



## LJMU Research Online

Piel, AK

**Primate Archaeology Evolves**

<http://researchonline.ljmu.ac.uk/7190/>

### Article

**Citation** (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

**Piel, AK (2017) Primate Archaeology Evolves. Nature Ecology and Evolution, 1. ISSN 2397-334X**

LJMU has developed [LJMU Research Online](#) for users to access the research output of the University more effectively. Copyright © and Moral Rights for the papers on this site are retained by the individual authors and/or other copyright owners. Users may download and/or print one copy of any article(s) in LJMU Research Online to facilitate their private study or for non-commercial research. You may not engage in further distribution of the material or use it for any profit-making activities or any commercial gain.

The version presented here may differ from the published version or from the version of the record. Please see the repository URL above for details on accessing the published version and note that access may require a subscription.

For more information please contact [researchonline@ljmu.ac.uk](mailto:researchonline@ljmu.ac.uk)

<http://researchonline.ljmu.ac.uk/>

1 **Primate archaeology evolves**

2

3 Michael Haslam<sup>1\*</sup>, R. Adriana Hernandez-Aguilar<sup>2</sup>, Tomos Proffitt<sup>1</sup>, Adrian Arroyo<sup>3</sup>, Tiago  
4 Falótico<sup>4</sup>, Dorothy Fragaszy<sup>5</sup>, Michael Gumert<sup>6,10</sup>, John W.K. Harris<sup>7</sup>, Michael Huffman<sup>8</sup>,  
5 Ammie K. Kalan<sup>9</sup>, Suchinda Malaivijitnond<sup>10</sup>, Tetsuro Matsuzawa<sup>11</sup>, William McGrew<sup>12</sup>,  
6 Eduardo B. Ottoni<sup>4</sup>, Alejandra Pascual-Garrido<sup>1</sup>, Alex Piel<sup>13</sup>, Jill Pruett<sup>14</sup>, Caroline Schuppli<sup>15</sup>,  
7 Fiona Stewart<sup>13</sup>, Amanda Tan<sup>6,16</sup>, Elisabetta Visalberghi<sup>17</sup>, Lydia V. Luncz<sup>1</sup>

8

9 <sup>1</sup>Primate Archaeology Research Group, University of Oxford, Oxford OX1 3QY, UK

10 <sup>2</sup>Centre for Ecological and Evolutionary Synthesis, University of Oslo, Oslo NO-0316, Norway

11 <sup>3</sup>Institute of Archaeology, University College London, London, WC1H 0PY, UK

12 <sup>4</sup>Institute of Psychology, University of São Paulo, São Paulo CEP 05508-030, Brazil

13 <sup>5</sup>Department of Psychology, University of Georgia, Athens, GA 30602, USA

14 <sup>6</sup>Division of Psychology, Nanyang Technological University, Singapore 637332, Singapore

15 <sup>7</sup>Anthropology Department, Rutgers University, New Brunswick, NJ 08901, USA

16 <sup>8</sup>Primate Research Institute, Kyoto University, Inuyama 484-8506, Japan

17 <sup>9</sup>Max Planck Institute for Evolutionary Anthropology, Leipzig 04103, Germany

18 <sup>10</sup>Department of Biology, Chulalongkorn University, Bangkok 10330, Thailand

19 <sup>11</sup>Institute for Advanced Study, Kyoto University, Kyoto 606-8501, Japan

20 <sup>12</sup>School of Psychology & Neuroscience, University of St Andrews, Fife KY16 9JP, UK

21 <sup>13</sup>School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool L3  
22 3AF, UK

23 <sup>14</sup>Department of Anthropology, Iowa State University, Ames 50011, USA

24 <sup>15</sup>Department of Anthropology, University of Zürich, Zürich 8057, Switzerland

25 <sup>16</sup>Department of Anthropology, Dartmouth College, New Hampshire 03755-3529, USA

26 <sup>17</sup>Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, Rome  
27 00197, Italy

28

29 \*Corresponding author

30

31

## 32 Introduction

33 Archaeology gives humanity access to its past, helping to define who we are. Its method -  
34 the scientific study of the material remains of past behaviour – has been extraordinarily  
35 successful, resulting in the systematic recovery and interpretation of evidence for human  
36 evolution covering more than three million years<sup>1</sup>. It is puzzling, therefore, that only  
37 recently has the idea emerged that the same approach could be applied to the behaviour of  
38 non-human animals. Here, we discuss the development, current state and possible future of  
39 the first attempt to move archaeology beyond its anthropocentric borders: primate  
40 archaeology<sup>2</sup>.

41

42 Archaeologists looking to expand their discipline at the close of the twentieth century  
43 followed the path of early evolution-minded biologists<sup>3</sup>, by turning to humanity's close  
44 relatives: the chimpanzees (*Pan troglodytes*). Initially focused on the spatial patterning of  
45 chimpanzee artefacts and behaviour<sup>4,5</sup>, this work saw a breakthrough in 2002 with the  
46 excavation of a chimpanzee nut-cracking site in the Taï Forest, Ivory Coast<sup>6</sup>. The same site  
47 and nearby locations were then further excavated in 2003, producing the first radiocarbon  
48 dates for non-human tool use of over 4000 years before the present (BP)<sup>7</sup>. Building on  
49 decades of research on the Taï chimpanzee communities<sup>8</sup> as well as a single community at  
50 Bossou in Guinea<sup>9</sup>, stone tools became a central research focus, under both natural<sup>10</sup> and  
51 human-controlled<sup>11</sup> conditions. Along with work on non-stone artefacts, such as nests<sup>12,13</sup>  
52 and plant tools<sup>14,15</sup>, this research demonstrated that chimpanzees created long-lasting  
53 patterns of material culture that could be directly linked to their behaviour.

54

55 In 2009, a review of this incipient work outlined the potential for 'ethoarchaeology'<sup>6,16-18</sup> –  
56 the study of how animal behaviour produces durable, patterned material signatures – to  
57 encompass other non-human primates (hereafter, primates)<sup>2</sup>. The discovery only a few  
58 years earlier of wild stone-tool-using monkeys – bearded capuchins<sup>19</sup> (*Sapajus libidinosus*) in  
59 Brazil and Burmese long-tailed macaques<sup>20</sup> (*Macaca fascicularis aurea*) in Thailand – meant  
60 that for the first time the social and environmental contexts of lithic technology in multiple  
61 primate species could be compared with that of humans and our direct ancestors (the  
62 hominins) (Fig. 1). That review, and subsequent elaborations<sup>21-24</sup>, identified two main areas  
63 that could benefit from an archaeological approach to the primate past: (i) a deeper

64 understanding of the specific technological and cultural trajectories taken by other primate  
65 species, and (ii) the collection of comparative primate data useful to palaeoanthropologists  
66 and archaeologists working on the emergence of hominin tool use<sup>1</sup>. There were also specific  
67 goals proposed in the review, namely greater collaboration (including joint fieldwork)  
68 between primatologists, archaeologists and palaeoanthropologists, standardization of site  
69 and artefact recording procedures, and a greater focus on use-damage patterns as a means  
70 of analysing recovered tools<sup>2</sup>. As outlined below, each of these goals has seen rapid  
71 advancement in recent years, although fundamental challenges still remain.

72

73

74 **Figure 1: Locations and examples of stone-tool-use by wild non-human primates and early**  
75 **hominins.** (A) Bearded capuchin monkey (*Sapajus libidinosus*), Brazil. Photo by MH. (B) West  
76 African chimpanzee (*Pan troglodytes verus*), Guinea. Photo by TM. (C) Burmese long-tailed  
77 macaque (*Macaca fascicularis aurea*), Thailand. Photo by MH. (D) Stone tools from Lomekwi  
78 3, Kenya, dated to 3.3 million years ago. From ref. <sup>1</sup>. (E) Stone tool from Gona, Ethiopia,  
79 dated to 2.6 million years ago. From ref. <sup>25</sup>.

80

### 81 **The role of primate archaeology**

82 Primatology was established in the first half of the twentieth century initially as an  
83 interdisciplinary field by researchers trained in zoology, psychology and physical  
84 anthropology<sup>26–28</sup>. In its formative years, it lacked significant inter-disciplinary collaboration  
85 with archaeology, despite the latter being also sometimes considered a branch of  
86 anthropology<sup>29</sup>, a situation that saw little improvement up to the 1990s<sup>16</sup>. As primatology  
87 developed into the premier field for the study of primates, it therefore did so as a discipline  
88 rooted firmly in the present. Where past primates were considered, it was their bones that  
89 typically drew attention, rather than their tools<sup>30</sup>. This focus on close observation of  
90 behaviour, physiology, social relationships and diets in living animals meant that reports  
91 from both wild and captive animals could be considered, despite the drastically altered  
92 living conditions of the latter<sup>31</sup>. However, it left a situation rife with temporal uncertainty,  
93 concisely summarised by McGrew: ‘Termite fishing [in Gombe] may just as well have been  
94 invented in 1959, the year before Jane Goodall arrived, or a million years ago’<sup>16</sup>.

95

96 Adding time-depth to primate behaviour is one of the novel contributions made by  
97 researchers using primate archaeological methods. Taking a long-term perspective allows us  
98 to identify when and where tool use innovation or tool use loss may have occurred within a  
99 primate population, and to track the spread of such behaviour between groups. To  
100 chimpanzee nut-cracking, we can now add macaque shellfish-pounding in Thailand<sup>32</sup>,  
101 capuchin stone-on-stone percussive<sup>33</sup>, and capuchin cashew processing<sup>34</sup> to the list of  
102 archaeologically excavated and reconstructed primate behaviours (Fig. 2). The latter has  
103 been traced back at least 700 years in northeast Brazil, recording around 100 generations of  
104 capuchin social transmission. There is every reason to expect that earlier sites and forms of  
105 tool use will be found; recall that it took centuries of investigation into the human  
106 archaeological record to push its origins back into the Pliocene<sup>1</sup>. As with all excavations,  
107 context is key, and identification of older sediments likely to preserve primate tools<sup>35</sup> will be  
108 important in refining this process. However, archaeology is not only concerned with the  
109 distant past. For example, analysis of activity areas recently abandoned by non-habituated  
110 chimpanzees in the Tai Forest allowed reconstruction of their cultural preference for stone  
111 versus wooden nut-cracking hammers<sup>36</sup>. By recording the ratio of wood to stone tools at  
112 abandoned sites, this report was first to enumerate chimpanzee cultural differences solely  
113 from archaeological deposits, a practice that is commonplace in hominin archaeology.

114

115

116 **Figure 2: Archaeologically excavated stone tools used in percussive activities.** (A) Lomekwi  
117 3 site (Kenya), 3.3 million years old, tool user unknown but possibly *Kenyanthropus*  
118 *platyops*. From ref. <sup>1</sup>. (B) Panda 100 site (Ivory Coast), used by West African chimpanzees  
119 (*Pan troglodytes verus*). Photos by TP. (C) LS5 site (Thailand), used by Burmese long-tailed  
120 macaques (*Macaca fascicularis aurea*). From ref. <sup>32</sup>. (D) Lasca OIT2 site (Brazil), used by  
121 bearded capuchin monkeys (*Sapajus libidinosus*). From ref. <sup>33</sup>. All scales are in cm.

122

123 The fact that we can now demonstrate how multiple, phylogenetically-diverse species  
124 produce distinct lithic records across parts of Africa, Asia and South America opens up new  
125 opportunities for identifying unsuspected primate tool use in the past. It also offers a  
126 chance to explore why few populations have adopted tool use, even where it seems primed  
127 to develop from closely related forms such as stone handling in three species of macaque<sup>37</sup>.

128 In each instance, stone-tool-using primates have lived alongside hominins, leaving  
129 archaeological records that may be either separate but contemporaneous<sup>34</sup>, or even  
130 intermingled<sup>7</sup>. For now, we should assume that the same circumstance occurred at other  
131 times and places, over the millions of years that hominins and other primates have shared  
132 landscapes<sup>38</sup>. The primates that happened to be alive during the geologically recent birth of  
133 primatology as a science are very likely not the only ones that used or potentially even  
134 made stone tools. Further, we should not assume that the hominin stone tool record is  
135 somehow comprised of a single unbroken lineage of tool use from first appearance to the  
136 modern day. The primate evidence indicates that we should expect multiple, independent  
137 inventions of hominin stone tool use.

138

139 Time-depth can be assessed either directly, for example using radiocarbon dating of organic  
140 material found with stone tools<sup>7,34</sup>, or indirectly, for example through genetic data. Genetic  
141 studies can estimate the longevity of individual primate communities, and based on Y-  
142 chromosome data a number of East African chimpanzee (*P. t. schweinfurthii*) communities  
143 were found to likely have existed as stable entities for hundreds to thousands of years<sup>39</sup>.  
144 Decoding of chimpanzee subspecies genomes makes it clear that Central African  
145 chimpanzees (*P. t. troglodytes*) retain ancestral genes, with West African *P. t. verus* as a later  
146 offshoot<sup>40</sup>. Since West African chimpanzees are the only known *Pan* stone tool users  
147 (possibly along with the even more recently-diverged Nigerian-Cameroon *P. t. ellioti*<sup>41</sup>),  
148 current evidence puts the emergence of chimpanzee stone technology in the late Middle  
149 Pleistocene, perhaps as recently as 200,000-150,000 years ago<sup>42</sup>. In the same line of  
150 reasoning, when comparing chimpanzees with their close relatives the bonobos (*Pan*  
151 *paniscus*), there is no clear stone-tool-use link back to their common ancestor with  
152 humans<sup>42</sup>. The bonobo-chimpanzee-human common ancestor may have used stone tools –  
153 although we have no evidence for it as yet – but as things stand we cannot assess whether  
154 its behaviour resembled the tool use actions of modern chimpanzees<sup>43</sup>. Recognising just  
155 which parts of the chimpanzee (or any primate species) behavioural repertoire are actually  
156 valid for use in referential models is an ongoing process<sup>44,45</sup>, and progress will require  
157 primatologists and archaeologists to more regularly engage with each other, in the field and  
158 in the scientific literature.

159

160 Using the same genetic dating approach as that applied to *Pan*, the origins of robust  
161 capuchin stone tool use very likely post-dates the emergence of *S. libidinosus* and its  
162 occupation of the semi-arid Brazilian interior during the Middle Pleistocene<sup>21,46</sup>. If this turns  
163 out to be the case, then it may be that the subsequent Late Pleistocene expansion of these  
164 capuchins north into the Amazon forests, where no tool use has been observed, reflects a  
165 loss of cultural knowledge in the Amazonian groups owing to a change of environment<sup>46</sup>. A  
166 similar process of forest variation through time has been proposed to help explain the  
167 absence of probe tool use, common among almost all chimpanzee communities<sup>47</sup>, in the  
168 modern Sonso chimpanzee community in Uganda<sup>48</sup>.

169

170 When primates make use of durable raw materials, they generate landscape-scale patterns  
171 of artefact discard that are amenable to archaeological surveys. Again, with a few notable  
172 exceptions<sup>13,49–52</sup>, these patterns have been typically not investigated by primatologists.  
173 Archaeologists are familiar with the kind of mixed assemblages that this repeated behaviour  
174 creates, but the additional feature of being able to observe living animals creating these  
175 palimpsests puts primate archaeology in a unique position. Foraging activities that occur  
176 across multiple tool-use areas require knowledge of material transport in particular, and  
177 recently both capuchin<sup>53</sup> and chimpanzee studies<sup>54</sup> have demonstrated the cumulative  
178 effects of long-term stone tool transport. In the chimpanzee example, the weight  
179 distribution of hammerstones used for cracking *Panda* nuts in the Taï Forest was found to  
180 follow a similar distance-decay curve to that seen at hominin sites in East Africa<sup>55</sup>. This  
181 finding suggests that, just as chimpanzee short-term planning of tool movements<sup>56</sup> is  
182 obscured in their archaeological record, there are likely to be similar hidden components to  
183 hominin transport events. For capuchins, the repeated use of favoured natural sites not only  
184 guides foraging patterns and results in an archaeological signature, but it also acts to build  
185 up repositories of tools and anvils that scaffold the efforts of young monkeys learning to  
186 crack nuts<sup>57</sup>.

187

188 Much of primate archaeology can be differentiated from traditional primatology in its focus  
189 on ethoarchaeology<sup>18</sup>. This perspective combines detailed observations of modern animals  
190 with the 'lifeways' of the inanimate objects with which they interact, although in the case of  
191 unhabituated primates the emphasis is heavily on the latter type of evidence. For example,

192 a study of wild Thai macaques<sup>58</sup> found stone-tool-assisted consumption of up to 63 oysters  
193 by a macaque in a single feeding bout, while also recording how the distance moved by each  
194 individual tool contributed to the formation of archaeologically-recognisable sites. In  
195 another recent study, West African chimpanzees were observed accumulating stones in and  
196 around trees, leaving (unintentionally or otherwise) durable and salient landscape  
197 markers<sup>59</sup>. Of course, wild primates continue to use sites in the absence of human  
198 observers, meaning that surveys of materials accumulated as a result of natural primate  
199 activity are more directly comparable to the build-up of tools seen at hominin  
200 archaeological sites than the short-term recording of specific tool-use events or  
201 experiments<sup>11</sup>. Primate archaeologists can return repeatedly to the same site<sup>53</sup> to observe  
202 site formation as an active process.

203

#### 204 **Primate archaeology and hominin evolution**

205 One of the early aims of primate archaeology was the recovery and reporting of primate  
206 data in forms that would allow comparison with the evidence from early hominin  
207 behaviour<sup>4,5</sup>. In recent years, this aim has been advanced in three primary areas: identifying  
208 and interpreting tools versus natural stones, framing the emergence of hominin stone  
209 flaking, and ascertaining which primate species can act as models for hominin tool-use  
210 behaviour.

211

212 The question of how to identify a tool from an unused stone has vexed archaeology since its  
213 inception. In general, repeated conchoidal fracturing of a stone using controlled strikes<sup>60,61</sup>,  
214 whether or not this results in a pre-determined shape<sup>62</sup>, has been accepted as a sign of  
215 hominin agency (although see below regarding capuchin flake manufacture). For stones that  
216 have not been deliberately flaked, however, including those used by modern primates and  
217 past humans for simple food pounding tasks, the form of the stone gives little clue to its  
218 artefactual nature. Fortunately, the sophistication and specificity of use-wear investigations  
219 have seen significant advances in the past few years. These studies use either  
220 experimental<sup>63</sup> or surface morphology<sup>64–66</sup> analyses to locate the damaged portions of tools,  
221 and to reconstruct the behaviour that produced the damage. This method can identify likely  
222 pounding tools from any time period; for example, two stones from the Tulu Bor Member at  
223 Koobi Fora in Kenya<sup>64</sup> – a formation dated at over three million years<sup>67</sup> – possess use-wear



224 that matches patterns on Pleistocene and experimental pounding tools, and that differs  
225 significantly from natural damage. If verified by further study, these tools would be the  
226 oldest yet identified by use-wear damage alone, joining early flaked assemblages<sup>1</sup>.

227

228 Expanding out from tools to sites, primate archaeology gives us a new perspective on the  
229 densities of stone tools left behind by primate (including hominin) activities. Tool densities  
230 are fundamental to locating archaeological sites, and even for recognizing sites as discrete  
231 activity areas in the first place<sup>68</sup>. Research on modern nut-cracking sites at Bossou<sup>23</sup>  
232 revealed that chimpanzees left behind tools at a density of 0.002-0.05 tools/m<sup>2</sup>, while  
233 capuchin cashew processing sites at Serra da Capivara National Park (SCNP)<sup>34</sup> had orders of  
234 magnitude higher average stone tool densities of 0.45 m<sup>-2</sup>, with a maximum of 13 m<sup>-2</sup>.

235 Compared with artefact scatters from early hominin sites in East Africa<sup>69</sup>, which typically  
236 have densities of 1-10 m<sup>-2</sup> but in exceptional cases >100 m<sup>-2</sup>, the capuchins are towards the  
237 lower range of the hominins. This overlap means that traditional archaeological methods  
238 are apt for locating buried capuchin sites at SCNP, and this has proved to be the case<sup>34</sup>.

239 However, the Bossou chimpanzees discard such low numbers of tools – one stone in 20 m<sup>2</sup>  
240 at the densest<sup>23</sup> – that detecting and correctly interpreting such sites in an archaeological  
241 excavation will be more challenging. The contribution of use-wear data will be of greatest  
242 aid in such cases<sup>65</sup>.

243

244 Environmental variability likely played a leading role in the evolution of early hominin  
245 technologies<sup>70</sup>, and primate archaeology offers the opportunity to track the effects of  
246 environmental shifts on other technological primates. For example, the parts of coastal  
247 Thailand occupied by stone-tool-using macaques have seen dramatic changes in sea levels  
248 over the past twenty thousand years<sup>71,72</sup>. Given that these macaques are well adapted to  
249 foraging on inter-tidal resources, identifying when and where such resources existed will  
250 assist in identifying periods suitable for the spread of lithic technology in this taxon. Useful  
251 parallels for the macaque research in this regard may be found in archaeological debates  
252 over the importance of sea levels in the Bering Strait for human dispersal into North  
253 America<sup>73</sup>, and the importance of marine resources to the emergence of behaviourally  
254 modern humans in southern Africa<sup>74</sup>. In each of these cases, the exposure of coastal lands at  
255 times of lowered sea level, and the inundation of those lands during high stands, is critical

256 for assessing how archaeological sites were situated within the ancient landscape. Assessing  
257 the interconnectedness of past African forests is similarly important, to determine whether  
258 tool-use behaviours have multiple origin points or spread through contact between  
259 neighbouring chimpanzee communities<sup>21,48</sup>.

260

261 The initial emergence of hominin stone flaking is not considered the start of tool use in our  
262 lineage<sup>75,76</sup>, but it does remain the most visible manifestation of this phenomenon. There is  
263 no evidence that the last common ancestor of bonobos, chimpanzees and humans used  
264 stone tools<sup>42</sup>, and one of the stalwarts of hominin uniqueness has been the fact that we  
265 alone invasively flake stones<sup>77</sup> to obtain sharp edges. Chimpanzees damage the edges and  
266 corners of their stone hammers and anvils during use<sup>78</sup>, and may even split them into still-  
267 usable chunks<sup>11</sup>. These breakage events are essentially random and inadvertent, however,  
268 and no wild chimpanzee has been observed directly and repeatedly striking two stones  
269 together – an essential component of hominin flaking – in order to damage them. It is  
270 significant, therefore, that wild capuchins at SCNP have been documented performing  
271 precisely this behaviour<sup>79,80</sup>. The capuchins strike hammer stones onto other cobbles  
272 embedded within a natural conglomerate, unintentionally producing recurrent sharp-edged,  
273 conchoidally fractured flakes that are technologically indistinguishable from simple,  
274 intentionally made flakes<sup>33</sup>. In some cases, the capuchins use this technique to extract a  
275 cobble that is then used as a hammer in its own right<sup>79</sup>, although they have not been  
276 observed using the sharp-edged flakes that they produce.

277

278 The fact that capuchins perform activities that appear to resemble human flaking more than  
279 does chimpanzee stone tool use highlights one way that single-species comparative primate  
280 models may be limited in their usefulness for understanding hominin ancestors. By the  
281 same token, macaques use stone tools primarily to process animal prey<sup>81</sup>, a closer  
282 approximation to reconstructions of early hominin carcass processing<sup>77</sup> than the focus on  
283 nut-cracking seen among capuchins or chimpanzees. Overall, those characteristics  
284 universally (and convergently) shared by known stone-tool-using primates form a stronger  
285 analogical basis for reconstructing hominin stone tool use than any single species does  
286 referentially. At present, known stone-tool-use universals for primates include: (i) selective  
287 transport and accumulation of both modified and unmodified stones at activity areas; (ii)

288 use of stone tools by all members of a primate group at a given site, including females,  
289 males and juveniles; (iii) a multi-year learning process for juveniles to become fully  
290 proficient tool-users, with evidence of juvenile learning left at sites (e.g., inefficient  
291 materials and tool sizes, mis-struck stones); and (iv) use of stone anvils as pounding  
292 surfaces, even if wooden anvils are preferred at some sites. All species on occasion move  
293 food to hammers and anvils, hammers and anvils to food, and all three elements to a  
294 separate site<sup>11,34,58,82</sup>. There is no reason why these same behaviours should not have been  
295 present among hominins throughout their range and temporal distribution, and this  
296 fundamental knowledge can help guide both the search for, and interpretation of, hominin  
297 stone-tool-use sites.

298

299 In contrast, characteristics not shared among the extant lithic primates – including modern  
300 humans – require further explanation and justification if applied to extinct hominins. These  
301 species-specific characters include (i) the presence of human-level handedness<sup>83</sup>, (ii) a  
302 preference for wooded, grassy or coastal environments, (iii) the use of language to transmit  
303 tool traditions, (iv) a focus on plant vs animal prey, (v) a threshold for brain size, (vi)  
304 reliance on a particular form of locomotion (bipedal or quadrupedal), and (viii) the  
305 relationship between body size or strength and tool sizes. The size and hardness of primate  
306 stone tools are typically selected (when possible) to match the target food item<sup>10,84,85</sup>, to the  
307 extent that tool size is, on first principles, a proxy for the hardness of processed encased  
308 foods. The primary exception to this rule is found among capuchins that use heavier stone  
309 tools to process softer cashew nuts<sup>86</sup>. In that instance, it may be that the larger stones act  
310 more as a shield against the caustic liquid in these cashews than as a necessity for opening  
311 the nuts. Naturally, these character lists are not solely retrodictive, and they need to be  
312 tested against future discoveries of additional stone-tool-using species, to assess their  
313 robustness in the face of new data.

314

### 315 **Challenges for the future**

316 Despite the steps taken in the past decade or so, there is much left to do in bringing  
317 primatology, palaeoanthropology and archaeology closer together, and fundamental  
318 questions remain unanswered. For example, it is not yet clear how we should measure  
319 change in primate tool use through time, when their technologies are (in comparison to

320 modern humans) far simpler to begin with. This question is tied to the fact that our search  
321 image for past primate tools is heavily guided by our knowledge of present-day tools, to the  
322 extent that changes may be difficult to recognize in the first place. However, the same  
323 issues confront researchers dealing with simple hominin technologies, where debates over  
324 the extent and meaning of possible changes during the first million years of the Oldowan  
325 are longstanding and unresolved<sup>60,87,88</sup>. One solution is to continue extending the primate  
326 archaeological record further back in time, assessing it for change at major climatic  
327 boundaries (e.g., the Pleistocene-Holocene transition), and using present-day ties between  
328 primate tool sizes and processed foods to assess past variation. Another solution is to  
329 investigate species dispersals into new environments; for example, bearded capuchin tool  
330 use may have evolved in concert with their expansion into more arid environments,  
331 increasing their encounters with and potential reliance on hard, encased palm nuts<sup>89</sup>.

332

333 Primate archaeology is much more reliant on stone tool evidence than is traditional human  
334 archaeology, at least for the past few thousand years, because of human innovations in the  
335 use of shell, bone, ceramic, metal, glass and synthetic materials. For example, in terms of  
336 tool types the majority of chimpanzee technology is based on plant materials<sup>47,77,90</sup>, and  
337 while hominins have also long made use of wood and fragile organic artefacts<sup>91,92</sup>, the  
338 added contextual information derived from non-lithic hominin artefacts has enriched our  
339 understanding of how hominin behaviour evolved. This problem is confounded by primate  
340 habitation of tropical zones, especially forests, where organic materials are rapidly recycled  
341 back into the biosphere<sup>90</sup>. The result is that forested early primate sites may not be  
342 recognized (or recognizable), whereas the presence of artificial materials such as ceramics  
343 or even elaborately shaped stone tools immediately signal past hominin presence. In these  
344 circumstances, the main positive aspect is that extant primate non-lithic tools can suggest  
345 possible missing elements of the hominin record, particularly as the great apes in general  
346 are more prolific plant than stone tool users<sup>93-95</sup>.

347

348 A final challenge lies in distinguishing hominin from non-hominin tools. In some cases, this  
349 may be relatively straightforward even within the one site, for example when the fracture  
350 characteristics of intentionally flaked stones contrast with the blocky fractures produced by  
351 chimpanzees<sup>7,78</sup>. In other cases there is no easy solution, and for the earliest stone tools

352 there are no directly associated hominin bones that may give confidence in assigning a  
353 particular species as their creator<sup>1,96</sup>. If an ancestor of any primate was breaking stones (for  
354 whatever reason) more than two million years ago in Eastern or Southern Africa, we simply  
355 would not know. The ability of primates to make use of materials provided by humans –  
356 seen repeatedly in studies of captive animals<sup>31</sup> – increases the likelihood that early primate  
357 stone tool behaviour may involve the same raw materials, and even the same sites, as those  
358 exploited by hominins. The rationale for such behaviour may also be difficult to discern or  
359 unexpected; for example, the stone-flaking wild capuchins of SCNP do not use the sharp  
360 edges they create, instead they lick and sniff the damaged stone surfaces. These behaviours  
361 have not been posited for Pliocene hominins, yet these and other as-yet-unimagined  
362 activities may have been exhibited by them in the past. Primate traditions can be  
363 ephemeral, lasting only a few generations<sup>97,98</sup>, yet in that time a primate group could easily  
364 create thousands of damaged stones across their home range. Hundreds<sup>34</sup> to thousands<sup>7</sup> of  
365 years of primate activity will leave a correspondingly greater footprint.

366

367 The assignation of particular sites and assemblages to particular species, or even more  
368 problematically cultural groups within a species, is an unresolved issue. However, when  
369 researchers of different backgrounds work together at the same locations and on the same  
370 material, it can help diminish the effect of any discipline-specific biases, increasing the  
371 chance of producing a more accurate understanding of the studied behaviour. For example,  
372 primatologists and archaeologists with experience of wild capuchin nut cracking have  
373 applied their field methods directly to wild macaque nut processing<sup>99</sup>, and archaeologists  
374 have conducted site formation experiments with wild monkeys as a guide to excavating  
375 former sites produced by that same monkey group<sup>58,100</sup>. This cross-pollination of people and  
376 ideas was, as noted earlier, a tenet of the original establishment of primate archaeology as a  
377 discipline, and its continuation and expansion will undoubtedly provide unforeseen  
378 solutions to currently intractable issues.

379

380 At the turn of the twenty-first century, we possessed an archaeological record for only one  
381 lineage, our own. Fewer than two decades later, we now have four primate lineages with  
382 excavated archaeological evidence, adding the New World monkeys, Old World monkeys,  
383 and apes to what had been for centuries an exclusively human club. Other animals will

384 inevitably also be added in, including from outside the primates<sup>101</sup>. The question is  
 385 therefore no longer whether the archaeology of non-human animals is possible, but which  
 386 questions should be the next ones to address using these methods. Whatever answers we  
 387 come up with, the crucial ethoarchaeological component of this work needs to continue,  
 388 and even accelerate, as anthropogenic forces constantly reduce the chances for primates'  
 389 survival<sup>102</sup>. Increasing anthropogenic modification of primate habitats provides an  
 390 opportunity to observe whether and how these animals adjust their technologies in  
 391 response to environmental and social disturbances<sup>37,103</sup>, but this is a poor trade for  
 392 ultimately losing the animals themselves. It is not enough to ensure the existence of cultural  
 393 species in isolated zoos or sanctuaries, where they are divorced from the social and physical  
 394 environments that produced their unique characteristics. Instead, culturally-healthy free-  
 395 ranging populations need to be preserved, maintaining the ability of animals to transfer  
 396 naturally between groups and to access the foods and tool materials on which their  
 397 traditions depend. Only then will we ensure that the remarkable behaviour of primates  
 398 continues to evolve.

399

#### 400 **Acknowledgements**

401 Funding was received from European Research Council Grant no. 283959 (Primate  
 402 Archaeology) awarded to MH.

403

#### 404 **Author contributions**

405 MH, AHA, LL and TP conceived the paper. MH wrote the paper, with contributions from all  
 406 other authors. TP prepared the figures, with assistance from MH.

407

#### 408 **References**

- 409 1. Harmand, S. *et al.* 3.3-million-year-old stone tools from Lomekwi 3, West Turkana,  
 410 Kenya. *Nature* **521**, 310–315 (2015).
- 411 2. Haslam, M. *et al.* Primate archaeology. *Nature* **460**, 339–344 (2009).
- 412 3. Huxley, T. H. *Evidence as to Man's Place in Nature*. (Williams and Norgate, 1863).
- 413 4. Joulain, F. in *Modelling the Early Human Mind* (eds. Mellars, P. & Gibson, K.) 173–189  
 414 (McDonald Institute for Archaeological Research, 1996).
- 415 5. Sept, J. Was there no place like home? A new perspective on early hominid

- 416 archaeological sites from the mapping of chimpanzee nests. *Curr. Anthropol.* **33**, 187–  
417 207 (1992).
- 418 6. Mercader, J., Panger, M. & Boesch, C. Excavation of a chimpanzee stone tool site in  
419 the African rainforest. *Science* **296**, 1452–1455 (2002).
- 420 7. Mercader, J. *et al.* 4,300-year-old chimpanzee sites and the origins of percussive  
421 stone technology. *Proc. Natl. Acad. Sci. USA* **104**, 3043–3048 (2007).
- 422 8. Boesch, C. & Boesch-Achermann, H. *The Chimpanzees of the Tai Forest. Behavioral*  
423 *Ecology and Evolution*. (Oxford University Press, 2000).
- 424 9. Matsuzawa, T., Humle, T. & Sugiyama, Y. *The Chimpanzees of Bossou and Nimba*.  
425 (Springer, 2011).
- 426 10. Luncz, L., Mundry, R. & Boesch, C. Evidence for cultural differences between  
427 neighboring chimpanzee communities. *Curr. Biol.* **22**, 922–926 (2012).
- 428 11. Carvalho, S., Cunha, E., Sousa, C. & Matsuzawa, T. Chaînes opératoires and resource-  
429 exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *J. Hum. Evol.* **55**,  
430 148–163 (2008).
- 431 12. Stewart, F., Piel, A. & McGrew, W. C. Living archaeology: artefacts of specific nest site  
432 fidelity in wild chimpanzees. *J. Hum. Evol.* **61**, 388–395 (2011).
- 433 13. Hernandez-Aguilar, A. Chimpanzee nest distribution and site reuse in a dry habitat:  
434 implications for early hominin ranging. *J. Hum. Evol.* **57**, 350–364 (2009).
- 435 14. Hernandez-Aguilar, A., Moore, J. & Pickering, T. Savanna chimpanzees use tools to  
436 harvest the underground storage organs of plants. *Proc. Natl. Acad. Sci. USA* **104**,  
437 19210–19213 (2007).
- 438 15. Pruett, J. D. *et al.* New evidence on the tool-assisted hunting exhibited by  
439 chimpanzees (*Pan troglodytes verus*) in a savannah habitat at Fongoli, Senegal. *R. Soc.*  
440 *Open Sci.* **2**, 140507 (2015).
- 441 16. McGrew, W. C. *Chimpanzee Material Culture: Implications for Human Evolution*.  
442 (Cambridge University Press, 1992).
- 443 17. McGrew, W. C. *The Cultured Chimpanzee: Reflections on Cultural Primatology*.  
444 (Cambridge University Press, 2004).
- 445 18. McGrew, W. C. *et al.* Ethoarchaeology and elementary technology of unhabituated  
446 wild chimpanzees at Assirik, Senegal, West Africa. *PaleoAnthropology* **2003**, 1–20  
447 (2003).

- 448 19. Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. & de Oliveira, M. Wild capuchin  
449 monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *Am. J. Primatol.* **64**,  
450 359–366 (2004).
- 451 20. Malaivijitnond, S. *et al.* Stone-tool usage by Thai long-tailed macaques (*Macaca*  
452 *fascicularis*). *Am. J. Primatol.* **69**, 227–233 (2007).
- 453 21. Haslam, M. Towards a prehistory of primates. *Antiquity* **86**, 299–315 (2012).
- 454 22. McGrew, W. C. Chimpanzee technology. *Science* **328**, 579–580 (2010).
- 455 23. Carvalho, S. & McGrew, W. C. in *Stone Tools and Fossil Bones* (ed. Dominguez-  
456 Rodrigo, M.) 201–221 (Cambridge University Press, 2012).
- 457 24. McGrew, W. C. & Foley, R. A. Palaeoanthropology meets primatology. *J. Hum. Evol.*  
458 **57**, 335–336 (2009).
- 459 25. Semaw, S. *et al.* 2.6-million-year-old stone tools and associated bones from OGS-6  
460 and OGS-7, Gona, Afar, Ethiopia. *J. Hum. Evol.* **45**, 169–177 (2003).
- 461 26. Imanishi, K. Identification: a process of enculturation in the subhuman society of  
462 *Macaca fuscata*. *Primates* **1**, 1–29 (1957).
- 463 27. Yerkes, R. M. & Yerkes, A. W. *The Great Apes*. (Yale University Press, 1929).
- 464 28. Kohler, W. *The Mentality of Apes*. (Harcourt, Brace, 1925).
- 465 29. Willey, G. R. & Phillips, P. *Method and Theory in American Archaeology*. (University of  
466 Chicago Press, 1958).
- 467 30. Fleagle, J. *Primate Adaptation and Evolution*. (Academic Press, 2013).
- 468 31. Haslam, M. ‘Captivity bias’ in animal tool use and its implications for the evolution of  
469 hominin technology. *Philos. Trans. R. Soc. B* **368**, 20120421 (2013).
- 470 32. Haslam, M. *et al.* Archaeological excavation of wild macaque stone tools. *J. Hum.*  
471 *Evol.* **96**, 134–138 (2016).
- 472 33. Proffitt, T. *et al.* Wild monkeys flake stone tools. *Nature* **539**, 85–88 (2016).
- 473 34. Haslam, M. *et al.* Pre-Columbian monkey tools. *Curr. Biol.* **26**, R521–R522 (2016).
- 474 35. Santos, J. C., Barreto, A. M. F. & Suguio, K. Quaternary deposits in the Serra da  
475 Capivara National Park and surrounding area, Southeastern Piau  state, Brazil. *Geol.*  
476 *USP. S rie Cient fica* **12**, 115–132 (2012).
- 477 36. Luncz, L., Wittig, R. & Boesch, C. Primate archaeology reveals cultural transmission in  
478 wild chimpanzees (*Pan troglodytes verus*). *Philos. Trans. R. Soc. B* **370**, (2015).
- 479 37. Huffman, M. A., Leca, J.-B. & Nahallage, C. A. D. in *The Japanese Macaques* 191–219



- 480 (2010). doi:10.1007/978-4-431-53886-8\_9
- 481 38. Bobe, R. & Behrensmeyer, A. K. The expansion of grassland ecosystems in Africa in  
482 relation to mammalian evolution and the origin of the genus *Homo*. *Palaeogeogr.*  
483 *Palaeoclimatol. Palaeoecol.* **207**, 399–420 (2004).
- 484 39. Langergraber, K. E. *et al.* How old are chimpanzee communities? Time to the most  
485 recent common ancestor of the Y-chromosome in highly patrilocal societies. *J. Hum.*  
486 *Evol.* **69**, 1–7 (2014).
- 487 40. Prado-Martinez, J. *et al.* Great ape genetic diversity and population history. *Nature*  
488 **499**, 471–475 (2013).
- 489 41. Morgan, B. & Abwe, E. Chimpanzees use stone hammers in Cameroon. *Curr. Biol.* **16**,  
490 R632–R633 (2006).
- 491 42. Haslam, M. On the tool use behavior of the bonobo-chimpanzee last common  
492 ancestor, and the origins of hominine stone tool use. *Am. J. Primatol.* **76**, 910–918  
493 (2014).
- 494 43. Sayers, K., Raghanti, M. A. & Lovejoy, O. Human evolution and the chimpanzee  
495 referential doctrine. *Annu. Rev. Anthropol.* **41**, 119–138 (2012).
- 496 44. Whiten, A. *et al.* Studying extant species to model our past. *Science* **327**, 410 (2010).
- 497 45. Moore, J. in *Great Ape Societies* (eds. McGrew, W. C., Marchant, L. F. & Nishida, T.)  
498 275–292 (Cambridge University Press, 1996).
- 499 46. Lynch Alfaro, J. W. *et al.* Explosive Pleistocene range expansion leads to widespread  
500 Amazonian sympatry between robust and gracile capuchin monkeys. *J. Biogeogr.* **39**,  
501 272–288 (2012).
- 502 47. Whiten, A. *et al.* Cultures in chimpanzees. *Nature* **399**, 682–685 (1999).
- 503 48. Gruber, T. Historical hypotheses of chimpanzee tool use behaviour in relation to  
504 natural and human-induced changes in an East African rain forest. *Rev. Primatol.* **5**,  
505 (2013).
- 506 49. Hernandez-Aguilar, R. A., Moore, J. & Stanford, C. B. Chimpanzee nesting patterns in  
507 savanna habitat: environmental influences and preferences. *Am. J. Primatol.* **75**, 979–  
508 994 (2013).
- 509 50. Pascual-Garrido, A., Buba, U., Nodza, G. & Sommer, V. Obtaining raw material: plants  
510 as tool sources for Nigerian chimpanzees. *Folia Primatol.* **83**, 24–44 (2012).
- 511 51. Stewart, F. A. & Piel, A. K. Termite fishing by wild chimpanzees: new data from Ugalla,

- 512 western Tanzania. *Primates* **55**, 35–40 (2014).
- 513 52. McBeath, N. & McGrew, W. C. Tools used by wild chimpanzees to obtain termites at  
514 Mt Assirik, Senegal: the influence of habitat. *J. Hum. Evol.* **11**, 65–72 (1982).
- 515 53. Visalberghi, E. *et al.* Use of stone hammer tools and anvils by bearded capuchin  
516 monkeys over time and space: construction of an archeological record of tool use. *J.*  
517 *Archaeol. Sci.* **40**, 3222–3232 (2013).
- 518 54. Luncz, L. V., Proffitt, T., Kulik, L., Haslam, M. & Wittig, R. M. Distance-decay effect in  
519 stone tool transport by wild chimpanzees. *Proc. R. Soc. B Biol. Sci.* **283**, 20161607  
520 (2016).
- 521 55. Blumenschine, R. J., Masao, F. T., Tactikos, J. C. & Ebert, J. I. Effects of distance from  
522 stone source on landscape-scale variation in Oldowan artifact assemblages in the  
523 Paleo-Olduvai Basin, Tanzania. *J. Archaeol. Sci.* **35**, 76–86 (2008).
- 524 56. Sirianni, G., Mundry, R. & Boesch, C. When to choose which tool: multidimensional  
525 and conditional selection of nut-cracking hammers in wild chimpanzees. *Anim. Behav.*  
526 **100**, 152–165 (2015).
- 527 57. Frigaszy, D. *et al.* The fourth dimension of tool use: temporally enduring artefacts aid  
528 primates learning to use tools. *Philos. Trans. R. Soc. B* **368**, (2013).
- 529 58. Haslam, M., Pascual-Garrido, A., Malaivijitnond, S. & Gumert, M. Stone tool transport  
530 by wild Burmese long-tailed macaques (*Macaca fascicularis aurea*). *J. Archaeol. Sci.*  
531 *Reports* **7**, 408–413 (2016).
- 532 59. Kühl, H. S. *et al.* Chimpanzee accumulative stone throwing. *Sci. Rep.* **6**, 22219 (2016).
- 533 60. Delagnes, A. & Roche, H. Late Pliocene hominid knapping skills: the case of Lokalalei  
534 2C, West Turkana, Kenya. *J. Hum. Evol.* **48**, 435–472 (2005).
- 535 61. Harris, J. W. K. Cultural beginnings: Plio-Pleistocene archaeological occurrences from  
536 the Afar, Ethiopia. *African Archaeol. Rev.* **1**, 3–31 (1983).
- 537 62. Dibble, H. L. *et al.* Major fallacies surrounding stone artifacts and assemblages. *J.*  
538 *Archaeol. Method Theory* (2016). doi:10.1007/s10816-016-9297-8
- 539 63. de la Torre, I., Benito-Calvo, A., Arroyo, A., Zupancich, A. & Proffitt, T. Experimental  
540 protocols for the study of battered stone anvils from Olduvai Gorge (Tanzania). *J.*  
541 *Archaeol. Sci.* **40**, 313–332 (2013).
- 542 64. Caruana, M. V. *et al.* Quantifying traces of tool use: a novel morphometric analysis of  
543 damage patterns on percussive tools. *PLoS One* **9**, e113856 (2014).

- 544 65. Benito-Calvo, A., Carvalho, S., Arroyo, A., Matsuzawa, T. & de la Torre, I. First GIS  
545 analysis of modern stone tools used by wild chimpanzees (*Pan troglodytes verus*) in  
546 Bossou, Guinea, West Africa. *PLoS One* **10**, e0121613 (2015).
- 547 66. Haslam, M., Gumert, M., Biro, D., Carvalho, S. & Malaivijitnond, S. Use-wear patterns  
548 on wild macaque stone tools reveal their behavioural history. *PLoS One* **8**, e72872  
549 (2013).
- 550 67. McDougall, I. & Brown, F. H. Geochronology of the pre-KBS Tuff sequence, Omo  
551 Group, Turkana Basin. *J. Geol. Soc. London*. **165**, 549–562 (2008).
- 552 68. Isaac, G. L. in *Patterns of the Past* (eds. Hodder, I., Isaac, G. L. & Hammond, N.) 131–  
553 155 (Cambridge University Press, 1981).
- 554 69. Plummer, T. Flaked stones and old bones: biological and cultural evolution at the  
555 dawn of technology. *Yearb. Phys. Anthropol.* **47**, 118–164 (2004).
- 556 70. Potts, R. Environmental and behavioral evidence pertaining to the evolution of early  
557 Homo. *Curr. Anthropol.* **53**, S299–S317 (2012).
- 558 71. Voris, H. K. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems  
559 and time durations. *J. Biogeogr.* **27**, 1153–1167 (2000).
- 560 72. Scheffers, A. *et al.* Holocene sea levels along the Andaman Sea coast of Thailand. *The*  
561 *Holocene* **22**, 1169–1180 (2012).
- 562 73. Hoffecker, J. F., Elias, S. A., O'Rourke, D. H., Scott, G. R. & Bigelow, N. H. Beringia and  
563 the global dispersal of modern humans. *Evol. Anthropol.* **25**, 64–78 (2016).
- 564 74. Will, M., Kandel, A. W., Kyriacou, K. & Conard, N. J. An evolutionary perspective on  
565 coastal adaptations by modern humans during the Middle Stone Age of Africa. *Quat.*  
566 *Int.* **404**, 68–86 (2016).
- 567 75. Panger, M., Brooks, A., Richmond, B. G. & Wood, B. Older than the Oldowan?  
568 Rethinking the emergence of hominin tool use. *Evol. Anthropol.* **11**, 235–245 (2002).
- 569 76. Marchant, L. F. & McGrew, W. C. in *Stone Knapping: The Necessary Conditions for a*  
570 *Uniquely Hominin Behaviour* (eds. Roux, V. & Bril, B.) 341–350 (McDonald Institute  
571 for Archaeological Research, 2005).
- 572 77. Wynn, T., Hernandez-Aguilar, R. A., Marchant, L. F. & McGrew, W. C. 'An ape's view of  
573 the Oldowan' revisited. *Evol. Anthropol.* **20**, 181–197 (2011).
- 574 78. Arroyo, A., Hirata, S., Matsuzawa, T. & de la Torre, I. Nut cracking tools used by  
575 captive chimpanzees (*Pan troglodytes*) and their comparison with Early Stone Age

- 576 percussive artefacts from Olduvai Gorge. *PLoS One* **11**, e0166788 (2016).
- 577 79. Mannu, M. & Ottoni, E. B. The enhanced tool-kit of two groups of wild bearded  
578 capuchin monkeys in the Caatinga: tool making, associative use, and secondary tools.  
579 *Am. J. Primatol.* **71**, 242–251 (2009).
- 580 80. Falótico, T. & Ottoni, E. B. The manifold use of pounding stone tools by wild capuchin  
581 monkeys of Serra da Capivara National Park, Brazil. *Behaviour* **153**, 421–442 (2016).
- 582 81. Gumert, M. & Malaivijitnond, S. Marine prey processed with stone tools by Burmese  
583 long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. *Am. J. Phys.*  
584 *Anthropol.* **149**, 447–457 (2012).
- 585 82. Visalberghi, E. *et al.* Characteristics of hammer stones and anvils used by wild  
586 bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. *Am. J. Phys.*  
587 *Anthropol.* **132**, 426–444 (2007).
- 588 83. Marchant, L. F. & McGrew, W. C. Handedness is more than laterality: lessons from  
589 chimpanzees. *Ann. N. Y. Acad. Sci.* **1288**, 1–8 (2013).
- 590 84. Gumert, M. D. & Malaivijitnond, S. Long-tailed macaques select mass of stone tools  
591 according to food type. *Philos. Trans. R. Soc. B* **368**, 20120413 (2013).
- 592 85. Visalberghi, E. *et al.* Selection of effective stone tools by wild bearded capuchin  
593 monkeys. *Curr. Biol.* **19**, 213–217 (2009).
- 594 86. Luncz, L. V. *et al.* Wild capuchin monkeys adjust stone tools according to changing nut  
595 properties. *Sci. Rep.* **6**, 33089 (2016).
- 596 87. Semaw, S. The world's oldest stone artefacts from Gona, Ethiopia: their implications  
597 for understanding stone technology and patterns of human evolution between 2.6–  
598 1.5 million years ago. *J. Archaeol. Sci.* **27**, 1197–1214 (2000).
- 599 88. de la Torre, I., Mora, R., Domínguez-Rodrigo, M., de Luque, L. & Alcalá, L. The  
600 Oldowan industry of Peninj and its bearing on the reconstruction of the technological  
601 skills of LowerPleistocene hominids. *J. Hum. Evol.* **44**, 203–224 (2003).
- 602 89. Spagnoletti, N. *et al.* Stone tool use in wild bearded capuchin monkeys, *Cebus*  
603 *libidinosus*. Is it a strategy to overcome food scarcity? *Anim. Behav.* **83**, 1285–1294  
604 (2012).
- 605 90. Haslam, M. in *The Archaeology of African Plant Use* (eds. Nixon, S., Murray, M. A. &  
606 Fuller, D.) 25–35 (Left Coast Press, 2014).
- 607 91. Thieme, H. Lower Palaeolithic hunting spears from Germany. *Nature* **385**, 807–810

- 608 (1997).
- 609 92. Joordens, J. C. A. *et al.* *Homo erectus* at Trinil on Java used shells for tool production  
610 and engraving. *Nature* **518**, 228–231 (2014).
- 611 93. van Schaik, C. *et al.* Orangutan cultures and the evolution of material culture. *Science*  
612 **299**, 102–105 (2003).
- 613 94. Furuichi, T. *et al.* Why do wild bonobos not use tools like chimpanzees do? *Behaviour*  
614 **152**, 425–460 (2015).
- 615 95. Schuppli, C. *et al.* Development of foraging skills in two orangutan populations:  
616 needing to learn or needing to grow? *Front. Zool.* **13**, 43 (2016).
- 617 96. Semaw, S. *et al.* 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature* **385**,  
618 333–336 (1997).
- 619 97. Nishida, T., Matsusaka, T. & McGrew, W. C. Emergence, propagation or  
620 disappearance of novel behavioral patterns in the habituated chimpanzees of  
621 Mahale: a review. *Primates* **50**, 23–36 (2009).
- 622 98. Perry, S. & Manson, J. H. Traditions in monkeys. *Evol. Anthropol.* **12**, 71–81 (2003).
- 623 99. Falótico, T. *et al.* Analysis of sea almond (*Terminalia catappa*) cracking sites used by  
624 wild Burmese long-tailed macaques (*Macaca fascicularis aurea*). *Am. J. Primatol.*  
625 (2017). doi:10.1002/ajp.22629
- 626 100. Haslam, M., Cardoso, R. M., Visalberghi, E. & Fragaszy, D. Stone anvil damage by wild  
627 bearded capuchins (*Sapajus libidinosus*) during pounding tool use: a field experiment.  
628 *PLoS One* **9**, e111273 (2014).
- 629 101. Emslie, S. D., Polito, M. J., Brasso, R., Patterson, W. P. & Sun, L. Ornithogenic soils and  
630 the paleoecology of pygoscelid penguins in Antarctica. *Quat. Int.* **352**, 4–15 (2014).
- 631 102. Estrada, A. *et al.* Impending extinction crisis of the world's primates: why primates  
632 matter. *Sci. Adv.* **3**, e1600946 (2017).
- 633 103. Hockings, K. J. *et al.* Tools to tipple: ethanol ingestion by wild chimpanzees using leaf-  
634 sponges. *R. Soc. Open Sci.* **2**, 150150 (2015).
- 635
- 636