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AUTHOR(S):

McGrew, William C.

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Chimpanzees digging up termites: A problematic but persisting issue

William C. McGrew

School of Psychology and Neuroscience, University of St Andrews, Scotland, UK
(✉ E-mail: wcm21@cam.ac.uk)

Every chimpanzee researcher knows of the value of our study species in modelling the evolutionary origins of humanity. As our nearest living relations, with a Last Common Ancestor about 7–8 mya, *Pan* is the sensible starting point for etho-archaeology, that is, linking their behavior and artefacts to hominins who provide the latter but not the former. The aim of this essay is to show that such modelling should be done with care, lest we go astray, even in the simplest ways. A case study exemplifies this cautionary note.

This year marks the 20th anniversary of published findings inferring that *Australopithecus (Paranthropus) robustus* in South Africa used bone tools to dig into termite mounds in extractive foraging (Backwell & d’Errico 2001, d’Errico *et al.* 2001). Citing Goodall (Figure 1), the authors’ conclusion was based on analyses of the use-wear patterns on the bones, that is, striations revealed by microscopy to have come from repeated abrasion with termite earth. They used experimental replicates of the artefacts to test their origin, by digging into extant termite mounds. Their conclusion was straight-forward: “Our results suggest that early hominids used a bone technology as a part of their dietary adaptations, and they maintained a bone tool termite-foraging cultural tradition in

southern Africa for nearly a million years.” (Backwell & d’Errico 2001, p. 1362).

So, how has this assertion fared over the last two decades? Eight years later, the authors modified their claims, based on further analysis, but still stuck to the termite extraction hypothesis: “*Swartkrans and Drimolen tools may have been used to forage for termites, which remains the closest match, but also extract tubers, process fruits and conduct other, as yet unidentified tasks.*” (d’Errico & Backwell 2009, p. 1772). Others also continue to restate the argument: Lesnik (2011) has done the most extensive and sophisticated experimental study of bone tools and termite foraging, comparing *Macrotermes* and *Trinervitermes* (see below). She concludes that the evidence for termite foraging is stronger than tuber-digging in the Swartkrans bone tools. Also, “*South African weathered bone splinters used in unmodified form or occasionally shaped through grinding and implemented in foraging activities such as termite extraction.*” (Pante *et al.* 2020, p. 2).

These and other archaeological papers cite studies of chimpanzees using tools to get termites, so how apt is this linkage?

Chimpanzees consuming termites via tool use has been known for over 50 years, since Goodall (1964) first described termite fishing. Since then scores of papers have shown it to be the prevalent form of ape extractive technology, found from Tanzania to Senegal. New studies continue to report it in more populations and with more behavioral diversity (Boesch *et al.* 2020). So, what is the problem with Backwell *et al.*’s analogy?

First, wild chimpanzees have yet to be reported to use bone tools. Nor have captive chimpanzees, though some experiments have been done with other species in captivity, with mixed success.

Second, chimpanzees have not been seen to dig up termite mounds, with or without tools. They are well-known to do more than simple fishing with flexible probes: Some use tool sets of a



Figure 1. Gombe chimpanzees’ termite ‘fish-in’. (Photo taken by Robert O’Malley)

stout perforating/puncturing tool to access underground termite chambers, followed by prey extraction with a standard fishing probe (Sanz *et al.* 2004). But why is this activity not digging? If digging is defined as *excavation*, that is, displacing soil from the substrate, thus creating a cavity, then *compressing* soil by thrusting a stick into the ground is different (Estienne *et al.* 2017, Table 1, *cf.* McLennan *et al.* 2020, Table A).

Third, Backwell and d’Errico chose *Trinervitermes trinervoides* for their experimental digging into termite mounds (d’Errico *et al.* 2001). I can find no confirmed record of this genus being eaten by chimpanzees, either with or without tools, or from observations or fecal analysis. The genus appears to be absent from at least nine sites of chimpanzee research (Bogart & Pruettz 2008, Table II). *Trinervitermes* is in a different sub-family (Nasutitermitinae) of Termitidae than is *Macrotermes* (Macrotermitinae), which is overwhelmingly the preferred choice of chimpanzees across Africa (e.g. Collins & McGrew 1985, Lesnik 2011). *Trinervitermes* is small-bodied and squirts noxious chemicals from its snout; *Macrotermes* has the largest body-size of all termite genera and tastes palatable (Figures 2 and 3).

Fourth, carbon isotope data show that *Paranthropus* in South African had a diet of about 35% C₄ foods (Sponheimer *et al.* 2005), while chimpanzees almost exclusively consume C₃ foods, in both East and West Africa (Schoeninger *et al.* 1999, Sponheimer *et al.* 2006). Termite taxa vary greatly from pure C₃ to C₄ consumers, with the highest C₄ values coming from harvester (grass-eating) termites, such as *Trinervitermes* (Sponheimer *et al.* 2005). Thus, on multiple grounds, *Trinervitermes* seems to have been an unfortunate choice for modelling.

But how to explain the striated use-wear on the South African bone tools from antiquity, especially as the authors’ original experimental replications indicate that it comes from digging in a different but similar substrate, that is, a particular one in which soil particles are uniform in size and structure, as in the composition of termite mounds. (It seems likely that the size of such particles in mounds reflects the width of the gape of the mandibles of worker termites of any given species, but this idea seems not to have been tested.) Perhaps from digging up other dietary items in very sandy soil?

Another alternative (2) is that the hominins *did* use bone tools to dig into termite mounds, but for another reason. Perhaps for *geophagy*, which does yield micro-nutrients, at least in *Macrotermes* (Seymour *et al.* 2014) but need not entail accompanying termitivory? In southern Africa, *Macrotermes* mounds show enrichment of multiple micro-nutrients compared with *Trinervitermes*, which show none (Mills *et al.* 2009). Neither of these alternatives has been investigated systematically for *Pan*, but chimpanzees *do* dig wells for drinking water in sandbars in riverbeds (McGrew *et al.* 2013), and chimpanzees (Reynolds *et al.* 2019) and humans (Hunter 1993) *do* consume termite earth, without digging, especially from *Macrotermes*.

Wild chimpanzees *do* dig for other social insects,



Figure 2. Close-up of *Macrotermes* soldiers ('Big Macs'). (Photo taken by Robert O'Malley)



Figure 3. *Macrotermes* sp. Mound, Lui Kotale, DRC. (Photo taken by Linda Marchant)

such as stingless honey-bees using tools (e.g. Estienne *et al.* 2017), as revealed by camera trap data that provide both the behavior and its products. Primate archaeological data from unhabituated chimpanzees suggest digging into the nests of army ants (Pascual-Garrido *et al.* 2013). But all such cases seem to be the result of using tools of vegetation, not bone. (No one seems to have recorded the availability of weathered bone as a potential raw material for chimpanzees in nature, but many chimpanzee field projects seem to accumulate a collection of such specimens in the process of research, especially at dry and open sites.)

Captive chimpanzees will use tools to dig for food

rewards buried by experimenters in contrived settings (e.g. Motes-Rodrigo *et al.* 2019), but their study made available only woody vegetation for use as tools to dig up fruits. The obvious actualistic experiment to be done might be to give captive chimpanzees a range of raw materials, including bone, horn core, and ivory, as potential tools to do their digging in various substrates, and then to subject the tools used to the same analyses employed by the archaeologists. Thus, the behavior could be matched to the use-wear. An even more comprehensive study also would involve the same raw materials applied to an experimental task involving vertical downward compression into the substrate.

So, my conclusion, subject to correction by better-informed readers, is that the use of chimpanzees to model extinct hominin use of bone tools in termitivory was perhaps over-reaching, and that the topic merits further investigation. A lesson to primatologists is that such modelling of extinct hominids based on extant primates should be done carefully and precisely, that is, with focused etho-archaeology. A more general lesson is to tread carefully into cognate disciplines and to consult colleagues across disciplinary lines.

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