



Pliocene hominin biogeography and ecology



Gabriele A. Macho

Research Laboratory for Archaeology (RLAHA), University of Oxford, England, UK

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ABSTRACT

Australopithecus bahrelghazali, its origin and palaeobiology are not well understood. Reported from only one location some several thousand kilometres away from East African Pliocene hominin sites, it appears to have predominantly fed on C_4 sources. Yet, it lacks the morphological adaptations of other primate C_4 consumers like *Paranthropus boisei* and *Theropithecus oswaldi*. Furthermore, although considered to belong to *Australopithecus afarensis* by most researchers, *A. bahrelghazali* appears to differ from the former in a key aspect of its morphology: enamel thickness. To assess the phylogeny and palaeobiology of *A. bahrelghazali*, I first evaluate the dietary adaptations and energetics of *A. bahrelghazali* using empirical data of the feeding ecology of extant baboons, *Papio cynocephalus*. Information published on *A. bahrelghazali* morphology and habitat preference is used to select C_4 foods with the appropriate mechanical properties and availability within the environment to create the models. By altering the feeding time on various food categories, I then test whether *A. bahrelghazali* could have subsisted on a C_4 diet, thus accounting for the $\delta^{13}C$ composition of its dental tissue. The effects of body mass on the volume of food consumed are taken into account. The outcomes of these simulations indicate that *A. bahrelghazali* could have subsisted on a diet of predominantly sedges, albeit with limitations. At higher energy requirements, i.e., above 3.5 times the BMR, it would be difficult for a medium-sized primate to obtain sufficient energy from a sedge-based diet. This is apparently due to constraints on foraging/feeding time, not because of the nutritional value of sedges per se. These results are discussed against the backdrop of *A. bahrelghazali* biogeography, palaeoenvironment, and phylogeny. The combined evidence makes it plausible to suggest that Northern Chad may have been a refugium for migrating mammals, including hominins, and throws new light on the deep history of *A. bahrelghazali*.

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1. Introduction

The study of hominin dispersal(s) is one of the hot topics in palaeoanthropology today (Fleagle et al., 2010; Palombo, 2013). Central to these investigations is an understanding of hominin energetics, i.e., diet (Antón et al., 2002), either by itself or in relation to the cost of locomotion, brain size and life history (Pontzer, 2012a), the role played by climate (deMenocal, 2004; Donges et al., 2011) and the concomitant changes in topography (Bergner et al., 2009; Trauth et al., 2010), overall wood cover (Cerling et al., 2011a) and vegetation types (Bonnefille, 2010; Feakins et al., 2013). Disentangling these interactions is not straightforward and is compounded further by the fact that although correlates with other migrating large-bodied mammals exist (Vrba, 1992; Turner and Wood, 1993; Bromage and Schrenk, 1995; Strait and Wood,

1999), hominins did not always travel in the same direction as these mammals. Thus insights from different lines of enquiry are necessary to arrive at reasonable inferences about migration patterns and dispersals in the past, as well as their underlying causes. This becomes more difficult as one goes back in time, because of the paucity of fossil remains and environmental information, unresolved phylogenies (Strait and Wood, 1999), and taphonomic biases (Behrensmeyer and Reed, 2013). Yet, dispersals did occur throughout our evolutionary history and were not restricted to *Homo*. South African australopithecids can most certainly be traced back to East Africa from where they migrated southwards (Bromage and Schrenk, 1995; Reed et al., 2013), although biogeographic details have yet to be determined. A westward dispersal is implicated by the hominin remains from Koro Toro, Chad (Brunet et al., 1995). The evidence for such a dispersal is even less secure. When, why, and how did *Australopithecus bahrelghazali* come to be in Central Africa? An integrating approach that combines information from different lines of research together with a more detailed

E-mail address: gabriele.macho@rlaha.ox.ac.uk.

assessment of the species' dietary adaptations and energetics may provide some answers. To do so is the aim of the present study.

Specimens of *A. bahrelghazali*, a mandibular fragment and an isolated tooth, from the Chad were originally assigned to *Australopithecus* aff. *afarensis* and were suggested to represent a local population of a widely dispersed *A. afarensis* (Brunet et al., 1995); only later were the fossils assigned to a new species (Brunet et al., 1996). The well-vegetated green belt, which repeatedly extended across the Sahara from the Atlantic to East Africa during the Pliocene (Larrasoana et al., 2013) and the successive wet and arid periods in Northern Chad (Schuster et al., 2009), could have led East African hominins to periodically expand and contract their ranges. Whether the morphological differences in the cross-sectional shape of the mandibular symphysis and in tooth root morphology (Brunet et al., 1996; Guy et al., 2008) between the specimens from Koro Toro and *A. afarensis* (Fig. 1) constitute snapshots of a morphocline or reflect species differences is, however, unclear. Most palaeoanthropologists argue that species distinction is not warranted (e.g., Ward et al., 2001; Kimbel et al., 2006; Wood and Lonergan, 2008), thus explicitly or implicitly, favouring a dispersal scenario for *A. afarensis*. In contrast, and adding to this discussion, are considerations that it cannot be ruled out that *A. bahrelghazali* may not be related to East African hominins at all but may be derived from an as yet unidentified stem hominin west of the Rift Valley (Strait, 2013), a suggestion previously alluded to by Brunet et al. (2010a, 2010b). The limited fossil material available and the lack of hominin-bearing sites in Central and Western Africa makes it difficult, if not impossible, to resolve these issues. A combined palaeontological, palaeobiological, and paleoenvironmental perspective may however inform this debate. For such an approach to be meaningful, the dietary niche of *A. bahrelghazali* must be conceptualised as best as possible.

A. bahrelghazali, unlike other hominins, appears to have had intermediate-thin enamelled teeth, i.e., somewhere between those of modern chimpanzees and australopiths, as evident in the published line drawings of the holotype mandible KT-12-95-H1 also (Brunet, 2010a, 2010b; Fig. 1). It derived 55–80% of its tissues' $\delta^{13}\text{C}$ from C_4 sources (Lee-Thorp et al., 2012), similar to *Theropithecus oswaldi* (Cerling et al., 2013a) and *Paranthropus boisei* (Cerling et al., 2011b). The C_4 sources eaten by *Theropithecus* and *Paranthropus* differ in material properties but both are abrasive, either due to phytoliths (grasses) or starches (Underground Storage Organs) or both. Lacking the hypsodont teeth of *T. oswaldi*, *A. bahrelghazali* could not have subsisted on large quantities of tough, abrasive grasses. Lacking the hyper-thick enamel of *P. boisei* (as well as their large teeth and—presumably—cranial robusticity), *A. bahrelghazali* could not have subsisted on the nutrient-rich below-ground sources that are rich in starches (Macho, 2014a);

Underground Storage Organs (USOs) can be either tough or hard/brittle (Dominy et al., 2008). It also needs to be borne in mind that a dietary change towards stenotopy tends to be unusual among mammals (Price et al., 2012), even more so if *A. bahrelghazali* is derived from *A. afarensis*, either as a regional variant or through cladogenesis. *A. afarensis* was a eurytopic species that occupied different habitats (Reed, 2008; Kimbel and Delezene, 2009; Behrensmeier and Reed, 2013) and successfully negotiated fluctuating environmental conditions during its lifetime (Bonnefille et al., 2004). It too incorporated C_4 foods into its diet (Wynn et al., 2013), although—on average—considerably less so than *A. bahrelghazali* (Lee-Thorp et al., 2012). While sample sizes are small and may have biased the outcomes of these isotope studies, the differences between the two species seem real: *A. bahrelghazali* falls outside one standard deviation of *A. afarensis* (Fig. 2) and, when the two taxa are considered together, the total range of variation exceeds that seen in any other hominin, with $\delta^{13}\text{C}$ values ranging from -0.8‰ to -13.0‰ (stippled box in Fig. 2) and spanning almost across the entire hominin range. Perhaps most importantly, *A. afarensis* showed great fidelity in the selection of foods, at least with regard to its material properties and as judged by microwear analyses (Grine et al., 2006); microwear data are not

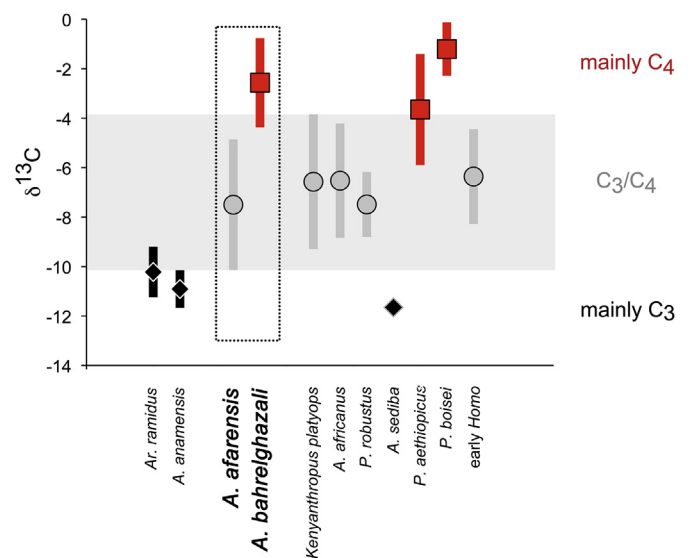


Figure 2. Mean values and standard deviations of isotope values of hominin teeth, calculated from Sponheimer et al. (2013). The upper and lower bounds of the stippled box indicate the maximum and minimum values of the combined sample of *A. bahrelghazali* and *A. afarensis*, i.e., when they are regarded as one species.

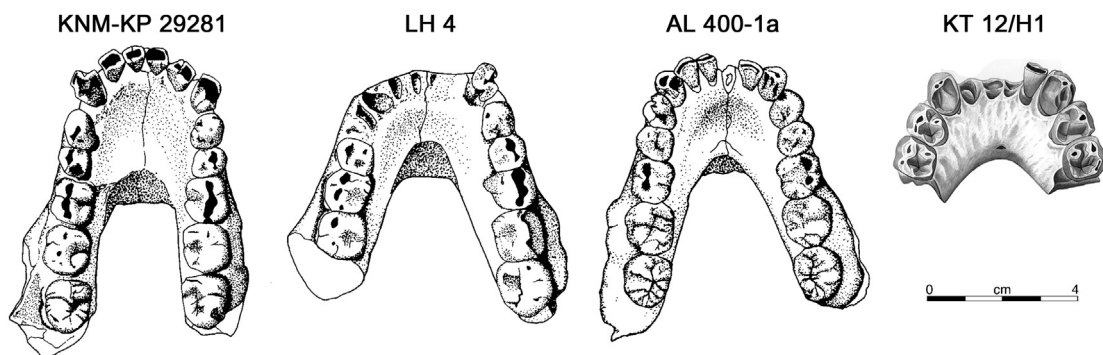


Figure 1. Drawings of *A. anamensis* from Kanapoi (KNM-KP 29281), *A. afarensis* from Laetoli (LH4), *A. afarensis* from Hadar (AL 400-1a), and *A. bahrelghazali* (KT 12/H1), reproduced from Ward et al. (2001) and Brunet (2010b) with permission.

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