4,300-Year-old chimpanzee sites and the origins of percussive stone technology

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Archaeological research in the African rainforest reveals unexpected results in the search for the origins of hominoid technology. The ancient Panin sites from Côte d'Ivoire constitute the only evidence of prehistoric ape behavior known to date anywhere in the world. Recent archaeological work has yielded behaviorally modified stones, dated by chronometric means to 4,300 years of age, lodging starch residue suggestive of prehistoric dietary practices by ancient chimpanzees. The "Chimpanzee Stone Age" pre-dates the advent of settled farming villages in this part of the African rainforest and suggests that percussive material culture could have been inherited from an common human–chimpanzee clade, rather than invented by hominins, or have arisen by imitation, or resulted from independent technological convergence.

Tool use among modern wild ape populations, first reported in the early 19th century (1), has been documented throughout tropical Africa, and chimpanzees from West Africa are known for their use of stone tools for nut cracking (2–6). In 2002, the publication of recent buried remains of unintentionally fractured stone left behind by modern chimpanzees from Côte d'Ivoire outlined the potential of using archaeological methods in cultural primatological research and also identified the type of material assemblage that would allow archaeologists to detect and characterize ancient chimpanzee nut-cracking behavior. To test the feasibility and scope of the new methodology, we conducted further work in Taï National Park, and investigated the existence of ancient chimpanzee sites and whether these sites would offer an answer to the long-standing question of the antiquity of nut-cracking behavior (6, 7). The archaeological evidence retrieved consists of behaviorally modified stones, dated by chronometric means to 4,300 years of age, whose attached food residue suggests chimpanzee manipulation, rather than natural causes or human intervention. This discovery speaks of true prehistoric great ape behavior that predates the onset of agriculture in this part of Africa (8). The chimpanzee assemblages are contemporaneous with the local Later Stone Age (8); thus, they represent a parallel "Chimpanzee Stone Age" that prompts us to ask whether percussive material culture could have been inherited from a common human–chimpanzee clade rather than invented by hominins (cf. 9, 10), have arisen by imitation, or resulted from independent technological convergence.

The Archaeological Horizon: Age and Composition

The sites of Noulo, Sacoglotis B, and Panda 100 (Fig. 1) are located at 5°N /7°E, and 200 m above sea level; in the lowland rainforest of Taï National Park, Côte d'Ivoire, on the flood plain traversed by a small meandering black water stream called Audrenisrou; within the chimpanzee territory known as "North Group." Archaeological excavation took place over the course of two field seasons in 2001 and 2003, following standard paleolithic archaeology techniques. The research area is in a closed-canopy environment that receives ≈2,000 mm of annual precipitation (11). As part of the West African Craton, the region's geological configuration is dominated by igneous and metamorphic rocks of Precambrian origin (12). The archaeological sites studied here are located on a flat riverbank that gets regularly inundated. Sedimentation is thicker than 4 m, alternating silty sands, muddy sands, and sandy silts that include patches of pebbles and cobbles. Small fires affecting isolated trees and caused by lightning are common occurrences throughout the Guineo–Congolian rainforest (13); leaving behind a ubiquitous record of former vegetation and forest composition as well as a source of datable material. Numerous pits excavated throughout the Audrenisrou valley bottom document the effects of past forest fires that charred one or several trees, and at the sites of Noulo, Panda 100, and Sacoglotis B, a total of 15 ^{14}C assays performed on excavated charcoal samples (Table 1) indicate that (*i*) sedimentary deposition in this part of the landscape is older than 6,000 years, (*ii*) the archaeological assemblage studied in this paper dates back 4,300 years, and (*iii*) this assemblage is composed of relict materials deposited at different times over the course of >2,000 years.

We present stone assemblages from three sites east of the Audrenisrou, <200 m apart from each other (Fig. 1). Most of these

Table 1. List of radiometric ages by ^{14}C from the sites of Noulo, Panda 100, and Sacoglotis B

Provenance	Sample data	^{13}C/^{12}C, per mil	Conventional radiocarbon age, years B.P.
Noulo			
Uppermost part of profile	Beta-196391	−27.3	230 ± 40
	Beta-195439	−27.2	270 ± 40
	Beta-196390	−26.4	410 ± 40
Main archaeological horizon	Beta-196953	−27.5	2,200 ± 40
	Beta-195444	−26.7	2,890 ± 40
	Beta-196392	−26.3	2,910 ± 40
	Beta-195441	−28.9	2,970 ± 40
	Beta-195440	−25.9	4,240 ± 120
Underneath archaeological horizon	Beta-195442	−28.1	6,290 ± 40
Panda 100	Beta-172916	−27.6	2,330 ± 40
	Beta-164876	−27.9	2,440 ± 40
	Beta-164877	−27.2	2,440 ± 40
	Beta-172913	−26.8	3,750 ± 40
	Beta-164879	−25	4,280 ± 40
Sacoglotis B	Beta-195443	−28.6	1,280 ± 40

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Table 2. Technological features of the stone assemblage excavated in the Taï National Park, Côte d'Ivoire

		Blind test					Dimensions, mm		
ID	Site	Starch	Stone	Fragments, *n*	Depth, cm	Technological by-product of thrusting percussion	Length	Height	Width
1	Noulo			1	60	Chunk	70	60	35
2	Noulo			1	70	Edge/corner	85	120	20
3	Noulo			1	70	Edge/corner	65	65	22
4	Noulo			1	70	Edge/corner	80	25	15
5	Noulo	31–32	4	1	70	Chunk	110	60	50
6	Noulo			2	70	Edge/corner	50	40	30
7	Noulo	34–36	NT	1	78	Complete piece	130	40	40
8	Noulo			3	84	Chunk	90	90	30
9	Noulo			1	70	Chunk	150	150	60
10	Noulo			1	60	Flake	30	50	15
11	Noulo			1	62	Flake	30	45	10
12	Noulo			1	62	Flake	15	15	8
13	Noulo	30	11	1	76	Chunk	100	80	80
14	Noulo	33	8	1	63	Complete piece	100	70	70
15	Noulo			1	76	Chunk	100	50	40
16	Noulo			1	83	Flake	30	40	15
17	Noulo			1	80	Chunk	100	90	50
18	Noulo			1	90	Chunk	100	90	50
19	Noulo			1	70	Edge/corner	55	20	20
20	Noulo			1	83	Chunk	70	60	30
21	Noulo	37	32	1	68	Chunk	100	50	50
22	Noulo			1	83	Flake	70	90	10
23	Noulo	3–9	3	1	70	Chunk	220	80	55
24	Noulo	10–20	NT	1	80	Almost complete piece	70	60	60
25	Noulo			1	80	Edge/corner	100	80	30
26	Noulo			1	74	Chunk	100	80	60
27	Noulo	38	6	1	29	Edge/corner	70	70	60
28	Noulo	28–29	NT	1	50	Chunk	140	70	70
29	Sacoglotis B	1–2	14	1	15	Complete piece	190	80	80
30	Panda 100			1	121	Edge/corner	80	90	45
31	Panda 100			1	125	Chunk	110	60	60
32	Panda 100	21–27	NT	1	110	Edge/corner	70	70	25
33	Noulo			1	57	Edge/corner	50	20	35

stones, however, come from one site alone: Noulo (three specimens came from Panda 100; and one from the site of Sacoglotis B). At Noulo, we excavated a 10-m grid down to 1 m of depth, and unearthed a stone-rich horizon at 60–90 cm (three specimens were found at 29–57 cm). This horizon produced 23,168 g of modified stone (206 pieces) (Table 2). Its physical condition is fresh, except for some instances of chemical weathering in the form of surface desquamation. Stones from all size categories and diverse raw materials were excavated with shatter $<$20 mm excluded (mean length: 68 mm; range: 25–220 mm). Granitoid rocks represent 62%; quartz and quartzite represent 36%; laterite represents 1%, and feldspar represents 1%. The horizontal scattering of this collection clusters around three areas rich in granitoid shatter, with two smaller outliers to the north and south of these higher density spots (Fig. 1). About half of the quartz–quartzite assemblages concentrated in the southwest corner of the grid. The granitoid pieces broke off rocks that, generally, are not susceptible to percussive fracture (nonconchoidal, 88%; 20,370 g); a smaller portion of the assemblage (12%; 2,799 g) was from quartz and quartzite; rocks whose fracture results in a curved, rippled breakage surface (conchoidal). Average concentration of nonconchoidal pieces is 1.2 per m^2; mean concentration for conchoidal pieces is $\approx$0.7 per m^2.

Can the archaeological evidence from the Taï forest be attributed to natural or behavioral agency? If behavioral, can we discriminate between stone modifications such as those produced by nut-cracking versus those derived from systematic flaking? What is the direct evidence for nut-cracking, and especially, do these stone assemblages represent mid-Holocene human or chimpanzee agency?

Fluvial Geofact versus Behavioral Accumulation

Fine sands, silt, and clay are indicative of very low energy fluvial regimes such as floods and standing pools associated with braided and meandering streams. Grain size from the excavated matrix corresponds with the "Ingram–Wentworth" sedimentological profile known as "muddy sands" (14) and indicates that pebble-, cobble-, and boulder-sized rock fragments would be naturally lacking. This prediction is corroborated by the results from excavation in 26 off-site ground-truthing pits (area: 0.5–6.25 m^2 taken to a maximum depth of 2 m) along a 220-m transect around the site of Noulo, in which cobble-sized stones were found in 5 pits only; the remaining 21 pits yielded ceramics, lithics, iron, or nothing. To test the proposition that the accumulation of stones reported here took place by means other than fluvial agency, a triple blind test was carried out. The lead author (J.M.) and two independent observers (J.H. and S.K.) classified stone specimens randomly numbered by J.M. as coming from (*i*) nonartifactual objects shaped exclusively by geological forces, (*ii*) objects produced by systematic flaking, or (*iii*) objects generated by cracking (thrusting percussion). The test collection comprised 90 rock specimens, of which 60 were not from the Taï forest. To the extent of our possibilities, we included raw materials that are likely to be found in a granitic domain, such granites, diorites, quartzite, and quartz, but limited access to geofact collections led us to include other rocks as well. Of these, 30 came from a high-energy, undisturbed glacial till in the Canadian Rockies, near Banff, Alberta, where silicified limestone pebbles and cobbles show several kinds of natural modification that gives them the appearance of artifacts (15). The other 30 came from a demonstrated behavioral site dated to the mid-Holocene (site FiPo-147; Royal Alberta Museum) that yielded hundreds of artifacts including lithic debitage in quartz and quartzite, among other raw materials (16). The remainder of 30 specimens came from the Ivorian sites of Noulo (n = 28), Panda 100 (n = 1), and Sacoglotis B (n = 1), and these were previously selected by J.M.

Table 2. (continued)

PML	Mass for thr. perc. elements*	Raw material		Starch		Proposed agency
		Nonconchoidal	Conchoidal	Botanical origin: Nut	≥1 nut species cracked by chimpanzees	
280	202.9 (by 4) = **811.6**	Granitoid		X	X	C
391	622.8 (by 4.6) = **2,864.88**	Granitoid		X	X	C
325	186 (by 5) = **930**	Granitoid		X	X	C
368	102.1 (by 4.6) = **469.66**	Granitoid		X	X	C
440	358.1 (by 4) = 1,432.4		Quartz	X	X	C
250	83.1 (by 5) = **415.5**	Granitoid		N/A	NRE	C
130	849.4	Granitoid		X	X	Unclear
405	395 (by 4.5) = **1,777.5**	Granitoid		Unclear	Unclear	C
525	1,928.7 (by 3.5) = 6,750.4	Feldspar		X	X	C
N/A	2.9	Granitoid		N/A	NRE	Unclear
N/A	22.9	Granitoid		N/A	NRE	Unclear
N/A	3.6	Granitoid		N/A	NRE	Unclear
150	927.6 (by 1.5) = **1,391.4**	Laterite		X	X	Unclear
100	1014.8	Granitoid		X	X	Unclear
300	295.5 (by 3) = **886.5**	Quartz-rich granitoid		X	X	C
N/A	20.7	Quartz-rich granitoid		N/A	NRE	Unclear
230	670.8 (by 2.3) = **1,542.84**	Quartz-rich granitoid		X	X	C
300	742.4 (by 3) = **2,227.2**	Granitoid		X	X	C
247.5	119.7 (By 4.5) = 538.65	Laterite		N/A	NRE	C
245	233.2 (by 3.5) = **816.2**		Quartz	X	X	C
300	956.6 (by 3) = **2,869.8**		Quartz	X	X	C
n/a	90.5	Granitoid		N/A	NRE	Unclear
660	1,686.9 (by 3) = **5,060.7**	Granitoid		X	X	C
70	556.9	Granitoid		X	X	Unclear
500	435.4 (by 5) = **2,177**		Quartzite	X	X	C
450	904.5 (by 4.5) = **4,070.26**	Granitoid		X	X	C
231	557.6 (by 3.3) = **1,840**	Diorite		X	X	C
420	1,525.9 (by 3) = **4,577.7**	Granitoid		X	X	C
190	3761.5	Feldspar		X	X	C
320	394.2 (by 4) = **1,576.8**	Quartz-rich granitoid		Barren sample	No residue detected after two sonication cycles	C
495	937.9 (by 4.5) = **4,220.5**	Quartz-rich granitoid		X	X	C
350	159.1 (By 5) = **795.5**	Granitoid		X	X	C
250	29.5 (by 5) = **147.5**	Granitoid		N/A	NRE	C

PML, projected maximum length; NRE, no residue extracted; NT, not tested. For the complex data set, see supporting information (SI) Table 3.

*Boldface figures are projected.

as stone pieces that could be behaviorally modified, comprising all types and morphological variables. Criteria for this part of the triple exercise focused on worn, rounded stones with surface damage or removals, and >50% of cortical cover. Then, the examiners sought a minimum of two additional attributes thought to be common on geofacts (17): four or fewer flake scars, lack of platform preparation, differential weathering of removals, random scar alignment, striations on surfaces, or entirely cortical flakes. Statistical analysis demonstrates very high levels of agreement among all three examiners: 90.00% (κ test > 0.799; $n = 90$, $P < 0.000$). In other words, the Ivorian stones are not geofacts, as confirmed by three independent observers.

Discriminating Systematic Flaking from Thrusting Percussion Products

Systematic flaking is an exclusive behavioral characteristic of Plio–Pleistocene hominins (18–21). During the Holocene, Later Stone Age lithic assemblages from the African rainforest (22) demonstrate that systematic flaking can be identified beyond any doubt when one or more of the following criteria are present: cores that display logical reduction strategies (e.g., radial), cores with more than five flake scars, intentional creation or preparation of platforms, bifacial reduction, retouch, or blade production. Agreement among three observers (J.M., J.H., and S.K.) through a blind test designed to identify systematic flaking is 93.33% (κ test < 0.754; $n = 30$; $P < 0.000$). One examiner (S.K.) interpreted 10% of the stones that were known to have been produced by systematic flaking as derived from thrusting percussion, and the other stone examiner (J.H.) interpreted a separate 10% also as fashioned by thrusting percussion. Systematic flaking can be distinguished from the products of thrusting percussion of unknown agency. The three examiners agreed that 35 of 64 stone specimens larger than 20 mm were produced by thrusting percussion, whereas 28 stones resulted from systematic flaking. Because chimpanzees have not yet been observed to flake stone intentionally, it is unquestionable that human lithic reduction is present at the site. Therefore, the possibility that humans could be the sole culprit of our stone collections must be carefully examined. For the entire sedimentary package, the amount of human lithics amounts to 0.77 per m^3. This figure alone is telling; for we know that systematic quartz reduction from Later Stone Age sites in comparable geographical and ecological environments yields contrasting higher numbers, often consisting of thousands of specimens per m^3 (22) (number of sites, 10; mean, 1,030; range, 70–5,000). In addition, this part of the landscape, a frequently inundated riverbank, probably was not a preferred site for humans, and its occupation seems sporadic; brief visits to the river bed to collect pebbles that could be tested or reduced for flakes. Typical archaeological features commonly found in Later Stone Age sites from the African rainforest (23, 24) were not found here, such as inhabitation structures, activity areas, hearths, or charred food remains. That is, the presence of a limited number of lithics is not, by itself, proof of agency for the other technologies present at the site. It does suggest that humans were present in this area and that, over time, they visited the river bank where the rest of the archaeological remains were also deposited.

Identifying and Classifying the Products of Thrusting Percussion

Could some of these stone pieces have been used and discarded by chimpanzees? The maximum length, three-dimensional volume,

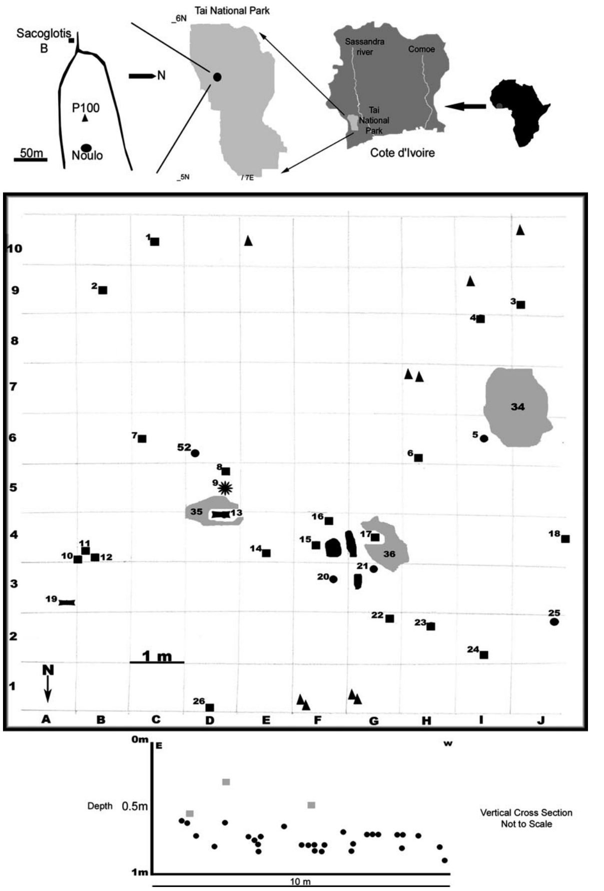

Fig. 1. Map of Noulo. Excavation grid covers 100 m^2. Solid black squares indicate granitoid specimens. Circles represent quartz specimens. Asterisks indicate feldspar-rich granitoids, and diamonds indicate laterite pieces. Each spot represents one piece, but in the case of shatter or refitted specimens, the number of specimens per spot is as follows: no. 6, 2; no. 8, 3; no. 34, 59; no. 35, 29. Light gray shading indicates granitoid shatter. Triangles and dark gray shading indicate quartz shatter, representing specimens reduced by humans shown on Table 2 as nos. 35, 29; 38, 27; and 45, 26.

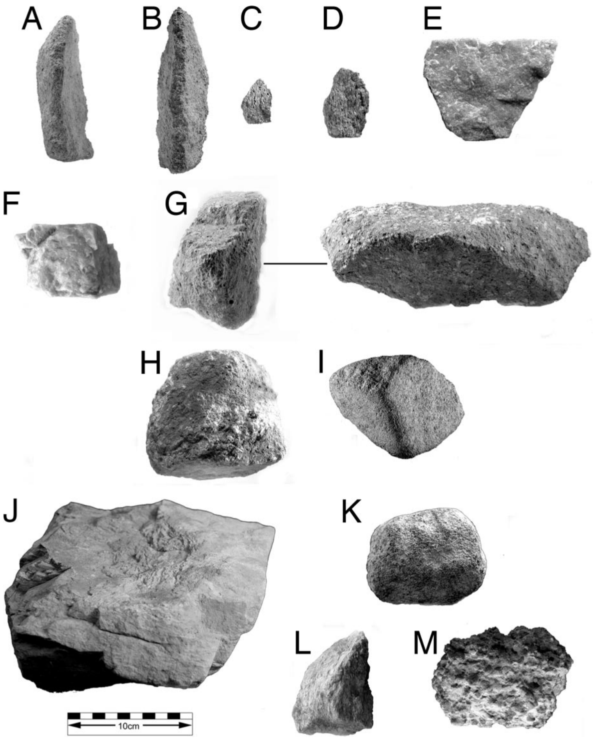

Fig. 2. Selected thrusting percussion products. Stone specimen ID, as it appears on Table 2: *A*, 2; *B*, 4; *C*, 11; *D*, 12; *E*, 25; *F*, 20; *G* (two pieces), 23; *H*, 17; *I*, 28; *J*, 29; *K*, 14; *L*, 27; *M*, 13. (Photograph by Gerald Newlands, Department of Archaeology, University of Calgary.)

and total mass of stone products can help elucidate the agency that generated them. A review of hammer metrics from early sites (9, 10, 25) indicates that the hominin hand accommodates hammerstone up to 12 cm in maximum length, often <8 cm. Hominin hammers typically weigh <400 g, and even anvils, the largest component of this bimodal technology, on average, reach a maximum weight of 1,000 g, but often weigh much less. We know that hominins do intentionally select tabular rocks and raw materials such as quartz and quartzite for their hammers and anvils at sites such as Olduvai (Bed 1) (10). In contrast, a 1-year study of nut-cracking sites (n = 1434) and hammers (n = 133) among modern chimpanzees (26) indicates both a strong preference for granitoid rocks, and large/heavy hammers (65% weigh 1,000–9,000 g; 23% weigh <1,000 g; 12% weigh >9,000 g; the limit is 24,000 g). This marked difference probably is related to the larger size of the chimpanzee hand, its morphology, and the overall arm strength, which are several times superior to that of any hominin species known to have used hammers and anvils.

To classify the products of thrusting percussion, we modified published work on the different modalities of products generated by bashing technologies (10) and distinguished complete pieces, "chunks" (significant portion of the hammer/anvil has been preserved), "edges/corners," flakes, and shatter (Fig. 2). Our blind test reveals that independent observers agree on the classification of thrusting percussion by-products in 70% of the cases (κ values between 0.508 and 0.565; $n = 20, P < 0.001$), which shows that stone pieces unintentionally generated by thrusting percussion and stone pieces intentionally produced by systematic flaking can be differentiated. The majority of the stones excavated at Noulo are the unintentional by-products of bashing technologies. To discriminate human from chimpanzee agency, we used reconstructions of original size and mass of the stone fragments before breakage. These estimates were subject to blind testing as well, and our results indicate a high level of confidence in the maximum projected length and mass by three independent observers (65%, 75%, and 90%; κ values of 0.493, 0.636, and 0.851, respectively; n = 20; $P < 0.000$). The mean maximum length of stone by-products derived from thrusting percussion is 97 mm (range, 35–220 mm), and the average mass is 710 g (range, 21–3,761 g). Flakes generated by thrusting percussion average 33.5 mm. Therefore, our reconstructed totals for thrusting percussion products suggest a projected maximum length of ≈320 mm (range, 70–660 mm), and maximum mass or ≈2,030 g (range, 145–6,750 g), well above what is known for by-products of hominin thrusting percussion.

Starch Residues as Direct Evidence for Nut-Cracking

Can we demonstrate that such stones were used by chimpanzees? Present-day chimpanzees crack five nut species that, except for one (*Coula edulis*), are not cracked by local human populations (26). If part of the stone assemblage retrieved at Noulo was used to crack starch-bearing nuts open, those pieces might shelter ancient starch residue still lodged in the stone crevices. If so, this may represent direct evidence for both ancient plant usage and stone function. To test this proposition, our research design followed field and laboratory protocols used by numerous researchers in the study of ancient starch grains throughout the world (see *Materials and Methods*) (27–33). Once all examiners achieved a reasonable familiarity with the reference collection, we asked two examiners (H.B. and R.T.) to inspect 40 starch granules (10.8% of the total

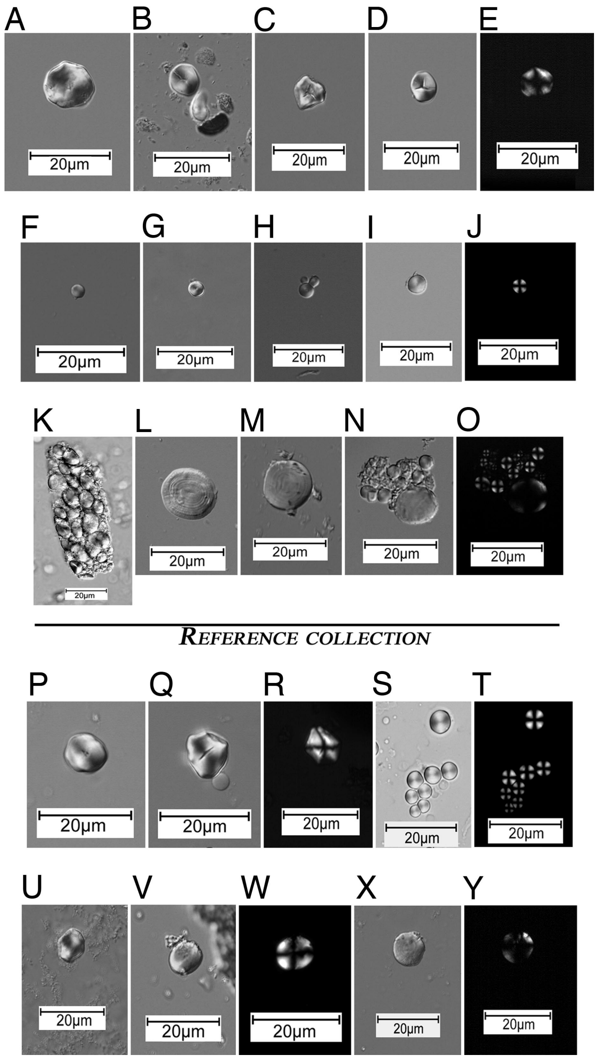

Fig. 3. Starch grains extracted from archaeological specimens amount to 370 grains, and these can be classified into three types: Type 1 (*A*–*E*), comprising subrounded to subangular, medium size grains (10–25 μm) with a smooth to rugose surface and distinct quandrangular, hexagonal, or octagonal faceting. The hylum (or geometric centre of the grain) often supports a single cavity, a slit, or several fissures forming a Y, cross, or star-like patterns. The arms of the cross are often straight, but sometimes they take on wavy and hooked morphologies. Type 2 (*F*–*J*) is a small (5–10 μm) to medium (10–25 μm) spherical grain with a smooth surface. It shows a centric slit or fissures. Its arms are straight and widen out toward the periphery. Type 3 (*K*–*O*) is a medium (10–25 μm) to large (25 μm) lenticular grain with a characteristic wide and diffuse cross; sometimes smooth, sometimes with variably marked lamellae. Micrographs from the reference collection illustrate selected examples of one or several morphotypes from the nuts of *Parinari excelsa* (*P*, *Q*, *W*, and *X*), *Detarium senegalense* (*R* and *V*), *Coula edulis* (*S* and *T*), and *Panda oleosa* (*U*). Stone specimen identification, as it appears on Table 2: *A*, 20; *B*, 29; C, 32, *D* and *E*, 35; *F*, 15; *G*, 7; *H*, 23; *I*, 5; *J*, 7; *K*, 34; *L*, 27; *M*, 3; *N*, 24; *O*, 24. (Micrographs by J.M. and Gerald Newlands.)

available granule population extracted from the archaeological stone; $n = 370$) previously processed, quantified, classified, and identified by J.M. to test the degree to which these granules could be consistently interpreted to typify specific plant usage. Agreement over starch grain classification has been estimated by pairing up the results produced by the different observers separately. Classification at the level of botanical origin (nut versus legume and tuber) yields high agreement (>77.8%; higher to a 50% agreement criterion, binomial test: $P < 0.000$, and equal to 85% agreement criterion, binomial test $P > 0.2$). Several nut species yielded morphotypes of very similar characteristics, making single-species identification inconsistent between analysts; a problem that can be minimized by proposing two to four species as likely identifications (J.M. and R.T. agreement = 92.5%, binomial 85% criterion, $P > 0.4$; yet, agreement for all three examiners is 48%, binomial 50% criterion, $P > 0.5$). In general, our data indicate that at least 3/4 of the tested sample derived from nuts (Fig. 3), not tubers or legumes. Moreover, all three observers agreed that three nut species cracked exclusively by chimpanzees (*Parinari excelsa*, *Panda oleosa*, and *Detarium senegalense*) are the only candidates 7 of 40 times (17.5%), with two observers (J.M. and R.T.) agreeing that these species could be present an additional 17 times (extra 42.5%).

Discussion and Implications

From a stone perspective, it can be said that the choice of raw materials displayed in the mid-Holocene thrusting percussion assemblage from the Taï forest mirrors the choices made today by local chimpanzee populations, to whom granitoid rocks are the preferred choice for ≈3/4 of their assemblages (7). The rest is made up of laterite, diorite, feldspar, and quartz. The density of stone pieces within the excavated horizon per m^2 (1.27) matches that observed in known chimpanzee nut-cracking sites excavated with identical methodologies (1.46 per m^2) (7). For the same raw materials, maximum flake length at Noulo (33.5 mm) resembles maximum flake length produce in known modern chimpanzee nut-cracking assemblages (35 mm) (7). The percent of shatter <20 mm produced at Noulo is 74%, which is very similar to the percent of shatter <20 mm produced in demonstrated chimpanzee assemblages (79%) (7). Likewise, use-wear patterns from chimpanzee nut cracking include small pits and hollow concavities (6, 34), which are found in Noulo along with systematic edge and corner damage. In addition, stone metrics at Noulo are indicative of large hand size and great strength and follow the metrics of chimpanzee hammers more closely than they follow human ones.

The majority of the starch grains retrieved from the by-products of thrusting percussion comes from a set of nuts typically found at chimpanzee nut-cracking sites. In a 1-year study, Boesch and Boesch (26) reported 1,434 sites where chimpanzees exploited *Coula edulis* (52%), *Panda oleosa* (32%), *Detarium senegalense* (9%), *Parinari excelsa* (6%), and *Sacoglotis gabonensis* (1%). This is the set of nuts seen in the prehistoric starch sample. By contrast, human rain forest dwellers rely very heavily on starch-producing tubers and legumes, as well as the "incense" tree *Canarium schweinfurthii* (17.5% of oily–starchy food consumed among Congolese pygmies) and the African oil palm *Elaeis guineensis* (10% of oily–starchy food consumed among Congolese pygmies) (35, 36). Chimpanzees in Bossou, Republic of Guinea, >250 km north of Taï, have been observed cracking the kernels of *Elaeis guineensis* (37). Considering how closely associated this plant seems to be with African forest farming communities, some have gone further to suggest that chimpanzees learned to nut-crack from forest farmers (38). However, the starch assemblage from Noulo predates the appearance of farming in this part of the African forest, and yields no significant evidence of species that correspond to modern human forager or farming use. Two starch grains were matched with reference materials of the genus *Dioscorea*. These were recovered from stones at two separate archaeological sites, Noulo and Panda 100, and belong to wild evergreen rainforest lianas whose tubers could have accidentally came in contact with the stones, and thus are best interpreted as background noise. Moreover, none of the pounding, grinding, and pestling tools that human foragers and farmers use to process starchy foods appears at Noulo.

In conclusion, the geological, morphological, technological, metric, and mass parameters for the nut-cracking stone assemblage reported in this study rule out human or natural agency. The nut species cracked all belong to a set of taxa known to be exploited by modern chimpanzees, and part of the starch assemblage may belong to species exclusively consumed by chimpanzees. The full implications of this line of work require a reevaluation of the terms under which we can make meaningful comparisons of Oldowan and Chimpanzee cultures. The behavioral variables documented at Noulo indicate that chimpanzees and hominins share cultural attributes (39–41), including the transport of stones across the landscape for a projected use elsewhere; the optimal combination of raw material, size, and weight criteria to perform a predicted activity; the re-occupation of focal points (the accumulation and concentration of both stone and botanical debris is artificially created by behavior); creation of activity areas; the use of locally available resources; and the curation and selection of specific types of stones that are most optimal for specific technological activities.

The systematic archaeological study of prehistoric chimpanzee cultures suggests that the "Chimpanzee Stone Age" started at least 4,300 years ago, that nut-cracking behavior in the Taï forest has been transmitted over the course of >200 generations, and that chimpanzee material culture has a long prehistory whose deep roots are only beginning to be uncovered. These findings substantiate the contribution of rainforest archaeology to human evolutionary studies in areas other than the classical savanna-woodlands of East and Southern Africa and add support to fossil discoveries from these other regions indicative of an ancient chimpanzee past (42).

Materials and Methods

For ancient starch analysis, we processed a large collection of residue extracted from 31 behaviorally modified stone pieces from a pool of 38 specimens, 7 of which have been positively identified by all examiners as derived from thrusting percussion. Second, we used multiple lines of control samples (30–32) to test whether the tools were the primary source of starch grains, rather than random contamination. Although we cannot rule out the possibility that some of the starch discovered on the stones comes from redeposition unrelated to use (e.g., background starch derived from roots coming in contact with the stone over hundreds of years), the differential preservation of starch granules on the stone specimens compared with that in their surrounding free-standing matrix indicates that a large part of the assemblage is genuine prehistoric residue (30–32). Third, for all examiners to propose potential identification for the grains, we worked with a reference collection that included not just the five nut species known to be cracked by chimpanzees, but also two other types of starch-producing plants typically used by human foragers in the African rainforest. Thus, we included all nut and tuber species relevant to modern hominoid starch use plus other species present in our study area totaling 18 nut species, 1 palm pith, and 8 rainforest yams. The specimens used for the test were made available to the examiners on 13 separate microscope slides, and these represented 37% of the total residue (n = 370 grains) obtained from the sites of Noulo (11 stones providing 37 grains), Panda 100 (1 stone providing 1 starch grain), and Sacoglotis B (1 stone providing 2 grains). Extraction protocols for both sediment and residue samples follow the methodology of Zarrillo and Kooyman (33) with minor modifications. Quantity of sediments used ranged from 0.5 g (residue samples extracted from stones through sonication) to 1 g (free-standing sediments). Column samples (n = 5) were taken at 10-cm intervals from the North wall at the site of Noulo. Modern deposits formed around decomposing, natural piles of nuts (n = 4) from *Detarium senegalense*, *Sacoglotis gabonensis*, *Panda oleosa*, and *Coula edulis*/*Parinari excelsa* were scraped off to a maximum depth of 2.5 cm. Modern chimpanzee hammers (n = 3) came from the uppermost levels of two sites, Loukoum and Panda 100, and were all excavated to a maximum depth of 5 cm. Natural stones on-site (n = 2), off-site (n = 1), Later Stone Age lithics (radial cores) (n = 3), stone sharpener fashioned by humans (n = 1), and matrix samples retrieved around archaeological specimens, but not in contact with them (n = 4), provided the rest of our control samples. The amount of starch granules found in these control samples varies, and the types found are similar to those seen in the archaeological specimens. Values below represent an average for a given type of control. For example, four sediment samples collected around stone specimens yielded no grains. Five free-standing, on-site column samples yielded an average of 0.4 grains. Four naturally occurring nut piles yielded a mean ≈0.5 grains. Three unmodified on- and offsite stones yielded no grains, whereas four Later Stone Age stone tools yielded a mean of 0.2 grains. In contrast, residue extracted from 31 archaeological stone produced by thrusting percussion contains a mean of 12 grains per stone (3 of the 31 stones yielded no grains; 28 stones yielded 1–90 grains).

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