



# From the Forests to the Coast – Multidisciplinary Investigation of Human Adaptations at the Mini-athiliya Shell Midden, Sri Lanka

**Patrick Roberts<sup>1,2,3\*</sup>, Jay Stock<sup>4\*</sup>, Samanti Kulatilake<sup>5</sup>, Nicole Boivin<sup>2,3,6,7</sup>, Michael D. Petraglia<sup>8,3,6</sup>, Siran Deraniyagala<sup>9</sup>, Nimal Perera<sup>10,11\*</sup>**

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<sup>1</sup> isoTROPIC Research Group, Max Planck Institute for Geoanthropology, Kahlaische Str. 10, 07745 Jena, Germany.

<sup>2</sup> Department of Archaeology, Max Planck Institute for Geoanthropology, Kahlaische Str. 10, 07745 Jena, Germany.

<sup>3</sup> School of Social Sciences, University of Queensland, St. Lucia, Brisbane, QLD 4072, Australia.

<sup>4</sup> Department of Anthropology, Western University, London, Ontario, N6A 3K7, Canada.

<sup>5</sup> Department of Sociology and Anthropology, Mount Royal University, Alberta, Canada

<sup>6</sup> Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA

<sup>7</sup> Department of Anthropology and Archaeology, University of Calgary, Alberta, Canada

<sup>8</sup> Australian Research Centre for Human Evolution (ARCHE), Griffith University, Brisbane, Australia

<sup>9</sup> Department of Archaeology, Sir Marcus Fernando Mawatha, Colombo 00700, Sri Lanka.

<sup>10</sup> Postgraduate Institute of Archaeology, 407 Bauddhaloka Mawatha, Colombo 00700, Sri Lanka.

<sup>11</sup> Department of Archaeology, School of Philosophical and Historical Inquiry (SOPHI), The University of Sydney, A14 – Quadrangle, NSW 2006 Australia

\*Corresponding authors' email addresses:

[roberts@shh.mpg.de](mailto:roberts@shh.mpg.de)

[jay.stock@uwo.ca](mailto:jay.stock@uwo.ca)

[nimalach@hotmail.com](mailto:nimalach@hotmail.com)

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## Abstract

Over the last three decades, Sri Lanka has risen to international prominence as a key area for exploring past forager adaptations. Much of this discussion has focused on the lowland rainforests of the Wet Zone of the island, and their preservation of the earliest fossils of our species, bone tools, and microlithic technologies in the region ca. 45,000 years ago. It has been recognized that the northern and southern coasts of Sri Lanka represent crucial locales for studying human occupation and adaptation through the Pleistocene and Holocene. Here, we revisit the important shell midden site of Mini-athiliya (dating to ca. 4,000 cal. years BP), on the southern coast of Sri Lanka, which has yielded human remains alongside microlithic stone tools and animal remains. We present a comparative analysis of body size variation of the human remains belonging to the HMA 6 adult skeleton from Mini-athiliya with a wider database of foragers to investigate local adaptations. We also apply stable carbon and oxygen isotope analysis to the tooth enamel of four other individuals documented at Mini-athiliya in order to determine their dietary reliance on forest, grassland, or coastal resources. Together, our results highlight that, rather than a clear distinction between earlier forest adaptations and later coastal specialisation, the Mini-athiliya individuals provide evidence for a plastic spectrum of ecological adaptation. We argue for continued research on how human populations in different parts of the island interacted and adapted to its diverse tropical settings across space and time.

## Introduction

The work of S. U. Deraniyagala, and that of his father P. E. P. Deraniyagala, laid the groundwork for the catapulting of Sri Lanka to international significance in discussions of human ecological adaptations during the Pleistocene and the Holocene (P.E.P. Deraniyagala, 1956; S.U. Deraniyagala, 1992). Much of this attention has focused on the early human habitation of the wet evergreen lowland tropical rainforests of the island from 48,000-45,000 years ago, through to at least 3,000 years ago (Langley et al., 2020; Perera, 2010; Perera et al., 2011; Roberts et al., 2015a, 2017; Wedage et al., 2019, 2020;). Here, the study of microliths, bone tools, faunal records, and palaeodietary archives in human fossils have revealed that the earliest confidently dated members of our species thus far recorded in Sri Lanka developed well-tuned, specialised adaptations to these forest environments, practising dedicated hunting of arboreal and semi-arboreal prey and the use of starchy plant foods (Perera et al., 2011; Wedage et al., 2019). This work has helped to overturn global stereotypes that have often seen 'extreme' environments such as tropical rainforests as 'barriers' to human occupation and dispersal (cf. Bailey et al., 1989; Gamble, 1993), while also demonstrating that classic 'human' behaviours, such as bow and arrow technology, did not just develop in open grassland 'savannah' settings or in coastal areas (Langley et al., 2020; Roberts and Stewart, 2018). Yet, S. U. Deraniyagala's pioneering work (1992) involved the survey of the whole spectrum of environments that Sri Lanka has to offer, necessitating detailed, context-specific approaches to human occupation across the island.

Since the 1980s, it has been recognized that the northern and southern coasts of Sri Lanka, in particular, represent crucial locales for exploring human occupation and adaptation through the Pleistocene and Holocene. Proximity to rich medium to large game in the grasslands of the Dry Zone (Deraniyagala, 1992) and diverse mangrove and coastal ecosystems (Primavera et al. 2004; Satyanarayana et al. 2013), likely provided a rich variety of food sources as they continue to do today. Surveys by S. U. Deraniyagala identified geometric microliths at two sites within the Iranamadu Formation (1992). These sites, so-called Sites 49 and 60, were dated to around 28,000 years ago based on thermoluminescence dating, although further confirmation of these results is required. It is from the Middle-Late Holocene that occupation of the coastal areas intensified, with archaeological investigation and dates from sites such as Matota (Mantai), Patirajawela Site 50, Henagahapugala Site 57, Arnakallu Site 30, Udamalala, Karagan Lewaya, and Pallemalla revealing an expanding 'Mesolithic' occupation of these parts of the island ca. 6,700 and 2,900 years BP (Deraniyagala 1992, p. 692; Katupotha 1995; Kulatilake 2009; Somadeva and Ranasinghe 2006;), just following the stabilisation of Holocene sea levels (Katupotha 1995; Kulatilake 2009; Somadeva and Ranasinghe 2006;). Nevertheless, a lack of systematic zooarchaeological or archaeobotanical analysis, limited human remains, and debates relating to the anthropogenic origin of shell deposits have made determining the ecological reliance of human societies at these sites somewhat challenging.

Mini-athiliya, near Hungama, is a shell midden site in the Southern Province of Sri Lanka that has not only yielded prehistoric human remains (Kulatilake et al., 2018), but also microlithic stone tools and anthropogenically utilised animal remains, dating to around 4,000 cal. years BP (Kulatilake et al., 2014). Large quantities of molluscs from a variety of habitats, as well as the remains of crustaceans, fish, reptiles, birds and mammals have been discovered in association with human skeletal elements (Kulatilake et al., 2018), including one individual that has been interpreted as a deliberate burial (Kulatilake et al., 2014). The site thus offers a major opportunity to determine the ecological adaptations of populations living in Sri Lankan coastal regions during the Middle Holocene, potentially at a challenging time of climatic aridity (Premathilake, 2006). Recently, stable isotope analysis of human tooth enamel has proven to have major potential for determining dietary reliance in the tropics. Stable carbon isotope analysis ( $\delta^{13}\text{C}$ ), in particular, has shown itself to be particularly useful in distinguishing between human individuals dependent on dense canopy or more open rainforests and those reliant on coastal or tropical grassland settings. This methodology has been successfully used in the tropical forest environments of Sri Lanka, as well as in Wallacea in Southeast Asia, to explore the changing adaptations of our species across space and time (Roberts et al., 2015a, 2017, 2020).

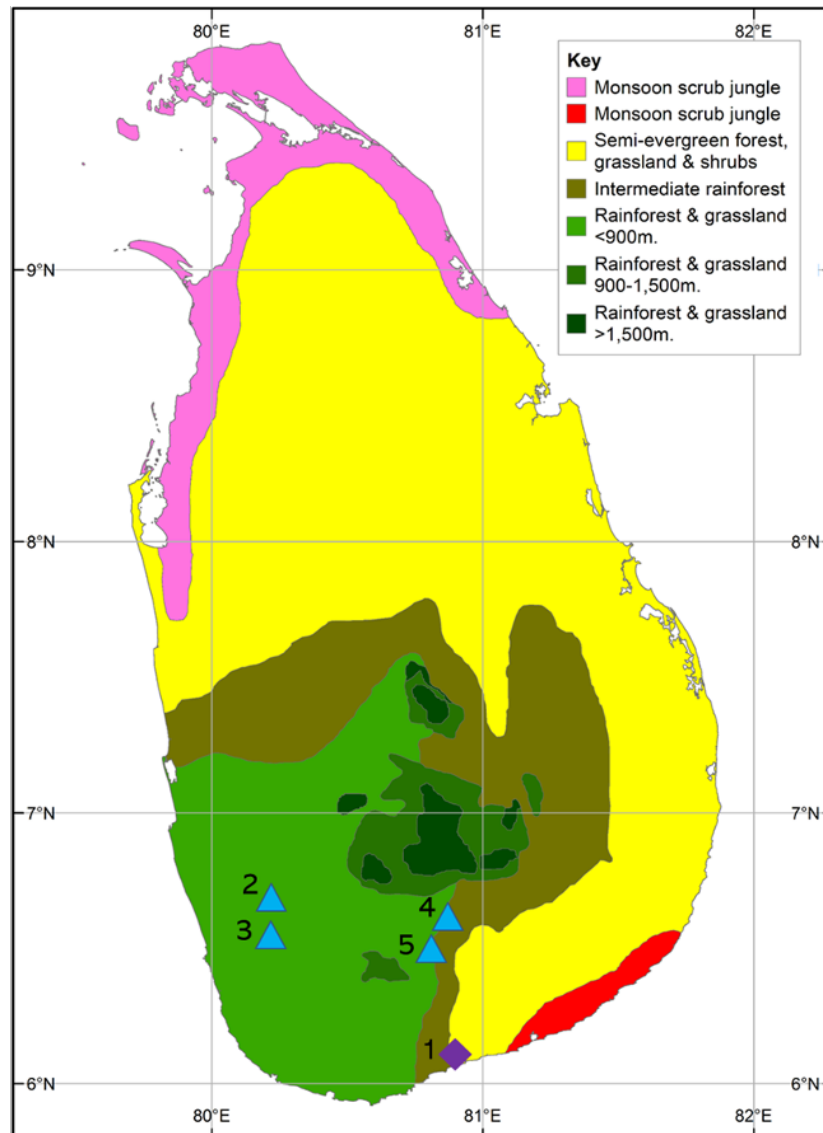
In this study we seek to reinforce the emphasis on shell middens along Sri Lanka's coasts as sites of major significance for the island's prehistory (Deraniyagala, 1992). We present a comparative analysis of stable body size variation of the human remains belonging to the HMA 6 adult skeleton from Mini-athiliya with a wider database of foragers to investigate local adaptations and to stimulate further work by Sri Lankan scholars in this regard. We also apply stable carbon and oxygen isotope analysis to the tooth enamel of four other individuals documented at Mini-athiliya (Kulatilake et al., 2018) in order to determine their dietary reliance on forest, grassland, or coastal resources during their younger years. We also sought to undertake

experimental collagen extraction from two of the same skeletons to determine the potential for future direct dating of human remains in these contexts as well as more detailed isotopic reconstruction of past diets. This represents the first time that this multidisciplinary approach to human remains has been applied beyond the Wet Zone rainforests of Sri Lanka and should stimulate future research that follows S. U. Deraniyagala's calls (1992) to assess and investigate all of the varied environments that this 'Resplendent Isle' had to offer past human societies, from the Pleistocene to the Holocene.

## **Background**

### *Coastal ecologies of Sri Lanka*

The different climatic zones of Sri Lanka determine the spatial patterning of animal and plant resources available to humans (Deraniyagala, 1992). As a consequence of the Indian Ocean Monsoon, and the topographic influence of the Central Highlands, Sri Lanka is divided into three climatic zones (Puvaneswaran and Smithson 1993; Roberts et al., 2015b). The southwestern Coastal Plain and the Central Highlands receive the highest annual precipitation (4,840 – 2,201 mm) as the 'Wet Zone'. This Wet Zone hosts closed-canopy wet deciduous and tropical evergreen mixed dipterocarp rainforests (Ashton and Gunatilleke 1987; Gunatilleke et al. 2005). The 'Dry Zone' (1,700 – 1,001 mm) comprises the majority of the rest of the island, covering the northern and southeastern coastlines as well as most of the northern interior. Reliant on the northeastern winter monsoon, this portion of Sri Lanka is prone to major variability in rainfall and can face major drought conditions. Vegetation communities are dominated by arid-adapted shrubs and grasslands as well as 'arid zone' forest, with some mangrove forests appearing along the more mesic coasts (Erdelen, 1988; Somaratne and Dhanapala 1996). An 'Intermediate Zone' forms a strip between the Wet and Dry Zone and receives a mean annual rainfall of 2,201-1,701 mm. Species composition of the forests of this zone are similar to the Wet Zone, though with a great domination of drier deciduous forests and tree species (Erdelen, 1988) (Figure 1).



**Figure 1.** Vegetation zones of Sri Lanka and location of key sites mentioned in the text: 1) Mini-athiliya; 2) Fa Hien-lena; 3) Batadomba lena; 4) Balangoda Kuragala; 5) Bellan-bandi Palassa (Following Erdelen, 1998 and Roberts et al. 2015a, b).

Although prone to climatic variation, S. U. Deraniyagala emphasised the large concentrations of medium-sized ungulate fauna available across the Dry Zone (Phillips, 1980), with spotted deer and hare being the most abundant (Eisenberg and Lockhart, 1972). Other faunal resources include cervids (sambhur, mouse-deer, barking deer), bovids (buffalo), the giant squirrel, monkeys (gray langur, toque macaque), elephant, and wild boar (Bambaradeniya, 2006; Dittus, 1977; Eisenberg and Lockhart, 1972). Also present are diverse reptiles (e.g., hard and soft-shelled terrapins, star tortoise, python, ratsnake, land monitor, crocodile), fish (e.g., snakehead, catfish, eels), and bird communities (Eisenberg and Lockhart 1972; Nyrop et al. 1971). Significantly, humans living along the coasts of the Dry Zone would also have had access to the biodiverse fish and invertebrate species in mangrove

ecologies (Primavera et al. 2004), as well as a marine fauna proper that includes diverse mollusc species (Kelaart, 1852; Tennant, 1861), fish of various sizes and ecologies, over 50 species of sea bird (Kotagama and De Silva, 2006), over 60 shark species and over 30 ray species (De Silva, 2006). Marine mammals, including dolphins and the dugong, would also have been available for humans (Ilangakoon, 2006). Thus, the coastal environments of the Dry Zone represent a potential patchwork of resources that could have been variably relied upon by past human societies.

### *The site of Mini-athiliya*

Mini-athiliya (6° 07' 12" N, and 80° 56' 47" E) is situated near the town of Hungama on the southern coast in the Hambantota District of Sri Lanka's Dry Zone (Figure 1), today surrounded by paddy fields for rice cultivation. Although the site is currently located four kilometres from the present-day coastline, reconstruction of past sea-level changes suggest that it may have been closer to the shore during the Middle Holocene (Kulatilake et al., 2014). The site was discovered by local shell miners, exploiting shell beds for lime-based fertiliser, building material, and chicken-feed. The Department of Archaeology of the Government of Sri Lanka then began a rescue operation in 2007 that uncovered the fragmented remains of five human individuals associated with commingled faunal remains (Kulatilake et al., 2018), the original context of which had been disturbed by shell mining activities. In addition, an undisturbed, complete human burial (HMA 6) was excavated as a single block. This burial (Context 8) was found in association with stone tools, burnt molluscs, and faunal remains (Kulatilake et al., 2014), with charred material providing dates of ca. 4,000 cal. years BP (see Kulatilake et al., 2014 for summary).

Preliminary faunal analyses have demonstrated that prehistoric human societies at the site exploited molluscs from a variety of terrestrial, estuarine and marine habitats, including genera such as *Acavus*, *Pila*, *Turbinella*, and *Cerithedea* (Kulatilake et al., 2014). Although future detailed zooarchaeological work is still to be undertaken, the remains of crabs, fish, reptiles, birds and mammals were also found throughout the site. The stone tool assemblage was composed of flakes, cores, geometric microliths, hammerstones, and grinding stones, characteristic of 'Mesolithic' (microlithic) cultures identified elsewhere along the Sri Lankan coast (Kulatilake et al., 2014, pp. 3). Overall, Kulatilake et al. (2014) interpreted the archaeological evidence at the site as being indicative of a human population relying upon 'a suite of varied subsistence strategies for their survival', perhaps facilitating survival through a period of Middle Holocene arid conditions recognised for the 'Dry Zone', although the varying reliance on marine versus terrestrial resources remains uncertain.

### *The samples from Mini-athiliya*

A complete human skeleton of an adult male, designated HMA 6, was excavated from the shell midden site of Mini-athiliya in 2007. This discovery was preceded by the recovery of fragmentary remains of five individuals, designated HMA 1 through 5, from shell miner's pits (Kulatilake, 2009, Kulatilake et al., 2018). The complete HMA 6 burial was cast in plaster, crated, and removed in block, and was carefully excavated to expose the burial (Kulatilake et al., 2014), which is on display in matrix in the Matara Star Fort Museum. Beyond morphometric analyses (Kulatilake et al., 2014, Kulatilake et al., 2018), to date, none of the skeletal remains from Mini-athiliya have been studied in detail using scanning technologies and biomolecular approaches. There is considerable potential for 3D surface scanning to document the precise burial position and strategic removal and replacement of individual skeletal elements to allow for more detailed analyses of remains while preserving the integrity of the museum display. Before this careful work is conducted, it is possible to place existing skeletal data within the context of other Holocene forager skeletal remains to better understand the specific adaptations of coastal foragers within Sri Lanka.

## **Methods**

### *Stable body variation analysis*

At present, the only skeletal measurements available for the HMA 6 skeleton are from the left femur, which is sufficiently exposed from the matrix to allow for accurate measurement of the femoral head and femur maximum length. These measurements are important indicators of general differences in body size. Femoral head diameter is strongly correlated with adult body mass at the time of puberty, as the proximal epiphysis of the femur grows in proportion to weight bearing during skeletal development (Ruff et al., 1997; Young et al., 2018). Maximum femur length is also strongly correlated with stature and can be used to investigate ecological and temporal variation in human height (Stock et al., 2011). Measurements for the dimensions of the left femur of HMA 6 were: maximum length - 445 mm, maximum head diameter - 42 mm (Kulatilake et al., 2014). The application of a standard stature estimation equation (Byers, 2002) led to an estimated stature of 167.32 cm +/- 3.27 (Kulatilake et al., 2014). Regression equations for the estimation of body mass and stature are a useful heuristic device to compare general aspects of phenotypic variation through time and space, but they also introduce bias based on the composition of the samples used to develop the regression equations. In this context, it is desirable to use different regression equations that have been derived from local populations with similar body proportions.

When comparing body size from populations globally, such locally relevant equations do not exist for each population, and it becomes necessary to use more generic regression equations derived from the analysis of a range of human populations. Here, we have applied the standard stature estimation equation of Feldesman & Fountain (1996), which provides a stature estimate of 165.63 cm, which corresponds very closely to the previous stature estimate of 167.32 cm +/- 3.27 of Kulatilake et al. (2009). Application of one sex-specific and two generic body mass

estimation equations for femoral head diameter (Ruff et al., 1997) lead to an average estimated mass of 55.7 kg. We compare the ratio of estimated stature and body mass of Mini-athiliya HMA 6 to a globally representative dataset of 453 late Pleistocene to late Holocene hunter-gatherer skeletons representing 21 populations. To investigate ecological influences on the relationship between body mass and stature, we have grouped the populations into broad categories representing a combination of climate and subsistence strategy. These include cold climate coastal-marine foragers, cold-temperate riverine foragers, temperate coastal foragers, rainforest foragers, arid environment terrestrial foragers, and arid riverine populations (Table 1). To provide a more specific comparison of skeletal dimensions relating to phenotype, but that are unbiased by regression equations, we also directly compared femoral head diameters and maximum femur length between populations.

<b>Ecological Context</b>	<b>Population</b>	<b>Sample Size n (m, f, indet)</b>
Cold coastal marine	Sadlermiut	27 (13,9,5)
	Yaghan, Tierra del Fuego	25 (13,9,3)
Cold-temperate riverine	Archaic Great Lakes	14 (5,5,4)
	Kitoi, Siberia	55 (30,19,6)
	Serovo-Glazkovo, Siberia	33 (16,16,1)
Temperate coastal	Later Stone Age, South Africa	53 (25,28,0)
	Jomon, Japan	36 (17,12,7)
	Mesolithic, France	8 (5,3,0)
Rainforest	Andaman Islanders	31 (16,15,0)
	Aeta, Philippines	15 (10,5,0)
	Efe, DRC	4 (2,2,0)
Arid terrestrial	Natufian, Levant	20 (8,6,6)
	Early-Mid Epipalaeolithic, Levant	6 (4,2,0)
	Later Stone Age, Kenya	10 (4,4,2)
	Later Stone Age, Tanzania	9 (8,1,0)
	Iberomarusian, Morocco, Algeria	38 (16,8,14)
	Masai pastoralists, Tanzania	9 (8,1,0)
Arid riverine	Jebel Sahaba, Sudan	7 (6,0,1)
	Aboriginal Australian	19 (3,3,13)
	Aboriginal Tasmanian	1 (1,0,0)
	Badarian Neolithic, Egypt	10 (3,3,4)

**Table 1.** Comparative data for other global foragers (Stock, 2013).



### Stable isotope analysis

$\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  isotope analysis of animal (including human) tooth enamel has been increasingly applied in tropical settings to explore past diets and palaeoecologies (Lee-Thorp et al., 1989, 1994; Levin et al., 2006, 2008; Roberts et al., 2015a, 2017, 2020; Sponheimer et al., 2013). In terrestrial tropical ecosystems, variation in  $\delta^{13}\text{C}$  is driven by the photosynthetic pathways of  $\text{C}_3$  (including trees and shrubs that dominate tropical forest, woodland, or shrubland ecosystems) and  $\text{C}_4$  vegetation (including grasses that often dominate open tropical grasslands) (Codron et al., 2014; Smith and Epstein, 1971; Sponheimer et al., 2009). Within  $\text{C}_3$  ecosystems themselves, the 'canopy effect' can lead to further variation in plant  $\delta^{13}\text{C}$ , with those plants growing under a dark shaded canopy having lower values (van der Merwe and Medina, 1991). These distinctions are passed up into the tissues of the consumers of these plants meaning that an animal's ecological behaviour and reliance on different habitats can be discerned through the isotopic measurement of its bones and teeth (Cerling et al., 2004; Lee-Thorp et al., 1989, 1994; Lee-Thorp, 2008). Marine producer biomass has higher  $\delta^{13}\text{C}$  than all  $\text{C}_3$  terrestrial plants, thanks to a different source of  $\text{CO}_2$  in these ecosystems, more closely mimicking  $\text{C}_4$  consumers (Kusaka et al., 2015; Roberts et al., 2020).

Although diet-tissue spacing has been shown to be variable between species (Schoeninger, 2014), and there is currently a lack of experimental models for humans, we expect pre-industrial humans relying completely on tropical forest, open  $\text{C}_3$  resources, and marine resources to have tooth enamel  $\delta^{13}\text{C}$  values of ca. -14‰, ca. -11‰, and ca. -4‰, respectively (Lee-Thorp et al., 1989; Levin et al., 2008; Roberts et al., 2017, 2020). Interpretations can be complicated by the fact that some studies of mangrove ecosystems have shown fish and plants growing in these coastal settings to have  $\text{C}_3$ -like  $\delta^{13}\text{C}$  (Krigbaum, 2001; Rodelli et al., 1984;). Furthermore,  $\delta^{13}\text{C}$  in freshwater ecosystems is unpredictable (Fry and Sherr, 1984; Fry, 2006). Nevertheless, established variation in  $\delta^{13}\text{C}$  should still enable this approach to tease apart human reliance on terrestrial  $\text{C}_3$  ecosystems as opposed to  $\text{C}_4$  grassland/marine habitats.  $\delta^{18}\text{O}$  data from human tooth enamel has been argued to provide further palaeoecological insights into water and food, and prevailing environmental conditions, and has even been argued to enable distinction between terrestrial and marine consumers (Clementz and Koch, 2001).

Bone collagen is typically poorly preserved in tropical contexts as a result of high temperatures and high hydrological activity. Consequently, although stable isotope analysis in temperate areas frequently focuses on bone collagen, tooth enamel is often preferred as a more reliable archive in the tropics (Krigbaum, 2003, 2005). The bioapatite of tooth enamel is considered to be particularly resistant to post-mortem diagenesis (Lee-Thorp et al., 1989; Lee-Thorp, 2008) and isotopic signatures of *in vivo* diet have been argued to be preserved in hominins as far back as 7-5 million years ago in the tropics (Lee-Thorp et al., 1989; Lee-Thorp, 2008; Levin et al., 2008; Nelson, 2007; White et al., 2009). Importantly, while  $\delta^{13}\text{C}$  of bone collagen is often heavily weighted towards protein components of the diet, and can thus be biased towards foodstuffs that are high in protein,  $\delta^{13}\text{C}$  of enamel bioapatite reflects the 'whole diet' signature, including lipids, carbohydrates, and protein (Lee-Thorp et al., 1989; Ambrose & Norr, 1993). The exact period of life recorded in the isotopic measurements of enamel bioapatite will vary depending on the tooth studied, with

late maturing teeth such as second and third molars providing insights into a period spanning approximately 8-16 years of age (Hillson, 1996).

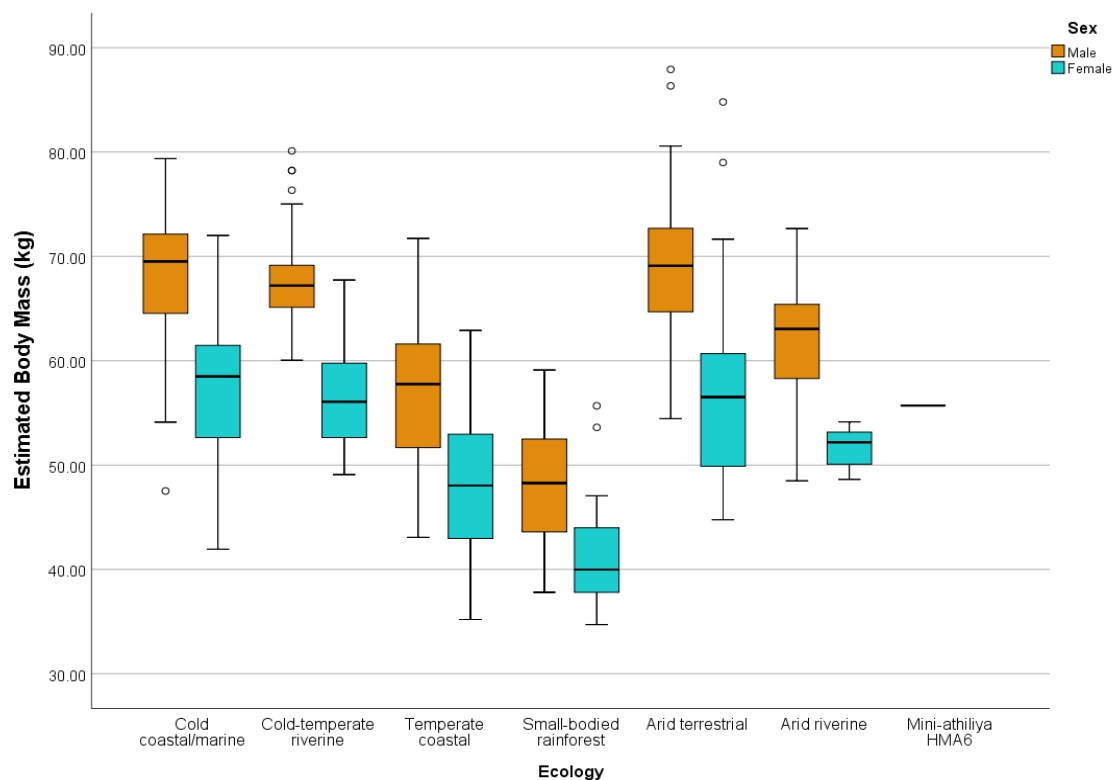
Stable carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotope analysis were performed on four of the five commingled human remains discovered at Mini-athiliya so as to avoid destructive sampling of the curated skeleton. Permissions for limited destructive sampling procedures were given by the Department of Archaeology, Sri Lanka (N. Perera, S.U. Deraniyagala). Although these individuals come from disturbed contexts, their isotopic results should still provide a broad overview of the dietary reliance of human populations living at the site during the Middle Holocene (Kulatilake et al., 2018). All available evidence suggests that all remains are derived from contexts that are similar temporally and culturally. The 2<sup>nd</sup> or 3<sup>rd</sup> molars were sampled in each case in order to avoid the influence of the 'weaning effect' on  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values (Wright and Schwarcz, 1998). The full details of the specimens sampled are provided in Table 2. All human remains are currently housed with the Department of Archaeology, Government of Sri Lanka, with the exception of the complete skeleton of HMA 6 that is curated at the Matara Star Fort Museum. Unfortunately, no fauna was available for isotopic analysis as a baseline at the time. Collagen extraction was also attempted for a skull fragment and tooth dentine, respectively, from two of the individuals (Table 3).

All sampled teeth or teeth fragments were first cleaned to remove any adhering external material. Enamel powder was obtained using gentle abrasion with a diamond-tipped drill along the full length of the buccal surface to produce a 'bulk' sample covering the entire period of enamel formation. Standard pretreatment protocols, applied to Pleistocene and Holocene tooth enamel elsewhere in Sri Lanka, were utilised to remove organic or secondary carbonate contaminants and to make sure that data was comparable to existing studies in the region (Roberts et al., 2015a, 2017). Samples were washed in 1.5% sodium hypochlorite for 60 minutes, followed by three rinses in purified  $\text{H}_2\text{O}$  and centrifuging, before 0.1M acetic acid was added for 10 minutes, followed by another three rinses in purified  $\text{H}_2\text{O}$ . Samples were then lyophilized for 24 hours. Bone collagen extraction following a modified Longin protocol (1971) was also attempted for two samples as mentioned above (Table 3), though no collagen was extracted in either case suggesting a lack of preservation.

Gases evolved from the samples following reaction with 100% phosphoric acid were measured by stable carbon and oxygen isotope analysis using a Thermo Gas Bench 2 connected to a Thermo Delta V Advantage Mass Spectrometer at the Department of Archaeology, Max Planck Institute for Geoanthropology (formerly the Max Planck Institute for the Science of Human History).  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values were compared against International Standards (IAEA-603 ( $\delta^{13}\text{C} = 2.5$ ;  $\delta^{18}\text{O} = -2.4$ ); IAEA-CO-8 ( $\delta^{13}\text{C} = -5.8$ ;  $\delta^{18}\text{O} = -22.7$ ); USGS44 ( $\delta^{13}\text{C} = -42.2$ )) and an in-house standard (MERCK ( $\delta^{13}\text{C} = -41.3$ ;  $\delta^{18}\text{O} = -14.4$ )) using Isodat 3.0 software from Thermo Electron Corporation. Replicate analysis of MERCK carbonate standards suggests that machine measurement error is ca.  $\pm 0.1\text{‰}$  for  $\delta^{13}\text{C}$  and  $\pm 0.2\text{‰}$  for  $\delta^{18}\text{O}$ . Overall reproducibility for tooth enamel samples was studied based on repeat extracts from an in-house bovid tooth enamel standard ( $n = 20$ ;  $\delta^{13}\text{C} = -12.4 \pm 0.2\text{‰}$ ;  $\delta^{18}\text{O} = -8.0 \pm 0.3\text{‰}$ ).

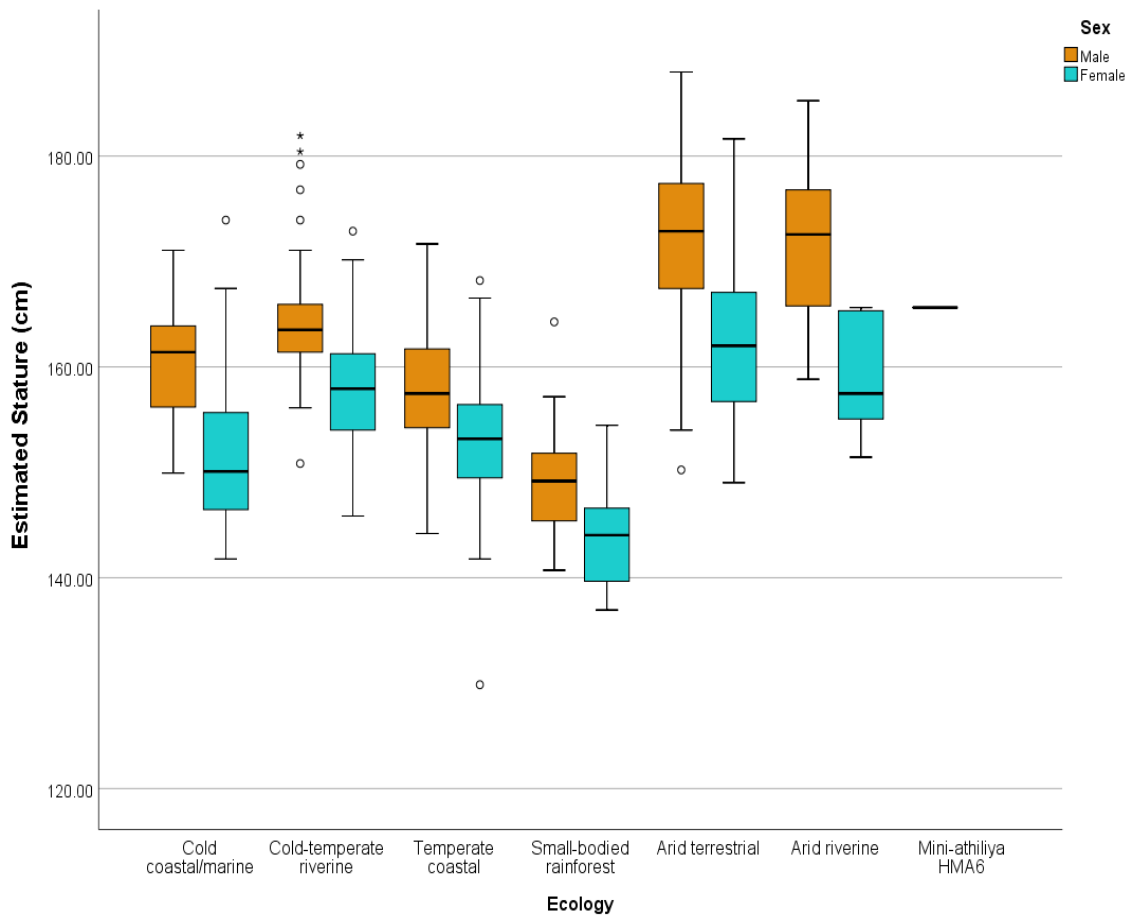
## Results

The size estimates of the Mini-athiliya HMA 6 skeleton place the estimated body mass (55.7 kg) very close to the average body mass for a hunter-gatherer globally (Figure 2). Within a more specific context, this mass would be very high for a male tropical rainforest forager, based on existing measurements of Andaman Islanders, the Aeta of the Philippines, and Efé communities of the Congo Basin (Stock, 2013), but falls slightly below male averages for more arid environment terrestrial or riverine/coastal foragers. In this context, body mass alone is not overly informative of the specific ecological adaptations of the HMA 6 individual.



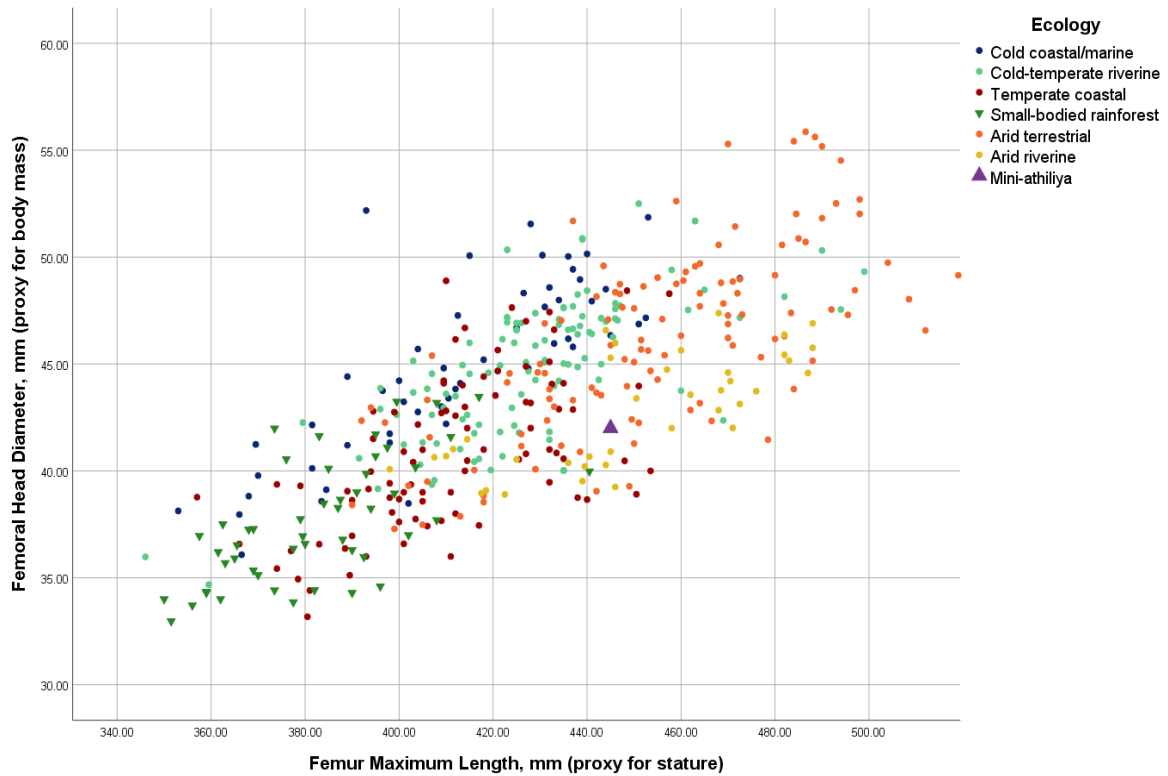
**Figure 2.** Estimated body mass of Hungama Mini-athiliya HMA 6 compared to variation in hunter-gatherer populations globally.

The estimated stature Mini-athiliya HMA 6 (165.6 cm) is high when compared to all foragers globally (Figure 3). It falls above the interquartile ranges of cold coastal, cold-temperate riverine, and temperate coastal foragers globally, and is above the entire range found among three populations of rainforest foragers. The stature of HMA 6 is near the middle of the range found among arid environment terrestrial foragers and arid riverine/coastal foragers globally but within the lower interquartile range for males.



**Figure 3.** Estimated stature of -Mini-athilya HMA 6 compared to variation in hunter-gatherer populations globally.

To compare the specific femoral skeletal measurements to these populations more broadly, femoral head diameter (a proxy for body mass) and maximum femur length (a proxy for stature) of the Mini-athilya HMA 6 skeleton are plotted against a globally representative sample of hunter-gatherer and coastal forager skeletons in Figure 4. The femoral head diameter of 42 mm is near the median of the global range of variation. Within a more specific context, this mass would be very high for a male tropical rainforest forager, but falls slightly below male means for more arid environment terrestrial or riverine/coastal foragers. In this context, as we saw in Figure 2, body mass alone is not that informative of the specific ecological adaptations of the HMA 6 individual. The combination of body mass and stature, however, places HMA 6 near the centre of the range of arid-riverine / coastal foragers globally. This suggests that HMA 6 possessed long term adaptations to the tropical coastal environment that were either the result of consistent presence and interaction with these habitats or plasticity achieved during the period of growth and development as a result of living within this coastal environment.



**Figure 4.** Femoral head diameter, which is a proxy for adult body mass, plotted against femur maximum length, a proxy for adult stature Mini-athiliya HMA 6 is represented by a purple triangle, and is compared to global variation among hunter-gatherers.

#### *Stable isotope analysis*

The  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values obtained for the four human individuals analysed can be found in Table 2 and Figure 5. The  $\delta^{13}\text{C}$  range of the individuals spans from -12.5 to -10.1‰ (mean = -11.1‰, SD= 1.1‰). When this is compared to existing datasets from the Wet Zone of Sri Lanka and the coastal settings of Timor in Wallacea it is evident that the Mini-athiliya humans sampled present an overall dietary reliance on terrestrial  $\text{C}_3$  (including perhaps mangrove or some estuarine resources – Rodelli et al., 1984) with some small contribution of  $\text{C}_4$  or marine resources. Further resolution would require analysis of an associated faunal baseline.  $\delta^{18}\text{O}$  of the humans span -4.7 to -3.8‰, which is consistent with estimates of variation within a single human population living at a given locality (Lightfoot & O’Connell, 2016).

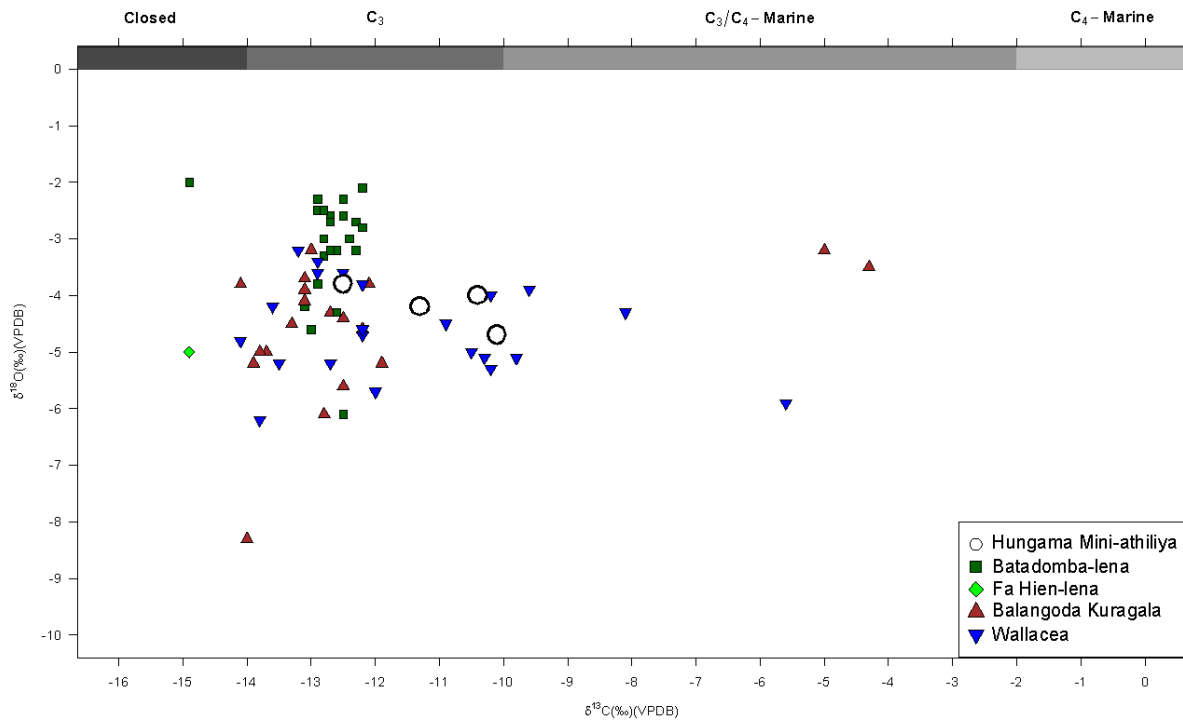
Sample name	Tooth	$\delta^{13}\text{C}$ (‰) (VPDB)	SD	$\delta^{18}\text{O}$ (‰) (VPDB)	SD
Skeleton 5 (child)	Right maxilla M2	-12.5	0.1	-3.8	0.1
Skeleton 4	<i>Right mandible M3</i>	-11.3	0.1	-4.2	0.1
Skeleton 2 (Bag 20)	M2	-10.1	0.1	-4.7	0.1
Skeleton 3 (Bag 24)	M3	-10.4	0.1	-4.0	0.1

**Table 2.** Sample information and  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  data from the Mini-athiliya humans analysed in this study.

Although a pilot study of collagen extraction was undertaken for two human individuals, no collagen was preserved following extraction (Table 3), further highlighting the challenges of protein preservation in these conditions (Krigbaum, 2003, 2005).

Sample name	Element	Collagen extracted? (Yes/No)
Skeleton 4	Skull fragment	No
Skeleton 5 (child)	M2 dentine	No

**Table 3.** Sample information for the two specimens on which collagen extraction was attempted at Mini-athiliya.



**Figure 5.** Mini-athiliya human  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  plotted relative to human data from the Sri Lankan Wet Zone Pleistocene-Holocene sequences of Batadomba-lena, Fa Hien-lena, and Balangoda Kuragala (Roberts et al., 2015a, 2017) and Wallacean Pleistocene-Holocene sequences (Roberts et al., 2020). Approximate cut-offs for diets reliant on closed canopy resources,  $\text{C}_3$  resources, a mixture of  $\text{C}_3$  and  $\text{C}_4$ /marine resources, and  $\text{C}_4$ /marine resources are shown based on the references mentioned in the text.

## Discussion

Existing work on the relatively complete HMA 6 skeleton from Mini-athiliya has involved a basic description of the burial and its context (Kulatilake et al., 2014). However, we have been able to place HMA 6 into a broader context to interpret aspects of physical adaptation to the ecology in this region. Femoral head diameter is strongly correlated with body mass at the time of puberty when epiphyses fuse, while femur length is correlated with adult stature (Ruff et al., 1997; Young et al., 2018). From these parameters we can investigate the height and weight of HMA 6 during life. The analysis demonstrates that the height of HMA 6 is similar to other hunter-gatherers found in arid terrestrial or arid-riverine or coastal environments. In contrast, the body mass of HMA 6 is relatively light, more typical of hunter-gatherers from temperate coastal environments. When these two parameters are combined they demonstrate phenotypic adaptations to a relatively arid coastal environment, suggesting long-term adaptation to life on the southern coast, and that this individual lived in the region throughout their lifespan. This analysis provides only a preliminary assessment of the HMA 6 skeleton. Future analyses of the human remains from Mini-

athiliya will provide much more detailed interpretations of the life and lifestyle of the mid-Holocene people of the southern coastal region.

The appearance of microliths at shell midden sites along the coasts of Sri Lanka during the Middle-Late Holocene have seemed to represent a stark break from the long record of tropical rainforest foraging that preceded them (Deraniyagala, 1992; Perera, 2010; Roberts et al., 2015b). In other coastal contexts around the world, the emergence of dense shell midden layers during the Holocene have frequently been associated with increasingly dense, and perhaps also increasingly sedentary, populations making the most of reliable protein opportunities (Bicho et al., 2010; Wicks et al., 2014). However, the stable carbon and oxygen isotope data presented here suggest that, for Mini-athiliya at least, the use of molluscs were just one part of what was undoubtedly a diverse ecological adaptation. A strong reliance on C<sub>3</sub> resources suggests the hunting of game living in nearby dry tropical forest settings or browsers living in shrublands, alongside the foraging of useful plants. This apparent 'C<sub>3</sub>' component may also be the product of the exploitation of mangrove resources or estuarine settings. Smaller additions of C<sub>4</sub> (perhaps grazing mammals) or marine resources are apparent in at least two of the individuals. Therefore, while a more detailed animal, including molluscan, isotopic baseline is necessary to obtain more detailed information, as predicted by Kulatilake et al. (2014), it seems clear that the humans living at Mini-athiliya were practising a highly diverse subsistence strategy, one that was not purely reliant on resources from the ocean.

Together, the comparative morphological analysis of HMA 6, and the isotopic analysis of other fragmentary human remains from Mini-athiliya, highlight the importance of multidisciplinary approaches to prehistoric ecological adaptations in Sri Lanka. Rather than a clear distinction between earlier forest adaptations and later coastal specialisation, the Mini-athiliya individuals provide evidence for a plastic spectrum of ecological adaptation that involved the continued use of inland dry forest and scrubland resources, alongside the addition of marine foods into the diet. There is no evidence for dedicated coastal reliance such as that seen at the Late Pleistocene Wallacean site of Asitau Kuru (Roberts et al., 2020) (Figure 5) or in prehistoric Japan (Kusaka et al., 2015). This may accord well with Kulatilake and colleagues' (2014) proposal that the use of molluscs at Mini-athiliya was an important adaptive response to increasingly unpredictable climates in the drier areas of Sri Lanka, supplementing the diet alongside an ongoing reliance on game and plant foods. Future analyses should prioritise the isotopic analysis of different terrestrial and marine animals present at the site to confirm these observations, as well as isotopic analysis of the HMA 6 individual itself as the most-securely-dated human occupant of the site. However, we hope to have demonstrated the kind of nuanced insights that can be attained through the application of comparative osteological measurement and stable isotopic approaches, in addition to more traditional zooarchaeological and archaeological approaches. Given the likelihood that plants played an important role in these humans' diets, microbotanical and archaeobotanical research is likely to represent a further promising avenue for research.

S. U. Deraniyagala's (1992) programme of research emphasised the important role Sri Lanka has to play in global discussions of Pleistocene human technology and ecological adaptation. However, while his work in cave and rockshelter sites, such as Batadomba-lena and Fa-Hien Lena, and subsequent detailed research at these sites



by his successors (Perera, 2010; Perera et al., 2011; Wedage et al., 2019, 2020), received some of the most attention, his worked spanned the vast variety of ecological settings the island has to offer. His seminal 1992 volume *'The Prehistory of Sri Lanka'* called for an integration of *all* of the climatic zones and ecological habitats in the narrative of our species' arrival and subsequent adaptations. Although the importance of the coasts for the first hominin settlement of Sri Lanka remains up for debate (Deraniyagala, 1992; Roberts et al., 2015b), they undoubtedly became increasingly important to expanding human populations in the Middle Holocene up until Sri Lanka's integration in vast Indian Ocean trading networks through sites such as Mantai from the historical period (Deraniyagala, 2007). However, in the same way that shark teeth and marine shell beads at rainforest sites (Perera, 2010) highlight complex inter-habitat social networks between populations from the Late Pleistocene, the evidence from Mini-athiliya suggests that Holocene foraging populations maintained one foot in the Sri Lankan interior even as they probed the types of resources the oceans had to offer.

## Conclusion

Our data from a comparative analysis of stable body size variation of HMA 6 and stable carbon and oxygen isotope analysis of other associated individuals, provides further insights into Sri Lankan foraging adaptations during the Holocene. A fluorescence of shell midden sites on the coasts of the island during the Middle-Late Holocene have often been seen as representing an intensification of marine resource use and growing populations associated with microlithic technologies. However, few multidisciplinary studies and limited human remains have made the investigation of the ecological reliance of human societies at these enigmatic sites difficult. Our body size and isotopic data provide different but compatible insights into forager adaptations at the site of Mini-athiliya, one of the few such shell midden sites to have preserved human remains. While the osteoarchaeological data suggests a phenotypic adaptation to a relatively arid coastal environment, the isotopic data highlights the likely procurement of a mixture of resources from inland forest and shrubland plant and animals as well as marine, mangrove, and estuarine settings. Together, this emphasises the ongoing relationship between interior and coastal habitats that may have characterised the ecological adaptations and social networks of our species since its first arrival in Sri Lanka ~45,000 years ago. Furthermore, it supports S. U. Deraniyagala's emphasis on scholars continuing to investigate how human populations in different parts of the island interacted and adapted to its diverse tropical settings across space and time, and what this meant for patterns of technological and cultural change and stability witnessed in the archaeological record.

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This work is a tribute to the remarkable scholar, Siran Deraniyagala, who set the agenda for prehistoric archaeology in Sri Lanka for the last four decades and whose work will continue to do so for many to come. We hope it emphasises that to truly appreciate S. U. Deraniyagala's impact on the discipline of Archaeology in Sri Lanka, we must continue looking at how human populations in different parts of the island interacted and adapted to its diverse tropical settings. We thank the Department of Archaeology, Government of Sri Lanka for permission to conduct this collaborative study, which was performed as part of an established formal agreement between the Department of Archaeology and the Max Planck Institute for Geoanthropology (formerly Max Planck Institute for the Science of Human History).

## References

- Ambrose, S. H., & Norr, L. (1993). Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In J.B. Lambert, G. Grupe (Eds.), *Prehistoric Human Bone Archaeology at the Molecular Level*. Berlin: Springer-Verlag. Pp. 1-37.
- Ashton, P. S., & Gunatilleke, C. V. S. (1987). New light on the plant geography of Ceylon I. Historical Plant Geography. *Journal of Biogeography*, 14, 249-285.
- Bailey, R. C., Head, G., Jenike, M., Owen, B., Rechtman, R., & Zechenter, E. (1989). Hunting and gathering in tropical rain forest; Is it possible? *American Anthropologist* 91, 59-82.
- Bambaradeniya, C. N. B. (Ed). (2006). *The Fauna of Sri Lanka: Status of Taxonomy, Research and Conservation*. Colombo, Sri Lanka: The World Conservation Union (IUCN) and the Government of Sri Lanka.
- Bicho, N., Umbelino, C., Detry, C., & Pereira, T. (2010). The emergence of Muge Mesolithic shell middens in central Portugal and the 8200 cal. yr BP cold event. *The Journal of Island and Coastal Archaeology*, 5, 86-104.
- Byers, S. N. (2002). *Introduction to Forensic Anthropology: A Textbook*. Allyn and Bacon.
- Cerling T. E., Hart, J. A., & Hart, T. B. (2004). Isotope ecology in the Ituri forest. *Oecologia*, 138, 5-12.
- Clementz, M. T., & Koch, P. L. (2001). Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel. *Oecologia*, 129, 461-472.
- Codron, J., Codron, D., Sponheimer, M., Kirkman, K., Duffy, K.J., Raubenheimer, E.J., Melice, J-L., Grant, R., Clauss, M., & Lee-Thorp, J.A. (2014). Stable isotope series from elephant ivory reveal lifetime histories of a true dietary generalist. *Proceedings of the Royal Society B-Series*. doi:10.1098/rspb.2011.2472
- Deraniyagala, P. E. P. (1956). Some aspects of the prehistory of Ceylon. Part 5: the Balangoda Culture. *Spolia Zeylanica*, 28, 117-120.
- Deraniyagala, S. U. (1992). *The Prehistory of Sri Lanka: An Ecological Perspective*, second ed. Department of Archaeological Survey, Colombo.

- Deraniyagala, S. U. (2007). The prehistory and protohistory of Sri Lanka. In P.L. Prematilleke, S. Bandaranayake, S.U. Deraniyagala, R. Silva (Eds.), *The Art and Archaeology of Sri Lanka, 1*. Colombo: Central Cultural Fund. Pp. 1-96.
- De Silva, R. I. (2006). Taxonomy and status of the sharks and rays of Sri Lanka. In C. N .B. Bambaradeniya (Eds.), *The fauna of Sri Lanka: Status of taxonomy, research and conservation* (pp. 294–301). Colombo: World Conservation Union (IUCN)/Government of Sri Lanka.
- Dittus, W.P.J. (1977). The socioecological basis for the conservation of the Toque Monkey (*Macaca sinica*) of Sri Lanka (Ceylon). In H.S.H.O. Rainer, G.H. Bourne (Eds.), *Primate Conservation*. New York: Academic Press. Pp. 237-265.
- Eisenberg, J. F., & Lockhart, M. (1972). An ecological reconnaissance of Wilpattu National Park, Ceylon. *Smithsonian Contributions to Zoology, 101*, 1–119.
- Erdelen, W. (1988). Forest ecosystems and nature conservation in Sri Lanka. *Biological Conservation, 43*, 115-135.
- Feldesman, M. R., & Fountain, R. L. (1996). “Race” specificity and the femur/stature ratio. *American Journal of Physical Anthropology, 100*, 207-224.
- Fry, B. (2006). *Stable isotope ecology*. New York: Springer.
- Fry, B., & Sherr, E. B. (1984).  $\delta^{13}\text{C}$  measurements as indicators of carbon flow in marine and freshwater ecosystem. *Contributions to Marine Science, 27*, 13-47.
- Gamble, C. (1993). *Timewalkers: The prehistory of global colonization*. Stroud: Alan Sutton.
- Gunatilleke, I. A. U. N., Gunatilleke, C. V. S., & Dilhan, M. A. A. B. (2005). Plant biogeography and conservation of the South-western hill forests of Sri Lanka. *The Raffles Bulletin of Zoology, 12*, 9-22.
- Hillson, S. (1996). *Dental Anthropology*. Cambridge: Cambridge University Press.
- Ilangakoon, A. D. (2006). Taxonomy and current status of marine mammals in Sri Lanka. In C. N. B. Bambaradeniya (Ed.), *The Fauna of Sri Lanka: Status of Taxonomy, Research and Conservation* (pp. 302–308). Colombo: World Conservation Union (IUCN)/Government of Sri Lanka.
- Katupotha, J. (1995). Evolution and geological significance of Holocene emerged shell beds on the southern coastal zone of Sri Lanka. *Journal of Coastal Research, 11*, 1042–1061.
- Kelaart, E. F. (1852). *Prodromus faunae Zeylanicae: Being contributions to the zoology of Ceylon*. Colombo: Observer Press.
- Kotagama, S. W., & De Silva, R. I. (2006). The taxonomy and status of offshore birds (seabirds) of Sri Lanka. In C. N. B. Bambaradeniya (Eds.), *The fauna of Sri Lanka: Status of taxonomy, research and conservation* Colombo: World Conservation Union (IUCN)/Government of Sri Lanka. Pp. 288–293.
- Krigbaum, J. (2001). *Human paleodiet in tropical Southeast Asia; Isotopic Evidence from Niah Cave and Gua Cha*. PhD thesis, New York University.
- Krigbaum, J. (2003). Neolithic subsistence patterns in northern Borneo reconstructed with stable carbon isotopes of enamel. *Journal of Anthropological Archaeology, 22*, 292–304.
- Krigbaum, J. (2005). Reconstructing Human Subsistence in the West Mouth (Niah Cave) Sarawak) Burial Series Using Stable Isotopes of Carbon. *Asian Perspectives, 44*, 73-89.

- Kulatilake, S. (2009). Early occupation of coastal Sri Lanka: Human remains from the Mini-athiliya shell midden. In A. R. Sankhyan (Eds.). *Asian perspectives on Human Evolution*. New Delhi: Serials. Pp. 207–214.
- Kulatilake, S., Perera, N., Deraniyagala, S. U., & Perera, J. (2014). The discovery and excavation of a human burial from the Mini-athiliya shell midden in southern Sri Lanka. *Ancient Asia*, 5, 1-8. <http://dx.doi.org/10.5334/aa.12319>
- Kulatilake, S., Peiris, R., Perera, H. N., Perera, H. J. (2018). Out of context, in association: Human remains salvaged from the Mini-athiliya shell midden, Sri Lanka. *Asian Perspectives*, 57, 51-82. <https://doi.org/10.1353/asi.2018.0002>
- Kusaka, S., Uno, K. T., Nakano, T., Nakatsukasa, M., & Cerling, T.E. (2015). Carbon isotope ratios of human tooth enamel record the evidence of terrestrial resource consumption during the Jomon period, Japan. *American Journal of Physical Anthropology*, 158, 300-311.
- Langley, M., Amano, N., Wedage, O., Deraniyagala, S., Pathamalal, M., Perera, N., Boivin, N., Petraglia, M., & Roberts, P. (2020). Bows-and-arrows and complex symbolic displays at 48,000-years-ago in the South Asian tropics. *Science Advances*, 6: <https://doi.org/10.1126/sciadv.aba3831> .
- Lee-Thorp, J. A. (2008). On isotopes and old bones. *Archaeometry*, 50, 925-950.
- Lee-Thorp, J. A., Sealy, J.C., & van der Merwe, N.J. (1989). Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *Journal of Archaeological Science*, 16, 585-599.
- Lee-Thorp, J. A., van der Merwe, N. J., & Brain, C. K. (1994). Diet of *Australopithecus robustus* at Swartrans deduced from stable carbon isotope ratios. *Journal of Human Evolution*, 27, 361-372.
- Levin, N.E., Cerling, T. E., Passey, B.H., Harris, J. M., & Ehleringer, J. R. (2006). A stable isotope aridity index for terrestrial environments. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 11201-11205.
- Levin, N.E., Simpson, S.W., Quade, J., Cerling, T.E., & Frost, S.R. (2008). Herbivore enamel carbon isotopic composition and the environmental context of *Ardipithecus* at Gona, Ethiopia. In J.Quade, & J.G. Wynn (Eds.), *The Geology of Early Humans in the Horn of Africa*. Boulder, Colorado: Geological Society of America Special Paper 446. Pp. 215-234.
- Lightfoot, E., & O'Connell, T. C. (2016). On the use of biomineral oxygen isotope data to identify human migrants in the archaeological record: Intra-sample variations, statistical methods and geographical considerations. *PLoS ONE*: <https://doi.org/10.1371/journal.pone.0153850>
- Longin, R. (1971). New Method of Collagen Extraction for Radiocarbon Dating. *Nature*, 230, 241–242.
- Nelson, S. (2007). Isotopic reconstructions of habitation change surrounding the extinction of *Sivapithecus*, a Miocene hominoid, in the Siwalik Group of Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 243, 204-222.
- Nyrop, R. F., Benderly, B.L., Cort, A. S., Parker, N. B., Perlmutter, J. L., Shinn, R. S., & Shivanandan, M. (1971). *Area handbook for Ceylon*. Washington, DC: US Government Printing Office.
- Premathilake R. T. (2006). Relation of environmental changes in central Sri Lanka to possible land use and climate changes. *Palaeogeography, Palaeoclimatology and Palaeoecology*, 240, 468–496.

- Primavera, J. H., Sadaba, R. B., Leбата, M. J. H. L., & Altamirano J. P. (2004). *Handbook of mangroves in the Philippines – Panay*. Iloilo, Philippines: SEAFDEC Aquaculture Department (Philippines) and UNESCO Man and the Biosphere ASPACO Project.
- Perera, N. (2010). *Prehistoric Sri Lanka: Late Pleistocene rockshelters and an open air site*. BAR International Series. Oxford: Archaeopress.
- Perera, N., Kourampas, N., Simpson, I.A., Deraniyagala, S.U., Bulbeck, D., Kamminga, J., Perera, J., Fuller, D.Q., Szabo, K., & Oliveira, N.V. (2011). People of the ancient rainforest: Late Pleistocene foragers at the Batadomba-lena rockshelter, Sri Lanka. *Journal of Human Evolution*, 61, 254-269.
- Phillips, W. W. A. (1980). *Manual of the Mammals of Sri Lanka* (volumes 1, 2 and 3) (2<sup>nd</sup> edition). Wildlife and Nature Protection Society of Sri Lanka, Sri Lanka.
- Puvaneswaran, K. M., & Smithson, P. A. (1993). Controls on precipitation distributions in Sri Lanka. *Theoretical and Applied Climatology*, 47, 105-115.
- Roberts, P., & Stewart, B. (2018). Defining the ‘generalist-specialist’ niche for Pleistocene *Homo sapiens*. *Nature Human Behaviour* DOI: [10.1038/s41562-018-0394-4](https://doi.org/10.1038/s41562-018-0394-4)
- Roberts, P., Perera, N., Wedage, O., Deraniyagala, S. U., Perera, J., Eregama, S., Gledhill, A., Petraglia, M.D., & Lee-Thorp, J.A. (2015a). Direct evidence for human reliance on rainforest resources in late Pleistocene Sri Lanka. *Science*, 347, 1246-1249.
- Roberts, P., Boivin, N., & Petraglia, M.D. (2015b). The Sri Lankan ‘Microlithic’ tradition c. 38,000 to 3000 years ago: Tropical technologies and adaptations of *Homo sapiens* at the southern edge of Asia. *Journal of World Prehistory*, 29, 69-112.
- Roberts, P., Perera, N., Wedage, O., Deraniyagala, S. U., Perera, J., Eregama, S., Gledhill, A., Petraglia, M., & Lee-Thorp, J. (2017). Fruits of the forest: human stable isotope ecology and rainforest adaptations in Late Pleistocene and Holocene (~ 36 to 3 ka) Sri Lanka. *Journal of Human Evolution*, 106, 102-118.
- Roberts, P., Louys, J., Zech, J., Shipton, C., Kealy, S., Samper Carro, S., Hawkins, S., Boulanger, C., Marzo, S., Fiedler, B., Boivin, N., Mahirta, Aplin, K., & O’Connor, S. (2020). Isotopic evidence for initial coastal colonization and subsequent diversification in the human occupation of Wallacea. *Nature Communications* DOI: [10.1038/s41467-020-15969-4](https://doi.org/10.1038/s41467-020-15969-4).
- Rodelli, M. R., Gearing, J. N., Gearing, P. J., Marshall, N., & Sasekumar, A. (1984). Stable isotope ratio as a tracer of mangrove carbon in Malaysian ecosystems. *Oecologia*, 61, 326-333.
- Ruff, C. B., Trinkaus, E., & Holliday, T. W. (1997). Body mass and encephalization in Pleistocene *Homo*. *Nature*, 387, 173–176. <https://doi.org/10.1038/387173a0>
- Satyanarayana, B., Mulder, S., Jayatissa, L. P., & Dahdouh-Guebas, F. (2013). Are the mangroves in the Galle-Unawatuna area (Sri Lanka) at risk? A social-ecological approach involving local stakeholders for a better conservation policy. *Ocean and Coastal Management*, 71, 225–237.
- Schoeninger, M. J. (2014). Stable Isotope Analyses and the Evolution of Human Diets. *Annual Review of Anthropology*, 43, 413-430.
- Smith, B.N., & Epstein, S. (1971). Two categories of <sup>13</sup>C/<sup>12</sup>C ratios for higher plants. *Plant Physiology*, 47, 380-384.
- Somadeva, R., & Ranasinghe. R. (2006). An excavation of a shell midden at Pallemalla in southern littoral area of Sri Lanka. *Ancient Asia*, 1, 14–24.

- Somararatne, S., & Dhanapala A.H. (1996). Potential impact of global climate change on forest in Sri Lanka. In L. Erda, W. Bolhofer, S. Huq, S. Lenhart, S.K. Mukherjee, J.B. Smith, & J. Wisniewski (Eds.). *Climate change variability and adaptation in Asia and the Pacific*. Dordrecht: Kluwer. Pp. 129–135.
- Sponheimer, M., Codron, D., Passey, B. H., de Ruiter, D. J., Cerling, T. E., & Lee-Thorp, J. A. (2009). Using carbon isotopes to track dietary change in modern, historical, and ancient primates. *American Journal of Physical Anthropology*, 140, 661-670.
- Sponheimer, M., Alemseged, Z., Cerling, T. E., Grine, F. E., Kibel, W. H., Leakey, M. G., Lee-Thorp, J. A., Manthi F. K., Reed, K. E., Wood, B. A., & Wynn, J. G. (2013). Isotopic evidence of early hominin diets. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 10513-10518.
- Stock, J. T. (2013). The skeletal phenotype of “Negritos” from the Andaman islands and Philippines relative to global variation among hunter-gatherers. *Human Biology*, 85, <https://doi.org/10.3378/027.085.0304>
- Stock, J. T., O’Neill, M. C., Ruff, C. B., Zabecki, M., Shackelford, L., & Rose, J. C. (2011). Body Size, Skeletal Biomechanics, Mobility and Habitual Activity from the Late Palaeolithic to the Mid-Dynastic Nile Valley. In *Human Bioarchaeology of the Transition to Agriculture*. <https://doi.org/10.1002/9780470670170.ch14>
- Tennant J. E. (1861). *Sketches of the natural history of Ceylon*. London: Longman.
- Van der Merwe, N. J., & Medina, E. (1991). The canopy effect, carbon isotope ratios and foodwebs in Amazonia. *Journal of Archaeological Science*, 18, 249-259.
- Wedage, O., Amano, N., Langley, M. C., Douka, K., Blinkhorn, J., Crowther, A., Deraniyagala, S., Kourampas, N., Simpson, I., Perera, N., Picin, A., Boivin, N., Petraglia, M., & Roberts, P. (2019). Specialized rainforest hunting by *Homo sapiens* 45,000 years ago. *Nature Communications*, 10, 739 DOI: [10.1038/s41467-019-08623-1](https://doi.org/10.1038/s41467-019-08623-1).
- Wedage, O., Roberts, P., Faulkner, P., Crowther, A., Douka, K., Picin, A., Blinkhorn, J., Deraniyagala, S., Boivin, N., Petraglia, M., & Amano, N. (2020). Late Pleistocene to early-Holocene rainforest foraging in Sri Lanka: Multidisciplinary analysis at Kitulgala Beli-Lena. *Quaternary Science Reviews*, 231, 106200. DOI: [10.1016/j.quascirev.2020.106200](https://doi.org/10.1016/j.quascirev.2020.106200).
- White, T. D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Owen Lovejoy, C., Suwa, G., & WoldeGabriel, G. (2009). *Ardipithecus ramidus* and the Paleobiology of Early Hominids. *Science*, 326, 75-86.
- Wicks, K., Pirie, A., & Mithen, S. J. (2014). Settlement patterns in the late Mesolithic of western Scotland: the implications of Bayesian analysis of radiocarbon dates and inter-site technological comparisons. *Journal of Archaeological Science*, 41, 406-422.
- Wright, L. E., & Schwarcz, H. P. (1998). Stable carbon and oxygen isotopes in human tooth enamel: Identifying breastfeeding and weaning in prehistory. *American Journal of Physical Anthropology*, 106, 1-18.
- Young, M., Johannesdottir, F., Poole, K., Shaw, C., & Stock, J. T. (2018). Assessing the accuracy of body mass estimation equations from pelvic and femoral variables among modern British women of known mass. *Journal of Human Evolution*, 115, <https://doi.org/10.1016/j.jhevol.2017.10.011>