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LETTER TO THE EDITOR

Primate archaeology 3.1

Primate archaeology is the comparative study of material remains left by past and present primates, including humans. The field was created over a decade ago to promote better coordination between the long-term focus of those pursuing human origins research, and the typically modern focus of primatologists working with living creatures (Haslam et al., 2009). Recently, Pascual-Garrido et al. (2023) outlined their vision of a third version of this field, or "Primate archaeology 3.0" as they name it. Their review is timely and valuable, emphasizing details of the primate social, spatial and organic worlds that are among the great strengths of having living behavioral models.

As part of their discussion of shared and derived tool behaviors, Pascual-Garrido et al. (2023, fig. 2) present a cladogram titled "Primates with documented tool use." This diagram includes the four extant great ape genera (*Pongo*, *Gorilla*, *Pan*, and *Homo*) as well as two monkey genera (*Sapajus* and *Macaca*). However, both it and the report as a whole leave out some tool-using taxa that could have important bearing on evolutionary and ecological reconstructions. Further, this phylogenetic perspective may inadvertently contribute to a supposition that while the human lineage has gone through significant technological change, other primates have not done so.

1 | TECHNOLOGICAL PRIMATES

The most prominent missing primate genera from Pascual-Garrido et al.'s review, both in their cladogram and elsewhere, is the gracile capuchin monkey, *Cebus*. Comprehensive work in Panama has shown that wild white-faced capuchins (*Cebus capucinus imitator*) use stone tools at intertidal and inland sites on islands in Coiba National Park (e.g., Barrett et al., 2018; Monteza-Moreno, Crofoot, et al., 2020b; Monteza-Moreno, Dogandžić, et al., 2020a). As they do so, they create durable archeological sites across the landscape, including combinations of tools, anvils and broken shells (Monteza-Moreno, Dogandžić, et al., 2020a). *Cebus* and the more robust *Sapajus* capuchins split some 5.8 million years ago (Lima et al., 2017), and are therefore as similarly diverged in time as humans and chimpanzees or bonobos, meaning that they should not be combined into an all-purpose capuchin category. The stone-tool-using *Sapajus* for which we have an archeological record (Falótico et al., 2019; Haslam, Luncz, Staff, et al., 2016a) most likely only moved into the relevant Brazilian habitat in the last 200,000 years, separating them significantly in time and space from the island-dwelling *Cebus* stone tool users (Lima et al., 2017).

Macaca fascicularis and *Cebus capucinus* are two of the four best-studied non-human primate species that use stone tools in the wild. Both only do so on islands, which raises questions about the importance of complex intertidal and nearshore environments for the emergence and past distribution of this behavior. This topic ties directly into the issues of landscape archaeology—"which includes the physical environment as well as [species] interactions with other plants and animals"—raised by Pascual-Garrido et al., who briefly discuss coastal use without mentioning islands in their review. There are also sex biases in some of the Panamanian *Cebus* groups, with males using tools more than females (Barrett et al., 2018), which joins examples such as male bias in probing tools among some *Sapajus* groups (Falótico et al., 2021) to aid discussions going beyond technology into the social and developmental realms of past primates. While the most recent reports of *Cebus* tool use appeared too late for inclusion in the review (e.g., Goldsborough, Crofoot, Alavi, et al., 2023; Goldsborough, Crofoot, & Barrett, 2024), others have been in the literature for some years. By not including *Cebus* in their report, Pascual-Garrido et al. diminish an already shallow pool from which primate archeological comparisons can be drawn.

A second important primate genus largely missing from Pascual-Garrido et al.'s article is *Papio*. Baboons are known to be only sporadic tool-users in the wild, although no less so than the gorillas included in the cladogram. For example, Goodall reported use of both plant and stone tools for self-maintenance by baboons in Gombe Stream National Park (Lawick-Goodall et al., 1973), and baboon throwing displays have been noted by several researchers (King, 2022). A key upside of including known baboon tool use alongside the other primates is that we have decades of intensive research on baboon socioecology, fossils, landscape use, and plant use (see, for example, the volume introduced by Fischer & Zinner, 2020), all of which forms a rich point of comparison for an expanded primate archaeology. Pascual-Garrido et al. acknowledge this value by including an image of baboon-stripped bark in their fig. 3, although baboons are not discussed in the text. Even if *Papio* tool users are unusual outliers, if the aim is to find the best analogs for comparing living and extinct primate species, then every step beyond a chimpanzee or great ape focus is a positive one.

2 | THE ETERNAL PRESENT

One of the reasons for the creation of primate archaeology was to explore the time depth of non-human primate behavior through material remains. This aim has had a successful start, with archeological excavation and recovery of stone tools used by past western

chimpanzees (*Pan troglodytes verus*; Mercader et al., 2002, 2007; Proffitt et al., 2018), bearded capuchins (*Sapajus libidinosus*; Haslam, Luncz, Staff, et al., 2016a; Falótico et al., 2019) and Burmese long-tailed macaques (*Macaca fascicularis aurea*; Haslam, Luncz, Pascual-Garrido, et al., 2016b). Beyond finding such evidence, though, there is a need to better understand the emergence and loss of tool use among non-human animals. The hominin archeological record is sufficiently extensive to posit the (patchy) origin of stone tool use at least 3.4 million years ago, well after the split of our lineage from the other living apes (Harmand et al., 2015; McPherron et al., 2010). However, caveats about the potential non-linearity of non-human primate tool behaviors, and the likelihood of these having little to do with their phylogenetic split from humans, are rare. The result can be an overly simplified view, in which activities seen in living populations are projected wholesale back to the origins of a species, or even genus.

Cladograms are effective at highlighting probable ancestral traits when they based on clearly defined physical characteristics, or relatively well-studied processes, such as genetic mutation. The lineage divergence times given in Pascual-Garrido et al.'s review are derived from just such insights, including fossil morphology and mutation rates, and their diagram is explicitly referenced in relation to these ages: "given that the use of perishable implements is shared among all extant great apes, it is possible that plant technology may date as far back as their earliest divergence in the Miocene (fig. 2)." But it is not clear that the behaviors emphasized in the review—including landscape use, plant tool making and use, and cultural history—are tied strongly enough to morphology or genetics to make a cladogram a useful theorizing device in this instance.

Data presentation matters, and the cladogram obscures specifics of key processes that motivate the review, including the dynamics of plant tool use and the opportunities for primate archaeology that this provides. One potential source of information is the DNA of past tool-users, with genetic material from living wild chimpanzees already recovered from the surface of termite fishing tools in the absence of direct observation of their use (Stewart et al., 2018). Recovery of human DNA from tool surfaces reaches back at least 19,000 years (Essel et al., 2023), and the rapid development of this field suggests that the timeframe of recovered material will only get older. This kind of analysis would help to track shifting tool-use patterns, such as for chimpanzees of the Budongo Forest in Uganda that appear not to use stick tools. Many of their neighbors and fellow chimpanzees further afield do so, suggesting a loss of this trait in the Budongo communities (Gruber, 2019). Yet the Sonso community in Budongo Forest also recently innovated and spread a moss sponging tool (Lamon et al., 2017). Tool lists for non-human primates too often assume that the current set of behaviors seen in a community is fixed, suitable for comparison with environmental factors or gene flow as an unchanging and unchangeable whole. This is not the case.

If tool use is always a direct and rapid result of speciation, then diagrams such as the one presented by Pascual-Garrido et al. would allow us to not only generate hypotheses about ancestral states and derived traits among technological primates, but to draw conclusions from them. If not, this kind of data display could end up implying connections and earlier states that do not exist. For instance, if stone tool use has only arisen in *Sapajus* capuchins since their occupation of the Caatinga and Cerrado environments in the past 200 kya (Lima et al., 2017), and potentially began in the western chimpanzee subspecies (*Pan troglodytes verus*) in the same timeframe (Haslam, 2014), then any evidence for earlier or geographically distant primate lithic technologies in Brazil or tropical Africa should be viewed as independent inventions (as the Coiba capuchins demonstrate for Central America).

The hypothesis that certain types of primate tool use derive from speciation events is a testable one. It is in fact the kind of hypothesis that primate archaeology was designed to address, and ideally we will one day know whether or not it is supported. Until that time, we need to be wary of promoting the idea that the animals we currently see are representative of their ancestors across evolutionary timescales. Previous similar reviews have either included (e.g., Panger et al., 2002) or avoided (e.g., Haslam et al., 2017; McGrew et al., 2019; Wynn et al., 2011) tree diagrams, and I realize that Pascual-Garrido et al. may have been using their cladogram primarily to concisely display timeframes of species divergence, despite the Miocene hypothesis. However, primate archaeology may be better served by avoiding the implicit or explicit connotations of placing behavioral traits on a tree, unless the full suite of tool activities is modeled to allow for independent inventions and loss. Hominin archaeology has revealed deeply complex and unpredictable shifts in tool materials and forms (Shea, 2017), and associated landscape activity patterns (Faith et al., 2021), and the non-human primate record may well have equally unexpected shifts in store.

3 | CONCLUSION

Pascual-Garrido et al.'s review is an important update on primate archaeology, and it contains much of significance for advancing the field. This letter is intended less as a corrective than as an addendum to that work, hence the title: Primate archaeology 3.1. We should all look forward to versions 3.2, 4.0, and so on as rapid progress continues.

AUTHOR CONTRIBUTIONS

Michael Haslam: Conceptualization (lead); writing – original draft (lead); writing – review and editing (lead).

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DATA AVAILABILITY STATEMENT

Not applicable.

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