Human Evolution and Population Dynamics in Northeast Africa at the End of the Pleistocene and the Beginning of the Holocene

Évolution humaine et dynamiques de population dans le nord-est africain à la fin de Pléistocène et au début de l'Holocène

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Abstract: Although subjected to growing interest, the debates related to *Homo sapiens'* evolution in Africa during the Late Pleistocene and the beginning of the Holocene are currently mainly tied to the success of palaeogenetic studies of Holocene skeletons from sub-Saharan Africa. These genetic results have opened new perspectives pertaining the origin of present-day African diversity and the nature of such diversity in the past, confirming previous assumptions based on the study of African fossils suggesting deep sub-structuration of human populations.

In Northeast Africa, the end of the Late Pleistocene and the beginning of the Holocene were marked by major climatic changes whose effects on human settlements are still poorly understood. Geological evidence support generally dry conditions during the Last Glacial Maximum followed by the so-called African Humid Period which ends abruptly with the second half of the Holocene and the onset of more arid conditions. In parallel with these climatic fluctuations, this transitional period witnessed the emergence of new subsistence strategies with the introduction of pastoralism.

However, the scarcity of human remains in northeast Africa has limited our understanding of modern human diversity and population processes during this transitional period. Through a review of the key human fossils and assemblages associated to the Late Pleistocene and the Early Holocene period in Egypt, Sudan, Ethiopia, Somalia and the Republic of Djibouti, this contribution aims at discussing phenotypic and cultural diversity, addressing hypotheses of population isolation, replacement and/or continuity.

Keywords: Phenotypic diversity, Late Pleistocene, Early Holocene, Nile Valley, Horn of Africa, populations processes, adaptation, environmental changes.

Résumé : Bien que soumis à un intérêt croissant, les débats concernant l'évolution d'*Homo sapiens* en Afrique durant le Pléistocène supérieur et le début de l'Holocène sont actuellement principalement liés au succès des études paléogénétiques sur des squelettes holocènes d'Afrique sub-saharienne. Ces résultats génétiques ont ouvert de nouvelles perspectives concernant l'origine de la diversité africaine actuelle et la nature de cette diversité dans le passé, confirmant les hypothèses antérieures fondées sur l'étude des fossiles africains, suggérant une sous-structuration profonde des populations humaines sur ce continent depuis le Pléistocène moyen.

En Afrique du nord-est, la fin du Pléistocène supérieur et le début de l'Holocène ont été marqués par des changements climatiques majeurs dont les effets sur populations humaines sont encore mal connus. Les données géologiques indiquent des conditions environnementales plutôt arides pendant le dernier maximum glaciaire, suivies à partir de 15000 ans de la période humide africaine qui se termine abruptement avec la seconde moitié de l'Holocène et le retour de conditions plus arides. Parallèlement à ces fluctuations climatiques, cette période de transition a vu l'émergence de nouvelles stratégies de subsistance avec notamment l'introduction du pastoralisme.

Cependant, la rareté des restes humains en Afrique du nord-est a limité notre compréhension de la diversité phénotypique des populations à l'origine de la diversité actuelle, et des processus démographiques qui ont structuré cette diversité durant cette période de transition. À travers un examen des principaux fossiles et échantillons de populations, associés à la fin du Pléistocène supérieur et au début de l'Holocène en Égypte, au Soudan, en Éthiopie, en Somalie et en République de Djibouti, cette contribution vise à discuter de la diversité phénotypique et culturelle de ces derniers groupes de chasseurs-pêcheurs-cueilleurs, en abordant les hypothèses d'isolement, de remplacement et/ou de continuité populationnelle.

Mots-clés : diversité phénotypique, Pléistocène supérieur, Holocène, vallée du Nil, Corne de l'Afrique, dynamique de peuplement, adaptation, changements environnementaux.

1. NORTHEAST AFRICA PHENOTYPIC DIVERSITY DURING THE LATE PLEISTOCENE

The African Late Pleistocene fossil record is extremely sparse for the period that is supposed to have witnessed modern human diversification in Africa and dispersions outside the African continent (Grine, 2016). Archaeological sites with human remains attributed to the first half of the Late Pleistocene (i.e. MIS 5, 130-71 ka; Lisiecki and Raymo, 2005) are essentially located in North Africa (Dar-es-Soltan II and La Grotte des Contrebandiers in Morocco; e.g. Vallois and Roche, 1958; Debénath, 1976 and 2000; Ferembach, 1976 and 1998), East Africa (Ngaloba and Eyasi in Tanzania, Panga ya Saidi in Kenya and Aduma in Ethiopia; Magori and Day, 1983; Mehlman, 1987; Haile-Selassie et al., 2004; Martinón-Torres et al., 2021), and South Africa (Blind River, Blombos and Sea Harvest; e.g. Grine and Kein, 1993; Henshilwood et al., 2001; Grine and Henshilwood, 2002; Wang et al., 2008). Even if we add to the list the sites with a wider chronological range, for which the associated human remains can be dated from at least the marine oxygen-isotope stages (MIS) 5 to 4 (black and full green dots from figure 1; for discussion about their dating see Grine, 2016), the fossil record from the first half of the Late Pleistocene is mostly documented by fragmentary human remains (incomplete cranial remains, isolated teeth or infra-cranial fragments). Comparative morphometric studies of these fossils have delivered partial information about past modern human diversity during this period. The results suggest a high level of phenotypic diversity with the persistence of plesiomorphic features in some specimens (e.g. Rightmire and Deacon, 1991; McCrossin, 1994; Pearson et al., 1998; Royer et al., 2009; Harvati and Hublin, 2012; Hublin et al., 2012), while others are described as fully modern (e.g. De Villiers, 1973; Grine and Klein, 1985; Bräuer and Mehlman, 1988; Bräuer and Singer, 1996). This situation limits our understanding of past modern human phenotypic diversity during this crucial period of modern human African diversification. In addition, no data exists from West and Central Africa, which together characterize the largest part of the African continent.

The situation is even worse for the second half of the Late Pleistocene until the end of the Last Glacial Maximum (i.e. from MIS 4 to MIS 2). Only four sites with human remains are securely associated with MIS 4 (light green dots in figure 1), and seven for MIS 3 (light red dots in figure 1; for discussion about their dating see Grine, 2016). With the exception of the Nazlet Khater 2 and Hofmeyr specimens (light red stars in figure 1), these sites preserved very fragmentary human remains, some still unpublished, that have nonetheless contributed to palaeoanthropological discussions about the phenotypic diversity of past modern humans in Africa at that time (e.g. Grine, 2000; Hublin et al., 2012; Verna et al., 2013, Pleurdeau et al., 2014; Harvati et al., 2015; Willoughby et al., 2018; Reiner et al., 2017). The Nazlet Khater 2 (NK 2) skeleton from Egypt and the Hofmeyr (HOF) cranium from South Africa are the only two reasonably complete and well-dated African specimens from the MIS 4-MIS 3 interval. During MIS 2 and until the peak of the Last Glacial Maximal (~ 20 ka; Clark et al., 2009), five additional sites can be added to the African fossil record (light blue points and stars in figure 1). After 20 ka, the number of sites with human remains gradually increases until the end of MIS 2, although a large portion of the African continent remains undocumented. During the Holocene, the fossil record increases substantially, and homogenization of cranio-morphological features has been documented, particularly within sub-Saharan African populations, with its peak both during and after the Bantu expansion from 6 ka onwards (Ribot, 2011).

The paucity of human remains found in Africa from the last glacial period (MIS 4-MIS 2) is probably multifactorial. Historical factors involving unequal attention paid to specific African regions could have played a role, as well as taphonomic bias (Surovell et al., 2009). Another hypothesis relates to the intense environmental and climatic changes that occurred in Africa during this period, that may have affected human population adaptation and survival in some areas (Carto et al., 2009). From MIS 6 to the LGM, a growing amount of paleoclimatic evidence indicates increasing aridity that correlates with the onset of the northern hemisphere glaciation (e.g. deMenocal et al., 2000; Moreno et al., 2002; Battarbee et al., 2004; Carto et al., 2009). However, the climatic changes in Africa were not synchronous, and interregional differences are recorded in the timing of alternance between humid and arid conditions (Blome et al., 2012). In North Africa, the density of sites appears to be inversely correlated with the expansion of the Sahara, with the exception of the Nile Valley (Blome et al., 2012; Leplongeon et al., 2020; Leplongeon, 2021). Whatever the cause, the sparse

fossil record for the Late Pleistocene is clearly a limitation in discussing modern human evolution in Africa.

In northeast Africa, the only site with well-preserved and securely dated human remains during the MIS 3 is Nazlet Khater 2 (Egypt; Vermeersch et al., 1984; Vermeersch, 2002). It is penecontemporaneous from Hofmeyr (South Africa; Grine et al., 2007), the only other site from this time range with dated and substantial human remains. The NK 2 skeleton has been directly dated by ESR on tooth enamel fragments to 38 ± 6 ka (Crevecoeur, 2008), while the Hofmeyr skull has been dated to 36.2 ± 3.3 ka by a combination of optically stimulated luminescence and uranium-series methods (Grine et al., 2007). Both specimens are anatomically modern, but they also display cranial plesiomorphic features that put them on the brink of extant modern human African phenotypic diversity (Grine et al., 2007; Crevecoeur, 2012a). Regarding the infra-cranial remains of Nazlet Khater 2, the main characteristics express adaptation to high biomechanical strength and specialized activities (Crevecoeur, 2008 and 2012a). Together with the mining archaeological context, these results support the hypotheses of well-organised settlements and planned specialized activities in the Nile Valley during the MIS 3 (Van Peer, 1998).

The Hofmeyr specimen exhibits the greatest overall similarities to Upper Palaeolithic specimens from Europe rather than Holocene San populations from South Africa (Grine et al., 2007; Grine et al., 2010). Similarly, the Nazlet Khater 2 individual presents plesiomorphic features on the cranium and the mandible more comparable to those of Late Middle Pleistocene and early Late Pleistocene fossils than to chronologically closer recent African populations (Crevecoeur, 2008 and 2012a). However, their morphometric characteristics do not particularly draw them together. On the contrary, the two specimens appear to reflect different aspects of Late Pleistocene African phenotypic variation (Crevecoeur et al., 2009). While we can observe a community of robustness related to temporal trends compared to Holocene populations, they exhibit different morphological conformation, as illustrated by the following examples of craniofacial and inner ear morphology comparisons (fig. 2 to fig. 4). The face of NK 2 is particularly robust, with notable height and width dimensions. The projection of the two first principal components of the PCA performed on seven cranio-facial dimensions (fig. 3; for details of the analysis see Crevecoeur, 2012a) shows that the position of NK 2 is closer to Middle Pleistocene hominin and early *Homo sapiens* specimens than chronologically closer specimens. Hofmeyr occupies a transitional position between the earlier specimens and the extant population, lying closer to European Upper Palaeolithic specimens, and North African fossil samples from the end of the Late Pleistocene (LPNEA and LPNWA, < 20-11 ka). This dispersion along the first axis illustrates a temporal trend of a reduction in facial dimensions over time. The result is consistent with studies on the evolution of human craniofacial morphological variation (e.g. Enlow, 1990; Freidline et al., 2012; von Cramon-Taubadel, 2014; Bastir and Rosas, 2016). In
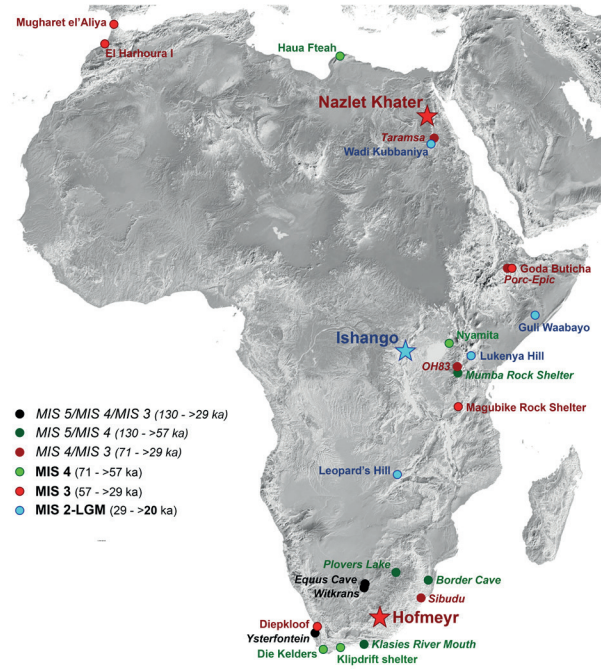

Fig. 1 – African map with the location of human remains dated from the Marine Isotopic Stage 4 (MIS 4) to the Last Glacial Maximum (LGM) peak. The stars identify sites that are detailed in the text.
Fig. 1 – Carte de l'Afrique avec l'emplacement des restes humains datés depuis le stade isotopique marin 4 (MIS 4) au Dernier Maximum glaciaire (DMG). Les étoiles signalent les sites qui sont décrits dans le texte.

this regard, the position of Nazlet Khater 2 is somewhat anachronic.

Comparison of the inner ear structures of Pleistocene *Homo* have allowed the reconstruction of the phenetic and phylogenetic relationships between hominin specimens (e.g. Spoor et al., 1994 and 2003; Braga et al., 2013; Wu et al., 2014). While earlier studies have mainly focused on archaic specimens, several studies have since highlighted phenotypic variations on small regional and temporal scales, emphasizing the importance of this structure to discuss genetic distances and population affiliation in *Homo sapiens* (Spoor et al., 2003; Bouchneb and Crevecoeur, 2009; Crevecoeur et al., 2016; Ponce de León et al., 2018). Analysis of the Nazlet Khater 2 inner ear showed that it exhibits a set of labyrinthine characteristics that put it closer to European Upper Paleolithic specimens than to recent modern human populations, notably regarding the width of the anterior semicircular canal (Bouchneb and Crevecoeur, 2009; Crevecoeur et al., 2012a). On the other hand, the more recent MIS 2 specimen from Ishango 37 (ISH 37; fig. 1) showed greater affinity with the bony labyrinth morphology of the Qafzeh and Skhul (Q-S) samples (Crevecoeur et al., 2016). The characteristic that set ISH 37, apart from the recent and chronologically closer modern human samples, is the position of the cochlea together with its morphology. In addition to being more coronally oriented in the transversal plane, Ishango 37 possesses a larger cochlea basal turn (Creve-
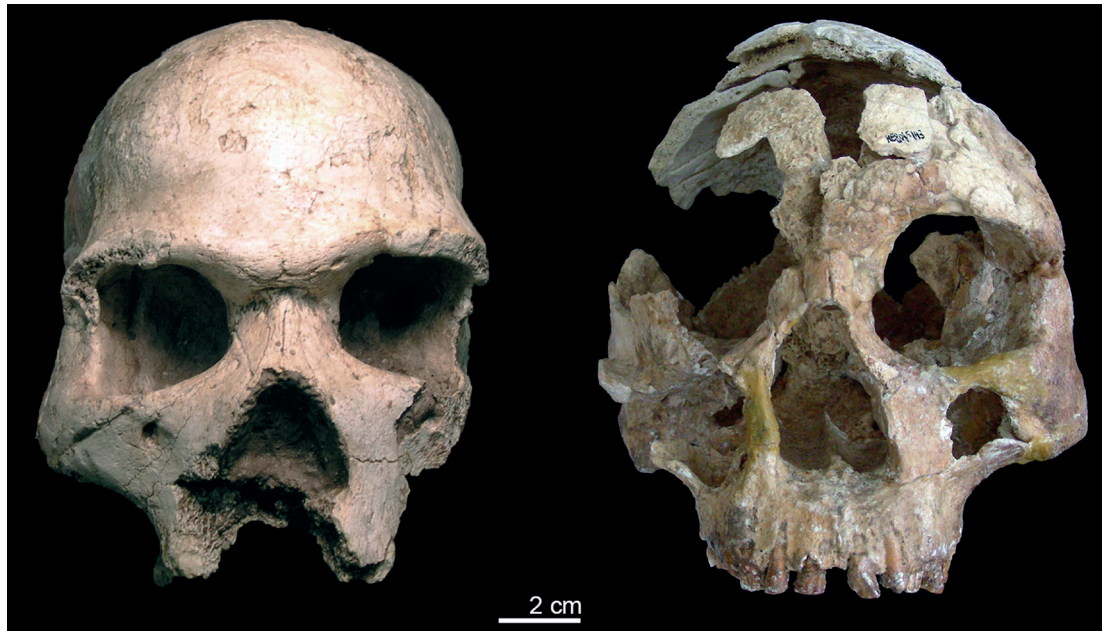
Fig. 2 – Composite picture of Hofmeyr (left) and Nazlet Khater 2 (right) cranium in frontal view.
Fig. 2 – *Image composite des crânes d'Hofmeyr (à gauche) et de Nazlet Khater 2 (à droite), en vue frontale.*
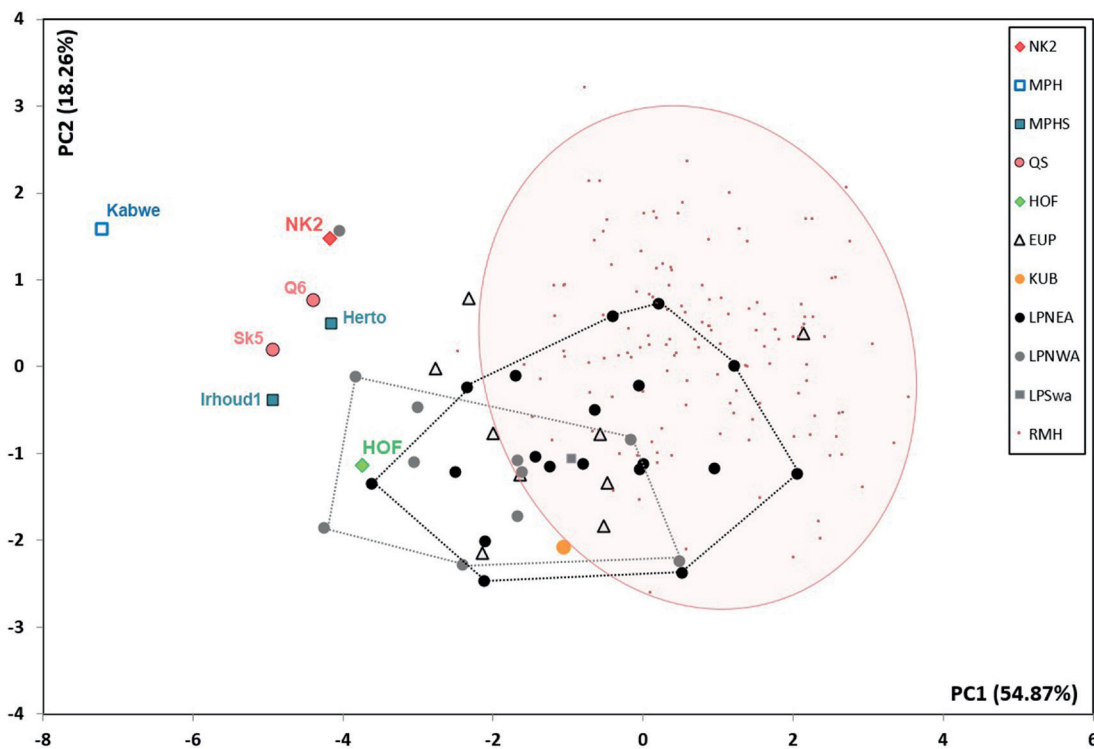

Fig. 3 – Bivariate plot of the projection of the first and second principal component of the PCA on seven cranio-facial dimensions. NK2 = Nazlet Khater 2, MPH = Middle Pleistocene Hominin, MPHS = Middle Pleistocene early *Homo sapiens*, QS = Qafzeh and Skhul, HOF = Hofmeyr, EUP = European Upper Palaeolithic fossils, KUB = Wadi Kubbaniya, LPNEA = Late Pleistocene specimens from north-east Africa (i.e. Jebel Sahaba and Wadi Halfa), LPNWA = Late Pleistocene specimens from north-west Africa (i.e. Taforalt and Afalou), LPSwa = Late Pleistocene from south-west Asia (i.e. Natufian; see Bocquentin, 2003), RMH = Recent modern human (here Egyptian population; see Howells, 1996). The ellipse represents 95% of the RMH variation.
Fig. 3 – *Diagramme bivarié de la projection de la première et de la deuxième composante principale de l'ACP sur sept dimensions cranio-faciales. NK2 = Nazlet Khater 2, MPH = hominines du Pléistocène moyen, MPHS = premiers* Homo sapiens *du Pléistocène moyen, QS = Qafzeh and Skhul, HOF = Hofmeyr, EUP = fossiles* Homo sapiens *du Paléolithique supérieur européen, KUB = Wadi Kubbaniya, LPNEA = spécimens de la fin du Pléistocène supérieur du nord-est de l'Afrique (à savoir Jebel Sahaba et Wadi Halfa), LPNWA = spécimens de la fin du Pléistocène supérieur du nord-ouest de l'Afrique (à savoir Taforalt et Afalou), LPSwa = spécimens de la fin du Pléistocène supérieur d'Asie du sud-ouest (à savoir les Natoufiens ; voir Bocquentin, 2003), RMH =* Homo sapiens *récents (ici population égyptienne ; voir Howells, 1996). L'ellipse représente 95 % de la variation du group RMH.*

coeur et al., 2016). F. Spoor et al. (2003) highlighted this characteristic in a smaller comparative sample consisting of Qafzeh and Skhul specimens. Similar morphologies have been observed in the Hofmeyr specimens (Crevecoeur et al., 2022). An enlarged anterior semi-circular canal, like Nazlet Khater 2, and a wide cochlea that is positioned more inferiorly with respect to the level of the lateral semi-circular canal, like Ishango 37, characterize the Hofmeyr inner ear. As illustrated by their position in the lower left quadrant of the first two principal component projections in figure 4, these inner ear characteristics, shared by the EUP and Q-S specimens, also influenced the position of the early Holocene fossil from Shum Laka (SE II) which exhibits a genetic signal of deep ancestry (A00 Y-chromosome lineage; Lipson et al., 2020). Located close to Qafzeh 11, this member of the Early Holocene African (EHA) comparative sample is separated from the other individual from Shum Laka (SE I), whose Y-chromosome haplogroup (B) is common among recent hunter-gatherers from Central Africa. Interestingly, the similarities of Hofmeyr to Nalet Khater

or Ishango differ in relation to the part of the bony labyrinth investigated, namely the semi-circular canals or the cochlea. The independent physiological roles of each component of the inner ear likely imply that they could have evolved separately as noted within the Neanderthal clade (Quam et al., 2016; Conde-Valverde et al., 2019). The affinities of Hofmeyr with EUP and Q-S regarding the size and proportions of the semi-circular canals, and its similarity with Ishango based on its large cochlea could be interpreted as reflecting different paths within Late Pleistocene modern human evolution (Crevecoeur et al., 2022). Given that the strong phylogenetic signal of cochlear dimensions may be confidently used to assess biological affinities between human populations (Braga et al., 2015; Conde-Valverde et al., 2019), we believe that these results help to support the hypotheses of a certain level of phylogenetic discontinuity between Late Pleistocene and present-day populations, even those that are geographically proximate, within the African continent.

Despite the fragmentary nature of the Late Pleistocene fossils, these results echo the paleogenetic hypotheses
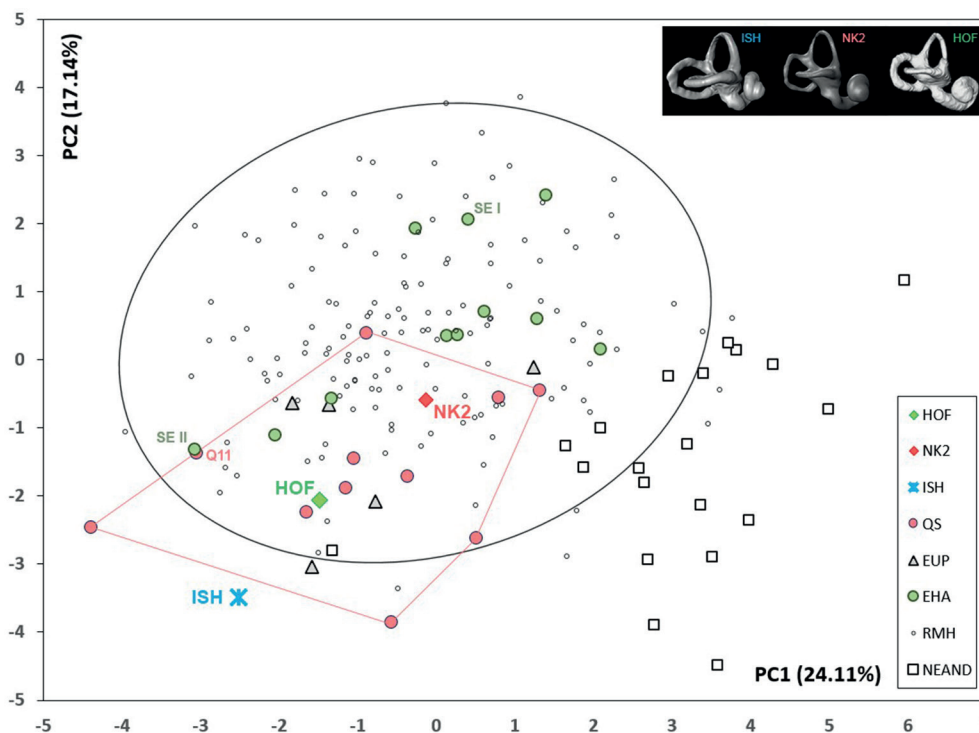

Fig. 4 – Bivariate plot of the projection of the first and second principal component of the PCA on fourteen variables that account for the general size and shape of the bony labyrinth. Composite image of the virtual reconstruction of Ishango, Nazlet Khater 2 and Hofmeyr bony labyrinth structure. HOF = Hofmeyr, NK2 = Nazlet Khater 2, ISH = Ishango 37, QS = Qafzeh and Skhul, EUP = European Upper Palaeolithic fossils, EHA = Early to mid-Holocene specimens from north-east and central Africa (Shum Laka, Lothagam, Gogoshiis Qabe, Hara Idé 2), RMH = Recent modern human, NEAND = Neandertal specimens (see Crevecoeur et al., 2022). The black ellipse represents 95% of the RMH variation. The pink line delimits the Q-S convex hull.

Fig. 4 – Diagramme bivarié de la projection de la première et de la deuxième composante principale de l'ACP sur quatorze variables rendant compte de la taille et de la forme du labyrinthe osseux. Image composite de la reconstruction virtuelle de la structure du labyrinthe osseux des fossiles d'Ishango, de Nazlet Khater 2 et d'Hofmeyr. HOF = Hofmeyr, NK2 = Nazlet Khater 2, ISH = Ishango 37, QS = Qafzeh et Skhul, EUP = fossiles Homo sapiens *du Paléolithique supérieur européen, EHA = spécimens du début de l'Holocène d'Afrique du nord-est et d'Afrique centrale (à savoir Shum Laka, Lothagam, Gogoshiis Qabe, Hara Idé 2), RMH =* Homo sapiens *récents, NEAND = Néandertaliens (voir Crevecoeur* et al.*, 2022). L'ellipse noire représente 95 % de la variation du groupe RMH. La ligne rose délimite le polygone convexe contenant les individus de Q-S.*

about deeply divergent, geographically separated populations in Africa during the Late Pleistocene (e.g. Quintana-Murci et al., 2008; Scheinfeldt et al., 2010; Schlebusch et al., 2017; Skoglund et al., 2017; Schlebush and Jakobsson, 2018; Lipson et al., 2020). The fossils under study are distinct from both extant African populations and many Holocene specimens. They exhibit diverse biological affinities with earlier Middle to Late Pleistocene fossils and European Upper Paleolithic *Homo sapiens* that appear related to plesiomorphic morphologies or part of the phenotypic diversity that is no longer documented in more recent populations. Similar observations made for some individuals from the terminal part of the Pleistocene (Crevecoeur et al., 2009; Harvati et al., 2011; Tryon et al., 2015) suggest that deep population substructures in Africa lasted at least until the mid-Holocene period and that some populations might not have contributed to present day diversity. In this regard, the metapopulation model of African population history is currently the best-fitting theory to reconcile palaeoanthropological and ancient and recent genetic data (Scerri et al., 2019).

It is of course possible that some of the observations made about Nazlet Khater 2, or others Late Pleistocene fossils could be interpreted as indicating signs of admixture with a "ghost archaic" population as some studies have suggested (e.g. Harvati et al., 2011; Durvasula and Sankararaman, 2020). However, given our poor understanding of African Late Pleistocene phenotypic and genetic diversity, as well as the recent work of M. Lipson et al. (2020) which also suggested the presence of a "ghost modern" population input in present day variation, we favor a conservative approach regarding these assertions. The identification of admixed phenotypes is currently limited by the absence of fossils from this "ghost archaic" population and will only be possible once African modern human past phenotypic diversity is properly encompassed.

2. NILE VALLEY POPULATION PROCESSES AT THE END OF THE PLEISTOCENE AND THE BEGINNING OF THE HOLOCENE

As described above, geological evidence points to generally dry conditions in Africa during the Last Glacial Maximum (LGM, ~ 23-18 ka; Gasse, 2000). The LGM was then followed by the African Humid Period (~ 15-5.5 ka) which ended abruptly with the second half of the Holocene and the onset of more arid conditions (DeMenocal et al., 2000). In the Nile Valley, climatic conditions are depicted as hyper-arid during the second half of the Late Pleistocene (Paulissen and Vermeersch, 1987). During the MIS 2 (27.8-14.7 ka; Sanchez Goñi et al., 2010), the Nile Valley probably functioned as a refuge for human populations. This is attested by the high density of archaeological contexts in Upper Egypt and Lower Nubia dated to the aridity peaks of the LGM and the second part of the Heinrich Stadial 1 (HS1b; 16-14.5 ka;

Hoelzmann et al., 2004; Vermeersch and Van Neer, 2015; Castañeda et al., 2016; Vermeersch, 2020; Leplongeon, 2021). The Blue Nile and the White Nile were then highly seasonal rivers and the Sudd swamps had yet to develop (Williams et al., 2000, Hoelzmann et al., 2004). Around 15-14 ka, the present Nile-flow regime was re-established by the sudden overflow of lake Victoria in the White Nile, which caused severe flooding in the Nile Valley as far as Egypt (Williams et al., 2006). This period of hydrological instability was interrupted by a short-term return of drier and colder climatic condition that coincides with the Younger Dryas interval (YD; ~ 12.9-11.7 ka; Rasmussen et al., 2006). It was only after the Younger Dryas (~ 12.9-11.7 ka) that the monsoon conditions of the African Humid Period became more stable for human presence in the Nile Valley, as evidenced by the scarcity of traces of human occupation at the end of the Late Pleistocene and the beginning of the Holocene (~ 15-10.5 ka). Archaeological sites from this period are restricted to the floodplain in Upper Egypt and Lower Nubia (Nicoll, 2004; Kuper and Kröpelin, 2006; Schild and Wendorf, 2010; Vermeersch and Van Neer, 2015, Vermeersch, 2020; Leplongeon, 2021), and only a few sites have yielded complete human remains. Among these, the most emblematic are Jebel Sahaba (JS, site 117), Tushka (site 8905), Wadi Kubbaniya, and Wadi Halfa (WH, site 6B36; fig. 5; Hewes et al., 1964; Wendorf, 1968; Wendorf and Schild, 1986).

Culturally, a large variety of lithic assemblages, linked to Late Paleolithic, or Late Stone Age, industries based on the production of flakes and elongated products of small dimensions, including high proportions of backed tools (Schild and Wendorf, 2010; Leplongeon, 2021), has been identified in sites associated with the end of the Late Pleistocene (e.g. the Fakhurian, the Kubbaniyan, the Idfuan, the Ballanan-Silsilian, the Afian, the Isnan and the Qadan; Wendorf, 1968; Lubell, 1974; Wendorf et al., 1989; Schild and Wendorf, 2010; Vermeersch, 2010). The great variability of typological characteristics of these lithic assemblages has led to the recognition of different industries that seem to be regionally and chronologically constrained, with some industries occurring only in Lower Nubia or in Upper Egypt (Leplongeon, 2021). Archaeozoological analysis of these Late Pleistocene settlements indicate similar human subsistence strategies based on the exploitation of the Nilotic environment (Schild and Wendorf, 2010). Seasonally adapted fishing activities, shellfish consumption, medium and large ungulate hunting and plant tuber processing are documented at various locations (Van Neer et al., 2000; Linseele and Van Neer, 2010; Yeshurun, 2018). In this framework of limited subsistence strategy options and constrained geographical habitable environment, the development of a wide range of lithic cultural traditions is interesting. They don't seem to be related to specific activities and are characterized by distinctive sets of lithic tools and/or technology that could be associated with small hunting-fishing-gathering groups (Vermeersch, 2010). It has therefore been suggested that each of these lithic entities could represent
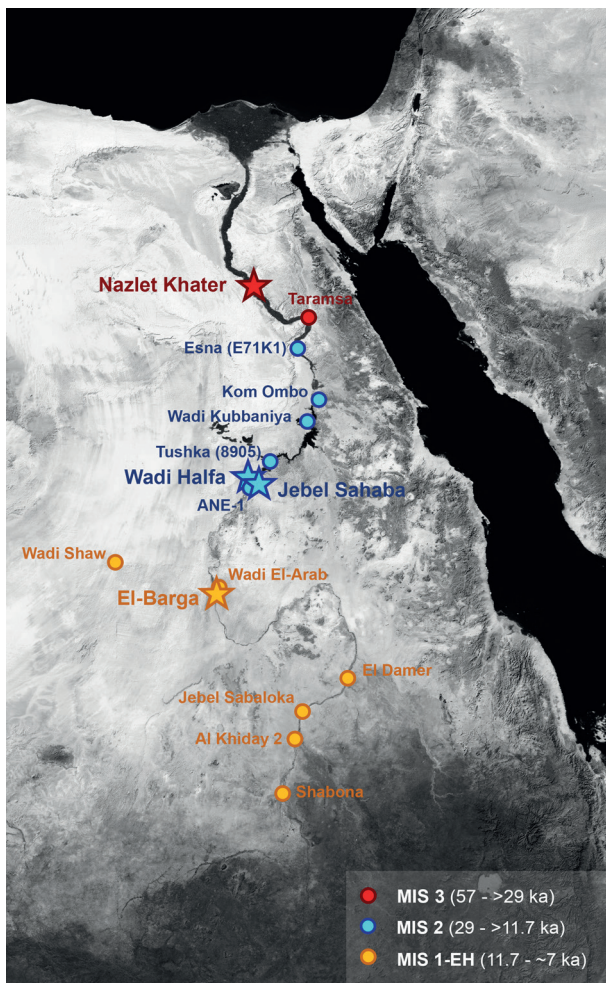
Fig. 5 – Map of the Nile Valley with the location of sites preserving human remains dated from the MIS 3 to the end of the early Holocene period (MIS 1-EH). Stars identify sites that are discussed in the text.

Fig. 5 – Carte de la vallée du Nil avec la localisation des sites ayant livré des restes humains datés depuis le MIS 3 jusqu'au début de l'Holocène (MIS 1-EH). Les étoiles signalent les sites qui sont discutés dans le texte.

a cultural tradition reflecting the structuration of human group identity in this restricted habitable area (Schild and Wendorf, 2010). The concomitant occurrence of large graveyards at the end of the Late Pleistocene in this area reinforces the hypothesis of strong social units of residential groups (Wendorf and Schild, 2004).

As mentioned earlier, the more numerous and best preserved human remains from this period come from the graveyard of Jebel Sahaba (site 117, MNI = 61; Wendorf, 1968), the Wadi Halfa cemetery (site 6B36, MNI = 36; Hewes et al., 1964) and the Tushka burial ground (site 8905; MNI = 12; Wendorf 1968). All are associated with the Qadan industry. The Qadan sequence is documented in Upper Egypt and Lower Nubia from the end of the Late Pleistocene (~ 18 ka) until the Holocene (Wendorf, 1968; Schild and Wendorf, 2010). In Jebel Sahaba, direct dating of five individuals based on the collagen and mineral fraction of the bones and teeth give a time range of between 18 ka and 11 ka (Wendorf and Schild,

2004; Zazzo, 2014). The oldest Tuskha human remains are dated between ~ 15-11 ka, based on geological and archaeological data, taphonomic observations and several radiocarbon dating results (Albritton and Wendorf, 1968). Although not directly dated, the Wadi Halfa cemetery is considered to be of equivalent age given its archaeological consistency with Jebel Sahaba and Tushka (Greene and Armelagos, 1972). The partial skeleton from Wadi Kubbaniya, also associated with the Qadan artefacts, represents the last and maybe the oldest well-preserved human remains from MIS 2 in the region. Sedimentological and lithic technological evidence could indicate a date as early as 20 ka for this deposit (Wendorf and Schild, 1986). The other human remains from this period (Kom Ombo, Esna and ANE-1) are fragmentary and/or poorly preserved (Reed, 1965; Wendorf, 1968; Lubell, 1974).

Since the first publications related to their find, the individuals from Wadi Halfa and Jebel Sahaba have been described as part of a highly robust population exhibiting a distinctive assemblage of cranial and dental traits compared to recent modern humans (Greene et al., 1967; Anderson, 1968; Greene and Armelagos, 1972). The dental elements are massive and exhibit high frequencies of complex traits that can be related to mass additive features (Greene et al., 1967; Irish, 2005). The cranial remains are also characterised by plesiomorphic features and robust morphologies in relation to powerful masticatory apparatus. Moreover, the level of similarity between the Wadi Halfa and the Jebel Sahaba individuals supports their association with the same Nubian Late Pleistocene population (Anderson, 1968; Greene and Armelagos, 1972). As J.L. Angel and J.O. Kelley (1986) later argued, given its large face and robust mandible, the Wadi Kubbaniya skeleton would fit perfectly in the center of this Nubian Late Pleistocene variation. This robust phenotype is associated with a high average stature (~ 1 m 67) and structural conformation of the lower limb that suggests an active and mobile lifestyle (Shackelford, 2007; Holliday, 2015). In addition, these populations appear to exhibit a higher phenotypic variation than the more recent Holocene populations (Crevecoeur et al., 2009). The figure 6 illustrates the extreme dental size and the range of variation shown by the Nubian Late Pleistocene sample (LPNAE, here composed of Jebel Sahaba, Wadi Halfa and Tuskha) with regard to the lower second molar crown diameters.

These dental dimensions may be related to the complexity of the crown morphology exhibited by Jebel Sahaba and Wadi Halfa, with a high frequency of six-cusped lower first molars and at least five-cusped lower second molars (Greene et al., 1967; Irish, 2000 and 2005). The number of cusps on the lower molars is one of the most suitable non-metric dental trait for identifying population affinities as it preserves the maximum number of neutral genetic signals (Rathmann and Reyes-Centeno, 2020). Interestingly, Nazlet Khater 2 fits in the center of the LPNAE variation, as do several African specimens attributed to the MIS 5 to MIS 3 period, here referred
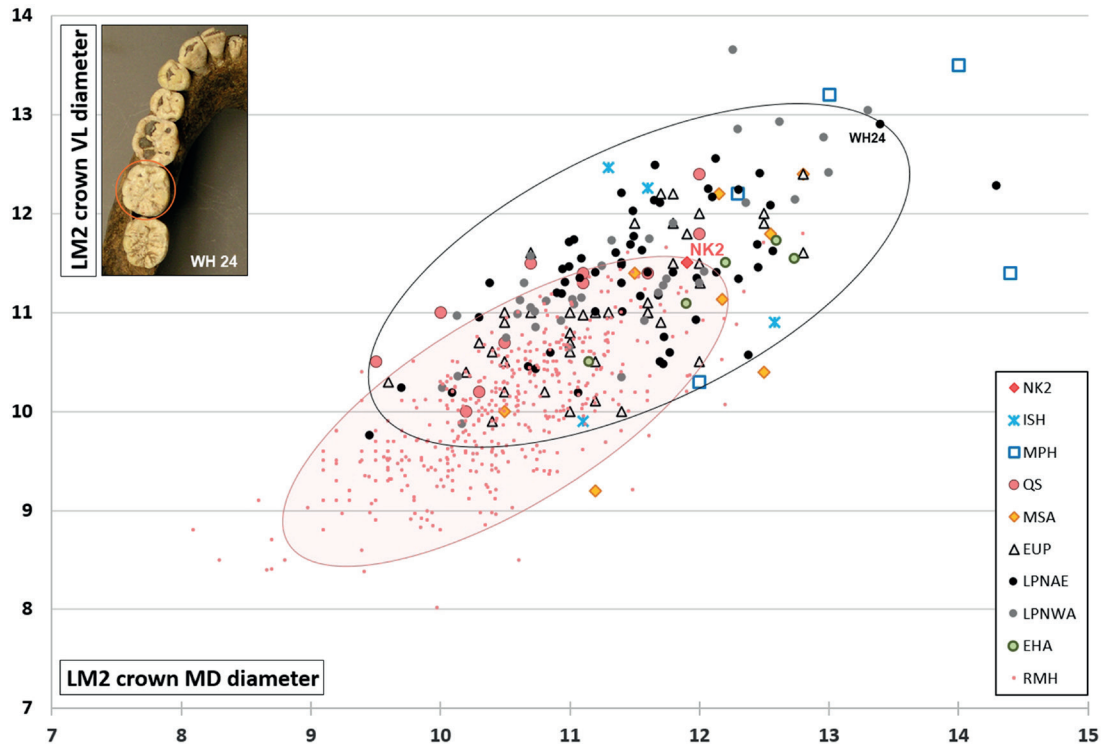
Fig. 6 – Bivariate plot of the lower second molar crown dimensions in centimeters. VL = vestibule-lingual, MD = mesiodistal. NK2 = Nazlet Khater 2, ISH = Ishango, MPH = Middle Pleistocene Hominin, QS = Qafzeh and Skhul, MSA = African specimens attributed to the MIS 5 to MIS 3 period (i.e. Temara, Dar-es-Soltan, Haua Fteah, Klasies River Mouth, Mumba Rock Shelter, Equus Cave and Witkrans), EUP = European Upper Palaeolithic fossils, LPNEA = Late Pleistocene specimens from north-east Africa (i.e Jebel Sahaba and Wadi Halfa), LPNWA = Late Pleistocene specimens from north-west Africa (i.e. Taforalt and Afalou), EHA = Early to mid-Holocene specimens from northeast Africa (Lothagam, Gogoshiis Qabe, Mille Logghia and Lake Besaka 2), RMH = Recent modern human (database, see Kieser, 1990). The ellipses represent 95% of the sample variation.

Fig. 6 – Diagramme bivarié des dimensions de la couronne de la deuxième molaire inférieure en centimètres. VL = vestibulo-lingual, MD = mésiodistal. NK2 = Nazlet Khater 2, ISH = Ishango, MPH = hominines du Pléistocène moyen, QS = Qafzeh et Skhul, MSA = spécimens africains attribués à la période allant du MIS 5 au MIS 3 (à savoir Temara, Dar-es-Soltan, Haua Fteah, Klasies River Mouth, Mumba Rock Shelter, grotte d'Equus et Witkrans), EUP = fossiles Homo sapiens du Paléolithique supérieur européen, LPNEA = spécimens de la fin du Pléistocène supérieur du nord-est de l'Afrique (à savoir Jebel Sahaba et Wadi Halfa), LPNWA = spécimens de la fin du Pléistocène supérieur du nord-ouest de l'Afrique (à savoir, Taforalt et Afalou), EHA = spécimens du début de l'Holocène d'Afrique du nord-est (à savoir Lothagam, Gogoshiis Qabe, Mille Logghia et lac Besaka 2), RMH = Homo sapiens récents (base de données, voir Kieser, 1990). Les ellipses représentent 95 % de la variation de l'échantillon.

to as the MSA sample (i.e. Dar-es-Soltan, Equus Cave, Haua Fteah, Klasies River Mouth, Mumba X, and Witkrans).

In line with what was observed for Nazlet Khater 2, the combination of plesiomorphic and unique morphometric features in the LPNAE sample, that sit on the fringe, or outside, recent phenotypic diversity, could be the consequence of population isolation and division/fragmentation in Middle Nile Valley at a time of extreme climatic conditions (Kuper and Kröpelin, 2006; Crevecoeur, 2008; Vermeersch and Van Neer, 2015; Pagani and Crevecoeur, 2019). In this context of environmental pressure and geographic constraints, the identification of traces of interpersonal violence on the bones of individuals from different LPNAE sites have attracted a great deal of attention and generated debate about Late Pleistocene warfare (Anderson, 1968, Keeley, 1996; Thorpe, 2003; Wendorf and Schild, 2004; Guilaine and Zammit, 2005; Daković, 2014). The oldest case is documented on the

partial skeleton from Wadi Kubbaniya where two bladelets were found inside the volume of the body between the rib cage and the lumbar vertebrae. A chip of flint was also found embedded in a partially healed trauma on the left humerus. Finally, this individual also exhibits a healed fracture of the right ulna (Angel and Kelley, 1986; Wendorf and Schild, 1986). Similar observations of embedded lithic and healed fractures have been documented on some individuals buried in the Wadi Halfa cemetery (Hewes et al., 1964; Saxe, 1971; Greene and Armelagos, 1972). However, the most emblematic case is clearly the cemetery of Jebel Sahaba, where anthropological examinations of the skeletons by J. E. Anderson (1968) and B. Butler (1968) revealed the presence of traces of interpersonal violence on the bones of at least half of the Jebel Sahaba individuals. In addition, abundant lithic artefacts were discovered within the body volume or directly embedded in the bones (Wendorf, 1968). On these issues, we can confirm that more than half of

the injured Jebel Sahaba individuals undoubtedly exhibit projectile impact marks (61%), and almost all of them showing signs of trauma (92.7%). We also confirmed that these individuals exhibit clear signs of acts of interpersonal violence involving projectile weapons. The injuries are independent of the age-at-death and sexual diagnosis of the individuals. In addition, the concomitant occurrence of healed and unhealed traumas on the same individuals increases through time, with adolescents, young adults and adults exhibiting this association progressively more frequently (Crevecoeur et al., 2021 and this volume). This observation suggests that acts of interpersonal violence were repeated over time. We suggest that adaptation of the subsistence strategies to territorial and environmental stresses triggered by climatic changes at the end of MIS 2 may be responsible for these sporadic, but recurrent, small-scale conflictual events between semi-sedentary hunter-fisher-gatherer groups.

With the stabilization of more humid conditions during the Early Holocene period (~ 10.5-7.3 ka), Prehistoric settlements moved to the eastern Sahara that turned into a savannah-like environment, probably more hospitable than the Nile Valley (Nicoll, 2001 and 2004; Kuper and Kröpelin, 2006; Bubenzer and Riemer, 2007; Manning and Timpson, 2014). No precisely dated archaeological sites are documented in the Egyptian Nile Valley during the Early Holocene, but only periodic traces of human presence related to seasonal activities are suspected (Vermeersch, 2001; Kuper and Kröpelin, 2006; Dittrich, 2015). The only two regions that have yielded clear archaeological records of human occupations near the Nile Valley during this Saharan exodus are central Sudan and Nubia (fig. 5). Evidence includes several archaeological sites related to the Khartoum Mesolithic culture that were excavated near the confluence of the White Nile and Blue Nile in central Sudan (Clark, 1989; Haaland, 1993; Usaï et al., 2010; Salvatori, 2012; Suková and Varadzin, 2012; Williams et al., 2015) and sites near Kerma, like Wadi El-Arab and El-Barga, that document human occupation near the Nile Valley between ~ 10.5-7.3 ka (Honegger, 2006, 2011 and 2012; Honegger and Williams, 2015). The decline in human occupation in the Sahara from 7.3 ka to 5.5 ka relates to the cessation of regular monsoon rains that forced human populations to relocate to new ecological niches and/or to begin the exodus to the Sudanese plains and the Egyptian Nile Valley (Nicoll, 2001 and 2004; Vermeersch, 2001; Kuper and Kröpelin, 2006; Manning and Timpson, 2014).

In parallel with these climatic fluctuations, the beginning of the Holocene witnessed the appearance of new subsistence strategies with the emergence of herding activities. The origin and spread of pastoralism in North Africa is the subject of intense debate about whether it results from one or several independent African domestication centers or is linked to the diffusion and adoption of the practice from other continents (Wendorf and Schild, 1998; Kuper and Riemer, 2013; Stock and Gifford-Gonzales, 2013; Brass, 2018). Circumstantial evidence of early cattle domestication is reported from Nabta Playa

and Bir Kiseiba about ~ 10-8 ka, which corresponds to the period of stabilization of more humid climatic conditions (Wendorf and Schild, 1980; Gautier, 2001; Jórdeczka et al., 2013). While there is a lack of data on early domestic Holocene bovid remains, large bovids have been documented in association with archaeological contexts from the end of the Late Pleistocene in the Nile Valley, suggesting that bovids had specific significance prior to domestication (e.g. Tuskha, site 8905; Wendorf, 1968; Marshall and Hildebrand, 2002). In addition, the early dates for potential cattle domestication at Nabta Playa and Bir Kiseiba are concomitant with the apparition of the oldest form of pottery in the Sahara and the Nile Valley (Jesse, 2010; Haaland, 2015). Wavy-line and dotted wavy-line potteries are recorded in the earliest phases at Nabta Playa and Bir Kiseiba (Close and Wendorf, 2001; Jesse, 2010). These behavioral changes at the beginning of the Holocene among hunter-gatherer communities might therefore be viewed as a way to accommodate the new climatic conditions of subtle rainfall variations compared to the preceding period of probably more stable, acute aridity by way of more predictable food availability and storage (Marshall and Hildebrand, 2002; Jesse, 2010). The introduction of domestic sheep and goats in Africa is clearly an exogenous contribution, since no wild ancestor is present in Africa (Marshall and Hildebrand, 2002; Lesur-Gebremariam, 2010; Lesur et al., 2014). The oldest occurrence of bones from domestic ovicrapines are documented in the Red Sea mountains (Marinova et al., 2008; Vermeersch et al., 2015) and in the western desert (Gautier, 2001 and 2014) from ~ 8.2 ka onwards. These dates are consistent with the oldest remains recorded in the south Sinai and are earlier than domestic goat and sheep remains from Northern Egypt, which would suggest their introduction to southern Egypt and north Sudan from southwestern Asia prior to the major diffusion of fully-fledged pastoralism along the Nile Valley around ~ 7.0 ka, originating from the Levant (e.g. Close, 2002; Marshall and Hildebrand, 2002; Kuper and Kröpelin, 2006; Kuper and Riemer, 2013; Lesur et al., 2014).

While changes in subsistence strategies emerged in the western desert and the Red Sea mountains at the beginning of the Holocene, they do not seem to be related to a fundamental break in the hunter-fisher-gatherer tradition since in many of these contexts, hunting of wild mammals and gathering of wild seeds were still dominant food procurement activities (Kuper and Riemer, 2013; Vermeersch et al., 2015). It was only in the second half of the Holocene (after 7.0 ka), concomitant to the decrease in the monsoonal rains and the resettlement of populations in the Nile Valley refuge zone, that northeast African populations truly developed pastoral ways of life (Kuper and Kröpelin, 2006; Kuper and Riemer, 2013). Evidence of cultural convergence in terms of material uses and funerary practices can be observed in the Neolithic of the Nile Valley from the same period (i.e. during the 5th millennium BCE; Wengrow et al., 2014). This timescale (~ 7.3-5.7 ka) also corresponds to the expansion period of the Y-chromosome haplogroup R-V88 into

the Sahelian/Savannah pastoralist gene pool that seems to be associated with an Asia-to-Africa back migration (Cruciani et al., 2010; Kulichová et al., 2017).

Given this climatic, behavioral and cultural framework of change at the beginning of the Holocene in the Nile Valley, the cranio-facial phenotypic differences documented between Nubian Late Pleistocene individuals (Jebel Sahaba, Wadi Halfa) and mid-Holocene to recent populations in this region have been widely discussed. For some authors, the differences in cranial and dental morphology are linked to a gradual adaptation to changes in subsistence activities (Greene et al., 1967; Carlson and Van Gerven, 1977; Galland et al., 2016). This morpho-functional hypothesis postulates population continuity in the Nile Valley during the Holocene and attributes the strong morphological differences to changes in diet, caries-related selection and gracilization processes (Carlson and Van Gerven, 1977). For others, these differences, notably in non-metric dental trait variations, are genetically related and suggest some level of population discontinuity at the beginning of the Holocene (Groves and Thornes, 1999; Irish, 2000 and 2005; Holliday, 2015). However, the absence of Early Holocene samples in these studies that would allow the hypotheses of continuity or replacement of populations in the Nile Valley to be tested limits the discussion.

The Early Holocene site of El-Barga, situated in Nubia more than 10 km east of the city of Kerma, offers a unique opportunity to address these questions of Early Holocene population processes in the Nile Valley (fig. 5). Excavated since 2001 by the Swiss archaeological mission in Sudan (Honegger, 2006), the site has preserved two archaeological assemblages, a Mesolithic settlement with habitat structures and burials, and an Early Neolithic cemetery. The two occupations are located in the same area and dated by radiocarbon isotopic analyses on shells and ostrich eggshells directly associated with the burials (Honegger and Williams, 2015). The Mesolithic assemblage, situated at the top of the hill, has been dated to ∼ 10.2-9.1 ka, and the Early Neolithic cemetery is dated to 8.1-7.5 ka, which corresponds to the earliest Neolithic occupation in Nubia (Salvatori and Usaï, 2008). Preliminary analyses of funerary practices, associated artefacts, as well as morphometric comparisons of the human remains, suggest substantial biological and cultural differences between the two human occupations, separated by about a millennium (Honegger, 2006 and 2011; Crevecoeur, 2012b).

Morphometrically, the El-Barga Mesolithic skeletons (EBK_M) can be described as extremely robust. They exhibit strong muscular attachments on the cranium and the infra-cranium skeleton. Regarding dental dimensions and morphology, the Mesolithic sample possesses higher dental diameters on average than the Early Neolithic group (EBK_N). In addition, there is a statistically significant difference in terms of shape of the lower second molars (LM2) and the lower second premolars (LP2). The latter observation is related to the fact that Mesolithic individuals exhibit a higher frequency of lower

second molars with fifth cusps compared to the Neolithic group, while differences in the shape of the LP2s depend on the proportionally wider bucco-lingual diameters of the Epipalaeolithic individuals (Benoiston et al., 2018). Comparative morphometric analyses of dental remains show strong biological affinities between the Mesolithic sample from El-Barga and the Nubian Late Pleistocene population from Jebel Sahaba. These characteristics significantly differentiate the Mesolithic and Early Neolithic samples at El-Barga (Benoiston et al., 2018). In-depth investigations of the dental tissue proportions between both El-Barga samples have highlighted variations in size and conformation of these inner structures that support the hypothesis of a biological differentiation between the two El-Barga populations. For instance, the results from the permanent upper central incisors (UI1s) show that the Mesolithic sample exhibits higher values of crown, enamel and dentine volumes than the Neolithic sample, as illustrated in figure 7. The latter figure also maps the repartition of the enamel in both samples. The Mesolithic UI1s possess a significantly higher enamel thickness on average than the Early Neolithic group, notably on the buccal surface of the tooth. This result indicates a difference in conformation of the dental tissue that is independent of the size of the tooth (Benoiston et al., 2018). Although the development of the permanent incisor is more plastic than the posterior teeth (Braga and Heuzé, 2007), the dominance of genetic factors compared to environmental ones in the dental crown development is underscored (e.g. Townsend and Brown, 1978; Dempsey and Townsend, 2001; Hlusko et al., 2004; Townsend et al., 2009). Thus, it is unlikely that the differences in dental tissue proportion would only be related to dietary changes in the El-Barga case in such a short timescale and at the onset of pastoralism. On the contrary, we believe that these results indicate major biological differences between both groups, suggesting possible biological discontinuity between the Mesolithic and the Neolithic populations from El-Barga.

This hypothesis is supported by the results of craniometric comparisons. The Mesolithic individuals from El-Barga exhibit long and wide mandibles, characterized by high mandibular corpus and wide ramus, while the Neolithic mandibles differ significantly with regard to these dimensions. Their mandibles are shorter, narrower and characterized by a consistently low height of the mandibular corpus. Differences in craniofacial morphology are also striking, as illustrated in figure 8 and by the results of a PCA anlysis on seven size-adjusted variables (fig. 8). In the projection of the first and third principal components in figure 8, the El-Barga individuals cluster in very different areas of the plot in relation to their chronological affinities. The El-Barga Mesolithic group cluster with Late Pleistocene specimens from north-east Africa (LPNAE; i.e. Jebel Sahaba, Wadi Halfa) along the positive value of the PC1 that correlates with the relative length and breadth of the face compared to the neurocranial conformation. On the other hand, the El-Barga Neolithic individuals are clearly dissociated from this positive
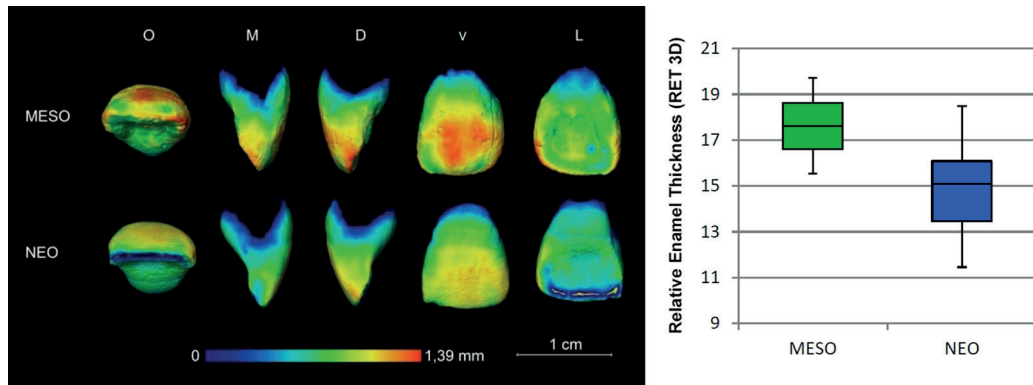
Fig. 7 – Right: Cartographic representation of the enamel thickness variation for the El-Barga Mesolithic and Neolithic UI1s. The teeth are represented in occlusal (O), medial (M), distale (D), vestibular (V) and lingual (L) views. Left: Boxplot of the mean and range of variation of the relative enamel thickness (RET 3D) of the UI1s for the Mesolithic and Neolithic samples of El-Barga (following Benoiston et al., 2018).
Fig. 7 – À droite : représentation cartographique de la variation de l'épaisseur de l'émail pour les UI1 mésolithiques et néolithiques d'El-Barga. Les dents sont représentées en vues occlusale (O), médiale (M), distale (D), vestibulaire (V) et linguale (L). À gauche : Boxplot de la moyenne et de l'écart-type de l'épaisseur relative de l'émail (RET 3D) des UI1 pour les échantillons mésolithiques et néolithiques d'El-Barga (d'après Benoiston et al., 2018).
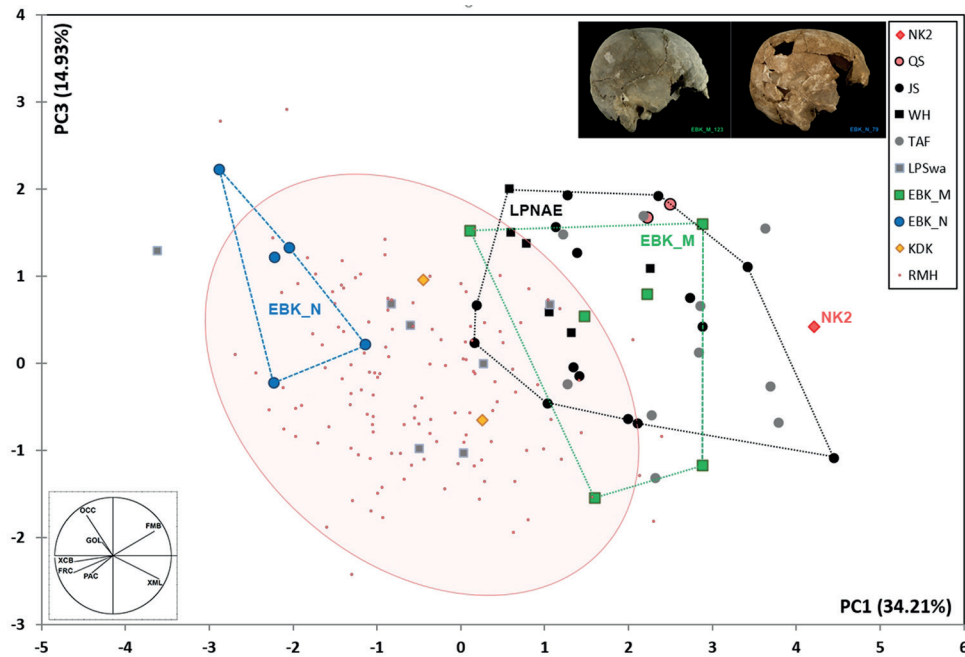

Fig. 8 – Bivariate plot of the projection of the first and third principal component of the PCA on size-adjusted cranial dimensions. Bottom left: Correlation circle showing the position of the variables in relation to the two plotted PCs. FMB, bifrontal breadth; XML, malar length; FRC, frontal chord; PAC, parietal chord; OCC, occipital chord; XCB, maximum cranial breadth; GOL, maximum cranial length. NK2 = Nazlet Khater 2, QS = Qafzeh and Skhul, JS = Jebel Sahaba, WH = Wadi Halfa, TAF = Taforalt, LPSwa = Late Pleistocene from southwest Asia (i.e. Natufian; see Bocquentin, 2003), EBK_M = Mesolithic from El-Barga, EBK_N = Neolithic from El-Barga, KDK = Kadruka 1 sample, RMH = Recent modern human (here Egyptian population; see Howells, 1996). The pink ellipse represents 95% of the RMH variation (Howells, 1996). The dotted lines delimit convex hulls of selected samples. Photograph inserted in the top right part of the graph illustrates the cranium of EBK_M_123 and EBK_N_79 individuals in lateral view.
Fig. 8 – Diagramme bivarié de la projection de la première et de la troisième composante principale de l'ACP sur les dimensions crâniennes normées. En bas à gauche : cercle de corrélation montrant la position des variables par rapport aux deux composantes principales projetées. FMB, largeur bifrontale ; XML, longueur malaire ; FRC, corde frontale ; PAC, corde pariétale ; OCC, corde occipitale ; XCB, largeur crânienne maximale ; GOL, longueur crânienne maximale. NK2 = Nazlet Khater 2, QS = Qafzeh et Skhul, JS = Jebel Sahaba, WH = Wadi Halfa, TAF = Taforalt, LPSwa = spécimens de la fin du Pléistocène supérieur d'Asie du sud-ouest (à savoir les Natoufiens ; voir Bocquentin, 2003), EBK_M = individus mésolithiques d'El-Barga, EBK_N = individus néolithiques d'El-Barga, KDK = individus néolithiques de Kadruka 1, RMH = Homo sapiens récents (ici population égyptienne ; voir Howells, 1996). L'ellipse rose représente 95 % de la variation du groupe RMH. Les lignes pointillées délimitent les polygones convexes contenant les individus des échantillons sélectionnés. La photographie insérée dans la partie supérieure droite du graphique illustre les crânes des individus EBK_M_123 et EBK_N_79 en vue latérale.

PC1 grouping. Their position in the upper left quadrant is influenced by their proportionally longer occipital chord. It is worth noting that the Late Pleistocene individuals from southwest Asia (LPSwa), as well as the individuals from the later Nubian Neolithic site of Kadruka 1 (KDK) are included, with most of the EBK_N specimens in the Egyptian recent human variation used here as a reference.

All the anthropological evidence points to significant craniofacial and dental differentiation in terms of size and conformation between both El-Barga samples. Following D. S. Carlson and D. P. Van Gerven (1977), and more recently, M. Galland et al. (2016), the strong phenotypic differences observed on more chronologically separated samples (namely, the LPNAE sample in comparison to the Mid-Holocene (< 5.5 ka) Nile Valley populations) are related to changes in masticatory function and diet. Analysis of the only anthropological sample from the beginning of the Holocene in the Nubian part of the Nile Valley calls this hypothesis into question. El-Barga fills a chronological gap in the Early Holocene record and the comparative analyses of the human remains from both occupations underline strong phenotypic differences between them. These changes are documented on a short timescale (one millennium) and during a period of limited climatic and environmental change. In addition, while incipient pastoralism can be identified during the EBK-N period, both El-Barga populations still seem to have relied mainly on Nilotic resources (Linseele, 2012), leaving little evidence of a radical change in lifestyle or diet between the Mesolithic and the Neolithic groups. It is only by the end of the 6th millennium that evidence establishes the development of fully-fledged pastoralism in Nubia (Kuper and Kröpelin, 2006). Therefore, we consider that our results support the hypotheses of biological discontinuity between the two El-Barga groups. Without excluding the possibility of a certain level of continuity, the anthropological study of the El-Barga assemblage suggests a complex history of population processes in the Nile Valley during this crucial, but poorly documented period of the beginning of the Holocene.

3. THE HORN OF AFRICA AT THE END OF THE PLEISTOCENE AND THE BEGINNING OF THE HOLOCENE

Ideally located between Africa and Eurasia, the Horn of Africa has the potential to play a crucial role as a migratory corridor out of and back to Africa. However, the level of resolution offered by the Nile Valley to discuss population processes and phenotypic diversity at the end of the Late Pleistocene and the beginning of the Holocene is currently unavailable in the Horn of Africa. While the region is well-known for its Plio-Pleistocene hominin record and the discovery of the early representative of *Homo sapiens* (e.g. Asfaw et al., 1999 and 2002; White et al., 2003; Alemseged et al., 2006), research into the Late Pleistocene and Early Holocene periods is less

frequent. The earliest major contribution to our understanding of the MSA and LSA archaeological sequences in this area was proposed by J. D. Clark (1954), and although research increased from the 1970s onward, relatively few well-dated Late Pleistocene human occupations have been identified compared to other African regions (Brandt, 1986; Assefa, 2006; Ménard et al., 2014; Pleurdeau et al., 2014; Brandt et al., 2017; Leplongeon et al., 2017; Tribolo et al., 2017). If we focus on the number of sites preserving Late Pleistocene and Early Holocene human remains, the dearth of paleoanthropological data is striking (fig. 9).

For the beginning of the Late Pleistocene, the number of sites with securely dated archaeological sequences is
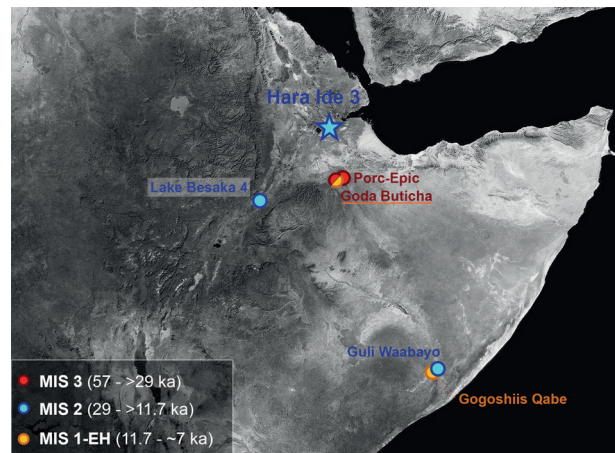

Fig. 9 – Map of the Horn of Africa with the location of sites preserving human remains dated from the MIS 3 to the end of the early Holocene period (MIS 1-EH). Star identifies the Hara Idé 3 site discussed in the text.
Fig. 9 – Carte de la Corne de l'Afrique avec la localisation des sites ayant livré des restes humains datés depuis le MIS 3 jusqu'au début de l'Holocène (MIS 1-EH). L'étoile indique le site Hara Idé 3 évoqué dans le texte.

very low and the quasi absence of sites dating to MIS 4 also raises questions about the possible absence of human presence in vast areas of the Horn of Africa (Brandt et al., 2017). During MIS 3, archaeological sequences provide evidence of continued occupation by hunter-gatherer groups (Assefa, 2006). Among these sites, only two in the Dire Dawa region have yielded human remains: Porc-Épic and Goda Buticha (fig. 10; Vallois, 1951; Pleurdeau, 2003; Pleurdeau et al., 2014).

In Porc-Épic, a poorly preserved mandibular corpus fragment was found in 1933 during H. Breuil, P. Teilhard de Chardin and P. Wernert's excavations (fig. 10a; Clark and Williamson, 1984). H.-V. Vallois (1951) noted the absence of mental protuberance, the presence of archaic features on the symphysis, and the size and robustness of the corpus which led him to propose an association with archaic populations. The stratigraphic position of the mandibular fragment is unknown, but a high-resolution low-background gamma-ray spectrometry applied
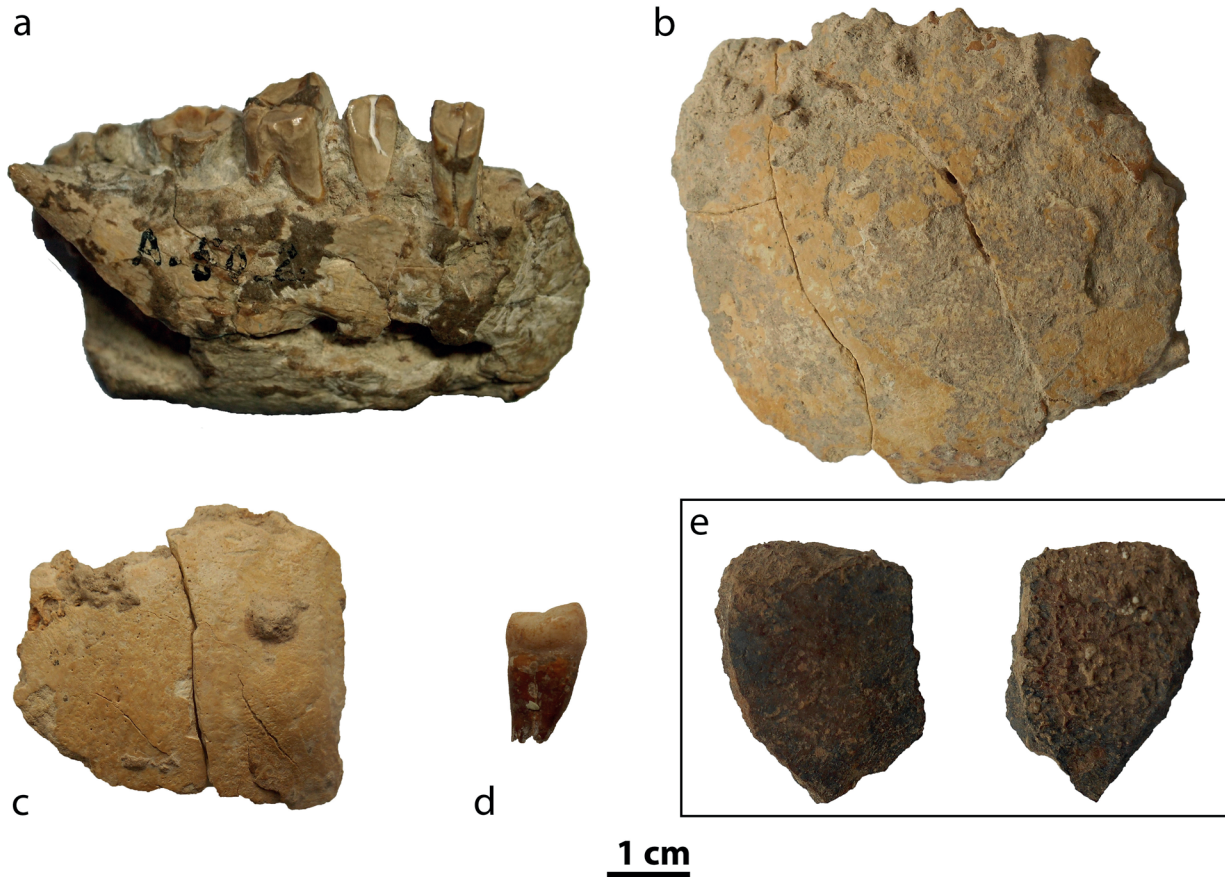
Fig. 10 – Composite image of MIS 3 human remains from Porc-Épic (a to d) and Goda Buticha (e): a, mandibular corpus described by H.-V. Vallois (1951); b, left parietal fragment; c, left occipital fragment; d, first upper left premolar; e, cranial vault fragments.
Fig. 10 – Image composite des restes humains MIS 3 de Porc-Épic (a à d) et de Goda Buticha (e) : a, corps mandibulaire décrit par H.-V. Vallois (1951) ; b, fragment de pariétal gauche ; c, fragment d'occipital gauche ; d, première prémolaire supérieure gauche ; e, fragments de voûte crânienne.

directly to the mandible yielded a date of 50 ka that is consistent with the chronological time range of the sedimentary accumulation dated by obsidian hydratation and radiocarbon between ~ 77-40 ka (Michels and Marean, 1984; Assefa, 2006; Leplongeon, 2014). Three additional unpublished human remains from Porc-Épic, two cranial fragments and a first upper left premolar (UP1) were discovered during the 1998 fieldwork conducted by Z. Assefa and D. Pleurdeau to obtain new data on Porc-Épic's stratigraphic sequence (fig. 10b, 10c and 10d; Pleurdeau, 2003 and 2004). They are associated with Unit III, dated by radiocarbon around 40 ka (Pleurdeau, 2005; Assefa, 2006; Leplongeon, 2014). The last human remain, a cranial vault fragment, dated from MIS 3, comes from the nearby cave of Goda Buticha (fig. 10e). It is associated with Level IID whose *terminus ante quem* of 36.6-33 ka is given by two radiocarbon dates on charcoal (Assefa et al., 2014; Pleurdeau et al., 2014). Given the state of preservation and the fragmentary nature of these MIS 3 human remains, it seems impossible to char-

acterize the phenotypic diversity of human populations in this area in the Late Pleistocene. While the mandibular corpus of the Porc-Épic mandible is indeed robust, with corpus dimensions on the edge of recent human variation (fig. 11), the first upper premolar crown does not exhibit any complexity and its diameters are included in the Late Pleistocene and Early Holocene African variation.

The figure 11 also illustrates the position of the mandibular remains from the other Late Pleistocene and early Holocene Horn of Africa specimens (LPHA and HHA samples). All of them cluster close to Porc-Épic and Nazlet Khater 2, exhibiting robust mandibular corpus dimensions.

Human remains associated with MIS 2 in the Horn of Africa are as scarce as those from MIS 3, although more complete (fig. 9). One reason is probably tied to the stratigraphic hiatus documented in several sites in this region between ~ 30-11 ka (Assefa, 2006; Pleaurdeau et al., 2014; Brandt et al., 2017; Tribolo et al., 2017; Jones, 2020; Khalidi et al., 2020). In Somalia, the sites
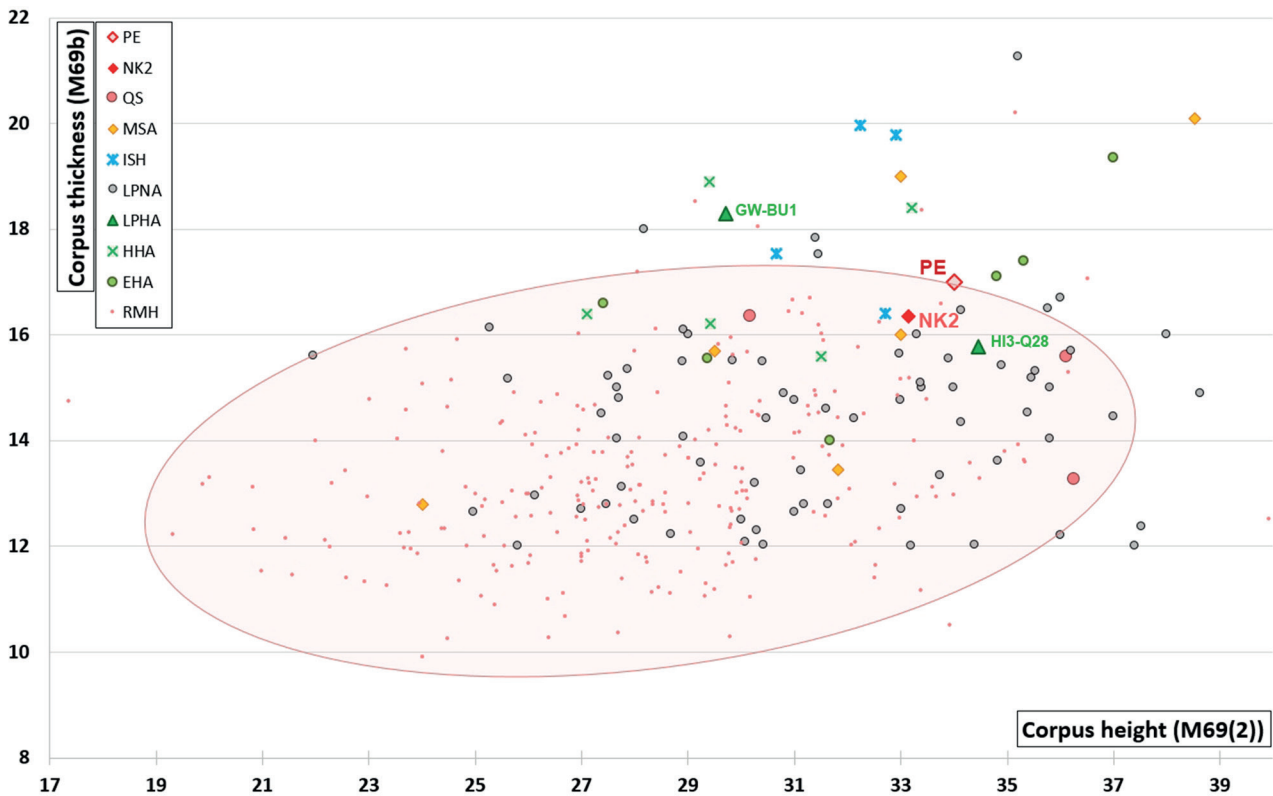
Fig. 11 – Bivariate plot of the mandibular corpus dimensions between the first and second lower molars in centimeters [M69b = corpus thickness; M69(2) = corpus height; see Braüer, 1988]. PE = Porc-Épic, NK2 = Nazlet Khater 2, QS = Qafzeh and Skhul, MSA = African specimens attributed to the MIS 5 to MIS 3 period (i.e. Border Cave, Temara, Dar-es-Soltan, Klasies River Mouth, Loiyangalani and Mumba Rock Shelter), ISH = Ishango, LPNA = compilation of LPNAE and LPNAW samples (i.e. Jebel Sahaba, Wadi Halfa, Wadi Kubbaniya and Taforalt), LPHA = Late Pleistocene specimens from the Horn of Africa (i.e. Guli Waabayo, GW-BU1, and Hara Idé 3, HI3-Q28), HHA = Early and Mid-Holocene samples from the Horn of Africa (i.e. Lake Besaka 2, Gogoshiis Qabe and Mille-Logghia), EHA = Early to Mid-Holocene specimens from east Africa (Lothagam), RMH = Recent *Homo sapiens* (see Ribot , 2011). The ellipse represents 95% of the variation.

Fig. 11 – Diagramme bivarié des dimensions du corps mandibulaire entre la première et la deuxième molaire inférieure en centimètres [M69b = épaisseur du corps ; M69(2) = hauteur du corps ; voir Braüer, 1988]. PE = Porc-Épic, NK2 = Nazlet Khater 2, QS = Qafzeh et Skhul, MSA = spécimens africains attribués à la période allant du MIS 5 au MIS 3 (à savoir Border Cave, Temara, Dar-es-Soltan, Klasies River Mouth, Loiyangalani et Mumba Rock Shelter), ISH = Ishango, LPNA = compilation d'échantillons LPNAE et LPNAW (à savoir Jebel Sahaba, Wadi Halfa, Wadi Kubbaniya et Taforalt), LPHA = spécimens de la fin du Pléistocène supérieur de la Corne de l'Afrique (à savoir Guli Waabayo, GW-BU1, et Hara Idé 3, HI3-Q28), HHA = spécimens de la première moitié de l'Holocène de la Corne de l'Afrique (à savoir lac Besaka 2, Gogoshiis Qabe et Mille-Logghia), EHA = spécimens du début de l'Holocène d'Afrique du nord-est (à savoir Lothagam), RMH = Homo sapiens récents (ici base de données africaine Ribot, 2011). L'ellipse représente 95% de la variation.

from Rifle Range and Guli Waabayo preserved sedimentary records covering the Last Glacial Maximum (Jones et al., 2018; Jones, 2020). The latter also delivered the oldest human remains from MIS 2. Direct dating on bone apatite of the remains from Guli Waabayo Burial 1 (GW-BU1) was achieved during the ANR Big Dry program (18683 ± 82 BP, UBA-34897 Muse17239). The result is consistent with chronological reassessment of the Guli Waabayo rock shelter, indicating human activity between ~ 26-6 ka (Brandt, 1986; Jones, 2020). The ANR program also provided a chronological background to a deciduous upper central incisor identified in the faunal collection from the Lake Besaka 4 locality (fig. 9) with the dating of an associated ostrich eggshell to 11699 ± 47 BP (UBA-34907 Muse17252; Clark and Williams, 1978; Brandt, 1982).

The limited record of human occupation in the Horn of Africa during the Last Glacial Maximum may be related to partial abandonment of the area during this period of extreme aridity (Tierney and DeMenocal, 2013). Analyses of lacustrine sediments, isotopic proxy for hydroclimate and pollen sequences have provided a clear image of the impact of large-scale climate changes in the Horn of Africa. The results consistently highlight dramatic hydroclimate changes from MIS 3 until the end of the African Humid Period (e.g. Gasse, 1977 and 2000; Lamb et al., 2002; Marshall et al., 2009; Tierney and DeMenocal, 2013; Foerster et al., 2015; Fersi et al., 2016). Arid conditions prevailed during MIS 3 until the Last Glacial Maximum, followed by a severe dry period associated with the Heinrich Event 1 in the North Atlantic. The abrupt transition to more humid conditions was

interrupted by a return to a dryer environment during the Younger Dryas. The strong climatic variations and hydrological instability, notably documented by the fluctuation in lake levels, unquestionably challenged the adaptation capacities of human groups in this area (Gasse, 1977 and 2000; Marshall et al., 2011; Khalidi et al., 2020).

Two exceptions are currently known from the Horn of Africa, that suggest the region experienced heterogenous human responses to the environmental changes caused by the cooling and drying of MIS 2. G. Ossendorf et al. (2019) documented MSA occupations of the Fincha Habera rock shelter in the Bale mountains (~ 4,000 m above sea level) between 47-31 ka with intensive hunting of giant mole rats. E.A. Hensel et al. (2021) reported an occupation throughout the LGM of Sidocho rock shelter (1,930 m above sea level) in the southwestern Ethiopian highlands. The MIS 2 lithic assemblage from Sidocho rock shelter is dominated by microblades lacking retouch and made from obsidian (Hensel et al., 2021). Thus, the lithic industry differs substantially from that at Porc-Épic and Goda Buticha, in which microliths are present, but the assemblages are dominated by larger, retouched tools and small, narrow unifacially or bi-facially flaked points made predominately on chert (Pleurdeau, 2004 and 2005; Leplongeon, 2014; Leplongeon et al., 2017; Pleurdeau et al., 2014). The other exception lies in Somalia. The continuous occupations documented in Somalia appear to correlate with more stable climate conditions in this specific area (Reid et al., 2019). Arguments in favor of the possible absence of human occupation, or the splitting up and maybe isolation of human groups in the Horn of Africa at the end of the Late Pleistocene and the beginning of the Holocene, are found in late occurrence pottery, herding (< 4 ka) and agricultural activities (< 3 ka) compared to adjacent African regions (Cauliez et al., 2008; Lesur et al., 2014; Gutherz et al., 2015; Khalidi et al., 2020). In addition, reduced mobility and specialized hunting strategies are documented in sites preserving archaeological records from this period, such as Guli Waabayo (Jones et al., 2018; Jones, 2020). Finally, the hypotheses of possible long-term isolation and adaptation of populations from this region are also supported by genetic studies (Luis et al., 2004; Rowold et al., 2007; Gallego Llorente et al., 2015).

Within this context, the discovery of a new site in the Republic of Djibouti in 2003, Hara Idé 3 (HI3), tentatively associated with the end of the Late Pleistocene and the beginning of the Holocene, with well preserved human remains, was fortuitous (fig. 9). Hara Idé 3 is located on the southern shore of the Dagadlé oued in the Gobaad basin, 30 km southeast of lake Abhe. The Gobaad basin is a large complex of basaltic grabens that document the fluctuation of lake Abhe during the Pleistocene (Gasse, 1977; Vellutini and Piguet, 1994). This depression has been extensively surveyed for Prehistoric occupation since the 1980s and the discovery of Oldowan assemblages (Chavaillon et al., 1987). Later archaeological programs succeeded one another, focused on identifying occupation sites in relation to first food production

societies in the region (Gutherz and Joussaume, 2000; Gutherz, 2008; Gutherz et al., 2015, Cauliez et al., 2018; Cauliez, 2019). From MIS 4 to the Holocene, the Gobaad basin was repeatedly, and to various extents, filled by the transgressions of Abbe lake in relation to paleoclimatic fluctuations (Gasse, 1977 and 2000). Changes in the lake-shore levels affected human occupation in this region and are responsible for the burying and/or erosion of archaeological evidence preceeding the last great transgression (~ 10 ka; fig. 12; Gasse, 2000; Gutherz et al., 2015; Coudert et al., 2018). This is why the discovery of hundreds of human bones and tooth fragments embedded in a lacustrine limestone matrix at Hara Idé 3, together with various faunal remains and lithic artifacts that were initially associated with Late Pleistocene and Early Holocene deposits, was so exceptional. These remains were collected between 2003 and 2005 during rescue excavations directed by H. Duday in the framework of the franco-djiboutian archaeological mission. Given the potential importance of the site, additional archaeological campaigns were organized between 2016 and 2019 in order to clarify the geological and chronological context of these remains.

The geological data from the new excavation campaigns and the dating results allowed the chronostratigraphic context of the Hara Idé 3 archaeological site to be secured. Given the scarcity of human remains in the Horn of Africa for the end of the Late Pleistocene, the discovery of new human remains dated to the Late Upper Pleistocene (~ 18-13.5 ka) in this poorly documented part of the world is crucial to the discussion about the adaptation and/or isolation of human populations in Africa during these times of intense climatic variation (Crevecoeur et al., 2019). Preliminary morphometric investigations of the most complete mandible from the site and found in the pit structure (HI3-Q28; fig. 13) highlighted the robustness of the corpus and the mandibular ramus (Matu et al., 2017). In multivariate comparative analyses, the Hara Idé 3 mandible shows affinities with earlier specimens from the Late Pleistocene, characterized by a relatively long and thick mandibular corpus and a short wide ramus. This conformation explains its position on the upper left quadrant of the graph in figure 13. HI3-Q28 mandible lies at the edge of extant human variation and, given these proportions, can be differentiated from Holocene individuals from the Horn of Africa (HHA) as well as from Nile Valley Late Pleistocene specimens (fig. 13).

These results show that HI3 shares some features with NK2 or Ishango, but seems to differ from the variation in the Late Pleistocene sample from the Nile Valley (LPNAE). Its mandible possesses morphometric characteristics that distinguish it from extant populations. The HHA specimens (here represented by Gogoshiis Qabe, Mille-Logghia and Lake Besaka 2) exhibit great variability, two of them being at the edge of extant human variation, but none of them plots close to Hara Idé 3. This variation in conformation is mirrored by great variation in size. While the latter specimens have a thick and wide mandible associated with large teeth (fig. 13), oth-

ers, like individuals from Goda Buticha, are characterized by medium to small post-cranial and dental remains (Pleurdeau et al., 2014). These observations of large variations in size and shape between the different sites, although based on limited data from the Holocene period in the Horn of Africa, call into question the relationship between Late Pleistocene specimens like Hara Idé 3 and the Holocene populations in this region, as well as their level of isolation.

4. CONCLUSIONS

In this review of the paleoanthropological data available in northeast Africa during the second half of the Late Pleistocene and the beginning of the Holocene, we sought to highlight general trends regarding past modern human phenotypic variation, leading to a discussion of population diversity, adaptation and affinities during this period of major climatic and cultural changes.

In the Nile Valley, anthropological data indicate the persistence of robust phenotypes associated with plesi-
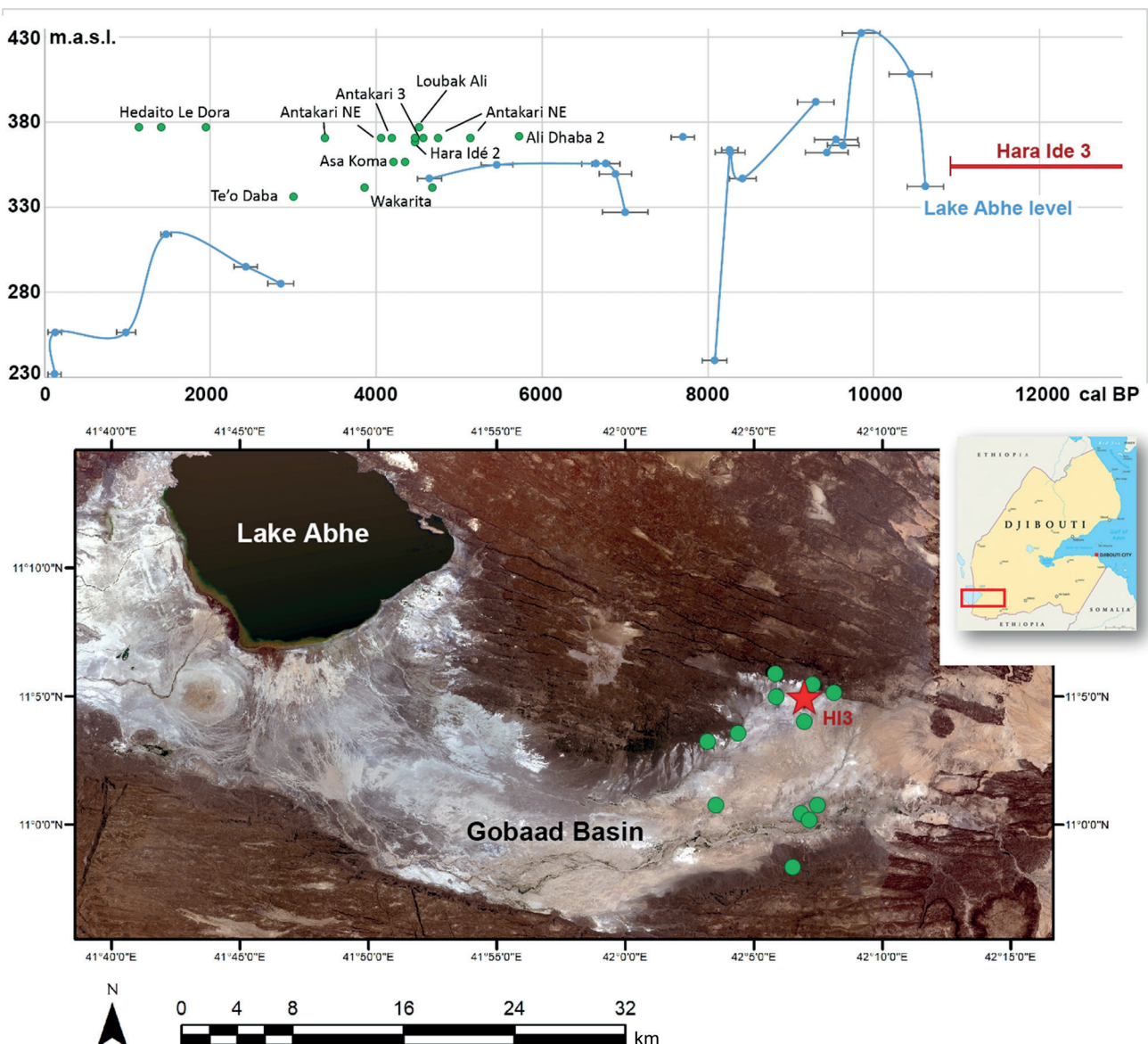

Fig. 12 – Top: Lake Abhe fluctuation level (blue line; see Gasse, 1975) during the Holocene and altitudinal position of Hara Idé 3 and Mid-Holocene archaeological sites investigated by the PSPCA project (Cauliez, 2019). Bottom: Localisation of the sites in the Gobaad basin (following Bruxelles and Mologni, 2019). m a.s.l.: meters above sea level.
Fig. 12 – En haut : niveau de fluctuation du lac Abhé au cours de l'Holocène (ligne bleue ;voir Gasse, 1975) et position altitudinale du site archéologique d'Hara Idé 3 et des sites datant du milieu de l'Holocène fouillés dans le cadre du projet PSPCA (Cauliez, 2019). En bas : localisation des sites dans le bassin de Gobaad (d'après Bruxelles et Mologni, 2019). m a.s.l. : mètres au-dessus du niveau de la mer.
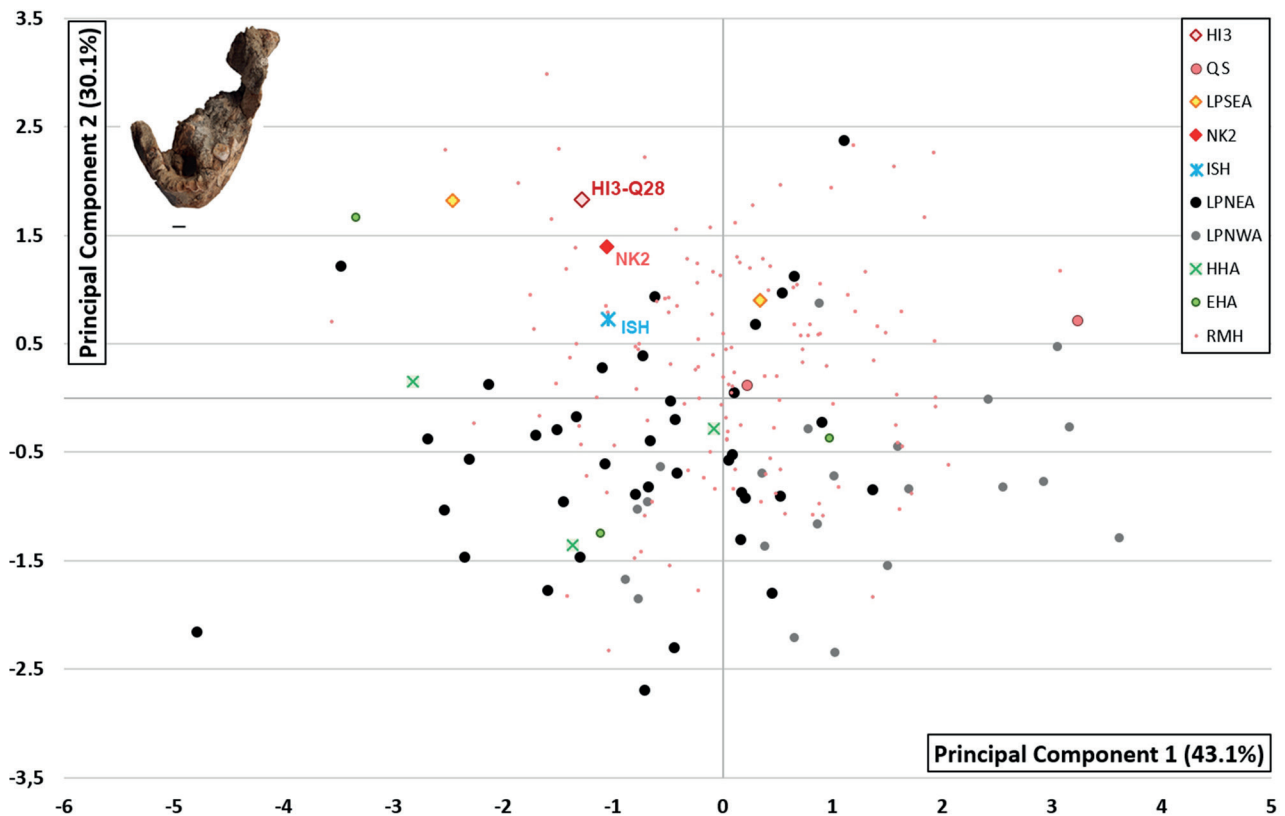
Fig. 13 – Bivariate plot of the first and second principal component of the PCA on size-adjusted mandibular dimensions. HI3 = Hara Idé 3 (HI3-Q28), QS = Qafzeh and Skhul, LPSEA = Late Pleistocene specimens from east and south Africa (i.e. Olduvai Hominid 1 and Springbok Flats), NK2 = Nazlet Khater 2, ISH = Ishango, LPNEA = Late Pleistocene specimens from north-east Africa (i.e. Jebel Sahaba and Wadi Halfa), LPNWA = Late Pleistocene specimens from north-west Africa (i.e. Taforalt and Afalou), HHA = Early and Mid-Holocene samples from the Horn of Africa (Lake Besaka 2, Gogoshiis Qabe and Mille-Logghia), EHA = Early to Mid-Holocene specimens from east and south Africa (Lothagam, Gamble Cave and Fish Hoek Cave), RMH = Recent *Homo sapiens* (see Ribot, 2011). Photograph inserted in the top left part of the graph illustrates the mandible HI3-Q28 in superior view.

Fig. 13 – Diagramme bivarié de la première et de la deuxième composante principale de l'ACP sur les dimensions mandibulaires normées. HI3 = Hara Idé 3 (HI3-Q28), QS = Qafzeh et Skhul, LPSEA = spécimens du Pléistocène supérieur d'Afrique de l'Est et du Sud (Olduvai Hominid 1 et Springbok Flats), NK2 = Nazlet Khater 2, ISH = Ishango, LPNEA = spécimens de la fin du Pléistocène supérieur du nord-est de l'Afrique (à savoir Jebel Sahaba et Wadi Halfa), LPNWA = spécimens de la fin du Pléistocène supérieur du nord-ouest de l'Afrique (à savoir, Taforalt et Afalou), HHA = spécimens de la première moitié de l'Holocène de la Corne de l'Afrique (à savoir lac Besaka 2, Gogoshiis Qabe et Mille-Logghia), EHA = spécimens de la première moitié de l'Holocène d'Afrique de l'Est et du Sud (à savoir Lothagam, Gamble Cave, Fish Hoek Cave), RMH = Homo sapiens récents (voir Ribot, 2011). La photographie insérée dans la partie supérieure gauche du graphique illustre la mandibule HI3-Q28, en vue supérieure.

omorphic features related to size and shape from MIS 3 until the end of the Late Pleistocene. These characteristics that lie at the edge of recent modern human diversity are also present in the only Early Holocene sample from the Nile Valley. Although based on a very limited number of fossils, the data support hypotheses of population isolation and biological continuity of human groups in the Nile Valley from the end of the Late Pleistocene until the beginning of the Holocene. After ~ 8 ka, human remains from Nubia, notably, show a more gracile cranio-dental phenotype, whose origin could be related to the arrival of new populations in the area concomitant with the spread of pastoralism.

While changes in climate conditions also influenced human settlements in the Horn of Africa, dynamic popu-lation issues are more difficult to address with the limited fossil records available. Scattered morphological information from a few Late Pleistocene fossils from Ethiopia, Somalia and the Republic of Djibouti seem to indicate overall robust phenotypes, while Holocene specimens express greater diversity in terms of shape and size dimorphism. Cultural changes in the Horn of Africa in relation to herding and agriculture appear quite late compared to the Nile Valley region. In addition, although ideally situated between Africa and Asia, the role of the Horn of Africa as a migratory corridor during the Late Pleistocene and the beginning of the Holocene is currently little supported by genetic or cultural data. Rather, scenarios involving population isolation and the development of specific adaptation are favored.

The combination of plesiomorphic and unique morphometric features seen in Late Pleistocene African specimens in the Nile Valley and the Horn of Africa from MIS 3 to the Holocene could be the consequence of population isolation and division/fragmentation, whose origin could be at least partially related to climate variations. In this regard, paleoanthropological data are consistent with a genetically-driven model of modern human origin and diversification that support hypotheses of African multi-regionalism and deep population substructures. The paleoanthropological data from the Nile Valley and the Horn of Africa have potential implications concerning the debate about plausible population dynamics that could have led to the out-of-Africa expansion. The genomes of non-Africans harbor the signature of a bottleneck, or a reduction in overall diversity, which can be dated to around 70 ka (Malaspinas et al., 2016). Putting together genetic evidence for a Northern exit OoA (Pagani et al., 2015), archaeological and palaeoclimatic evidence for a drastic reduction in human presence along the lower Nile Valley from MSI 4 (70-60 ka) until ~ 25 ka (Vermeersch et al., 1990; Van Peer, 2004; Vermeersch and Van Neer, 2015), as well as the paleoanthropological data presented here suggesting isolation and fragmentation of Late Pleistcocene human populations in the Nile Valley, we may postulate that the progressive drying out of the North-East African region from 70 ka triggered a population bottleneck (Pagani and Crevecoeur, 2019). The majority of these fragmented human groups may eventually have died out or merged back with the broader sub-Saharan population. A small subset of them may instead have reached the Mediterranean shores and subsequently expanded west, along the North African coast, and east towards Eurasia. Such a scenario would imply that the potential cause of the genetic bottleneck that characterizes all non-African groups was the gradual increase in aridity of the Nile corridor rather than the out-of-Africa expansion of a few wanderers during environmentally permissive conditions. It also suggests that this bottleneck did not take place at the gateways of Africa, but rather, within Africa (along the Nile basin). This highly speculative scenario should now be confronted to comparative analyses of Late Pleistocene specimens from Eurasia to outline possible affinities and illustrate how the analysis of African human remains from MIS 3 onwards is crucial to further understanding the evolutionary history of our species.

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