

1 **Interpreting phytoliths assemblages at chimpanzee (*Pan troglodytes verus*) nut-cracking sites**
2 **in Bossou Forest, Guinea**

3

4 Phillips C¹, Almeida-Warren K¹, Bamford MK²

5 1. School of Anthropology and Museum Ethnography, University of Oxford
6 Institute, University of the Witwatersrand

7

8 **Abstract**

9 The nut-cracking behaviour of the chimpanzees of Bossou Forest has been long documented and
10 studied in order to understand ultimate drivers for this form of durophagy by these apes. At sites in
11 which they break open the nuts of the oil palm (*Elaeis guineaeensis*) on stone anvils with stone
12 hammers, fragments of the tools as well as remnants of the nuts may be deposited into local
13 sediments; however, they may become less visible at the macroscopic level as these sites are no
14 longer used (become dormant). We build upon work that has been done to document this unique
15 cultural heritage in West African chimpanzees by interpreting phytolith assemblages in sediments at
16 active nut-cracking sites (used within the last two months). We compare these assemblages with
17 those found in sediments of sites that have been dormant for ~10 years and sites where
18 chimpanzees have not been observed to access and crack open oil palm nuts with stone tools. We
19 predicted that larger assemblages of spheroid echinates, a phytolith associated with palms, would
20 be found at active nut-cracking sites, however we found no statistical difference between total
21 spheroid echinates (measured as total number found per gram of dry sediment) assemblages
22 produced across active nut-cracking, dormant, or non-nut-cracking sites. This may have been due to
23 small sample size (N≤6 sediment samples for each of the three sites) and so further sample
24 collection and analyses are needed for inter-site comparisons. We also measured 2D area (μm^2),
25 perimeter and maximum diameter of spheroid echinates found in nut endocarps (shells) and leaflets
26 from an oil palm frond. Intra-specific differences from all three measurements were found with
27 these phytoliths being larger in the nut endocarp than the leaflet. This has implications for
28 (re)interpreting the assemblages of spheroid echinate phytoliths at the three sites to determine if
29 there is a greater productivity larger-sized spheroid echinates that fall within the size range of those
30 measured for the nut endocarp (mean maximum diameter of 14.9 μm versus 7.8 μm for those found
31 in oil palm leaflet). Finally, we argue for the importance of initialising and continuing the
32 interpretation of phytolith assemblages in local sediments that are located near sites where directed
33 plant input by non-human taxa has occurred, in this case, chimpanzees cracking open oil palm nuts

34 using stone tools. This is important to refine our interpretation of phytolith assemblages where
35 human and non-human taxa who use complex foraging strategies share ecological spaces.

36

37 **Introduction**

38 **Durophagy in extant primates**

39 The eating of nuts by our close primate relatives has received much attention to progress our
40 understanding of their dietary ecology and material culture (Spagnoletti et al. 2012; McGraw et al.
41 2014), as well as to model aspects of diet, ecological niche, material culture, and cognitive abilities of
42 human ancestors (Jolly 1985; Peters 1987; Yamakoshi 2008; Daegling et al. 2011; Bril et al. 2012).
43 This form of durophagy has been observed in multiple primates including the Sooty mangabey
44 (*Cercocebus atys*), bearded capuchin (*Sapajus libidinosus*), tufted capuchin (*Cebus apella*),
45 Panamanian white-faced capuchin (*C. imitator*), western (*Pan troglodytes verus*) and Nigerian-
46 Cameroon chimpanzee (*P. t. elliotii*), Japanese macaque (*Macaca fuscata*) and Burmese long-tailed
47 macaque (*Macaca fascicularis aurea*). How they extract the kernel (endosperm) from their hard
48 outer casing (endocarp) with tools (e.g., bearded capuchins using stone hammers and boulders as
49 anvils: Langguth & Alonso 1997; Fragaszy et al. 2004; Panamanian white-faced capuchin using stone
50 hammers and stone or wooden anvils: Barrett et al. 2018; and western chimpanzees using stone or
51 wooden hammers and anvils: Sugiyama & Koman 1979; Boesch & Boesch 1983) or without tools
52 (e.g., tufted capuchins hitting nuts directly on branches or against each other: Struthsaker & Leland
53 1977; Japanese macaques using teeth: Tamura 2020) continues to be documented. For primates
54 who access and process nuts with tools, known as nut-cracking, this involves an individual selecting a
55 nut (due to size, hardness and/or availability), and as mentioned, a stone/wooden hammer and a
56 stone/wooden anvil (latter may be transportable or fixed e.g., tree root or branch, rock outcrops;
57 Carvalho et al. 2008). The individual places the nut on the anvil and strikes the endocarp to access
58 and feed on the endosperm. Successful individuals develop a greater spatial awareness between the
59 hammer and nut and the nut and anvil (Matsuzawa 2001; Fragaszy et al. 2004). Indirect evidence
60 e.g. fragmented refuse of nuts, indents or percussion marks on tools, foot and handprints near the
61 nut remains or tools (Humble & Matsuzawa 2004; Morgan & Abwe 2006; Benitio-Calvo et al. 2015;
62 Falótico et al. 2017), and direct observation of nut-cracking (Sugiyama & Koman 1979; Carvalho et al.
63 2008; Fragaszy et al. 2013; Luncz et al. 2017; Proffitt et al. 2018) have provided insight into how they
64 access, process and ingest nuts. In turn, workers have addressed questions relating to social,
65 cultural and ecological selection pressures that have driven primate durophagy and how an
66 adaptation to feed on this hard-to-access food has shaped cognitive, anatomical and morphological

67 traits (Carvalho et al. 2008; Wynn et al. 2011; Duarte et al. 2012; Fragaszy et al. 2013; Visalberghi &
68 Fragaszy 2013; Sirianni et al. 2015; Fragaszy et al. 2017; Lombard et al. 2019). If we look at the Sooty
69 mangabeys in Taï Forest, Ivory Coast as an example: they bite-through the endocarp of *Sacoglottis*
70 *gabonensis* (Baill.) Urb. with their molars and premolars to access and eat the endosperm. These
71 primates feed on this nut more frequently than any other food-item each month and across the year
72 (McGraw & Daegling 2014) which has opened our questioning on how we categorise fallback foods
73 (i.e., foods that are argued to be consumed when preferred foods are scarce) based on enamel
74 thickness and tooth morphology (Daegling et al. 2011; McGraw et al. 2014). In addition, nuanced
75 aspects of dietary related adaptations such as sex differences in ability to access harder nuts
76 (Geissler et al. 2021), selection for gape ability and its impact on hard-food eating (Taylor et al. 2018)
77 and the scavenging of plant matter, in this case on *Coula* (Baill.) and *Panda* (Pierre.) nut fragments
78 left by chimpanzees and river hogs in Taï Forest (Bryndan et al. 2018) have also been explored. This
79 example highlights the complexity in proximate and ultimate explanations of durophagy by primates
80 (discussed further for chimpanzees below).

81 **Utilisation of the oil palm by primates (including humans)**

82 The focus of our study is the nut-cracking sites created by chimpanzees in Bossou Forest, Guinea,
83 (Sugiyama & Koman 1979, Matsuzawa 1994, Matsuzawa et al. 2001, Biro et al. 2003) but
84 chimpanzee nut-cracking sites have been found across West Africa in Cameroon (Morgan & Abwe
85 2006), Sierra Leone (Whitesides 1985), and Liberia (Anderson et al. 1983; artefacts found for recent
86 extirpated Ganta community: Smith et al. 2010); notably, nut-cracking by the North, South and East
87 chimpanzee communities in Tai Forest, Ivory Coast has been observed across five decades
88 (Struthsaker and Hunkeler 1971; Boesch & Boesch 1983; Luncz et al. 2018). As to how far reaching
89 this foraging strategy originally occurred across the range of *P.t. sp.*, and why this behaviour has only
90 been documented in extant populations in West Africa remains unresolved. It has been suggested
91 that natural barriers such as the N'Zo-Sassandra River in the Ivory Coast may have impacted the
92 diffusion of this behaviour (Boesch *et al.* 1994; Humle and Matsuzawa 2004), or that it was
93 innovated or devolved in pockets across populations (McGrew et al. 1997; Morgan & Abwe 2006).
94 For context, dating of excavated nut-cracking sites with nut refuse and tool artefacts indicate
95 durophagy and nut-cracking in western chimpanzees for at least 4300 years (Mercader et al. 2007 vs.
96 3000 years for bearded capuchins: Falótico et al. 2019); for humans, for at least 780,000 years (at
97 Geshar Benot Ya'aqov, Israel: Goren-Inbar et al. 2002). As well as co-evolution of nut-cracking across
98 the order, Primates, percussive technology origins in our lineage argued to predate the earliest
99 stone tool artefacts dated to 3.3 million years (Harmond et al. 2015) allude that nut-cracking was a

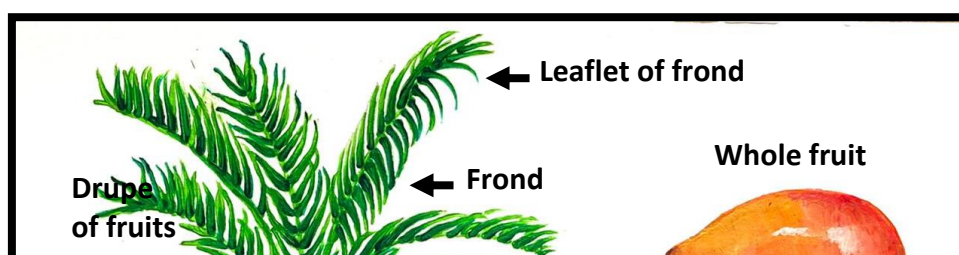
100 persistent foraging strategy across multiple hominin taxa (Wynn & McGrew 1989; Schroer 2012; Brill
101 et al. 2015; Arroyo et al. 2016).

102 One nut that is accessed and processed by the Bossou chimpanzee community is that of the oil palm
103 (*Elaeis guineensis* Jac q., family Arecaceae, subfamily Arecoideae; illustration of parts in Fig. 1). The
104 oil from this nut is high in fatty acids and a good source of energy due to a high carbohydrate
105 content (Atatsie et al. 2009; Dian et al. 2017). Oil palms are a single-branch monocot native to West
106 and Central Africa but have since dispersed across parts of Africa (Robins 2021). Possible fossilised
107 pollen of this palm occurs in late Miocene sediments in Nigeria (Zeven 1964, 1972), as well as Late
108 Holocene sediments and pottery artefacts across parts of West Africa (Sowunmi & Awosina 1991;
109 D'Andrea et al. 2006; Garcin et al. 2018). Although likely to be a combination of factors, debate
110 continues as to whether expansion of oil palm across Africa in the late Holocene was due to human
111 activity (Hartley 1988), animal dispersal agents (Zons & Henderson 1989), that it is a pioneer species
112 in disturbed areas, or in areas impacted by climate change such as the Dahomey Gap (Maley &
113 Brenac 1998; Maley & Chepstow-Lusty 2001; Salzmann & Hoelzmann 2005; Blach-Overgaard et al.
114 2010). It is now cultivated worldwide across the humid tropics for oil which is extracted from the
115 fibrous mesocarp of the fruit and the endosperm of the nut (Meijaard et al. 2018). Demand for palm
116 oil has caused largescale deforestation and biodiversity loss (Fitzherbert et al. 2008; Koh and Wilcove
117 2008; Yapp et al. 2010; Vijay et al. 2016) with devastating impacts on the survivorship of primates
118 (Wich et al. 2014; Linder & Palkovitz 2016; Supriatna et al. 2017), but like many palm species, faces
119 the threat of decline with climate change (Murphy et al. 2021; Paterson 2021). Here, it should be
120 noted that multiple primates feed on parts of the oil palm including the nut, flower, leaf and fruit
121 (e.g., tufted capuchins: Struthsaker & Leland 1977; vervets (*Chlorocebus aethiops*): McGrew 1985;
122 lesser white-nosed guenon (*Cercopithecus petaurista*), *Diana guenon* (*Cercopithecus diana*): Humle
123 and Matsuzawa 2004; long-tailed macaque: Mathews et al. 2007; Panamanian white-faced capuchin:
124 Estrada et al. 2012; Bornean orangutan (*Pongo pygmaeus*): Ancrenaz et al. 2014; Southern pig-tailed
125 macaque (*Macaca nemestrina*): Ruppert et al. 2018, and chimpanzees (*P.t.* spp at various sites: Tai
126 Forest Reserve, Ivory Coast: Boesch & Boesch 1983; Lopé Reserve, Gabon: Tutin et al. 1995; Ndoki
127 Forest, Democratic Republic of Congo: Kuroda et al. 1996; Mahale and Gombe, Tanzania: Goodall
128 1986, Zamma et al. 2011). Chimpanzees and orangutans also build arboreal beds in oil palm trees
129 (Sousa et al. 2008; Ancrenaz et al. 2014; Carvalho et al. 2015); whether due to necessity or
130 opportunity remains unclear.

131

132

133



134

135

136

137

138

139

140

141

142

143

144

145

146

147

148

149

150

Figure 1: Parts of the oil palm (*Elaeis guineensis*). Illustration by Elodie Freymann.

151

152

153

154

155

156

157

158

159

160

161

162



163

Figure 2: Bossou chimpanzees using stone tools (hammer and anvil) to crack open nuts. Photo by Katarina Almeida-Warren

164

165

166

167

The Bossou chimpanzee community not only feed on the oil palm nut, but also the leaflets and pith of the frond. Nuts and pith are eaten when preferred foods are scarce (Yamakoshi 1998) and the

168 eating of these plant parts has become ever more prevalent in this ape community, partly driven by
169 long-term anthropogenic activities (Hockings et al. 2009; Leblan & Soiret 2021). Many Bossou village
170 inhabitants rely on swidden agriculture (i.e., cutting and burning of vegetation in a forested
171 environment) (Yamakoshi & Leblan 2013) and the heterogeneric landscape that has been created
172 has resulted succession of food resources in most habitats (Bryson-Morrison et al. 2016; Leblan &
173 Soiret 2021), including oil palms that have thrived in disturbed local habitat. Many are heavily reliant
174 on this resource (Yamakoshi 2011, 2013). Oil palms are also found in what has been referred to as ‘a
175 buffer zone’ between core areas used by the chimpanzees and the villagers themselves, they have
176 been considered ‘common property’ to both humans and chimpanzees, and historically, this inter-
177 species resource sharing has facilitated co-existence between them to some degree (Yamakoshi
178 2005; 2011). The Bossou chimpanzees also access the youngest shoot tip (the apical meristem)
179 located in the leaf bases of the crown shaft (Tomlinson et al. 2011). The chimpanzees first
180 laboriously pull up older shoots and feed on the petiole and leaf base of these. This creates a hole in
181 what looks like a vertical cylinder, and they access the flesh of the newest tip in the crown shaft by
182 pounding it with one of the pulled-out, older shoots (Yamakoshi 2011). This behaviour is known as
183 pestle-pounding, so far, only observed for this ape community and a neighbouring community in
184 Kpala, Liberia (Sugiyama 1994; Yamakoshi & Sugiyama 1995; Yamakoshi 2011; Ohashi 2015). As well
185 as the Bossou chimpanzees, neighbouring chimpanzee communities in Diéké and Yealé, (Humble and
186 Matsuzawa 2004; Matsuzawa et al. 2008; Humle 2011; Carvalho 2013) also practice nut-cracking of
187 the oil palm nut; however, not all seem to (Humble & Matsuzawa 2001; Koops et al. 2013; Phillips C
188 personal observation for Nimba community).

189
190 Nut-cracking behaviour by the Bossou chimpanzees has been observed for over four decades
191 (Sugiyama & Koman 1979; Biro et al. 2010; Bryson-Morrison et al. 2020) and has contributed to
192 revealing complexities in understanding proximate and ultimate explanations for the practice of
193 durophagy of nuts by these apes. The chaînes opératoires of this phenomenon (Carvalho et al.
194 2008), as well as ontogeny and proficiency of nut-cracking (Biro et al. 2006), transportation and re-
195 use of tools (Sakura & Matsuzawa 1991; Carvalho et al. 2009), tool selection and function, forms of
196 locomotion used and laterality of nut-crackers (Humble & Matsuzawa 2009; Carvalho et al. 2012)
197 have all been studied to understand proximate mechanisms to consider ultimate explanations for
198 ecological, biological adaptations e.g. nutrition (Bryson-Morrison et al. 2020), mental mapping of
199 availability of nuts and tools as observed for Taï Forest communities (Boesch & Boesch 1984), as well
200 as cultural and social selection pressures (Bossou Forest: Biro et al. 2003; Matsuzawa et al. 2008; Taï
201 Forest: Boesch et al. 1994; Luncz et al. 2012) for increased fitness and reproductive success.

202
203 A key observation by Mercader et al. (2002) from their excavations of chimpanzee nut-cracking sites
204 in Taï Forest was that “*chimpanzees left behind stone and plant refuse that accumulated in specific*
205 *loci*”. Our work aims to build on this observation by exploring further the plant refuse accumulated
206 from nut-cracking by the Bossou chimpanzees; however, at the microscopic level rather than the
207 macroscopic level which may reveal greater insight from localised, decomposed plant refuse no
208 longer visible to the naked eye. We achieved this by analysing oil palm phytoliths produced in
209 specific loci sediments at chimpanzee nut-cracking sites in Bossou Forest (further details below).

210

211 **Why phytoliths? Overview and application of phytoliths across Africa**

212 Phytoliths are opal silica microfossils (‘phyto’ meaning plant and ‘lith’ meaning stone: Baker, 1959)
213 and are formed when aqueous monosilic acid ($\text{Si}(\text{OH})_4$) enters the plant during water, nutrient and
214 other mineral uptake and is then deposited within cell lumina, in the cells’ wall or in between cells.
215 The deposited silica then solidifies producing silica plant-cell-structure formations to varying degrees
216 of silicification (Madella & Lancelotti 2012) during evapotranspiration. Phytoliths encountered in
217 soils have normally accumulated due to deposition by local, phytolith-producing plants as they
218 decompose, although some translocation can occur vertically and horizontally by water and air
219 movement, and translocation distance can vary between different phytoliths (Fishkis et al. 2009,
220 2010; Lui et al. 2019). Organic carbon can be occluded (i.e., blocked) in phytoliths which can impact
221 soil carbon sequestration (Par & Sullivan 2005) and deposited phytoliths can breakdown or dissolve
222 in soils due to many factors including pH, surface bulk ratio (i.e., surface area to volume ratio of
223 phytolith shapes; Cabanes et al. 2011; Cabanes & Shahack-Gross 2015; Strömberg et al. 2018). Such
224 factors can help maintain equilibrium in concentrations of silica in soils (Farmer et al. 2005), but they
225 can also evade these processes and therefore, remain preserved and undisturbed in soils and
226 paleosols worldwide (Runge & Fimbel 2001; Piperno 2006; Cabanes et al. 2011). Furthermore,
227 phytoliths can survive charring, mineralisation, oxidisation (unlike pollen in more tropical regions)
228 and when ingested, mastication, digestion and defaecation (Cabanes et al. 2011; Hart 2016; Cabanes
229 2020). This, along with the fact that they can be distinctive in chemistry, size and morphology
230 (known as morphotypes: Rovner 1971; Piperno 1988; Piperno 2006; Hodson 2016) allow workers to
231 diagnose and associate phytoliths to plant type (e.g., grass), to family and genus, and with more
232 recent morphometric work, potentially to species (Hart 2016; Cai & Ge 2017; Hořková et al. 2021).
233 Additionally, phytolith indices have been created using combinations of phytolith morphotypes to
234 indicate aridity and climate (Twiss et al. 1992), and tree cover (Alexandre et al. 1997; Barboni et al.
235 2007). Thus, phytoliths are a powerful palaeoecological tool to reconstruct diet and environments of

236 extant and extinct taxa (Aleman et al. 2012; de Silva Neto et al. 2020) including humans and our past
237 activity (Pearsall 1994; Piperno 1994; Jiang, 1995; Runge 2001; Madella et al. 2002; Wanget et al.
238 2003; Barboni et al. 2010).

239
240 Phytoliths have been studied across Africa, but relatively more recently compared to work done on
241 other continents (Piperno 2006). A key focus has been to document phytolith morphotypes across
242 African flora and create reference libraries of multiple morphotypes that are associated with or indicate
243 vegetation structures and habitats to assist reconstruction of modern and past environments across
244 Africa (Runge & Runge 1997; Runge 1999; Mercader et al. 2000; Bremond et al. 2008; Barboni &
245 Bremond 2009; Aleman et al. 2012; Bremond et al. 2017; Bremond et al. 2020). For palm phytoliths,
246 work has focused on morphotypes in *Hyphaene* and *Pheonix* at African archaeological and modern sites,
247 particularly on their presence, preservation, and abundance in sediments due to taphonomic processes
248 and size of phytoliths (Olduvai Gorge, Tanzania: Bamford et al. 2006; Albert et al. 2009, Barboni et al.
249 2010, 2014) as well as their presence in relation to surface groundwater levels (multiple sites in East
250 Africa: Albert et al. 2015; Barboni et al. 2019). This work builds upon phytolith analyses of multiple palm
251 species globally (e.g. phytolith variability in Amazonian palms and their use by humans: Piperno 1989;
252 Morcote-Rios et al. 2013, 2016; Witteveen et al. 2022; morphotype analyses of palms at archaeological
253 sites in Papua New Guinea and Rapa Nui: Delhon & Orliac 2010; Fenwick et al. 2011; Bowdery 2015).
254 Such attention to palms is unsurprising as they are high phytolith producers (Hodson et al. 2006, 2015),
255 their phytoliths are relatively robust to chemical and physical processes pre- and post-deposition due to
256 factors such as having a surface bulk ratio >1 (Barboni et al. 2019). Furthermore, they have relatively
257 distinct taxonomic phytolith morphotypes, including the spheroid echinate. As described and identified
258 using Neumann et al.'s (2019) Code for Phytolith Nomenclature (IPCN) 2.0, these phytoliths have a basic
259 shape representing a sphere, and the echinate denotes the surface texture and ornamentation of having
260 conical projections that "vary in size which can be pointed or rounded" (Fig. 5). For spheroid echinates
261 associated with the palm family, Arecaceae, they range in size of 6-25 μm (Piperno 2006; Benvenuto et
262 al. 2015), and their conical formations are generally large and closely distributed (Neumann et al. 2019).

263
264 As well as building upon Mercader et al.'s (2000) observation at Tai Forest to consider the
265 microscopic level of oil palm nut refuse, we also highlight a component of plant input that requires
266 further attention; that is *directed* plant input that results from complex foraging behaviours of non-
267 human taxa, such as accessing, processing of foods with lithic and perishable tools, which we argue
268 is not equivalent to natural or anthropic plant input (Zurro et al. 2016). Directed plant input caused
269 in this case, by the chimpanzees repeatedly crushing nut endocarp and possibly the kernel (if the nut

270 is hit too hard) with a stone tool could enter sediments and as Madella and Lancelotti (2012) argue
271 for anthropic plant input could, “*produce phytolith assemblages that are normally much larger than*
272 *those produced from the natural vegetation [i.e., natural input] or the phytolith soil bank*”. As
273 remarked by these workers, we acknowledge that there is a spectrum of anthropic plant input that
274 depends on specific practices across human societies. This would, therefore, have implications for
275 phytolith assemblages produced, for example, cracking open nuts of oil palms might produce a
276 ‘weaker’ (i.e. produce phytolith assemblages that are normally less large) anthropic plant input than
277 heating up of oil palm over an open fire (with palm parts as fuel), but if the former was repeated at a
278 highly localised sites, this deserves consideration when interpreting phytolith assemblage in
279 associated sediments. Work on the impact of bioturbation by fossorial insects on phytolith
280 production in sediments indicate the importance to understand how multiple non-human taxa
281 influence sediment phytolith assemblages (Hart 2003; Jouquet et al. 2020). For primates, such work
282 would acknowledge the mutual roles that they play in shared ecological spaces with humans
283 (Fuentes 2012). Our aim was to analyse oil palm phytoliths at: 1) active sites where nut-cracking has
284 been observed in the last five years; 2) dormant sites where nut-cracking has not been observed for
285 10 years); and 3) non-nut-cracking sites where this form of durophagy has never been observed to
286 determine if resultant accumulation of oil palm nut refuse from nut-cracking by chimpanzees
287 provides a phytolith signature in “specific loci” (Mercader et al. 2000). We tested H₁: Production of
288 spheroid echinate phytoliths will be larger in localised sediments collected in close proximity to
289 visible remains of cracked oil palm nuts (within 10cm of remains). We predicted a larger production
290 of spheroid echinate phytoliths at the active nut-cracking sites based on the assumption that oil
291 palm nut refuse fragments pre- and post-deposition, would be present in greater frequency in
292 localised sediments.

293

294 We also endeavour to build upon work undertaken to reconstruct diets of extant primates using
295 micro remains such as phytoliths (reviewed Henry 2012). Diet composition estimates using phytolith
296 reference libraries from plants eaten by extant primates been recently explored. Phytolith
297 assemblages have been correlated with primate enamel thickness (Power et al. 2015), and
298 interpretations of phytolith assemblages in faeces of east and west African chimpanzees (Phillips &
299 Lancelotti 2014; Power et al. 2021) have revealed components of diet that are less detectable at the
300 macroscopic level. Relevant for this study and for future work is Power et al.’s (2021) findings for the
301 nut-cracking chimpanzees of Tai Forest; oil palm phytoliths were “overrepresented” in dietary
302 composition estimates based on analyses of their faeces and dental calculus. These apes access
303 endosperms of oil palm nuts as well as non-palm nuts of *Coula* and *Panda* through nut-cracking; it

304 was suggested the spines of the spheroid echinate phytoliths from oil palms could perhaps embed
305 themselves more easily in dental plaque versus phytoliths with a smoother (psilate) surface (Power
306 et al. 2021). Such work is vital for continued efforts to create high-resolution dietary comparatives of
307 non-human taxa using phytolith analyses, yet ethnographic comparatives beyond consumption
308 remain lacking – in this case, directed oil palm nut input into sediments associated with nut-cracking
309 tool-use behaviour of western chimpanzees.

310

311 Finally, we aim to complement work done on the behavioural and technological landscape of the
312 Bossou chimpanzees which provides support for the favoured places hypothesis for patterns of
313 landscape use in relation to nut-cracking (Almeida-Warren et al. 2021) and contribute to the
314 continued documentation of the behavioural ecology and unique cultural heritage of this ape
315 community. Few individuals remain (see methods below) and their sharing of ecological space with
316 the people of Bossou is also motive to document and interpret phytolith assemblages from directed
317 plant input of these non-human primates. Anthropogenic plant input could potentially result in directed
318 input by these primates being overlooked.

319

320 **Methods**

321 **Study site:** Situated near the border of Ivory Coast and Liberia, Bossou Forest surrounds the village
322 which is located in the sub-prefecture of Lola, South-Eastern Republic of Guinea (7°38'71.7'N -
323 8°29'38.9'W) at an attitude of 550m above sea level (Humble 2011). In terms of geology, in this
324 southern part of the West African Craton, the Archaean rocks (dated 2.8Ga) are defined by Tonalite-
325 Trondhjemite-Granodiorite (TTG) gneisses (Rollinson 2016). There are also supracrustal belts
326 containing greenstone, and iron formation sequences dated 2.7Ga. Paleoproterozoic (dated 2.3Ga)
327 reworking of the Archaean rocks are also found in the form of an intrusion of Macenta Batholith
328 (White & Leo 1969), which consists of coarse-grained, igneous granitoids (Rollinson 2016). Leptosols
329 which are typically shallow soils over hard bedrock are recorded for this area, but a detailed analyses
330 of soil type is yet to be done for Bossou and possibly there could be anthrosols i.e., soils that have
331 been heavily modified from human activity (WRB 2022). Analyses of a section of soil in Bossou
332 indicated moderately acidic soil (pH range: 4.9-5.7) with sand to silt-sized particles (SM Table 1).
333 Application of the feel method on-site, indicated a loam soil texture (Brady & Weil 1996).
334 Furthermore, the yellow-red hue (5-7.5YR Munsell Colour Chart) of the soil reflects iron oxidation.
335 Soil temperatures are isomegathemic (Jones et al. 2013) which means $\leq 5^{\circ}\text{C}$ difference between the
336 dry season (November to February), and the wet season (March to October). In terms of
337 topography, the home range of the Bossou chimpanzees includes four hills (Gban, Gbouton and

338 Guein) with elevations between 70-150m (Fig. 3). Vegetation across their range is a mosaic of
339 primary (found only on Gban), secondary and gallery forest across 6km². Secondary forest at
340 different successional stages is the most prevalent habitat (Bryson-Morrison et al. 2016) where
341 patches of fallow, coffee plantations and cultivated areas of varying degrees are found (Sugiyama &
342 Koman 1992; Hockings et al. 2009). Dominant trees include: *Albizia zygia* (DC.) J.F.Macbr., *Sterculia*
343 *tragacantha* Lindl. and various species of *Ficus* spp. *Thaumatococcus daniellii* (Benn.) Benth. and
344 *Aframomum latifolium* K. Schum. are terrestrial herbaceous vegetation found across their home
345 range and are eaten by the Bossou chimpanzees (Bryson-Morrison et al. 2016). Oil palms have been
346 recorded on three of the hills of the forest. Palms located on the top of the hills are not used or cut
347 down by humans due to traditional beliefs (see below; Yamakoshi & Leblan 2013); Schnell (1946)
348 suggests that the Bossou chimpanzees have been key dispersal agents for these particular oil palms.

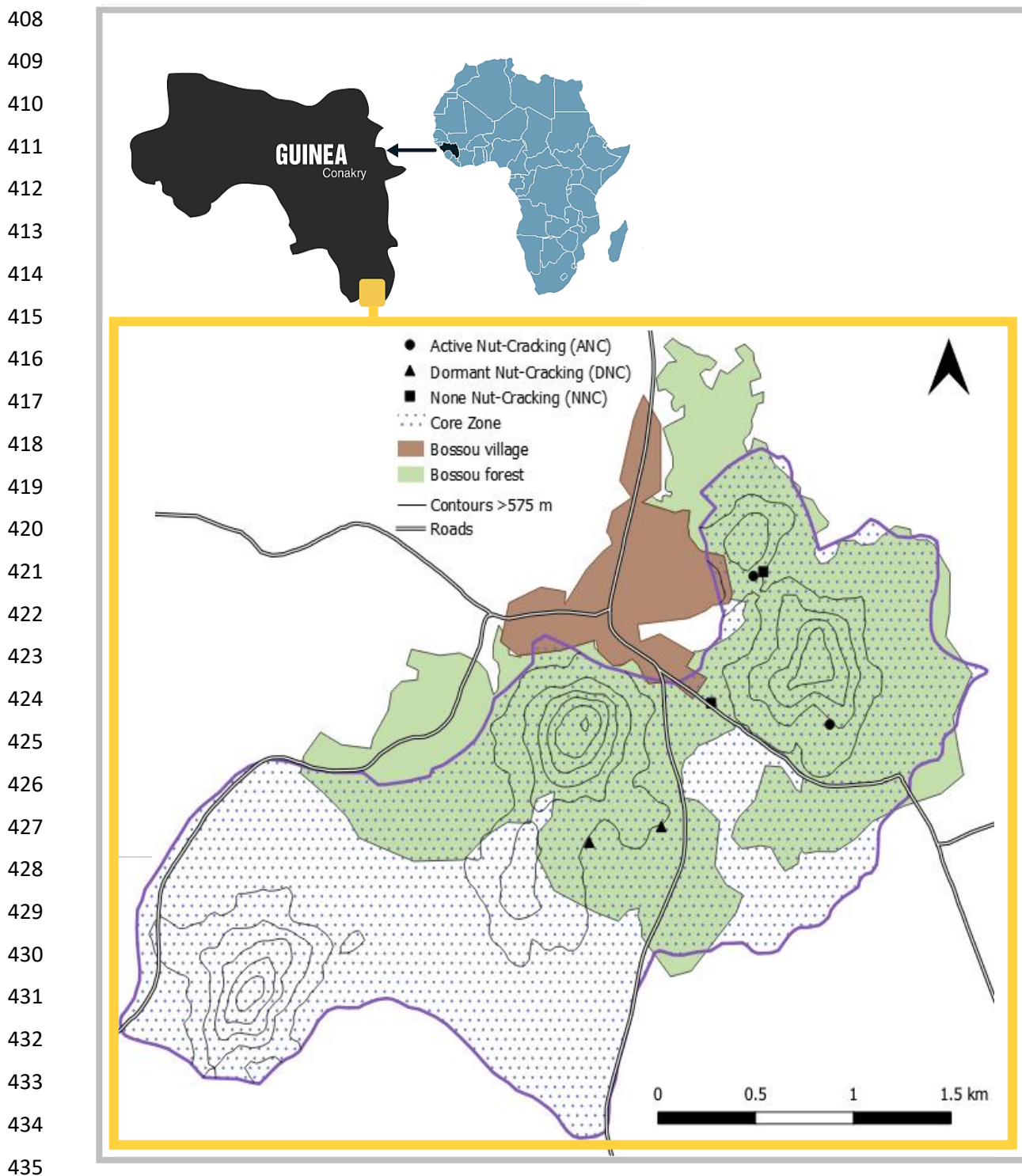
349 **People and chimpanzees:** The Bossou chimpanzees have been studied for almost 45 years with
350 longer-term studies beginning in 1976 (Sugiyama and Koman 1979; Sugiyama & Fujita 2011). During
351 this time, community size has been no more than 23 individuals, but they have experienced
352 significant losses due to disease since 2003 (Humble 2011; Matsuzawa 2020) and current numbers are
353 less than 10. They are fully habituated and so tolerate select human observers at close proximity
354 (Williamson et al. 2011), allowing diurnal follows to be undertaken within their 15km² home range.
355 These apes have a long tradition of sharing ecological and social space with the people of Bossou.
356 Currently, the village comprises of people of multiple backgrounds and ethnicities including Muslim
357 Fula, Malinke, Sus, Yakuba, Kono and Manon (Granier & Martinez 2011; Yamakoshi & Leblan 2013).
358 The traditional animist religion is practised by some and the Bossou chimpanzees have not been
359 hunted for meat due to a long-standing ban initiated by clans as well as the belief that the
360 chimpanzees are ancestral inhabitants who have changed form (Yamakoshi 2006; Yamakoshi &
361 Leblan 2013). Chimpanzees mostly utilise and inhabit the upper forested parts of three of the hills in
362 their home range, however, lower down swidden agriculture is practiced, and resource competition
363 is observed through crop damage by the chimpanzees, including oil palm fruits (Hockings et al.
364 2009). Whether sustainable co-existence between the Bossou people and the last remaining
365 chimpanzees is achievable remains to be seen. This is ever more imperative when savannah and
366 further patches of plantations and fallow surround Bossou Forest and the village where *Pennisetum*
367 *purpureum* Schumach., *Harungana madagascariensis* Lam. ex Poir., and *Sarcocephalus latifolius*
368 (Sm.) E.A.Bruce are dominant (Morimura et al. 2014). Biogeographically, the nearest continuous
369 primary and secondary montane forest, gallery forest and neighbouring chimpanzee communities
370 are southeast of Bossou and are 6km away in the Guinean Nimba Mountains which is part of a Strict
371 Nature Reserve and UNESCO World Heritage Site (Humble 2011).

372 **Taphonomy of phytoliths:** Despite their robusticity, oil palm phytoliths with varying degrees of
373 silicification may have been deposited into sediments through natural input (e.g., parts falling of the
374 palm, parts dropped when animals are feeding oil palm or when the palm dies and decomposes).
375 With directed input of oil palm phytoliths from nut-cracking activity of the chimpanzees, the
376 percussive action to open the nuts with stone tools could have caused damage to some of the
377 phytoliths pre-deposition. Regarding post-deposition, recent work indicates that rate of dissolution
378 of phytoliths in oil palm fronds is lower than in phytoliths detected in rainforest litter (von der Lühe
379 et al. 2022) which may, albeit tentatively, provide support for greater survivorship of oil palm
380 phytoliths to occur in sediments of the primary, secondary and gallery forests of Bossou. As
381 mentioned, particle size appears to indicate sand and silt-sized particles in the shallow soils of this
382 forest which might have implications for the movement of phytoliths of $\leq 62\text{-}2\ \mu\text{m}$ moving
383 downwards to deeper strata depth in sediments. The impact of hitting nuts on stone anvils with
384 stone hammers on such phytolith movement in surrounding sediments remains unknown but
385 warrants further investigation if spheroid echinates of palms could fall between these particles
386 based on their estimated size of 6-25 μm . Bioturbation by fossorial insects such as *Macrotermes* spp.
387 and *Dorylus* spp. are also a consideration for interpretation of phytolith assemblages in Bossou
388 Forest; for this study, we did not measure how close nests of both were to the palms and sediments
389 sampled. Both insects are eaten by the Bossou chimpanzees using perishable tools (Humble 1999;
390 Humle et al. 2009) and their locality to sampled areas in future warrants attention.

391

392 **Sample collection:** In 2018 KAW collected sediment samples for phytolith analyses from six palms
393 within the Bossou chimpanzee home range (Fig 3): two were palms where chimpanzees actively nut-
394 cracked in the last two months (ANC), two dormant palms, where they had not been observed nut
395 cracking since 2009 (DNC) and two where the chimpanzees had never been observed to nut crack as
396 our control samples (NNC). Previous studies have used a 2m (Koop et al. 2013; Almeida-Warren et al.
397 2021), or 5m radius at nut-cracking sites (Humble & Matzusawa 2004); we applied the shortest radius
398 as this is where we encountered tools and oil palm nut remains close to tools at active nut-cracking
399 sites (Fig 4 a-b). Maximum sediment sample depth was determined using a Van Walt Auger (57mm
400 diameter) which indicated a maximum soil depth of 23cm before the auger hit bedrock; hence, KAW
401 collected at depths of 0-5cm, 5-10cm and 10-15cm by creating a small soil profile and removing
402 samples using disposable spatulas (N=17: Fig 4c). Two samples of oil palm nut endocarp and two
403 leaflets from a frond were collected by CP in 2013. All samples were placed in double, pre-labelled
404 plastic zip-lock bags. This work was permitted under the Direction Nationale de la Recherche
405 Scientifique et Technique and the Institut de Recherche Environnementale de Bossou, Republic of

406 Guinea. Sample size of plant and sediments collected was minimised to reduce disturbance to the
407 Bossou chimpanzees.



436 **Figure 3: Map of Bossou Forest in Guinea with location of active nut-cracking sites (ANC) which**
437 **had been used within 2 months of sampling, dormant nut-cracking sites (DNC) which had not been**
438 **observed to be used at a nut-cracking site by the Bossou chimpanzees for ~10 years and non-nut-**
439 **cracking sites (NNC) which have not been observed to be used as a nut-cracking site. Map also**
440 **depicts home range of the Bossou chimpanzees (purple) which was adapted from Humle (2011).**
441 **Contours of hills (thin black lines), village (brown), forested area which includes primary,**

442 secondary and gallery forest, as well as some cultivated areas (green) and roads adapted from
443 ©OpenStreetMap and NASA (2013). Map of Africa and Guinea created on Visme.

444

445

446

447

448

449

450

451

452

453

454

455

456

457

458

459

460

461

462

463

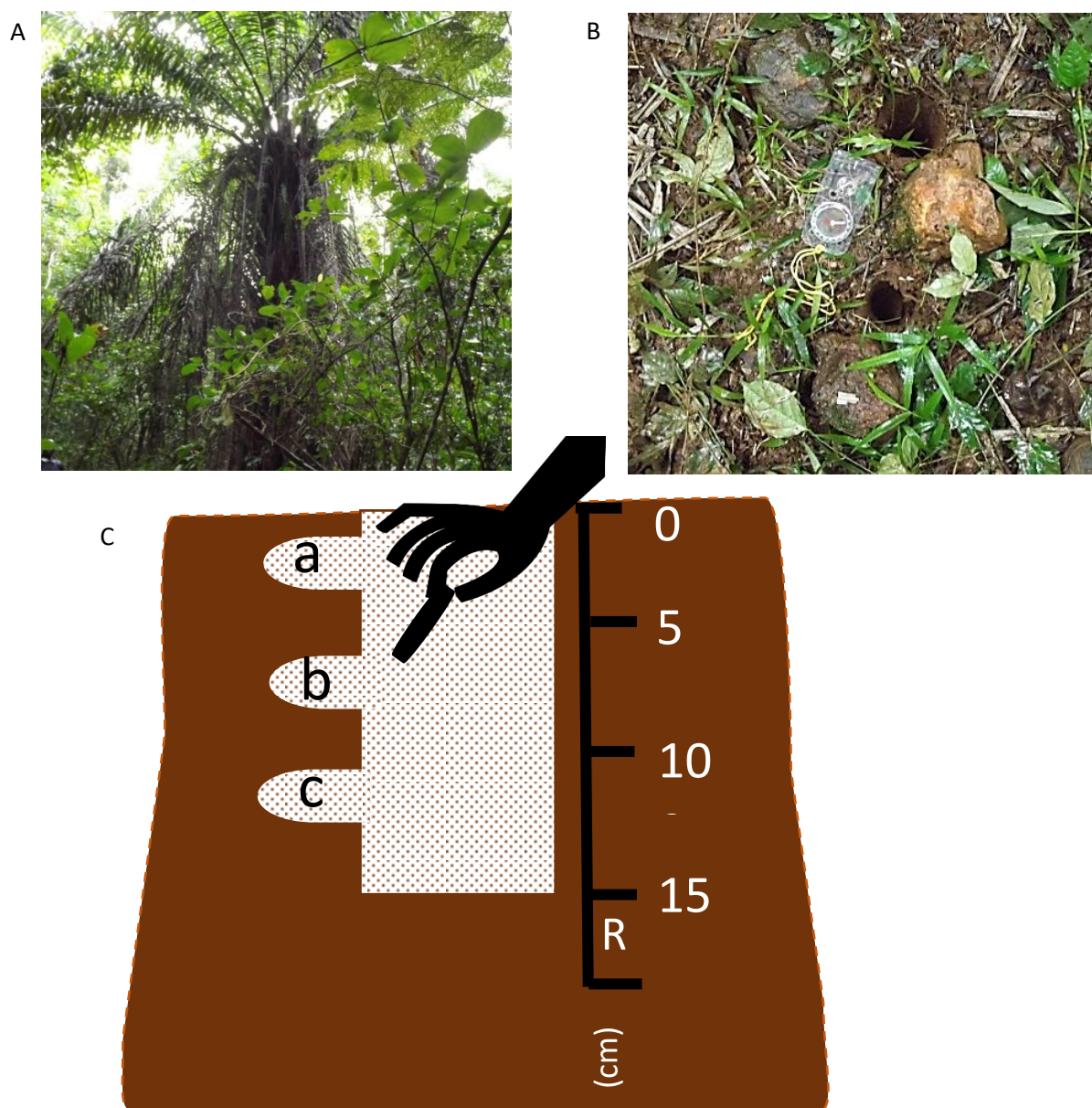
464

465

466

467

468



469 **Figure 4: One of the oil palm trees (a) in which sediment samples were collected and (b) soil**
470 **sample collection sites located in the vicinity of a stone tool and oil palm nut remains. Procedure**
471 **for soil sample collection at different depths (c).**

472

473 **Sample processing:** We separated collected plant parts and prepared and extracted phytoliths from
474 these four ashed plant samples (550°C to burn away organic matter in a muffle furnace) using
475 Lancelotti's (2010) dry ash extraction method (protocol outlined Phillips & Lancelotti 2014). For

476 sediment samples, we applied Albert et al.'s (1999) extraction method but adapted it by: 1) running
477 samples at 450°C in a muffle furnace rather than oven drying to remove organic matter; 2) after
478 heating samples in boiling water to remove phosphates and calcium carbonates, using Jackson's
479 (1956) equation for clay fractionation in the centrifuge which resulted in running samples at
480 1000rpm x 4 mins x 30 cycles; 3) using sodium polystungstate solution of 2.3g/ml density to extract
481 phytoliths; 4) running at 3000rpm for 10 mins instead of 5 mins until there was no more visible
482 mineral particles in the supernatant. We then applied their AIF/g equation to provide a standardised
483 total weight of acid insoluble fraction (containing extracted spheroid echinate phytoliths) per gram
484 of dry sediment and dry plant for each sample (SM 2). Mounting medium used for slides and as a
485 sealant was Entellan™. Phytolith processing of the four plant samples was done in the Palynology
486 and Phytolith Laboratory at the Evolutionary Studies Institute, University of the Witwatersrand. The
487 remaining samples were processed in the Oxford Long-term Ecology Laboratory at Dept. of Biology,
488 University of Oxford.

489

490 **Phytolith taxonomy and analyses:** We observed extracted phytoliths from both plant and sediment
491 samples under a transmitted light MI5B-P Swift microscope at 40x and any photographs were taken
492 using D-Moticam 10 camera and on Motic Images Plus 2.0. The description and identification
493 outlined in Neumann et al.'s (2019) International Code for Phytolith Nomenclature (IPCN) 2.0 was
494 used for this study of spheroid echinate phytoliths associated with oil palm. We counted complete
495 spheroid echinate phytoliths along nine random vertical transects per slide, resulting in a total of 351
496 view fields (39 view fields per transect) based on a minimum count of 350 for valid sample material
497 representation per slide (Van der Veen & Fieller 1982). This included the individual counting of these
498 phytoliths within parts of plant cells where they were still articulated. These phytoliths are normally
499 associated with the stegmata which is a cell found near vascular bundles and fibres in various parts
500 of the palm (Schmitt et al. 1995; Neumann et al. 2019).

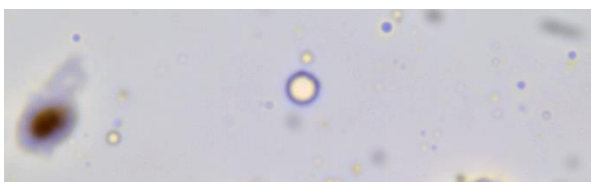
501

502 During the counting of the spheroid echinate phytoliths in both the nut and leaflet samples, there
503 appeared to be a visible size-difference for each palm part. We therefore took an approximate
504 measure of the 2D area (μm^2) (Hart 2016), perimeter (μm) and approximate maximum diameter
505 (μm) (Benvenuto et al. 2015) of 30 spheroid echinate phytoliths from a nut and leaflet sample to
506 determine if this could give a preliminary indication to intra-species size differences for this

507

A

B



508

509

Figure 5: Spheroid echinates detected in (a) nut endocarp and (b) leaflet of the oil palm (*Elaeis guineensis*). Approximated measurement of 2D area (μm^2), perimeter (μm) and maximum diameter of phytolith (μm) taken on Motic Images Plus 2.0.

510

511

512

513

514

515

516

517

518

519

520

521

522

523

524

525

526

527

528

529

530

531

532

533

534

535

536

537 morphotype in the oil palms at Bossou Forest (SM 3). We used the 'irregular' function on the Motic
538 Images Plus 2.0 to draw around the echinoid surface of each phytolith to determine an
539 approximated 2D area and perimeter, and the 'line' function for approximated maximum diameter
540 of measured phytoliths (Fig. 5).

541

542 **Data Analyses**

543 To test if there were a larger production of spheroid echinate phytoliths in localised sediments at
544 active nut-cracking sites (ANC) versus non-nut-cracking (NNC) and dormant nut-cracking sites (DNC),
545 we carried out a Kruskal Wallis Test to compare mean AIF/g of collective sediments at ANC sites, DO
546 sites and NNC sites as one-way ANOVA normality assumption was not met. To compare size
547 variation between nut and leaflet spheroid echinates, a Wilcoxon signed rank test was performed for
548 2D area (μm^2) and for the perimeter (μm) and maximum diameter (μm), a paired t-test (two-tailed).
549 Analyses was done on (STATA IC 15.0), Shapiro-Wilk tests were done for normality due to sample
550 size (<50) and $\alpha = 0.05$ (SM 3).

551

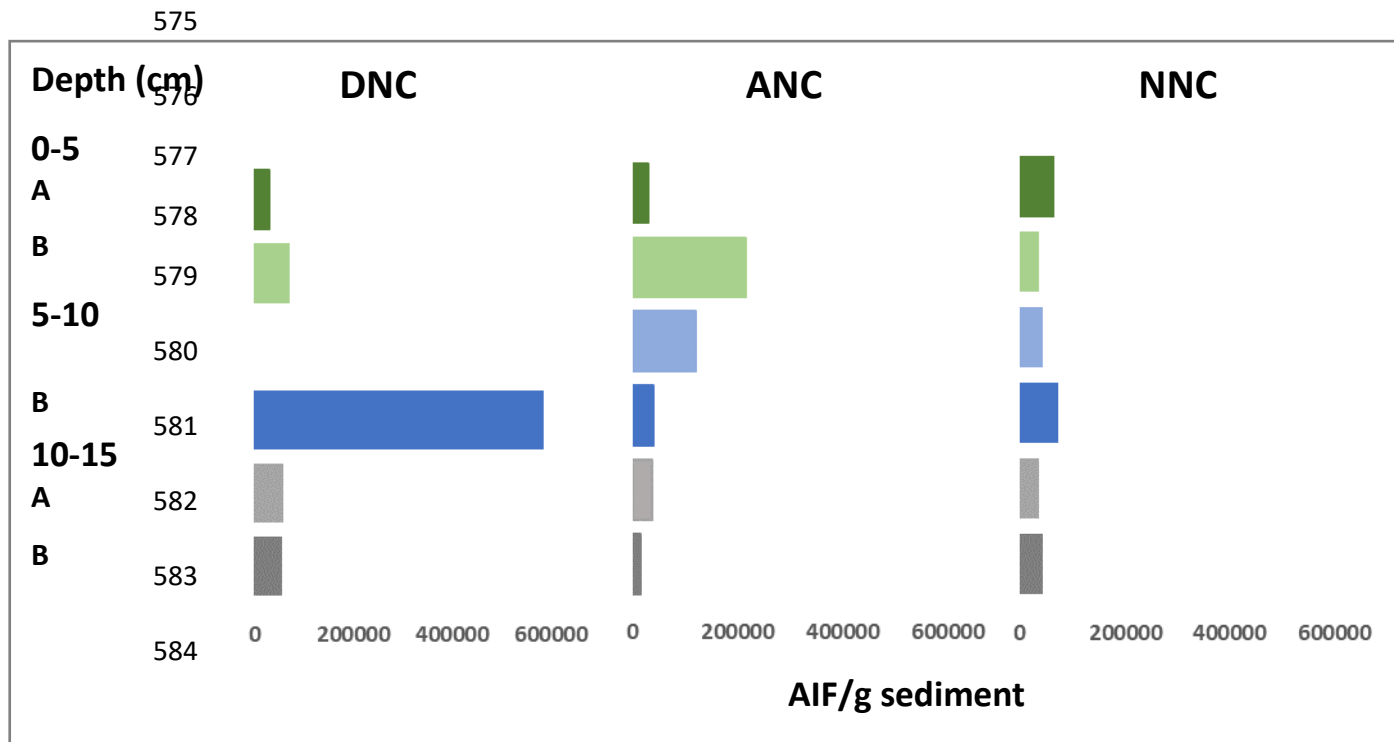
552 **Results**

553 Total spheroid echinates per gram of dry sediment (AIF/g) in ANC, DNC and NNC sediment samples
554 are outlined in Figure 6. From this, it would appear that the AIF/g of spheroid echinate phytoliths
555 across the different depths at the two non-nut-cracking sites appear relatively uniform, but no
556 statistical analyses could be done on possible intra- and inter-site differences with this small sample
557 size. No statistical difference was found between ANC, DNC or NNC sites for the combining of
558 sediment sample AIF/g values at each site ($\chi^2 = 0.982$, $df = 2$, $p = 0.621$). Total spheroid echinates in
559 AIF/g nut endocarp was 4876 and in leaflet it was 53529; many of the spheroid echinates within the
560 leaflet remained articulated in silica skeleton compared to those detected in the nut endocarp. This
561 aligns with other palm phytolith work on intra-specific productivity, with leaflets having greater
562 numbers of palm phytoliths (Delhon & Orliac 2010).

563

564 For 2D area of nut and leaf spheroid echinates ranged between 18.0-404.6 μm^2 and 17.9-83.3 μm^2
565 respectively and were statistically different (Wilcoxon signed rank test: $z=4,960$, $p < 0.001$, $N=30$,
566 effect size 0.85). Their perimeter ranges were 20.7-80.7 μm and 18.0-38.7 μm respectively and again
567 were statistically different (Paired t-test (two-sided): $T=10.79$, $df = 30$, $p < 0.001$, effect size 1.97,
568 power 0.754). Maximum diameter of spheroid echinate phytoliths between the plant parts were also
569 statistically significant (Paired t-test (two-sided): (Paired t-test (two-sided): $T=9.353$, $df = 29$, p
570 < 0.001 , effect size 1.71, power 0.754); maximum diameter range: 5.0-25.1 μm for nut and 4.9-11.6
571 μm for leaf. Generally, these approximate maximum diameter ranges align with the 6-25 μm for
572 spheroid echinates of Arecaceae proposed in Neumann et al. (2019), on two, especially with mean
573 maximum diameters of 14.9 μm and 7.8 μm for the nut and leaflet sample respectively.

574



586 **Figure 6: Bar graphs indicating total spheroid echinates recorded per gram of dry sediment (AIF/g)**
587 **at oil palms (A + B) for each of the type of site: dormant nut-cracking site (DNC), active nut-**
588 **cracking (ANC) and non-nut-cracking site (NNC). The green bars indicate AIF/g at sediment depth**
589 **of 0-5cm, blue bars for 5-10cm and grey bars for sediment depth 10-15cm.**

590

591 Discussion

592 This study has provided initial findings to interpret phytolith assemblages from directed plant input
593 by non-human taxa, in this instance as a result of the Bossou chimpanzees cracking open oil palm
594 nuts using stone tools. Our prediction that there would be a larger production of spheroid echinate
595 phytoliths in the localised sediments in close proximity to stone tools and oil palm nut remains at
596 active nut-cracking sites was not met. It could be that the directed plant input by these apes may
597 produce a relatively small phytolith assemblage as argued by Madella and Lancelotti (2012) for
598 hunter-gather *versus* agrarian societies in relation to interpreting phytolith assemblages from
599 anthropic plant input. However, our sample sizes were small (N=5 combined sediment samples for
600 DNC; N=6 for combined sediment samples NNC; and N=6 for ANC sites). This has implications for
601 effect size and type 1 error (Makin & Orban de Xivry 2019), and so a next step will be to increase
602 sample size. First, in terms of the number of oil palms that localised sediment samples are collected
603 from and second, to explore the phytolith productivity in sediments of the various depths, which
604 although were collected in this study, were not fully analysed due to limitation of sample size.

605 Almeida-Warren et al. (2021) highlight that there are multiple oil palm trees (~40) that have been
606 utilised by the Bossou chimpanzees to access and process oil palm nuts, and so there is great
607 potential to explore and further interpret phytolith assemblages produced from nut-cracking activity
608 by these apes. Further sampling of sediments at oil palms not used by the chimpanzees for nut-
609 cracking are needed as continued control samples, but this will require some consideration in terms
610 of their location and historical use. Oil palms in this region are under various stages of succession
611 due to land management practices (Yamakoshi & Leblan 2013; Leblan & Soiret 2021), and some may
612 be older than the usual 20–25-year-old oil palms at large-scale plantations (Jourdan & Rey 1997). As
613 this is a resource shared by the people and chimpanzees of Bossou (Humble & Matsuzawa 2004;
614 Hockings et al. 2009), there is the risk of anthropic input of phytolith assemblages produced. This will
615 have to be carefully factored in to ensure initial interpretations of phytolith assemblages from
616 directed input can be done that are independent from anthropic input.

617

618 In terms of analyses of production of phytolith assemblages at different sediment depths in relation
619 to the nut-cracking sites at Bossou, AIF/g of the various depths appears to indicate some possible
620 variation in phytolith productivity, with non-nut-cracking sites having a more similar AIF/g of
621 spheroid echinates across the depths sampled, compared to the dormant and active nut-cracking
622 sites which visually appear to be more productive in near surface sediment depths (Fig. 6). We could
623 not determine this statistically in this study due to sample size, but again, an increased sample size
624 and study of spheroid echinates across the different depths would clarify if variation of phytolith
625 productivity across the depths results from nut-cracking activity by chimpanzees. The movement of
626 phytoliths from the surface down to deeper sediments has understandable received long-standing
627 attention and has indicated how burning, size of phytoliths, pH, bioturbation, water exposure and
628 draining, and soil particle size all support Hart & Humphreys (1997) mobile phytolith hypothesis
629 (Rovner 1986; Fishkis et al. 2009, 2010; Cabanes et al. 2011) and whether we observe gradual
630 decrease or increase in phytolith movement (Hart & Humphreys 2003). Does the physical impact of
631 repeated use of percussive technology, cause smaller spheroid echinate phytoliths to move further
632 down in deeper sediments? Although work has been done to explore the surfaces of percussive
633 technology such as grinding stones and the use of large pestle and mortars for recent humans
634 (Hayes et al. 2018; Tsartsidou & Ktsakis 2020), as well as for stone tools of our ancestors
635 (Domínguez-Rodrigo et al. 2001), no published literature could be found to address this question.

636

637 Our preliminary data on approximated 2D area of the spheroid echinates as well as perimeter and
638 maximum diameter all indicated intra-specific differences in the size of this phytolith morphotype in
639 the nut and leaflet of the oil palm. This is rather a crude approximation compared to the detailed
640 work done using phytolith morphometrics (Ball et al. 2016; Yansheng et al. 2019) and on globular
641 and palm phytoliths (Fenwick et al. 2011; Benvenuto et al. 2015; Huisman et al. 2018; Witteveen et
642 al. 2022), however, published data on detailed morphometrics of oil palm phytoliths does not seem
643 available. Should there be intra-specific differences between nut endocarp phytoliths and that of
644 other parts of the oil palm in that the former are generally larger as indicated in this study, this
645 would have major implications for interpretations of phytolith assemblages in sediments associated
646 with processing oil palm nuts by both human and non-human taxa. Our next step is to measure a
647 proportion of the spheroid echinates in existing sediment samples, particularly comparing phytolith
648 2D area and maximum diameter for surface sediments at the nut-cracking and non-nut-cracking
649 sites; in addition, to collect additional samples as discussed and to also carry out further
650 measurements across multiple parts of the oil palms of Bossou Forest.

651 There are multiple future directions in which to take this work, some described already in relation to
652 increasing sample size at Bossou Forest, collecting samples at additional sites where chimpanzee
653 nut-cracking has occurred, completing an in-depth study of phytolith assemblages at different
654 sediment depths at Bossou, particularly in sediments in localities where repeated use of percussive
655 technology takes place, and obtaining detailed measurements on oil palm phytolith morphometrics.
656 There are additional future directions to explore for the directed input of oil palms by nut-cracking
657 activity of the Bossou chimpanzees, such as how the use of percussive technology impacts the
658 structure of phytoliths that are being processed (i.e. if there would be an increase in partial spheroid
659 echinates pre- and post-deposition due to possible damage from the crushing the oil palm nut). The
660 scope to explore directed input from other aspects of their complex foraging strategies such as the
661 insectivory component of their diet (using perishable tools for ant-dipping and termite fishing) also
662 awaits further attention. Finally, there are *Raphia* palms in Bossou Forest where the chimpanzees
663 feed on the gum as a result of visiting farms and causing crop damage (Hockings et al. 2009). There
664 phytoliths could also be studied to compare with oil palms phytoliths.

665

666 **Conclusion**

667 In the study of directed input by non-human taxa and the interpretation of phytolith assemblages
668 produced, this work has immense potential to explore ecological spaces shared by human and non-
669 human taxa, such as primates and highlight the mutual roles they play (Fuentes 2012) and highlight

670 the unique cultural heritage of our close relatives to work towards ensuring the survival of as many
671 primates as possible (Estrada et al. 2017; Kühl et al. 2019; Hockings and McLennan 2019; Carvalho et
672 al. 2022). This is ever more crucial and urgent for the Bossou chimpanzees who remain
673 biogeographically isolated from most neighbouring chimpanzee communities. Furthermore, it also
674 has potential to contribute and build upon work done at existing primate archaeological sites for
675 chimpanzees such as that in Tai Forest, Ivory Coast (Mercader et al. 2000; 2007), but also provide
676 insight into the interpretation of phytolith assemblages at nut-cracking sites yet to be discovered for
677 extirpated chimpanzees of West Africa (Smith et al. 2010) and at other sites where such directed
678 plant input is observed for primates, for example for the bearded capuchins at Boa Vista, Brazil who
679 use stone hammers and wooden and boulder anvils to crack open various palm nuts, or the long-
680 tailed macaques who crack open oil palm nuts in Ao Phang-Nga National Park, Thailand (Luncz et al.
681 2017). Finally, it highlights that there are many future directions needed to expand work on
682 interpreting phytolith assemblages from directed input of non-human taxa.

683 **Acknowledgements** We thanks Fromo Dore and Pascal Goumi for support in the field and the
684 Direction Nationale de la Recherche Scientifique, the Institut de Recherche Environnementale de
685 Bossou (Guinea), and the Kyoto University Primate Research Institute, for research permissions. CP
686 was funded by the NRF DST Centre of Excellence in Palaeosciences and the Leverhulme Trust. CP is
687 the main author and was responsible for conceptualisation, methodology, and writing of most of the
688 manuscript. KAW was responsible for most of the primary data collection, and logistical support in
689 the field. MB was responsible for logistical support for laboratory work in the Palynology and
690 Phytolith Lab at the Evolutionary Studies Institute, University of the Witwatersrand and supervision
691 of CP during this postdoctoral work. We thank Katherine Willis for allowing us to analyse sediment
692 samples in the Oxford Long-Term Ecology Lab, in Dept. of Biology, University of Oxford as well as
693 Steve Boreham and Chris Rolfe for allowing us to analyse sediment samples in the Geography
694 Science Laboratories, University of Cambridge.

695

696

697 **References**

698 Albert, R.M., Lavi, O., Estroff, L., Weiner, S., Tsatskin, A., Ronen, A. and Lev-Yadun, S., 1999. Mode of
699 occupation of Tabun Cave, Mt Carmel, Israel during the Mousterian period: a study of the sediments
700 and phytoliths. *Journal of Archaeological Science*, 26(10), pp.1249-1260.

- 701 Albert, R.M., Bamford, M.K. and Cabanes, D., 2009. Palaeoecological significance of palms at Olduvai
702 Gorge, Tanzania, based on phytolith remains. *Quaternary International*, 193(1-2), pp.41-48.
- 703 Albert, R.M., Bamford, M.K. and Esteban, I., 2015. Reconstruction of ancient palm vegetation
704 landscapes using a phytolith approach. *Quaternary International*, 369, pp.51-66.
- 705 Aleman, J., Leys, B., Apema, R., Bentaleb, I., Dubois, M.A., Lamba, B., Lebamba, J., Martin, C.,
706 Ngomanda, A., Truc, L. and Yangakola, J.M., 2012. Reconstructing savanna tree cover from pollen,
707 phytoliths and stable carbon isotopes. *Journal of Vegetation Science*, 23(1), pp.187-197.
- 708 Alexandré, A., Meunier, J.D., Lézine, A.M., Vincens, A. and Schwartz, D., 1997. Phytoliths: indicators
709 of grassland dynamics during the late Holocene in intertropical Africa. *Palaeogeography,*
710 *Palaeoclimatology, Palaeoecology*, 136(1-4), pp.213-229.
- 711 Almeida-Warren, K., Matsuzawa, T. and Carvalho, S., 2021. Landscaping the behavioural ecology of
712 primate stone tool use. *bioRxiv*.
- 713 Anderson, J. R., E. A. Williamson & J. Carter, 1983. Chimpanzees of Sapo Forest, Liberia: Density,
714 nests, tools and meat-eating. *Primates*, 24: pp594–601.
- 715 Ancrenaz, M., Oram, F., Ambu, L., Lackman, I., Ahmad, E., Elahan, H., Kler, H., Abram, N.K. &
716 Meijaard, E. 2015. Of Pongo, palms and perceptions: a multidisciplinary assessment of Bornean
717 orang-utans *Pongo pygmaeus* in an oil palm context. *Oryx*, 49(3), pp.465-472.
- 718 Arroyo, A., Hirata, S., Matsuzawa, T. & De La Torre, I. 2016. Nut cracking tools used by captive
719 chimpanzees (*Pan troglodytes*) and their comparison with Early Stone Age percussive artefacts from
720 Olduvai Gorge. *PLoS One*, 11(11), p.e0166788.
- 721 Atasie, V.N. and Akinhanmi, T.F. 2009. Extraction, compositional studies and physico-chemical
722 characteristics of palm kernel oil. *Pakistan Journal of Nutrition*, 8(6), pp.800-803.
- 723 Baker, G. 1959. A contrast in the opal phytolith assemblages of two Victorian soils. *Australian Journal*
724 *of Botany*, 7(1), pp.88-96.
- 725 Ball, T.B., Davis, A., Evett, R.R., Ladwig, J.L., Tromp, M., Out, W.A. and Portillo, M., 2016.
726 Morphometric analysis of phytoliths: recommendations towards standardization from the
727 International Committee for Phytolith Morphometrics. *Journal of Archaeological Science*, 68, pp.106-
728 111.

- 729 Bamford, M.K., Albert, R.M. and Cabanes, D., 2006. Plio–Pleistocene macroplant fossil remains and
730 phytoliths from Lowermost Bed II in the eastern palaeolake margin of Olduvai Gorge, Tanzania.
731 *Quaternary International*, 148(1), pp.95-112.
- 732 Barboni, D., Bremond, L. and Bonnefille, R., 2007. Comparative study of modern phytolith
733 assemblages from inter-tropical Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 246(2-
734 4), pp.454-470.
- 735 Barboni, D. and Bremond, L., 2009. Phytoliths of East African grasses: an assessment of their
736 environmental and taxonomic significance based on floristic data. *Review of Palaeobotany and*
737 *Palynology*, 158(1-2), pp.29-41.
- 738 Barboni, D., Ashley, G.M., Dominguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z. and Baquedano, E.,
739 2010. Phytoliths infer locally dense and heterogeneous paleovegetation at FLK North and
740 surrounding localities during upper Bed I time, Olduvai Gorge, Tanzania. *Quaternary Research*, 74(3),
741 pp.344-354.
- 742 Barrett, B.J., Monteza-Moreno, C.M., Dogandžić, T., Zwyns, N., Ibáñez, A. and Crofoot, M.C., 2018.
743 Habitual stone-tool-aided extractive foraging in white-faced capuchins, *Cebus capucinus*. *Royal*
744 *Society open science*, 5(8), p.181002.
- 745 Benito-Calvo, A., Carvalho, S., Arroyo, A., Matsuzawa, T. and de la Torre, I. 2015. First GIS analysis of
746 modern stone tools used by wild chimpanzees (*Pan troglodytes verus*) in Bossou, Guinea, West
747 Africa. *PLoS One*, 10(3), p.e0121613.
- 748 Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C. & Matsuzawa, T. 2003. Cultural
749 innovation and transmission of tool use in wild chimpanzees: evidence from field experiments.
750 *Animal Cognition*, 6(4), pp.213-223.
- 751 Biro, D., Sousa, C. & Matsuzawa, T. 2006. Ontogeny and cultural propagation of tool use by wild
752 chimpanzees at Bossou, Guinea: Case studies in nut cracking and leaf folding. In *Cognitive*
753 *development in chimpanzees* (pp. 476-508). Springer, Tokyo.
- 754 Biro, D., Carvalho, S. & Matsuzawa, T. 2010. Tools, traditions, and technologies: interdisciplinary
755 approaches to chimpanzee nut-cracking. *The mind of the chimpanzee: ecological and experimental*
756 *perspectives*, pp.141-155.
- 757 Boateng, L., Ansong, R., Owusu, W. and Steiner-Asiedu, M., 2016. Coconut oil and palm oil's role in
758 nutrition, health and national development: A review. *Ghana medical journal*, 50(3), pp.189-196.

- 759 Boesch C, Boesch H. 1983. Optimisation of nut-cracking with natural hammers by wild chimpanzees.
760 *Behaviour*, 83(3-4):265-86.
- 761 Boesch, C., Marchesi, P., Marchesi, N., Fruth, B. and Joulian, F., 1994. Is nut cracking in wild
762 chimpanzees a cultural behaviour?. *Journal of Human Evolution*, 26(4), pp.325-338.
763
- 764 Bowdery, D., 2015. An enigma revisited: identification of palm phytoliths extracted from the 1983
765 Rapa Nui, Rano Kao2 core. *Vegetation History and Archaeobotany*, 24(4), pp.455-466.
- 766 Brady, N.C. and Weil, R.R., 1996. Elements of the nature and properties of soils. 11th edition, prentice
767 hall inc, New Jersey. p109.
- 768 Bremond, L., Alexandre, A., Peyron, O. and Guiot, J., 2008. Definition of grassland biomes from
769 phytoliths in West Africa. *Journal of Biogeography*, 35(11), pp.2039-2048.
- 770 Bremond, L., Bodin, S.C., Bentaleb, I., Favier, C. and Canal, S., 2017. Past tree cover of the Congo
771 Basin recovered by phytoliths and $\delta^{13}C$ along soil profiles. *Quaternary International*, 434, pp.91-101.
- 772 Benvenuto, M.L., HONAIN, M.F., Osterrieth, M.L. and Morel, E., 2015. Differentiation of globular
773 phytoliths in Areaceae and other monocotyledons: morphological description for paleobotanical
774 application. *Turkish Journal of Botany*, 39(2), pp.341-353.
- 775 Bril, B., Smaers, J., Steele, J., Rein, R., Nonaka, T., Dietrich, G., Biryukova, E., Hirata, S. and Roux, V.,
776 2012. Functional mastery of percussive technology in nut-cracking and stone-flaking actions:
777 experimental comparison and implications for the evolution of the human brain. *Philosophical*
778 *Transactions of the Royal Society B: Biological Sciences*, 367(1585), pp.59-74.
- 779 Bril, B., Parry, R. & Dietrich, G. 2015. How similar are nut-cracking and stone-flaking? A functional
780 approach to percussive technology. *Philosophical Transactions of the Royal Society B: Biological*
781 *Sciences*, 370(1682), p.20140355.
- 782 Bryson-Morrison, N., Matsuzawa, T. & Humle, T. 2016. Chimpanzees in an anthropogenic landscape:
783 Examining food resources across habitat types at Bossou, Guinea, West Africa. *American Journal of*
784 *Primatology*, 78(12), pp.1237-1249.
- 785 Bryson-Morrison, N., Beer, A., Gaspard Soumah, A., Matsuzawa, T. & Humle, T. 2020. The
786 macronutrient composition of wild and cultivated plant foods of West African chimpanzees (*Pan*
787 *troglodytes verus*) inhabiting an anthropogenic landscape. *American Journal of Primatology*, 82(3),
788 p.e23102.
- 789 Cabanes, D., 2020. Phytolith analysis in Paleoecology and Archaeology. In *Handbook for the Analysis*
790 *of Micro-Particles in Archaeological Samples* (pp. 255-288). Springer, Cham.

- 791 Cabanes, D. and Shahack-Gross, R., 2015. Understanding fossil phytolith preservation: the role of
792 partial dissolution in paleoecology and archaeology. *PloS one*, 10(5), p.e0125532.
- 793 Cabanes, D., Weiner, S. and Shahack-Gross, R., 2011. Stability of phytoliths in the archaeological
794 record: a dissolution study of modern and fossil phytoliths. *Journal of Archaeological Science*, 38(9),
795 pp.2480-2490.
- 796 Carvalho JS, Meyer CF, Vicente L, Marques TA. 2015. Where to nest? Ecological determinants of
797 chimpanzee nest abundance and distribution at the habitat and tree species scale. *American Journal*
798 *of Primatology*. 7(2):186-99.
- 799 Carvalho, S., Cunha, E., Sousa, C. and Matsuzawa, T., 2008. Chaînes opératoires and resource-
800 exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of Human Evolution*,
801 55(1), pp.148-163.
- 802 Carvalho, S., Wessling, E.G., Abwe, E.E., Almeida-Warren, K., Arandjelovic, M., Boesch, C., Danquah,
803 E., Diallo, M.S., Hobaiter, C., Hockings, K. and Humle, T., 2022. Using nonhuman culture in
804 conservation requires careful and concerted action. *Conservation Letters*, 15(2), p.e12860.
- 805 Daegling DJ, McGraw WS, Ungar PS, Pampush JD, Vick AE, Bitty EA . 2011. Hard-Object Feeding in
806 Sooty Mangabeys (*Cercocebus atys*) and Interpretation of Early Hominin Feeding Ecology. *PLoS ONE*
807 6(8): e23095. <https://doi.org/10.1371/journal.pone.0023095>
- 808 D'Andrea, A.C., Logan, A.L. & Watson, D.J. 2006. Oil palm and prehistoric subsistence in tropical
809 West Africa. *Journal of African Archaeology*, 4(2), pp.195-222.
- 810 da Silva Neto, E.C., Calegari, M.R., Pereira, M.G., Maranhão, D.D.C., Schiavo, J.A., Fontana, A. and
811 Fernandes, J.C.F., 2018. Phytoliths as indicators of pedogenesis and paleoenvironmental changes in
812 Spodosols of the state of Rio de Janeiro, Brazil. *Science of the Total Environment*, 636, pp.1070-1080.
- 813 Delhon, C. and Orliac, C., 2010. The vanished palm trees of Easter Island: new radiocarbon and
814 phytolith data. In *The Gotland Papers-Selected Papers from the VII International Conference on*
815 *Easter Island and the Pacific: Migration, Identity, and Cultural Heritage* (pp. 97-110). Uppsala:
816 Gotland University Press.
- 817 Dian, N.L.H.M., Hamid, R.A., Kanagaratnam, S., Isa, W.A., Hassim, N.A.M., Ismail, N.H., Omar, Z. &
818 Sahri, M.M. 2017. Palm oil and palm kernel oil: Versatile ingredients for food applications. *Journal of*
819 *Oil Palm Research*, 29(4), pp.487-511.

- 820 Domínguez-Rodrigo, M., Serrallonga, J., Juan-Tresserras, J., Alcalá, L. and Luque, L., 2001.
821 Woodworking activities by early humans: a plant residue analysis on Acheulian stone tools from
822 Peninj (Tanzania). *Journal of Human Evolution*, 40(4), pp.289-299.
- 823 Duarte, M., Hanna, J., Sanches, E., Liu, Q. and Fragaszy, D., 2012. Kinematics of bipedal locomotion
824 while carrying a load in the arms in bearded capuchin monkeys (*Sapajus libidinosus*). *Journal of*
825 *Human Evolution*, 63(6), pp.851-858.
- 826 Estrada, A., Garber, P.A., Rylands, A.B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekarís, K.A.I.,
827 Nijman, V., Heymann, E.W., Lambert, J.E. and Rovero, F., 2017. Impending extinction crisis of the
828 world's primates: Why primates matter. *Science advances*, 3(1), p.e1600946.
- 829 Falótico, T., Proffitt, T., Ottoni, E.B., Staff, R.A. and Haslam, M., 2019. Three thousand years of wild
830 capuchin stone tool use. *Nature Ecology & Evolution*, 3(7), pp.1034-1038.
- 831 Falótico T, Spagnoletti N, Haslam M, Luncz LV, Malaivijitnond S, Gumert M. 2017. Analysis of sea
832 almond (*Terminalia catappa*) cracking sites used by wild Burmese long-tailed macaques (*Macaca*
833 *fascicularis aurea*). *American Journal of Primatology*. 79(5):e22629.
- 834 Fenwick, R.S., Lentfer, C.J. and Weisler, M.I., 2011. Palm reading: a pilot study to discriminate
835 phytoliths of four *Arecaceae* (Palmae) taxa. *Journal of Archaeological Science*, 38(9), pp.2190-2199.
- 836 Fishkis, O., Ingwersen, J. & Streck, T. 2009. Phytolith transport in sandy sediment: experiments and
837 modeling. *Geoderma*, 151(3-4), pp.168-178
838
- 839 Fishkis, O., Ingwersen, J., Lamers, M., Denysenko, D. & Streck, T. 2010. Phytolith transport in soil: a
840 field study using fluorescent labelling. *Geoderma*, 157(1-2), pp.27-36.
841
- 842 Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Brühl, C.A., Donald, P.F. & Phalan, B. 2008.
843 How will oil palm expansion affect biodiversity?. *Trends in Ecology & Evolution*, 23(10), pp.538-545.
- 844 Fragaszy DM, Liu Q, Wright BW, Allen A, Brown CW, Visalberghi E. 2013. Wild bearded capuchin
845 monkeys (*Sapajus libidinosus*) strategically place nuts in a stable position during nut-cracking. *PLoS*
846 *One*. 8(2): e56182.
- 847 Fragaszy, D.M., Eshchar, Y., Visalberghi, E., Resende, B., Laity, K. and Izar, P., 2017. Synchronized
848 practice helps bearded capuchin monkeys learn to extend attention while learning a tradition.
849 *Proceedings of the National Academy of Sciences*, 114(30), pp.7798-7805.
- 850 Fuentes, A., 2012. Ethnoprimatology and the anthropology of the human-primate interface. *Annual*
851 *Review of Anthropology*, 41, pp.101-117.

- 852 Geissler, E., Daegling, D.J., Polvadore, T.A. & McGraw, W.S. 2021. Seed choice differs by sex in sooty
853 mangabeys (*Cercocebus atys*). *Primates*, 62(2), pp.361-367.
- 854 Goren-Inbar, N., Sharon, G., Melamed, Y. & Kislev, M., 2002. Nuts, nut cracking, and pitted stones at
855 Gesher Benot Ya 'aqov, Israel. *Proceedings of the National Academy of Sciences*, 99(4), pp.2455-
856 2460.
- 857 Harmand, S., Lewis, J.E., Feibel, C.S., Lepre, C.J., Prat, S., Lenoble, A., Boës, X., Quinn, R.L., Brenet, M.,
858 Arroyo, A. & Taylor, N. 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya.
859 *Nature*, 521(7552), pp.310-315.
- 860 Hart, D.M. and Wallis, L., 2003. The influence of soil fauna on phytolith distribution in an Australian
861 soil. *Phytolith and starch research in the Australian-Pacific-Asian regions: The state of the art*, pp.83-
862 91.
- 863 Hart D.M. & Humphreys G.S. 1997. The mobility of phytoliths in soils: Pedological considerations. In:
864 PINILLA A., JUAN-TRESSERRAS J. & MACHADO M.J. eds. *The State-of-the-art of Phytoliths in Soils and*
865 *Plants*. Centro de Ciencias Medioambientales (CSIC) Monograph, 93-100
- 866 Hart, T.C., 2016. Issues and directions in phytolith analysis. *Journal of Archaeological Science*, 68,
867 pp.24-31.
- 868 Hayes, E., Fullagar, R., Mulvaney, K. and Connell, K., 2018. Food or fibercraft? Grinding stones and
869 Aboriginal use of *Triodia* grass (*spinifex*). *Quaternary International*, 468, pp.271-283.
- 870 Hartley, C.W.S., 1988. *The oil palm (Elaeis guineensis Jacq* (No. 3. ed.). Longman scientific and
871 technical.
- 872 Henry, A.G., 2012. Recovering dietary information from extant and extinct primates using plant
873 microremains. *International journal of primatology*, 33(3), pp.702-715.
- 874 Hockings, K.J., Anderson, J.R. & Matsuzawa, T. 2009. Use of wild and cultivated foods by
875 chimpanzees at Bossou, Republic of Guinea: feeding dynamics in a human-influenced environment.
876 *American Journal of Primatology: Official Journal of the American Society of Primatologists*, 71(8),
877 pp.636-646.
- 878 Hockings, K.J. and McLennan, M.R., 2019. Inclusive chimpanzee conservation. *Science*, 364(6445),
879 pp.1040-1040.

- 880 Hodson, M.J., 2016. The development of phytoliths in plants and its influence on their chemistry and
881 isotopic composition. Implications for palaeoecology and archaeology. *Journal of Archaeological*
882 *Science*, 68, pp.62-69.
- 883 Hošková, K., Pokorná, A., Neustupa, J. and Pokorný, P., 2021. Inter-and intraspecific variation in grass
884 phytolith shape and size: a geometric morphometrics perspective. *Annals of botany*, 127(2), pp.191-
885 201.
- 886 Huisman, S.N., Raczka, M.F. and McMichael, C.N., 2018. Palm phytoliths of mid-elevation Andean
887 forests. *Frontiers in Ecology and Evolution*, 6, p.193.
- 888 Humle, T. 2011. The 2003 epidemic of a flu-like respiratory disease at Bossou. In *The chimpanzees of*
889 *Bossou and Nimba* (pp. 325-333). Springer, Tokyo.
- 890 Humle, T. 1999. New Record of Fishing for Termites (*Macrotermes*) by the Chimpanzees of Bossou
891 (*Pan troglodytes verus*), Guinea.. *Pan Africa News*. 6(1): pp3-4
- 892 Humle, T. and Matsuzawa, T., 2004. Oil palm use by adjacent communities of chimpanzees at Bossou
893 and Nimba Mountains, West Africa. *International Journal of Primatology*, 25(3), pp.551-581.
- 894 Humle, T., Snowdon, C.T. and Matsuzawa, T., 2009. Social influences on ant-dipping acquisition in
895 the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition*,
896 12(1), pp.37-48.
- 897 Humle, T. and Matsuzawa, T., 2009. Laterality in hand use across four tool-use behaviors among the
898 wild chimpanzees of Bossou, Guinea, West Africa. *American Journal of Primatology: Official Journal*
899 *of the American Society of Primatologists*, 71(1), pp.40-48.
- 900 Jackson, M. L. 1956. Soil chemical analysis-Advanced course, (Fourth printing, 1968) Published by the
901 author, Department of Soil Science, University of Wisconsin, Madison, Wisconsin.
- 902 Jolly, A., 1985. The evolution of primate behavior: a survey of the primate order traces the
903 progressive development of intelligence as a way of life. *American Scientist*, 73(3), pp.230-239.
- 904 Jones, A., Breuning-Madsen, H., Brossard, M., Dampha, A., Deckers, J., Dewitte, O., Gallali, T., Hallett,
905 S., Jones, R., Kilasara, M., Le Roux, P., Micheli, E., Montanarella, L., Spaargaren, O., Thiombiano, L.,
906 Van Ranst, E., Yemefack, M., Zougmore R., (eds.),2013, Soil Atlas of Africa. European Commission,
907 Publications Office of the European Union, Luxembourg. 176 pp.

- 908 Jouquet, P., Jamoteau, F., Majumdar, S., Podwojewski, P., Nagabovanalli, P., Caner, L., Barboni, D.
909 and Meunier, J.D., 2020. The distribution of Silicon in soil is influenced by termite bioturbation in
910 South Indian forest soils. *Geoderma*, 372, p.114362.
- 911 Jourdan, C. and Rey, H., 1997. Architecture and development of the oil-palm (*Elaeis guineensis* Jacq.)
912 root system. *Plant and soil*, 189(1), pp.33-48.
- 913 Koops, K., McGrew, W.C. & Matsuzawa, T. 2013. Ecology of culture: do environmental factors
914 influence foraging tool use in wild chimpanzees, *Pan troglodytes verus*?. *Animal Behaviour*, 85(1),
915 pp.175-185.
- 916 Koh, L. P., & Wilcove, D. S. 2008. Is oil palm agriculture really destroying tropical biodiversity?
917 *Conservation Letters*, 1: pp 60–64.
- 918 Kühn, H.S., Boesch, C., Kulik, L., Haas, F., Arandjelovic, M., Dieguez, P., Bocksberger, G., McElreath,
919 M.B., Agbor, A., Angedakin, S. and Ayimisin, E.A., 2019. Human impact erodes chimpanzee
920 behavioral diversity. *Science*, 363(6434), pp.1453-1455.
- 921
- 922 Kuroda S, Nishihara T, Suzuki S, and Oko RA (1996) Sympatric chimpanzees and gorillas in the Ndoki
923 Forest, Congo. In WC McGrew, LF Marchant, and T Nishida (eds.): *GreatApe Societies*. Cambridge:
924 Cambridge University Press, pp.71–81
- 925
- 926 Langguth A, Alonso C. 1997. Capuchin monkeys in the Caatinga: tool use and food habits during
927 drought. *Neotropical Primates* 5: pp77–78.
- 928
- 929 Leblan, V. & Soiret, S.P.K. 2021. The future of human-chimpanzee coexistence in West Africa:
930 Reconsidering the role of shifting agriculture in chimpanzee (*Pan troglodytes verus*) conservation
931 planning. *Conservation Science and Practice*, 3(9), p.e496.
- 932
- 933 Linder, J.M. & Palkovitz, R.E. 2016. The threat of industrial oil palm expansion to primates and their
934 habitats. In *Ethnoprimatology*. Springer, Cham. p21-45.
- 935
- 936 Lombard, M., Högberg, A. and Haidle, M.N., 2019. Cognition: From Capuchin rock pounding to
937 Lomekwian flake production. *Cambridge Archaeological Journal*, 29(2), pp.201-231.
- 938
- 939 Liu, L., Li, D., Jie, D., Liu, H., Gao, G. & Li, N. 2019. Translocation of Phytoliths Within Natural Soil
940 Profiles in Northeast China. *Frontiers in Plant Science*, 10.

- 941 Luncz, L.V., Svensson, M.S., Haslam, M., Malaivijitnond, S., Proffitt, T. and Gumert, M., 2017.
942 Technological response of wild macaques (*Macaca fascicularis*) to anthropogenic change.
943 *International Journal of Primatology*, 38(5), pp.872-880.
944
- 945 Luncz LV, Sirianni G, Mundry R, Boesch C. 2018. Costly culture: differences in nut-cracking efficiency
946 between wild chimpanzee groups. *Animal Behaviour*. 1;137:63-73.
947
- 948 Madella, M., Jones, M.K., Goldberg, P., Goren, Y. and Hovers, E., 2002. The exploitation of plant
949 resources by Neanderthals in Amud Cave (Israel): the evidence from phytolith studies. *Journal of*
950 *Archaeological Science*, 29(7), pp.703-719.
951
- 952 Madella, M. & Lancelotti, C. 2012. Taphonomy and phytoliths: a user manual. *Quaternary*
953 *International*, 275, pp.76-83.
- 954 Makin, TR, & Orban de Xivry J. 2019. Science Forum: Ten common statistical mistakes to watch out
955 for when writing or reviewing a manuscript, *eLife* 8: e48175.
- 956 Maley, J., & Chepstow-Lusty, A. 2001. *Elaeis guineensis* Jacq. (oil palm) fluctuations in central Africa
957 during the late Holocene: Climate or human driving forces for this pioneering species? *Vegetation*
958 *History and Archaeobotany*, 10, pp117–120.
- 959 Maley J, & Brenac P. 1998. Vegetation dynamics, palaeoenvironments and climatic changes in the
960 forests of western Cameroon during the last 28,000 years BP. *Review of Palaeobotany and*
961 *Palynology*. 99(2):pp157-87.
- 962 Matsuzawa, T., 2020. Jokro: The death of a wild infant chimpanzee from respiratory disease.
963 *Primates*, 61(3), pp.339-346.
- 964 Matsuzawa, T., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R. & Yamakoshi, G. 2008.
965 Emergence of culture in wild chimpanzees: education by master-apprenticeship. In *Primate origins*
966 *of human cognition and behavior* (pp. 557-574). Springer, Tokyo.
- 967 Mathews, J., Yong, K.K. & Nurulnihar, B.E. 2007. Preliminary investigation on biodiversity and its
968 ecosystem in oil palm plantation. In *International Palm Oil Congress*, pp. 1112-1158.
- 969 McGraw, W.S., Vick, A.E. and Daegling, D.J., 2014. Dietary variation and food hardness in sooty
970 mangabeys (*Cercocebus atys*): implications for fallback foods and dental adaptation. *American*
971 *Journal of Physical Anthropology*, 154(3), pp.413-423.
972

- 973 McGrew WC 1985. The chimpanzee and the oil palm: patterns of culture. *Soc Biol & Hum Affairs*,
974 50:7–23.2.
- 975 McGrew WC 1992. Chimpanzee Material Culture: Implications for Human Evolution. Cambridge
976 University Press, Cambridge.
- 977 McGrew, W.C., Ham, R.M., White, L.J.T., Tutin, C.E.G. and Fernandez, M., 1997. Why don't
978 chimpanzees in Gabon crack nuts?. *International Journal of Primatology*, 18(3), pp.353-374.
- 979 Meijaard, E., Garcia-Ulloa, J., Sheil, D., Wich, S.A., Carlson, K.M., Juffe-Bignoli, D., & Brooks, T.M.
980 2018. *Oil palm and biodiversity. A situation analysis by the IUCN Oil Palm Task Force*. IUCN Oil Palm
981 Task Force Gland, Switzerland: IUCN.
- 982 Mercader, J., Runge, F., Vrydaghs, L., Doutrelepon, H., Ewango, C.E. and Juan-Tresseras, J., 2000.
983 Phytoliths from archaeological sites in the tropical forest of Ituri, Democratic Republic of Congo.
984 *Quaternary Research*, 54(1), pp.102-112.
- 985 Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R. & Boesch, C., 2007. 4,300-year-old
986 chimpanzee sites and the origins of percussive stone technology. *Proceedings of the National
987 Academy of Sciences*, 104(9), pp.3043-3048.
- 988 Morimura N, Ohashi G, Matsuzawa T.2014. A Survey of the Savanna Vegetation in Bossou, Guinea.
989 *Pan Africa News* 21(2):22-24
- 990 Morcote-Ríos, G., Bernal, R. and Raz, L., 2016. Phytoliths as a tool for archaeobotanical,
991 palaeobotanical and palaeoecological studies in Amazonian palms. *Botanical journal of the Linnean
992 Society*, 182(2), pp.348-360.
- 993
- 994 Morgan BJ, Abwe EE. 2006. Chimpanzees use stone hammers in Cameroon. *Current Biology*.
995 16(16):R632-3.
- 996
- 997 Murphy, D.J., Goggin, K. & Paterson, R.R.M., 2021. Oil palm in the 2020s and beyond: challenges and
998 solutions. *CABI Agriculture and Bioscience*, 2(1), pp.1-22.
- 999
- 1000 NASA JPL. 2013. *NASA Shuttle Radar Topography Mission Global 1 arc second*. 2013, distributed by
1001 NASA EOSDIS Land Processes DAAC, <https://doi.org/10.5067/MEaSURES/SRTM/SRTMGL1.003>.
1002 Accessed 2022-11-10.
- 1003

1004 International Committee for Phytolith Taxonomy (ICPT) Neumann Katharina k. neumann@ em. uni-
1005 frankfurt. de Strömberg Caroline AE Ball Terry Albert Rosa Maria Vrydaghs Luc Cummings Linda
1006 Scott, 2019. International code for phytolith nomenclature (ICPN) 2.0. *Annals of Botany*, 124(2),
1007 pp.189-199.

1008

1009 Novello, A., Bamford, M.K., van Wijk, Y. and Wurz, S., 2018. Phytoliths in modern plants and soils
1010 from Klasies River, cape region (South Africa). *Quaternary International*, 464, pp.440-459.

1011

1012 Ohashi, G. 2015. Pestle-pounding and nut-cracking by wild chimpanzees at Kpala, Liberia. *Primates*,
1013 56(2), pp.113-117.

1014

1015 Paterson, R.R.M. 2021. Longitudinal trends of future climate change and oil palm growth: empirical
1016 evidence for tropical Africa. *Environmental Science and Pollution Research*, 28(17), pp.21193-21203.

1017

1018 Pearsall, D.M., 1994. Investigating New World tropical agriculture: Contributions from phytolith
1019 analysis. *Tropical Archaeobotany*, Routledge, London, pp.115-138.

1020

1021 Peters, C.R., 1987. Nut-like oil seeds: Food for monkeys, chimpanzees, humans, and probably
1022 ape-men. *American Journal of Physical Anthropology*, 73(3), pp.333-363.

1023

1024 Piperno, D.R., 2006. *Phytoliths: a comprehensive guide for archaeologists and paleoecologists*.

1025 Rowman Altamira.

1026

1027 Phillips, C. and Lancelotti, C., 2014. Chimpanzee diet: phytolithic analysis of feces. *American Journal*
1028 *of Primatology*, 76(8), pp.757-773.

1029

1030 Power, R.C., Salazar-García, D.C., Wittig, R.M., Freiberg, M. and Henry, A.G., 2015. Dental calculus
1031 evidence of Tai Forest Chimpanzee plant consumption and life history transitions. *Scientific Reports*,
1032 5(1), pp.1-13.

1033

1034 Power, R.C., Wittig, R.M., Stone, J.R., Kupczik, K. and Schulz-Kornas, E., 2021. The representativeness
1035 of the dental calculus dietary record: insights from Tai chimpanzee faecal phytoliths. *Archaeological*
1036 *and Anthropological Sciences*, 13(6), pp.1-11.

1037

- 1038 Proffitt T, Luncz VL, Malaivijitnond S, Gumert M, Svensson MS, Haslam M. 2018. Analysis of wild
1039 macaque stone tools used to crack oil palm nuts. *Royal Society Open Science*. 5(3):171904.
1040
1041
1042 Rollinson, H., 2016. Archaean crustal evolution in West Africa: A new synthesis of the Archaean
1043 geology in Sierra Leone, Liberia, Guinea and Ivory Coast. *Precambrian Research*, 281, pp.1-12.
1044
1045 Rovner I. 1986. Downward percolation of phytoliths in stable soils: a non-issue. In: ROVNER I. ed.
1046 Plant Opal Phytolith Analysis in Archaeology and Paleoecology. Proceedings of the 1984 Phytolith
1047 Research Workshop, North Carolina State University, Raleigh. Occasional Papers No. 1 of the
1048 Phytolitharien, 23-28.
1049
1050 Runge, F., 1999. The opal phytolith inventory of soils in central Africa—quantities, shapes,
1051 classification, and spectra. *Review of Palaeobotany and Palynology*, 107(1-2), pp.23-53.
1052
1053 Runge, F., 2001. Evidence for land use history by opal phytolith analysis: examples from the central
1054 African tropics (eastern Kivu, DR Congo). *Phytoliths: Applications in Earth Science*, pp.73-85.
1055
1056 Runge, F. and Runge, J., 1997. Opal phytoliths in East African plants and soils. *The state-of-the-art of*
1057 *phytoliths in soils and plants. Madrid: Centro de Ciencias Medioambientales*, pp.71-81.
1058
1059 Sakura, O. & Matsuzawa, T. 1991. Flexibility of wild chimpanzee nut-cracking behavior using stone
1060 hammers and anvils: An experimental analysis. *Ethology*, 87(3-4), pp.237-248.
1061
1062 Salzmann, U. and Hoelzmann, P., 2005. The Dahomey Gap: an abrupt climatically induced rain forest
1063 fragmentation in West Africa during the late Holocene. *The Holocene*, 15(2), pp.190-199.
1064
1065 Schnell R (1946). Notes sur le palmier à huile, sa répartition et sa dissémination dans la région
1066 forestière. *Notes Africaines* 31, 30.
1067
1068 Sirianni, G., Mundry, R. & Boesch, C. 2015. When to choose which tool: multidimensional and
1069 conditional selection of nut-cracking hammers in wild chimpanzees. *Animal Behaviour*, 100, pp.152-
1070 165.
1071

- 1072 Smith, C.C., Morgan, M.E. & Pilbeam, D., 2010. Isotopic ecology and dietary profiles of Liberian
1073 chimpanzees. *Journal of Human Evolution*, 58(1), pp.43-55.
1074
- 1075 Spagnoletti, N., Visalberghi, E., Verderane, M.P., Ottoni, E., Izar, P. and Fragaszy, D., 2012. Stone tool
1076 use in wild bearded capuchin monkeys, *Cebus libidinosus*. Is it a strategy to overcome food scarcity?
1077 *Animal Behaviour*, 83(5), pp.1285-1294.
1078
- 1079 Sowmmai MA & Awosina EO. 1991. Pollen analysis of Kariya Wuro rock shelter, Bauchi State.
1080 *Nigerian Field* 56 (3-4):pp 163-170
1081
- 1082 Soumah, A.G., Humle, T. & Matsuzawa, T. 2014. *Oil Palm Use Among the People and Wild*
1083 *Chimpanzes of Bossou, Guinea, West Africa*.
1084
- 1085 Sousa J, Barata AV, Sousa C, Casanova CCN, & Vicente L. 2011. Chimpanzee Oil-Palm Use in Southern
1086 Cantanhez National Park, Guinea-Bissau. *American Journal of Primatology*, 73: pp485–497.
- 1087 Strömberg, C.A., Dunn, R.E., Crifò, C. and Harris, E.B., 2018. Phytoliths in paleoecology: analytical
1088 considerations, current use, and future directions. In *Methods in paleoecology* (pp. 235-287).
1089 Springer, Cham.
- 1090 Struhsaker, T. T. & P. Hunkeler, 1971. Evidence of tool-using by chimpanzees in the Ivory Coast. *Folia*
1091 *Primatol.*, 15: 212–219.
- 1092 Struhsaker, T.T. & Leland, L. 1977. Palm-nut smashing by *Cebus a. apella* in Colombia. *Biotropica*,
1093 pp.124-126.
- 1094 Sugiyama, Y. 1994. Tool use by wild chimpanzees. *Nature*, 367(6461), pp.327-327.
- 1095 Sugiyama Y, Koman J. 1979. Tool-using and-making behavior in wild chimpanzees at Bossou, Guinea.
1096 *Primates*. 20(4):513-24.
- 1097 Sugiyama, Y., Fujita, S. (2011). The Demography and Reproductive Parameters of Bossou
1098 Chimpanzees. In: Matsuzawa, T., Humle, T., Sugiyama, Y. (eds) *The Chimpanzees of Bossou and*
1099 *Nimba*. Primatology Monographs. Springer, Tokyo. https://doi.org/10.1007/978-4-431-53921-6_4
- 1100 Supriatna, J., Dwiyahreni, A.A., Winarni, N., Mariati, S. & Margules, C. 2017. Deforestation of primate
1101 habitat on Sumatra and adjacent islands, Indonesia. *Primate Conservation*, 31(71-82).
- 1102 Tamura, M. 2020. Extractive foraging on hard-shelled walnuts and variation of feeding techniques in
1103 wild Japanese macaques (*Macaca fuscata*). *American Journal of Primatology*, 82(6), p.e23130.

- 1104 Taylor, A.B., Terhune, C.E., Toler, M., Holmes, M., Ross, C.F. & Vinyard, C.J. 2018. Jaw-muscle fiber
1105 architecture and leverage in the hard-object feeding Sooty Mangabey are not structured to facilitate
1106 relatively large bite forces compared to other papionins. *The Anatomical Record*, 301(2), pp.325-342.
1107
- 1108 Tomlinson PB, Horn JW, Fisher JB. 2011. *Palm constriction and classification*. In: The Anatomy of
1109 Palms. Tomlinson PB, Horn JW, Fisher JB (Eds), Oxford University Press, Oxford: pp 12-16.
1110
- 1111 Tsartsidou, G. and Kotsakis, K., 2020. Grinding in a hollow? Phytolith evidence for pounding cereals
1112 in bedrock mortars at Paliambela Kolindros, an Early Neolithic site in Macedonia, North Greece.
1113 *Archaeological and Anthropological Sciences*, 12(8), pp.1-16.
1114
- 1115 Tsuji, Y. and Takatsuki, S., 2012. Interannual variation in nut abundance is related to agonistic
1116 interactions of foraging female Japanese macaques (*Macaca fuscata*). *International Journal of*
1117 *Primatology*, 33(2), pp.489-512.
1118
- 1119 Tutin, C.E., Fernandez, M., Rogers, M.E., Williamson, E.A. & McGrew, W.C. 1991. Foraging profiles of
1120 sympatric lowland gorillas and chimpanzees in the Lope Reserve, Gabon. *Philosophical Transactions*
1121 *of the Royal Society of London. Series B: Biological Sciences*, 334(1270), pp.179-186.
1122
- 1123 Twiss, P.C., 1992. Predicted world distribution of C 3 and C 4 grass phytoliths. In *Phytolith*
1124 *systematics* (pp. 113-128). Springer, Boston, MA.
1125
- 1126 UNEP-WCMC and IUCN (2022), Protected Planet: The World Database on Protected Areas (WDPA)
1127 and World Database on Other Effective Area-based Conservation Measures (WD-OECM) [Online],
1128 August 2022, Cambridge, UK: UNEP-WCMC and IUCN. Available at: www.protectedplanet.net.
1129
- 1130 Visalberghi, E. & Fragaszy, D. 2013. 10 The Etho-Cebus Project: Stone-tool use by wild capuchin
1131 monkeys. *Tool Use in Animals: Cognition and Ecology*, p.203.
1132
- 1133 Visalberghi, E., Fragaszy, D., Ottoni, E., Izar, P., de Oliveira, M.G. and Andrade, F.R.D., 2007.
1134 Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus*
1135 *libidinosus*) to crack open palm nuts. *American Journal of Physical Anthropology: The Official*
1136 *Publication of the American Association of Physical Anthropologists*, 132(3), pp.426-444.
1137

- 1138 Van der Veen, M. and Fieller, N., 1982. Sampling seeds. *Journal of Archaeological Science*, 9(3),
1139 pp.287-298.
1140
- 1141 van Pinxteren BO, Sirianni G, Gratton P, Després-Einspenner ML, Egas M, Kühl H, Lapuente J, Meier
1142 AC, Janmaat KR. Sooty mangabeys scavenge on nuts cracked by chimpanzees and red river hogs—An
1143 investigation of inter-specific interactions around tropical nut trees. *American journal of*
1144 *primatology*. 2018 Aug;80(8):e22895.
1145
- 1146 Vijay V, Pimm SL, Jenkins CN, Smith SJ. 2016. The impacts of oil palm on recent deforestation and
1147 biodiversity loss. *PLoS one*. 11(7):e0159668.
1148
- 1149 von der Lühe, B., Bezler, K., Hughes, H.J., Greenshields, B., Tjoa, A. and Sauer, D., 2022. Oil-palm and
1150 Rainforest Phytoliths Dissolve at Different Rates-with Implications for Silicon Cycling After
1151 Transformation of Rainforest Into Oil-palm Plantation. *Silicon*, pp.1-8.
1152
- 1153 Wich, S.A., Garcia-Ulloa, J., Kühl, H.S., Humle, T., Lee, J.S. & Koh, L.P. 2014. Will oil palm's
1154 homecoming spell doom for Africa's great apes? *Current Biology*, 24(14), pp.1659-1663.
1155
- 1156 Witteveen, N.H., Hobus, C.E.M., Philip, A., Piperno, D.R. and McMichael, C.N.H., 2022. The variability
1157 of Amazonian palm phytoliths. *Review of Palaeobotany and Palynology*, 300, p.104613.
1158
- 1159 Wood, B. and Schroer, K., 2012. Reconstructing the diet of an extinct hominin taxon: the role of
1160 extant primate models. *International Journal of primatology*, 33(3), pp.716-742.
1161
- 1162 Wynn, T., Hernandez-Aguilar, R.A., Marchant, L.F. and McGrew, W.C., 2011. "An ape's view of the
1163 Oldowan" revisited. *Evolutionary Anthropology: Issues, News, and Reviews*, 20(5), pp.181-197.
1164
- 1165 Yamakoshi, G., Sugiyama, Y. 1995. Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea:
1166 A newly observed tool-using behavior. *Primates* 36, pp489–500.
- 1167 Yamakoshi G. 2011. *Pestle-Pounding Behavior: The Key to the Coexistence of Humans and*
1168 *Chimpanzees*. In: Matsuzawa T., Humle T., Sugiyama Y. (eds) *The Chimpanzees of Bossou and Nimba*.
1169 *Primate Monographs*. Springer, Tokyo.

- 1170 Yamakoshi G. 2008. *Ecology of Tool Use in Wild Chimpanzees: Toward Reconstruction of Early*
1171 *Hominid Evolution*. In: Matsuzawa T. (eds) Primate Origins of Human Cognition and Behavior.
1172 Springer, Tokyo.
- 1173 Yamakoshi, G. & Leblan, V. 2013. Conflicts between indigenous and scientific concepts of landscape
1174 management for wildlife conservation: human-chimpanzee politics of coexistence at Bossou, Guinea.
1175 *Revue de primatologie*, (5).
- 1176 Yansheng, G., Yabin, J., Shuo, G., Hongye, L., Yuchuan, M., Hanlin, W. and Rencheng, L. 2019. An
1177 introduction to the research and application of phytolith morphometrics. *Quaternary Sciences*, 39(1),
1178 pp.12-23.
- 1179 Yaap B, Struebig MJ, Paoli G, Koh LP, Koh LP. 2010. Mitigating the biodiversity impacts of oil palm
1180 development. *CAB Reviews*. 5(19):1-1.
- 1181 Zamma, K., Nakashima, M. & Romadhani, A. 2011. < Note> Mahale Chimpanzees Start to Eat Oil
1182 Palm. *Pan Africa News* , 18(1): p6-8
- 1183 Zeven AC. 1964. On the origin of the oil palm (*Elaeis guineensis* Jacq.). *Grana*. 1;5(1):121-3.
- 1184 Zona, S. & Henderson, A. 1989. A review of animal-mediated seed dispersal of palms. *Selbyana*, pp.6-
1185 21.
- 1186 Zurro, D., García-Granero, J.J., Lancelotti, C. and Madella, M., 2016. Directions in current and future
1187 phytolith research. *Journal of Archaeological Science*, 68, pp.112-117.
1188
- 1189 Savage, T. S. & J. Wyman, 1843/44. Observations on the external characters and habits of
1190 the *Troglodytes niger*, Geoff.—and on its organization. *Boston J. Nat. Hist.*, 4: 362–386.