Use-wear and residue analysis of pounding tools used by wild capuchin monkeys (*Sapajus libidinosus*) from Serra da Capivara (Piauí, Brazil)

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Abstract

Bearded capuchin monkeys (*Sapajus libidinosus*) from Serra da Capivara National Park (Brazil), perform the widest range of activities using stone tools of all the non-human tool-using primates. The behaviours behind this range of tool use have been closely documented, but little is known about the characteristics of the tools themselves. Here we redress this imbalance and adopt an archaeological perspective to the analysis of capuchin pounding tools. We apply, for the first time, systematic microscopic techniques to the analysis of capuchin stone tools used for digging, cracking cashew nuts and seed processing to characterise their damage patterns combined with residue spatial distribution and micro-remains analysis. This work presents a standardized methodology for future primate archaeological use-wear studies as well as forming a reference collection which can be used to identify different activities within the primate archaeological record. Furthermore, understanding the archaeologically visible traces of

primate percussive behaviours represents an initial step in developing a methodology to investigate if similar activities were practiced by early hominins and to help identify these activities in the Plio-Pleistocene archaeological record.

Keywords: Primate archaeology; *Sapajus libidinosus*; percussive activities; use-wear analysis; residues.

1. Introduction

During the last decade, primate archaeology (Haslam et al., 2009, 2017) has been established as a robust discipline to study past and present non-human primate tool-use. Research within this field has shown that chimpanzees (*Pan troglodytes verus*) have been using stones to crack nuts for at least 4,300 years (Mercader et al., 2007), whilst the earliest evidence of stone tool use for bearded capuchins (*Sapajus libidinosus*) is at least 3,000 years old (Falótico and Proffitt et al., 2019). Moreover, there have been reports of stone tool use to process shellfish (at least since the 19th century), to crack sea almonds, and more recently oil palm nuts, by long-tailed macaques (Carpenter,1887; Gumert et al., 2009; Tan et al., 2015; Falótico et al., 2017b; Luncz et al., 2017). The hominin archaeological record also preserves evidence of varying percussive behaviour including bone breaking (e.g. Blumenschine and Selvaggio, 1988), and nut cracking (Goren-Inbar et al., 2002), with the earliest reported flaked stone tools also possessing a significant percussive element (Harmand et al, 2015). These parallels have led different scholars to underline the evolutionary implications that pounding activities had on the course of human evolution (Panger et al., 2002; DeBeaune, 2004; Marchant and McGrew, 2005; de la Torre and Hirata, 2015; Thompson et al., 2019). Hence, a key aim of primate archaeology is to investigate the similarities and differences between the percussive behaviour of extant primates and those of early hominins (Haslam et al, 2009).

The earliest references to stone tool use by capuchin monkeys date to the 16th century (Urbani, 1998), with additional reports of tool-use in the 18th and 19th centuries (Visalberghi, 1990). However, systematic primatological studies of tool-use by wild capuchin monkey (*Sapajus* spp. and *Cebus* spp.) were not undertaken until the 2000s, when long-term research studies were established at two locations in Brazil: Fazenda Boa Vista (FBV) and Serra da Capivara National Park (SCNP). Capuchin tool use is also known to occur at other areas within the Brazilian Cerrado and Caatinga environments including Serra das Confusões (Falótico et al., 2018), Serra Talhada (de Moraes et al., 2014) and various locations in Bahia (Canale et al., 2009). Additionally, it has been shown that some white-faced capuchins (*Cebus imitator*) from Panama also use stones to process encased foods (Méndez-Carvajal and Valdés-Díaz, 2017; Barrett et al., 2018; Monteza-Moreno et al., 2020), increasing substantially the geographic distribution of this behaviour among the New World primates.

Capuchins at SCNP perform a range of stone tool use, including pounding cashew nuts (*Anacardium occidentale*), processing cactuses to consume the inner pith, and cracking seeds (*Manihot* sp. and *Cordia rufescens*) and fruits such as jatobá (*Hymenaea courbaril*) (Moura and Lee, 2004; Mannu and Ottoni, 2009; Falótico and Ottoni, 2016). In addition, stone are used to dig shallow holes to access small tubers (*Thiloa glaucocarpa*), roots (*Ocotea* sp.) and trapdoor spiders (Mannu and Ottoni, 2009; Falótico et al., 2017), as throwing implements for sexual displays (Falótico and Ottoni, 2013), and as pounding tools to pulverize other quartzite cobbles (Mannu and Ottoni, 2009; Proffitt et al., 2016).

The use of stones to process plant food resources and underground storage organs (USOs) is a well-documented behaviour for capuchin monkeys at SCNP (Mannu and Ottoni, 2009; Falótico and Ottoni, 2016; Falótico et al., 2017). These activities provide a source of proteins and carbohydrates, although representing only a small percentage within their total foraging and feeding time strategy (Spagnoletti et al., 2012). Plant food processing with stones has been considered as one of the main dietary adaptations in primates (Haslam, 2012) in which terrestrially, influenced by foraging strategy, would have played an important role in the development of tool use by capuchins (Visalberghi et al., 2005).

This wide range of stone tool use in multiple primate species highlights that percussive tooluse is not exclusive to the *Homo* genus or indeed to hominins, but instead may be a characteristic adaptation of primates, including hominins. Despite detailed reports describing the behavioural aspects of capuchin stone-use, little attention has been paid to the physical characteristics of the tools themselves, with only a few presenting comprehensive technological analyses (Visalberghi et al., 2007; Haslam et al., 2014; Proffitt et al., 2016; Falótico and Proffitt et al., 2019).

Since the identification of capuchin stone tool use, nut cracking has been the focus of systematic studies at both SCNP and FBV. These studies have shown that capuchins select hammerstones based on weight and size depending on the hardness and type of nut processed (Visalberghi et al., 2009; Ferreira et al., 2010; Luncz et al., 2016). These hammerstones can weigh over three kilograms, with boulders and logs used as anvils (Fragaszy et al., 2004; Visalberghi et al., 2007). During nut cracking the monkeys adjust the position of the nut on the anvil to be stable (Liu et al., 2011; Fragaszy et al., 2013) and then perform a motion in which they lift the hammerstone using both hands and use the kinetic energy generated when dropping to break the nut (Liu et al., 2009; Mangalam et al., 2018, 2019). When processing softer fruits and seeds, however, capuchins tend to select smaller tools and adjust the motion to pound them (Falótico and Ottoni, 2016).

Microwear studies have long been used within the field of archaeology to characterize and differentiate the use related damage on prehistoric stone tools (Semenov,1964; Keeley, 1980; Vaughan, 1985). The first comprehensive use-wear studies applied to ground stone tools were undertaken in the 1980's and highlighted the importance of plant-food processing activities to early humans (e.g. Adams, 1988, 1989; Dubreuil, 2004 among others). Recently it has been shown that these analytical techniques can be applied to various primate stone tool types, including hammerstones and anvils used for chimpanzee nut cracking (Benito-Calvo et al., 2015; Arroyo et al., 2016; Proffitt et al., 2018) and hammerstones used by macaque during pounding behaviours (Haslam et al., 2013; Proffitt et al., 2018b). Within this framework, we aim to broaden the application of primate use-wear studies to the analysis of pounding tools used by wild capuchin monkeys. Here we present an integrated study of a used stone assemblage from Serra da Capivara National Park, describing the use-wear traces and residues developed on their surfaces and applying a microscopic methodology based on a low (<100×) and high (>100×) magnification approaches. This work contributes to our understanding of the technological attributes associated with various percussive behaviours and establishes a reference collection of use-wear patterns for capuchin stone tools which can be used to identify activities within the primate archaeological record. The ultimate aim of this study, as with previous primate tool use-wear studies, is to develop a greater understanding of the damage patterns associated with a wide range of potential percussive behaviours, which in turn might allow greater insight into the range of percussive behaviours practiced by early hominins.

2. Materials and Methods

2.1 Capuchin groups from Serra da Capivara

Serra da Capivara National Park, located in the State of Piauí (NE of Brazil) over an area of nearly 130 ha, is a nature reserve and World Heritage site well-known for its valuable natural and cultural heritage. The environment is dominated by the Caatinga, a biome exclusive to Brazil and characterized by a landscape predominated by xerophytic and scrub vegetation, as well as deciduous forest with a semi-arid climate (average rainfall between 240-900 mm/year). The Caatinga has been considered as a seasonally dry tropical forest biota (Santos et al., 2011).

The pounding tool collection was conducted between 2007 and 2009 as part of a wider study of two groups of capuchin monkeys (*Sapajus libidinosus*) from SCNP: I) The Pedra Furada group, formed by forty-five individuals; II) The Bocão group, formed of twenty-seven individuals. Observations of these groups have documented that they are sympatric, and frequently met and foraged together (Falótico and Ottoni, 2016).

2.2 The lithic assemblage

The capuchin pounding tool assemblage analysed in this study was selected from a larger sample of capuchin tools (Falótico and Ottoni, 2016) and collected at SCNP by one of us (TF). All tools were collected immediately after an observed percussive behaviour event, and individually stored in plastic bags (see Falótico and Ottoni (2016) for details about the data collection during fieldwork).

An additional sample of six stone tools were collected during the 2019 field season at the Oitenta area (OIT) as a reference collection of tools where use-wear traces and residues were newly developed. A total of twenty-nine tools used exclusively for pounding (n = 16), digging for roots, spiders and arthropods (n = 12) and stone-on-stone (SoS) percussion (n = 1) were included in this analysis (see Fig. 1 and details in Table 1). For comparative purposes between the three activities, we included additional data (general dimensions and macroscopic traces) from sixteen hammerstones used for SoS percussion formerly analyzed elsewhere (Proffitt et al., 2016). All pounded food resources (jatobá fruit, seeds and cashew nuts) were locally available and selected by the monkeys without human interaction.

To geologically characterise the lithic specimens, a sample of available stones matching the size and raw material properties of the capuchin stone tools were collected from the study area. These were prepared as 30 µm petrographic thin sections and studied under the polarising light microscope. Their elemental composition was characterised via non-destructive portable X-ray fluorescence (pXRF).

The technological analysis of the stone tool assemblage is based on the general classification of pounding tools proposed by Chavaillon (1979) that distinguish two categories: active and passive elements, used as synonyms for hammerstones and anvils respectively. Additional technological attributes were analysed, including general metrics, raw material, blank type and macroscopic surface traces such as fractures, impact points (and hertzian cones), battered areas (formed by superposed impacts) and location of the percussive marks.

2.3 Residue analysis: sample preparation and spatial distribution

Each tool was macro- and microscopically inspected to identify residues, six were selected for micro-remains analysis, including phytoliths, starches, pollens and non-pollen palynomorphs (NPP) analysis based on the abundance of residues present on their surfaces. To process the samples, we adapted standard protocols for preparation and extraction of different micro-remains from archaeological materials (e. g. Kooyman, 2015; Pearsall, 2019). The extraction process was done from the active surfaces. Each tool was deposited in a glass container with distilled water and sonicated in an ultrasonic tank for fifteen minutes. All distilled water was decanted and centrifuged at 2500 rpm for three minutes. Finally, sediment remains were dried in a furnace at 40º for 24-48 hours. Dried residues were mounted homogenously on a slide with phenolated glycerin and sealed with a coverslip. Observations were made with an optical microscope IS.1152-PLi at 600× and photographs were taken with a CMOS 10MP Euromex. At least three sections of each sample were analysed using plane polarized light (PPL) and cross polarized light (XPL). Phytolith identification and description follow the International Code for Phytolith Nomenclature (ICPN) 2.0 (Neumann et al., 2019), while fossil pollen, spores and non-pollen palynomorphs (NPP) were identified using previous terms (Reille, 1995; van Geel, 1978, 1986; Jarzen and Elsik, 1986; Miola, 2012) and modern pollen reference collection.

Spatial distribution analysis of the residues was done adapting the methods proposed by de la Torre and colleagues (2013). Digital images of the tools were georeferenced in a local spatial coordinate system. Then, single points were assigned for each residue cluster. Only on tools used to crack cashew nuts was it possible to draw and quantify the complete areas covered by oil residues. Finally, we computed spatial parameters such as distance of the clusters to the center of the tool (DAC), distance to the edge (DAE), residue area quantification and percentage of the surface covered by residues (PCR).

2.4 Microwear analysis: Stone sample cleaning and microscopic equipment

Prior to microscopic analysis, protocols of stone tool cleaning were applied following the procedures outlined by Ollé and Vergés (2008, 2014). First, tools were cleaned in an ultrasonic bath in hydrogen peroxide (H_2O_2); then cleaned in neutral phosphate-free detergent Derquim®; and finally, an ultrasonic bath in acetone ($CH_3(CO)CH_3$) to eliminate residues from handling. We repeated the process several times at intervals of 15 minutes until surfaces were clean enough to conduct the microscopic analysis.

Observations to characterize use-wear marks was done using three types of microscopes: 1) Euromex binocular microscope with a magnification range between 1× - 8× equipped with a Scemex camera and 10× lenses. 2) Zeiss Axio Scope A1 reflected light microscope with differential interference contrast (DIC) system, and a Nomarski interference contrast filter, that ensures better results with translucent materials (Pignat and Plisson, 2000; Araújo Igreja, 2009; Knutsson et al., 2015; Fernández Marchena and Ollé, 2016). This microscope is equipped with objectives EC Epiplan ranging from 5×/ 0.13 to 50×/0.5 HD DIC, allowing observations from 50× to 500×. 3) HIROX KH-8700 digital microscope supplied with MXG-5000REZ triple objective with a magnification range from 35× to 5000×.

Terminology used to describe the microscopic traces follow nomenclature used when analyzing percussive objects (Adams et al., 2002, 2009; de la Torre et al., 2013; Arroyo and de la Torre, 2018). Among these we have focused on the identification of marks produced by the tribological mechanisms of fatigue wear (micro-fractures, crystal crushing, impact points) and by process of abrasive motion (linear traces, scratches, grain edge rounding), following Adams et al. (2009). Additionally, identified polish traces are based on descriptions of similar wear on quartzite raw materials (e.g. Sussman, 1988; Knutsson, 1988; Ollé et al., 2016).

3. Results

3.1 General characteristics of the wild capuchin assemblage

Thin section petrographic analysis conducted on a sample of five stone samples collected at SCNP showed that they are composed almost entirely of interlocking recrystallized quartz and polycrystalline quartz with metamorphic foliation (Supplementary Online Material [SOM] Text 1). Geochemical characterisation via portable X-ray fluorescence spectrometry (pXRF) confirmed their extremely high silica content. It therefore appears that all wild capuchin pounding tool blanks were complete or fractured quartzite cobbles. This raw material is found in large quantities across SCNP, and belong to an extensive conglomerate deposited above the Palaeozoic sandstone massif that dominates the landscape (Oliveira and Santos, 2019).

Pounded tools analysed here were used as active elements, as generally capuchin monkeys at SCNP use embedded conglomerates or large blocks as passive elements. Most of the tools (75.9%, n = 22) were used by males and six (20.7%) by females, while it was not possible to determine the sex of the individual that used one tool (3.4%). Nineteen (65.5%) of the individuals that manipulated the tools were adult (> 7 years old) and ten (34.5%) were juvenile (2-5 years old). Regarding laterality most individuals (41.4%, *n* = 12) tended to use tools bimanually, however, both exclusively right-handed (34.5%, *n* = 10) and left-handed (13.8%, *n* = 4) tool use was also observed, not being possible to determine the laterality on three of the tools (10.3%)

Previous analysis of a larger assemblage of pounded tools from SCNP has shown differences in the size of the pounding tools dependent on the properties (hardness and size) of the material being processed. Furthermore, wild capuchins at SCNP select stones of particular size ranges compared to the locally available raw material (Falótico and Ottoni, 2016). Considering only the assemblage examined here, there is no significant difference in dimensions(see Fig. 2 and SOM Table S1) between the active elements used for pounding activities and those used for digging (see details in Table 2). Significant differences are found, however, when comparing all three activities, pounding, digging and SoS percussion (Table 2), with SoS active elements possessing larger mean dimensions (Fig. 2).

3.2 Residue and micro-remains analysis

Macroscopic remains of residues were documented on ten pieces (22.2%), and represent three types of residues: a) kernels/shell fragments adhering to the surface, possessing a compressed appearance and clustered distribution (Fig. 3A-C); b) oil residues (Fig. 3C); c) sediment patches adhered to the active areas of the digging tools (Fig. 3D).

Active elements used to process cashew nuts showed the greatest frequency of residue remains caused by the oil located between the pericarp and the nut, which can be corrosive to the skin due to the anacardic acids (Akinhanmi et al., 2008; Sirianni and Visalberghi, 2013; Falótico and Ottoni, 2016). The oil residues of the nuts are present across large sections of the tools surface, covering up to 62.7% of the surfaces (see details on SOM Table S2). Occasionally, this residue coated the entire surface, as documented on two pounded tools. Indeed, even after significant and thorough cleaning of the tools, such oil residues were still clearly identifiable (Fig. 4).

The GIS spatial distribution of residue performed on ten tools indicated that seed pounding hammerstones possessed greater frequencies of residue clusters. These tended, however, to be clustered independently of the material processed (Fig. 5).Tools used to process cashew nuts and those used for digging differed, with residue located primarily on the peripheral areas of working surfaces. This is indicated by the low mean values of the distance to the tool edge (mean DAC< 0.60 cm, see details on Fig. 6 and SOM Table S2), and is reflected by the higher values for the distance of residue mean centre to the tool centre (EMNC-AC).

Table 3 details the plant micro-remains identified on the selected tools highlighting the variability and richness of remains. Non-pollen palynomorphs are the most abundant remains, dominated by fungi forms such as *Pluricellaesporites*, hyphae, *Polyadosporites* and *Polyporisporites*. It is noteworthy that on three samples there is also atypical evidence of *Pinus* pollen, a species currently absent in SCNP and whose presence can be attributed to post-collection contamination (Fig. 7).

Phytoliths are less abundant, identified only on one sample. Starch grains, however, are notable, showing homogeneous distributions across samples (Fig. 8). Although present on the stone tools themselves, the lack of a controlled reference collection for phytoliths and starch grains for SCNP prohibits detailed taxonomic identification.

3.3 Use-wear characterization of wild capuchin pounding tools

Pounding and digging tools are characterized by a low degree of modification. From a macroscopic perspective, all SoS percussive tools and one of the tools used to process seeds possessed concentrations of superimposed impacts, occasionally developing into battered areas. Overall, it was possible to identify impact points on 71.1% (n = 32) of the tools, the majority on pounding and SoS active elements. Most digging tools (n = 9) showed no significant macroscopic modifications. Fracture negatives were not common among the analysed collection. We identified a total of eight tools (17.8%, tools for pounding = 5; SoS = 1; digging tools = 2) with non-invasive, short and wide fractures , often with feather (and less frequently step) terminations (Fig. 9).

Digging stones

Digging stones are characterized by a specific use-wear pattern (Fig. 10 and Fig. 11). They possessed primarily one active zone of use (only one object was reoriented during its use and had two active zones). The morphology of the active zone is often a naturally occurring edge or pointed convex surface, with concentrated use wear marks located on these distal areas.

From a microscopic perspective, tools used for digging possessed fewer conspicuous use-wear marks on their surfaces. Of the stone tools studied, three showed no significant use-wear traces. Crushing of the quartz crystals which were also occasionally associated with microfractures caused by impacts between the hammerstone and pebbles within the sediment were the most frequent (66.7%, n = 8) use wear traces. Both pits and incipient hertzian cones were absent on all digging tools.

Overall, digging stones possessed worn and rough areas across their surfaces caused by natural weathering. However, five tools from this assemblage possessed traces that are not related to natural weathering processes. Three possessed small areas of polish with a scattered distribution within the active zone (Fig. 11C), and two possessed sub-parallel linear traces / scratches (Fig. 11F and G). These use wear traces can be seen as the result of an abrasive process caused by the motion performed during digging.

Tools used to pound soft fruits and cashew nuts

Soft fruit and cashew nut processing tools possess a wider spatial distribution of pounding marks compared to digging tools, however, they also possess a low degree of physical modification (Fig. 12). Microwear traces are characterized by the presence of singular impact points (with a low presence of incipient hertzian cones) and crushed crystals. These are frequently associated to micro-fractures with a stepped morphology and, less frequently, to small pits (caused by the detachment of small fragments) (Fig. 10). Furthermore, use-wear traces related to abrasive motion, such as linear traces and polish, are completely absent in this category of pounding tools. Flat horizontal surfaces were primarily used on almost all stone tools within this category with only one example showing damage (crushed crystals and stepped microfractures) on both angular ends (Fig. 12E). This contracts heavily with the observed preferential use of angular surfaces for digging tools. .

Tools used on SoS percussion

Only one active element collected during 2019 and used for SoS percussion was included in this study. Nonetheless, its use-wear analysis follows similar observations described by Proffitt et al. (2016), with impacts (incipient hertzian cones) and crushing on the ridges occasionally associated to detachments and stepped microfractures (Fig. 13). Within the wild capuchin assemblage, incipient hertzian cones are more frequent on tools used for SoS percussion than other pounding tools, a similar use-wear pattern as identified in previous research (Proffitt et al, 2016). Following the terminology proposed by Byous (2013), the hertzian cones identified on the capuchin SoS tool show crushed craters surrounded by hackles that can also develop crushing.

Particular use wear features also occur independently of the target material processed. These are associated with the mechanical processes of crystal crushing through impacts during a thrusting motion. First, we identified iridescences located on the outer areas of hertzian cones and around crushed areas (Figure 13C). This feature was identifiable only using an optical light microscope and is formed by the light reflexion when passing through fractured crystals (Fernández-Marchena and Ollé, 2016). Additionally, fracture lines were identified towards the exterior zones of the crushed areas formed by the propagation of the impact force that produced fissuring of the crystals without being detached (see Fig. 12F).

4. Discussion

4.1 Characterization of primate use-wear patterns

The analysis of the wild capuchin pounding tool assemblage presented here establishes patterns of use-wear traces based on different activity types and allows for an understanding of their formation processes. The main differences between the three activities centres on the location of the percussive traces. Pounding tools bear marks mainly on the horizontal surfaces, while digging tools are primarily used on distal and angular areas, indicating that capuchin monkeys adjust not only the size of the tools but also the use of specific areas of the hammerstones based on the activity. This type of stone morphology mediated tool use has been identified amongst long-tailed macaques, where flat board surfaces are used for pounding and sharper edges used for oyster processing (Luncz et al., 2019; Gumert et al, 2009). This study highlights that, not only do capuchins, similarly to macaques and chimpanzees, select hammerstones based on the hardness of the target object, but also use specific stone morphologies for different tasks. This selection criteria, however, is less visible compared to macaque stone tool selection, as the raw material used at SCNP develops macro use-wear traces at a much lower rate compared to the limestone used by macaques (Luncz et al., 2019).

The scattered patterns of microwear traces documented on the tools used to process soft fruits and seeds is explained by the frequent contact between the active and the passive element when performing the activity.

The exceptionally low modification of the tools used for digging activities can be explained by the short duration of the activity itself, with more substantial use-wear traces potentially being formed when impacting pebbles embedded within the substrate. Additional marks were formed through abrasion produced by the motion of the activity. The formation of use-wear marks on digging tools is also highly dependent on the duration of the action. Digging is normally a quick (<5 min) activity in which the tool is abandoned after use, therefore, if use time is low and there is an absence of contact with other pebbles, very few wear traces will develop, making the recognition of this activity in the primate record challenging although in some cases, not impossible.

Tools used for SoS percussion show higher surface modifications, as the activity requires striking two cobbles together. In this case, the presence of the hertzian cones and fractures on the surface of the stones can be used as an index to distinguish the activity, as they are highly frequent on tools used for this activity (Proffitt et al., 2016), whilst being less frequent on tools used for pounding and absent on digging tools.

It is also significant that nine tools did not show any macroscopic modification, and four did not bear significant microwear traces. Most of these tools were used for digging, and one for pounding. The lack of clear physical damage patterns on these tools highlights the potential difficulties of identifying these pounding activities within the primate archaeological record. Furthermore, it is clear that the material processed heavily influences the development of use-wear patterns on these tools. The evidence presented in this paper suggests that digging would be the most difficult to too use behavior to identify archaeologically, as it is performed against a softer and less consolidated material producing superficial microscopic marks. Based on these results it is likely that identification of such behaviours, which rely solely on the interpretations of associated stone tools, in a primate archaeological context will be under representative of the true frequency of primate tool use. Following this same argument, it is also likely that percussive tasks performed on soft targets by early hominins are also under represented in the plio-pleistocene archaeological record.

Equally interesting are the results of the micro-remains analysis. On one side, it is noticeable that there is a low level of pollen from the seeds and fruits processed (*Hymenaea* sp., *Buchenavia grandis* and *Anacardium occidentale*), as they are all entomophilous species, with a restricted pollen production and dispersion. The low level of pollens can also be explained by the action of pounding, which may have mechanically "cleaned" the surface of the tools. Conversely, however, non-pollen palynomorphs and charcoal remains are representative of the local environmental conditions in which each tool was used. Moreover, the abundance of fungi spores and chitinous faunal remains from insects or acari can be explained by their high presence in the environment. The identification of palynomorphs and the limited dispersion of this type of micro-remains has the potential to characterize and differentiate the area and environment where tool use was undertaken.Phytolith and starch granules are the micro-remains that can be considered as directly related to the pounding activities as they don ´t have a natural dispersal mechanism (Pearsall, 2019), and have been widely recognized in the analysis of ground stone tools in archaeological contexts (Dubreuil, 2004; Pearsall et al., 2004; Revedin et al., 2010; Portillo et al., 2013). Despite the fact starch grains were recovered from all analysed tools, it was not possible for these to be taxonomically identified, making it difficult to correlate them to specific pounded fruits. Further, the near absence of phytolith remains in the capuchin pounding stone assemblage can be explained by multiple factors: i) fruits and seeds processed by capuchins have different production levels of phytoliths; ii) differences in the deterioration process of the organic element that allow the release of phytoliths; iii) the intensity of the activity was not enough in terms of length and/or concentration to allow the deposition of phytoliths on the surface. Having said this, however, the presence of substantial levels of starch grains highlights the potential for future studies, as they may represent better markers for identifying plant residues on primate pounding tools, as was also documented on chimpanzee pounding tools (Mercader et al., 2007).

Considering a wider primatological record, variations in the size of the tools based on the type of food processed have been documented also by long-tailed macaques (Proffitt et al., 2018b; Gumert et al, 2009), while chimpanzees select their tools based on the nut hardness (Luncz et al., 2012, 2019b). Besides the differences in the activities, a Welch t test also revealed significant inter-species differences in the size of the tools (see Table 4). Bossou chimpanzee pounding tools show the largest mean dimensions (Fig. 14), although some variables can explain these differences such as raw material availability and the type of material processed. Nevertheless, chimpanzee (i.e. Benito-Calvo et al., 2015; Proffitt et al., 2018) and macaque tools (Haslam et al., 2013; Proffitt et al., 2018b) also have specific use-wear patterns that, along with the ones presented in this paper can be used as reference to recognise archaeological primate sites.

4.2 Implications for understanding early hominin activities

Pounding is a behaviour that does not require any intentional shaping of an object into a standardized form. Any suitable stone (or even wooden branch) available in the surrounding landscape can be selected and, as primatology has shown, their use can be based on a complex chaîne opératoire which include selection, transport, use and discard of the percussive tools (Carvalho et al., 2008). Comparative models involving extant primates are highlighting that the spectrum of percussive activities using movable tools within the early hominin record could have been far wider than previously expected, while the archaeological record supports that pounding activities may have been a significant behaviour during the Lower Pleistocene (Mora and de la Torre, 2005). Paleoanthropological evidence suggests that the consumption of plant food resources by early hominins was equally significant (Ungar, 2012; Ungar and Berger, 2018 among others). A key aspect required for the identification of these behaviours in the hominin archaeological record will be the correlation of pounding tools and their food target.

To date, analogies between early hominins and extant primate activities can be made for two behaviours: digging and nut cracking. Digging has been studied in four groups of wild capuchin monkeys from SCNP where the behaviour was directly observed (Mannu and Ottoni, 2009; Falótico et al., 2017). In addition, the use of digging tools made on organic raw materials by wild chimpanzees has been documented in Bulindi (Uganda; McLennan et al., 2020), through indirect evidence at Ugalla (Tanzania; Hernández-Aguilar et al., 2007) and on captive chimpanzees (Motes-Rodrigo et al., 2019). From an evolutionary perspective, it has been argued that digging for USO's may have played a significant role in human evolution (e.g. Wrangham et al., 1999; Laden and Wrangham, 2005), while environmental similarities between the Ugalla chimpanzees and *Australopithecus* spp. were considered as a significant factor in suggesting this type of behaviour in the latter (Hernández-Aguilar et al., 2007). However, the perishable nature of the potential wooden tools used makes the direct identification of this behaviour in the early hominin archaeological record increasingly difficult. The use of other materials as digging tools such as bones for termite foraging has been documented in the South African sites of Swartkrans, dated to 1.8-1 Ma (Backwell and d'Errico 2001, 2005), and Drimolen, with a chronology of 2-1.5 Ma (Backwell and d'Errico, 2008). The fact that a tool using primate species, capuchin monkeys, use stones as digging tools, opens up the potential for their use and identification in the archaeological record. A strength of primate archaeological studies lies in identifying uses of material that have previously been overlooked. Natural unmodified stones used as a digging implement is one such behaviour.

The potential importance of nut consumption for early hominins has long been recognised (Peters, 1987).To date, direct evidence of nut consumption by ESA hominins is only identified at Gesher Benot Ya'aqov (Israel) (Goren-Inbar et al., 2002) and highlights the variability in the hominin diets. By developing a comprehensive characterisation of the macro and microscopic damage patterns associated with primate nut processing stone tools it increases the likelihood of identifying identify similar wear patterns in the hominin archaeological record.

Overall, increasing evidence from the primatological stone tools use record supports the possibility that there are a range of archaeologically 'hidden' activities that early hominins may have performed in relation to their foraging strategies. Analyses such as the one presented in this study can be taken as a proof of concept for a means of identifying these types of activities. The future application of analyses designed to identify these percussive behaviours on primate stone tools to the hominin archaeological record may elucidate a wider exploitation of plant resources and fallback foods for our earliest ancestors. Having said, this, however, merely identifying the characteristics of various percussive activities on a range of stone tools cannot be solely used to interrogate the ESA archaeological record. Future work must develop robust methods of understanding the effect that millennia scale post depositional factors have on ephemeral and fragmented hominins percussive assemblages.

5. Conclusions

This study represents the first work to systematically characterize the use-wear patterns of pounding tools produced by extant wild capuchin monkeys, applying a combination of microwear as well as residue spatial distribution and micro-remains analysis.

Our results show that different patterns of use-wear marks can be distinguished between three stone tool activities performed by these primates. Micro-residue analysis applied to extant primate stone assemblages can offer a multiscale approach of local and regional vegetation, environment and the percussive activities. Although identification of phytoliths and pollen was not positive in all samples, starch grains and non-pollen palynomorphs extracted from the tools offered better results. We acknowledge that this represents just a small step within this field and that future work is required to expand the sample of tools, processed foods and behaviours, in which additional protocols should be established to implement an exhaustive sampling process and build a detailed reference collection.

The analyses presented here have wider applications within the field of primate archaeology. These patterns can be tested on the earliest capuchin tools recently documented (Falótico and Proffitt et al., 2019), to assess the persistence of specific activities through time. In addition, these techniques can be used to assess inter-group stone tool use variability of any of these behaviours between modern capuchin populations, as well as to identify capuchin activities in areas where populations are non-habituated or no longer present.

Overall, as a common behaviour associated with early hominins and extant primates, the study of pounding activities can provide valuable information about the ecological factors that allowed the emergence of stone tool use, and has the potential to shed light on the identification of the subsistence strategies developed by different hominin species including past primates. While chimpanzees evolutionarily are the closest primate to our linage and have been extensively used to model past hominin behaviours, this work highlights that capuchin monkeys can also contribute to our understanding of hominin tool use.

Acknowledgments

Fieldwork at SCNP was approved by Brazilian environmental protection agencies (IBAMA/ICMBio authorizations 14825-1 and 60134-1). Support for fieldwork and analysis was provided by FUMDHAM and funded by a Leakey Foundation Grant and British Academy Fellowship (to T.P.). Support was also provided by the Max Planck Society (Technological Primates Research Group to T.P). T.F. is supported by grant #2018/01292-9, São Paulo Research Foundation (FAPESP). T.P. is supported by a British Academy Postdoctoral fellowship (No. pf170157). A.A. is supported the by Spanish Ministry of Science, Innovation and Universities (IJCI-2017-33342, Subprograma Juan de la Cierva-Incorporación). A.B.-C. research is funded by Fundación Atapuerca. This research was framed in the Spanish MICINN-FEDER project PGC2018-093925-B-C32, the Generalitat de Catalunya-AGAUR projects 2017-SGR-1040, 2017-SGR-836 and the URV project 2018PFR-URV-B2-91. We also thank M. D. Guillén (PEJ2018-005216-A) for her assistance photographing the lithic assemblage and the reviewers for their comments to improve the manuscript.

References

Adams, J., 1988. Use-wear analyses on manos and hide-processing stones. J. Field Archaeol. 15, 307-315.

Adams, J., 1989. Methods for improving ground stone artifacts analysis: experiments in mano wear patterns, in: Amick, D.S., Mauldin, R.P. (Eds.), Experiments in Lithic Technology. Archaeopress, Oxford, pp. 259-276..

Adams, J., 2002. Mechanisms of wear on ground stone surfaces, in: Procopiu, H., Treuil, R. (Eds.), Moudre et broyer: L'Interprétation Fonctionelle de l'Outillage de Mouture et de Broyage dans la Préhistoire et l'Antiquité. CTHS, Paris, pp. 57-68.

Adams, J., Delgado, S., Dubreuil, L., Hamon, C., Plisson, H., Risch, R., 2009. Functional analysis of macro-lithic artefacts: a focus on working surfaces, in: Costa, L.J., Eigeland, L., Sternke, F. (Eds.), Non-flint Raw Material Use in Prehistory: Old Prejudices and New Directions. Proceedings of the XV Congress of the U.I.S.P.P. Archaeopress, Oxford, pp. 43-66.

Akinhanmi, T.F., Atasie, V.N., Akintokun, P.O., 2008. Chemical composition of physicochemical properties of cashew nut (*Anacardium occidentale*) oil and cashew nut shell liquid. J. Agri. Food. Environ. Sci. 2, 1-10.

Araújo Igreja, M., 2009. Use-wear analysis of non-flint stone tools using DIC microscopy and resin casts: a simple and effective technique, in: Clemente, I., Araújo Igreja, M. (Eds.), Recent Functional Studies on Non-flint Stone Tools: Methodological Improvements and Archaeological Inferences. Proceedings of the Workshop 23-25 May 2008, Lisboa.

Arroyo, A., de la Torre, I., 2018. Pounding tools in HWK EE and EF-HR (Olduvai Gorge, Tanzania): Percussive activities in the Oldowan-Acheulean transition. J. Hum. Evol. 120, 402-421.

Arroyo, A., Hirata, S., Matsuzawa, T., de la Torre, I., 2016. Nut cracking tools used by captive chimpanzees (*Pan troglodytes*) and their comparison with Early Stone Age percussive artefacts from Olduvai Gorge. PloS One 11, e0166788. doi:10.1371/journal.pone.0166788

Backwell, L., d'Errico, F., 2001. Evidence of termite foraging by Swartkrans early hominids. Proc. Natl. Acad. Sci. USA 98, 1358-1363.

Backwell, L., d'Errico, F., 2005. The origin of bone tool technology and the identification of early hominid cultural traditions, in: d'Errico, F., Backwell, L. (Eds.), From Tools to Symbols: From early hominids to modern humans. Witwatersrand University Press, Johannesburg, pp. 238-275.

Backwell, L., d'Errico, F., 2008. Early hominid bone tools from Drimolen, South Africa, J. Archaeol. Sci. 35, 2880-2894.

Barrett, B.J., Monteza-Moreno, C.M., Dogandzic, T., Zwyns, N., Ibáñez, A., Crofoot, M.C., 2018. Habitual stone-tool-aided extractive foraging in white-faced capuchins, *Cebus capucinus*. R. Soc. Open Sci. 5, 181002. doi:10.1098/rsos.181002.

Benito-Calvo, A., Carvalho, S., Arroyo, A., Matsuzawa, T., de la Torre, I., 2015. First GIS analysis of modern stone tools used by wild chimpanzees (*Pan troglodytes verus*) in Bossou, Guinea, West Africa. PloS One 10, e0121613. doi:10.1371/journal.pone.0121613

Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominid behaviour. Nature 333, 763-765.

Byous, J., 2013. Hertzian fractures and related terms - A glossary, Dowd Research/AAtR Publishing, Savannah, GA.

Canale, G.R., Guidorizzi, C.E., Martins Kierulff, M.C., Ferreira Rodrigues Gatto, C.A., 2009. First record of tool use by wild populations of the yellow-breasted Capuchin monkey (*Cebus xanthosternos*) and new records for the Bearded capuchin (*Cebus libidinosus*). Am. J. Primatol. 71, 366-372.

Carpenter, A., 1887. Monkeys opening oysters. Nature 36, 53.

Carvalho, S., Cunha, E., Sousa, C., Matsuzawa, T., 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. J. Hum. Evol. 55, 148-163.

Chavaillon, J., 1979. Essai pour une typologie du matériel de percussion. Bull. Soc. Prehist. Fr. 76, 230-233.

de Beaune, S.A., 2004. The invention of technology: Prehistory and cognition. Curr. Anthropol. 45, 139-162.

de la Torre, I., Benito-Calvo, A., Arroyo, A., Zupancich, A., Proffitt, T., 2013. Experimental protocols for the study of battered stone anvils from Olduvai Gorge (Tanzania). J. Archaeol. Sci. 40, 313-332.

de la Torre, I., Hirata, S., 2015. Percussive technology in human evolution: an introduction to a comparative approach in fossil and living primates. Philos. Trans. R. Soc. London, Ser. B. 370(1682), 20140346. doi: 10.1098/rstb.2014.0346.

de Moraes, B.L.C., da Silva Souto, A., Schiel, N., 2014. Adaptability in stone tool use by wild capuchin monkeys (Sapajus libidinosus). Am. J. Primatol. 76, 967-977.

Dubreuil, L., 2004. Long-term trends in Natufian subsistence: a use-wear analysis of ground stone tools. J. Archaeol. Sci. 31, 1613-1629.

Falótico, T., Coutinho, P.H.M., Bueno, C.Q., Rufo, H.P., Ottoni, E., 2018. Stone tool use by wild capuchin monkeys (*Sapajus libidinosus*) at Serra das Confusões National Park, Brazil. Primates 59, 385-394.

Falótico, T., Ottoni, E., 2013. Stone throwing as a sexual display in wild female bearded capuchin monkeys, *Sapajus libidinosus*. PloS One 8, e79535. doi:10.1371/journal.pone.0079535

Falótico, T., Ottoni, E., 2016. The manifold use of pounding stone tools by wild capuchin monkeys of Serra da Capivara Nartional Park, Brazil. Behaviour 153, 421-442.

Falótico, T., Proffitt, T., Ottoni, E.B., Staff, R.A., Haslam, M., 2019. Three thousand years of wild capuchin stone tool use. Nat. Ecol. Evol. 3, 1034-1038.

Falótico, T., Siqueira, J.O., Ottoni, E., 2017. Digging up food: excavation stone tool use by wild capuchin monkeys. Sci. Rep. 7, 1-10.

Falótico, T., Spagnoletti, N., Haslam, M., Luncz, L.V., Malaivijitnond, S., Gumert, M.D., 2017b. Analysis of sea almond (*Terminalia catappa*) cracking sites used by wild Burnese long-tailed macques (*Macaca fascicularis aurea*). Am. J. Primatol. 79, e22629. https://doi.org/10.1002/ajp.22629

Fernández-Marchena, J.L., Ollé, A., 2016. Microscopic analysis of technical and functional traces as a method for the use-wear analysis of rock crystal tools. Quat. Int. 424, 171-190.

Ferreira, R.G., Almeida Emidio, R., Jerusalinsky, L., 2010. Three stones for three seeds: Natural occurrence of selective tool use by capuchins (*Cebus libidinosus*) based on an analysis of the weight of stones found at nutting sites. Am. J. Primatol. 72, 270-275.

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E., Gomes de Oliveira, M., 2004. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. Am. J. Primatol. 64, 359-366.

Fragaszy, D., Liu, Q., Wright, B., Allen, A., Welch Brown, C., Visalberghi, E., 2013. Wild bearded capuchin monkeys (*Sapajus libidinosus*) strategically place nuts in a stable position during nut-cracking. PloS One 8, e56182. doi:10.1371/journal.pone.0056182

Goren-Inbar, N., Sharon, G., Melamed, Y., Kislev, M.E., 2002. Nuts, nut cracking, and pitted stones at Gesher Benot Ya'aqov, Israel. Proc. Natl. Acad. Sci. USA 99, 2455-2460.

Gumert, M.D., Kluck, M., Milaivijitnond, S., 2009. The physical characteristics and usage patterns of stone axe and pounding hammers used by long-tailed macaques in the Andaman sea region of Thailand. Am. J. Primatol. 71, 549-608.

Harmand, S., Lewis, J.E., Feibel, C.S., Lepre, C.J., Prat, S., Lenoble, A., Boës, X., Quinn, R.L., Brenet, M., Arroyo, A., Taylor, N., Clément, S., Daver, G., Brugal, J.-P., Leakey, L., Mortlock, R.A., Wright, J.D., Lokorodi, S., Kirwa, C., Kent, D.V., Roche, H., 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. Nature 521, 294-310.

Haslam, M., 2012. Towards a prehistory of primates. Antiquity 86, 299-315.

Haslam, M., Gumert, M.D., Biro, D., Carvalho, S., Malaivijitnond, S., 2013. Use-wear patterns on wild macaque stone tools reveal their behavioural history. PloS One 8, e72872. doi:10.1371/journal.pone.0072872

Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de la Torre, I., DeStefano, A., Du, A., Hardy, B., Harris, J., Marchant, L., Matsuzawa, T., McGrew, W.C., Mercader, J., Mora, R., Petraglia, M., Roche, H., Visalberghi, E., Warren, R., 2009. Primate archaeology. Nature 460, 339-344.

Haslam, M., Hernandez-Aguilar, R.A., Proffitt, T., Arroyo, A., Falótico, T., Fragaszy, D., Gumert, M., Harris, J.W.K., Huffman, M.A., Kalan, A.K., Malaivijitnond, S., Matsuzawa, T., McGrew, W., Ottoni, E.B., Pascual-Garrido, A., Piel, A., Pruetz, J., Schuppli, C., Stewart, F., Tan, A., Visalberghi, E., Luncz, L.V., 2017. Primate archaeology evolves. Nat. Ecol. Evol. 1, 1431-1437.

Haslam, M., Moura Cardoso, R., Visalberghi, E., Fragaszy, D., 2014. Stone anvil damage by wild bearded capuchins (*Sapajus libidinosus*) during pounding tool use: A field experiment. PloS One 9, e111273. doi:10.1371/journal.pone.0111273

Hernández-Aguilar, A., Moore, J., Pickering, T.R., 2007. Savanna chimpanzees use tools to harvest the underground storage organs of plants. Proc. Natl. Acad. Sci. USA 104, 19210-19213.

Humle, T., Matsuzawa, T., 2004. Oil palm use by adjacent communities of chimpanzees at Bossou and Nimba Mountains, West Africa. Int. J. Primatol. 25, 551-581.

Jarzen, D.M., Elsik, W.C., 1986. Fungal palynomorphs recovered from recent river deposits, Luangwa valley, Zambia. Palynology, 35-60.

Keeley, L.H., 1980. Experimental determination of stone tool uses: a microwear analysis. University of Chicago Press, Chicago.

Knutsson, H., Knutsson, K., Taipale, N., Tallavaara, M., Darmark, K., 2015. How shattered flakes were used: micro-wear analysis of quartz flake fragments. J. Archaeol. Sci.: Rep. 2, 517-531.

Knutsson, K., 1988. Patterns of tools use. Scanning Electron Microscopy of Experimental Quartz Tools. Societas Archaeologica Upsaliensis, Uppsala.

Kooyman, B., 2015. Phytoliths: preparation and archaeological extraction, in: Chee Tak Yeung, E., Stasolla, C., Sumner, M.J., Quan Huang, B. (Eds.), Plant Microtechniques and Protocols. Springer International Publishing, Switzerland, pp. 507-524.

Laden, G., Wrangham, R.W., 2005. The rise of the hominids as an adaptive shift in fallback foods: Plant underground storage organs (USOs) and australopith origins. J. Hum. Evol. 49, 482-498.

Liu, Q., Fragaszy, D., Wright, B., Wright, K., Izar, P., Visalberghi, E., 2011. Wild bearded capuchin monkeys (*Cebus libidinosus*) place nuts in anvils selectively. Anim. Behav. 81, 297-305.

Liu, Q., Simpson, K., Izar, P., Ottoni, E., Visalberghi, E., Fragaszy, D., 2009. Kinematics and energetics of nut-cracking in wild capuchin monkeys (*Cebus libidinosus*) in Piauí, Brazil. Am. J. Phys. Anthropol. 138, 210-220.

Luncz, L.V., Falótico, T., Pascual-Garrido, A., Corat, C., Mosley, H., Haslam, M., 2016. Wild capuchin monkeys adjust stone tools according to changing nut properties. Sci. Rep. 6, 33089. https://doi.org/10.1038/srep33089

Luncz, L.V., Gill, M., Proffitt, T., Svensson, M.S., Kulik, L., Malaivijitnond, S., 2019. Group-specific archaeological signatures of stone tool use in wild macaques. eLife 8, e46961. https://doi.org/10.7554/eLife.46961

Luncz, L.V., Mundry, R., Boesch, C., 2012. Evidence for cultural differences between neighboring chimpanzee communities. Curr. Anthropol. 22, 922-926.

Luncz, L.V., Mundry, R., Soiret, S., Boesch, C., 2019b. Cultural diversity of nut-cracking behaviour between two populations of wild chimpanzees (*Pan troglodytes verus*) in the Côte d'Ivoire, in: Boesch, C., Wittig, R.M., Crockford, C., Vigilant, L., Deschner, T., Leendertz, F. (Eds.), The chimpanzees of the Taï Forest. 40 years of Research. Cambridge University Press, Cambridge, pp. 194-220.

Luncz, L.V., Svensson, M.S., Haslam, M., Malaivijitnond, S., Proffitt, T., Gumert, M., 2017. Technological response of wild macaques (*Macaca fascicularis*) to anthropogenic change. Int. J. Primatol. 38, 872-880.

Mangalam, M., Pacheco, M.M., Izar, P., Visalberghi, E., Fragaszy, D., 2018. Unique perceptuomotor control of stone hammers in wild monkeys. Biol. Lett. 14, 20170587. https://doi.org/10.1098/rsbl.2017.0587

Mangalam, M., Roles, L.K.R., Fragaszy, D., 2019. Distinct perceptuomotor features of percussive tooling in humans (*Homo sapiens*) and wild bearded capuchin monkeys (*Sapajus libidinosus*). J. Comp. Psychol. 134, 84-97.

Mannu, M., Ottoni, E., 2009. The enhanced tool-kit of two groups of wild bearded capuchin monkeys in the Caatinga: Tool making, associative use, and secondary tools. Am. J. Primatol. 71, 242-451.

Marchant, L.F., McGrew, W.C., 2005. Percussive technology: Chimpanzee baobab smashing and the evolutionary modelling of hominin knapping, in: Roux, V., Brill, B. (Eds.), Stone knapping, the necessary conditions for a uniquely hominin behaviour. McDonald Institute for Archaeological Research, Cambridge, pp. 341-350.

McLennan, M.R., Rohen, J., Satsias, Z., Sabiiti, T., Baruzaliire, J.-M., Cibot, M., 2019. ‘Customary’ use of stick tools by chimpanzees in Bulindi, Uganda: update and analysis of digging techniques from behavioural observations. Rev. Primatol. 10, http://journals.openedition.org/primatologie/6706

Méndez-Carvajal, P., Valdés-Díaz, S., 2017. Use of anvils and other feeding behaviour observed in Cebus imitator, Coiba Island, Panama. Tecnociencia 19, 5-18.

Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R., Boesch, C., 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology, Proc. Natl. Acad. Sci. USA 104, 3043-3048.

Miola, A., 2012. Tools for non-pollen palynomorphs (NPPs) analysis: A list of Quaternary NPP types and reference literature in English language (1972-2011), Rev. Palaeobot. Palynol. 186, 142-161.

Monteza-Moreno, C.M., Dogandzic, T., McLean, K.A., Castillo-Caballero, P.L., Mijango-Ramos, Z., Del Rosario-Vargas, E., Crofoot, M.C., Barrett, B.J., 2020. White-faced capuchin, *Cebus capucinus imitator*, hammerstone and anvil tool use in Riparian habitats on Coiba Island, Panama. Int. J. Primatol. 41, 429-433.

Motes-Rodrigo, A., Majlesi, P., Pickering, T.R., Laska, M., Axelsen, H., Minchin, T.C., Tennie, C., Hernandez-Aguilar, A., 2019. Chimpanzee extractive foraging with excavating tools: Experimental modeling of the origins of human technology. PloS One 14, e0215644. https://doi.org/10.1371/journal.pone.0215644

Mora, R., de la Torre, I., 2005. Percussion tools in Olduvai Beds I and II (Tanzania): Implications for early human activities. J. Anthropol. Archaeol. 24, 179-192.

Moura, A.C.A., Lee, P.C., 2004. Capuchin stone tool use in caatinga dry forest. Science 306, 1909.

Neumann, K., Strömberg, C.A.E., Ball, T., Albert, R.M., Vrydaghs, L., Cummings, L.S., 2019. International Code for Phytolith Nomenclature (ICPN) 2.0. Ann. Bot. 124, 189-199.

Oliveira, M.A.T. de, Santos, J.C., 2019. GPR stratigraphy and quaternary morphogenesis in the semiarid Brazil. Mercator (Fortaleza) 18, e18027. https://doi.org/10.4215/rm2018.e18027.

Ollé, A., Pedergnana, A., Fernández-Marchena, J.L., Martin, S., Borel, A., Aranda, V., 2016. Microwear features on vein quartz, rock crystal and quartzite: A study combining Optical Light and Scanning Electron Microscopy. Quat. Int. 424, 154-170.

Ollé, A., Vergès, J.M., 2008. SEM functional analysis and the mechanism of microwear formation, in: Longo, L., Skakun, N. (Eds.), 'Prehistoric technology' 40 years later: Functional Studies and the Russian legacy. Archaeopress, Oxford, pp. 39-49.

Ollé, A., Vergès, J.M., 2014. The use of sequential experiments and SEM in documenting stone tool microwear. J. Archaeol. Sci. 48, 60-72.

Panger, M.A., Brooks, G.E., Richmond, B.G., Wood, B., 2002. Older than the Oldowan? Rethinking the emergence of hominin tool use. Evol. Anthropol. 11, 235-245.

Pearsall, D.M., 2019. Case studies in paleoethnobotany. Routledge, United Kingdom.

Pearsall, D.M., Chandler-Ezell, K., Zeidler, J.A., 2004. Maize in ancient Ecuador: results of residue analysis of stone tools from the Real Alto site. J. Archaeol. Sci. 31, 423-442.

Peters, C.R., 1987. Nut-Like oil seeds: Food for monkeys, chimpanzees, humans, and probably ape-men. Am. J. Phys. Anthropol. 73, 333-363.

Pignat, G., Plisson, H., 2000. Le quartz pour quel usage? L'outillage mesolithique de Vionnaz (CH) et l'apport de la traceologie, in: Crotti, P. (Ed.), MESO 97. Actes de la Table Ronde: epipaleolithique et mesolithique, vol. 81. Cahiers d'Archeologie Romande, Lausanne, pp. 65-78.

Portillo, M., Bofill, M., Molist, M., Albert, R.M., 2013. Phytolith and use-wear functional evidence for grinding stones from the Near East, in: Anderson, N., Cheval, C., Durand, A. (Eds.), Regards croisés sur les outils liés au travail des végetaux. An interdisciplinary focus on plant-working tools. Editions APDCA, Antibes.

Proffitt, T., Haslam, M., Mercader, J.F., Boesch, C., Luncz, L.V., 2018. Revisiting Panda 100, the first archaeological chimpanzee nut-cracking site. J. Hum. Evol. 124, 117-139.

Proffitt, T., Luncz, L.V., Falótico, T., Ottoni, E., de la Torre, I., Haslam, M., 2016. Wild monkeys flake stone tools. Nature 539, 85-88.

Proffitt, T., Luncz, L.V., Malaivijitnond, S., Gumert, M., Svensson, M.S., Haslam, M., 2018b. Analysis of wild macaque stone tools used to crack oil palm nuts. R. Soc. Open Sci. 5, 171904.

Reille, M., 1995. Pollen et Spores d'Europe et d'Afrique du Nord (Supplément 1). Laboratoire de Botanique Historique et Palynologie, CNRS, Marsaille.

Revedin, A., Aranguren, B., Becattini, R., Longo, L., Marconi, E., Mariotti, M., Skakun, N., Sinitsyn, A., Spiridonova, E., Svodoba, J., 2010. Thirty thousand-year-old evidence of plant food processing. Proc. Natl. Acad. Sci. USA 107, 18815-18819.

Santos, J.C., Leal, I.R., Almeida-Cortez, J.S., Fernandes, G.W., Tabarelli, M., 2011. Caatinga: the scientific negligence experienced by a dry tropical forest. Trop. Conserv. Sci. 4, 276-286.

Semenov, S.A., 1964. Prehistoric technology: an experimental study of the oldest tools and artefacts from traces of manufacture and wear. Redwood Press Limited, Great Britain.

Sirianni, G., Visalberghi, E., 2013. Wild bearded capuchins process cashew nuts without contacting caustic compounds. Am. J. Primatol. 75, 387-393.

Spagnoletti, N., Visalberghi, E., Verderane, M.P., Ottoni, E., Izar, P., Fragaszy, D., 2012. Stone tool use in wild bearded capuchin monkeys, *Cebus libidinosus*. Is it a strategy to overcome food scarcity? Anim. Behav. 83, 1285-1294.

Sukura, O., Matsuzawa, T., 1991. Flexibility of wild chimpanzee nut-cracking behavior using stone hammers and anvils: an experimental analysis. Ethology 87, 237-248.

Sussman, C., 1988. A Microscopic Analysis of Use-Wear and Polish Formation on Experimental Quartz Tools. Archaeopress, Oxford.

Tan, A., Hoon Tan, S., Vyas, D., Malaivijitnond, S., Gumert, M.D., 2015. There is more than one way to crack an oyster: identifying variation in Burmese long-tailed macaque (*Macaca fascicularis aurea*) stone-tool use. PloS One 10, e0124733. doi:10.1371/journal.pone.0124733

Thompson, J.C., Carvalho, S., Marean, C.W., Alemseged, Z., 2019. Origins of the human predatory pattern. The transition to large-animal exploitation by early hominins. Curr. Anthropol. 60, 1-23.

Ungar, P.S., 2012. Dental evidence for the reconstruction of diet in African early Homo. Curr. Anthropol. 53, S318-S329.

Ungar, P.S., Berger, L.R., 2018. Brief communication: Dental microwear and diet of *Homo naledi*. Am. J. Phys. Anthropol. 166, 228-235.

Urbani, B., 1998. An early report on tool use by neotropical primates. Neotrop. primates 6, 123-124.

van Geel, B., 1978. A palaeoecological study of Holocene peat bog sections in Germany and The Netherlands, based on the analysis of pollen, spores and macro and microscopic remains of fungi, algae, cormophytes and animals. Rev. Palaeobot. Palynol. 25, 1-120.

van Geel, B., 1986. Application of fungal and algal remains and other microfossils in palynological analyses, in: Berglund, B.E. (Ed.), Handbook of Holocene Palaeoecology and Palaeohydrology. John Wiley & Sons Ltd., Chichester, pp. 497-505.

Vaughan, P.C., 1985. Use-wear analysis of flaked stone tools. University of Arizona Press, Tucson.

Visalberghi, E., 1990. Tool use in *Cebus*, Folia Primatol. 54, 146-154.

Visalberghi, E., Fragaszy, D., Izar, P., Ottoni, E., 2005. Terrestriality and tool use. Science 308, 951-952.

Visalberghi, E., Fragaszy, D., Ottoni, E., Izar, P., de Oliveira, M.G., Andrade, F.R.D., 2007. Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. Am. J. Phys. Anthropol. 132, 426-444.

Visalberghi, E., Spagnoletti, N., Ramos da Silva, E.D., Andrade, F.R.D., Ottoni, E., Izar, P., Fragaszy, D., 2009. Distribution of potential suitable hammers and transport of hammer tools and nuts by wild capuchin monkeys. Primates 50, 95-104.

Wrangham, R.W., Holland Jones, J., Laden, G., Pilbeam, D., Conklin-Brittain, N., 1999. The raw and the stolen: cooking and the ecology of human origins. Curr. Anthropol. 40, 567-594.

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Figure 1. Overview of the different activities performed by capuchin monkeys from SCNP using quartzite pounding tools and the corresponding typical archaeological signature. A) Digging; B) Seed pounding; C) Stone-on-stone percussion; D) Nut-cracking.

Figure 2. Box plots for dimensions (A-C) and weight (D) of all analysed pounding objects in this study. Boxes represent the interquartile range, whiskers indicate variability outside the upper and lower quartiles. Outliers are represented by circles and stars.

Figure 3. Residues observed on the surface of the tools used for processing seeds (A), jatobá (B), cashew nuts (C) and digging (D).

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Figure 10. Seriation with the use-wear marks identified on the capuchin lithic assemblage. Note that three capuchin digging tools and one tool used for pounding bear no significant microscopic traces.

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Figure 12. Use-wear traces of tools used for pounding. A) Object with small disperse crushed areas associate occasionally with small detachments. Microscopic photos B and D are details of crushed crystals at 50× (scale = 700 µm), while photo C is a detail at 100× (scale = 350 µm). E) Pounding tool utilised on both ends with presence of crushing on the edges (F; 50×, scale = 700 µm) and stepped fractures (G; 30×, scale = 800 µm).

Figure 13. Use-wear marks on the SoS-percussion tool, characterized by surface modification characterized by: A) step fractures (10×, scale = 3 mm); B) Edge crushing

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Figure 14. Box plots comparing general dimensions of percussive tools from Bossou chimpanzees (BF1 and BF2) (Sakura and Matsuzawa, 1991; Humle and Matsuzawa, 2004), long-Thai macaques (Falótico et al., 2017b; Haslam et al., 2013; Proffitt et al., 2018b) and the capuchin assemblage analysed here.