

Primate archaeology evolves

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Since its inception, archaeology has traditionally focused exclusively on humans and our direct ancestors. However, recent years have seen archaeological techniques applied to material evidence left behind by non-human animals. Here, we review advances made by the most prominent field investigating past non-human tool use: primate archaeology. This field combines survey of wild primate activity areas with ethological observations, excavations and analyses that allow the reconstruction of past primate behaviour. Because the order Primates includes humans, new insights into the behavioural evolution of apes and monkeys also can be used to better interrogate the record of early tool use in our own, hominin, lineage. This work has recently doubled the set of primate lineages with an excavated archaeological record, adding Old World macaques and New World capuchin monkeys to chimpanzees and humans, and it has shown that tool selection and transport, and discrete site formation, are universal among wild stone-tool-using primates. It has also revealed that wild capuchins regularly break stone tools in a way that can make them difficult to distinguish from simple early hominin tools. Ultimately, this research opens up opportunities for the development of a broader animal archaeology, marking the end of archaeology's anthropocentric era.

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 3 Myr¹. 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 archaeology².

Archaeologists looking to expand their discipline at the close of the twentieth century followed the path of early evolution-minded biologists³, 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 Tai Forest, Ivory Coast⁶. The same site and nearby locations were then further excavated in 2003, producing the first radiocarbon dates for non-human tool use of over 4 kyr BP⁷. Building on decades of research on the Tai chimpanzee communities⁸ as well as a single community at Bossou in Guinea⁹, stone tools became a central research focus, under both natural¹⁰ and human-controlled¹¹ 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)³. The discovery only a few years earlier of wild stone-tool-using monkeys — bearded capuchins¹⁹ (*Sapajus libidinosus*) in Brazil and Burmese long-tailed macaques²⁰ (*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 those 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: (1) a deeper understanding of the specific technological and cultural trajectories taken by other primate species; and (2) the collection of comparative primate data useful to palaeoanthropologists and archaeologists working on the emergence of hominin tool use¹. 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 tools². As outlined below, each of these goals has seen rapid advancement in recent years, although fundamental challenges still remain.

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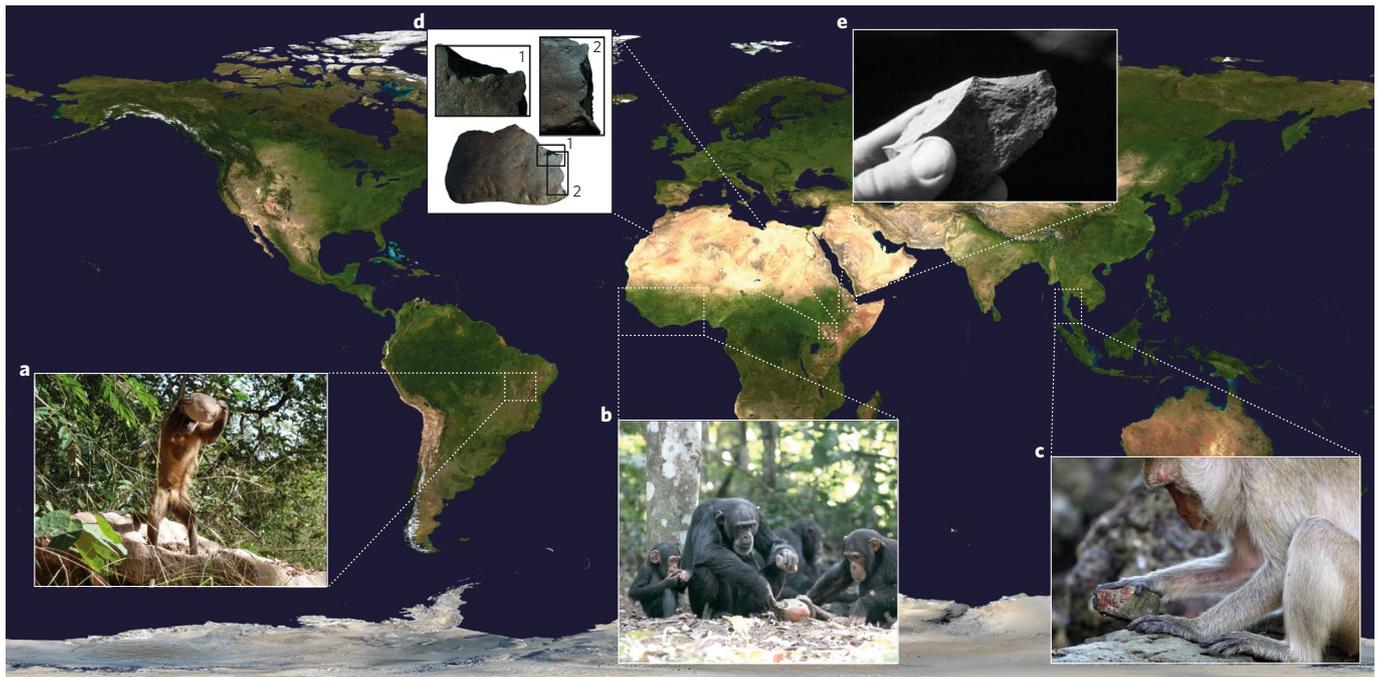


Fig. 1 | Locations and examples of stone tool use by wild non-human primates and early hominins. **a**, Bearded capuchin monkey (*S. libidinosus*), Brazil. **b**, West African chimpanzee (*P. t. verus*), Guinea. **c**, Burmese long-tailed macaque (*M. f. aurea*), Thailand. **d**, Stone tools from Lomekwi 3, Kenya, dated to 3.3 Myr ago. **e**, Stone tool from Gona, Ethiopia, dated to 2.6 Myr ago. Figure reproduced from: **d**, ref. ¹, Macmillan Publishers Ltd; **e**, ref. ¹⁰⁴, Elsevier.

The role of primate archaeology

Primate archaeology was established in the first half of the twentieth century initially as an interdisciplinary field by researchers trained in zoology, psychology and physical anthropology^{25–27}. In its formative years, it lacked significant interdisciplinary collaboration with archaeology, despite the latter being also sometimes considered a branch of anthropology²⁸, a situation that saw little improvement up to the 1990s¹⁶. 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 tools²⁹. 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 latter³⁰. However, it left a situation rife with temporal uncertainty, concisely summarized 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 new contributions made by researchers using primate archaeological methods. Taking a long-term perspective allows us to identify when and where tool-use innovation or 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 Thailand³¹, capuchin stone-on-stone percussion³², and capuchin cashew processing³³ to the list of archaeologically excavated and reconstructed primate behaviours (Fig. 2). The last in this list 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 epoch¹. As with all excavations, context is key, and identification of older sediments that are likely to preserve primate tools³⁴ 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 hammers³⁵. By recording the ratio of wood to stone tools at abandoned sites, this report was the first to enumerate chimpanzee cultural differences solely from archaeological deposits, a practice that is commonplace in hominin archaeology.

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 macaque³⁶. In each instance, stone-tool-using primates have lived alongside hominins, leaving archaeological records that may be either separate but contemporaneous³³, or even intermingled⁷. 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 landscapes³⁷. The primates that happened to be alive during the geologically recent birth of primatology as a science are very probably not the only ones that used or potentially even made stone tools. Further, we should not assume that the hominin stone tool record somehow comprises 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^{7,33}, 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 (*Pan troglodytes schweinfurthii*) communities were found to probably have existed as stable entities for hundreds to thousands

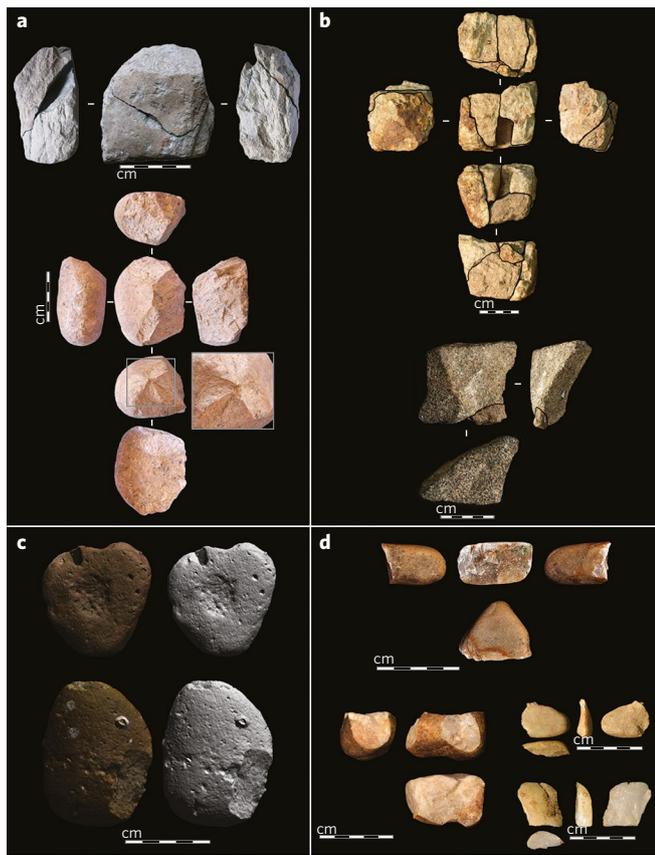


Fig. 2 | Archaeologically excavated stone tools used in percussive activities. **a**, Lomekwi 3 (Kenya); 3.3 Myr old, tool user unknown but possibly *Kenyanthropus platyops*. **b**, Panda 100 (Ivory Coast); used by West African chimpanzees (*P. t. verus*). **c**, Laem Son 5 (Thailand); used by Burmese long-tailed macaques (*M. f. aurea*). **d**, Lasca OIT2 (Brazil); used by bearded capuchin monkeys (*S. libidinosus*). Figure reproduced from: **a**, ref. ¹, Macmillan Publishers Ltd; **c**, ref. ³¹, Elsevier; **d**, ref. ³², Macmillan Publishers Ltd.

of years³⁸. 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 offshoot³⁹. As West African chimpanzees are the only known *Pan* stone tool users (possibly along with the even more recently diverged Nigerian-Cameroon *P. t. ellioti*⁴⁰), current evidence puts the emergence of chimpanzee stone technology in the late middle Pleistocene, perhaps as recently as 200–150 kyr ago⁴¹. 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 humans⁴¹. The bonobo-chimpanzee-human common ancestor may have used stone tools — although we have no evidence for it yet — but as things stand we cannot assess whether its behaviour resembled the tool-use actions of modern chimpanzees⁴². Recognizing just which parts of the chimpanzee (or any primate species) behavioural repertoire are actually valid for use in referential models is an ongoing process^{43,44}, and progress will require primatologists and archaeologists to engage with each other more regularly, 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 probably post-dates the emergence of *S. libidinosus* and its occupation of the semi-arid Brazilian interior during the middle Pleistocene^{21,45}. 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 environment⁴⁵. 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 communities⁴⁶, in the modern Sonso chimpanzee community in Uganda⁴⁷.

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^{13,48–51}, these patterns have typically not been 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 capuchin⁵² and chimpanzee studies⁵³ 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 Africa⁵⁴. This finding suggests that, just as chimpanzee short-term planning of tool movements⁵⁵ 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 also acts to build up repositories of tools and anvils that scaffold the efforts of young monkeys learning to crack nuts⁵⁶. A similar process can guide stone handling in Japanese macaques (*Macaca fuscata*)⁵⁷.

Much of primate archaeology can be differentiated from traditional primatology in its focus on ethoarchaeology¹⁸. 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 macaques⁵⁸ 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 recognizable sites. In another recent study, West African chimpanzees were observed accumulating stones in and around trees, leaving (unintentionally or otherwise) durable and salient landscape markers⁵⁹. 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 experiments¹¹. Primate archaeologists can return repeatedly to the same site⁵² 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 shape⁶², 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 experimental⁶³ 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 Kenya⁶⁴ — a formation dated at over 3 Myr⁶⁷ — 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 assemblages¹.

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 place⁶⁸. Research on modern nut-cracking sites at Bossou²³ 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)³³ 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 Africa⁶⁹, 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 case³³. However, the Bossou chimpanzees discard such low numbers of tools — one stone in 20 m² at the densest²³ — 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 cases⁶⁵.

Environmental variability probably played a leading role in the evolution of early hominin technologies⁷⁰, 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 20 kyr^{71,72}. Given that these macaques are well adapted to foraging on intertidal 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 America⁷³, and the importance of marine resources to the emergence of behaviourally modern humans in southern Africa⁷⁴. 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^{21,47}.

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 tools⁴¹, and one of the stalwarts of hominin uniqueness has been the fact that we alone invasively flake stones⁷⁷ to obtain sharp edges. Chimpanzees damage the edges and corners of their stone hammers and anvils during use⁷⁸, and may even split them into still-usable chunks¹¹. 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 — 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 flakes³¹. In some cases, the capuchins use this technique to extract a cobble that is then used as a hammer in its own right⁷⁹, although they have not been observed using the sharp-edged flakes that they produce.

The fact that capuchins perform activities that seem 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 prey⁸¹, a closer approximation to reconstructions of early hominin carcass processing⁷⁷ 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: (1) selective transport and accumulation of both modified and unmodified stones at activity areas; (2) use of stone tools by all members of a primate group at a given site, including females, males and juveniles; (3) a multi-year learning process for juveniles to become fully proficient tool users, with evidence of juvenile learning left at sites (for example, inefficient materials and tool sizes, mis-struck stones); and (4) 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^{11,33,58,82}. 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: (1) the presence of human-level handedness⁸³; (2) a preference for wooded, grassy or coastal environments; (3) the use of language to transmit tool traditions; (4) a focus on plant versus animal prey; (5) a threshold for brain size; (6) reliance on a particular form of locomotion (bipedal or quadrupedal); and (7) 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 nuts⁸⁶. 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 with 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 (for example, 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 nuts⁸⁹.

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^{46,77,90}, 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 biosphere⁹⁰. 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 non-human primate was breaking stones (for whatever reason) more than 2 Myr 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 animals³⁰ — 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. Hundreds³³ to thousands⁷ of years of primate activity will leave a correspondingly greater footprint.

The assignment 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 processing⁹⁹, 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 primates¹⁰¹. 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' survival¹⁰². 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^{36,103}, 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.

Received: 14 February 2017; Accepted: 19 July 2017;
Published online: 21 September 2017

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Acknowledgements

Funding was received from European Research Council Starting Grant no. 283959 (Primate Archaeology) awarded to M.H.

Author contributions

M.H., R.A.H.-A., L.V.L. and T.P. conceived the paper. M.H. wrote the paper, with contributions from all other authors. T.P. prepared the figures, with assistance from M.H.

Competing interests

The authors declare no competing financial interests.

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