Journal of Human Evolution 106 (2017) 102–118

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Fruits of the forest: Human stable isotope ecology and rainforest adaptations in Late Pleistocene and Holocene (~36 to 3 ka) Sri Lanka

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ARTICLE INFO

Article history:
Received 7 September 2016
Accepted 26 January 2017
Available online 21 March 2017

Keywords:
South Asia
Rainforests
Stable isotope analysis
Homo sapiens
Microlithic

ABSTRACT

Sri Lanka has yielded some of the earliest dated fossil evidence for *Homo sapiens* (~38-35,000 cal. years BP [calibrated years before present]) in South Asia, within a region that is today covered by tropical rainforest. Archaeozoological and archaeobotanical evidence indicates that these hunter-gatherers exploited tropical forest resources, yet the contribution of these resources to their overall subsistence strategies has, as in other Late Pleistocene rainforest settings, remained relatively unexplored. We build on previous work in this tropical region by applying both bulk and sequential stable carbon and oxygen isotope analysis to human and faunal tooth enamel from the sites of Batadomba-lena, Fa Hien-lena, and Balangoda Kuragala. Tooth enamel preservation was assessed by means of Fourier Transform Infrared Spectroscopy. We use these data to produce a detailed stable isotope ecology for Late Pleistocene–Holocene foragers in Sri Lanka from ~36-29,000 to 3000 cal. years BP, allowing us to test the degree of human tropical forest resource reliance over a considerable time period. Given that non-human primates dominate the mammalian assemblages at these sites, we also focus on the stable isotope composition of three monkey species in order to study their ecological preferences and, indirectly, human hunting strategies. The results confirm a strong human reliance on tropical forest resources from ~36-29,000 cal. years BP until the Iron Age ~3 cal. years BP, while sequential tooth data show that forest resources were exploited year-round. This strategy was maintained through periods of evident environmental change at the Last Glacial Maximum and upon the arrival of agriculture. Long-term tropical forest reliance was supported by the specialised capture of non-human primates, although the isotopic data revealed no evidence for niche distinction between the hunted species. We conclude that humans rapidly developed a specialisation in the exploitation of South Asia's tropical forests following their arrival in this region.

1. Introduction

Tropical rainforests have often been ignored in discussions of the evolution and adaptations of our genus, *Homo* (Roberts et al., 2016), while open savannah environments, or mixed forest-open mosaics, have been a focus for the emergence and migration of hominins within and beyond Africa (Gamble, 1993; Finlayson, 2014; Bird et al., 2005; Dennell and Roebroeks, 2005; Basell, 2008; Blome et al., 2012; Boivin et al., 2013; Domínguez-Rodrigo, 2014). Potential obstacles for human foragers in tropical forests are argued to include limited starch and protein-rich resources, navigational difficulties, seasonal resource fluctuations, and widely-spaced resources (Hutterer, 1983; Bailey et al., 1989; Bailey and Headland, 1991). In the last two decades, however, archaeological evidence has suggested that *Homo sapiens* utilised tropical rainforests from at least 45,000 years ago in Southeast Asia and Melanesia (Barker et al., 2007; Summerhayes et al., 2010, 2016;

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http://dx.doi.org/10.1016/j.jhevol.2017.01.015

Barker, 2013), and possibly even 200,000 years ago in Africa (Mercader, 2002a,b).

Despite early evidence for rainforest use, poor organic preservation (Tappen, 1994) makes it difficult to test the extent of human reliance on these biomes. Indirect linkage of archaeological remains to 'off-site' pollen, microcharcoal, and geochemical studies from lake and marine settings is one common approach (Mercader, 2002a,b), yet the correlation of these records with human activity is problematic (Roberts and Petraglia, 2015). Where archaeological material is preserved within rare cave and rockshelter sequences, more direct insights into human rainforest resource use can be obtained from archaeobotanical and archaeozoological remains (Barker et al., 2007; Summerhayes et al., 2010), as well as typological and use-wear analysis of stone and bone tool technologies (Barker, 2013; O'Connor et al., 2014). Yet, these remains are frequently absent beyond the Holocene. Furthermore, it remains almost impossible to estimate overall dietary importance of tropical forest resources on the basis of archaeobotanical and archaeozoological snapshots alone.

Stable carbon and oxygen isotope analysis can, on the basis of a distinction between the C_3 and C_4 photosynthetic pathways at the base of tropical food webs, as well as the 'canopy effect', provide direct insight into long-term human forest reliance in tropical environments. This methodology has been widely applied to hominin fossil tooth enamel in Africa to determine when early hominins moved from C_3 forest resources to open C_4 savannah reliance (White et al., 2009; Lee-Thorp et al., 2010; Sponheimer et al., 2013; Levin et al., 2015). It has also been used to elucidate the forest adaptations of the early extinct apes *Gigantopithecus* and *Sivapithecus* (Nelson, 2003, 2007; Bocherens et al., 2015), as well as to discern forest niche distinctions in extant faunal communities (Cerling et al., 2004), including primates (Sandberg et al., 2012; Krigbaum et al., 2013).

The systematic application of this methodology to questions relating to rainforest adaptations in our own species, however, remains limited to just a few case studies (Krigbaum, 2003, 2005; Roberts et al., 2015a). Krigbaum (2001, 2003, 2005) first applied stable carbon and oxygen isotope analysis to questions of human diet following the onset of the Neolithic in a rainforest context in Southeast Asia. Sri Lanka has one of the richest human fossil records, spanning from ~38,000 to 3000 years ago, in a modern rainforest setting worldwide (Deraniyagala, 1992; Perera et al., 2011). Recently, stable isotope analysis of human tooth enamel from this region provided the earliest direct evidence for human rainforest reliance anywhere in the world from 20,000 to 3000 years ago (Roberts et al., 2015a). However, stable isotope methodologies are yet to be extended back to the earliest encounters of *H. sapiens* with tropical forests in Sri Lanka, as well as more globally, and there has been little attempt to explore, in detail, the stable isotope ecology of humans and their associated fauna in these settings.

1.1. The Sri Lankan Microlithic tradition and primate specialisation

Sri Lanka is divided into three broad climate-driven precipitation and vegetation zones. The 'Wet Zone' receives between 2200 and 4800 mm of annual rainfall and is home to wet deciduous and tropical evergreen rainforest (Ashton and Gunatilleke, 1987; Gunatilleke et al., 2005; Roberts et al., 2015b), while the 'Intermediate Zone' receives 1700–2200 mm and supports moist tropical deciduous and semi-evergreen intermediate rainforest (Erdelen, 1988; Roberts et al., 2015b). The remaining 'Dry Zone' (still very wet by most standards) receives rainfall of ~1000–1700 mm and is characterised by open forest and large expanses of shrubs and grassland (Erdelen, 1988; Somaratne and Dhanapala, 1996) (Fig. 1). Although the majority of the rain in the Wet Zone comes between May and October, as a result of the southwest monsoon, there is no real dry season. By contrast, the northern Dry Zone of the island faces regular periods of drought between May and September (Mueller-Dombois, 1968; Dittus, 1977). The position of these boundaries in the past is relatively poorly understood, however, with well-dated palynological information coming from only the Horton Plains in the highlands of Sri Lanka (Premathilake and Risberg, 2003; Premathilake, 2012).

The 'Microlithic' characterizes a tradition of small, less than 2 cm long, stone tools found at sites in Sri Lanka from 38,000 to 35,000 cal. years BP (calibrated years before present) until the onset of the Iron Age ~3000 cal. years BP (Deraniyagala, 1992; Lewis et al., 2014; Roberts et al., 2015b). Thus far no direct use-wear studies have been carried out on the microliths, although they have been associated with projectile weaponry (Perera et al., 2011; Roberts et al., 2015b). In contrast to many tropical regions of the world, the archaeological sequences in which these tools are found are rich in organic material (Kennedy and Deraniyagala, 1989; Deraniyagala, 1992; Wijeyapala, 1997; Kennedy, 2000; Perera et al., 2011, 2017), potentially linked to the formation of gneiss rockshelter and cave sites out of the Precambrian Highland Complex of the island (Cooray, 1984). This facilitates the detailed construction of human subsistence choices at these tropical sites.

The evidence uncovered to date indicates the use of tropical forest tree resources, such as *Canarium* sp. nuts, freshwater molluscs from fast-flowing rivers, and the exploitation of small-medium arboreal and semi-arboreal mammals (Perera, 2010; Perera et al., 2011). In particular, primate taxa consistently make up to 70–80% of the mammalian kill assemblage at the Microlithic sites of Fa Hien-lena and Batadomba-lena (Perera, 2010; Perera et al., 2011). This proportion is unprecedented, even with rifles in many parts of the African and Amazonian rainforests today (ProWildlife, 2007; Lu, 2010; Papworth et al., 2013), with perhaps one exception amongst the Raute of Nepal (Fortier, 2014). Ethnographies of hunter-gatherers highlight primates as a potentially valuable source of protein in tropical environments, extracted using a variety of techniques, including projectile hunting, trapping, or nets (Harako, 1982; Noss, 1997, 1998; Fortier, 2014). Clearly then, forest resources were an important component of hunter-gatherer subsistence at these sites. However, from technological, archaeobotanical and archaeozoological evidence alone it is not yet clear whether Late Pleistocene and Holocene human populations were reliant on these rainforest resources, or whether they were just one, seasonal, strategy.

1.2. Batadomba-lena rockshelter

One of the most important sites to produce early human fossils associated with rainforest foraging in Sri Lanka is Batadomba-lena. This gneiss rockshelter (80°12′E, 6°46′N) is 10 × 15 m in area and lies near the banks of a stream in the Wet Zone rainforest of Sri Pada, Ratnapura District (Fig. 1). It is currently surrounded by dense, lowland evergreen forest (Perera, 1975). Excavations in the 1980s indicated the presence of geometric microliths from the earliest horizon upwards, while bone tools, animal bones, archaeobotanical remains and human fossils were found throughout the sequence (Deraniyagala, 1992). Initial radiocarbon dates from wood charcoal indicated a period of occupation from ~28,000 to ~12,000 cal. years BP (Deraniyagala, 1992) but these dates were subsequently recalibrated alongside additional AMS (Accelerator Mass Spectrometry) radiocarbon dates on wood charcoal to produce a stratigraphic sequence of Layers 7c to 1, dated from 36,000 cal. years BP to 12,000 cal. years BP (Perera, 2010; Perera et al., 2017). Perera et al. (2011) used a combination of one bulk