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 origin 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 for 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.

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 Neandertals and Denisovans (Green et al., 2010; Reich et al., 2011). Although the Eurasian record, particularly in Central Asia, includes large gaps, the Late Pleistocene African record, 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.

Genetic studies of African populations, derived from a growing number of samples and regions (Gurdasani et al., 2014), document extensive migrations, complex interactions and genetic sub-structure 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; Twiesselman, 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 25-20 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.

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) (Figure 1).

- Insert Figure 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 (Figure 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 Figure 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 2m by 2m square excavations, one near the junction of the two trenches (1985) and one ca. 10 meters further into the cliff (1986), were performed by Brooks and members of the Semliki Research Expedition to obtain materials for dating (Brooks and Smith, 1987; Boaz, 1990).

The stratigraphy established by de Heinzelin was later confirmed by the work of the Semliki Research Expedition (Brooks and Smith 1987; Brooks et al., 1995). The lithostratigraphic units are, as follows, from top to bottom: Recent deposits (symbol R) / Museya Gravels Formation (symbol TP) / Ishango Gravels Formation (symbol TT) / Lusso Formation (symbol L), (de Heinzelin and Verniers, 1996; Figure 2).

- Insert Figure 2 -

The top part of the sequence comprises Recent deposits (R) correlated to the uppermost Holocene. They include the Post-Emersion Zone (ZPEm) archaeological occupation level and are dated between ca 1,700 and ca. 3,200 BP based on four calibrated ^{14}C dates on charcoal ($1,680 \pm 80$ CalBP, 2200 ± 80 CalBP, 3140 ± 80 CalBP and $3,170 \pm 90$ CalBP (CAMS 3235-3237, Beta 54933-35, -37); Brooks et al., 1995). The informal Semliki Lower Terrace Complex (T), which precedes the Recent unit, regroups the earlier Ishango Gravels Formation (TT) and the later Museya Gravels Formation (TP). These fluvial deposits are located ca. 9.5-12 meters above the present-day Semliki River (de Heinzelin and Verniers, 1996). The Museya Gravels Formation is correlated with the middle Holocene and is immediately posterior to the volcanic tuffs (de Heinzelin and Verniers, 1996).

Although the Museya Gravels Formation is present in the cliffs to the NW of the site, both it and the widespread thick deposits of ash from the Katwe volcanic field in Uganda are absent from the lower terrace complex at the Ishango site itself. Their absence may be correlated with the major erosional unconformity represented by the base of the Post-Emersion Zone due either to a climate-related lake highstand or a catastrophic flood and intense tectonic activity during deposition of the massive ash deposits. The top of the ash is dated at Kabale, ca. 3 km

downstream from Ishango to $6,890 \pm 75$ BP by ^{14}C on charcoal (SI-7066) suggesting that most of the early to middle Holocene is not represented in the Ishango site sequence (Brooks and Smith, 1987).

The Ishango Gravels Formation (TT) is a fluvial deposit with linked deltaic and slope deposits, and volcanic admixture. It is dated from the uppermost Pleistocene to the early Holocene (de Heinzelin and Verniers, 1996). At the time of its deposition, the course of the Semliki River was inverted (southflowing) compared with the present day (de Heinzelin, 1957; Helgren, 1997). The detailed lithological and stratigraphic descriptions of the Ishango Gravels Formation levels are provided by de Heinzelin (1955, 1957) and can be summarized as follows from the uppermost (youngest) to the lowermost (oldest) (cf. Figure 2):

- N.TUF (Tuffaceous Levels) refers to a group of layers made of silty fine sand, small white gravels and a thick bed of accumulated shells, cemented with tuffaceous material and carbonate deposits (de Heinzelin, 1955, 1957). The base of the tuffaceous level has been directly dated by ^{14}C on mollusk shells to $20,155 \pm 245$ CalBP (SI-7062, Brooks et al., 1995).
- SD-SFM (Hardened Sand – Fine Micaceous Sand) corresponds to an interstratified, variably cemented bank of sand. The contact with the NFPr is variably indurated.
- NFPr (Principal Fossiliferous Level) is the principal human occupation layer of the site, consisting of a dense accumulation of bone debris and shells. All of the remains are encrusted in their upper part by cement made of fine and saline materials that precipitated at this level. The bones are heavily mineralized. A series of five radiocarbon dates on NFPr mollusk shells all fall between 19,540 and 24,145 BP (de Heinzelin 1957, Brooks and Smith, 1987; Brooks and Robertshaw, 1990; Brooks et al., 1995). In the 1950s, a bulk radiocarbon date on nacreous mollusk shells from the modern beach yielded a date of 3,000 BP (de Heinzelin, 1957). As the waters of Lake Edward contained three times more carbonate ions than water from the Congo River, this anomalous result was thought to be due to the incorporation of carbonate material from non-biogenic, volcanic sources, leading to the argument that the age of the NFPr should be reduced by $2/3$ to ca. 7000 BP. It is not clear if the current concentration of old carbon in the lake water dates to before the flood or high water stand following the formation of the TT (and TP), particularly if the “emersion”, which also radically affected the fish fauna (Stewart, 1989), was due to massive volcanic inputs into the lake. Brooks and colleagues applied both amino acid racemization and radiocarbon dating to

equally fresh shells from the modern beach, using experimentally-derived Arrhenius equations for the conversion of isoleucine to D-alloisoleucine at the mean annual temperature of Lake Edward. The ^{14}C ages of the modern shell samples were 1695 ± 80 and $2,030 \pm 55$ BP, but all the modern shells including those directly dated by ^{14}C had ratios of D-alloisoleucine/isoleucine that were close to 0, consistent with their modern status. The archaeological shells from the NFPr and NTUF, however, had ratios consistent with ages in the low 20,000s, clustering between .40 to .48 for the bound amino acids (hydrolysates) and .55 to .68 for the free amino acids. In 1990, a rare NFPr ostrich eggshell fragment, which derives its carbon from the bird's diet rather than from the lake water, was also dated by both epimerization of isoleucine and ^{14}C , yielding an age consistent with, and even slightly older than, the NFPr mollusc dates. The hydrolysates ratio was .43, the free amino acids .59, and the ^{14}C age $25,570 \pm 350$ CalBP (AA-3300). Thus the true age of the NFPr as well as that of the NTUF likely fall between 20,000 and 26,000 BP (Brooks and Smith, 1987; Brooks and Robertshaw, 1990; Brooks et al., 1995). The eggshell itself is interesting as its rarity in an eLSA context argues that ostriches were not generally found along the Semliki River in the Late Pleistocene but their eggshells may have been traded over large distances. Finally, the terrestrial fauna are consistent in size and species representation with a Late Pleistocene rather than a Holocene age (Peters, 1990).

- G.INF (Inferior Gravels) are lightly cemented gravels containing numerous fragments of reworked fossils from the Lusso Formation (de Heinzelin, 1955; Greenwood, 1959; Stewart, 1989), together with some Late Stone Age artifacts and fauna.

The lower level of the Ishango Gravels Formation (namely the G.INF layer) lies unconformably above and cuts into the oldest fossiliferous deposits identified in the Upper Semliki Basin, the Lusso Formation (L). The Lusso Formation, first identified as Kaiso beds (Fuch, 1934), is composed of lake deposit mudstones with sands and ironstones (de Heinzelin and Verniers, 1996; Verniers and de Heinzelin, 1990), and has an estimated age of 2.0-2.4 Ma based on the associated fauna (Boaz et al., 1992).

The Principal Fossiliferous Level (NFPr) yielded an exceptional eLSA archaeological assemblage consisting of thousands of fauna remains (fish and mammals) and numerous lithic and bone artifacts in association with more than one hundred heavily mineralized human remains (de Heinzelin, 1957; Twiesselmann, 1958; Greenwood, 1959; Hopwood and

Misonne, 1959; Verheyen, 1959; Stewart, 1989, Peters, 1990; Mercader and Brooks, 2001). The faunal assemblages attest to intensive fishing activity and fish consumption, both of smaller fish likely caught in nets, weirs or dams, and of very large fish most likely harpooned during spawning runs as a seasonal activity that has been interpreted as incipient or semi-sedentary behavior, returning and remaining at specific locations in the landscape on a seasonal basis (Stewart, 1989). Some of the unbarbed bone points resemble fish gorges or hooks (de Heinzelin, 1957). The high quantity of bone, both fish and mammal in the NFPr, combined with a focus on fish species most easily caught during their spawning seasons, suggests multiple closely spaced occupations “separated by very short intervals of time” (Stewart 1989:209). While transport of large mammal carcasses for meat consumption is also documented (Peters, 1990), Stewart (1989:213) argues that fish “processing, preparation and consumption all took place at the site”.

The lithic industry is a microlithic LSA, including both quartz microliths and about 80 grinding tools (pestles, mortars or grindstones) in quartz, quartzite, basalt or various raw materials (Mercader and Brooks, 2001; Cornelissen, 2002). Some of these are especially massive and heavily used. The bone industry is characterized by the production of standardized bone tools including harpoons (with basal notches for holding a line), hafts, barbed points, and unbarbed points. They are manufactured through grinding, which differs from the older Middle Stone Age Katanda points that were made by scraping (Yellen, 1998; Brooks et al., 2004). The most fascinating artifacts of Ishango are not the harpoon points but the manufactured engraved bones that were found in the NFPr layer and in the interstratified tuffaceous yellow sands (SD-SFM) just above the Principal Fossiliferous Level (de Heinzelin, 1962; Cornelissen et al., 2008). The most famous engraved bone incorporates three columns of parallel notches and is surmounted by a quartz fragment that may or may not have been retouched or backed. The regularity of these notches and their grouping by prime numbers and multiples of two is not random. They have been interpreted as possible indications of mathematical concepts such as prime numbers, multiplication and the duodecimal system (de Heinzelin, 1962; Pletser and Huylebrouck, 1999).

The archaeological assemblage present in the Ishango eLSA layers depicts a population that showed complex social and cognitive behaviors and a lifestyle involving repeated closely spaced occupations of the site (Stewart, 1989). Given the poverty of the human fossil record in Africa for the second half of the Late Pleistocene, the paleoanthropological interest and potential of this collection for understanding the process of morphological diversification and

population dispersion in Africa during the drastic climate and environmental changes of the Last Glacial Maximum is considerable (Johnson et al., 1996; Gasse, 2000).

Materials and methods

Inventory of the human remains from the NFPr layer

The human remains published by Twiesselmann in 1958 included the most complete bones. At that time, both archaeological levels (NFPr and ZPEm) were thought to be close in age, and the human remains were examined as a whole.

This paper will focus on only the early Late Stone Age assemblage of the Ishango Terrace complex. The new inventory includes the NFPr human remains from the original collections of the Royal Belgian Institute of Natural Sciences (Brussels, Belgium) and the Smithsonian Institution's National Museum of Natural History (Washington D.C., USA) that were identified during each excavation campaign, together with newly recognized human remains found by sorting the fauna collections from both repositories. The reassessment of the Ishango collections led to the identification of 138 human remains attributed to the NFPr layer (cf. Supplementary Online Material (SOM) 1). The numbers of mature and immature bones by anatomical part are given in Figure 3.

- Insert Figure 3 -

The cranial remains are fragmented (the largest skull portion, made of three refitting fragments, is 10 cm long), as are many of the infra-cranial remains, with the exception of one complete mandible (#Ish15), two humeri (one mature #Ish31 and one immature #Ish32), one tibia (#Ish33), two immature forearm long bones (#Ish26 and #Is11-818), the patella and most of the hand and foot bones.

The Minimal Number of Individuals (MNI; White, 1953) was calculated by counting the most frequent element on one side. This MNI of frequency by bone category was then adjusted according to association and exclusions, largely based on the age-at-death criterion. The estimation of the age-at-death was based on bone maturation following the standards of Maresh (1970). Immature individuals were grouped by quinquennial age groups with the exception of the youngest individuals, who were separated into two groups: age class [0-<1] for an age-at-death of less than one year, and age class [1-4] (Sellier, 1996). The term

perinatal is used for an immature individual whose age at death is situated between the 7th lunar month of gestation and the 28th day after birth. In the latter case, age estimates were based on long bone measurements (Sellier, 1993). Given the absence of pelvic remains, it was not possible to reliably estimate the sex and age-at-death of the adults (Brůžek, 2002; Schmitt, 2005). Because senescence processes are strongly dependent on population, environmental and behavioral factors (Brůžek et al., 2005), we chose to include all of the mature remains in one age group [>20].

Table 1 provides the MNI for each age class. The human remains from Ishango represent a minimum number of twelve individuals: two perinatals, four children, one adolescent and five adults.

- Insert Table 1 -

Three immature individuals span two age groups based on bone maturation standards and the exclusion of possible association with the individuals already identified in each age group. The final count of the Minimum Number of Individuals for each age class is provided following the principle of minimization of anomalies (Sellier 1996). Individuals who could be associated with either of two age groups are included in the most likely age class based on the theoretical mortality rates of Ledermann (1969) for a population with a life expectancy at birth of between 25 and 35 years. If we compare the mortality quotient before adulthood ($20q_0$) of the Ishango assemblage with the Ledermann standards, the proportion of immature individuals (58.3%) is close to the theoretical mean values of between 45% and 64% for a population with a life expectancy at birth of between 25 and 35 years (Ledermann, 1969). The distribution of remains by age class also follows the theoretical values more generally; therefore, no demographic anomaly, whose causality could be multifactorial (post-depositional processes, excavation limits, or biological and cultural factors), can be detected.

Two hypotheses have been proposed to explain the site formation processes and the deposition of the NFPr archaeological assemblage. Following de Heinzelin (1957), the accumulation process occurred on the shoreline of a rising lake, and the Ishango NFPr layer could have resulted from the dumping of residential debris either into the lake or onto a small adjacent beach (de Heinzelin, 1957). Most of the NFPr bones are covered with a cemented crust on their superior side, and this fact, together with the presence of some heavily rolled bones, suggested instead secondary deposition in a beach context (Brooks and Smith, 1987).

The latter researchers therefore argued that it was unlikely that most of the debris was directly associated with a residential camp, although the density of artifacts and fauna suggest otherwise and the numerous human remains with some matches and articulations argue for a localized burial ground that was minimally disturbed by beach formation.

The hypothesis of a secondary deposit was also challenged by Peters (1990) in his analysis of the faunal remains. He observed that only a few specimens from the NFPr layer were rolled. Fine morphological characteristics were recognizable and used to identify species, and smaller bones were entirely preserved. As outlined by Peters (1990), the notion of secondary deposition implies that the original thanatocoenosis has been reworked, transported, and then finally deposited by natural processes (Peters, 1990). The same principle defines a secondary deposit in archaeothanatology (Duday, 2009), where the term is used when the evidence suggests that skeletal elements were partially or completely disarticulated when deposited in the place of discovery (Boulestin and Duday, 2006). This implies that the decomposition of the corpse occurred in a separate, temporary location before the final deposition of the human remains.

Despite partial spatial information on the precise planar location and orientation of every human remain in the excavated portion of the NFPr layer, some bone associations could be proposed based on secondary anatomical connections, bone maturation, symmetry and morphology (cf. SOM 1). The preservation of the perinatal remains is exceptional given their fragility. Among the nine perinatal remains inventoried, six bones from the upper and lower limb and from the pelvic girdle could be associated with the same individual based on morphology and robustness criteria. The complete mature mandible, humerus and tibia, in addition to their morphometric similarities, were all found in the same area of the site, in Zone A at the corner of both trenches within a two-meter square radius (cf. Figure 1; de Heinzelin, 1957). Additionally, the human remains exhibit no cut marks, few traces of rolling and although incomplete, most of the long bones preserved substantial portions. Moreover, the absence of selection concerning age group representation and the good anatomical representation of hand and foot bones, some of which could be refitted, support the taphonomic hypothesis of a primary deposit (used here also in the archaeothanatology sense, i.e., intentional deposit of corpses in their final place of deposition, where they decomposed and are discovered, cf. Duday, 2009), on the lake shore at a location of low energy level, partially protected from predators. As suggested by Peters (1990), it is likely that the coating of the bones and artifacts with sand and poorly sorted clastics and its encrustation with

sediments and mollusks occurred when the assemblage was already partly embedded in the deltaic sediments.

Comparative samples

To describe the human remains from the NFPr layer and highlight their morphometric characteristics, we used a broad Eurasian and African modern human sample from the Middle Pleistocene to the Holocene periods, as well as Neandertal specimens as an outside group. SOM 2 presents both the nature and sample size of all comparative groups used for the statistical analyses. The groups were generated based on chronology and geographical origins and are labeled as followed: EMH (Early modern humans from Africa and Southwest Asia) includes MPHS (Late Middle to Mid-Late Pleistocene specimens from North Africa and Southwest Asia) and MSA (Late Middle to Mid-Late Pleistocene specimens from Sub-Saharan Africa); LPH (Late Pleistocene modern humans from Europe and North Africa) regroups the specimens of NK2 (Nazlet Khater 2) and HOF (Hofmeyr), as well as the samples EUP (European Early and Middle Upper Paleolithic modern humans) and LPA (Late Pleistocene specimens from North Africa and Southwest Asia). The latter group is sometimes subdivided in three groups based on the geographic location (LPAne: from Northeast Africa; LPAnw: from Northwest Africa, and LPSwa: from Southwest Asia). The remaining samples are LSA (Late Pleistocene/Early Holocene specimens from Sub-Saharan Africa); RMH (Recent modern humans from Africa and Eurasia) and NEAND (Neandertal specimens from Eurasia).

Data from Ishango, El Fakhuri, Jebel Sahaba, Lothagam, Lukenya Hill, Olduvai Hominid 1, Singa, Spy, Taforalt, Tongo and Wadi Halfa were measured on the original fossils and tomographic acquisitions. The measurements of Wadi Kubbania were taken on a cast from the Smithsonian Institution (Washington, DC). The additional classic linear measurements, inner ear data and cross-sectional geometric properties of the fossil comparative sample come from published data from Alekseeva and Bader (2000), Basabe (1966), Billy (1975), Bocquentin (2003), Bouchneb and Crevecoeur (2009), Braüer (1983), Crevecoeur (2008), Daura et al. (2005), de Lumley (1973), de Villiers (1973), Doboş et al. (2010), Garralda and Vandermeersch (2000), Grine et al. (2010), Guipert et al. (2010), Hambucken (1993), Heim (1982), Howells (1996), Hublin (1991), Hublin et al. (1996), Hughes (1990), Leakey (1942,1970), Leroi-Gourhan (1958), Magori and Day (1983), Mallegni et al. (1999, 2000), Matiegka (1938), McCown and Keith (1939), Pap et al. (1996), Pearson et al. (2008),

Radovic et al. (1998), Rightmire and Deacon (1991), Schepers (1939), Sergi and Ascenzi (1955), Shackelford (2005), Singer and Wymer (1982), Sládek et al. (2000, 2002), Spoor (1993), Spoor et al. (2002a, 2002b, 2003), Stansfield and Gunz (2010), Teschler-Nicola (2006), Teschler-Nicola and Trinkaus (2001), Tillier (1991), Tobias (1967), Trinkaus (1983), Trinkaus and Ruff (1999), Trinkaus et al. (2003a, 2003b, 2006, 2013a, 2013b), Vallois (1951, 1952), Vallois and Billy (1965), Vallois and Roche (1958), Vandermeersch (1981), Velemínská and Brůžek (2008), Viola et al. (2004), Walker et al. (2008, 2010, 2011), and White et al. (2003). Finally, cranial measurements of the recent modern human samples (RMH) come from Howells (1996) and Twiesselmann (1941). The mandibular data from the RMH were collected by Isabelle Ribot, and the infra-cranial RMH database was provided by Anne Hambucken (Pers. Comm.).

Methods

Cranial and infra-cranial measurements were taken following Howells (1973), Twiesselmann (1941) and Martin (in Braüer, 1988). The sample of the Ishango collection stored in the Royal Belgian Institute of Natural Science was digitized at the Erasme Hôpital (Brussels, Belgium) using a Siemens Somatom Sensation 64. The remains from Ishango and Lothagam stored at the Department of Anthropology of the Smithsonian Institution and the comparative sample from Tongo housed in the Department of Anthropology of the George Washington University were scanned at the Siemens Training and Development Center in Cary (NC, USA) by a Somatom Definition AS. Finally, the skeleton of Olduvai Hominid 1 was digitized at the University Hospital Munich Grosshadern/Innenstadt by a GE Healthcare Discovery.

The cranial and infra-cranial computed tomography data acquisitions followed the protocols of Spoor and Zonneveld (1995) and Ruff and Leo (1986) concerning the orientation of the human remains. Semi-automatic, threshold-based segmentation with manual corrections was conducted using Avizo 7 (Visualization Sciences Group, SAS). Threshold values between segmented components were found according to the half-maximum height method (Spoor et al., 1993; Coleman and Colbert, 2007). The linear and angular measurements of the labyrinth were taken with ArteCore (NESPOS Society) from planar reformatted images in the transverse and sagittal planes according to the CT-morphometric method described by Spoor (1993) and Spoor and Zonneveld (1995, 1998). Measurements of the cross-sectional geometric properties of the long bones at mid-diaphysis were taken with ImageJ 1.47v

software and the macro «Moment MacroJ v1.4» (<http://www.hopkinsmedicine.org/FAE/mmacro.htm>).

Adjusted z-scores were used to assess the position of the Ishango remains relative to mean and range of variation of the comparative groups. The method is based on the Student t-test that accounts for sample sizes (Scolan et al., 2012). Multivariate analyses were performed with Statistica 8.0 (StatSoft, Inc). Each variable was first tested for normality. The principal component analysis (PCA) was performed on size-adjusted variables following Darroch and Mosimann's (1985) ratio for shape analysis (Jungers et al., 1995). Discriminant analysis (DA) was used to determine the posterior probability of Ishango belonging to each of the predefined groups. The distance used was the squared Mahalanobis distance to each centroid. Finally, a random resampling procedure with replacement was performed on a sample-size-corrected coefficient of variation ($V^* = (1 + 1/4n) * CV$). The latter coefficient allows comparison of relative variation in samples with different means while correcting for small sample size (Sokal and Braumann, 1980; Sokal and Rohlf, 1995).

Results and discussion

The neurocranium

Neurocranium remains are represented by fragments of mature and immature frontal, parietal, temporal and occipital bones. Nineteen pieces have been undoubtedly identified as human cranium remains, some of which refit, none of which is greater than 36 cm² (cf. SOM 1).

One characteristic of these fragments is the general thickness of the vault for the mature remains (average of 8.4 ± 1.5 mm, $n=12$). Comparative measurements at the level of the parietal eminence could be taken on the refitted #Ish3-4 fragments. The value (TPE = 11 mm) stands outside the published range of variation for both a sample of recent African specimens (Twisselmann, 1941) and for that of the LPH sample (Table 2). Compared with our reference groups, the fragment from Ishango falls within the LSA dispersion, which seems to stand apart from the other comparative samples (Figure 4). As with NK2, the thickness of the Ishango cranial fragments does not seem to be associated with abnormal bone remodeling (Crevecoeur, 2008). Non-pathological high cranial thickness is a common characteristic of Late Pleistocene modern humans and may reflect elevated activity levels compared with recent populations (Lieberman, 1996).

- Insert Table 2 and Figure 4 -

Two fragments of frontal bone representing two different individuals (#Ish1 and #Is11-564/567) preserved part of, respectively, the right and left orbits (Figure 5).

- Insert Figure 5 -

#Ish1 presents a moderate, but visible, superciliary ridge close to the grade ST2 defined by Lahr (1996). Two supra-orbital foramina are present. The medial supra-orbital foramen is close to the superior orbital margin and crosses it to come out in the orbital roof. The lateral one lies close to the lateral border of the fragment which occurs approximately halfway from the superior orbital margin length. A half centimeter up from the lateral supra-orbital foramen is the starting point of a frontal groove running upward and laterally. #Is11-564/567 is made of two pieces. The largest one (#Is11-564) remains covered with a fine dusting of matrix. A slight superciliary eminence is visible, corresponding to the first grade of expression (ST1) of Lahr (1996). A supra-orbital foramen is present at mid-distance between the frontal maxillary and zygomatic processes, but is only visible on the CT scans. #Is11-564 preserved the left zygomatic process. The suture area is 112 mm^2 and the thickness of the frontal trigone is 7.4 mm. The superior orbital border seems to exhibit a very large, blurred medial notch that does not fit entirely the definition of Hauser and De Stefano (1989). However, it is not clear whether this notch is actually induced by the morphology of the orbital margin more laterally. The latter presents a sinuous outline that protrudes in two points in the frontal plane. The endocranial surface is characterized by a well-developed frontal crest.

The interorbital breadth (DKB; Howells, 1989) could be estimated on both fragments as the double of the best-preserved half from the dacryon to the frontal crest in projection. As illustrated in Figure 6, #Ish1 lies in the upper part of the RMH variation, whereas #Is11-564/567 stands outside. They both align with the Pleistocene range of variation characterized by large inter-orbital dimensions (Table 2 and Figure 6).

- Insert Figure 6 -

The study of the inner structures through CT-scanner acquisitions shows that both frontal fragments present a frontal sinus aplasia. The frequency of bilateral and unilateral absence of the frontal sinus ranges from 2.5% (with an average between 5-15% in most populations) to

43% (among Inuit populations) for the bilateral case, and 1-15% for the asymmetric case (Tillier, 1977; Hanson and Owsley, 1980; Aydinhoğlu et al., 2003; Fatu et al., 2006). The etiology of the anatomical variations of the frontal sinus pneumatization is still debated, that is, whether it is related to mechanical, structural, climatic, pathological or genetic factors (Tillier, 1977; Shapiro and Schorr, 1980; Harris et al., 1987; Aydinhoğlu et al., 2003; Balzeau, 2005; Fatu et al., 2006; Rae et al., 2011). According to recent studies (Balzeau, 2005; Rae et al., 2011), it seems that the pneumatization of the frontal bone has more to do with individual variation rather than functional or taxonomical reasons.

However, the absence of the frontal sinus in the only two Ishango fragments preserving this part, and representing two different individuals, cannot be ignored, given the small percentage of this occurrence in extant populations. As underlined by Tillier (1977) for the Skhul sample (two crania out of four present frontal sinus aplasia), individual variation may not be sufficient to explain such a pattern. The same observation applies to the Late Pleistocene-Early Holocene Wadi Halfa sample. This population, characterized by heavy masticatory musculature and marked dental attrition, like the Ishango cranial remains, possesses a frequency of frontal sinus aplasia that is extremely high (94%, $n=18$; Greene and Scott, 1973), supporting a possible epigenetic etiology of this feature.

The bony labyrinth

Among the cranial fragments from the NFPr layer is a right petrous bone, #Ish37. The latter encloses a complete right bony labyrinth that was examined based on high resolution CT scanning. As underlined by previous studies, the bony labyrinth has a strong genetic component (Sporer et al., 1994; Spoor, 2003). Together with its postnatal relative independence to environmental factors (Jeffery and Spoor, 2004), this structure provides important information for assessing phylogenetic affinities between taxa (Sporer and Zonneveld, 1995; Ekdale, 2010; Lebrun et al., 2010; Ni et al., 2010) and between hominid groups (e.g., Spoor and Zonneveld, 1994; Hublin et al., 1996; Spoor et al., 2003; Urquiza et al., 2005; Bouchneb and Crevecoeur, 2009).

The three-dimensional reconstruction of the #Ish37 bony labyrinth is shown in lateral and superior view in Figure 7.

- Insert Figure 7 -

The absolute and relative dimensions and angles of the #Ish37 bony labyrinth are provided in Table 3, together with the mean value, the standard deviation and the sample size of the comparative data. Adjusted z-scores between #Ish37 and the reference groups have also been computed.

- Insert Table 3 -

The dimensions and the shape of the anterior and lateral semicircular canals of #Ish37 stand within the recent modern human range of variation. The size of the anterior semicircular canal is slightly smaller than the MPHS, LPH and RMH average, whereas the dimensions of the lateral one are just above their means. The shape ratio (h/w) of both canals follows the same pattern, indicating a slightly wider anterior and lateral semicircular canal in relation to their height compared with the RMH average. The particularities of #Ish37 are related to the size and shape of both the posterior semicircular canal and the cochlea.

The height of the posterior semicircular canal lies in the upper part of the LPH and recent modern human variation, and outside of the MPHS one, whereas its width is below the comparative group means. Consequently, the shape of the posterior semicircular canal, whose height and width ratio lies outside that of all of the comparative samples, is characterized by an unusually narrow and elongated form. However, the radius of curvature of the PSC is within the modern human range of variation. Conversely, the cochlea of #Ish37 is extremely wide (outside the limit of all comparative groups). This characteristic is not compensated for by equivalent increase in height, leading to a shape ratio and a radius of curvature that lie outside the LPH and recent modern human variation (Figures 8 and 9).

- Insert Figures 8 and 9 -

Following Spoor and Zonneveld (1998), the size of the cochlea is positively correlated with the size of the posterior and lateral canals. In Figure 8, Ishango is clearly isolated from the recent modern human sample concerning the cochlea size compared with the radius of the posterior semi-circular canal. The MPHS individuals seem to exhibit the same relationship and cluster on the edge of this variation, close to #Ish37. This larger size of the cochlea basal turn (CO-R) of the specimens from Qafzeh and Skhul compared with Holocene modern humans has already been underlined by Spoor et al. (2003) in a smaller comparative sample.

Interestingly, the Late Stone Age specimen from Lothagam seems to exhibit a comparable morphology of its cochlea and posterior semicircular canal to that of Ishango. However, although the shape of the posterior semicircular canal follows the same trend as #Ish37, the shape ratio of the cochlea in this case is conditioned by the proportionally small height (lying outside the lower limit of our comparative groups).

With respect to the relative dimensions of the three semicircular canals, #Ish37 possesses a proportionally larger posterior semicircular canal than the anterior one. None of the average comparative samples exhibits this pattern (Figure 10). However, this conformation is not exceptional in the recent modern human sample.

- Insert Figure 10 -

The size of the lateral semicircular canal (LSC) is always inferior to that of the vertical canals. However, the relative dimension of #Ish37 LSC is higher than the recent modern human average and lies between the percentages of the Middle and Late Pleistocene groups (MPHS and LPH). The Lothagam specimen shows semicircular canal proportions similar to Ishango. The sagittal labyrinthine index (SLI) of #Ish37 and the orientations of the common crus ($CCR < LSC_m$) and the vertical canals ($VC < LSC_m$) fall clearly within both past and extant modern human variation. The inclination of the ampular line in relation to the lateral canal is more vertical than the means of the comparative sample. #Ish37 lies in the upper part of the MPHS and RMH sample variation and outside the LPH one. The principal characteristic concerning the labyrinthine shape of Ishango is related to the orientation of the cochlea compared with any other structure (it lies outside of the variation in every case). It is illustrated in Table 3 by the more vertical position of the cochlea ($COs < LSC_m$) compared with the lateral canal in the sagittal plane. In the transversal plane, the cochlea is more coronally oriented than in any of our comparative groups compared with the vertical canals.

We assessed the affinities of #Ish37 labyrinthine morphology by performing a discriminant analysis based on 23 variables of the labyrinth, among which 12 were selected by the stepwise method to best discriminate between the predefined groups. The posterior probabilities of #Ish37 to belong to each of these samples have been computed based on the Mahalanobis distances. The results of the classification matrix in cross-validation are provided in the Table 4.

For a correct classification of 78.3% in cross-validation, #Ish37 has the highest probability to belong to the MPHS sample ($p = 0.944$), whereas its probability of being associated with the recent modern human sample is very low ($p = 0.035$). In contrast, although Lothagam exhibits some shared characteristics with Ishango, it shows rather the highest affinity with recent modern humans ($p = 0.993$).

Spoor et al. (2003) underlined that there seems to be a temporal variation in modern human labyrinthine morphology if we compare the Holocene humans with the Late Pleistocene modern sample. They also noted that the LP sample does not occupy an intermediate position between Holocene humans and Neandertals for the features that differ among the three groups. Actually, it seems that the labyrinthine morphologies of both early modern humans and European Upper Paleolithic specimens differ more from the Neandertals than do those of the Holocene humans (Spoor et al., 2003). The comparative study of #Ish37's bony labyrinth confirms this previous statement. Moreover, the results from the univariate and bivariate analyses showed that #Ish37 exhibits traits that are unusual in all of the comparative groups. Given this latter observation, it seems more likely that, rather than an actual phylogenetic relationship with the Qafzeh and Skhul specimens, the affinity of #Ish37 with the MPHS sample in the multivariate analysis is instead related to the fact that the morphology of this specimen samples part of the modern human labyrinthine variation that is no longer expressed in extant diversity.

The mandibles

Four mandibular remains have been recovered from the NFPr (Figure 11, Table 5). With the exception of #Ish22, which comes from the expedition of Damas, they all originate from de Heinzelin's excavation in 1950. The four remains, #Ish15, #Ish16, #Ish18 and #Ish22, were described in detail by Twiesselmann (1958) and Orban et al. (2001). These authors provided an exhaustive morphological description of the fragments and biometric comparative analyses. The comparative samples used by Twiesselmann (1958) and Orban et al. (2001) were restricted to a limited number of recent African individuals and a few Late Pleistocene African fossils. Here, we describe the main morphometrical characteristics of the Ishango mandibles compared to an African sample extended geographically (cf. SOM 2) and chronologically.

- Insert Figure 11 and Table 5 -

The main characteristics underlined previously relate to the overall robustness of the mandibular remains. A lateral torus is present on each fragment and is particularly well-developed for #Ish15. The lateral torus is always associated with a well-marked lateral prominence. A marginal torus is also visible, but less expressed than the lateral torus. The sub-complete mandible #Ish15 possesses a strong lateral torus that forms, together with the lateral prominence, a real lateral projection. On the same individual, a tuberculum marginal anterior is clearly individualized on the right side of the mandibular corpus. On the same side and posteriorly, the inferior border is characterized by well-marked platysmatic striae that are only slightly present on the left side. These morphological features provide a general impression of the robustness of the mandibular corpus, which is confirmed by the robustness index at the level of M_1 and M_2 's sockets (the ratio of breadth and height of the corpus; data in Table 5). Even the more gracile individual, #Ish15, possesses a robustness index superior to the mean of the recent modern human sample (Figure 12).

- Insert Figure 12 -

For #Ish15, the robustness indices of the corpus decrease anteriorly until the symphysis, with a breadth-height ratio at the symphysis falling in the lower part of the comparative group variation. This is due largely to the proportionally high height dimensions of the mandibular corpus and symphysis, medial to the M_1 .

The sub-complete mandible is the only piece that preserved both the symphysis and the mandibular ramus. The anterior part of the symphysis is characterized by a well-developed trigonum mentale. The incisura mandibular anterior is present together with a tuber symphyseos extending bilaterally, but the lateral tubercles are barely visible. The maximum projection is above the basilar margin, which corresponds to a rank 4 of Dobson and Trinkaus (2002), the most frequent rank observed among Late Pleistocene modern human fossils (Trinkaus et al., 2003b). The lingual aspect of the symphysis exhibits plesiomorphic morphology with respect to the expression of two transversal tori and a genioglossa fossa. The superior transversal torus is less developed than is the inferior one. The mental spines are located in the fossa and on the superior margin of the inferior transversal torus. Finally, a lingual foramen is present beneath the inferior transversal torus. The expression of the latter

torus is rare among recent modern humans, with a frequency close to 2% among African populations ($n=141$; Ali, 2005). In our comparative groups, the highest frequency of combined genioglossa fossa and inferior transversal torus is present in the NEAND and MPHS samples (86%, $n=14$, and 80%, $n=5$, respectively). Nazlet Khater 2 and Loyangalani exhibit the same archaic conformation. Within the Late Pleistocene groups, the LPAn sample shows the highest number of cases (17%; $n=42$). Finally, among the LSA sample, two mandibles from Lothagam present an inferior transversal torus, but only one also exhibits a genioglossa fossa.

The medial surfaces of #Ish15's mandibular ramus are characterized by a well-marked planum triangulare that continues in two sharp endocoronoid and encondyloid crests up to the tips of the coronoid processes and condyles. At the same level on the external side, the planum triangulare is mirrored by a well-marked ovoid imprint.

Metrically, #Ish15 can be defined as elongated (dolichostenomandibular) and massive, with a proportionally thick mandibular ramus and corpus, distal to the M_1 , and a proportionally high corpus and symphysis medially. The overall conformation of #Ish15 is unusual compared with recent modern humans, as illustrated by Figure 13 with the mandibular corpus length in relation to the bimental breadth. #Ish15 stands outside the 95% confidence interval ellipse of the recent African modern human sample, clustering near the presumed chronologically close specimen of Mumba X (mx) and Olduvai Hominid 1(oh) (Mumba X is dated by association to Bed III, see Gliganic et al., 2012; and Olduvai Hominid 1 was dated by radiocarbon by Protsch in 1974). Note that all of the LSA individuals included in the RMH ellipse are post-Pleistocene specimens and that the Wadi Kubbaniya (wk) mandible is clearly isolated from the rest of the LPAn sample.

- Insert Figure 13 -

Apart from their unique robustness, note that some of the Ishango's mandibles present lesions reflecting age and/or diet. The condyles of #Ish15 are affected by temporomandibular joint osteoarthritis. The left condyle is flattened and expanded antero-posteriorly, forming a circular outline. Its superior surface is rough and porous. On the right side, the condyle is partly broken, but the same pathological changes are also visible. In addition, the alveolar margin at the level of the right M_2 shows the scar of an abscess. Degenerative changes at the temporomandibular joint are often observed in association with severe dental attrition (i.e., Richards, 1990; Hodges, 1991), as is true for #Ish15. All of the remaining teeth are heavily

worn (stages 7 to 8; Smith, 1984), with the right M₂ and the left M₁ having their roots functioning in the occlusal surface buccally. The plane of wear is oblique in the lingual-buccal direction, with an angle of ~20-25°. The mandibular corpus #Ish16 also possesses heavily worn teeth (stages 6 to 8; Smith, 1984), with the roots of the M₂s exposed, but the wear-plane is less inclined for #Ish16. A similarly severe wear pattern with marked inclination is common among agriculturalists (Smith, 1984) or Late Pleistocene-Early Holocene populations living in a desert environment (Ferembach et al., 1962; Greene et al., 1967). It is suggested that these similarities are related to the inclusion of abrasive particles in food preparation, by the use of grinding stones for agriculturalists, or related to unintentional inclusion of sand originating from the desert (Greene et al., 1967; Smith, 1984). At Ishango, grinding stones, pestles and mortars may indicate intensified plant processing, but may also have been used for processing mineral substances and in the manufacturing of the bone implements (de Heinzelin, 1957; Cornelissen, 2002). However, various other causes, such as paramasticatory habits, cannot be ruled out.

The infra-cranium

Diversity Analyzing infra-cranial remains is problematic because of the complex interaction between the genetic factors and the plasticity of the bone in adapting to different environments or lifestyles (Churchill, 1996; Pearson 2000a, 2000b). The infra-cranial remains of Ishango have been previously described as slender by Twiesselmann (1958), who only noted one robust radius fragment. His conclusions were largely based on the study of the two most complete long bones, namely the humerus #Ish31 and the tibia #Ish33, that likely belonged to the same individual. However, the examination of the entire collection, including all fragmented pieces, underlines the presence of highly robust individuals. Together with peculiar morphological features, the infra-cranial assemblage of Ishango seems to account for a high level of diversity.

To quantify the size variation observed among the infra-cranial remains from Ishango and discuss this dimorphism, we selected the radius, which allowed us to include the maximum number of mature individuals from the NFPr layer (MNI=5). The five selected radii from the right side all have at least the proximal part of the diaphysis preserved, allowing the measurement of the transversal diameter of the radial neck (M.4(2); Braüer, 1988). We used the coefficient of variation corrected for small samples (V*; Sokal and Braumann, 1980) in

conjunction with a resampling procedure to assess the size variation among this sample (Lockwood et al., 1996; Table 6).

- Insert Table 6 -

The coefficient of variation of the Ishango radial neck transverse diameters ($V^*=22.4$) has been compared with different reference samples through the resampling analysis. Four comparative groups were selected for this purpose, based on available data. The first one is a recent sample including 229 individuals representing 12 populations from different geographical origins (Hambucken, 1993; SOM 2). The three other groups consist of Late Pleistocene-Early Holocene populations from North Africa of Taforalt, Jebel Sahaba and Wadi Halfa.

To assess the probability of finding five radii with the same coefficient of variation exhibited by the Ishango sample, we performed a random resampling procedure with replacement. We repeatedly (1,000 times) drew a sample of five radii from the reference populations and computed their adjusted coefficient of variation. The distribution ranges of the expected V^* for each comparative sample are provided in Figure 14.

- Insert Figure 14 -

The four reference samples are normally distributed (Shapiro-Wilk test, $p<0001$). The mean and variance of the distributions significantly differ between samples (F-Snedecor and T-test). The recent modern human group has the highest level of variance, which can be explained by its inter-population and heterogeneous nature. However, the mean of the Jebel Sahaba population is significantly higher than the means of the other distributions. Concerning Ishango, the null hypothesis of similar size variation could be rejected in all cases. The probability of sampling at random the same level of variation as observed in the Ishango sample is less than 1% ($p<0.01$) in the four cases. The rejection of the null hypothesis supports the observation of a greater size variation in the Ishango sample. This size dimorphism exceeds the intra-population size variation seen in the comparative African groups dated from the Late Pleistocene up to the Holocene. Moreover, Ishango's high level of size variation also surpasses the inter-population variation seen in present-day populations. Similar observations have been made for the Middle Stone Age population of Klasies River Mouth and the Early Upper Pleistocene population from Skhul based on the dimension of the

mandibular corpus (Royer et al., 2009). The Ishango infra-cranial size variation is therefore consistent with the hypothesis of a higher level of size dimorphism in some aspect of the skeleton in Pleistocene populations, notably from Africa, in comparison to extant modern humans. The persistence of a high level of size variation in the Ishango sample, comparable to what was present during the MIS 5-4, suggests a recent and rapid reduction in size dimorphism to reach current levels, or questions the potential relationship between the Ishango group and present day populations.

The infra-cranial remains from Ishango also exhibit unusual morphological characteristics whose etiology is debated and whose frequency among recent modern populations is low. This is well illustrated by the conformation of the distal extremity of the humerus. Compared with the diaphysis, articular extremities are supposedly less plastic (Lieberman et al., 2001), and the distal part of the humerus has received particular attention for reconstructing hominid phylogeny (McHenry and Corruccini, 1975; Senut, 1981; Bacon, 2000; Rosas et al., 2015). If the locomotion-related functional component of the morphometric differences observed among fossil hominoids and hominins is debatable (Lague and Jungers, 1996; Drapeau, 2008), a significant differentiation exists within the genus *Homo* (Yokley and Churchill, 2006; Carretero et al., 2009; Bermudez de Castro et al., 2012; Trinkaus, 2012). A most distinct morphology is seen in Neandertals compared with recent modern humans. Neandertal distal humeral extremities are characterized by a relatively large olecranon fossa and a narrow medial pillar (Yokley and Churchill, 2006), and these morphological differences find their counterparts in the conformation of the ulnar proximal extremity (Churchill et al., 1996). However, these supposedly derived Neandertal features do not seem to be specific to this group since they have been observed in some African early modern ulnae (Churchill et al., 1996; Pearson and Grine, 1996). Concerning the distal extremity of the humerus, the fossil record is rather abundant, and Early to Middle Pleistocene specimens from Africa and Europe show a high range of variation that overlaps both modern human and Neandertal diversity, suggesting that the so-called Neandertal traits could have been selected from a highly polymorphic ancestral population (Bermudez de Castro et al., 2012).

In addition to a strong size dimorphism, the two mature humeri from Ishango (#Ish31 and #Ish160) display very different morphologies of the distal extremity. The most striking feature relates to the thickness of the medial pillar, but the overall distal conformations of both humeri are dissimilar both to one another and to modern human variation. Table 7

includes the inventory of the humerus remains and the recorded dimensions of their distal extremities.

- Insert Table 7 -

As illustrated in Figure 15, the humerus #Ish31 exhibits an extremely narrow medial pillar compared with the size of the olecranon fossa.

- Insert Figure 15 -

The low value of its medial pillar Index (MPI = 15.40) lies outside all comparative ranges of variation, whereas the Index of #Ish160 (MPI = 33.95) stands within past and recent modern human diversity, as does the Index of both immature humeri from the site (#Ish32 and #Ish177; Figure 15). As underlined by Bermudez de Castro et al. (2012), the archaic pattern (the E-MPleis group) is highly variable, and the separation between *Homo heidelbergensis* and the Neandertals compared with Late Pleistocene and recent modern humans could be considered as a differentiation from a highly polymorphic ancestral population. However, Figure 15 also shows that the Late Pleistocene populations from North Africa (LPA groups) are closer to the Neandertal variation than the recent human one.

To assess the overall conformation of the distal extremities from the Ishango mature humeri, we performed a principal component analysis on the seven measurements from Table 7 that were size-adjusted (Darroch and Mosimann, 1985). The projection of the two first principal components is provided in Figure 16 and accounts for 59.27% of the total sample variation.

- Insert Figure 16 -

The ellipse represents 95% of the recent modern human diversity, and both adult specimens from Ishango lie outside this comparative variation. If #Ish160 stands at the edge of the RMH ellipse, #Ish31 is isolated along the left part of the first axis. A clear differentiation is visible between the recent modern sample group and many Neandertal specimens and most of the Late Pleistocene individuals from North Africa in the upper left quadrant. This separation reflects a difference in conformation concerning the breadth of the distal extremity and the olecranon fossa in relation to the pillar thickness, and particularly the medial pillar thickness. The position of the Neandertals, somewhat more isolated in the lower-left quadrant, is related

to the shape of the olecranon fossa, which is more circular than oval. The two LSA individuals, Olduvai Hominid 1 (oh) and Lothagam 4b (lo), exhibit different morphologies, with Olduvai Hominid 1 aligning with the Late Pleistocene variation, whereas the Holocene humerus from Lothagam is included in recent modern human variation.

Similarities between distal humeral extremity of recent individuals from hunter-gatherer populations and Neandertals have been described by Yokley and Churchill (2006). Although functional significances of this conformation have been neglected in the study of distal humerus morphology, our results tend to support that epigenetic factors might actually be involved in the expression of this supposedly plesiomorphic trait. The strong morphological differentiation between both mature Ishango humeri, the absence of a narrow medial pillar in the immature individuals from Ishango regardless of the age group, and the distal humeral conformation of the LPA groups suggest that functional hypothesis should be acknowledged in further studies.

Mobility Cross-sectional geometric properties have been widely used to characterize infra-cranial robustness and adaptation to biomechanical strengths (e.g., Ruff et al., 1993; Trinkaus, 1997; Holliday, 2002; Stock and Pfeiffer, 2004). In particular, the inner structure morphologies of the limb bones were shown to reflect mobility and activity patterns (e.g., Holt, 2003; Shackelford, 2007; Shaw and Stock, 2013). The shape of the section at mid-diaphysis reflects the resistance of the shaft to bending strengths (I_x/I_y , or I_{max}/I_{min}), the polar second moment of area (J) reflects the resistance to torsional strengths, and the proportion of cortical area (%CA) is related to axial – tensile and compressive – strengths (Ruff, 2008). The latter proportion is partly influenced by body mass, body size and genetic and aging factors (Peck and Stout, 2007; Ruff, 2008). Therefore, in the case of incomplete skeletons or fragmented bones, the comparison of cross-section geometric properties is challenged by the difficulties in standardizing the data (Shaw and Stock, 2013).

At Ishango, the most complete infra-cranial remains from the site, the humerus #Ish31 and the tibia #Ish33, were described as gracile by Twiesselmann (1958). The tibia #Ish33 exhibits a robustness index that falls in the lower part of the comparative sample range of variation (as is true for the #Ish31 humerus; Table 8).

- Insert Table 8 -

Comparing the cross-sectional properties of the tibia at mid-diaphysis highlights marked resistance to axial loads, but a limited resistance to torsion and bending. The shape of the section at mid-diaphysis ($I_{\max}/I_{\min} = 2.0$) is closer to the post-industrial population mean (2.1 ± 0.4 , $n=59$; Ledger et al., 2000) than to that of hunter-gatherers and pre-industrial populations (2.55 ± 0.5 , $n=57$; Ledger et al., 2000). The more circular shape of the section in post-industrialized populations has been interpreted by several authors as reflecting their less mobile lifestyle (Ledger et al., 2000; Holt, 2003).

To compare the activity-related information of the cross-sectional geometric properties of the Ishango most complete infra-cranial remains, we used the relative tibial rigidity ratio (TibJ/HumJ) proposed by Shaw and Stock (2013) to assess differences in the distribution of robusticity and encompass standardization problems. The association of these two long bones (#Ish31 and #Ish33) with the same individual is supported by their spatial repartition, their morphology, and biometric correlations as illustrated by their lengths in Figure 17.

- Insert Figure 17 -

Following the data of Shaw and Stock (2013), Ishango relative tibial rigidity (TibJ/HumJ = 2.06) falls between the means of the Swimmer group (1.84, $n=15$) and the Andaman Islanders means (2.36, $n=15$). The Ishango ratio expresses a decrease in tibial rigidity relative to the humeral one. Figure 18 shows the regression slopes of humerus rigidity in relation to the tibial rigidity based on two comparative groups defined by their adaptation to different mobility patterns, as well as data from a sample of South African LSA and Protohistoric Andaman Islanders individuals.

- Insert Figure 18 -

The Ishango rigidity values plot close to the Andaman Islanders regression slope. The Andamanese can be described as having marine mobility and fishing activities (Radcliffe-Brown, 1922; Stock and Pfeiffer, 2001). They are habitual paddlers and swimmers, and occasional foragers. They use canoes for transportation and procuring food (Stock and Pfeiffer, 2001). Although avoiding a strict correlation between the Ishango data and Andamanese mobility patterns, it is noticeable that, although limited to one individual, the infra-cranial information from Ishango suggests a different ecological adaptation (aquatic

mobility) compared with the extreme terrestrial mobility pattern exhibited by Late Pleistocene and Holocene foragers (Shaw and Stock, 2013).

Conclusions

The Ishango collection represents the oldest sample of modern humans in Late Pleistocene Central Africa. The human remains are associated with an exceptional archaeological context characterizing a hunter-fisher-gatherer community showing 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. In the framework of growing interest in understanding of African Late Pleistocene modern human diversification and dispersion, the comparative study of these human remains offers a unique opportunity to document past modern human diversity and adaptation during the period of drastic environmental changes in many parts of Africa related to the Last Glacial Maximum.

To summarize, the comparative study of the Ishango human remains underlines the unusual morphometrical characteristics of this population. The cranial and mandibular remains are robust and characterized by plesiomorphic features more frequently seen in Late-Middle to early Late Pleistocene comparative fossils. The bony labyrinth morphology exhibits stronger affinities with Middle Paleolithic specimens from Qafzeh and Skhul rather than with recent, chronologically and geographically closer modern human populations. The infra-cranial remains exhibit a high level of size dimorphism and peculiar characteristics that are unusual in recent modern human groups. Concerning past modern human phenotypic diversity, the Ishango collection, although fragmentary and isolated, opens a window on Late Pleistocene variation that suggests a complex evolutionary history of diversification and isolation in Africa that lasted at least until the LGM. In addition, the morphometric study of the infra-cranial remains provides more insights on the mobility and activity patterns of the Ishango population, complementing the behavioral inferences that could be made through the analysis of their archaeological context. Therefore, the antiquity and diversification of aquatic adaptations are supported here even more with the paleoanthropological data extracted from Ishango's infra-cranial skeletons, which may reflect an adaptive response to a specific environment.

Finally, our results are consistent with genetic theories about the deep sub-structure of Late Pleistocene African populations, the complex history of isolation and diversification, and a

possible archaic admixture. Indeed, the plesiomorphic trait expressions, the morphometric variations and adaptations exhibited by the Ishango sample could relate to the isolation of modern human groups in Africa during the end of the Late Pleistocene, when many parts of the continent became extremely hostile to human life. This collection may represent the tip of the iceberg of modern human biological and cultural diversity that once existed in Central Africa during this crucial period preceding large Holocene migration and morphological homogenization within Africa.

The Ishango collection adds to growing Late Pleistocene fossil evidence that seems to sample some of the aspects of modern human variation no longer present in extant Africa diversity. Understanding these aspects is crucial to the definition of anatomically modern human variation.

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Figure captions

Figure 1: Location of the Ishango 11 archaeological site along the Semliki River (left) and excavation plan of the site (right), modified following de Heinzelin (1957). A: area preserving only the basal part of the Ishango Gravels Formation. B: area where the tuffaceous levels were present in addition to the previous ones. No grid system was laid out in areas A and B.

Figure 2: Schematic stratigraphic section of the first ten meters of Ishango N43GE trench, modified following de Heinzelin and Verniers (1996). R: Recent Formation; TP: Museya Gravels Formation; TT: Ishango Gravels Formation; L: Lusso Formation. ZPEm: Post Emersion Zone; N.TUF: Tuffaceous levels; SD-SFM: Hardened Sand – Fine Micaceous Sand; NFPr: Principal Fossiliferous level; G.INF: Inferior Gravels. Stars: archaeological assemblages containing human remains.

Figure 3: Histogram of the anatomical representation of the Ishango NFPr human material.

Figure 4: Boxplot of the median and range of variation of the thickness of the cranium at the parietal eminence (TPE) for Ishango (ISH) and the comparative samples. Comparative group abbreviations as in SOM 2.

Figure 5: Photographs of the two frontal bones from Ishango preserving an orbital portion and the glabella. Left: Endocranial views of the two fragments (#Is11-564/567 and #Ish1); Right: external view. The scale represents 1 cm.

Figure 6: Boxplot of the median and range of variation of the interorbital breadth (DKB) for the two Ishango frontal fragments and the comparative samples. Comparative group abbreviations as in SOM 2.

Figure 7: Three-dimensional reconstruction of the complete right bony labyrinths from the right petrous bone (#Ish37) in lateral (upper) and superior (lower) views.

Figure 8: Bivariate diagram of the shape of the posterior semicircular canal (PSCh/w) in relation to the shape of the cochlea (COh/w). Comparative group abbreviations as in SOM 2.

Figure 9: Bivariate diagram of the radius of the posterior semicircular canal (PSC-R) in relation to the radius of the cochlea (CO-R). Comparative group abbreviations as in SOM 2.

Figure 10: Histograms of the relative proportions of the anterior (ASC-%R), posterior (PSC-%R) and lateral (LSC-%R) semicircular canals of #Ish37 compared with the average value of the comparative sample groups. Comparative group abbreviations as in SOM 2.

Figure 11: Photographs of the lateral side of the four mandibular remains from the Ishango NFPr layer. The scale represents 1 cm.

Figure 12: Boxplot of the median and range of variation of the index of robustness of the corpus between the first and second lower molars (IRM1/M2) for three Ishango mandibles and the comparative samples. Comparative group abbreviations as in SOM 2.

Figure 13: Bivariate diagram of the mandibular corpus length (MCL) in relation to the bi-mental breadth (BMB). Comparative group abbreviations as in SOM 2. lo= Lothagam 4b; mx=Mumba X; wk=Wadi Kubbania; oh=Olduvai Hominid 1.

Figure 14: Histogram of the dispersion of the expected coefficient of variation, corrected for small samples (V^*), of the transversal diameter of the radial neck (TDN) during a random resampling (1,000 iterations with replacement) of five individuals among the Recent modern human sample (RMH), and the Late Pleistocene North African populations of Wadi Halfa (WH), Jebel Sahaba (JS) and Taforalt (TAF). The black line illustrates the coefficient of variation for the five Ishango radii.

Figure 15: Boxplot of the median and range of variation of the medial pillar Index (MPI) of the mature (ISHm) and immature (ISHi) humeri from Ishango, and the comparative samples. Comparative group abbreviations as in SOM 2. E-MPleis: Bodo, Gombore, ATD-6, and Nariokotome (Senut, 1981; Walker and Leakey, 1993; Carretero et al., 2009; Bermudez de Castro et al., 2012); Hhed: *Homo heidelbergensis* (Carretero et al., 1997).

Figure 16: Bivariate projection of the two first principal components from the principal component analysis on the distal humerus conformation. Comparative group abbreviations as in SOM 2. lo= Lothagam 4b; oh=Olduvai Hominid 1.

Figure 17: Bivariate diagram of the relation between the humerus and tibia maximum lengths of #Ish31 and #Ish33 compared to the reference sample (REF). The latter sample includes all African fossils from our database for which associated tibia and humerus data were available.

Figure 18: Bivariate diagram of the least squares linear regressions of midshaft tibial rigidity (J) in relation to midshaft humeral rigidity (J) for modern human athletes (runners and swimmers), protohistoric Andaman Islanders (ANDAM ISL), and Late Stone Age southern African specimens (LSA SA). Slope equations based on Shaw and Stock (2013). The position of Ishango is indicated by the black dot and cross.

Table captions

Table 1: Minimum number of individuals by age class.

The gray rectangles represent immature individuals who span two age groups based on bone maturation standards and whose association with the individuals already identified in each age group is excluded.

Table 2: Cranial measurements of the Ishango remains and the comparative samples.

Measures TPE = vault thickness at parietal eminence (Twisselmann, 1941); DKB (inter-orbital breadth) follows Howells (1973). M = Mean, Sd = Standard Deviation; n = Number.

*Adjusted z-scores of ISH relative to the variation range of the four comparative groups; the values in bold and italic (<-1 or >1) are outside 95% of the comparative sample range of variation (Scolan et al., 2012). Adjusted z-scores of the DKB value for #Ish1 are provided in the middle column, whereas the Adjusted z-scores of #Ish11-564/567 are in the right column.

° two fragments that refit together.

Table 3: Labyrinth dimensions of Ishango and the comparative samples.

The variable abbreviations and definitions of the labyrinth are as described by Spoor (1993). Bold values in the Adjusted z-scores section are outside 95% of the comparative sample range of variation.

*Values of Lothagam (skeleton 4b) that lie outside of the RMH range of variation.

Table 4: Results of the discriminant analysis on the Labyrinth dimensions.

In cross-validation, each case is classified by the functions derived from all cases other than that case. Variables active in the analysis: LSC-%R; SLI; ASCw, LSCh; CO-R; PSCtor; PSCw; APA<LSCm; ASCh/w; ASC-R; COw and COh/w.

Table 5: Mandibular measurements of the Ishango remains and the comparative samples.

MFP = Mental foramen position. Measurements follow Martin (Braüer, 1988): MCL = Mandibular Corpus Length (M68); BMB = Bi-mental Breadth (M67); IMD = Index of the mandible ($M68/M65 \times 100$); IMR = Index of the mandibular ramus ($M71/M70 \times 100$); IRS = Index of robustness at the symphysis; IRT = Index of robustness of the corpus at the level of the mental foramen; IRM1/M2 = Index of robustness of the corpus between M_1 and M_2 . M = Mean, Sd = Standard Deviation; n = Number. *Adjusted z-scores of ISHs relative to the variation range of the recent modern human sample; the values in bold (<-1 or >1) are outside 95% of the comparative sample range of variation (Scolan et al., 2012).

Table 6: Ishango radius fragments and measurements of the transversal diameter of the radial neck (TDN; M4(2), Braüer, 1988).

⌘ Individual not included in the resampling analyses;

° The pathology of the radial head does not affect the transversal measure of the radial neck;

V* = corrected coefficient of variation $\times 100$; R = right; L = left.

Table 7: Humerus measurements of the Ishango remains.

*Dimensions without the distal epiphysis. M = mature; L = left; R = right; BB = Biepicondylar Breadth (M4); TB = Trochlear Breadth (M11); CB = Capitatum Breadth (M12); OFB = Olecranon Fossa Breadth (M14); OFH = Olecranon Fossa Height; MPT = Medial Pillar Thickness; LPT = Lateral Pillar Thickness; OFI = Olecranon Fossa Index ($OFB/BB \times 100$); PI = Pillar Index ($MPT/BB \times 100$); MPI = Medial Pillar Index ($MPT/OFB \times 100$).

Table 8: Tibia linear measurements and cross-sectional geometric properties of the Ishango remains.

M = mature; L = left; R = right; Lo4a = Lothagam, burial 4, Individual 1; n = number (right one corresponds to the minimal number of individual used for the comparison of classic measurements; the left one relates to the cross-sectional geometric property comparisons); LMAX = Maximal Length (M1a); RI = Robustness Index ($M10b/M1a$); CI = Cnemic Index

(M9a/M8a); %CA_50 = percentage of cortical area at mid-diaphysis; Ix/Iy_50 = ratio of the antero-posterior and mesio-lateral second moment of area at mid-diaphysis; J_50 = Mid-diaphyseal rigidity. Data for the LSA cross-sectional properties from Stock & Pfeiffer (2001) and Shaw & Stock (2013).

*Adjusted z-scores of ISH relative to the variation range of the recent modern human sample; the values in bold (<-1 or >1) are outside 95% of the comparative sample range of variation (Scolan et al., 2012).

Supplementary Online Material

SOM 1: Inventory of the NFPr human remains.

Not included, seven undetermined and possibly human fragments (#Ish38-40; #Ish42-45; #Ish179).

SOM 2: Composition of the comparative samples and description of the comparative group abbreviations.

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Table1

	Immature					Mature
Minimum Number of Individuals	[0-<1]	[1-4]	[5-9]	[10-14]	[15-19]	[>20]
	2	1	1	-	-	5
	1					
			1			
				1		
Total	2	2	2	-	1	5

Table2

Bone number	Identification	TPE	DKB	
#Ish1	Frontal	-	23.8	
#Is11-564/567	Frontal	-		27.6
#Ish3°	Parietal	11.0	-	
#Ish4°	Parietal	11.0		
Comparative groups				
EMH	M	8.8	27.5	
	Sd	2.2	2.8	
	<i>n</i>	6	8	
LPH	M	7.24	26.0	
	Sd	1.3	2.2	
	<i>n</i>	69	64	
LSA	M	10.0	24.4	
	Sd	0.7	2.9	
	<i>n</i>	5	15	
RMH	M	7.7	22.4	
	Sd	1.0	2.6	
	<i>n</i>	64	506	
Adjusted Z-scores*				
ISH vs EMH		0.3537	-0.5304	0.0125
ISH vs LPH		1.4938	-0.4954	0.3465
ISH vs LSA		0.4429	-0.0985	0.4924
ISH vs RMH		1.6339	0.2756	1.0094

Table3

		SLI	ACSh/w	ASC-R	PSCh	PSCh/w	PSC-R	LSCh/w	LSC-R
ISH (#Ish37)		48.60	85.63	3.20	7.40	129.60	3.28	89.35	2.49
LSA (Lo4b)		52.09	81.01	2.96	6.6	120.15*	3.03	79.69	2.3
MPHS	M	53.0	88.5	3.3	6.0	99.7	3.0	83.4	2.4
	Sd	6.2	6.9	0.2	0.4	7.9	0.2	9.7	0.2
	N	11	11	11	11	11	11	11	11
LPH	M	43.7	89.6	3.3	6.4	107.5	3.0	94.1	2.5
	Sd	9.4	6.8	0.2	0.5	7.5	0.3	6.3	0.2
	N	10	9	10	8	8	9	9	10
RMH	M	50.6	90.2	3.2	6.5	105.0	3.2	91.6	2.3
	Sd	6.9	5.0	0.2	0.6	7.5	0.3	6.1	0.2
	N	145	145	145	145	145	145	145	145
NEAND	M	62.1	93.8	3.0	5.7	100.7	2.8	92.2	2.6
	Sd	7.9	5.0	0.2	0.6	10.0	0.2	7.3	0.2
	N	26	27	27	25	27	27	27	27
ISH vs MPHS		-0.3052	-0.1790	-0.2701	1.3300	1.6341	0.6546	0.2674	0.2821
ISH vs LPH		0.2191	-0.2397	-0.2306	0.8270	1.1681	0.3399	-0.3076	-0.0642
ISH vs RMH		-0.1479	-0.4573	-0.0892	0.7750	1.6604	0.2188	-0.1890	0.3808
ISH vs NEAND		-0.8093	-0.7751	0.5113	1.3643	1.3785	1.0322	-0.1891	-0.1810

Table4

Classification matrix (cross validation)*°						
	<i>n</i>	RMH	EUP	MPHS	NEAND	% Correct
RMH	145	113	13	7	12	77.9
LPH	6	2	4	0	0	66.7
MPHS	10	1	1	7	1	70.0
NEAND	23	2	0	1	20	87.0
						78.3
Posterior probability						
ISH37		0.035	0.021	0.944	0.001	
LSA (Lo)		0.993	0.001	0.005	0.002	

Table5

Number	MFP	MCL	BMB	IMD	IMR	IRS	IRT	IRM1/M2
#Ish15	P ₄ /M ₁	94.5	51.2	79.2	72.9	37.5	38.3	50.1
#Ish16	P ₄	-	-	-	-	-	47.0	60.1
#Ish22	P ₃ /P ₄	-	-	-	-	-	51.5	61.9
Comparative groups								
EMH	M	95.4	50.3	82.4	66.7	44.4	45.3	50.0
	Sd	11.2	6.2	4.8	12.4	8.6	8.6	7.2
	n	6	5	3	5	10	7	9
LPH	M	82.1	46.2	67.7	64.0	44.8	39.2	46.7
	Sd	8.5	3.3	7.4	9.7	5.4	5.8	7.6
	n	107	158	73	91	167	107	107
LSA	M	83.9	45.5	73.2	67.0	47.6	41.7	50.3
	Sd	5.0	5.0	3.4	8.5	4.7	6.6	5.9
	n	20	19	14	16	5	8	7
RMH	M	79.8	44.5	71.3	65.8	46.1	41.1	47.7
	Sd	5.8	3.0	5.8	7.8	11.1	6.7	6.9
	n	296	277	279	169	10	189	247
Adjusted Z-scores*								
ISH15 vs RMH		1.2788	1.1285	0.6873	0.4558	-0.3258	-0.2047	0.1784
ISH16 vs RMH		-	-	-	-	-	0.4500	0.9113
ISH22 vs RMH		-	-	-	-	-	0.7915	1.0429

Table6

Number	Side	TDN (M4(2))	Comment
#Ish28	R	11.93	Radial head deformed°
#Ish136	R	12.25	
#Ish137	R	10.74	
#Is11-530 ^h	L	-	
#Is11-677	R	10.01	Immature [1-4]/[5-9]
#Is11-818 ^h	R	11.14	
#Is11-4084	(R)	16.75	
V*		22.36	

Table 7

[illegible]

Table8

Number	Maturation	Side	LMAX	RI	CI	%CA_50	Ix/Iy_50	J_50
#Ish33	M	R	380.0	17.4	70.2	86.3	1.91	20822.8
#Ish184	[0-1]	L	-	-	83.2	81.9	1.27	98.1
Is11-3621	[1-4]/[5-9]	R	-	-	89.9	65.0	1.55	2099.8
Lo4a	M	L	-	-	70.7	73.8	2.39	84310.0
Adjusted Z-scores*	Number		LMAX	RI	CI	%CA_50	Ix/Iy_50	J_50
Ish33 vs MPHS	$n \geq 4; n \geq 6$		-0.9713	-0.8055	0.4274	0.9377	-0.1143	-1.1944
Ish33 vs EUP	$n \geq 26; n \geq 13$		-0.0917	-0.9635	0.7261	0.4000	-0.2655	-0.6465
Ish33 vs LPA	$n \geq 54; n \geq 41$		0.0077	-0.5993	0.2169	0.2964	-0.4317	-0.7155
Ish33 vs LPSwa	$n \geq 14; n \geq 7$		0.2822	-1.5103	0.4041	0.5369	-0.4084	-0.5613
Ish33 vs LSA	$n \geq 18; n \geq 19$		-0.4723	-	0.6009	-	-0.5239	-0.6539
Ish33 vs NEAND	$n \geq 10; n \geq 5$		0.5275	-2.4333	-0.1193	0.3825	0.0706	-0.4672

Figure1

Figure2

Figure3

Figure4

Figure5

Figure6

Figure7

Figure8

Figure9

Figure10

Figure11

Figure12

Figure13

Figure14

Figure15

Figure16

Figure17

Figure18