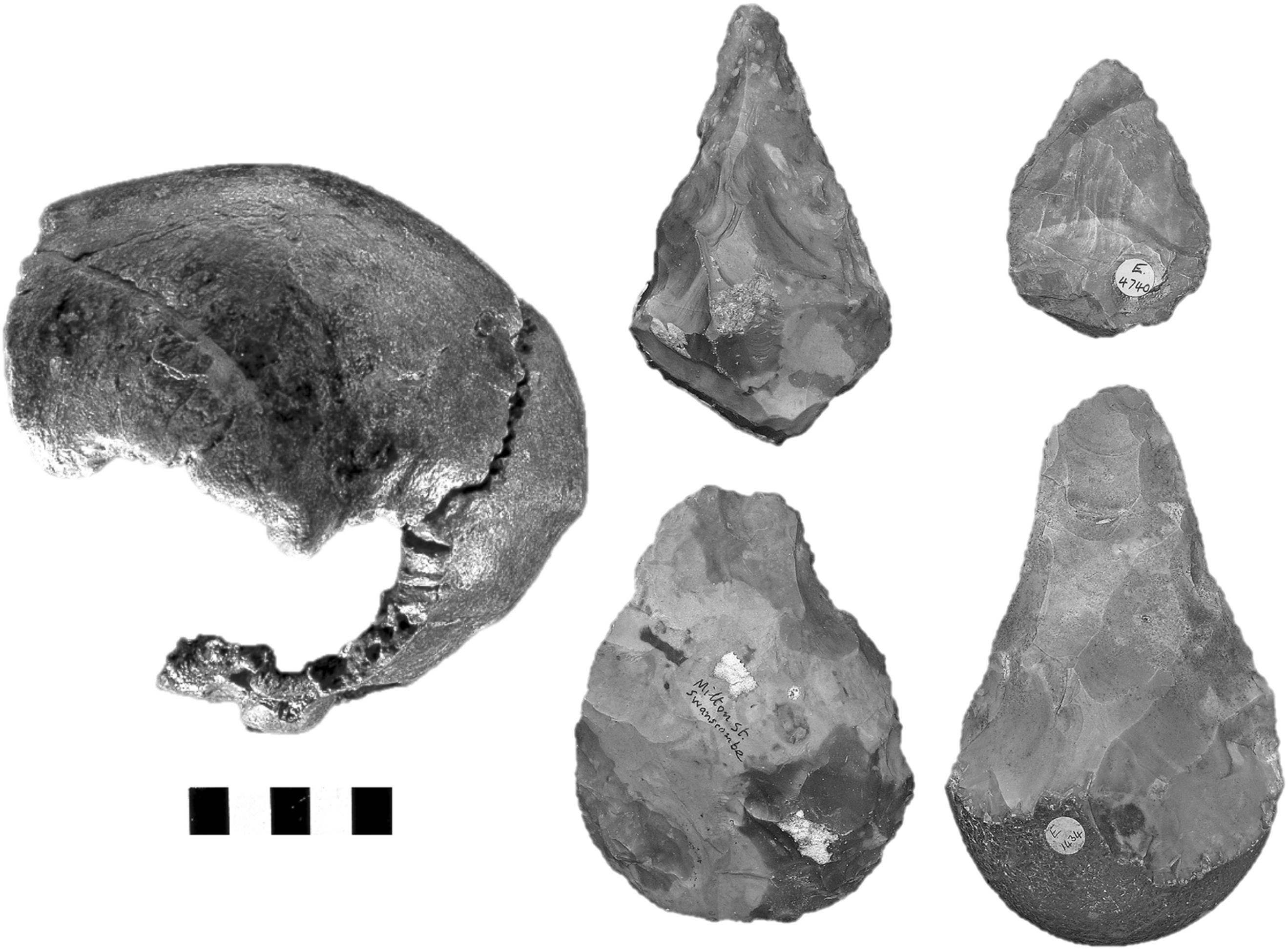


Fig. 6 Swanscombe, Kent. The partial cranium belonging to an early Neanderthal, probably female, and a selection of handaxes recovered at Swanscombe (courtesy of NHM, London) / *Swanscombe, Kent. Le crâne partiel appartenant à un Néanderthalien ancien, probablement de sexe féminin et une sélection de bifaces découverts à Swanscombe (of NHM, London)*

Hominins

The oldest fossil evidence for Neanderthals in the British Isles is the partial skull from Swanscombe. The three cranial bones were discovered between 1935 and 1955; the articulated bones form the back of the skull of what is believed to be an early Neanderthal female and were found close to a number of flint handaxes [23]. Despite its chronological association with the Middle Pleistocene, the occipital bone carries Neanderthal features: a weak occipital torus with bilateral projection, a central suprainiac depression and a strongly convex occipital plane. This makes the Swanscombe hominin one of the earliest primitive Neanderthals and supports an ancient root for the Neanderthal clade. The early emergence of these Neanderthal features in Swanscombe, while other roughly contemporary fossil hominins from Italy, Hungary and Germany display less derived Neanderthal morphology, suggests a more complex pattern of human evolution than has generally been assumed [20,23]. Neanderthal fossils were also found in *Pontnewydd Cave*, North Wales. The nineteen hominin teeth were associated with bifacial and Levallois artefacts and belonged to both juveniles and adults. The teeth are taurodont and the overall dental morphology shows clear affinities with Neanderthals and the pre-Neanderthal Middle Pleistocene teeth from the Sima de los Huesos, Atapuerca, Spain.

The founding people (40,000 – 10,000 years ago)

An island established

Neanderthals had returned to the British Isles by about 60,000 years ago, and although MIS 3 climate was variable and complex, conditions did not improve permanently until

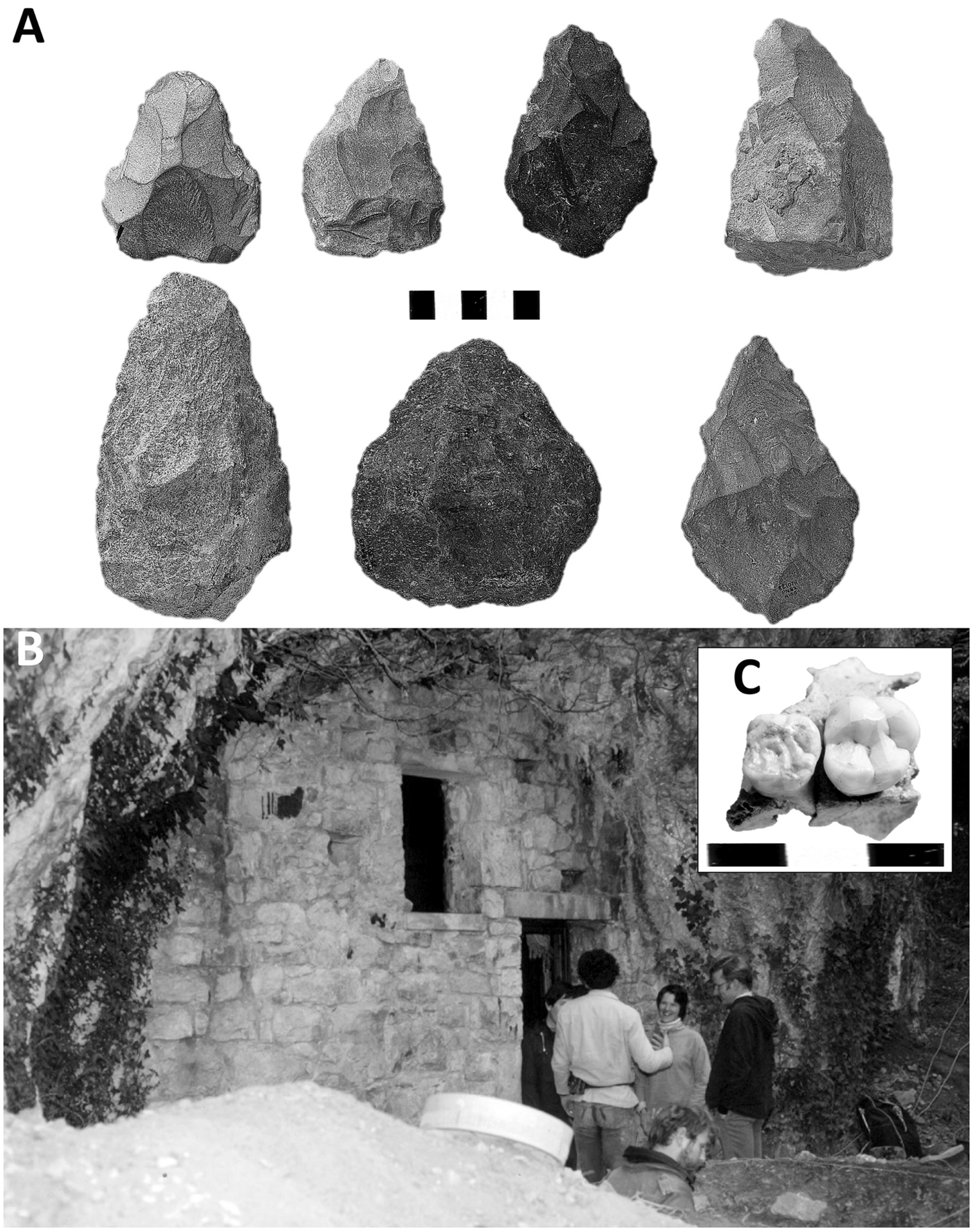


Fig. 7 Pontnewydd Cave, North Wales. A. Handaxes discovered at Pontnewydd Cave (courtesy of the National Museum of Wales). B. The cave entrance during excavations. C. A juvenile Neanderthal maxilla is part of the assemblage of 19 teeth discovered at the site (courtesy of the NHM, London) / *Pontnewydd Cave, North Wales. A. Bifaces découverts dans la grotte de Pontnewydd (National Museum of Wales). B. L'entrée de la grotte durant les fouilles. C. Un maxillaire de Néanderthalien immature fait partie des 19 dents découvertes dans le site (NHM, London)*

the end of the glacial period (MIS 2), which reached its cold peak around 20,000 years ago, the Last Glacial Maximum (Fig. 1C). During the early part of the current interglacial, the Holocene, Doggerland, the exposed land area in the present-day North Sea region, gradually disappeared as the ice melted and sea levels slowly rose to those of today (Fig. 1D). Well before this time (around 40,000 years ago), we see the demise of the Neanderthals and the arrival of *Homo sapiens* in Europe [38]. The role of modern humans in the physical extinction of the Neanderthals is the subject of much debate [38], but genetic data show that Neanderthal DNA entered the modern human gene pool through interbreeding events. At present, no evidence of overlap exists for the occupation of Britain by Neanderthals and modern humans; any interbreeding probably happened more centrally within the Neanderthal range rather than at its geographical limits.

Still coming and going

The oldest modern human fossil in Britain, a fragment of maxilla, was found at *Kent's Cavern* (Fig. 8) and dates back to at least 40,000 years ago [39]. The "Red Lady of *Paviland*" (actually the skeleton of a young man initially wrongly identified as a female) was discovered at Goat's Hole, South Wales, in 1823. The skeleton was coated in red ochre and the body had been buried wearing jewellery made from mammoth tusks; recent dating to about 33,000 years makes this discovery the oldest ceremonial burial in western Europe [40]. During the Last Glacial Maximum much of northern Britain and upland Wales would have been under an ice sheet that was up to 1 km thick in places, and cold winds and dry air would have prevailed across Britain. This severe environment seems to have been too difficult to deal with, even for the resourceful first modern humans, and Britain was deserted once more, probably by around 28,000 years ago [41].

Around 15,000 years ago the climate started to improve and the ice gradually retreated making Britain, once again, a welcome place for large game and the hunters who followed them [42]. *Gough's Cave* in Cheddar Gorge was one of the first settlements for Magdalenian modern humans after the peak of the last glacial stage [43]. Not only did these humans bring with them finely decorated bone tools, like batons and needles, they also made cups out of human skulls [44,45]. For a long time, it was believed that one of the main differences between early British and mainland European modern human sites was the absence of figurative art, such as figurines and cave paintings or engravings. In 2004 however, an engraving at least 13,000 years old of a bison, similar in style to those found in European caves, was found at *Church Hole* in the English midlands [46]. Shortly after 13,000 years ago another brief cold period hit Europe, but by about 11,700 years ago the current interglacial had started and temperatures gradually reached what they are today [47,48]. Prehistoric hunter-gatherers coming from Europe had to deal with new challenges. The animals they were used to hunting on the European Steppe, such as reindeer and horse, were replaced by forest dwelling taxa such as deer and wild boar. Around 6000 years ago, new ideas of agriculture and animal husbandry arrived from Europe leading to the decline of the hunter-gathering way of life and the beginning of the Neolithic [49,50]. As well as the adoption of agriculture, technological advances and a more sedentary way of life, these farming communities also implemented the construction of the first monuments in the landscape, such as Stonehenge 4600 years ago [49].

Fig. 8 The maxilla from Kent's Cavern, Devon, including three teeth of the earliest known modern human in Britain, discovered during excavations in 1927 / *Le Maxillaire de la grotte de Kent, Devon, qui comprend trois dents et correspond au plus ancien Homme moderne connu en Grande-Bretagne, trouvé lors de fouilles en 1927*

Conclusion

This review has laid out how human occupation of the British Isles during the last one million years is a story of repeated migration. The changing environment, with temperatures decreasing and recovering during the glacials and interglacials, would have posed challenges to the humans and fauna that they would not have encountered in more southerly parts of Europe. Not only would the English Channel land area have been submerged or dissected by large rivers at times, making accessing Britain difficult or impossible, but also when the ice sheets were at their thickest the extreme cold would have made the area uninhabitable for long periods of time. The first hominins to venture into the British Isles, probably *Homo antecessor* and *Homo heidelbergensis*, would have been unable to survive these long cold periods. Even Neanderthals, a human species well adapted to living in the cold northwest European plains, seem to have been unable to survive in Britain during MIS 6. Modern humans, despite their controlled use of fire, building of shelters and advanced lithic technology, still needed several attempts before being able to settle because life at the western edge of the Old World was not easy. The prehistory of the British Isles is a tale of coming and going of deserted, lands and recurring migrations.

Acknowledgements We would like to thank Simon Parfitt and also the Photography Unit at the Natural History Museum, London, for some of the images used; John Sibbick for the Happisburgh and Boxgrove reconstructions; Elizabeth Walker and Kay Kays from the National Museum of Wales for the Pontnewydd lithics image. CBS and ML's research work was supported through the AHOB Project, funded by the Leverhulme Trust, and Pathways to Ancient Britain, funded by the Calleva Foundation.

Conflict of interest: None.

References

1. Stringer C (2006) *Homo britannicus*. London, Allen Lane, London. 319 pp.
2. Gupta S, Collier JS, Garcia Moreno D, et al (2017) Two-stage opening of the Dover Strait and the origin of island Britain. Nat Commun 8:e15101
3. Ashton N, Lewis SG, De Groote I, et al (2014) Hominin footprints from early pleistocene deposits at happisburgh, UK. PLoS One 9:e88329
4. Parfitt SA, Ashton NM, Lewis SG, et al (2010) Early Pleistocene human occupation at the edge of the boreal zone in northwest Europe. Nature 466:229–33
5. Lee JR, Rose J, Hamblin RJ, et al (2004) Dating the earliest lowland glaciation of eastern England: a pre-MIS 12 early Middle Pleistocene Happisburgh glaciation. Quat Sci Rev 23:1551–66
6. Huddart D, Roberts G, Gonzalez S (1999) Holocene human and animal footprints and their relationships with coastal environmental change, Formby Point, NW England. Quat Int 55:29–41
7. Parfitt SA, Barendregt RW, Breda M, et al (2005) The earliest record of human activity in northern Europe. Nature 438:1008–12
8. Ashton N, Lewis SG (2012) The environmental contexts of early human occupation of northwest Europe: The British Lower Palaeolithic record. Quat Int 271:50–64
9. Stuart A, Lister AM (2001) The mammalian faunas of Pakefield/Kessingland and Corton, Suffolk, UK: evidence for a new temperate episode in the British early Middle Pleistocene. Quat Sci Rev 20:1677–92
10. Lister AM, Stuart AJ (2010) The West Runton mammoth (Mammuthus trogontherii) and its evolutionary significance. Quat Int 228:180–209
11. Roberts MB, Parfitt SA (1999) Boxgrove: A Middle Pleistocene Hominid site at Eartham Quarry, Boxgrove, West Sussex, English Heritage. In: English Heritage. 484 pp
12. Stringer CB (1996) The Boxgrove tibia: Britain's oldest hominid and its place in the Middle Pleistocene record. In: Gamble C and Lawson AJ (eds): The English Palaeolithic Reviewed. Trust for Wessex Archaeology Ltd, pp. 52–6
13. Roberts MB, Stringer CB, Parfitt S (1994) A hominid tibia from Middle Pleistocene sediments at Boxgrove, UK. Nature 369:311
14. Fernandez-Jalvo Y, Carlos Diez J, Cacares I, et al (1999) Human cannibalism in the Early Pleistocene of Europe (Gran Dolina, Sierra de Atapuerca, Burgos, Spain). J Hum Evol 37:591–622
15. Lorenzo C, Arsuaga JL, Carretero JM (1999) Hand and foot remains from the Gran Dolina Early Pleistocene site (Sierra de Atapuerca, Spain). J Hum Evol 37:501–22
16. Carretero JM, Lorenzo C, Arsuaga JL (1999) Axial and appendicular skeleton of *Homo antecessor*. J Hum Evol 37:459–99
17. Arsuaga J-L, Martínez I, Lorenzo C, et al (1999) The human cranial remains from Gran Dolina lower Pleistocene site (Sierra de Atapuerca, Spain). J Hum Evol 37:431–57
18. Hillson S, Parfitt S, Bello S, et al (2010) Two hominin incisor teeth from the middle Pleistocene site of Boxgrove, Sussex, England. J Hum Evol 59:493–503
19. Trinkaus E, Stringer C, Ruff C, et al (1999) Diaphyseal cross-sectional geometry of the Boxgrove 1 Middle Pleistocene human tibia. J Hum Evol 37:1–25
20. Buck LT, Stringer CB (2014) *Homo heidelbergensis*. Curr Biol 24:R214–R5
21. Stout D, Apel J, Commander J, et al (2014) Late Acheulean technology and cognition at Boxgrove, UK. J Archaeol Sci 41:576–90
22. Ashton N (2002) Absence of humans in Britain during the last interglacial (oxygen isotope stage 5e). Publications du CERP 8:93–103
23. Stringer C, Hublin JJ (1999) New age estimates for the Swanscombe hominid, and their significance for human evolution. J Hum Evol 37:873–7
24. Scott B, Ashton N, Penkman KE, et al (2010) The position and context of Middle Palaeolithic industries from the Ebbsfleet Valley, Kent, UK. J Quat Sci 25:931–44
25. Green H, Stringer C, Collcutt S, et al (1981) Pontnewydd Cave in Wales — a new Middle Pleistocene hominid site. Nature 294:707–13
26. Compton T, Stringer C (2015) The morphological affinities of the Middle Pleistocene hominin teeth from Pontnewydd Cave, Wales. J Quat Sci 30:713–30
27. Roe DA (2014) The Lower and Middle Palaeolithic periods in Britain, Routledge. In: The Lower and Middle Palaeolithic periods in Britain, Routledge. 358 pp.
28. Chandler R (1916) The implements and cores of Crayford. Proc Prehist Soc 2:240–8
29. White M, Scott B, Ashton N (2006) The Early Middle Palaeolithic in Britain: archaeology, settlement history and human behaviour. J Quat Sci 21:525–41
30. Scott B, Bates M, Bates R, et al (2014) A new view from La Cotte de St Brelade, Jersey. Antiquity 88:13–29
31. Bates M, Pope M, Shaw A, et al (2013) Late Neanderthal occupation in North-West Europe: rediscovery, investigation and dating of a last glacial sediment sequence at the site of La Cotte de Saint Brelade, Jersey. J Quat Sci 28:647–52
32. Callow P, Cornford JM, McBurney CBM (1986) La Cotte de St. Brelade, 1961–1978: Excavations by C.B.M. McBurney, Geo Books, Norwich, 433 p
33. Wenban-Smith FF, Bates MR, Schwenninger JL (2010) Early Devensian (MIS 5d–5b) occupation at Dartford, southeast England. J Quat Sci 25:1193–9
34. White MJ, Pettitt PB (2011) The British Late Middle Palaeolithic: an interpretative synthesis of Neanderthal occupation at the northwestern edge of the Pleistocene world. J World Prehist 24:25–97
35. Boismier W, Schreve DC, White MJ, et al (2003) A Middle Palaeolithic site at Lynford Quarry, Mundford, Norfolk: Interim statement. Proc Prehist Soc 69:315–24
36. Schreve DC (2006) The taphonomy of a Middle Devensian (MIS 3) vertebrate assemblage from Lynford, Norfolk, UK, and its implications for Middle Palaeolithic subsistence strategies. J Quat Sci 21:543–56
37. Boismier WA, Gamble C, Coward F (2012) Neanderthals among mammoths: excavations at Lynford Quarry, Norfolk UK, English Heritage Monographs. In: English Heritage Monographs. 529 pp
38. Higham T, Douka K, Wood R, et al (2014) The timing and spatiotemporal patterning of Neanderthal disappearance. Nature 512:306–9
39. Higham T, Compton T, Stringer C, et al (2011) The earliest evidence for anatomically modern humans in northwestern Europe. Nature 479:521–4
40. Jacobi R, Higham T (2008) The "Red Lady" ages gracefully: New ultrafiltration AMS determinations from Paviland. J Hum Evol 55:898–907
41. Jacobi R, Higham T (2011) The British earlier Upper Palaeolithic: Settlement and chronology. In: Ashton NM, Lewis SG, Stringer CB (eds) The Ancient Human Occupation of Britain. Elsevier, Amsterdam, pp 181–222
42. Jacobi R, Higham T (2009) The early Lateglacial re-colonization of Britain: New radiocarbon evidence from Gough's Cave, southwest England. Quat Sci Rev 28:1895–913
43. Currant A, Jacobi R, Stringer CB (1989) Excavations at Gough's Cave, Somerset 1986 7. Antiquity 63:131–6

44. Bello SM, Saladié P, Cáceres I, et al (2015) Upper Palaeolithic ritualistic cannibalism at Gough's Cave (Somerset, UK): The human remains from head to toe. J Hum Evol 82:170–89
45. Bello SM, Parfitt SA, Stringer CB (2011) Earliest directly-dated human skull-cups. PLoS One 6:e17026
46. Ripoll S, Muñz F, Bahn P, et al (2004) Palaeolithic Cave Engravings at Creswell Crags, England. Proc Prehist Soc 70:93–105
47. Woodward J (2014) The Ice Age: A very short introduction, OUP Oxford, 63 p
48. Shennan I, Horton B (2002) Holocene land- and sea-level changes in Great Britain. J Quat Sci 17:511–26
49. Bradley R (2014) The Prehistoric Settlement of Britain, Routledge, London, 172 p
50. Cramp LJE, Jones J, Sheridan A, et al (2014) Immediate replacement of fishing with dairying by the earliest farmers of the northeast Atlantic archipelagos. Proc R Soc B 281:e20132372
51. Penkman KE, Preece RC, Bridgland DR, et al (2011) A chronological framework for the British Quaternary based on Bithynia opercula. Nature 476:446–9
52. Debenham NC, Atkinson T, Grun R, et al (2012) Dating. In: Aldhouse-Green S, Peterson R, Walker EA (eds) Neanderthals in Wales: Pontnewydd and the Elwy Valley Caves. Oxbow Books, Oxford, pp 283–319
53. Pike AW, Gilmour M, Pettitt P, et al (2005) Verification of the age of the Palaeolithic cave art at Creswell Crags, UK. J Archaeol Sci 32:1649–55

BMSAP (2018) 30:14-16
DOI 10.3166/bmsap-2018-0005

INTRODUCTION / *INTRODUCTION*

Biological Anthropology of the African Continent: From the First Hominins to Extant Populations

Anthropologie biologique du continent africain : des premiers hominines aux populations actuelles

F. Marchal · I. Crevecœur · F. Détroit · S. Prat · F. Ramirez Rozzi

Received: 15 January 2018; Accepted: 29 January 2018

"The biological anthropology of the African continent: from the first hominins to extant populations" is a vast undertaking not only because Africa is a vast continent, but also because Africa, as the "cradle of humanity", is the only continent that encompasses the full chronological depth of the history of humankind from its earliest origins. This was the theme of one of the two thematic scientific sessions of the 1842nd SAP meeting held in Paris, at the National Institute of the History of Art, from 25 to 27 January 2017. The seven articles published together in this issue of BMSAP[1] are from papers submitted during this session. Obviously, neither the papers read nor these articles can fully cover such a wide topic. The idea, rather, was to present, with some examples, an overview of current research conducted by our community on the African continent. This resulted in a rich session, with guest speaker Professor Robert A. Foley, 15 oral presentations and 6 poster presentations.

Human evolution was naturally one of the topics explored in this session, with two oral presentations and three poster presentations. Robert A. Foley (Cambridge University) [1] presented his Afrotropical Model for Hominin Evolution, explaining why Africa is so central to the issue of hominin evolution through an approach mainly based on evolutionary geography (the spatial and distributional properties of evolutionary processes). Also devoted to hominin evolution was the paper given by Prat and Caparros (UMR 7194 HNHP) [2], who used cladistic analyses to assess the taxonomy of the earliest representatives of the genus *Homo*. In their poster presentation, Louail and Prat (UMR 7194 HNHP) [3] discussed the relevance of the ASUDAS standard scoring system when applied to hominin teeth and proposed some adaptations to encompass their morphological variability. Another poster, by Verna (UMR 7194 HNHP) [4], presented the use of this ASUDAS standard scoring system together with a morphometric analysis to compare dental morphology between humans from northern and southern Africa during the Pleistocene (MIS 5–3). Finally, the poster by Matu et al. (UMR 5199 PACEA) [5] presented new human remains from the Holocene site of Hara Idé 3 (Djibouti) documenting the morphological variability of African *Homo sapiens* and the issue of continuity or discontinuity at the Pleistocene–Holocene boundary.

Five oral and three poster communications dealt with mortuary or funerary practices of past African populations from various periods and geographical origins, illustrating both the variety of these practices as well as the close involvement of SAP members in the field in Africa. Chronologically speaking, the first of these communications was the poster by Hanon et al. (UMR 7194 HNHP) [6], showing the experimental taphonomic approach they developed to reassess the intentionality of the process that produced the linear marks on the South African hominin Stw53. The talk by Chalamon de Bernardy et al. (UMR 7194 HNHP) [7] then presented new Later Stone Age human remains from

F. Marchal (✉)
UMR 7268 ADES, Aix-Marseille université, CNRS, EFS,
Faculté de médecine de Marseille, secteur Nord, bât. A CS80011,
bld Pierre-Dramard, 13344 Marseille cedex 15, France
e-mail : francois.marchal@univ-amu.fr

I. Crevecœur
UMR 5199 PACEA, CNRS, université de Bordeaux,
ministère de la Culture et de la Communication,
allée Geoffroy-Saint-Hilaire, 33615 Pessac Cedex, France

F. Détroit · S. Prat
UMR 7194 HNHP, CNRS, MNHN, UPVD, Sorbonne
universités, Musée de l'homme,
17, place du Trocadéro, 75016 Paris, France

F. Ramirez Rozzi
UMR 5288 AMIS, Faculté de chirurgie dentaire,
1, rue Maurice-Arnoux, 92120 Montrouge, France

---

[1] Articles relating to this specific session were produced with the associated editors (F. Marchal, I. Crevecoeur, F. Détroit, S. Prat and F. Ramirez Rozzi).

the Leopard Cave in Namibia. These document a previously unknown mortuary *chaine opératoire* for the southern African Later Stone Age. Probably also from the Holocene is the Fossil man from Asselar (Mali). With their poster, Dumesnil et al. (UMR 7194 HNHP) [8] proposed new insights into the archaeology of the deaths of these individuals whose remains were discovered in 1927. Sellier et al. (UMR 7206 Eco-Anthropology and Ethnobiology) [9] presented some results of their fieldwork in Sudan in the Kadruka 23 cemetery, including newly discovered Neolithic funerary practices in Sudan such as pre- and post-burial practices that imply wrapping and carrying of the dead. Le Roy et al. (UMR 5140 ASM) [10] documented the Egyptian area, presenting evidence from new fieldwork at Kom Abu Billou of funerary practices in the Nile delta during the Roman period. Gleize et al. (INRAP) [11] are involved in fieldwork in Lalibela, Ethiopia, and presented new data from the Qedemt cemetery bringing more in-depth knowledge on the influence of Christianization on funerary practices in mediaeval Ethiopia. Ardagna and Maillot (UMR 7268 ADÉS) [12] co-authored a poster presenting the mediaeval necropolis of Mouweiss in Sudan. They notably document a very rare case of leprosy in mediaeval Nuba. Finally, for the most recent period, Polet et al. (IRSNB) [13] presented results from Kindoki in the Democratic Republic of Congo, describing two cases of DISH for the first time in an African archaeological sample.

The African continent also displays such a wide diversity of human populations that it is an inexhaustible source for research on the biological anthropology of living humans, as illustrated by the nine papers given during this session. West Africa was represented in five of these. The first, by Cohen et al. (UMI 3189 ESS) [14], presented results on the biocultural determinants of excess weight in Senegal, arguing in favour of local and global policies to fight obesity in that country, where a nutritional transition is in progress. The second study, by Macia et al. (UMI 3189 ESS) [15], compared the prevalence of obesity and body size perceptions between urban and rural areas, which enabled them to explain how and why obesity is becoming a health problem in rural areas in Senegal. A third study from the UMI 3189 ESS team in Senegal was presented by Duboz et al. [16]. They compared the determinants of self-rated health between urban and rural areas in order to determine whether self-rated health is a relevant indicator of actual individual health in Senegal. Moving from Senegal to Ivory Coast, the work of Kouassi et al. (ISAD) [17] shows that the interaction between parity and physical self-esteem of the mother significantly influences the physical development of children. Kouadio et al. (ISAD) [18] also dealt with children's development, comparing the environments of children living in different socio-sanitary conditions and confirming that these factors strongly influence the children's development. Ramirez Rozzi (UMR 5288 AMIS) [19] is working on the life history of the Baka Pygmies in Cameroon. Based on chronological age, he shows that tooth eruption proceeds at an early age, suggesting that growth diversity in modern humans is larger than previously thought, as his work on body proportions in Pygmies confirms. From South Africa, Ridel et al. (University of Pretoria) [20] presented a computer-assisted method for the approximation of the nose, based on an analysis of the anatomical variability of nasal shapes among South African groups, with some forensic anthropological implications. The great diversity of human populations in Africa is also the result of a complex history of peopling and migration. This can be analyzed by genetic anthropology, as exemplified by the last two communications of this session. Verdu et al. (UMR 7206 Eco-Anthropology and Ethnobiology) [21] studied the trajectories of genetic and linguistic admixture in Kriolu speakers in Cape Verde and propose combining the two trajectories to reconstruct the complex admixture processes that have shaped the wide diversity of human populations living in this archipelago. The last communication, by Fortes-Lima et al. (UMR 7206 Eco-Anthropology and Ethnobiology) [22], offered new insights into the genetic legacy of African–American populations. They showed that Noir Marron communities have a strong African genetic legacy, and more specifically that they are linked to the populations residing today in the historical Gold Coast and Bight of Benin.

The number of communications and the variety of topics covered during this session clearly demonstrated the close involvement of our community in every aspect of anthropological research in Africa and also emphasized the major importance of research conducted in the field. Field research is, and will always be, the most important source of primary data ensuring high-level scientific output. We hope that by illustrating this with examples from across a whole continent, we will have given further encouragement to all our colleagues already engaged in field research and helped to motivate those who aim to do so in future.

References

1. Foley RA (2017) Evolutionary geography: The dynamic role of the African environment in becoming human. BMSAP 29(S1):S9
2. Prat S, Caparros M (2017) Taxinomie des premiers représentants du genre *Homo* : apport des analyses cladistiques. BMSAP 29 (S1):S28–9
3. Louail M, Prat S (2017) Précision du système de codage de référence ASUDAS pour prendre en compte la variation morphologique des hominines fossiles. BMSAP 29(S1):S24
4. Verna C (2017) Morphologie dentaire au Nord et au Sud de l'Afrique au Pléistocène (MIS 5–3). Une fenêtre sur une structuration des populations d'Hommes anatomiquement modernes ? BMSAP 29(S1):S32

5. Matu M, Bruxelles L, Cauliez J, et al (2017) Les derniers chasseurs-cueilleurs en République de Djibouti : étude des restes humains inédits du site d'Hara Idé 3 (Bassin du Gobaad). BMSAP 29(S1):S25
6. Hanon R, Péan S, Prat S (2017) Réévaluation du traitement intentionnel de l'hominine sud-africain Stw53. BMSAP 29(S1):S19
7. Chalamon de Bernardy M, Détroit F, Lesur J, et al (2017) Modifications anthropiques de restes humains à Leopard Cave (Namibie) et une chaîne opératoire mortuaire inédite au Later Stone Age en Afrique australe. BMSAP 29(S1):S12
8. Dumesnil J, Vialet A, Valentin F (2017) Le squelette de l'Homme d'Asselar (Mali) : premières réflexions archéothanatologiques. BMSAP 29(S1):S15
9. Sellier P, Aoudia L, Gilon A, et al (2017) Pratiques pré- et post-dépositionnelles du Néolithique de Haute-Nubie : enveloppement et transport des corps dans le cimetière Kadruka 23 (Soudan). BMSAP 29(S1):S31
10. Le Roy M, Picavet P, Dhennin S (2017) La reprise des fouilles de Kom Abu Billou (Égypte) : des données anthropologiques inédites. BMSAP 29(S1):S23
11. Gleize Y, Bosc-Tiessé C, Derat ML, et al (2017) Le cimetière médiéval de Qedemt à Lalibela (Éthiopie) : christianisation et pratiques funéraires. Apports de la campagne 2014. BMSAP 29 (S1):S17–8
12. Ardagna Y, Maillot M (2017) La nécropole médiévale de Mouweiss (Region de Shendi, Soudan) : données bioarchéologiques. BMSAP 29(S1):S10
13. Polet C, Clist B, Bostoen K (2017) Étude des restes humains de Kindoki (République Démocratique du Congo, 18^{e} s.). BMSAP 29(S1):S18
14. Cohen E, Ndao A, Ndiaye S, et al (2017) Déterminants bioculturels du surpoids dans un contexte de transition nutritionnelle au Sénégal. BMSAP 29(S1):S13
15. Macia E, Cohen E, Gueye L, et al (2017) Prévalences d'obésité et images du corps en milieu urbain et en milieu rural au Sénégal. BMSAP 29(S1):S24
16. Duboz P, Macia E, Gueye L, et al (2017) Les déterminants de l'auto-évaluation de la santé au Sénégal : comparaison entre milieux urbain et rural. BMSAP 29(S1):S15
17. Kouassi FK, Kouadio JK, Kobenan DAN, et al (2017) Estime de soi physique de la mère, parité et niveau d'activation biophysique chez des nourrissons de 6 à 11 mois en milieu urbain abidjanais. BMSAP 29(S1):S21
18. Kouadio JK, Kouassi FK, Kouame NP, et al (2017) Milieu de vie et développement physique chez des enfants vivant dans des conditions socio-sanitaires différentes dans la commune de Koumassi en Côte d'Ivoire. BMSAP 29(S1):S21
19. Ramirez Rozzi F (2017) Stratégie de vie et croissance dentaire chez les pygmées Baka. Le polymorphisme humain. BMSAP 29 (S1):S29
20. Ridel A, Oettlé AC, L'Abbé EN, et al (2017) Une méthode assistée par ordinateur pour l'approximation du nez, appliquée aux groupes de populations modernes d'Afrique du Sud, à partir de données tomographiques volumiques à faisceau conique. BMSAP 29(S1):S29
21. Verdu P, Jewett EM, Pemberton TJ, et al (2017) Trajectoires parallèles de l'histoire des métissages linguistiques et génétiques chez les locuteurs Kriolu au Cap Vert. BMSAP 29(S1):S32
22. Fortes-Lim C, Schroeder H, Ruiz-Linares A, et al (2017) New insights into the genetic legacy of Africa-American populations: Origin and admixture. BMSAP 29(S1):S16–7

BMSAP (2018) 30:17-31
DOI 10.3166/bmsap-2018-0001

NOTE / *NOTE*

Evolutionary Geography and the Afrotropical Model of Hominin Evolution

Géographie évolutionnaire et le modèle afro-tropical de l'évolution des hominines

Robert A. Foley

Received: 28 July 2017; Accepted: 27 October 2017

Abstract During the second half of the twentieth century, the evidence that Africa was central to hominin evolution became overwhelming. The earliest occurrences of most of the fossil hominin taxa and lithic technologies are to be found in Africa, and there is also strong evidence that humans are closely related to African apes, and that the genetic origins of modern humans lie in Africa. The aim of this article is to consider the possible evolutionary and ecological basis for this — why should Africa be so central? After considering biases in the record that might promote an African record, this article uses evolutionary geography – the spatial and distributional properties of the evolutionary process — to consider the factors that lead to higher rates of speciation, novelty and dispersals, as well as the way in which the African ecological context is structured and changes through time. Critical factors identified are the variable role of the Sahara, the different extent of the Afrotropical realm as climate changes, the impact of basin structure, and the effect of variable topography and surface water distribution. The key factor is biogeographic regionalisation and the shared evolutionary histories that reflect this. It is proposed that hominin evolution is globally part of the Afrotropical realm and its history, and that biogeographical variation within Africa is a key to understand the diverse nature of African hominins and their potential to disperse beyond the continent. More broadly, this article shows the importance of placing hominin evolution into a comparative and theoretical framework, particularly evolutionary geography, and proposes a more general basis for the Afrotropical Model of Hominin Evolution.

Keywords Human evolution · Evolutionary geography · Biogeography · African ecology

Résumé Au cours de la seconde moitié du xx^{e} siècle, le fait que l'Afrique occupait une place centrale pour la question de l'évolution humaine est devenu une hypothèse soutenue par des témoignages de plus en plus incontournables. Les plus anciennes occurrences de la plupart des taxons d'hominines et des technologies lithiques se trouvent en Afrique. En plus, il existe des preuves très solides du fait que les plus proches parents des humains sont les grands singes africains et que les origines génétiques des humains actuels sont africaines. L'objectif de cet article est d'en considérer les fondements évolutionnaires et écologiques — pourquoi l'Afrique occupe-t-elle une place si centrale ? Après avoir pris en compte les biais fossiles qui peuvent déformer les enregistrements en faveur de l'Afrique, cet article s'appuie sur la géographie évolutionnaire — les propriétés de localisation et de distribution des processus évolutionnaires — pour appréhender les facteurs à l'origine des taux supérieurs de spéciation, de nouveauté et de dispersion, ainsi que la façon dont le contexte écologique africain est structuré et varie au cours du temps. Les facteurs critiques qui ont pu être identifiés sont le rôle variable du Sahara, les différentes extensions du royaume afro-tropical en fonction des changements climatiques, l'impact de la structure en bassin, et l'effet de la grande variabilité de la topographie aussi bien que de la distribution en eau. Le facteur clé est la régionalisation biogéographique et les histoires évolutionnaires partagées que cela reflète. Il est ici proposé que l'évolution des hominines s'inscrit globalement dans le royaume afro-tropical et son histoire, et que la variabilité biogéographique à l'échelle de l'Afrique est un facteur clé pour comprendre la diversité des hominines et leur potentiel pour se disperser à terme au-delà du continent africain. Plus généralement, cet article montre l'importance de placer l'évolution des hominines dans un cadre théorique et comparatif, notamment dans une perspective de géographie évolutionnaire, et propose

---

Robert A. Foley (✉)
Leverhulme Centre for Human Evolutionary Studies,
Department of Archaeology and Anthropology,
University of Cambridge, Fitzwilliam street,
Cambridge CB2 1QH, UK
e-mail : raf10@cam.ac.uk

des fondements plus généraux en faveur du Modèle Afrotropical de l'évolution des Hominines.

Mots clés Evolution humaine · Géographie évolutionnaire · Biogéographie · Écologie africaine

Introduction: the Afrotropical Model of hominin evolution

When Raymond Dart described the first fossil hominin in 1924 at Taung [1], few would have predicted that by the end of the last century Africa would have moved from a peripheral to a central role in human evolution. Both theory and data seemed to point Eurasia as a more probable place of origins [2]. Ironically, Darwin's prediction that Africa would be the place of human origins had largely been forgotten.

Now, no-one would challenge the substantial role of Africa — especially sub-Saharan Africa — in the evolution of the hominin lineage. A simple measure is to look at the first appearances (Table 1). The earliest hominins, the earliest (and only) australopithecines, the earliest genus *Homo*, the earliest hominin with significantly larger brain size and human body proportions, the earliest anatomically modern humans. Against that, Eurasia can claim one definite palaeontological first appearance — *H. neanderthalensis* — plus the genetic ghost lineage, the Denisovans. *Homo georgicus, H. antecessor*, *H. floresiensis*, *H. erectus* and *H. heidelbergensis* are hard to place, as it depends upon taxonomic definitions, but could have Eurasian origins. Of the 28 taxa so far identified in the hominin fossil record [3,4], 24 occur in Africa, and 21 exclusively in Africa. All hominin genera have African origins.

Table 1 Occurrence of first appearances in Africa during the course of hominin evolution / *Occurrence des premières apparitions en Afrique au cours de l'évolution des hominines*

First appearances	Age (Ma)	Reference
Earliest modern human behaviours	0.16–0.1	[62]
Earliest *Homo sapiens*	~0.3–0.2	[17,27,63]
Earliest Mode 3 technologies	~0.3	[64]
Earliest *Homo heidelbergensis*	~0.7	[65]
Earliest Acheulean	1.7	[66]
Earliest *Homo ergaster/erectus*	1.9	[67]
Earliest Oldowan technologies	2.5	[68]
Earliest *Homo*	2.8–2.3	[69]
Earliest technology	3.3	[70]
Origins and radiation of australopithecines	4.2–2	[71]
Earliest hominins	~7–5	[22]

A similar story can be found among the lithic traditions (Table 1) — the first stone tool technology (Lomekwian), the first Oldowan, the earliest Mode 2 technologies and the earliest Mode 3. Looking more broadly at the archaeological record, fire, use of ochre and microliths are all found earlier in Africa than elsewhere, and there is widespread acceptance of the evidence for what might broadly be called modern human behaviour in Africa by around 100,000 years ago.

It is not just the palaeontological and archaeological records that underpin the Afrotropical model of human evolution. Comparative genetics have shown that the sister clade of the hominins is the chimpanzee/bonobo one [5], and that in turn is part of an African ape clade, suggesting, in line with Darwin's proposal [6], that hominin origin is an African event.

Currently, genetics cannot inform on australopithecine diversity, or the early evolution of *Homo*, but both ancient and contemporary DNA has also shown a) that the ancestral population of modern humans was in Africa [7]; b) that Africans have much larger genetic diversity than all Eurasia [8]; c) that Eurasian populations are descended from African ones [9,10]; and d) that African ancestral populations did not interbreed with Neanderthals and Denisovans [11]. This has been made clear for some time from the uniparental markers, mtDNA and *Y*-chromosome, and now it has been firmly confirmed by whole genomes and multiple autosomal markers.

Even when the focus moves beyond Africa, the framework remains African. Eurasian evolution and prehistory is defined in terms of "out of Africa" models — Out of Africa 1 (*H. ergaster/erectus*) [12], Out of Africa 2 (modern humans) [13] and more extensively, "out of Africa again and again" (multiple dispersals) [14].

There is, on current evidence, little chance of this Afrocentric model being overturned, although there may be challenges to some elements of it — for example, that the African apes were in fact "recent" Eurasian immigrants [15], or that *H. erectus* (defined broadly) evolved in Asia and subsequently dispersed into Africa [16], or that northern rather than sub-Saharan Africa may have played an important role in modern human origins [17,18]. Neither is there much to be gained by thinking of this pattern in terms of "importance"; it is not that Africa is more important than other regions, but that the ecological and demographic conditions in different regions prompt different evolutionary processes. Higher latitudes, for example, are subject to more magnified habitat change, and so responses are likely to be different (often extinction), compared to tropical regions. Cold climates demand particular adaptive responses which may be less likely to lead to novelty. This is certainly the pattern across broader biological systems, leading to such patterns as the declining levels of diversity with latitude [19].

A more profitable approach is to examine how and why Africa seems to have been, for hominins, such a promotor of change and diversity. The framework adopted here is broadly speaking referred to as evolutionary geography. Evolutionary geography investigates the role of spatial factors in the evolutionary process [20]. It differs from biogeography in which it operates at a variety of scales. While phylogenetic patterns are an important element, its primary focus is the investigation of the environmental (biotic and abiotic) and demographic conditions for both range expansions and contractions in the history of a lineage, and the way this plays out from the micro to the macroevolutionary levels [20]. Geographical approaches to evolution are significant because spatial distributions and their context underlie most processes. "Evolutionary change occurs first as a result of spatial distribution — population dispersals and contractions, fragmentation and isolation in response to vicariance, shifting habitat boundaries, and so on. Changes in distribution result in altered selective pressures, different demographic parameters, new levels of gene flow or discontinuities, and as such, evolutionary change through time is the end product of geographical processes" [21] (Fig. 1). This article will examine the primacy of Africa in human evolution in the context of geographical patterns, and in particular that hominins share the evolutionary history and processes of the biogeographical area to which they belonged, and that is the basis for an Afrotropical Model of Hominin Evolution.

Africa and the evolutionary process

Before considering the particular role of Africa in hominin evolution, it is necessary to examine some broader issues that may influence both the visibility of African fossil history and the probability of an evolutionary event taking place. The former are issues of sampling and taphonomy, while the latter are largely about biogeography and evolutionary processes.

Taphonomic bias

One possibility that should be entertained is that the Afrotropical model is an artefact of preservation. The uneven nature of the fossil record is well-established — preservation of fossils is rare, exposure to discovery is very rare, and furthermore, it is highly patchy in relation to both species and time. Perhaps Africa is not just a good place for hominins to have lived, but simply a good place for them to have subsequently died in terms of becoming part of the fossil records. Africa may have particularly good conditions for fossilisation and discovery. Support for that view could be found in the patchy distribution of the record of hominin evolution. By and large, what is known comes from three major sources — the East African Rift System (EARS), the limestone caves of the Transvaal, and the rock shelters and

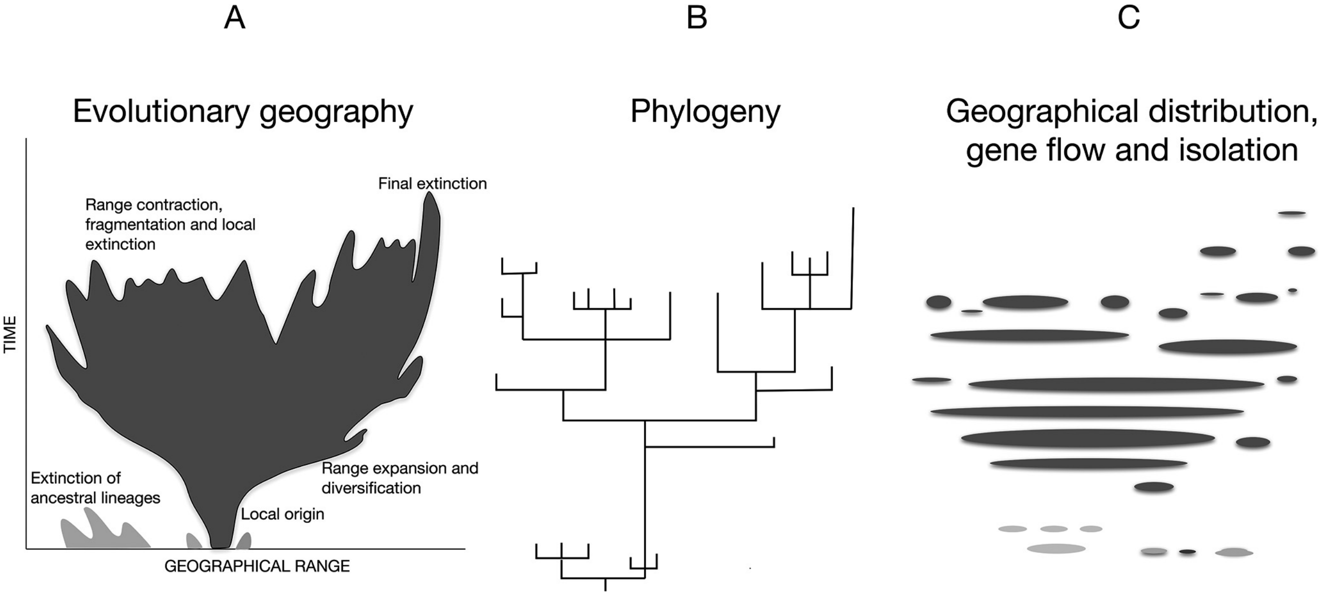


Fig. 1 Evolutionary geography focuses on the way in which change occurs first as a result of spatial distribution (A); resulting in demographic and adaptive divergence through lineages (B); with variable levels of gene flow or discontinuities, and as such evolutionary change through time (C). See [20] and [21] for further details / *La géographie évolutionnaire se concentre sur la façon dont des changements ont lieu en fonction de la distribution spatiale (A) ; impliquant des divergences adaptatives et démographiques à travers les lignées (B) ; avec différents niveaux de flux géniques et de discontinuités, aboutissant à terme à des changements évolutionnaires au cours du temps (C). Voir [20] et [21] pour plus de détails*

caves of the Cape. This does not mean that there are no other important regions — Chad, for example, is the source of the oldest potential hominin (*Sahelanthropus tchadensis*) [22], and the north African coastal caves, such as Haua Fteah and Jabel Irhoud [23,24] — but that these regions are particularly rich, and probably account for well over 90% of all hominin fossils.

The reasons for this are largely geological. The EARS has created numerous fluvial and lacustrine systems that have subsequently been buried and re-exposed by rifting, ideal conditions for both fossilisation and research [23]. The Pliocene and Pleistocene caves in the Transvaal are one of the few karstic systems in Africa, and are highly fossiliferous [24]. The Cape has many caves which record the more recent elements of human evolution [25,26]. Much of the rest of Africa is either covered with dense rainforest which has highly lateritic sediments that do not preserve fossils, or have been denuded by erosion. Hominins have been found in none of these regions.

We cannot exclude the case for taphonomic exceptionalism, but there are a number of points that can be made against it. The most important of these are based on genetics. This is entirely independent of taphonomic factors, yet both the close relationship between humans and African apes and the greater human diversity and inferred time depth among African populations would point strongly to Africa as being significant for both early hominins and modern human evolution. There is a good match between the estimates for the divergence of the last common ancestor of chimpanzees/bonobos and hominins and the fossil record, so the timing fits as well [5]. There is also a consistency for the dates of the last common ancestral population of modern humans and Neanderthals — in the region of 300-600 Ka [18,27–30], the earliest anatomically modern humans. Equally, the dates of both archaic hominins and modern humans in Eurasia are consistent with this pattern [31–33]. The centrality of Africa in the human story may benefit from geological history, but, at a comparative scale, it is likely to be correct. What is uncertain is that whether the regional, within-Africa pattern is not an artefact of that history.

Size and chance

When it is stated that humans — or hominins — evolved in Africa, it is not a particularly discriminating perspective. Africa is a very large continent. The Afrotropical Model narrows down the origins to approximately one quarter of the Old World, and once one has excluded the high latitudes where it is unlikely such origins would be found, probably to half the Old World. Africa is larger than Europe, China and the USA combined. A null model would be that given its size, it should be expected that a very large proportion of evolutionary events should occur there by chance. While this must be a possibility, it can only be tested by excluding other environmental hypotheses.

Latitudinal gradients and the importance of the tropics

One such is the latitude diversity gradient hypothesis. It has long been observed that there are many more species at the tropics, and that species diversity declines with increasing latitude. There are many explanations for this observation, but the pattern is remarkably robust across taxa, trophic level and habitat [19]. Whatever the ultimate causation — energetics, climatic stability, land area, etc. — the implication of all is that rates of speciation are higher in the tropics than at high latitudes. The adaptive corollary of this is that there is a higher rate of evolutionary novelty. As Africa has the highest land mass of tropical and sub-tropical environments, the pattern seen for hominins could be said to reflect a much broader evolutionary process; hominins are simply following general evolutionary principles. Rolland et al [34] have shown that the latitudinal gradient is not just a reflection of ecological equilibrium, but rates of speciation. There is a higher speciation rate in the tropics than in temperate zones, and this can be seen for mammals as a whole, and in particular orders. In effect, mammalian species diversity reflects an “out of the tropics” model, and such a model will necessarily show a strong signal in Africa. Hominin evolution reflects both the latitudinal gradient in terms of taxic diversity, and the high rate of endemism.

This pattern is not found solely for inter-specific diversity. Studies of cultural and linguistic diversity among humans have shown a similar latitudinal gradient, from tropics to high latitudes [35–37]. This suggests there are at least analogous processes occurring in the way in which boundaries are formed between human groups, with a higher probability of such boundaries in tropical latitudes. Nettle [35] has argued that this is a product of risk reduction in high latitudes; a complimentary hypothesis is that niche partitioning and isolation is possible at smaller scales in low latitudes [38]. This would suggest that the higher rate of speciation among hominins may not only reflect the environmental factors, but also integrates with evolving aspects of human cultural behaviour.

Endemism: Africa as a species factory

Endemism is the central concept in the Afrotropical Model — most hominin taxa are endemic to Africa, having originated there. This high level of endemism is an African characteristic; endemism levels at family rank (proportion of endemic families per biome) is highest in the Oceanic biome, followed by Neotropics. The Ethiopian biome is ranked next. However, what is perhaps most striking is that at family level there are no endemics in the Palaearctic. Eurasia, in terms of the origins of higher taxa, is a recipient and not a donor. The same pattern is seen at species level for zoogeographic regions [39].

In an analysis of global patterns of endemism, Kier et al. [40] showed that species endemism was generally higher in island zones, but among the mainland regions it was the tropics that had the highest levels of endemism, and within Africa, parts of East Africa had the highest levels among mammals. Fortelius et al. [41] have introduced the idea of "species factories" — in particular, suggesting that the Turkana Basin is one such; specific conditions of isolation, resilience and resource availability provided the balance between survivorship (so species did not become extinct), but sufficient changes in conditions to prompt evolutionary novelty. If this is the case — particularly for tropical Africa — then the high level of African endemism among hominins would be part of a more general evolutionary pattern.

Community and co-evolution

A final factor is that no lineage evolves in isolation, but as part of a community and through co-evolutionary interactions. Such co-evolutionary processes can be intimate, intense and obligatory — for example, the co-evolution of acacia trees and ants. More general long term patterns have also been observed among predators and prey – for example, in changes in limb lengths across the Cenozoic [42]. At a broader level, there is a process of community evolution, where many lineages coevolve as a response to changing environmental conditions [43]. The expansion of the grasslands in the Late Miocene and Pliocene in East Africa created conditions suitable for many mid to large body-sized mammals, and an increase in grazing [44], although the detailed sequence may have been complex [45]. The typical African savanna or Ethiopian fauna evolved concurrently in response to this, and hominins in Africa are likely to have been a part of that process, and should be considered a member of the African later Cenozoic biome. In a more speculative manner, whether there were more intense competitive interactions between lineages so that this community evolution took place in a Red Queen framework [43,46].

In summary, the evolutionary record of Africa is a product of many factors, some of which may inhibit our understanding (for example, areas with no fossil preservation), while others may promote it. Equally, some intrinsic characteristics of the evolutionary process may have promoted great evolutionary change than it was to be expected in other areas (Fig. 2).

The evolutionary geography of Africa

Against this broad evolutionary background, we can examine the role of Africa in hominin evolution more specifically, and, in particular, how its geography has been significant in this. We can consider how Africa, as an evolutionary unit, is neither constant nor homogenous.

The two Africas

Africa is, geologically speaking, a single continent, and has been a unit in plate tectonics since the split from South America around 100 Ma. Until the Early Miocene Africa was essentially an island continent, unconnected to Eurasia. From the Early Miocene a land bridge was established, and faunal exchanges occurred, including by Hominoids. In that context, Africa is a continent with a deep evolutionary history separated from Eurasia. However, Africa is also divided into two biogeographical regions, created by the proximity of the north to the Mediterranean, and the presence of the Sahara as a major barrier. The result is two distinct zoogeographic zones — Saharo-Arabian and Afrotropical (more colloquially known as northern Africa and sub-Saharan Africa [39] (Fig. 3).

In practice, discussion of the role of Africa in hominin evolution actually refers to sub-Saharan Africa, or more formally the Afrotropical Zoogeographic Zone (approximately the same as Wallace's Ethiopian Region) [39], for, with the exception of the fossils from Chad [22] (which are effectively on the boundary of the Afrotropical Zone), and, for more recent times, the North African coastal region, all hominin fossils of any significance come from sub-Saharan Africa.

Two points arise from the dual nature of Africa [47]. The first point is that the Sahara is a major barrier, creating isolation of the sub-Saharan element. The Sahara was formed in the late Miocene, and was a progressively major barrier to movement and range expansion from the south (or indeed the north). Strictly speaking, while talking about African origins during the course of hominin evolution, it should be more clearly specified as the sub-Saharan Africa or the Afrotropical Zone. The second point is that although the Sahara is a major barrier, this has not been a constant. Based on the last glacial cycle, it is clear that in the cold phases Africa becomes arid, and the desertification intensifies and expands; conversely, at the beginning of periods of deglaciation, the region becomes much more humid, and as a result the Sahara contracts and is replaced by savannas — basically an expansion of the Afrotropical fauna [48]. At this point, there is much greater connectivity between sub-Saharan Africa and Eurasia, and it is then that range expansion northward occurs.

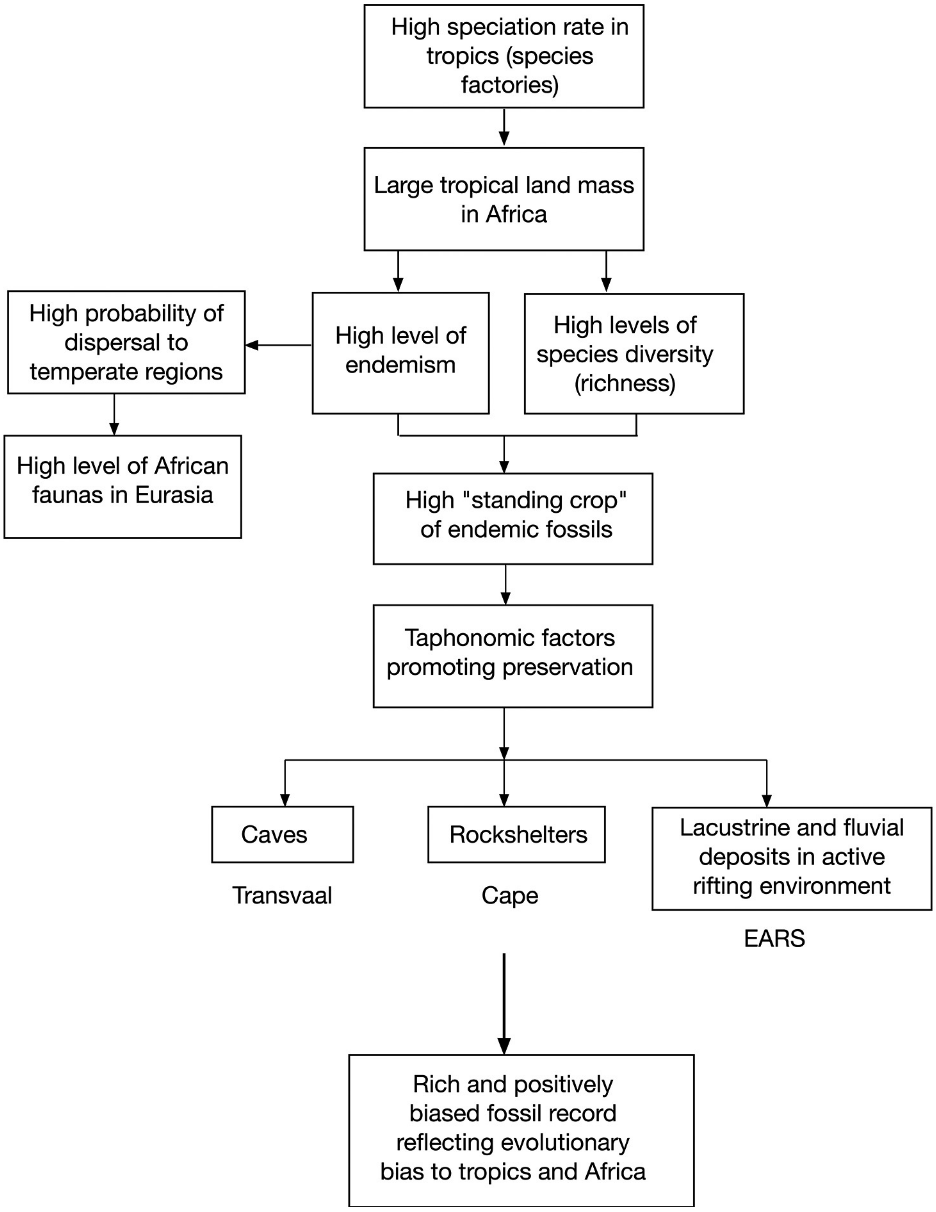


Fig. 2 Factors influencing the biological and taphonomic processes resulting in a rich Afrotropical model of hominin evolution / *Facteurs influençant les processus biologiques et taphonomiques, contribuant à la richesse du modèle afro-tropical de l'évolution des hominines*

What seems clear across many faunas is that this is the directionality — from south to north, with few taxa making the journey in the opposite direction [47].

The 'two Africas' model is therefore a dynamic model, with periods of both isolation and connectivity. That connectivity is still through particular corridors — the Nile and the montane regions of the Central Sahara, most importantly creating the conditions for both isolation and range expansion and dispersals towards Eurasia [20,47]. The pulses — multiple dispersals — out of Africa are likely to have been regulated by the opening and closing of this barrier.

Greater and lesser Africa

The variable nature of Africa biogeographically — sometimes two distinct zoogeographic zones, sometimes one continuum — can be extended further. When the Sahara is a barrier, then in effect Africa — as in the Afrotropical Zoogeographic Zone — is reduced. During warm wet phases, it is greatly enlarged, and extends beyond the actual boundaries of the continent. If the Afrotropical faunas spread into the Saharo-Arabian regions, then these distributions will also extend further still. Dennell and Roebroecks

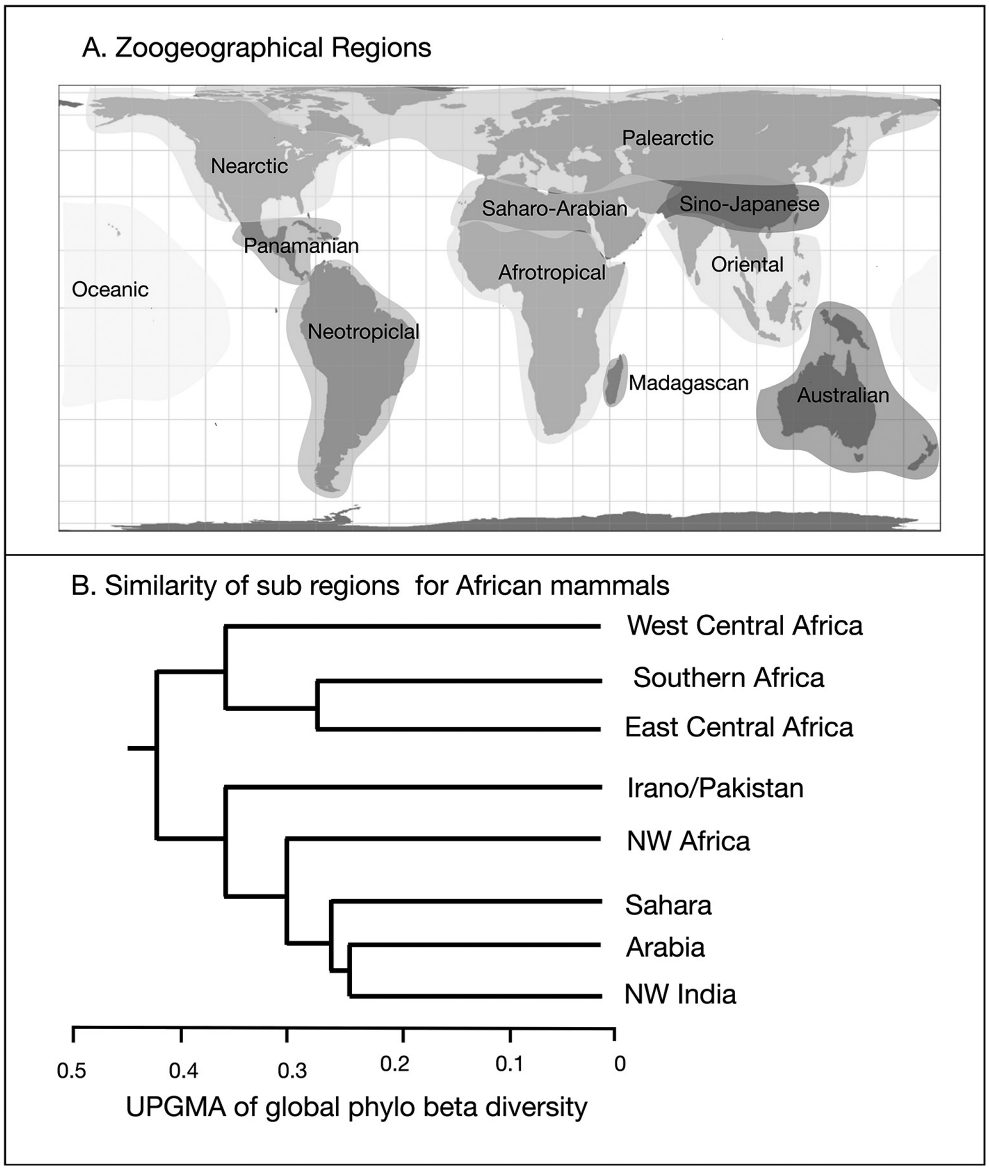


Fig. 3 A. Zoogeographical zones of the world. B. Similarities between African zoogeographical zones and adjacent Eurasian ones. Adapted from [39] / *A. Zones zoogéographiques du monde. B. Similarités entre les zones zoogéographiques africaines et les zones adjacentes d'Eurasie. Adapté de [39]*

have referred to 'savannastan' [16], as the total range of continuous habitat, stretching from East Africa as far as the north-west frontier of India, and possibly beyond. While the distinctive zoogeographic zones suggest that there was never a complete swamping of the Palearctic by African fauna, nonetheless it is important to recognise that evolution operates on ecological boundaries, not geo-political and geological units. At various times — principally in the warmer marine isotope stages — "evolutionary Africa" was larger than the continent, and at other times — during cold phases — it was smaller (Fig. 4).

African basins

Another geographical perspective on Africa is to view it as a series of basins, each of which may form a distinct biogeographic zone. Although the formation of the EARS in the last five million years has altered some of these basins, and the Nile is both recent and unstable as a basin, they represent, in relation to hominin evolution, a long-term feature of the African landscape, with strong evolutionary consequences [49]. These basins have their own distinct responses to climatic change (as they largely relate to precipitation and

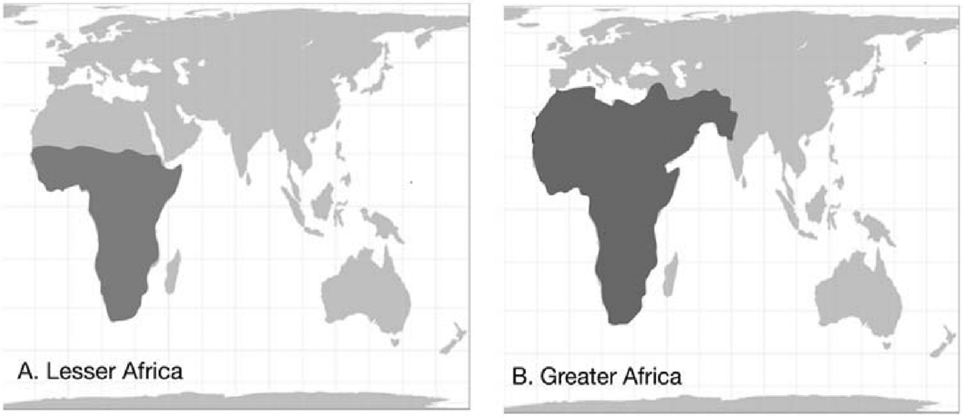


Fig. 4 "Lesser" and "Greater" Africa: during the Pleistocene biogeographic distributions varied extensively in relation to climatic conditions. A. During more arid phases the Sahara was a barrier, and Eurasian and North African/Saharan Zones extended into Africa. B. During more humid phases the Sahara was less of a barrier and the Afrotropical Zone extended into Southern Eurasia (Peters projection system) / *La « petite » et la « grande » Afrique : au cours du Pléistocène, les distributions biogéographiques ont énormément varié en fonction des conditions climatiques. A. Pendant les phases les plus arides, le Sahara constituait une barrière, et les zones eurasienne et nord-africaine/saharienne s'étendaient en Afrique. B. Pendant les phases plus humides, le Sahara représentait moins une barrière et la zone afro-tropicale s'étendait jusqu'au sud de l'Eurasie (système de projection de Peters)*

run-off), and as a result, high levels of endemism in some cases. If hominins are both responding to environmental changes as other taxa, and subject to distance effects, then there may well have been asynchrony between basins, refugia networks occurring between adjacent basins, and particular patterns of dispersals between adjacent basins [50–52]. In this regard, two basins stand out as particularly interesting – Turkana and the Nile. These two have boundaries with four other basins, more than is the case for any other basin. They may therefore both act as refugia, and also have the greatest potential for dispersal. It should be added that both these basins are, relatively speaking, recent; the Turkana was an open fluvial system until the Lower Pleistocene [53], and the Nile has varied in size and catchment over time, at various periods being much more reduced. It is also the only major basin that connects beyond Africa (Fig. 5).

Biogeographic relationships across Africa

Although we have characterised Africa as having two major zoogeographic regions, within those there is a considerable amount of diversity, part of which maps on to the basin structure. In a wide-ranging analysis across multiple taxa of animals and plants, Linder et al [54] have used a bottom-up approach to determine what these regions are, and how are they related to each other. They identified eight major regions — Saharan, Sudanian, Somalian, Zambezian, Congolian, Guinean, Kalaharian and South African (Fig. 6). Their analysis shows the "relatedness" of the regions, which in effect indicates the degree of contact through dispersals or the presence of closely related species. In the analysis of mammals, the two forested regions of Central and West Africa are the most similar. The savanna regions are also similar, but divide quite strongly into northern (Sudanian) and southern (Zambezian) zones, suggesting a natural break in evolutionary patterns. The Saharan and Somalian zones link next to the savannas, and it is the southern African zones (Kalaharian and South African) that are the most disparate. The 'savanna' regions are the most similar to each other (Fig. 6). Other groups of plants and animals show slightly different patterns. These analyses would suggest that eastern Africa is, in terms of mammalian evolution and ecology, more loosely linked to northern rather than southern Africa, and, as discussed above, the Sahara is a variable barrier. An interesting question is that the nature of the barriers between equatorial and southern Africa, whether these are the result of biotic competition or some more physical or climatic effect.

East-West versus North-South

The analysis of biogeographical zonation of Africa is based on current distributions, but, as discussed above, this is not stable. At certain times Africa is more arid, and the more open environments expand at the expense of the more humid ones. When this happens, the 'corridors of sub-Saharan Africa' are north-west, cutting the equatorial rainforests into eastern and western parts [46]. However, at that time the Sahara is expanded, acting as a barrier to further northern expansion. When the climate is more humid, in contrast, the tropical

Fig. 5 Africa is comprised of a number of large basins that act as biogeographical units (see text for discussion). Adapted from [51] / *L'Afrique comporte un certain nombre d'immenses bassins qui se comportent comme des unités biogéographiques (voir le texte pour discussion). Adapté de [51]*

forests expand, and cut the savanna regions into northern (Sudanian) and southern (Zambezian), creating a continuous forested distribution from coast to coast. At these times, however, the Sahara would have been an extension of the Sudanian region, and therefore a conduit to the north and Eurasia. This oscillation would mean that Africa alternates between a region with a north-south axis of movement, with a northern cap, and periods when it has an east-west-axis, but reduced barriers to the north [21].

Mosaic environments

Another perspective on Africa is as a set of mosaic environments. Where Eurasia is dominated by latitudinally-banded habitats, Africa is a more patchy set of environments, shaped by not just latitude, but also topography, relief and rainfall patterns. The result, particularly on the eastern side of the continent, is a mosaic structure of habitats. Mosaic environments are effectively regions with high environmental diversity, where it is possible to travel relatively short distances and cross a number of habitat boundaries. It has been argued that these mosaic habitats can promote local adaptations, form refugia and high levels of endemism, and will consequently have high rates of speciation. These mosaic habitats often coincide with biodiversity hotspots and also areas with high extinction risk. Palaeoanthropologists have often proposed that the mosaic environments played a critical role in the early stages of hominin evolution [55,56], and the EARS is particularly noted for the high level of habitat diversity occurring within it. And in particular greater seasonality, a key selective pressure [57].

Topography

One of the variables that promote a high level of mosaicism in a region is a variable topography, or high relief. King and

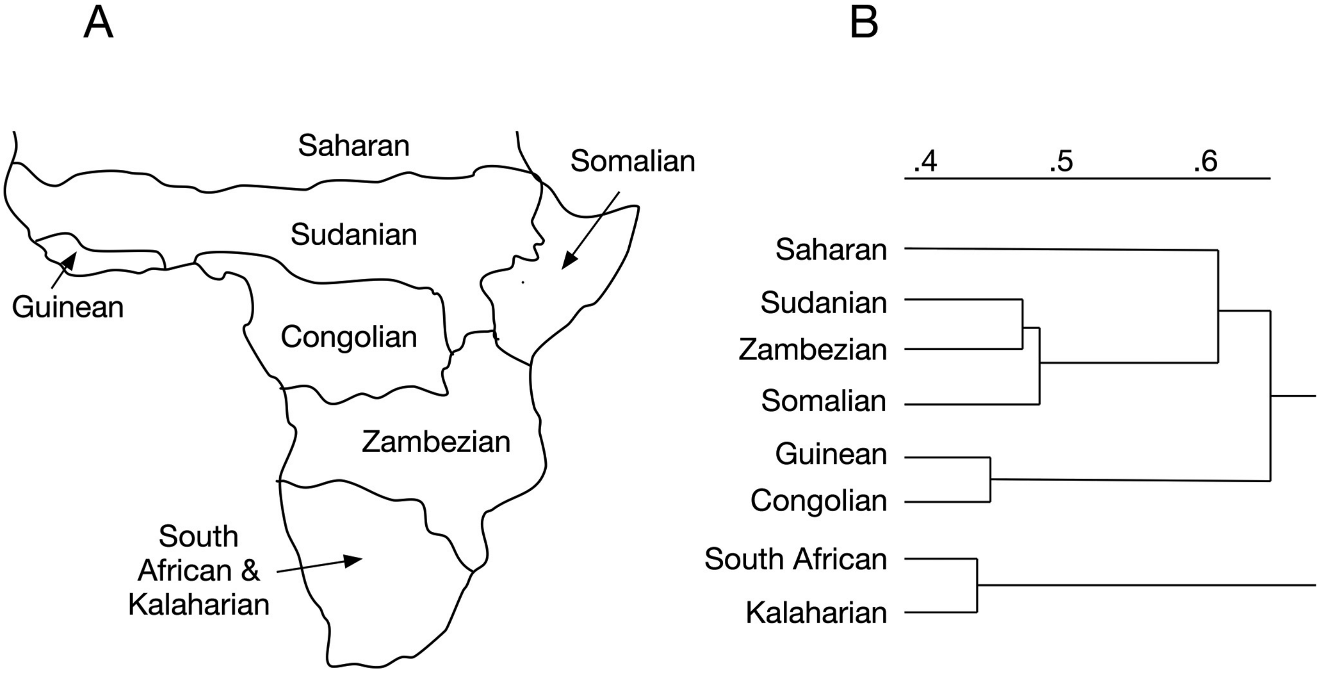


Fig. 6 Map showing statistically. A. Defined biogeographical regions of Africa. B. The degree of similarity between these. Adapted from [54] / *Carte montrant les régions biogéographiques d'Afrique. A. Définies statistiquement. B. Le degré de similarité entre elles. Adapté de [54]*

colleagues have made a strong case for linkage between high relief and hominin evolution in Africa [57–59]. The argument is that traits such as bipedalism are advantageous in regions with high relief, as well as providing suitable habitats in terms of resource availability and distribution. They also suggest that the distribution of hominin occupation, and the regions to which they disperse tend to be ones with high topographic relief. As always, there may be taphonomic factors involved, but there are also good ecological reasons for such a correlation, including the presence of water, shelter and protection, and good hunting conditions.

Water

While the requirements and availability for food resources will vary with habitat, water is a constant. Hominins are strongly water-dependent animals [55], and there are arguments that their dependence upon sweating for thermoregulation makes them particularly water-dependent. Access to surface water is critical, and this in turn varies enormously. In deserts, the mean distance between water sources is over 30 km; for most other habitats it is between 3 and 5 km, and in the savanna/bush environments in which it is hypothesised much of human evolution occurs, it is between 5 and 10 km [60] (Fig. 7). These average figures, of course, conceal considerable variation, and it is likely that actual landscape distributions of hominins will have been patchily determined by water distribution.

Ecological and biogeographic context for hominin evolution in Africa

The abundant genetic, archaeological and palaeontological evidence that places the Afrotropical realm at the centre of many aspects of hominin evolution implies that there are many reasons for focusing on the ecological and biogeographic context of Africa to understand why this is the case. Several factors contribute to that context, and these emphasise not only the homogeneity of Africa relative to the rest of the world, but also the variable and dynamic nature of it. That variability can explain not just the importance of the Afrotropical realm, but why particular parts of it may play key roles in hominin evolution. Among these are:

- areas of high diversity, which occur both in the rain forests and in the EARS, may act as sources for evolutionary novelty, with higher rates of speciation, and therefore the potential for dispersals of new populations to their zones of endemism. These areas of high diversity may relate to broader climatic, topographic variables, habitat distribution and diversity and water availability;
- from the perspective of evolutionary geography, Africa is neither homogenous nor stable. As an evolving

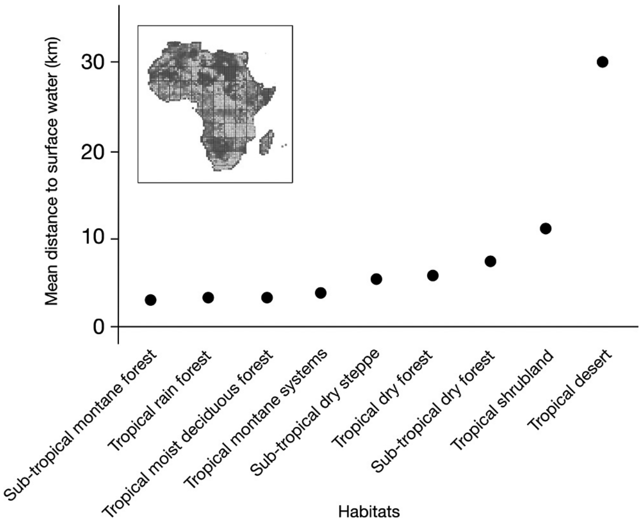


Fig. 7 Mean distance to the nearest surface water for different habitats in Africa. Inset map shows the density of surface water locations across Africa (red represents lowest, green highest). Adapted from [60] / *Distance moyenne de la plus proche source d'eau pour différents habitats en Afrique. La carte en encart montre la densité des eaux de surface en Afrique (le rouge représente les densités les plus faibles, le vert les plus fortes). Adapté de [60]*

community of plants and animals, geographical facts have shaped the patterns observed, and in turn these patterns show a strong spatial structure. Large scale basin structures play a strong role, although there are also broader zoogeographic structures. Changes in these over time result in different configurations of Africa and the Afrotropical realm – 'greater' and lesser, with or without a Saharan barrier, and with either a north-south continuity of open savannas, or an east-west continuity of forests. These shifts are important in terms of isolation and patterns of gene flow;

- actual geographical position is also an important factor. The similarity coefficients of mammalian regions [54] showed, for example, southern Africa was relatively isolated from the rest, while Holt et al [39] also showed how the Sahara was more closely related to the south-western parts of Asia. The implication is that these are distance effects, and are likely to have shaped hominin population relationships and probabilities of dispersal. Put simply, it is impossible to disperse into Eurasia without going through north-eastern Africa.

African evolutionary geography and hominin evolution

Hominin evolution is a complex and multiphase process that occurs over more than seven million years on current evidence. As stated at the outset, much of that occurs in the Afrotropical realm. How much can the evolutionary geography and ecology of Africa described above provide insights into these events. Table 2 shows the principal elements of African evolutionary geography discussed, and the implications for patterns of hominin evolution.

Many of the underlying ecological principles and hominin implications relate primarily to distributions and diversity – broadly speaking macroevolutionary patterns that are shaped by geographical factors. This is, in essence, the contribution of evolutionary geography. Most of the expectations for hominin evolution are that there should be greater diversity, endemism and evolutionary novelty in Africa compared to other regions, and in tropical Africa relative to other parts of Africa. The expectations from evolutionary geography can apply to all phases — the diversity of the earliest hominins with several genera, probably associated with the emerging adaptations to ground-dwelling through bipedalism, the peak diversity of Plio-Pleistocene hominins, the complex biogeography of early *Homo* across eastern Africa and into the Caucasus, and the multiple dispersals of novel taxa from Africa into Eurasia during the Pleistocene. They are all broadly consistent with the current data, although, as stressed at the outset, it is not possible entirely to disentangle these from taphonomic factors.

What is less clear is the extent to which the adaptive trends of hominin evolution — as opposed to macroevolutionary patterns — are also influenced strongly by the African context. In general terms they must be, as the adaptive traits of hominins are solutions to the problems of survival and reproduction at particular times and in particular places in Africa. For this a different approach is required, one that is based more closely on the adaptive traits of hominins — bipedalism, technology, changes in life history strategy, changes in diet, encephalisation and the development of an enhanced capacity for culture — in other words whether this approach relates only to macroevolutionary patterns, or microevolution and adaptation. For example, what are the particular elements of the African evolutionary and ecological environment that makes bipedalism an optimal solution for a hominoid? Or, what adaptive problems does the development of lithic technology solve for hominins in East Africa around or before 3.3 Ma? To put it another way, while the evolutionary geography might predict a higher rate of speciation and evolutionary novelty in Africa compared to other regions, further components and a much more fine-grained analysis would need to be added to the model to explain why that novelty might be bipedalism or larger brains.

Conclusions

Conclusive evidence from genetics, archaeology and palaeontology has shown the central role of Africa in hominin evolution. That centrality can be measured by the

Table 2 Evolutionary processes and patterns discussed in the text, and applications to hominin evolution / Processus et modèles discutés dans le texte, et implication concernant l'évolution des hominines

Evolutionary geography component	Hominin applications and hypotheses
Latitudinal gradient: higher taxic diversity in equatorial Africa relative to both northern and southern Africa, and Eurasia	More hominin species have African origins More hominin species occur only in Africa There is higher hominin diversity in tropical Africa compared to northern and southern Africa
Sahara as a variable barrier: under warmer and wetter conditions, the Sahara is an extension of Sudanian Zone, and does not act as a barrier-open	Continuity of hominin populations across Africa and into southern Eurasia during wet phases Out of Africa dispersals during wet phases Admixture and cultural contact between northern African and southern Eurasian populations during wet phases
Sahara as a variable barrier: under drier and colder conditions the Sahara expands and forms a barrier between northern and southern Africa	Isolation of sub-Saharan hominin populations Early hominins limited to sub-Saharan Africa Divergence of Eurasian and sub-Saharan lineages, such as Neanderthal/Denisovans and ancestors of anatomically modern humans
Greater Africa: the more open environment elements of Africa to the east and north expand into Eurasia ('Savannastan')	Northern Africa and southern Eurasia could have formed a hominin metapopulation during these times This may fit the observed complex diversity of early *Homo* between 2 and 1.6 Ma Some genetic evidence may indicate a similar metapopulation after the early dispersals of modern humans, but prior to the separation of Eurasians and Papuans/Australians
Lesser Africa: environmental differences and barriers such as the Sahara lead to a more restricted Afrotropical geographical range	Restricted and fragmented populations in sub-Saharan Africa may have created the conditions for population structuring implied by the human evolutionary genetics The African and Eurasian phylogeny proposed for Lower and Middle Pleistocene *Homo* may reflect the sustained nature of 'lesser Africa' at various periods
Inter-continental endemism: tropical areas such as Africa have higher levels of endemism relative to Eurasia *Intra-Africa endemism:* East Africa has higher levels of endemism than other parts of Africa	Most hominin taxa originate in Africa Most hominin taxa occur in Africa Relative to other parts of Africa, East Africa has higher rates of origin of taxa and higher diversity If hominin lineages evolved primarily in eastern Africa, then there would be a greater correlation between co-evolutionary and dispersal events in that region compared to other parts of Africa
Co-evolution: due to competitive interactions and shared environmental dynamics, there will be co-evolution among lineages in the same regions	If hominin lineages evolved primarily in eastern Africa, then there would be a greater correlation between co-evolutionary and dispersal events in that region compared to other parts of Africa

(Suite page suivante)

Table 2 *(suite)*

Evolutionary geography component	**Hominin applications and hypotheses**
African basins and biogeographic phylogeny: biogeographical zonation in Africa is structured to a large extent by major topographic basins, which determine levels of endemism and zoogeographic relationships between basins	Patterns of hominin physiology, affinity and dispersals should match the distribution of African basins, and their proximity to each other The relative isolation of the southern African biomes; the split between Zambian and Sudanian savannas Southern Africa should have a hominin evolutionary history that reflects greater levels of isolation and terminal refugia, possibly with later extinction dates
East-West humid connectivity versus north-south savanna connectivity: during arid phases the primary routes for range dispersals are north-south, by open habitat organisms; during humid phases it is east-west and dominated by forest organisms	If hominins were largely adapted to the more open environments of sub-Saharan Africa, then during more arid phases there would have been range expansion and dispersals from eastern to southern Africa (and vice-versa); during warmer and wetter phases, eastern and southern Africa would have been less connected Little is known about the western extensions of hominins, but these would have been more likely during more arid phases
Mosaic environments: some African regions have high environmental diversity, which promotes local adaptations, form refugia and high levels of endemism	Although taphonomy may well be a factor, the high level of hominin diversity in East Africa coincides with the high levels of habitat diversity found in the EARS
Topographic variation: variation in relief promotes habitat diversity and isolation, and thus species diversity and endemism	Hominins may have had a preference for areas with relatively high relief, although this would be difficult to disentangle from taphonomic factors
Water: water is one of the primary determinants of distribution and habitat, and in addition to its broader impact on productivity, surface water availability constrains water-dependent species	At the meso- and microscale, hominin distributions (and their archaeological record) will be restricted to areas with surface water

number of significant first appearances, by the high levels of evolutionary endemism, by the high level of taxonomic diversity, and the strong directionality of dispersals from Africa to Eurasia across the Pleistocene. Evolutionary genetics is also showing that Africa was the source for the ancestral modern human populations, and that genetic diversity declines from Africa. These are straightforward facts, and appear to be as secure as any major finding in evolutionary history. There is inevitably a form of phylogenetic bias involved; given the original African origin of the hominin clade and its solely African distribution for several million years. However, that this pattern continues after the first Eurasian dispersals remains an interesting observation.

These facts sum together as the Afrotropical model of hominin evolution, namely that hominin evolution is rooted in a distinct zoological region. The challenge addressed in this article has been to connect this model to a broader range of evolutionary theory and biology. Evolutionary geography provides one such body of theory; using the way in which evolutionary processes play out over different spatial scales provides the basis for exploring whether what is seen for hominin evolution reflects the broader rules of biogeography — the higher levels of endemism and speciation in the tropics, the operation of latitudinal gradient rules and comparisons with evolutionary patterns in other groups of plants and animals. All of these lead to the conclusion that there are good reasons why it might be expected that such phenomena as higher hominin diversity occurs in Africa compared to other continents, or why dispersals tend to be from Africa to Eurasia. This approach, while largely confirming the current findings, could be extended to develop more detailed predictions for hominin evolution. What might be the next challenge would be considering the cases in hominin evolution that do not conform to these general rules — the possibility of dispersals from Eurasia into Africa at the base of the African ape/human lineage, the possibility of convergence in behaviour between Eurasian and African hominins, the Eurasian divergence of Neanderthal and

Denisovan lineages – in other words, developing an evolutionary geography framework for Eurasia.

Finally, it is worth emphasising what is not claimed in this article – that hominin evolution could only have occurred in Africa. The broad rules of evolution that have been used to understand why there is a consistency between principles and observations within hominin evolution are not fixed and deterministic rules, but statistical properties, patterns and trends that are more likely to occur than not. But evolution is also full of exceptions, of unusual conditions, of chance and convergence. If — to develop Gould's thought experiment [61] — we were to rerun the tape of life a million times, in most of those evolutionary histories "hominin" evolution probably would not occur. Among those where it did, there would, no doubt, be histories where the emergence of a highly intelligent and cultural creature occurred under different geographical conditions, in Asia, in Europe, in the Americas. But, the largest proportion of alternative histories are likely to be in the tropics and in Africa.

Acknowledgements: this article is part of Marta Mirazón Lahr's European Research Council Advanced Award (IN-AFRICA, ERC 295907), and also received support from the Leverhulme Trust. I thank the Société d'Anthropologie de Paris for the invitation to address this topic at their annual meeting in 2017, and Marta Mirazón Lahr for input of ideas and discussion.

Link of interest: None.

References

1. Dart RA (1925) *Australopithecus africanus*: The Man-Ape of South Africa. Nature 115:195–9
2. Reader J (2011) Missing links. OUP, Oxford, 538 p
3. Gould SJ (1991) Wonderful life: The Burgess Shale and the nature of history. Penguin, London, 347 p
4. Richter D, Grün R, Joannes-Boyau R, et al (2017) The age of the hominin fossils from Jebel Irhoud, Morocco, and the origins of the Middle Stone Age. Nature 546:293–6
5. McDougall I, Brown FH, Fleagle JG (2005) Stratigraphic placement and age of modern humans from Kibish, Ethiopia. Nature 433:733–6
6. McBrearty S, Brooks AS (2000) The revolution that wasn't: A new interpretation of the origin of modern human behavior. J Hum Evol 39:453–563
7. Day MH, Stringer CB (1991) The Omo Kibish cranial remains and classification within the genus *Homo*. Anthropologie 95:573–94
8. Tryon CA, McBrearty S (2002) The Middle Stone Age of the southern Kapthurin Formation, Baringo, Kenya. J Hum Evol 42: A37–A37
9. Asfaw B (1983) A new hominid parietal from Bodo, Middle Awash Valley, Ethiopia. Am J Phys Anthropol 61:367–71
10. Lepre CJ, Roche H, V. Kent D, et al (2011) An earlier origin for the Acheulian. Nature 477:82–5
11. Brown F, Harris J, Leakey R, Walker A (1985) Early *Homo erectus* skeleton from West Lake Turkana, Kenya. Nature 316:788–92
12. Semaw S, Renne P, Harris JW, et al (1997) 2.5-million-year-old stone tools from Gona, Ethiopia. Nature 385:333–6
13. Villmoare B, Kimbel WH, Seyoum C, et al (2015) Paleoanthropology. Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. Science 347:1352–5
14. Harmand S, Lewis JE, Feibel CS, et al (2015) 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. Nature 521:310–5
15. Brunet M, Guy F, Pilbeam D, et al (2002) A new hominid from the upper Miocene of Chad, central Africa. Nature 418:145–51
16. Boyle E, Wood B (2017) Human evolutionary history. Evolution of nervous systems, Vol. 4. In: Kaas J (ed) The evolution of the human brain: Apes and other ancestors, 2nd ed. Academic Press, New York, pp 19–36
17. Wood B, Boyle EK (2016) Hominin taxic diversity: Fact or fantasy? Yearb Phys Anthropol Phys Anthropol 159:S37–S78
18. Prado-Martinez J, Sudmant PH, Kidd JM, et al (2013) Great ape genetic diversity and population history. Nature 499:471–5
19. Darwin C (1871) Descent of man and selection in relation to sex. Murray, London, 528 p
20. Cann RL, Stoneking M, Wilson AC (1987) Mitochondrial DNA and human evolution. Nature 325:31–5
21. Botigué LR, Henn BM, Gravel S, et al (2013) Gene flow from North Africa contributes to differential human genetic diversity in southern Europe. PNAS 110:11791–6
22. Seguin-Orlando A, Korneliussen TS, Sikora M, et al (2014) Genomic structure in Europeans dating back at least 36,200 years. Science 346:1113–8
23. Fu Q, Moorjani P, Jay F, et al (2014) Genome sequence of a 45,000-year-old modern human from western Siberia. Nature 514:445–9
24. Wang CC, Farina SE, Li H (2013) Neanderthal DNA and modern human origins. Quat Int 295:126–9
25. Fleagle JG, Shea JJ, Grine FE, et al (2010) Out of Africa I. The first Hominin colonization of Eurasia, Springer, Dordrecht, 293 p
26. Stringer CB, Andrews P (1988) Genetic and fossil evidence for the origin of modern humans. Science 239:1263–8
27. Mirazon Lahr M, Foley RA (1994) Multiple dispersals and modern human origins. Evol Anthropol Issues, News, Rev 3:48–60
28. Fuss J, Spassov N, Begun DR, et al (2017) Potential hominin affinities of *Graecopithecus* from the Late Miocene of Europe. PLoS One 12:e0177127
29. Dennell R, Roebroeks W (2005) An Asian perspective on early human dispersal from Africa. Nature 438:1099–104
30. Hublin JJ, Ben-Ncer A, Bailey SE, et al (2017) New fossils from Jebel Irhoud, Morocco and the pan-African origin of *Homo sapiens*. Nature 546:289–92
31. Hillebrand H (2004) On the generality of the latitudinal diversity gradient. Am Nat 163:192–211
32. Mirazon Lahr M, Foley RA (1998) Towards a theory of modern human origins: geography, demography, and diversity in recent human evolution. Am J Phys Anthropol Suppl 27:137–76
33. Foley RA (1999) Evolutionary geography of pliocene African hominids. In: Bromage TG, Schrenk F (eds). African biogeography, climate change & human evolution. Oxford University Press, Oxford, pp 1–26
34. Maslin MA, Brierleya CM, Milner AM, et al (2014) East African climate pulses and early human evolution. Quat Sci Rev 101:1–17
35. Brain CK (1981) The Hunters or the Hunted?: An Introduction to African Cave Taphonomy. University of Chicago Press, Chicago, 365 p
36. Deacon HJ, Shuurman R (1992) The origins of modern people: The evidence from Klasies River. In: Brauer G, Smith FH (eds). Continuity or Replacement. Controversies in Homo sapiens Evolution. Balkema, Rotterdam, pp 121–29

37. d'Errico F, Henshilwood C, Nilssen P (2001) An engraved bone fragment from c. 70,000-year-old Middle Stone Age levels at Blombos Cave, South Africa : Implications for the origin of symbolism and language. Antiquity 75:309–18
38. White TDT, Asfaw B, DeGusta D, et al (2003) Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. Nature 423:742–7
39. Fu Q, Mittnik A, Johnson PLF, et al (2013) A revised timescale for human evolution based on ancient mitochondrial genomes. Curr Biol 23:553–59
40. Stringer C (2016) The origin and evolution of *Homo sapiens*. Philos Trans R Soc B Biol Sci 371:20150237
41. Higham T, Douka K, Wood R, et al (2014) The timing and spatiotemporal patterning of Neanderthal disappearance. Nature 512:306–9
42. Hershkovitz I, Marder O, Ayalon A, et al (2015) Levantine cranium from Manot Cave (Israel) foreshadows the first European modern humans. Nature 520:216–19
43. Nigst PR, Haesaerts, P, Damblon F, et al (2014) Early modern human settlement of Europe north of the Alps occurred 43,500 years ago in a cold steppe-type environment. PNAS 111: 14394–9
44. Rolland J, Condamine FL, Jiguet F, Morlon H (2014) Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. PLoS Biol [in press]
45. Nettle D (1998) Explaining global patterns of language diversity. J Anthropol Archaeol 17:354–74
46. Collard I, Foley RA (2002) Latitudinal patterns and environmental determinants of recent human cultural diversity: Do humans follow biogeographical rules? Evol Ecol Res 4:371–83
47. Amano T, Sandel B, Eager H, et al (2014) Global distribution and drivers of language extinction risk. Proc Biol Sci 281:20141574
48. Foley RA (2004) The evolutionary ecology of linguistic diversity in human populations. In: Jones M (ed) Traces of Ancestry: Studies in honour of Colin Renfrew. Cambridge University Press, Cambridge, pp 61–71
49. Holt BG, Lessard JP, Borregaard MK, et al (2013) An update of Wallace's zoogeographic regions of the world. Science 339:74–8
50. Kier G, Kreft H, Lee TM, et al (2009) A global assessment of endemism and species richness across island and mainland regions. PNAS 106:9322–27
51. Fortelius M (2016) An ecometric analysis of the fossil mammal record of the Turkana Basin. Philos Trans R Soc London Ser B 371:20150232
52. Janis CM, Wilhelm PB (1993) Were there mammalian pursuit predators in the tertiary? Dances with wolf avatars. J Mamm Evol 1:103–25
53. Foley RA (1984) Early man and the Red Queen: Tropical African community evolution and ecology. In: Foley RA (ed) Hominid evolution and community ecology: Prehistoric human adaptation in biological perspectives. Academic Press, New York and London, pp 85–110
54. Se galen L, Lee-Thorp JA, Cerling T (2007) Timing of C4 grass expansion across sub-Saharan Africa. J Hum Evol 53:549–59
55. Blumenthal SA, Levin NE, Brown FH, et al (2017) Aridity and hominin environments. PNAS 1:201700597. http://www.pnas.org/content/114/28/7331.abstract - aff-2
56. Foley RA (1999) The evolutionary geography of Pliocene hominids. In: Bromage TG, Schrenk F (eds) African biogeography, climate change and human evolution. Oxford University Press, Oxford, pp 328–48
57. Mirazon Lahr M (2010) Saharan corridors and their role in the evolutionary geography of "Out of Africa I." In: Fleagle JG, Shea JJ, Grine FE, et al (eds) Out of Africa I. The first hominin colonization of Eurasia. Springer, Dordrecht, pp 27–46
58. Armitage SJ, Drake NA, Stokes S, et al (2007) Multiple phases of North African humidity recorded in lacustrine sediments from the Fazzan Basin, Libyan Sahara. Quat Geochronol 2:181–6
59. Kingdon J (1989) Island Africa: The evolution of Africa's rare animals and plants. Academic Press, London, 287 p
60. Foley RA (2013) Comparative evolutionary models and the "Australopith Radiations". In: Reed KE, Fleagle JG, Leakey RE (eds) The paleobiology of *Australopithecus*. Springer, Dordrecht, pp 163–74
61. Foley RA, Maíllo-Fernández JM, Mirazon Lahr M (2013) The Middle Stone Age of the Central Sahara: Biogeographical opportunities and technological strategies in later human evolution. Quat Int 300:153–70
62. Mirazón Lahr M, Foley RA (2016) Human evolution in Late Quaternary Eastern Africa. In: Jones SC, Stewart BA (eds) Africa from MIS 6-2: Population dynamics and paleoenvironments. Springer, Dordrecht, pp 215–31
63. Feibel CS (2011) A geological history of the Turkana Basin. Evol Anthropol Issues, News, Rev 20:206–16
64. Linder HP, de Klerk HM, Born J, et al (2012) The partitioning of Africa: Statistically defined biogeographical regions in sub-Saharan Africa. J Biogeogr 39:1189–205
65. Foley RA (1987) Another unique species: Patterns in human evolutionary ecology. Longman, Harlow, 313 p
66. Reynolds SC, Wilkinson DM, Marston CG, et al (2015) The mosaic habitat concept in human evolution: Past and present. Trans R Soc South Africa 326:57–69
67. Foley RA (1993) The influence of seasonality on hominid evolution. In: Ulijaszek SJ, Strickland S (eds) Seasonality and human ecology. Cambridge University Press, Cambridge, pp 17–37
68. Winder IC, Devès MH, King GCP, et al (2015) Evolution and dispersal of the genus *Homo*: A landscape approach. J Hum Evol 87:48–65
69. Kübler S, Rucina S, Reynolds S, et al (2016) Edaphic and topographic constraints on exploitation of the Central Kenya Rift by large mammals and early Hominins. Open Quat [in press]
70. King G, Bailey G (2006) Tectonics and human evolution. Antiquity 80:265–86
71. Lennard J (2011) Surface water distribution in Africa and its impact on human evolution: A GIS approach, M. Phil Dissertation, University of Cambridge, 70 p

BMSAP (2018) 30:32-48
DOI 10.3166/bmsap-2018-0002

NOTE / *NOTE*

Readjustment of the Standard ASUDAS to Encompass Dental Morphological Variations in Plio-Pleistocene Hominins

Précision du système de référence ASUDAS pour prendre en compte la variation morphologique des hominines plio-pléistocènes

M. Louail · S. Prat

Received: 30 April 2017; Accepted: 22 November 2017

Abstract The standard ASUDAS scoring system (Arizona State University Dental Anthropology System) is used to assess dental morphological variations in modern humans. It is also frequently used to study, score, and compare morphological variations in fossil hominin taxa and to examine their phylogenetic relationships. However, using ASUDAS in studies of this type is under debate because it is based on modern *Homo sapiens* populations and does not appear to cover all variations observed in fossil Plio-Pleistocene hominins. Our observations and coding of 178 dentals casts of Plio-Pleistocene specimens based on ASUDAS and from the literature have confirmed the need to adapt the standard system to fossil hominins. In this initial study, we propose that the scoring procedures for some morphological characters need to be readjusted, while others could be standardized following the ASUDAS system.

Keywords Dental morphology · Plio-pleistocene hominins · ASUDAS

Résumé Le système de codage de référence des caractères morphologiques dentaires ASUDAS (Arizona Stade University Dental Anthropology System) est un outil fréquemment utilisé pour étudier, coder et comparer les différents groupes d'hominines fossiles. Or, ce système étant basé sur des populations d'hommes actuels, il ne couvre pas l'ensemble de la variation morphologique observée sur les hominines plio-pléistocènes. Une adaptation du système de référence à ces derniers permettrait de renforcer la pertinence de son utilisation dans les études paléoanthropologiques. Suite à l'examen morphologique et au codage d'un échantillon de 178 moulages dentaires de spécimens plio-pléistocènes selon les plaques ASUDAS et les données de la littérature, nous avons pu confirmer la nécessité d'adapter le système de référence ASUDAS. Dans cette première étude, nous montrons que certains caractères morphologiques nécessitent un réajustement de leurs procédures de codage et que d'autres peuvent faire l'objet d'une standardisation sur le modèle ASUDAS.

Mots clés Morphologie dentaire · Hominines plio-pléistocènes · ASUDAS

Introduction

The Arizona State University Dental Anthropology System (ASUDAS) is frequently used in taxonomic and phylogenetic studies on fossil hominins [1,2]. Published in 1991 by G. Richard Scott and Christy G. Turner II, ASUDAS covers > 30 characters considered to be representative of morphological variations in modern *Homo sapiens* [3–5]. The authors describe discrete dental characters and their grades of expression. For most of the characters, scoring is easier with the reference plaque, which represents the different grades of expression. This system is particularly useful because it makes it possible to standardize scoring, thus facilitating comparisons between morphological studies: the primary purpose of the standard ASUDAS is in fact to standardize the scoring of morphological characters that are easily and reliably observable. In addition, when taken together, these traits can be used to characterize populations [3]. Therefore, dental morphological traits may be relevant either to distinguish between geographic populations within a species, or to distinguish between taxa at a higher level [1,6].

This scoring system has also been used to describe dental morphological variations in fossil hominins. However, some studies consider that it may not be appropriate for morphological descriptions of fossil hominin teeth [1,2,6,7] because it is based on modern human populations (initially, mainly

---

M. Louail (✉) · S. Prat
UMR 7194, 17, place du Trocadéro, 75016, Paris, France
e-mail : louailmargot@gmail.com

Lavoisier

Native South American and Arctic populations) [4,5]. Therefore, it seems important to test whether ASUDAS can encompass the wide morphological variations found in the different Plio-Pleistocene hominin species.

Many studies have described the dental morphology of fossil specimens and estimated how dental morphological variations were distributed across fossil hominin taxa [e.g.], [8,9]. However, since the publication of ASUDAS [3] and apart from uploaded versions [4,5], very few authors have attempted to adapt the system or to propose new standards that would be required for studies of fossil hominins [2,6,7,10–14]. This paper reports on our study to test whether ASUDAS is appropriate to the morphological coding of Upper Pliocene and Lower Pleistocene hominins, and to propose possible readjustments to the system.

Materials and Methods

The initial sample was made up of a collection of more than 200 high-resolution silicone (©President light body) dental crown casts belonging to Sandrine Prat. Because postcanine teeth have a larger number of morphological characters than canines and are less subject to sexual dimorphism, this study focused on premolars and molars. The specimens are from Upper Pliocene and Lower Pleistocene South and East African sites (mainly Sterkfontein, Swartkrans and the Omo valley). One specimen from Dmanisi (D 211) was also included in the study. The taxa in our sample are *Australopithecus*, *Paranthropus* and early *Homo* (Table 1).

From the initial collection, we selected maxillary and mandibular premolars and molars. We excluded third molars because of their complex and irregular morphology. Teeth with limited wear or fragmentation (i.e., on which we were able to observe and score at least one character) were included in the study. We thus used a sample of 178 teeth: 34 upper premolars, 41 upper molars, 43 lower premolars, 60 lower molars (Table 1).

We scored 22 characters following the standard scoring procedure developed by Scott and Turner [3–5]. We also included 11 additional, or revised, characters described in the literature after the publication of ASUDAS in 1991 [2,6,7,10–14]. These studies described the types of expression of some additional characters that were relevant to morphological descriptions of fossil hominins and were not included in ASUDAS [3–5]. The authors [2,6,7,10–14] proposed descriptions and standardizations to complement ASUDAS, but usually with no reference plaques. We did not take taxonomic attribution into account during our observations in order to minimize observer subjectivity, and we did not analyze and describe characters that appeared to be constant in our sample (Table 2). Concerning the revised or new characters presented in this study, we tested both intra-observer variability (scored three times by M.L.) and inter-observer variability (scored by S.P. and M.L.). Inter-trait correlations were estimated with Kendall's τ test using only one tooth from each district. The frequencies of dental traits are provided for each taxon in our sample. Specimens with uncertain taxonomic attribution, as for "non-robust" specimens, are not counted in the trait frequencies. The distribution of frequencies between taxa is estimated and compared by means of a Fisher exact test, as the very small samples prevented us from applying a chi-squared test. Groups with < 2 specimens were not included in the Fisher exact test.

Results and discussions

We propose an initial approach for several dental characters and additional grades for existing traits that would allow more accurate assessments of dental morphological variations in Plio-Pleistocene hominins, and a standardization of their scoring procedures. We observed that 19 ASUDAS characters are well suited to studies focusing on Plio-Pleistocene hominins (Table 2), which means that the standard system can be used to score Plio-Pleistocene hominins. Three ASUDAS characters needed a readjustment of their scoring procedures (Table 3). A new scoring procedure for the protostylid is proposed, to combine the ASUDAS reference plaque and the types of expression described by Hlusko [7] (see below). Seven additional characters are well suited when applied to Plio-Pleistocene hominins (Table 4). We argue that three characters already described in the literature (Table 5) are observed in particular in Plio-Pleistocene hominins [6,14] and should therefore be integrated into the standard system with their initial scores. This study also proposes descriptions and scoring procedures for three new characters (Table 6), including disto-buccal cusplets on lower premolars as described in Suwa's thesis on upper premolars.

With regard to intra- and inter-observer errors, we found very high replicability for a single observer and no less than 77% replicability between the two authors. No significant differences were apparent. Inter-observer errors were estimated at 88% and 98% for disto-buccal cusplets on upper and lower premolars, respectively, 93% for hypocone reduction, >99% for double cusp 5, 81% for the distal fovea, 80 % for the hypoconulid, 89% for the protostylid, 98% for double cusp 6, and 77% for the mesial marginal ridge. Concerning inter-trait correlations, most significant correlations ($p<0.05$) do not exceed $\tau=0.4$ or -0.4 (LM1 double cusp 6 and mesial marginal ridge, LM1 mesial marginal ridge and cusp 7, LM1 mesial marginal ridge and deflecting wrinkle, LM1 hypoconulid and Y-pattern, LM1 mesial marginal ridge and protostylid, LM2 double cusp 6 and cusp 6, UM1 distal fovea and crista obliqua, LM2 cusp 5 and cusp 7, UM1 double cusp

Table 1 List of Plio-Pleistocene hominins studied in this paper / *Liste des hominines plio-pléistocènes étudiés dans cet article*

Au. afarensis and aff. *afarensis*		*Au. africanus*			
AL 128–23	RP$_3$	MLD 2	LM$_1$		
	RP$_4$		LM$_2$		
	RM$_1$	Sts 8	LM^1		
	RM$_2$		LM^2		
AL 145–35	LM$_1$	Sts 9	RM$_1$		
	LM$_2$	Sts 24	LP^3		
AL 199–1	RP^3		LM^1		
	RP^4		LP$_3$		
	RM^1		RM$_1$		
	RM^2	Sts 51	RP$_3$		
AL 200–1a	LP^3	Sts 55	LP^3		
	LP^4	Sts 56	LM^1		
	LM^1	Stw 151	LM$_1$		
	LM^2	Stw 252	LP^3		
AL 333w–1b	RP$_4$		LP^4		
	RM$_1$		LM^1		
	RM$_2$		LM^2		
B7–39A	LP^3	Taung 1	LM$_1$		
B7–39B	LP^4	TM 1511	RP^3		
B7–39C	LM^1	TM 1523	LP$_4$		
B8–23A	LP^4				
B8–23B	LM^1				
B8–4q	LP^4				
B8–49	LP^4				
LH 2	RM$_1$				
W7–23	LP$_4$				
W7–508	RM$_1$				
W8–751	LP$_4$				
W8–978	RP$_3$				
W8–749	RM$^{1 \text{ or } 2}$				
W8–988	LP^4				
Au. bahrelghazali					
KT1	LP$_3$				
	LP$_4$				
P. aethiopicus			*P. boisei*		
F22–1a	RM$_2$		L628–9	LM$_{1 \text{ or } 2}$	
L51–79	RP$_4$		L628–10	LM$_1$	
L62–17	RM$_2$		L726–11	RP^3	lingual fragment
L338x35	RP^3		WT 37747	RM^1	
L338x40	LP$_4$		WT 47844	RM$_1$	
L398–120	RP$_3$	lingual fragment			
L398–1223	RP$_4$	lingual fragment			
L420–15	LP$_4$	buccal fragment			
L465–111	LP$_3$				
Omo 18–68–31	RP$_3$				
Omo 18–68–33	LP$_3$				

(Suite page suivante)

Table 1 *(suite)*

Omo 18–68–34	LM$_{1 \text{ or } 2}$			
Omo 18–70–1799	LM^1			
Omo 33–71–508	LP$_4$			
Omo 136–2	LM$_{2 \text{ or } 3}$			
P. robustus		*Early Homo*		
SK 1	LM$_2$	K7–19	LM$_2$	
SK6	LP$_4$	L26–1G	LM$_2$	
	LM$_1$	OH 7	LP$_3$	
	LM$_2$		LP$_4$	
SK 7	RP$_4$		LM$_1$	
SK 9	LP$_4$		LM$_2$	
SK 24	LP^3	OH 13	RP^3	
SK 33	RP^3		RP^4	
SK 61	RM$_1$		LM^1	
	RM$_2$		LM^2	
SK 88	LP$_4$	OH 21	LM^1	Germ
SK 89	LM^1	OH 22	RP$_3$	
SK 98	LM^2		RP$_4$	
SK 102	LM^1		RM$_1$	
SK 104	RM$_1$		RM$_2$	
SK 823	RP^3	Omo 29–1968–43	RP$_3$	
SK 824	LP^4	Omo 74–18	RP$_4$	
SK 825	LP^4	Omo 123N–1973–5495	RP$_3$	
SK 831	RP$_3$	Omo 177–4525	RP$_3$	
SK 832	LM^1	Omo SH1–1–17	LM^1	
SK 834	RM^2	P933–1	LM^1	
SK 835	LM^2	SE 255	RM^1	
	RM$_1$	SK 15	RM$_1$	
	RM$_2$		RM$_2$	
SK 837	RM^2	SK 27	LP^3	
SK 843	LM$_1$		RM^2	
	LM$_2$	SKW 3114	LM^2	
SK 857	RP$_3$	SKX 258	LM$_1$	
SK 3974	RM$_1$	SKX 268	RM^1	
SK 3976	LM$_2$	WT 42718	RM$_1$	
SK 13114	RP^3	WT 47767	LM^2	
	RP^4			
	LM^1			
	RM^2			
SK 1587a	LP$_4$			
	LM$_1$			
	LM$_2$			
SKW 5	RP$_3$			
	RP$_4$			
	RM$_1$			
	RM$_2$			
SKW 4767	RM$_1$			
SKW 4772	RP^4			
SKW 14129	RM^1			

(Suite page suivante)

Table 1 *(suite)*

SKX 162	RP^3		
	RP^4		
SKX 4446	RP_4		
	RM_1		
	RM_2		
SKX 26625	LP^4		
TM 1517	LP^3		
	LP^4		
	LM^1		
	LM^2		
	LP_3		
	LP_4		
	RM_1		
	RM_2		
H. georgicus		*Uncertain*	
D211	LP_3	KB 5223	RM^2
	LP_4		LM_1
	LM_1	L28–31	$RM_{1 \text{ or } 2}$
	LM_2	L45–2	$RM_{1 \text{ or } 2}$
		L50–2	$LM^{1 \text{ or } 2}$
		L51–1	LM_1
		L51–2	$LM^{1 \text{ or } 2}$
		L51–4	$LM^{1 \text{ or } 2}$
		L51–80	RP_4
		L795–1	$RM_{2 \text{ or } 3}$
		Omo 69–900	LP^4
		Omo 212–1950	LM_1

5 and cusp 5, LP4 disto-buccal cusplet and metaconid placement, UP4 disto-buccal cusplet and accessory marginal tubercles). Those ranging from (−)0.4 to (−)0.6 are not judged to be high enough to discard any character [5] (LM1 double cusp 6 and cusp 6, LM1 double cusp 6 and cusp number, LM1 mesial marginal ridge and cusp 6, LM1 mesial marginal ridge and cusp number, LM2 double cusp 6 and deflecting wrinkle, UM1 hypocone and lingual paracone tubercle, LP4 disto-buccal cusplet and mesio-lingual groove, LP4 disto-buccal cusplet and crown asymmetry). The highest significant correlations were found between LM1 cusp 6 and double cusp 6 ($\tau=0.6$, $p=0.00007$) and between cusp 6 and mesial marginal ridge ($\tau=0.6$, $p=0.0002$). The lowest significant correlation was found between LM1 mesial marginal ridge and protostylid ($\tau=-0.3$, $p=0.02$).

Readjustment of scoring procedures for ASUDAS characters

Concerning the readjustment of the scoring procedure, our observations suggest adding a sixth development grade for two characters: the hypocone on upper molars and the hypoconulid on lower molars. Additional grades described by Hlusko [7] are confirmed for the protostylid expression on lower molars.

Hypocone, upper molars (Table 3)

A large proportion of modern humans show an extreme reduction, and sometimes the complete absence [3], of this distolingual cusp, or hypocone, on upper molars. In our sample, only one molar (e.g., SK 27, *Paranthropus robustus*) shows a significant reduction of this cusp whereas the majority of the sample has either a large or very large hypocone, i.e., grades 4 and 5. In ASUDAS, the expression types are described according to the absolute size of the cusp. However, some Plio-Pleistocene hominins show a fourth cusp that exceeds the size of the grade 5 (*n*=17). We propose to add a sixth development grade described as: “Cusp 4 is much larger than metacone and shows a distolingual projection” (Fig. 1). Because this character is not illustrated in the current ASUDAS although it is observed on several specimens, it should be incorporated into the standard system.

Table 2 List of constant ASUDAS dental characters used in this study [3–5,11] / *Liste des caractères morphologiques dentaires ASUDAS constants utilisés dans cette étude [3–5,11]*

Upper premolars
Disto-sagittal ridge [3–5] Presence of a ridge from the apex of the buccal cusp to the distal occlusal border at the sagittal sulcus Grades: 0 (absence), 1 (presence) **Secondary marginal tubercles [3,4]** Presence of a secondary mesial or distal tubercle on the marginal ridge 21. Grades: 0 (absence), 1(presence) **Tricuspid premolars [3]** Presence of an additional distolingual cusp Grades: 0 (absence), 1 (presence)
Lower premolars
Lingual cusp number [3–5] Number and relative size of lingual cusps Grades: A (absence), 0 (one lingual cusp), 1 (one or two lingual cusps), 2 (two lingual cusps; mesial cusp much larger than distal cusp), 3 (two lingual cusps; mesial cusp larger than distal cusp), 4 (two lingual cusps; mesial and distal cusps equal in size), 5 (two lingual cusps; distal cusp larger than mesial cusp), 6 (two lingual cusps; distal cusp much larger than mesial cusp), 7 (two lingual cusps; distal cusp very much larger than mesial cusp), 8 (three lingual cusps; cusps equal in size), 9 (three lingual cusps; mesial cusp larger than medial and/or distal cusp) **Secondary mesial ridge [4,11]** Development of a secondary ridge on the mesiolingual border of the tooth Grades: 0 (absence), 1 (presence) **Secondary distal ridge [4,11]** Development of a secondary ridge on the distolingual border of the tooth Grades: 0 (absence), 1 (presence)
Upper molars
Metacone [3,5] Presence and size of the disto-buccal cusp Grades: 0 (absence), 1 (an attached ridge is present but there is no free apex), 2 (a slight cusplet with a free apex is present), 3 (slight cusp is present), 3.5 (medium-sized cusp), 4 (large cusp), 5 (very large cusp) **Parastyle [3–5]** Development of a cingular remnant on the buccal surface of the paracone Grades: 0 (absence), 1 (a pit is present in the buccal groove between cusps 2 and 3), 2 (small cusp with an attached apex), 3 (medium-sized cusp with a free apex), 4 (large cusp with a free apex), 5 (very large cusp) **Carabelli's cusp [3–5]** Development of a cingular remnant on the lingual surface of the protocone Grades: 0 (absence), 1 (a groove is present), 2 (a pit is present), 3 (small Y-shaped depression), 4 (large Y-shaped depression), 5 (small cusp without a free apex), 6 (medium-sized cusp with an attached apex making contact with the medial lingual groove), 7 (large free cusp) **Cusp 5 [3–5]** Presence and size of a fifth cusp between cusps 3 and 4 Grades: 0 (absence), 1 (slight cusplet), 2 (trace cusplet), 3 (small cusplet), 4 (small cusp), 5 (medium-sized cusp) **Secondary mesial marginal tubercles [4]** Presence of secondary tubercles on the mesial marginal ridge Grades: 0 (absence), 1 (mesial paracone tubercle), 2 (protoconule), 3 (secondary mesial tubercle), 4 (lingual paracone tubercle)
Lower molars
Groove pattern [3–5] Grades: Y (cusps 2 and 3 are in contact), + (cusps 1 to 4 are in contact), X (cusps 1 and 4 are in contact)

(Suite page suivante)

Table 2 *(suite)*

Cusp 6 [3–5]
Presence and size of the entoconulid, between the hypoconulid and the entoconid
Grades: 0 (absence), 1 (cusp 6 much smaller than cusp 5), 2 (cusp 6 smaller than cusp 5), 3 (cusps 6 and 5 equal in size), 4 (cusp 6 larger than cusp 5), 5 (cusp 6 much larger than cusp 5)

Cusp 7 [3–5]
Presence and size of cusp 7, or metaconulid, between cusps 2 and 4
Grades: 0 (absence), 1 (slight cusp), 2 (small cusp), 3 (medium-sized cusp) to 4 (large cusp)

Cusp number [3–5]
Cusp number does not include cusp 7.
Grades: 4 (protoconid, metaconid, entoconid, hypoconid), 5 (with hypoconulid), 6 (with entoconulid)

Deflecting wrinkle [3–5]
Presence and shape of the medial ridge on cusp 2
Grades: 0 (absence), 1 (medial ridge is straight but with a midpoint constriction), 2 (medial ridge is deflected distally but does not make contact with cusp 4), 3 (medial ridge is distally deflected forming an L-shaped ridge and comes in contact with cusp 4)

Anterior fovea [3–5]
Development of a triangular depression distal to the mesial marginal ridge
Grades: 0 (absence), 1 (faint groove), 2 (groove deeper than in grade 1), 3 (groove longer than in grade 2), 4 (groove is very long and mesial ridge is robust)

Distal trigonid crest [3–5]
Presence of a ridge connecting the distal borders of cusps 1 and 2
Grades: 0 (absence), 1 (presence)

Mid-trigonid crest [5,10,11,13]
Presence and shape of a ridge connecting the mesial aspects of cusps 1 and 2
Grades: 0 (absence), 1 (interrupted crest), 2 (crest forms a complete bridge)

Table 3 List of ASUDAS characters for which scoring procedures need readjustment [3–7] / *Liste des caractères ASUDAS nécessitant un réajustement de leurs procédures de codage [3–7]*

Upper molars

Hypocone [3–5]
Presence and size of the distolingual cusp
Grades: 0 (absence), 1 (slight ridging present at the site), 2 (slight cusplet), 3 (small cusp), 3.5 (medium-sized cusp), 4 (large cusp), 5 (very large cusp)
Grade 6 (this study): cusp 4 is much larger than metacone and shows a disto-buccal projection

Lower molars

Hypoconulid [3–5]
Presence and size of the most distal cusp between cusps 3 and 4
Grades: 0 (absence), 1 (very small cusp), 2 (small cusp), 3 (medium-sized cusp), 4 (large cusp), 5 (very large cusp)
Grade 6 (this study): cusp 5 is larger than the hypoconid and the entoconid

Protostylid [3–7]
Development of a cingulum derivative on the buccal surface [7], or a paramolar cusp according to the ASUDAS description [3–5].
Grades: 0 (absence), 1 (buccal pit), 2 (very slight swelling), 3 (slight positive expression), 4 (moderate positive expression), 5 (strong positive expression), 6 (pronounced positive expression), 7 (most distinctive form of protostylid, expressed as tubercle)
Additional grades ([7], this study): 4A (V-cleft centrally located on the buccal groove. The bottom of the groove is covered with enamel), 4B (robust cingulum parallel to the occlusal surface and centrally located on the buccal groove, with a cusplet frequently observed), 6A (deep linear cleft parallel to the occlusal surface and extending mainly onto the protoconid. The bottom of the buccal groove is covered with enamel), 7A (linear cleft extends onto the mesial border of the protoconid and expands on the buccal side)

Fig. 1 ASUDAS reference plaque, hypocone, upper molars [3–5] and grade 6 (this study). Scoring: grade 0 (absence) to 5 (very large cusp); grade 6 (mirror image of Sts 8, *Au. africanus*, LM2): cusp 4 is much larger than metacone and shows a distolingual projection. Occlusal views. Scale bar = 1 cm / *Plaque de référence ASUDAS pour le caractère hypocone sur les molaires supérieures [3–5] et stade 6 (cette étude). Codage : 0 (absence) à 5 (très large) ; Stade 6 (image en miroir de Sts 8*, Au. africanus, *LM2) : l'hypocone est plus large que le metacone et présente une projection distolinguale. Vues occlusales. Echelle = 1 cm*

Frequencies of grade 6 for this character are 1/4 for *Australopithecus africanus* M^1 and 2/2 for M^2 (Table 7). Frequencies for *P. robustus* M^1 are 3/6 and 4/6 for M^2. It seems less frequent on *Australopithecus afarensis* (1/5 for M^1 and 1/2 for M^2) and early *Homo* (2/6 for M^1 and 0/4 for M^2) upper molars. With regard to grade 6, we did not find any significant differences between taxa (p>0.07), even for all upper molars and species grouped together (p>0.05).

Hypoconulid, lower molars (Table 3)

Cusp 5, or the hypoconulid, is the most distal cusp and occurs on lower molars between the hypoconid and the entoconid. It is scored according to the absolute size of the cusp and only if cusp 6 is absent. It is variable in size in modern humans and may be absent [3]. However, cusp 5 occurs in all of our samples, the majority at grade 3 (medium-sized) or more. Grade 5 was described by Scott and Turner as "cusp 5 is very large", but if we try to score our sample against the reference plaque, some molars show a cusp 5 that is larger than the maximum grade. We therefore suggest adding a sixth grade for this character. To facilitate the scoring procedure and to limit bias arising from the size parameter, grade 6 is described as "cusp 5 is larger than the hypoconid and the entoconid" (Fig. 2). Our results show that grade 6 is mostly observed on *Paranthropus* specimens (Table 7). Among the seven molars with a hypoconulid scored as grade 6, three (2/11 M_1 and 1/9 M_2) are attributed to *P. robustus*, two (2/3 M_1) to *Paranthropus boisei*, one (1/3 M_2) to *Paranthropus aethiopicus* and one (1/3 M_2) to *Au. afarensis*. None of the early *Homo* specimens in our sample have a grade 6 hypoconulid. We did not find any significant differences with regard to grade 6 between taxa (p>0.1) or when lower molars and species were grouped together (p>0.2).

Protostylid, lower molars (Table 3)

According to the description made by Scott and Turner [3], the protostylid is a paramolar cusp that occurs on the buccal surface of lower molars. It is frequently associated with the

Fig. 2 ASUDAS reference plaque, hypoconulid, lower molars [3–5] and grade 6 (this study). Scoring: grade 0 (absence) to 5 (very large cusp); Grade 6 (mirror image of KB 5223, uncertain attribution, LM1): cusp 5 is larger than the hypoconid and/or the entoconid. Occlusal views. Scale bar = 1 cm / *Plaque de référence ASUDAS pour le caractère hypoconulide sur les molaires inférieures [3–5] et stade 6 (cette étude). Codage : 0 (absence) à 5 (très large cuspide) ; Stade 6 (image en miroir de KB 5223, attribution incertaine, LM1) : l'hypoconulide est plus large que l'hypoconide et/ou l'entoconide. Vues occlusales. Echelle = 1 cm*

buccal groove separating cusps 1 (protoconid) and 3 (hypoconid) and the buccal surface of cusp 1. However, a more recent study [7] showed that in Plio-Pleistocene hominins, the types of expression of this character were more similar to the development of a cingular remnant than to that of a cusp. Hlusko shows that in early hominins, the protostylid is more closely linked to the buccal groove than in modern humans and develops parallel to the occlusal surface. In our sample, almost half (48 %) of lower molars have a developed enamel crest or a large bulge centrally located on the buccal surface, extending onto both the mesial and distal cusps and almost parallel to the occlusal surface, but no apex development. When these descriptions and scoring procedures are applied [3–7], it appears that the types of expression described by Hlusko are more accurate for our sample. Our study thus confirms the readjustment of the scoring procedure that Hlusko proposed for the protostylid [7] for Plio-Pleistocene hominins. Indeed, one specimen, at least, can be associated with each grade she proposed, unlike Scott and Turner's grades. Our proposal is to incorporate some of her newly described developmental stages in the ASUDAS protostylid reference and to assign a "model specimen" to each grade described (Fig. 3).

The following four stages are described in addition to the reference plaque:

- 4A (similar to Hlusko's grade 2): V-cleft centrally located on the buccal groove. The bottom of the groove is covered with enamel;
- 4B (similar to Hlusko's grade 3): Robust cingulum centrally located on the buccal groove with no detached apex but a cusplet frequently observed;

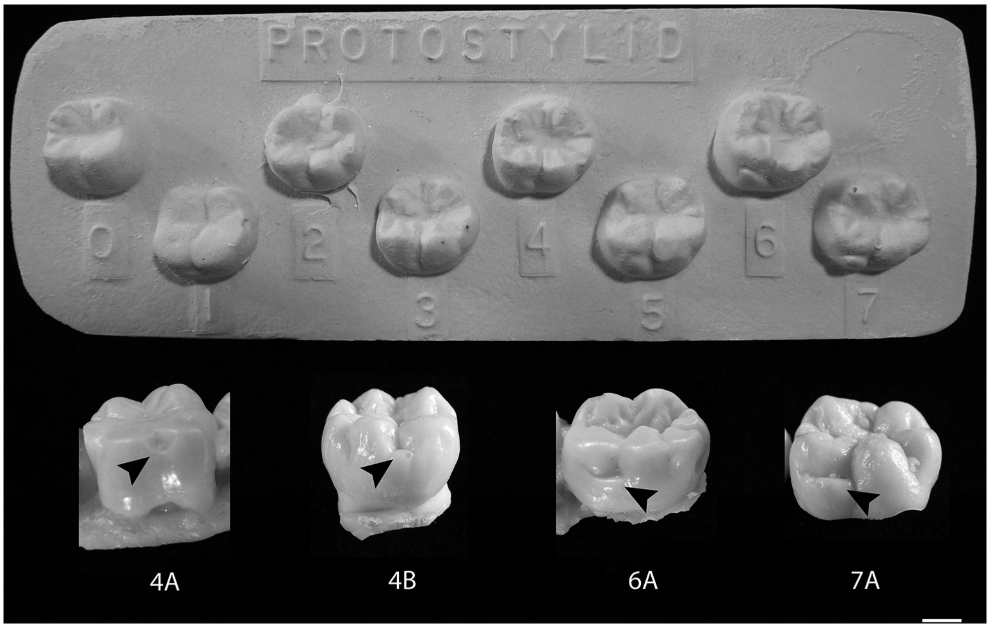


Fig. 3 New reference plaque of protostylid expression in Plio-Pleistocene hominins. ASUDAS reference plaque ([3–5]; occlusal view) and additional grades (this study and [7]; buccal views). Scoring: 4A. V-cleft centrally located on the buccal groove. The bottom of the groove is covered with enamel (mirror image of AL 333w-1b, *Au. afarensis*, RM1); 4B. Robust cingulum centrally located on the buccal groove with no apex detached but a cusplet is frequently observed (mirror image of SK 3974, *P. robustus*, RM1); 6A. Deep linear cleft is almost parallel to the occlusal surface and extends mainly onto the protoconid. The bottom of the buccal groove is covered with enamel (SK 1587a, *P. robustus*, LM2); 7A. Deep linear cleft extends onto the mesial border of the protoconid and is buccally expanded. It is almost parallel to the occlusal surface and does not show a free apex as described for the maximum grade in modern humans (MLD 2, *Au. africanus*, LM2). Scale bar = 5 mm / *Développement du caractère protostylide sur les molaires inférieures chez les hominines plio-pléistocènes. Plaque de référence ASUDAS ([3–5] ; vue occlusale) et stades supplémentaires (cette étude et [7] ; vues vestibulaires). Codage : 4A. Fissure "en V" centrée sur le sillon vestibulaire. Le bas du sillon est recouvert d'émail (image en miroir de AL 333w–1b*, Au. afarensis, *RM1) ; 4B. Cingulum robuste centré sur le sillon vestibulaire sans apex mais fréquemment associé à des cuspules accessoires (image en miroir de SK 3974*, P. robustus, *RM1) ; 6A. Fissure linéaire profonde plutôt parallèle à la surface occlusale et principalement étendue sur le protoconide. Le bas du sillon vestibulaire est recouvert (SK 1587a*, P. robustus, *LM2) ; 7A. Fissure linéaire profonde étendue sur le bord mésial du protoconide et projetée vestibulairement. La fissure est plutôt parallèle à la surface occlusale et ne présente pas d'apex libre tel qu'observé sur les hommes modernes (MLD 2*, Au. africanus, *LM2). Echelle = 5 mm*

- 6A (similar to Hlusko's grade 4): Deep linear cleft is almost parallel to the occlusal surface and extends mainly onto the protoconid. The bottom of the buccal groove is covered with enamel;
- 7A (similar to Hlusko's grade 5): Deep linear cleft extending to the mesial border of the protoconid and buccally expanded. It is almost parallel to the occlusal surface and does not have a free apex as described for the maximum grade in modern humans.

See Table 7 for details of frequencies for each grade and species. Note that grade 4A is mainly observed on *P. robustus* (5/9 M_1 and 1/10 M_2) and is also scored on 1/5 *Au. africanus* M_1, 1/3 *P. boisei* M_1, 1/4 early *Homo* M_1 and 2/3 *Au. afarensis* M_2. Grade 4B is also mainly observed on *P. robustus* (2/9 M_1 and 2/10 M_2) and is scored on 1/2 *P. aethiopicus* M_2, but it is not observed on other species. Grade 6A is also mainly scored on *P. robustus* specimens (6/10 M_1 and 1/9 M_2) and on 1/3 *P. boisei* M_1 and 1/5 *Au. africanus* M_1. It is not observed on *Au. afarensis* and early *Homo* molars. Grade 7A seems more randomly distributed: it is observed on 1/5 *Au. afarensis* M_1, 1/5 *Au. africanus* M_1 and 1/1 M_2, 1/9 *P. robustus* M_1 and 1/2 *P. aethiopicus* M_2. It is not observed on early *Homo* molars.

Fisher exact tests did not reveal any significant differences between taxa on all lower molars graded 4A ($p>0.7$), 4B ($p>0.1$), 6A ($p>0.07$) or 7A ($p>0.2$).

Incorporation of supplementary morphological dental characters

Six morphological characters that are not included in ASUDAS and their types of expression are described (Table 2). An accessory distal cusp on molars had already been described and used for scoring in Bailey and Wood's study [6] as "double cusp 6" on lower molars and "cusp 6" on upper molars.

Disto-buccal cusplet, upper premolars (Table 4); Disto-buccal cusplet, lower premolars (Table 5)

As ASUDAS scores the number of lingual cusps on lower premolars [3–5], we propose to take the possible expression of a secondary buccal cusp into account, on both upper and lower premolars. In his thesis, Suwa described and scored the "development of a disto-buccal cusplet" on second upper premolars [14], but this character can be observed on

Table 4 List of constant additional characters described in the literature [2,10–12] / *Liste des caractères supplémentaires constants décrits dans la littérature [2,10–12]*

Upper premolars
Essential crest [11] Presence and shape of the essential crest scored on both buccal and lingual cusps Grades: 0 (absence), 1 (single crest), 2 (bifurcating crest) **Secondary ridges [12]** Presence of secondary mesial and/or distal ridges on the buccal cusp Grades: 0 (absence), 1 (truncated ridge), 2 (continuous but barely discernable ridge), 3 (thin continuous ridge), 4 (medium-sized continuous ridge), 5 (thick continuous ridge)
Lower premolars
Transverse crest [10,11] Presence and shape of a ridge connecting the buccal and lingual cusps Grades: 0 (absence), 1 (interrupted crest), 2 (moderate expression), 3 (marked expression) **Mesiolingual groove [11]** Presence of a groove on the mesiolingual aspect of the tooth Grades: 0 (absence), 1 (presence) **Metaconid placement [10,11]** Position of the metaconid relative to the protoconid Grades: 1 (mesial), 2 (medial), 3 (distal) **Crown asymmetry [10,11]** Shape of the lingual contour of the tooth in occlusal view Grades: 0 (symmetrical), 1 (asymmetrical), 2 (very asymmetrical)
Upper molars
Crista obliqua [2] Presence and shape of a crest connecting the protocone and metacone Grades: 0 (absence), 1 (continuous crest)

Table 5 List of additional dental characters described in the literature and observed in particular on Plio-Pleistocene hominins [6,14] / *Liste des caractères dentaires additionnels décrits dans la littérature et particulièrement observés chez les hominines plio-pléistocènes [6,14]*

Upper premolars
Disto-buccal cusplet [14] Presence of a secondary buccal cusp detached from the main buccal cusp Grades: 0 (absence), 1 (marked groove on the disto-buccal surface but no or minimal projection), 2 (disto-buccal cusplet with a free apex)
Upper molars
Double cusp 5 [6] Presence of a secondary distal cusp, in addition to cusp 5 [6]. Scored only if cusp 5 is also present Grades: 0 (absence), 1 (presence)
Lower molars
Double cusp 6 [6] Presence of a secondary distal cusp between cusps 5 and 6 [6] Grades: 0 (absence), 1 (presence)

both first and second upper and lower premolars. A large proportion of upper and lower premolars (40 % and 13 %, respectively) in our sample have a single buccal cusp. However, we observed that a buccal occlusal projection is present on several premolars on the distal side, which in some respects can be considered as an apex because it is detached from the main buccal cusp. Some premolars have a groove on the buccal surface between the main and secondary cusps. This groove is marked but the secondary cusp does not seem to be detached from the main one. Thus, as proposed by Suwa, the expression of a disto-buccal cusplet on second upper premolars [14] can be described by three grades for all the premolars. These two characters on both upper premolars (Fig. 4) and lower premolars (Fig. 5) are scored as follows:

- 0: No disto-buccal cusplet;
- 1: Marked groove on the disto-buccal surface but no or minimal projection;
- 2: Disto-buccal cusplet with a free apex.

Our results show that this character is mainly scored as present on *P. robustus* upper and lower premolars (Table 7). Grade 2 is observed on 3/6 *P. robustus* P^3 and 6/7 P^4, and on 2/4 P_3 and 7/8 P_4.

It is also frequently observed on *P. aethiopicus* (1/1 P^3, 3/4 P_3, and 3/3 P_4). It is much less common in other taxa and more frequent on lower premolars. No *Homo* specimens express a grade 2 on upper premolars (0/2 P^3 and 0/1 P^4), and only 2/7 on lower premolars (1/4 P_3 and 1/3 P_4). Concerning *Au. afarensis*, the frequencies for a disto-buccal cusplet scored as grade 2 are 0/10 on P^3 and P^4, 1/2 P_3 and 2/4 P_4. It is observed on 1/4 *Au. africanus* P^3 and 1/2 P_3.

Grades 0 and 1 seem more randomly distributed, but note that 2/3 P^3 *Au. africanus* and 5/7 P^4 are scored as grade 0 whereas it seems less common on other taxa (Table 4).

With regard to grade 0 and grade 2 on upper premolars, we found a significant difference between *Australopithecus* and *Paranthropus* (p=0.02 and p=0.0005, respectively). No significant differences appeared for grade 1 on upper premolars (p>0.4). On lower premolars, Fisher exact tests revealed significant differences between *Paranthropus* and early *Homo* for grades 0 and 2 (p=0.006 and p=0.01, respectively), but not for grade 1 (p>0.6).

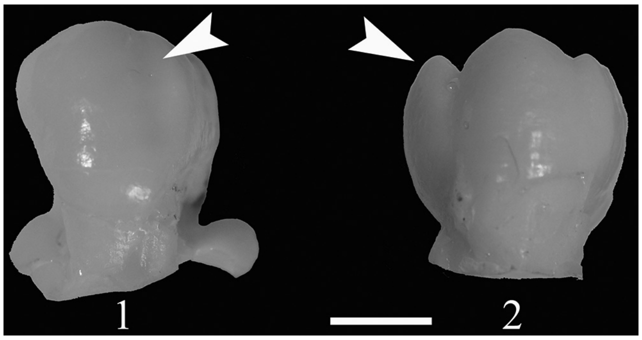


Fig. 4 Disto-buccal cusplet, upper premolars [14]. Scoring: 1. Marked groove on the disto-buccal surface but no or minimal projection (B7–39A, *Au. aff. afarens*is, LP3); 2. Disto-buccal cusplet with a free apex (SK 824, *P. robustus*, LP4). Buccal views. Scale bar = 5 mm / *Cuspide disto-vestibulaire sur les prémolaires supérieures [14]. Codage : 1. Sillon marqué sur la surface vestibulaire mais pas d'apex libre (B7–39A*, Au. aff afarensis, *LP3) ; 2. Cuspide disto-vestibulaire avec apex libre (SK 824*, P. robustus, *LP4). Vues vestibulaires. Echelle = 5 mm*

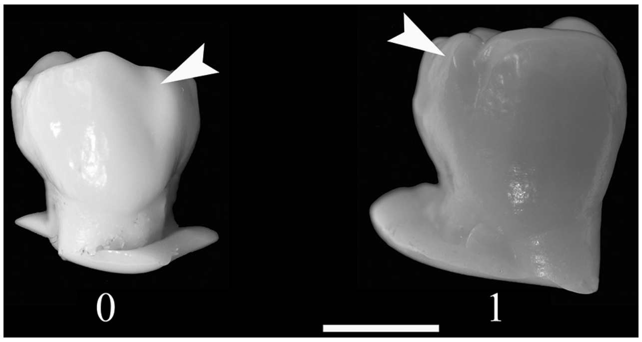


Fig. 5 Disto-buccal cusplet, lower premolars. Scoring: 1. Marked groove on the disto-buccal surface but no or minimal projection (TM 1523, *Au. africanus*, LP4); 2. Disto-buccal cusplet with a free apex (SK 7, *P. robustus*, RP4). Buccal views. Scale bar = 5 mm / *Cuspide disto-vestibulaire sur les prémolaires inférieures. Codage : 1. Sillon marqué sur la surface vestibulaire mais pas d'apex libre (TM 1523*, Au. africanus, *LP4); 2. Cuspide disto-vestibulaire avec apex libre (SK 7*, P. robustus, *RP4). Vues vestibulaires. Echelle = 5 mm*

Double cusp 5, upper molars (Table 4)

"Cusp 6" on upper molars had already been described and used for scoring in Bailey and Wood's study [6]. To avoid confusion, we prefer to use the term "double cusp 5" on upper molars rather than "cusp 6", which is described on lower molars. Our study provides statistical comparisons of trait frequencies between taxa, and also shows that some hominin upper molars have a small distal cusp, in addition to cusp 5. As proposed by Bailey and Wood, we scored the expression of this character on upper molars as absent (grade 0) or present (grade 1) (Fig. 6). Double cusp 5 is scored as present on 2/6 *P. robustus* M^1 and 1/6 M^2. Grade 1 is also observed on 1/5 *Au. afarensis* M^1 and 1/6 early *Homo* M^1. Except for *P. robustus* specimens, it is not observed on any other taxa M^2s (Table 7).

We did not find any significant differences between taxa for this character ($p>0.3$).

Distal fovea, upper molars (Table 5)

On a large proportion of upper molars, a triangular fossa is present on the occlusal surface and distally to the metacone

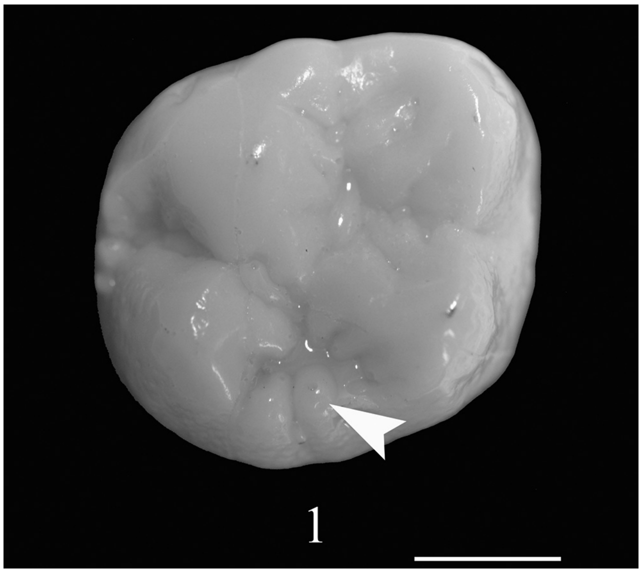


Fig. 6 Occurrence of a secondary distal cusp on upper molars [6]. Scoring: 1. Presence (SK 832, *P. robustus*, LM1). Occlusal view. Scale bar = 5 mm / *Présence d'une cuspide accessoire distale sur les molaires supérieures [6]. Scoring: 1. Présence (SK 832*, P. robustus, *LM1). Vue occlusale. Echelle = 5 mm*

Table 6 List of new non-metric dental characters described in this study / *Liste des nouveaux caractères dentaires proposés dans cette étude*

Lower premolars
Disto-buccal cusplet Presence of a secondary buccal cusp detached from the main buccal cusp Grades: 0 (absence), 1 (marked groove on the disto-buccal surface but no or minimal projection), 2 (disto-buccal cusplet with a free apex)
Upper molars
Distal fovea Development of a triangular depression mesial to the distal marginal ridge Grades: 0 (absence), 1 (small distal fovea), 2 (large distal fovea. Distal crests on hypocone and metacone converge to form a large fovea which extends almost to the summits of distal cusps)
Lower molars
Mesial marginal ridge Development of the mesial marginal ridge Grades: 0 (absence), 1 (ridge is continuous and thin), 2 (ridge is uninterrupted, thick and sometimes closes the anterior fovea)

Table 7 Trait frequencies for each character for all groups / *Distributions des fréquences de chaque caractère pour chacun des groupes*

			Au. afarensis	*Au. africanus*	*Au. bahrelghazali*	*P. aethiopicus*	*P. boisei*	*P. robustus*	*Early Homo*	*H. georgicus*
Maxilla										
	P^3 Disto-buccal cusplet	0	2/3	1/4	–	0/1	–	1/6	1/2	–
		1	1/3	2/4	–	0/1	–	2/6	1/2	–
		2	0/3	1/4	–	1/1	–	3/6	0/2	–
	P^4 Disto-buccal cusplet	0	5/7	1/1	–	–	–	1/7	1/1	–
		1	2/7	0/1	–	–	–	0/7	0/1	–
		2	0/7	0/1	–	–	–	6/7	0/1	–
	M^1 Hypocone	3	0/5	0/4	–	0/1	0/1	0/6	0/6	–
		4	1/5	0/4	–	0/1	0/1	0/6	0/6	–
		5	3/5	3/4	–	0/1	0/1	3/6	4/6	–
		6	1/5	1/4	–	1/1	1/1	3/6	2/6	–
	M^1 Double Cusp 5	0	4/5	4/4	–	1/1	0/1	4/6	5/6	–
		1	1/5	0/4	–	0/1	1/1	2/6	1/6	–
	M^1 Distal Fovea	0	1/5	0/4	–	0/1	1/1	0/6	0/6	–
		1	4/5	2/4	–	1/1	0/1	6/6	1/6	–
		2	0/5	2/4	–	0/1	0/1	0/6	5/6	–
	M^2 Hypocone	3	0/2	0/2	–	–	–	0/6	1/4	–
		4	0/2	0/2	–	–	–	0/6	0/4	–
		5	1/2	0/2	–	–	–	2/6	3/4	–
		6	1/2	2/2	–	–	–	4/6	0/4	–
	M^2 Double Cusp 5	0	2/2	2/2	–	–	–	5/6	4/4	–
		1	0/2	0/2	–	–	–	1/6	0/4	–
	M^2 Distal Fovea	0	1/2	0/2	–	–	–	1/6	0/4	–
		1	1/2	2/2	–	–	–	4/6	2/4	–
		2	0/2	0/2	–	–	–	1/6	2/4	–
Mandible										
	P$_3$ Disto-buccal cusplet	0	0/2	0/2	0/1	0/4	–	0/4	1/4	1/1
		1	1/2	1/2	0/1	1/4	–	2/4	2/4	0/1
		2	1/2	1/2	1/1	3/4	–	2/4	1/4	0/1
	P$_4$ Disto-buccal cusplet	0	1/4	–	0/1	0/3	–	0/8	1/3	1/1
		1	1/4	–	0/1	0/3	–	1/8	1/3	0/1
		2	2/4	–	1/1	3/3	–	7/8	1/3	0/1
	M$_1$ Hypoconulid	3	0/5	0/5	–	0/1	1/3	0/11	0/4	0/1
		4	0/5	0/5	–	0/1	0/3	3/11	1/4	0/1
		5	5/5	5/5	–	1/1	0/3	6/11	3/4	1/1
		6	0/5	0/5	–	0/1	2/3	2/11	0/4	0/1

(Suite page suivante)

Table 7 *(suite)*

		Au. afarensis	*Au. africanus*	*Au. bahrelghazali*	*P. aethiopicus*	*P. boisei*	*P. robustus*	*Early Homo*	*H. georgicus*
M_1 Protostylid	0	0/5	2/5	–	0/1	1/3	0/9	2/4	0/1
	1	0/5	0/5	–	0/1	0/3	0/9	0/4	0/1
	2	0/5	0/5	–	0/1	0/3	0/9	0/4	0/1
	3	0/5	0/5	–	0/1	0/3	0/9	0/4	0/1
	4	4/5	0/5	–	0/1	0/3	0/9	0/4	0/1
	4A	0/5	1/5	–	0/1	1/3	5/9	1/4	0/1
	4B	0/5	0/5	–	0/1	0/3	2/9	0/4	0/1
	5	0/5	0/5	–	0/1	0/3	0/9	0/4	0/1
	6	0/5	0/5	–	1/1	0/3	0/9	1/4	1/1
	6A	0/5	1/5	–	0/1	1/3	1/9	0/4	0/1
	7	0/5	0/5	–	0/1	0/3	0/9	0/4	0/1
	7A	1/5	1/5	–	0/1	0/3	1/9	0/4	0/1
M_1 Double Cusp 6	0	4/4	4/5	–	1/1	1/3	10/11	5/5	1/1
	1	0/4	1/5	–	0/1	2/3	1/11	0/5	0/1
M_1 Mesial Marginal Ridge	0	0/5	1/5	–	0/1	0/3	0/7	1/4	1/1
	1	3/5	1/5	–	1/1	0/3	2/7	1/4	0/1
	2	2/5	3/5	–	0/1	3/3	5/7	2/4	0/1
M_2 Hypoconulid	3	0/3	0/1	–	0/3	–	0/9	0/4	0/1
	4	2/3	0/1	–	1/3	–	4/9	2/4	0/1
	5	0/3	1/1	–	1/3	–	4/9	2/4	1/1
	6	1/3	0/1	–	1/3	–	1/9	0/4	0/1
M_2 Protostylid	0	0/3	0/1	–	0/2	–	0/10	4/4	0/1
	1	0/3	0/1	–	0/2	–	0/10	0/4	0/1
	2	0/3	0/1	–	0/2	–	0/10	0/4	0/1
	3	0/3	0/1	–	0/2	–	0/10	0/4	0/1
	4	0/3	0/1	–	0/2	–	0/10	0/4	0/1
	4A	2/3	0/1	–	0/2	–	1/10	0/4	1/1
	4B	0/3	0/1	–	1/2	–	2/10	0/4	0/1
	5	1/3	0/1	–	0/2	–	0/10	0/4	0/1
	6	0/3	0/1	–	0/2	–	1/10	0/4	0/1
	6A	0/3	0/1	–	0/2	–	6/10	0/4	0/1
	7	0/3	0/1	–	0/2	–	0/10	0/4	0/1
	7A	0/3	1/1	–	1/2	–	0/10	0/4	0/1
M_2 Double Cusp 6	0	3/3	1/1	–	2/3	–	5/9	4/4	1/1
	1	0/3	0/1	–	1/3	–	4/9	0/4	0/1
M_2 Mesial Marginal Ridge	0	0/3	0/1	–	0/2	–	0/9	0/4	1/1
	1	1/3	0/1	–	0/2	–	1/9	2/4	0/1
	2	2/3	1/1	–	2/2	–	8/9	2/4	0/1

and the hypocone. We propose scoring the expression of the distal fovea on upper molars as follows (Fig. 7):

- 0: Absence, or very slight development;
- 1: Small distal fovea;
- 2: Large distal fovea, distal crests of distal cusps converging to form a large fossa that extends almost to the summit of the distal cusps.

The distal fovea seems to be well developed on the majority of early *Homo* (5/6 M^1 and 2/4 M^2 scored as grade 2). *P. robustus* specimens mainly express a grade 1: 6/6 M^1 and 4/6 M^2. We scored the distal fovea as grade 1 on 2/4 *Au. africanus* M^1 and 2/2 M^2. *Au. afarensis* specimens are only scored as grades 0 (1/5 M^1 and 1/2 M^2) and 1 (4/5 M^1 and 1/2 M^2). The single *P. boisei* specimen (M^1) is scored as grade 0 and the single *P. aethiopicus* specimen (M^1) as grade 1 (Table 7).

Fisher exact tests revealed significant differences in grade 2 between *Australopithecus* and early *Homo* (p=0.01) and between *Paranthropus* and early *Homo* (p=0.002). For grade 1, we found a significant difference only between *Paranthropus* and early *Homo* (p=0.02). No significant differences appeared for grade 0 (p>0.5).

Double cusp 6, lower molars (Table 4)

A small secondary distal cusp located between cusps 5 and 6 is often observed on several lower molars. This character had already been described as "double cusp 6" in several studies [6,15,16]. Bailey and Wood's study on occlusal morphology points out that it is useful for distinguishing between taxa or assessing phenetic relationships [6]. Our study provides statistical comparisons of trait frequencies between taxa. This character was scored only if cusps 5 and 6 were present, so that a distinction could be made between these cusps instead of scoring the same cusp twice. As proposed by Bailey and Wood, we scored this character as absent (grade 0) or present (grade 1) (Fig. 8).

This character is observed mostly on *P. robustus* specimens (Table 7). It is observed on 4/9 M_2 but only 1/11 M_1. Concerning *P. boisei* specimens, 2/3 M_1 have a double cusp 6. It is only observed on 1/5 *Au. africanus* M_1 and not on M_2. It is not observed on any *Au. afarensis* (0/4 M_1 and 0/3 M_2) or early *Homo* (0/5 M_1 and 0/4 M_2). There is no significant difference between groups with regard to the presence or absence of double cusp 6 (p>0.08).

Mesial marginal ridge, lower molars (Table 5)

In our sample, Plio-Pleistocene hominin lower molars have different types of expression of the mesial marginal ridge, which is absent on some molars but can also be more or less developed. In a few cases, we observed a thick marginal ridge that obliterates the anterior fovea.

We propose the following scoring procedure for the expression of this character (Fig. 9):

- 0: Mesial marginal ridge absent or very slight;
- 1: Mesial marginal ridge is continuous and thin;
- 2: Mesial marginal ridge is continuous, thick and can sometimes close the anterior fovea.

A mesial marginal ridge (grades 1 and 2) is frequently observed on Plio-Pleistocene molars (n=42). In our sample, it was absent only on two M_1, and never absent on M_2 (Table 7). We scored this character as grade 2 on 5/7 *P. robustus* M_1 and 8/9 M_2. 2/4 early *Homo* M_1 and 2/4 M_2 express a grade 2. The three *P. boisei* molars (M_1) express a grade 2. The frequencies for grades 1 are 3/5 M_1 and 1/3 M_2 for *Au. afarensis*, and 1/5 M_1 for early *Homo*. The

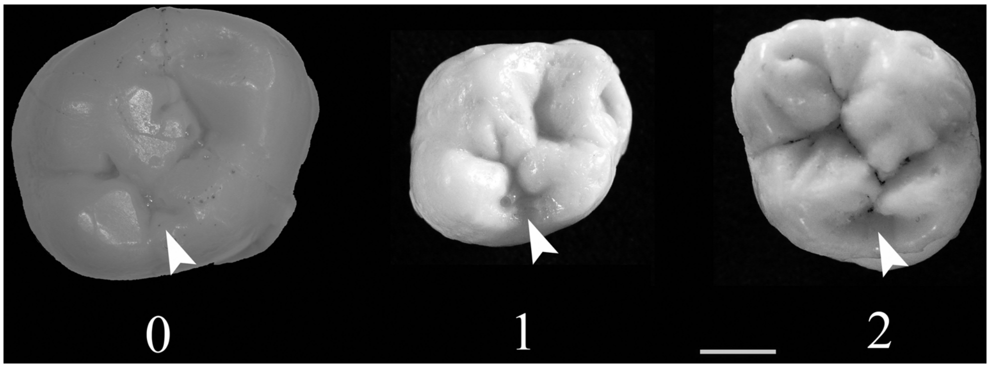


Fig. 7 Distal fovea, upper molars. Scoring: 0. Absence or very slight development (SK 835, *P. robustus*, LM2); 1. Small distal fovea (B8–23B, *Au. aff. afarensis*, LM1); 2. Large distal fovea, distal crests of distal cusps converging to form a large fossa which extends almost to the summits of distal cusps (KB 5223, uncertain attribution, RM2). Occlusal views. Scale bar = 5 mm / *Fosse distale sur les molaires supérieures. Codage : 0. Absence ou très faible développement (SK 835,* P. robustus, *LM2) ; 1. Petite fosse distale (B8-23B,* Au. aff afarensis, *LM1) ; 2. Large fosse distale. Les crêtes distales des cuspides distales se rejoignent à distance formant une large fosse qui s'étend presque jusqu'aux sommets des cuspides distales (KB 5223, attribution incertaine, RM2). Vues occlusales. Echelle = 5 mm*

frequencies for grade 2 are 2/5 M_1 and 2/3 M_2 for *Au. afarensis* and 3/5 M_1 and 1/1 M_2 for early *Homo*. We found significant differences between *Paranthropus* and early *Homo* for grades 0 (p=0.02) and 2 (p=0.04), but not for grade 1 (p>0.2).

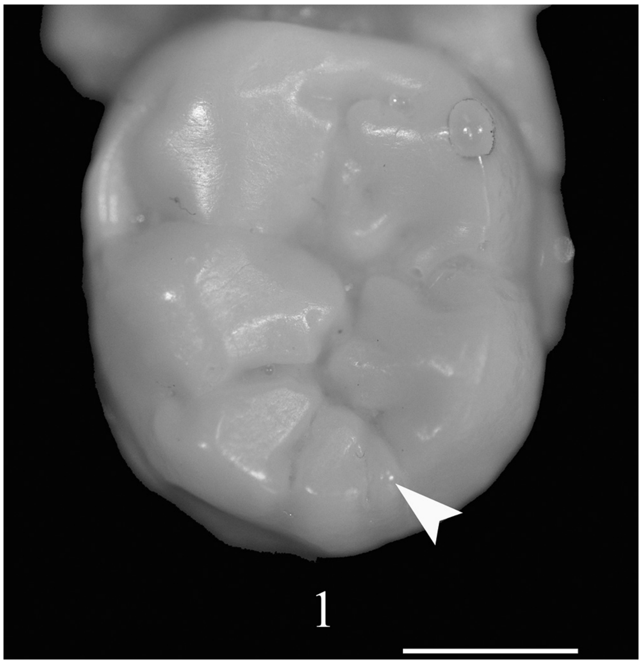


Fig. 8 Occurrence of a secondary distal cusp on lower molars [6]. Scoring: 1. Presence (SK 1587a, *P. robustus*, LM2). Occlusal view. Scale bar = 5 mm / *Présence d'une cuspide accessoire distale sur les molaires inférieures [6]. Scoring: 1. Présence (SK 1587a,* P. robustus, *LM2). Vue occlusale. Echelle = 5 mm*

Conclusion

Our study based on observations and scoring of 178 premolars and molars demonstrates that the standard scoring system for dental morphological characters (ASUDAS) does not cover all morphological variations in Plio-Pleistocene hominins. The purpose of this note is to emphasize the need to develop standard scoring for these characters, which are useful to assess variations in premolars and molars in fossil hominins. We propose to readjust this standard scoring system by, firstly, adding grades for the types of expression of dental characters already described, and secondly, by including the new types of expression described by Hlusko [7] on the protostylid reference plaque, and finally by describing six characters that are not included in the standard system.

Firstly, our observations suggest that there is a size parameter that creates a bias in the scoring procedure for some characters. This is because ASUDAS was established for the study of modern human teeth, which are smaller than those of extinct hominins. Therefore, in order to score every molar in our sample accurately, we suggest adding a sixth grade for two characters: the hypocone on upper molars and the hypoconulid on lower molars. We propose a description based on the size of the cusp relatively to the adjacent cusp, in order to limit the bias arising from the size parameter.

Furthermore, our study confirms the new scoring procedure developed by Hlusko for the protostylid on lower molars [7]. According to Hlusko, the expression of this character in *Australopithecus* is more similar to that of a cingular remnant than to that of a cusp as initially described in ASUDAS for modern humans. Our observations re-confirm that

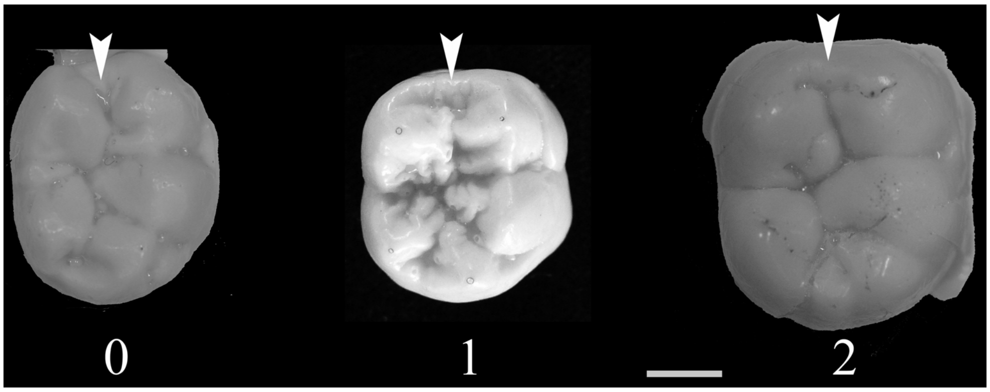


Fig. 9 Types of expression of the mesial marginal ridge, lower molars. Scoring: 0. Mesial marginal ridge absent or very slight (Stw 151, *Au. africanus*, RM1); 1. Ridge is continuous and thin (W7–508, *Au. aff. afarensis*, RM1); 2. Ridge is continuous, thick, and can obliterate the anterior fovea (SKW 4767, *P. robustus*, RM1). Occlusal views. Scale bar = 5 mm / *Développement de la crête marginale mésiale sur les molaires inférieures. Codage : 0. Absence ou faible développement (Stw 151*, Au. africanus, *RM1) ; 1. Crête continue et fine (W7–508*, Au. aff afarensis, *RM1) ; 2. Crête continue et robuste, pouvant combler la fosse antérieure (SKW 4767*, P. robustus, *RM1). Vues occlusales. Echelle = 5 mm*

the types of expression described by Hlusko should be illustrated in the standard system to allow accurate and standardized scoring for Plio-Pleistocene hominins.

Our study describes six characters that are not included in the standard ASUDAS [3–5]. A secondary distal cusp on upper and lower molars has already been described [6] and our observations also suggest that it may have the potential to establish distinctions between taxa. We believe that the disto-lingual cusplet on second upper premolars described by Suwa [14] can be recorded on both first and second upper and lower premolars. However, our results suggest that it is useful for distinguishing *P. robustus* upper premolars, but that it is more randomly distributed on lower premolars. We have kept a basic present/absent description for double cusp 5 on upper molars and double cusp 6. However, we stress the need to propose more accurate scoring procedures that are not based solely on the occurrence (or not) of the character.

Acknowledgments: The authors wish to thank the Ditsong National Museum (South Africa) for allowing us access to the cast and original specimens, and ANR ARCHOR (ANR-12-CULT-006) for their support.

Conflict of interest: none.

References

1. Irish JD, Guatelli-Steinberg D (2003) Ancient teeth and modern human origins: An expanded comparison of African Plio-Pleistocene and recent world dental samples. J. Hum Evol 45:113–44
2. Martinón-Torres M, De Castro JB, Gomez-Robles A, et al (2012) Morphological description and comparison of the dental remains from Atapuerca-Sima de los Huesos site (Spain). J. Hum Evol 62:7–58
3. Turner CG, Nichol CR, Scott GR (1991) Scoring procedures for key morphological traits of the permanent dentition: The Arizona State University dental anthropology system. In: Kelley MA, Larsen CS (eds) Advances in dental anthropology. Wiley-Liss, New York, pp 13–31
4. Scott GR, Turner CG (1997) The anthropology of modern human teeth: Dental morphology and its variation in recent human populations. Cambridge University Press, Cambridge, England, 382 p
5. Scott GR, Irish JD (2017) Human tooth crown and root morphology. Cambridge University Press, Cambridge, England, 334 p
6. Bailey SE, Wood BA (2007) Trends in postcanine occlusal morphology within the hominin clade: The case of *Paranthropus*. In: Bailey SE, Hublin JJ (eds) Dental perspectives on human evolution: State of the art research in dental paleoanthropology. Springer, Netherlands, pp 33–52
7. Hlusko LJ (2004) Protostylid variation in *Australopithecus*. J. Hum Evol 46:579–94
8. Wood BA, Abbott SA (1983) Analysis of the dental morphology of Plio-Pleistocene hominids. I. Mandibular molars: crown area measurements and morphological traits. J. Anat 136:197–219
9. Wood BA, Engleman CA (1988) Analysis of the dental morphology of Plio-Pleistocene hominids. V. Maxillary postcanine tooth morphology. J Anat 161:1–35
10. Bailey SE (2002) A closer look at Neanderthal postcanine dental morphology: The mandibular dentition. Anat Rec 269:148–56
11. Bailey SE (2006) Beyond shovel-shaped incisors: Neanderthal dental morphology in a comparative context. Period Biol 108:253–67
12. Burnett SE, Hawkey DE, Turner CG (2010) Brief communication: Population variation in human maxillary premolar accessory ridges (MxPAR). Am J. Phys Anthropol 141:319–24
13. Martinón-Torres M, De Castro JB, Gomez-Robles A, et al (2007) Dental evidence on the hominin dispersals during the Pleistocene. Proc Natl Acad Sci U S A 104:13279–82
14. Suwa G (1990) A comparative analysis of hominid dental remains from the Shungura and Usno Formations. Omo Valley, Ethiopia, 521 p
15. Skinner MM, Wood BA, Boesch C, et al (2008) Dental traits expression at the enamel-dentine junction of lower molars in extant and fossil hominoids. J. Hum Evol 54:173–86
16. Skinner MM, Gunz P (2010) The presence of accessory cusps in chimpanzee lower molars is consistent with a patterning cascade model of development. J. Anat 217:245–53

BMSAP (2018) 30:49-58
DOI 10.3166/bmsap-2018-0013

NOTE / *NOTE*

Reassessment of Anthropic Modifications on the Early Pleistocene Hominin Specimen Stw53 (Sterkfontein, South Africa)

Réévaluation des modifications anthropiques sur le fossile d'hominine du Pleistocène Inférieur Stw53 (Sterkfontein, Afrique du Sud)

R. Hanon · S. Péan · S. Prat

Received: 3 May 2017; Accepted: 10 January 2018

Abstract Linear marks were observed on the maxillary zygomatic process of the early Pleistocene hominin fossil Stw53 from the Sterkfontein cave site. The taxonomic allocation of this specimen is still under debate, as it has been attributed either to the genus *Homo* or *Australopithecus*. Two alternative hypotheses have been proposed regarding the taphonomic agent responsible for the linear marks observed on this specimen. These modifications were initially assigned to anthropic cutmarks inflicted by stone tools, thus representing the earliest cutmarks discovered on hominin remains. Conversely, these linear marks were interpreted by others as non-anthropic modifications. In order to better understand the origin of the linear marks, a new taphonomic appraisal of these modifications was conducted using a multivariate statistical approach complemented by butchery and trampling experiments on extant mammal bones. This new study of Stw53 linear marks does not provide evidence for anthropic activities but, rather, supports the unintentional origin hypothesis.

Keywords Taphonomy · Cutmarks · Trampling · Stw53 · Sterkfontein

Résumé Des traces linéaires ont été observées sur le processus zygomatique de l'os maxillaire de l'hominine fossile sud-africain Stw53 découvert dans le site de Sterkfontein. L'attribution taxinomique de ce spécimen fait l'objet de nombreux débats. Il est attribué, selon les auteurs, soit au genre *Homo*, soit au genre *Australopithecus*. Deux hypothèses alternatives ont été proposées concernant l'identification de l'agent taphonomique responsable des marques linéaires de Stw53. La première les attribue à des traces de découpe produites par un artefact lithique. Elles pourraient alors représenter les plus anciennes marques de découpe retrouvées sur des restes d'hominine. À l'inverse, ces marques linéaires ont été interprétées comme des modifications non anthropiques. Afin de mieux comprendre l'origine des marques observées sur le fossile Stw53, une étude préliminaire a été menée en appliquant des expérimentations taphonomiques afin de produire des marques de découpe et des marques de piétinement sur des os de mammifères actuels complétées par une approche statistique multivariée. Cette nouvelle étude des marques linéaires de Stw53 remet en cause leur origine anthropique et soutient plutôt l'hypothèse d'une origine non intentionnelle.

Mots clés Taphonomie · Marques de découpe · Piétinement · Stw53 · Sterkfontein

Introduction

Since the description of anthropic modifications on the middle Pleistocene Bodo cranium from Ethiopia [1], several taphonomic studies have focused on possible perimortem damage observed on hominin fossil remains [e.g. 2–11]. The early Pleistocene Stw53 hominin cranium specimen is one of them. Moreover, in late Pliocene and early Pleistocene African contexts, the anthropic origin of linear marks observed on vertebrate remains has been debated by many authors [12–19].

Stw 53 hominin cranium was discovered by Alan Hughes in 1976 in the dolomitic cave of Sterkfontein (South Africa). It comes from either calcified and decalcified breccia, stratigraphically derived from either Member 5 [20] or the hanging remnant of non-tool-bearing Member 4 (Stw53 Infill) [10,21]. According to different authors, an age between 2.6 and

R. Hanon (✉) · S. Péan
Muséum national d'Histoire naturelle, UMR 7194,
1, rue René Panhard, 75013 Paris, France
e-mail : raphael.l.hanon@gmail.com

S. Prat
CNRS, UMR 7194, 17, place du Trocadéro, 75116 Paris, France

1.49 million years old is proposed for this specimen [21–23]. No stone tools have been found in association with Stw53 [21].

The taxonomic allocation of this specimen is under debate. At the time of its discovery, Stw53 was attributed to *Homo* aff. *H. habilis* [20]. More recently, an allocation to the genus *Australopithecus* has been suggested [21], based on cranial capacity, a braincase frontally narrow and restricted, a flattened nasal skeleton and large teeth. However, new analyses based on cladistic [24] and comparative approaches [25] confirm the previous allocation to the *Homo* genus and the species *habilis*. Following these studies, a new species, *Homo gautengensis*, was defined [26], with the Stw53 specimen as the holotype.

Linear marks were described on the maxillary zygomatic process of Stw53 and interpreted by Pickering and colleagues as "cutmarks inflicted by a stone tool such as a sharp flake edge" [6]. The interpretation of Stw53 linear marks was based on macro- and microscopic (i.e. stereo microscope and scanning electron microscope, SEM) observations of the morphology and orientation of the grooves, their anatomical location, as well as the lack of any other linear mark on the macromammalian assemblage associated with the hominin specimen [6]. The striae are located in the masseter muscle insertion area and have been attributed to a mandibular disarticulation [6]. Several hypotheses were raised to explain their presence, including "cannibalism, curation, mutilation, and/or funerary procedures" [6, p. 583].

This assumption has far-reaching implications in terms of early hominin behaviours, as it would represent the earliest bone modifications of anthropic origin observed on hominin fossil [6,27]. Except Sterkfontein with Stw53, only TD6 level (between 800 and 900 ka) of the Gran Dolina site, at Atapuerca (Spain), has yielded hominin remains bearing cutmarks for the early Pleistocene period [3–5,8].

Conversely, it was mentioned that the zygomatic bone of Stw53 was discovered together with sharp-edged blocks lying against it, which could produce linear marks under sedimentary pressure and therefore without the action of any anthropic agent [10]. This raises the question of the distinction between cutmarks on this bone inflicted intentionally (i.e. by another hominin) and 'produced naturally by a small chert block' [10].

Many authors already showed that marks resulting from non-anthropic processes (e.g. sedimentary pressure, sedimentary abrasion, trampling) can mimic cutmarks (equifinality) [12–14,16,17,19,28–30]. Some criteria are recurrent and efficient to distinguish anthropic and trampling modifications. Among these criteria (Table 1), we can cite the number of marks in the assemblage and/or in a specimen [15,29],

Table 1 Morphological criteria used in this study to describe taphonomical linear marks on bones / *Critères morphologiques utilisés dans cette étude pour décrire les marques linéaires taphonomiques sur os*

Criteria	Variables
1. Number of specimens	
2. Bone type	1 = long; 2 = short; 3 = flat
3. Position of marks	1 = shaft; 2 = epiphyses; 3 = variable
4. Association with others marks	0 = absence; 1 = fracture; 2 = polished surface; 3 = scraped surface; 4 = abraded surface; 5 = gnawed surface; 6 = digested surface; 7 = perforated surface; 8 = variable
5. Number of marks	1 = numerous (≥ 5); 2 = few (< 5)
6. Distribution of marks	1 = the whole bone surface; 2 = grouped; 3 = individual; 4 = variable
7. Orientation of marks	1 = parallel to the bone axis; 2 = perpendicular to the bone axis; 3 = oblique to the bone axis; 4 = variable
8. Length	1 = long (> 7 mm); 2 = medium (3–7 mm); 3 = short (≤ 3 mm); 4 = variable
9. Width	1 = large (≥ 1 mm); 2 = small (< 1 mm); 3 = variable
10. Depth	1 = large; 2 = medium; 3 = small; 4 = variable
11. Mark trajectory	1 = sinuous; 2 = straight; 3 = curved; 4 = variable
12. Division of groove ends	0 = absence; 1 = presence
13. Mark cross-section	1 = V-shaped; 2 = dissymmetric V-shaped; 3 = wide V-shape (with a flat bottom _/); 4 = U-shaped; 5 = variable
14. Shoulder effect	0 = absence; 1 = presence
15. Flaking effect	0 = absence; 1 = presence
16. Internal microstriations	0 = absence; 1 = presence
17. Location of microstriations	1 = on the mark walls; 2 = on the mark bottom; 3 = on both places
18. Shape of microstriations	1 = continuous; 2 = discontinuous; 3 = variable
19. Trajectory of microstriations	1 = sinuous; 2 = straight; 3 = variable

the random position and orientation of the mark [15,28], the variation in the dimensions [29,31,32], the shoulder effect [15], the cross-section shape of the marks and microstriations [30].

In this paper, we propose to further test these two hypotheses by (1) conducting a taphonomic study on the original fossil Stw53 cranium from South Africa and (2) developing butchery and trampling experiments on extant mammal bones in order to better clarify the origin of the marks observed on the Stw53 specimen. This paper is focused on the descriptions and interpretations of the modifications observed on the early Pleistocene Stw53 hominin. Thus, this article does not aim at describing hominin specimens bearing cutmarks such as the middle Pleistocene Bodo [1].

Materials and methods

We studied 21 specimens from a reference taphonomic collection, which is hosted at the Institut de paléontologie humaine (Institute of Human Palaeontology) and the Muséum national d'Histoire naturelle (National Museum of Natural History), nine experimental specimens and the original Stw53 hominin cranium (Table 2). Material from the taphonomic collection is composed of long (radius, ulna, metapodial), flat (mandible, scapula) and short (carpal, phalanx) bones from large mammals (reindeer (*Rangifer tarandus*), ox (*Bos Taurus*) and medium sized species) and one reindeer antler. This sample bears anthropic ($N = 15$), carnivore ($N = 4$) and rodent ($N = 2$) linear marks. Experimentation was conducted on long, flat and short bones: pig (*Sus domesticus*) femur, rib and vertebra of ox and pig.

Two experiments were conducted. Firstly, the trampling experimental protocol consisted of placing dry bones (pig vertebra, rib and tibia) in three kilograms of (1) flour and (2) sand, containing 108 sharp-edged blocks (83g), in order to observe the impact of the flakes present inside a soft and abrasive matrix. Flakes using Oldowan techniques were obtained by Adrian Arroyo with raw material (chert) from the Sterkfontein Valley. Bones were exposed to trampling by one of the authors (R. Hanon) for two minutes following the protocol established by Domínguez-Rodrigo et al. [30], which was to place dry bones in different sediments and expose them to trampling for two minutes. Pickering et al. [6] assumed that the cheek bone is "an area that we argue was naturally protected, unlikely to acquire the types of random scratches imparted by animals trampling around the cave floor and pushing the bone across abrasive sediments." Based on this assumption, we decided to apply experiments on vertebra, which present the best example of naturally protected bone area. Furthermore, ribs were also used due to their flat morphology similar to cranial bones.

Secondly, the butchery experiment was also conducted by one of the authors (R. Hanon) by defleshing fresh bones with meat still on them, in order to produce cutmarks on the same types of anatomical elements as the trampled ones (pig vertebra, rib and tibia), with experimental Oldowan stone flakes made of the same chert from the Sterkfontein Valley.

Specimens were described using a list of 19 criteria following several existing ones available in the literature [15,28–30,33] and personal observations (R. Hanon) (Table 2) in order to identify the taphonomic agent(s) responsible for the marks. All comparative specimens were observed under Motic SMZ-143 binoculars (10× to 40×) and photographed using a AD7013MTL Dino-Lite microscope. In addition to Dino-Lite microscope acquisitions on the original Stw53 specimen (S. Prat), silicone (©President light body) high resolution moulds were made by one of us (S. Prat). Four specimens from the reference taphonomic collection (IPH/MNHN), four experimental pieces (two butchered and two trampled bones) and Stw53 moulds, were observed with an environmental scanning electron microscope (ESEM), Tescan Vega 2 LSU. These analyses were undertaken at the Electron Microscopy Technical Platform of the Collections Direction of the Muséum of Natural History in Paris. ESEM acquisition was conducted according to methods applied by White [1] on Bodo and Pickering et al. [6] on Stw53.

Furthermore, unlike the previous study on Stw53 [6], we compared Stw53 marks with our reference taphonomic collection and experimental material, and we applied statistical methods. Hierarchical cluster analyses [UPGMA (unweighted pair group method with arithmetic mean), single linkage and neighbour joining method] were performed using PAST (version 2.17) software. The UPGMA is an agglomerative clustering approach, based on grouping the most similar specimens together, but with three different algorithms, which permit the testing of the strength of the clusters between the three methods. Moreover, multiple correspondence analysis (MCA) was performed to cluster the marks according to their similarities using XLSTAT (version 2013) software. All analyses were applied to the same taphonomic database (Table 2).

Results

Using both Dino-Lite and SEM acquisitions on Sterkfontein specimen Stw53, we observed three groups of linear marks, as described by Pickering et al. [6] (Fig. 1A–B). All of them are located on the zygomatic process of the right maxilla, referred to as Stw53c.

The first set of linear marks observed on Stw53c is a group of striations composed of a main mark with a wide V-shaped cross-section (Fig. 1C), which is usually observed in trampling marks [15]. The main groove is less than 3 mm

Table 2 Database of the studied bone specimens bearing taphonomical linear marks. Groups are indicated as follows: A = anthropic; C = carnivore; R = rodent; T = trampling / *Base de données des pièces osseuses étudiées portant des marques linéaires taphonomiques. Les groupes sont enregistrés comme suit : A = anthropique ; C = carnivore ; R = rongeur ; T : piétinement*

ITERIA	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**GROUP**
TAPH - 12	1	2	0	2	3	3	2	2	1	2	0	5	1	1	1	3	1	2	A
TAPH - 13	2	1	0	2	4	2	2	2	1	2	1	5	1	0	1	3	1	2	A
TAPH - 15	2	0	0	2	3	2	1	2	1	2	0	5	1	0	1	3	1	2	A
TAPH - 10	1	2	0	1	2	4	4	1	1	2	0	2	1	0	1	1	1	2	A
TAPH - 11	1	2	0	2	3	3	4	2	1	2	1	2	1	0	1	1	1	2	A
TAPH - 16	2	2	0	2	2	4	2	2	1	2	0	2	1	0	1	1	1	2	A
TAPH - 17	2	1	0	2	3	2	2	1	1	2	0	3	0	0	1	2	2	1	A
TAPH - 18	2	2	0	2	2	2	2	1	1	2	0	2	1	0	1	1	1	2	A
TAPH - 19	3	0	0	1	2	0	1	2	2	4	0	5	1	1	0	0	0	0	A
TAPH - 23	3	1	0	1	2	3	1	2	2	4	0	3	1	1	1	2	1	2	A
TAPH - 24	3	1	0	2	2	3	1	2	2	4	0	5	1	1	0	0	0	0	A
TAPH - 25	3	1	3	2	3	3	1	2	2	2	1	2	1	1	1	1	1	2	A
TAPH - 8	1	1	8	1	2	2	1	3	4	4	0	5	0	0	0	0	0	0	A
TAPH - 9	1	1	1	1	2	2	1	3	4	4	0	5	0	0	0	0	0	0	A
G.1919 - 1 LE PLACARD	1	3	8	2	3	4	2	3	1	1	0	5	0	0	1	2	2	1	C
CRITERIA	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**GROUP**
G.1919 - 1 COLL. H. BREUIL	1	3	4	1	1	2	2	1	4	1	0	5	0	0	1	2	1	1	C
G.1919 - 1 COLL. H. BREUIL PHOTO°11	1	3	8	1	1	2	1	1	4	1	0	4	0	0	0	0	0	0	C
MDA / RDG / 61	1	1	4	1	1	1	1	2	2	1	0	3	1	0	1	2	1	1	C
SCP-R, E. 1930. 2, CANGO CAVE	3	3	0	1	1	2	1	1	2	1	0	3	0	0	0	0	0	0	R
BOIS-R	1	3	1	1	2	2	1	1	1	1	0	3	0	0	0	0	0	0	R
EXPA-1	3	1	0	2	2	4	4	3	4	4	0	5	1	1	0	0	0	0	A
EXPA-2	2	2	0	1	2	3	1	2	4	4	0	2	1	0	1	1	1	1	A
EXPA-3	1	1	0	1	2	4	1	2	4	4	0	2	0	0	1	1	1	3	A
EXPC-1	1	1	0	2	4	4	4	2	3	4	0	5	1	0	0	0	0	0	T
EXPC-2	2	1	0	2	4	3	4	2	3	1	0	5	0	0	1	1	2	1	T
STW53 SET1	3	1	0	2	2	3	3	2	3	1	0	3	0	0	1	1	2	1	Stw53
STW53 SET2	3	1	0	2	2	3	3	2	3	1	0	3	0	0	0	0	0	0	Stw53
STW53 SET3	3	1	0	2	2	3	3	2	3	1	0	5	0	0	0	0	0	0	Stw53

long, less than 1 mm wide and shallow. A few ancillary shorter striae are present along the main mark. Those are sinuous and their cross-sections are relatively wide V-shaped. Sinuous and discontinuous microstriations are visible on mark walls.

The second set is composed of two overlapping narrower and longer striae than the first set (Fig. 1D). They are slightly more than 3 mm long, less than 1 mm wide and shallower than Set 1. We clearly observed relatively wide V-shaped striae, which can have been produced by trampling [34], without internal microstriations. One stria has a sinuous trajectory while the other one has a curvy ending (named barb) which is rarely observed (6/251 marks) in trampling experimental marks [30].

The third set described by Pickering et al. [6] was difficult to finely observe (Fig. 1E), even with a Dino-Lite

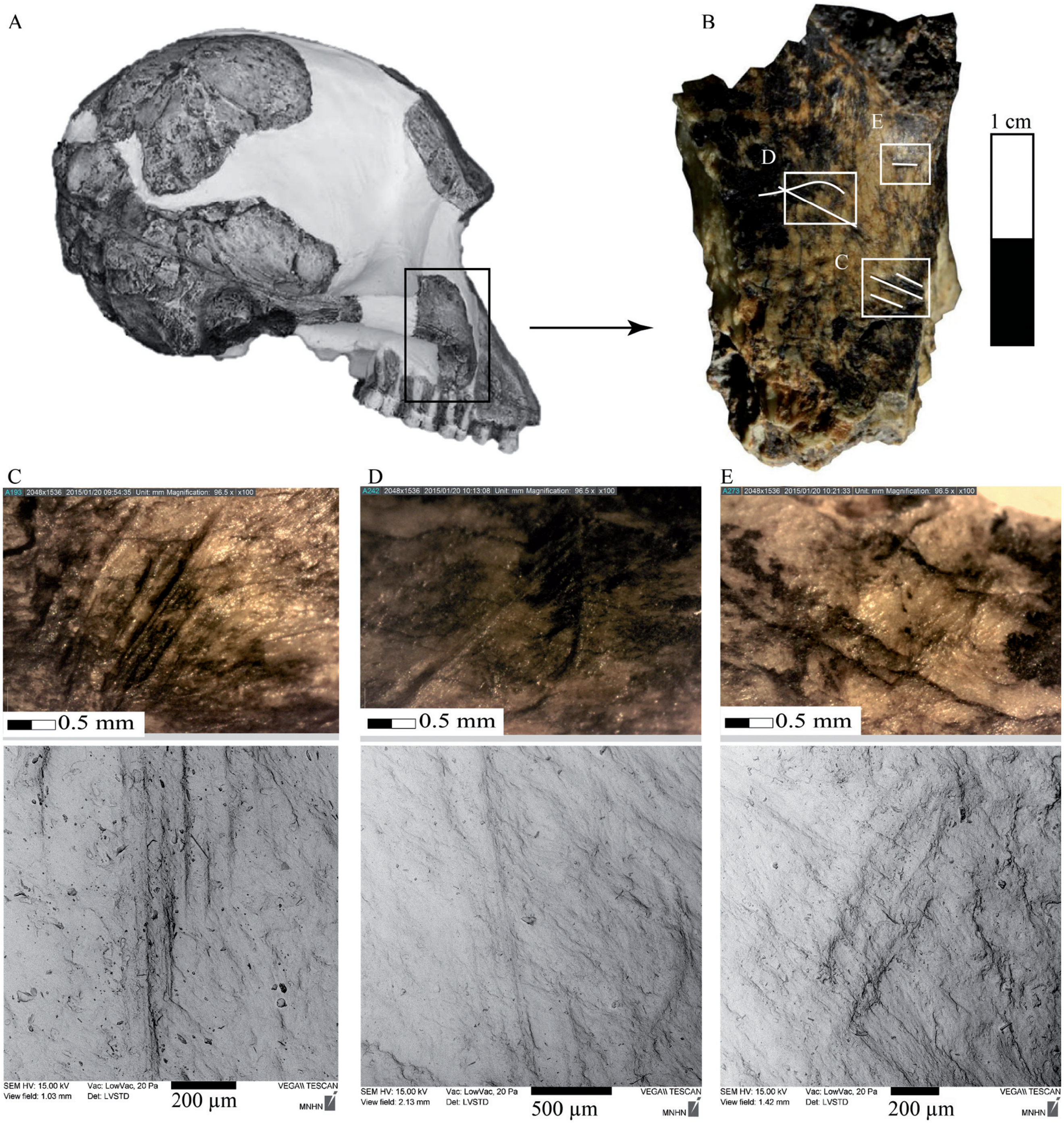


Fig. 1 A: Reconstitution of early Pleistocene hominin cranium Stw53 [15]. B: Stw53c maxillary zygomatic process and location of the 3 sets of linear marks (pictures taken by S. Prat). C: Set I under Dino-Lite and SEM; D: Set II; E: Set III / *Une reconstitution du cranium Stw53, hominine du Pléistocène inférieur* [15]. *B : Processus zygomatique de l'os maxillaire Stw53c et la localisation des trois groupes de marques linéaires* (*photo S. Prat. C : Groupe I sous Dino-Lite et MEB ; D : Groupe II ; E : Groupe III*)

microscope. Using the SEM, we observed three very short striae with a variable cross-section along their length, very irregular and without microstriation or shoulder effect. The marks are less than 3 mm long, less than 1 mm wide and shallow.

No stria was observed on the surface of the right temporal bone belonging to Stw53 specimen, despite microscopic investigation under Dino-Lite.

Experimental trampling in flour did not produce linear marks on bones, despite the presence of sharp-edged

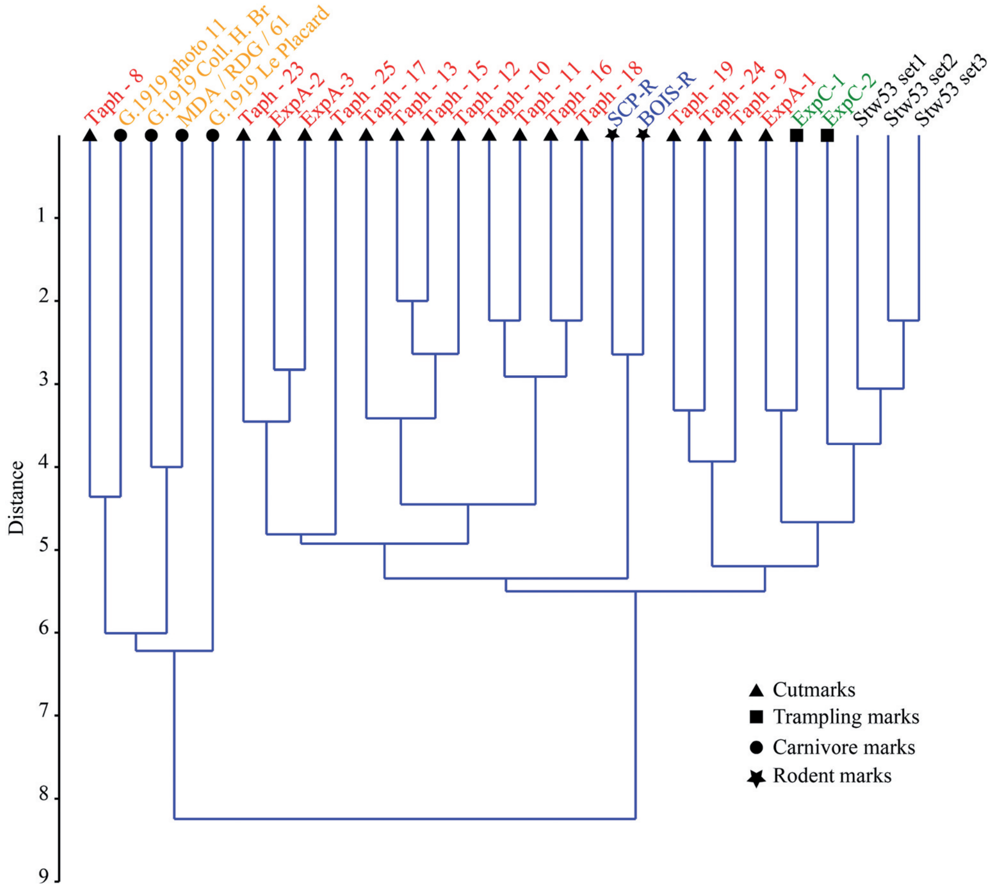


Fig. 2 UPGMA diagram of taphonomic linear marks observed on the Stw53c fossil and comparative bone sample / *Diagramme UPGMA des marques linéaires taphonomiques observées sur le fossile Stw53c et dans l'échantillon de comparaison*

blocks. Flour is probably too fine to bring a strong contact between sharp-edged blocks and bone surface. Concerning the experimental trampling in sand, we observed several of the typical morphological characteristics associated with trampling [mentioned by: 15,28,30] such as a variation of the cross-section, the trajectory and the dimensions of linear marks, although they were produced during one experimental event.

During the butchery experiment, we produced several linear marks with many typical cutmark criteria such as dissymmetric V-shaped cross-section, shoulder effect, flaking and continuous microstriations on groove walls [30]. Trajectories of most striae are straight or oblique relatively to the bone axis.

Hierarchical clusters (Figs 2–4) permit the highlighting of the existence of groups of marks according to their taphonomic agents. We observed that carnivore and rodent marks are grouped together, except for the single linkage method which splits carnivores into two different groups (Fig. 3). There is an overlapping between all cutmarks and one trampling mark (ExpC-2), which could be explained by the presence of microstriations inside the groove, absent in the other trampling mark. Linear marks presented on the Stw53 specimen are linked to one trampling mark.

Four groups were distinguished by multiple correspondence analysis (MCA; Fig. 5). They correspond to the four taphonomic modifications: carnivore, rodent, butchery and trampling processes (Fig. 5). Stw53 marks are closer to trampling marks than to the majority of butchery ones. It seems that a combination of several criteria contributed to the axis F1 and F2. The main factors which contributed to the F1 axis are the straight trajectory of the groove (.06), the absence of internal microstriations (.06) and the position of the marks on the epiphyses (.04). On the contrary, the main contributing factors to the F2 axis are the variable position of the mark (.06), the presence of sinuous microstriation (.04) in the bottom of the groove (.05), the presence of flaking effect (.05) and the high width of the groove (.05).

The morphological variations (in terms of dimensions, trajectory and cross-section) of linear marks, cluster and MCA analyses are all in accordance, showing that Stw53 cranium marks are more similar to experimental trampling (using abrasive sediment and sharp-edged blocks) than to butchery marks.

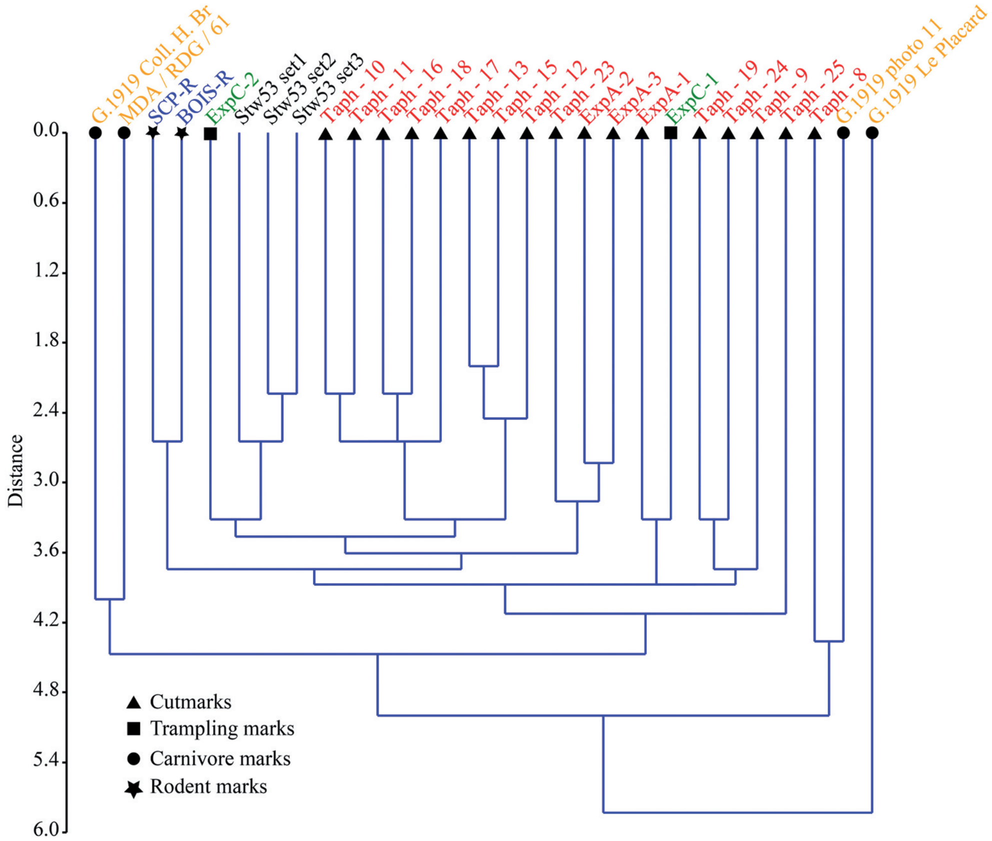


Fig. 3 Single linkage diagram of taphonomic linear marks observed on the Stw53c fossil and comparative bone sample / *Diagramme single linkage des marques linéaires taphonomiques observées sur le fossile Stw53c et dans l'échantillon de comparaison*

Discussion and conclusion

Linear marks are present on the right hominin maxillary zygomatic process (Stw53c) from Sterkfontein as three distinct sets of short striations. Two alternative hypotheses have been proposed to identify the taphonomic agent responsible for them: (1) anthropic [6] or (2) 'produced naturally by a small chert block' [10].

The unintentional abrasion of the bone against sharp-edged blocks by trampling or under sedimentary pressure was rejected by Pickering et al. [6]. They based their argument on: (1) the lack of random striae caused by sedimentary abrasion on all 763 macromammalian fossils associated with Stw53, and on the more exposed surface of the Stw53 specimen; (2) 'the depths, nonrandom orientation, and discrete placements of these sets of striae (i.e. three sets, with different orientations)' [6, p.583]. Nevertheless, it was mentioned that, in the Stw53 breccia faunal assemblage, 'most fragmentation was incurred by geological forces such as sediment compaction and rock fall while the bones were lying on the cave talus slope' [35, p. 111]. This is consistent with Pickering's observations of linear marks on the masseteric fossa of Stw498 mandible [35], an *Australopithecus prometheus* from Member 4, morphologically similar to those on Stw53 [10], and considered to have been 'caused by dynamic contact with the jagged surface of a rock antiquity' and the author adds that 'there is no reason to believe that the marks were inflicted intentionally by stone tool' [35, p. 45]. As Stw 53c was discovered with sharp-edged blocks against it [10], these arguments are not strong enough to reject a non-anthropic origin for the linear marks on Stw53.

The longest mark on Stw53 specimen, which comprises a part of the Set 2, is 3 mm long, and the other marks are less than 3 mm. Cutmarks are generally longer (more than 10 mm) than trampling marks (less than 5 mm) [36,37], except for sinew removal, which can produce shorter cutmarks [33]. Thus, the lengths of linear marks on Stw53c correspond rather to the trampling marks range than to the cutmarks one. However, recent experiments tend to show that the length is not a discriminant criterion for distinguishing cutmarks and trampling marks [38]. Stw53 marks depths are very variable and can correspond, in fact, to a trampling process as well [15,28,29,31]. The location of the marks on the zygomatic process of the maxilla was presented as evidence against the trampling hypothesis [6]. It would not be valid if the bone fragmentation had happened before the

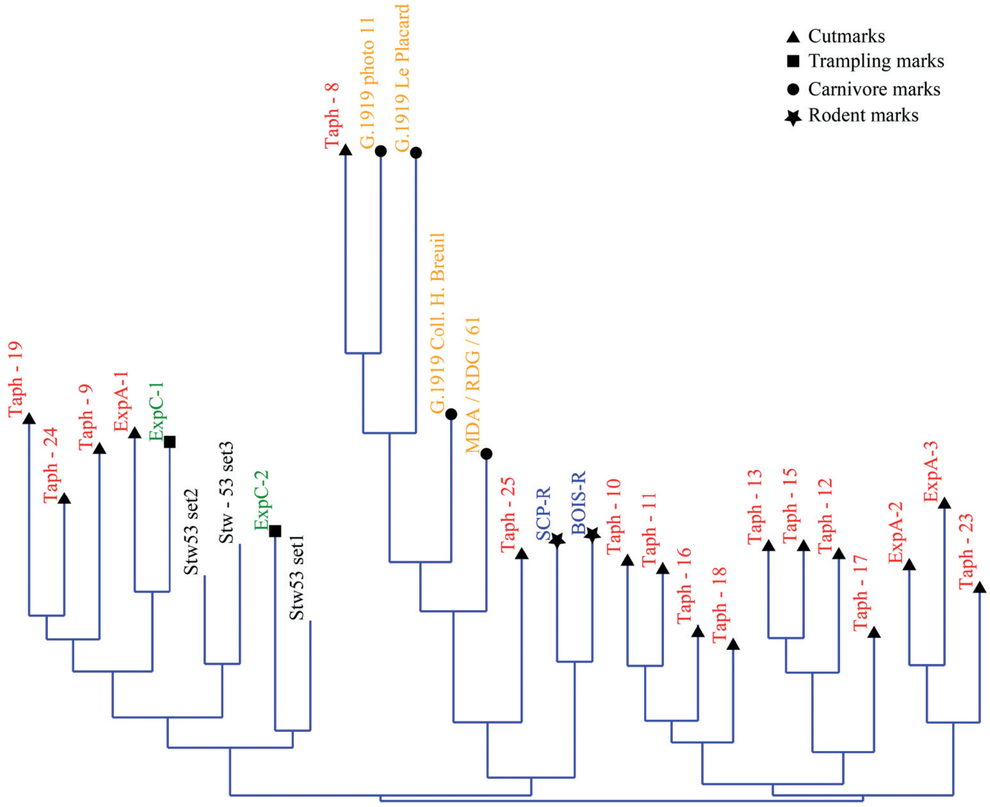


Fig. 4 Neighbour joining diagram of taphonomic linear marks observed on the Stw53c fossil and comparative bone sample / *Diagramme Neighbour Joining des marques linéaires taphonomiques observées sur le fossile Stw53c et dans l'échantillon de comparaison*

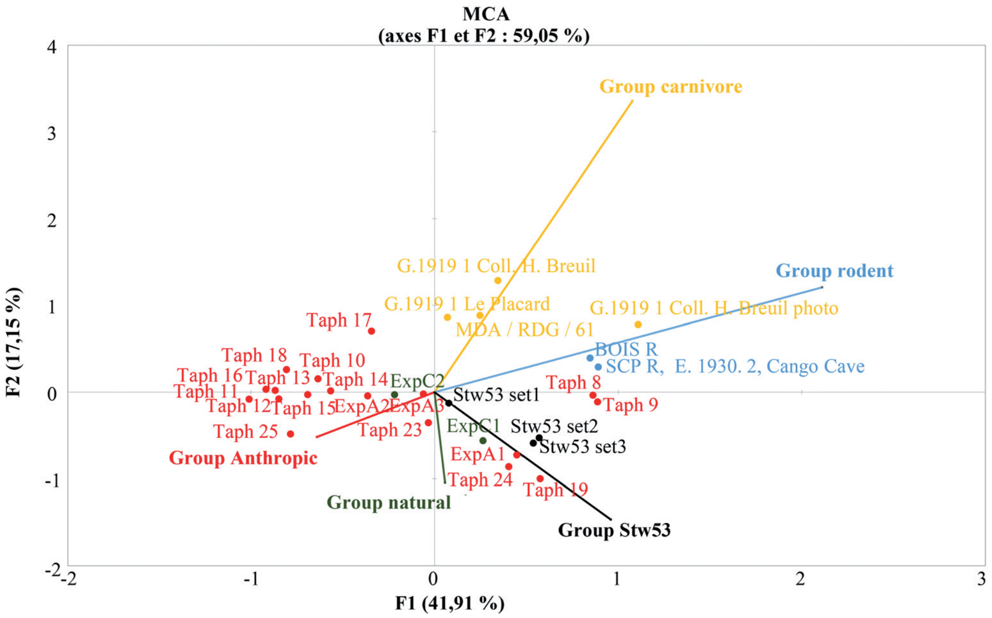


Fig. 5 MCA diagram of taphonomic linear marks on bones observed on the Stw53c fossil and comparative sample / *Diagramme ACM des marques linéaires taphonomiques observées sur le fossile Stw53c et dans l'échantillon de comparaison*

mark occurrence. Furthermore, the calcified breccia context and decalcification process in South African sites, which could alter bone surface, require more careful taphonomic interpretations [39].

We support the hypothesis that a morphological variation of the linear marks (i.e. dimensions, trajectory, cross-section) in one assemblage and/or on one specimen is an accurate indicator of trampling processes [29,31,32]. Our study shows that the morphological variations of linear marks on Stw53c are consistent with a non-anthropic origin.

Moreover, because of the position of the marks on the masseter muscle insertion of the zygomatic maxillary process, we also attempted to observe marks on the temporal bone [40,41]. Thus, the lack of linear marks on the masseter muscle insertion of the temporal bone on the Stw53 specimen does not support the cutmarks hypothesis resulting from disarticulation or defleshing, which can produce similar marks [42,43].

To conclude, based on statistically supported morphological comparisons of macro- and microscopic observations, our results allow us to interpret the linear marks present on the early Pleistocene hominin cranium Stw53 as trampling marks rather than cutmarks modifications. Based on these results, Stw53 would not exhibit the earliest unambiguous evidence of anthropic modifications on hominin remains.

Acknowledgments The authors would like to thank Professor Henry de Lumley (Institut de Paléontologie Humaine), Stéphanie Renault and Carole Vercoutère (Muséum national d'Histoire naturelle) for the authorization to study the comparative material, Bernhard Zipfel and the University of the Witwatersrand to study the Stw53 original specimen, Sylvain Pont and the Service de microscopie électronique à balayage de la direction des Collections of the Muséum national d'Histoire naturelle in Paris for the access to the scanning electron microscope and Adrian Arroyo (UCL) for producing the flakes and sharp-edge blocks. We thank the ANR ARCHOR (ANR-12-CULT-006) for support. We also thank Aurore Val and the second anonymous reviewer for their useful comments.

Conflict of interest: The authors do not have any conflict of interest to declare.

References

1. White TD (1986) Cut marks on the Bodo cranium: a case of prehistoric defleshing. Am J Phys Anthropol 69:503–9
2. White TD, Toth N (1989) Engis: preparation damage, not ancient cutmarks. Am J Phys Anthropol 78:361–7
3. Fernández-Jalvo Y, Díez C, Bermúdez de Castro JM, Carbonell E (1996) Evidence of early cannibalism. Science 271:277–8
4. Fernández-Jalvo Y, Díez C, Cáceres I, Rosell J (1999) Human cannibalism in the early Pleistocene of Europe (Gran Dolina, Sierra de Atapuerca, Burgos, Spain). J Hum Evol 37:591–622
5. Fernández-Jalvo Y, Andrews P (2001) Atapuerca, le conte de deux sites. L'Anthropologie 105:223–36
6. Pickering TR, White TD, Toth N (2000) Brief communication: Cutmarks on a Plio-Pleistocene hominid from Sterkfontein, South Africa. Am J Phys Anthropol 111:579–84
7. Le Mort F (2003) Modifications artificielles et restes humains préhistoriques : signification et interprétations. Revue archéologique de Picardie 21:117–23
8. Carbonell E, Cáceres I, Lozano M, Saladié P, et al (2010) Cultural cannibalism as a paleoeconomic system in the European lower Pleitocene. Curr Anthropol 51:539–49
9. Clarke RJ (2012) A brief review of history and results of 40 years of Sterkfontein excavations. In: Reynolds S, Gallagher A (eds) African genesis: perspectives on hominin evolution. Cambridge University Press, Cambridge, pp 120–43
10. Clarke RJ (2013) Australopithecus from Sterkfontein caves, South Africa. In: Reed KE, Fleagle JG, Leakey RE (eds) The paleobiology of Australopithecus. Springer, Dordrecht, pp 105–23
11. Bello SM, Wallduck R, Dimitrijević V, Živaljević I, et al (2016) Cannibalism versus funerary defleshing and disarticulation after a period of decay: comparisons of bone modifications from four prehistoric sites. Am J Phys Anthropol 161:722–43
12. Shipman P, Potts R (1981) Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania. Nature 291:577–80
13. Behrensmeyer AK, Gordon KD, Yanagi GT (1986) Trampling as a cause of bone surface damage and pseudo-cutmarks. Nature 319:768–71
14. Behrensmeyer AK, Gordon KD, Yanagi GT (1989) Nonhuman bone modification in Miocene fossils from Pakistan. In: Bonnichsen R, Sorg MH (eds) Bone modification. University of Maine Center for the Study of the First Americans, Orono, pp 99–120
15. Njau JK, Blumenschine RJ (2006) A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai Basin, Tanzania. J Hum Evol 50:142–62
16. McPherron SP, Alemseged Z, Marean CW, et al (2010) Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. Nature 466:857–60
17. Dominguez-Rodrigo M, Pickering TR, Bunn HT (2010) Configurational approach to identifying the earliest hominin butchers. PNAS 107:20929–34
18. Thompson JC, McPherron SP, Bobe R, et al (2015) Taphonomy of fossils from the hominin-bearing deposits at Dikika, Ethiopia. J Hum Evol 86:112–35
19. Sahle Y, El Zaatari S, White TD (2017) Hominid butchers and biting crocodiles in the African Plio-Pleistocene. PNAS, doi: 10.1073/pnas.1716317114
20. Hughes A, Tobias P (1977) A fossil skull probably of the genus Homo from Sterkfontein, Transvaal. Nature 265:310–2
21. Kuman K, Clarke RJ (2000) Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. J Hum Evol 38:827–47
22. Schwarcz HP, Grün R, Tobias PV (1994) ESR dating studies of the australopithecine site of Sterkfontein, South Africa. J Hum Evol 26:175–81
23. Herries AIR, Shaw J (2011) Palaeomagnetic analysis of the Sterkfontein palaeocave deposits: implications for the age of the hominin fossils and stone tool industries. J Hum Evol 60:523–39
24. Prat S (2004) Les premiers représentants du genre Homo, en quête d'une identité. Apports de l'étude morphologique et de l'analyse cladistique. BMSAP 16:7–35

25. Curnoe D, Tobias PV (2006) Description, new reconstruction, comparative anatomy, and classification of the Sterkfontein Stw53 cranium, with discussions about the taxonomy of other southern African early Homo remains. J Hum Evol 50:36–7
26. Curnoe D (2010) A review of early Homo in southern Africa focusing on cranial, mandibular and dental remains, with the description of a new species (*Homo gautengensis* sp. nov.). Homo 61:151–77
27. Pickering TR (2013) Rough and tumble: aggression, hunting, and human Evolution. University of California Press, Los Angeles, 208 p
28. Olsen S, Shipman P (1988) Surface modification on bone: Trampling versus butchery. J Archaeol Sci 15:535–53
29. Fischer JW (1995) Bone surface modifications in zooarchaeology. J Archaeol Method Theory 2:7–68
30. Domínguez-Rodrigo M, de Juana S, Galan AB, Rodríguez M (2009) A new protocol to differentiate trampling marks from butchery cut marks. J Archaeol Sci 36:2643–54
31. Andrews P, Cook J (1985) Natural modifications to bones in a temperate setting. Man 20:675–91
32. Patou-Mathis M (2002) Retouchoirs, compresseurs, percuteurs… Os à impressions et éraillures, Cahier X. Éditions Société préhistorique française, Paris, 136 p
33. Valensi P (1991) Étude des stries de boucherie sur les ossements de cerf élaphe des niveaux supérieurs de la grotte du Lazaret (Nice, Alpes-Maritimes). L'Anthropologie 95:797–830
34. Andrews P, Fernández-Jalvo Y (2012) How to approach perimortem injury and other modifications. In: Bell LS (ed) Forensic microscopy for skeletal tissues: Methods and protocols. Human Press, Totowa, NJ, 191–225
35. Pickering TR (1999) Taphonomic interpretations of the Sterkfontein early hominid site (Gauteng, South Africa) reconsidered in light of recent evidence. PhD dissertation, Department of Anthropology, University of Wisconsin, Madison, 557 p
36. Monnier GF, Bischoff E (2014) Size matters: An evaluation of descriptive and metric criteria for identifying cut marks made by unmodified rocks during butchery. J Archaeol Sci 50:305–17
37. Fernández-jalvo Y, Andrews P (2016) Atlas of taphonomic identifications. Springer Netherlands, 359 p
38. Orlikoff ER, Keevil TL, Pante MC (2017) A quantitative assessment of templing-induced modification to bone surfaces. Poster conference: Paleoanthropology Society
39. Val A, Stratford DJ (2015) The macrovertebrate fossil assemblage from the Name Chamber, Sterkfontein: taxonomy, taphonomy and implications for site formation processes. Palaeontol Afr 50:1–17
40. Villa P, Bouvill C, Courtin J, et al (1986) Cannibalism in the Neolithic. Science 233:431–7
41. Pérez VR (2012) The taphonomy of violence: recognizing variation in disarticulated skeletal assemblages. IJPP 2:156–65
42. Nilssen P (2000) An actualistic butchery study in South Africa and its implications for reconstructing hominid strategies of carcass acquisition and butchery in the Upper Pleistocene and Plio-Pleistocene. PhD Thesis, University of Cape Town 649 p
43. Soulier MC, Costamagno S (2017) Let the cutmarks speak! Experimental butchery to reconstruct carcass processing. J Arch Sci Reports 11:782–802

BMSAP (2018) 30:59-69
DOI 10.3166/bmsap-2018-0006

ARTICLE / *ARTICLE*

Large Body Size as a Socially Valued Factor Determining Excess Weight and Obesity in the Context of the Nutritional Transition in Senegal

La valorisation sociale de l'embonpoint comme déterminant du surpoids et de l'obésité dans un contexte de transition nutritionnelle au Sénégal

E. Cohen · A. Ndao · B. Faye · S. Ndiaye · E.H.M. Ndiaye · G. Ezan · L. Gueye · G. Boëtsch · P. Pasquet · N. Chapuis-Lucciani

Received: 18 April 2017; Accepted: 06 November 2017

Abstract Like most African countries, Senegal is experiencing a nutritional transition. Global drivers of sedentary behavior and high-calorie dietary intake, together with local anthropological drivers of large body size as a socially valued characteristic could be exposing the population to obesity. This study therefore set out to assess the impact of this sociocultural factor on the nutritional status of Senegalese adults. We set up 14 focus groups (*n*=84 participants) and a cross-sectional quantitative survey (*n*=313 women; *n*=284 men) of adults in three different socio-ecological areas in Senegal (rural: *n*=204; suburban: *n*=206; urban: *n*=187). We also assessed perceptions of body weight (Body Size Scale) and weight status (anthropometric measures). Middle-aged and older Senegalese people value excess weight more than younger Senegalese in all the areas studied. Being female, older, living in urban/suburban areas and valuing excess weight/obesity were independently associated with being overweight/obese. A higher socio-economic status was also associated with being overweight/obese. A nutritional transition is under way in Senegal in urban/suburban areas, particularly affecting older urban women, with specific cultural factors contributing to this phenomenon. This suggests a need for local measures targeting women and is accounted for by specific anthropological characteristics in the Senegalese population.

Keywords Senegal · Excess weight · Obesity · Body image · Determining factors

Résumé Le Sénégal fait face à la transition nutritionnelle car des facteurs globaux tels que la sédentarité et l'alimentation calorique, et des facteurs locaux d'ordre anthropologique comme la valorisation sociale de l'embonpoint, peuvent exposer la population à l'obésité. L'objectif de cette étude est d'évaluer l'impact de ce facteur socioculturel sur le statut nutritionnel des adultes sénégalais. Nous avons mené 14 focus-groups (*n*=84 participants) et une étude quantitative transversale (*n*=313 femmes ; *n*=284 hommes) auprès d'adultes vivant dans trois milieux socio-écologiques au Sénégal (rural : *n*=204 ; périurbain : *n*=206 ; urbain : *n*=187). Nous avons aussi mesuré les perceptions du volume corporel (Body Size Scale) et évalué la catégorie staturo-pondérale des individus. Les femmes d'âge mûr et âgées

---

E. Cohen (✉) · L. Gueye · G. Boëtsch · N. Chapuis-Lucciani
CNRS, UMI 3189 « environnement, santé, sociétés »,
faculté de médecine, UCAD, BP 5005, Dakar-Fann, Sénégal
e-mail : emmcohen@outlook.fr

E. Cohen
MRC/Wits Developmental Pathways for Health Research Unit,
Department of Paediatrics, Faculty of Health Sciences,
University of the Witwatersrand, 7 York Road, Parktown,
Johannesburg 2193, South Africa

A. Ndao
CNRS, UMR 8177, IIAC-LAIOS,
École des hautes études en sciences sociales (EHESS),
190-198, avenue de France, F-75244 Paris cedex 13, France

Raum IG 551, Norbert-Wollheim-Platz 1,
university of Frankfurt am Main,
institute of ethnology, DE-60629 Frankfurt/Main, Germany

B. Faye · S. Ndiaye
Département de sociologie, faculté de lettre, UCAD,
BP 5005, Dakar-Fann, Sénégal

E.H.M. Ndiaye · G. Ezan
Laboratoire de physiologie et d'exploration fonctionnelle,
faculté de médecine, UCAD, BP 5005, Dakar-Fann, Sénégal

P. Pasquet
CNRS, UMR-MNHN 7206 « Éco-anthropologie
et ethnobiologie », muséum national d'histoire naturelle,
musée de l'homme, 17, place du Trocadéro,
F-75116 Paris, France

sénégalaises valorisaient davantage le surpoids que les jeunes sénégalais dans les trois zones investiguées. De plus, être femme, plus âgé, urbain/ périurbain et valoriser le surpoids étaient des facteurs indépendamment associés à la surcharge pondérale. Enfin, le haut niveau socioéconomique était aussi associé à cette surcharge. La transition nutritionnelle en cours au Sénégal dans les zones urbanisées affecte surtout les femmes matures par des facteurs culturels spécifiques contribuant au développement de ce phénomène. Des interventions locales envers celles-ci sont donc nécessaires, en tenant compte des spécificités anthropologiques du pays.

Mots clés Sénégal · Surpoids · Obésité · Image du corps · Déterminants

Introduction

Obesity has become a global public health challenge, which is now reaching pandemic proportions [1]. High income countries (HICs) were the first to experience the phenomenon of rising obesity. Low and middle income countries (LMICs) are now facing a similar but faster process of nutritional transition [2] involving rapid short-term adaptive strategies potentially causing obesity [3,4]. African populations are experiencing increasing levels of obesity [5,6] that may exceed even those found in some HICs [7].

Growing urbanization, rural exodus and increasing internal migration in most African countries have exposed new migrants to non-communicable diseases [8]. In addition, rural migrants bring with them a sociocultural preference for stoutness (excess weight/obesity), which is not always suited to the urban ecosystem [9]. Accordingly, body fat is increasingly valued socially [10,11] and becoming a risk factor of excess weight/obesity in Africa [12,13]. The fact that a large body size involving a high-calorie diet [14,15] and low physical activity is socially valued [16,17] could therefore be considered as a biocultural determinant of excess weight/obesity [18], especially in African populations [19,20].

The social value of large body size had been identified several decades ago in African traditional societies [21], and still persists today despite the influence of modern lifestyles. Several studies conducted recently in Cameroon, Nigeria and Ghana [12,22,23] have brought evidence of the social value attached to excess weight, especially among middle-aged and elderly subjects, which could raise serious public health issues in the context of urbanization and the nutritional transition across the continent. Historically, a large body size became socially valued in preindustrial societies in which weight gain could have been an advantage in a context of recurrent periodic shortages [9,24]. However, in the context of mass industrialization and easy access to processed high-calorie food, as in Western societies, thinness, and even emaciation in extreme cases, has become the social norm while stoutness is negatively perceived [25].

This study focuses on Senegal in West Africa, where little research has been attempted to assess the determinants of excess weight/obesity in perceptions of body size [26]. However, a nutritional transition is under way in this region [27,28] with intensifying urbanization together with internal migration [29]. As a result, overweight/obesity has become prevalent in urban areas, where the lifestyle has become obesogenic with the development of transport and cheap processed high-calorie foods [30] that affordable to working class people living in poor urban neighborhoods [31–33]. Twenty-five years ago, the prevalence of excess weight and obesity was 16.3% and 6.1%, respectively, among women living in Pikine [28], a peripheral working-class neighborhood of Dakar. Fifteen years later, in a similar sample, the figures had risen to 26.6% and 18.6% [34]. The overall prevalence of excess weight and obesity among women in Dakar as a whole was recently found to be 24.5% and 16.5% [35], a trend similar to that found in France [36].

While the industrialization of the greater Dakar area could expose its populations to obesity, this could be compounded by obesogenic body weight norms, since a large body size is valued by women living in the peripheral neighborhoods of Dakar [34,37], who therefore deliberately seek to gain weight. In the traditional view of body size in Senegal, particularly in the Wolof region, stoutness in women symbolizes a peaceful and wealthy household [38]; this has persisted with the current rural exodus [39], with the result that processed, high-calorie foods are highly valued among low socio-economic status (SES) populations in Dakar [14,15]. An anthropological investigation of the development of obesity in Senegal could identify how a sociocultural factor – body image – might be exposing the population to obesity and related diseases. This study therefore investigated the impact of valuing large body size on the nutritional status of Senegalese adults in the context of the nutritional transition from a rural to an urban/suburban context in Dakar.

To do so, we compared two specific and contrasting geographical areas: the Dakar urban area (city center and suburbs) and a rural area in the Wolof region (three villages in the Kaolack region: Diamaguene, Keur Ndary Ndiaye and Gandiaye), where the socio-economic conditions of the inhabitants are among the poorest in the country [40]. Using this framework, we conducted (i) a qualitative study to identify body weight norms and (ii) a quantitative study to assess the value attached to stoutness, in relation with (iii) anthropometric measurements. Overall, the results from these integrated analyses facilitated comparisons between the cultural reality of Senegalese adults and their nutritional health status.

Materials and Methods

Qualitative study

Study design

This analysis aimed to define the sociocultural determinants of excess weight/obesity by (i) describing the different vernacular conceptions associated with body weight: fertility, power, well-being, good health and beauty [11] and (ii) detecting a potential acculturation process driven by the influence of modern lifestyles on these body weight norms. This phase was also instrumental to the completion of the quantitative study, since the variables tested by our measurement tools (Body Size Scale [BSS] and questionnaire) cannot be isolated from their sociocultural context.

Sampling and process

To determine these local norms and identify how they are influenced by the modern lifestyle, a qualitative study using focus groups explored local representations of excess weight/obesity determinants in depth [41]. Fourteen focus group discussions were held, with six participants per group recruited from different neighborhoods in the two study areas according to three criteria: age (< 25 years, > 45 years); sex and educational level (< high school level: low education, ≥ high school level: high education) or, if necessary, occupational category (low occupational level, e.g. manual trades, small traders; high occupational level, e.g. senior executive level, healthcare professional). The sample presented a balanced sex ratio and all the participants were Wolof speakers. The focus group discussions were held within the neighborhoods so that participants could express themselves in a familiar context without outside pressure, and recorded with a handheld recorder. The focus group discussions (and all other methods) were conducted in Wolof, the participants' vernacular language, then transcribed and translated into French.

Quantitative survey

Perceptions of corpulence

To accurately assess body perceptions and identify the social value potentially attributed to excess weight/obesity, we used a BSS. This validated tool presents photographs of real human body sizes for both sexes, covering the entire gradient of the body mass index (BMI) [42]. We then built up a body image assessment guide (BIAG) to compare local Senegalese norms with scientific body weight norms measured by the BSS, as in one of our previous studies [43]. The BIAG consists of three questions about current body size (CBS), desired body size (DBS) and ideal body size (IBS) for oneself and for one's partner (for polygamous households, we included the first wife only). We compared the responses of participants living in urban, suburban and rural areas to assess possible changes in corpulence norms with the urbanization process. In addition, an *index of social value attached to excess weight/obesity* was constructed from the BSS to accurately assess the desire to gain weight.

Perceptions of nutritional health status

Using the BSS, a *body self-satisfaction index* was calculated to identify subjects as satisfied with their body weight, wanting to gain weight or wanting to lose weight. This BSS index was compared with BMI categories to assess the accuracy of perceived body weight.

Anthropometry

A series of anthropometric measurements was taken by trained fieldworkers, using standardized procedures [44]. Height was measured to the nearest millimeter using a portable stadiometer (Siber Hegner, Zurich, Switzerland). Weight was measured, in very light clothing, to the nearest 100 g, using a digital beam scale (Tanita, Tokyo, Japan). This anthropometric protocol allowed us to assess the nutritional status of each respondent.

Samples. We assembled one sample in the Dakar urban area (city center and suburbs) of 393 adults (200 men/193 women; 187 urban and 206 suburban subjects) and one sample of 204 adults in the Kaolack region (84 men/120 women). For both areas, we used a quota sampling strategy, according to three criteria (age, sex and neighborhood) from the 2002 National Senegalese Census. In the Dakar urban area, participants were selected from all parts of the city and its peripheral region (e.g. Sacré Coeur, Cambérène). Rural subjects were strictly inhabitants of the three villages indicated above. Pregnant women were not included in the sample in order to collect reliable biological and cultural data.

Data analysis

Main analyses

For the qualitative study, analyses were performed from thematic groupings to identify relevant themes that emerged for each potential determinant of obesity [45]. After identifying the main themes, we summarized the main information from each theme and compared the social representations and practices related to these in our three subsamples.

For the quantitative study, we used the ANOVA, ANCOVA, *t*-test, chi^2 and Fisher exact tests to assess anthropometric characteristics, body size standards and prevalence of excess weight/obesity. The average comparisons between CBS and DBS/IBS were done with paired *t*-tests.

Socio-economic status

A proxy index of household wealth was constructed using principal component analysis (PCA) of a set of variables: e.g. owner/tenant, type of house, car/truck, mobile phone, electricity. In the total sample, the first principal component explained 40.1% of the variance with an eigenvalue of 19.7 (5.3% for the second principal component). Households were classified into three distinct groups: "low," "middle" and "high" SES according to terciles of the variable calculated from the first principal component.

Body image. The BSS was treated as a metric value, with each photograph of humans scoring 1–9 according to increasing BMI categories. The *index of social value attached to excess weight/obesity* was constructed as follows: 4 − DBS; since the fifth silhouette on the scale corresponds to excess weight/obesity. The *body self-satisfaction index* was then calculated by subtracting the CBS and DBS (CBS−DBS) [46].

Relationships between beliefs, practices and body weight

The relationships (adjusted odds ratios, 95% confidence intervals) between excess weight/obesity and their possible determinants (sex, age, area of residence, proxy index of household wealth, educational level, index of social value attributed to excess weight/obesity) were assessed with a binary logistic regression model.

For the qualitative analyses, we used NVivo 7 software (QSR International, Melbourne, Australia) to synthesize the main focus group outcomes. For the quantitative analyses we used Statistica 7 software (Statsoft Inc, Tulsa, OK, USA) to produce descriptive statistics and PCA(s), and MyStat 12 software (Systat Software Inc, San Jose, CA, USA) for the logistic regression. Finally, equal weight was assigned to the qualitative and quantitative approaches in the interpretation of our findings.

Results

Qualitative study

Traditional value of large body size

Stoutness is traditionally perceived as a sign of wealth and prosperity in the household. Excess weight is associated with strength, good physical and mental health and vitality. Stoutness represents fertility in women and their ability to maintain a peaceful atmosphere in their household, and in men their ability to support their family.

> *"In principle, ngande [being fat], this is not a disease in our culture. The opposite, tuuti [being small], is a disease here because am yaram [being fat] is really important, especially for women. A big body shows that you have a good life. People consider that if you are not am yaram, it is because you are not well in your life. You have problems, you do not have peace of mind [xel mu dal]. For you and your family, nothing works. For us, body weight reflects economic status." [Older urban woman, high SES]*
>
> *"The man, he has to be a boss. But being a boss at work, in the neighbourhood or at home is not the same. At work, he must command, he must exert his power; at home, he demonstrates his power. This is the birru patron [chicken belly]. This is the belly that shows you eat a lot of chicken." [Younger rural man, low level of education]*

Urbanization and the value of large body size

The development of urban areas in Senegal implies an ideal conception of the modern lifestyle, where success is seen as possible for rural and migrant populations who idealize Western culture. Integrating into an urban lifestyle is associated with weight gain, which is rare in the village context, as a symbol of integration into the city, of doing well from its abundance. But in rural areas, only moderate corpulence is valued, since being very fat is not suited to rural labor. Therefore, the social value of stoutness has increased with the emergence of the modern lifestyle, seen as a symbol of wealth and prosperity, especially in middle-aged and older married women with a lower SES.

> *"Nowadays, women want to gain weight. Before, it was not like this. Now, a woman who is not fat tries to put on weight, for instance by using medication (corticosteroids). This is very dangerous. You put on weight very quickly; but later your face and the rest of your body become deformed. And these women want to be beautiful… [dieekk: a stout married woman who is content in her household]." [Older rural woman, high SES]*
>
> *"Women today, especially married women; most of them do not want to be tuuti [thin]. Sometimes, you see a tuuti [slim] woman, and people say that she is HIV positive or has many problems in her life. People say a lot of nonsense about her. This is why tuuti women take medications to put on weight." [Younger rural woman, high educational level]*

Competition in the household

With migration to the city and excess weight becoming overvalued, middle-aged and older married women compete to demonstrate their well-being and the success of their husband and household to others. This competitive atmosphere can be found outside the home, but particularly between co-wives in the household.

> *"If you are a co-wife and you are wow [thin], your co-wife will tend to give you the evil eye. If you have an argument with her, she will always have something bad to say to you, by criticising your thinness. To her, you are skinny. This will hurt you. That's why to find a way out, you will be looking for medication to become ngande [fat] yourself." [Younger rural woman, high educational level]*
>
> *"Even though we know the serious consequences of taking medication to put on weight, a jealous co-wife will want to put on weight to rival another co-wife and stop her from criticising her as not a real woman." [Younger rural man, low educational level]*

How female stoutness is valued

Gaining weight during marriage is important and particularly expected in women, since an overweight woman is a symbol of her husband's wealth through economic success. Therefore, there is more social pressure on women to become fat, as their weight is the symbol of household prosperity.

> *"We don't like wow [thin] people, especially women. It is better to be wow [thin] for a man than a woman. If you say to a women that she is wow [thin], she will be angry with you all the rest of her life. She wants to be am yaram [fat]." [Older urban man, low SES]*
>
> *"The woman should gain weight. When a woman is wow [thin], people say that her husband will soon be looking for a co-wife." [Younger urban woman, low educational level]*

Acculturation of young people

Nevertheless, with the influence of western media and medical discourse, young people are beginning question the social value of a large body size. Some educated urban women devalue stoutness to the point of becoming "obesophobic":

> *"Most series, like Telenovelas, are set on beaches where young women have beautiful bodies. Now with the summer arriving, young Senegalese women also want to have a beautiful body. They all start dieting so they can wear their two-piece bathing suits on the beach." [Younger urban woman, high educational level]*
>
> *"Now there's the sports ground phenomenon. The young men go to the beach to train. They go just to build up their muscles. They don't have money so they work on their appearance." [Younger urban man, low educational level]*

Quantitative survey

Sociodemographic characteristics

The sex ratio for the urban and suburban samples was approximately even, while women were moderately over-represented in the three rural samples, with about one quarter of the subjects over 45 years of age. Most urban and suburban subjects had at least attended primary school and had electricity at home, whereas almost half of the rural subjects had never been to school and the majority did not have electricity. Finally, we observed an over-representation of both second- and third-generation migrants in the urban and suburban samples (Table 1).

Perceptions of corpulence

Concerning men's perceptions (Fig. 1), all groups considered themselves to be in the normal weight category. The desire to become overweight was significant only in the urban and rural groups (CBS *vs* DBS: $p < 0.01$ and $p < 0.001$), and slight in the suburban group. Overall, the participants in the three groups selected DBS and IBS in the normal weight category. The suburban group had the lowest DBS and IBS averages and the highest CBS average. There was no significant difference between CBS and IBS in this group, unlike the two others, which had a higher IBS than CBS (urban: $p < 0.001$, rural: $p < 0.001$) (Fig. 1).

Concerning women's perceptions (Fig. 2), the urban and suburban groups saw themselves on the lower threshold of excess weight whereas rural women considered themselves to be in the normal weight category ($p < 0.001$) and wanted to gain weight ($p < 0.001$). The IBS averages were on the lower threshold of excess weight, except for rural women who clearly preferred the overweight category ($p < 0.001$) with an IBS significantly higher than DBS ($p < 0.05$) and CBS ($p < 0.001$) (Fig. 2).

Anthropometry

Excess weight and obesity in the total sample were more prevalent in the urban and suburban areas (Table 2).

Table 1 Sociodemographic characteristics of the three samples / *Caractéristiques démographiques des trois échantillons*

	Urban area		**Suburban area**		**Rural area**	
Sex						
	N	**%**	***N***	**%**	***N***	**%**
Men	96	51.3	104	50.5	84	41.2
Women	91	48.7	102	49.5	120	58.8
Age						
	N	**%**	***N***	**%**	***N***	**%**
[18–25]	49	26.2	60	29.1	65	31.9
[26–45]	92	49.2	95	46.1	84	41.2
≥46	46	24.6	51	24.8	55	27.0
Education						
	N	**%**	***N***	**%**	***N***	**%**
University	24	12.8	18	8.7	4	2.0
High school	18	9.6	20	9.7	13	6.4
Secondary school	44	23.5	43	20.9	40	19.6
Primary school	61	32.6	68	33.0	46	22.5
Koranic school	1	0.5	1	0.49	0	0.0
None	39	20.9	56	27.2	101	49.5
Socio-economic status						
	N	**%**	***N***	**%**	***N***	**%**
Family house	185	98.9	200	97.1	3	1.5
No data	2	1.1	4	1.9	9	4.4
Tap water	172	92.0	199	96.6	3	1.5
No data	6	3.2	6	2.9	11	5.4
Electricity	179	95.7	200	97.1	3	1.5
No data	1	0.5	0	0.0	13	6.4
Migration status						
	N	**%**	***N***	**%**		
1st generation	35	18.7	49	23.8	N/A	N/A
2nd generation	82	43.9	99	48.1	N/A	N/A
3rd generation	68	36.4	57	27.7	N/A	N/A
No data	2	1.07	1	0.5		

N/A: Not Applicable

Perceptions of nutritional health status

The majority of overweight subjects were not able to identify their nutritional status. Almost half of the overweight subjects (48.7%) and more than half of the obese subjects (57.5%) were satisfied with their body weight (Table 3). Using the *index of social value attached to excess weight/obesity*, we observed that the majority of subjects who valued excess weight/obesity were women (urban men/women: 41.8 vs 58.0%, $p < 0.05$; suburban men/women: 35.7 vs 55.7%, $p < 0.01$; rural men/women: 52.6 vs 62.7%, NS). In women only, we observed that the DBS was significantly higher in the > 25-year-old age group (women: 5.2 ± 1.8 vs 4.5 ± 1.7, $p < 0.01$; men: 4.3 ± 1.6 vs 4.3 ± 1.7) (Table 3).

Analysis of excess weight/obesity determinants

The comparison of overweight/obese (≥ 25 kg/m^2) with non-overweight subjects, using binary logistic regression analysis (Table 4), showed independent effects of gender, age, living area and the value given to excess weight/obesity. Finally, univariate analyses showed that a high SES was more likely to be associated with being overweight/obese ($p < 0.05$) (Table 4).

Discussion

This study investigated a specific biocultural determinant of obesity – the value attached to large body size – in the context

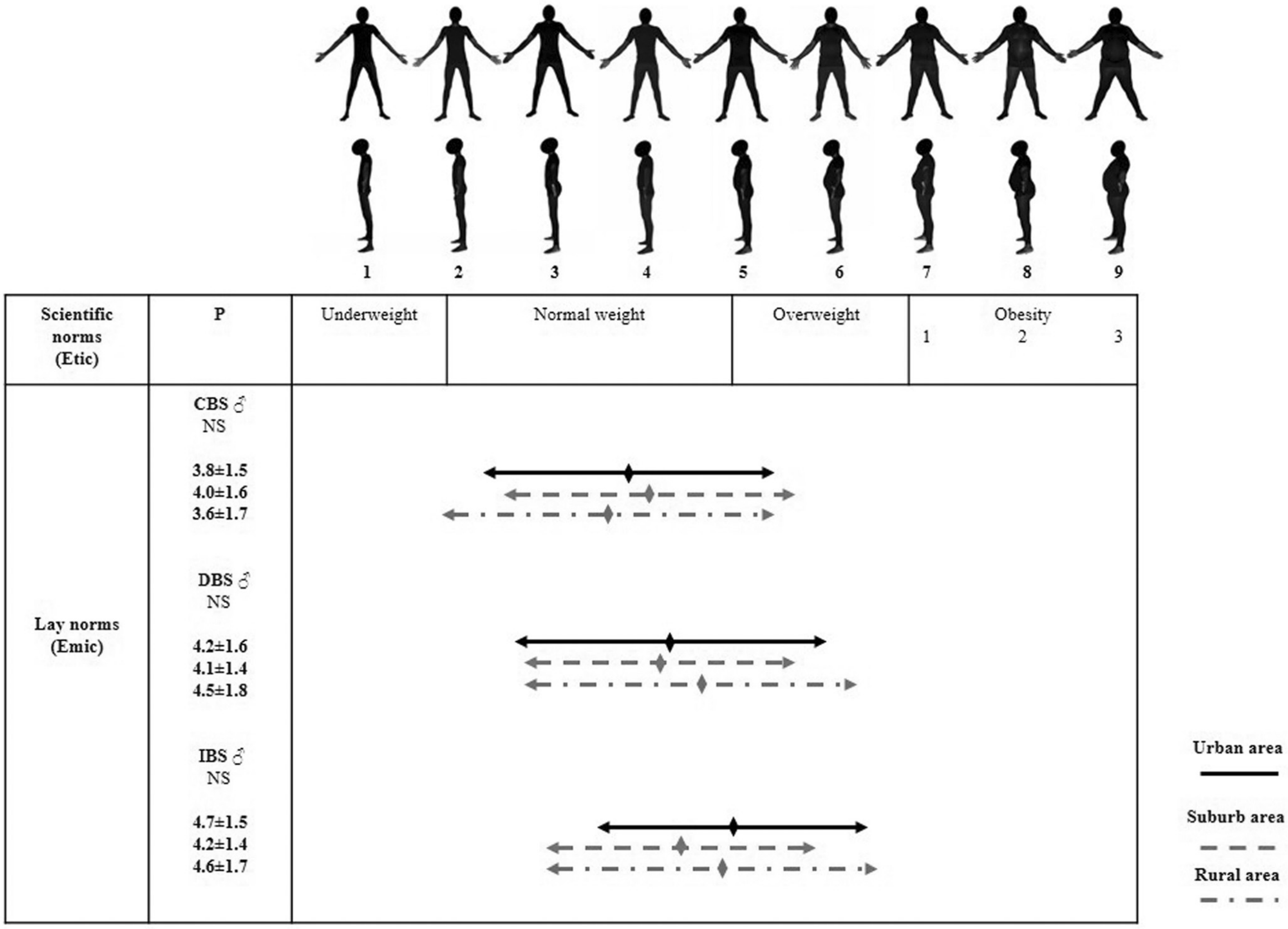


Fig. 1 Perceptions of body size for male BSS. CBS: Current body size, DBS: Desired body size, IBS: Ideal body size. NS: Not significant / *Perceptions du volume corporel sur la planche masculine BSS. CBS :* Current Body Size *(volume corporel actuel), DBS :* Desired body size *(volume corporel désiré), IBS :* Ideal body size *(volume corporel idéal). NS :* not significant *(Non significatif)*

of the nutritional transition in Senegal. Overall, we observed that our study population experienced health consequences from this change in lifestyle where there was a higher degree of urbanization. More precisely, this was associated with a dynamic socio-ecological obesogenic context, through internal migration from a rural area (Kaolack region) to an urban area (Dakar). Senegalese people who have settled in suburban and urban areas have higher rates of excess weight and obesity, with several determinants acting in different ways influencing the spread of excess weight/obesity, as has been observed in other migrant populations in urban areas of LMICs and HICs [47]. The nutritional transition seems to be under way among urban/suburban Senegalese women with a mean BMI of ~25 kg/m^2, a tendency already recently observed in Dakar [35]. This suggests that women are more sensitive to the obesogenic effects of the nutritional transition that accompanies an urban lifestyle [48], as in most LMICs [49], and that this is exacerbated by the value they attach to excess weight/obesity.

Nevertheless, despite the social value attached to excess weight/obesity in traditional Senegalese culture, accentuated by the current portrayal of Dakar as an Eldorado (based on our qualitative study), the value attached to excess weight/obesity seems to be decreasing overall in Dakar (urban/suburban areas), particularly among young women, even though women initially desired a higher average body size than men. Senegalese people seem to be adapting their body size norms to the obesogenic urban environment and to modern perceptions of body size, like other African populations [50,51], since the younger generations, unlike older people, are no longer valuing excess weight/obesity [52]. This is happening to such an extent among young Senegalese people exposed to Western media and medical discourse that some are beginning to develop the first symptoms of anorexia nervosa and body dysmorphic disorder, according to the literature on African urban youth [38,53,54]. Thus, the desire to lose weight observed in many subjects of normal weight might be linked to the

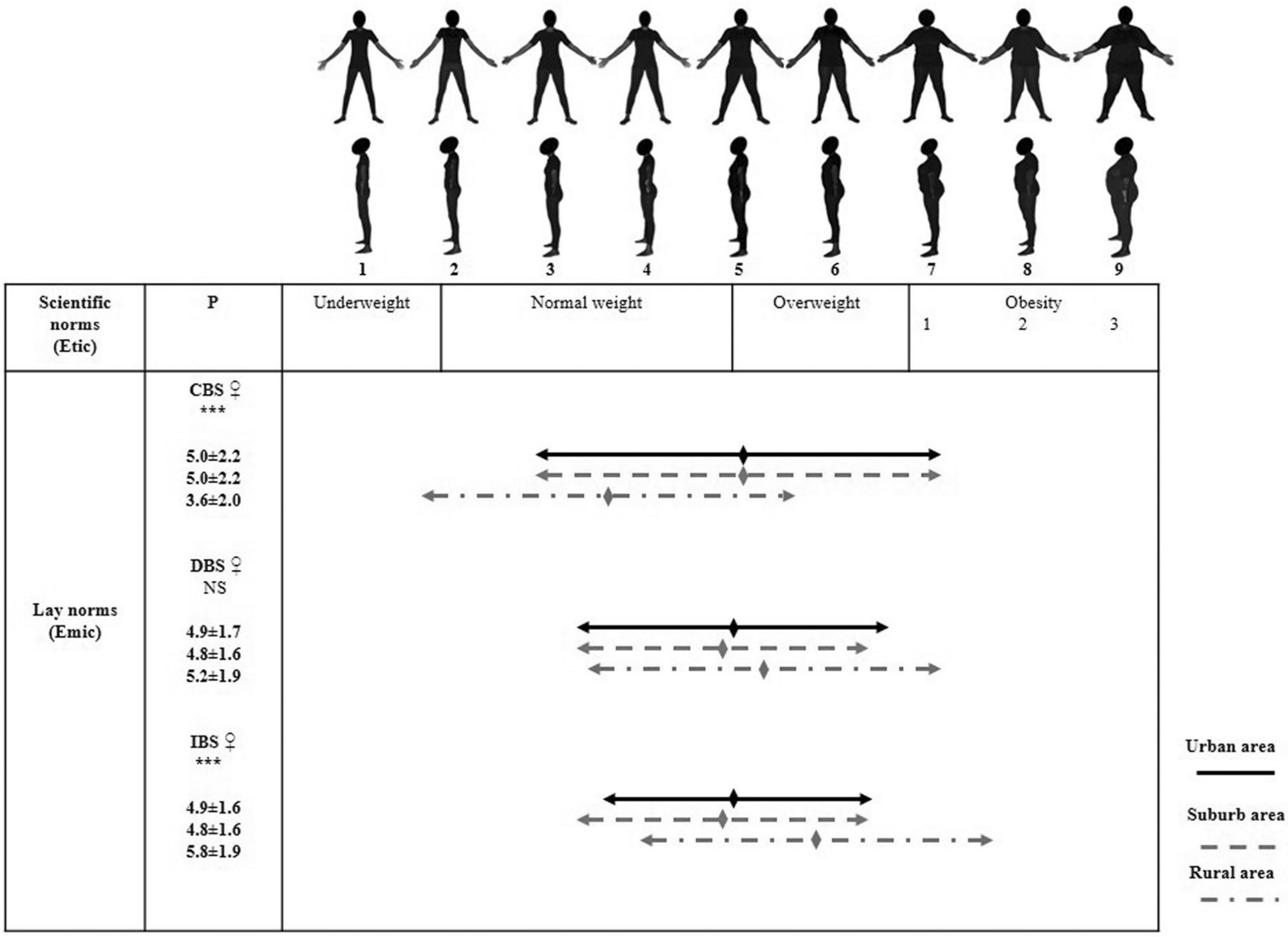


Fig. 2 Perceptions of body size for female BSS. CBS: Current body size, DBS: Desired body size, IBS: Ideal body size. NS: Not significant. ***: p<0.001 / *Perceptions du volume corporel sur la planche féminine BSS. CBS :* Current Body Size *(volume corporel actuel), DBS :* Desired body size *(volume corporel désiré), IBS :* Ideal body size *(volume corporel idéal). NS :* Not significant *(non significatif). *** : p<0,001*

Table 2 Prevalence of overweight and obesity / *Prévalence du surpoids et de l'obésité*

%	No excess weight	Excess weight	*p*
Urban	70.4 (131)	29.6 (55)	
Suburban	70.4 (143)	29.6 (60)	
Rural	91.5 (184)	8.5 (17)	***
	No obesity	**Obese**	***p***
Urban	88.2 (164)	11.8 (22)	
Suburban	88.2 (179)	11.8 (24)	
Rural	98.0 (197)	2.0 (4)	***

***: *p* < 0.001

emerging modern cult of thinness. Nevertheless, in the Dakar urban area, both desired and ideal body sizes were still close to excess weight, as observed in other African urban areas [12], while the prevalence of excess weight was higher than in the rural areas, as also in several other African countries [6]. The social value attached to excess weight/obesity is an independent risk factor of excess weight/obesity [23] and, not surprisingly, the majority of overweight/obese subjects do not want to lose weight [34]. Middle-aged and older women seem to represent the main group displaying this high-risk behavior, as also observed in Nigeria [22].

Various practices are used in Senegal to put on weight. As observed by Rguibi and Belahsen [16] among Sahraoui women in Morocco, corticosteroids are commonly taken by married women to prove by their corpulence that their household is peaceful. Another strategy to gain weight is to decrease physical activity by promoting and adopting idleness, especially among women of low SES living in the peripheral area of Dakar. Indeed, to these urban working-class women, staying peacefully at home, being fat and surrounded by cleaning women is the way to success, as also

Table 3 Self-assessment of health status / *Auto-appréciation de l'état de santé*

BMI	Want to lose weight	Satisfied	Want to gain weight	*p*
Underweight	27.8 (30)	8.3 (9)	63.9 (69)	
Normal weight	52.6 (170)	15.2 (49)	32.2 (104)	
Overweight	43.4 (33)	48.7 (37)	7.9 (6)	
Obese	36.2 (17)	57.5 (27)	6.4 (3)	***

***: $p < 0.001$

Table 4 Odds ratio and 95% confidence limits for overweight/obese subjects, adjusted by binomial logistic regression analysis, and compared to subjects who are not overweight / *Odds ratio et intervalles de confiance à 95 % pour les sujets en surpoids et obèses, ajustés par une régression logistique et comparés avec les sujets qui ne le sont pas*

Determinants	Categories	Excess weight/obesity			
		Odds ratio	*Confidence intervals*		
Gender**	Men†				
	Women	**3.8**	**2.2**	**6.3**	c
Age***		**1.1**	**1.1**	**1.1**	c
Living area***	Rural area†				
	Urban/suburban areas	**8.2**	**4.1**	**16.5**	c
Educational level	None/primary†				
	Secondary/University	1.2	0.7	2.0	
Socio-economic level*	Low/Middle†				
	High	0.8	0.5	1.4	
Stoutness value**	Excess weight not valued†				
	Excess weight valued	**1.7**	**1.1**	**2.8**	a
***N*=561**					

Crude analysis significant effect (p<0.05, p<0.01 and p<0.001, respectively) In bold: binomial logit analysis significant effects (a, b, c): p<0.05, p<0.01, p<0.001, respectively. † Category taken as reference / Effets significatifs des analyses directes univariées (p<0,05, p<0,01 et p<0,001, respectivement). En gras : effets significatifs des analyses logistiques binomiales (a, b, c) : p<0,05, p<0,01, p<0,001, respectivement. † Catégorie prise comme référence

observed by Rguibi and Belahsen [16] in Morocco and by Cohen et al. in Cameroon [23].

Some specific traditional dietary practices also exist to gain weight, especially among Senegalese women, such as consuming high-calorie meals like *ruy [millet porridge without grains]* and *foõdé [millet porridge with grains]*. However, this is more common among Senegalese women living in suburban areas, as a way of showing off the economic success of their household, than among rural women who still have to take on manual activities that demand physical fitness [55,56]. It seems obvious that dietary practices are changing with urbanization, since the population is more exposed to processed high-calorie food. Consuming modern high-calorie food and adding processed oil to all recipes in the Dakar urban area could be another strategy to gain weight. However, another study focusing on this determinant would be needed to identify this factor, especially in the light of the value attached to stoutness, which is identified as a determinant of excess weight/obesity in middle-aged married women.

The Senegalese living in Dakar are thus exposed to both physical and social obesogenic environments. As observed in other populations [3], the duration of urban residence is a risk factor for obesity to which subjects who tend to value excess weight/obesity, especially women, are more exposed. This study therefore suggests that public health policies for obesity prevention need to be adapted to the specific characteristics of migrant populations [57,58] to ensure that evolving biocultural determinants in different socio-ecological areas in Senegal [59,60] are taken into account. To achieve this goal in the future, we propose a set of general recommendations [61] in two areas: public health practice and research targeted to public health personnel in academia, community-based contexts and government agencies. The findings from this study could clarify the exposure levels of urban Senegalese to excess weight and obesity according to their anthropological specificities, and thus help to promote health initiatives among Senegalese migrants or immigrants to the Dakar urban area, in order to connect individuals with healthcare services in urban Senegal [62].

Conclusion

This study demonstrates that the social value attached to large body size is a driver of excess weight and obesity in rural to urban migrants in Senegal. Comparative studies of migrants in other African countries would be needed to provide more evidence on whether this is a general trend. To identify the exposure levels of migrants to obesity, local and global health policies need to take the anthropological specificities of migration pathways into account, such as perceptions of food and body weight in particular.

Acknowledgments : Emmanuel Cohen is supported by the South African DST/NRF Centre of Excellence in Human Development. Particular thanks to Luisa Michelotti and other investigators in the field.

Conflict of Interest: No conflict of interest and no competing financial interests.

References

1. Popkin BM, Adair LS, Ng SW (2012) Global nutrition transition and the pandemic of obesity in developing countries. Nutr Rev 70:3–21
2. Morris K (2010) UN raises priority of non-communicable diseases. Lancet 375:1859
3. Olszowy KM, Pomer A, Dancause KN, et al (2015) Impact of modernization on adult body composition on five islands of varying economic development in Vanuatu. Am J Hum Biol 27:832–44
4. Downey G (2016) Being human in cities: Phenotypic bias from urban niche construction. Curr Anthropol 57:52–64
5. Stevens GA, Singh GM, Lu Y, et al (2012) National, regional, and global trends in adult overweight and obesity prevalences. Popul Health Metr 10:22
6. Steyn NP, Mchiza ZJ (2014) Obesity and the nutrition transition in Sub-Saharan Africa. Ann N Y Acad Sci 1311:88–101
7. Connor Gorber S, Tremblay M, Moher D, Gorber B (2007) A comparison of direct vs. self-report measures for assessing height, weight and body mass index: A systematic review. Obes Rev 8:307–26
8. Oyebode O, Pape UJ, Laverty AA, et al (2015) Urban and migrant differences in non-communicable disease risk-factors in middle income countries: A cross-sectional study of WHO-SAGE Data. PLoS One 10:0122747
9. De Garine I (1990) Adaptation biologique et bien-être psychoculturel. BMSAP 2:151–73
10. Blocker DE, Freudenberg N (2001) Developing comprehensive approaches to prevention and control of obesity among low-income, urban, African-American women. J Am Med Womens Assoc 56:59–64
11. Mvo Z, Dick J, Steyn K (1999) Perceptions of overweight African women about acceptable body size of women and children. Curationis 22:27–31
12. Appiah CA, Otoo GE, Steiner-Asiedu M (2016) Preferred body size in urban Ghanaian women: Implication on the overweight/obesity problem. Pan Afr Med J [in press]
13. Cohen E, Boetsch G, Palstra FP, Pasquet P (2013) Social valorisation of stoutness as a determinant of obesity in the context of nutritional transition in Cameroon: The Bamileke case. Soc Sci Med 96:24–32
14. Bricas N (2008) La pluralité des références identitaires des styles alimentaires urbains en Afrique. Les nouvelles figures des marchés agroalimentaires. Apports Croisés L'économie Sociol Gest 149–59
15. Ndoye F, Diop A (2001) Evolution des styles alimentaires à Dakar. ENDA-GRAF/CIRAD, Dakar, 62 p
16. Rguibi M, Belahsen R (2006) Fattening practices among Moroccan Saharawi women. East Mediterr Health J 12:619–24
17. Warnier JP (2009) Régner au Cameroun : le roi-pot, Karthala Editions, Paris, 338 p
18. Brewis AA (2011) Obesity: cultural and biocultural perspectives. Rutgers University Press, New Brunswick, New Jersey, 232 p
19. Flynn K, Fitzgibbon BM (1998) Body images and obesity risk among black females: a review of literature. Ann Behav Med 20:13–24
20. Krauss RC, Powell LM, Wada R (2012) Weight misperceptions and racial and ethnic disparities in adolescent female body mass index. J Obes 205393
21. De Garine I, Pollock NJ (1995) Social aspects of obesity. Gordon and Breach Publishers, Amsterdam, 352 p
22. Okoro EO, Oyejola BA, Etebu EN, et al (2014) Body size preference among Yoruba in three Nigerian communities. Eating and Weight Disorders-Studies on Anorexia. Bulim Obes 19:77–88
23. Cohen E, Amougou N, Ponty A, et al (2017) Nutrition transition and biocultural determinants of obesity among Cameroonian migrants in urban Cameroon and France. Int J Environ Res Public Health [in press]
24. Brown PJ, Konner M (1987) An anthropological perspective on obesity. Ann N Acad Sci 499:29–46
25. Boetsch G (2006) Les variations historiques et culturelles de la morphologie corporelle. Médecine et nutrition 42:29–35
26. Macia E, Cohen E, Gueye L, et al (2017) Prevalence of obesity and body size perceptions in urban and rural Senegal: new insight on the epidemiological transition in West Africa. Cardiovasc J Afr [in press]
27. Abubakari AR, Lauder W, Agyemang C, et al (2008) Prevalence and time trends in obesity among adult West African populations: A meta-analysis. Obes Rev 9:297–311
28. Maire B, Delpeuch F, Cornu A, et al (1992) Urbanisation et transition nutritionnelle en Afrique sub-saharienne: les exemples du Congo et du Sénégal. Rev D'épidémiologie Santé Publique 40:252–8
29. Duboz P, Macia E, Chapuis Lucciani N, et al (2012) Migration and hypertension in Dakar, Senegal. Am J Phys Anthropol 149:250–8
30. Macia E, Duboz P, Gueye L (2010) Prevalence of obesity in Dakar. Obes Rev 11:691–4
31. Sobal J, Stunkard AJ (1989) Socio-economic status and obesity: A review of the literature. Psychol Bull 105:260–75
32. Drewnowski A (2009) Obesity, diets, and social inequalities. Nutr Rev 67:36–9
33. Temple NJ, Steyn NP (2011) The cost of a healthy diet: A South African perspective. Nutrition 27:505–8

34. Holdsworth M, Gartner A, Landais E, et al (2004) Perceptions of healthy and desirable body size in urban Senegalese women. Int J Obes 28:1561–8
35. Macia E, Gueye L, Duboz P (2016) Hypertension and obesity in Dakar, Senegal. PloS One 11:0161544
36. Eschwege E, Charles MA, Basdevant A (2012) ObEpi: Enquête Epidémiologique Nationale sur le Surpoids et L'obésité, Roche, Basel, 60 p
37. Gning SB, Thiam M, Fall F, et al (2007) Le diabète sucré en Afrique subsaharienne. Aspects épidémiologiques, difficultés de prise en charge. Médecine Trop 67:607–11
38. Ndiaye L (2006) Les représentations sociales du corps de la femme en pays wolof sénégalais : « tradition et modernité ». In: Ly B (ed) Sociétés en devenir. Presses Universitaire de Dakar, Dakar, pp 213–34
39. Duboz P, Macia E, Gueye L, et al (2011) Migrations internes au Sénégal. Caractéristiques socioéconomiques, démographiques et migratoires des Dakarois. Divers Urbaine 11:113–35
40. AG/GRN-GTZ (2004) Convention locale de la gestion des ressources naturelles du terroir communautaire de Taïba Niassène, République du Sénégal, 21 p
41. Stewart D, Shamdasani P (1990) Focus group: Theory and practice. Sage Publications, Newburg Park, 153 p
42. Cohen E, Bernard JY, Ponty A, et al (2015) Development and validation of the body size scale for assessing body weight perception in African populations. Rev PLoS One 10:0138983
43. Cohen E, Pasquet P (2011) Development of a new body image assessment scale in urban Cameroon: An anthropological approach. Ethn Dis 21:288
44. Weiner JS, Lourie JA (1981) Practical human biology. Academic Press, New York, 439 p
45. Mason J (2002) Qualitative researching. Sage, London, 232 p
46. Williamson DA, Gleaves DH, Watkins PC, Schlundt DG (1993) Validation of self-ideal body size discrepancy as a measure of body dissatisfaction. J Psychopathol Behav Assess 15:57–68
47. Siervo M, Grey P, Nyan OA, Prentice AM (2006) A pilot study on body image, attractiveness and body size in Gambians living in an urban community. Eat Weight Disord-Stud Anorex Bulim Obes 11:100–9
48. Fezeu LK, Assah FK, Balkau B, et al (2008) Ten-year changes in central obesity and BMI in rural and urban Cameroon. Obesity 16:1144–7
49. Monteiro CA, Conde WL, Lu B, Popkin BM (2004) Obesity and inequities in health in the developing world. Int J Obes Relat Metab Disord 9:1181–6
50. Renzaho AM, McCabe M, Swinburn B (2012) Intergenerational differences in food, physical activity, and body size perceptions among African migrants. Rev Qual Health Res 22:740–54
51. Szabo CP, Allwood CW (2006) Body figure preference in South African adolescent females: A cross cultural study. Afr Health Sci 6:201–6
52. Dapi LN, Omoloko C, Janlert U, et al (2007) "I eat to be happy, to be strong, and to live." Perceptions of rural and urban adolescents in Cameroon, Africa. J Nutr Educ Behav 39:320–6
53. Hitzeroth V, Wessels C, Zungu Dirwayi N, et al (2001) Muscle dysmorphia: a South African sample. Psychiatry Clin Neurosci 55:521–3
54. Sow AM (2002) Médecine interne et image de soi: canons de beauté ou indicateurs de santé ? Médecine Trop 62:577–81
55. De Garine I (1962) Usages alimentaires dans la région de Khombole (Sénégal). Cahiers d'études africaines 218–65
56. Sear R, Marlowe FW (2009) How universal are human mate choices? Size does not matter when Hadza foragers are choosing a mate. Biol Lett 5:606–9
57. Delavari M, Farrelly A, Renzaho A, et al (2013) Experiences of migration and the determinants of obesity among recent Iranian immigrants in Victoria, Australia. Rev Ethn Health 18:66–82
58. Delavari M, Sonderlund AL, Mellor D, et al (2015) Migration, acculturation and environment: determinants of obesity among Iranian migrants in Australia. Rev Int J Env Res Public Health 12:1083–98
59. Abraido-Lanza AF, Armbrister AN, Florez KR, Aguirre AN (2006) Toward a theory-driven model of acculturation in public health research. Am J Public Health 96:1342–46
60. Himmelgreen DA, Pérez Escamilla R, Martinez D, et al (2004) The longer you stay, the bigger you get: Length of time and language use in the US are associated with obesity in Puerto Rican women. Am J Phys Anthropol 125:90–6
61. Lara M, Gamboa C, Kahramanian MI, et al (2005) Acculturation and Latino health in the United States: A review of the literature and its sociopolitical context. Annu Rev Public Health 26:367–97
62. Frisillo Vander Veen D (2015) Obesity, obesity health risks, resilience, and acculturation in black African immigrants. Int J Migr Health Soc Care 11:179–93

BMSAP (2018) 30:70-89
DOI 10.1007/s13219-017-0193-x

ARTICLE / *ARTICLE*

Étude des restes humains de Kindoki (République démocratique du Congo, fin XVII^{e}–début XIX^{e} siècle)

Study of the Human Remains from Kindoki (Democratic Republic of Congo, End 17th–Early 19th Century AD)

C. Polet · B. Clist · K. Bostoen

Reçu le 2 mai 2017 ; accepté le 11 septembre 2017

Résumé Nous présentons l'étude anthropologique de dix individus provenant d'un cimetière situé sur la colline de Kindoki au Kongo central (RDC). Ils ont été exhumés en 2012 et 2013 dans le cadre du projet KongoKing qui consistait en une approche interdisciplinaire de l'histoire ancienne du royaume Kongo. Ce cimetière contient des inhumations datées du XVII^{e} au XIX^{e} siècle, très probablement celles de nobles de haut rang. Les défunts étaient accompagnés d'un mobilier funéraire (perles de verre, sabres, bijoux en or, mousquet). Les restes humains sont malheureusement très mal conservés. Certains ne sont représentés que par quelques fragments osseux ou dentaires. Parmi les dix défunts, on note la présence de deux femmes et de huit hommes. Deux individus masculins présentent des usures dentaires qui résulteraient de l'utilisation d'une pipe. Les deux femmes seraient âgées de plus de 40 ans et se caractérisent par des signes vertébraux évocateurs de DISH (*diffuse idiopathic skeletal hyperostosis*). Cette pathologie est actuellement associée à une alimentation riche, à l'obésité et au diabète de type II. Il n'est donc pas surprenant qu'elle touche ces individus de statut élevé. Le DISH n'avait encore jamais été décrit dans une population ancienne d'Afrique centrale.

Mots clés République démocratique du Congo · Archéologie historique · Époque contemporaine · Royaume Kongo · Statut social

Abstract This paper presents an anthropological study of ten individuals from a cemetery situated on Kindoki Hill in the central Kongo region (DRC). They were excavated in 2012 and 2013 as part of the KongoKing project (2012–2016), which applied an interdisciplinary approach to the ancient history of the Kingdom of Kongo. The cemetery contains graves dated to the 17th–19th century, very probably those of high-ranking nobles. The dead were buried with various grave goods (glass beads, swords, gold jewels and muskets). The human remains were unfortunately very badly preserved. Some were represented only by a few bone fragments and/or teeth. Of the ten bodies, two were female and eight were male. Two of the men showed dental wear as a result of pipe-smoking. The two women were probably more than 40 years of age at the time of death. The vertebrae showed signs that evoke diffuse idiopathic skeletal hyperostosis (DISH), a pathological condition associated today with a rich diet, obesity and type II diabetes. It is therefore not surprising that these conditions might have affected high-status individuals. Until now, DISH had never been described in an ancient Central African population.

Keywords Democratic Republic of Congo · Modern period · Historical archaeology · Kingdom of Kongo · Social status

Introduction

Cette étude fait partie du projet interdisciplinaire KongoKing (2012–2016) qui visait à mieux connaître l'origine et l'histoire du royaume Kongo, principalement d'un point de vue politique, linguistique et économique [1]. Ce projet réunissait six institutions : l'Université de Gand, l'Université libre de Bruxelles et le Musée royal d'Afrique centrale, du côté belge ; l'Université de Kinshasa, l'Université Kongo et l'Institut des Musées Nationaux du Congo, du côté congolais. L'Institut royal des Sciences naturelles de Belgique (IRSNB)

C. Polet (✉)
Institut royal des Sciences naturelles de Belgique,
29, rue Vautier, B-1000 Bruxelles, Belgique
e-mail : caroline.polet@sciencesnaturelles.be

B. Clist · K. Bostoen
BantUGent – Centre d'études bantoues de l'UGent,
Département de Langues et Cultures, Université de Gand

a été contacté en cours de projet pour réaliser l'étude anthropologique des restes humains exhumés.

Partant du constat que les recherches sur l'urbanisation en Afrique centrale ont jusqu'à présent suscité peu d'intérêt, les chercheurs du projet KongoKing ont mis en commun leurs potentiels pour tenter de combler une partie de ces lacunes [2]. Leur choix s'est porté sur le royaume Kongo qui figure parmi les rares structures politiques précoloniales de l'Afrique centrale à être historiquement documentées dès le début du XVI^e siècle. Ce royaume, fondé au XIV^e siècle, occupait un territoire qui est actuellement celui de l'Angola et de la République démocratique du Congo (RDC) [3]. Si l'on excepte les cités historiques de Mbanza Kongo, de Mbanza Soyo et de Ngongo Mbata qui ont fait anciennement l'objet de fouilles archéologiques [4–7], l'histoire des anciennes agglomérations kongo demeure assez méconnue.

Les recherches archéologiques de ce projet se sont concentrées depuis 2012 sur le bassin de l'Inkisi, l'un des principaux affluents du fleuve Congo dans la province du Kongo central (appelée Bas-Congo jusqu'en 2015). Les capitales des provinces de Mbata, de Nsundi et de Mpangu du royaume Kongo se sont en effet établies dans cette vallée [2,3].

Cet article présente les premiers résultats de l'étude des restes humains exhumés lors de ces campagnes de fouilles. Elle porte sur les squelettes découverts sur la colline de Kindoki.

Matériel

La colline de Kindoki (05 04'069" S ; 15°01'403" E) est actuellement située en RDC, plus particulièrement dans la province du Kongo central (Fig. 1AB). Elle s'étend sur une superficie d'environ 30 ha. Son substrat géologique est composé de schiste calcaire de l'unité Bangu. Son sous-sol contient des sables qui sont plus ou moins argileux, avec souvent des galets à la base [8]. La province du Kongo central est caractérisée par un climat tropical humide (selon le système de classification de Köppen, elle appartient au type climatique Aw_4) [9]. La saison pluvieuse alterne avec la saison sèche. La température moyenne annuelle oscille autour de 25 °C. La moyenne annuelle des précipitations s'élève à environ 1 600 mm. L'humidité relative sur l'ensemble de la province se situe autour de 80 % pour tous les mois de l'année [10].

Au temps du royaume Kongo, la colline était située dans la province de Nsundi (Fig. 1C), une zone probablement densément peuplée avec des sols relativement fertiles et une végétation mixte constituée de savanes et de forêts [11]. Depuis le XVI^e siècle, elle faisait vraisemblablement partie de l'ancienne capitale de cette province (Mbanza Nsundi) [2,3].

L'équipe du projet KongoKing a réalisé des fouilles en 2012, en 2013 et en 2015 sur le site de Kindoki [2]. Les fouilles ont été installées sur un axe est–ouest de 700 m et sur un axe nord–sud de 450 m. Elles ont combiné le creusement de tranchées tests systématiques et des carroyages à grande échelle. Un cimetière fut ainsi découvert et fit l'objet d'une fouille exhaustive sur une superficie d'environ 279 m^2. Des zones d'habitat datées du XIII^e au XIX^e siècle ont également été mises au jour à proximité du cimetière.

Ce cimetière contenait 11 sépultures qui ont été numérotées 1, 2, 4, 5, 6, 7, 8, 9, 11, 12 et 13 (Fig. 2). Elles présentaient toutes la même orientation (SW–NE), étaient très proches les unes des autres et avaient été édifiées de manière identique [2]. Une fois le corps déposé, avec son matériel funéraire à plus ou moins 2 m de profondeur, la fosse était entièrement rebouchée ; puis on installait une série de petites dalles matérialisant le rectangle de la fosse. À l'intérieur de cet espace, on plaçait ensuite un pavement de dalles plus grandes. Pour finir, on empilait sur le pavement des pierres irrégulières pour former un cairn. Ces données suggèrent que ce cimetière a été constitué dans un faible laps de temps et que les individus inhumés étaient liés les uns aux autres d'une manière qui reste à identifier.

Quelques indices archéologiques et pédologiques témoignent du traitement des défunts. Dans les sédiments des tombes 1, 8 et 11, la présence d'une zone ovalaire de couleur foncée entourant les restes humains suggère la décomposition de couches de tissus emballant le corps (des restes textiles ont d'ailleurs été découverts dans la sépulture 8) (Tableau 1). Cette pratique est attestée par des textes datant du début du XX^e siècle, qui mentionnent que les personnages de statut social élevé étaient emballés dans des dizaines, voire des centaines de couches de tissus (tapis importés, nattes, etc.) [2,3]. La tombe 4 a livré des clous en fer entourant le défunt, témoins d'un cercueil en bois. Les sept autres tombes n'ont livré aucune structuration particulière, laissant penser à un dépôt simple des corps en pleine terre ou à un appareil funéraire dont les traces n'étaient plus perceptibles au moment de la fouille.

Les défunts étaient accompagnés d'un mobilier funéraire dont la composition varie d'une sépulture à l'autre (les tombes 1 et 13 en étaient toutefois dépourvues) (Tableau 1). Cinq tombes recelaient une épée de fer (n^{os} 4–7 et 12), symbole important de la noblesse kongo illustré sur les gravures d'époque (XVI^e–XVIII^e siècles), et une sixième renfermait un mousquet (n^o 9). Si l'on se fonde sur ces mêmes gravures, ces attributs seraient caractéristiques de tombes masculines. Des bijoux en or ont été retrouvés dans deux tombes (n^{os} 1 et 8) et des médailles religieuses dans trois autres (n^{os} 2, 6 et 12). Une croix et un crucifix se trouvaient aussi dans la tombe 12. Quatre tombes ont livré des perles en verre (n^{os} 8, 9, 11 et 12) qui étaient des symboles de richesse et/ou de féminité [12]. Les tombes 8 et 11 contenaient également

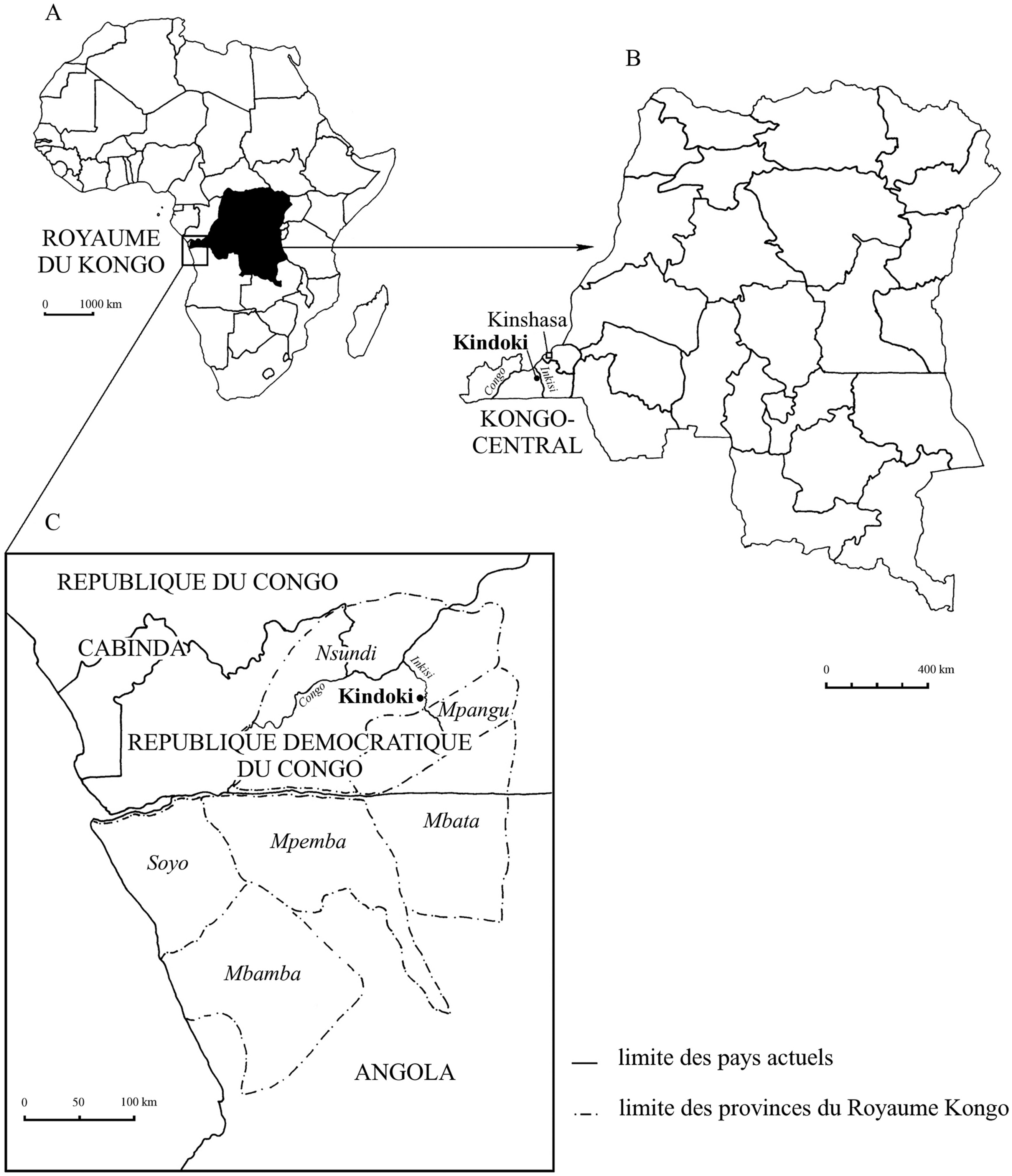


Fig. 1 A. Localisation de la République démocratique du Congo (RDC). B. Carte actuelle de la RDC avec localisation du site de Kindoki dans la province du Kongo central. C. Royaume du Kongo et délimitation de ses provinces aux XVIe–XVIIe siècles (dessin : A.-M. Wittek [ADIA], d'après Clist et al. [2]) / A. Location of the Democratic Republic of the Congo (DRC). B. Current map of the DRC with the location of the Kindoki site in the province of Central Kongo. C. Kingdom of Kongo and its boundaries in the 16–17th centuries (drawing : A.-M. Wittek (ADIA) from Clist et al [2])

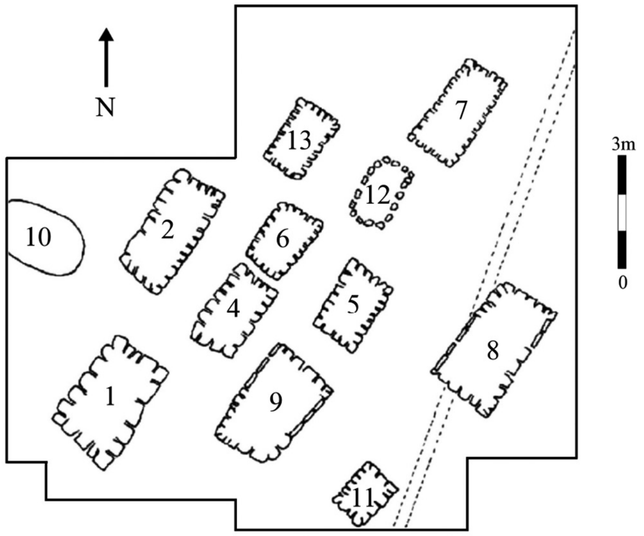


Fig. 2 Plan du cimetière de Kindoki [2] / Map of the cemetery at Kindoki [2]

des perles en coquilles de gastéropodes marins ainsi que des chevillères en fer d'un modèle identique. Les armes, les médailles, la croix, le crucifix et les perles de verre sont d'origine européenne. Cela n'est pas surprenant, car le royaume Kongo était en contact avec les Portugais dès 1483, et depuis lors, les échanges de biens avec les Européens étaient largement répandus [13]. La présence de médailles religieuses, de croix et de crucifix n'est, elle aussi, pas inattendue étant donné que les Bakongo se sont graduellement volontairement christianisés à la suite de la conversion du roi Joao Ier en 1491 [14].

L'étude du mobilier funéraire a permis de proposer des dates dites terminus post quem, à savoir les dates à partir desquelles les inhumations ont pu avoir lieu [2] (Tableau 1). Deux tombes (nos 5 et 9) renfermaient du charbon de bois qui a été daté par le radiocarbone (Tableau 1). Les dates calibrées à deux sigma, en tenant compte des tables de calibration de l'hémisphère sud avec le programme Calib 7.0.4., ont donné :

Poz–60769 (tombe 5) : 200 ± 30 BP. 1658AD–1712AD (25 %), 1718AD–1814AD (56 %), 1835AD–1891AD

Tableau 1 Résultat de l'étude archéologique des 11 tombes de Kindoki : composition du mobilier funéraire, attributions chronologique et sexuelle (genre) / Result of the archaeological study of the 11 graves from Kindoki: composition of the grave goods, chronological and gender attributions

Tombe	Mobilier funéraire	Chronologie	Genre
1	–	–	–
2	1 médaille religieuse, 1 chaîne en or (perdues sur le chantier)	?	?
4	1 épée	Fin XVIIe–début XVIIIe siècle (épée)	♂
5	1 épée	1658–1814 (^{14}C ; 81 % de probabilité), XVIIe–XVIIIe siècles (épée)	♂
6	1 médaille religieuse, 1 épée	fin XVIIIe–début XIXe siècle (médaille), XVIe–XVIIe siècles (épée)	♂
7	1 épée, 2 fragments de métal en fer	XVIIe siècle (épée)	?/♂
8	1 159 perles de verre, 1 perle en cuivre, 32 cloches crotales, 660 perles de coquillage (*Pusula depauperata*), 1 coquillage des mangroves *(Tympanotonus fuscatus radula)*, 1 chevillère en fer, 1 collier en fer, 1 chaîne en cuivre, 1 chaîne en or, plusieurs fragments d'un linceul	1825–1845 (perles)	♀
9	1 mousquet, 2 bracelets en fer, 18 perles de verre	1690–1725 (mousquet), 1725–1850 (perles), 1665–1816 (^{14}C ; 71 % de probabilité)	♂
11	268 perles de verre, 272 perles de coquillage (*Pusula depauperata*), 6 bracelets de cheville en fer	1825–1845 (perles)	♀
12	16 perles de verre, 2 perles d'ivoire, 1 crucifix en cuivre, 1 croix en cuivre, 1 médaille religieuse, 1 chaîne en cuivre, 2 fragments de fer, 1 épée	1650–1750 (perles), XVIIe– XVIIIe siècles (crucifix), XVIIe siècle (médaille), XVIIe siècle (épée)	♂
13	–	–	–

(13 %) et 1924AD–1949 AD (6 %). Bêta–333285 (tombe 9) : 190 ± 30 BP. 1665AD–1816AD (71 %), 1830AD–1892AD (20 %) et 1922AD–1949AD (9 %).

La présence dans plusieurs sépultures de vestiges ou d'objets connotant un statut social très élevé dans la tradition kongo actuelle et subactuelle, de nobles dans l'esprit du royaume Kongo (épées, couches multiples de tissus, bracelets de fer au bras droit, centaines de perles en verre et en coquilles marines), amène à conclure que nous avons affaire à des nobles kongo, sinon à des tombes ducales datées entre la fin du XVII^{e} et le début du XIX^{e} siècle [2].

Méthodes

Pour quantifier l'état de préservation des squelettes, nous avons utilisé l'indice de conservation anatomique (ICA) de Dutour [15] (pp. 26–29). Afin de décrire l'état de préservation des surfaces osseuses, nous avons appliqué la méthode de McKinley [16].

Le sexe n'a malheureusement pas pu être déterminé à partir des os coxaux, car ils sont généralement très fragmentés, voire absents. Nous avons donc utilisé le bloc craniofacial, la mandibule, les os longs et les dents. Les déterminations du sexe à partir de la tête osseuse se sont fondées sur des critères morphologiques et métriques. Pour le bloc craniofacial, nous avons appliqué la méthode de Ferembach et al. [17]. Pour la mandibule, nous avons appliqué la méthode de Gilles citée par Krogman et İşcan [18] (p. 200), mise au point sur des Afro-Américains, et celle de Franklin et al. calculée pour des Zoulous d'Afrique du Sud [19]. Les diagnostics réalisés à partir des os longs ont fait appel à des fonctions discriminantes, comme celles de Dibennardo et Taylor calculées sur la base de fémurs d'Afro-Américains [20] et celles d'İşcan et Miller-Shaivitz établies sur des tibias d'Afro-Américains [21]. Les déterminations du sexe fondées sur les dents ont été effectuées grâce :

- aux fonctions discriminantes de Macaluso fondées sur deux mesures réalisées sur les M1 et M2 supérieures de Noirs sud-africains [22] ;
- à la méthode graphique d'Orban et al., mise au point sur une population européenne et faisant appel à deux mesures relevées sur la PM2 supérieure et la C inférieure [23].

En fonction de l'état de préservation des individus, les estimations de l'âge au décès ont été fondées sur l'usure dentaire [24], l'oblitération des sutures crâniennes [18] (pp. 120–121), l'ossification du cartilage thyroïdien [18] (pp. 127–129) et l'état de fusion des épiphyses [25] (pp. 293–295).

Les statures ont été estimées à partir de la longueur des os longs, grâce aux formules de Trotter et Gleser destinées aux femmes et aux hommes afro-américains [26]. Lorsque les os étaient incomplets, nous avons appliqué la méthode de Steele et McKern pour estimer leur longueur [27].

Pour élaborer le profil biologique, nous avons privilégié des méthodes anthropologiques mises au point à partir de populations de référence africaines. En l'absence de celles-ci, nous avons employé des méthodes largement utilisées en anthropologie biologique. Se pose dans ce cas la question de la transposition à des échantillons africains. Ce point est particulièrement crucial dans le cas de l'usure dentaire, puisqu'elle dépend principalement du régime alimentaire. Comme les chasseurs-cueilleurs amérindiens étudiés par Lovejoy [24] n'avaient pas le même régime que les agriculteurs-éleveurs de Kindoki, les stades d'usure dentaire ne seront pas utilisés pour leur attribuer un âge précis, mais pour les répartir en trois classes d'âge (16–25 ans, 26–40 ans et > 40 ans), en tenant également compte des résultats obtenus par les autres méthodes d'estimation de l'âge et de la présence de pathologies dégénératives.

Les pathologies osseuses traumatiques, infectieuses, métaboliques et dégénératives ainsi que les pathologies dentaires ont été étudiées à l'échelle macroscopique [28–31]. Les variations anatomiques dentaires et osseuses ont également été examinées [32] tout comme les marqueurs d'activité [33].

Des analyses par microscopie électronique à balayage couplée à la microanalyse par spectroscopie à rayons X à dispersion d'énergie (MEB-EDS = FEI Quanta 200 équipé de système EDAX, modèle Apollo 10 SDD® Silicon Drift Detectors, 23 kV) ont été effectuées à l'IRSNB, afin de déterminer l'origine des colorations que présentent certains restes osseux et dentaires [34].

Résultats

Neuf des 11 sépultures du cimetière de Kindoki ont livré des restes humains (les tombes 4 et 13 en étaient dépourvues). Sept d'entre elles ne renfermaient qu'un seul défunt (1, 2, 5, 6, 9, 11 et 12). La tombe 7 contenait des vestiges appartenant à deux individus (7A et 7B).

Une monographie présentant les résultats du projet KongoKing est en préparation [35]. Le chapitre consacré à l'étude des squelettes de Kindoki reprendra l'étude descriptive détaillée de chaque individu, les mesures osseuses et dentaires individuelles ainsi que de nombreuses photographies.

État de préservation

Les défunts des tombes 1, 2, 5, 6, 7 et 12 sont très incomplets et très fragmentaires. Ils ne sont généralement constitués que de restes dentaires, de fragments de diaphyse et de la tête osseuse (Tableau 2). Leur ICA varie entre 1,1 et 10,2 % (Tableau 2), ce qui correspond à un état de conservation

Tableau 2 Résultats de l'étude anthropologique des dix individus de Kindoki : inventaire des restes dentaires et osseux (F = os incomplet, FF = quelques fragments osseux), indice de conservation anatomique (ICA), état de préservation des surfaces osseuses (PSO), détermination du sexe, stade d'usure dentaire de Lovejoy [24], classe d'âge, pathologie et particularité anatomique / Results of the anthropological study of the 10 individuals from Kindoki: dental and bone inventory (F = incomplete bone, FF = several bone fragments), Anatomical Preservation Index (ICA), bone surface preservation (PSO), sex determination, Lovejoy dental wear phase [24], age class, age estimation, pathology and anatomically distinctive traits

Individu n°	*N* dents	Os long	Tête osseuse	Autres os	ICA (%)	PSO	Sexe	Usure dentaire	Classe d'âge (années)	Pathologie	Particularité
1	30	FF	FF	–	10,2	5	♂	F	26–40	Carie, tartre	Torus mandibulaire, usure pipe
2	15	FF	FF	–	4,5	5+	♂	G-H	26–40	–	–
5	22	FF	–	–	4,0	5+	♂	E	26–40	Tartre	Usure pipe
6	11	–	–	–	2,3	–	?	C	16–25	–	–
7A	12	FF	FF	–	2,8	5+	♂	G	26–40	–	LSAMAT
7B	12	–	–	–	1,1	–	♂	>I	> 40	–	–
8	31	F	F	F	34,1	3–5	♀	H	> 40	Parodontite, DISH ? Arthrose, tartre	13 vertèbres thoraciques, LSAMAT
9	24	F	F	F	43,2	2–3	♂	G	> 40	Carie, arthrose	Suture métopique
11	25	F	F	F	38,1	1–3	♀	H	> 40	Parodontite, DISH, arthrose	Courbure du fémur
12	6	FF	FF	FF	4	1–3	?	B2–C	16–25	–	–

allant de mauvais à médiocre [15]. De plus, leurs surfaces osseuses sont très érodées (Fig. 3, Tableau 2). On note la présence de fissures dans presque toutes les couronnes dentaires. Les racines sont friables, souvent très érodées et parfois même absentes (individus 5, 6 et 7B).

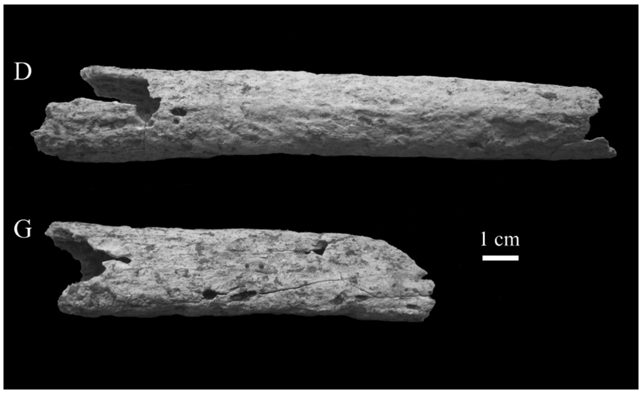


Fig. 3 Tibias droit (D) et gauche (G) de l'individu de la tombe 2 de Kindoki. Ils se caractérisent par une très forte érosion des surfaces / Right (D) and left (G) tibias of individual 2 from Kindoki. Both have severely eroded surfaces

Les squelettes des tombes 8, 9 et 11 situées à l'est du cimetière sont bien mieux conservés que les précédents (Tableau 2). Leurs ICA varient entre 34,1 et 43,21 %, ce qui correspond à un assez bon à bon état de conservation [15]. Ils sont néanmoins incomplets, de nombreux ossements sont fragmentaires (Annexes A–C), et leurs surfaces sont érodées (Tableau 2). Les os des mains et des pieds (sauf pour l'individu 9), les patellas et le sacrum font défaut. Les épiphyses des os longs sont aussi généralement absentes. Les couronnes dentaires sont fissurées et ont perdu de nombreux éclats d'émail. Les racines sont légèrement érodées.

Chez l'individu 9, une concrétion métallique (oxyde de fer) en forme d'anneau entoure la diaphyse humérale droite au niveau de son tiers supérieur (Annexe B, Fig. 4).

Coloration des restes humains

Les squelettes 8, 9 et 11 présentent des colorations vertes (Annexes A–C). Chez l'individu 9, elles concernent même les dents. Les analyses au MEB-EDS montrent que ces colorations sont dues à la présence d'un ou de plusieurs oxydes de cuivre.

Fig. 4 Humérus droit de l'individu de la tombe 9 de Kindoki. A. Vue antérieure. B. Vue postérieure / Right humerus from the individual in grave n° 9 at Kindoki. A. Anterior view. B. Posterior view

L'individu 8 se caractérise également par des colorations roses (Annexe A). Les analyses au MEB-EDS ont révélé des teneurs élevées en plomb et en fer. Le plomb n'est pas responsable de cette coloration. Des oxydes de fer à faible concentration pourraient être à l'origine des teintes roses.

Les squelettes 9 et 11 présentent aussi des teintes brun foncé au niveau des membres inférieurs (Annexes B,C). Les analyses au MEB-EDS montrent que ces colorations sont liées à la présence d'oxydes de fer.

Détermination du sexe

Les déterminations du sexe des individus 1, 2, 5, 6, 7 et 12 ont été réalisées uniquement à partir des mensurations dentaires. Celles des individus 8, 9 et 11 ont aussi fait appel à des méthodes fondées sur la tête osseuse et les os longs (Tableau 3).

Six individus ont été diagnostiqués comme masculins : 1, 2, 5, 7A, 7B et 9. Les défunts des tombes 8 et 11 ont été déterminés comme étant de sexe féminin. Les individus 6 et 12 sont de sexe indéterminé (Tableau 2).

Estimation de l'âge au décès

La présence exclusive de dents permanentes usées (y compris des M3) indique que les individus sont adultes. Seul l'individu 12, qui présente des M1 et M2 peu usées, pourrait être un adolescent.

Pour estimer leur âge au décès, nous nous sommes principalement fondés sur l'usure dentaire (Tableau 4), avec les réserves énoncées dans le chapitre « Méthodes ». Pour les individus des tombes 8, 11 et 12, nous avons aussi employé respectivement l'ossification du cartilage du larynx, l'oblitération des sutures crâniennes et l'état de fusion de l'épiphyse distale du radius (Tableau 4). Les résultats sont rassemblés dans le tableau 2.

Les individus 5, 6 et 12 seraient les plus jeunes, alors que les individus 7B, 8 et 11 seraient les plus âgés.

Le fait que les individus 8 et 9 présentent des atteintes arthrosiques de la colonne vertébrale (voir ci-dessous) indique, par analogie aux connaissances cliniques actuelles, qu'il s'agirait d'adultes ayant au moins atteint 40 ans [36–38] (p. 459 de [37]).

Estimation de la stature

Les statures n'ont pu être estimées que pour les trois individus les mieux préservés.

La stature de l'individu 11 calculée à partir de la longueur du fémur vaut 155,3 ± 3,41 cm.

L'estimation de la stature des individus 8 et 9 a nécessité deux étapes : l'estimation de la longueur du fémur et l'estimation de la stature. L'erreur associée à l'estimation de la longueur du fémur est de 1,31 cm pour les sujets masculins et de 1,02 cm pour les sujets féminins [27]. La stature de la femme de la tombe 8 vaut 157,2 ± 3,41 cm (cette valeur est probablement sous-estimée étant donné que l'individu présentait une vertèbre surnuméraire). L'homme de la tombe 9 aurait mesuré 161,5 ± 3,94 cm.

Tableau 3 Méthodes appliquées pour déterminer le sexe des dix individus de Kindoki / Methods used to determine the sex of the 10 individuals from Kindoki

	Dents (biométrie)		**Bloc craniofacial**	**Mandibule**		**Os longs (biométrie)**	
Individu n°	**Molaires [22]**	**Prémolaire et canine [23]**	**Morphologie [17]**	**Biométrie [18] (p. 200)**	**Biométrie [19]**	**Fémur [20]**	**Tibia [21]**
1	X	X					
2	X						
5	X	X					
6	X						
7A	X						
7B	X						
8	X	X	X	X	X	X	X
9	X		X		X	X	
11	X	X	X	X		X	
12	X						

Tableau 4 Méthodes appliquées pour estimer l'âge au décès des dix individus de Kindoki / Methods used to estimate the age at death of the 10 individuals from Kindoki

Individu n°	**Usure dentaire [24]**	**Sutures crâniennes [18] (pp. 120–121)**	**Cartilage thyroïdien [18] (pp. 127–129)**	**Fusion épiphyse [25] (pp. 293–295)**
1	X			
2	X			
5	X			
6	X			
7A	X			
7B	X			
8	X		X	
9	X			
11	X	X		
12	X			X

Pathologie buccodentaire

Seuls deux individus étaient atteints de caries dentaires. Chez le sujet 1, elle concerne la PM1 inférieure gauche. La lésion a détruit toute la couronne (stade 4 de Metress et Conway [39]) (Fig. 5A). Chez le sujet 9, deux caries sont à signaler : la couronne de la M3 supérieure gauche est à moitié détruite (stade 2), alors que celle de la M2 supérieure gauche a totalement disparu (stade 4). Le taux de dents cariées s'élève à 1,6 % (3/188).

Trois individus présentent des dépôts de tartre dentaire. Chez l'individu 1, le dépôt est léger [31] (pp. 153–154) et concerne la face vestibulaire des PM1 supérieures et la face linguale des dents inférieures (Fig. 5A). Chez l'individu 5, le dépôt est moyen et se situe sur les faces linguales et vestibulaires de la majorité des 22 dents. Chez l'individu 8, on note un léger dépôt de tartre sur la face linguale des incisives supérieures.

On observe chez les individus 8 et 9 une parodontopathie généralisée. Elle s'exprime par une résorption de l'os alvéolaire [29,30,40] (pp. 260–269 de [30]), qui atteint au moins le stade 1 de Brabant et Sahly (régression sur moins d'un tiers de la racine [41]). Chez l'individu 8, l'os montre une porosité, signe que le processus de remodelage était encore en cours.

On relève également chez l'individu 8 une hypercémentose, c'est-à-dire un épaississement anormal du cément dentaire [30,42] (pp. 205–206 de [30] ; pp. 255–256 de [42]). Elle est particulièrement visible au niveau des canines (Fig. 6B).

Les femmes 8 et 11 présentent des atteintes périapicales. Chez l'individu 8, on observe six cavités à paroi rugueuse (abcès ? [43]) : au niveau de la M2 et de la C inférieures

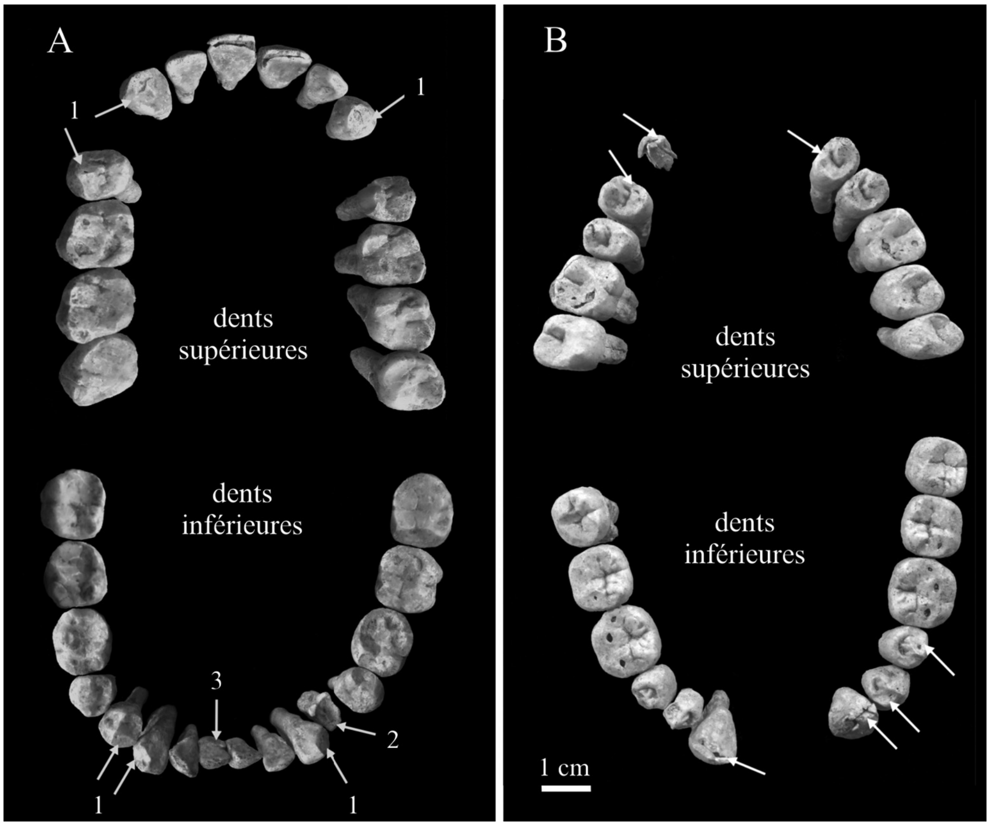


Fig. 5 A. Denture de l'individu de la tombe 1 de Kindoki (1 = usures semi-circulaires ; 2 = carie ; 3 = tartre). B. Denture de l'individu de la tombe 5 de Kindoki. Les flèches indiquent la localisation des usures semi-circulaires / A. Teeth of the individual from grave n° 1 at Kindoki (1 = semicircular wear, 2 = caries, 3 = dental calculus). B. Teeth of the individual from grave n° 5 at Kindoki. The arrows show the location of semicircular wear

droites (Fig. 6A), de la M1 (avec perforation du plancher du sinus) et de la C supérieures droites, des M1 et M3 supérieures gauches (Fig. 6B). L'individu 11 présente deux cavités périapicales à paroi lisse (kyste ? [43]) (Fig. 7) : au niveau de la PM1 et de la M2 inférieures gauches. Dans ce dernier cas, la destruction de l'os alvéolaire est telle qu'elle a permis le déplacement de cette molaire. Elle a pu pencher légèrement mésialement (Fig. 7Ba) ou totalement basculer jusqu'à reposer sa face mésiale sur l'os alvéolaire (Fig. 7Bb). Elle n'était, de toute façon, plus en contact avec la dent antagoniste supérieure, étant donné qu'elle est nettement moins usée que sa correspondante droite. Les bascules antérieures sont habituellement observées lors de la perte d'une molaire : la molaire suivante bascule vers le site de la dent manquante [44]. Ce n'est pas le cas de notre sujet, puisque sa M1 est présente et en place : c'est l'espace dégagé postérieurement par la destruction de l'alvéole (Fig. 7Bc) qui a rendu possible le déplacement de la dent.

Chez l'individu 11, on note la présence d'une ligne d'hypoplasie de l'émail dentaire [30] (pp. 165–177) sur les PM1 et PM2 inférieures gauches (la droite est trop mal préservée), les M1 et M2 inférieures droites, la M2 supérieure gauche et les M3 (Fig. 7A).

Usures dentaires particulières

Deux individus de sexe masculin présentent des usures dentaires de forme semi-circulaire. Chez l'individu 1, elles concernent les C, la PM1 inférieure droite (la gauche a été détruite par une carie, et les PM1 supérieures sont manquantes) et la PM2 supérieure droite (Fig. 5A). Chez l'individu 5, les usures touchent les canines, les prémolaires et les premières molaires (Fig. 5B).

Les incisives supérieures des individus 7A et 8 présentent une usure qui s'étend sur leur face linguale. Ce type d'usure des dents antérosupérieures a été dénommé LSAMAT (*lingual surface attrition of the maxillary anterior teeth*) [45].

Pathologie osseuse

Les deuxième et troisième vertèbres thoraciques de l'individu 8 présentent une zone de fusion (Fig. 8A). Cette fusion est localisée antérieurement et restreinte au côté droit des corps vertébraux. L'espace entre les deux vertèbres est conservé. Deux côtes droites sont fusionnées avec les corps vertébraux sur lesquels elles s'articulent (Fig. 8B).

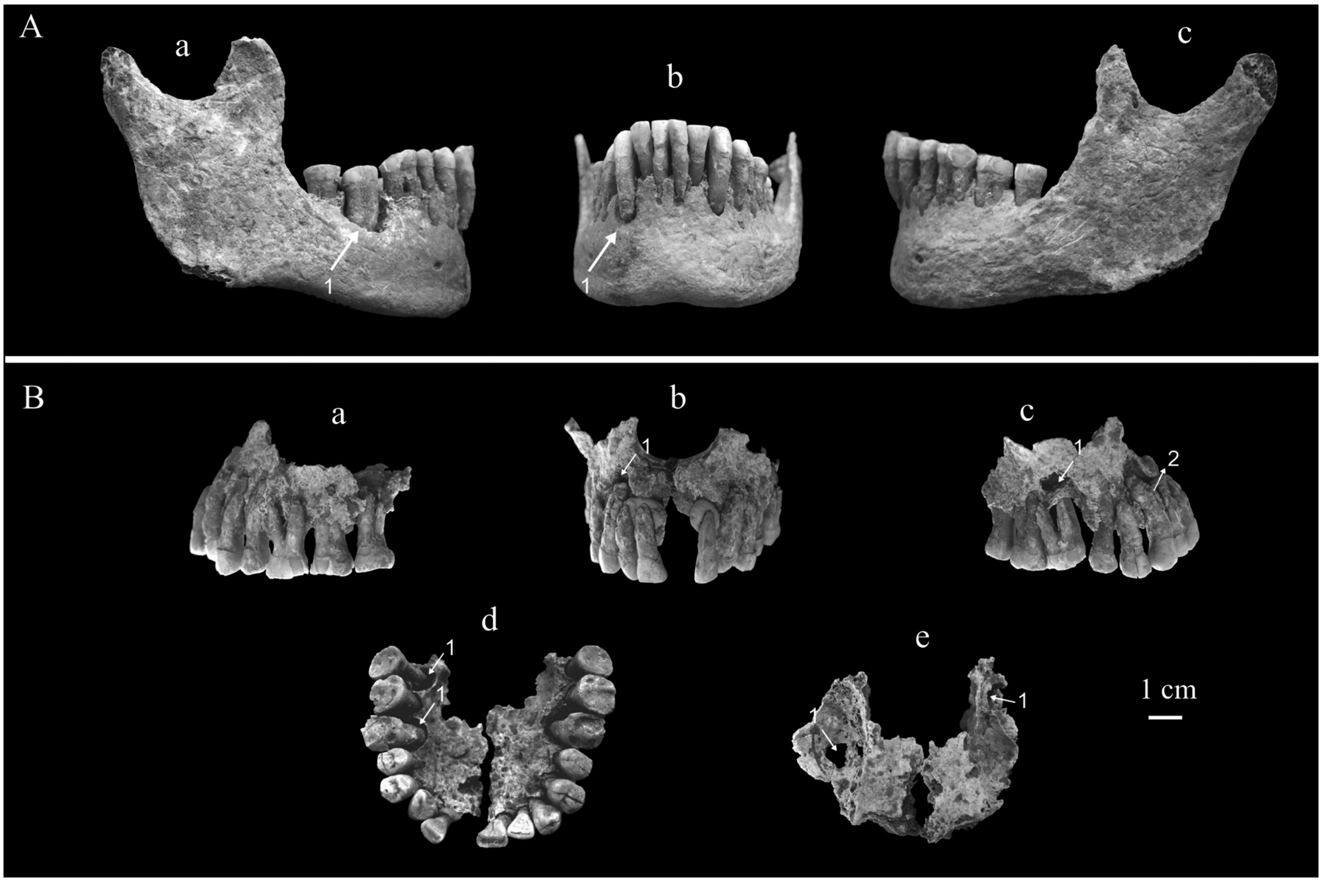


Fig. 6 Mandibule et maxillaires de l'individu de la tombe 8 de Kindoki. Les flèches indiquent la localisation des atteintes périapicales (1) et l'hypercémentose (2). A. Mandibule ; a : vue latérale droite ; b : vue antérieure ; c : vue latérale gauche. B. Maxillaires (de la plasticine a été appliquée pour fixer les dents antérieures) ; a : vue latérale gauche ; b : vue antérieure ; c : vue latérale droite ; d : vue inférieure ; e : vue supérieure / Mandible and maxillae of the individual from grave nº 8 at Kindoki. The arrows show the location of the periapical lesions (1) and hypercementosis (2). A. Mandible; a: right side view; b: anterior view; c: left side view. B. Maxillae (plasticine was applied to fix the anterior teeth); a: left side view; b: anterior view; c: right side view; d: inferior view; e: superior view

Au moins sept vertèbres thoraciques de la femme de la tombe 11 montrent des zones de fusion (Fig. 9). Comme dans le cas de l'individu 8, les fusions sont localisées antérieurement et restreintes au côté droit des corps vertébraux. Elles s'expriment sous forme de ponts osseux qui ont l'aspect d'une coulée de cire. Les espaces entre les vertèbres sont conservés.

Les vertèbres de l'individu 8 présentent des signes d'ostéoarthrose modérée qui affecte les différents étages du rachis. Le sujet 9 est aussi atteint de maladie articulaire dégénérative au niveau du seul corps préservé de vertèbre cervicale et au niveau de la cavité glénoïde droite.

Particularités anatomiques

L'individu 1 présente un torus mandibulaire composé de trois nodules : un situé à droite au niveau de la PM2, deux à gauche, respectivement au niveau de la PM1 et de la PM2. L'individu 8 se caractérise par 13 vertèbres thoraciques au lieu de 12 (Annexe A). L'os frontal de l'individu 9 comporte une suture métopique. Les fémurs de l'individu 11 accusent une courbure antérieure prononcée.

Discussion

Neuf des 11 tombes de la colline de Kindoki ont livré des restes humains, mais la majorité présente un très mauvais état de conservation. Ces détériorations sont à imputer aux conditions d'enfouissement des sites de plein air localisés dans cette région au climat tropical humide (province du Kongo central et province du Zaïre en Angola) [46]. Le degré de préservation serait, de plus, lié à leur durée de séjour dans ce type de sol. Jusqu'à présent, aucun reste humain antérieur au XVII^{e} siècle n'y a été retrouvé. Pour ceux datant plus ou moins de 150 ans (comme la tombe 9), l'ICA

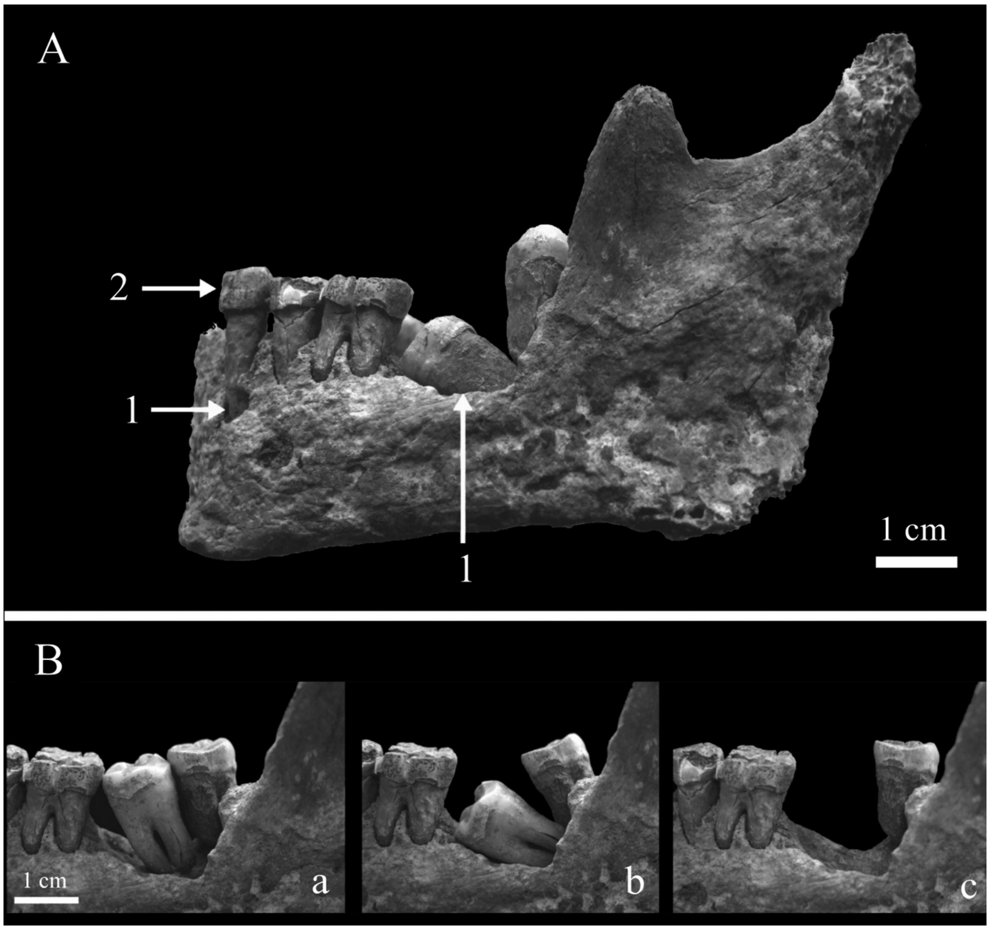


Fig. 7 Mandibule de l'individu de la tombe 11 de Kindoki. A. Vue latérale gauche (1 = lésions périapicales, 2 = ligne d'hypoplasie de l'émail). B. Vues latérales gauches rapprochées. Deux scénarii (a et b) sont proposés en ce qui concerne la position de la seconde molaire ; a : la dent était encore plus ou moins dans sa position initiale ; b : la dent avait totalement basculé sur sa face mésiale ; c : vue de la cavité sans la deuxième molaire / Mandible of the individual from grave n° 11 at Kindoki. A. Left side view (1 = periapical lesions, 2 = enamel hypoplasia line). B. Close-up lateral views. Two hypotheses (a and b) are proposed concerning the position of the second molar; a: the tooth was still more or less in its original position ; b: the tooth had twisted entirely onto its mesial face; c: view of the cavity without the second molar

atteint à peine les 40 %, et les surfaces osseuses sont généralement dégradées.

L'étude anthropologique est de ce fait très limitée, et les résultats obtenus sont à considérer avec prudence.

Le nombre minimum d'individus s'élève à dix, car la tombe 7 contenait les restes de deux individus. L'étude anthropologique montre que, parmi ces dix individus, six seraient de sexe masculin, deux de sexe féminin et deux de sexe indéterminé. Une comparaison de ces déterminations du sexe avec celles réalisées à partir du mobilier funéraire aboutit à une bonne concordance (Tableaux 1,2). Trois tombes, déterminées comme masculines sur la base de la présence d'armes (5, 7 et 9), ont livré des restes humains attribués au sexe masculin par l'étude anthropologique. Il en est de même pour les deux tombes diagnostiquées féminines sur la base de l'absence d'arme et la présence de nombreuses perles de verre (8 et 11). Les individus 6 et 12, dont l'analyse métrique des restes dentaires n'a pas permis de déterminer le sexe, sont diagnostiqués de sexe masculin sur la base de l'étude du mobilier funéraire. En combinant l'étude des squelettes et du mobilier funéraire, il y aurait donc deux femmes et huit hommes. Les individus les plus jeunes ont été inhumés au centre du cimetière : il s'agit d'adolescents ou de jeunes adultes.

La couleur verte des os des individus 8, 9 et 11 et des dents de l'individu 9 peut s'expliquer parfois par la présence d'objets en cuivre dans la tombe (Tableau 1, tombe 8). De même, la couleur brune des os des membres inférieurs des sujets 9 et 11 résulterait de la migration d'oxydes provenant d'objets en fer au contact des défunts (Tableau 1). La teinte rose présente chez l'individu 8 pourrait être aussi liée à la présence d'oxydes de fer ou provenir de colorants présents

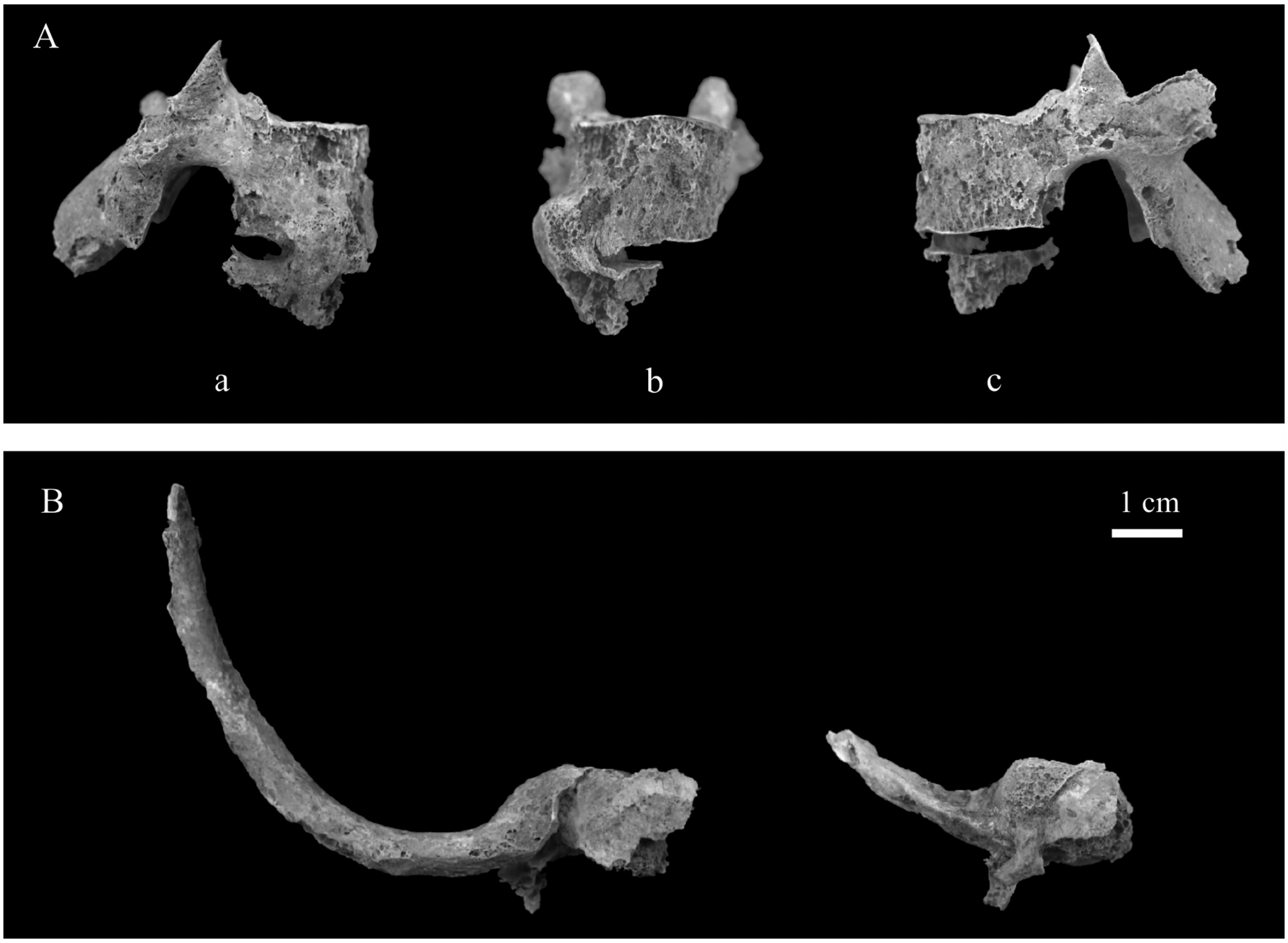


Fig. 8 Vertèbres de l'individu de la tombe n°8 de Kindoki. A. Deuxième et troisième vertèbres thoraciques ; a : vue latérale droite ; b : vue antérieure ; c : vue latérale gauche. B. Vue supérieure des côtes soudées aux dernières vertèbres thoraciques / Vertebrae of the individual from grave 8 at Kindoki. A. Second and third thoracic vertebrae; a: right side view ; b: anterior view ; c: left side view. B. Superior view of the ribs fused to the last thoracic vertebrae

dans les tissus qui entouraient le cadavre (chapitre « Matériel » et Tableau 1).

Quatre particularités osseuses ont été relevées à Kindoki : un torus mandibulaire, une suture métopique, une vertèbre surnuméraire et une courbure accentuée du fémur. Elles seraient d'origine génétique, environnementale [47,48] (pp. 41–44 de [48]) ou, pour la dernière, biomécanique [49]. Reginato et al. [50] mentionnent que le torus affecte 3,2 % des Africains, alors que Corruccini [51] cite une fréquence deux fois plus élevée. La suture métopique est présente chez 1 à 3,4 % des individus africains [52]. La vertèbre surnuméraire serait plus fréquente chez les Africains [32] (pp. 218–219). En général, cette variabilité s'accompagne d'un phénomène de compensation : quand il y a une vertèbre thoracique en plus, il y a une vertèbre lombaire en moins [53] (pp. 234–235), mais ce n'est pas le cas chez notre individu. Walensky [54] a relevé des valeurs de courbure du fémur les moins élevées chez les individus d'origine africaine. Des caractères discrets ont permis d'identifier des groupements familiaux dans un cimetière soudanais datant du III^{e} au VI^{e} siècle [55]. Ce type d'étude n'est malheureusement pas envisageable à Kindoki, étant donné le faible effectif et la mauvaise préservation des restes osseux.

Les individus masculins des tombes 1 et 5 présentent des usures dentaires semi-circulaires révélatrices de l'utilisation d'une pipe [56]. Cette dernière, surtout lorsqu'elle est en matériau dur, peut en effet entraîner des usures dentaires au niveau des positions préférentiellement adoptées. Fumer le tabac au royaume Kongo est attesté dès 1612 [57], et des exemplaires de pipes en terre cuite et en pierre ont été découverts par l'équipe du projet KongoKing lors des fouilles de la colline de Kindoki [2].

L'étude de la stature ainsi que des pathologies osseuses et dentaires constitue le point de départ d'une recherche plus vaste qui portera sur le régime alimentaire, l'état sanitaire, le statut social et leurs interconnexions. En effet, pour l'instant,

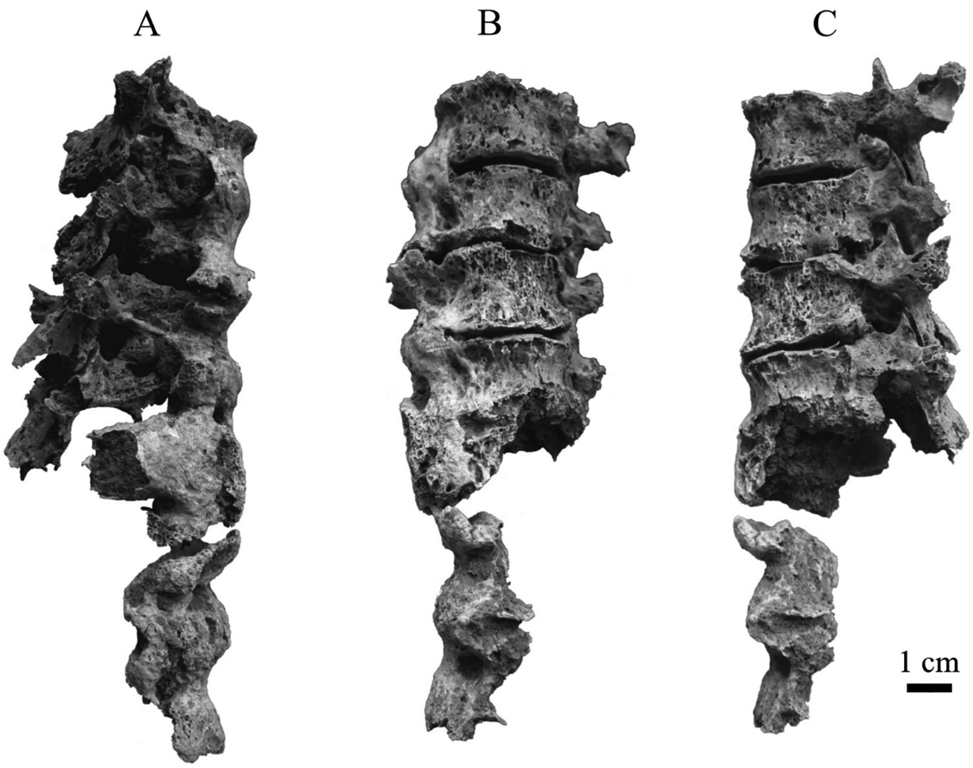


Fig. 9 Sept vertèbres thoraciques de l'individu de la tombe 11 de Kindoki. A. Vue latérale droite. B. Vue antérieure. C. Vue latérale gauche / Seven thoracic vertebrae of the individual from grave n° 11 at Kindoki. A. Right side view. B. Anterior view. C. Left side view

on ne dispose de pratiquement aucune information sur l'alimentation et la santé de ces aristocrates du royaume Kongo. Les comparaisons réalisées avec d'autres populations d'Afrique centrale (voir ci-dessous) sont, à ce stade, exploratoires. Elles ont pour but de mettre en évidence si l'échantillon privilégié de Kindoki se démarque des autres populations de la région.

Les deux statures féminines de Kindoki qui avoisinent 1 m 55–1 m 60 sont comparables à celles des populations actuelles d'Afrique centrale (à l'exception des Pygmées) comme les Bakiga vivant au sud-ouest de l'Ouganda et au nord du Rwanda (moyenne féminine = 155,1 cm) [58], les Lese de RDC (153 cm), les Bagandu et Issongo de la République centrafricaine (154 cm) [59]. La stature masculine qui est de l'ordre de 1 m 60 est par contre inférieure à celle des populations actuelles d'Afrique centrale comme les Bakiga (moyenne masculine = 165,4 cm) et les Luba (165,7 cm) [60] ainsi qu'à celle des populations de la RDC datées du VIII^{e} au XV^{e} siècle comme les Sanga (165,7 cm) et les Katoto (165,8 cm) [61]. Elle est néanmoins similaire à celle des Lese (161 cm) et des Bagandu et Issongo (159 cm) [62].

Les fusions vertébrales principalement localisées du côté droit chez les individus féminins des tombes 8 et 11 sont évocatrices de DISH ou de maladie hyperostosique [29] (pp. 47–54 et 62–64). Ses manifestations rachidiennes consistent en une ossification du ligament vertébral commun antérieur. Au niveau thoracique, celle-ci est limitée au côté droit suite aux pulsations de l'aorte [65]. Le diagnostic de DISH repose sur la présence d'une coulée osseuse impliquant au moins quatre vertèbres thoraciques consécutives [63]. Il est donc confirmé pour l'individu 11, mais reste probable pour l'individu 8. Les fusions costovertébrale et sternocostale du sujet 8 ne font pas partie des signes attribués habituellement au DISH. Elles sont par contre associées à des spondylarthropathies comme la spondylarthrite ankylosante [66]. Le DISH est également caractérisé par des manifestations extrarachidiennes comme des ossifications de diverses enthèses (au niveau des talons, des coudes, des chevilles, des genoux et des épaules) [64,67], mais le mauvais état de conservation des individus ne nous permet pas de les observer. Actuellement, cette affection touche généralement les individus masculins (sex-ratio : 2/1) de plus de 50 ans et est associée à une alimentation riche, à l'obésité et au diabète de type II [68]. Il est donc envisageable que les deux femmes inhumées dans ce cimetière aient eu, de par leur statut social, accès à une alimentation très riche et qu'elles étaient en surpoids. Des cas archéologiques de DISH ont déjà été associés à un statut social élevé [69–73]. Les données actuelles montrent qu'environ 4 % des Noirs africains présentent cette pathologie [65]. Des cas archéologiques de DISH ont été décrits en Afrique du Nord [74,75] et au Botswana [76], mais encore jamais en Afrique centrale.

Le LSAMAT serait dû à la mastication d'aliments très abrasifs comme les tubercules [44,45]. Irish et Turner [77] l'ont observé chez des Sénégalais d'époque contemporaine (XIX^e siècle) et l'ont mis en relation avec la consommation de manioc. Cela pourrait avoir aussi été le cas à Kindoki, car cette plante originaire d'Amérique du Sud fut introduite dans le bassin du Congo par les Portugais au XVI^e siècle [78] (pp. 60–87).

Deux des dix individus de Kindoki présentaient des caries dentaires, et le taux de dents cariées s'élève à 1,6 %. Il n'existe malheureusement pas de données comparatives pour l'Afrique centrale à l'époque concernée (fin XVII^e–début XIX^e siècle). On dispose toutefois de données pour des échantillons plus anciens et plus récents. Les fréquences sont toutes plus élevées qu'à Kindoki. Ainsi, Gutierrez et Valentin ont relevé 6,3 % de dents cariées chez des Angolais de statut social élevé décédés entre le XVI^e et le XVII^e siècle [79]. L'étude menée par Dlamini et al. sur les Sanga et les Katoto, des agriculteurs du Katanga (province la plus méridionale de la RDC) datés du VIII^e au XV^e siècle, a montré des taux de carie respectifs de 17,1 et 3,9 % [80]. Brabant, qui a étudié des crânes hutus du Rwanda datés du début du XX^e siècle, mentionne une fréquence de dents cariées de 4,6 % qui affectaient 20 % des individus (comme à Kindoki) [81]. Walker et Hewlett ont relevé à la fin du XX^e siècle des fréquences de dents cariées de 5,2 à 6 % chez les Pygmées chasseurs-cueilleurs et de 8,1 % chez les Bantous agriculteurs [82]. Ils ont aussi observé que les Pygmées de statut social plus élevé présentaient moins de dents cariées que les autres individus (5,7 contre 7,7 %).

Trois individus de Kindoki présentent des dépôts de tartre mais, étant donné le mauvais état de préservation, certains autres individus pourraient l'avoir perdu post mortem. Des squelettes inhumés dans des conditions plus favorables (en grotte) présentent des prévalences plus élevées comme les Hutus du Rwanda, dont la moitié montrait des dépôts de tartre [81].

Chez les trois individus les mieux conservés de Kindoki, il a été possible de mettre en évidence un mauvais état de santé buccodentaire via la présence de maladie parodontale et de lésions périapicales. Les parodontites sont liées à des facteurs génétiques, hormonaux, systémiques (diabètes de types I et II et ostéoporose), locaux (problèmes occlusaux et présence de tartre), sociaux et comportementaux (tabagisme, stress et mauvaise hygiène buccodentaire) [83]. Il est donc probable qu'à Kindoki le tabagisme, la présence de tartre et peut-être du diabète (souvent associé au DISH) aient accru le risque de développer une maladie parodontale. Près de la moitié des Hutus du Rwanda présentait des signes de cette affection [81]. Les atteintes périapicales infectieuses peuvent faire suite à une carie, à un traumatisme dentaire, à une usure importante ou à la propagation depuis un foyer infectieux voisin (gingivite, parodontite, sinusite) [42] (pp. 143–146). À Kindoki, aucune carie ne semble à l'origine de lésions périapicales. Il est donc possible que ces dernières soient plutôt liées à la parodontopathie. Ces lésions périapicales étaient aussi présentes dans d'autres populations archéologiques d'Afrique centrale, comme les Hutus du Rwanda (16,8 %) [81].

Les hypercémentoses sont généralement causées par des surcharges mécaniques ou une inflammation périapicale [42] (pp. 255–256). Les deux types de facteurs (consommation d'aliments durs et inflammation de l'os alvéolaire) pourraient avoir joué un rôle à Kindoki.

Seul un individu présente de l'hypoplasie de l'émail dentaire, un marqueur de maladie et/ou une malnutrition pendant la croissance. Cette faible prévalence pourrait être liée à leur statut social privilégié, comme cela a été mis en évidence dans d'autres échantillons anciens [84,85] ou récents [86,87].

Conclusion

Les fouilles réalisées sur la colline de Kindoki ont permis la découverte d'un petit cimetière qui renfermait au moins 11 tombes d'aristocrates datées du XVII^e au XIX^e siècle. Comme dans de nombreux autres sites de plein air localisés en climat tropical humide, les restes humains sont très mal conservés. Deux tombes étaient même dépourvues de restes humains. Les études anthropologique et archéologique ont néanmoins révélé la présence de huit hommes et de deux femmes.

Au moins deux de ces hommes étaient des fumeurs de pipe. Une femme était atteinte de DISH, et il est probable que la seconde souffrait aussi de cette maladie. Cette pathologie, qui n'avait pas encore été décrite chez des populations archéologiques d'Afrique centrale, est probablement en relation avec leur statut élevé. Les faibles taux de carie dentaire et d'hypoplasie de l'émail dentaire pourraient, eux aussi, être liés à cette position sociale favorisée. Leur stature, par contre, n'est pas élevée et est comparable (voire inférieure) à celle d'individus vivant actuellement ou il y a quelques centaines d'années en Afrique centrale.

Le tabagisme et le déséquilibre glycémique pourraient être à l'origine de leur mauvais état de santé buccodentaire.

L'étude des particularités anatomiques osseuses n'a pas permis d'identifier d'éventuels liens de parenté au sein des individus inhumés dans ce cimetière. Une étude des caractères discrets dentaires et des analyses d'ADN pourraient apporter des éléments supplémentaires à cette problématique.

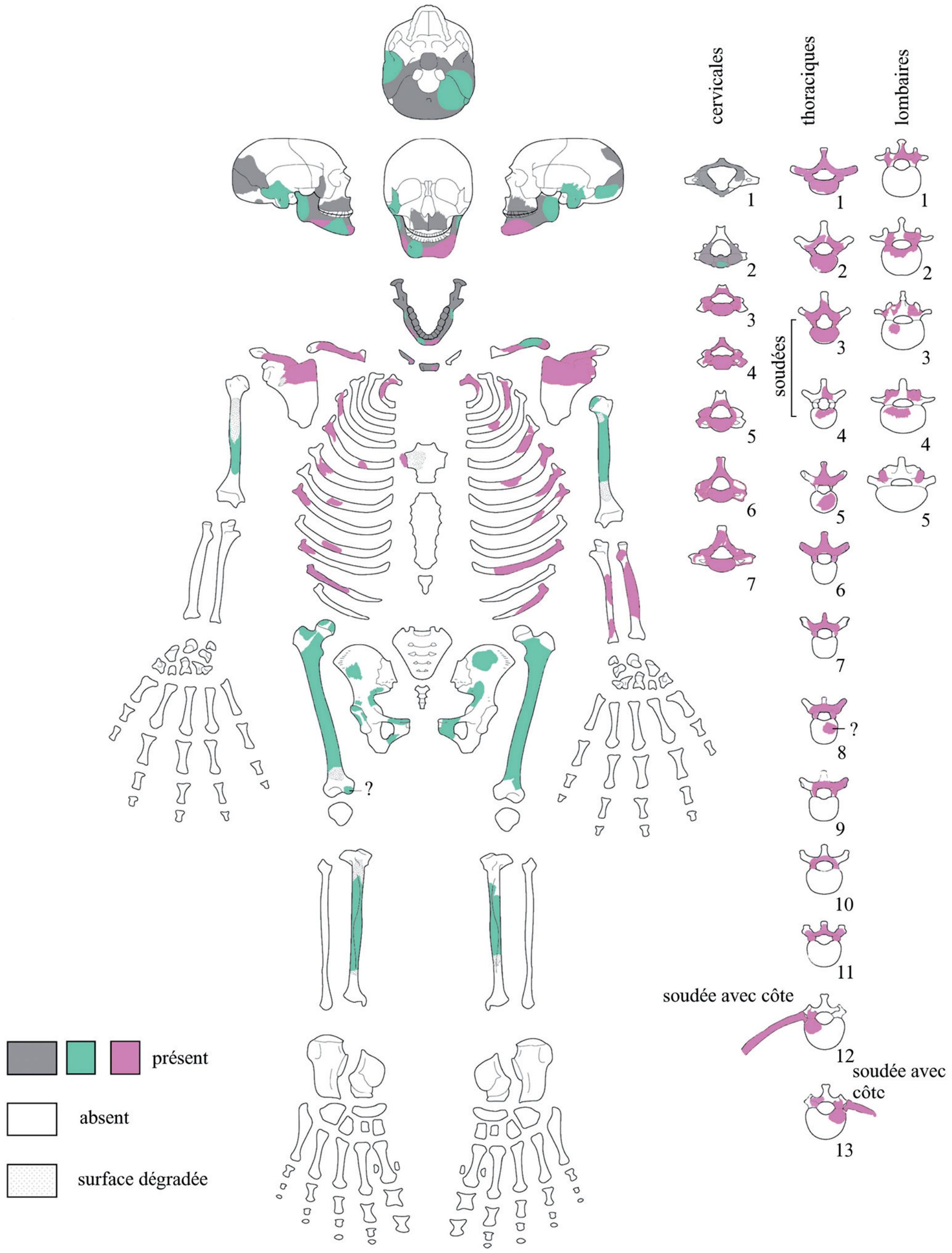
L'usure particulière des incisives supérieures (LSAMAT) indique la consommation d'aliments abrasifs comme le manioc. L'étude des microfossiles végétaux emprisonnés dans le tartre dentaire et des analyses isotopiques du collagène osseux sont en cours. Elles pourraient permettre de confirmer cette hypothèse et d'apporter de nouvelles informations sur le régime alimentaire de ces dignitaires du royaume Kongo.

Remerciements Le projet KongoKing a été financé par le Conseil européen de la recherche (European Research Council Starting Grant No. 284126). Nous adressons nos remerciements à Hélène Déom (UCL/University of Sheffield), Mélodie Ducastelle (ULB), Camille Delmarcelle (UCL) et Nathan Van Kerkhoven (ULB) pour leur aide lors du nettoyage et de l'étude des squelettes. Nous remercions Anne-Marie Wittek (ADIA) pour la réalisation des dessins et Thierry Leduc (IRSNB) pour les analyses chimiques des restes osseux. Les commentaires constructifs des deux relecteurs anonymes ont permis d'améliorer cet article.

Liens d'intérêts : les auteurs déclarent ne pas avoir de lien d'intérêt.

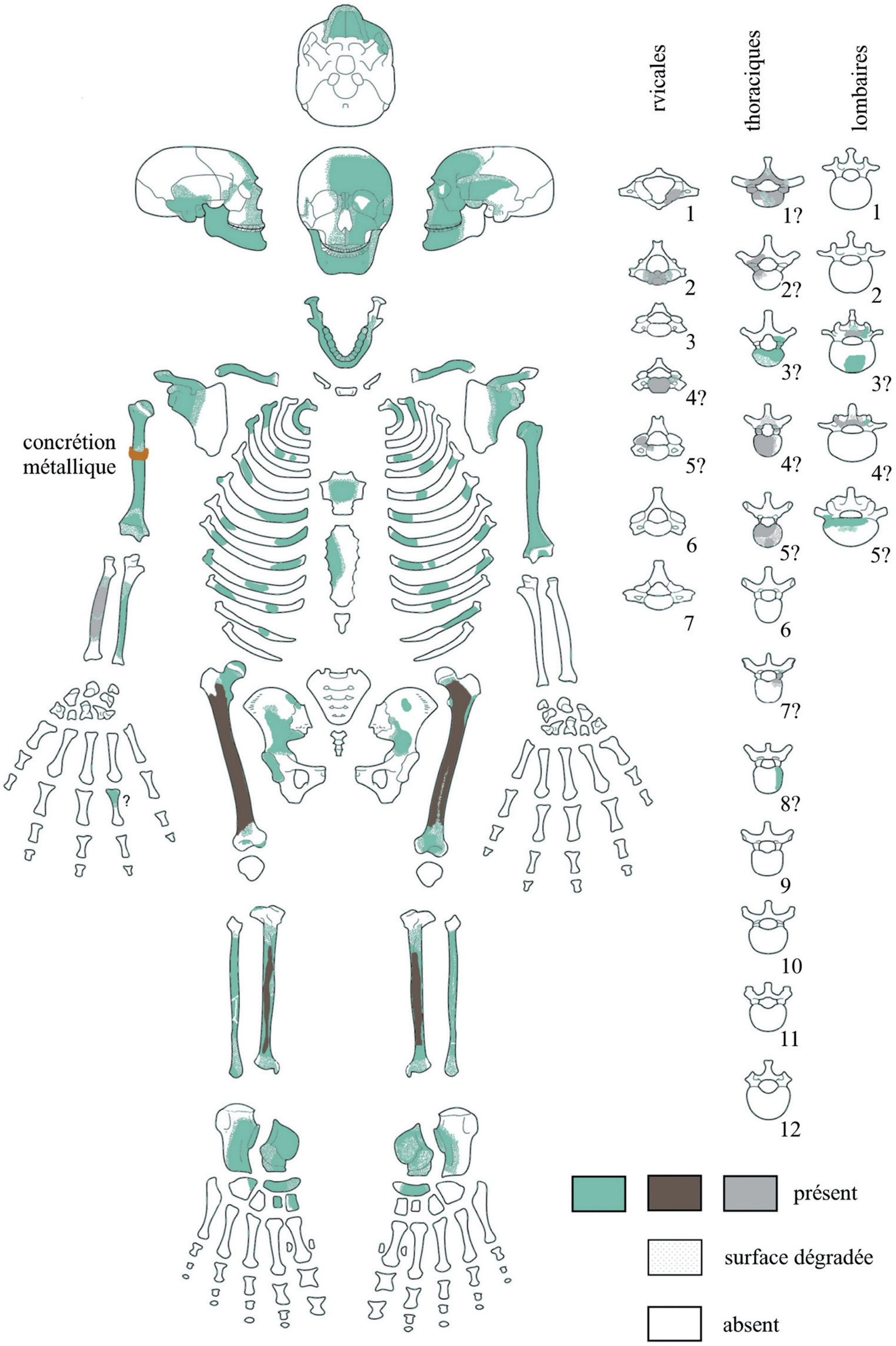
Annexe A

Représentation schématique du squelette de la tombe 8 de Kindoki. Les couleurs des restes osseux y sont figurées : les os de teinte « normale » sont en gris (dessin : M. Coutureau [INRAP] et A.-M. Wittek [ADIA]) / Diagram of the skeleton from grave n$^{\mathrm{o}}$°8 at Kindoki, indicating the colours of the bone remains: the bones of “normal” colour are in grey (drawing : M. Coutureau [INRAP] and A.-M. Wittek [ADIA])



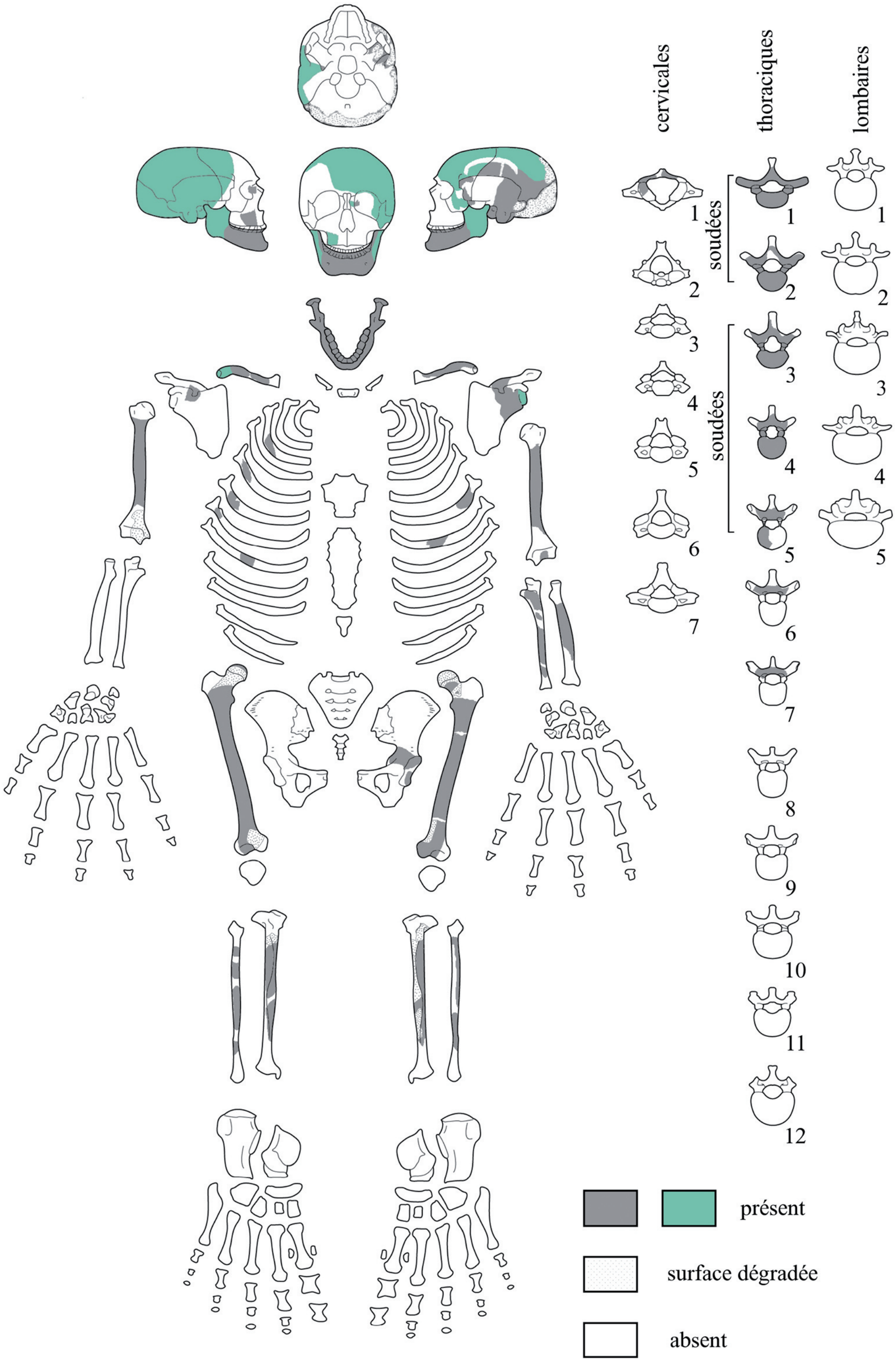
Annexe B

Représentation schématique du squelette de la tombe 9 de Kindoki. Les couleurs des restes osseux y sont figurées : les os de teinte « normale » sont en gris (dessin : M. Coutureau [INRAP] et A.-M. Wittek [ADIA]) / Diagram of the skeleton from grave n°°9 at Kindoki, indicating the colours of the bone remains: the bones of "normal" colour are in grey (drawing : M. Coutureau [INRAP] and A.-M. Wittek [ADIA])



Annexe C

Représentation schématique du squelette de la tombe 11 de Kindoki. Les couleurs des restes osseux y sont figurées : les os de teinte « normale » sont en gris (dessin : M. Coutureau [INRAP] et A.-M. Wittek [ADIA]) / Diagram of the skeleton from grave n°°11 at Kindoki, indicating the colours of the bone remains: the bones of "normal" colour are in grey (drawing : M. Coutureau [INRAP] and A.-M. Wittek [ADIA])



Références

1. Bostoen K, KongoKing. http://research.flw.ugent.be/en/projects/kongoking
2. Clist B, Cranshof E, de Schryver GM, et al (2015) The elusive archaeology of Kongo urbanism: the case of Kindoki, Mbanza Nsundi (Lower Congo, DRC). Afr Archaeol Rev 32:369–412
3. Thornton J (2001) The origins and early history of the Kingdom of Kongo. Int J Afr Hist Stud 34:89–120
4. Clist B, Cranshof E, de Schryver GM, et al (2015), African-European contacts in the Kongo Kingdom (sixteenth-eighteenth centuries): new archaeological insights from Ngongo Mbata (Lower Congo, DRC). Int J Hist Archaeol 19:464–501
5. Esteves E (1989) Mbanza Kongo, ville archéologique. Nsi 6:159–64
6. Souindoula S (1992) Mbanza Soyo: pesquisas arqueolôgicas. Leba 7:277–82
7. Vandenhoute J (1972–1973) De begraafplaats van Ngongo-Mbata (Neder-Zaire). Opgravningsverslag en historische situering. Thèse de master non publiée, Rijksuniversiteit Gent, Gand (Belgique)
8. Ladmirant H, Annaert A (1970) Carte géologique du Congo. Feuille Inkisi S.6/15. Institut géographique militaire de Belgique, Bruxelles
9. Bultot F (1950) Carte des régions climatiques du Congo belge établie d'après les critères de Köppen. INEAC, Publications du Bureau climatique 9, Bruxelles, 15 p
10. Wamuini Lunkayilakio S (2010). Ichtyofaune de l'Inkisi (Bas-Congo / RDC) : diversité et écologie. Thèse de doctorat en sciences non publiée de l'Université de Liège (Belgique), 351 p
11. de Maret P (2002) Urban origins in central Africa — The case of Kongo. In: Sinclair PJJ (ed) The development of urbanism from a global perspective. University of Uppsala, Uppsala, pp 1–15
12. Verhaeghe C, Clist B, Fontaine C, et al (2014) Shell and glass beads from the tombs of Kindoki, Mbanza Nsundi, Lower Congo. Beads 33:22–33
13. Bontinck F, Castro Segovia J (1972) Histoire du royaume du Congo (c. 1624). Études d'Histoire africaine IV, Éditions Nauwelaers, Beauvechain (Belgique), 145 p
14. Thornton J (2013) Afro-christian syncretism in the Kingdom of Kongo. J Afr Hist 54:53–77
15. Dutour O (1989) Hommes fossiles du Sahara : peuplements holocènes du Mali septentrional. Éditions du CNRS, Paris, 342 p
16. McKinley JI (2004) Compiling a skeletal inventory: disarticulated and co-mingled remains. In: Brickley M, McKinley JI (eds) Guidelines to the standards for recording human remains. BABAO and Institute of Field Archaeologists, Southampton (UK), IFA Paper No. 7, pp 14–7
17. Ferembach D, Schwidetzky I, Stloukal M (1979) Recommandations pour déterminer l'âge et le sexe sur le squelette. Bull Mem Soc Anthropol Paris 6:7–45
18. Krogman WM, İşcan MY (1986) The human skeleton in forensic medicine. 2nd edition. CC Thomas, Springfield, 551 p
19. Franklin D, O'Higgins P, Oxnard CE, et al (2006) Determination of sex in South African Blacks by discriminant function analysis of mandibular linear dimensions: a preliminary investigation using the Zulu local population. Forensic Sci Med Pathol 2:263–8
20. Dibennardo K, Taylor JV (1982) Classification and misclassification in sexing the Black femur by discriminant function analysis. Am J Phys Anthropol 58:145–51
21. İşcan MY, Miller-Shaivitz P (1984) Determination of sex from the tibia. Am J Phys Anthropol 64:53–7
22. Macaluso PJ Jr (2010) Sex discrimination potential of permanent maxillary molar cusp diameters. J Forensic Odontostomatol 28:22–31
23. Orban R, Semal P, Molleson T (1989) La nécropole médiévale de Coxyde (Belgique) : propos sur la détermination du sexe. Anthropol Prehist 100:57–70
24. Lovejoy CO (1985) Dental wear in the Libben population: its functional pattern and role in the determination of adult skeletal age at death. Am J Phys Anthropol 68:47–56
25. Scheuer L, Black S (2000) Developmental juvenile osteology. Academic Press, San Diego, 587 p
26. Trotter M, Gleser G (1952) Estimation of stature from long bones of American Whites and Negroes. Am J Phys Anthropol 10:463–514
27. Steele DG, McKern TW (1969) A method for assessment of maximum long bone length and living stature from fragmentary long bones. Am J Phys Anthropol 31:215–27
28. Aufderheide AC, Rodríguez-Martín C (1998) The Cambridge encyclopedia of human paleopathology. Cambridge University Press, Cambridge, 478 p
29. Rogers J, Waldron T (1995) A field guide to joint disease in archaeology. John Wiley & Sons, Chichester, 119 p
30. Hillson S (1996) Dental anthropology. Cambridge University Press, Cambridge, 373 p
31. Brothwell, DR (1963) Digging up bones. The excavation, treatment and study of human skeletal remains. British Museum, Londres, 194 p
32. Olivier G (1960) Pratique anthropologique. Vigot frères, Paris, 299 p
33. Capasso L, Kennedy KAR, Wilczak CA (1999) Atlas of occupational markers on human remains. Atto, Teramo (Italie), 183 p
34. Dupras TL, Schultz JJ (2013) Taphonomic bone staining and color changes in forensic contexts. In: Pokines J, Symes SA (eds) Manual of forensic taphonomy. CRC Press, Boca Raton (USA), pp 315–40
35. Clist B, de Maret P, Bostoen K (eds) Archéologie des provinces septentrionales du royaume Kongo. Oxford, Archaeopress [in press]
36. Stewart TD (1957) Rate of development of vertebral hypertrophic arthritis and its utility in age estimation. Am J Phys Anthropol 15: 433
37. Simon L, Claustre J, Blotman F (1984) Abrégé de rhumatologie. 4^{e} éd. Masson, Paris, 592 p
38. Mikkelsen WM, Duff IF, Dodge HJ (1970) Age-sex specific prevalence of radiographic abnormalities of the joints of the hands, wrists and cervical spine of adult residents of Tecumseh, Michigan, Community Health Study area, 1962–1965. J Chronic Dis 23:151–9
39. Metress JF, Conway T (1975) Standardized system for recording dental caries in prehistoric skeletons. J Dent Res 54:908
40. Duyninh T, Jame O, Bousquet P, et al (2005) Classification des maladies parodontales. EMC–Odontologie 1:58–66
41. Brabant H, Sahly A (1962) La paléostomatologie en Belgique et en France : essai de synthèse de recherches personnelles. Acta Stomatol Belg 59:286–355
42. Piette E, Goldberg M (2001) La dent normale et pathologique. De Boeck Université, Bruxelles, 392 p
43. Dias G, Tayles N (1997) "Abscess cavity" — a misnomer. Int J Osteoarchaeol 7:548–54
44. Becker A, Karnei-R'em RM (1992) The effects of infraocclusion: Part 1. Tilting of the adjacent teeth and local space loss. Am J Orthod Dentofacial Orthop 102:256–64
45. Turner CG 2nd, Machado LM (1983) A new dental wear pattern and evidence for high carbohydrate consumption in a Brazilian archaic skeletal population. Am J Phys Anthropol 61:125–30

46. Dent BB, Forbes SL, Stuart BH (2004) Review of human decomposition processes in soil. Environ Geol 45:576–85
47. Hassett B (2006) Torus mandibularis: etiology and bioarcheological utility. Dental Anthropology 19:1–14
48. Hauser G, De Stefano GF (eds) (1989) Epigenetic variants of the human skull. Schweizerbart, Stuttgart, 301 p
49. Chapman T, Sholukha V, Semal P, et al (2015) Femoral curvature variability in modern humans using three-dimensional quadric surface fitting. Surg Radiol Anat 37:1169–77
50. Reginato A, Roques JC, Pommereau X, et al (1987) Le torus mandibularis. Bull Mem Soc Anthropol Paris 4:25–32
51. Corruccini RS (1974) An examination of the meaning of cranial discrete traits for human skeletal biological studies. Am J Phys Anthropol 40:425–45
52. Ajmani ML, Mittal RK, Jain SP (1983) Incidence of the metopic suture in adult Nigerian skulls. J Anat 137:177–83
53. Olivier G (1965) Anatomie anthropologique. Vigot frères, Paris, 488 p
54. Walensky NA (1965) A study of anterior femoral curvature in man. Anat Rec 151:559–70
55. Crubézy É, Telmon N, Sevin A, et al (1999) Microévolution d'une population historique. Étude des caractères discrets de la population de Missiminia (Soudan, III^e^–VI^e^ siècle). Bull Mem Soc Anthropol Paris 11:1–213
56. Scott GR, Turner II CG (1988) Dental anthropology. Annu Rev Anthropol 17:99–126
57. Jones A (1983) Samuel Brun's voyages of 1611–20. In: Jones A (ed) German sources for West-African history, 1599–1669. Wiesbaden, Franz Steiner, pp 60–1
58. Perry GH, Foll M, Grenier JC, et al (2014) Adaptive, convergent origins of the pygmy phenotype in African rainforest hunter-gatherers. Proc Natl Acad Sci 111: E3596–E603
59. Eveleth PB, Tanner JM (1990) Worldwide variation in human growth. Cambridge University Press, Cambridge, 2nd edition, 397 p
60. Hiernaux J (1964) Luba du Katanga et Luba du Kasai (Congo) ; comparaison de deux populations de même origine. Bull Mem Soc Anthropol Paris 6:611–22
61. Hiernaux J, Plantier M, De Buyst J (1992) Étude ostéométrique des restes humains de Sanga et Katoto (âge du fer, Zaïre). Anthropol Prehist 103:9–44
62. Holgate RL, Steyn M (2016) Diffuse idiopathic skeletal hyperostosis: diagnostic, clinical and paleopathological considerations. Clin Anat 29:870–7
63. Crubézy É, Crubézy-Ibáñez E (1993) Évaluation sur une série de squelettes de critères diagnostiques de la maladie hyperostosique. Implications épidémiologiques. Rev Rhum 60:586–90
64. Resnick D, Niwayama G (1976) Radiographic and pathologic features of spinal involvement in diffuse idiopathic skeletal hyperostosis (DISH). Radiology 119:559–68
65. Utsinger PD (1985) Diffuse idiopathic skeletal hyperostosis. Clin Rheum Dis 11:325–51
66. Olivieri I, D'Angelo S, Palazzi C, et al (2009) Diffuse idiopathic skeletal hyperostosis: differentiation from ankylosing spondylitis. Curr Rheumatol Rep 11:321–8
67. Mader R, Sarzi-Puttini P, Atzeni F, et al (2009) Extraspinal manifestations of diffuse idiopathic skeletal hyperostosis. Rheumatology 48:1478–81
68. Burner TW, Rosenthal AK (2009) Diabetes and rheumatic diseases. Curr Opin Rheumatol 21:50–4
69. Rogers J, Waldron T (2001) DISH and the monastic way of life. Int J Osteoarchaeol 11:357–65
70. Jankauskas R (2003) The incidence of diffuse idiopathic skeletal hyperostosis and social status correlations in Lithuanian skeletal materials. Int J Osteoarchaeol 13:289–93
71. Giuffra V, Giusiani S, Fornaciari A, et al (2010) Diffuse idiopathic skeletal hyperostosis in the Medici, Grand Dukes of Florence (XVI century). Eur Spine J 19:S103–S7
72. Blondiaux J, Alduc-Le Bagousse A, Demondion X, et al (2007) Maladie hyperostosique et maladie goutteuse, une diathèse familiale en Normandie : Thaon, Calvados. Bull Mem Soc Anthropol Paris 19:7–20
73. Kacki S, Villotte S (2006) Maladie hyperostosique et mode de vie : intérêt d'une démarche bioarchéologique. Exemple du cimetière du couvent des Sœurs Grises de Beauvais (Oise), XV^{e}–XVIII^{e} siècles. Bull Mem Soc Anthropol Paris 18:55–64
74. Dupras TL, Williams LJ, Willems H, et al (2010) Pathological skeletal remains from ancient Egypt: the earliest case of diabetes mellitus? Practical Diabetes Int 27:358–63a
75. Saleem SN, Hawass Z (2014) Ankylosing spondylitis or diffuse idiopathic skeletal hyperostosis in royal Egyptian mummies of 18th–20th Dynasties? CT and archaeology studies. Arthritis Rheumatol 66:3311–6
76. Mosothwane MN, Steyn M (2009) In sickness or in health? Assessment of Early Iron Age human skeletons from Toutswe sites, east central Botswana. Int J Osteoarchaeol 19:66–77
77. Irish JD, Turner CG 2nd (1997) First evidence of LSAMAT in non-native Americans: historic Senegalese from West Africa. Am J Phyl Anthropol 102:141–6
78. Jones W (1959) Manioc in Africa. Stanford University Press, Stanford, 315 p
79. Gutierrez M, Valentin F (1995) Archéologie et anthropologie des tumulus de Kapanda (Angola). J Africanistes 65:145–69
80. Dlamini N, Morris AG, Sealy J (2016) Carbon isotopes and dental caries as evidence for regional variation in the diets of early farming communities from Katanga, Democratic Republic of the Congo. J Afr Archaeol 14:135–53
81. Brabant H (1963) Observations anthropologiques et odontologiques sur les dents des Hutus du Rwanda. Musée royal de l'Afrique centrale, Tervuren (Belgique), Annales, séries in-8°. Sciences humaines, n^{o} 47, 30 p
82. Walker PL, Hewlett BS (1990) Dental health, diet and social status among Central African foragers and farmers. Am Anthropol 92:383–98
83. Nunn ME (2003) Understanding the etiology of periodontitis: an overview of periodontal risk factors. Periodontol 2000 32:11–23
84. Nakayama N (2016) The relationship between linear enamel hypoplasia and social status in 18th to 19th Century Edo, Japan. Int J Osteoarchaeol 26:1034–44
85. Miszkiewicz JJ (2012) Linear enamel hypoplasia and age-at-death at Medieval (11th–16th Centuries) St. Gregory's Priory and Cemetery, Canterbury, UK. Int J Osteoarchaeol 25:79–87
86. Skinner MF, Hung JTW (1989) Social and biological correlates of localized enamel hypoplasia of the human deciduous canine tooth. Am J Phyl Anthropol 79:159–75
87. Lukacs JR (1991) Localized enamel hypoplasia of human deciduous canine teeth: prevalence and pattern of expression in rural Pakistan. Hum Biol 63:513–22

BMSAP (2018) 30:90-101
DOI 10.3166/bmsap-2018-0009

ARTICLE / *ARTICLE*

De l’est à l’ouest de l’Afrique, une seule morphologie pygmée qui diffère de celle des Non-Pygmées

From East to West Africa, a Single Pygmy Morphology that Differs from Non-Pygmies

F.V. Ramirez Rozzi · A. Froment · J. Ghesquière

Reçu le 5 septembre 2017 ; accepté le 25 janvier 2018

Résumé En plus de leur taille réduite, les groupes pygmées ont été décrits comme présentant des proportions corporelles particulières qui pourraient résulter d’une réduction d’échelle (allométrie) au cours de la croissance. Cependant, les groupes pygmées pourraient ne pas partager la même morphologie. À partir de l’analyse des mensurations corporelles et des allométries de trois groupes pygmées de différentes régions d’Afrique et d’un groupe non pygmée, nous avons testé a) s’il existe plus d’une morphologie chez les Pygmées et b) si la différence avec les Non-Pygmées peut être expliquée par des processus allométriques. Nos résultats suggèrent que les groupes pygmées partagent la même morphologie : la diversité morphologique chez les Pygmées s’opère au long d’un même axe qui est isométrique. Par contre, chez les Non-Pygmées, la conformation se modifie en fonction de la variation de la taille, car la taille et le tronc présentent un rapport allométrique. Donc, la différence de conformation entre Pygmées et Non-Pygmées ne peut pas être expliquée par une réduction d’échelle, elle indique plutôt deux modalités distinctes de constitution corporelle.

Mots clés Pygmées · Proportion corporelle · Conformation · Taille · Allométrie

Abstract Besides their small body size, the various Pygmy groups found across different African regions have generally been described as presenting particular body proportions. This could result from a reduction of scale (allometry) during growth, relatively to non-Pygmy groups. However, morphological differences may also exist between the Pygmy groups. In this study, we have analyzed body measurements and allometries in Pygmy groups from different regions and also in a non-Pygmy group, to test whether: a) Pygmies have more than one morphology (intra-Pygmy variability), and b) differences with non-Pygmies can be explained by allometric processes. Our results suggest that all Pygmies share the same morphology, with morphological variations occurring along the same axis, which is isometric. In non-Pygmies, on the other hand, changes in shape occur with changes in size: the trunk shows an allometric relationship with size. Thus, the differences in body shape between Pygmies and non-Pygmies cannot be explained only by a reduction of scale, but rather it suggests two different patterns of morphological development.

Keywords Pygmies · Body proportion · Shape · Size · Allometry

Le terme « pygmée » a longtemps été utilisé pour désigner les populations d’Afrique équatoriale ayant une taille moyenne adulte inférieure à 1,55 m [1]. Il comprend des groupes répartis en deux ensembles géographiques, l’un à l’ouest (Baka, Aka, Kola, Bongo, Bedzan et Koya) et l’autre à l’est (Aka, Efé, Sua et Twa). Le groupe Twa habitant dans la zone du lac Tumba en République démocratique du Congo (RDC) est aussi considéré comme groupe pygmée [2] ; Vallois [3] les nommait les Pygmées du « centre ». Tous ces groupes parlent des langues différentes et sont reconnus comme des Pygmées non seulement en raison de leur petite taille, mais encore et surtout par leurs caractéristiques sociales et économiques. Ce sont à l’origine des groupes de chasseurs-cueilleurs semi-nomades qui se caractérisent aussi par des rapports très particuliers, complexes et très divers, avec les groupes voisins non pygmées [4].

F.V. Ramirez Rozzi (✉)
UMR 5288 AMIS, faculté de chirurgie dentaire,
1 rue Maurice-Arnoux, 92120 Montrouge, France
e-mail : fernando.ramirez-rozzi@cnrs.fr

A. Froment
UMR 7206, Musée de l’Homme, 17, place du Trocadéro,
75116 Paris, France

J. Ghesquière
Faculty of Kinesiology and Rehabilitation Sciences,
Tervuursevest 101, box 1500, 3001 Leuven, Belgium

Lavoisier

Les études en génétique des populations ont révélé que, bien que l'utilisation d'une taille adulte moyenne comme critère de distinction entre groupes pygmées et non pygmées soit arbitraire, elle reflète assez correctement l'existence d'entités biologiques distinctes. En effet, Patin et al. [5,6], en comparant l'ADN nucléaire de cinq groupes pygmées, trois originaires de l'Ouest et deux de l'Est, et de cinq groupes non pygmées, ont suggéré que la lignée pygmée s'est séparée de celle non pygmée il y a environ 60 000 ans et que les sous-ensembles est et ouest de groupes pygmées ont divergé depuis environ 20 000 ans. Verdu et al. [7,8], analysant les microsatellites des groupes pygmées et non pygmées de l'Ouest, arrivent à des conclusions semblables et ont suggéré que les groupes pygmées de l'Ouest sont issus d'une population ancestrale qui s'est diversifiée il y a près de 2 800 ans.

La taille réduite des Pygmées résulte de fondements génétiques [9,10]. Les études sur les facteurs de croissance responsables du phénotype pygmée ont été réalisées en considérant que les processus endocriniens étaient les mêmes dans les deux ensembles [11–18]. Or, les études sur la croissance somatique ont révélé que la taille réduite des Pygmées est un phénomène de convergence évolutive, les modalités de croissance étant différentes entre les groupes de l'Est et de l'Ouest [19]. En effet, tandis que dans les groupes de l'Est [20] la croissance intra-utérine a été restreinte, les groupes de l'Ouest se caractérisent par une croissance ralentie pendant la petite enfance.

Depuis les premières descriptions des Pygmées, les auteurs ont été étonnés non seulement par la taille réduite, mais aussi par des proportions corporelles particulières [21,22]. Bien que ces premières impressions ne fussent pas supportées par des analyses, Poutrin [23] pour les Pygmées de l'Ouest et Pagezy [2] pour les Twa du lac Tumba ont confirmé que les Pygmées présentent, par rapport au tronc, des membres inférieurs plus courts que chez les Non-Pygmées, tandis qu'il n'y a pas de différences pour les membres supérieurs.

La conformation particulière des Pygmées ne résulterait pas pour autant de modifications importantes dans la dimension des différentes parties corporelles. Shea et Bailey [24] ont comparé la conformation chez les Pygmées Efé et les groupes non pygmées. Disposant d'individus adultes, mais aussi de subadultes, ils ont pu établir l'allométrie ontogénique des Efé et ont observé que les adultes non pygmées se situent dans le prolongement de cette allométrie. La conformation particulière des Pygmées Efé résulte donc principalement d'une réduction d'échelle au long de la croissance allométrique (*ontogenetic scaling*). En d'autres mots, tout Non-Pygmée qui aurait arrêté sa croissance avec une taille semblable à celle des Pygmées présenterait la même conformation qu'un Pygmée adulte.

Vallois [3], en comparant les Pygmées de l'Ouest et de l'Est, a observé que les premiers présentent une plus grande stature et un tronc plus long. Mais il ne peut pas affirmer que ceux de l'Ouest sont des Pygmées avec des traits moins marqués que ceux de l'Est, car le tronc des Pygmées occidentaux, bien que plus long, est plus étroit que celui des Pygmées de l'Est (argument pour refuser l'hypothèse de l'existence des Pygmées et des Pygmoïdes de Schebesta [25]). Vallois suggère donc la présence de plus d'un type dans la conformation pygmée.

L'objectif de ce travail est de comparer les proportions des Pygmées de l'Est, de l'Ouest et du centre pour confirmer ou infirmer l'existence de plusieurs conformations. La conformation des Pygmées est aussi comparée à celle des Non-Pygmées vivant dans le même environnement.

Matériel

La comparaison des rapports métriques entre populations ne peut pas s'effectuer à partir des mesures de la tendance centrale ; les allométries ontogéniques et statiques (qui se réfèrent à une seule étape de la croissance) ne peuvent se calculer qu'avec les données individuelles. Après avoir compilé les archives de différentes institutions, nous avons pu obtenir les données individuelles de plusieurs enquêtes biométriques. Ayant pour objectif la comparaison de la conformation des groupes pygmées de différents ensembles, nous présentons ici les données des Pygmées Baka du Cameroun, des Efé de l'Ituri et des Twa du lac Tumba (RDC).

Les mensurations des Baka (80 femmes, 61 hommes) ont été obtenues en 2010 et 2015 (AF et FRR) lors d'une étude longitudinale de la croissance dans la localité du Bosquet (Cameroun) [19,26]. Les mesures des Efé (31 femmes, 35 hommes) ont été fournies par Bailey et correspondent à celles qui ont été utilisées par Shea et Bailey [24]. Bailey n'a pas mesuré la taille en position assise. L'un de nous (JG) a mesuré des Twa de sexe masculin lors de ses séjours dans les années 1960 au lac Tumba [27,28] ; les mesures des femmes ont été fournies par les travaux de Pagezy [2]. Un total de 59 Twa (29 femmes, 30 hommes) sont inclus dans cette étude, mais certaines mesures manquent pour quelques individus. Pour le groupe non pygmée, nous avons utilisé, comme Shea et Bailey [24], les données publiées par Czekanowski [29]. Cet anthropologue polonais n'avait examiné que des hommes adultes, donc la comparaison avec les Pygmées sera limitée à 50 hommes du groupe Hiru mesurés dans la région de Toro, à l'ouest de Fort Portal, zone frontière entre l'Ouganda et la RDC.

Méthodes

Les mesures corporelles classiques ont été considérées pour effectuer l'analyse de la conformation : poids, taille, taille assise, hauteur à l'épine iliaque antérieure (Heias) qui permet d'estimer la hauteur des membres inférieurs, longueur maximale du membre supérieur, largeur entre les épaules (diamètre biacromial) et largeur au niveau du bassin (diamètre bicrête, entre les crêtes iliaques) (Tableau 1).

Les Baka ont des âges connus [19] et les Efé, des âges estimés [24]. Nous avons retenu les individus à partir de 14 ans. Une étude reposant exclusivement sur des individus adultes ne permettrait d'obtenir que l'allométrie statique pour cette étape de la croissance, tandis que l'inclusion des individus subadultes permet de caractériser au moins la dernière phase de l'allométrie ontogénique. Les autres groupes ne sont représentés que par des individus adultes, et donc leurs analyses se réfèrent à l'allométrie statique.

Dans une première étape, seuls les individus adultes (≥ 18 ans) ont été inclus dans l'analyse, afin d'évaluer le dimorphisme sexuel des variables et des proportions dans chaque groupe (*t*-test). La comparaison entre les groupes a aussi été effectuée en considérant seulement les adultes (*t*-test).

Il faut préciser que nous considérons comme analyse des allométries la comparaison entre la taille (totale ou d'une variable) et la conformation (proportion d'un trait sur la taille) selon l'école Gould-Mosimann [30]. La comparaison de deux mensurations ne conduit pas à déterminer des allométries (école Huxley-Jolicœur) [31,32]. Les courbes de régression des moindres carrés entre taille et conformation représentent la croissance allométrique qui peut être :

- isométrique si le ratio entre deux variables (conformation) ne se modifie pas (régression non significative) au cours de la modification de la variable indépendante (taille) ;
- allométrique si la conformation se modifie (régression significative) au cours de la modification de la variable indépendante (taille).

Tableau 1 Mesures et abréviations / *Measurements and abbreviations*

Et = écart-type = *SD = standard deviation*
Es = erreur standard = *SE = standard error*
BMI = indice de masse corporelle = *body mass index*
T = taille = size Tassis = taille assise = *seated height*
Heais = hauteur à l'épine iliaque antérieure = *height anterior iliac spine*
LMS = longueur du membre supérieur = *upper member length*
Biacro = diamètre biacromial = *biacromial breadth*
Bicrête = diamètre des bicrêtes iliaques = *biiliac diameter*
ND = non disponible = *not available*
NS = non significative = *not significant*
TassT = ratio Tassis / Taille = *Seated height/Size ratio*
HeiasT = ratio Heais / Taille = *HeiasT/size ratio*
LMSTass = ratio LMS / Tassis = *LMS/seated height ratio*
BiacroTass = ratio Biacro / Tassis = *Biacro/seated height ratio*

Donc, tout d'abord des régressions entre les variables et la taille (conformation) ont été calculées pour les adultes de chaque sexe de chaque groupe ; les régressions ont été comparées entre les sexes au sein de chaque groupe et entre les groupes. Si l'observation de Vallois [3] est correcte, on s'attendra à ce que les Baka diffèrent des Efé au moins dans les régressions qui prennent en compte le diamètre biacromial. Ensuite, pour établir la croissance allométrique statique (adultes), des régressions ont été obtenues entre la conformation et la taille pour chaque sexe de chaque groupe. Enfin, ces régressions allométriques ont été comparées entre les groupes pygmées et le groupe non pygmée. Si les régressions ne montrent pas de différence significative ($p \leq 0{,}05$), il n'est pas possible de distinguer plus d'un type de morphologie.

La comparaison entre les régressions a été effectuée avec le logiciel SPSS. Le degré de signification dans la différence de pente et d'interception de l'axe Y entre deux lignes de régression peut être obtenu avec l'analyse de covariance (ANCOVA), appelée « modèle linéaire général univarié » dans la version française de SPSS. Mais ce logiciel permet aussi de comparer des régressions à partir d'une analyse de variance (ANOVA) dans laquelle une variable factice codée de façon binaire (0, 1) et une autre variable résultant du produit entre la variable factice et la variable indépendante accompagnent celle-ci comme covariables. La variable factice sert à séparer les deux groupes à comparer [33]. Pour effectuer cette analyse, il faut partir d'une régression linéaire. Dans le tableau résultant, le coefficient de la variable factice indique le degré de signification de la différence des interceptions avec l'axe Y, tandis que celui du produit de cette variable avec l'indépendante donne la comparaison des coefficients de régression (pente).

Une dernière analyse concerne l'allométrie ontogénique. Elle a été obtenue chez les Baka et les Efé en incluant les individus subadultes pour caractériser l'allométrie ontogénique, au moins pendant la dernière étape de la croissance. Nous avons testé si les Hiru se situent dans le même axe de croissance que les groupes pygmées [24]. Pour cette comparaison, bien évidemment, seulement les hommes Baka et Efé ont été considérés.

Résultats

Le même type de dimorphisme sexuel existe dans les trois groupes pygmées (Tableau 2), les différences sont significatives, excepté pour l'indice de masse corporelle et le diamètre bicrête. Par contre, le dimorphisme sexuel des proportions corporelles ne semble pas suivre la même modalité selon les groupes. Chez les Baka et les Efé, la longueur du membre supérieur est proportionnellement plus importante que la taille, et la longueur du membre inférieur est plus

Tableau 2 Dimorphisme sexuel des variables chez les Pygmées / *Sexual dimorphism in Pygmy traits*

Groupe	**Variable**	**Sexe**	***n***	**Moyenne**	**Et**	**Es**	***p***
Baka	Poids	H	42	48,7	4,86	0,75	**
		F	64	44,3	5,16	0,64	
	Taille	H	42	154,4	4,03	0,62	**
		F	64	147,0	5,23	0,65	
	BMI	H	42	20,38	1,43	0,22	NS
		F	64	20,44	1,61	0,20	
	Tassis	H	42	81,1	2,71	0,42	**
		F	64	77,0	2,89	0,36	
	Heais	H	42	87,6	2,62	0,40	**
		F	64	83,6	3,86	0,48	
	LMS	H	42	71,7	2,39	0,37	**
		F	64	66,9	3,56	0,45	
	Biacro	H	42	35,9	1,59	0,25	**
		F	64	33,0	1,80	0,23	
	Bicrête	H	42	24,5	1,45	0,22	NS
		F	64	24,2	1,20	0,15	
Twa	Poids	H	27	48,0	5,11	0,98	**
		F	29	42,9	6,20	1,15	
	Taille	H	27	159,0	5,38	1,04	**
		F	29	148,7	5,26	0,98	
	BMI	H	27	18,98	1,79	0,35	NS
		F	29	19,36	2,16	0,40	
	Tassis	H	23	83,0	2,79	0,58	**
		F	28	77,7	2,59	0,49	
	Heais	H	23	88,8	4,61	0,96	**
		F	29	83,5	4,64	0,86	
	LMS	H	23	70,3	3,09	0,64	**
		F	29	65,1	2,85	0,53	
	Biacro	H	23	34,1	1,54	0,32	**
		F	29	30,7	2,64	0,49	
	Bicrête	H	23	23,3	1,16	0,24	*
		F	29	22,5	1,46	0,27	
Efé	Poids	H	25	42,9	4,82	0,96	**
		F	29	38,1	4,26	0,79	
	Taille	H	25	146,0	5,61	1,12	**
		F	29	138,9	3,90	0,73	
	BMI	H	25	20,07	1,42	0,28	NS
		F	29	19,74	1,86	0,35	
	Tassis	H					
		F					
	Heais	H	25	79,7	3,70	0,74	**
		F	29	76,0	2,82	0,52	
	LMS	H	24	65,5	3,22	0,66	**
		F	29	61,4	2,49	0,46	
	Biacro	H	25	34,5	6,60	1,32	**
		F	29	29,7	5,37	1,00	
	Bicrête	H	24	22,8	1,05	0,21	NS
		F	23	22,7	1,09	0,23	

*: $p \leq 0,05$; **: $p \leq 0,01$

Tableau 3 Dimorphisme sexuel des proportions / *Sexual dimorphism in body proportions*

	Tassise Taille	Heias Taille	LMS Taille	LMS Tassise	Biacro Tassise	Bicrête Tassise	LMS Heias	Biacro Taille	Bicrête Taille
Baka	NS	NS	**	NS	**	**	**	**	**
Efe	nd	NS	*	nd	nd	nd	**	NS	**
Twa	NS	NS	NS	NS	*	*	NS	*	*

*: P ≤ 0,05, **: P ≤ 0,01

Tableau 4 Différences entre les groupes Pygmées / *Differences among Pygmy groups*

Homme									
	Poids	**T**	**BMI**	**Tassis**	**Heias**	**LMS**	**Biacro**	**Bicrête**	**TassT**
Baka–Twa	NS	**	**	*	NS	*	**	**	NS
Baka–Efé	**	**	NS	ND	**	**	NS	**	ND
Twa–Efé	**	**	*	ND	**	**	NS	NS	ND
	HeiasT	**LMST**	**LMSTass**	**BiacroTass**	**BicrêtTass**	**LMSHeias**	**BiacroT**	**BicrêteT**	
Baka–Twa	*	**	**	**	**	**	**	**	
Baka–Efé	**	**	ND	ND	ND	NS	NS	NS	
Twa–Efé	**	*	ND	ND	ND	**	*	**	
Femmes									
	Poids	**T**	**BMI**	**Tassis**	**Heias**	**LMS**	**Biacro**	**Bicrête**	**TassT**
Baka–Twa	NS	NS	**	NS	NS	**	**	**	NS
Baka–Efé	**	**	NS	ND	**	**	**	**	ND
Twa–Efé	**	**	NS	ND	**	**	NS	NS	ND
	HeiasT	**LMST**	**LMSTass**	**BiacroTass**	**BicrêtTass**	**LMSHeias**	**BiacroT**	**BicrêteT**	
Baka–Twa	*	**	**	**	**	**	**	**	
Baka–Efé	**	**	ND	ND	ND	NS	NS	NS	
Twa–Efé	**	NS	ND	ND	ND	**	**	**	

*: *p* ≤ 0,05 ; **: *p* ≤ 0,01

grande chez les hommes que chez les femmes (Tableau 3). Chez les Twa et les Baka, les hommes ont par rapport au tronc des épaules plus larges et une ceinture pelvienne plus étroite que les femmes. Ces aspects n'ont pas pu être étudiés chez les Efé. Pour combler cette lacune, nous avons examiné les proportions des diamètres biacromial et bicrête avec la taille. Les résultats pour les Baka et les Twa sont semblables en ce qui concerne la taille assise, c'est-à-dire un dimorphisme sexuel élevé pour les Baka et moins marqué pour les Twa. Les Efé présentent comme les Baka un dimorphisme marqué pour le rapport bicrête et taille, mais il n'y a pas de dimorphisme sexuel pour le rapport entre biacromial et taille.

Les différences entre les groupes sont présentées dans le tableau 4. La plupart des variables montrent des différences significatives. On peut remarquer que les Efé se distinguent des deux autres groupes par leur taille et leur poids et que le groupe Twa présente des proportions qui le distinguent des deux autres. Contrairement à ce qui a été observé par Vallois [3], les Baka (Pygmées de l'Ouest) ont un diamètre

Tableau 5 Comparaison des régressions entre les sexes / *Comparisons of linear regressions between sexes*

	Conformation	***Coefficient***	***Intersection***
		p	***p***
Baka	Heias/Taille	0,179	0,192
	LMS/Taille	0,989	0,902
	Biacro/Taille	0,532	0,449
	Bicrêt/Taille	0,666	0,606
	Tassis/Taille	0,093	0,108
Twa	Heias/Taille	0,432	0,471
	LMS/Taille	0,602	0,648
	Biacro/Taille	0,822	0,742
	Bicrêt/Taille	0,235	0,275
	Tassis/Taille	0,971	0,944
Efé	Heias/Taille	0,822	0,784
	LMS/Taille	0,643	0,681
	Biacro/Taille	0,627	0,593
	Bicrêt/Taille	0,58	0,514

biacromial plus large que les Efé (Pygmées de l'Est), mais la différence n'est significative que pour les femmes. Le rapport entre la hauteur du membre inférieur et la taille distingue les trois groupes, de même que le rapport entre la taille et la longueur du membre supérieur pour les hommes.

Les résultats pour les régressions entre les variables et la taille sont présentés dans le tableau 5 (entre les sexes) et le tableau 6 (entre les groupes). Les régressions ne sont dissemblables ni entre les sexes ni entre les groupes pygmées (Fig. 1). Donc, la conformation ne change pas significativement ni entre les sexes d'un même groupe ni entre les groupes de Pygmées ; leurs différences sont fortement influencées par les modifications de taille. Quand les groupes pygmées sont comparés avec les Hiru (Non-Pygmées), la seule différence observée concerne le rapport entre la taille assise et la taille chez les Baka, mais pas chez les Twa (la taille assise n'a pas été obtenue chez les Efé). Pour ce qui est de la comparaison entre la conformation et la taille (rapport allométrique), toutes les régressions entre les groupes pygmées montrent que la conformation (ratio entre les variables) ne change pas significativement quand la taille (variable indépendante) se modifie (p < 0,05) (Tableau 7) (Fig. 2). L'unique exception est le rapport du ratio taille assise/taille avec la taille chez les femmes Baka et Twa, dont les coefficients de détermination (R2) sont de toute façon bas. En d'autres termes, les modifications sont isométriques, les corps changent de taille, mais gardent toujours une conformation semblable. Par contre, chez les Non-Pygmées, les ratios des diamètres et de la taille assise avec la stature montrent une allométrie statique négative par rapport à la stature (Tableau 7). Ainsi, le coefficient de détermination signale que les équations de régression ne montrent pas une forte prédiction de la distribution des points, l'augmentation en taille s'accompagne clairement d'une diminution proportionnelle des diamètres et de la taille assise, ce qui produit un changement de conformation.

Tableau 6 Comparaison des régressions entre les groupes pygmées et les Hiru / *Comparisons of linear regressions among Pygmy groups and the Hiru*

Comparaison	**Conformation**	**Hommes**		**Femmes**	
		Coefficient	***Intersection***	***Coefficient***	***Intersection***
		p	***p***	***p***	***p***
Baka/Twa	Heias/Taille	0,381	0,349	0,245	0,211
	LMS/Taille	0,998	0,816	0,438	0,78
	Biacro/Taille	0,573	0,722	0,462	0,611
	Bicrêt/Taille	0,789	0,921	0,124	0,069
Baka/Efé	Heias/Taille	0,263	0,171	0,671	0,801
	LMS/Taille	0,452	0,361	0,853	0,709
	Biacro/Taille	0,938	0,945	0,113	0,108
	Bicrêt/Taille	0,91	0,949	0,791	0,84
Twa/Efé	Heias/Taille	0,9	0,954	0,24	0,255
	LMS/Taille	0,486	0,556	0,539	0,559
	Biacro/Taille	0,818	0,87	0,16	0,202
	Bicrêt/Taille	0,809	0,948	0,21	0,15
Hiru/Baka	Heias/Taille	0,463	0,568		
	LMS/Taille	0,64	0,657		
	Biacro/Taille	0,222	0,301		
	Bicrêt/Taille	0,261	0,279		
	Tassis/Taille	0,015	0,033		
Hiru/Efé	Heias/Taille	0,765	0,497		
	LMS/Taille	0,294	0,24		
	Biacro/Taille	0,524	0,573		
	Bicrêt/Taille	0,214	0,188		
Hiru/Twa	Heias/Taille	0,71	0,579		
	LMS/Taille	0,67	0,557		
	Biacro/Taille	0,526	0,52		
	Bicrêt/Taille	0,364	0,284		
	Tassis/Taille	0,511	0,718		

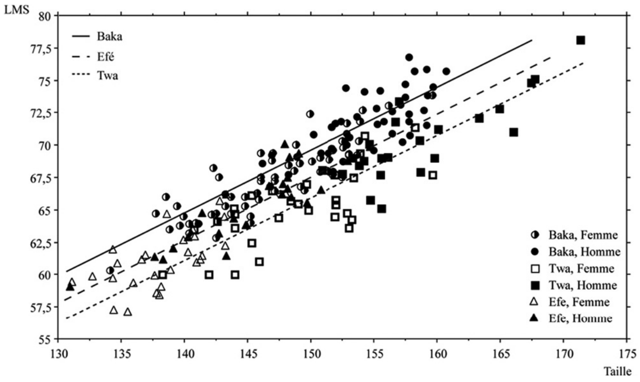


Fig. 1 Rapport entre la longueur du membre supérieur (LMS) et la taille dans les trois groupes de Pygmées par sexe. Les lignes de régression correspondent aux hommes. Elles ne sont pas différentes ($p < 0,05$) ni entre les sexes ni entre les groupes. Les trois groupes présentent le même rapport (conformation) / *Ratio between upper member length (LMS) and size in the three Pygmy groups by sex. Only regressions for males are shown. Regressions do not differ by sex or by group. The same ratio is observed for all three groups (shape)*

L'isométrie chez les groupes pygmées contraste avec l'allométrie des dimensions du tronc chez le groupe non pygmée. La comparaison entre ces régressions allométriques permet de déterminer si ces différences sont significatives. Les résultats de cette comparaison sont présentés dans le tableau 8. Bien que les allométries des diamètres chez les Hiru ne montrent pas une différence significative avec les isométries chez les groupes pygmées, les régressions allométriques concernant le ratio taille assise/taille avec la taille sont significativement différentes entre les Hiru et les Baka. La différence de conformation révélée par les régressions significativement différentes entre la taille assise et la taille (tableau 6) se traduit par un rapport allométrique distinct entre ces groupes (Tableau 8). Donc, les Baka diffèrent du groupe non pygmée par un tronc plus long par rapport à la taille (Fig. 3).

La présence d'une allométrie négative chez les Hiru signale que l'augmentation en taille n'est pas suivie d'une augmentation des dimensions du tronc, mais qu'elle résulte principalement d'une variation importante dans la taille des membres inférieurs. Chez les Baka, l'isométrie suggère que la quantité de variation de la taille et celle du tronc sont proportionnelles. Le tableau 9 donne les écarts de variations de différentes mesures chez les Baka et les Hiru. L'écart de la taille assise est semblable dans les deux groupes, tandis que celui de la taille chez les Hiru correspond au double, en valeurs absolues, de celui chez les Baka, fortement influencé par la variation de la longueur des membres inférieurs.

Quand les individus subadultes des Baka et des Efé sont inclus dans l'analyse, on observe, comme il a été décrit pour l'allométrie statique adulte, que les régressions ne sont pas significatives (Tableau 10), ce qui indique que les allométries ontogéniques suivent une croissance isométrique. Il n'existe pas de différence significative ni entre les sexes ni entre les groupes. Donc, les Baka et les Efé (hommes et femmes) partagent la même allométrie ontogénique pendant la dernière étape de la croissance. Quand ces allométries ontogéniques sont comparées à l'allométrie statique des Hiru, les différences entre les Baka et ce groupe non pygmée s'accentuent (Tableau 11). En effet, en plus du ratio taille assise/taille, les rapports des diamètres avec la taille deviennent très dissemblables (Fig. 3). Le diamètre entre les crêtes iliaques par rapport à la taille distingue aussi les Efé des Hiru. Ces résultats mettent en évidence que les proportions du tronc par rapport à la taille chez les Baka suivent une croissance allométrique (isométrique) qui se distingue des rapports observés chez les Hiru. Ceux-ci ne se placent pas dans la continuité de la croissance ontogénique des Baka (Fig. 3).

Discussion

Les premières observations biométriques signalaient que, en plus de leur petite taille, les Pygmées se distinguent des Non-Pygmées par leurs proportions corporelles [22]. Poutrin [34] a été le premier à proposer des valeurs qui suggéraient que le tronc des Pygmées de l'Ouest était, par rapport aux membres inférieurs, plus long que celui des Non-Pygmées. Vallois [3] a même suggéré que la conformation du tronc différait entre les Pygmées de l'Est et de l'Ouest. Toutes ces analyses se sont limitées à comparer les valeurs moyennes, aucun traitement statistique n'a été réalisé pour comprendre si les résultats indiquaient une différence significative. Plus récemment, Shea et Bailey [24], fondés sur une ANCOVA, ont suggéré que des différences significatives dans la conformation existent entre les Efé et les Non-Pygmées, mais ces différences correspondent à des variations sur la même droite ontogénique. D'après Shea et Bailey, la conformation des Non-Pygmées et celle des Efé, bien que dissemblables, se situent dans le même axe de croissance.

Nous avons comparé trois groupes de Pygmées provenant de trois régions différentes et un groupe de Non-Pygmées (Hiru) qui habite comme les Pygmées la forêt équatoriale. Nos résultats suggèrent que les trois groupes de Pygmées se différencient par de nombreux aspects, qu'il s'agisse des mensurations ou des rapports entre les mensurations. Contrairement aux observations de Vallois [3], les Baka montrent des diamètres plus grands que les Efé. Cependant, les régressions de la conformation avec la taille (allométrie statique chez les adultes) montrent toutes que les changements au sein de chaque groupe sont isométriques. La conformation ne change pas entre hommes et femmes ni

Tableau 7 Régressions entre la conformation et la taille (allométrie statique, adultes) / *Regressions between shape and size (static allometry, adults)*

Groupe	Sexe	Allométrie	Régression	p	R^2
Baka	Hommes	HeiasTaille/Taille	$y = 61{,}578 - 0{,}032x$	0,427	0,016
		LMSTaille/Taille	$y = 47{,}747 - 0{,}008x$	0,832	0,001
		BiacroTaille/Taille	$y = 27{,}239 - 0{,}026x$	0,468	0,013
		BicrêteTaille/Taille	$y = 17{,}023 - 0{,}008x$	0,821	0,001
		TassisTaille/Taille	$y = 51{,}340 + 0{,}008x$	0,86	0,001
	Femmes	HeiasTaille/Taille	$y = 50{,}426 + 0{,}044x$	0,182	0,029
		LMSTaille/Taille	$y = 46{,}357 - 0{,}004x$	0,859	0,001
		BiacroTaille/Taille	$y = 21{,}742 + 0{,}005x$	0,831	0,001
		BicrêteTaille/Taille	$y = 20{,}932 - 0{,}030x$	0,077	0,05
		TassisTaille/Taille	$y = 66{,}306 - 0{,}095x$	0,008	0,108
Twa	Hommes	HeiasTaille/Taille	$y = 49{,}586 + 0{,}040x$	0,595	0,014
		LMSTaille/Taille	$y = 43{,}788 + 0{,}003x$	0,942	0,000
		BiacroTaille/Taille	$y = 27{,}881 - 0{,}040x$	0,229	0,068
		BicrêteTaille/Taille	$y = 16{,}560 - 0{,}012x$	0,606	0,013
		TassisTaille/Taille	$y = 66{,}934 - 0{,}092x$	0,06	0,158
	Femmes	HeiasTaille/Taille	$y = 37{,}733 + 0{,}123x$	0,052	0,132
		LMSTaille/Taille	$y = 47{,}636 - 0{,}026x$	0,588	0,011
		BiacroTailleTaille	$y = 24{,}113 - 0{,}023x$	0,697	0,006
		BicrêteTaille/Taille	$y = 11{,}229 + 0{,}026x$	0,322	0,036
		TassisTaille/Taille	$y = 67{,}977 - 0{,}106x$	0,022	0,187
Efé	Hommes	HeiasTaille/Taille	$y = 47{,}764 + 0{,}047x$	0,189	0,074
		LMSTaille/Taille	$y = 38{,}502 + 0{,}044x$	0,239	0,062
		BiacroTaille/Taille	$y = 24{,}940 - 0{,}009x$	0,956	0,000
		BicrêteTaille/Taille	$y = 17{,}768 - 0{,}015x$	0,425	0,029
	Femmes	HeiasTaille/Taille	$y = 50{,}583 + 0{,}030x$	0,605	0,01
		LMSTaille/Taille	$y = 42{,}024 + 0{,}016x$	0,797	0,002
		BiacroTaille/Taille	$y = 9{,}591 + 0{,}090x$	0,052	0,133
		BicrêteTaille/Taille	$y = 22{,}025 - 0{,}041x$	0,306	0,05
Hiru	Hommes	HeiasTaille/Taille	$y = 56{,}98 + 0{,}007x$	0,803	0,001
		LMSTaille/Taille	$y = 50{,}909 - 0{,}03x$	0,354	0,018
		BiacroTaille/Taille	$y = 32{,}748 - 0{,}07x$	0,003	0,17
		BicrêteTaille/Taille	$y = 22{,}367 - 0{,}043x$	0,002	0,181
		TassisTaille/Taille	$y = 66{,}554 - 0{,}108x$	0,0003	0,24

entre les groupes ; les différences dans les mensurations ne seraient qu'une conséquence d'échelle. Par contre, le groupe non pygmée se caractérise par une conformation qui diffère notamment de celle des Baka. Les Hiru présentent un tronc moins long par rapport à la taille. Les allométries statiques négatives des Non-Pygmées indiquent que la variation en taille ne s'accompagne pas d'une variation proportionnelle du tronc, mais implique un allongement de membres plus important que celui du tronc. Chez les Pygmées, l'allométrie statique du corps suit des processus isométriques, le tronc garde une proportion identique avec la taille. Ce phénomène explique dans une certaine mesure l'observation souvent mentionnée des membres plus courts chez les Pygmées que chez les Non-Pygmées [2,23].

Shea et Bailey [24] ont suggéré que la croissance des Efé et des Non-Pygmées ne suit pas la ligne isométrique ; pour cette raison Efé et Non-Pygmées présentent des conformations différentes. Par contre, ces auteurs ont suggéré qu'ils se placent sur la même trajectoire de croissance. Nous avons utilisé les données de Shea et Bailey pour les Efé, et contrairement aux observations de ces auteurs, nos analyses suggèrent que l'allométrie statique (adulte) et l'allométrie ontogénique chez les Efé suivent l'axe isométrique ou en tout cas ne s'en écartent pas significativement. Les différentes interprétations des résultats sont liées à des divergences sur ce qu'est une allométrie.

Toute analyse allométrique se réfère à l'étude de la variation de la conformation par rapport à la taille (*change in*

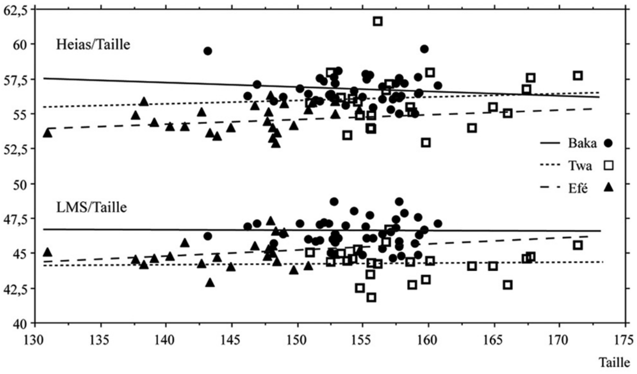


Fig. 2 Allométrie statique chez les Pygmées (hommes). Les changements de taille ne s'accompagnent pas de modifications dans la conformation, il y a un rapport isométrique. La comparaison entre groupes indique que les régressions ne sont pas différentes (α = 0,05). L'allométrie statique est la même pour les groupes pygmées / *Static allometry in Pygmies (males). Changes in size are not paralleled by changes in shape: the relationship is isometric. Comparison among groups shows that the regressions are not dissimilar (α = 0.05). Static allometry is the same in the three Pygmy groups*

Tableau 8 Comparaison des allométries statiques entre Pygmées et Non-Pygmées / *Comparisons of static allometry between Pygmies and non-Pygmies*

	Baka/Hiru	**Efe/Hiru**	**Twa/Hiru**
Allométrie	***p***	***p***	***p***
HeiasTaille/Taille	0,483	0,459	0,629
LMSTaille/Taille	0,723	0,24	0,616
BiacroTaille/Taille	0,34	0,592	0,521
BicrêteTaille/Taille	0,293	0,283	0,277
TassisTaille/Taille	0,044		0,787

shape and size) [30,32, 35–38]. Shea et Bailey [24] parlent de croissance allométrique, cependant ils n'analysent pas ce type de rapport. En observant les figures, il est clair qu'ils n'ont pas effectué une véritable analyse allométrique, mais ont comparé la variation entre deux mensurations ; cette comparaison peut en effet donner un aperçu de la conformation. La lecture attentive des figures montre que l'augmentation d'une variable s'accompagne d'une augmentation proportionnelle de l'autre variable. Ces résultats n'indiquent cependant pas une allométrie, ils indiquent que les variables gardent le même rapport, la conformation est toujours la même, ce qui veut dire qu'il s'agit d'isométries.

Ces auteurs ont suggéré que les Non-Pygmées se placent dans la continuation de la croissance ontogénique des Efé [24]. Il est vrai que, en ce qui concerne le rapport des membres avec la taille, l'allométrie statique des Hiru ne se distingue pas de l'axe de croissance ontogénique des Pygmées (Baka et Efé) (Tableau 10). Par contre, la croissance ontogénique des Baka diffère clairement de celle des Hiru dans le rapport que le tronc présente avec la taille. Il est très intéressant de remarquer que dans la figure 9 du travail de Shea et Bailey [24] (p. 321), dans laquelle le diamètre biacromial est comparé à la hauteur sternale, la droite qui représente les adultes non pygmées s'éloigne de la ligne isométrique suivie par le groupe pygmée, ce qui indique le rapport allométrique de ce diamètre par rapport à d'autres mesures.

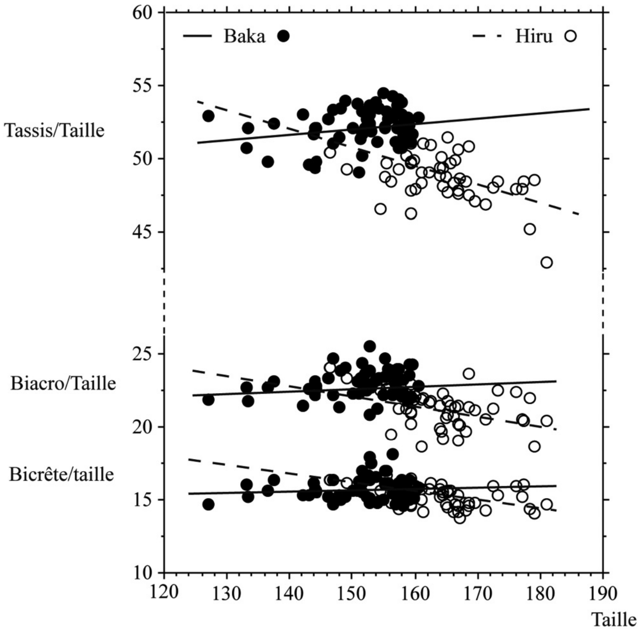


Fig. 3 Allométrie ontogénique chez les Baka et allométrie statique chez les Hiru. Les variables du tronc présentent un rapport isométrique avec la taille chez les Baka. Par contre, la variation chez les adultes Hiru s'effectue en suivant un rapport allométrique. Les Hiru ne se placent pas sur l'axe de la croissance ontogénique des Baka / *Ontogenic allometry in the Baka and static allometry in the Hiru. Trunk dimensions in the Baka vary isometrically with size, while the pattern of variation in adult Hiru is allometric. The Hiru do not follow the same axis of ontogenic growth as the Baka*

Conclusion

Les groupes pygmées montrent un dimorphisme sexuel semblable. Les différences observées entre les groupes dans les mensurations et les proportions corporelles semblent correspondre plutôt à des différences de taille, d'échelle et, dans une moindre mesure, à la variation de la conformation qui est semblable dans les trois groupes pygmées. Il n'y a pas de différence significative entre les rapports des variables, ce

Tableau 9 Écart de la variation des variables chez les Baka et les Hiru / *Range of variation of variables in the Baka and the Hiru*

		Taille	**Tassis**	**Heias**	**LMS**	**Biacro**	**Bicrête**	**TassisTaille**
Hiru	Minimum	146,5	72	81,4	66,4	30,1	22,7	42,9
	Maximum	181,1	86,8	105,8	84,6	39,9	28,4	52,7
	Écart	34,6	14,8	24,4	18,2	9,8	5,7	9,75
Baka	Minimum	143,2	71	82,3	66,2	31,9	22	49,6
	Maximum	160,7	85,2	95,3	76,8	39	28,3	54,6
	Écart	17,5	14,2	13	10,6	7,1	6,3	5

Tableau 10 Allométries ontogéniques chez les Baka et les Efé / *Ontogenic allometry in the Baka and the Efe*

Groupe	**Sexe**	**Allométrie**	**Régression**	***p***
Baka	Hommes	HeiasTaille/Taille	$y = 60{,}134 - 0{,}021x$	0,285
		LMSTaille/Taille	$y = 42{,}8 + 0{,}024x$	0,145
		BiacroTaille/Taille	$y = 18{,}535 + 0{,}029x$	0,072
		BicrêteTaille/Taille	$y = 14{,}285 + 0{,}01x$	0,495
		TassisTaille/Taille	$y = 46{,}238 + 0{,}039x$	0,079
	Femmes	HeiasTaille/Taille	$y = 50{,}024 + 0{,}047x$	0,112
		LMSTaille/Taille	$y = 45{,}068 + 0{,}005x$	0,802
		BiacroTaille/Taille	$y = 22{,}541 - 0{,}001x$	0,97
		BicrêteTaille/Taille	$y = 19{,}451 - 0{,}021x$	0,152
Efé	Hommes	HeiasTaille/Taille	$y = 60{,}36 - 0{,}038x$	0,149
		LMSTaille/Taille	$y = 41{,}746 + 0{,}023x$	0,274
		BiacroTaille/Taille	$y = 15{,}506 + 0{,}054x$	0,513
		BicrêteTaille/Taille	$y = 16{,}11 - 0{,}003x$	0,761
	Femmes	HeiasTaille/Taille	$y = 51{,}834 + 0{,}021x$	0,648
		LMSTaille/Taille	$y = 45{,}295 - 0{,}008x$	0,873
		BiacroTaille/Taille	$y = 15{,}892 + 0{,}045x$	0,218
		BicrêteTaille/Taille	$y = 20{,}894 - 0{,}033x$	0,273

Tableau 11 Allométrie ontogénique des Pygmées comparée à l'allométrie statique des Hiru / *Ontogenic allometry in Pygmies compared to static allometry in the Hiru*

Allométrie	**Baka/Hiru**			**Efé/Hiru**		
	Coefficient	***Intersection***		***Coefficient***	***Intersection***	
	p	***p***	R^2	***p***	***p***	R^2
HeiasTaille/Taille	0,395	0,549	0,194	0,247	0,567	0,573
LMSTaille/Taille	0,117	0,141	0,06	0,199	0,153	0,096
BiacroTaille/Taille	0,000	0,001	0,457	0,098	0,132	0,148
BicrêteTaille/Taille	0,008	0,01	0,168	0,026	0,024	0,209
TassisTaille/Taille	0,000	0,000	0,65			

qui infirme l'idée de plusieurs conformations chez les Pygmées. Les analyses des allométries statiques chez les trois groupes pygmées et des allométries ontogéniques chez les Efé et les Baka indiquent que les changements corporels chez les Pygmées se font en suivant des rapports isométriques. Tout indique donc que les différents groupes pygmées partagent une même morphologie.

Par contre, le groupe non pygmée présente une allométrie statique négative du tronc par rapport à la taille. La comparaison des allométries statiques signale que les Baka se distinguent des Hiru dans le rapport que la longueur du tronc présente avec la taille. Les différences du rapport du tronc avec la taille s'accentuent si l'allométrie ontogénique est considérée. L'observation répandue des Pygmées ayant des membres inférieurs courts résulterait donc d'une croissance isométrique du tronc par rapport à la taille chez les Pygmées, tandis que la variation chez les Non-Pygmées adultes suit une allométrie statique négative. En d'autres termes, le tronc et les jambes grandissent et varient proportionnellement chez les Pygmées, tandis que les jambes s'allongent de façon plus importante que le tronc chez les adultes non pygmées. Un changement d'échelle chez les Pygmées, comme il a été suggéré [24], ne suffit pas à expliquer cette différence qui indique plutôt deux modalités distinctes de constitution corporelle.

Remerciements Nous tenons à remercier R. Bailey pour avoir partagé ses données. Nous pensons très particulièrement à H. Pagezy. Nous remercions deux rapporteurs anonymes dont les commentaires ont aidé à améliorer ce travail. Nos remerciements vont aussi au personnel de l'IRD à Yaoundé et aux sœurs spiritaines du Bosquet par leur chaleureux accueil. Nous n'oublions pas nos collaborateurs sur le terrain Kalo, Etoa, Pierre et Basile. Ce travail a été soutenu financièrement en partie par une bourse de la National Geographic (#8 863–10), une bourse de la Wenner-Gren Foundation (Gr7810) et le projet ANR Blanc SVSE7-2011 « GrowinAP ».

Liens d'intérêt : Les auteurs déclarent de pas avoir de liens d'intérêt.

Références

1. Cavalli-Sforza LL (1986) African Pygmies. Academic Press, New York, 461 p
2. Pagezy H (1973) Adaptation physique et organisation des activités quotidiennes de femmes pygmoïdes Twa et de Non pygmoïdes Oto de la forêt équatoriale (lac Tumba, Zaïre). Thèse, Paris VII, 149 p
3. Vallois HV (1940) New research on the western Negrilles. Am J Phys Anthropol 26:448–71
4. Robillard M, Bahuchet S (2012) Les Pygmées et les autres : terminologie, catégorisation et politique. J Africanistes 82:15–51
5. Patin E, Laval G, Barreiro LB, et al (2009) Inferring the demographic history of African farmers and Pygmy hunter-gatherers using a multilocus resequencing data set. PLoS Genet 5: e1000448
6. Patin E, Siddle KJ, Laval G, et al (2014) The impact of agricultural emergence on the genetic history of African rainforest hunter-gatherers and agriculturalists. Nat Commun 5:3163
7. Verdu P, Austerlitz F, Estoup A, et al (2009) Origins and genetic diversity of pygmy hunter-gatherers from Western Central Africa. Curr Biol 19:312–8
8. Verdu P, Becker NS, Froment A, et al (2013) Sociocultural behavior, sex-biased admixture, and effective population sizes in Central African Pygmies and Non-pygmies. Mol Biol Evol 30:918–37
9. Becker NS, Verdu P, Froment A, et al (2011) Indirect evidence for the genetic determination of short stature in African Pygmies. Am J Phys Anthropol 145:390–401
10. Becker NS, Verdu P, Georges M, et al (2012) The role of GHR and IGF1 genes in the genetic determination of African pygmies' short stature. Eur J Hum Genet 21:1–6
11. Merimee TJ, Hewlett BS, Wood W, et al (1989) The growth hormone receptor gene in the African Pygmy. Trans Assoc Am Physicians 102:163–9
12. Baumann G, Shaw MA, Merimee TJ (1989) Low levels of high-affinity growth hormone-binding protein in African Pygmies. N Engl J Med 320:1705–9
13. Bowcock A, Sartorelli V (1990) Polymorphism and mapping of the IGF1 gene, and absence of association with stature among African Pygmies. Hum Genet 85:349–54
14. Schneid H, Le Bouc Y, Seurin D, et al (1990) Insulin-like growth factor-I gene analysis in subjects with constitutionally variant stature. Pediatr Res 27:488–91
15. Geffner ME, Bersch N, Bailey RC, Golde DW (1995) Insulin-like growth factor1 resistance in immortalized T cell lines from African Efé Pygmies. J Clin Endocrinol Metab 80:3732–8
16. Hattori Y, Vera JC, Rivas CI, et al (1996) Decreased insulin-like growth factor I receptor expression and function in immortalized African Pygmy T cells. J Clin Endocrinol Metab 81:2257–63
17. Dulloo AG, Shahkhalili Y, Atchou G, et al (1996) Dissociation of systemic GH-IGF-I axis from a genetic basis for short stature in African Pygmies. Eur J Clin Nutr 50:371–80
18. Bozzola M, Travaglino P, Marziliano N, et al (2009) The shortness of Pygmies is associated with severe under-expression of the Growth Hormone receptor. Mol Genet Metab 98:310–3
19. Ramírez Rozzi F, Koudou Y, Froment A, et al (2015) Growth pattern from birth to adulthood in African pygmies of known age. Nat Commun 6:7672
20. Bailey RC (1991) The comparative growth of Efé pygmies and African farmers from birth to age 5 years. Ann Hum Biol 18:113–20
21. Schweinfurth G (1874) Im Herzen von Afrika, vol. II. FA Brockhaus, Leipzig, 564 p
22. Regnault M (1911) Les Babenga. L'Anthropologie 22:261–88
23. Poutrin L (1911) Contribution à l'étude des pygmées d'Afrique : les Négrilles du Centre africain. L'Anthropologie 22:421–549
24. Shea BT, Bailey RC (1996) Allometry and adaptation of body proportions and stature in African Pygmies. Am J Phys Anthropol 100:311–40
25. Schebesta P (1938) Die Bambuti-Pygmaën von Ituri. Mémoires vol I, Institut royal colonial belge, 438 p
26. Ramírez Rozzi FV (2016) Diversity in tooth eruption and life history in humans: illustration from a Pygmy population. Sci Rep 6:27405
27. Austin DM, Ghesquiere J (1976) Heat tolerance of Bantu and Pygmoid groups of the Zaire River Basin. Hum Biol 48:439–53
28. Austin D, Ghesquiere J, Azama M (1979) Work capacity and body morphology of Bantu and Pygmoid groups of Western Zaire. Hum Biol 51:79–89
29. Czekanowski J (1922) Ethnographie–Anthropologie. In: Forschungen im Nil-Kongo-Zwischengebeit Anthropologische Beobachtungen Wissenschaftliche ergebnisse der Deutschen Zentral-Afrika-Expedition 1907–1908, volume IV, Klinkhardt & Biermann, Leipzig, pp. 143–473
30. Gould SJ (1966) Allometry and size in ontogeny and phylogeny. Biol Rev Camb Philos Soc 41:587–640
31. Joli cœur P (1963) The multivariate generalization of the allometry equation. Biometrics 19:497–9
32. Godfrey LR, Sutherland MR (1995) What's growth got to do with it? Process and product in the evolution of ontogeny. J Hum Evol 29:405–31

33. Introduction to SAS. UCLA: Statistical Consulting Group. from https://stats.idre.ucla.edu/spss/faq/how-can-i-compare-regression-coefficients-between-two-groups
34. Poutrin L (1911) Anthropologie, ethnographie, linguistique. In: Cottes A (ed) Travaux scientifiques de la mission Cottes au Sud-Cameroun. Ernest Leroux, Paris, pp 125–219
35. Gould SJ (1977) Ontogeny and phylogeny. Cambridge MA, Harvard University Press, 501 p
36. Godfrey LR, Sutherland MR (1996) The paradox of peramorphic paedomorphosis: heterochrony and human evolution. Am J Phys Anthropol 99:17–42
37. Klingenberg CP (1998) Heterochrony and allometry: the analysis of evolutionary change in ontogeny. Biol Rev Camb Philos Soc 73:79–123
38. Ramírez Rozzi FV (2000) Hétérochronies : état des lieux. Primatologie 3:479–512

BMSAP (2018) 30:102-106
DOI 10.1007/s13219-017-0199-4

NOTE / *NOTE*

Le squelette de l'homme fossile d'Asselar (Mali, Holocène ancien) : observations archéothanatologiques

Archeothanatological Observations on the Human Skeleton from Asselar (Early Holocene, Mali)

J. Dumesnil · F. Valentin · A. Vialet

Résumé L'homme fossile d'Asselar, découvert en 1927 dans l'actuel Mali, n'a été que peu exploité depuis l'étude de Boule et Vallois (1932). Daté de l'Holocène ancien, il est, avec la série d'Hassi-el-Abiod, un témoin des populations vivant dans un Sahara alors « vert », bien différent de celui que nous connaissons aujourd'hui. L'hypothèse d'un dépôt funéraire, écartée dès la première étude au profit de celle d'une noyade et d'un enfouissement accidentel, est considérée pour la première fois selon les principes de l'anthropologie de terrain et grâce à l'imagerie médicale qui permet un accès complet et non invasif aux parties du squelette toujours incluses dans le sédiment.

Mots clés Mali · Sahara · Holocène ancien · Archéothanatologie · Imagerie 3D

Abstract The fossilized human skeleton of Asselar was discovered in 1927 in present-day Mali. This specimen has been very little studied since it was first described by Boule and Vallois (1932). Dated to the early Holocene, it provides, together with the Hassi-el-Abiod series, evidence of the human groups who lived in then the fertile Sahara, which was very different from the desert we know today. The hypothesis of a deliberate burial, which was ruled out by the first study that considered it to be a case of drowning, is assessed for the first time in light of field anthropology principles and thanks to the medical imaging techniques which allowed full and non-invasive access to parts of the skeleton that are still naturally embedded in the sediment.

Keyword Mali · Sahara · Ancient Holocene · Archaeothanatology · 3D Imaging techniques

Introduction

Le squelette de l'homme d'Asselar a été découvert en 1927 lors de la mission Augiéras–Draper, dont le but était « *d'aller vers l'inconnu* » en traversant le Sahara entre Alger et Dakar [1]. En suivant les indications fournies par les militaires au nord du Mali, non loin de la frontière algérienne, deux membres de l'équipe (T. Monod et V. Besnard) ont en effet repéré, à proximité du poste d'Asselar, des ossements humains affleurants, qu'ils ont prélevés. Le contexte géologique et la faune associée permettent aujourd'hui d'attribuer le squelette d'Asselar à l'Holocène ancien (entre 9500 et 7000 BP) [2,3]. Il s'agit d'une époque à laquelle le Sahara était humide, présentant une faune et une flore différentes de l'actuel, comme en témoignent les cuvettes environnantes dont le fond contient une couche de marne grise à mollusques d'eau douce [4], indiquant la présence probable d'un lac.

Le squelette a été ramené à Paris et donné à l'Institut de paléontologie humaine où il a été confié pour étude à Marcellin Boule (1861–1942) et Henri-Victor Vallois (1889–1981). Il est constitué de « *plusieurs blocs et de quelques os et fragments recueillis isolément à la surface du sol* » [4]. Conformément au paradigme du moment, son étude a suivi une approche raciologique. Il a alors été mis en relation avec les Hottentots, les Bochimans d'Afrique du Sud et les hommes de Grimaldi, considérés comme des ancêtres de la « race noire » [5]. C'est sans doute par son inscription au service de tels paradigmes tombés en désuétude dans les années 1960 [6] que ce squelette a été oublié jusqu'à une période récente. En 2013, Vialet et al. [3] ont mené une étude historiographique et un réexamen général de ce spécimen, mettant en évidence l'absence de questionnement sur son

---

J. Dumesnil
MNHN, UMR 7194, UPVD, 1,
rue René-Panhard, F-75013 Paris, France

F. Valentin
CNRS, UMR 7041, 21, allée de l'Université,
F-92023 Nanterre cedex, France

A. Vialet (✉)
MNHN, UMR 7194, UPVD, CERP, 1,
rue René-Panhard, F-75013 Paris, France
e-mail : amelie.vialet@mnhn.fr

éventuel contexte funéraire. En effet, la question d'un dépôt funéraire a été écartée par les découvreurs qui affirment dans leur « livre de bord » qu'« *il n'y a aucun indice de sépulture* » [1]. Par la suite, faisant référence au contexte géologique (paléolac), c'est une noyade qui est évoquée par Boule et Vallois pour expliquer la bonne conservation du squelette [4].

L'« anthropologie de terrain » permet de reconsidérer ces propositions et de préciser les conditions d'enfouissement de l'homme d'Asselar grâce à l'étude des relations spatiales entre les os formant une articulation [7–9]. Déjà, les observations réalisées par Vialet et al. en 2013 [3] avaient permis d'argumenter un dépôt primaire et un enfouissement rapide sur la base de la bonne conservation du squelette, de la position du corps et de la préservation des volumes principaux (thorax et bassin). Nous proposons ici de nous concentrer sur l'analyse des relations articulaires entre les os des pieds et de la main droite encore engagés dans un bloc de sédiment induré et donc maintenus dans la position de leur découverte. Pour cette analyse, nous avons eu recours au scanner médical et à l'imagerie 3D.

Matériel

Rappelons que l'ensemble du squelette est bien conservé même si les premiers auteurs précisent que « *les eaux avaient emporté quelques débris et les avaient dispersés sur plusieurs mètres de la pente* » [4]. Il est aujourd'hui constitué d'os isolés et d'os encore inclus dans la gangue gréseuse. Un bloc vertébral contient cinq cervicales (C2 à C6), un autre comprend C7 et six vertèbres thoraciques et les portions postérieures des côtes droites, un troisième renferme les vertèbres thoraciques basses et les premières lombaires (T7 à L2), un quatrième contient les autres lombaires, le sacrum et l'ilium gauche, et un cinquième inclut les côtes gauches.

Au niveau des extrémités, deux blocs comprennent, l'un, le cinquième métacarpien droit ainsi qu'une partie du cunéiforme latéral droit et deux fragments des métatarsiens, et l'autre, la partie distale des tibias, l'extrémité distale de la fibula gauche, des os des deux pieds et de la main droite (Fig. 1). Un fragment de la fibula gauche (quart distal de la diaphyse) est détaché de ce dernier bloc qui est également cassé au niveau de la partie distale des pieds manquante. Ce bloc présente un intérêt considérable, car les os se trouvent encore dans la position qui était la leur lors de la découverte. Son examen donne la possibilité d'obtenir des indications sur l'état des connexions articulaires des extrémités du squelette d'Asselar.

Méthode

Afin de discuter des modalités de dépôt du squelette d'Asselar, nous nous sommes concentrés sur le bloc comprenant l'extrémité distale de la fibula gauche, des tibias et les os des pieds et de la main droite, pour lequel Boule et Vallois avaient effectué un inventaire [4] que nous avons complété

Fig. 1 Le squelette de l'homme d'Asselar tel qu'il est conservé à l'IPH, c'est-à-dire respectant la disposition donnée par Boule et Vallois pour les besoins photographiques de leur publication [4], en haut à gauche : le bloc comprenant les extrémités distales de la fibula gauche, des tibias, les os des pieds et de la main droite, qui a été tomographié (photographie A. Vialet) / The Asselar skeleton as preserved at the IPH in the position recommended by Boule and Vallois for photographic purposes [4]. Upper left: the block containing the distal ends of the left fibula, tibias and bones from the feet and the right hand. This block was CT-scanned (picture A. Vialet)

grâce aux données tomographiques. Les paramètres techniques de ces dernières sont les suivants : épaisseur des coupes : 0,8 mm ; espace entre les coupes : 0,4 mm ; kVp : 120 ; X-Ray Tube Current : 108 mA ; taille des pixels : 0,37 × 0,37 mm ; largeur et hauteur : 285,00 mm (768 pixels). Une segmentation manuelle a été effectuée pour l'ensemble des 768 coupes en utilisant le logiciel Aviso 9.0.1, car les valeurs de densité entre l'os et la matrice se sont avérées trop proches pour appliquer une segmentation semi-automatique.

Résultats

État de conservation

Notons préalablement que nos déterminations anatomiques concordent avec celles des premiers auteurs [3]. De plus, les observations effectuées grâce à la tomographie sur le bloc contenant la fibula gauche, les tibias, les os des deux pieds et de la main droite permettent d'ajouter une phalange distale de la main droite au premier inventaire.

D'une façon générale, toutes les régions du squelette ainsi que les différents éléments osseux sont bien représentés. Les extrémités en particulier sont relativement complètes. Ainsi, pour la main gauche, seuls manquent deux os du carpe, deux phalanges moyennes et les cinq phalanges distales tandis que pour la main droite, quatre os du carpe ainsi que le deuxième métacarpien, et la majorité des phalanges n'ont pas été identifiés. Tous les tarses sont présents ainsi que, de façon fragmentaire, deux métatarses à droite et cinq à gauche. Les phalanges moyennes et distales ne sont pas conservées.

Ces absences relèvent sans doute principalement de dégradations taphonomiques remarquées dès la découverte et dues à l'affleurement du squelette à la surface du sol et au ruissellement des eaux de pluie [3].

Bilan articulaire

L'analyse du bloc grâce aux données tomographiques permet d'observer la bonne cohérence anatomique des éléments osseux composant les deux pieds et la main droite. Ainsi, l'articulation persistante de la cheville droite est maintenue (Fig. 2) ; la cheville gauche est en connexion lâche (Fig. 3). Les articulations talo-calcanéennes sont disjointes, alors que celles joignant les autres tarsiens sont maintenues. Les os du carpe sont en connexion stricte, et les fragments de métacarpiens, parallèles les uns aux autres (Fig. 4). Deux phalanges (moyenne et distale) de la main se succèdent selon la logique anatomique (Fig. 4).

Cette analyse permet également de définir les positions relatives des pieds et de la main droite. Ainsi, les chevilles sont étendues, et les deux pieds sont parallèles et rapprochés l'un de l'autre, le pied droit en position basse par rapport au gauche. La main droite, phalanges fléchies, est au contact du pied droit, sa face dorso-latérale se situant contre la face latéroplantaire du pied (Figs 3, 4). Cet arrangement est compatible avec la flexion des hanches visible sur la figure 1 et encore plus nette dans la monographie de Boule et Vallois [4]. L'association main droite–pieds implique de plus une hyperflexion latérale des genoux ramenant les pieds vers le bassin.

Fig. 2 Vue latérale gauche du bloc comprenant les extrémités distales de la fibula gauche, du tibia, les os des pieds et de la main droite après séparation par imagerie 3D entre les os (en vert) et la matrice gréseuse (en jaune). On distingue nettement dans la partie supérieure les tarses et la moitié proximale des métatarses du pied gauche, l'extrémité distale du tibia et la malléole de la fibula gauche. Capture d'écran sur Aviso 9.0.1 / Left lateral view of the block containing the distal ends of the left fibula and tibia and bones from the feet and the right hand, after virtual separation, by 3D imaging techniques, of the bones (green) from the matrix (yellow). The left foot can be clearly distinguished in the upper part: the tarsus and the proximal half of the metatarsus and the distal ends of the tibia and the fibula. Generated by Aviso 9.0.1

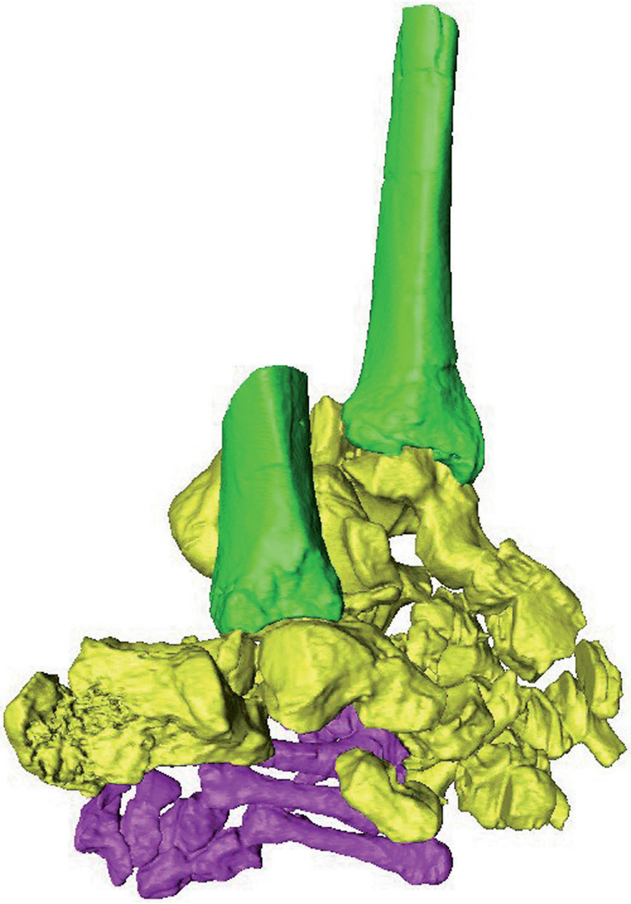


Fig. 3 Vue latérale droite du bloc comprenant les extrémités distales, des tibias, les os des pieds et de la main droite après dégagement virtuel des ossements par imagerie 3D. Tibias (en vert), pieds (en jaune), main droite (en violet). Capture d'écran sur Aviso 9.0.1 / Right lateral view of the block containing the distal ends of the tibias and bones from the feet and the right hand, virtually removed from the matrix by 3D imaging techniques. Tibias (green), foot (yellow), right hand (purple). Generated by Aviso 9.0.1

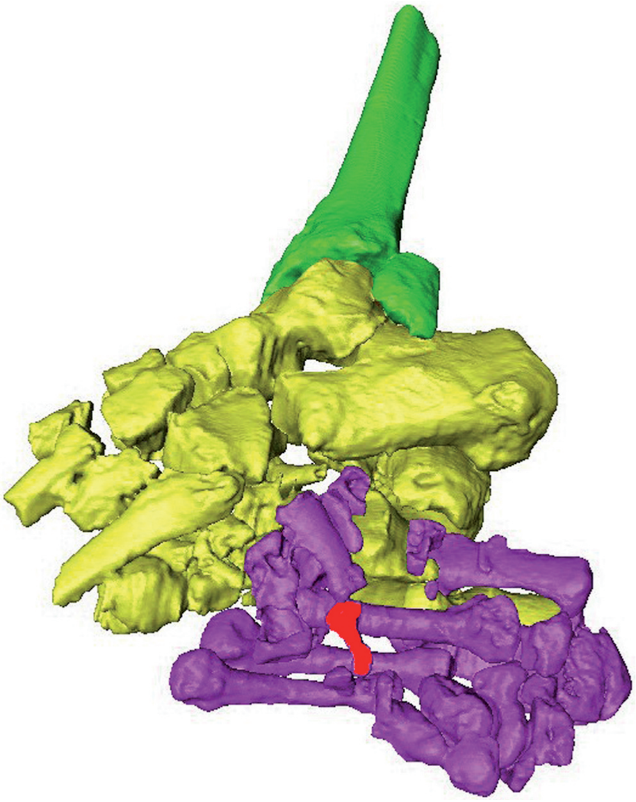


Fig. 4 Vue latérale gauche du bloc comprenant les extrémités distales de la fibula et du tibia gauches, les os des pieds et de la main droite après dégagement virtuel des ossements par imagerie 3D. Tibia et fibula (en vert), pieds (en jaune), main droite (en violet). La phalange distale de la main (rouge) est celle qui était totalement incluse dans le sédiment et qui a pu être identifiée grâce aux données CT. Capture d'écran sur Aviso 9.0.1 / Left lateral view of the block containing the distal ends of the left fibula, and tibia, bones from the feet and the right hand, virtually removed from the matrix by 3D imaging techniques. Tibia and fibula (green), foot (yellow), right hand (purple). The intermediate hand phalanx (red), embedded in the sediment, was discovered thanks to the CT-data. Generated by Aviso 9.0.1

Discussion

Depuis la reprise de l'étude du squelette d'Asselar par Vialet et al. en 2013 [3], la question posée est celle des conditions de dépôt et d'enfouissement de cet individu. Boule et Vallois [4], dont la publication ne traite que très peu de cette interrogation, avaient émis l'hypothèse d'une noyade pour expliquer la bonne conservation du squelette. Or, cette proposition recouvre deux notions qui ne sont pas discutées à l'époque : celle des conditions d'enfouissement et celle de la cause de la mort. Les caractéristiques observées pour cet individu (bonne représentation du squelette, maintien en connexion d'articulations labiles et conservation des volumes thoracique et pelvien) témoignent d'un enfouissement précoce (antérieur à la décomposition des articulations) du cadavre dans le sédiment, alors qu'un séjour long dans l'eau conduit à une dislocation du squelette et à une dispersion des os en commençant par ceux des pieds et des mains [10]. Cependant, Duday [8,11] décrit le corps d'une femme morte par noyade, dont le squelette est bien représenté (mains conservées jusqu'aux sésamoïdes) et les articulations, même labiles, sont maintenues en connexion stricte. Mais, dans le cas d'Asselar, la position du bas du corps (hanches fléchies et hyperflexion des genoux ramenant les pieds vers le bassin) est peu compatible avec l'hypothèse de la noyade, car les noyés (par accident) se présentent généralement en procubitus, membres étendus [10]. L'extrême flexion des genoux d'Asselar et la proximité pieds–bassin évoqueraient plutôt une position « donnée » au corps à l'occasion de sa mise en terre soit immédiatement après le décès, soit de 24 à 48 heures après, lorsque la rigidité cadavérique a disparu. Notons qu'une flexion prononcée des genoux semble commune aux sépultures de la région saharienne telles, en Tunisie, celles du site de SHM-1 à Hergla [12] et, au Mali, celles d'Hassi-el-Abiod [13] datées de 7000 BP.

Enfin, la proximité main droite–pieds observée à Asselar invite à s'interroger sur l'éventuelle présence d'une contention. En effet, ce cas a été récemment évoqué pour le site de Nataruk au Kenya (9500–10500 BP) où deux individus sont décrits, en raison du rapprochement étroit de leurs poignets et de la position de leurs mains, comme ayant eu les mains ligotées [14].

Conclusion

Cette étude, réalisée sur un individu issu de collections anciennes pour lequel nous disposions de nouvelles données grâce à la tomographie du bloc de sédiment comprenant les os des membres inférieurs (fibula gauche, tibias), des pieds et de la main droite, a permis de mieux définir les conditions de son enfouissement. Ainsi, la bonne représentation du squelette d'Asselar, la conservation de connexions articulaires, la position des membres inférieurs et des pieds et le maintien de la main droite au contact des pieds évoquent une attitude du corps qui semble incompatible avec l'hypothèse d'une noyade suivie d'un enfouissement accidentel, émise par Boule et Vallois [4]. Au contraire, nos observations, précisées par l'analyse des données tomographiques des os des extrémités des membres inférieurs encore pris dans le sédiment, permettent d'envisager un ensevelissement précoce du corps et la possibilité de son inhumation intentionnelle. En effet, la position rapprochée des deux pieds et la main droite aux doigts fléchis, placée sous le pied droit, impliquent une flexion prononcée des membres inférieurs donnée à l'individu peu de temps après son décès. La récurrence de cette position observée dans les sépultures d'un autre site malien de l'Holocène ancien, celui d'Hassi-el-Abiod, sort le squelette d'Asselar de son isolement et incite à conclure à la pratique d'une sépulture.

Remerciements Les acquisitions ont été réalisées le 27 juillet 2013 à l'hôpital de la Pitié-Salpêtrière (Paris, 13) grâce à Mme Huynh-Charlier et à son équipe que nous remercions. Notre gratitude va également à Patricia Wils du plateau Accès scientifique à l'imagerie (ASIM) du Muséum national d'histoire naturelle qui a contribué au traitement des données tomographiques. Les résultats présentés sont en grande partie issus du Master (MNHN, QP) de Justine Dumesnil dont le stage a été financé par l'UMR 7194. Enfin, nous sommes très reconnaissants envers la SOGEDA pour son intérêt pour ce programme de recherche et le soutien procuré.

Liens d'intérêts : les auteurs déclarent ne pas avoir de lien d'intérêt.

Références

1. Augiéras EM, Draper WP, Gierzynski ME, et al (1931) D'Algérie au Sénégal. Mission Augiéras-Draper, 1927–1928. Société de géographie de Paris, 293 p
2. Petit-Maire D (2002) Sahara, sous le sable… des lacs. Un voyage dans le temps, CNRS Éditions, Paris, France, 127 p
3. Vialet A, André L, Aoudia L (2013) L'homme fossile d'Asselar (actuel Mali). Étude critique, mise en perspective historique et nouvelles interprétations. Anthropologie 117:345–61
4. Boule M, Vallois HV (1932) L'homme fossile d'Asselar (Sahara). Archives de l'Institut de paléontologie humaine, Paris, France, 90 p
5. Verneau R (1906) Les grottes de Grimaldi (Baoussé-Roussé). Anthropologie. Imprimerie de Monaco, tome 2, fascicule 1, 324 p
6. Legoux P (1962) Nouvelle étude anthropologique des « négroïdes de Grimaldi ». Comptes rendus des séances de l'Académie des sciences de Paris 255:2276–7
7. Duday H (1990) Observations ostéologiques et décomposition du cadavre : sépulture colmatée ou en espace vide. Rev Archeol Centre Fr, 29:193–6
8. Duday H (1995) Anthropologie de « terrain », archéologie de la mort. La mort, passé, présent, conditionnel, GVEP, La Roche-sur-Yon, France, 33–58
9. Duday H, Courtaud P, Crubézy E, et al (1990) Anthropologie « de terrain » : reconnaissance et interprétation des gestes funéraires. Bull Mem Soc Anthropol Paris 2:29–49
10. Hamilton S J, Green M A (2017) Gross post-mortem changes in the human body. In: Schotsmans EMJ, Márquez-Grant N, Forbes SL (eds.) Taphonomy of human remains: forensic analysis of the dead and the depositional environment. John Wiley & Sons, pp 11–25
11. Duday H (2009) Archaeology of the dead. Oxbow Books, Oxford, Angleterre, 230 p
12. Munoz O, Candilio F, Roudesli-Chebbi S (2013) Les restes humains de SHM-1 (campagnes 2002-2007) : étude archéo-anthropologique. In: Mulazzani S (Éd) Le capsien de Hergla (Tunisie). Culture, environnement, économie. Reports in African Archaeology. Africa Magna Verlag, Franckfurt, pp 299–314
13. Dutour O (1989) Hommes fossiles du Sahara : peuplements holocènes du Mali septentrional, Éditions du CNRS, Paris, France, 342 p
14. Mirazón Lahr M, Rivera F, Power R K, et al (2016) Inter-group violence among early Holocene hunter-gatherers of West Turkana, Kenya. Nature 529:394–8

BMSAP (2018) 30:107
DOI 10.3166/bmsap-2018-0008

Liste des thèses d'anthropologie soutenues en 2017

Muséum national d'Histoire naturelle

Christophe Coste : *The costs of reproduction in evolutionary demography: An application of Multitrait Population Projection Matrix models*

Goki Ly : *Du système de parenté à la diversité génétique dans les populations humaines d'Asie du Sud-Est*

Nina Marchi : *A la croisée de l'anthropologie et de la biologie évolutive : diversité génétique et comportements migratoires en Asie Intérieure*

Valentin Thouzeau: *Inférer l'histoire des populations humaines à partir des diversités génétiques et linguistiques*

Université de Bordeaux

Elsa Garot : *Distinction entre processus pathologique de type MIH (molar incisor hypomineralisation) et processus taphonomique par différentes méthodes de micro-analyse de l'émail dentaire*

Université Paris 1 Panthéon-Sorbonne

Marie Dejonghe : *Les nécropoles phéniciennes de méditerranée occidentale. Architectures et pratiques funéraires*

Université Paris Nanterre

Nathalie Del Socorro : *Les rites funéraires dans le royaume des Téménides et ses environs à la période archaïque*

Université Paul Valery Montpellier 3

Elsa Ciesielski : *La pratique celtique des « têtes coupées » en France Méditerranéennes : l'exemple du site du Cailar (Gard) au III*^{e} *siècle avant notre ère. Approche archéothanatologique et traitements informatiques des données*

Université Toulouse III Paul Sabatier

Barbara Da Costa : *Caractérisation de modèles pouvant modifier la bio-énergétique mitochondriale : syndrome de Leigh et haplogroupe de l'ADNmt*

Etienne Cavaignac : *Etude de la variabilité en fonction du sexe, de l'âge et de l'origine géographique de l'extrémité distale du fémur*

Pradiptajati Kusuma : *A la recherche des ancêtres asiatiques des Malgaches en Indonésie*

Fatima-Zohra Mokrane : *L'angioscanner* pos-mortem *et ses diverses applications : de l'imagerie archéologique à l'étude de la population pédiatrique* post-mortem

Nicolas Reina : *Les contraintes de charge asymétriques chez l'Homme moderne. Étude microCT sur l'os trabéculaire*

Frédéric Savall : *Estimation de l'âge au décès d'individus français contemporains. Apport d'un échantillon virtuel à la méthode de Brooks et Suchey*

Bulletins et Mémoires de la Société d'Anthropologie de Paris (BMSAP)

Recommandations aux auteurs

La Société d'Anthropologie de Paris publie dans ses* Bulletins et Mémoires *des articles originaux, des revues de synthèse ou des notes concernant le champ disciplinaire de l'anthropologie biologique, depuis la paléoanthropologie jusqu'à l'écologie humaine, en passant par la génétique des populations et l'histoire de la discipline. Tous les manuscrits soumis à la revue font l'objet d'un processus d'évaluation* (reviewing)*. Pour être publié, chaque article doit :

- ***recueillir les avis favorables des membres du Comité de lecture auquel ils sont soumis***
- ***obéir aux normes de présentation exposées ci-dessous***

1 - Soumission électronique du manuscrit

Le **manuscrit** doit être soumis en un seul fichier au format DOC comprenant successivement texte, légendes des tableaux et des figures, tableaux, illustrations (300 DPI), par e-mail à l'adresse suivante : **redacchef@sapweb.fr**

La **version acceptée du manuscrit** devra être envoyée en plusieurs fichiers distincts : un unique fichier Word (DOC) correspondant au texte, aux tableaux et aux légendes d'une part, et les figures sous la forme de fichiers JPEG, EPS ou TIFF séparés d'autre part.

Il est explicitement convenu que tout manuscrit soumis aux ***Bulletins et Mémoires de la Société d'Anthropologie de Paris*** est un travail original qui n'a pas été publié et qui n'est pas en cours d'évaluation par une autre revue.

2 - Préparation du manuscrit

Le manuscrit sera rédigé en français ou en anglais. Il devra comporter successivement : un **titre** en anglais **et** en français, les **nom, prénom et adresse des auteurs,** l'adresse **e-mail** du contact, des **mots clés** (6 maximum) en français **et** en anglais, un **résumé** en anglais **et** en français (1500 caractères maximum espaces compris), une **version abrégée** facultative (4000 caractères maximum espaces compris) en anglais **ou** en français (dans la langue non utilisée pour l'article), le texte du manuscrit, la liste des références bibliographiques, la liste des tableaux, la liste des figures, les tableaux et les figures. Les pages et les lignes du manuscrit seront numérotées de façon continue dès la page de titre.

Le **texte** du manuscrit (texte, titres et intertitres, notes infrapaginales, abréviations ou sigles, références bibliographiques, légendes des tableaux et figures) n'excédera pas 50 000 caractères (espaces compris) pour un article et 20 000 caractères (espace compris) pour une note. Il sera de préférence rédigé avec la police Times New Roman, 12 pt, en double interligne, et mis en page au format A4 avec des marges de 25 mm.

Titres et intertitres. Le titre principal de l'article n'excédera pas 200 caractères (espaces compris). En outre, le corps du texte de chaque article comportera au maximum 2 niveaux de titres que l'auteur veillera à bien rendre distincts sur son manuscrit. Ceux-ci ne seront pas numérotés.

Les **notes infrapaginales** sont appelées dans le texte par un numéro en chiffres arabes et en exposant, sans crochets ni parenthèses. Elles seront rejetées en bas de page et devront être limitées en nombre et en longueur.

Les **abréviations ou sigles** doivent être explicités lorsqu'ils apparaissent pour la première fois. Les termes scientifiques et techniques, ainsi que les unités de mesures et les symboles statistiques, doivent être conformes aux normes internationales.

Les **références bibliographiques** sont signalées entre [crochets] et numérotées par ordre d'apparition.

- Dans le corps du texte, seul le premier auteur est mentionné suivi de « et al. » lorsqu'il y a plusieurs auteurs (par exemple : « Fisher a montré que… [1] ; Cette hypothèse due à Jablonski et al… [2] ; Deux articles de paléoanthropologie… [3] et [4] »). Dans la mesure du possible, les numéros des références seront placés en fin de phrase.
- Dans la liste des références, celles-ci seront agencées par ordre d'apparition dans le texte. S'il y a quatre auteurs ou plus, seuls les trois premiers seront mentionnés, suivis d'une virgule et de la mention « et al ». Seules les références appelées dans le texte doivent figurer dans la liste de références en fin d'article. Les titres des périodiques sont écrits en respectant les abréviations standard (List of Serial Title Word Abbreviations).

Le **modèle de présentation** est illustré par les exemples suivants :

- Pour un article dans un périodique : Hershkovitz I, Smith P, Sarig R, et al (2011) Middle pleistocene dental remains from Qesem Cave (Israel). Am J Phys Anthropol 144(4):575-92
- Pour un ouvrage : Scheuer JL, Black S (2000) Developmental Juvenile Osteology, Academic Press, San Diego, California, 587 p
- Pour un article dans un ouvrage collectif :
Gomila J (1980) L'Afrique subsaharienne. In: Hiernaux J (ed) La diversité biologique humaine. Masson, Paris, pp 107-196

Les **légendes des tableaux et figures** seront portées en fin de manuscrit, sur une feuille séparée du texte avec leur traduction en anglais ou en français. Chaque légende doit être suffisamment explicite par elle-même, sans qu'il soit nécessaire de se référer au texte. Les auteurs veilleront toutefois à limiter leur longueur. La numérotation des tableaux (en chiffres arabes) et des figures (en chiffres arabes) se fait selon leur ordre d'apparition dans le texte.

Les **tableaux** seront fournis au format word, présentés sur des pages séparées et placés à la fin du document texte.

Les **illustrations** seront fournies aux formats JPEG, AI ou EPS, avec une résolution minimale de 600 dpi et doivent être composées avec une largeur correspondant à une colonne (8,5 cm), une colonne et demi (12 cm) ou deux colonnes (17,5 cm) de l'article imprimé ; les textes des illustrations sont écrits en police Times New Roman, 10 pt (taille d'impression) et 11 pt pour les titres.

Les images seront reproduites par défaut en couleur dans la version électronique et en noir et blanc dans la version imprimée. Les images couleur devront être fournies dans une qualité permettant le transfert en niveaux de gris.

Rappel des points à vérifier avant de soumettre votre article :

- Titres, résumés et mots clés en français et en anglais
- Affiliation et coordonnées complètes de chacun des auteurs, auteur correspondant et co-auteurs
- Références citées dans le texte, numérotées par ordre d'apparition dans le texte et mises en forme selon les règles
- Appels dans le texte entre crochets du numéro des références citées
- Titres des tableaux et appels des tableaux dans le texte
- Légendes des figures et appels des figures dans le texte
- Attention spéciale à la qualité de la langue utilisée, français et/ou anglais

Bulletins et Mémoires de la Société d'Anthropologie de Paris (BMSAP)

Guidelines to authors

The Société d'Anthropologie de Paris publishes in its **Bulletins et Mémoires** ***original articles, reviews of works or notes in the field of biological anthropology, from the palaeoanthropology to the human ecology and population genetics, and the history of the discipline. All submitted manuscripts are evaluated during a reviewing process. Publication of articles is subject to the following conditions:***

- ***approval by members of the Review Committee to which it is submitted;***
- ***adherence to the standards of presentation set out below.***

1 - Electronic submission of Manuscript

The **manuscript** including text, tables, illustrations (300 DPI) and their captions must be submitted as a single DOC file by e-mail to **redacchef@sapweb.fr**

The **accepted version of the manuscript** will be sent as separate files: a single Word text file (DOC) including the text, tables and captions on the one hand, and the illustrations as separate JPEG, EPS or TIFF files on the other hand.

The author guarantees that his/her contribution is original. It is assumed that all manuscripts sent to the ***Bulletins et Mémoires de la Société d'Anthropologie de Paris*** is an original paper which has not been published before and which is not evaluated in another Journal.

2 - Preparation of manuscript

The manuscript must be written in either English or French. It must include successively: the **title** in both English **and** French, the **name**, **surnames** and **address of the authors,** the **email** address of the corresponding author, keywords (maximum of 6) in both English **and** French, an **abstract** in both English **and** French (1,500 characters including spaces), a facultative **abridged version** (4,000 characters including spaces) in either English **or** French (depending on the language of the manuscript), the text of the manuscript, the list of bibliographic references, the list of tables, the list of figures, the tables and the figures. Each page and line of the manuscript must be sequentially numerated from the title page.

The **text** of the manuscript (text, titles and headings, footnotes, abbreviations, bibliogaphical references, captions for tables and figures) should not exceed 50,000 characters (including spaces) for an article and 20,000 characters (including spaces) for a note. It will be preferentially written using the font Times New Roman 12 pt, double spaced, A4 page size with margin of 25 mm.

Titles and headings. The main title of the article will not exceed 200 characters (including spaces). In addition, the text of each article will contain a maximum of 2 clearly distinct title levels. They will not be numbered.

Footnotes are noted in the text by Arabic numerals and in superscript, without brackets or parenthesis. They are to be placed at the bottom of the page and should be limited in number and in length.

Abbreviations or **initials** must be explained when they appear for the first time. Scientific and technical terms, as well as units of measurement and statistical symbols, must conform to international norms.

Bibliographical references are indicated using [brackets] and numbered in their order of appearance in the text.

- In the text, only the first author is listed. It is followed by a comma and the words "et al." When there are many authors (example: "Fisher showed that… [1] ; This hypothese formulated by Jablonski et al… [2] ; Two articles in paleoanthropology… [3] and [4]"). Wherever possible, the numbers of references are to be placed at the end of the sentence.
- The reference list is organised in alphabetical order of the authors cited and in chronological order of the publications for each author. All authors are listed if there are three or less. If there are more than three, only three are listed first, followed by a comma and the words "et al". The titles of journals should be abbreviated according to standard abbreviations (List of Serial Title Word Abbreviations).

The **presentation model** is illustrated by the following examples:

- For an article in a journal: Hershkovitz I, Smith P, Sarig R, et al (2011) Middle pleistocene dental remains from Qesem Cave (Israel). Am J Phys Anthropol 144(4):575-592
- For a book: Scheuer JL, Black S (2000) Developmental Juvenile Osteology, Academic Press, San Diego, California, 587 p
- For an article in a collective work: Gomila J (1980) L'Afrique subsaharienne. In: Hiernaux J (ed) La diversité biologique humaine. Masson, Paris, pp 107-196

The **captions for tables and figures** will be presented on a separate page at the end of the manuscript, with a French or English translation. Each caption must be explicit enough in itself, so that reference to the text is not necessary. The numbering of the tables (in Arabic numerals) and figures (in Arabic numerals) must follow the order in which they appear.

The **tables** must be presented in Word format, on separated pages, and provided at the end of the text document.

The **illustrations** must be provided in JPEG, AI or EPS format, with a minimum resolution of 600 DPI. Illustrations must be composed with a width of one column (8,5cm), one column and half (12cm) or two columns (17,5cm) of the printed paper. The text of illustrations must be written in police Times New Roman, 10 pt (printed size) and 11pt for titles.

Color art is free of charge for online publication. If black and white will be shown in the print version, make sure that the main information will still be visible. Many colors are not distinguishable from one another when converted to black and white. A simple way to check this is to make a xerographic copy to see if the necessary distinctions between the different colors are still apparent. If the figures will be printed in black and white, do not refer to color in the captions. Color illustrations should be submitted as RGB (8 bits per channel).

Items to verify before manuscript submission:

- Title, keywords and abstract in both French and English
- Full contact details of each author, corresponding author and co-authors
- References numbered alphabetically and formatted following the guidelines
- Quotations in the text of the reference number in square brackets
- Title of tables and call for tables in the text
- Caption of figures and call for figures in the text
- Special attention to the quality of the language used, French and/or English.

Lavoisier

Lavoisier

Abonnez-vous en 2018 !

Bulletins et Mémoires de la Société d'Anthropologie de Paris (BMSAP)

Les ***Bulletins et Mémoires de la Société d'Anthropologie de Paris*** ont pour objectif de rendre compte de l'activité scientifique internationale dans le domaine de l'« histoire naturelle de l'homme » comprise comme l'étude de l'origine et de la diversité biologique de l'espèce humaine. Ils couvrent de manière pluridisciplinaire le champ de l'anthropologie biologique, depuis la paléoanthropologie jusqu'à l'écologie humaine, en passant par la génétique des populations. Ils publient des articles originaux, des revues de synthèse, des comptes rendus de lecture ou de congrès et possèdent une rubrique consacrée à l'histoire de la discipline.

- ***BMSAP* est indexé dans :** SCOPUS, Google Scholar, Academic OneFile, Anthropolocial Index Online, Anthropological Literature, Biological Abstracts, BIOSIS, ERIH PLUS, GeoRef, OCLC, SCImago, Summon by ProQuest.

Disponible sur internet :

VERSION ÉLECTRONIQUE
http://bmsap.revuesonline.com/

ACCÈS À LA VERSION ÉLECTRONIQUE INCLUS !

je m'abonne aux ***Bulletins et Mémoires de la Société d'Anthropologie de Paris* (BMSAP)** pour l'année 2018, 2 numéros doubles :

☐ **Abonnement individuel :**

France **110 € TTC**

Abonnement institutionnel :

Contactez le Service Abonnement Lavoisier : pascal.pinard@lavoisier.fr

Frais de port inclus.
Pour les **tarifs à l'étranger**, veuillez vous reporter à l'adresse suivante :
http://bmsap.revuesonline.com ; rubrique : "Abonnements"

ISSN papier : 0037-8984 - ISSN électronique : 1777-5469

Retournez votre bulletin d'abonnement accompagné de votre règlement à :

Service Abonnement Lavoisier - 14 rue de Provigny - 94236 Cachan cedex - France
Fax : +33 (0)1 47 40 67 02 - E-mail : pascal.pinard@lavoisier.fr

NOM/PRÉNOM ....

E-MAIL ....

ADRESSE ....

....

CP |_|_|_|_|_| VILLE ....

PAYS ....

☐ **Oui, je souhaite recevoir les informations de Lavoisier par e-mail**

Je joins mon règlement à la commande

☐ Chèque bancaire payable en France à l'ordre de LAVOISIER S.A.S.

☐ Carte bancaire n° (Visa, Mastercard)

|_|_|_|_|_|_|_|_|_|_|_|_|_|_|_|_|

Date d'expiration : |_|_| |_|_|

Cryptogramme : |_|_|_|

Date et signature obligatoires

Pour plus d'informations :

pascal.pinard@lavoisier.fr
Tél. : +33 (0)1 47 40 67 68

Demande d'abonnement à renvoyer à :

Service Abonnement Lavoisier
14 rue de Provigny - 94236 Cachan cedex - France

Lavoisier