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table S1

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Excavation of a Chimpanzee Stone Tool Site in the African Rainforest

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Chimpanzees from the Taï forest of Côte d'Ivoire produce unintentional flaked stone assemblages at nut-cracking sites, leaving behind a record of tool use and plant consumption that is recoverable with archaeological methods. About 40 kilograms of nutshell and 4 kilograms of stone were excavated at the Panda 100 site. The data unearthed show that chimpanzees transported stones from outcrops and soils to focal points, where they used them as hammers to process foodstuff. The repeated use of activity areas led to refuse accumulation and site formation. The implications of these data for the interpretation of the earliest hominin archaeological record are explored.

Ape ethoarchaeology uses primatological data to formulate archaeological hypotheses (1–3). For example, several authors have studied stone tools used by chimpanzees for nut cracking and have discussed similarities between them and early hominin tools (1–3). This paper reports on the nature and content of a naturally buried stone assemblage produced by the nut-cracking activities of chimpanzees (*Pan troglodytes*) in the wild. We describe the behavioral data unearthed at the chimpanzee

stone tool site of Panda 100 (hereafter P100) at Taï National Park, Côte d'Ivoire, which was excavated with the same techniques that are applied to the recovery of early archaeological sites and yielded preserved activity areas containing a large amount of plant refuse and 479 stone pieces.

Several West African chimpanzee populations use stone tools to crack open hard-shelled nuts. Nut-cracking technology allows chimpanzees to obtain more than 3000 calories per day (2) and has been extensively studied at Taï National Park, Côte d'Ivoire (2, 4). At Taï, chimpanzees are known to crack nuts from *Panda oleosa*, *Coula edulis*, *Parinari excelsa*, *Sacoglottis gabonensis*, and *Detarium senegalense* (2). On soft shells (such as those of *Coula*),

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Table 1. Size of stone pieces from P100 and selected Early Oldowan assemblages.

Size range (mm)	P100 (%) (granitoid rocks laterite; n = 479)	Omo 123 (%) [quartz (15); n = 223]*	Shungura formation, Ftj1 (%) [quartz (16); n = 130]	KBS (%) [basalt (17); n = 139]†
1–10	49	36	19	16
11–20	30	46	60	27
21–30	7	16	18	19
31–40	4	2	3	14
41–50	4	0.1	0	8
51–60	3	0	0	9
61–70	1	0	0	3
71–80	1	0	0	2
81–90	0.3	0	0	1
91–100	0.3	0	0	0
101–110	0.3	0	0	1

*Numbers only include excavation data. †Flakes = 97.7% of the total assemblage; estimates are based on interpretation of Fig. 1.

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chimpanzees use both soft and hard hammers, but access to *Panda oleosa* (abbreviated as *Panda*) seeds requires the use of stone hammers. *Panda* kernels (5) are the toughest in sub-Saharan Africa, require an average compression force of 1100 kg to crack open (6), and contain three seeds (5, 7). *Panda* trees rarely cluster, and they grow in undisturbed lowland forest along valley bottoms and swamps (6). The average distance between *Panda* trees across the site and the surrounding 30 hectares is ~100 m (4).

The nut-cracking season for the Tai chimpanzees is from February to August. A single chimpanzee may crack up to 100 fruits in one day, and refuse heaps form at processing locations around anvils. Learning to crack *Panda* nuts takes up to 7 years (2), and females crack more often than males (2). Typically, chimpanzees use stone hammers of igneous rocks (weighing 3 to 15 kg) and lateritic soil crust (weighing up to 6 kg) on nonmovable anvils that are used repeatedly over time, such as roots from hardwood trees and outcropping

rocks. The stones used as hammers are obtained from local igneous outcrops and ferrallitic soil exposures and are then taken to processing locations within nut-cracking sites. These hammers are curated intensively (4) and transported between nut-cracking sites, sometimes involving distances of several hundred meters (4). The total distance between the geological or pedological source from which a stone is collected and the last nut-cracking location in which a given hammer stone is used and exhausted is unknown. Hammers and anvils used to crack *Panda* nuts often have distinctive use wear consisting of pitting (3) and/or flaking.

The site of P100 is in Tai National Park, Côte d'Ivoire, in a lowland rainforest environment that receives around 2000 mm of annual precipitation (8). This region is part of the West African craton, specifically the "Man shield" composed of igneous and metamorphic rocks of Precambrian origin (9). The site of P100 is situated on the inside loop of a subsidiary meandering stream that surrounds the site on three sides and flows into the Audrenisrou River (Fig. 1). The platform on which the site is located was formed by Quaternary sedimentary infill and slopes westward, with an area of 9000 m². The sedimentary matrix (10) is texturally homogeneous with clay, silt, and rounded fine and coarse quartz sands and has no apparent stratification. Soil formation is typically hydromorphic with weakly developed horizons (10).

We used conventional archaeological techniques to recover stone and organic evidence from a nut-processing site consisting of one source tree and six associated anvil groups (10) (Fig. 1). The site is known to have been intermittently occupied by chimpanzees from at least 1975, when behavioral work began, until the death of the *Panda* tree in 1996, when nut cracking ceased at P100. Four of the six excavated anvil groups (with a total of 12 individual anvil surfaces) were visible before excavation. However, two additional anvil groups were discovered through excavation alone. The anvils occurred on hard tropical woods such as *Pentaclethra macrophylla* (Mimosaceae), *Bussea occidentalis* (Caesalpiniaceae), and *Diospyros soubreana* (Ebenaceae). The maximum distance between the source tree and any of its associated anvils is 20.2 m.

The excavated remains at P100 comprise 39,600 g of nutshell (10, 11) and 4500 g of fractured stone. At anvil 1, the remains formed a lenticular accumulation covering 9 m² that was, on average, 17 cm thick. Anvil 4 was an oblong mound extending 1.3 m² and was 21 cm thick. The average thickness of the matrix containing

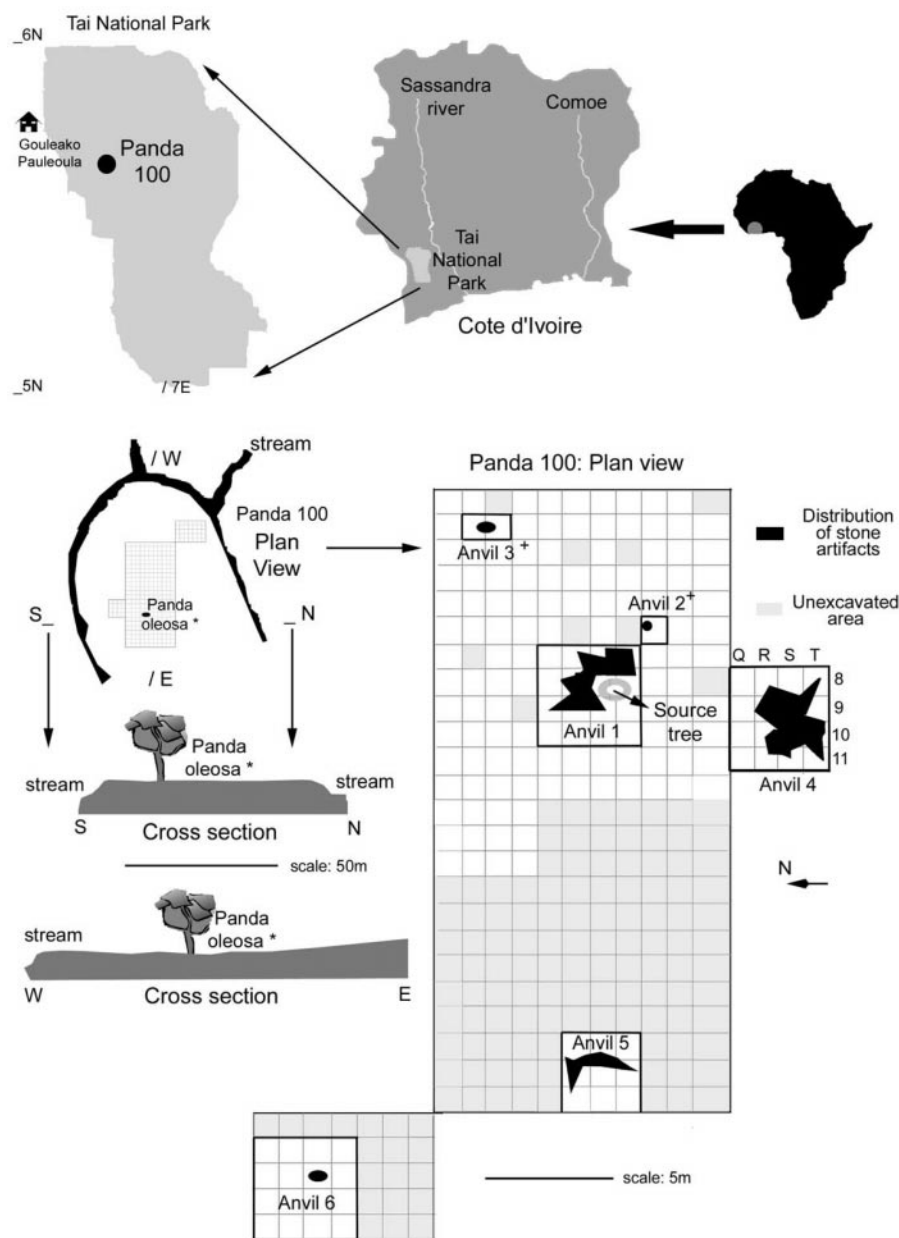


Fig. 1. Map of P100. Coordinates: 5°52.564'N, 7°19.5'W at 200 m above sea level. The excavation grid covers 327 m². The excavation of anvils 1, 4, and 6 covered 16 m² per anvil, with smaller grids for anvils 2 (1 m²), 3 (2 m²), and 5 (9 m²). Asterisk (*) indicates a currently decomposing stump; plus sign (+) indicates an anvil system not visible before excavation. Bold outlines within the grid indicate the anvil areas.

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stone is 16 cm (range = 8 to 22 cm), although most materials appeared within the upper 5 cm. In anvil areas, the average stone concentration per m² across the entire chimpanzee level is 8.1 for stone (range = 0 to 191) and 670 g for nutshell (range = 0 to 4000 g). At anvil 1, 3 stones were found partially buried and 85 were completely buried. Neither anvil 2 nor 3 had any surface stones but contained one and five buried stone pieces, respectively. Anvil 4 yielded 26 surface pieces and 291 buried in the matrix (12). Anvil 5 produced 3 surface stones and 52 buried ones. Anvil 6 yielded no surface stone but had 13 buried stone pieces.

Chimpanzees used raw materials from various sources, including granite (10) (79%), laterite (16.5%), diorite (2%), quartz (1.5%), and feldspar (1%). The nearest probable raw material sources were within a radius of 0.1 to 2 km from P100. The stone assemblage from P100 (Figs. 2 and 3) consisted of 479 pieces and included the following stone types, which in a conventional archaeological site would be classified as hammer edges (33, or 6.9%), cortical and noncortical flakes (25, or 5.2%), tabular products (9, or 1.9%), angular shatter (30, or 6.3%), amorphous shatter (8, or 1.7%), and microshatter smaller than 20 mm (374, or 78%). Within the fraction larger than 20 mm, the most common morphology is tabular ($n = 40$), followed by pyramidal ($n = 19$), amorphous ($n = 13$), cubical ($n = 6$), and spheroid ($n = 3$). The mean weight of hammer edges is 90.6 g (range = 6 to 322 g). Flakes are, on average, 35 mm long (range = 20 to 83 mm), 27 mm wide (range = 12 to 71 mm), and 10 mm thick (range = 1 to 27 mm) and weigh 21 g (range = 3 to 162 g). More than half of the flakes retrieved ($n = 15$) show one side entirely covered by cortex. Seven flakes have partial cortex on the dorsal face, and three show an entirely noncortical dorsal side. Striking platforms are on average 18 mm thick (range = 4 to 47 mm) and are mostly cortical, but in one case (flake no. 59, Fig. 3D) the platform is dihedral.

Refitted breaks and fragments from the same hammer include seven groups with a total of 16 pieces, comprise three different raw materials, and are represented at two anvils only. The horizontal and vertical distances that separate these refitted pieces suggest movements between 5 to 160 cm in the horizontal and 1 to 4.5 cm in the vertical. There is spatial segregation of raw materials among the anvils. Granitoid rocks were not used at anvils 2 and 6 but were the only type of rock present at anvil 1; diorite, except for one piece, is limited to anvil 4; feldspar only appears at anvil 4; laterite was the predominant raw material at anvil

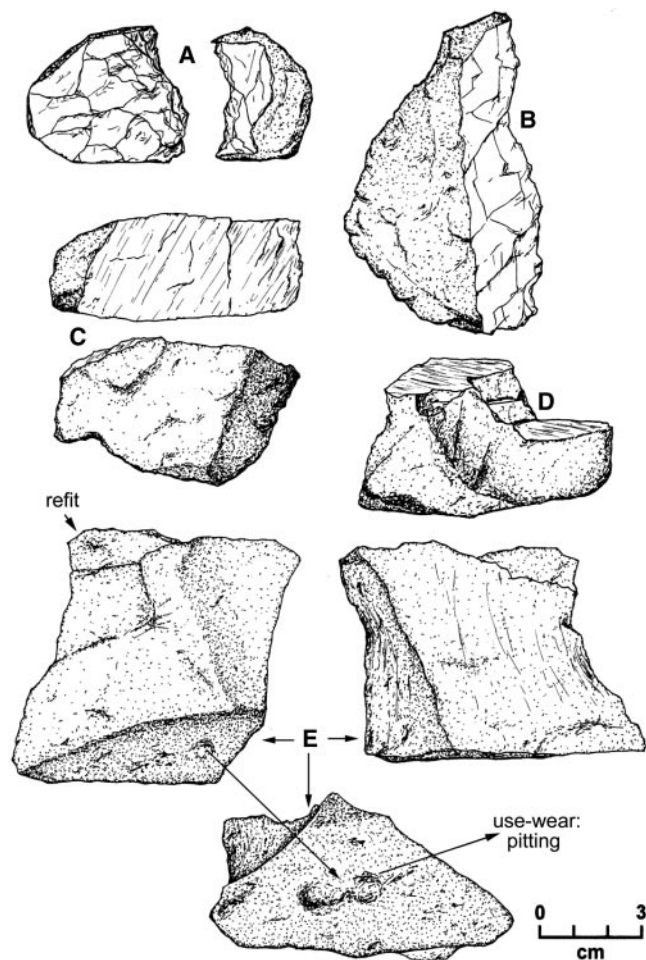


Fig. 2. Stone pieces. (A) Laterite hammer fragment. Specimen number: R9, spit 1, no. 43. (B) Laterite hammer fragment. Specimen number: N6, spit 1, no. 1. (C) Quartz hammer fragment. Specimen number: S9, spit 1, no. 30. (D) Granite hammer fragment. Specimen number: K24, spit 0. (E) Diorite hammer fragment with multiple fractures, pitting, and refit. Specimen number: S10, spit 2, no. 52. Refit: R10, spit 1, no. 44. [Drawings by Dennis Knepper]

5, was much scarcer at all other anvils, and was totally absent from anvil 1; and quartz was not used at anvils 1 and 2.

Several lines of evidence indicate that stone and *Panda* nutshells were behaviorally associated and that stone hammers were intentionally brought to the anvils. Outside anvil zones, we excavated 119 m² in which no stone and only a small amount of nutshells were found (an average of 10.8 g per m², SD = 22, range = 0 to 64 g). Around the anvils, the amount of shell refuse was significantly higher in trenches that contained stone (an average of 633 g of nutshells per m² and an artificial excavation layer or "spit"; SD = 916, range = 1 to 4000 g), than in trenches that contained no stone (an average of 53 g of nutshells per m² and spit; SD = 143, range = 0 to 1000 g) (Mann-Whitney U test: $U = 1226$, $z = -7.5$, $P < 0.0001$). In addition, the stones occur in localized horizontal and vertical clusters with abrupt edges, and all the stones are limited to the areas that surround the anvils (Fig. 1). The remains appear in a low-energy sedimentary matrix in which shattered granitoid rocks, laterite, and nutshells are naturally lacking. More-

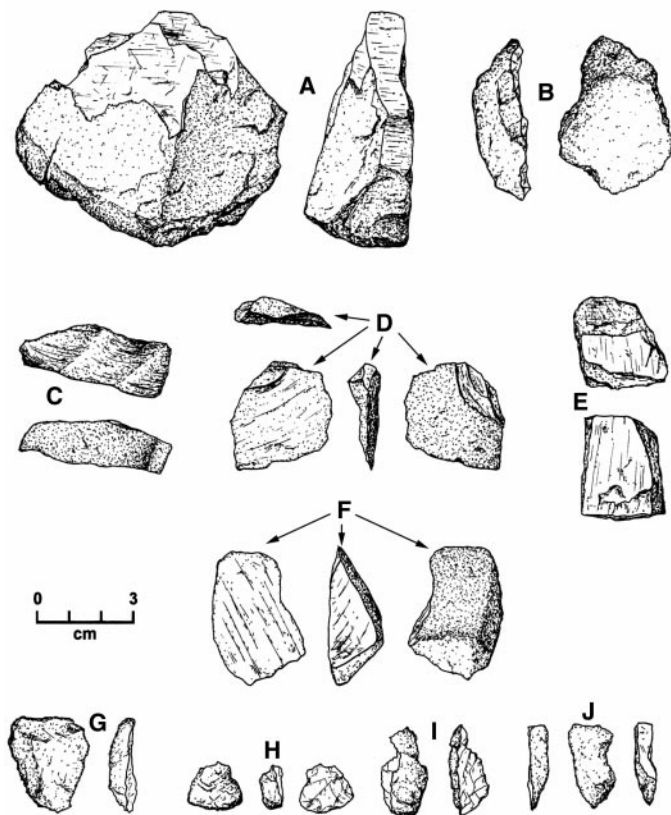
over, the physical condition of the stone is fresh, so the assemblage cannot be interpreted as waterborne.

McGrew (13) and Kortland (14) report human and chimpanzee nut-cracking sites, but systematic studies to distinguish between both types of sites are not available. In Guinea-Bissau and Tanzania, the target species is the African palm, and nut cracking occurs near villages and trails (13, 14). The reasons for inferring chimpanzee agency at P100 are, first, the existence of an extensive behavioral record of chimpanzee nut cracking at the site that covers several years of observation. Second, no humans have been observed cracking *Panda* or palm nuts at Tai (2). Third, P100 is in a deep forest location removed from villages and trails.

We compared the size ranges observed among the technologically simplest Oldowan stone assemblages from the Omo valley (15), Shungura formation (16), and KBS (17) with the stones retrieved from P100 (Table 1). We excluded the more sophisticated industries from Gona (18), Lokalalei (19), and Olduvai (20). In this exercise, we compared the accidental stone

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Fig. 3. Stone pieces. (A) Granite flake with dorsal side partially covered by cortex and evidence of previous removals. Specimen number: R10, spit 1, no. 24. (B) Diorite cortical flake with natural platform. Specimen number: S9, spit 0, no. 1. (C) Diorite piece with evidence of three removals. Specimen number: R11, spit 1, no. 42. (D) Diorite flake with dorsal side partially covered by cortex and evidence of previous extractions. Dihedral platform of percussion. Specimen number: S11, spit 3, no. 59. (E) Granite tabular piece. Specimen number: K7, spit 0. (F) Diorite cortical flake. Specimen number: R11, spit 0, no. 23. (G) Laterite cortical flake. Specimen number: S10, spit 1, no. 32. (H) Laterite cortical flake. Specimen number: T11, spit 1, sieve. (I) Laterite cortical flake. Specimen number: R10, spit 1, no. 45. (J) Diorite flake. Specimen number: L23, spit 1, sieve. [Drawings by Dennis Knepper]



by-products of P100 with intentionally fractured stone, raw materials with different conchoidal properties, and various percussion types (P100: stone on wood; Oldowan sites: stone on stone). But despite these differences, the stone by-products of chimpanzee nut cracking fall within the size spectrum and morphological parameters observed in a subset of the earliest known hominin technological repertoires. Additional similarities include the abundance of cortical flakes and natural platforms (21), the density of stone per m² (17, 22–24), and the size of the stone clusters (17, 22–24). Thus, chimpanzees engage in cultural activities that leave behind a stone record that mimics some Oldowan occurrences and invite us to speculate whether some of the technologically simplest Oldowan sites could be interpreted as nut-cracking sites or, more generally, if some subsets of artifacts from the more sophisticated Oldowan assemblages could be interpreted as evidence of hard-object feeding by early hominins.

Chimpanzee nut-cracking behavior leaves a durable and detectable record. Archaeology has proved to be a feasible method for uncovering past chimpanzee sites and activity areas in rainforest environ-

ments. This introduces the possibility of tracing the development of at least one aspect of ape culture through time (25). At P100, chimpanzees evidently transported stones from various sources to focal points, moved stone hammers and foodstuff to these processing locations, reoccupied spatially congruent activity areas, and unintentionally flaked and shattered stone hammers. As a result, chimpanzees left behind stone and plant refuse that accumulated in specific loci. These patterns resemble some of the behavioral landmarks (26) of early hominin stone assemblages and site formation.

The full implications of this work will require additional evidence and further elaboration. As new data from chimpanzee sites become available, the “type” assemblage discovered at P100 might merit the name “Pandan.” Additionally, further excavations may shed light on the tentative evolutionary implications of this type of evidence; for example, nut cracking during the Miocene and Plio-Pleistocene could have generated by-products that eventually became the “cutting” tools of Oldowan hominins. It is also likely that panins may have been capable of producing assemblages that mimic some of the earliest hominin artifacts.

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11. A single *Panda* fruit, with a diameter of about 5.5 cm, yields three seeds and 30 g of shell.
12. Anvil 4 yielded the richest surface assemblage, with 26 stone pieces (surface stone density, 1 to 14 per m²; average, 3.25 per m²), of which 15 were partly buried to depths ranging from 5 to 40 mm.
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Materials and Methods

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