Evidence of termite foraging by Swartkrans early hominids

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Previous studies have suggested that modified bones from the Lower Paleolithic sites of Swartkrans and Sterkfontein in South Africa represent the oldest known bone tools and that they were used by *Australopithecus robustus* to dig up tubers. Macroscopic and microscopic analysis of the wear patterns on the purported bone tools, pseudo bone tools produced naturally by known taphonomic processes, and experimentally used bone tools confirm the anthropic origin of the modifications. However, our analysis suggests that these tools were used to dig into termite mounds, rather than to dig for tubers. This result indicates that early hominids from southern Africa maintained a behavioral pattern involving a bone tool material culture that may have persisted for a long period and strongly supports the role of insectivory in the early hominid diet.

bone tools | *Australopithecus robustus* | southern Africa | Lower Paleolithic

Exactly where, when, for what purpose, and by whom the first bone tools were used, and what the evolutionary, adaptive, and cognitive implications of such a use are, are questions that have provoked considerable debate among researchers interested in early human culture. The main reason for this debate is that nonhuman taphonomic processes are known to produce pseudotools: objects that appear morphologically similar to humanly modified and used tools (1–4). To distinguish between pseudotools and true tools it is necessary to combine taphonomic analysis of the associated fossil assemblages, microscopic studies of possible traces of manufacture and use, and the experimental replication of the purported tools. Using the purported bone tools identified by Brain and his coworkers (5–7) from the Lower Paleolithic sites of Swartkrans (Members 1–3; ca. 1.8–1 million years ago) and Sterkfontein (11, 12) (Member 5, ca. 1.7–1.4 million years ago), we reanalyze the evidence for their being tools and reappraise their probable function. Although Brain and Shipman's (7) work was based on microscopic analysis of a number of specimens, their interpretation of these bones as tools used for digging up tubers and working skins was not supported by a comparison of the purported tool morphology and wear pattern with those produced by natural processes known to mimic anthropic modifications. Brain and Shipman did not consider alternative functional interpretations, nor did they test them experimentally by using appropriate analytical methods. Other potentially relevant data (species, type of bone used, fracturing patterns, degree of weathering, bone flake morphometry, spatial distribution) were not collected or discussed by Brain and Shipman in the context of the site's taphonomy. The aim of the present study is to provide a multidisciplinary framework for assessing the origin of the wear patterns recorded on the Swartkrans purported bone tools.

Materials and Methods

Swartkrans and Sterkfontein Material. High-resolution dental impression material (13) (Coltene President microSystem light body surface activated silicone paste for molds, and Araldite M resin and HY 956 Hardener for casts) was used to replicate the 68 Swartkrans (SKX) and 1 Sterkfontein (SE) purported bone tools, and optical and scanning electron microscopy was used to identify their surface modifications. Microscopic images of the transparent resin replicas were digitized at 40× magnification on a sample of 18 fossils from Swartkrans. The orientation and dimension of all visible striations were recorded by using MICROWARE image analysis software (14). Because accurate measurements require a relatively flat surface, we preferred to measure those aspects of the specimens guaranteeing reliability of results. Microscopic inspection of the wear patterns on the remaining specimens and measurements taken randomly on these objects indicate that extending the quantification analysis to all of the collection would not have significantly changed our results.

The collection of 23,000 bone fragments from Swartkrans (10) was then taphonomically studied and examined for specimens with a wear pattern similar to that recorded on the purported bone tools from the same site. Comparative taphonomic analysis was conducted on Swartkrans because most of the putative tools come from this site, and because the stratigraphic provenance of both tools and faunal remains is reliable. In the course of research, 16 additional specimens from Swartkrans Members 1–3 that had wear comparable to that of the 69 previously described specimens (7) were identified, bringing the total to 85.

Comparative Material. After investigation of the content and context of the Swartkrans material, the next step involved the examination of 35 reference collections of modern and fossil bones (15–27) from open air and cave contexts (13,301 specimens) modified by 10 nonhuman agents (hyena, dog, leopard, cheetah, porcupine, river gravel, spring water, flood plain, wind, and trampling) without evidence of human involvement. At a macroscopic scale, 24 of the pieces examined appeared similar to the SKX/SE specimens. Resin replicas of these pseudotools were made and examined microscopically. A comparison was then made between the wear patterns on the SKX/SE fossils, those on two antelope long bone shaft fragments used by Brain to dig up bulbs of *Scilla marginata* and *Hypoxis costata* (7), and those on bone tools experimentally used by the authors. This last sample included 11 antelope limb bone shaft fragments and horn cores, used to dig for tubers in a wide range of soil types, to scrape and pierce animal hides, and to excavate termites from termite mounds found in the Sterkfontein Valley today. The worn tips of these bones were each replicated with dental impression material after 5, 15, 30, and 60 min of use. Resin replicas of the SKX/SE fossils and

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experimental tools were made, and then examined under transmitted light. Image analysis was conducted on digitized images of the wear patterns on 18 SKX/SE fossils, 9 of our experimental tools, and both of the experimental tools used by Brain to dig up bulbs. Microscopic analysis of all of the experimental tools was conducted to verify that they would have provided comparable results.

Results

Microscopic analysis revealed that the SKX/SE specimens had distinctive wear patterns (Fig. 1a). The specific elements that constitute the wear pattern include the following: (*i*) a single rounded end with smoothing/polishing confined to an area of between 5 and 50 mm from the tip, (*ii*) individual striations covering the worn tip, including any recessed areas, 5–40 μm wide and running parallel or subparallel to the long axis of the bone, decreasing in number away from the tip, and (*iii*) absence of similar striations from the remainder of the bone. A very small number of striations oriented perpendicular to the main axis of the bone, generally posterior to the longitudinal parallel striations and ranging between 100 and 400 μm in width, were recorded on some specimens. The localized wear pattern on all 85 specimens was established as being distinctly different from the patterns created by nonhominid taphonomic processes such as carnivore gnawing and bone weathering that affect the remainder of the assemblage. In addition, the low percentage of tip wear (0.5%, $n = 16,535$) in the Swartkrans faunal assemblage makes it unlikely that such wear is related to a common or currently recognized form of depositional sedimentary abrasion of the type associated with South African cave deposits (28, 29).

It was found that the wear patterns on bones from river gravel and flood plain contexts, as well as those from spotted hyena dens, showed gross morphological similarity to the SKX/SE specimens, in that they had smoothly rounded or pointed tips. None of them, however, had the distinctive microwear pattern observed on the SKX/SE specimens. From this we conclude that the damage found on the 85 SKX/SE fossils was not caused by known nonhuman agents.

The wear patterns on the SKX/SE specimens and all of the experimental tools used to dig in the ground and the termite mounds were similar in that they all had a rounded tip with smoothing/polishing confined to an area between 5 and 50 mm from the tip. They also had individual striations confined to the worn tip and absent from the remaining bone surface. There were, however, two distinct striation patterns (Fig. 1).

All experimental tools used for digging tubers and insects from the ground recorded superimposed, randomly oriented striations of various widths (ca. 30–80 μm). Examples are show in Fig. 1 *b* and *c* and in Fig. 7, which is published as supplemental data on the PNAS web site, www.pnas.org. This striation pattern is the result of repeated tangential impacts of the tool tip against soil with mixed particle sizes, including angular dolomite blocks. In contrast, the experimentally created tools used exclusively to excavate termite mounds had a different wear pattern that closely matched that of the fossils (Fig. 2; Table 1). The striations

radiated from the tip, were finer (ca. 5–30 μm), and ran parallel or subparallel to the long axis of the bone.

These striations appear to result from repeated abrasion caused by angular fine-grained sediment with a limited range in particle size, such as that found in the presorted sediment constituting the hard outer crust of termite mounds (30). The subparallel arrangement of the striations is due to the fact that a motion parallel to the main axis is the most efficient way to perforate and flake off the crust of a mound, an activity that encourages the swarming of termites to the surface. When the digging activity stops, the termites cease to emerge.

These distinctive striations were evident on the experimentally created tools after only 15–30 min of use—the time necessary to dig in one medium-sized termite mound. The wear pattern on the SKX/SE specimens and that on the experimentally created termite-digging tools are virtually indistinguishable (see Fig. 1 *a* and *d*).

An unpaired *F* test confirms that a significant difference ($P < 0.0001$) exists among the variance of the orientation of the striations on Swartkrans bone tools, those on the bulb digging experimental tools used by Brain, and those on tools used by us to dig in soil in search of tubers. In contrast, the test indicates that the orientation variability of striations on experimental tools used to dig termites is comparable with that recorded on the Swartkrans tools ($P = 0.731$).

Because the values for striation width are not normally distributed, a nonparametric Mann–Whitney *U* test was carried out to compare the Swartkrans tools with each of the experimental tool types. While showing significant differences between Swartkrans tools and those used by Brain or by us to dig for tubers, this test also detects a difference between Swartkrans fossils and tools used to dig in termite mounds, in that experimental tools were apparently used in a sedimentary environment composed of slightly smaller abrasive particles. This difference may be due to the known variability in the sedimentological composition of termite mounds located in different areas and belonging to different species (30) and therefore does not affect our interpretation. Differences in the orientation of the striations between Brain's and our experimental tools used to dig up tubers and insects depend on the two distinct tasks for which they were used. Extraction of *Scilla marginata* and *Hypoxis costata*, as carried out by Brain, required scratching out the soil around these large bulbs and the removal of angular dolomitic blocks, an activity implying motions perpendicular or oblique to the bone main axis. Our random search for tubers and buried larvae was conducted with motions parallel or subparallel to the bone axis resulting in striations relatively parallel to the main axis of the bone.

Analysis of the breakage patterns on the SKX/SE bone tools indicates that the early hominid users selected heavily weathered bone fragments of a particular size range (13–19 cm) and shape (long, straight bone flakes and horn cores). Metric analysis of the Swartkrans faunal collection also suggests that the bone tools are a discrete population in that the lengths of the few complete worn bones fall outside the range of the length of the unworn long bone fragments from the site,

Table 1. Comparison between experimental and archeological tools in the orientations and widths of the striations

Tools	No. of striations	Orientations, 0–90°		Widths, μm	
		Mean	SD	Mean	SD
Digging *Scilla* and *Hypoxis* bulbs	330	44.2	27.7	63.1	56.0
Digging soil	336	61.3	21.1	46.7	44.7
Gathering termites	525	77.7	17.6	13.7	9.3
Swartkrans	816	75.2	22.2	18	14.6

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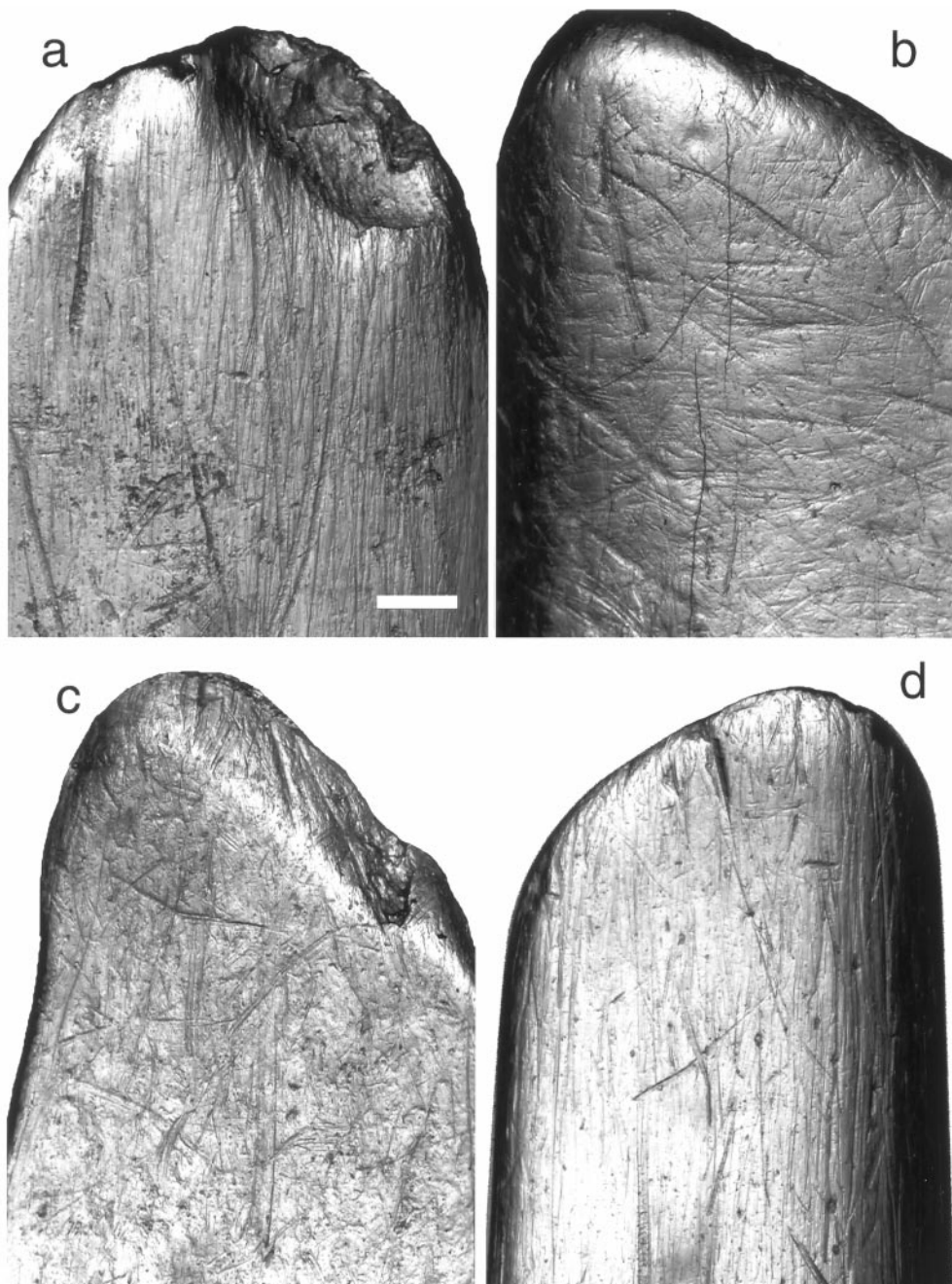
Fig. 1. Wear pattern on Swartkrans and experimental bone tool tips photographed in transmitted light from transparent resin replicas. (*a*) Bone tool from Swartkrans Member 3 (SKX 38830). (*b*) Tip of a tool used in Brain's experiment (7) to dig up *Scilla marginata* bulbs. (*c*) Experimental bone tool used to dig the ground in search of tubers and larvae. (*d*) Experimental bone tool used to dig in a termite mound. Note the similarity in the orientation and the width of the striations in *a* and *d*. (Scale bar, 2 mm.) Related figures are published as supplemental data on the PNAS web site, www.pnas.org: Fig. 4, Swartkrans bone tools; Fig. 5, use of a bone tool to dig a termite mound; and Fig. 6, wear patterns as in *a* and *d* above.

and even the broken putative tools are generally longer (Fig. 3). A similar result is obtained when the widths of the tools are compared with those of the other fragments, or the thickness of the compact bones in the two populations, suggesting that the wear occurs on longer, wider, and more robust bone fragments only.

Discussion

The above results suggest not only that SKX/SE specimens were real tools but also that they were predominantly used to dig termite mounds found in the Swartkrans area. The same

interpretation may apply to the 23 undescribed, but similarly worn, bone tool pieces, recently found at the Drimolen early hominid site (31), suggesting that bone tool-assisted termite extraction was a persistent component of the subsistence behaviors of early hominids in this area. It is clear that termites were present in this region during the deposition of Swartkrans Members 1–3 by the direct evidence of termite-feeding taxa such as *Proteles* sp. (aardwolf; Members 1 and 3), *Orycteropus afer* (antbear; Members 1, 2, and 3), and *Manis* sp. (pangolin; Member 3) represented in the Swartkrans faunal collection (32). Circumstantial evidence is provided by termite
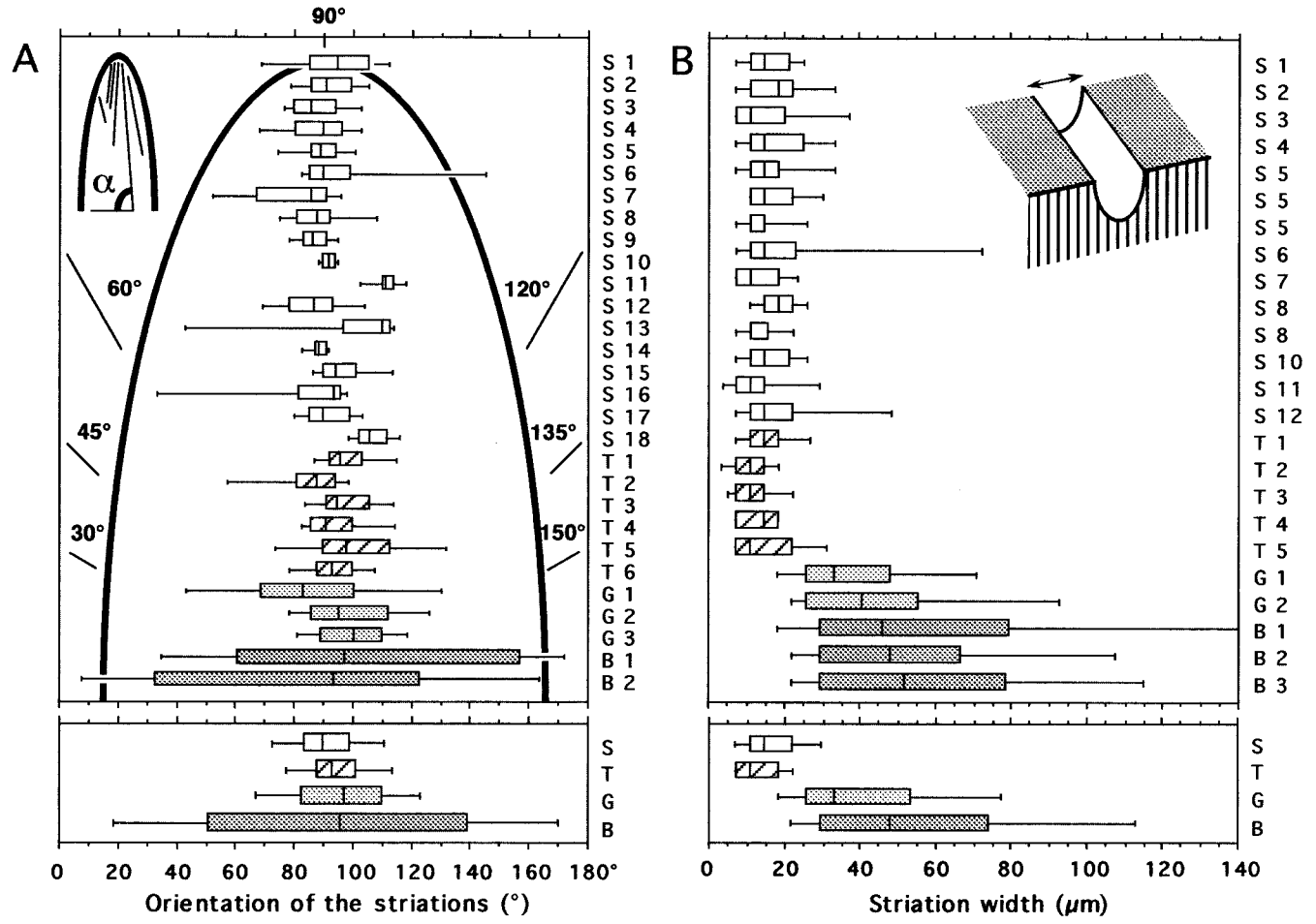
Fig. 2. Image analysis of the wear patterns on the Swartkrans fossils and on experimental bone tools. (*A*) Variability (*Upper*) and mean (*Lower*) in the orientation of the striations on the Swartkrans tools (S) and on experimental tools used to dig termite mounds (T), to excavate the ground in search of tubers and larvae (G), and to extract bulbs (B) [Brain's experimental tools (7)]. An unpaired *t* test has shown the orientation of the striations on the Swartkrans and termite digging tools to be the most similar, and significantly different from the other experimental tools. (*B*) Striation width as measured at 40× magnification on all of the striations visible. A nonparametric statistical test has shown the striation widths on all of the experimental tools to be significantly different from each other, but with the closest similarity recorded between the Swartkrans and termite digging tools. This figure is shown in color as Fig. 8 in the supplemental data on the PNAS web site, www.pnas.org.

damage identified on some fossils in the Swartkrans faunal collection (33).

Alternative explanations are unlikely for two reasons. They would require digging exclusively in a fine-grained, stoneless soil matrix, such as that of termite mounds, a feature unlikely to occur in the colluvial or fluviatile deposits of the Sterkfontein Valley or inside the SKX/SE caves (34). Second, although limb bone shaft fragments are suitable for breaking the hard crusts of termite mounds, they appear inefficient for other digging activities compared with the long, stout, and often heavy digging sticks used by modern hunter-gatherers to extract buried tubers, larvae, and small game (35). Digging experiments that we have conducted have shown slender and pointed bone artifacts to be the most efficient way to penetrate a mound, as opposed to the use of stone tools similar to those found at Swartkrans, which present an unsuitably large surface area, inefficient for perforating the hard crust of a termite mound.

The deposition of Swartkrans members 1–3 occurred over a period of more than half a million years, suggesting that the South African Plio-Pleistocene hominids incorporated termites

in their diet over an extended period. Termites are a valuable source of protein, fat, and essential amino acids in the diets of both primates and modern humans (36). While a rump steak yields 322 Calories per 100 grams, and cod fish 74, termites provide 560 Calories per 100 grams (37). Chimpanzees are known to "fish" for termites by using grass stalks as well as to perforate and dig termite mounds in a variety of ways (38–41), but never with bone implements. By digging termites out of their nests, hominids would have made use of a rich food source that was otherwise accessible only after rain when the insects emerge from their nests for breeding.

Similar pieces are unreported from East African sites of roughly the same age. Only some pieces from Olduvai Beds I and II may be equally old, and these are very different in form (42, 43) from those in South Africa. One possible reason is that the East African sites have been inadequately sampled, considering that the bone collections tend to be small compared with the large Swartkrans assemblage. Alternatively, this may be due to differences in tool usage, as exist amongst chimpanzee cultural traditions (38–41), or to the fact that termites were not a regularly utilized resource.

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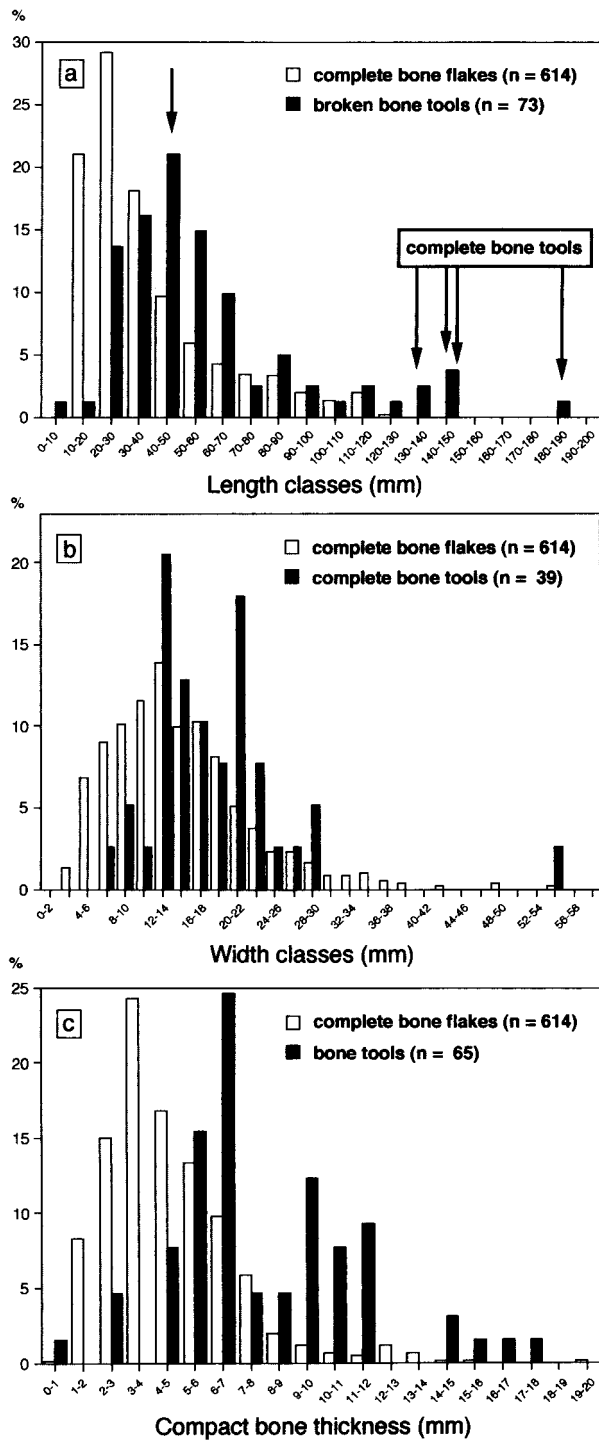
Fig. 3. Comparison between the length (*a*), width (*b*), and thickness of the compact bone (*c*) of Swartkrans bone tools and of a representative sample of bone fragments from Swartkrans members 1–3 showing no postdepositional breakage. Arrows in *a* indicate the length of the complete bone tools. This figure is shown in color in Fig. 9, which is published as supplemental data on the PNAS web site, www.pnas.org.

It is not easy at this stage to identify the hominid responsible for the use of the bone tools. The archaeological context of the three sites (Swartkrans, Sterkfontein, and Drimolen) where the bone tools have been found so far does not allow a clear-cut identification of the user. At all three sites there is evidence of the occurrence of *Homo* and *Australopithecus robustus*. At Swartkrans and Drimolen, where the majority of bone tools have been found, the co-occurrence of *Australopithecus robustus* and *Homo* is well established. The evidence from Sterkfontein is less secure. At Swartkrans and Drimolen, *Australopithecus robustus* constitutes the majority of hominid remains recovered (10, 31). Some hand bones from Swartkrans attributed to *Australopithecus robustus* have been described as capable of tool use (44). This evidence has, however, been disputed by other authors (45). There is no clear evidence of a change in occurrence of bone tools, stone tools, or hominid remains through Members 1, 2, and 3 of the Swartkrans Formation. The only site where stone tools have not been found is Drimolen. This seems to represent the only faint indication that the bone tool culture belonged to *Australopithecus robustus*. However, further excavation may well change our present interpretation.

Independent evidence of the probable user of these tools may also derive from dietary analysis based on carbon isotopes. *Australopithecus robustus* has been traditionally considered a vegetarian species (46–51). However, recent isotopic analyses (52, 53) have found a significant proportion of dietary carbon from C4 plants (i.e., with a photosynthesis using four-carbon molecules) indicative of a protein component, in the remains of both *Homo* and *Australopithecus robustus*. C4 plant carbon may be provided by grass-eating herbivores, but also by grass-eating termites. Only a detailed characterization of the isotopic signatures of different species of termites may establish whether only one or both of these hominids were utilizing this resource.

Conclusion

The results discussed here strongly support the role of insectivory in the early hominid diet. Pioneering statements predicting tool use for the gathering of termites by early hominids were made by Goodall as far back as 1963 (54), but until now empirical support has remained elusive. 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.

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