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Who were the Nataruk people? Mandibular morphology among late Pleistocene and early Holocene fisher-forager populations of West Turkana (Kenya)

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A B S T R A C T

Africa is the birthplace of the species *Homo sapiens*, and Africans today are genetically more diverse than other populations of the world. However, the processes that underpinned the evolution of African populations remain largely obscure. Only a handful of late Pleistocene African fossils (~50-12 Ka) are known, while the more numerous sites with human fossils of early Holocene age are patchily distributed. In particular, late Pleistocene and early Holocene human diversity in Eastern Africa remains little studied, precluding any analysis of the potential factors that shaped human diversity in the region, and more broadly throughout the continent. These periods include the Last Glacial Maximum (LGM), a moment of extreme aridity in Africa that caused the fragmentation of population ranges and localised extinctions, as well as the 'African Humid Period', a moment of abrupt climate change and enhanced connectivity throughout Africa. East Africa, with its range of environments, may have acted as a refugium during the LGM, and may have played a critical biogeographic role during the heterogene`ous environmental recovery that followed. This environmental context raises a number of questions about the relationships among early Holocene African populations, and about the role played by East Africa in shaping late hunter-gatherer biological diversity. Here, we describe eight mandibles from Nataruk, an early Holocene site (~10 Ka) in West Turkana, offering the opportunity of exploring population diversity in Africa at the height of the 'African Humid Period'. We use 3D geometric morphometric techniques to analyze the phenotypic variation of a large mandibular sample. Our results show that (i) the Nataruk mandibles are most similar to other African hunter-fisher-gatherer populations, especially to the fossils from Lothagam, another West Turkana locality, and to other early Holocene fossils from the Central Rift Valley (Kenya); and (ii) a phylogenetic connection may have existed between these Eastern African populations and some Nile Valley and Maghrebian groups, who lived at a time when a Green Sahara may have allowed substantial contact, and potential gene flow, across a vast expanse of Northern and Eastern Africa.

1. Introduction

Africa is the birthplace of our species, *Homo sapiens*, from where all human populations diversified. The earliest fossils that show the unique, universal characteristics of a modern human morphology are found in East Africa 200,000–160,000 years ago (Ka) (Day, 1969; Leakey, 1969; White et al., 2003; Fleagle et al., 2008), while recent proposals for an earlier origin for the species would extend this date to ca. 300 Ka (Hublin et al., 2017). Africans today are genetically more diverse than other populations of the world, reflecting the population size and time-depth of modern human presence in the continent (Liu et al., 2006; Li et al., 2008). Genetic data further point to significant population change associated with

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the expansion of food-producing populations in the last 4000 years (Tishkoff et al., 2009). However, between these two extremes in time, the historical, ecological and adaptive processes that underpinned the evolution of African populations remain largely unknown. Only a handful of late Pleistocene sites (~50-12 Ka) with human remains are known (Grine, 2016), and these are mostly located in North or South Africa. This period includes the Last Glacial Maximum, a moment of extreme aridity in Africa (Gasse, 2000; Clark et al., 2009) that caused the fragmentation of population ranges and localised extinctions. East Africa, with its diversity of environments and high relief, may have acted as a refugium (Mirazón Lahr and Foley, 2016), thus playing a critical biogeographic role within the continent during phases of late Pleistocene aridity. Contrastingly, the early-to-mid Holocene (12-5 Ka) – the 'African Humid Period' (AHP) – was a moment of abrupt climate change (de Menocal et al., 2000) and enhanced connectivity throughout Africa, including the expansion of productive biomes and greening of the Sahara (Larrasoaña et al., 2013). However, the timing of environmental recovery was not synchronous throughout the continent (Carolin et al., 2013), creating the opportunity for the differential expansion of those populations who first experienced ameliorated conditions (Mirazón Lahr, 2016). This environmental context raises a number of questions about the relationships among early Holocene African populations and, in particular, about the role played by East Africa in shaping late hunter-gatherer biological diversity in the continent. The number of sites and human fossil remains of early Holocene age in Africa is greater than earlier phases, but these are patchily distributed. In particular, the late Pleistocene and early Holocene human diversity of Eastern Africa is still poorly known, precluding any analysis of the potential factors that shaped human diversity in the region, and more broadly throughout the continent.

This paper describes the variation and affinities of a new group of fossil mandibles from the site of Nataruk in West Turkana, Kenya, dating to ~10 Ka (Mirazón Lahr et al., 2016). In the context of a scarce African fossil record, the discovery in August 2012 of this new Kenyan site is important. Nataruk is located ~30 km southwest of Lake Turkana, and ~2 km from the paleoshore of Lake Turkana during the AHP. The site is at the Eastern edge of a small depression that would have formed a lagoon during periods of high precipitation, abutting small dunes rising ~4 m above the surface. Small-to medium-sized gravel, lying loosely over a layer of lake sediments, covers the surface of the ridge and mounds largely characterized by shell and carbonate deposits. The majority of the fragmentary faunal remains recovered are aquatic/lake-edge species. The site has been dated using radiocarbon from shells and sediment samples associated with the human remains, optical luminescence dating and uranium-series dates that yielded an age estimate of ~10.5–9.5 Ka (Mirazón Lahr et al., 2016). A minimum of 27 fossil individuals, among which 12 are represented by partially complete skeletons, were uncovered at Nataruk. Ten skeletons show evidence of human-inflicted trauma and the site was described as being the scene of inter-group conflict between hunter-fisher-gatherer groups and the earliest evidence of warfare (Mirazón Lahr et al., 2016). Most of the 12 articulated skeletons are reasonably well-preserved; however, the crania are broken or partly missing. For four specimens (KNM-WT 71258, 71259, 71260, and 71265), the skull is fragmentary; another four individuals lack most of the upper face (KNM-WT 71251, 71255, 71256 and 71263), KNM-WT 71253 lacks most of the occipital and basicranium, and KNM-WT 71254 preserves only the right parietal, the frontal and the right zygomatic. KNM-WT 71257 and 71264 skulls are almost complete, but their calvaria are deformed due to trauma. However, with the exception of KNM-WT 71258, 71259, 71260 and 71265, all the specimens have well-preserved mandibles that exhibit minimal traumatic lesions, although most mandibular condyles are missing; the right ascending ramus of KNM-WT 71254 has a linear perforation on its antero-lateral surface (Figs. 1 and 2, Table 2; Mirazón Lahr et al., 2016), but this lesion has not affected its overall shape. Therefore, while the cranial remains from Nataruk are either fragmentary or show evidence of violent trauma, which precludes unbiased morphometric study, the well-preserved mandibular remains offer the opportunity of exploring population diversity in Africa at the height of the 'African Humid Period'.

In this paper we examine the phenotypic variation of the people of Nataruk in order to understand their phenetic affinities with worldwide populations, and, more specifically with African populations. The population affinities of the people of Nataruk have not been explored before, although our expectation is that they will show a close relationship to neighboring fisher-forager groups from the early Holocene of Turkana, and more broadly, to early Holocene eastern African forager groups. While this hypothesis is based on the spatial and temporal proximity that would have promoted the connectivity among these groups, the potential relationships of the Nataruk population to other African populations is unmapped. Thus, this paper aims to test both this hypothesis and describe the broad phenetic relationships among some Holocene African populations, both of which depend on the presence of a signal of population history in mandibular morphology.

1.1. The mandible as a source of evolutionary information

The human cranium is often used to reconstruct morphological and phylogenetic affinities among populations and species because variation in its morphology is largely explained by a model of neutral evolution, i.e., the result of stochastic processes of mutation and genetic drift (Roseman and Weaver, 2004; Nicholson and Harvati, 2006; Smith, 2009; von Cramon-Taubadel, 2009a; Betti et al., 2010; Galland, 2013; Katz et al., 2017). However, skull morphology must still be compatible with a number of different functions. These include protection of the brain and sensory organs, food processing and maintenance of the respiratory airways (Daegling, 2010). As a consequence, certain regions of the skull also reflect those functions and the external factors that influence them, to different degrees (von Cramon-Taubadel, 2014; Noback and Harvati, 2015b). Notably, it has been suggested that the upper face – especially the nasal cavity (Noback et al., 2011; Zaidi et al., 2017) – is influenced by climate, while the mandible together with general cranial shape might be more influenced by diet (Harvati and Weaver, 2006; Smith, 2009; von Cramon-Taubadel, 2009b, 2011; Noback and Harvati, 2015a). Nevertheless, such shape differences associated with climatic (Zaidi et al., 2017) and dietary pressures (Katz et al., 2017) are relatively small, most strongly expressed at the extremes of the adaptive range (i.e., among populations who live in very extreme environments), and overlap between populations is considerable, indicating that the impact of these factors on skull morphology may be less significant than previously hypothesised.

A recent study by Katz et al. (2017) suggests that the phenotypic differences due to diet in both mandible and cranium tend to be smaller than typical differences between sexes, groups of average relatedness and between individuals, further indicating that differences attributable to subsistence strategy may appear somewhat magnified when comparing populations which are closely related. The study, nevertheless, points towards modest directional shape differences between foragers and farmers, as has been advocated before (see von Cramon-Taubadel, 2011). This can be explained by a decrease in masticatory stress associated with the transition from tougher or harder foraged foods to tender or soft processed agricultural ones (González-José et al., 2005; Lieberman, 2008; von