

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

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40 **Abstract**

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

57

58 Keywords:

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

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65 **1. Introduction**

66 South Asia has emerged as a crucial region for understanding the timing and nature of human
67 dispersals from Africa and the Middle East into Southeast Asia and Australasia (Petraglia et
68 al., 2012; Blinkhorn et al., 2013, 2019; Roberts et al., 2017a). In addition to it being located at
69 a key geographical juncture, it also sits at a major biogeographic boundary between the
70 Sahara-Arabian and Afrotropical regions to the west and Palearctic and Sino-Japanese regions
71 to the north (Watts, 1984; Holt et al., 2013; Blinkhorn et al., 2013). Archaeological research
72 in South Asia over the past two decades has pointed to potential multiple, early routes of
73 dispersal into the region (Petraglia et al., 2010; Boivin et al., 2013; Bae et al., 2017; Blinkhorn
74 and Petraglia 2017), and emphasized the varied and complex local patterns of technological
75 and cultural change (Petraglia et al., 2010, 2012; Blinkhorn et al., 2013), as well as the
76 diversity of the types of terrestrial environments, utilized by early humans (Blinkhorn et al.,
77 2016; Roberts et al., 2015a, 2017b). This is in contrast to a prominent model that assumes a
78 rapid, coastal *ca.* 60 ka dispersal of humans, associated with uniform technological features
79 around the Indian Ocean Rim (Mellars, 2006; Mellars et al., 2013).

80

81 Research in Sri Lanka, an island at the southern tip of South Asia, has highlighted how early
82 members of our species employed adaptive strategies to take full advantage of their
83 environments such as tropical rainforests. Traditional anthropological and archaeological
84 assumptions have viewed rainforests as barriers to human occupation due to a scarcity of
85 resources, including calorie-rich plants and large animals (Bailey et al., 1989; Gamble, 1993).
86 Nevertheless, Sri Lanka has produced the earliest clear evidence for *Homo sapiens* fossils in
87 tropical rainforest environments in South Asia (Kennedy, et al., 1987; Kennedy and
88 Deraniyagala, 1989; Deraniyagala, 1992; Kennedy, 2000) as well as evidence for heavy
89 reliance on rainforest resources, including specialized hunting of arboreal and semi-arboreal

90 fauna from ~45,000 years ago through to 3,000 years ago (Roberts et al., 2015a,b, 2017b;
91 Wedage et al., 2019a) facilitated by microlithic and osseous technologies (Deraniyagala,
92 1992, Wijeyapala, 1997, Perera et al., 2011, Wedage et al., 2019a; Langley et al., 2020).
93 However, knowledge of the scale of Late Pleistocene tropical rainforest occupations in the
94 region remains limited since multidisciplinary analyses of archaeological sequences are
95 restricted to two sites: Fa Hien-lena, dated to *ca.* 45,000 years ago (Wedage et al., 2019a) and
96 Batadomba-lena, dated to *ca.* 38,000-36,000 years ago (Roberts et al., 2015b).

97

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

115 reveal a more complete picture of Late Pleistocene and Holocene human adaptation and
116 presence in this increasingly significant region for human evolutionary research.



117

118 **Figure 1.** Map of Sri Lanka showing the location of Kitulgala Beli-lena and the island's
119 vegetation zones (Ashton et al., 1987, Erdelen, 1988) (A), the 2017 excavation of the
120 rockshelter (B) and the plan showing the location of the excavation squares of the site (C).
121

122 2. Kitulgata Beli-lena Rockshelter: History of Research

123 Kitulgala Beli-lena is located in the Kegalle district of Sri Lanka's Sabaragamuwa Province,
124 approximately 85 km east of Colombo (Figure 1). With a ca. 30 x 15 m north facing entrance,
125 the rockshelter is formed from gneiss bedrock, part of the metamorphic terrain of Sri Lanka's
126 Highland Complex (Cooray, 1984). Kitulgala Beli-lena is situated in the island's lowland Wet

127 Zone with a mean annual precipitation between 2500-3500 mm/year (Dömros, 1974; Roberts
128 et al., 2015b), surrounded by humid tropical rainforest. The rockshelter was first explored by
129 P.E.P. Deraniyagala in 1960-1961, who excavated several test pits and noted an abundance of
130 historic and prehistoric archaeological materials. However, no detailed description of this first
131 investigation was ever published. Systematic excavation of the rockshelter continued in 1978
132 by the Department of Archaeology of the Government of Sri Lanka under the supervision of
133 S.U. Deraniyagala. Excavations continued in 1979, 1983, 1985 and in 1986 (under W. H.
134 Wijeyapala). The Department of Archaeology, this time led by Oshan Wedage, carried out a
135 small excavation of 1 m² in the southeast corner of the rockshelter in 2013. Collectively, these
136 excavations sampled depths of more than 3 m of cultural deposits and produced a total of 25
137 radiocarbon dates (Table 1), indicating a chronology extending back to *ca.* 31,000 cal. years
138 BP. Two thermoluminescence dates ($17,217 \pm 3300$ and $18,565 \pm 2610$) have also been
139 reported (Abeyratne, 1994).

140

141 Excavations of Terminal Pleistocene sediments of the site, with associated charcoal dated to
142 $12,260 \pm 870$ years BP, had previously yielded several human remains including a partial
143 skeleton of an adult of indeterminate sex, a skull of a child 10-11 years of age at the time of
144 death, and bones and teeth from at least ten different individuals (Kennedy et al., 1987;
145 Kennedy and Deraniyagala, 1989; Wijeyapala, 1997). Sparse microlithic tools, manufactured
146 from quartz, were also recorded from the beginning of site occupation (Wijeyapala, 1997).
147 However, these technologies, as well as osseous tools, were not systematically analysed. In
148 2017, a new excavation in Kitulgala Beli-lena was conducted by the Max Planck Institute for
149 the Science of Human History and University of Sri Jayewardenepura in collaboration with
150 the Department of Archaeology, Government of Sri Lanka. The aim of the excavation was to
151 recover new materials to produce a refined chronology for the site, using appropriate pre-

152 treatment methodologies for charcoal samples as well to conduct systematic
 153 zooarchaeological, archaeomalacological and archaeobotanical analyses. Three 1 x 1 m
 154 squares were opened in the inner western section of the rockshelter, close to the wall,
 155 following the grid laid out during the 1980s excavation (Figure 1). The excavation reached a
 156 final depth of 192 cm from the surface rockshelter deposits.

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

Stratum	Lab Code	$^{14}\text{C}^\dagger$	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 ± 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	-

160
 161 †Radiocarbon dates were from charcoal samples *All samples were calibrated using the OxCal 4.3
 162 software (Bronk Ramsey 2017) and IntCal calibration curve (Reimer et al., 2013)
 163
 164

165 **3. Methods**

166 **3.1 Excavation**

167 The 2017 excavation of Kitulgala Beli-lena aimed to recover new archaeological material in
168 order to refine/revise the chronology of the site and better understand human culture,
169 technology, and subsistence strategies. The excavation was situated in the inner western
170 section of the rockshelter, some 5 m from the wall. Following the excavations in the
171 rockshelter in 1985, the exposed sections were covered by stone walls to preserve the
172 integrity of the site. The only portion that was not protected was a 2 m² excavation square
173 (grid code: G12-G11) which was sampled for micromorphology in 2005 and 2009 (Perera,
174 2010, Kourampas et al., 2009). The new excavation extended this unprotected square
175 southward, opening excavation square G12 and the previously unexcavated squares H14 and
176 I14 (Figure 1) and allowing for the correlation of the results with the micromorphological
177 analyses of Kourampas et. al (2009).

178

179 Excavations were conducted using hand tools dividing artefacts and sediment samples into
180 discrete sediment units, or subdividing discrete sediment units into 5cm arbitrary horizons,
181 where single contexts were deeper than 5cm. Three dimensional recording of the excavated
182 area, the interface between sediment deposits and major artefacts (>20 mm) was undertaken
183 using a Leica Builder 505 total station. After removal, excavated sediments were placed on
184 polythene sheeting and a 10-20 liter sub-sample was taken for flotation. A total of 1120 liters
185 of sediment were floated (using a 250 micron mesh) during the excavation. The remainder of
186 the excavated sediments was wet sieved to allow for the recovery of cultural materials. In
187 addition, samples of approximately 100 g were recovered at 5 cm intervals to enable a range
188 of sediment analyses (including ongoing analyses i.e. laser particle size analyses, phosphate
189 analyses etc.).

190

191 ***3.2 Radiocarbon dating***

192 Fourteen charcoal fragments recovered during excavation were submitted for dating to the
193 Oxford Radiocarbon Accelerator Unit. The charcoal samples were prepared using the acid–
194 base oxidation/stepped combustion (ABOx-SC) protocol (Bird et al., 1999; Higham et al.,
195 2008). Of these, 13 samples yielded ¹⁴C measurements that were calibrated using the IntCal13
196 calibration curve and the OxCal 4.3 programme (Reimer et al., 2013; Bronk Ramsey 2017).

197

198 ***3.3 Zooarchaeological analysis and osseous technology analysis***

199 All recovered bone fragments from the 2017 excavation of Kitulgala Beli-lena were analysed,
200 including fragmentary remains as well as diaphyses and rib shafts. All specimens were sorted,
201 counted, and measured (length, width, and thickness) using a digital caliper (Mitutoyo 500–
202 463). Identified specimens were recorded in detail using codes for anatomic zones following a
203 zonation system modified from Dobney and Reilly (1988) to allow for the description of
204 fragmentation patterns. Diagnostic skeletal elements were identified using comparative
205 vertebrate specimens from the Field Museum of Natural History and American Museum of
206 Natural History and from the Laboratory of Comparative Anatomy of the Muséum national
207 d’Histoire naturelle (MNHN). Naming of identified taxa follows the nomenclature published
208 by Wilson and Reeder (2005). The identified taxa were classified to size class based on live
209 weight following a modification of the criteria established by Thomas (1969) and Grayson
210 (1984): (a) micromammals: 100 g to 1 kg, (b) small mammals: 1 kg to 25 kg, (c) large
211 mammals class 1: 25 kg to 200 kg, (d) large mammals class 2: 200 kg to 1000 kg, and (e)
212 large mammals class 3: > 1000 kg.

213

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

222

223 In terms of zooarchaeological quantifications, the minimum number of element (MNE) and
224 minimum number of individual (MNI) counts were calculated following a modification of
225 Dobney and Rielly's (1998) zonation system. This system is based on the recording of distinct
226 morphological zones in a skeletal element. The MNE was taken as the total number of non-
227 overlapping zones (i.e., greater than 50% of the diagnostic zone present) for every skeletal
228 element of a taxon. The highest MNE value, considering side and age (epiphyseal fusion and
229 dental wear, following Klein and Cruz-Uribe (1984), was used to estimate the MNI. The
230 MNE counts were converted to minimum animal unit (MAU) values by taking into account
231 the number of times the element occurs in the skeleton. The normalized MAU values (%
232 MAU) were used to compare skeletal part representation in the different phases of cave
233 occupation (Lyman, 1994).

234

235 ***3.4 Molluscan Analysis***

236 The invertebrate assemblage of Kitulgala Beli-lena consists of all remains collected during the
237 2017 excavation of the site, including fragmentary specimens recovered from dry and wet
238 sieving of sediments. Prior to analysis, all samples were washed to remove excess sediment

239 and air-dried for 24-48 hours. As a physical comparative reference collection was not
240 available for specimen identification, all taxonomic attributions were made following the
241 descriptions and/or illustrations provided in Hausdorf and Perera (2000), Naggs and Raheem
242 (2000), Raheem and Naggs (2006) and Starmuhlner (1974). Recent correspondence with Dr
243 Dinarzarde Raheem (Natural History Museum, London) indicates that significant taxonomic
244 revision of the Sri Lankan terrestrial and freshwater mollusc fauna is needed.

245

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

253

254 ***3.5 Archaeobotanical analysis***

255 The archaeobotanical assemblage analysed in this study comprises materials from flotation
256 samples from five sedimentary contexts spanning the Pleistocene sequence of Kitulgala Beli-
257 lena, namely contexts 10, 17, 21, 24, 23. The flotation samples were sieved into >4mm, 2-
258 4mm, 1-2mm, and <1mm fractions. The >4mm and 2-4mm fractions were sorted under low
259 magnification (x8–x40) using an Olympus SZ61 stereozoom microscope and the 1-2mm
260 fraction was scanned for any smaller remains. Analysis of this material is ongoing and subject
261 to the establishment of a comparative ethnobotanical reference collection for Sri Lanka.
262 Where possible, taxonomic identifications were based on published descriptions (e.g., Kahn

263 and Ragone 2013; Kajale 1988; Levin 2015) and available comparative botanical material in
264 the University of Queensland's Archaeobotany Laboratory.

265

266 **3.6 Lithic analysis**

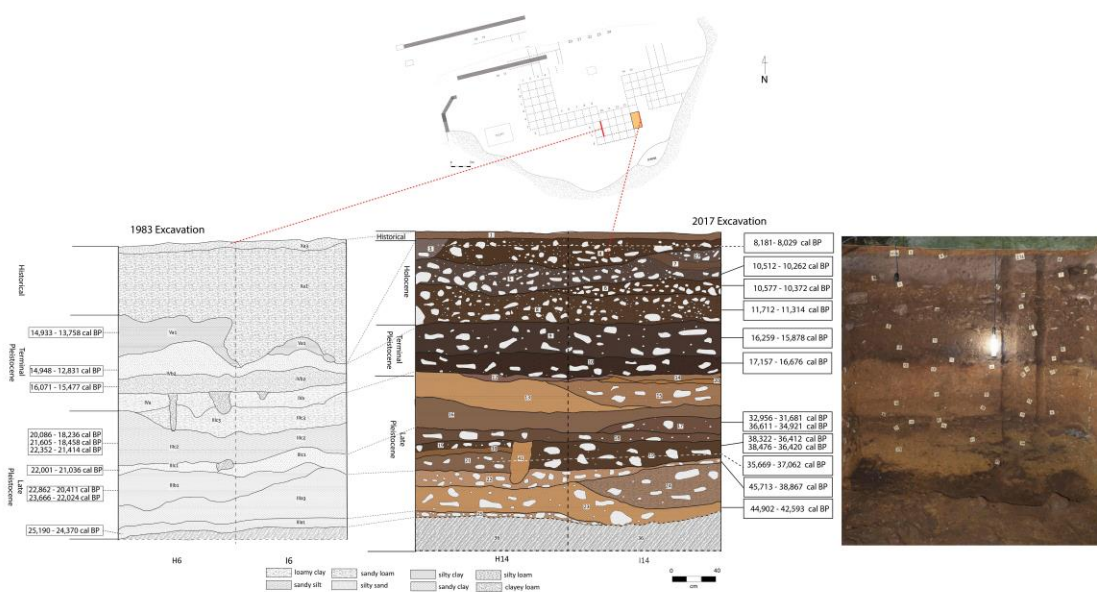
267 The technological analysis of the lithic assemblages was performed using the *chaîne*
268 *opératoire* concept, a methodological framework that defines the reconstruction of the various
269 processes of flake production from the procurement of raw materials through to discard
270 (Lemonnier, 1986; Pelegrin et al., 1988). The assemblages were firstly discriminated by raw
271 material units, defined according to variety of stone and macroscopic features including type
272 of cortex, colour, grain size, and texture (Roebroeks, 1988). The technological features were
273 then reconstructed through the diacritic analysis of the scar pattern organization on the cores'
274 flaking surfaces and on the flakes' dorsal side. Previous studies on the lithic collections in Sri
275 Lanka report the extensive use of the bipolar method (Lewis, 2017; Wedage et al., 2019a;
276 2019b). In order to address the variability of this lithic reduction strategy, the analysis was
277 performed following more recent definitions based on experimental knapping data (Crabtree,
278 1972; de la Peña, 2015; Donnart et al., 2009; Mourre, 1996). The flake assemblages were
279 classified by dimensional criteria and only the lithic items greater than 1 cm were analysed.
280 Bladelets are considered elongated blanks in which the ratio length to width is ≥ 2 , and with a
281 percussion axis length of less than 4 cm (Petraglia et al., 2009). A distinction has not been
282 made between bladelets produced from true bladelet cores and flake-bladelets. Siret knapping
283 accidents were distinguished following the criteria of Mourre (1996) whereas *bâtonnet* flakes
284 (or bipolar spalls) and splinter flakes were defined following Brun-Ricalens (2006).

285

286 **4. Results**

287 **4.1 A Revised Chronostratigraphy for Kitulgala Beli-lena**

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



295 **Figure 2.** Comparison of the 1983 (Wijeyapala, 1997) and 2017 stratigraphy for Kitulgala
 296 Beli-lena.

297
 298 **Table 2.** New radiocarbon dates on (charcoal) from the 2017 excavation of Kitulgala Beli-
 299 lena

Context	Labcode (OxA)	Measured Date	Calibrated (cal. BP)*
3	37930	7,309 ± 34	8,181 - 8,029
5	37932	9,230 ± 40	10,512 - 10,262
6	37933	9,280 ± 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

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

302
 303 **Table 3.** Major phases of Kitulgala Beli-lena occupation based on radiocarbon dates and site
 304 stratigraphy.

Occupational Phase	Sedimentary Stratum (1983)	Dates (cal. BP)*	Sedimentary Context (2017)	Dates (cal. BP) *
Historical	Xa3	-	1	-
Holocene	-	-	3	8,181- 8,029
			5	10,512-10,262
			6	10,577- 0,372
			8	11,712-11,314
			7, 27	-
Terminal Pleistocene	V	-	9	16,259 -15,878
	IVb3	13,816-13,481;	10	17,157 -16,676
	IVb2	14,948-12,831		
	IVb2	16,071-15,477		
	IVa	-		
Late Pleistocene	IIIc3	16,084-15,435;	12, 13, 14, 15, 20	-
	IIIc2	20,086-18,236; 21,605-18,458; 22,352-21,414	-	-
	IIIc1	22,001-21,036	17	32,956 - 31,681; 36,611 - 34,921
			19	38,322 - 36,412; 38,476 - 36,420
			21	37,062- 35,669
			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†	-	-

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

307 †uncalibrated

308 *Late Pleistocene Phase*

309 The Late Pleistocene phase of the rockshelter represents intermittent/episodic human
310 occupation, from around *ca.* 44,000 to 31,000 cal. BP. It is characterized by pebbly clayey
311 loams with angular gneiss slabs and subhorizontal layers of yellowish brown, sandy clay to
312 sandy silt deposits. Just above the gneiss bedrock is a *ca.* 10 cm clast-supported conglomerate
313 with well-rounded imbricated pebbles that is hypothesized (Wijeyapala, 1997; Kourampas,
314 2009) to have been deposited by a stream that at the present flows 60 m below the level of the
315 rockshelter's entrance. This layer, notably devoid of any cultural materials, is overlain by a
316 series of sandy loam and sandy clay deposits containing angular gneiss slabs and abundant
317 charcoal.

318

319 Kourampas et al. (2009) suggest that these layers most likely represent an admixture of roof
320 fall and colluvial deposits reworked by bioturbation and rockshelter floor processes including
321 trampling and surface runoff. The first in the series, Context 23, returned dates as early as
322 42,593-44,902 cal. BP. These sedimentary layers, referred to as phases IIIa(2)-IIIc(3) by
323 Wijeyapala (1997), were previously dated to 25,190 - 18,236 cal. BP. New dates now place
324 these layers as being deposited between *ca.* 44,902-31,600 cal. BP (Figure 2). Evidence of
325 human activities in the Late Pleistocene phase includes artefacts (ochre fragments and stone
326 tools) and macrobotanical remains. No faunal remains were recovered in the Late Pleistocene
327 layers during the 2017 excavations.

328

329 *Terminal Pleistocene Phase*

330 The Terminal Pleistocene phase of site occupation is characterized by dark greyish brown
331 sandy loam and silty clay deposits notable for a heavy concentration of quartz microliths and
332 macrobotanical remains (e.g. contexts 9-10). This *ca.* 30 cm phase of occupation correlates to
333 sedimentary layers IV and V from the 1983 excavation which were dated to 13,600-12,100

334 cal. BP (Wijeyapala, 1997) and contain the densest occupation debris in terms of charcoal and
335 lithic materials. Discrete patches of burnt sediments and ashes point to possible hearths within
336 the layers. Angular gneiss slabs most likely from roof fall or wall disintegration are also
337 abundant in these layers. Charcoal from these layers recovered from the 2017 excavation
338 returned dates between 17,157-11,314 cal. BP. Kourampas (2009), in his micromorphological
339 analyses of the stratigraphy from the 1986 excavation, interpreted these layers as resulting
340 from accelerated sedimentation brought about by human activity, high rates of colluvation,
341 and accelerated water seepage.

342

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

351

352 *Holocene Phase*

353 The Holocene Phase of Kitulgala consists of at least six distinct sedimentary layers with
354 abundant charcoal, quartz microlith, and ochre content. These layers, previously dated to
355 9,070-3,550 cal. BP (layer VI to VII), have been re-dated to 10,577-8,029 cal. BP. Unlike the
356 underlying sedimentary layers, the Holocene layers yielded numerous faunal materials. *In situ*
357 hearths with burnt seeds and animal bone fragments were also recorded. The lowermost layer,
358 a compact mid-yellowish brown sandy loam, contains frequent mid-sized (up to 15 cm)

359 angular gneiss slabs suggestive of a roof-fall episode that happened sometime during the
360 onset of the Holocene. Overlying this is a series of almost horizontal loamy clay and silty
361 sand layers rich in debris from human activity.

362

363 *Historical Phase*

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

375

376 **4.2 Vertebrate Fauna**

377 A total of 5502 animal bone fragments were recovered from the 2017 excavation of Kitulgala
378 Beli-lena. As noted above, all of the vertebrate remains were recorded from sedimentary
379 contexts dated to the Early Holocene. Small mammals (< 25kg) dominate the faunal
380 assemblage, accounting for 70.5% (Total number of fragments, TNF= 3859, Number of
381 identified specimens, NISP=2156) of the remains recorded, suggesting deliberate targeting of
382 these animals by the people that settled in Kitulgala (Table 4, Figure 3). Large mammals
383 account for 3.9% of the recovered animal bones and micromammals (mostly murids and bats)

384 account for 10.7%. Reptiles (11.1% NISP), fish (4.8% NISP) and birds (2.1% NISP) were
 385 also identified in the assemblage.

386 **Table 4.** Vertebrate remains recovered from the 2017 excavation of Kitulgala Beli-lena.
 387

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

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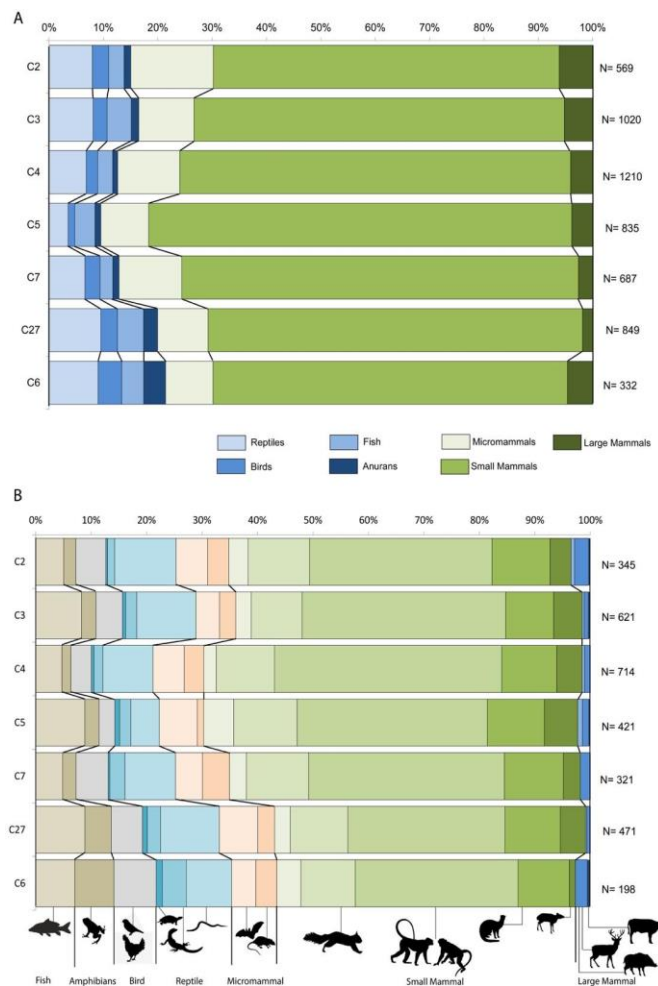
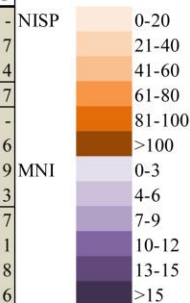


Figure 3. Distribution of animal taxa identified in different Holocene sedimentary contexts of Kitulgala Beli-lena based on (A) the total number of bone fragments recovered (TNF) and (B) number of identified specimens (NISP).

424 **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%)	-
				2	1	3	1	4	1	2	1	1	1	1	1	5	1	18 (0.6%)	7
				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		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
				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
Reptilia	Squamata	Bataguridae	<i>Varanus</i> sp.	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	2	1	5	2	6	2	30 (1.0%)	11
				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
				21	1	37	2	32	1	10	1	8	1	16	1	28	1	152 (4.9%)	8
				14	1	21	1	29	2	8	1	7	1	14	1	21	2	114 (3.7%)	9
				92	7	173	12	254	18	105	11	46	5	104	9	118	10	892 (28.9%)	72
Mammalia	Primates	Cercopithecidae	<i>Macaca sinica</i>	7	1	18	3	14	2	10	1	6	1	9	1	10	2	74 (2.4%)	11
				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	Hystricidae	<i>Ratufa cf. macroura</i>	76	8	157	15	127	10	109	12	39	4	41	5	88	6	637 (20.6%)	60
				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	Leporidae	<i>Lepus</i>	1	1	-	-	-	-	1	1	-	-	-	-	2	1	4 (0.1%)	3
				18	3	22	4	42	5	24	3	8	2	15	3	32	5	161 (5.2%)	25
	Chiroptera	Hipposideridae	Rhinolophidae	1	1	-	-	-	-	-	-	-	-	1	1	-	-	2 (0.1%)	2
				-	-	1	1	1	1	-	-	-	-	-	-	-	-	2 (0.1%)	2
	Carnivora	Viverridae	<i>Paradoxurus</i> sp.	34	4	45	4	64	5	35	4	22	2	37	2	49	4	286 (9.3%)	25
				1	1	4	1	3	1	3	1	-	-	1	1	1	1	13 (0.4%)	6
	Artiodactyla	Tragulidae	<i>Moschiola</i> sp.	12	4	30	4	33	4	21	2	6	2	10	2	21	3	133 (4.3%)	21
				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
1				1	2	1	-	-	1	1	1	1	-	-	-	-	5 (0.2%)	4	
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



427 From the 5502 vertebrate remains recovered from the site, 3091 (56.2%) can be confidently
428 assigned to family, genus, or species (Table 5). Cercopithecoid monkeys dominate the Early
429 Holocene assemblage of the site, with a total of 1001 remains from at least 91 individuals
430 recorded. Both cercopithecines (macaque) and colobines (langurs) were identified in the
431 assemblage based on teeth and certain post-cranial elements. However, the high degree of
432 fragmentation prohibits confident identification of these elements to species. Only 74 (7.4 %,
433 MNI= 11) specimens can be confidently identified as representing *Macaca sinica* and 35
434 (3.5%, MNI=8) were identified as coming from langurs (*Semnopithecus/Trachypithecus*). All
435 skeletal elements were represented in the assemblage suggesting that complete monkey
436 carcasses were brought in and processed on the site.

437

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

448

449 Sciurids represent the second most common taxa in the Holocene faunal assemblage of
450 Kitulgala with a total of 654 dental and skeletal elements identified. 97.4% of the elements
451 correspond in terms of size and morphology, particularly for dental elements, to comparative

452 specimens of the grizzled giant squirrel (*Ratufa macroura*) while the rest (NISP= 17)
453 represent flying squirrels (*Petinomys/Petaurista*). Burning and calcination were observed in
454 12.3% and 5.4% of the identified sciurid specimens, respectively. Other small mammals
455 identified in the assemblage include civet cats (9.3% NISP, MNI=25), otters (0.4% NISP,
456 MNI=6), chevrotains (4.3% NISP, MNI=21) and porcupines (2.7% NISP, MNI=15). Similar
457 to cercopithecids, these animals are represented mostly by dental and dense postcranial
458 elements.

459
460 A total of 222 specimens representing large mammals were recorded in the assemblage. From
461 these, 23.4% can be assigned confidently to taxa. These include 11 (0.4% NISP, MNI=5) suid
462 specimens, 36 (1.2% NISP, MNI=9) cervid and 5 (0.2% NISP, MNI=4) bovid fragments.
463 Anthropogenic modifications were mostly restricted to burning (12.6%). Butchery marks were not
464 observed in any large mammal bone fragments, albeit a proximal cervid metatarsal exhibited
465 evidence of impact fractures and two bovid and one cervid metapodial fragments showed
466 evidence of modifications consistent with tool/artefact production.

467
468 Non-mammalian fauna represents 15.2% (19.7% NISP) of the animal remains from the site.
469 Fish (NISP=149) are represented mostly by cyprinids (carps), identified from pharyngeal
470 teeth and certain cranial elements. Silurid (catfish) specimens (spine) were also identified,
471 albeit in very low frequency (NISP=4). Reptiles (11.1% NISP) on the other hand are
472 represented by varanids, pond/river turtles, agamid/iguanid lizards, pythons and colubrid
473 snakes (Table 5). The fish bones recorded in the site exhibited a high degree of burning
474 (40.9%). Likewise, several reptile bone fragments, particularly varanids and *Python*,
475 exhibited evidence of burning and calcination (11%), suggesting that they were probably also
476 utilized as a food source. Although bird skeletal elements are present in all sedimentary

477 contexts dated to the Holocene (2.1% NISP), only 20 (23.8%) fragments can be confidently
478 identified to taxa. These include owls (Strigidae), swifts (Apodidae) and jungle fowls
479 (Phasianidae).

480

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

486

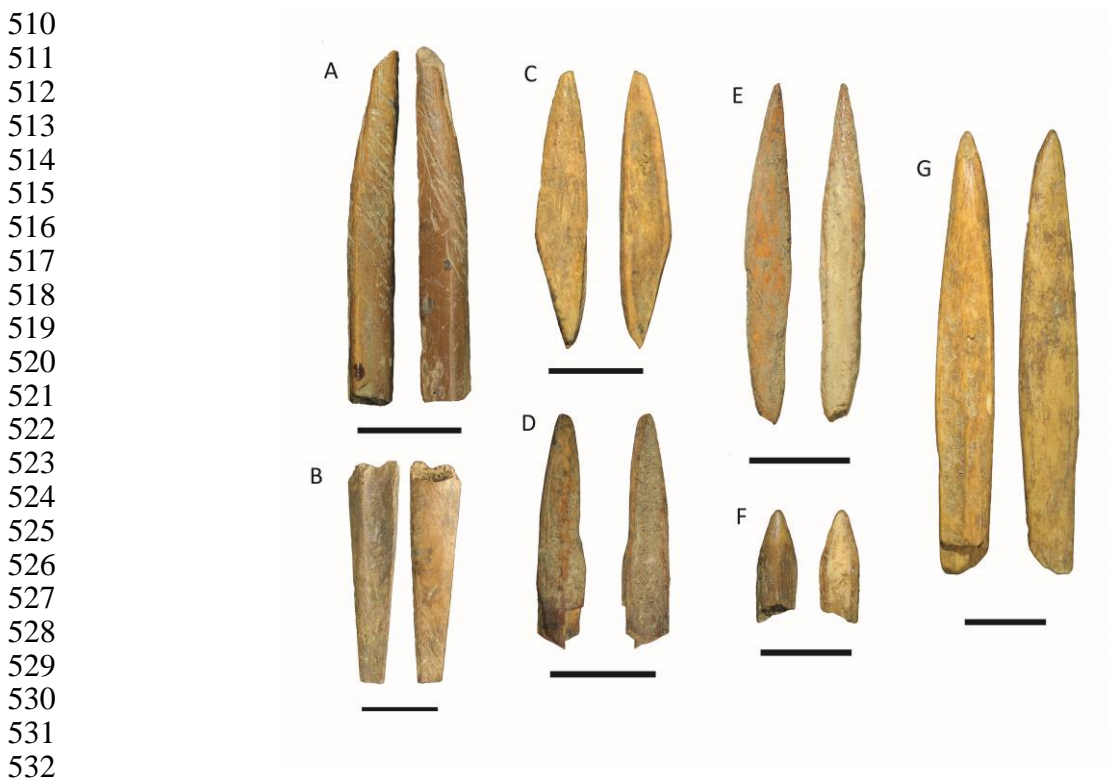
487 ***4.3 Osseous Technology***

488 A total of 21 (0.38% of the bone assemblage studied) finished tools manufactured from small
489 mammal long bones were identified in the site, including 10 finished unipoints, seven
490 bipoints, and four geometrics (Figure 4). Morphological features retained in some of the
491 unipoints in the assemblage suggest that they were manufactured from cercopithecoid fibulae
492 (Figure 4A) and ulnae (Figure 4B). The bipoints and the geometrics (Figure 4C-G), on the
493 other hand, were most likely manufactured from cercopithecoid humerus or femur shaft
494 fragments. However, further studies are needed to confirm this. At Fa Hien-lena, the bipoints
495 and geometric bone tools from the Terminal Pleistocene and Early to Mid-Holocene layers
496 were manufactured from cercopithecoid femur shaft fragments, based on the presence of
497 blanks and unfinished tools (Wedage et al., 2019; Langley et al., 2020).

498

499 In terms of typology, the osseous tools recorded in Kitulgala Beli-lena are identical to those
500 identified at Fa Hien-lena (Wedage et al., 2019a; Langley et al., 2020) and Batadomba-lena
501 (Perera et al., 2011). The unipoints exhibit side notches suggesting that they were hafted to a

502 shaft by ligature. These hafted bone points, again like those found in Fa Hien, most likely
503 represent projectile points that were used by hunter-gatherers to selectively target certain
504 arboreal animals (Wedage et al., 2019a; Langley et al., 2020). This is also consistent with the
505 high-impact fracture observed in some of these specimens. However, unlike in Fa Hien-lena
506 where 1.7% (N=246) of the faunal remains studied exhibited modifications consistent with
507 tool manufacture (grinding/polishing) (Wedage et al., 2019a), only finished tools were
508 identified in Kitulgala Beli-lena. This suggests that the tools were not manufactured in the
509 site, or at least in this part of the rockshelter.



533 **Figure 4.** Osseous tools manufactured from cercopithecoid appendicular skeletal elements
534 recovered during the 2017 excavation of Kitulgala Beli-lena (A-B unipoints C-G bipoints).
535 Scale bars in microphotographs= 1 cm. (context 3: A, F; 4: B,E; 5:C, D; 27- E,G)
536

537 In addition to finished tools manufactured from small mammal bones, three bone tool
538 fragments manufactured from cervid metapodial shafts were also recorded in the Holocene
539 layers of the site. The fragments represent scraper and spatula-type tools, again similar to
540 those recorded in Fa Hien-lena. The use wear on the edges of the tools identified at Kitulgala

541 resembles the use wear of flaked tools recorded in Fa Hien-lena, such as striations suggestive
 542 of use as scrapers (Langley et al., 2020). Overall, the similarity of the osseous tools recovered
 543 from Kitulgala Beli-lena to those from Fa Hien-lena as well as those from Batadomba-lena
 544 suggests a shared technology that facilitated hunting and foraging in the rainforest
 545 environments of Sri Lanka.

546

547 **4.4 Invertebrate Fauna**

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

554

555

556 **Table 6.** Taxonomic categories and total quantification data of the invertebrate remains from
 557 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 chilinooides</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
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

Weight

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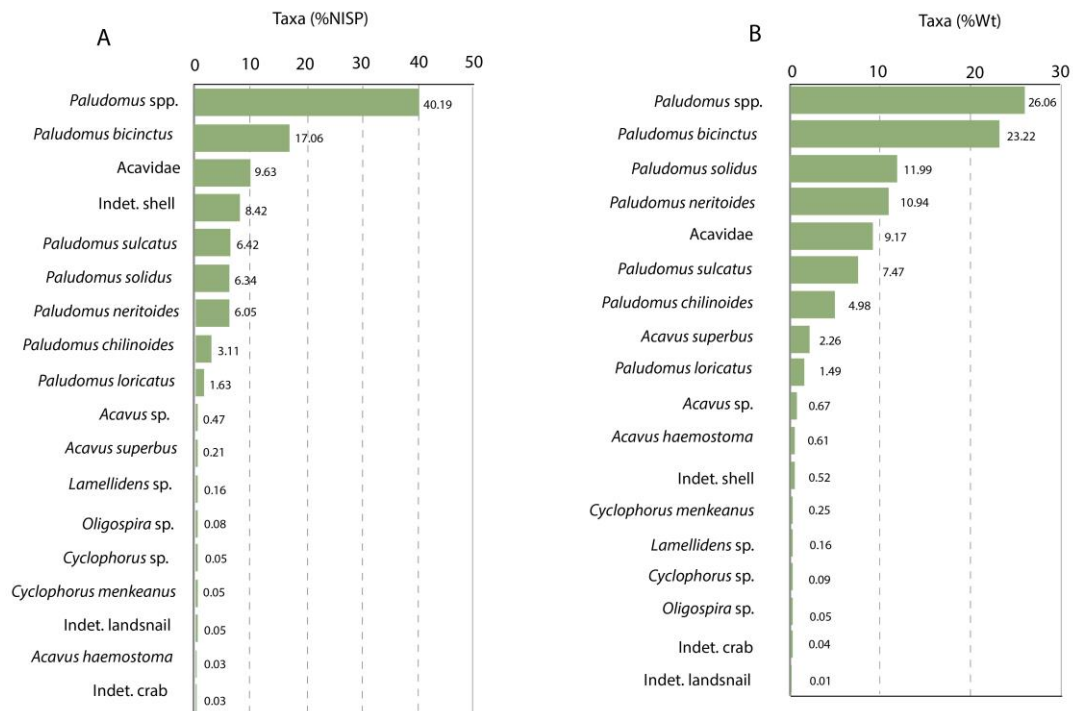
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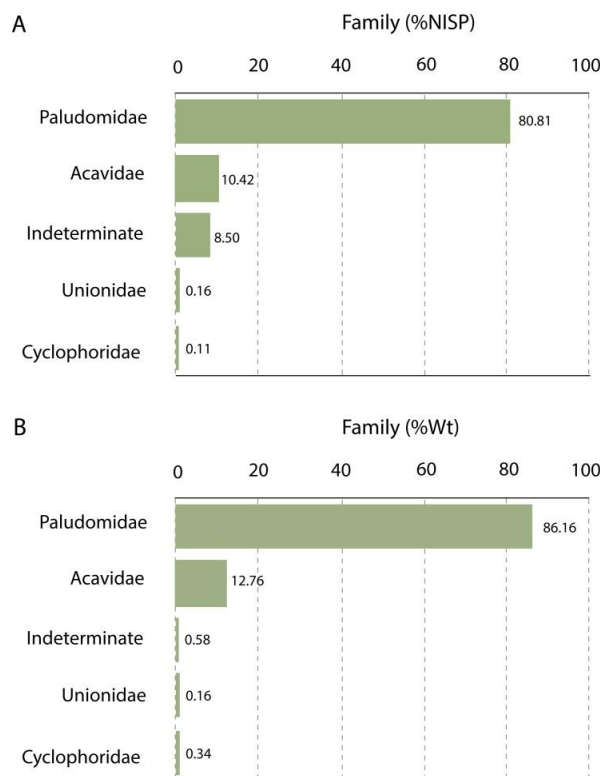
562 Breaking down the identified taxonomic groups, there is one category at the family level
563 (9.63% NISP, 9.17% Wt), five categories at the genus level (40.96% NISP, 27.03% Wt), nine
564 categories at the species level (40.91% NISP, 63.23% Wt), and three indeterminate categories
565 (8.50% NISP, 0.58% Wt). The latter category encompasses indeterminate crab, land snail, and
566 shell, all of which do not retain key characteristics for identification beyond these broad
567 attributions. Figure 5 graphs the taxonomic categories in descending order (highest to lowest)
568 by %NISP (Figure 5A) and %weight (Figure 5B). Taxonomic rank order varies based on the
569 quantification measure used, a factor that relates to shell size and morphology, robusticity,
570 and also likely the differential degree of taphonomic modification within and between taxa.

571

572 Regardless of the quantification measure used, the dominant taxa are the Paludomidae
573 (freshwater gastropods) and the Acavidae (terrestrial gastropods). In many respects this is not
574 unexpected, particularly given the similar trends reported for the Batadomba-lena rockshelter
575 invertebrate assemblage (Perera et al. 2011). This dominance is also apparent when the
576 assemblage is rank ordered by family (Figures 6A and 6B), where the Paludomidae and
577 Acavidae are ranked first and second, followed by the indeterminate categories, by both
578 %NISP and %weight. In combination with the occurrence of freshwater Unionidae bivalves,
579 these data indicate the presence of flowing freshwater and lowland rainforest habitats around
580 Kitulgala Beli-lena during the Holocene.



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582 **Figure 5.** Kitulgala Beli-lena mollusc taxa by %NISP (A) and %Weight (B).
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607 **Figure 6.** Kitulgala Beli-lena mollusc taxa at the family taxonomic level by %NISP (A) and
608 %Weight (B).
609

610
611 The distribution of the freshwater and terrestrial molluscs by context is presented in Table 7.

612 These data are based on family or genus level, to account for some of the issues surrounding

613 accurate identification to species level noted earlier. Based on these data, there would appear
614 to be a level of consistency in taxonomic representation and habitat exploitation throughout
615 the Holocene sequence at Kitulgala Beli-lena. The *Paludomus* spp. (range 76.9-86.3% NISP)
616 and Acavidae (range 8.4-13.7% NISP) dominate the assemblage and occur relatively
617 consistently across these contexts, with the freshwater bivalve *Lamellidens* sp. and the
618 terrestrial gastropod *Cyclophorus* spp. occurring at very low percentages. The ratio of
619 freshwater to terrestrial molluscs through the sequence also stays relatively consistent as a
620 result, ranging between 6.2 and 7.4 in contexts 7/5, 4, 3 and 2, with a minor increase in
621 freshwater taxa occurring in context 27 (with a ratio value of 9.7).

622

623 **Table 7.** *Kitulgala Beli-lena* taxonomic distribution at family or genus level by sedimentary context (contexts 7 and 5 combined).
 624

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	

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

644

645 ***4.5 Plant Remains***

646 Preliminary assessment of the macrobotanical assemblage from the Pleistocene sedimentary
647 contexts of Kitulgala Beli-lena revealed the presence of charred plant remains in all contexts
648 analysed. These remains included charred fragments of wood, nutshell, fruits, and seeds.
649 Overall, preservation in these contexts is limited with the macroremains generally exhibiting a
650 high degree of fragmentation. The identification of these remains is ongoing, but initial
651 assessment indicates the likely presence of economic taxa including cf. *Artocarpus* sp.
652 (breadfruit) and cf. *Canarium* sp. ('kekuna' nut).

653

654 Charred fragments of fruit exocarp comprising distinctive roundish to polygonal nodules or
655 disks, *ca.* 1-2mm in size, with a small central perforation were identified in all five
656 Pleistocene contexts analysed. Based on published descriptions including of previously

657 identified archaeobotanical material from Holocene contexts at Kitulgala, these are tentatively
658 identified as breadfruit (*Artocarpus* sp.) skin. Fissuring of the nodules is consistent with the
659 fracture patterns observed in experimentally cooked and charred breadfruit cultivars in
660 Oceania (Kahn and Ragone 2013), suggesting the charred Kitulgala fragments were also
661 produced by roasting, though additional experiments with Sri Lankan wild varieties is needed
662 to replicate these observations. In addition, a single fragment of cf. *Canarium* sp. endocarp
663 (nutshell) was identified in Context 10. The fragment was <3mm in size and identified
664 tentatively based on the presence of a distinctive cellular pattern observed on the inner seed
665 locule (Fairbairn pers. comm. 2018). Additional comparative work with modern reference
666 material is needed to confirm this identification. Other nutshell fragments were also observed
667 in other contexts but these have not yet been identified.

668

669 The presence of cf. *Artocarpus* sp. and cf. *Canarium* sp. in the archaeobotanical assemblages
670 is consistent with a rainforest plant food economy being practised at Kitulgala throughout the
671 Late Pleistocene, as also observed at other rockshelter sites in the Wet Zone (Perera et al.
672 2011; Kajale 1988). Previous archaeobotanical studies at Kitulgala also identified charred
673 breadfruit and *Canarium* remains, as well as wild banana (*Musa* sp.) in Holocene deposits
674 dating to at least 12,500 BP. Whilst additional work is needed to confirm the identifications of
675 some of the new Kitulgala samples, the present study tentatively extends the chronology of
676 the rainforest plant gathering into the Pleistocene. Furthermore, it indicates that at least wild
677 breadfruit was probably exploited from initial occupation of the site at around 44,000 years
678 ago. Wild breadfruit (*Artocarpus nobilis*) and kekuna nut (*Canarium zeylanicum*) are both
679 endemic to Sri Lanka and grow today in the lowland rainforest (Gunatilleke et al. 2008).
680 Together these provide a rich source of starch, fats and protein, and require little processing
681 other than cooking (in the case of breadfruit), making them high ranked food resources. The

682 storability and transportability of *Canarium* nuts would have made them an attractive resource
683 for a mobile hunter-gatherer population.

684

685 ***4.6 Lithic Technology***

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

694

695 The technological reconstruction of the lithic *chaîne opératoire* indicates the continuous use
696 of the bipolar-on-anvil method from the Late Pleistocene to the Holocene. The cores are
697 characterized by the typical battering marks of the hammerstones on the proximal end and by
698 small breakages produced by the contact with the anvil. Generally, the quartz pebbles were
699 exploited along their longer axis in order to maximize the length of the by-products. At times,
700 during the knapping events, the striking platforms were shifted in order to achieve a better
701 stability on the anvil. This behaviour is common in the different chronological phases and
702 several examples document the opportunistic use of striking platforms opposed to flat
703 surfaces, natural or created during the reductions (Figure 7, 2-3), and the rotations of the cores
704 of 90° degrees (Figure 7, 1), producing flakes with orthogonal scars on the dorsal surfaces.

705

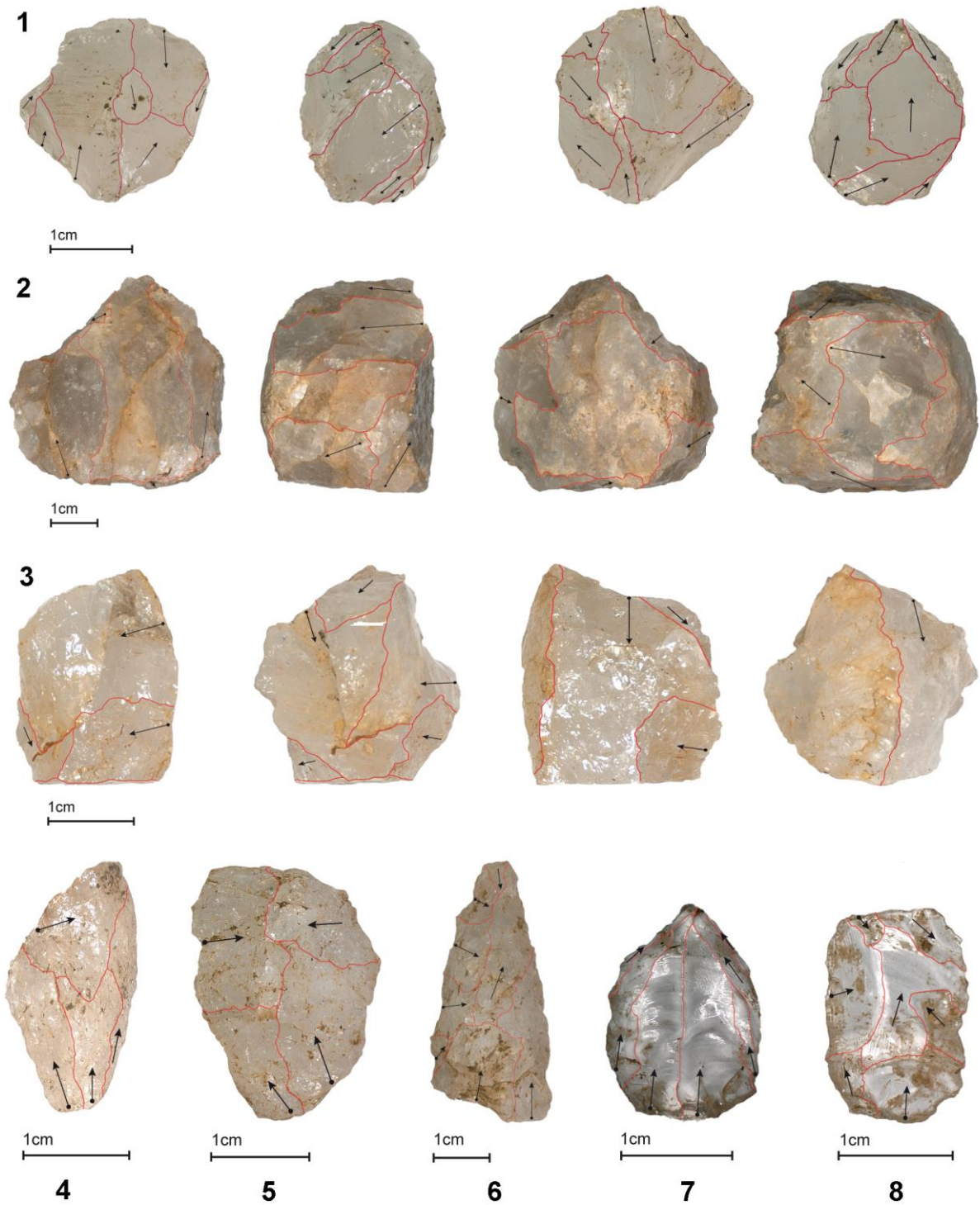
706 The flake assemblage is composed mostly of fragments and small chips whereas complete
707 flakes and flake bladelets are recorded in lower frequencies (Table 8, Figure 7, 4-8).
708 Comparison of unbroken flakes by length intervals indicates that the knapping events were
709 aimed to produce small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

722

723 **Table 8.** Total number and percentage of the lithic assemblages of Kitulgala Beli-lena by
724 chronological phases.
725

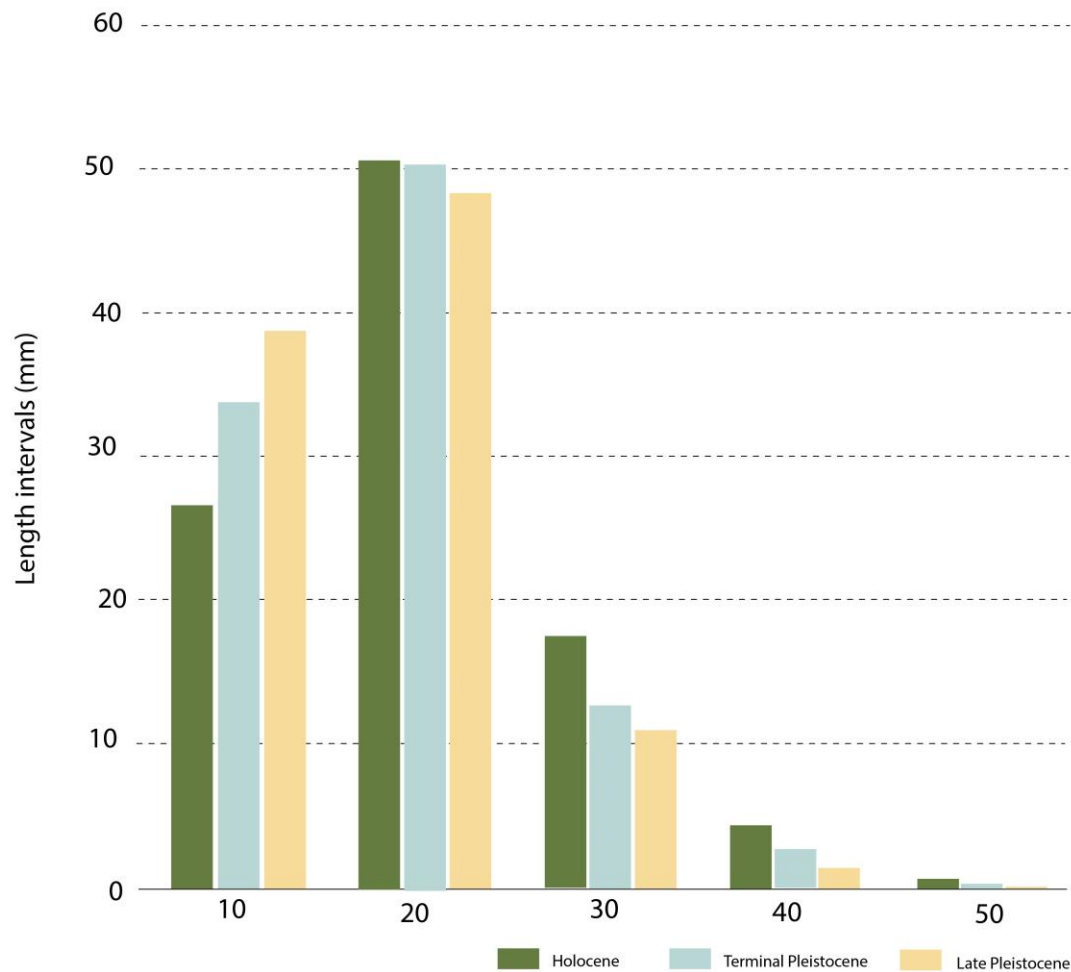
Phase	Flake	Flake Bladelet	Fragment	Debris	Core	Core Frag.	Hammer	Total
Holocene	523	9	2367	620	43	34	7	3603
%	14.5	0.2	65.7	17.2	1.2	0.9	0.2	100
Terminal Pleistocene	592	1	2635	3230	68	45	6	6577
%	9	0	40.1	49.1	1	0.7	0.1	100
Late Pleistocene	544	2	2324	1998	57	67	20	5012
%	10.9	0	46.4	39.4	1.1	1.3	0.4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

726



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

730
 731
 732
 733



734
 735 **Figure 8.** Histogram of the frequency of complete flakes by length intervals during the
 736 different chronological phases at Kitulgala Beli-lena.
 737

738
 739 Although they were documented, albeit in low frequencies, in previous fieldwork and
 740 analyses (Roberts et al., 2015a; Lewis, 2017), retouched tools and backed microliths are
 741 absent in the lithic assemblage analysed. From the 24,772 artefacts and more than 500,000
 742 pieces of debris recorded in previous excavations, only 28 were identified as retouched tools.
 743 The technological continuity recorded at Kitulgala Beli-lena is in accordance with the
 744 evidence documented in other cave sites located in the modern Wet Zone rainforest of Sri
 745 Lanka. At Fa Hien-lena Cave, the lithic production was aimed at small blanks, and the
 746 bipolar-on-anvil method on quartz, with the expedient technique of rotating the core and
 747 changing the striking platform, was used from ~48-45 ka up to the Holocene (Wedage et al.,

748 2019a; 2019b). At Batadomba-lena Cave, bipolar cores were found in association with
749 freehand flake and bladelet cores along with numerous backed microliths, a type of artefact
750 that is not generally found in the other two sites (Lewis, 2017).

751

752 **5. Discussion**

753 *Human behaviour and adaptations at Kitulgala Beli-lena*

754 Our data provide new insights into the foraging strategies and material culture of human
755 populations living at the site of Kitulgala Beli-lena. Firstly, our new radiocarbon dating
756 programme has dramatically revised the dates for the site, making it now one of the oldest
757 dated rockshelter/cave sites in Sri Lanka, and indeed South Asia more broadly. Indeed, the
758 earliest occupation date of 44,000 cal. years BP places it approximately contemporaneous to
759 Fa Hien-lena Cave and now earlier than the 38,000-36,000 cal. years BP recorded for
760 Batadomba-lena (Perera et al., 2011; Roberts et al., 2015a). This re-dating emphasises the
761 importance of applying robust pre-treatment methodologies in the tropics (as also highlighted
762 by Higham et al. (2008) for the Niah Caves, Borneo), in order to avoid erroneously young
763 dates as a result of detrital contamination. In the context of charcoal, this involves the
764 application of the Acid Base Oxidation (ABOX) pre-treatment steps (Higham et al., 2008).
765 Moreover, the re-dating of Kitulgala Beli-lena confirms the early presence of humans in the
766 Wet Zone rainforests of Sri Lanka as early as *ca.* 45,000 years ago, an assertion that was
767 previously solely based on the record at Fa Hien-lena (see also Wedage et al., 2019a).

768 The multidisciplinary approach presented here also enables us to confirm that this early
769 record of human presence at Kitulgala Beli-lena is associated with clear evidence for
770 rainforest plant gathering and manufacture of quartz flakes using the bipolar-on-anvil method
771 in the Pleistocene and targeting of arboreal animals starting with the onset of the Holocene.
772 Archaeobotanical evidence from the Late Pleistocene and Holocene levels demonstrates the

773 likely continued extraction and use of wild breadfruit (*Artocarpus nobilis*) and possibly also
774 kekuna nut (cf. *Canarium zeylanicum*) by foragers at the site. Both of these plants provide a
775 rich source of starch, fats, and protein, and require little processing. This makes them highly
776 productive food resources in an environment that has often been considered to lack reliable
777 plant-based sources of carbohydrate and protein (Bailey et al., 1989; Gamble, 1993).
778 *Canarium* sp. nuts have also been documented at Fa Hien-lena and Batadomba-lena (Perera et
779 al., 2011; Wedage et al., 2019a), as well as Late Pleistocene sites in Southeast Asia and New
780 Guinea (Summerhayes et al., 2010; Barker and Farr, 2013), highlighting their potential
781 significance to early human tropical foragers in these parts of the world.

782

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

796

797 The osseous and lithic technological remains recovered from Kitulgala Beli-lena further
798 confirm evidence from Fa Hien-lena that Late Pleistocene and Holocene foragers in Sri Lanka
799 had developed a sophisticated repertoire for the exploitation of their immediate landscapes.
800 Osseous tools were found within the Holocene levels of Kitulgala Beli-lena, including
801 finished unipoints, bipoints and geometrics. The bone points were most likely utilized as
802 projectile points similar to those found in Fa Hien-lena (Wedage et al., 2019a; Langley et al.,
803 2020). The lithic materials, while not representing any backed microliths, show a bipolar-on-
804 anvil reduction method on quartz with stark similarities to those seen at Fa Hien-lena and
805 Batadomba-lena where microlithic points appear to have been the final goal (Lewis et al.,
806 2014; Lewis, 2017; Wedage et al., 2019a; 2019b). The absence of retouched tools and backed
807 flakes in this area of the site may indicate that tool-use occurred in a different part of the
808 rockshelter or at another location altogether. Since faunal remains were recorded previously
809 in the Pleistocene deposits (Wijeyapala, 1997) and they are lacking in the area excavated in
810 2017, it is probably that butchering activities, microlith preparation, and gear retooling were
811 carried out in task-specific locations of the rockshelter.

812

813 Albeit a preliminary evaluation, this different spatial distribution of the remains suggests a
814 complex organization of the site that is common in prolonged (long-term) settlements
815 (Bartram et al., 1991; O'Connell et al., 1991). This, alongside the lack of bone tools and faunal
816 remains from the Late Pleistocene layers, supports the differential use of space by Late
817 Pleistocene and Holocene foragers at Kitulgala Beli-lena. Recent analysis of the lithic
818 assemblages of the previous excavations recorded the presence of 27 microliths in the Late
819 Pleistocene, and four in the terminal Pleistocene. Similarly, where bone tools are present in
820 Holocene levels, there is no *débitage* evidence implying that they were manufactured
821 elsewhere. As a result, while material culture and archaeobotanical and zooarchaeological

822 evidence at Kitulgala Beli-lena, and its neighbouring sites, demonstrates a well-tuned,
823 persistence foraging adaptation to the rainforest environments of Sri Lanka, there appears to
824 be spatial complexity into how this adaptation was practised on a site and landscape basis,
825 represented within a given site, in a given period, and, indeed, perhaps across the landscape.
826 Given that systematic lithic, material culture, and subsistence analysis has now taken place at
827 Fa Hien-lena (Deraniyagala, 1992; Roberts et al., 2015b; Wedage et al., 2019a,b),
828 Batadomba-lena (Perera, 2010; Perera et al., 2011; Roberts et al., 2017a), and, here, Kitulgala
829 Beli-lena (sites that lie within 100km² radius of each other in the Wet Zone evergreen
830 rainforests), future, systematic comparative work promises to further enrich understandings of
831 the spatial organisation of tropical rainforest use by Late Pleistocene and Holocene hunter-
832 gatherers on the island of Sri Lanka.

833

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

836 The multidisciplinary evidence from Kitulgala Beli-lena, Fa Hien-lena, and Batadomba-lena
837 now demonstrates the persistent use of tropical rainforest resources from 48,000-45,000 years
838 ago through to 3,000 years ago in the Wet Zone of Sri Lanka (Wedage et al., 2019a). Stable
839 isotope evidence of human and animal tooth enamel from Batadomba-lena, Fa Hien-lena, and
840 Balangoda Kuragala demonstrates that between 36,000 and 3,000 years ago human foragers
841 were reliant on tropical rainforest resources year round (Roberts et al., 2015a, 2017b), while
842 detailed zooarchaeological and archaeobotanical information demonstrates that this lifestyle
843 was supported by a heavy focus on semi-arboreal and arboreal primates and tree products and
844 supplemented by freshwater molluscs and squirrel taxa (Perera et al., 2011; Wedage et al.,
845 2019a). This research, as well as finds in East Africa, Southeast Asia, and Melanesia (Barker
846 et al., 2007; Summerhayes et al., 2016; Shipton et al., 2018), has gone a significant way to

847 rehabilitating tropical rainforests as key habitats for *Homo sapiens* during its dispersal within
848 and beyond Africa - environments that were once considered barriers to human dispersal
849 (Gamble, 1993; Bird et al., 2005; Boivin et al., 2013). The scale and intensity of rainforest
850 occupation and exploitation in Sri Lanka during the Late Pleistocene remains to be fully
851 elucidated. Although one could argue that this occupation is characterized by highly-mobile
852 and low density human populations, growing evidence, including from stable isotope analyses
853 (Roberts et al., 2017a), as well as intense evidence of occupation of rockshelter and cave sites
854 (Perera et al., 2011; Wedage et al., 2019a; 2019b), suggests the persistent presence of groups
855 fully adapted to the dynamics of a rainforest environment.

856

857 Such a specialized adaptation is supported by evidence reported here from Kitulgala Beli-lena
858 that tool production and faunal butchery may have taken place across a wider social and
859 economic landscape in the Wet Zone rainforests of Sri Lanka. It is possible that Kitulgala
860 Beli-lena, Fa Hien-lena, and Batadomba-lena all formed part of a network of hunting ranges,
861 plant exploitation routes, and settlement strategies that were likely also augmented by open-
862 air sites that may never be discovered (see Mercader et al., 2003 for pessimism in this regard
863 in the Central African rainforest). The existence of the formation of social and economic
864 networks between different groups, potentially operating simultaneously, is also supported by
865 growing evidence for contact between foraging communities in the rainforest and populations
866 on the coast. Evidence for marine shell beads and shark teeth has emerged in the Pleistocene
867 and Holocene levels of Fa Hien-lena and Batadomba-lena (Perera, 2010; Perera et al., 2011;
868 Langley et al., 2020), as well as the Dry Zone site of Bellan-bandi Palassa (Perera, 2010).
869 These items were most likely obtained by trade with communities present in Sri Lanka's
870 southern coast, identified in sites such as Bundala, Patirajawela and Minihagalkanda
871 (Deraniyagala, 1992), given that isotopic evidence points to year-round reliance to rainforest

872 resources by communities in the island's Wet Zone (Roberts et al., 2015a, 2017a). As a result,
873 it seems that the Wet Zone rainforests were home to an established population that was part of
874 wider social and symbolic networks with groups living in other Sri Lankan biomes, not only
875 on the coast but potentially also in the drier north and south-eastern reaches given the lack of
876 Pleistocene investigation of these regions to-date (Deraniyagala, 1992; Roberts et al., 2015b).

877

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

897

898 *A Wider South Asian and Asian Perspective*

899 From earlier assumptions of a rapid coastal arrival in South Asia *ca.* 60 ka (Mellars, 2005,
900 2006; Field et al., 2007), our understanding of the appearance of our species in this part of the
901 world have become much more complex over the course of the last decade (Groucutt et al.
902 2015; Blinkhorn & Petraglia 2017; Roberts et al., 2017a). Significantly, given the data
903 available from Kitulgala Beli-lena and the other Wet Zone sites of Sri Lanka, it is now clear
904 that *H. sapiens* occupied and utilized a diversity of terrestrial environments, away from the
905 coast, from its earliest arrival in South Asia. This includes the arid environments of the Thar
906 Desert, from potentially as early as *ca.* 114 ka, perhaps supported by increased precipitation
907 and the freshwater of palaeochannels and lakes (Blinkhorn et al., 2013, 2017, 2019). The
908 Jurreru River Valley has also provided evidence for human populations in mosaic of dry
909 forest, grassland, and riparian habitats, with fluctuating periods of aridity from 77 ka through
910 to the Holocene (Petraglia et al., 2007; 2010, 2012; Clarkson et al., 2012). It is perhaps in Sri
911 Lanka, however, that human adaptability to different extremes is most evident in South Asia.
912 Here, sites producing the earliest current evidence for human fossils in the entirety of South
913 Asia, as well as long-term records of human behaviour, are associated with specialized
914 adaptations to tropical rainforest environments from 48-45,000 years ago through to 3,000
915 years ago. This is not to say that coasts were irrelevant to late Pleistocene human occupations
916 in this part of the world (Blinkhorn et al. 2017, 2019), and indeed future work on Sri Lankan
917 coastal sites is likely to reveal prehistoric settlements in these parts of the island as well
918 (Deraniyagala, 1992). It is now clear that the peopling of South Asia was far more complex
919 than a coastal highway that rapidly brought uniform populations and technological strategies
920 throughout this diverse region.

921

922 Research in South Asia over the past two decades points to a complex pattern of cultural and
923 technological change following the initial *H. sapiens* colonization of the region. In western
924 India, the Son Valley of north-central India and in the Jurreru Valley of southern India, it has
925 been argued that Late Palaeolithic and microlithic toolkits transitioned from Middle
926 Palaeolithic technologies (Sali 1989, Clarkson et al., 2009; Petraglia et al., 2012; Blinkhorn
927 2018; Clarkson et al. 2018). This can be clearly seen in the Jurreu Valley, where Middle
928 Palaeolithic occupations span 77-38ka, with the younger assemblages sharing features that
929 become central to subsequent Late Palaeolithic industries from 35ka onwards (Petraglia et al.,
930 2007; Clarkson et al. 2012). It also appears that microlithic and osseous tool technologies
931 were utilized by communities occupying a diverse range of terrestrial environments far from
932 the South Asian coast. Bone tools were recorded in the Jwalapuram Locality 9 site alongside
933 Late Palaeolithic stone tools (Clarkson et al., 2009). Likewise, bone technology including
934 projectile points presumed to have been utilized to hunt arboreal fauna, alongside quartz
935 microliths, has been recorded in the earliest phase of occupation of the rock shelter sites in Sri
936 Lanka's Wet Zone region (Deraniyagala, 1992; Perera, 2010; Perera et al., 2011; Wedage et
937 al., 2019a; Langley et al., 2020). The sophisticated microlithic and osseous technologies, as
938 well as ochre and symbolic beads, documented in these sites would not be out of place in the
939 caves of western Europe 45,000 years ago (Conard, 2010) or in southern Africa from 100,000
940 years ago (Henshilwood et al., 2011), perhaps causing us to reorient our ideas of which
941 ecological adaptations accompanied symbolic, technological, and economic hallmarks of our
942 species.

943 Evidence for Late Pleistocene rainforest occupation and resource utilization, akin to evidence
944 from Sri Lanka's Wet Zone sites, has also been documented in Southeast Asia and Melanesia.
945 The most comprehensive evidence for Late Pleistocene rainforest subsistence foraging
946 strategies in the region comes from Niah Caves in Sarawak, Borneo. Niah Caves produced

947 one of the earliest human fossils in Southeast Asia, dated to c. 44,000–40,000 cal. years BP
948 (Barker et al., 2007; Higham et al., 2008; Reynolds and Barker, 2015). Results of detailed
949 analyses looking at a wide range of archaeological materials including fauna, pollen,
950 pytholiths, starch grains, and macrobotanical remains, point to complex foraging behaviours
951 tailored to take full advantage of the rainforest environment (Barker and Farr, 2016). These
952 include exploitation of an array of plant resources for food and possibly clothing, processing
953 of toxic plants such as taros and yams, specialized targeting of wild boar, hunting of arboreal
954 taxa including monkeys and civet cats, as well as collection and processing of freshwater
955 molluscs (Barker et al., 2007; Barton et al., 2009; Barton, 2016; Hunt et al., 2012; Piper and
956 Rabett, 2014; 2016; Szabó, 2016). These activities were facilitated by some of the earliest
957 bone tools found in Southeast Asia (Rabett and Piper, 2012; Rabett, 2016) in addition to flake
958 based stone tool technologies (Reynolds, 2016; Barton, 2016). The earliest human occupation
959 of Melanesia is also associated with rainforest foraging. Sites in the Ivane Valley region of
960 Papua New Guinea produced evidence for processing of *Dioscorea* yams and *Pandanus* nuts
961 as early as 49,000–43,000 cal. years BP (Summerhayes et al., 2010). Human occupation of
962 rainforests have also been recorded in the Bismarck Archipelago at sites in New Ireland dated
963 to c. 40,000 cal. years BP (Leavesley, 2005) and in West New Britain c. 35,000 cal. years BP
964 (Pavlides, 2004; Summerhayes et al., 2017).

965

966 It is now becoming increasingly apparent that what truly characterises our species is its
967 emergence at a time of increasing climatic and environmental variability in Africa (Potts et
968 al., 2018). Not only did this act as the background for the evolution of diverse human
969 populations in different parts of this continent (Scerri et al., 2016), but it is also the situation
970 that met members of *H. sapiens* moving into Europe, Asia, Australasia, and the Americas
971 during the Late Pleistocene (Roberts and Stewart, 2018). While in some cases coastal

972 environments or savannah settings may have been significant to human populations utilizing
973 new projectile technologies, and developing novel symbolic networks (Shea, 2011; Marean,
974 2016), these behaviours also supported the movement of populations into more ‘extreme’
975 environments including high-altitude settings (Stewart et al., 2016), desert settings (Hiscock
976 and Wallis, 2005; Nash et al., 2016), the arctic (Pitulko et al., 2016), and tropical rainforests
977 (Barker et al., 2007; Roberts and Petraglia, 2015; Roberts et al., 2017a; Westaway et al.,
978 2017). While research focus on these latter environments was for long lacking in contrast to
979 temperate and grassland parts of Europe and Africa, two decades of research has revealed a
980 vast wealth of information into human subsistence, technological adaptations, and symbolic
981 behaviours (Hunt and Barker, 2014; Aubert et al., 2014; 2018; Langley et al., 2020).
982 Increased multidisciplinary excavation, and analysis in parts of the world dominated by these
983 more ‘extreme’ habitats in the present, as well as the past, has the possibility to enable us to
984 build a more complete picture of the ecological and social adaptations that make us human,
985 and enabled us to colonize nearly the entirety of the planet by the end of the Pleistocene.

986

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998
999 **Author contributions**

1000 OW, PR, SD, NB, MP and NA designed the study with AP and JB in collaboration with PF,
1001 AC and KD. OW, AP, JB and NA conducted the site excavation and the recording of
1002 stratigraphy and artefact distribution with supervision from PR, SD, NB and MP. The lithic
1003 materials were analysed by AP and OW. AC looked at the archaeobotanical remains.
1004 Molluscan remains were studied by PF. NA studied the vertebrate faunal remains and the
1005 bone tools. KD was responsible for the radiocarbon dating. OW, PR, PF, AC, KD, AP, JB,
1006 SD, NB, MP and NA wrote the paper.

1007
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