

## REVIEW ARTICLE

## On the Tool Use Behavior of the Bonobo-Chimpanzee Last Common Ancestor, and the Origins of Hominine Stone Tool Use

MICHAEL HASLAM\*

*Research Laboratory for Archaeology and the History of Art, University of Oxford, Oxford, United Kingdom*

The last common ancestor (LCA) shared by chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) was an Early Pleistocene African ape, which, based on the behavior of modern chimpanzees, may be assumed to be a tool-using animal. However, the character of tool use in the *Pan* lineage prior to the 20th century is largely unknown. Here, I use available data on wild bonobo tool use and emerging molecular estimates of demography during *Pan* evolution to hypothesise the plausible tool use behavior of the bonobo-chimpanzee LCA (or “*Pancestor*”) at the start of the Pleistocene, over 2 million years ago. This method indicates that the common ancestor of living *Pan* apes likely used plant tools for probing, sponging, and display, but it did not use stone tools. Instead, stone tool use appears to have been independently invented by Western African chimpanzees (*P. t. verus*) during the Middle Pleistocene in the region of modern Liberia-Ivory Coast-Guinea, possibly as recently as 200,000–150,000 years ago. If this is the case, then the LCA of humans and chimpanzees likely also did not use stone tools, and this trait probably first emerged among hominins in Pliocene East Africa. This review also suggests that the consistently higher population sizes of Central African chimpanzees (*P. t. troglodytes*) over the past million years may have contributed to the increased complexity of wild tool use seen in this sub-species today. *Am. J. Primatol.* © 2014 Wiley Periodicals, Inc.

**Key words:** *Pan paniscus*; *Pan troglodytes*; genetics; demography; primate archaeology

## INTRODUCTION

The last common ancestor (LCA) of our closest animal relatives—bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*)—was an African ape living in the Early Pleistocene [Langergraber et al., 2012; Mailund et al., 2012; Prufer et al., 2012]. We have no fossil evidence for this “*Pancestor*” ape, and its potential behavioral traits are rarely discussed [Doran et al., 2002], in contrast to frequent behavioral reconstructions of the Miocene LCA shared by the *Pancestor* and modern humans [Boesch et al., 2009; Ghiglieri, 1987; McGrew, 1992, 2010b; Moore, 1996; Panger et al., 2002; Sayers et al., 2012; Stanford, 2012; Whiten et al., 2009; Wrangham, 1987; Wrangham & Pilbeam, 2001]. Comparisons have also been directly made between chimpanzees and more recent, Early Stone Age hominins [Joulian, 1996; Whiten et al., 2009; Wynn & McGrew, 1989; Wynn et al., 2011]. However, a better understanding of *Pancestor* behavior is valuable for avoiding a bias toward chimpanzees in reconstructions of the human-*Pan* LCA. In particular, the tool-using proficiency of wild chimpanzees has resulted in their playing an almost exclusive role over other apes in reconstructing human-*Pan* LCA tool use [McGrew, 2010b; Whiten, 2011].

Wild chimpanzees demonstrate the widest variety of tool use activities of any non-human

animal [Shumaker et al., 2011], a finding that may in part relate to the intensity of field study devoted to this species, but also to the cultural variation displayed by chimpanzee groups [McGrew, 2010a; Whiten et al., 2001]. In contrast, wild bonobos have been found to use tools relatively rarely [Hohmann & Fruth, 2003], especially for the kinds of extractive foraging tasks at which chimpanzees excel, and despite the presence of suitable tools and prey species [McGrew et al., 2007]. This situation can cause anomalies in phylogenetic reconstructions: for example, Duda & Zrzavy [2013, Table IV] recently used a broad suite of characters to assess ape life history and behavioral evolution, concluding that there is

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\*Correspondence to: Michael Haslam, Research Laboratory for Archaeology and the History of Art, University of Oxford, Dyson Perrins Building, South Parks Road, Oxford, United Kingdom. E-mail: michael.haslam@rlaha.ox.ac.uk

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statistically significant support for simple tool use in the LCAs of all great apes, all African great apes, and the human-*Pan* LCA, but not the *Pan* ancestor ape, in which tool use is considered “likely” instead. This situation arises because of the apparent simplicity and rarity of bonobo tool use, but in assessing the overall degree of tool use it does not take into account the actual activities carried out with tools by living *Pan* apes. In this review, I use the limited available data on wild bonobo tool use, in combination with recent molecular estimates of demography during *Pan* evolution, to present an initial hypothesis on the tool-use behavior of the *Pan* ancestor ape. It is hoped that this hypothesis and its attendant predictions will, in turn, assist in refining our behavioral picture of the human-*Pan* LCA.

The behavior of extinct species can be modeled on a combination of anatomical, ecological, archaeological, and comparative ethological data. In this regard, available data on the hominin and panin lineages (respectively those ancestral taxa closer to us than they are to living *Pan*, and vice versa) are starkly different in both quantity and quality. Discussions of human behavioral evolution benefit from a multi-million-year record of tool use by our hominin ancestors [Ambrose, 2001], and a fossil record that includes a growing variety of hominin species [Wood & Lonergan, 2008]. On the other side of the equation, however, for the panins we have no artefacts older than a few thousand years [Mercader et al., 2007] and an almost complete absence of fossils [McBrearty & Jablonski, 2005]. Discussions of evidence for *Pan* ancestor tool use must therefore rely strongly upon ethological information from extant populations [Haslam, 2012], using parsimony to reconstruct ancestral behavioral states [Duda & Zrzavy, 2013; Harvey & Pagel, 1991]. Genetic mutation rates inferred from modern populations are also proving increasingly valuable for providing broad temporal boundaries to past species divergence processes [Prado-Martinez et al., 2013; Sun et al., 2012], although these ages should always be treated as estimates subject to revision.

This study considers only published observations on wild primate subjects, as captive ape activities are affected by factors such as provisioning, increased terrestriality, and human contact and may not directly reflect natural tool use behavior [Haslam, 2013; Meulman et al., 2012]. For example, bonobos have shown an ability to use tools in several captive (e.g., laboratory, zoo) settings [Boose et al., 2013; Gruber et al., 2010; Herrmann et al., 2008; Jordan, 1982; Toth et al., 1993]. Note that behavioral reconstruction is conducted here by comparing bonobo and chimpanzee characters without the aid of computational statistics, a method that has limitations—explicit outgroups are not considered, for example—but which has been previously successfully employed in developing hypotheses about the

human-chimpanzee LCA [Begun, 2004; McGrew, 2010b; Moore, 1996; Whiten, 2011].

## DATING AND DEMOGRAPHIC HISTORY

The temporal framework of panin evolution has been improved markedly by genetic and genomic results published in the past few years, adding to both field-based and molecular reconstructions of chimpanzee demographic history that provide a broad framework within which any innovation, maintenance, or loss of tool use behavior may be considered [Gruber et al., 2010; Wrangham, 2006]. Based on emerging molecular data, the panin split leading to the separate bonobo and chimpanzee lineages may have occurred somewhere between 2.5 and 1.5 million years ago (mya) [Becquet et al., 2007; Bjork et al., 2011; Gonder et al., 2011; Langergraber et al., 2012; Sun et al., 2012; Wegmann & Excoffier, 2010]. Note that these ages are considerably older than some previous estimates of even a few years ago, which used a faster genetic mutation rate that placed the *Pan* ancestor split at around 2–1 mya [Caswell et al., 2008; Stone et al., 2010], or even just under a million years ago [Becquet & Przeworski, 2007; Hey, 2010; Won & Hey, 2005]. The divergence of bonobos from chimpanzees followed the establishment of the Congo River [Myers Thompson, 2003; Prufer et al., 2012; Stankiewicz & de Wit, 2006], with modern bonobos isolated to the south of the river. The bonobo-chimpanzee split appears to have been relatively rapid and allopatric, unlike the more drawn out divergence seen, for example, among eastern and western gorillas, Bornean and Sumatran orangutans, and the human-*Pan* split [Mailund et al., 2012; Prufer et al., 2012].

Chimpanzees are currently known to have diverged into four subspecies following the split from bonobos, although the genetically derived ages given here for these divergent processes may be in need of reassessment upwards using lower mutation rates, and should be considered minimums only. First, around 1–0.5 mya the Western chimpanzees (*P. t. verus*) split from the rest of the population, with the Nigeria-Cameroon chimpanzees (*P. t. ellioti*) then splitting from *P. t. verus* during the Middle Pleistocene. Finally, the Eastern chimpanzees (*P. t. schweinfurthii*) diverged from the Central subspecies (*P. t. troglodytes*) around 0.4–0.2 mya [Bjork et al., 2011; Caswell et al., 2008; Gonder et al., 2011; Prado-Martinez et al., 2013; Stone et al., 2010]. Putative fossil chimpanzee teeth found far to the east of the modern chimpanzee range in Kenya, and dated to 0.5–0.3 mya [McBrearty & Jablonski, 2005], may provide evidence that the Eastern chimpanzee split was earlier than these molecular estimates suggest, or they may represent a now-extinct *Pan* lineage. Further, one recent autosomal microsatellite study suggests that a population of chimpanzees found in

southern Cameroon may have separately diverged from the Central chimpanzees during the last interglacial period, around 110,000 years ago [Gonder et al., 2011], but testing this hypothesis will require further sampling of the populations in this region.

All chimpanzees therefore appear to be ultimately derived via founder events from the Central African population, which unlike the Western and Eastern subspecies did not suffer a substantial Pleistocene demographic bottleneck [Wegmann & Excoffier, 2010], and maintained the highest genetic diversity of all chimpanzee subspecies [Becquet et al., 2007; Caswell et al., 2008; Prado-Martinez et al., 2013; Won & Hey, 2005]. Using an Approximate Bayesian Computation approach based on coalescent simulations, Prado-Martinez et al. [2013] found that the *Pancestor* population size was decreasing prior to the chimpanzee-bonobo split, with bonobos experiencing a further bottleneck in effective population size following that divergence. Based on the genetic data the chimpanzee common ancestor likely lived somewhere in the region currently occupied by Central chimpanzee groups, and gene flow studies suggest that once separated, the divided species and subspecies had limited (though likely non-zero) interaction [Becquet & Przeworski, 2007; Caswell et al., 2008; Wegmann & Excoffier, 2010].

The timing of population splits and bottlenecks is relevant not only for understanding the development of the current geographic distribution of *Pan* taxa, but also for the potential effects of chimpanzee demographic history on tool use. Researchers examining the causes of human technological complexity and diversity in the archaeological record have highlighted the role of population size and interactions as critical variables in ensuring the continuation and spread of innovations, and preventing the loss of existing technical traits [Dean et al., 2014; Derex et al., 2013; Henrich, 2004; Kline & Boyd, 2010; Muthukrishna et al., 2014; Powell et al., 2009; Shennan, 2001]. Bottlenecks associated with founder effects have been postulated to simplify and reduce tool diversity in dispersing human groups [Clarkson, 2014; Lycett & von Cramon-Taubadel, 2008; Mellars, 2006], and tolerant interactions between individuals correlate strongly with the number of customary and habitual behavioral variants displayed by wild orangutans and chimpanzees [van Schaik et al., 2003]. In chimpanzees, it may be that the number of females in a community is more important than overall community size, given their position as a transmission vector to their young and between groups [Lind & Lindenfors, 2010].

On a more general level, social interactions and their attendant support of social learning processes have been argued to underpin much of the maintenance of customary tool use in primates [van Schaik & Pradhan, 2003], while homoplasy in multi-regional

chimpanzee behavioral data may point to stochastic trait loss associated with demographic declines [Lycett et al., 2009], and recent analysis of cultural nestedness suggests the same for orangutans [Kamilar & Atkinson, 2014]. Collectively, these studies suggest that all the chimpanzee subspecies except *P. t. troglodytes*, as well as the bonobos, may have seen a reduction in the complexity and diversity of their technological behavior during population divergence events in the Early to Middle Pleistocene.

## TOOL USE OF THE BONOBO-CHIMPANZEE LAST COMMON ANCESTOR

Tool use in wild chimpanzees has been comprehensively catalogued and discussed by McGrew [1992, 2004], with recent important data also coming from the lesser-known Central African [Boesch et al., 2009; Sanz & Morgan, 2007] and Nigeria-Cameroon [Fowler et al., 2011; Pascual-Garrido et al., 2012] groups. Chimpanzee tool use behaviors may be divided into universal and localized types, with the former not recorded as absent in any well-studied group, and the latter differing from site to site or group to group, thereby forming the basis for discussions of cultural differentiation. In the most comprehensive survey to date [Whiten et al., 1999, 2001], “universal” tools were found to include, (i) branch-dragging during social display, (ii) holding a detached plant stem while inviting another individual to play, and (iii) the use of a collected mass of leaves to absorb and drink water. These are strong candidates for behavior present in the common ancestor of all chimpanzees around 1 mya, following the divergence of bonobos from the *Pancestor* population. All wild chimpanzee tool use other than these three cases may have either arisen in specific groups following subspecies divergence, or have been lost from certain populations as part of founder effects or cultural drift. For example, leaf-clipping with the mouth is customary or habitual in all but one of the long-studied chimpanzee sites [Whiten et al., 1999], with a parsimonious conclusion is that this was also a universal trait at one point, prior to its loss in the Late Pleistocene from the Eastern Gombe group.

The loss of tool use traits is difficult to demonstrate without archaeological evidence, but we can consider chimpanzee use of investigatory probes as an example. This behavior, an aid to exploration and structurally similar to a number of extractive probing behaviors including termite fishing and ant-dipping, was also initially identified as a potential “universal” trait [Whiten et al., 2001]. It has since been reported as absent among the Eastern Budongo chimpanzees [Gruber et al., 2012; Reynolds, 2005], as stick tool use for extraction of either prey species or fluids has not been observed at the long-term Sonso site in the Budongo Forest. This finding is supported by

preliminary results from two other sites in the same forest, even when field experiments provided incentives for this behavior [Gruber et al., 2012]. Chimpanzee use of stick tools for extractive foraging at the nearby Bulindi site [McLennan, 2011], and at other Ugandan sites, argues in favor of the loss of probing activities specifically in the Budongo Forest, perhaps occurring as recently as the early Holocene following fragmentation of the region's tropical forests [Gruber et al., 2012].

Moving away from universal behaviors, however, many types of chimpanzee tool-use are patchier in their distribution. Where these restrictions fall entirely within one subspecies, it is reasonable to suggest that the trait arose within that subspecies alone, with the time since emergence of the trait post-dating the split from the parent population. The most-discussed such trait is the use of stone tools to open nuts, which has only been observed within a group of sites clustered near the intersection of Liberia, Ivory Coast and Guinea, with an additional site in Sierra Leone [Carvalho & McGrew, 2012]. All these sites are occupied by Western chimpanzees. An outlier is the single report of nut cracking from Cameroon [Morgan & Abwe, 2006], which may be a retained or innovated behavior and which must be treated as tentative evidence at present [Wrangham, 2006]. The simplest explanation for the current distribution of chimpanzee stone tool use is that it arose following the emergence of *P. t. verus* as a distinct subspecies [Haslam, 2012], possibly prior to the split from *P. t. ellioti*.

The possible causes of this invention require further investigation. If demographic history plays a role in chimpanzee innovation and cultural retention, and given the extreme rarity with which stone tool use emerges among wild animals [Shumaker et al., 2011], then the emergence of Western chimpanzee stone tool use may relate to the maximum *P. t. verus* population peak suggested by genetic data, around 150,000 years ago [Prado-Martinez et al., 2013]. However, the likelihood of genetic effects lagging demographic processes [Storz et al., 2002] suggests that the actual population peak may have occurred prior to its genetically detectable effect. An earlier peak, perhaps around 200,000 years ago toward the end of the warmer Marine Isotope Stage 7, is also more realistic in light of vegetation reconstructions that show highly reduced and fragmented West African rainforests 150,000 years ago, during the colder Marine Isotope Stage 6 [Dupont et al., 2000]. Critically, stone tool use is highly unlikely to have been present in the ancestral chimpanzee taxon around 1 mya, and therefore not present at the time of the earlier *Pancestor* ape.

While demographic history and frequency of social interaction help explain the maintenance of tool use traditions, we can also consider three main hypotheses that are currently proposed for tool use

emergence, especially among primates and birds. These are necessity, opportunity, and relative profitability, with tool use in different groups respectively driven by a need to overcome food scarcity, to exploit available resources, or to gain an adaptive advantage over non-tool-users [Biro et al., 2013]. For example, the Western chimpanzee population in the Nimba Mountains, Guinea, has been suggested to follow an opportunity-based rather than necessity-based pattern because their insectivorous tool use behavior does not track food scarcity [Koops et al., 2013]. A similar conclusion, with additional support for relative profitability, was drawn for the Central Goulougo chimpanzees [Sanz & Morgan, 2013]. Neither of these chimpanzee populations uses stone tools, unlike the Nimba group's closest neighbors at Bossou, where the necessity of exploiting palm nuts during periods of low fruit production has been emphasized [Yamakoshi, 1998]. Necessity has also been suggested to explain variations in stick tool use among Ugandan Eastern chimpanzees [Gruber et al., 2012]. Outside *Pan*, the opportunity hypothesis has been favored for Brazilian capuchins [Spagnoletti et al., 2012] and Sumatran orangutans [Fox et al., 2004], and the profitability hypothesis for tool-using New Caledonian crows [Rutz & St Clair, 2012].

As with many such debates, we can take these instances of support for competing ideas as evidence that each has a role to play in an ultimate explanation. However, the rarity of chimpanzee stone tool use suggests that we should add an element of historical (or cultural or random) contingency, and propose that this behavior likely initially required: (1) the persistent co-occurrence of encased foods and suitable stones; (2) the availability of those foods at times of other food scarcity, and preferably year-round, to increase chances of the behavior being repeatedly performed and observed; (3) an overall energetic, nutritional or fitness gain, or at least lack of detriment, from stone tool use versus other feeding behaviors that were forgone; (4) a social network sufficient to support the multi-year learning process that sustains this activity; and (5) the acceptance of stone tool use as a social norm, perhaps independently of the other listed factors. Only some Western chimpanzee groups currently fit these criteria, although the first four factors are available to other chimpanzee groups [McGrew et al., 1997], suggesting that the fifth factor, or an equivalent mechanism such as stone tool use as a cultural "fad" or bias [Gruber et al., 2011; Luncz & Boesch, 2014], must be involved. Genetic explanations are insufficient, as shown by non-stone-tool-using Western chimpanzees, such as those of the Nimba Mountains. Of course, for a comprehensive explanation of observed chimpanzee stone tool use, a further factor may also be included: the presence of human observers during the timeframe of the

behavior's existence, prior to its loss through cultural drift, environmental change or extinction of its practitioners.

An assessment of wild chimpanzee population structure through time suggests that the most complex and diverse tool use behavior should be found among *P. t. troglodytes* groups, which maintained relatively high effective population sizes throughout the Pleistocene [Caswell et al., 2008; Prado-Martinez et al., 2013; Wegmann & Excoffier, 2010]. Until recently, a lack of long-term field sites for this species has hampered efforts to compare them to other wild chimpanzee groups: only one site, Lope, was included in the surveyed sites discussed above, and many data were unavailable for comparison at that time. However, findings from the Goualougo and Loango sites in the Republic of Congo and Gabon are now beginning to address that issue [Boesch et al., 2009; Sanz & Morgan, 2007]. Interestingly, they show that these chimpanzees do regularly employ complex tool use strategies, where complexity is defined as the use of multiple tools in sequence for one task, and the use of a single tool for multiple functions. For example, sequential tool sets of up to five tools were used by chimpanzees at both sites to gather honey—including pounding, enlarging or levering and dipping or collecting tools—and at Goualougo sets were also employed to forage on army ants, and to extract termites from both underground and above-ground nests [Boesch et al., 2009; Sanz & Morgan, 2009; Sanz et al., 2004]. Goualougo chimpanzees also used a single tool to dip, pound and lever during honey gathering [Sanz & Morgan, 2009]. It remains to be seen if other chimpanzee subspecies will ultimately be found to have similar levels of tool diversity, but for the moment at least, a demographic explanation prompts the prediction that the tool use behavior seen among *P.t. troglodytes* is related to their long-term population stability. Intra-subspecies comparisons may help in testing this prediction, for example between the Budongo chimpanzees and the Eastern Bili-Uele chimpanzees in the Democratic Republic of the Congo, the latter of which display multiple kinds of plant tool behavior and may represent one of the world's largest chimpanzee cultures [Hicks, 2010].

Against the backdrop of multiple and complex chimpanzee tool-use variants, wild bonobo tool-use certainly appears sparse. Wild *Pan paniscus* field sites are few and many more data are needed before robust comparisons with the chimpanzee ethological record can be made. Nevertheless, initial studies of wild bonobo groups have found that several tool use behaviors are present, even if they have not been found to be habitual or customary [Hohmann & Fruth, 2003; Ingmanson, 1996; Kano, 1982]. Of relevance to this paper, reported wild bonobo tool use includes branch dragging, water sponging, play initiation, and leaf-clipping. As these match those

traits hypothesized for the chimpanzee ancestor, each of these is therefore posited here to be putative characteristic *Pancestor* behaviors, likely originating at least 2 million years ago. Additional tool use traits found in bonobos and some of the chimpanzee groups surveyed include use of detached vegetation as a seat, and use of a leafy twig to fan away flies—as these are present only in isolated Western and Eastern chimpanzee groups it is likely that their display by bonobos is the result of behavioral convergence in tasks that increase personal comfort, rather than continuation from the *Pancestor* ape. A further trait that was likely independently invented by bonobos is the use of rain covers or hats, in which vegetation is held or arranged over the body during rainfall. A similar activity is seen in orangutans [Fox et al., 1999] and the Goualougo population of chimpanzees [Sanz & Morgan, 2007], suggesting it may also be a “self-maintenance” convergent behavior in these apes.

Wild bonobos have not been observed using investigative or extractive probes, or any other extractive technology. As this behavior is posited here to have been present in the ancestral chimpanzee population, three possibilities may explain its observed absence: (i) probing arose in chimpanzees after the bonobos split from that group in the Early Pleistocene; (ii) probing was lost or severely reduced in early *P. paniscus* through founder effects; or (iii) bonobos do use probes but research into wild bonobo tool use has not yet discovered this behavior. The intensity of research effort certainly plays a part in behavioral discovery, but targeted searches for bonobo probing for insects have been unsuccessful [McGrew et al., 2007], indicating that even if it survives in unstudied groups then probing is not a common bonobo trait at present. The other two explanations may be considered equally probable, based on the extremely limited available evidence. The possibility that a founder effect reduced tool use diversity among the early bonobo population through cultural drift, and the known ability of captive bonobos to use probes [Gruber et al., 2010], however, suggest that the most appropriate hypothesis at this point is as follows: the *Pancestor* engaged in investigative probing activities that were subsequently reduced in wild *P. paniscus*, just as they later were in the Budongo Forest chimpanzees [Gruber et al., 2012]. Under this scenario, and given the near universality and dietary importance of wild *P. troglodytes* probing, we may separately predict that following this reduction there remains strong potential for re-discovery of probing tasks, and that some form of investigative use of plant tools by bonobos will therefore be found as research data accumulate in the future. A key question for future debate on this topic is the nature of the environment in which the *Pancestor* apes that would subsequently give rise to the bonobos found themselves isolated,

and whether it offered either lowered returns from probing behavior or an absence of previously targeted prey.

To summarize, at a minimum the *Pan* ancestor ape likely made use of vegetation tools for social displays and play, and for extractive tasks such as sponging and most probably probing. Plants were also likely used as tools to increase personal comfort, but the nature of such tool use is not clear from present day distributions. The bonobo-chimpanzee LCA did not use stone tools, possibly in part because of a paucity of stones in the ancestral Congo basin region [Sanz & Morgan, 2007], and may not have used pounding tools at all. By extension, and in the continuing absence of hominin artifactual evidence from near the time of the Miocene human-*Pan* LCA [McPherron et al., 2010; Panger et al., 2002], it is logical to suggest that the human-*Pan* LCA may also not have used stone pounding tools [contra Whiten, 2011]. The related behavior of smashing foods directly onto stone or wooden anvils may be one that comes and goes in the *Pan* lineage, as it is currently found in some Eastern groups and most Western groups, where it may be related to hammer use [e.g., Marchant & McGrew, 2005].

Of the more than one million catalogued animal species [Mora et al., 2011], regular wild stone tool use is currently known in multiple populations of only three non-human primate species or subspecies: *Sapajus libidinosus* (bearded capuchins), *Macaca fascicularis aurea* (long-tailed macaques) and *P. t. verus*, in addition to a handful of non-primate species including Egyptian vultures, Californian sea otters and digger wasps [Gumert et al., 2009; Haslam et al., 2013; Shumaker et al., 2011; Visalberghi et al., 2007, 2013]. Western chimpanzees in the region of modern Liberia-Ivory Coast-Guinea appear to have independently converged on stone tool use for pounding behavior, as did hominins at some point in our lineage prior to the appearance of stone flaking around 2.6 mya in Ethiopia [Haslam et al., 2009; Panger et al., 2002]. In contrast, Central and Eastern chimpanzees, and bonobos, gorillas, orangutans and around 99% of other living primate species [Perelman et al., 2011] apparently did not.

## CONCLUSION

Consideration of available but scarce wild bonobo tool use evidence, and demographic information provided by recent molecular studies of the living panins, provides a new perspective on the tool use behavior of the bonobo-chimpanzee LCA. At a minimum, this Early Pleistocene ape likely used stick and leaf tools for probing and sponging tasks, self-maintenance, and socially targeted activities such as branch dragging, leaf clipping, and play initiation. Probing behavior was subsequently at least partially

lost in the bonobo lineage and some chimpanzee populations, but it remains a credible candidate activity for reconstructions of tool use by the human-*Pan* LCA. Stone tool use, for pounding or other activities, is not a plausible trait for the *Pan* ancestor ape. The stone tools we observe today likely only began to be regularly included in the panin toolkit following the separation of Western chimpanzees from the Central African population in the Middle Pleistocene, and may be related to an even more recent *P. t. verus* population spike prior to the last interglacial period. A continued search for archaeological (artifact and fossil) evidence of the evolution of primate tool use, further investigation of wild bonobo behavior, and refinement of molecular dating and demographic history methods are required to test the behavioral model hypothesized here.

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