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

Oshan Wedage^{a, b, **}, Patrick Roberts^{a, c, ***}, Patrick Faulkner^{a, d}, Alison Crowther^{a, c}, Katerina Douka^{a, e}, Andrea Picin^{a, f}, James Blinkhorn^{a, g}, Siran Deraniyagala^h, Nicole Boivin^{a, c, i, j}, Michael Petraglia^{a, c, i, ****}, Noel Amano^{a, *}

^a Department of Archaeology, Max Planck Institute for the Science of Human History, Jena, Germany

^b Department of History and Archaeology, University of Sri Jayewardenepura, Gangodawila, Nugegoda, Sri Lanka

^c School of Social Science, The University of Queensland, Brisbane, Australia

^d Faculty of Arts and Social Sciences, University of Sydney, Sydney, Australia

^e Research Laboratory for Archaeology and the History of Art, University of Oxford, Oxford, United Kingdom

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

^g Department of Geography, Royal Holloway, University of London, United Kingdom

^h Department of Archaeology, Government of Sri Lanka, Colombo, Sri Lanka

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

^j Department of Anthropology and Archaeology, University of Calgary, Calgary, Canada

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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.

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1. Introduction

South Asia has emerged as a crucial region for understanding

* Corresponding author.

** Corresponding author. Department of Archaeology, Max Planck Institute for the Science of Human History, Jena, Germany.

*** Corresponding author. Department of Archaeology, Max Planck Institute for the Science of Human History, Jena, Germany.

**** Corresponding author. Department of Archaeology, Max Planck Institute for the Science of Human History, Jena, Germany.

E-mail addresses: wedage@shh.mpg.de (O. Wedage), roberts@shh.mpg.de (P. Roberts), petraglia@shh.mpg.de (M. Petraglia), amano@shh.mpg.de (N. Amano).

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 boundary 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, early routes of dispersal into the region (Petraglia et al., 2010; Boivin et al., 2013; Bae et al., 2017; Blinkhorn and Petraglia, 2017), and emphasized 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 (Roberts et al., 2015a, 2017b). This is in contrast to a prominent model that assumes a rapid, coastal ca. 60 ka dispersal of humans, associated with uniform technological features around the Indian Ocean Rim (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 have 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 ~45,000 years ago through to 3000 years ago (Roberts et al., 2015a,b, 2017b; Wedage et al., 2019a) facilitated by microlithic and osseous technologies (Deraniyagala, 1992; Wijeyapala, 1997; Perera et al., 2011; Wedage et al., 2019a; Langley et al., 2020). 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. 45,000 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 overlooked in recent debates given that existing radiocarbon dates place this sequence considerably later (31,000 years ago – Kourampas et al., 2009). Moreover, a lack of published zooarchaeological, archaeobotanical (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 provide 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 indicate 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 reveal 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: history of research

Kitulgala Beli-lena is located in the Kegalle district of Sri Lanka's Sabaragamuwa Province, approximately 85 km east of Colombo (Fig. 1). With a ca. 30 × 15 m north facing entrance, the rockshelter is formed from 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 and 3500 mm/year (Domrös, 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). 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 depths of 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 ± 3300 and 18,565 ± 2610) have also been reported (Abeyratne, 1994).

Excavations of Terminal Pleistocene sediments of the site, with associated charcoal dated to 12,260 ± 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, and 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 × 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 (Fig. 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 (Fig. 1) and allowing for the correlation of the results with the micromorphological analyses of Kourampas et al. (2009).

Excavations were conducted using hand tools dividing artefacts and sediment samples into discrete sediment units, or subdividing discrete sediment units into 5 cm arbitrary horizons, where single contexts were deeper than 5 cm (Harris, 1989). Three dimensional recording of the excavated area, the interface between sediment deposits and major artefacts (>20 mm) was undertaken using a

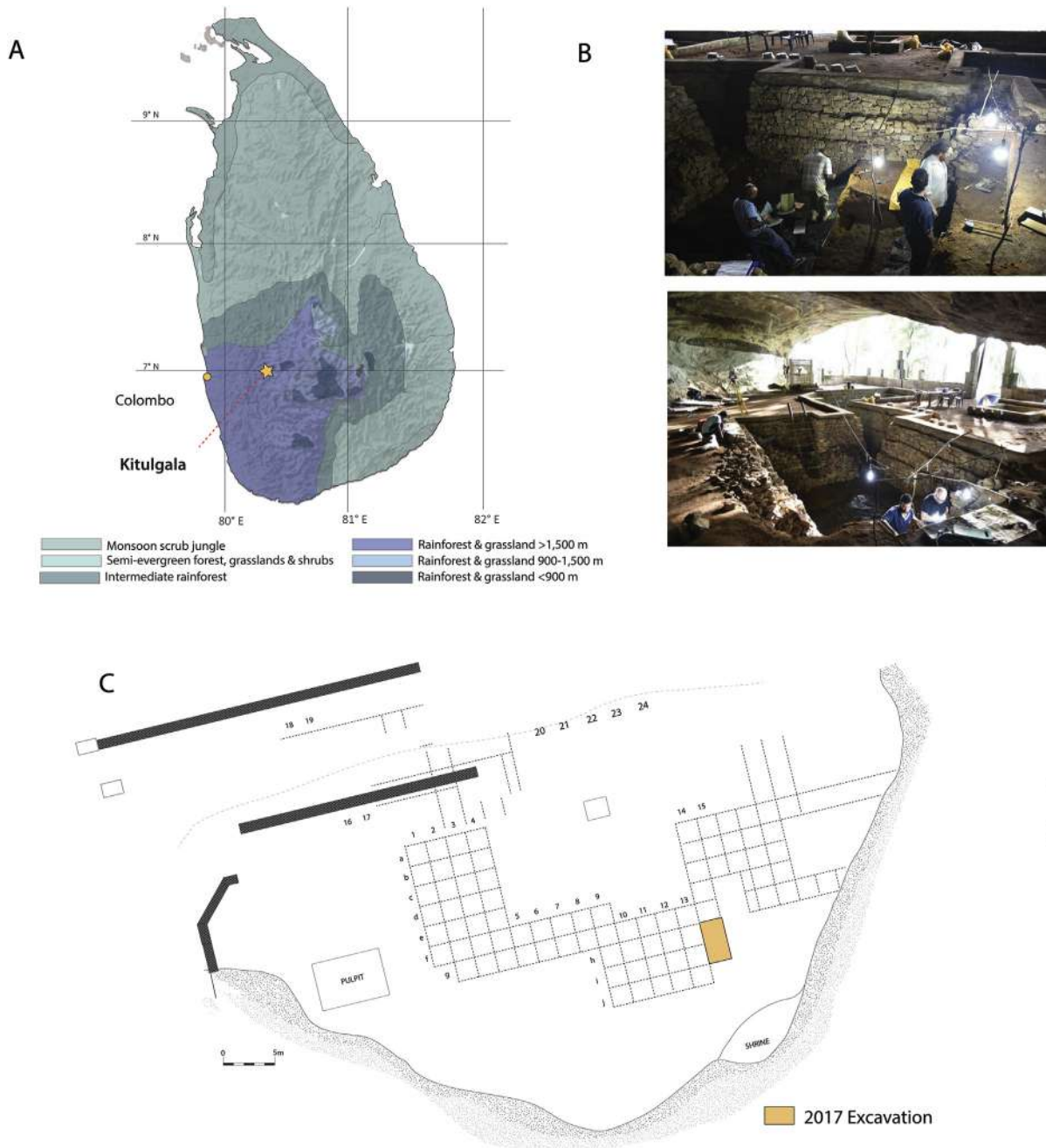


Fig. 1. Map of Sri Lanka showing the location of Kitulgala Beli-lena and the island's vegetation zones (Ashton and Gunatilleke, 1987; Erdelen, 1988) (A), the 2017 excavation of the rockshelter (B) and the plan showing the location of the excavation squares of the site (C).

Leica Builder 505 total station. After removal, excavated sediments were placed on polythene sheeting and a 10–20 L sub-sample was taken for flotation. A total of 1120 L of sediment were floated (using a 250 μm mesh) during the excavation. The remainder of the excavated sediments was 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 (including 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,

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

| Stratum | Lab Code | ¹⁴ C ^a | cal. BP ^b |
|---------|------------|------------------------------|----------------------|
| VIIa2 | Beta 18448 | 3640 ± 60 | 4150–3829 |
| VIIa1 | PRL 1012 | 3170 ± 120 | 3691–3661 |
| VIb1 | Beta 18446 | 8160 ± 80 | 9407–8976 |
| VIa1 | Beta 18445 | 7040 ± 80 | 8000–7698 |
| Va3 | BS 287 | 10,200 ± 170 | 12,517–12,493 |
| Va3 | BS 288 | 10,280 ± 170 | 12,571–11,394 |
| Va3 | BS 289 | 10,010 ± 160 | 12,156–11,146 |
| Va3 | PRL 861 | 11,910 + 430/-410 | 15,298–12,981 |
| Va3 | BS 290 | 11,550 ± 180 | 13,751–13,076 |
| Va3 | Fra-91 | 11,780 ± 220 | 14,155–13,151 |
| Va3 | BS-292 | 11,570 ± 210 | 13,933–13,901 |
| Va2 | BS-292 | 11,520 ± 220 | 13,825–12,901 |
| Va1 | BS-293 | 12,240 ± 160 | 14,933–13,758 |
| IVb3 | Beta 33287 | 11,860 ± 70 | 13,816–13,481 |
| IVb2 | BS-294 | 11,750 ± 390 | 14,948–12,831 |
| IVb2 | Beta 33286 | 13,150 ± 80 | 16,071–15,477 |
| IIIc3 | Beta 33285 | 13,150 ± 90 | 16,084–15,435 |
| IIIc2 | Fra-163 | 15,780 ± 400 | 20,086–18,236 |
| IIIc2 | Fra 164 | 16,400 ± 650 | 21,605–18,458 |
| IIIc2 | Beta 18443 | 18,050 ± 180 | 22,352–21,414 |
| IIIc1 | Beta 18442 | 17,810 ± 170 | 22,001–21,036 |
| IIIb1 | PRL 1013 | 17,870 + 510/-530 | 22,862–20,411 |
| IIIb1 | Beta 18441 | 18,900 ± 350 | 23,666–22,024 |
| IIIa3 | Beta 33283 | 20,560 ± 130 | 25,190–24,370 |
| IIIa2 | Beta 18439 | older than 26,425 | – |

^a Radiocarbon dates were from charcoal samples.

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

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) micro-mammals: 100 g to 1 kg, (b) small mammals: 1 kg–25 kg, (c) large mammals class 1: 25 kg–200 kg, (d) large mammals class 2: 200 kg–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, 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-Uribe \(1984\)](#), 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. Molluscan 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 h. 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 Dinarzade 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. While 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 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 >4 mm, 2–4 mm, 1–2 mm, and <1 mm fractions. The >4 mm and 2–4 mm fractions were sorted under low magnification (x8–x40) using an Olympus SZ61 stereozoom microscope and the 1–2 mm 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. Where possible, taxonomic identifications were based on published descriptions (e.g., [Kahn and Ragone, 2013](#); [Kajale, 1988](#); [Levin, 2016](#)) 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](#); [Pelegri 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 (Fig. 2). 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).

4.1.1. 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 et al., 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 (Fig. 2). 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.

4.1.2. 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. contexts 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 contain 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 et al. (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 our excavation unit at the site resulted from natural taphonomic processes as abundant macrobotanical remains and unweathered quartz flakes were recovered in the same layers.

4.1.3. 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 9070–3550 cal. BP (layer VI to VII), have been re-dated to 10,577–8029 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.

4.1.4. 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

Table 2
New radiocarbon dates on (charcoal) from the 2017 excavation of Kitulgala Beli-lena.

| Context | Labcode (OxA) | Measured Date | Calibrated (cal. BP) ^a |
|---------|---------------|---------------|-----------------------------------|
| 3 | 37930 | 7309 ± 34 | 8181–8029 |
| 5 | 37932 | 9230 ± 40 | 10,512–10,262 |
| 6 | 37933 | 9280 ± 37 | 10,577–10,372 |
| 8 | 37934 | 10,015 ± 39 | 11,712–11,314 |
| 9 | 37935 | 13,360 ± 50 | 16,259–15,878 |
| 10 | 37936 | 13,960 ± 50 | 17,157–16,676 |
| 17 | 37808 | 28,420 ± 180 | 32,956–31,681 |
| 17 | 37789 | 31,880 ± 390 | 36,611–34,921 |
| 19 | 37809 | 33,120 ± 330 | 38,322–36,412 |
| 19 | 37810 | 33,230 ± 390 | 38,476–36,420 |
| 21 | 37724 | 32,410 ± 260 | 35,669–37,062 |
| 22 | X-2782-17 | 37,500 ± 1700 | 45,713–38,867 |
| 23 | 37483 | 39,900 ± 700 | 44,902–42,593 |

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

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 |

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 coming 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/iguanaid 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 (<1 kg) 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 (Fig. 4). Morphological features retained in some of the unipoints in the assemblage suggest that they were manufactured from cercopithecoid fibulae (Fig. 4A) and ulnae (Fig. 4B). The bipoints and the geometrics (Fig. 4C–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., 2019a, b; Langley et al., 2020).

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., 2020) and Batadomba-lena (Perera et al., 2011; Perera et al., 2016). 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., 2020). This is also consistent with the

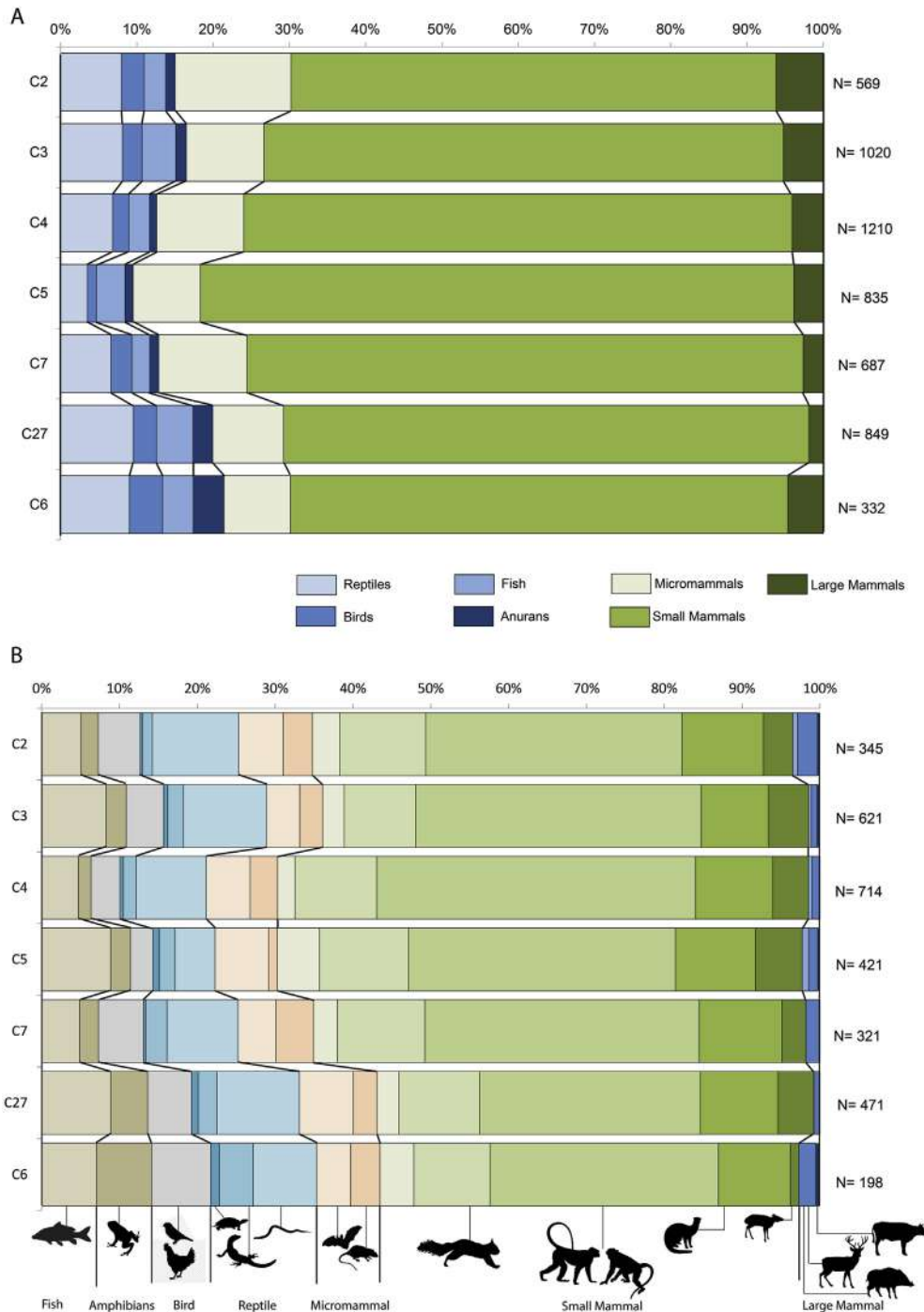


Fig. 3. Distribution of animal taxa identified in different Holocene sedimentary contexts of Kitulgala Beli-lena based on (A) the total number of bone fragments recovered (TNF) and (B) number of identified specimens (NISP).

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 at Kitulgala resembles the use wear of flaked tools recorded in Fa Hien-lena, such as striations suggestive of use as scrapers (Langley et al., 2020). 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.

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 | | 27 | | 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%) | - | |
| | | | Siluriformes | 2 | 1 | 3 | 1 | 4 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 5 | 1 | 18 (0.6%) | 7 | |
| | | | Siluridae | 1 | 1 | 1 | 1 | - | - | 1 | 1 | - | - | - | - | 1 | 1 | 4 (0.1%) | 4 | |
| Amphibia | Anura | | 2 | 1 | 7 | 2 | 11 | 4 | 9 | 3 | 8 | 3 | 4 | 1 | 10 | 3 | 51 (1.6%) | 17 | | |
| Aves | Apodiiformes | Apodidae | | 5 | - | 5 | - | 4 | - | 4 | - | 2 | - | 5 | - | 5 | - | 30 (1.0%) | - | |
| | | | Phasianidae | 1 | 1 | 3 | 1 | - | - | 1 | 1 | 3 | 1 | 2 | 1 | 1 | 1 | 11 (0.4%) | 6 | |
| | | | Galliformes | 3 | 1 | 4 | 2 | 2 | 1 | 1 | 1 | 2 | 1 | 4 | 2 | 4 | 1 | 20 (0.6%) | 9 | |
| | | | Strigiformes | 1 | 1 | - | - | - | - | 1 | 1 | - | - | - | - | 1 | 1 | 3 (0.1%) | 3 | |
| Reptilia | Testudines | Bataguridae | | 1 | 1 | 3 | 1 | 3 | 1 | 3 | 1 | 2 | 1 | 1 | 1 | 4 | 1 | 17 (0.5%) | 7 | |
| | | | Squamata | 2 | 1 | 8 | 2 | 4 | 1 | 3 | 2 | 2 | 1 | 5 | 2 | 6 | 2 | 30 (1.0%) | 11 | |
| | | | Varamidae | 1 | 1 | 2 | 1 | 5 | 2 | 4 | 1 | 4 | 1 | 3 | 1 | 4 | 1 | 23 (0.7%) | 8 | |
| | | | Agamidae | 1 | 1 | 1 | 1 | 2 | 1 | - | - | 2 | 1 | 1 | 1 | 1 | 1 | 8 (0.3%) | 6 | |
| | | | Geckonidae/Scincidae | 21 | 1 | 37 | 2 | 32 | 1 | 10 | 1 | 8 | 1 | 16 | 1 | 28 | 1 | 152 (4.9%) | 8 | |
| | | | Pythonidae | 14 | 1 | 21 | 1 | 29 | 2 | 8 | 1 | 7 | 1 | 14 | 1 | 21 | 2 | 114 (3.7%) | 9 | |
| | | | Colubridae/Viperidae | | | | | | | | | | | | | | | | | |
| Mammalia | Primates | Cercopithecoidea | | 92 | 7 | 173 | 12 | 254 | 18 | 105 | 11 | 46 | 5 | 104 | 9 | 118 | 10 | 892 (28.9%) | 72 | |
| | | | <i>Macaca sinica</i> | 7 | 1 | 18 | 3 | 14 | 2 | 10 | 1 | 6 | 1 | 9 | 1 | 10 | 2 | 74 (2.4%) | 11 | |
| | | | <i>Semnopithecus/Trachypithecus</i> | 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%) | 15 | |
| | | | Rodentia | Hystriidae | 76 | 8 | 157 | 15 | 127 | 10 | 109 | 12 | 39 | 4 | 41 | 5 | 88 | 6 | 637 (20.6%) | 60 |
| | | | Sciuridae | <i>Ratufa cf. macroura</i> | 2 | 1 | 3 | 2 | 4 | 2 | 4 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 17 (0.5%) | 10 |
| | | | | 12 | 2 | 16 | 3 | 24 | 5 | 4 | 2 | 7 | 2 | 16 | 3 | 14 | 4 | 93 (3.0%) | 21 | |
| | | | | | | | | | | | | | | | | | | | | |
| | | | Lagomorpha | Muridae | 1 | 1 | - | - | - | - | 1 | 1 | - | - | - | - | 2 | 1 | 4 (0.1%) | 3 |
| | | | Chiroptera | Leporidae | 18 | 3 | 22 | 4 | 42 | 5 | 24 | 3 | 8 | 2 | 15 | 3 | 32 | 5 | 161 (5.2%) | 25 |
| | | | | Hipposideridae | 1 | 1 | - | - | - | - | - | - | - | - | - | 1 | 1 | - | 2 (0.1%) | 2 |
| | | | | Rhinolophidae | - | - | 1 | 1 | 1 | 1 | - | - | - | - | - | - | - | - | 2 (0.1%) | 2 |
| | | | Carnivora | Viverridae | 34 | 4 | 45 | 4 | 64 | 5 | 35 | 4 | 22 | 2 | 37 | 2 | 49 | 4 | 286 (9.3%) | 25 |
| | | | | Mustelidae | 1 | 1 | 4 | 1 | 3 | 1 | 3 | 1 | - | - | 1 | 1 | 1 | 1 | 13 (0.4%) | 6 |
| | | | Artiodactyla | Tragulidae | 12 | 4 | 30 | 4 | 33 | 4 | 21 | 2 | 6 | 2 | 10 | 2 | 21 | 3 | 133 (4.3%) | 21 |
| | Suidae | 2 | 1 | 2 | 1 | 3 | 1 | 3 | 1 | - | - | - | - | 1 | 1 | 11 (0.4%) | 5 | | | |
| | Cervidae | 8 | 2 | 4 | 1 | 7 | 2 | 4 | 1 | 4 | 1 | 6 | 1 | 3 | 1 | 36 (1.2%) | 9 | | | |
| | Bovidae | 1 | 1 | 2 | 1 | - | - | 1 | 1 | 1 | 1 | - | - | - | - | 5 (0.2%) | 4 | | | |
| Total | | | | 345 | 52 | 621 | 71 | 714 | 73 | 421 | 60 | 198 | 35 | 321 | 44 | 471 | 59 | 3091 | 394 | |

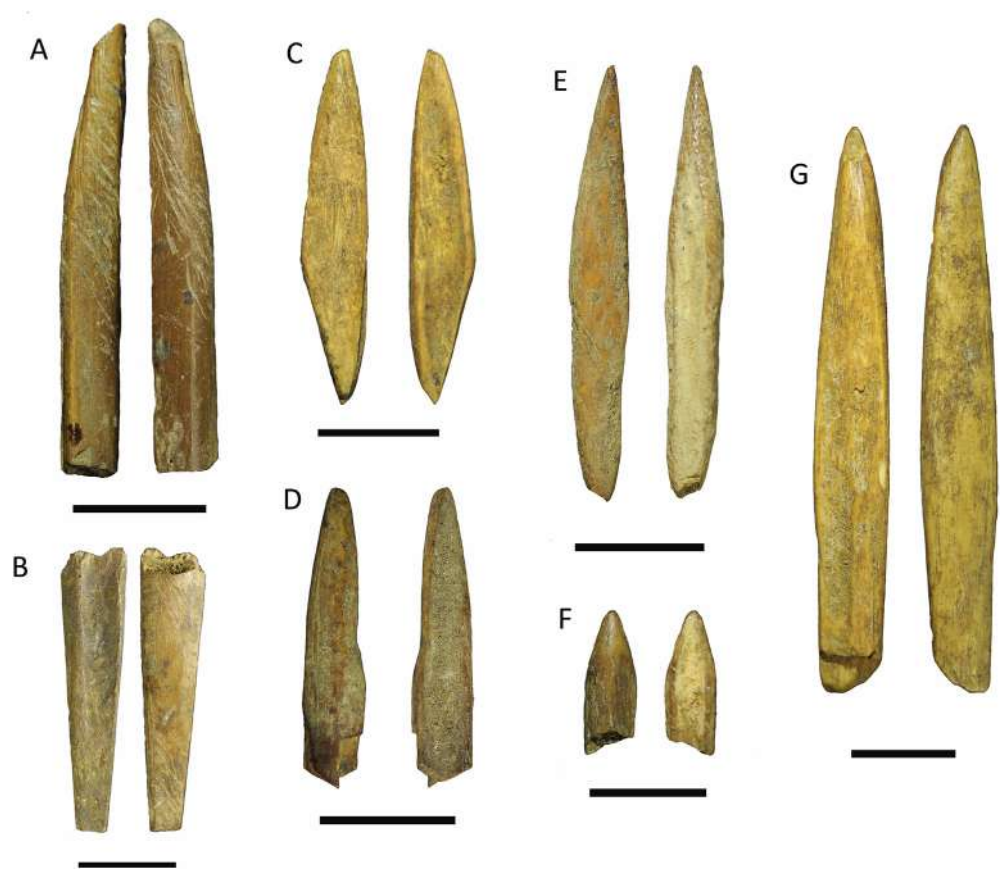
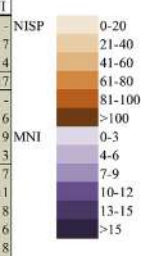


Fig. 4. Osseous tools manufactured from cercopithecoid appendicular skeletal elements recovered during the 2017 excavation of Kitulgala Beli-lena (A-B unipoints C-G bipoints). . Scale bars in microphotographs = 1 cm. (context 3: A, F; 4: B,E; 5:C, D; 27- E,G).

4.4. Invertebrate fauna

The total data for the invertebrate assemblage recovered from the 2017 excavation of Kitulgala Beli-lena are 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 2002.90 g (or ca. 2 kg). 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. Fig. 5 graphs the taxonomic categories in descending order (highest to lowest) by %NISP (Fig. 5A) and %weight (Fig. 5B). 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 (Fig. 6A and B), 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,

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 |
| | | <i>Paludomus bicinctus</i> | 648 | 17.06 | 465.16 | 23.22 |
| | | <i>Paludomus chilinoides</i> | 118 | 3.11 | 99.79 | 4.98 |
| | | <i>Paludomus loricatus</i> | 62 | 1.63 | 29.86 | 1.49 |
| | | <i>Paludomus neritoides</i> | 230 | 6.05 | 219.17 | 10.94 |
| | | <i>Paludomus solidus</i> | 241 | 6.34 | 240.22 | 11.99 |
| | | <i>Paludomus sulcatus</i> | 244 | 6.42 | 149.65 | 7.47 |
| | Unionidae | <i>Lamellidens</i> sp. | 6 | 0.16 | 3.3 | 0.16 |
| Terrestrial | Acavidae | Acavidae | 366 | 9.63 | 183.59 | 9.17 |
| | | <i>Acavus</i> spp. | 18 | 0.47 | 13.42 | 0.67 |
| | | <i>Acavus haemostoma</i> | 1 | 0.03 | 12.2 | 0.61 |
| | | <i>Acavus superbus</i> | 8 | 0.21 | 45.32 | 2.26 |
| | | 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 | |

NISP

- 0-200
- 200-400
- 400-600
- 600-800
- 800-1000
- >1000

Weight

- 0-100
- 100-200
- 200-300
- 400-500
- 500-600

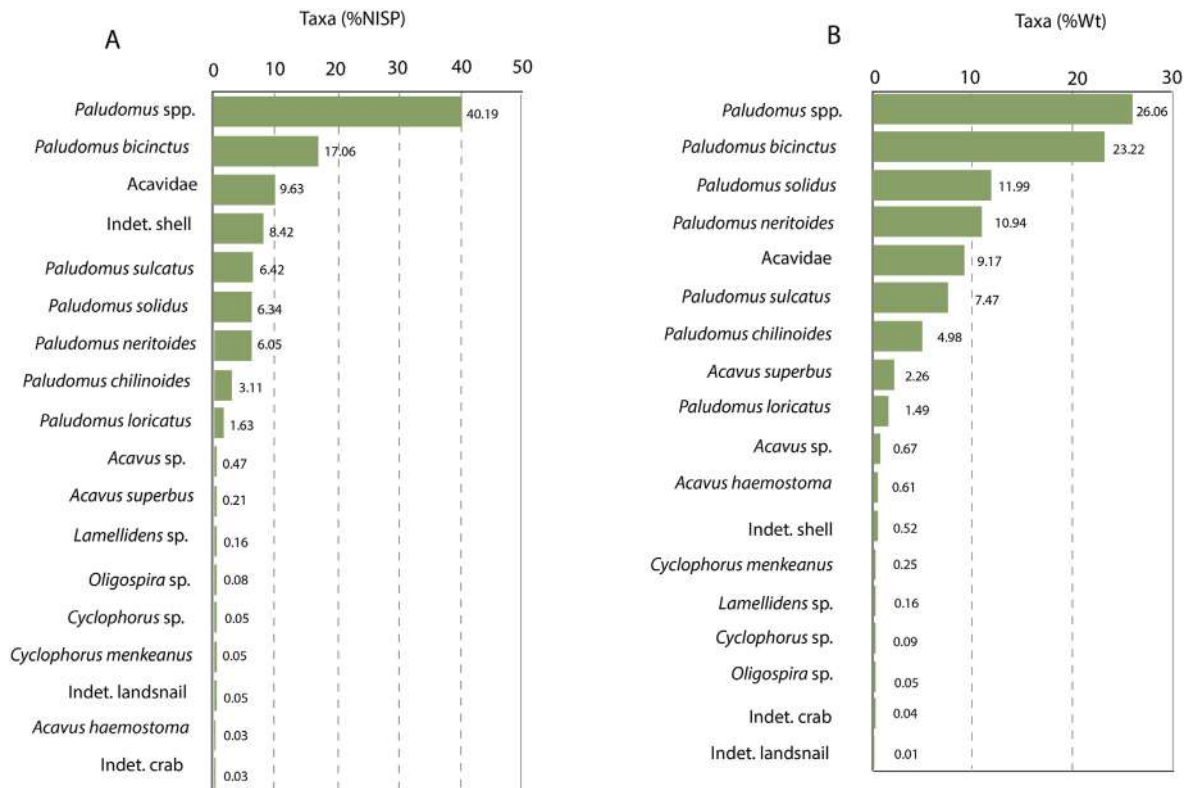


Fig. 5. Kitulgala Beli-lena mollusc taxa by %NISP (A) and %Weight (B).

but 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. 1–2 mm 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 <3 mm 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 some of the new Kitulgala samples, the present study tentatively extends the chronology of the

rainforest plant gathering 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

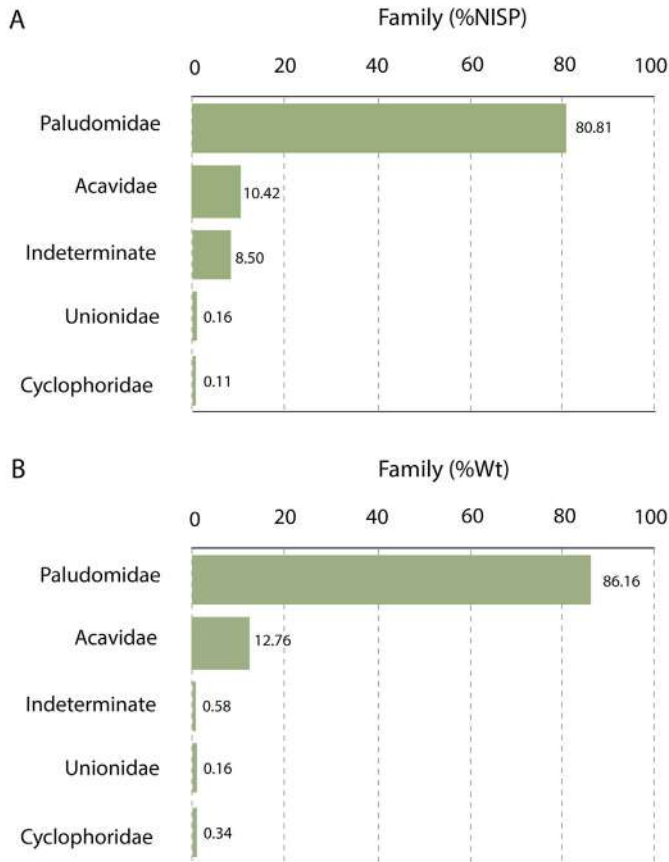


Fig. 6. Kitulgala Beli-lena mollusc taxa at the family taxonomic level by %NISP (A) and %Weight (B).

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 (Fig. 7, 2-3), and the rotations of the cores of 90° degrees (Fig. 7, 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 8, Fig. 7, 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 (Fig. 8). 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 (Fig. 8). 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 pieces 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).

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

| Habitat | Taxon | Context | | | | | | | | | |
|------------------------------|-------------------------|---------|-------|------|-------|------|-------|------|-------|------|-------|
| | | 2 | | 3 | | 4 | | 27 | | 7/5 | |
| | | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % |
| 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 |

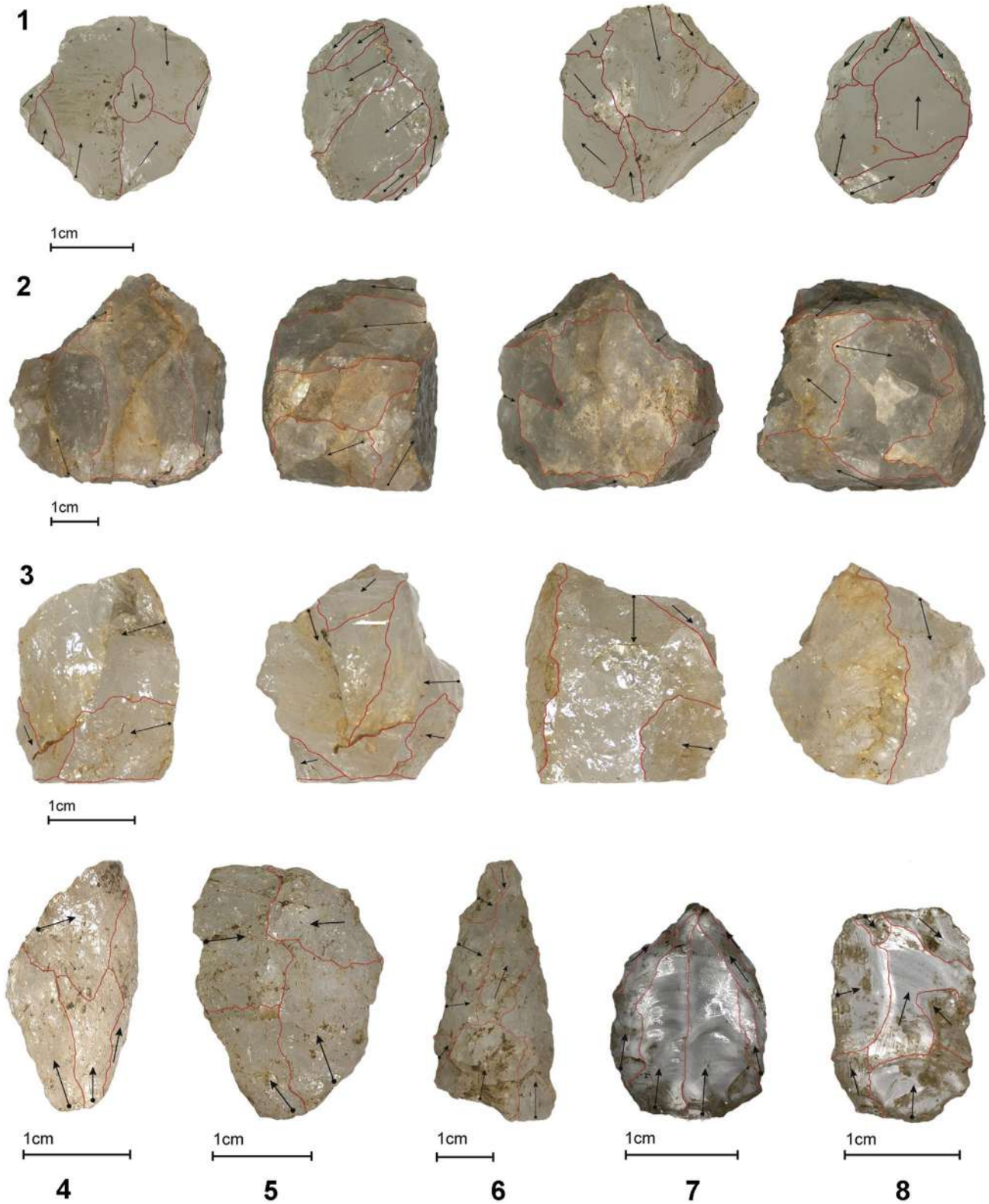


Fig. 7. Bipolar-on-anvil cores (1 – Holocene; 2 – Terminal Pleistocene; 3 Late Pleistocene) and bipolar flakes (4, 5 – Holocene; 6 – Terminal Pleistocene; 7-8 Late Pleistocene) from Kitulgala Beli-lena.

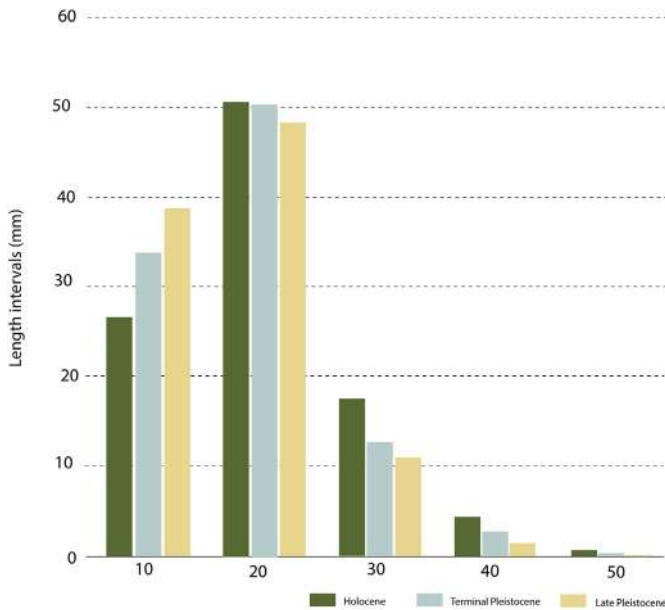


Fig. 8. Histogram of the frequency of complete flakes by length intervals during the different chronological phases at Kitulgala Beli-lena.

5. Discussion

5.1. 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 confirms 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 plant gathering and manufacture of quartz flakes using the bipolar-on-anvil method in the Pleistocene and targeting of arboreal animals starting with the onset of the Holocene. Archaeobotanical evidence from the Late Pleistocene and Holocene levels demonstrates the likely continued extraction and use of wild breadfruit (*Artocarpus nobilis*) and possibly also kekuna nut (cf. *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, 2016), highlighting their potential significance to early human tropical foragers in these parts of the world.

Zooarchaeological and taphonomic insights from the Holocene layers (8029–10,577 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 were 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., 2020). 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 task-specific locations of the rockshelter.

Albeit a preliminary evaluation, 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 100 km² 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.

5.2. 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 3000 years ago in the Wet Zone of Sri Lanka (Wedage et al., 2019a). Stable isotope evidence of human and animal tooth enamel from Batadomba-lena, Fa Hien-lena, and Balangoda Kuragala demonstrates that between 36,000 and 3000 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). The existence of the formation of social and economic networks 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., 2020), as well as the Dry Zone site of Bellan-bandi Palassa (Perera, 2010). These items were most likely obtained by trade with communities present in Sri Lanka's southern coast, identified in sites such as Bundala, Patirajawela and Minihagalkanda (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-bandi 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; Perera, 2010). Bone tools, supposedly of a similar nature to those found in the Wet Zone, have also been documented at Bellan-bandi Palassa (Perera, 2010). On top of isotopic evidence for the persistence of rainforest reliance at Batadomba-lena and Fa Hien-lena until 3000 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 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).

5.3. 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), our understanding 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 and 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. 114 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 77 ka through to the Holocene (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 3000 years ago. This is not to say that coasts were irrelevant to late Pleistocene human occupations in this part of the world (Blinkhorn et al., 2017, 2019), 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 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 (Sali, 1989; Clarkson et al., 2009; Petraglia et al., 2012; Blinkhorn, 2018; Clarkson et al., 2018). This can be clearly seen in the Jurreru Valley, where Middle Palaeolithic occupations span 77–38ka, with the younger assemblages sharing features that become central to subsequent Late Palaeolithic industries from 35ka onwards (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, has 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., 2020). 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 accompanied 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 (Pavlidis, 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., 2018). 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., 2017), 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 was for long 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 (Hunt and Barker, 2014; Aubert et al., 2014, 2018; Langley et al., 2020). 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.

Author contributions

OW, PR, SD, NB, MP and NA designed the study with AP and JB in collaboration with PF, AC and KD. OW, AP, JB and NA conducted the site excavation and the recording of stratigraphy and artefact distribution with supervision from PR, SD, NB and MP. The lithic materials were analysed by AP and OW. AC looked at the archaeobotanical remains. Molluscan remains were studied by PF. NA studied the vertebrate faunal remains and the bone tools. KD was responsible for the radiocarbon dating. OW, PR, PF, AC, KD, AP, JB, SD, NB, MP and NA wrote the paper.

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