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Late Stone Age human remains from Ishango (Democratic Republic of Congo): New insights on Late Pleistocene modern human diversity in Africa

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ABSTRACT

Although questions of modern human origins and dispersal are subject to intense research within and outside Africa, the processes of modern human diversification during the Late Pleistocene are most often discussed within the context of recent human genetic data. This situation is due largely to the dearth of human fossil remains dating to the final Pleistocene in Africa and their almost total absence from West and Central Africa, thus limiting our perception of modern human diversification within Africa before the Holocene.

Here, we present a morphometric comparative analysis of the earliest Late Pleistocene modern human remains from the Central African site of Ishango in the Democratic Republic of Congo. The early Late Stone Age layer (eLSA) of this site, dated to the Last Glacial Maximum (25–20 Ky), contains more than one hundred fragmentary human remains. The exceptional associated archaeological context suggests these remains derived from a community of hunter-fisher-gatherers exhibiting complex social and cognitive behaviors including substantial reliance on aquatic resources, development of fishing technology, possible mathematical notations and repetitive use of space, likely on a seasonal basis.

Comparisons with large samples of Late Pleistocene and early Holocene modern human fossils from Africa and Eurasia show that the Ishango human remains exhibit distinctive characteristics and a higher phenotypic diversity in contrast to recent African populations. In many aspects, as is true for the inner ear conformation, these eLSA human remains have more affinities with Middle to early Late Pleistocene fossils worldwide than with extant local African populations. In addition, cross-sectional geometric properties of the long bones are consistent with archaeological evidence suggesting reduced terrestrial mobility resulting from greater investment in and use of aquatic resources.

Our results on the Ishango human remains provide insights into past African modern human diversity and adaptation that are consistent with genetic theories about the deep sub-structure of Late Pleistocene African populations and their complex evolutionary history of isolation and diversification.

1. Introduction

The diversification and dispersion of modern humans throughout the world during the Late Pleistocene is a major topic in genetic, paleontological and archaeological studies of the past. Recent papers have documented the interaction and interbreeding between early migrants to Eurasia and pre-existing archaic populations, such as Neanderthals and Denisovans (Green et al., 2010; Reich et al., 2010). Although the Eurasian record, particularly in Central Asia, includes large gaps, the Late Pleistocene African record, the putative core area for modern human origin and diversification (e.g., Underhill et al., 2000; Garrigan and Hammer, 2006; Manica et al., 2007; Li et al., 2008), is even more poorly documented in all three domains of study.

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Genetic studies of African populations, derived from a growing number of samples and regions (Gurdasani et al., 2015), document extensive migrations, complex interactions and genetic substructure within the continent prior to and following the time of the major modern human expansion to other continents (Quintana-Murci et al., 2008; Cox et al., 2009; Tishkoff et al., 2009; Scheinfeldt et al., 2010; Henn et al., 2011; Schlebusch et al., 2012). It has been assumed that modern human populations had outcompeted other more archaic groups within Africa by the time of the expansion. However, recent genetic studies suggest that this assumption was likely false and that archaic groups might have shared the African continent with modern human groups for many millennia, possibly until at least the Marine Isotopic Stage (MIS) 3 (Hammer et al., 2011; Mendez et al., 2013).

Disparate archaeological sequences in the different regions of the African continent also suggest considerable regional diversity beginning in the Middle Stone Age (Clark, 1988; McBrearty and Brooks, 2000; Tryon and Faith, 2013) and interregional migrations (e.g., Robbins et al., 1994). The MSA (Middle Stone Age) record of lithic technology is highly variable and together with an increasing number of innovations (e.g., bladelet and microlithic technologies, projectile weapons, bone points, heat treatment of stone, regular exploitation of aquatic resources) and features that are possibly associated with symbolic behaviors (e.g., geometric engravings, personal ornaments, and extensive pigment transport and use), the Late Pleistocene African archaeological record seems to reflect significant behavioral diversity (McBrearty and Brooks, 2000; Shea, 2011; Tryon and Faith, 2013). Moreover, these innovations do not occur suddenly, all together, in one place, they are recorded in sites widely separated in space and time, suggesting that regional variations are the outcome of long-term interactions between populations and their environments (McBrearty and Brooks, 2000; Tryon and Faith, 2013).

Unfortunately, the African Late Pleistocene fossil record is extremely sparse for the period that is supposed to have witnessed modern human diversification within Africa and dispersions out of Africa (Soares et al., 2012; Rito et al., 2013). The African hominin sites attributed to the first half of the Late Pleistocene (i.e., from MIS 5 to the end of MIS 4) are essentially from North Africa (e.g., Debénath, 1975, 1979; Vermeersch et al., 1998), the Horn of Africa (e.g., Vallois, 1951; Haile-Selassie et al., 2004; Pleurdeau et al., 2014) and South Africa (e.g., de Villiers, 1973; Singer and Wymer, 1982; Grine and Klein, 1985). These cranial and infra-cranial remains are either highly fragmented or indirectly dated.

Recent comparative morphometric studies of some of these remains have suggested a high level of phenotypic diversity (Schillaci, 2008; Gunz et al., 2009; Royer et al., 2009; Harvati and Hublin, 2012; Hublin et al., 2012). However, our understanding of past modern human diversity during the Late Pleistocene in the entire African continent is extremely limited, with no data at all from West and Central Africa, which together characterize the larger part of the African continent.

For the second half of the Late Pleistocene and the period preceding the Last Glacial Maximum (LGM) (i.e., MIS 3), the only two sites with well preserved and securely dated human remains are Nazlet Khater 2 (38 ± 6 Ky, Egypt; Crevecoeur, 2008) and Hofmeyr (36.2 ± 3.3 Ky, South Africa; Grine et al., 2007). These fossils represent additional evidence for Late Pleistocene phenotypic variability of African sub-groups. The Hofmeyr specimen exhibits the greatest overall similarities to early modern human specimens from Europe rather than to Holocene San populations from the same region (Grine et al., 2007). Moreover, the Nazlet Khater 2 specimen preserves archaic 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, 2012). These specimens represent aspects of modern human phenotypic variation not found in current populations. This situation seems to have lasted until the beginning of the Holocene in the African fossil record, not only in the northeastern part of the continent (Crevecoeur et al., 2009) but also in the west central (Iwo Eleru, Nigeria, Harvati et al., 2011; Stojanowski, 2014) and eastern regions (Lukenya Hill, Kenya, Tryon et al., 2015). During the Holocene, an increased homogenization of cranio-morphological features is documented, particularly within sub-Saharan Africa, with its peak during and after the Bantu expansion from 6 Ky ago (Ribot, 2011). These glimpses of Late Pleistocene modern human diversity attest to our poor understanding of modern human diversification and adaptation in Africa during a time of abrupt environmental changes and archaeological transitions preceding the Holocene.

Here, we present a study of a large sample of Late Pleistocene human remains from the Central African site of Ishango 11, located at the junction of the north shore of Lake Edward and the Semliki River in the Virunga National Park, North Kivu Province, eastern Democratic Republic of Congo. This early Late Stone Age assemblage derives from two periods of excavation at the site: the 1950s excavations by J. de Heinzelin and colleagues (de Heinzelin, 1957; Twiesselmann, 1958) and the 1985–1986 excavations by co-author Brooks and colleagues (Brooks and Smith, 1987; Boaz et al., 1990). The two sets of human remains from the Late Pleistocene layers of the site, dated between 25 and 20 Ky, include 138 specimens representing at least 12 different individuals of multiple age groups, from perinatals to adults, and constitute the largest and oldest collection of human remains from Central Africa. After introducing the geological, geochronological and archaeological context of the material, we will show how new analytical approaches and technologies indicate the distinctive characteristics and possible affinities of this population, and lend support to current interpretations of the diversity of Late Pleistocene Africans.

1.1. *Ishango archaeological context*

Ishango 11 is located in the Democratic Republic of Congo, in the Western Rift, along the Semliki River where it flows out of Lake Rutanzige (or Lake Edward; see Boaz, 1990) (Fig. 1).

This valley is known for its early evidence for harpoons (Brooks et al., 1995; Yellen et al., 1995) and for the recent discovery of Plio-Pleistocene early hominin evidence (Crevecoeur et al., 2014). The site was first identified by Damas during his 1935–1936 expedition in the Upper Semliki, which focused on recent lake fauna and flora (Damas, 1940). The first formal excavations were performed by de Heinzelin in 1950 during his geological and archaeological expeditions in the Upper Semliki region (de Heinzelin, 1955, 1957, 1961). At Ishango, de Heinzelin excavated two trenches, one parallel (N143GE) and the other perpendicular (N43GE) to the river shoreline, and the area to the west of their junction (Fig. 1). De Heinzelin started his excavation in this western zone, noting later that most of the human remains, fauna and artifacts came from this area (de Heinzelin, 1957; zones A and B on Fig. 1). This area where the two trenches intersected preserved only the lower parts of the sequence (Ishango Gravels Formation, TT). De Heinzelin observed that the archaeological levels gradually disappear horizontally all around, although large remnants remain in both trenches and between the trench N43GE and the cliff.

Further excavations at Ishango include the 1959 extension of the N43GE trench by Splingaer, whose material is unpublished. In 1985–1986, two 2 m by 2 m square excavations, one near the junction of the two trenches (1985) and one ca. 10 m further into the cliff (1986), were performed by Brooks and members of the