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Primate Archaeobotany

The Potential for Revealing Nonhuman Primate Plant Use in the African Archaeological Record

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Recognition is growing that valuable comparative data on human evolution may be gained through an examination of the archaeological remains left by nonhuman species, including the closely related and technology-proficient chimpanzee (*Pan troglodytes*) and extending to more distant members of the human family tree (Haslam 2012; Haslam et al. 2009). Because much of the justification for extending archaeology to nonhuman primates comes from plant processing and plant-based technologies of species such as chimpanzees and capuchin monkeys (Mercader et al. 2007; Mercader, Panger, and Boesch 2002; Ottoni and Izar 2008; Visalberghi et al. 2007), it is therefore necessary to explore the extent to which the activities of such animals can be detected and interpreted in the archaeobotanical record. This perspective is important not just for understanding the intraspecies chronological development of nonhuman primate plant use but also because it bears on discussions of factors such as cooking and nonlithic tool use in human evolution. Because Africa was the primary centre for the evolution of both humanity and our closest primate relatives, African archaeobotanists have a central role to play in exploring primate archaeobotany.

PRIMATE ETHNOBOTANY AND ARCHAEOLOGICAL POTENTIALS

Archaeobotanical studies cover a number of overlapping categories, including diet, domestication, construction, fuel, plant-processing technologies, plant-tools, and non-subsistence exploitation of plant properties (for example, medicines, poisons). It would be impossible in a short chapter to review all such aspects of primate-plant interactions across Africa. Instead, here I focus on components of plant processing and exploitation (subsistence and technology) by the closest genetic relatives to humans, the chimpanzees, as a means of introducing the notion of primate archaeobotany. Possible extensions of these themes to other nonhuman primates are noted only where appropriate and are by no means systematic or exhaustive. Note that the term *ethobotany* is used here, in contrast to *ethnobotany*, to distinguish extant nonhuman plant exploitation.

CHIMPANZEE ETHOBOTANY: SUBSISTENCE

Chimpanzees occupy a broader range of environments than many primates do, including lowland and montane forests, savannah, and woodlands; however, as would be expected from forest-dwelling common ancestry (Milton 1993), most primate species live today in tropical forests, and fruits, leaves, flowers, and other vegetation make up the majority of the typical primate diet. Of the great apes, gorillas and orangutans consume only a very small

nonplant component (chiefly invertebrates), and, although chimpanzees eat a higher percentage of animal matter thanks to practices such as termite-fishing and the hunting of colobus monkeys, this amount is estimated to contribute at most around 5–10% of the total diet (Milton 1999, 2003; Tappen and Wrangham 2000). Evidence for bonobo (*Pan paniscus*) faunivory is rare (McGrew et al. 2007).

Chimpanzee diets, like those of the bonobo and gorilla, are preferentially composed of ripe tree-fruits (Laden and Wrangham 2005; Milton 2003). In contrast to the large gorillas and orangutans, however, chimpanzees also target nutrient-rich plant foods that require behavioural adaptations to access them. These include hard-shelled nut species that must be cracked using tools, palm pith pounded using a frond to produce an edible pulp, and underground storage organs (USOs) reached using digging sticks (Hernandez-Aguilar, Moore, and Pickering 2007; McGrew 1992; Yamakoshi and Sugiyama 1995). A non-exhaustive, selected list of plant taxa exploited for subsistence by chimpanzees is summarised in Table 2.1, providing an initial target list for archaeobotanical study of these apes. Foods processed using technology (for instance, *Strychnos* spp., *Coula edulis*, *Treculia africana*) have been emphasised, as these may leave processing residues (for example, Koops, McGrew, and Matsuzawa 2010) detectable on archaeologically recovered tools. More extensive species lists are provided in the primatological literature (for instance, McGrew, Baldwin, and Tutin 1988; Tweheyo, Lye, and Weladji 2004).

Recent emphasis on the role of 'fallback foods', typically low nutrient or difficult-to-access foods relied on at times of seasonal or other shortage, as drivers of evolutionary change (Laden and Wrangham 2005) has led to the suggestion that chimpanzee behavioural innovations such as tool use and fission-fusion foraging parties evolved to allow them to continue to subsist on high-quality foods year-round (Chapman, White, and Wrangham 1994; Lambert 2007). Tool use among New World capuchin monkeys (*Sapajus libidinosus*), including digging for tubers and cracking nuts with hammers and anvils (Ottoni and Izar 2008; Visalberghi et al. 2009), may represent an independently evolved approach similar to that of the chimpanzee (Lambert 2007), although food scarcity appears not to be a strong driver of nut-cracking among these monkeys (Spagnoletti et al. 2012). An alternative strategy, seen in gorillas, for example, involves anatomical (for instance, dental, digestive, and body-size) adaptations that permit processing of lower nutritional density but abundant foods such as mature leaves and bark (Harcourt and Stewart

2007). Clearly, *Homo sapiens* tend to the behavioural more than anatomical end of this adaptive continuum.

The potential for identifying nonhuman primate tools in the archaeobotanical record is discussed further later in the chapter, but first we consider the kinds of evidence that the chimpanzee and other primate diets may leave behind. The most direct evidence is found in fecal deposits, including seeds and chitinous insect exoskeletons, and plant remains integrated into dental calculus. There exists a substantial comparative record of fecal contents for many extant primate species (Behie, Pavelka, and Chapman 2010; Bradley et al. 2007; Moreno-Black 1978; Tutin and Fernandez 1993) collected over several decades, but high turnover of organic material within forested environments acts against long-term preservation. Drier areas inhabited by chimpanzees, such as Assirik (McGrew et al. 2003) and Fongoli (Pruetz and Bertolani 2007) in Senegal, may provide better opportunities for organic longevity. Perhaps the best opportunity for recognising past chimpanzee occupation via fecal material comes from build-up through repeated use of nesting sites (Sept 1998), since chimpanzees tend to defecate upon arising (McGrew et al. 2003). Dental calculus is receiving increasing attention as a degradation-resistant archaeobotanical trap, especially for plant microfossils (Cummings and Magennis 1997; Henry and Piperno 2008), with starches extracted and identified from the calculus of two recently deceased chimpanzees from Kibale, Uganda (Hardy et al. 2009). Claims have also been made for the recovery of diet-related phytoliths from the teeth of an extinct Asian ape, *Gigantopithecus* (Ciochon, Piperno, and Thompson 1990). The limits of this approach are as yet unknown, but the possibility cannot be ruled out that primate and ancestral human dietary niches and food acquisition strategies, including tool use where consumed foods are otherwise inaccessible to the studied species, may be identified dating back even millions of years.

A less direct form of evidence, but one that is potentially very important, is starch residues on artefacts. Starch residues have played an important role in the development of the emerging field of primate archaeology. It was the differentiation via palaeoamylogy (ancient starch analysis; Haslam 2004) of plants not consumed by humans that allowed for confidence in the attribution of 4,300-year-old stone tools to chimpanzee nut-cracking (Mercader et al. 2007). Excavated sites in Taï National Park, Côte d'Ivoire, contained both unquestionably human-manufactured flaked stone artefacts along with percussion-damaged stones, and the identification of starch residues from three

Table 2.1 Selected Plant Taxa Exploited by Chimpanzees (*Pan troglodytes*) for Subsistence, Maintenance, and Technological purposes.[†] (Note that variations exist between different chimpanzee subspecies, habitats, and cultural traditions and that this table is non-exhaustive in coverage.)

Taxa	Plant Part	Use	Area(s)
Ficus spp.	Fruit	Food	Kahuzi-Biega National Park, Democratic Republic of the Congo; Mt. Assirik, Senegal; Budongo Forest Reserve, Uganda; Mahale Mountains National Park, Tanzania; Ugalla, Tanzania
Myrianthus holstii *Rubus* spp.	Fruit	Food	Kahuzi-Biega National Park, Democratic Republic of the Congo
Coula edulis *Panda oleosa* *Parinari excelsa* *Sacoglottis gabonensis*	Nut	Food	Taï National Park, Côte de'Ivoire; Sapo National Park, Liberia
Detarium senegalense	Nut	Food	Taï National Park, Côte de'Ivoire; Tiwai Island, Sierra Leone
Dacryodes gabonensis *Trichoscypha arborea*	Fruit	Food	Taï National Park, Côte de'Ivoire
Elaeis guineensis	Nut	Food	Bossou, Guinea
Pseudospondias microcarpa	Fruit	Food	Kibale Forest, Uganda; Mt Assirik, Senegal
Uvariopsis congensis	Fruit	Food	Kibale Forest, Uganda
Strychnos spp.	Fruit	Food	Gombe National Park, Tanzania; Ugalla, Tanzania; Mt. Assirik, Senegal; Taï National Park, Côte de'Ivoire; Yealé, Côte de'Ivoire
Conopharyngia sp.	Fruit	Food	Gombe National Park, Tanzania; Kibale Forest, Uganda
Diplorhynchus condylocarpon	Seeds	Food	Gombe National Park, Tanzania
Balsamocitrus sp.	Fruit	Food	Budongo Forest Reserve, Uganda
Broussonetia papyrifera	Leaves, Fruit	Food	Budongo Forest Reserve, Uganda
Cynometra alexandri *Pterygota mildbraedii*	Fruit	Food	Virunga National Park, Democratic Republic of the Congo
Harungana madagascariensis	Fruit	Food	Mahale Mountains National Park, Tanzania
Adansonia digitata *Saba senegalensis,* *Cola cordifolia* *Lannea* spp. *Grewia lasiodiscus* *Hexalobus monopetalus* *Tamarindus indica* *Zizyphus* sp.	Fruit	Food	Mt. Assirik, Senegal
Pterocarpus erinaceus	Bark	Food	Mt. Assirik, Senegal
Detarium microcarpum	Nut	Food	Gashaka Gumti National Park, Nigeria
Treculia africana	Fruit	Food	Nimba Mountains, Guinea; Taï National Park, Côte de'Ivoire
Grewia spp. *Canthium hispidum*	Fruit	Food	Ugalla, Tanzania
Dolichos kilimandscharicus *Tacca leontopetaloides* *Raphionacme welwitschii* *Brachystegia bussei* *Smilax* sp. *Fadogia quarrei* *Costus macranthus*	Underground storage organs (USOs)	Food	Ugalla, Tanzania
Unspecified	*	Extractive foraging	All chimpanzee sites

Table 2.1 Continued

Taxa	Plant Part	Use	Area(s)
Thomandersia hensii	Sticks	Puncture termite nests	Nouabalé-Ndoki National Park, Republic of the Congo
Sarcophrynium spp. *Megaphrynium* sp.	Stalks	Termite-fishing, ant-dipping	Nouabalé-Ndoki National Park, Republic of the Congo
Ataenidia conferta *Haumania danckelmaniana*	Stalks	Termite-fishing	Nouabalé-Ndoki National Park, Republic of the Congo
Grewia lasiodiscus *Cissus* sp. *Pericopsis laxiflora* *Landolphia heudelotii* *Oxytenanthera abyssinica* *Pterocarpus erinaceous*	Twigs, leaf-stalks, vines, bark	Termite-fishing	Mt. Assirik, Senegal
Ficus vallis-choudae *Saba comorensis* *Landolphia owariensis* *Grewia flavescens*	Leaves	Water-sponge	Mahale Mountains National Park, Tanzania
Ficus thonningii	Fruit	Water-sponge	Mahale Mountains National Park, Tanzania
Elaeis guineensis	Palm frond	Pounding palm apex	Bossou, Guinea
Hybophrynium braunianum	Leaves	Water-sponge	Bossou, Guinea
Aspilia spp.	Leaves	Medicinal	Gombe and Mahale Mountains National Parks, Tanzania
Vernonia amygdalina	Shoots	Medicinal	Mahale Mountains National Park, Tanzania
Brachystegia bussei *Julbernardia globiflora* *Combretum molle* *Pterocarpus tinctorius*	Branches	Nesting	Ugalla, Tanzania
Crysophyllum albidum	Branches	Nesting	Virunga National Park, Democratic Republic of the Congo; Kibale Forest, Uganda
Cynometra alexandri	Branches	Nesting	Virunga National Park, Democratic Republic of the Congo
Garcinia sp.	Branch	Honey extraction	Loango National Park, Gabon
Thomandersia laurifolia *Milletia* sp.	Sticks	Puncture termite nest	Dzanga-Sangha region, Central African Republic
Haumania danckelmaniana *Sarcophrynium* spp. *Dalhousiea africana*	Sticks	Termite-fishing	Dzanga-Sangha region, Central African Republic
Ataenidia conferta *Sarcophrynium* spp.	Petiole; Sticks	Termite-fishing	Dja Biosphere Reserve, Cameroon; Dzanga-Sangha region, Central African Republic
Alchornea floribunda *Tabernaemontana crassa*	Sticks	Puncture termite nests	Dja Biosphere Reserve, Cameroon
Megaphrynium macrostachyum	Sticks	Termite-fishing	Dja Biosphere Reserve, Cameroon

*Many reports do not present data on plant taxa used for activities such as ant-dipping, termite-fishing, and honey-gathering; the tools are typically described only as sticks, twigs, branches, leaves, leaf mid-ribs, and so on. In some cases chimpanzees may not be selective in the taxa used for these activities, but modification to shape or trim the tool may still be practiced (for example, Boesch, Head, and Robbins 2009; Fowler and Sommer 2007; Sanz and Morgan 2007). A similar lack of botanical identification applies in many instances to plant parts used as weapons (for example, Pruetz and Bertolani 2007) or digging sticks (Hernandez-Aguilar, Moore, and Pickering 2007) and in social displays, and for a variety of self-directed maintenance and stimulation activities (McGrew 1992).

†Data compiled from (Anderson, Williams, and Carter 1983; Boesch and Boesch-Achermann 2000; Boesch, Head, and Robbins 2009; Deblauwe et al. 2006; Fay and Carroll 1994; Fowler and Sommer 2007; Hernandez-Aguilar 2009; Hernandez-Aguilar, Moore, and Pickering 2007; Huffman and Seifu 1989; Isabirye-Basuta 1988; Koops, McGrew, and Matsuzawa 2010; Marchant and McGrew 2005; Matsusaka et al. 2006; McBeath and McGrew 1982; McGrew 1992, 2004; McGrew, Baldwin, and Tutin 1988; McGrew et al. 1999; Nishida 1989; Sanz and Morgan 2007; Sept 1992; Sugiyama 1997; Tonooka 2001; Tweheyo, Lye, and Weladji 2004; Whiten et al. 2001; Whitesides 1985; Wrangham and Nishida 1983; Yamagiwa and Basabose 2009).

nut species exploited exclusively by chimpanzees (*Parinari excelsa*, *Panda oleosa*, and *Detarium senegalense*) provided the strongest evidence in favour of assigning these tools to chimpanzees. To date this study remains the only dated and confirmed nonhuman ape archaeological site, but the potential for further such work and resultant insights into the time-span and evolutionary role of ape (including human) technology are significant.

Starchy foods are preferentially targeted by technology-using nonhuman primates, including nut-cracking by chimpanzees and capuchins and more rarely digging for USOs by chimpanzees, capuchins, and, anecdotally, also by baboons (Hernandez-Aguilar, Moore, and Pickering 2007; Mannu and Ottoni 2009; Marlowe and Berbesque 2009). Plant residues, including starches and fibrous material from nut processing, are routinely embedded and retained on stone and wooden hammers and anvils during use (for example, Barton 2007). Plant use-residues can be differentiated even on wooden digging utensils, as demonstrated by study of ethnographic Australian digging sticks (Nugent 2006). Guidance as to sampling locations for primate archaeobotanical residues is provided by distinct wear traces left by pounding activities, such as cupule formation in sandstone anvils by capuchins (Visalberghi et al. 2007) and impact pitting on chimpanzee hammer stones (Haslam et al. 2009).

Starches also play a prominent role in discussions of the evolution of cooking and other behavioural adaptations by humans. Cooking improves foods for consumption by breaking down physical barriers, altering molecular structure, and reducing toxin load (Wrangham 2007; Wrangham et al. 1999), which in turn make more items edible and may reduce energetic expenditure on digestion. A preference for cooked foods, including starchy tubers, has been shown in a pilot study among all great apes (Wobber, Hare, and Wrangham 2008), suggesting that once cooking began in the hominin line it could have been taken up relatively rapidly and had follow-on effects on the life history and social behaviour of our ancestors. Documenting the effects of primate plant processing activities on starch residues (including pounding and grinding) may provide an avenue for identifying the entry and spread of cooked foods into the hominin diet and for differentiating hominin from nonhuman primate processing activities. However, further comparative work is required to document the effects of mechanical damage (Babot 2003), and gelatinisation through heat and moisture (Crowther 2012; Henry, Hudson, and Piperno 2009), on starches from different species.

Durable material surface remains also act as guides to the location of buried primate archaeological deposits, with present-day and recently buried nut-cracking localities liberally strewn with nutshells (Mercader, Panger, and Boesch 2002; Visalberghi et al. 2007) and broken hammer fragments. Under favourable conditions shells may survive for a considerable time, as evidenced by remains found with pitted stones at the Early-Middle Pleistocene hominin site of Gesher Benot Ya'aqov in Israel (Goren-Inbar et al. 2002). Of relevance here is that not all chimpanzee groups crack nuts, although the hypothesised restriction of this activity to sites west of the N'Zo-Sassandra River in Côte d'Ivoire has recently been shown to be incorrect (Morgan and Abwe 2006). Nevertheless, there remain chimpanzee groups with access to the relevant nut species and percussion materials that do not use these resources (Boesch, Head, and Robbins 2009; Whiten et al. 2001). Whether this absence results from local loss of technological proficiency, lack of innovative ability, or other explanations is currently unknown (Wrangham 2006).

CHIMPANZEE ETHOBOTANY: TECHNOLOGY

Vegetation is the primary raw material for nonhuman primate tools (McGrew 1992), although the relative roles of stones and plants vary between taxa (Mannu and Ottoni 2009). Greater recognition by archaeologists of the varied forms of primate plant technology is necessary to identify nonhuman contributions to the archaeobotanical record and aids both primatological and human evolution studies by building a record of technological development for extant species outside our own ancestral lineage. Chimpanzees were the first nonhuman species for which intensive observations of tool use were made, and some field sites (for example, Gombe and Mahale M in Tanzania) have mutlidecadal data (McGrew 2004), making this species arguably the most appropriate for discussing nonhuman plant-tool use.

The most comprehensive study of variation in extant chimpanzee behaviour (Whiten et al. 2001) identified 65 behaviour patterns that were present at multiple sites. These included such actions as probing, pounding, dipping, and clasping, although not all involved the use of external objects. It's important to note that 57 of these behaviours involve plants in some fashion, and 47 involve detached pieces of vegetation such as sticks and stems used to fish for insects, leaves used to collect water by sponging and wipe surfaces, and wooden hammers used to crack nuts (Whiten et al. 2001). Note also that 10 of the 19 'very likely cultural variants' identified for extant orangutan

populations (van Schaik et al. 2003) likewise involve detached plant tools. Table 2.1 summarises selected plant taxa used as tools by chimpanzees.

Modification and even standardisation of chimpanzee plant implements occurs for activities such as ant-fishing and honey extraction (Boesch and Boesch 1990; Boesch, Head, and Robbins 2009; McGrew 2004), and together with the location of discarded tools near extraction sites this purposeful modification allows primatologists to readily identify such items even in the absence of the tool user (for instance, Fowler and Sommer 2007). The same recognition should be feasible for archaeobotanists encountering these tools in archaeological contexts, provided taphonomic factors permit survival and the analyst is aware of the characteristics of nonhuman primate tools. Residue studies may be possible when such implements are identified, especially on tools used to access starchy foods or gather persistent materials such as honey (Boesch, Head, and Robbins 2009; Sanz and Morgan 2009). Residues (in the form of prey-species hair) have been observed adhering to a wooden tool used in the manner of a spear by savannah chimpanzees to immobilise lesser bushbabies (*Galago senegalensis*) (Pruetz and Bertolani 2007), and if this tradition persists then retention of blood and other bodily components on a subset of such tools is likely. As in the case of vegetal probes, the hierarchical manufacturing process employed for these 'hunting' tools may assist with their identification in the archaeological record.

A key element of the chimpanzee ethobotanical record, noted previously, for example, in the context of nut-hammering behaviour, is the presence of cultural variation between different communities. In this instance 'cultural' is defined as 'sufficiently frequent at one or more sites to be consistent with social transmission, yet absent at one or more others where environmental explanations [for the absence] were rejected' (Whiten et al. 2001, pp. 148–82). In practice cultural variation means that the full range of material culture employed by any given chimpanzee group (past or present) cannot be predicted in advance, even where full ecological information is known. It also means that the chimpanzee archaeobotanical record in any one region is expected to show cultural drift over time, with tool-forms coming in and out of fashion within functional constraints. The pace at which this occurs is very unlikely to be anywhere near as rapid as that seen in modern humans, especially since chimpanzees appear to lack a strong 'ratchet effect' for cumulative cultural accumulation over generations (Tennie, Call, and Tomasello 2009). Nevertheless, any longitudinal data collected by

archaeobotanists that bear on this issue would provide useful guiding parameters as to the rate of cultural change for early hominin technologies. It has been noted that primatology benefits significantly over archaeology in having living subjects to study (Haslam et al. 2009); however, from an evolutionary perspective this supposition is valid only to the extent that extant primate populations are seen as socially and technologically representative of past behaviours. Archaeobotanical study of chimpanzees, and other potentially cultural primates such as orangutans and capuchin monkeys, will help ascertain if the recognised fallacy of uncritically projecting modern human activities back into prehistory also holds for nonhuman primates (Haslam 2012).

A final category of botanical exploitation likely to have bearing on our views of human evolution is the construction of nests (Sept 1998). All great apes daily construct nests from bent and interwoven branches and leaves for resting and sleeping (Fruth and Hohmann 1994; van Schaik et al. 2003; Yamagiwa 2000). The precise function of arboreal chimpanzee nests is not well understood (McGrew et al. 2003), with hypotheses including thermoregulation or predator avoidance, but the spatial patterning and repeated use of ape nesting sites can broaden our perspective on early human site formation (Hernandez-Aguilar 2009; Sept 1992; Stewart, Piel, and McGrew 2011). Nesting sites act as foci for activity and potentially for accumulation of plant-food debris such as seeds and other feeding or self-maintenance debris, with the nests themselves surviving typically for a few weeks to several months or even years depending on the tree species used, the season of construction, and whether the branches used were broken during construction (McGrew et al. 2003). Nests are, of course, extremely unlikely to be observed archaeologically unless a fallen tree or ground nest is covered under anaerobic conditions; it is the spatial and temporal shaping of other behaviours that is of greater interest.

DEVELOPING PRIMATE ARCHAEOBOTANY

For all archaeobotanical studies there is a prime concern with taphonomy. Most ephemeral actions of chimpanzee and other primates of relevance to human evolution (by way of relatedness or technological aptitude) do not typically leave material traces that survive natural nutrient recycling processes. However, primate stone tools demonstrably are recoverable several thousand years after their use (Mercader et al. 2007; Mercader, Panger, and Boesch 2002), and microbotanical residues on these offer

a rare opportunity to record nonhuman technological and subsistence behaviour in the distant past. Hard woods selected and/or modified for use as digging sticks and probes, and dense scatters of primate-targeted nut-shells, provide the most promising nonlithic avenues for recovery. These materials have the same likelihood of survival as artefacts and debris created by humans from the same materials, with the exception that charring is less likely for the nonhuman assemblage. Hominin Middle Pleistocene wooden artefacts and nut-cracking debris are known but rare (Goren-Inbar et al. 2002; Thieme 1997), and recognition of past chimpanzee or other primate behaviours even much more recent than this would still be valuable. Although taphonomy is not unproblematic, the importance of archaeobotanists analysing primate records to reconstruct evolutionary and ethological data lies in the fact that in most instances plant remains will be the only evidence of activity at primate sites. Whether this means that the time-depth of the identifiable primate archaeological record is limited to a few years in the absence of accompanying stone tools or, rarely, prey bones (Tappen and Wrangham 2000) is unknown at present.

Differentiating human records from those of nonhuman primates is likely to be unproblematic in many cases, given the human propensity for accumulating durable artefacts at most activity sites. Flaked stone artefacts have been the hominin calling card for 2.5 million years (Semaw et al. 1997), and no extant animal other than humans regularly creates them. Yet long-term sympatry of humans with other apes means that not all hominin sites are necessarily exclusively hominin (Mercader et al. 2007), especially since humans and chimpanzees have similarities in their preference for nonrandomly distributed resources such as ripe fruits. An alternate avenue for differentiating primate archaeological remains may rely on the fact that human use of tools and fire to modify foods after extraction are also unique to our lineage. For example, if nut starch residues on a stone or wooden anvil display evidence of systematic grinding and not just incidental pounding, then they may potentially be attributed to human agency, as the chimpanzee and capuchin aim is to open a nut, not crush it. The same applies to gelatinised starches, which require both moisture and heat to gelatinise and would not ordinarily result from natural forest fires. Furthermore, although subsistence plants exploited by humans and nonhuman primates do have some overlap, this is not an intractable problem. For example, Peters and O'Brien (1981) found that of 461 genera of food plants consumed in eastern and southern Africa by humans,

chimpanzees, and baboons, 36% were consumed only by humans, 17% each were consumed solely by chimpanzees or baboons, and only 6% overlapped all three primates. At the time of that study the best chimpanzee-human comparison came from the Kasakati Basin/Mahale Mountains region of Tanzania, where of 161 genera 19% were consumed by humans only, 60% by chimpanzees only, and 21% by both (Peters and O'Brien 1981). Consideration of palaeobotanical (primarily palynological) analyses at the Pleistocene early hominin locales of Koobi Fora and Omo demonstrates that identification of leaf, shoot, and fruit food taxa exploited by modern humans and large primates is possible at such sites (Peters and O'Brien 1981).

Extraction of a chimpanzee or other primate botanical signature from background noise requires the same attention to primate plant exploitation practices as that traditionally afforded to humans, alongside ongoing study of botanical components of primate site creation and longevity.

Practical application of archaeobotanical methods to primate field sites does not require modifications of existing protocols or techniques. What is required are working collaborations with primatologists who have experience locating and working with their study species in its environment, in addition to extensive behavioural records. Reconstruction of site environments for past primate evolution is as important as that for hominins in determining causal from incidental ecological factors, and in this regard existing archaeobotanical approaches are appropriate. Even seemingly simple research into the longevity of a common activity, such as termite-fishing at the famous Gombe National Park, would be of great benefit to our understanding of primate traditions. As noted by McGrew (1992, p. 196), 'termite fishing may just as well have been invented in 1959, the year before Jane Goodall arrived, or a million years ago'. No living primate species is a direct model for early hominin behaviour or capabilities, but the more we examine the long-term behavioural trajectory of animals with genetically and anatomically similar constitutions to our own, the more chance we have of identifying truly unique aspects of human behaviour.

CONCLUSION

The notion of primate archaeobotany builds on current trends to integrate nonhuman primates more usefully into discussions of human evolution. It benefits from having living subjects to study, and an established primatological literature recording plant consumption and exploitation among a large number of species. Beyond diet, these

studies have demonstrated the importance of plant-processing and vegetation tools to extant African chimpanzees, Southeast Asian orangutans and South American capuchin monkeys in particular, and further discoveries among other taxa (such as bonobos and gorillas) are likely. Developing a more explicitly archaeobotanical approach to nonhuman primate species also benefits the study of primate evolution in its own right, and aids conservation efforts by increasing our understanding of changes in primate-plant interactions over time. Importantly, recognising the existence of a nonhuman archaeobotanical record provides comparative data for archaeologists working in areas with extant tool-using primates, giving an alternate perspective on ways that intelligent species with similar physiological adaptations to our own make use of the botanical environment.

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