

Alma Mater Studiorum Università di Bologna
Archivio istituzionale della ricerca

Late Pleistocene to early-Holocene rainforest foraging in Sri Lanka: Multidisciplinary analysis at Kitulgala Beli-lena

This is the final peer-reviewed author's accepted manuscript (postprint) of the following publication:

Published Version:

Wedage O., Roberts P., Faulkner P., Crowther A., Douka K., Picin A., et al. (2020). Late Pleistocene to early-Holocene rainforest foraging in Sri Lanka: Multidisciplinary analysis at Kitulgala Beli-lena. QUATERNARY SCIENCE REVIEWS, 231, 106200-106219 [10.1016/j.quascirev.2020.106200].

Availability:

This version is available at: <https://hdl.handle.net/11585/919153> since: 2023-02-28

Published:

DOI: <http://doi.org/10.1016/j.quascirev.2020.106200>

Terms of use:

Some rights reserved. The terms and conditions for the reuse of this version of the manuscript are specified in the publishing policy. For all terms of use and more information see the publisher's website.

This item was downloaded from IRIS Università di Bologna (<https://cris.unibo.it/>).
When citing, please refer to the published version.

(Article begins on next page)

Late Pleistocene to Early-Holocene Rainforest Foraging in Sri Lanka: Multidisciplinary analysis at Kitulgala Beli-lena

Oshan Wedage^{1,2*}, Patrick Roberts^{1,3*}, Patrick Faulkner^{1,4}, Alison Crowther^{1,3}, Katerina Douka^{1,5}, Andrea Picin^{1,6}, James Blinkhorn^{1,7}, Siran Deraniyagala⁸, Nicole Boivin^{1,3,9,10}, Michael Petraglia^{1,3,9*}, Noel Amano^{1*}

¹Department of Archaeology, Max Planck Institute for the Science of Human History, Jena, Germany.

²Department of History and Archaeology, University of Sri Jayewardenepura, Gangodawila, Nugegoda, Sri Lanka.

³School of Social Science, The University of Queensland, Brisbane, Australia.

⁴Faculty of Arts and Social Sciences, University of Sydney, Sydney, Australia.

⁵Research Laboratory for Archaeology and the History of Art, University of Oxford, Oxford, United Kingdom.

⁶Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

⁷Department of Geography, Royal Holloway, University of London, United Kingdom.

⁸Department of Archaeology, Government of Sri Lanka, Colombo, Sri Lanka.

⁹Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

¹⁰Department of Anthropology and Archaeology, University of Calgary, Calgary, Canada

*correspondence to: Oshan Wedage, Patrick Roberts, Michael Petraglia, Noel Amano,
email: wedage@shh.mpg.de, roberts@shh.mpg.de, petraglia@shh.mpg.de, amano@shh.mpg.de,

Abstract

Sri Lanka has produced the earliest clear evidence for *Homo sapiens* fossils in South Asia and research in the region has provided important insights into modern human adaptations and cultural practices during the last *ca.* 45,000 years. However, in-depth multidisciplinary analyses of Late Pleistocene and Holocene sequences remain limited to just two sites, Fa Hien-lena and Batadomba-lena. Here, we present our findings from the reinvestigation of a third site, Kitulgala Beli-lena. New chronometric dating from the site confirms the presence of humans as early as *ca.* 45,000 cal. BP. in the island's Wet Zone rainforest region. Our analyses of macrobotanical, molluscan, and vertebrate remains from the rockshelter show that this early human presence is associated with rainforest foraging. The Late Pleistocene deposits yielded evidence of wild breadfruit and kekuna nut extraction while the Holocene layers reveal a heavy reliance on semi-arboreal and arboreal small mammals as well as freshwater snails as a protein source. The lithic and osseous artefacts demonstrate that populations developed a sophisticated tool kit for the exploitation of their immediate landscapes. We place the rich Kitulgala Beli-lena dataset in its wider Sri Lankan context of Late Pleistocene foraging, as well as in wider discussions of our species' adaptation to 'extreme' environments as it moved throughout Asia.

Keywords:

Rainforest, Human adaptation, Modern human dispersal, South Asia, Pleistocene Archaeology

1. Introduction

South Asia has emerged as a crucial region for understanding the timing and nature of human dispersals from Africa and the Middle East into Southeast Asia and Australasia (Petraglia et al., 2012; Blinkhorn et al., 2013, 2019; Roberts et al., 2017a). In addition to it being located at a key geographical juncture, it also sits at a major biogeographic junction between the Sahara-Arabian and Afrotropical regions to the west and Palearctic and Sino-Japanese regions to the north (Watts, 1984; Holt et al., 2013; Blinkhorn et al., 2013). Archaeological research in South

Asia over the past two decades has pointed to potential multiple, earlier routes of dispersal into the region (Petraglia et al., 2010; Boivin et al., 2013; Bae et al., 2017; Blinkhorn and Petraglia 2017), and emphasizing the varied and complex local patterns of technological and cultural change (Petraglia et al., 2010, 2012; Blinkhorn et al., 2013), as well as the diversity of the types of terrestrial environments, utilized by early humans (Blinkhorn et al., 2016; Roberts et al., 2015a, 2017b). This is in contrast to a prominent model that assumes a rapid, coastal *ca.* 60 ka dispersal of humans, illustrated by uniform technological features (Mellars, 2006; Mellars et al., 2013).

Research in Sri Lanka, an island at the southern tip of South Asia, has highlighted how early members of our species employed adaptive strategies to take full advantage of their environments such as tropical rainforests. Traditional anthropological and archaeological assumptions viewed rainforests as barriers to human occupation due to a scarcity of resources, including calorie-rich plants and large animals (Bailey et al., 1989; Gamble, 1993). Nevertheless, Sri Lanka has produced the earliest clear evidence for *Homo sapiens* fossils in tropical rainforest environments in South Asia (Kennedy, et al., 1987; Kennedy and Deraniyagala, 1989; Deraniyagala, 1992; Kennedy, 2000) as well as evidence for heavy reliance on rainforest resources, including specialized hunting of arboreal and semi-arboreal fauna from ~48,000 years ago through to 3,000 years ago (Roberts et al., 2015a,b, 2017b; Wedage et al., 2019a) facilitated by microlith and osseous technologies (Deraniyagala, 1992, Wijeyapala, 1997, Perera et al., 2011, Wedage et al., 2019a; Langley et al., 2019). However, knowledge of the scale of Late Pleistocene tropical rainforest occupations in the region remains limited since multidisciplinary analyses of archaeological sequences are restricted to two sites: Fa Hien-lena, dated to *ca.* 48,000 years ago (Wedage et al., 2019a) and Batadomba-lena, dated to *ca.* 38,000-36,000 years ago (Roberts et al., 2015b).

Traditionally, a third site, Kitulgala Beli-lena, has been grouped with these other two sequences as a source of early human fossils (Kennedy et al., 1987; Kennedy and Deraniyagala, 1989; Wijeyapala, 1997) and microlith adaptations (Deraniyagala, 1992). Yet, this site has been somewhat neglected given that existing radiocarbon dates place this sequence considerably later (31,000 years ago – Kourampas et al., 2009). Moreover, a lack of published zooarchaeology, archaeobotany (though see Kajale, 1989), and detailed technological analysis, as well as the fact that the site required re-dating using methods better equipped to deal with contamination in tropical environments (see Higham et al., 2008), have meant comparisons of Kitulgala Beli-lena to Fa Hien-lena and Batadomba-lena are somewhat superficial. Here, we present the results of renewed excavation and multidisciplinary analyses of materials recovered from Kitulgala Beli-lena. We present a revised stratigraphy for the site as well as new chronological information. Alongside detailed insights into prey choices, plant use, and sedimentary formation processes at the site, lithic data from the site indicates that Kitulgala Beli-lena was potentially part of a social network of technological procurement and production. In addition, our research highlights possible differential spatial use of cave and rockshelter sites in the Sri Lankan rainforest in the Late Pleistocene and Holocene. By placing our data from Kitulgala Beli-lena in its wider Sri Lankan and Asian context we are able to present a more complete picture of Late Pleistocene and Holocene human adaptation and presence in this increasingly significant region for human evolutionary research.

2. Kitulgala Beli-lena Rockshelter

Kitulgala Beli-lena is located in the Kegalle district of Sri Lanka's Sabaragamuwa Province, approximately 85 km east of Colombo (Figure 1). With a *ca.* 30 x 15 m north facing entrance,

the rockshelter is formed within a gneiss bedrock, part of the metamorphic terrain of Sri Lanka's Highland Complex (Cooray, 1984). Kitulgala Beli-lena is situated in the island's lowland Wet Zone with a mean annual precipitation between 2500-3500 mm/year (Dömros, 1974; Roberts et al., 2015b), surrounded by humid tropical rainforest. The rockshelter was first explored by P.E.P. Deraniyagala in 1960-1961, who excavated several test pits and noted an abundance of historic and prehistoric archaeological materials. However, no detailed description of this first investigation was ever published. Systematic excavation of the rockshelter continued in 1978 by the Department of Archaeology of the Government of Sri Lanka under the supervision of S.U. Deraniyagala. Excavations continued in 1979, 1983, 1985 and in 1986 (under W. H. Wijeyapala) (Figure 1). The Department of Archaeology, this time led by Oshan Wedage, carried out a small excavation of 1 m² in the southeast corner of the rockshelter in 2013. Collectively, these excavations sampled more than 3 m of cultural deposits and produced a total of 25 radiocarbon dates (Table 1), indicating a chronology extending back to *ca.* 31,000 cal. years BP. Two thermoluminescence dates ($17,217 \pm 3300$ and $18,565 \pm 2610$) have also been reported (Abeyratne, 1994).

Excavations of Terminal Pleistocene sediments of the site, with associated charcoal dated to $12,260 \pm 870$ years BP, had previously yielded several human remains including a partial skeleton of an adult of indeterminate sex, a skull of a child 10-11 years of age at the time of death, bones and teeth from at least ten different individuals (Kennedy et al., 1987; Kennedy and Deraniyagala, 1989; Wijeyapala, 1997). Sparse microlithic tools, manufactured from quartz, were also recorded from the beginning of site occupation (Wijeyapala, 1997). However, these technologies, as well as osseous tools, were not systematically analysed. In 2017, a new excavation in Kitulgala Beli-lena was conducted by the Max Planck Institute for the Science of Human History and University of Sri Jayewardenepura in collaboration with the Department of Archaeology, Government of Sri Lanka. The aim of the excavation was to recover new materials to produce a refined chronology for the site, using appropriate pre-treatment methodologies for charcoal samples as well to conduct systematic zooarchaeological, archaeomalacological and archaeobotanical analyses. Three 1 x 1 m squares were opened in the inner western section of the rockshelter, close to the wall, following the grid laid out during the 1980s excavation (Figure 1). The excavation reached a final depth of 192 cm from the surface rockshelter deposits.

3. Methods

3.1 Excavation

The 2017 excavation of Kitulgala Beli-lena aimed to recover new archaeological material in order to refine/revise the chronology of the site and better understand human culture, technology, and subsistence strategies. The excavation was situated in the inner western section of the rockshelter, some 5 m from the wall. Following the excavations in the rockshelter in 1985, the exposed sections were covered by stone walls to preserve the integrity of the site. The only portion that was not protected was a 2 m² excavation square (grid code: G12-G11) which was sampled for micromorphology in 2005 and 2009 (Perera, 2010, Kourampas et al., 2009). The new excavation extended this unprotected square southward, opening excavation square G12 and the previously unexcavated squares H14 and I14 (Figure 1) and allowing for the correlation of the results to the micromorphological analyses of Kourampas et. al (2009).

Excavations were conducted using small hand tools and following the single context recording system (Harris 1989). Where the depths of single contexts were extensive (>5 cm), they were subdivided into spits to increase the resolution of artefact and sediment sampling. Three

dimensional recording of the sediment deposits and major artefacts was undertaken using a Leica Builder 505 total station. After removal, excavated sediments were placed on polythene sheeting and a sub-sample was taken for flotation. A total of 1120 liters of sediment were floated (using a 250 micron mesh) during the excavation. The rest of the excavated sediments were wet sieved to allow for the recovery of cultural materials. In addition, samples of approximately 100 g were recovered at 5 cm intervals to enable a range of sediment analyses (ongoing analyses i.e. laser particle size analyses, phosphate analyses etc.).

3.2 Radiocarbon dating

Fourteen charcoal fragments recovered during excavation were submitted for dating to the Oxford Radiocarbon Accelerator Unit. The charcoal samples were prepared using the acid–base oxidation/stepped combustion (ABOx-SC) protocol (Bird et al., 1999; Higham et al., 2008). Of these, 13 samples yielded ^{14}C measurements that were calibrated using the IntCal13 calibration curve and the OxCal 4.3 programme (Reimer et al., 2013; Bronk Ramsey 2017).

3.3 Zooarchaeological analysis and osseous technology analysis

All recovered bone fragments from the 2017 excavation of Kitulgala Beli-lena were analysed, including fragmentary remains as well as diaphyses and rib shafts. All specimens were sorted, counted, and measured (length, width, and thickness) using a digital caliper (Mitutoyo 500–463). Identified specimens were recorded in detail using codes for anatomic zones following a zonation system modified from Dobney and Reilly (1988) to allow for the description of fragmentation patterns. Diagnostic skeletal elements were identified using comparative vertebrate specimens from the Field Museum of Natural History and American Museum of Natural History and from the Laboratory of Comparative Anatomy of the Muséum national d'Histoire naturelle (MNHN). Naming of identified taxa follows the nomenclature published by Wilson and Reeder (2005). The identified taxa were classified to size class based on live weight following a modification of the criteria established by Thomas (1969) and Grayson (1984): (a) micromammals: 100 g to 1 kg, (b) small mammals: 1 kg to 25 kg, (c) large mammals class 1: 25 kg to 200 kg, (d) large mammals class 2: 200 kg to 1000 kg, and (e) large mammals class 3: > 1000 kg.

All fragments were examined for natural, animal, and anthropic modifications, including weathering (Behrensmeyer, 1978; Andrews, 1995), abrasion (Shipman and Rose, 1988), burning, staining, and butchery marks (Fernandez-Jalvo and Andrews, 2016). Bone surface modifications, including traces of bone tool manufacture, were recorded/observed using an Olympus BX53 light microscope. Bone artefacts were further examined under a Keyence VHX-6000 digital microscope to record traces of use. Bone surface modifications resulting from tool production and use were identified following published criteria (i.e. Shipman and Rose, 1988; Blasco et al., 2008; Bradfield and Brand, 2015; Langley et al., 2016).

In terms of zooarchaeological quantifications, the minimum number of element (MNE) and minimum number of individual (MNI) counts were calculated following a modification of Dobney and Reilly's (1998) zonation system. This system is based on the recording of distinct morphological zones in a skeletal element. The MNE was taken as the total number of non-overlapping zones (i.e., greater than 50% of the diagnostic zone present) for every skeletal element of a taxon. The highest MNE value, considering side and age (epiphyseal fusion and dental wear, following Klein and Cruz-Urbe (1984), was used to estimate the MNI. The MNE counts were converted to minimum animal unit (MAU) values by taking into account the number of times the element occurs in the skeleton. The normalized MAU values (% MAU)

were used to compare skeletal part representation in the different phases of cave occupation (Lyman, 1994).

3.4 Invertebrate analysis

The invertebrate assemblage of Kitulgala Beli-lena consists of all remains collected during the 2017 excavation of the site, including fragmentary specimens recovered from dry and wet sieving of sediments. Prior to analysis, all samples were washed to remove excess sediment and air-dried for 24-48 hours. As a physical comparative reference collection was not available for specimen identification, all taxonomic attributions were made following the descriptions and/or illustrations provided in Hausdorf and Perera (2000), Naggs and Raheem (2000), Raheem and Naggs (2006) and Starmuhlner (1974). Recent correspondence with Dr Dinarzarde Raheem (Natural History Museum, London) indicates that significant taxonomic revision of the Sri Lankan terrestrial and freshwater mollusc fauna is needed.

Although the resources currently available are useful for identifying genera and are likely to be of limited value for species level-identification, specimens were attributed to taxonomic categories (e.g. to species, genus, or family) based on the preservation of identifiable diagnostic features. Taphonomic indicators, such as dissolution, burning, and predatory boring, were also noted. Although the assemblage was recorded in such a way so as to enable the calculation of the MNI, due to the small sample size the quantification measures reported here are restricted to NISP and weight (in grams).

3.5 Archaeobotanical analysis

The archaeobotanical assemblage analysed in this study comprises of materials from flotation samples from five sedimentary contexts spanning the Pleistocene sequence of Kitulgala Beli-lena, namely contexts 10, 17, 21, 24, 23. The flotation samples were sieved into >4mm, 2-4mm, 1-2mm, and <1mm fractions. The >4mm and 2-4mm fractions were sorted under low magnification (x8–x40) using an Olympus SZ61 stereozoom microscope and the 1-2mm fraction was scanned for any smaller remains. Analysis of this material is ongoing and subject to the establishment of a comparative ethnobotanical reference collection for Sri Lanka. Taxonomic identifications where possible were based on published descriptions (e.g., Kahn and Ragone 2013; Kajale 1988; Levin 2015) and available comparative botanical material in the University of Queensland's Archaeobotany Laboratory.

3.6 Lithic analysis

The technological analysis of the lithic assemblages was performed using the *chaîne opératoire* concept, a methodological framework that defines the reconstruction of the various processes of flake production from the procurement of raw materials through to discard (Lemonnier, 1986; Pelegrin et al., 1988). The assemblages were firstly discriminated by raw material units, defined according to variety of stone and macroscopic features including type of cortex, colour, grain size, and texture (Roebroeks, 1988). The technological features were then reconstructed through the diacritic analysis of the scar pattern organization on the cores' flaking surfaces and on the flakes' dorsal side. Previous studies on the lithic collections in Sri Lanka report the extensive use of the bipolar method (Lewis, 2017; Wedage et al., 2019a; 2019b). In order to address the variability of this lithic reduction strategy, the analysis was performed following more recent definitions based on experimental knapping data (Crabtree, 1972; de la Peña, 2015; Donnart et al., 2009; Mourre, 1996). The flake assemblages were classified by dimensional criteria and only the lithic items greater than 1 cm were analysed. Bladelets are considered elongated blanks in which the ratio length to width is ≥ 2 , and with a percussion axis length of less than 4 cm (Petraglia et al., 2009). A distinction has not been made between bladelets

produced from true bladelet cores and flake-bladelets. Siret knapping accidents were distinguished following the criteria of Mourre (1996) whereas *bâtonnet* flakes (or bipolar spalls) and splinter flakes were defined following Brun-Ricalens (2006).

4. Results

4.1 A Revised Chronostratigraphy for Kitulgala Beli-lena

The fill of Kitulgala Beli-lena consists of *ca.* 192 cm of stratified detrital sediments deposited on a heavily weathered and phantomed gneiss bedrock over the last *ca.* 44,000 years. Thirteen new radiocarbon dates (Table 2) anchor the stratigraphy and resolve it into four phases, each corresponding to a major period of human occupation of the rockshelter (Figure 1). The sedimentary layers excavated in 2017 correspond to those recorded during the previous excavation of squares H6 and I6 as well as the micromorphological sequence reported by Kourampas et al. (2009) (Table 3).

Late Pleistocene Phase

The Late Pleistocene phase of the rockshelter represents intermittent/episodic human occupation, from around *ca.* 44,000 to 31,000 cal. BP. It is characterized by pebbly clayey loams with angular gneiss slabs and subhorizontal layers of yellowish brown, sandy clay to sandy silt deposits. Just above the gneiss bedrock is a *ca.* 10 cm clast supported conglomerate with well-rounded imbricated pebbles that is hypothesized (Wijeyapala, 1997; Kourampas, 2009) to have been deposited by a stream that at the present flows 60 m below the level of the rockshelter's entrance. This layer, notably devoid of any cultural materials, is overlain by a series of sandy loam and sandy clay deposits containing angular gneiss slabs and abundant charcoal.

Kourampas et al. (2009) suggest that these layers most likely represent an admixture of roof fall and colluvial deposits reworked by bioturbation and rockshelter floor processes including trampling and surface runoff. The first in the series, Context 23, returned dates as early as 42,593-44,902 cal. BP. These sedimentary layers, referred to as phases IIIa(2)-IIIc(3) by Wijeyapala (1997), were previously dated to 25,190 - 18,236 cal. BP. New dates now place these layers as being deposited between *ca.* 44,902-31,600 cal. BP (Figure 1). Evidence of human activities in the Late Pleistocene phase includes artefacts (ochre fragments and stone tools) and macrobotanical remains. No faunal remains were recovered in the Late Pleistocene layers during the 2017 excavations.

Terminal Pleistocene Phase

The Terminal Pleistocene phase of site occupation is characterized by dark greyish brown sandy loam and silty clay deposits notable for a heavy concentration of quartz microliths and macrobotanical remains (e.g. context 9-10). This *ca.* 30 cm phase of occupation correlates to sedimentary layers IV and V from the 1983 excavation which were dated to 13,600-12,100 cal. BP (Wijeyapala, 1997) and contains the densest occupation debris in terms of charcoal and lithic materials. Discrete patches of burnt sediments and ashes point to possible hearths within the layers. Angular gneiss slabs most likely from roof fall or wall disintegration are also abundant in these layers. Charcoal from these layers recovered from the 2017 excavation returned dates between 17,157-11,314 cal. BP. Kourampas (2009), in his micromorphological analyses of the stratigraphy from the 1986 excavation, interpreted these layers as resulting from

accelerated sedimentation brought about by human activity, high rates of colluvation, and accelerated water seepage.

Previous reports (Deraniyagala, 1992; Wijeyapala 1997) noted that faunal remains (both vertebrate and invertebrate) were recovered from the Terminal Pleistocene layers of Kitulgala. However, not a single piece of faunal material was recovered from the 2017 excavation. Kourampas et al. (2009) also reported an absence of microscopic bone fragments in the micromorphological sections from these layers. It is unlikely that the absence of animal bones and molluscan remains from the Late Pleistocene and Terminal Pleistocene phases of the site resulted from taphonomic processes as abundant macrobotanical remains and unweathered quartz flakes were recovered in the same layers.

Holocene Phase

The Holocene Phase of Kitulgala consists of at least six distinct sedimentary layers with abundant charcoal, quartz microlith, and ochre content. These layers, previously dated to 9,070-3,550 cal. BP (layer VI to VII), have been re-dated to 10,577-8,029 cal. BP. Unlike the underlying sedimentary layers, the Holocene layers yielded numerous faunal materials. *In situ* hearths with burnt seeds and animal bone fragments were also recorded. The lowermost layer, a compact mid-yellowish brown sandy loam, contains frequent mid-sized (up to 15 cm) angular gneiss slabs suggestive of a roof-fall episode that happened sometime during the onset of the Holocene. Overlying this is a series of almost horizontal loamy clay and silty sand layers rich in debris from human activity.

Historical Phase

A *ca.* 10 cm silty sand deposit represents the Historical Phase of occupation of Kitulgala Beli-lena. Much thicker near the entrance (i.e. *ca.* 50 cm in the previous excavation of H10/I10), this layer has been interpreted as reworked sediment and residue resulting from the extraction of guano-rich deposits used as fertilizer in nearby rubber plantations during colonial times (Wijeyapala, 1997). It is chronologically mixed, containing potsherds and abundant mollusc fragments as well as animal bones and quartz flakes most likely reworked from earlier phases of site occupation. The guano extraction digging had cut through Early Holocene deposits in some parts of the site (Wijeyapala, 1997). Kourampas et al. (2009) noted that the historical deposit did not penetrate below Mid-Holocene levels in the profile they studied. The new dates, however, suggested that much of the mid-Holocene deposits of Kitulgala Beli-lena were removed during the historical phase.

4.2 Vertebrate Fauna

A total of 5502 animal bone fragments were recovered from the 2017 excavation of Kitulgala Beli-lena. As noted above, all of the vertebrate remains were recorded from sedimentary contexts dated to the Early Holocene. Small mammals (< 25kg) dominate the faunal assemblage, accounting for 70.5% (Total number of fragments, TNF= 3859, Number of identified specimens, NISP=2156) of the remains recorded, suggesting deliberate targeting of these animals by the people that settled in Kitulgala (Table 4, Figure 2). Large mammals account for 3.9% of the recovered animal bones and micromammals (mostly murids and bats) account for 10.7%. Reptiles (11.1% NISP), fish (4.8% NISP) and birds (2.1% NISP) were also identified in the assemblage.

From the 5502 vertebrate remains recovered from the site, 3091 (56.2%) can be confidently assigned to family, genus, or species (Table 5). Cercopithecoid monkeys dominate the Early

Holocene assemblage of the site, with a total of 1001 remains from at least 91 individuals recorded. Both cercopithecines (macaque) and colobines (langurs) were identified in the assemblage based on teeth and certain post-cranial elements. However, the high degree of fragmentation prohibits confident identification of these elements to species. Only 74 (7.4 %, MNI= 11) specimens can be confidently identified as representing *Macaca sinica* and 35 (3.5%, MNI=8) were identified as from langurs (*Semnopithecus/Trachypithecus*). All skeletal elements were represented in the assemblage suggesting that complete monkey carcasses were brought in and processed on the site.

Distal articular ends of long bones and metapodials and other dense skeletal elements (carpals and tarsals) as well as teeth are slightly over-represented in the assemblage. In terms of anthropogenic signature, 35.8% of the identified cercopithecoid specimens exhibited evidence of burning. Cutmark frequency is relatively low, with only two specimens (a distal humerus and proximal femur fragment) exhibiting evidence of butchery. Age-at-death profile of cercopithecoid monkeys in the assemblage based on dental wear suggests deliberate targeting of sub-adults and adults. Most of the aged individuals fall within the age category J7 to A3 outlined by Ingicco et al., (2012) for the genus *Trachypithecus*. These individuals are of full sexual maturity, with completely erupted third molar (aged between 3 and 5 years old, Harvati, 2000; Bolter, 2011)

Sciurids represent the second most common taxa in the Holocene faunal assemblage of Kitulgala with a total of 654 dental and skeletal elements identified. 97.4% of the elements correspond in terms of size and morphology, particularly for dental elements, to comparative specimens of the grizzled giant squirrel (*Ratufa macroura*) while the rest (NISP= 17) represent flying squirrels (*Petinomys/Petaurista*). Burning and calcination were observed in 12.3% and 5.4% of the identified sciurid specimens, respectively. Other small mammals identified in the assemblage include civet cats (9.3% NISP, MNI=25), otters (0.4% NISP, MNI=6), chevrotains (4.3% NISP, MNI=21) and porcupines (2.7% NISP, MNI=15). Similar to cercopithecoids, these animals are represented mostly by dental and dense postcranial elements.

A total of 222 specimens representing large mammals were recorded in the assemblage. From these, 23.4% can be assigned confidently to taxa. These include 11 (0.4% NISP, MNI=5) suid specimens, 36 (1.2% NISP, MNI=9) cervid and 5 (0.2% NISP, MNI=4) bovid fragments. Anthropogenic modifications were mostly restricted to burning (12.6%). Butchery marks were not observed in any large mammal bone fragments, albeit a proximal cervid metatarsal exhibited evidence of impact fractures and two bovid and one cervid metapodial fragments showed evidence of modifications consistent with tool/artefact production.

Non-mammalian fauna represents 15.2% (19.7% NISP) of the animal remains from the site. Fish (NISP=149) are represented mostly by cyprinids (carps), identified from pharyngeal teeth and certain cranial elements. Silurid (catfish) specimens (spine) were also identified, albeit in very low frequency (NISP=4). Reptiles (11.1% NISP) on the other hand are represented by varanids, pond/river turtles, agamid/iguanid lizards, pythons and colubrid snakes (Table 5). The fish bones recorded in the site exhibited a high degree of burning (40.9%). Likewise, several reptile bone fragments, particularly varanids and *Python*, exhibited evidence of burning and calcination (11%), suggesting that they were probably also utilized as a food source. Although bird skeletal elements are present in all sedimentary contexts dated to the Holocene (2.1% NISP), only 20 (23.8%) fragments can be confidently identified to taxa. These include owls (Strigidae), swifts (Apodidae) and jungle fowls (Phasianidae).

Several animal taxa in the assemblage, such as frogs (1.6% NISP) and micromammals (<1kg) including murids (3% NISP) were most likely accumulated by non-human cave dwelling species (i.e. raptors). This is in addition to the colubrid snakes and small agamid lizards mentioned earlier. Swifts and bats (5.6%), on the other hand, most likely represent the rockshelter's natural faunal communities.

4.3 Osseous Technology

A total of 21 (0.38% of the bone assemblage studied) finished tools manufactured from small mammal long bones were identified in the site, including 10 finished unipoints, seven bipoints, and four geometrics (Figure 3). Morphological features retained in some of the unipoints in the assemblage suggest that they were manufactured from cercopithecoid fibulae (Figure 3A) and ulnae (Figure 3B). The bipoints and the geometrics (Figure 3C-G), on the other hand, were most likely manufactured from cercopithecoid humerus or femur shaft fragments. However, further studies are needed to confirm this. At Fa Hien-lena, the bipoints and geometric bone tools from the Terminal Pleistocene and Early to Mid-Holocene layers were manufactured from cercopithecoid femur shaft fragments, based on the presence of blanks and unfinished tools (Wedage et al., 2019; Langley et al., 2019).

In terms of typology, the osseous tools recorded in Kitulgala Beli-lena are identical to those identified at Fa Hien-lena (Wedage et al., 2019a; Langley et al., 2019) and Batadomba-lena (Perera et al., 2011). The unipoints exhibit side notches suggesting that they were hafted to a shaft by ligature. These hafted bone points, again like those found in Fa Hien, most likely represent projectile points that were used by hunter-gatherers to selectively target certain arboreal animals (Wedage et al., 2019a; Langley et al., 2019). This is also consistent with the high-impact fracture observed in some of these specimens. However, unlike in Fa Hien-lena where 1.7% (N=246) of the faunal remains studied exhibited modifications consistent with tool manufacture (grinding/polishing) (Wedage et al., 2019a), only finished tools were identified in Kitulgala Beli-lena. This suggests that the tools were not manufactured in the site, or at least in this part of the rockshelter.

In addition to finished tools manufactured from small mammal bones, three bone tool fragments manufactured from cervid metapodial shafts were also recorded in the Holocene layers of the site. The fragments represent scraper and spatula-type tools, again similar to those recorded in Fa Hien-lena. The use wear on the edges of the tools identified in Kitulgala resemble the use wear of flaked tools recorded in Fa Hien-lena, such as striations suggestive of use as scrapers (Langley et al., 2019). Overall, the similarity of the osseous tools recovered from Kitulgala Beli-lena to those from Fa Hien-lena as well as those from Batadomba-lena suggests a shared technology that facilitated hunting and foraging in the rainforest environments of Sri Lanka.

4.4 Invertebrate Fauna

The total data for the invertebrate assemblage recovered from the 2017 excavation of Kitulgala Beli-lena is presented in Table 6, listing the taxonomic categories and total quantification data (NISP and weight) for each. The sample size reported here is relatively small, with a total NISP of 3799 and total weight of 2002.90g (or *ca.* 2kg). Similar to animal bones, the invertebrate remains were recovered only in layers dating to the Holocene and no specimens were recovered from Pleistocene contexts.

Breaking down the identified taxonomic groups, there is one category at the family level (9.63% NISP, 9.17% Wt), five categories at the genus level (40.96% NISP, 27.03% Wt), nine categories at the species level (40.91% NISP, 63.23% Wt), and three indeterminate categories (8.50% NISP, 0.58% Wt). The latter category encompasses indeterminate crab, land snail, and shell, all of which do not retain key characteristics for identification beyond these broad attributions. Figure 4 graphs the taxonomic categories in descending order (highest to lowest) by %NISP (Figure 4A) and % weight (Figure 4B). Taxonomic rank order varies based on the quantification measure used, a factor that relates to shell size and morphology, robusticity, and also likely the differential degree of taphonomic modification within and between taxa.

Regardless of the quantification measure used, the dominant taxa are the Paludomidae (freshwater gastropods) and the Acavidae (terrestrial gastropods). In many respects this is not unexpected, particularly given the similar trends reported for the Batadomba-lena rockshelter invertebrate assemblage (Perera et al. 2011). This dominance is also apparent when the assemblage is rank ordered by family (Figures 5A and 5B), where the Paludomidae and Acavidae are ranked first and second, followed by the indeterminate categories, by both %NISP and %weight. In combination with the occurrence of freshwater Unionidae bivalves, these data indicate the presence of flowing freshwater and lowland rainforest habitats around Kitulgala Beli-lena during the Holocene.

The distribution of the freshwater and terrestrial molluscs by context is presented in Table 7. These data are based on family or genus level, to account for some of the issues surrounding accurate identification to species level noted earlier. Based on these data, there would appear to be a level of consistency in taxonomic representation and habitat exploitation throughout the Holocene sequence at Kitulgala Beli-lena. The *Paludomus* spp. (range 76.9-86.3% NISP) and Acavidae (range 8.4-13.7% NISP) dominate the assemblage and occur relatively consistently across these contexts, with the freshwater bivalve *Lamellidens* sp. and the terrestrial gastropod *Cyclophorus* spp. occurring at very low percentages. The ratio of freshwater to terrestrial molluscs through the sequence also stays relatively consistent as a result, ranging between 6.2 and 7.4 in contexts 7/5, 4, 3 and 2, with a minor increase in freshwater taxa occurring in context 27 (with a ratio value of 9.7).

These data suggest that there was a consistent focus on clean, flowing freshwater environments for the exploitation of molluscan resources, with some exploitation, albeit to a lesser extent, on lowland rainforest habitat gastropods. At Batadomba-lena, analyses of the invertebrate sample indicate that there was an increase in mollusc deposition after *ca.*16,000 cal. BP, with freshwater taxa increasing and terrestrial taxa decreasing into the terminal Pleistocene (Perera et al. 2011). While the Kitulgala Beli-lena molluscan assemblage does not extend beyond the Holocene, the dominance of the freshwater taxa would appear to correspond with the expectations derived from the molluscan faunal shifts seen at Batadomba-lena rockshelter. The Kitulgala Beli-lena invertebrate faunal assemblage presents a similar range and distribution of freshwater and arboreal/terrestrial taxa to that seen in other cave sites in southwest Sri Lankan rainforest environments, particularly Batadomba-lena rockshelter.

4.5 Plant Remains

Preliminary assessment of the macrobotanical assemblage from the Pleistocene sedimentary contexts of Kitulgala Beli-lena revealed the presence of charred plant remains in all contexts analysed. These remains included charred fragments of wood, nutshell, fruits, and seeds. Overall, preservation in these contexts is limited with the macroremains generally exhibiting a

high degree of fragmentation. The identification of these remains is ongoing however initial assessment indicates the likely presence of economic taxa including cf. *Artocarpus* sp. (breadfruit) and cf. *Canarium* sp. ('kekuna' nut).

Charred fragments of fruit exocarp comprising distinctive roundish to polygonal nodules or disks, ca. 1-2mm in size, with a small central perforation were identified in all five Pleistocene contexts analysed. Based on published descriptions including of previously identified archaeobotanical material from Holocene contexts at Kitulgala, these are tentatively identified as breadfruit (*Artocarpus* sp.) skin. Fissuring of the nodules is consistent with the fracture patterns observed in experimentally cooked and charred breadfruit cultivars in Oceania (Kahn and Ragone 2013), suggesting the charred Kitulgala fragments were also produced by roasting, though additional experiments with Sri Lankan wild varieties is needed to replicate these observations. In addition, a single fragment of cf. *Canarium* sp. endocarp (nutshell) was identified in Context 10. The fragment was <3mm in size and identified tentatively based on the presence of a distinctive cellular pattern observed on the inner seed locule (Fairbairn pers. comm. 2018). Additional comparative work with modern reference material is needed to confirm this identification. Other nutshell fragments were also observed in other contexts but these have not yet been identified.

The presence of cf. *Artocarpus* sp. and cf. *Canarium* sp. in the archaeobotanical assemblages is consistent with a rainforest plant food economy being practised at Kitulgala throughout the Late Pleistocene, as also observed at other rockshelter sites in the Wet Zone (Perera et al. 2011; Kajale 1988). Previous archaeobotanical studies at Kitulgala also identified charred breadfruit and *Canarium* remains, as well as wild banana (*Musa* sp.) in Holocene deposits dating to at least 12,500 BP. Whilst additional work is needed to confirm the identifications of the new Kitulgala samples, the present study tentatively extends the chronology of the rainforest subsistence economy into the Pleistocene. Furthermore, it indicates that at least wild breadfruit was probably exploited from initial occupation of the site at around 44,000 years ago. Wild breadfruit (*Artocarpus nobilis*) and kekuna nut (*Canarium zeylanicum*) are both endemic to Sri Lanka and grow today in the lowland rainforest (Gunatilleke et al. 2008). Together these provide a rich source of starch, fats and protein, and require little processing other than cooking (in the case of breadfruit), making them high ranked food resources. The storability and transportability of *Canarium* nuts would have made them an attractive resource for a mobile hunter-gatherer population.

4.6 Lithic Technology

The lithic assemblage of Kitulgala Beli-lena comprised of 15,151 lithic items and 33 quartz pebbles, probably utilized as hammerstones (Table 8). The main raw material used was quartz, with small numbers of chert artefacts identified, including four flakes and one fragment in the Holocene, five flakes, two chips and one core-on-flake in the Terminal Pleistocene, and three flakes and three fragments in the Late Pleistocene. Small and medium size quartz pebbles can be found in immediate vicinity of the site, including in the nearby stream and in open sedimentary sections. The primary source of chert is unresolved, and likely represents elements of toolkits that have been transported to the site.

The technological reconstruction of the lithic *chaîne opératoire* indicates the continuous use of the bipolar-on-anvil method from the Late Pleistocene to the Holocene. The cores are characterized by the typical battering marks of the hammerstones on the proximal end and by small breakages produced by the contact with the anvil. Generally, the quartz pebbles were

exploited along their longer axis in order to maximize the length of the by-products. At times, during the knapping events, the striking platforms were shifted in order to achieve a better stability on the anvil. This behaviour is common in the different chronological phases and several examples document the opportunistic use of striking platforms opposed to flat surfaces, natural or created during the reductions (Figure 6, 2-3), and the rotations of the cores of 90° degrees (Figure 6, 1), producing flakes with orthogonal scars on the dorsal surfaces.

The flake assemblage is composed mostly of fragments and small chips whereas complete flakes and flake bladelets are recorded in lower frequencies (Table 9, Figure 6, 4-8). Comparison of unbroken flakes by length intervals indicates that the knapping events were aimed to produce small blanks with the size of most of the artefacts smaller than 30 mm (Figure 7). However, some slight changes through time were documented. From the Late Pleistocene, there was a decrease in the frequency of flakes smaller than 20 mm and an increase in the frequency of artefacts in the intervals of 30 - 40 mm (Figure 7). Since during the bipolar-on-anvil reduction, the size of knapping by-products is not controlled as in other hierarchical technologies (Picin and Vaquero, 2016; Boëda, 2013), the greater number of larger flakes during the Terminal Pleistocene and Holocene could be linked to the gathering of bigger quartz nodules or the exploitation of different secondary outcrops where larger cobbles were available. Typical by-products of the bipolar-on-anvil reduction sequences are few in the flake assemblage. Siret knapping accidents represent 10.5% of the fragments from the Late Pleistocene, 8.4% from the Terminal Pleistocene and 7.1% from the Holocene. Conversely, splinter piece total only 32 blanks in Late Pleistocene, 33 blanks in the Terminal Pleistocene and 25 blanks in the Holocene.

Although they were documented, albeit in low frequencies, in previous fieldwork and analyses (Roberts et al., 2015a; Lewis, 2017), retouched tools and backed microliths are absent in the lithic assemblage analysed. From the 24,772 artefacts and more than 500,000 pieces of debris recorded in previous excavations, only 28 were identified as retouched tools. The technological continuity recorded at Kitulgala Beli-lena is in accordance with the evidence documented in other cave sites located in the modern Wet Zone rainforest of Sri Lanka. At Fa Hien-lena Cave, the lithic production was aimed at small blanks, and the bipolar-on-anvil method on quartz, with the expedient technique of rotating the core and changing the striking platform, was used from ~48-45 ka up to the Holocene (Wedage et al., 2019a; 2019b). At Batadomba-lena Cave, bipolar cores were found in association with freehand flake and bladelet cores along with numerous backed microliths, a type of artefact that is not generally found in the other two sites (Lewis, 2017).

5. Discussion

Human behaviour and adaptations at Kitulgala Beli-lena

Our data provide new insights into the foraging strategies and material culture of human populations living at the site of Kitulgala Beli-lena. Firstly, our new radiocarbon dating programme has dramatically revised the dates for the site, making it now one of the oldest dated rockshelter/cave sites in Sri Lanka, and indeed South Asia more broadly. Indeed, the earliest occupation date of 44,000 cal. years BP places it approximately contemporaneous to Fa Hien-lena Cave and now earlier than the 38,000-36,000 cal. years BP recorded for Batadomba-lena (Perera et al., 2011; Roberts et al., 2015a). This re-dating emphasises the importance of applying robust pre-treatment methodologies in the tropics (as also highlighted by Higham et al. (2008) for the Niah Caves, Borneo), in order to avoid erroneously young dates as a result of

detrital contamination. In the context of charcoal, this involves the application of the Acid Base Oxidation (ABOX) pre-treatment steps (Higham et al., 2008). Moreover, the re-dating of Kitulgala Beli-lena confirm the early presence of humans in the Wet Zone rainforests of Sri Lanka as early as *ca.* 45,000 years ago, an assertion that was previously solely based on the record at Fa Hien-lena (see also Wedage et al., 2019a).

The multidisciplinary approach presented here also enables us to confirm that this early record of human presence at Kitulgala Beli-lena is associated with clear evidence for rainforest foraging throughout the sequence. Archaeobotanical evidence from the Late Pleistocene and Holocene levels demonstrates the continued extraction and use of wild breadfruit (*Artocarpus nobilis*) and kekuna nut (*Canarium zeylanicum*) by foragers at the site. Both of these plants provide a rich source of starch, fats, and protein, and require little processing. This makes them highly productive food resources in an environment that has often been considered to lack reliable plant-based sources of carbohydrate and protein (Bailey et al., 1989; Gamble, 1993). *Canarium* sp. nuts have also been documented at Fa Hien-lena and Batadomba-lena (Perera et al., 2011; Wedage et al., 2019a), as well as Late Pleistocene sites in Southeast Asia and New Guinea (Summerhayes et al., 2010; Barker and Farr, 2013), highlighting their potential significance to early human tropical foragers in these parts of the world.

Zooarchaeological and taphonomic insights from the Holocene layers (8,029-10,577 cal. BP) of Kitulgala Beli-lena further support a specialized rainforest exploitation and use of small mammals, primarily semi-arboreal and arboreal primates and squirrels, that has been documented with striking similarities at Late Pleistocene and Holocene levels at Fa Hien-lena and Batadomba-lena. Wijeyapala (1997) reported the presence of animal bones in the Pleistocene layers of Kitulgala during his excavation of the outer, eastern section of the rockshelter. Although no systematic zooarchaeological analyses were conducted, he noted the presence of cercopithecoid bone fragments in the site's lower sediment layers. Interestingly, however, faunal remains were not recorded from the Pleistocene levels during the 2017 excavations of the inner western section of Kitulgala Beli-lena. The absence of any animal skeletal or dental remains was also noted in the sediment micromorphological analysis conducted by Kourampas et al. (2009). This seemingly indicates that animal butchery and processing was done in different parts of the site during the Pleistocene.

The osseous and lithic technological remains recovered from Kitulgala Beli-lena further confirm evidence from Fa Hien-lena that Late Pleistocene and Holocene foragers in Sri Lanka had developed a sophisticated repertoire for the exploitation of their immediate landscapes. Osseous tools were found within the Holocene levels of Kitulgala Beli-lena, including finished unipoints, bipoints and geometrics. The bone points were most likely utilized as projectile points similar to those found in Fa Hien-lena (Wedage et al., 2019a; Langley et al., 2019). The lithic materials, while not representing any backed microliths, show a bipolar-on-anvil reduction method on quartz with stark similarities to those seen at Fa Hien-lena and Batadomba-lena where microlithic points appear to have been the final goal (Lewis et al., 2014; Lewis, 2017; Wedage et al., 2019a; 2019b). The absence of retouched tools and backed flakes in this area of the site may indicate that tool-use occurred in a different part of the rockshelter or at another location altogether. Since faunal remains were recorded previously in the Pleistocene deposits (Wijeyapala, 1997) and they are lacking in the area excavated in 2017, it is probably that butchering activities, microlith preparation, and gear retooling were carried out in specific tasks locations of the rockshelter. This different spatial distribution of the remains suggests a complex organization of the site that is common in prolonged (long-term) settlements (Bartram et al., 1991; O'Connell et al., 1991). This, alongside the lack of bone tools and faunal remains

from the Late Pleistocene layers, supports the differential use of space by Late Pleistocene and Holocene foragers at Kitulgala Beli-lena.

Recent analysis of the lithic assemblages of the previous excavations recorded the presence of 27 microliths in the Late Pleistocene, and four in the terminal Pleistocene. Similarly, where bone tools are present in Holocene levels, there is no *débitage* evidence implying that they were manufactured elsewhere. As a result, while material culture and archaeobotanical and zooarchaeological evidence at Kitulgala Beli-lena, and its neighbouring sites, demonstrates a well-tuned, persistence foraging adaptation to the rainforest environments of Sri Lanka, there appears to be spatial complexity into how this adaptation was practised on a site and landscape basis, represented within a given site, in a given period, and, indeed, perhaps across the landscape. Given that systematic lithic, material culture, and subsistence analysis has now taken place at Fa Hien-lena (Deraniyagala, 1992; Roberts et al., 2015b; Wedage et al., 2019a,b), Batadomba-lena (Perera, 2010; Perera et al., 2011; Roberts et al., 2017a), and, here, Kitulgala Beli-lena (sites that lie within 100km² radius of each other in the Wet Zone evergreen rainforests), future, systematic comparative work promises to further enrich understandings of the spatial organisation of tropical rainforest use by Late Pleistocene and Holocene hunter-gatherers on the island of Sri Lanka.

Kitulgala Beli-lena in context - Late Pleistocene-Holocene rainforest foraging and its social context in Sri Lanka and South Asia

The multidisciplinary evidence from Kitulgala Beli-lena, Fa Hien-lena, and Batadomba-lena now demonstrates the persistent use of tropical rainforest resources from 48,000-45,000 years ago through to 3,000 years ago in the Wet Zone of Sri Lanka (Wedage et al., 2019a). Stable isotope evidence from human and animal tooth enamel from Batadomba-lena, Fa Hien-lena, and Balangoda Kuragala demonstrates that between 36,000 and 3,000 years ago human foragers were reliant on tropical rainforest resources year round (Roberts et al., 2015a, 2017b), while detailed zooarchaeological and archaeobotanical information demonstrates that this lifestyle was supported by a heavy focus on semi-arboreal and arboreal primates and tree products and supplemented by freshwater molluscs and squirrel taxa (Perera et al., 2011; Wedage et al., 2019a). This research, as well as finds in East Africa, Southeast Asia, and Melanesia (Barker et al., 2007; Summerhayes et al., 2016; Shipton et al., 2018) has gone a significant way to rehabilitating tropical rainforests as key habitats for *Homo sapiens* during its dispersal within and beyond Africa - environments that were once considered barriers to human dispersal (Gamble, 1993; Bird et al., 2005; Boivin et al., 2013). The scale and intensity of rainforest occupation and exploitation in Sri Lanka during the Late Pleistocene remains to be fully elucidated. Although one could argue that this occupation is characterized by highly-mobile and low density human populations, growing evidence, including from stable isotope analyses (Roberts et al., 2017a), as well as intense evidence of occupation of rockshelter and cave sites (Perera et al., 2011; Wedage et al., 2019a; 2019b), suggests the persistent presence of groups fully adapted to the dynamics of a rainforest environment.

Such a specialized adaptation is supported by evidence reported here from Kitulgala Beli-lena that tool production and faunal butchery may have taken place across a wider social and economic landscape in the Wet Zone rainforests of Sri Lanka. It is possible that Kitulgala Beli-lena, Fa Hien-lena, and Batadomba-lena all formed part of a network of hunting ranges, plant exploitation routes, and settlement strategies that were likely also augmented by open-air sites that may never be discovered (see Mercader et al., 2003 for pessimism in this regard in the

Central African rainforest). Such a network between different groups, potentially operating simultaneously, is also supported by growing evidence for contact between foraging communities in the rainforest and populations on the coast. Evidence for marine shell beads and shark teeth has emerged in the Pleistocene and Holocene levels of Fa Hien-lena and Batadomba-lena (Perera, 2010; Perera et al., 2011; Langley et al., 2019), as well as the Dry Zone site of Bellan-bandī Palassa (Perera, 2010). These items were most likely obtained by trade with groups present in Sri Lanka's southern coast, identified in sites such as Bundala, Patirajawela and Minihaḡalkanda (Deraniyagala, 1992), given that isotopic evidence points to year-round reliance to rainforest resources by communities in the island's Wet Zone (Roberts et al., 2015a, 2017a). As a result, it seems that the Wet Zone rainforests were home to an established population that was part of wider social and symbolic networks with groups living in other Sri Lankan biomes, not only on the coast but potentially also in the drier north and south-eastern reaches given the lack of Pleistocene investigation of these regions to-date (Deraniyagala, 1992; Roberts et al., 2015b).

Intriguingly, the basic lithic assemblage of bipolar flaked cores on quartz documented at the early rainforest sites in Sri Lanka, persists at postulated coastal sites, as well as at a number of Holocene hunter-gatherer sites (Roberts et al., 2015b). This includes the rockshelter site of Balangoda Kuragala in the Intermediate Zone, Bellan-bandī Palassa in the Dry Zone, a series of 'Microlithic' shell middens sites and, indeed, underlying contexts at the later Iron Age and urban site of Anuradhapura (Deraniyagala, 1992, 1997; Perera, 2010). Bone tools, supposedly of a similar nature to those found in the Wet Zone, have also been documented at Bellan-bandī Palassa (Perera, 2010). On top of isotopic evidence for the persistence of rainforest reliance at Batadomba-lena and Fa Hien-lena until 3,000 years ago and the arrival of the Iron Age in this part of the island (Roberts et al., 2015a), it therefore appears that human groups using similar technological repertoires persisted in the different biomes of Sri Lanka throughout the Late Pleistocene and into the Early and Mid-Holocene. Moreover, these groups apparently remained connected by exchange, and perhaps cultural affinities, throughout this period. Exploration of the scale and demography of these populations will require future work in different parts of the island. However, it seems reasonable to assume that the Wet Zone foragers were not isolated, mobile populations leaving ephemeral traces on their environment. Rather, their ability to persist in these settings, and not hunt primate populations to extinction, implies a certain sustainability of rainforest resource exploitation, perhaps in the form of spatial variation in hunting routes during different times of year or variation in targeted taxa (Roberts, 2016).

A Wider South Asian and Asian Perspective

From earlier assumptions of a rapid coastal arrival in South Asia *ca.* 60 ka (Mellars, 2005, 2006; Field et al., 2007), pictures of the appearance of our species in this part of the world have become much more complex over the course of the last decade (Groucutt et al. 2015; Blinkhorn & Petraglia 2017; Roberts et al., 2017a). Significantly, given the data available from Kitulgala Beli-lena and the other Wet Zone sites of Sri Lanka, it is now clear that *H. sapiens* occupied and utilized a diversity of terrestrial environments, away from the coast, from its earliest arrival in South Asia. This includes the arid environments of the Thar Desert, from potentially as early as *ca.* 120 ka, perhaps supported by increased precipitation and the freshwater of palaeochannels and lakes (Blinkhorn et al., 2013, 2017, 2019). The Jurreru River Valley has also provided evidence for human populations in mosaic of dry forest, grassland, and riparian habitats, with fluctuating periods of aridity from 120 ka through to 30 ka (Petraglia et al., 2007; 2010, 2012; Clarkson et al., 2012). It is perhaps in Sri Lanka, however, that human adaptability to different extremes is most evident in South Asia. Here, sites producing the earliest current

evidence for human fossils in the entirety of South Asia, as well as long-term records of human behaviour, are associated with specialized adaptations to tropical rainforest environments from 48-45,000 years ago through to 3,000 years ago. While this is not to say that coasts were irrelevant to late Pleistocene human adaptations in this part of the world (Blinkhorn et al. 2017), and indeed future work on Sri Lankan coastal sites is likely to reveal prehistoric settlements in these parts of the island as well (Deraniyagala, 1992). It is now clear that the peopling of South Asia was far more complex than a coastal highway that rapidly brought uniform populations and technological strategies throughout this diverse region.

Research in South Asia over the past two decades points to a complex pattern of cultural and technological change following the initial *H. sapiens* colonization of the region. In north-western India, the Son Valley of north-central India and in the Jurreru Valley of southern India, it has been argued that Late Palaeolithic and microlithic toolkits transitioned from Middle Palaeolithic technologies (Clarkson et al., 2009; Petraglia et al., 2012; Blinkhorn et al., 2013; Clarkson et al. 2018). This can be clearly seen in the site of Jwalapuram, in the Jurreru Valley of southern India, where evidence points to persistence of Middle Palaeolithic populations across a 74 ka stratum that were eventually to produce transitional Middle and Late Palaeolithic assemblages (Petraglia et al., 2007; Clarkson et al. 2012). It also appears that microlithic and osseous tool technologies were utilized by communities occupying a diverse range of terrestrial environments far from the South Asian coast. Bone tools were recorded in the Jwalapuram Locality 9 site alongside Late Palaeolithic stone tools (Clarkson et al., 2009). Likewise, bone technology including projectile points presumed to have been utilized to hunt arboreal fauna, alongside quartz microliths, have been recorded in the earliest phase of occupation of the rock shelter sites in Sri Lanka's Wet Zone region (Deraniyagala, 1992; Perera, 2010; Perera et al., 2011; Wedage et al., 2019a; Langley et al., 2019). The sophisticated microlithic and osseous technologies, as well as ochre and symbolic beads, documented in these sites would not be out of place in the caves of western Europe 45,000 years ago (Conard, 2010) or in southern Africa from 100,000 years ago (Henshilwood et al., 2011), perhaps causing us to reorient our ideas of which ecological adaptations accompany symbolic, technological, and economic hallmarks of our species.

Evidence for Late Pleistocene rainforest occupation and resource utilization, akin to evidence from Sri Lanka's Wet Zone sites, has also been documented in Southeast Asia and Melanesia. The most comprehensive evidence for Late Pleistocene rainforest subsistence foraging strategies in the region comes from Niah Caves in Sarawak, Borneo. Niah Caves produced one of the earliest human fossils in Southeast Asia, dated to c. 44,000–40,000 cal. years BP (Barker et al., 2007; Higham et al., 2008; Reynolds and Barker, 2015). Results of detailed analyses looking at a wide range of archaeological materials including fauna, pollen, pytholiths, starch grains, and macrobotanical remains, point to complex foraging behaviours tailored to take full advantage of the rainforest environment (Barker and Farr, 2016). These include exploitation of an array of plant resources for food and possibly clothing, processing of toxic plants such as taros and yams, specialized targeting of wild boar, hunting of arboreal taxa including monkeys and civet cats, as well as collection and processing of freshwater molluscs (Barker et al., 2007; Barton et al., 2009; Barton, 2016; Hunt et al., 2012; Piper and Rabett, 2014; 2016; Szabó, 2016). These activities were facilitated by some of the earliest bone tools found in Southeast Asia (Rabett and Piper, 2012; Rabett, 2016) in addition to flake based stone tool technologies (Reynolds, 2016; Barton, 2016). The earliest human occupation of Melanesia is also associated with rainforest foraging. Sites in the Ivane Valley region of Papua New Guinea produced evidence for processing of *Dioscorea* yams and *Pandanus* nuts as early as 49,000–43,000 cal. years BP (Summerhayes et al., 2010). Human occupation of rainforests have also been recorded

in the Bismarck Archipelago at sites in New Ireland dated to c. 40,000 cal. years BP (Leavesley, 2005) and in West New Britain c. 35,000 cal. years BP (Pavlides, 2004; Summerhayes et al., 2017).

It is now becoming increasingly apparent that what truly characterises our species is its emergence at a time of increasing climatic and environmental variability in Africa (Potts et al., 2019). Not only did this act as the background for the evolution of diverse human populations in different parts of this continent (Scerri et al., 2016), but it is also the situation that met members of *H. sapiens* moving into Europe, Asia, Australasia, and the Americas during the Late Pleistocene (Roberts and Stewart, 2018). While in some cases coastal environments or savannah settings may have been significant to human populations utilizing new projectile technologies, and developing novel symbolic networks (Shea, 2011; Marean, 2016), these behaviours also supported the movement of populations into more ‘extreme’ environments including high-altitude settings (Stewart et al., 2016), desert settings (Hiscock and Wallis, 2005; Nash et al., 2016), the arctic (Pitulko et al., 2016), and tropical rainforests (Barker et al., 2007; Roberts and Petraglia, 2015; Roberts et al., 2017a; Westaway et al., 2017). While research focus on these latter environments has been largely lacking in contrast to temperate and grassland parts of Europe and Africa, two decades of research has revealed a vast wealth of information into human subsistence, technological adaptations, and symbolic behaviours (Aubert et al., 2014; 2018; Langley et al., 2019). Increased multidisciplinary excavation, and analysis in parts of the world dominated by these more ‘extreme’ habitats in the present, as well as the past, has the possibility to enable us to build a more complete picture of the ecological and social adaptations that make us human, and enabled us to colonize nearly the entirety of the planet by the end of the Pleistocene.

Acknowledgements:

The authors thank the Max Planck Society and the University of Sri Jayewardenepura for funding the research. We acknowledge Prof. S. Dissanayake, Prof. P.B. Mandawala, Mr. S.A.T.G. Priyantha, Mr L.V.A. De Mel and other members at the Excavations Branch of the Department of Archaeology, Sri Lanka, for assistance and support of our fieldwork. We would also like to thank Mr. S. Eregama, Mr. K.K. Ruwan Pramod, Mr. P.G. Gunadasa, Mr Suranga Jayasinha, Mr. K.A.S Lakmal, Mr. Tiran Ananda and Mr. J. Perera for their participation during fieldwork. We like to thank Prof. Alexander Kapukotuwa and other faculty members of the Department of History and Archaeology of the University of Sri Jayewardenepura. In addition, we appreciate the cooperation of Mr. Sunil Kannangara (District Sectary) of the town of Yatiyanthota, Sabaragamuwa Province.

Figures and Tables.

Table 1. Previous radiocarbon dates for Kitulgala Beli-lena (from Deraniyagala, 1992, Wijeyapala, 1997, Perera, 2010).

Stratum	Lab Code	^{14}C	cal. BP*
VIIa2	Beta 18448	3640 ± 60	4,150 - 3,829
VIIa1	PRL 1012	3170 ± 120	3,691 - 3,661
VIb1	Beta 18446	8160 ± 80	9,407 - 8,976
VIa1	Beta 18445	7040 ± 80	8,000 - 7,698
Va3	BS 287	$10,200 \pm 170$	12,517 - 12,493
Va3	BS 288	$10,280 \pm 170$	12,571 - 11,394
Va3	BS 289	$10,010 \pm 160$	12,156 - 11,146
Va3	PRL 861	$11,910 + 430/-410$	15,298 - 12,981
Va3	BS 290	$11,550 \pm 180$	13,751 - 13,076
Va3	Fra-91	$11,780 \pm 220$	14,155 - 13,151
Va3	BS-292	$11,570 \pm 210$	13,933 - 13,901
Va2	BS-292	$11,520 \pm 220$	13,825 - 12,901
Va1	BS-293	$12,240 \pm 160$	14,933 - 13,758
IVb3	Beta 33287	$11,860 \pm 70$	13,816 - 13,481
IVb2	BS-294	$11,750 \pm 390$	14,948 - 12,831
IVb2	Beta 33286	$13,150 \pm 80$	16,071 - 15,477
IIIc3	Beta 33285	$13,150 \pm 90$	16,084 - 15,435
IIIc2	Fra-163	$15,780 \pm 400$	20,086 - 18,236
IIIc2	Fra 164	$16,400 \pm 650$	21,605 - 18,458
IIIc2	Beta 18443	$18,050 \pm 180$	22,352 - 21,414
IIIc1	Beta 18442	$17,810 \pm 170$	22,001 - 21,036
IIb1	PRL 1013	$17,870 + 510/-530$	22,862 - 20,411
IIb1	Beta 18441	$18,900 \pm 350$	23,666 - 22,024
IIa3	Beta 33283	$20,560 \pm 130$	25,190 - 24,370
IIa2	Beta 18439	older than 26,425	-

*All samples were calibrated using the OxCal 4.3 software (Bronk Ramsey 2017) and IntCal calibration curve (Reimer et al., 2013)

Table 2. *New radiocarbon dates from the 2017 excavation of Kitulgala Beli-lena*

Context	Labcode (OxA)	Measured Date	Calibrated (cal. BP)*
3	37930	7,309 \pm 34	8,181- 8,029
5	37932	9,230 \pm 40	10,512 - 10,262
6	37933	9,280 \pm 37	10,577 - 10,372
8	37934	10,015 \pm 39	11,712 - 11,314
9	37935	13,360 \pm 50	16,259 - 15,878
10	37936	13,960 \pm 50	17,157 - 16,676
17	37808	28,420 \pm 180	32,956 - 31,681
17	37789	31,880 \pm 390	36,611 - 34,921
19	37809	33,120 \pm 330	38,322 - 36,412
19	37810	33,230 \pm 390	38,476 - 36,420
21	37724	32,410 \pm 260	35,669 - 37,062
22	X-2782-17	37,500 \pm 1700	45,713 - 38,867
23	37483	39,900 \pm 700	44,902 - 42,593

*All samples were calibrated using the OxCal 4.3 software (Bronk Ramsey 2017) and IntCal calibration curve (Reimer et al., 2013)

Table 3. Major phases of Kitulgala Beli-lena occupation based on radiocarbon dates and site stratigraphy.

Occupational Phase	Sedimentary Context (2017)	Dates (cal. BP)	Sedimentary Stratum (1983)	Dates (cal. BP)*
Historical	1	-	Xa3	-
Holocene	3	8,181- 8,029	-	-
	5	10,512-10,262		
	6	10,577- 0,372		
	8	11,712-11,314		
Terminal Pleistocene	9	16,259 -15,878	IVb3	13,816-13,481;
			IVb2	14,948-12,831
	10	17,157 -16,676	IVb2	16,071-15,477
			IVa	
Late Pleistocene	12, 13, 14, 15, 20	-	IIIc3	16,084-15,435;
			IIIc2	20,086-18,236; 21,605-18,458; 22,352-21,414
	17	32,956 - 31,681; 36,611 - 34,921	IIIc1	22,001-21,036
	19	38,322 - 36,412; 38,476 - 36,420		
	21	35,669 - 37,062		
	18, 39, 41	-		
	22	45,713 - 38,867	IIIa3	25,190 - 24,370
	23	44,902 - 42,593		
	24	-		
	25	-	IIIa2	older than 26,425†

*All samples were calibrated using the OxCal 4.3 software (Bronk Ramsey 2017) and IntCal calibration curve (Reimer et al., 2013)

†uncalibrated

Table 4. Vertebrate remains recovered from the 2017 excavation of Kitulgala Beli-lena.

Context	Unidentifiable Bone Fragments					NISP	% NISP	TNF
	Micromammal	Small Mammal	Large Mammal	Non-Mammals	Total			
2	54	124	24	22	224	345	60.6%	569
3	61	244	45	49	399	621	60.9%	1020
4	68	327	38	63	496	714	59.0%	1210
5	41	341	27	5	414	421	50.4%	835
6	10	92	10	22	134	198	59.6%	332
7	45	287	14	20	366	321	46.7%	687
27	32	288	12	46	378	471	55.5%	849
Total	311	1703	170	227	2411	3091	56.2%	5502

Table 5. Number of identified specimens and minimum number of individuals of the different vertebrate taxa identified in Kitulgala Beli-lena.

Class	Order	Family	Taxon	2		3		4		5		6		7		≥7		TOTAL	
				NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Actinopterygii	Cypriniformes	Cyprinidae		8	-	28	-	21	-	27	-	7	-	10	-	26	-	127 (4.1%)	-
				2	1	3	1	4	1	2	1	1	1	1	1	5	1	18 (0.6%)	7
Amphibia	Anura	Syluridae		1	1	1	1	-	-	1	1	-	-	-	-	1	1	4 (0.1%)	4
				2	1	7	2	11	4	9	3	8	3	4	1	10	3	51 (1.6%)	17
Aves	Apodiformes	Apodidae		5	-	5	-	4	-	4	-	2	-	5	-	5	-	30 (1.0%)	-
				1	1	3	1	-	-	1	1	3	1	2	1	1	1	11 (0.4%)	6
Reptilia	Testudines	Testudinidae		3	1	4	2	2	1	1	1	2	1	4	2	4	1	20 (0.6%)	9
				1	1	-	-	-	-	1	1	-	-	-	-	1	1	3 (0.1%)	3
Mammalia	Primates	Cercopithecidae		1	1	3	1	3	1	3	1	2	1	1	1	4	1	17 (0.5%)	7
				2	1	8	2	4	1	3	2	1	1	5	2	6	2	30 (1.0%)	11
Mammalia	Rodentia	Hystriidae		1	1	2	1	5	2	4	1	4	1	3	1	4	1	23 (0.7%)	8
				1	1	1	1	2	1	-	-	2	1	1	1	1	1	8 (0.3%)	6
Mammalia	Rodentia	Sciuridae		21	1	37	2	32	1	10	1	8	1	16	1	28	1	152 (4.9%)	8
				14	1	21	1	29	3	9	1	7	1	14	1	21	2	114 (3.7%)	9
Mammalia	Rodentia	Sturnidae		32	7	172	12	254	18	105	11	46	5	104	9	119	10	892 (28.9%)	72
				7	1	18	3	14	2	10	1	6	1	9	1	10	2	74 (2.4%)	11
Mammalia	Rodentia	Sturnidae		5	1	8	2	9	1	5	1	2	1	3	1	3	1	35 (1.1%)	8
				10	2	13	2	12	2	18	3	8	1	10	2	11	3	82 (2.7%)	13
Mammalia	Rodentia	Sturnidae		76	8	157	15	127	10	109	12	39	4	41	5	68	6	637 (20.6%)	60
				2	1	3	2	4	2	4	2	1	1	2	1	1	1	17 (0.5%)	10
Mammalia	Rodentia	Sturnidae		12	2	16	3	24	5	4	2	7	2	16	3	14	4	93 (3.0%)	21
				1	1	1	1	1	1	1	1	1	1	1	1	1	1	4 (0.1%)	3
Mammalia	Rodentia	Sturnidae		18	3	22	4	42	5	24	3	8	2	15	3	32	3	161 (5.2%)	25
				1	1	-	-	-	-	-	-	-	-	1	1	-	-	2 (0.1%)	2
Mammalia	Rodentia	Sturnidae		1	1	1	1	1	1	-	-	-	-	-	-	-	-	2 (0.1%)	2
				34	4	45	4	64	5	35	4	22	2	37	2	49	4	286 (9.3%)	25
Mammalia	Rodentia	Sturnidae		1	1	4	1	3	1	3	1	1	1	1	1	1	1	13 (0.4%)	8
				12	4	30	4	33	4	21	2	6	2	10	2	21	3	133 (4.3%)	21
Mammalia	Rodentia	Sturnidae		2	1	2	1	3	1	3	1	-	-	-	-	1	1	11 (0.4%)	5
				8	2	4	1	7	2	4	1	4	1	6	1	3	1	36 (1.2%)	9
Mammalia	Rodentia	Sturnidae		1	1	2	1	-	-	1	1	1	1	-	-	-	-	5 (0.2%)	4
				345	52	621	71	714	73	421	60	198	35	321	44	471	59	3091	394

Table 6. Taxonomic categories and total quantification data of the invertebrate remains from Kitulgala Beli-lena.

Habitat	Family	Taxon	NISP	%NISP	Wt (g)	%Wt		
Freshwater	Paludomidae	<i>Paludomus</i> spp.	1527	40.19	521.89	26.06	NISP	0-200
		<i>Paludomus bicinctus</i>	648	17.06	465.16	23.22		200-400
		<i>Paludomus chilinoideis</i>	118	3.11	99.79	4.98		400-600
		<i>Paludomus loricatus</i>	62	1.63	29.86	1.49		600-800
		<i>Paludomus neritoides</i>	230	6.05	219.17	10.94		800-1000
		<i>Paludomus solidus</i>	241	6.34	240.22	11.99		>1000
		<i>Paludomus sulcatus</i>	244	6.42	149.65	7.47		
		Unionidae	<i>Lamellidens</i> sp.	6	0.16	3.3	0.16	Weight
	Terrestrial	Acavidae	Acavidae	366	9.63	183.59	9.17	
<i>Acavus</i> spp.			18	0.47	13.42	0.67		200-300
<i>Acavus haemostoma</i>			1	0.03	12.2	0.61		400-500
<i>Acavus superbus</i>			8	0.21	45.32	2.26		500-600
cf. <i>Oligospira</i> sp.			3	0.08	0.97	0.05		
Cyclophoridae		<i>Cyclophorus</i> spp.	2	0.05	1.86	0.09		
		<i>Cyclophorus menkeanus</i>	2	0.05	4.98	0.25		
		Indeterminate	Indet Crab	1	0.03	0.88	0.04	
Indet Landsnail	2		0.05	0.13	0.01			
Indet Shell	320		8.42	10.51	0.52			
Total			3799		2003			

Table 7. *Kitulgala Beli-lena taxonomic distribution at family or genus level by sedimentary context (contexts 7 and 5 combined).*

Habitat	Taxon	Context									
		2 NIS P	%	3 NIS P	%	4 NIS P	%	27 NIS P	%	7/5 NIS P	%
Freshwater	<i>Paludomus</i> spp.	349	84.91	1328	80.68	473	76.91	756	80.68	164	86.32
	<i>Lamellidens</i> sp.							6	0.64		
Terrestrial	Acavidae	49	11.92	178	10.81	64	10.41	79	8.43	26	13.68
	<i>Cyclophorus</i> spp.	1	0.24	2	0.12	1	0.16				
Total Context NISP		411		1646		615		937		190	
Freshwater:Terrestrial Ratio		6.98		7.38		7.28		9.65		6.31	

Table 8. *Total number and percentage of the lithic assemblages of Kitulgala Beli-lena by chronological phases.*

Phase	Flake	Flake Bladelet	Fragment	Debris	Core	Core Frag.	Hammer	Total
Holocene	523	9	2367	620	43	34	7	3603
%	14.5	0.2	65.7	17.2	1.2	0.9	0.2	100
Terminal Pleistocene	592	1	2635	3230	68	45	6	6577
%	9	0	40.1	49.1	1	0.7	0.1	100
Late Pleistocene	544	2	2324	1998	57	67	20	5012
%	10.9	0	46.4	39.4	1.1	1.3	0.4	100
Total	1659	12	7326	5848	168	146	33	15192
%	10.9	0.1	48.2	38.5	1.1	1	0.2	100

Figure 1. Map of Sri Lanka showing the location of Kitulgala Beli-lena and the country's vegetation zones (Ashton et al., 1987, Erdelen, 1988). Location of the 2017 excavation squares and comparison of the 1983 (Wijeyapala, 1997) and 2017 stratigraphy.

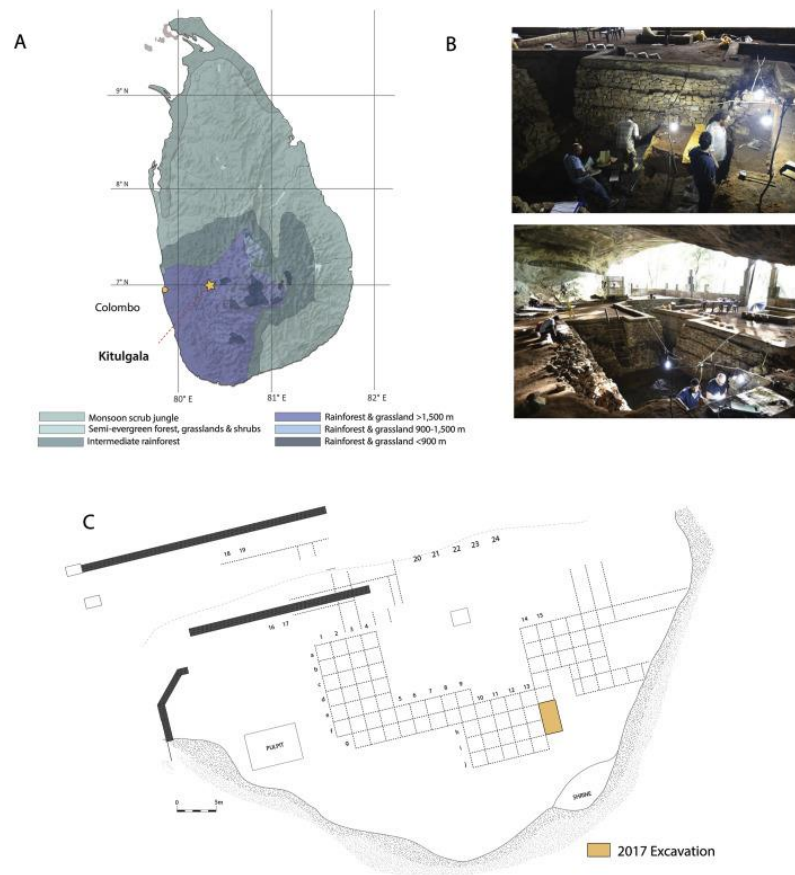


Figure 2. Distribution of animal taxa identified in different Holocene sedimentary contexts of Kitulgala Beli-lena based on the total number of bone fragments recovered (TNF, A) and number of identified specimens (NISP, B).

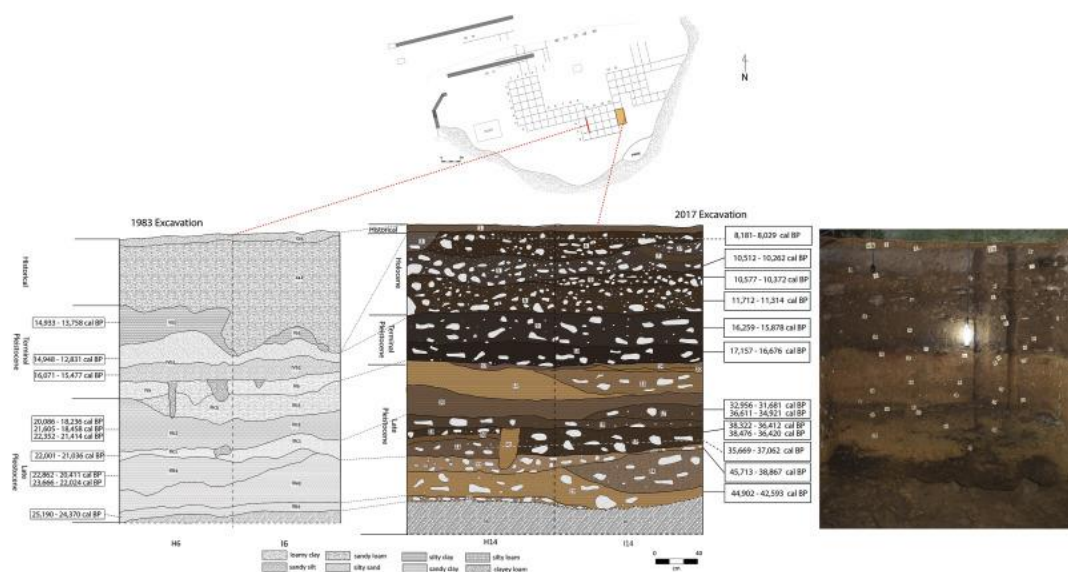


Figure 3. Distribution of animal taxa identified in different Holocene sedimentary contexts of Kitulgala Beli-lena based on (A) the total number of bone fragments recovered (TNF) and (B) number of identified specimens (NISP).

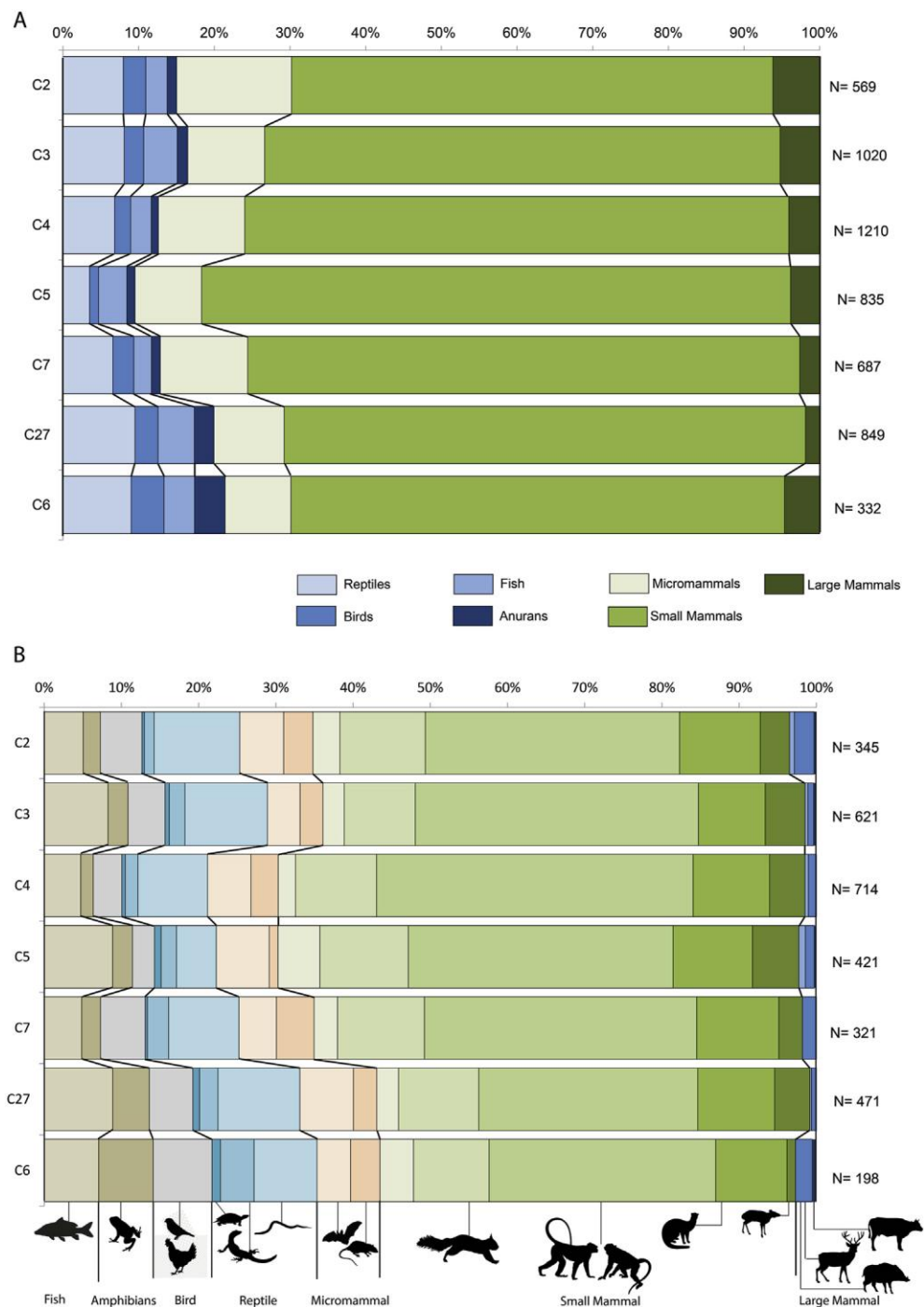


Figure 4. Osseous tools manufactured from cercopithecoid appendicular skeletal elements recovered during the 2017 excavation of Kitulgala Beli-lena (A-B unipoints C-G bipoints). . Scale bars in microphotographs= 1 cm.



Figure 5 Kitulgala Beli-lena mollusc taxa by %NISP (A) and %Weight (B).

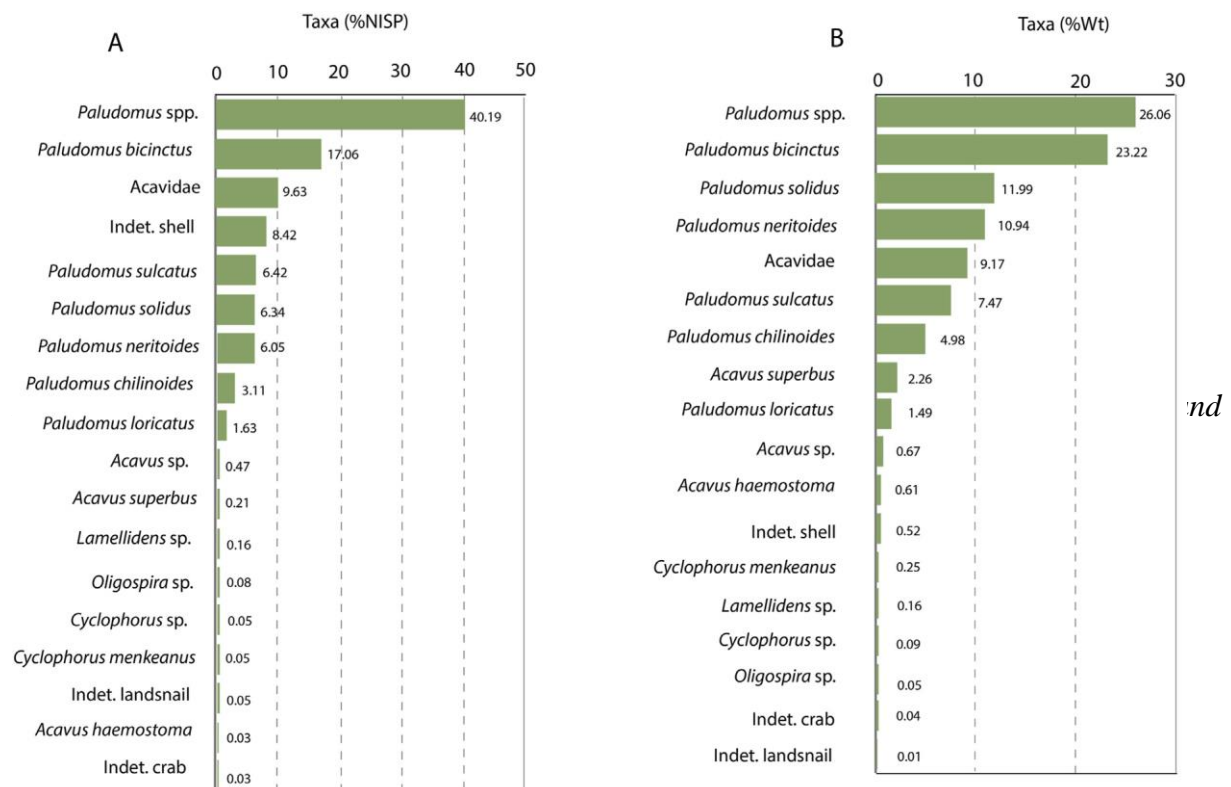


Figure 6. *Kitulgala Beli-lena* mollusc taxa at the family taxonomic level by %NISP (A) and %Weight (B).

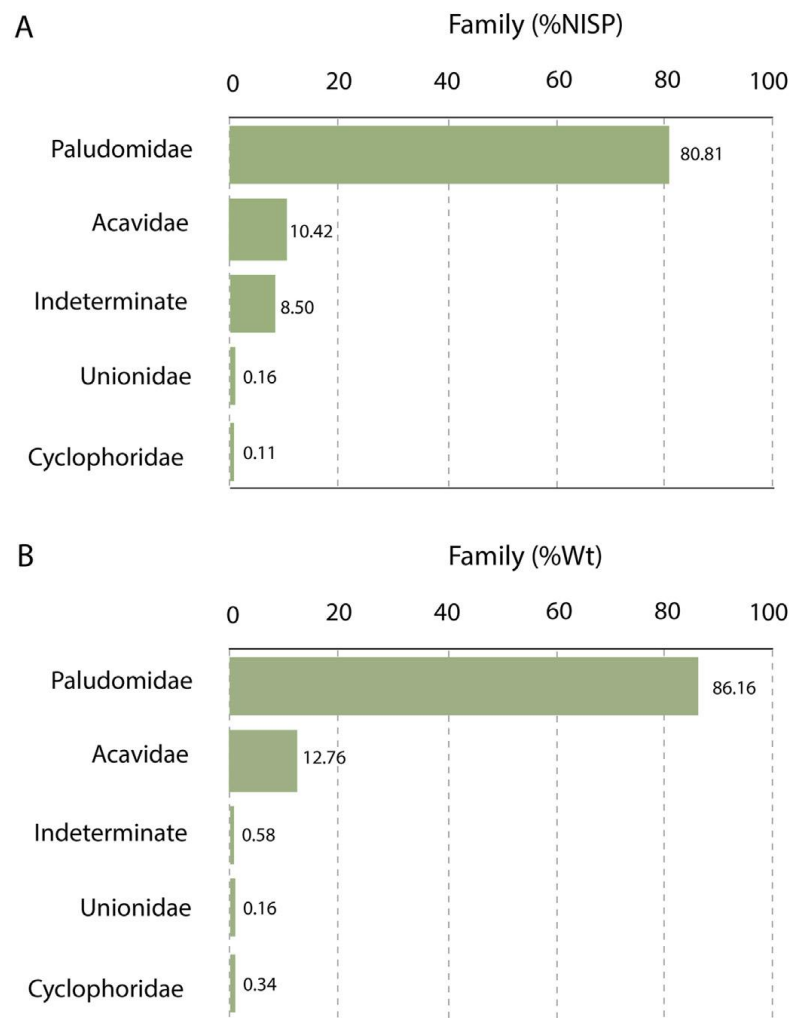


Figure 7. Bipolar-on-anvil cores (1 – Holocene; 2 – Terminal Pleistocene; 3 Late Pleistocene) and bipolar flakes (4, 5 – Holocene; 6 – Terminal Pleistocene; 7-8 Late Pleistocene) from Kitulgala Beli-lena.

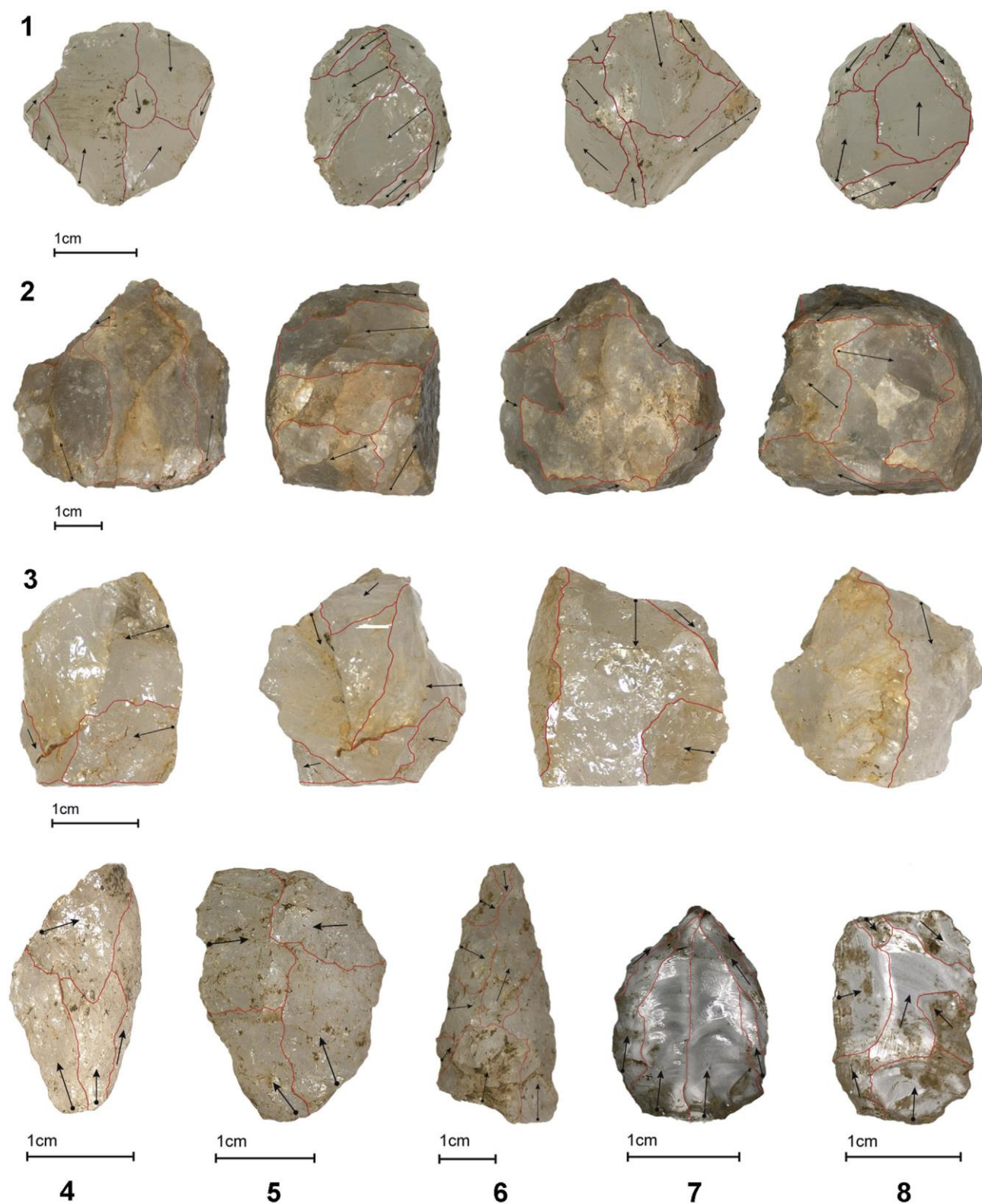
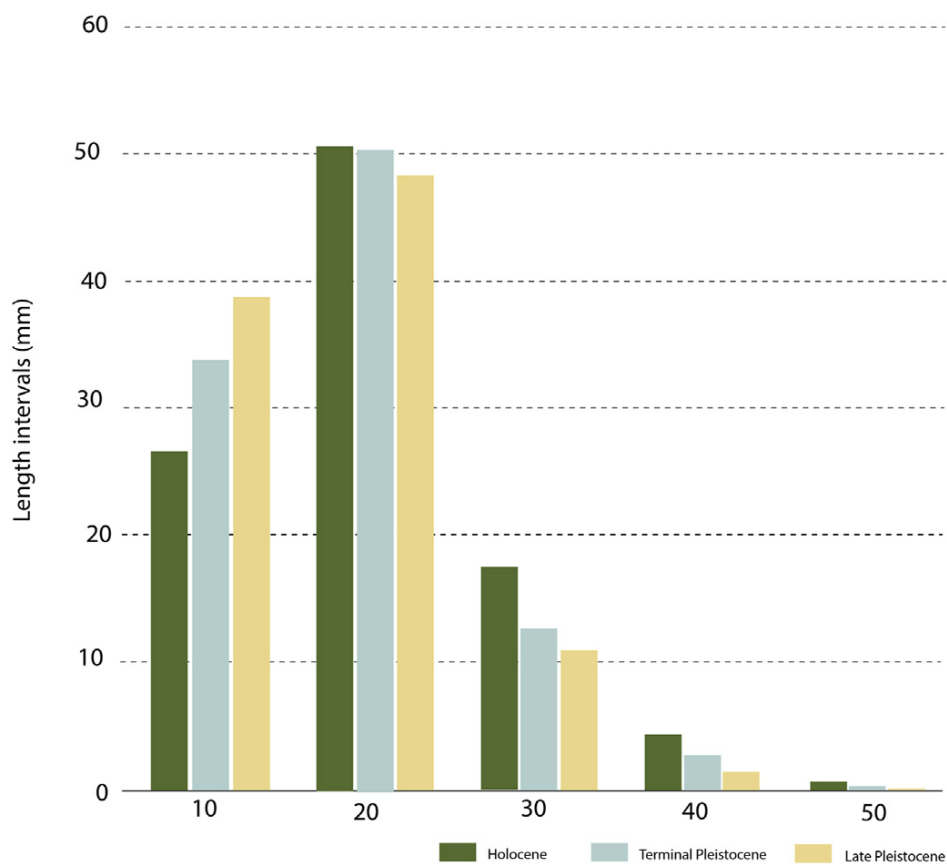


Figure 8. Histogram of the frequency of complete flakes by length intervals during the different chronological phases at Kitulgala Beli-lena.



References:

- Abeyratne, M. 1994. TL dating of Sri Lankan archaeological sites. *Quat. Sci. Rev.* 13(5-7), 585-588.
- Andrews, P. 1995. Experiments in taphonomy. *J. Arch. Sci.* 22, 147-153.
- Aubert, M., Brumm, A., Ramli, M., Sutikna, T., Saptomo E. W., Hakim, B., Morwood, M. J., van den Bergh, G. D., Kinsley, L., Dosseto, A. 2014. Pleistocene cave art from Sulawesi, Indonesia. *Nature*, 514(7521), 223.
- Aubert, M., Setiawan, P., Oktaviana, A.A., Brumm, A., Sulistyarto, P.H., Saptomo, E.W., Istiawan, B., Ma'rifat, T.A., Wahyuono, V.N., Atmoko, F.T. Zhao, J.X. 2018. Palaeolithic cave art in Borneo. *Nature* 564(7735), 254.
- Bae, C. J., Douka, K., Petraglia, M. D. 2017. On the origin of modern humans: Asian perspectives. *Science* 358(6368), 9067.
- Bailey, R. C., Head, G., Jenike, M., Owen, B., Rechtman, R., Zechenter, E. 1989. Hunting and gathering in tropical rain forest: Is it possible? *Am Anthropol.* 91:59-82.
- Barker, G., Barton, H., Bird, M., Daly, P., Datan, I., Dykes, A., Farr, L., Gilbertson, D., Harisson, B., Hunt, C., Higham, T., Kealhofer, L., Krigbaum, J., Lewis, H., McLaren, S., Paz, V., Pike, A., Piper, P., Pyatt, B., Rabett, R., Reynolds, T., Rose, J., Rushworth, G., Stephens, M., Stringer, C., Thompson, J., Turney, C., 2007. The 'human revolution' in lowland tropical Southeast Asia: the antiquity and behaviour of anatomically modern humans at Niah Cave (Sarawak, Borneo). *J. Hum. Evol.* 52, 243-261.
- Barker, G., Farr, L. (Eds) 2016. Archaeological Investigations in the Niah Caves, Sarawak. McDonald Institute for Archaeological Research, Cambridge.
- Barton, H. 2016. Functional analysis of stone tools from the West Mouth. In: Barker, G., Farr, L. (Eds.) Archaeological Investigations in the Niah Caves, Sarawak McDonald Institute for Archaeological Research, Cambridge. pp. 279-300.
- Barton, H., Piper, P.J., Rabett, R., Reeds, I., 2009. Composite hunting technologies from the Terminal Pleistocene and Early Holocene, Niah Cave, Borneo. *J. Archaeol. Sci.* 36, 1708-1714.
- Bartram, L. E., Kroll, E. M., Bunn, H. T. 1991. Variability in Camp Structure and Bone Food Refuse Patterning at Kua San Hunter-Gatherer Camps. In E. M. Kroll, & T. D. Price (Eds.), *The Interpretation of Archaeological Spatial Patterning*, Springer, Boston, MA. pp. 77-148.
- Behrensmeier, A. K. 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4, 150-162.
- Bird, M.I., Ayliffe, L.K., Fifield, L.K., Turney, C.S., Cresswell, R.G., Barrows, T.T., David, B. 1999. Radiocarbon dating of "old" charcoal using a wet oxidation, stepped-combustion procedure. *Radiocarbon*, 41(2), 127-140.

Bird, M., Taylor, D., Hunt, C. 2005. Palaeoenvironments of insular Southeast Asia during the last glacial period: a savanna corridor in Sundaland? *Quat. Sci. Rev.* 24, 2228–2242.

Blasco, R., Rosell, J., Fernández Peris, J., Cáceres, I., María Vergès, J. 2008. A new element of trampling: an experimental application on the Level XII faunal record of Bloomer Cave (Valencia, Spain). *J. Arch. Sci.* 35, 1605–1618.

Blinkhorn, J., Achyuthan, H., Petraglia, M., Ditchfield, P. 2013. Middle Palaeolithic occupation in the Thar Desert during the Upper Pleistocene: the signature of a modern human exit out of Africa?. *Quat. Sci. Rev.* 77, 233–238.

Blinkhorn, J., Petraglia, M. 2017. Environments and cultural change in the Indian subcontinent: implications for the dispersal of *Homo sapiens* in the Late Pleistocene. *Curr. Anthropol.* 58 (S17), S463–S479.

Blinkhorn, J., Achyuthan, H., Ditchfield, P., Petraglia, M. 2017. Palaeoenvironmental dynamics and Palaeolithic occupation at Katoati, Thar Desert, India. *Quat. Res.* 87(2), 298–313.

Blinkhorn, J., Ajithprasad, P., Mukherjee, A., Kumar, P., Durcan, J.A., Roberts, P., 2019. The first directly dated evidence for Palaeolithic occupation on the Indian coast at Sandhav, Kachchh. *Quat. Sci. Rev.* 224, 105975.

Boivin, N., Fuller, D.Q., Dennell, R., Allaby, R., Petraglia, M.D. 2013. Human dispersal across diverse environments of Asia during the Upper Pleistocene. *Quat. Int.* 300, 32–47.

Boëda, E. 2013. *Technologique & Technologie. Une Paléo-histoire des objets lithiques tranchants*. Archéo-éditions, Paris.

Bolter, D. R. A comparative study of growth patterns in crested langurs and vervet monkeys. *Anat. Res. Int.*, 1–12.

Bradfield, J., Brand, T. 2015. Results of utilitarian and accidental breakage experiments on bone points. *Archaeol. Anthropol. Sci.* 7, 27–38.

Brun-Ricalens, F. L. 2006. Les pièces esquillées: état des connaissances après un siècle de reconnaissance. *PALEO Revue d'archéologie préhistorique*. 18, 95–114.

Clarkson, C., Petraglia, M., Korisettar, R., Haslam, M., Boivin, N., Crowther, A., Ditchfield, P., Fuller, D., Miracle, P., Harris, C., Connell, K., James, H., Koshy, J. 2009. The oldest and longest enduring microlithic sequence in India: 35 000 years of modern human occupation and change at the Jwalapuram Locality 9 rockshelter. *Antiquity*. 83 (320), 326–48.

Clarkson, C., Jones, S., Harris, C. 2012. Continuity and change in the lithic industries of the Jurreru Valley, India, before and after the Toba eruption. *Quat. Int.* 258, 165–179.

Clarkson, C., Petraglia, M., Harris, C., Shipton, C., Norman, K. 2018. The South Asian Microlithic: *Homo sapiens* Dispersal or Adaptive Response?. In E. Robinson, E. and F. Sellet

(eds.) *Lithic Technological Organization and Paleoenvironmental Change*. Springer, Cham. pp. 37-61.

Cooray, P.G. 1984. *An introduction to the geology of Sri Lanka (Ceylon)*. National Museums of Sri Lanka Publication, Ceylon.

Conard, N.J. 2010. Cultural modernity: Consensus or conundrum?. *Proc. Nat. Acad. Sci* 107(17), 7621-7622.

Crabtree, D.E. 1972. An Introduction to Flintworking. Occasional Papers of the Idaho University Museum, Pocatello. No. 28

De la Peña, P. 2015. The interpretation of bipolar knapping in African Stone Age studies. *Curr. Anthropol.* 56(6), 911–923.

Deraniyagala, S. U. 1992. *The Prehistory of Sri Lanka: An Ecological Perspective*, 2nd Edition. Department of Archaeology, Colombo.

Dobney, K., Reilly, K. A. 1988. A method for recording archaeological animal bones: the use of diagnostic zones. *Circaea* 5, 79–96.

Domrös, M., 1974. *Agroclimate of Ceylon: a contribution towards the ecology of tropical crops*. Franz Steiner.

Donnart, K., Naudinot, N., Le Clézio, L. 2009. Approche expérimentale du débitage bipolaire sur enclume: caractérisation des produits et analyse des outils de production. *Bulletin de la Société Préhistorique Française* 106 (3), 517-533

Fernandez-Jalvo, Y., Andrews, P. 2016. *Atlas of Taphonomic Identifications*. Springer, New York.

Grayson, D. K. 1984. *Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas*. Academic Press, Cambridge.

Field, J.S., Petraglia, M.D., Lahr, M. M. 2007. The southern dispersal hypothesis and the South Asian archaeological record: examination of dispersal routes through GIS analysis. *J. Anthropol. Archaeol.* 26(1), 88-108.

Gamble, C. 1993. *Timewalkers: The Prehistory of Global Colonization*. Alan Sutton Press, Gloucester UK.

Gunatilleke, N., Pethiyagoda, R., Gunatilleke, S. 2008. Biodiversity of Sri Lanka. *J. Natn. Sci. Foundation Sri Lanka* 36, 25-62.

Harris, E. C. 1989. *Principles of archaeological stratigraphy, 2nd edition*. Academic Press, London.

Harvati, K. 2000. Dental eruption sequence among colobine primates. *Am. J. Phys. Anthropol.*, 112(1), 69-85.

Hausdorf, B., Perera, K. K., 2000. Revision of the genus *Acavus* from Sri Lanka (Gastropoda: Acavidae). *J. Molluscan Studies*, 66(2), 217-231.

Henshilwood, C.S., d'Errico, F., Van Niekerk, K.L., Coquinot, Y., Jacobs, Z., Lauritzen, S.E., Menu, M., García-Moreno, R. 2011. A 100,000-year-old ochre-processing workshop at Blombos Cave, South Africa. *Science* 334(6053), 219-222.

Higham, T.F.G, Barton, H., Turney, C.M.T., Barker, G., Bronk Ramsey, C., Brock, F. 2008. Radiocarbon dating of charcoal from tropical sequences: results from the Niah Great Cave, Sarawak and their broader implications. *J. Quat. Sci.* 24, 189–197.

Hiscock, P., Wallis, L., 2005. Pleistocene settlement of deserts from an Australian perspective In: P. Veth, M.A. Smith, P. Hiscock (Eds.), *Desert Peoples: Archaeological Perspectives*. Blackwell Publishing, Melbourne. pp. 34-57.

Holt, B.G., Lessard, J.P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.-H., Graham, C.H., Graves, G.R., Jonsson, K.A., Nogues-Bravo, D., Wang, Z., Whittaker, R.J., Fjeldsa, J., Rahbek, C. 2013. An update of Wallace's zoogeographic regions of the world. *Science* 339, 74-78.

Hunt, C.O., Gilbertson, D.D., Rushworth, G., 2012. A 50,000-year record of Late Pleistocene tropical vegetation and human impact in lowland Borneo. *Quat. Sci. Rev.* 37, 61–80.

Ingicco, T., Moigne, A.-M. & Gommery, D. 2012. A deciduous and permanent dental wear stage system for assessing the age of *Trachypithecus* sp. specimens (Colobinae, Primates). *J. Archaeol. Sci.* 39, 421-427.

Kahn, J.G., Ragone, D. 2013. Identification of carbonized breadfruit (*Artocarpus altilis*) skin: Refining site function and site specialization in the Society Islands, East Polynesia. *Journal of Ethnobiology*, 33(2), 237-259.

Kajale, M. D. 1988. Plant Economy. In: Dhavalikar MK, Sankalia HD, Ansari ZD (Eds) *Excavations at Inamgaon, Vol. 1, Part 2*. Deccan College Postgraduate and Research Institute, Pune. pp 727–821

Kajale, M.D. 1989. Mesolithic exploitation of wild plants in Sri Lanka: archaeobotanical study at the cave site of Beli-lena. In: D.R. Harris and G.C. Hillman (Editors), *Foraging and Farming: The evolution of plant exploitation*. Unwin Hyman, London, pp. 269-281.

Kennedy, K. A., Deraniyagala, S. U. 1989. Fossil remains of 28,000-year-old hominids from Sri Lanka. *Curr. Anthropol.* 30(3), 394-399.

Kennedy, K. A. R. 2000. *God-apes and Fossil Men*. University of Michigan Press, Ann Arbor.

Kourampas, N., Simpson, I. A., Perera, N., Deraniyagala, S. U., Wijeyapala, W. H. 2009. Rockshelter sedimentation in a dynamic tropical landscape: Late Pleistocene–Early Holocene

archaeological deposits in Kitulgala Beli-lena, southwestern Sri Lanka. *Geoarchaeology* 24(6), 677–714.

Klein, R. G., Cruz-Urbe, K. 1984. *The Analysis of Animal Bones from Archeological Sites*. Chicago University Press, Chicago, IL.

Langley M. C. (ed.) 2016. *Osseous Projectile Weaponry: Towards an Understanding of Pleistocene Cultural Variability*. Springer, Dordrecht, Netherlands.

Langley, M., Amano, N., Wedage, O., Deraniyagala, S., Pathmalal, M. M., Perera, N., Boivin, N., Petraglia, M., Roberts, P. 2019. Early Evidence for Bows-and-Arrows and Brilliant Symbolic Displays in the South Asian tropics. under review.

Langley, M.C., Clarkson, C., Ulm, S. 2019. Symbolic expression in Pleistocene Sahul, Sunda, and Wallacea. *Quat. Sci. Rev.* 221, 10588.

Langley, M.C., O'Connor, S. 2016. An Enduring Shell Artefact Tradition from Timor-Leste: *Oliva* Bead Production from the Pleistocene to Late Holocene at Jerimalai, Lene Hara, and Matja Kuru 1 and 2. *PLoS ONE* 11(8): e0161071.
<https://doi.org/10.1371/journal.pone.0161071>

Leavesley, M.G., 2005. Prehistoric hunting strategies in New Ireland, Papua New Guinea: the evidence of the cuscus (*Phalanger orientalis*) remains from Buang Merabak cave. *Asian Perspect.* 44, 207–218.

Lemonnier, P. 1986. The Study of Material Culture Today: Toward an Anthropology of Technical Systems. *J. Anthropol. Archaeol.* 5, 147–186.

Levin, M.J. 2016. Roasting breadfruit in the Pacific: A combined plant macroremain and phytolith analysis from Pohnpei, Federated States of Micronesia. *Archaeology in Oceania*, 51(1), 70-76.

Lewis, L., Perera, N., Petraglia, M. 2014. First technological comparison of Southern African Howiesons Poort and South Asian Microlithic industries: An exploration of inter-regional variability in microlithic assemblages. *Quat. Int.* 350, 7–25.

Lewis, L. 2017. *Early Microlithic Technologies and Behavioural Variability in Southern Africa and South Asia*. British Archaeological Reports International Series, Archaeopress, Oxford.

Lyman, R. L. 1994. *Vertebrate Taphonomy*. Cambridge University Press, Cambridge, UK.

Marean, C. 2016. The transition to foraging for dense and predictable resources and its impact on the evolution of modern humans. *Philos. Trans. Roy. Soc. B* 371, 1698.

Mellars, P. 2005. The impossible coincidence. A single-species model for the origins of modern human behavior in Europe. *Evolutionary Anthropology: Issues, News, and Reviews* 1(14), 12–27.

Mellars, P. 2006. Going East: New Genetic and Archaeological Perspectives on the Modern Human Colonization of Eurasia. *Science* 313(5788), 796–800.

Mellars, P., Gori, K. C., Carr, M., Soares, P. A., Richards, M. B. 2013. Genetic and archaeological perspectives on the initial modern human colonization of southern Asia. *Proc. Nat. Acad. Sci.* 110(26), 10699-10704.

Mercader, J., Martí, R., González, I.J., Sánchez, A., García, P. 2003. Archaeological site formation in rain forests: insights from the Ituri rock shelters, Congo. *J. Arch. Sci.* 30(1), 45-65.

Mourre, V. 1996. Les Industries en Quartz au Paléolithique. Terminologie, Méthodologie et Technologie. *Paléo.* 8, 205–223.

Naggs, F., Raheem, D. 2000. Land Snail Diversity in Sri Lanka. Department of Zoology, The NaturalHistory Museum, London.

Nash, D.J., Coulson, S., Staurset, S., Ulliyott, J.S., Babutsi, M., Smith, M.P. 2016. Going the distance: mapping mobility in the Kalahari Desert during the Middle Stone Age through multi-site geochemical provenancing of silcrete artefacts. *J. Hum. Evol.* 96, 113-133.

O'Connell, J. F., Hawkes, K., Jones, N. B. 1991. Distribution of Refuse-Producing Activities at Hadza Residential Base Camps. In E. M. Kroll, & T. D. Price (Eds.), *The Interpretation of Archaeological Spatial Patterning*, Springer, Boston, MA. pp. 61-76.

O'Connor, S., Ono, R., Clarkson, C., 2011. Pelagic fishing at 42,000 years before the present and the maritime skills of modern humans. *Science* 334, 1117–1121.

Pavlidis, C. 2004. From Misisil Cave to Eliva hamlet: rediscovering the Pleistocene in interior West New Britain. In: Auenbrow, V., Fullager, R. (Eds.), *A Pacific Odyssey: Archaeology and Anthropology in the Western Pacific. Papers in Honour of Jim Specht. Records of the Australian Museum, Supplement 29* Sydney, Australian Museum, pp. 97–108.

Pelegrin, J., Karlin, C., Bodu, P. 1988. *"Chaînes Opératoires": un outil pour le préhistorien.* Technologie Préstorique Notes et Monographies Techniques. Editions du CNRS, Paris.

Petraglia, M. D., Korisettar, R., Boivin, N., Clarkson, C., Ditchfield, P., Jones, S., Koshy, J., Lahr, M.M., Oppenheimer, D., Pyle, C., Roberts, R., Schwenninger, J.-L., Arnold, L., White, K. 2007. Middle Paleolithic assemblages from the Indian Subcontinent before and after the Toba super-eruption. *Science* 317, 114-116

Petraglia, M., Clarkson, C., Boivin, N., Haslam, M., Korisettar, R., Chaubey, G., Ditchfield, P., Fuller, D., James, H., Jones, S., Kivisild, T., Koshy, J., Lahr, M. M., Metspalu, M., Roberts, R. 2009. Population increase and environmental deterioration correspond with microlithic innovations in South Asia ca. 35,000 years ago. *Proc. Nat. Acad. Sci.* 106, 12261–6.

Petraglia, M.D., Haslam, M., Fuller, D.Q., Boivin, N., Clarkson, C. 2010. Out of Africa: new hypotheses and evidence for the dispersal of *Homo sapiens* along the Indian Ocean rim. *Annals of Human Biology* 37(3), 288-311.

Petraglia, M. D., Ditchfield, P., Jones, S., Korisettar, R., Pal, J.N. 2012. The Toba volcanic super-eruption, environmental change, and hominin occupation history in India over the last 140,000 years. *Quat. Int.* 258, 119-134.

Perera, N. 2010. *Prehistoric Sri Lanka: Late Pleistocene Rockshelters and an Open-air Site*. British Archaeological Reports International Series, Archaeopress, Oxford.

Perera, N., Kourampas, N., Simpson, I. A., Deraniyagala, S. U., Bulbeck, D., Kamminga, J., Perera, J., Fuller, D., Szabo, K., Oliveira, N. 2011. People of the ancient rainforest: Late Pleistocene foragers at the Batadomba-lena rockshelter, Sri Lanka. *J Hum Evol.* 61(3), 254–69.

Perera, N., Roberts, P., Petraglia, M. 2016. Bone Technology from Late Pleistocene Caves and Rockshelters of Sri Lanka. In: Langley MC, editor. *Osseous Projectile Weaponry: Towards an Understanding of Pleistocene Cultural Variability*. Springer, Dordrecht, Netherlands. pp. 173–88.

Picin, A., Vaquero, M. 2016. Flake productivity in the Levallois recurrent centripetal and discoid technologies: New insights from experimental and archaeological lithic series. *J. Arch. Sci. Reports* 8, 70-81.

Piper, P.J., Rabett, R.J., 2014. Late Pleistocene subsistence strategies in Island Southeast Asia and their implications for understanding the development of modern human behaviour. In: Dennell, R., Poor, M. (Eds.), *Southern Asia, Australia and the Search for Human Origins*. Cambridge University Press, Cambridge, pp. 118–134.

Piper, P.J., Rabett, R.J., 2016. Vertebrate fauna from the Niah Caves. In: Barker, G., Farr, L. (Eds.) *Archaeological Investigations in the Niah Caves*, Sarawak McDonald Institute for Archaeological Research, Cambridge. pp. 401-438.

Pitulko, V. Pavlova, E., Nikolskiy, P. 2017. Revising the archaeological record of the Upper Pleistocene Arctic Siberia: Human dispersal and adaptations in MIS 3 and 2. *Quat. Sci. Rev.* 165, 127-148.

Rabett, R. 2016. Bone and tusk tool from the West Mouth and Lobang Hangus. In: Barker, G., Farr, L. (Eds.) *Archaeological Investigations in the Niah Caves*, Sarawak McDonald Institute for Archaeological Research, Cambridge. pp. 301-324.

Rabett, R.J., Piper, P.J., 2012. The emergence of bone technologies at the end of the Pleistocene in Southeast Asia: regional and evolutionary implications. *Camb. Archaeol. J.* 22, 37–56.

Raheem, D., Naggs, F. 2006. The Sri Lankan endemic semi-slug *Ratnadvipia* (Limacoidea: Ariophantidae) and a new species from southwestern Sri Lanka. *Systematics and Biodiversity*, 4(1), 99-126.

Reimer, P. J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P. M., Guilderson, T. P., Hafliðason, H., Hajdas, I., Hatte, C., Heaton, T. J., Hofmann, D. L., Hogg, A. G., Hughen, K. A., Kaiser, K. F., Kromer, B., Manning, S. W., Niu, M., Reimer, R., Richards, D. A., Scott, E. M., Southon, J. R., Staff, R. A., Turney, C. S., van der Plicht, J. 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal. BP. *Radiocarbon* 55, 1869–188.

Reynolds, T., 2016. Lithic technologies: the West Mouth and Lobang Hangus assemblages. In: Barker, G., Farr, L. (Eds.) *Archaeological Investigations in the Niah Caves*, Sarawak McDonald Institute for Archaeological Research, Cambridge. pp. 251–278.

Reynolds, T., Barker, G., 2015. Reconstructing Late Pleistocene climates, landscapes, and human activities in northern Borneo from excavations in the Niah Caves. In: Kaifu, Y., Izuho, M., Goebel, T. (Eds.), *Emergence and Diversity of Modern Human Behavior in Paleolithic Asia*. Texas A & M University Press, College Station, pp. 140–157.

Roberts, P., Petraglia, M. D. 2015. Pleistocene rainforests: barriers or attractive environments for early human foragers? *World Archaeol.* 47, 718–739.

Roberts P., Perera N., Wedage O., Deraniyagala S., Perera J., Eregama S., Gledhill, A., Petraglia, M. Lee-Thorp, J. 2015a. Direct evidence for human reliance on rainforest resources in late Pleistocene Sri Lanka. *Science*. 347(6227), 1246–9.

Roberts, P., Boivin, N., Petraglia, M., 2015b. The Sri Lankan ‘Microlithic’ Tradition c. 38,000 to 3,000 Years Ago: Tropical Technologies and Adaptations of *Homo sapiens* at the Southern Edge of Asia. *J. World Prehis.* 28(2), 69–112.

Roberts, P., Perera, N., Wedage, O., Deraniyagala, S., Perera J., Eregama, S., Petraglia, M.D., Lee-Thorp, J.A., 2017a. Fruits of the forest: Human stable isotope ecology and rainforest adaptations in Late Pleistocene and Holocene (~ 36 to 3 ka) Sri Lanka. *J. Hum. Evol.* 106, 102–118.

Roberts, P., Gaffney, D., Lee-Thorp, J., Summerhayes, G., 2017b. Persistent tropical foraging in the highlands of terminal Pleistocene/Holocene New Guinea. *Nat. Ecol Evol.* 1:0044.

Roberts, P., Stewart, B. A. 2018. Defining the ‘generalist specialist’ niche for Pleistocene *Homo sapiens*. *Nat. Hum. Behav.* 2(8), 542–50.

Roebroeks, W. 1988. *From Find Scatters to Early Hominid Behaviour. A Study of Middle Palaeolithic Riverside Settlements at Maastricht-Belvédère (The Netherlands)*. *Analecta Praehistorica Leidensia* 21. Leiden University Press, Leiden.

Samper Carro, S.C., O'Connor, S., Louys, J., Hawkins, S., Mahirta, M., 2016. Human maritime subsistence strategies in the Lesser Sunda Islands during the terminal Pleistocene-early Holocene: new evidence from Alor, Indonesia. *Quat. Int.* 416, 64–79.

Scerri, E.M., Blinkhorn, J., Groucutt, H.S., Niang, K., 2016. The middle stone age archaeology of the Senegal river valley. *Quat. Int.* 408, 16–32.

- Shea, J. J. 2011. Homo sapiens is as Homo sapiens was: behavioral variability versus “behavioral modernity” in Paleolithic archaeology. *Curr. Anthropol.* 52, 1–35.
- Shipman, P., Rose, J. 1988. Bone tools: an experimental approach. In Olsen, S. L. (Ed.) *Scanning Electron Microscopy in Archaeology*. British Archaeological Reports International Series, Archaeopress, Oxford. pp. 303–335.
- Shipton, C., Roberts, P., Archer, W., Armitage, S.J., Bitu, C., Blinkhorn, J., Courtney-Mustaphi, C., Crowther, A., Curtis, R., d’Errico, F., Douka, K., Faulkner, P., Groucutt, H.S., Helm, R., Herries, A.I., Jembe, S., Kourampas, N., Lee-Thorp, J., Marchant, R., Mercader, J., Marti, A.P., Prendergast, M.E., Rowson, B., Tengeza, A., Tibesasa, R., White, T.S., Petraglia, M., Boivin, N. 2018. 78,000-year-old record of Middle and Later Stone Age innovation in an East African tropical forest. *Nat. Comms.* 9(1), 1832.
- Starmuhlner, F. 1974. *The freshwater gastropods of Ceylon*. Bulletin of the Fisheries Research Station, Sri Lanka (Ceylon).
- Stewart, B.A., Parker, A.G., Dewar, G., Morley, M.W., Allott, L.F. 2016. Follow the Senqu: Maloti-Drakensberg paleoenvironments and implications for early human dispersals into mountain systems. In S.C. Jones, B.A. Stewart (Eds.) *Africa from MIS 6-2: Population Dynamics and Paleoenvironments*. Springer, Dordrecht. pp. 247-271.
- Summerhayes, G.R., Field, J.H., Shaw, B. and Gaffney, D. 2016. The archaeology of forest exploitation and changes in the tropics during the Pleistocene: the case of Northern Sahul (Pleistocene New Guinea). *Quat. Int.* 53, 1-16.
- Summerhayes, G.R., Leavesley, M., Fairbairn, A., Mandui, H., Field, J., Ford, A., Fullagar, R. 2010. Human adaptation and plant use in highland New Guinea 49,000 to 44,000 years ago. *Science* 330(6000), 78-81.
- Szabó, K. 2016. Molluscan remains from the Niah Caves: Methods and approaches. In: Barker, G., Farr, L. (Eds.) *Archaeological Investigations in the Niah Caves*, Sarawak McDonald Institute for Archaeological Research, Cambridge. pp. 469-484.
- Thomas, D. H. 1969. Great basin hunting patterns: a quantitative method for treating faunal remains. *Am. Antiq.* 34, 392–401.
- Watts, D. 1984. The spatial dimension in biogeography. In J.A. Taylor (Ed.) *Biogeography: Recent Advances and Future Directions*. Barnes and Noble Books, Totowa, NJ. pp. 25–62
- Wedage, O., Amano, N., Langley, M. C., Douka, K., Blinkhorn, J., Crowther, A., Deraayanigala, S., Kourampas, N., Simpson, I., Perera, N., Picin, A., Boivin, N., Petraglia, M., Roberts, P. 2019a. Specialized rainforest hunting by Homo sapiens ~45,000 years ago. *Nat. Comms* 10(1), 739.
- Wedage O., Picin, A., Blinkhorn, J., Douka, K., Deraniyagala, S., Kourampas, N., Perera, N., Simpson, I., Boivin, N., Petraglia, M., Roberts, P., 2019b. Microliths in the South Asian rainforest~ 45-4 ka: New insights from Fa-Hien Lena Cave, Sri Lanka. *PLoS One*, 14(10), p.e0222606.

Westaway, K. E., Louys, J., Due Awe, R., Morwood, M. J., Price, G. J., Zhao, J.-x., Aubert, M., Joannes-Boyau, R., Smith, T.M., Skinner, M. M., Compton, T., Bailey, R.M., van den Bergh, G.D., de Vos, J., Pike, A.W.G., Stringer, C., Saptomo, E.W., Rizal, Y., Zaim, J., Santoso, W. D., Trihascaryo, A., Kinsley, L., Sulistyanto. B. 2017. An early modern human presence in Sumatra 73,000–63,000 years ago. *Nature* 548, 322-325.

Wijeyapala, W. 1997. *New light on the prehistory of Sri Lanka in the context of recent investigations of cave sites*. University of Peradeniya, Peradeniya, Sri Lanka.

Wilson, D. E., Reeder, D. M. 2005. *Mammal Species of the World*. John Hopkins University Press, Baltimore.