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Primate archaeology evolves

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Introduction

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

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

In 2009, a review of this incipient work outlined the potential for 'ethoarchaeology'[6,16–18] – the study of how animal behaviour produces durable, patterned material signatures – to encompass other non-human primates (hereafter, primates)[2]. The discovery only a few years earlier of wild stone-tool-using monkeys – bearded capuchins[19] (*Sapajus libidinosus*) in Brazil and Burmese long-tailed macaques[20] (*Macaca fascicularis aurea*) in Thailand – meant that for the first time the social and environmental contexts of lithic technology in multiple primate species could be compared with that of humans and our direct ancestors (the hominins) (Fig. 1). That review, and subsequent elaborations[21–24], identified two main areas that could benefit from an archaeological approach to the primate past: (i) a deeper understanding of the specific technological and cultural trajectories taken by other primate species, and (ii) the collection of comparative primate data useful to palaeoanthropologists and archaeologists working on the emergence of hominin tool use[1]. There were also specific goals proposed in the review, namely greater collaboration (including joint fieldwork) between primatologists, archaeologists and palaeoanthropologists, standardization of site and artefact recording procedures, and a greater focus on use-damage patterns as a means of analysing recovered tools[2]. As outlined below, each of these goals has seen rapid advancement in recent years, although fundamental challenges still remain.

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

The role of primate archaeology

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

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

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

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

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

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

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

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

Much of primate archaeology can be differentiated from traditional primatology in its focus on ethoarchaeology[18]. This perspective combines detailed observations of modern animals with the ‘lifeways’ of the inanimate objects with which they interact, although in the case of unhabituated primates the emphasis is heavily on the latter type of evidence. For example, a study of wild Thai macaques[58] found stone-tool-assisted consumption of up to 63 oysters by a macaque in a single feeding bout, while also recording how the distance moved by each individual tool contributed to the formation of archaeologically-recognisable sites. In another recent study, West African chimpanzees were observed accumulating stones in and around trees, leaving (unintentionally or otherwise) durable and salient landscape markers[59]. Of course, wild primates continue to use sites in the absence of human observers, meaning that surveys of materials accumulated as a result of natural primate activity are more directly comparable to the build-up of tools seen at hominin archaeological sites than the short-term recording of specific tool-use events or experiments[11]. Primate archaeologists can return repeatedly to the same site[53] to observe site formation as an active process.

Primate archaeology and hominin evolution

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

The question of how to identify a tool from an unused stone has vexed archaeology since its inception. In general, repeated conchoidal fracturing of a stone using controlled strikes[60,61], whether or not this results in a pre-determined shape[62], has been accepted as a sign of hominin agency (although see below regarding capuchin flake manufacture). For stones that have not been deliberately flaked, however, including those used by modern primates and past humans for simple food pounding tasks, the form of the stone gives little clue to its artefactual nature. Fortunately, the sophistication and specificity of use-wear investigations have seen significant advances in the past few years. These studies use either experimental[63] or surface morphology[64–66] analyses to locate the damaged portions of tools, and to reconstruct the behaviour that produced the damage. This method can identify likely pounding tools from any time period; for example, two stones from the Tulu Bor Member at Koobi Fora in Kenya[64] – a formation dated at over three million years[67] – possess use-wear that matches patterns on Pleistocene and experimental pounding tools, and that differs significantly from natural damage. If verified by further study, these tools would be the oldest yet identified by use-wear damage alone, joining early flaked assemblages[1].

Expanding out from tools to sites, primate archaeology gives us a new perspective on the densities of stone tools left behind by primate (including hominin) activities. Tool densities are fundamental to locating archaeological sites, and even for recognizing sites as discrete activity areas in the first place[68]. Research on modern nut-cracking sites at Bossou[23] revealed that chimpanzees left behind tools at a density of 0.002-0.05 tools/m^2, while capuchin cashew processing sites at Serra da Capivara National Park (SCNP)[34] had orders of magnitude higher average stone tool densities of 0.45 m^{-2}, with a maximum of 13 m^{-2}. Compared with artefact scatters from early hominin sites in East Africa[69], which typically have densities of 1-10 m^{-2} but in exceptional cases >100 m^{-2}, the capuchins are towards the lower range of the hominins. This overlap means that traditional archaeological methods are apt for locating buried capuchin sites at SCNP, and this has proved to be the case[34]. However, the Bossou chimpanzees discard such low numbers of tools – one stone in 20 m^2 at the densest[23] – that detecting and correctly interpreting such sites in an archaeological excavation will be more challenging. The contribution of use-wear data will be of greatest aid in such cases[65].

Environmental variability likely played a leading role in the evolution of early hominin technologies[70], and primate archaeology offers the opportunity to track the effects of environmental shifts on other technological primates. For example, the parts of coastal Thailand occupied by stone-tool-using macaques have seen dramatic changes in sea levels over the past twenty thousand years[71,72]. Given that these macaques are well adapted to foraging on inter-tidal resources, identifying when and where such resources existed will assist in identifying periods suitable for the spread of lithic technology in this taxon. Useful parallels for the macaque research in this regard may be found in archaeological debates over the importance of sea levels in the Bering Strait for human dispersal into North America[73], and the importance of marine resources to the emergence of behaviourally modern humans in southern Africa[74]. In each of these cases, the exposure of coastal lands at times of lowered sea level, and the inundation of those lands during high stands, is critical for assessing how archaeological sites were situated within the ancient landscape. Assessing the interconnectedness of past African forests is similarly important, to determine whether tool-use behaviours have multiple origin points or spread through contact between neighbouring chimpanzee communities[21,48].

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

The fact that capuchins perform activities that appear to resemble human flaking more than does chimpanzee stone tool use highlights one way that single-species comparative primate models may be limited in their usefulness for understanding hominin ancestors. By the same token, macaques use stone tools primarily to process animal prey[81], a closer approximation to reconstructions of early hominin carcass processing[77] than the focus on nut-cracking seen among capuchins or chimpanzees. Overall, those characteristics universally (and convergently) shared by known stone-tool-using primates form a stronger analogical basis for reconstructing hominin stone tool use than any single species does referentially. At present, known stone-tool-use universals for primates include: (i) selective transport and accumulation of both modified and unmodified stones at activity areas; (ii) use of stone tools by all members of a primate group at a given site, including females, males and juveniles; (iii) a multi-year learning process for juveniles to become fully proficient tool-users, with evidence of juvenile learning left at sites (e.g., inefficient materials and tool sizes, mis-struck stones); and (iv) use of stone anvils as pounding surfaces, even if wooden anvils are preferred at some sites. All species on occasion move food to hammers and anvils, hammers and anvils to food, and all three elements to a separate site[11,34,58,82]. There is no reason why these same behaviours should not have been present among hominins throughout their range and temporal distribution, and this fundamental knowledge can help guide both the search for, and interpretation of, hominin stone-tool-use sites.

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

Challenges for the future

Despite the steps taken in the past decade or so, there is much left to do in bringing primatology, palaeoanthropology and archaeology closer together, and fundamental questions remain unanswered. For example, it is not yet clear how we should measure change in primate tool use through time, when their technologies are (in comparison to modern humans) far simpler to begin with. This question is tied to the fact that our search image for past primate tools is heavily guided by our knowledge of present-day tools, to the extent that changes may be difficult to recognize in the first place. However, the same issues confront researchers dealing with simple hominin technologies, where debates over the extent and meaning of possible changes during the first million years of the Oldowan are longstanding and unresolved[60,87,88]. One solution is to continue extending the primate archaeological record further back in time, assessing it for change at major climatic boundaries (e.g., the Pleistocene-Holocene transition), and using present-day ties between primate tool sizes and processed foods to assess past variation. Another solution is to investigate species dispersals into new environments; for example, bearded capuchin tool use may have evolved in concert with their expansion into more arid environments, increasing their encounters with and potential reliance on hard, encased palm nuts[89].

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

A final challenge lies in distinguishing hominin from non-hominin tools. In some cases, this may be relatively straightforward even within the one site, for example when the fracture characteristics of intentionally flaked stones contrast with the blocky fractures produced by chimpanzees[7,78]. In other cases there is no easy solution, and for the earliest stone tools there are no directly associated hominin bones that may give confidence in assigning a particular species as their creator[1,96]. If an ancestor of any primate was breaking stones (for whatever reason) more than two million years ago in Eastern or Southern Africa, we simply would not know. The ability of primates to make use of materials provided by humans – seen repeatedly in studies of captive animals[31] – increases the likelihood that early primate stone tool behaviour may involve the same raw materials, and even the same sites, as those exploited by hominins. The rationale for such behaviour may also be difficult to discern or unexpected; for example, the stone-flaking wild capuchins of SCNP do not use the sharp edges they create, instead they lick and sniff the damaged stone surfaces. These behaviours have not been posited for Pliocene hominins, yet these and other as-yet-unimagined activities may have been exhibited by them in the past. Primate traditions can be ephemeral, lasting only a few generations[97,98], yet in that time a primate group could easily create thousands of damaged stones across their home range. Hundreds[34] to thousands[7] of years of primate activity will leave a correspondingly greater footprint.

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

At the turn of the twenty-first century, we possessed an archaeological record for only one lineage, our own. Fewer than two decades later, we now have four primate lineages with excavated archaeological evidence, adding the New World monkeys, Old World monkeys, and apes to what had been for centuries an exclusively human club. Other animals will inevitably also be added in, including from outside the primates[101]. The question is therefore no longer whether the archaeology of non-human animals is possible, but which questions should be the next ones to address using these methods. Whatever answers we come up with, the crucial ethoarchaeological component of this work needs to continue, and even accelerate, as anthropogenic forces constantly reduce the chances for primates' survival[102]. Increasing anthropogenic modification of primate habitats provides an opportunity to observe whether and how these animals adjust their technologies in response to environmental and social disturbances[37,103], but this is a poor trade for ultimately losing the animals themselves. It is not enough to ensure the existence of cultural species in isolated zoos or sanctuaries, where they are divorced from the social and physical environments that produced their unique characteristics. Instead, culturally-healthy free-ranging populations need to be preserved, maintaining the ability of animals to transfer naturally between groups and to access the foods and tool materials on which their traditions depend. Only then will we ensure that the remarkable behaviour of primates continues to evolve.

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Author contributions

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

References

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

archaeological sites from the mapping of chimpanzee nests. *Curr. Anthropol.* **33,** 187–207 (1992).

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

19. Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. & de Oliveira, M. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *Am. J. Primatol.* **64,** 359–366 (2004).

20. Malaivijitnond, S. *et al.* Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). *Am. J. Primatol.* **69,** 227–233 (2007).

21. Haslam, M. Towards a prehistory of primates. *Antiquity* **86,** 299–315 (2012).

22. McGrew, W. C. Chimpanzee technology. *Science* **328,** 579–580 (2010).

23. Carvalho, S. & McGrew, W. C. in *Stone Tools and Fossil Bones* (ed. Dominguez-Rodrigo, M.) 201–221 (Cambridge University Press, 2012).

24. McGrew, W. C. & Foley, R. A. Palaeoanthropology meets primatology. *J. Hum. Evol.* **57,** 335–336 (2009).

25. Semaw, S. *et al.* 2.6-million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *J. Hum. Evol.* **45,** 169–177 (2003).

26. Imanishi, K. Identification: a process of enculturation in the subhuman society of *Macaca fuscata*. *Primates* **1,** 1–29 (1957).

27. Yerkes, R. M. & Yerkes, A. W. *The Great Apes.* (Yale University Press, 1929).

28. Kohler, W. *The Mentality of Apes*. (Harcourt, Brace, 1925).

29. Willey, G. R. & Phillips, P. *Method and Theory in American Archaeology*. (University of Chicago Press, 1958).

30. Fleagle, J. *Primate Adaptation and Evolution*. (Academic Press, 2013).

31. Haslam, M. 'Captivity bias' in animal tool use and its implications for the evolution of hominin technology. *Philos. Trans. R. Soc. B* **368,** 20120421 (2013).

32. Haslam, M. *et al.* Archaeological excavation of wild macaque stone tools. *J. Hum. Evol.* **96,** 134–138 (2016).

33. Proffitt, T. *et al.* Wild monkeys flake stone tools. *Nature* **539,** 85–88 (2016).

34. Haslam, M. *et al.* Pre-Columbian monkey tools. *Curr. Biol.* **26,** R521–R522 (2016).

35. Santos, J. C., Barreto, A. M. F. & Suguio, K. Quaternary deposits in the Serra da Capivara National Park and surrounding area, Southeastern Piauí state, Brazil. *Geol. USP. Série Científica* **12,** 115–132 (2012).

36. Luncz, L., Wittig, R. & Boesch, C. Primate archaeology reveals cultural transmission in wild chimpanzees (*Pan troglodytes verus*). *Philos. Trans. R. Soc. B* **370,** (2015).

37. Huffman, M. A., Leca, J.-B. & Nahallage, C. A. D. in *The Japanese Macaques* 191–219

(2010). doi:10.1007/978-4-431-53886-8_9

38. Bobe, R. & Behrensmeyer, A. K. The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **207,** 399–420 (2004).

39. Langergraber, K. E. *et al.* How old are chimpanzee communities? Time to the most recent common ancestor of the Y-chromosome in highly patrilocal societies. *J. Hum. Evol.* **69,** 1–7 (2014).

40. Prado-Martinez, J. *et al.* Great ape genetic diversity and population history. *Nature* **499,** 471–475 (2013).

41. Morgan, B. & Abwe, E. Chimpanzees use stone hammers in Cameroon. *Curr. Biol.* **16,** R632–R633 (2006).

42. Haslam, M. On the tool use behavior of the bonobo-chimpanzee last common ancestor, and the origins of hominine stone tool use. *Am. J. Primatol.* **76,** 910–918 (2014).

43. Sayers, K., Raghanti, M. A. & Lovejoy, O. Human evolution and the chimpanzee referential doctrine. *Annu. Rev. Anthropol.* **41,** 119–138 (2012).

44. Whiten, A. *et al.* Studying extant species to model our past. *Science* **327,** 410 (2010).

45. Moore, J. in *Great Ape Societies* (eds. McGrew, W. C., Marchant, L. F. & Nishida, T.) 275–292 (Cambridge University Press, 1996).

46. Lynch Alfaro, J. W. *et al.* Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. *J. Biogeogr.* **39,** 272–288 (2012).

47. Whiten, A. *et al.* Cultures in chimpanzees. *Nature* **399,** 682–685 (1999).

48. Gruber, T. Historical hypotheses of chimpanzee tool use behaviour in relation to natural and human-induced changes in an East African rain forest. *Rev. Primatol.* **5,** (2013).

49. Hernandez-Aguilar, R. A., Moore, J. & Stanford, C. B. Chimpanzee nesting patterns in savanna habitat: environmental influences and preferences. *Am. J. Primatol.* **75,** 979–994 (2013).

50. Pascual-Garrido, A., Buba, U., Nodza, G. & Sommer, V. Obtaining raw material: plants as tool sources for Nigerian chimpanzees. *Folia Primatol.* **83,** 24–44 (2012).

51. Stewart, F. A. & Piel, A. K. Termite fishing by wild chimpanzees: new data from Ugalla,

western Tanzania. *Primates* **55,** 35–40 (2014).

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

65. Benito-Calvo, A., Carvalho, S., Arroyo, A., Matsuzawa, T. & de la Torre, I. First GIS analysis of modern stone tools used by wild chimpanzees (*Pan troglodytes verus*) in Bossou, Guinea, West Africa. *PLoS One* **10,** e0121613 (2015).

66. Haslam, M., Gumert, M., Biro, D., Carvalho, S. & Malaivijitnond, S. Use-wear patterns on wild macaque stone tools reveal their behavioural history. *PLoS One* **8,** e72872 (2013).

67. McDougall, I. & Brown, F. H. Geochronology of the pre-KBS Tuff sequence, Omo Group, Turkana Basin. *J. Geol. Soc. London.* **165,** 549–562 (2008).

68. Isaac, G. L. in *Patterns of the Past* (eds. Hodder, I., Isaac, G. L. & Hammond, N.) 131–155 (Cambridge University Press, 1981).

69. Plummer, T. Flaked stones and old bones: biological and cultural evolution at the dawn of technology. *Yearb. Phys. Anthropol.* **47,** 118–164 (2004).

70. Potts, R. Environmental and behavioral evidence pertaining to the evolution of early Homo. *Curr. Anthropol.* **53,** S299–S317 (2012).

71. Voris, H. K. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *J. Biogeogr.* **27,** 1153–1167 (2000).

72. Scheffers, A. *et al.* Holocene sea levels along the Andaman Sea coast of Thailand. *The Holocene* **22,** 1169–1180 (2012).

73. Hoffecker, J. F., Elias, S. A., O'Rourke, D. H., Scott, G. R. & Bigelow, N. H. Beringia and the global dispersal of modern humans. *Evol. Anthropol.* **25,** 64–78 (2016).

74. Will, M., Kandel, A. W., Kyriacou, K. & Conard, N. J. An evolutionary perspective on coastal adaptations by modern humans during the Middle Stone Age of Africa. *Quat. Int.* **404,** 68–86 (2016).

75. Panger, M., Brooks, A., Richmond, B. G. & Wood, B. Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evol. Anthropol.* **11,** 235–245 (2002).

76. Marchant, L. F. & McGrew, W. C. in *Stone Knapping: The Necessary Conditions for a Uniquely Hominin Behaviour* (eds. Roux, V. & Bril, B.) 341–350 (McDonald Institute for Archaeological Research, 2005).

77. Wynn, T., Hernandez-Aguilar, R. A., Marchant, L. F. & McGrew, W. C. 'An ape's view of the Oldowan' revisited. *Evol. Anthropol.* **20,** 181–197 (2011).

78. Arroyo, A., Hirata, S., Matsuzawa, T. & de la Torre, I. Nut cracking tools used by captive chimpanzees (*Pan troglodytes*) and their comparison with Early Stone Age

percussive artefacts from Olduvai Gorge. *PLoS One* **11,** e0166788 (2016).

79. Mannu, M. & Ottoni, E. B. The enhanced tool-kit of two groups of wild bearded capuchin monkeys in the Caatinga: tool making, associative use, and secondary tools. *Am. J. Primatol.* **71,** 242–251 (2009).

80. Falótico, T. & Ottoni, E. B. The manifold use of pounding stone tools by wild capuchin monkeys of Serra da Capivara National Park, Brazil. *Behaviour* **153,** 421–442 (2016).

81. Gumert, M. & Malaivijitnond, S. Marine prey processed with stone tools by Burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. *Am. J. Phys. Anthropol.* **149,** 447–457 (2012).

82. Visalberghi, E. *et al.* Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. *Am. J. Phys. Anthropol.* **132,** 426–444 (2007).

83. Marchant, L. F. & McGrew, W. C. Handedness is more than laterality: lessons from chimpanzees. *Ann. N. Y. Acad. Sci.* **1288,** 1–8 (2013).

84. Gumert, M. D. & Malaivijitnond, S. Long-tailed macaques select mass of stone tools according to food type. *Philos. Trans. R. Soc. B* **368,** 20120413 (2013).

85. Visalberghi, E. *et al.* Selection of effective stone tools by wild bearded capuchin monkeys. *Curr. Biol.* **19,** 213–217 (2009).

86. Luncz, L. V. *et al.* Wild capuchin monkeys adjust stone tools according to changing nut properties. *Sci. Rep.* **6,** 33089 (2016).

87. Semaw, S. The world's oldest stone artefacts from Gona, Ethiopia: their implications for understanding stone technology and patterns of human evolution between 2·6–1·5 million years ago. *J. Archaeol. Sci.* **27,** 1197–1214 (2000).

88. de la Torre, I., Mora, R., Domínguez-Rodrigo, M., de Luque, L. & Alcalá, L. The Oldowan industry of Peninj and its bearing on the reconstruction of the technological skills of LowerPleistocene hominids. *J. Hum. Evol.* **44,** 203–224 (2003).

89. Spagnoletti, N. *et al.* Stone tool use in wild bearded capuchin monkeys, *Cebus libidinosus*. Is it a strategy to overcome food scarcity? *Anim. Behav.* **83,** 1285–1294 (2012).

90. Haslam, M. in *The Archaeology of African Plant Use* (eds. Nixon, S., Murray, M. A. & Fuller, D.) 25–35 (Left Coast Press, 2014).

91. Thieme, H. Lower Palaeolithic hunting spears from Germany. *Nature* **385,** 807–810

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