A primate model for the origin of flake technology

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Abstract

When and how human ancestors first used tools remains unknown, despite intense research into the origins of technology. It has been hypothesized that prior to stone flaking hominins practiced various percussive behaviours resulting in accidental flake detachments, in turn leading to intentional flake production, named here the ‘By-Product Hypothesis’. The evolutionary root of technology therefore would have its origin in perucssive behaviour. In this study we tested the validity of accidental flake production as a by-product of percussive foraging and assess the role that raw material quality has on its efficacy. We applied archaeological lithic analysis to three experimental capuchin nut cracking assemblages of varying raw material quality. The resulting assemblage associated with percussive foraging is clearly identifiable as non-natural in origin. Capuchin nut cracking behavior can produce multiple conchoidal flakes which technologically resemble simple hominin flakes of the early archaeological record. Raw material quality and morphology significantly affect the rate of sharp-edged flake detachments as well as the resulting archaeological signature of this behavior. Our field experiments show that percussive tool use can lead to the unintentional production of substantial quantities of sharp cutting flakes and therefore directly support the ‘By-product-hypothesis’ for the emergence of hominin technology.

1. Introduction

Despite decades of investigations into the origins of hominin technology, the point in our evolutionary history in which tool use first appeared remains elusive. It is widely assumed that the production of sharp flakes is not the beginning of tool use. Simple pounding tools are likely to predate the creation of sharp flakes, pushing the invention of tools further back in time, towards our last common ancestor (LCA) with chimpanzees (Panger et al., 2002). The earliest tool behaviour has been documented only indirectly through cut marked animal bones from Dikika in Ethiopia (McPherron et al., 2010) dating to 3.39 Ma, arguing that naturally occurring sharp edges could have been used to facilitate subsistence butchering (McPherron et al., 2010). Similarly, the earliest evidence of stone tool production comes from the archaeological site of Lomekwi 3 (Kenya). Dated to 3.3 Ma, the Lomekwian technology is characterised by large stone flakes detached from cores (Harmand et al., 2015; Lewis and Harmand, 2016). Although both finds remain controversial amongst experts (Domínguez-Rodrigo et al., 2011, 2012; Domínguez-Rodrigo and Alcalá, 2016; 2019; Archer et al., 2020), Lomekwian technology and the Dikika cutmarks suggest that tool use and flake technology extend beyond the purview of early *Homo* and into the realm of hominins, during a period when Australopithecines (such as *A. afarensis* and *Kenyanthropus)* were occupying these east African landscapes.

The Lomekwian technology shows flake exploitation along the core margin, leading to repeated detachment of unidirectional conchoidal flakes (Harmand et al., 2015). This technology, however, lacks the variety of exploitation strategies seen later in the archaeological record. By 2.6 Ma systematic conchoidal flake production was clearly established (Braun et al, 2019; Semaw et al., 2000) and throughout the course of the Oldowan (2.6- 1.5 Ma), hominins employed a variety of different reduction strategies for the efficient production of sharp-edged flakes (Delagnes and Roche, 2005; de la Torre and Mora, 2005; de la Torre, 2004; Semaw et al., 2003; Stout et al., 2010; Toth, 1985).

Debates around the origin of technology has given rise to multiple different hypothesis. Some suggest that the emergence of hominin stone flake technology may have been a consequence of a relatively sudden cognitive development (de Lumley, 2006). Others suggest a more gradual evolution (Carbonell et al, 2007) with some arguing for a period of repeated technological invention prior to 2.6 Ma (Braun et al., 2019). The earliest evidences from Dikika (McPherron et al., 2010), Lomekwi (Harmand et al., 2015; Lewis and Harmand, 2016), as well as Bokol Dora 1 (Braun et al., 2019) and Gona (Semaw et al., 1997; 2003), supports the presence of a more gradual development throughout long periods of time and uptake of simple stone tool production.

Studying the material remains of tool-using non-human primates (hereafter primates) allows us to develop a broader understanding of the archaeological signature of percussive behaviors. The presence of tool use across several primate species, especially our closest living relative, the chimpanzee, has led to the suggestions that tool-use was within the behavioral repertoire of the LCA of *Pan* and *Homo* (e.g. Marchant and McGrew, 2005; McGrew, 2010; Rolian and Carvalho, 2017). For this reason, primates have been used as model organisms to better understand early hominin behaviour, including, the creation and use of hominin percussive artefacts (Arroyo et al, 2020; Arroyo and de la Torre, 2018; Arroyo et al., 2016; Proffitt et al., 2018, Proffitt et al., 2016). Primates use tools most frequently for extractive foraging, but they have also been reported in the context of communication, hygiene, and sexual display (Kühl et al., 2016; Luncz and Boesch 2014; Falótico and Ottoni, 2013; Humle et al., 2011). The use of stone tools, however, is scarce and is currently only known for four non-human primate taxonomic groups. These include the West African chimpanzee (*Pan trogoldytes verus*, Boesch and Boesch 1983; Matsuzawa et al., 1996), long-tailed macaques in Thailand and Myanmar (*Macaca fascicularis*, Malaivijitnond et al., 2005; Gumert et al., 2009), robust capuchin monkeys in Brazil (*Sapajus libidinosus*; Visalberghi et al., 2005, Falótico et al., 2015; *S. xanthosternos*; Canale et al., 2009) and white-faced capuchin monkeys in Panama (*Cebus capucinus*, Barrett et al., 2018). Although each species uses stone tools for a range of different behaviours all of these primates universally use stone tools to crack open nuts.

The emergence of stone flaking has been hypothesized to originate from a "pounding culture" dominated by the use of stones to process nuts or to fracture bones to access marrow (de Beaune, 2004; Marchant and McGrew, 2005; Thomson et al., 2019). Such pounding activities may have led to the accidental production of flakes, when the hammerstone misses the target food and accidently strikes on the stone anvil, or through a fatigue process produced by a repetitive impact. It has been hypothesized that these processes might have provided hominins with a supply of sharp edges within the vicinity of food processing locations (Merchant and McGrew 2005; Wynn and McGrew 1989; Wynn, 2011; Panger 2002; Carvalho et al. 2009). Repeated accidental production of flakes from percussive activities, along with an increasing necessity to use these flakes, may have offered an opportunity for the reverse engineering of intentional flake production. We will refer to this hypothesis as the 'By-Product Hypothesis' for the emergence of stone flake technology. Recent studies have, however, shown that chimpanzee nut cracking both in experimental (Arroyo et al, 2016) and natural (Carvalho et al., 2008; Proffitt et al, 2018) settings, results in only a small number of sharp cutting flakes.

To extend our understanding of the percussive signature of primate foraging behaviour we conducted controlled field experiments with capuchin monkeys in Brazil. Capuchins are known to exhibit different tools behaviours compared to chimpanzees and are therefore well suited to further insights into the likelihood of the 'By-product hypothesis'. These monkeys use stone tools for a wide range of behaviours, including digging for food, communication and for extractive foraging (Falótico and Ottoni, 2013; Falótico et al., 2017; Spagnoletti et al., 2015). Specifically, groups of capuchins (*Sapajus libidinosus*) from Serra da Capivara National Park in Brazil are the only extant primate species to produce substantial frequencies of conchoidal flakes as a by-product of striking two stones together, during a behaviour termed stone-on-stone percussion (Proffitt et al., 2016). Capuchins, however, are best known for their nut cracking behaviour which has been studied since 2005 in several wild and semi-wild ranging populations (Falótico and Ottoni, 2016; Falótico et al., 2018; Ottoni and Mannu, 2001; Visalberghi and Fragaszy, 2013). To date very little is known regarding the range of percussive signatures associated with capuchin nut cracking behaviour.

This study sets out to 1) investigate to what extent raw material quality affects the production of identifiable archaeological signatures during nut cracking; 2) describe the technological characteristics and archaeological signature of the resulting capuchin nut cracking percussive material, 3) investigate the similarities and differences between unintentional flakes produced during nut cracking to intentionally knapped flakes of modern humans and to Early Stone Age lithic assemblages. This work assesses the potential of the 'By-product hypothesis' and discusses its implications for the origin and evolution of technology.

2. Results

2.1 Behavioural analysis

Field experiments were set up along the natural foraging routes of one capuchin group in the Tiete Ecological Park. As travel routes were diverse throughout the study time, this resulted in five different experimental sites. A total of 20 individuals (5 adult males, 8 adult females, 6 juvenile males and 1 juvenile female) voluntarily participated in the nut cracking experiments. The anvils of high and medium isotropy (HI and MI) were used for a similar number of nuts whereas the anvil with low isotropy (LI), given its friable properties, was completely fractured shortly after initiating the experiments (counting a total of 78 strikes) and therefore removed from the experiment (for details see Table 1).

Independently of the raw material used, capuchins were consistent in displayed efficiency of opening the nut (around 1.6 hits per nut, ± 0.0607).

Table 1: Summary of strikes inflicted on the different anvil material.

	Isotropy	**Hits (total)**	**Missed hits (direct contact with anvil)**	**Missed hits (no contact with anvil)**	**Average hits per nut**
Chery Siltstone	Low (LI)	78	34	0	1.56 ± 0.338
Quartzite	Medium (MI)	1658	708	17	1.6 ± 0.0822
Ironstone	High (HI)	1483	824	0	1.54 ± 0.0809

2.2 Technological Analysis

2.2.1. Assemblage composition.

The technological categories for each raw material group are presented in Table 2 (see definitions in Supplementary Materials and Methods; Table S1). All detached technological categories typically associated with core and flake reduction in Early Stone Age assemblages are present in both the HI and MI materials. This includes complete and broken flakes, small debris and angular debris. Additionally, technological categories typically associated with percussive technology are also present such as the remaining anvil (for all raw materials) and spontaneous removals (for MI only). The HI raw material elicited the greatest frequency of complete flakes (*n* = 10, 22.2%) and broken flakes (*n* = 13, 28.9%). The MI raw material produced fewer complete flakes (*n* = 5, 10.6%) and broken flakes (*n* = 7, 14.9%), but produced a prevalence of small debris (*n* = 30, 63.8%) compared to the HI raw material (*n* = 16, 35.6%). The LI raw material stands out by the complete lack of flakes and the high predominance of small debris (*n* = 493, 87.7%) and angular debris (*n* = 38, 12.1%). The frequency of technological categories between all raw materials differed significantly ($\chi^2(8) = 152.53$, $p < 0.001$). Adjusted residuals on the Chi Square test indicate that this variation is derived from the increased frequency of flakes and broken flakes for HI raw material, and an increase of small debris for the MI raw material as well as the prevalence of angular debris for the LI raw material.

Table 2: Absolute and relative frequencies of all technological categories associated with each raw material quality.

	High Isotropic				**Medium Isotropic**				**Low Isotropic**			
	Frequency		**Weight**		**Frequency**		**Weight**		**Frequency**		**Weight**	
	n	**%**	**g**	**%**	***n***	**%**	**g**	**%**	***n***	**%**	**g**	**%**
Remaining anvil	2[a]	4.4	2639.3	92.4	1	2.1	2147.3	86.4	0	0	0	0.0
Complete flakes	10	22.2	154.7	5.4	5	10.6	184.6	7.4	0	0	0	0.0
Broken flakes	13	28.9	53.7	1.9	7	14.9	14.1	0.6	0	0	0	0.0
Small debris	16	35.6	3.5	0.1	30	63.8	4.3	0.2	493	87.7	22.9	1.0
Angular chunks	4	8.9	6.6	0.2	2	4.3	129.7	5.2	69	12.3	2276.9	99.0
Spontaneous removal	0	0.0	0	0.0	2	4.3	3.9	0.2	0	0	0	0.0
Total	**45**		**2857.8**		**47**		**2483.9**		**562**		**2299.8**	

[a] This anvil split into two halves.

2.2.2. Anvil analysis

Of the three anvils, the HI and MI raw materials are characterized by frequent battered marks on elevated areas of the anvil (Figure 1). On the contrary, the LI anvil showed a lower degree of percussive damage (Supplementary Materials and Methods). This is a result of the anvil being removed from the experiment after 50 nuts were processed as it had fragmented completely by this point and could no longer serve as an anvil. The surface modification on both the HI and MI anvils showed few differences in terms of extent, however, the HI anvil also developed a large shallow depression across the center of its active surface (Figure 1b; Supplementary Materials and Methods). Eventually, the anvil broke along the center of this depression. Refit analysis showed that further to the percussive damage on the surface of the anvils, there are considerable differences in fracture patterns of each raw material type. The LI anvil shattered in its entirety preventing a detailed sequential refit analysis (Figure 2a) and as such only the HI and MI anvils are considered in this analysis.

[Insert Figure 1]

Figure 1. Characterization of the use wear patterns. a) MI anvil bears battered areas on the active surface in which crystals appear crushed (1-4). Microscopic details taken at 10× (1. Scale 3 mm) and 20× (2-4. Scale 2 mm). b) HI anvil developed a large shallow depression on its surface. In this case, we identified remains of fibers from the nuts (1), and a process in which the grains compressed, fractures and detached during the use (2-3), showing scattered polished areas (4). Microscopic details were taken at 10× (1-2. Scale 2 mm and 3. Scale 3 mm) and 20× (4. Scale 2 mm)

Refitting of the MI anvil and detached pieces shows two separate flaking sequences during the percussive activity: (1) The first sequence results in the detachment of one large angular fragment truncated at its distal end by an internal fracture plane. (2) The second sequence consists of the detachment of 6 small flakes and broken flakes, unidirectionally detached along the margin of the active percussive surface. This sequence resulted in an anvil with non-invasive unidirectional removals obtained from one adjoining vertical plane that was used as an active surface during nut-cracking (Figure 2i).

The refit analysis of the HI anvil shows three separate removal sequences: (1) The first sequence consists of the detachment of three unidirectional removals from Plane B2. This is followed by the development of a significant area of percussive damage on Plane A developing into a substantial shallow pit (Supplementary Materials and Methods), during which time additional removals associated with a second sequence are detached. (2) The second sequence consists of six complete unidirectional flakes and one split flake, removed from Plane B. Following these removals, the anvil broke in two pieces (Half A and B) along the center of the depression that developed over the course of the experiment. (3) Following the fracture of the anvil, three non-invasive unidirectional flakes and one split flake were detached from the internal fracture plane of Half A (Figure 3; Supplementary Video 1).

The remaining flaked anvils (HI and MI) are characterized by significant areas of percussive damage on their horizontal plane (Plane A, the active surface). Frequent step scars across the vertical planes caused by a lack of force and a slight concavity on the vertical planes.

[Insert Figure 2]

Figure 2: Fully refitted anvils including the LI (a), MI (i), and a selection of associated detachments produced during the experiments (b-h and j-s).

[Insert Figure 3]

Figure 3: HI lithic material produced during capuchin nut cracking experiment. a. Fully refitted HI anvil. b-p. Detached products as a result of repeated capuchin percussive action.

2.2.3. Flake Analysis

Only HI and MI raw materials were used for comparisons of flake detachments as these are the raw material types which resulted in the production of by-products that can be classified technologically as flakes.

A comparison of flakes from both raw material groups (HI and MI) shows similarities in mean dimensions and mass, indicating no significant differences in the maximum and technological dimensions (Table S1 and Table S2). Furthermore, no significant difference in the platform dimensions nor external platform angle (EPA) between these flakes were found (Table S1 and Table S2). However, flakes from the HI raw material, tended to have a greater range of dimensions and platform angles compared to those produced from the MI raw material (Table S1).

Flakes from both raw materials showed fully cortical, flat, non-faceted platforms (Table 2). The HI flakes possessed an increased frequency of hinge and step terminations and prominent bulbs of percussion compared to the MI flakes. No significant differences, however, were found in the level of dorsal cortex and their flake types (based on Toth, 1982), with only the initial stages of reduction represented for both raw materials (Table 2).

Table 2: Absolute and relative frequencies of all technological attributes on HI and MI capuchin flakes.

Technological Attribute		**HI**		**MI**	
		n	**%**	**n**	**%**
Striking platform cortex	100%	10	100.0	5	100.0
Striking platform morphology	Flat	10	100.0	5	100.0
Striking platform facets	Non-Faceted	10	100.0	5	100.0
Striking platform shape	Rectilinear	10	100.0	5	100.0
Knapping accidents	None	5	50.0	5	100.0
	Hinge Termination	2	20.0	0	0.0
	Step Termination	3	30.0	0	0.0
Step scars present	No	9	90.0	5	100.0
	Yes	1	10.0	0	0.0
Bulb of percussion	Diffused	3	30.0	0	0.0
	Indeterminate	1	10.0	1	20.0
	Marked	6	60.0	4	80.0
Ventral face morphology	Convex	4	40.0	0	0.0
	Irregular	0	0.0	1	20.0
	Rectilinear	6	60.0	4	80.0
Dorsal cortex	0%	3	30.0	3	60.0
	<50%	2	20.0	0	0.0
	>50%	2	20.0	1	20.0
	100%	3	30.0	1	20.0
Flake category (following Toth, 1982)	I	3	30.0	1	20.0
	II	4	40.0	1	20.0
	III	3	30.0	3	60.0
	IV	0	0.0	0	0.0
	V	0	0.0	0	0.0
	VI	0	0.0	0	0.0

2.4 Comparison of unintentionally and intentionally produced flakes.

We compared the capuchin flakes that detached from the HI raw material during capuchin nut cracking to flakes produced by an experienced human freehand knapper, using the same raw material as the capuchin HI anvil. Comparisons show no significant difference between capuchin and experimental free-handed knapped flakes for maximum nor technological dimensions, as well as weight (Table 3). Moreover, no significant differences were found in edge length, platform dimensions, nor interior platform angle (Table 3), suggesting that from a general morphological perspective, the unintentional flakes produced by capuchins and the knapped flakes are superficially similar.

However, there are differences between the capuchin and knapped flakes in a range of technological attributes (Table 3). A significant difference was identified between the external platform angles (EPA; Table 3), with knapped flakes possessing a mean lower EPA (77.84° ± 14.36°) with a wider range compared to the capuchin flakes (87.8° ± 9.32°). Striking platforms on capuchin flakes were significantly different to those on knapped flakes (Table 3) and were non-faceted and cortical (n = 10, 100%), with a combination of centered (n = 6, 60%) and de-centered impact points (n = 4, 40%). This was compared to both non and uni-faceted platforms on knapped flakes which showed a higher frequency of centered impact points (n = 19, 76%) and a predominance of non-cortical (n = 15, 60%) platforms.

Step (n = 3, 30%) and hinge (n = 2, 20%) terminations were prominent on capuchin flakes, whilst the majority of knapped flakes displayed feather terminations (n = 24, 96%). Capuchin flakes also possessed an increased frequency of marked bulbs of percussion (n = 6, 60%), compared to a higher frequency of diffused bulbs on knapped flakes (n = 14, 56%). A Chi-Square test indicated significant differences for these attributes between both flake groups (Table 3). Although no significant difference was found in dorsal cortex coverage between capuchin and knapped flakes, when both dorsal cortex and platform cortex were combined a clear difference was, however, identified in the resulting flake types (Table 3). All capuchin flakes were fully or mostly cortical and fall within flake types I, II and III (following Toth, 1982), highlighting the predominance of early reduction flakes. Knapped flakes are, however, predominantly non-cortical in nature (Toth's, 1982 types IV, V, VI) with all phases of reduction represented.

Dorsal scars were present on both flake groups, indicating the repeated removal of flakes. An independent sample t-test indicated that capuchin flakes possessed a lower average (1.1 ± 0.88) number of dorsal flake scars compared to knapped flakes (1.9 ± 1.1), ($t(33) = -2.07$, $p = 0.046$), showing an increased frequency of 3 or more flake scars, whilst capuchin flakes possessed a maximum of 2 flake scars. These data corresponded to a lower degree of reduction associated with the flakes found in the capuchin assemblage. However, there was no significant difference in the flake scar directionality between the two flake groups, with unidirectional flaking being predominant for both ($\chi^2(3) = 1.029$, p = 0.794). This was mainly a consequence of the knapped flakes being the result of intentionally unidirectional exploitation. Bidirectional flaking was, however, represented albeit marginally only in the knapped assemblage, attributable to a degree of core rotation during reduction.

Table 3: Comparison between capuchin HI percussive flakes and conchoidal freehand knapping flakes.

Attribute	**Chi Square Test**		
	X(1)	**df**	***p***
Impact point location	11.9	3	**0.008**
Striking platform cortex	11.789	2	**0.003**
Striking platform morphology			
Striking platform facets	11.789	1	**0.001**
Striking platform shape			
Bulb of percussion	1.978	2	0.370
Knapping accidents	11.049	2	**0.004**
Step scars	0.028	1	0.867
Ventral face morphology	6.176	2	**0.046**
Dorsal cortex	1.898	3	0.594
Toth's 1982 flake category	12.972	5	**0.024**
	Mann Whitney U Test		
	U		***p***
Maximum length	120.5		0.872
Maximum width	114.5		0.706
Maximum thickness	105		0.483
Technological length	107.5		0.529
Technological width	121		0.900
Weight	110.5		0.602
Edge length	111		0.627
Platform length	171		0.097
Platform depth	146		0.460
Interior platform angle	146.5		0.439
Exterior platform angle	183.5		**0.031**

2.5 Comparison of capuchin nut cracking and hominin flakes

The technological analysis of the capuchin nut cracking assemblage allowed us to develop an inter-species comparison with published hominin assemblages. When comparing the capuchin HI flakes to Oldowan flake dimensions from a wide range of published Oldowan sites (Table S3), the results indicated no significant differences in mean length (U = 4, p = 0.385), width (U =18, p = 0.615), breadth (U = 22, p = 0.308) and weight (U = 18.5, p = 0.273). The metric similarities of both HI and MI capuchin flakes was highlighted as a clear overlap in a PCA biplot (Figure 4a). When compared to a smaller sample of Oldowan flake technological data from Koobi Fora (Režek et al., 2018) (Table S4) there was no significant difference in platform width (U = 1653, p = 0.822) and depth (U = 1850, p = 0.696). However, comparisons showed a significant difference in EPA between capuchin HI flakes and Oldowan flakes (U = 721, p = 0.002). Capuchin HI flakes possessed significantly larger (mean = 87.8°, SD = 9.32°) EPA compared to intentional Oldowan flakes (mean = 76.41°, SD = 10.72°). These technological differences between capuchin nut cracking and Oldowan flakes were again highlighted through a principal component analysis (Figure 4b).

[Insert Figure 4]

Figure 4: Principal components analysis (PCA) of a) Lomekwian, Oldowan, capuchin and experimental conchoidal flake dimensions conducted by experienced human knappers (length, width, and thickness) and b) flake platform measurements (width, depth and EPA) of a selection of Oldowan flake assemblages from Koobi Fora and capuchin HI and MI flakes. For data associated with each PCA plot see Table S3 and Table S4.

There were also qualitative technological differences between the capuchin percussive flakes and Oldowan technology. When considering a number of technological attributes of complete flakes (Table S5) it was clear that the capuchin flake assemblage technologically differed to that of Classic Oldowan flakes (Figure 5). Compared to Oldowan flakes, capuchin HI nut cracking flakes possessed exclusively non-faceted cortical platforms, and higher levels of cortex on the dorsal surface resulting in only the early stages of reduction being present. Additionally, Oldowan flakes possessed a higher range of dorsal extractions and a greater diversity in dorsal extraction directionality (Figure 5).

[Insert Figure 5]

Figure 5: Relative frequency of technological attributes on complete Classic Oldowan flakes from Olduvai Gorge (data from Proffitt, 2018) and unintentional capuchin nut cracking flakes. a) Platform cortex; b) platform facets; c) dorsal cortex; d) number of extractions; e) directionality of extractions; f) Flake categories (based on Toth, 1982). For a full table of data used see Supplementary table S5.

3. Discussion

The production of flaked stone tools was one of the key steps in our evolutionary history, leading to the unparalleled technological achievements of our species. The mechanisms behind the emergence of this technology, however, remain unknown (Panger et al, 2002). Percussive food processing was suggested to have played an important role in the foraging behavior of early hominins which might have led to the emerging of intentional stone tool knapping. This ‘By-Product hypothesis’ has been advanced as a potential mechanism behind the emergence of stone flake technology. Conversely, early hominins might have already used naturally sharp stones to process meat (McPherron et al., 2010). Accidental flake production through percussive behaviours may have, therefore, enabled the leap to intentional production of flakes. To date, there is no archaeological evidence to substantiate either hypothesis in deep time, with even the earliest technology being argued to represent intentional flake production (Harmand et al, 2015).

Through our controlled field experiments conducted with a group of capuchins in the Tiete Ecological Park in Brazil, we have shown that percussive foraging activity can lead to substantial production of sharp cutting flakes. We further explored the role of raw material quality in the production of unintentional flakes during nut cracking, by providing material of varying isotropy. Technological analysis of the resulting lithic assemblages allowed us to significantly refine the ‘By-product hypothesis’ as a mechanism for unintentional flake production, however, with important updated caveats. When a highly isotropic raw material is used as the passive element (anvil) during nut cracking, it increases the potential production of sequential and identifiable conchoidal flakes. These artefacts show similarities to flakes in the archaeological record, attributed to early hominins, where intentionality has previously been claimed. Conversely, the likelihood at which conchoidal flakes are produced

decreases as the raw material quality decreases. When less isotropic raw materials are used for the same task our results show a higher percentage of irregular fragments and chunks. These are a result of the irregular fracture properties of the raw material. Irregular fragments do not have a standardized shape nor morphological attributes typically associated with anthropogenic fracture mechanics. However, these fragments also exhibit defined characteristics of percussive behaviour through localized traces of battering marks on their surfaces, making them identifiable as artefacts in a lithic assemblage. Our findings substantiate previous observations of chimpanzee nut cracking assemblages in which less homogenous raw material was used, resulting in an assemblage characterized by a large percentage of non-conchoidal angular fragments (not suitable for cutting activities), however, possessing use-wear traces of percussive action (Proffitt et al., 2018).
The comparison of the high-isotropic flakes made by capuchin monkeys to intentionally produced conchoidal flakes made by an experienced human knapper shows significant overlap in a range of quantitative and qualitative attributes. Many capuchin flakes are conchoidal, possess bulbs of percussion, platforms with impact points and dorsal surfaces which retain previous removals. These comparisons demonstrate that identifiable sharp-edged flakes can be produced unintentionally during pounding activities, given the correct raw material, lending support for the ‘By-Product hypothesis’. There are, however, technological differences between the primate percussive flakes and those produced intentionally which mark them apart. Identifying these attributes is crucial for the interpretation of the archaeological record, if we want to advance the field towards identifying material that might have been contributing to the emergence of intentionality in tool production. By-product flakes found in capuchin assemblages are exclusively uni-directional, often exhibit multiple impact points (not associated with a bulb of percussion) on a single platform as well as occasionally retaining evidence of heavy battering on their platforms. They occasionally show double bulbs of percussion, as well as steep exterior platform angles (close to 90°). These technological attributes of unintentional percussive flakes are derived from the nature of their detachment, as by-products of heavy percussive battering. However, even these technological attributes differentiate them from natural angular fragments and therefore hold information when searching for percussive behaviour in lithic assemblages.

When comparing the high-isotropic raw material assemblage made by capuchins with the hominin archaeological record it becomes apparent that both groups exhibit sharp-edged flakes and attributes overlap substantially. Comparisons showed similarities in the physical characteristics of the flakes, such as length, width, breadth and weight. Additionally, there were no significant differences in platform width and depth. However, there are a range of marked differences that distinguish lithic assemblages found in the archaeological record from unintentionally produced primate flakes: (i) *Percussive marks*: the capuchin flakes exhibit percussive marks on their platforms because of multiple impacts received during nut cracking (before the detachment of the flake), while hominin flakes usually show one impact point only, which has been attributed to precisely placed hammerstone strikes to intentionally detach flakes; (ii) *Cortex on the dorsal face*: the capuchin flakes have high ratios of cortex on their dorsal faces, whilst hominins produced longer reduction sequences resulting in high ratios of flakes with an absence of cortex; However, the nut cracking experiment was artificially terminated after ~1000 nuts. With increasing exposure time to the same material, the amount of cortex on flakes would naturally decreases as material is further fragmented; (iii) *Core exploitations*: hominin cores show negative scars that show structured exploitation strategies. On the contrary, the capuchin flaked anvils exhibit heavy percussive damage on their surfaces and the negative scars tend to be randomly distributed.

When comparing the archaeological record with non-human primate tools it is important to highlight the fundamental functional differences of the performed tasks. Even though, early hominins and primates are selective in the use of raw material, early hominins selected raw materials with the appropriate fracture properties (Braun et al, 2009; de la Torre, 2004; Harmand, 2009a; 2009b) and morphology (Delagnes and Roche, 2005) to enable efficient exploitation of flakes. On the contrary, primates do not intend to break their tools when cracking nuts. This would significantly reduce their foraging success. Primates therefore select stones based on their morphological characteristics (i.e. size and weight, hardness), influential aspects for efficiently cracking nuts (Falótico and Ottoni, 2016; Fragaszy et al., 2010). Furthermore, primates do not use the flakes they produce and therefore do not modify them intentionally. Tools we attribute to hominins however are overwhelmingly thought to have been intentionally manufactured to be used in cutting activities (Keeley and Toth, 1981; Lemorini et al, 2014; 2019) and also occasionally exhibit intentional retouch in many Oldowan assemblages (de la Torre and Mora, 2005). If the LCA used percussive technology, future research must focus on, firstly identifying this stage of cultural evolution within the archaeological record, and secondly seek to understand the potential mechanisms by which unintentional production of un-utilised flakes develop into the intentional and systematic production of flakes for use.

4. Conclusions

Percussive behaviour has often been regarded as occasional among hominins (Shea, 2017). However, the identification of Lomekwi 3 showed that it is possible to identify low-density clusters of artefacts before 2.6 Ma. Excavations and analysis of primate sites (Mercader et al., 2002; Proffitt et al., 2018 Falótico et al., 2019) emphasizes that pounding activities can leave a clearly identifiable archaeological record. Developing a better understanding of the range of artefactual characteristics of percussive behaviours and their archaeological signature increases the possibility of identifying these behaviours in an early Pliocene context. Based on our results from a purely percussive assemblage we have identified the characteristics of a range of artefact types. In the archaeological record these would consist of accumulations of multiple active and passive elements, either complete or broken, but with significant percussive marks on their surfaces, potentially accumulated in specific locations in the landscape. Importantly, however, depending on the quality of the raw material used these active and passive elements may also be associated with identifiable detachments (flakes and irregular fragments).

The results from this study also urge for a note of caution when dealing with the known archaeological record. Where Plio-Pleistocene archaeological assemblages have a percussive component consisting of fractured anvils this study shows that associated flakes from early in the reduction sequence should not be automatically considered an intentional products as there are clear mechanisms whereby they may have been detached as a by-product of percussive behaviour and are indeed entirely unintentionally.

To fully understand the role and signature of percussive behaviours in the hominin archaeological record we must focus on developing methodologies that identify and characterize the evidence that percussive behaviours create, human, hominin and primate alike. In doing so our understanding of the potential range of archaeological signatures for the emergence of stone technology will develop. These techniques may be invaluable for investigating the archaeological record between 3.3 Ma and 2.6 Ma as well as identifying new archaeological horizons beyond the known archaeological record to date.

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Author Contributions

L.V.L, A.A and T.P conceived the study. L.V.L and T.F collected primate data. A.A and T.P conducted the technological, use wear and refit analysis and produced all figures. P.Q conducted XRF and thin section analysis. L.V.L, A.A and T.P wrote the paper and Supplementary material with contributions from T.F and P.Q.

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5. Methods

5.1 Materials

Three different raw materials were selected to be experimentally tested, a highly isotropic (HI) ironstone, a quartzite tabular block of medium isotropy (MI) and cherty siltstone of low isotropy (LI). The HI anvil and three rounded quartzite cobbles (hammerstones) were sourced from Tietê National Park, Sao Paulo, Brazil. The MI raw material was sourced from Naibor Soit (Olduvai Gorge, Tanzania) a metamorphic inselberg which was the primary source of quartzite at Olduvai in the Early Stone Age and widely used as cores to manufacture flakes (Leakey, 1971) and as anvils (Mora and de la Torre, 2005). In addition to this, three basalt river cobbles were sourced from cobble conglomerates at Olduvai. The LI anvil (cherty siltstone block) and three limestone beach cobbles were sourced from the south end of Boi Island, Phang Nga National Park, Thailand (see supplementary material for measurements and petrographic characterization of each raw material).

5.2 Experiments with monkeys:

Field site: The experiments took place at Tietê Ecological Park (PET), São Paulo, Brazil. The park covers an area of 14 km² and was created with the objective of preserving the Tietê river and some of its surrounding floodplains, as well as providing a leisure area for the population of the Metropolitan Region of São Paulo. Additionally, it has been used as place to release confiscated animals.

Group composition: One group of semi-free ranging capuchin monkeys (*Sapajus* sp) took part in the experiments. This group is fully habituated to human observers and habitually use stone tools to crack palm nuts (*Syagrus romanzoffina*). At the time of the experiment the group consisted of 33 individuals (10 adult males, 13 adult females, 10 juveniles and infants).

Experiments: Data collection took place from 7th until 20th of April 2017. Each experimental set-up was placed near known feeding areas and consisted of one anvil and three hammerstones of the same raw material. The capuchins were allowed to freely select the hammerstone during the experimental sessions.

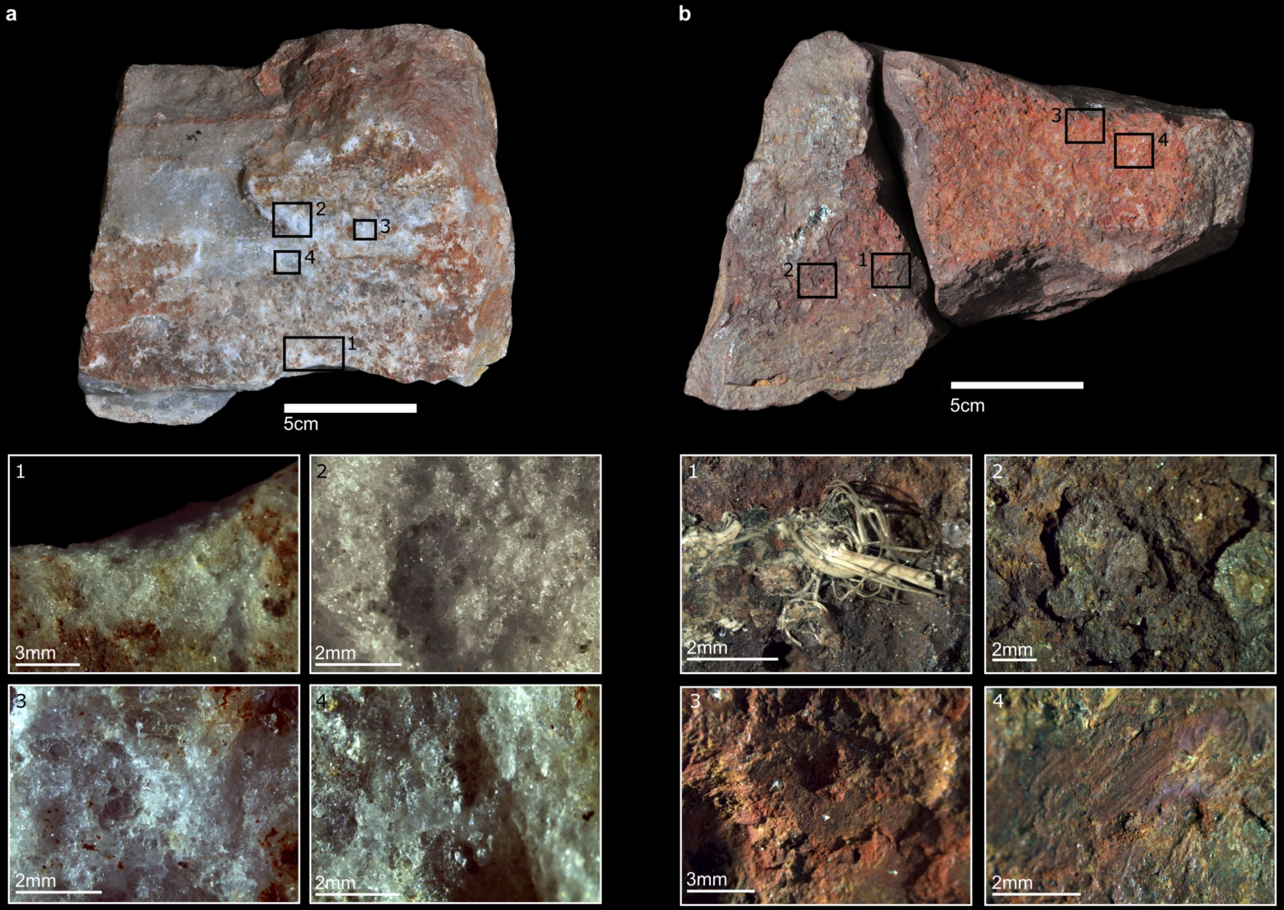
The experiment was designed for capuchins to crack open 1000 palm nuts (*Syagrus romanzoffina*) on each of the three anvils provided. During the course of the experiments one nut at a time was provided to the monkey present at the anvil to reduce dispersal of experimental tools by other group members and allow an accurate count of nuts processed on each anvil. After the monkeys left the site all fragments of the anvil and hammerstones were collected. One experimental setup consecutively was provided to the monkeys until ~ 1000 nuts had been cracked open on one anvil. Then the set up was changed to a different raw material.

All tool manipulation and use was filmed using a camcorder Canon Vixia HF R52 or a camera Canon EOS 70D mounted in tripods placed 6-7m from the anvil. This resulted in ~877 minutes of video footage over the course of 10 days. The video footage was coded, noting the individual, the tools used, the number of hits to crack the nut, number of miss hits, and visible fractures of the anvils.

All anvil material was subjected to a full use wear, technological and refit lithic analysis (for details see Supplementary Material and Methods). A visual display of the experimental set up can be seen in Supplementary Material and Methods. Controlled flaking experiments were conducted by an experienced human knapper to compare the technological attributes of unintentional capuchin nut cracking flakes and intentionally produced free hand knapped flakes using the same HI raw material. Finally, we compared this material to published Oldowan morphological and technological flake data to identify significant distinguishing attributes which would discriminate between the archaeological signature of flaking and percussive activities.

Anvils were preliminary photographed and studied after the experiments to record the presence of any residues left on their surfaces. After that, they were cleaned with rinse water and neutral soap using an ultrasonic bath. In those cases, in which the tool did not allow the use of the bath, surfaces were gently cleaning with a soft brush. Anvils were analyzed following protocols established by de la Torre et al. (2013) and which have been applied on other primate assemblages (Benito-Calvo, 2015; Arroyo et al., 2016; Proffitt et al., 2018).

Absolute and relative frequencies were established for all technological categories within each raw material. Statistical variation between skill levels in both categorical and numerical attributes was assessed. For categorical attributes a Chi-Square test or, where applicable, a Fisher’s Exact test (where a 2x2 contingency table was possible), were used, followed by a Post-Hoc assessment of the adjusted residuals (AR) to identify the source of any significant variation. Adjusted residual values represent the difference between the observed and expected frequencies for each variable divided by the standard error. Adjusted residual values of greater than +/-2 indicate significantly ($p = 0.05$) over or under representation of that variable from the expected frequency. Numerical data were subjected to a Kruskal-Wallis test.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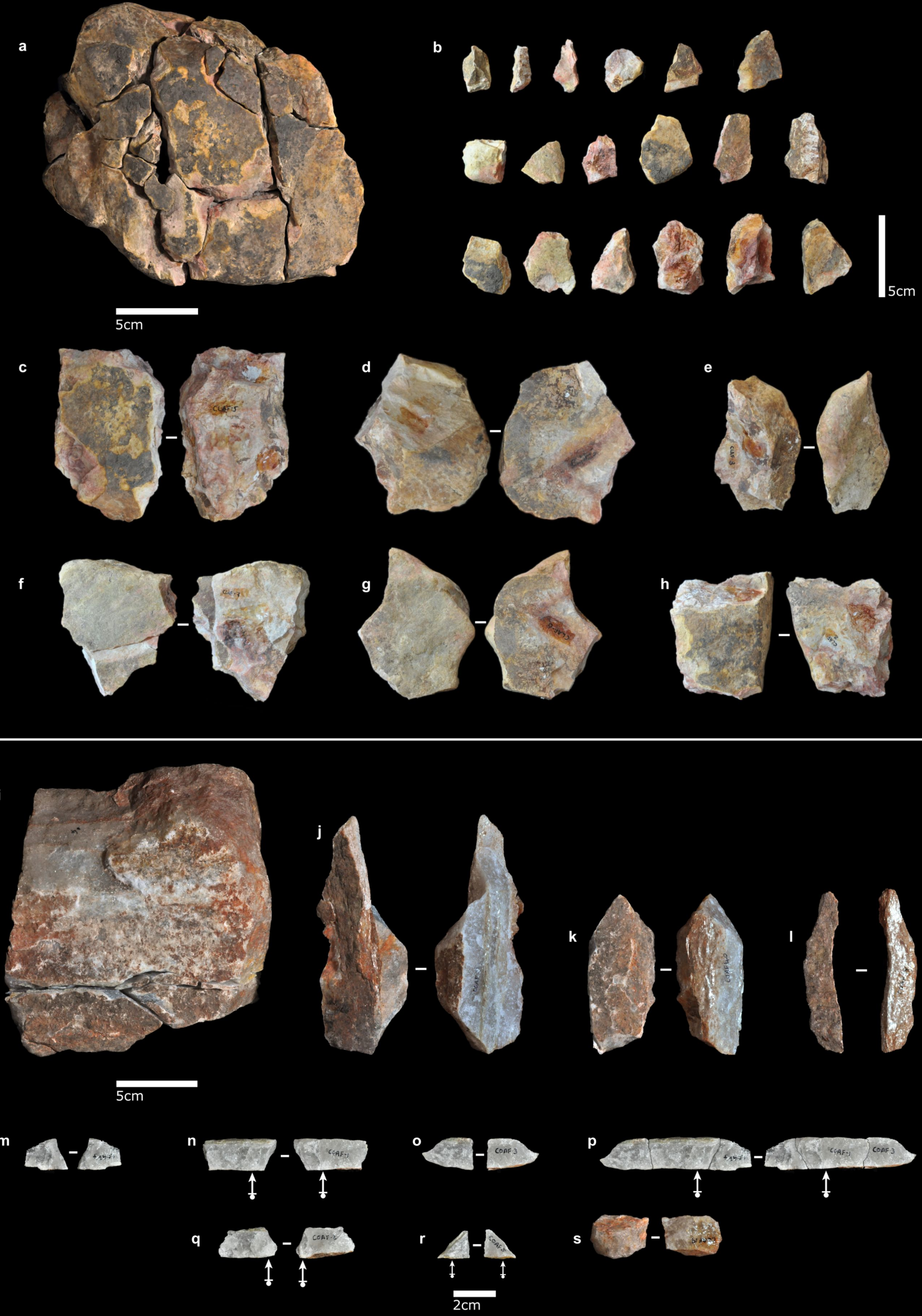
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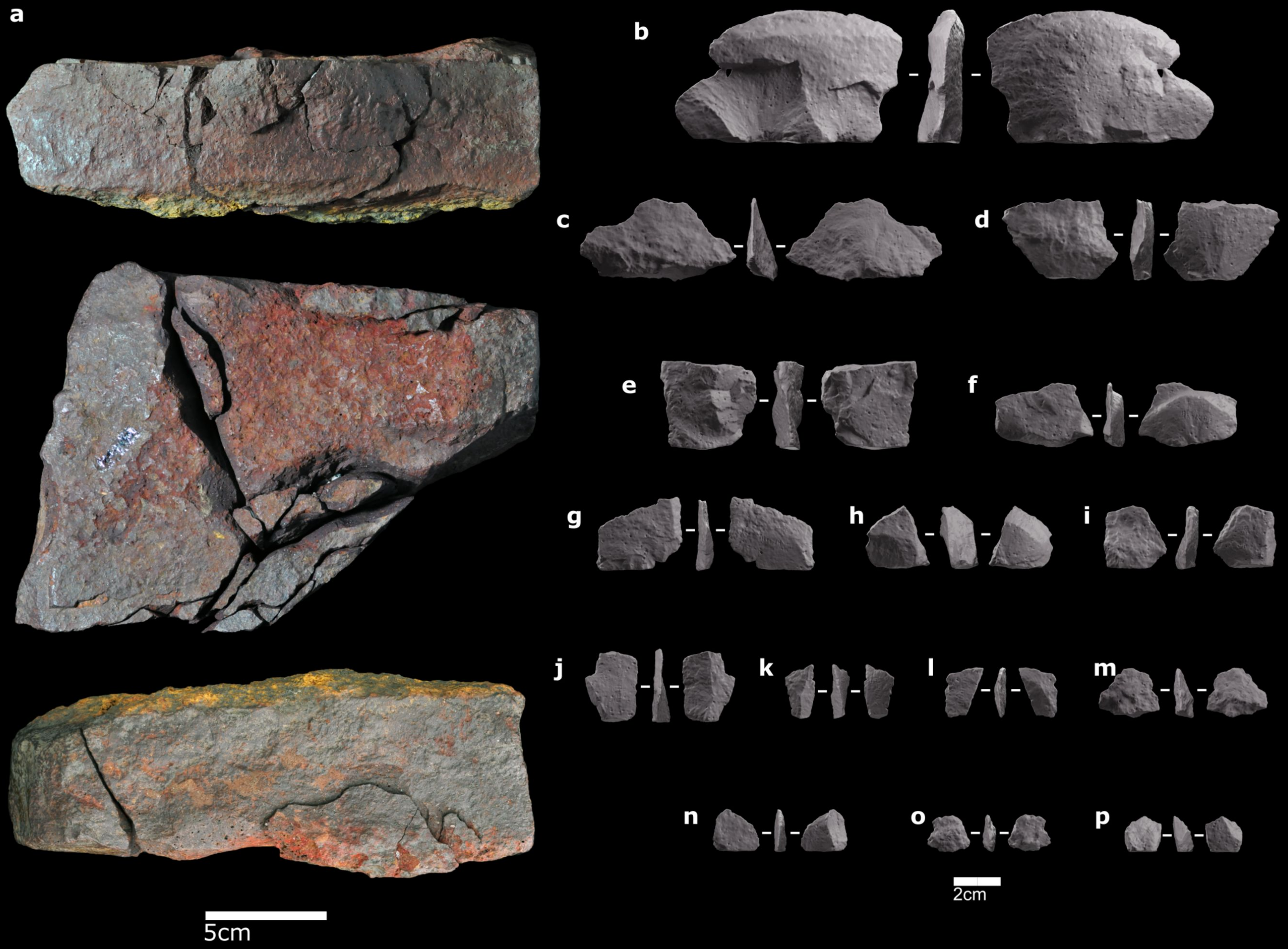
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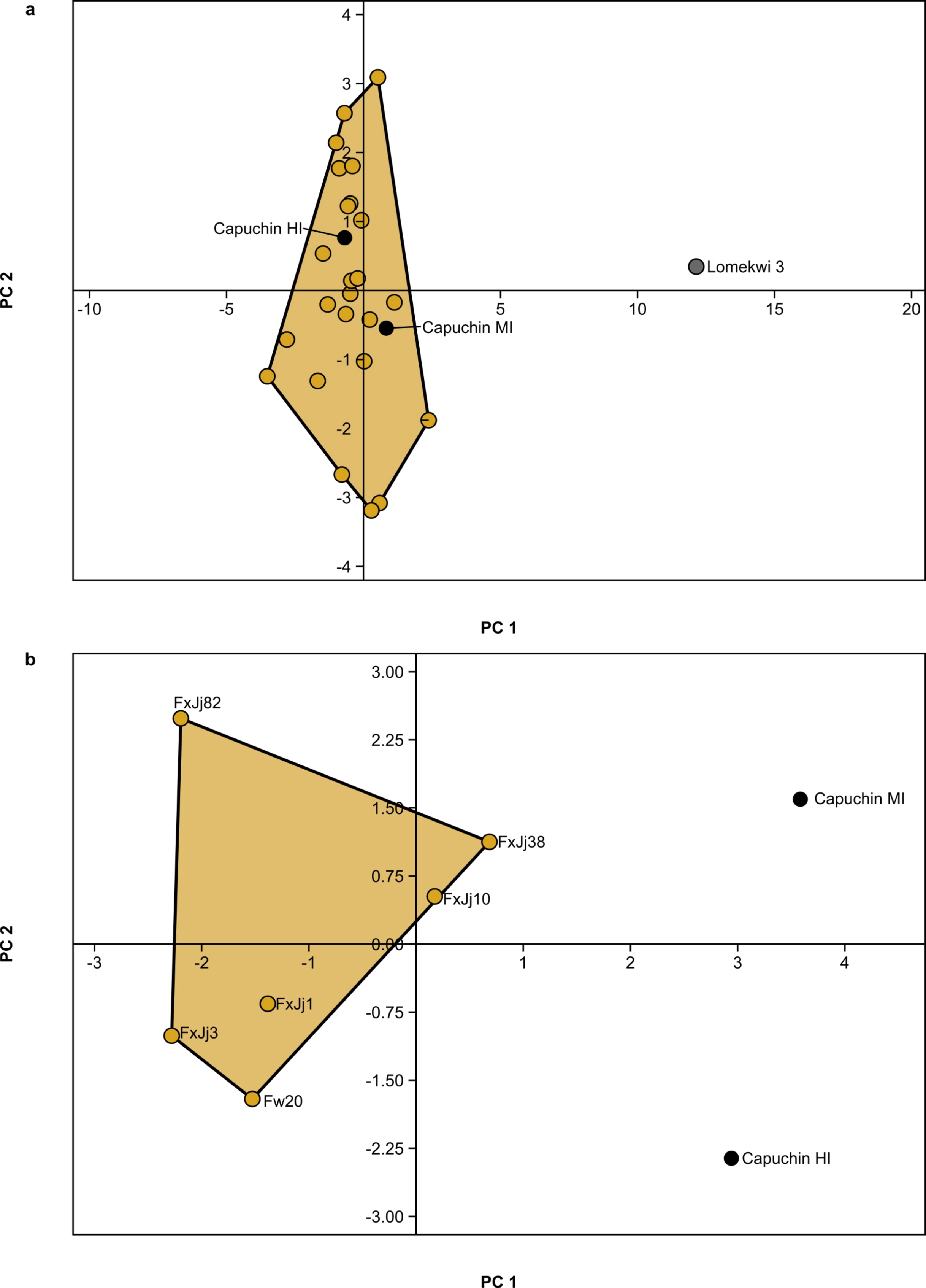
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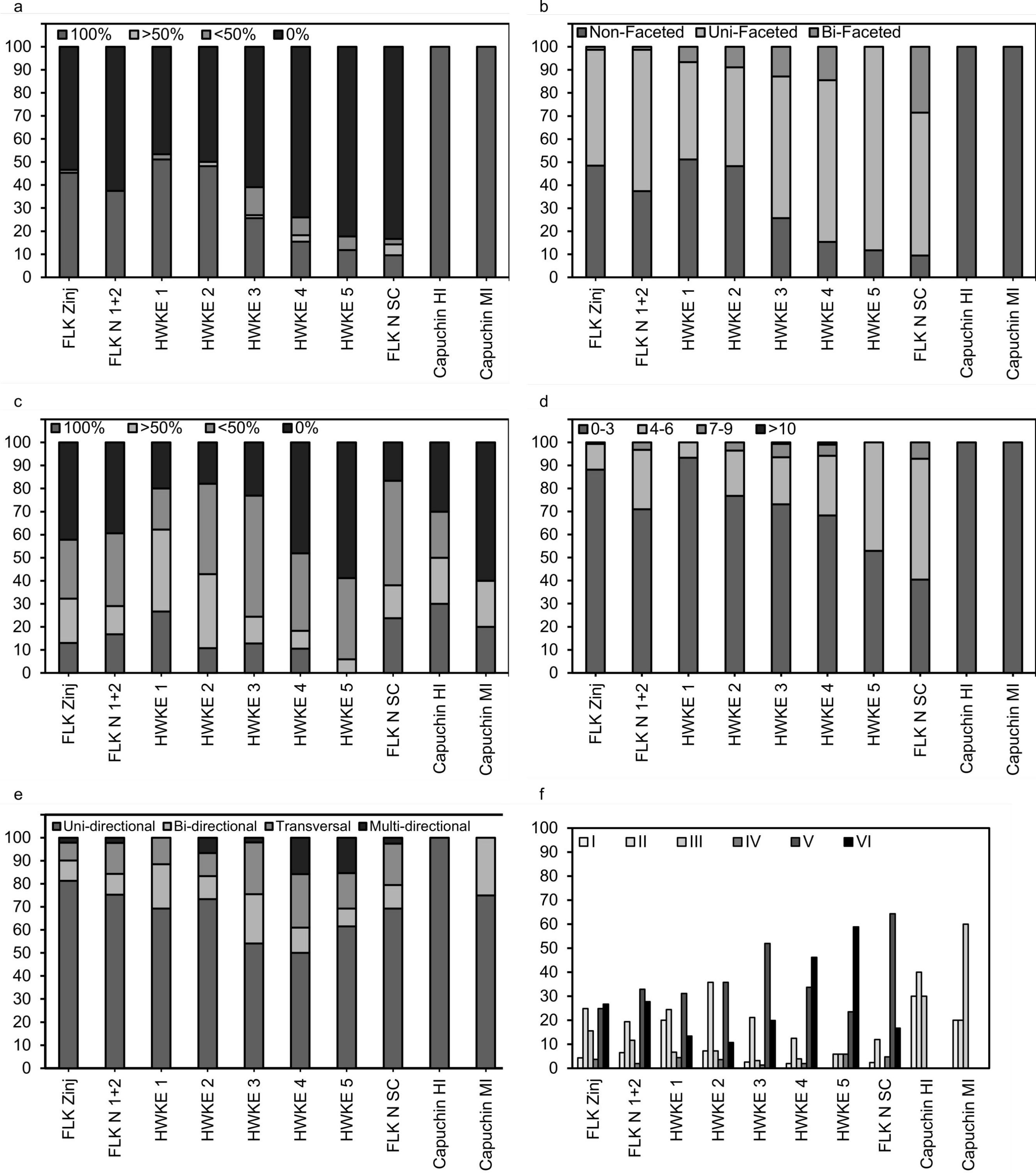
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