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The formation of the brush-sticks: modification of chimpanzees or the by-product of folding?

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Abstract Based on field research and experimental treatments of trees, we investigated the formation of the brush-like shape of digging sticks used by chimpanzees (*Pan troglodytes troglodytes*). Evidence obtained in the field consisted of digging sticks found in Mboete, Equatorial Guinea, which is a newly reported locality for this type of tool, and Campo, Cameroon. Digging sticks used by chimpanzees in these areas had a brush-like shape at one end, which was quite different from the other end that was probably used for digging. In our tree-breaking experiment, 8 out of 17 species acquired a typical brush-like shape without human modification when broken off, and the shapes of the stumps were similar to those found in the field. Other species did not acquire the brush-like shape naturally or even after human modifications, and the stumps had different shapes from those found in the field. Our findings suggest that the brush-like shapes of digging sticks are often naturally formed when broken off from trees, depending on the nature of the fibre structure, and that the brush-like end is not used as the digging tool. We conclude that the vegetation surrounding termite mounds might influence how chimpanzees combine different types of tools, i.e., digging stick, brush-stick and fishing tool, for obtaining termites.

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Introduction

Chimpanzees inhabiting central-west Africa use various types of tools and techniques for obtaining termites. Jones and Sabater Pi (1969) first reported that chimpanzees (*Pan troglodytes troglodytes*) in Equatorial Guinea used digging sticks to excavate termite mounds. Sugiyama (1985) reported the use of brush-sticks, i.e., sticks that have a brush-like shape at one end, in Cameroon. At several other sites, fishing tools have been found together with digging sticks (Fay and Carroll 1994; Suzuki et al. 1995; Bermejo and Illera 1999). Digging sticks are generally thick (≥1 cm in diameter), robust, and straight, without branches or leaves, and are often found inserted in termite mounds. In contrast, fishing tools are generally made of twigs or herbaceous plants. They are thin and flexible, and therefore not suitable for digging, and can easily be distinguished from digging sticks (Fay and Carroll 1994).

Digging sticks have been categorized into two types by their form. One has at least one brush-shaped end not encrusted with mud and the other is blunt with no brush-shaped ends (Sugiyama 1985). Brush-sticks have been reported from four sites in central-west Africa: Okorobiko in Equatorial Guinea (McGrew et al. 1979); Campo in Cameroon (Sugiyama 1985); Lossi in Republic of the Congo (Bermejo and Illera 1999); and Bai Hokou in Central Africa (Fay and Carroll 1994). In addition, brush-sticks presumably used for obtaining bees (larvae, pupae, and honey) or ants, but not termites, have been reported from Lopè, Gabon (Tutin et al. 1995). However, the means by which chimpanzees manufacture and use brush-sticks remain unclear, because direct observation of chimpanzees in central-west Africa has been extremely rare.

Two contradictory hypotheses have been proposed with respect to the development of the brush-like shape of the sticks. Based on field experiments, Sugiyama (1985, 1997) suggested that the brush is formed when a chimpanzee modifies the stick by biting or using a secondary tool. However, Muroyama (1991) suggested that the trees used by chimpanzees to make digging-sticks are often fibrous, so that broken sticks naturally attain a brush-like shape. Similarly, Bermejo and Illera (1999) reported that sticks from *Alchornea floribunda* trees become brush-like when they are broken off slowly.

A plausible explanation concerning the use of brush-sticks is that chimpanzees collect termites using the brush-like end (Sugiyama 1985). Fishing tools have been reported together with digging tools at several sites, and the brush-like shape of fishing tools is thought to be more efficient in collecting termites because it is easier for termites to bite the brushy ends (Suzuki et al. 1995). Bermejo and Illera (1999) directly observed a chimpanzee eating termites from the brush end of a digging stick. Adding to this single observation, further evidence supporting the use of the brush is required. An evaluation of whether the brush-shape was made by chimpanzees or not will be helpful information for a better understanding the use of brush-sticks for obtaining termites.

During research conducted in Equatorial Guinea, we found brush-sticks in Mboete, a new locality (Takemoto and Hirata, unpublished data, ECOFAC report, Equatorial Guinea). The present paper aims to clarify the way in which the brush-like shape is formed, namely whether or not this is the product of chimpanzee modification. We used the two following approaches to the problem: experimentally breaking sticks off 15 West African and 2 Japanese tree species, and re-examining digging sticks found in Equatorial Guinea and sticks found by Sugiyama (1985) in Campo, Cameroon.

Methods

Experimental breaking of trees

Breaking-off experiments were carried out for 15 species in Bossou, Guinea, West Africa and for 2 species in Japan. We selected tree trunks that were 10–13 mm in diameter (the range of size in which most digging sticks occurred according to previous studies) and by manually breaking sticks off the tree by bending them. Fifteen West African species were selected because they were abundant and of the appropriate diameter. Because there is no information on how chimpanzees break branches to make such tools, we broke them in the simplest way, i.e., merely bending the branch sharply with no twisting movements. It was not possible to control the speed of breaking because the hardness and flexibility of each tree species varied. Thus, we broke trees as quickly as possible. A stick about 40 cm long without branches was produced from each tree. We measured the length of the brush-like shape of the sticks and the stumps (remaining parts of the original trees). The brush-like shape was defined by the length of wood fibre frayed from the folding surface >0.5 cm. After breaking off a stick, we applied 10 iterations of one of five possible treatments to the ends of the sticks: chewing, pounding with a stone, pounding on a tree trunk, pressing to a tree trunk, and digging in the soil. The change in shape after each treatment was recorded.

We also experimentally removed sticks from two native Japanese species, *Eurya japonica* (Theacea), a small evergreen, and *Rhus sylvestris* (Anacardiacea), a small deciduous tree. These two species were selected because they are abundant in Japanese forests and were easy to find in sufficient numbers for this experiment. In addition, information on the xylem structure of these trees was available and we could evaluate the result of breaking off in terms of the xylem structure, while equivalent information was not available on African tree species.

Field observations

We conducted our investigation in continental Equatorial Guinea (Takemoto and Hirata, unpublished data, ECOFAC report, Equatorial Guinea) in March 2001, at the onset of the minor rainy season (Just et al. 1995). We searched throughout three regions in Rio Muni and found brush-sticks near Mboete (Fig. 1). This village is located in the southwestern part of the country (1°18′32″N, 9°36′12″E). Mboete is located approximately 35 km to the southwest of Okorobiko, where Sabater Pi conducted research during the 1960s, and approximately 16 km from the coast. The country covers 2,800 km^2 and has five protected areas. Mboete is not located in a protected area (Union mondiale pour la nature (UICN) 1996).

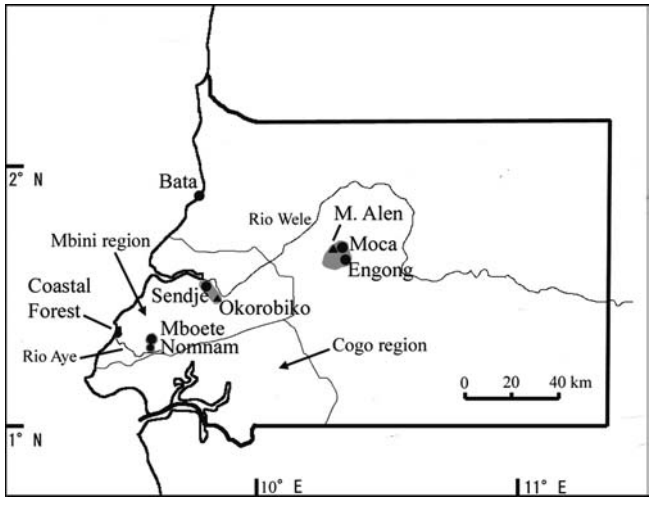

Fig. 1 Map of Rio Muni, Equatorial Guinea

Re-evaluation of the brush-sticks collected at Campo

The details of the geographical features of Campo, Cameroon, the study methods, and the results have been provided by Sugiyama (1985). Sugiyama's study was conducted in December and January, during a major dry season (Hoshino et al. 1984; Hoshino 1985).

Thirty-five of the original 52 brush-sticks collected at Campo by Sugiyama (1985) have been stored at the Primate Research Institute (PRI), Kyoto University. We re-examined the shapes of the sticks, and both ends were checked for evidence of modification by chimpanzees, such as teeth marks. Photographs of the 14 stumps taken during Sugiyama's study were also available for examination. We checked the shapes of the stumps and compared them with those observed at Mboete. Because it was obvious that the stumps were not used by chimpanzees to dig out termite mounds, it can be assumed that the shape of the stumps retain the natural shape when chimpanzees broke the sticks from the trees.

Comparison of digging sticks found in different localities

We examined local differences among digging sticks described in published studies. Specifically, we examined the ratio of brush-sticks to digging sticks, and the length of the brush-like shape. The sticks broken off in our experimental treatment were also included in the comparison for analysis of the length of the brush-like tip.

Results

Tree-breaking experiment

Trees from the same species showed virtually the same shape on both ends of sticks and stumps after breaking them off. Fifteen African tree species were divided into four types by the shape of the stump and the proximal end of the removed stick, though there were some intermediate cases (Table 1, Fig. 2a). Results of modifications for sticks were also roughly fixed within each type and differed among types. Table 2 shows measurements of all tree species.

Trees, which generally produced a brush-like shape when the stems were broken, were grouped into type A: the proximal end showed a brush-like shape in all cases, whereas the tip of the sticks (the distal end) lacked a brush-like shape in some cases. The brush-like shape was elongated and widened by chewing, pounding with a stone, or pressing to a tree trunk, but was not affected by pounding on a tree trunk or pressing to the ground. When we used the sticks for digging in the ground, the ends became bent and soil adhered to them. The sticks acquired a shape similar to that of the digging end of sticks observed in the Mboete forest. The fibres of the xylem were strong and did not break easily when bent (Fig. 2b), and they formed a long diagonal shape on the stump with bark. The mean length of the diagonal breaking point on the stumps was 20.1 (±3.4 SD) cm, similar in shape to those observed in the field.

Trees, which did not show a brush-like shape when broken off or after any kind of treatment, were grouped into type D. The sticks were light, and the fibres of these species were weak and easily broken (Fig. 2c). Because the fibres were weak, they were crushed by treatments such as pounding with a stone (Fig. 2d). Sometimes the ends of the stumps loosened to a certain degree and some bark remained, but generally they broke off horizontally and rarely produced the long diagonal scars observed in A type.

Trees of type B were similar to type A, but the length of brush and diagonal shape of the stump was less than a half of that of type A. Type C trees were similar to type D, but sometimes formed frayed ends with thick fibre (not typical brush-like shape) and rarely formed diagonal shaped stumps. One Japanese tree species (*E. japonica*) showed the same result as type A and another species (*R. sylvestris*) was classified as type D.

Chewing or pounding treatments left traces by teeth or crush marks on the fibres of all species. We carefully

Table 1 Experimental fabrication of the brush-like shape of the sticks removed from several tree species. > Brush-like shape became longer and wider, = brush-like shape did not change, × brush-like shape did not occur or lost its shape

Treatment	A type	B type	C type	D type
Breaking off (without modification)	Brush-like shape	Shorter brush-like shape with thin fiber	Sometimes frayed with thick fiber	No brush-like shape
Chew	>	>	×	×
Pound with stone	>	>	×	×
Dig in ground	×	×	×	×
Pound on tree trunk	=	=–>	× (frayed)	×
Press against tree trunk	=	=	× (frayed)	×
Stump	Diagonal shape	Shorter diagonal shape	Sometimes formed diagonal shape	No diagonal shape
Species	*M. puberula* *Coffea arabica* *E.japonica*	*Craterispermun laurinum* *Harungana madagascariensis* *G. brevis* *Alchornea cordifolia*	*M. libericus* *Rinorea oblongifolia* *Mareya spicata* *Trichilia heudelotii* *Parkia bicolour*	*S. monbin* *Pycnanthus angolensis* *Myrianthus arboreus* *Mangifera indica* *R. sylvestris*

Fig. 2 Breaking experiment. **a** Proximal ends of the sticks without modification. *Right to left*: *M. puberula* (A type), *Glyphaea brevis* (B type), *Myrianthus libericus* (C type), *Spondias monbin* (D type). **b** *M. puberula* (A type) showing fibrous structure after having been broken off. **c** *S. monbin* (D type) showing a shape different from that seen in *M. puberula* at the breaking point. *S. monbin* was easy to break, and no stump had a diagonal shape. **d** Modification treatment for *S. monbin* (D type). *Right to left*: dig in ground, pound with stone, chew, press against tree trunk, pound on tree trunk

examined 37 brush-sticks collected in Mboete and Campo, but such traces were not found, perhaps because they were rather old.

Field observations

Mboete in Equatorial Guinea

We found two brush-sticks that were presumably used by chimpanzees. The first stick was found on a termite mound 15 cm high, 95 cm long, and 50 cm wide. The stick was 41 cm long and 1.4 cm in diameter (Fig. 3a, b). One end of the stick had a brush-like shape, approximately 4 cm long, from which the bark was stripped. The other end (the digging end), which was half-buried in the soil, had a 5-cm long fray. This part was bent, and the bark and core remained intact. Some soil adhered to the surface of the digging end.

Approximately 1 m from the termite mound, we found the stump still erect in the ground. We also found the top of the tree entangled in vines, still retaining green foliage. From these leaves we identified that the stick had been broken off from young *Microdesmis* sp. The stump was 96 cm high, and was broken off diagonally, beginning at 80 cm. We found thin fibres at the end, but these did not have a brush-like shape. The 16-cm-long broken section matched the brush end of the stick. The top of the tree was 120 cm long and the bottom 20-cm section was also broken off diagonally. Thus, the stick had been removed from the 220-cm-high tree. The shapes of the brush-end and the stump were very similar to type A trees in our experiments.

Table 2 Tree-breaking experiment of African and Japanese trees (see text for details)

Species	*n*	Mean diameter (mm ± SD)	Length of brush end (cm ± SD)	Length of diagonal shape of the stump (cm ± SD)	Type
African species					
M. puberula	5	11.0 ± 1.0	Proximal end: 4.0 ± 2.0 Distal end: 1.2 ± 0.8 ($n = 3$)	20.1 ± 3.4	A
C. laurinum	5	11.4 ± 0.4	Proximal end: 1.0 ± 0.7	9.8 ± 5.3	B
M. libericus	5	11.4 ± 1.5	–	13.7 ± 3.1 ($n = 3$)	C
S. monbin	5	12.3 ± 1.2	–	–	D
Japanese species					
E. japonica	20	11.4 ± 0.4	Proximal end: 3.5 ± 1.8 Distal end: 2.6 ± 1.7 ($n = 11$)	15.5 ± 7.5	A
R. sylvestris	12	10.5 ± 2.9	–	–	D

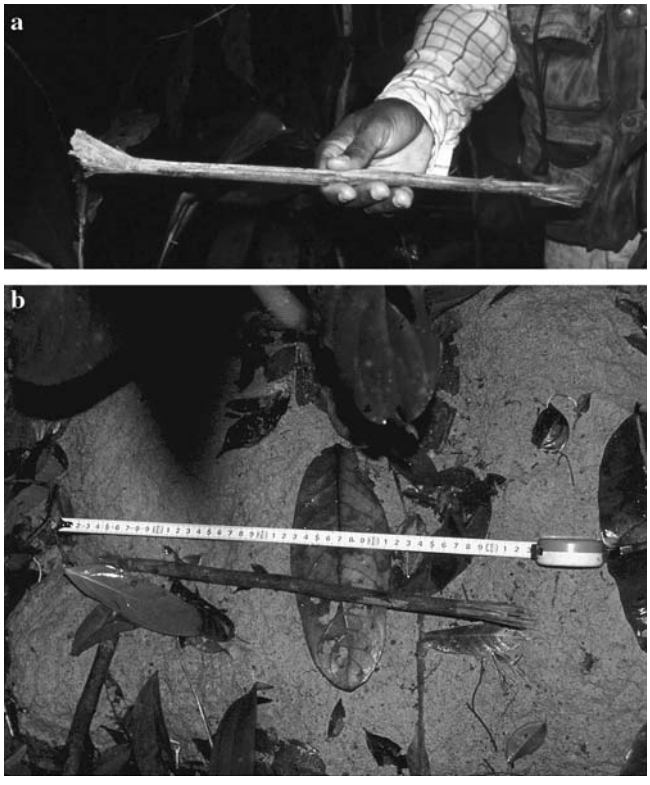

Fig. 3 **a** A brush-stick found in Mboete, Equatorial Guinea. **b** The brush-stick on the termite mound

The second digging stick was found about 50 m away from the first one. It was at the bottom of another termite mound (80 cm high, 200 cm long, and 150 cm wide). This stick was 35 cm long and straight, with a diameter of 1.0 cm. From the bark, we identified it as *Strombosiopsis* sp. The bark was stripped off at both ends over a length of 0.5 cm. One end of the stick had a short brush-like shape and the other end was rounded and had soil adhering to it. The stump could be categorized as B type.

The secondary forest where these sticks were found was adjacent to a farm. The forest interior was dark, no terrestrial herbaceous vegetation covered the forest floor, and few young trees made up the understory.

Campo

Two out of 14 stumps were broken off almost horizontally, and short, thin fibres were present at the ends of these two stumps, which we categorized as type D (Fig. 4a). A portion of the branch above the point of breakage connected to the stump was broken but not detached. If this part had actually been detached, the stick would have had a brush-like shape as seen in Fig. 4b. The other 11 stumps were broken off diagonally, and the breaking points were relatively long (10–20 cm; Fig. 4c), resembling to those found at Mboete and type A or B trees in our experiments.

We were able to identify the proximal and distal ends of 30 of the 35 sticks stored at PRI. Out of these 30 sticks, 21 were brushy at the proximal end (in other words, the distal end was the digging end), and four were brushy at the distal end (i.e., the proximal end was the digging end). The remaining 5 were suspected to have been used at both ends for digging, or neither end seemed to have been used.

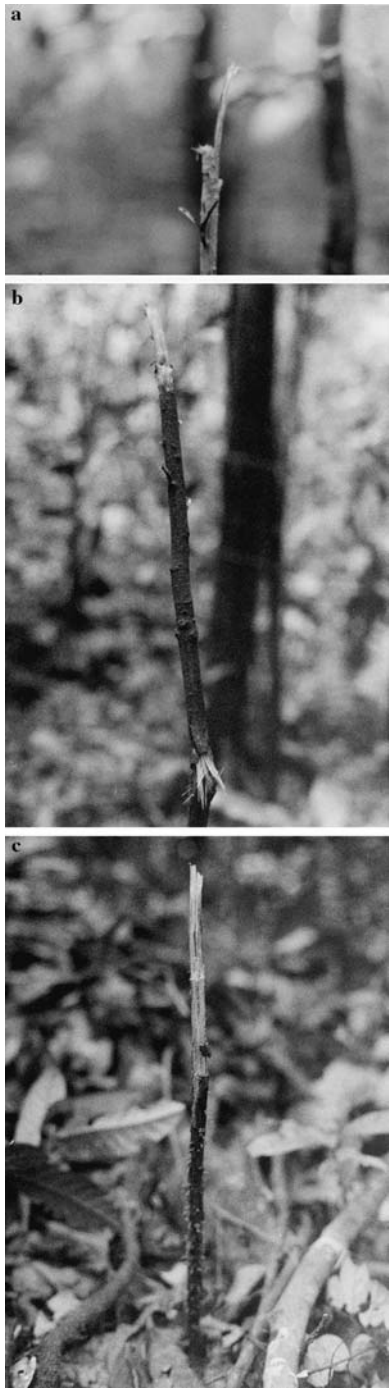

Fig. 4 Stumps from which brush-sticks were broken off, found at Campo, Cameroon. **a** Two of 14 stumps had a horizontal shape at the breaking point. **b** A stump showing a brush-like shape below the actual breaking point. **c** A diagonal shape at the breaking point of a stump

Table 3 Comparisons of digging tools among study sites

Research site	*n* (digging tools)	Mean diameter (mm ± SD)	Length of brush end (cm ± SD)	Ratio (%) (brush-sticks over digging sticks)	*n* (fishing tools)
Okorobiko [1]	155	11(range: 1–15, $n = 46$)	2–3	30.4 (14/46)	–[a]
Mayang River [2]	4	8.7 ± 0.8	–	–	–
Mboete [3]	2	14 and 10	4.0 and 0.5	100.0 (2/2)	0
Campo [4]	110	9.9 ± 1.6	5.4 ± 6.4	47.3 (52/110)	4
Campo [5]	81	9.0 ± 1.6	–	50.0 (33/66)	16
Lossi [6]	168	9.8 ± 2.3	3.8 ± 1.4	21.4 (36/168)	107
Bai Hokou [7]	74	12.3 ± 3.5	3.5 ± 2.0	20.3 (15/74)	62
Ndoki [8]	66	10.9 (range:0.5–1.8)	–	0.0 (0/66)	42
Belinga [9]	2	14–18[b]	–	–	23
Lopé [10, c]					
For Apis	95	15.7 ± 5.2	2.0 ± 0.9	80.0	–
For ants	28	11.2 ± 5.0	2.2 ± 1.2	82.2	–
For *Meliponula*	14	14.8 ± 7.4	2.6 ± 2.0	85.7	–
For *Trigona*	4	10.0 ± 3.9	1.2	75.0	–

[1]Equatorial Guinea (McGrew et al. 1979), [2]Equatorial Guinea (Gonzalez-Kirchner and de la Maza 1992), [3]Equatorial Guinea (this study) [4]Cameroon (Sugiyama 1985), [5]Cameroon (Muroyama 1991), [6]Congo (Bermejo and Illera 1999), [7]Central Africa (Fay and Carroll 1994), [8]Congo (Suzuki et al. 1995), [9]Gabon (McGrew and Rogers 1983), [10]Gabon (Tutin et al. 1995)

[a]Not mentioned or no observation
[b]Proximal diameter = 17 and 18 mm, distal diameter = 14 and 16 mm
[c]In Lopé, brush-sticks were used to obtain other invertebrates, and the lengths of the brush ends were measured only when the brush-like shape was > 10 mm long

Comparison of digging tools

The digging tools found across various study sites were compared (Table 3). The ratio of brush-sticks to digging sticks varied across areas. Some of the sticks found at Okorobiko might have been more aptly categorized as fishing tools, as they included relatively thin, flexible and herbaceous tools (Sabater Pi 1974). No brush-sticks were reported from Ndoki, Mayang River, or Belinga. Among four sites where large numbers of digging sticks were found (Bai Hokou, Campo, Ndoki, Lossi), there was a clear difference in the proportion of brush-sticks to digging sticks ($\chi^2 = 67.3$, $df = 3$, $P < 0.001$) and of digging sticks to fishing tools ($\chi^2 = 30.9$, $df = 3$, $P < 0.001$). The lengths of the brush-like shape at the proximal ends of *Microdesmis puberula* and *E. japonica* sticks in our experiment (before any treatments) did not differ significantly from those of the brush-sticks found at Campo, Lossi, and Bai Hokou, where information on length was available (*Microdesmis*: Campo, $t = 1.11$, n.s.; Lossi, $t = 0.28$, n.s.; Bai Hokou, $t = 0.48$, n.s., *Eurya*: Campo, $t = 1.95$, n.s.; Lossi, $t = 0.69$, n.s.; Bai Hokou, $t = 0.00$, n.s.). The lengths of the brushes at the distal ends of these species sticks were shorter than those found at Campo and Lossi (*Microdesmis*: Campo, $t = 4.39$, $P < 0.001$; Lossi, $t = 4.03$, $P < 0.001$; Bai Hokou, $t = 3.66$, $P < 0.001$, *Eurya*: Campo, $t = 2.73$, $P < 0.01$; Lossi, $t = 2.37$, $P < 0.05$; Bai Hokou, $t = 1.21$, n.s.).

Discussion

Our experiments and re-examination of previously published materials suggest that at least some of the brush-like shapes observed in the field could be the natural result of chimpanzees simply breaking branches off the tree trunks.

Generally, the wood of early seral trees has a soft texture and low density compared with the slower-growing tropical hard woods of the primary or mature forest, and the xylem of lianas show flexibility and great tensile strength (Richards 1996). The wood fibre that occupies most of the xylem produces these features. The proportion of xylem fibre, its size, proportion of cell wall, and structure largely affects the specific gravity, strength, and several other wood characteristics (Foster 1949). As each species has a given range of these variables in relation to their life forms or ecological status (i.e. pioneer or persistent), it will produce a specific shape when broken off. According to Hirai (1996), the xylem of *Eurya* (a species at the climax stage) has long libriform wood fibres (0.7–2 mm), thicker cell walls (3–7×10^{-3} mm), and thin, dense vessels (0.02–0.065 mm diameter). In contrast, the xylem of *Rhus* (an early seral tree) has short libriform wood fibres (0.3–1.1 mm), thinner cell walls (2–3×10^{-3} mm), and thick, sparse vessels (0.1–0.24 mm diameter). Although the growing stage must be considered, the xylem of *Eurya* may form the brush-like shape when broken off because the vertical structure of these xylem elements is long and complicated, and the cell wall is strong.

Our experiments also showed the possibility that the brush-like shape could be lost if it was used for digging. It is likely that, in most cases, the proximal end more easily produces the brush-like shape compared with the distal end and that chimpanzees use the distal end for digging.

In summary, our experiments did not provide the positive evidence that chimpanzees manufactured the brush ends of sticks by secondary modification; rather

the brush-ends are often naturally formed when trees are broken off. Comparison with two Japanese tree species suggests that the fibre structure is a major factor determining the forms of stick ends when broken off. In general, chimpanzees use materials found near the site where they are to be used (McBeath and McGrew 1982), and the digging stick is not an exception (Sabater Pi 1974). Therefore the available tree materials, and in consequence the forest structures around termite mounds may affect the difference in proportion of brush-sticks to digging sticks among each research site of chimpanzees. When considering the ecological influence of tool use, detailed analysis of vegetation around the place where chimpanzees use tools will be important.

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References

Bermejo M, Illera G (1999) Tool-set for termite—fishing and honey extraction by wild chimpanzees in the Lossi Forest, Congo. Primates 40:619–627

Fay JM, Carroll RW (1994) Chimpanzee tool use for honey and termite extraction in Central Africa. Am J Primatol 34:309–317

Foster AS (1949) Practical plant anatomy, 2nd edn. D. Van Nostrand, New York

Gonzalez-Kirchner JP, de la Maza MS (1992) Stick use by wild chimpanzees: a new locality in Rio Muni. Folia Primatol 58:99–102

Hirai S (1996) Encyclopedia of Japanese trees. Asakura-syoten, Tokyo (in Japanese)

Hoshino J (1985) Feeding ecology of mandrills (*Mandrillus sphinx*) in Campo Animal Reserve, Cameroon. Primates 26(3):248–273

Hoshino J, Mori A, Kudou H, Kawai M (1984) Preliminary report on the grouping of mandrills (*Mandrillus sphinx*) in Cameroon. Primates 25:295–307

Jones C, Sabater Pi J (1969). Sticks used by chimpanzees in Rio Muni, West Africa. Nature 223:100–101

Just J, Fa JE, perez del Val J, Castroviejo J (1995) Market dynamics of bushmeat species in Equatorial Guinea. J Appl Ecol 32:454–467

McBeath NM, McGrew WC (1982) Tools used by wild chimpanzees to obtain termites at Assirik, Senegal: the influences of habitat. J Hum Evol 11:65–72

McGrew WC, Rogers ME (1983) Chimpanzees, tools, and termites: new record from Gabon. Am J Primatol 5:171–174

McGrew WC, Tutin CEG, Baldwin PJ (1979) Chimpanzees, tools, and termites: cross-cultural comparisons of Senegal, Tanzania, and Rio Muni. Man 14:184–214

Muroyama Y (1991) Chimpanzees' choices of prey between two sympatric species of Macrotermes in the Campo Animal Reserve, Cameroon. Hum Evol 6(2):143–151

Richards PW (1996) The tropical rain forest, 2nd edn. Cambridge University Press, Cambridge

Sabater Pi J (1974) An elementary industry of the chimpanzees in the Okorobikó Mountains, Rio Muni (Republic of Equatorial Guinea), West Africa. Primates 15(4):351–364

Sugiyama Y (1985) The brush-stick of chimpanzees found in southwest Cameroon and their cultural characteristics. Primates 26(4):361–374

Sugiyama Y (1997) Social tradition and the use of tool-composites by wild chimpanzees. Evol Anthropol 6:23–27

Suzuki S, Kuroda S, Nishihara T (1995) Tool-set for termite-fishing by chimpanzees in the Ndoki Forest, Congo. Behaviour 132:219–235

Tutin CEG, Ham R, Wrogemann D (1995) Tool-use by chimpanzees (*Pan troglodytes*) in the Lopé Reserve, Gabon. Primates 36:181–192

Union mondiale pour la nature (UICN) (1996) "l'Atlas" pour la conservation des forêts tropicales d'Afrique. Jean-Pierre de Monza, Paris