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The archaeological visibility of chimpanzee (*Pan troglodytes*) nut-cracking

Tomos Proffitt [a], [b], [*], Serge Soiret Pacome [c], Jonathan S. Reeves [b], Roman M. Wittig [d], [e], Lydia V. Luncz [a]

[a] *Technological Primates Research Group, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig 04103, Germany*
[b] *Interdisciplinary Center for Archaeology and the Evolution of Human Behaviour (ICArEHB), Universidade do Algarve, Campus de Gambelas, Faro 8005-139, Portugal*
[c] *Centre de Recherche en Ecologie (CRE), Université Nangui Abrogoua, Abidjan, 08 BP 109 Abidjan 08, Côte d'Ivoire*
[d] *Ape Social Mind Lab, Institut des Sciences Cognitives, CNRS UMR 5229, 67 Boulevard Pinel, Bron 69675, France*
[e] *Taï Chimpanzee Project, Centre Suisse de Recherches Scientifiques, 01 BP 1301, Abidjan, Côte d'Ivoire*

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ABSTRACT

The earliest evidence for complex tool use in the archaeological record dates to 3.3 Ma. While wooden tools may have been used by our earliest ancestors, the evidence is absent due to poor preservation. However, insights into possible early hominin wooden tool use can be gained from observing the tool-use practices of our closest living relatives, chimpanzees (*Pan troglodytes*). By using stone hammers used to crack various nuts, chimpanzees leave a durable material signature comprised of formal tools and associated diagnostic fragments. While the archaeological evidence of chimpanzee wooden tool use is temporary, the combination of stone hammers and wooden anvils can create a more enduring lithic record. This study explores the lithic assemblages associated with wooden and stone anvil use at nut-cracking sites in Taï National Park, Côte d'Ivoire, using technological and use-wear analyses. Our results indicate clear differences in density, fracture patterns, and use-wear in the lithic records between wooden anvil and stone anvil sites. New archaeological excavations at six chimpanzee nut-cracking sites reveal that the anvils' material directly influences the visibility of nut-cracking evidence in the archaeological record. By examining the nature of the lithic signatures associated with wooden anvil and stone anvil use by chimpanzees, we can formulate hypotheses about the probability of such behaviors being preserved and identifiable in the Plio-Pleistocene hominin archaeological record. The variability in material signatures from nut-cracking on different anvils suggests that stone anvils leave a clear archaeological record. Evidence for wooden anvil use is likely underrepresented due to the more ephemeral nature of the associated percussive damage and material signature. It may, however, still be possible, albeit challenging, to identify wooden anvil use in the archaeological record.

1. Introduction

The majority of what we know about the behavior of Early Stone Age (ESA) hominins comes from our ability to identify, recover, and analyze durable stone tools and modifications of faunal remains (Blumenschine, 1988; Pante et al., 2018, 2020). These studies have shown that hominins had been producing sharp-edged stone tools as early as 3.3 Ma (Harmand et al., 2015) and certainly by between 3 and 2.6 Ma (Semaw, 2006; Braun et al., 2019; Plummer et al., 2023; Key and Proffitt, 2024). This core and flake technology was likely used for a variety of cutting tasks, including butchery (Blumenschine et al., 1996; Domínguez-Rodrigo et al., 2005) and plant processing (Keeley and Toth, 1981). A wider range of tool-use behaviors were, however, likely to have been undertaken during this stage of hominin evolution, including the use of organic materials such as grasses and wood (Keeley and Toth, 1981; Toth, 1985; Shea, 2007; Lemorini et al., 2014, 2019). However, their identification in the archaeological record remains difficult and largely unexplored.

Wooden tool use is documented in the middle and upper Paleolithic archaeological records and in modern ethnographic

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[*] Corresponding author.
E-mail address: tomos_proffitt@eva.mpg.de (T. Proffitt).

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literature (Oswalt, 1976; Goren-Inbar, 1991; Aranguren et al., 2018; Barham et al., 2023; Caruso Fermé et al., 2023; Hrnčíř, 2023; Milks et al., 2023a; Riede et al., 2023; Leder et al., 2024). However, evidence for its use as a tool material is largely lacking before 400 ka, where several wooden artifacts interpreted as spears, digging tools, and leather-working implements have been identified (Thieme, 1997; Bridgland et al., 1999; Richter and Krbetschek, 2015; Barham et al., 2023; Milks et al., 2023b; Leder et al., 2024). Recent identification of a wooden artifact associated with structural use dated to 476 ka (Barham et al., 2023), along with a potentially earlier example of a polished wooden plank (Goren-Inbar, 1991), suggests an earlier use of wood. Indirect evidence, however, suggests that wooden tool use was likely practiced during the Lower Pleistocene. A limited number of use-wear studies of Oldowan artifacts from Koobi Fora and Kanjera South (Kenya) suggest that flakes were used for scraping and cutting wood during the Lower Pleistocene (Keeley and Toth, 1981; Lemorini et al., 2014, 2019). However, the use of wooden tools is not exclusive to hominins and is prevalent among several contemporary nonhuman primate lineages including chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), orangutans (*Pongo pygmaeus*), and capuchin monkeys (*Sapajus libidinosus*; Goodall, 1964; Boesch and Boesch, 1990; Boesch, 2000; van Schaik et al., 2003; Breuer et al., 2005; Pruetz and Bertolani, 2007; Mannu and Ottoni, 2009; Pascual-Garrido et al., 2012; Samuni et al., 2022; Falótico, 2023), suggesting a wide range of uses for wooden tools in primates. Wild chimpanzees use wooden tools for a variety of tasks such as termite fishing and ant dipping (McGrew, 1974; Boesch and Boesch, 1990; Pascual-Garrido et al., 2012; Pascual-Garrido, 2019; Pascual-Garrido and Almeida-Warren, 2021), as spears for hunting (Pruetz and Bertolani, 2007), for digging for food (Yamagiwa et al., 1988; Hernandez-Aguilar et al., 2007; Hicks et al., 2019), and as hammers and anvils during nut-cracking (Boesch and Boesch, 1983; Boesch, 2000). Due to their close phylogenetic relatedness to humans, chimpanzees have often been used as analogs for understanding the potential range of early hominin behaviors (Carvalho and McGrew, 2012; Rolian and Carvalho, 2017).

The common use of wood as a tool material by modern nonhuman primates, modern hunter-gatherers (Hayden, 2015; Milks, 2020; Lew-Levy et al., 2022), and Plio-Pleistocene hominins (Thieme, 1997; Schoch et al., 2015; Rios-Garaizar et al., 2018; Milks, 2023; Milks et al., 2023b) suggests that this material may have been part of the behavioral repertoire of the last common ancestor of chimpanzees and hominins (Pascual-Garrido and Almeida-Warren, 2021; Luncz et al., 2022b) or may be a convergent evolutionary adaption in both lineages. Recent studies in primate archaeology aim to document chimpanzee wooden tool use, helping to infer the potential range of such behaviors among hominins and establish a referential framework for recognizing these behaviors in the Plio-Pleistocene record (Pascual-Garrido and Almeida-Warren, 2021; Luncz et al., 2022b). Therefore, identifying and understanding the material record associated with primate wooden tool use may provide a means by which to interrogate the Plio-Pleistocene archaeological record in search of these potentially hidden behaviors.

The wooden tools used by chimpanzees are unlikely to be preserved in the archaeological record, with the long-term preservation of wooden material requiring conditions not typically present in forested environments (Kortlandt, 1983; Retallack, 1991). Despite this, recent methodological advances have identified that the internal structure of robust, percussive wooden tools used for nut-cracking—which remain in the environment for several years—can develop permanent modifications (Luncz et al., 2022a, 2022b). This provides a means of identifying such wooden tools if they were to fossilize (Luncz et al., 2022a, 2022b).

Stone material used by chimpanzees, however, has the potential to be preserved more readily and over much longer periods of time. In West Africa, certain chimpanzee communities from Guinea, Liberia, and Côte d'Ivoire use stone material in conjunction with wooden and stone anvils to crack open a variety of nut species (Beatty, 1951; Sugiyama and Koman, 1979; Boesch and Boesch, 1983; Boesch, 2000; Luncz et al., 2012). This behavior creates a durable, landscape-wide material signature (Mercader, 2002, 2007; Luncz et al., 2016; Proffitt et al., 2018a; Reeves et al., 2021); in some places, this material has been dated to at least 4300 years ago (Mercader, 2007). When used in combination with wooden anvils, stone hammers and their resultant fragmentation patterns may create a distinct archaeological signature compared to their use on stone anvils.

Although chimpanzees are known to use stone and wooden hammers and anvils to crack nuts, there are some regional differences across groups (Luncz et al., 2012; Proffitt et al., 2022). For example, in the Taï National Park in Côte d'Ivoire, tool selection and material use differ between communities. In the north of the Taï Forest, within the groups of the Taï Chimpanzee Project (TCP), all group members of four neighboring communities preferentially use wooden anvils along with stone and wooden hammers, whereas chimpanzees in the Djouroutou Chimpanzee Project (DCP; ~60 km further south) use a combination of stone and wooden anvils but only stone hammers (Soiret et al., 2015). In both cases, wooden anvils are exclusively exposed roots of the nut-bearing trees, whereas stone anvils can be a combination of large, embedded boulders as well as smaller mobile stones.

This observed diversity of raw material selection provides a unique opportunity to study the potential variation in the lithic record associated with nut-cracking on both stone and wooden anvils. By identifying how anvil type can affect the preservation, visibility, composition, attributes, and use-wear of the durable lithic hammerstone assemblages, we aim to provide a better understanding of the material record of percussive foraging in primates. As such, this study seeks to address the following research questions: 1) How does the use of wooden and stone anvils affect the resulting lithic material signature of chimpanzee nut-cracking? and 2) Are these patterns recognizable in the primate archaeological record? To address these questions, we undertook a collection of the lithic material record associated with nut-cracking behavior from two chimpanzee groups in the Taï National Park. We then conducted a comparative analysis of artifacts resulting from different tool material combinations, specifically stone hammers used in conjunction with both wood and stone anvils. Furthermore, to better understand how these anvil types influence the diachronic archaeological signature of nut-cracking, we carried out new archaeological excavations at contemporary wooden and stone anvil nut-cracking sites.

2. Materials and methods

2.1. Study sites

To address whether wooden anvils influence the lithic material signature of nut-cracking, stone assemblages from 12 modern nut-cracking sites were collected. These surface assemblages were collected from both the Taï and Djouroutou chimpanzee field sites located within the Taï National Park in western Côte d'Ivoire (Fig. 1a). Chimpanzees in the Taï National Park crack open five different nut species (Luncz et al., 2019). These include *Coula* (*Coula edulis*), *Panda* (*Panda oleosa*), *Parinari* (*Parinari excelsa*) *Sacoglottis* (*Sacoglottis gabonensis*), as well as *Detarium* (*Detarium senegalense*; Soiret et al., 2015). The TCP is located in a large area of primary forest, which is home to four different groups of habituated

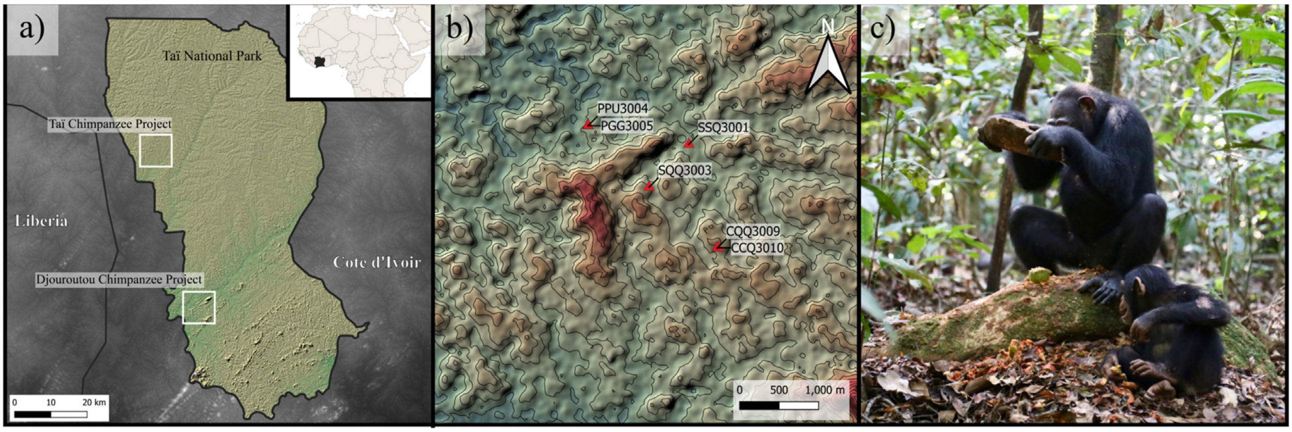

Figure 1. a) Location of the Taï National Park in Cote d'Ivoire and the location of all excavated sites within the Djouroutou Chimpanzee Project; b) locations where wild chimpanzees have undertaken nut-cracking; c) wild chimpanzee at Djouroutou using stone tools to crack a nut (image courtesy of Liran Samuni).

chimpanzees (Wittig, 2017). The chimpanzees within the TCP territories crack nuts using both stone and wooden hammers while predominantly using wooden anvils (Luncz et al., 2019; Fig. 1b).

The DCP is located around 60 km south of the Taï groups. Currently, around 60 chimpanzees inhabit this territory, which equates to ~25 km^2 of this part of the Taï Forest (Soiret et al., 2015). Here, the chimpanzees only use stone hammers. However, in contrast to the Taï communities, the Djouroutou group uses both wooden and stone anvils frequently.

The assemblages reported in this study derive from anvil sites used to crack three separate nut species, *Coula*, *Panda*, and *Sacoglottis*. The three different nut species included in this study each occupy different ecological settings within the forest. Specifically, both *Panda* and *Sacoglottis* trees tend to grow in areas with seasonal floods (Harris, 2002). *Coula* trees, however, grow in well-drained soil, often found at higher elevations in areas dominated by coarse pebbles and cobbles (Harris, 2002). In addition to these ecological variations, chimpanzee behavioral differences have also been observed during the processing of each nut species. Although the overarching tool-use behavior remains the same, the way the percussive activity is practiced differs between nut species. *Panda* nuts are the hardest nuts currently known, requiring ca. 12 kN to crack open (Boesch, 2012); therefore, requiring large heavy wooden or stone hammers (Luncz et al., 2018). As such, *Panda* nut-cracking is often a solitary activity, undertaken either alone or in small groups. This is likely due to the widespread distribution of *Panda* trees within the landscape coupled with the rarity of suitable raw materials large/heavy enough to be used to process this nut species (Luncz et al., 2018). As *Coula* trees are often found in clustered groups within the landscape, and the nut requires considerably less force to open, smaller hammerstones are adequate. Therefore, suitable tool material is more abundant, and this activity is often undertaken by multiple individuals and sometimes at a group level (Boesch, 2012). This nut-cracking behavior is also facilitated by the underlying high concentration of suitable raw material in areas where *Coula* trees grow (Reeves et al., 2021). *Sacoglottis* nuts (and tress), which are softer than *Panda* nuts and harder than *Coula* nuts (Boesch and Boesch, 1983; McGraw et al., 2014), show no preference for specific elevations or soil composition and, as such, tend to be widely distributed (Reeves et al., 2021).

2.2. Data collection

To address the two research questions posed in this study, we use a combination of data from different sources. To examine whether there is a different material signature associated with stone anvil vs. wooden anvil nut-cracking sites, we used lithic assemblages collected from surface contexts of 12 sites located in both the TCP and DCP (Fig. 1a), which represent a contemporary material signature of this behavior. The combined lithic assemblages of each anvil type were then compared. To evaluate whether this material signature is preserved in the archaeological record, we conducted excavations on a sample of six of these sites (from the Djouroutou Chimpanzee Project; Fig. 1b) and compared the lithic assemblages between surface and excavated contexts grouped by anvil type (Supplementary Online Material [SOM] Table S1).

Contemporary nut-cracking site data collection To address how the use of wooden and stone anvils affect the resulting lithic material signature of chimpanzee nut-cracking, a sample of 12 modern nut-cracking sites was collected. This included all lithic material found on the surface surrounding a central anvil. A total of six wooden anvil and six stone anvil locations were sampled from the TCP and DCP (Fig. 1a; SOM Table S1). As the aim of this study was to identify potential differences between stone and wooden anvil locations, the nut species being cracked was not controlled for, resulting in the final lithic assemblage being associated with three different nut species: *P. oleosa*, *C. edulis*, and *S. gabonensis*. In each case, a nut-cracking site was defined by the co-occurrence of a wooden or stone anvil, one or more complete or fragmented stone hammer(s), and evidence of cracked nut debris (Fig. 1c; Luncz et al., 2012). Data collection was undertaken during two separate field seasons, one in 2017 and the other in 2022. During 2017, three wooden-anvil sites were sampled from the TCP territories, and three stone anvil sites were sampled from the DCP territories. The location of each anvil was taken as the center of a 3 × 3 m square, within which all lithics were collected. An additional three wooden anvil and stone anvil sites were sampled and subsequently excavated from the DCP in 2022. The surface lithics collected from these anvil locations were combined with the data from 2017 to assess the material variation associated with wooden anvil and stone anvil sites (SOM Table S1 for details of how the assemblages are used).

Archaeological excavations After we investigated the diversity of assemblages associated with stone and wooden anvils, we further assessed the durability of this archaeological signature. To assess the degree to which an archaeological record is visible at both stone anvil and wooden anvil locations, six archaeological investigations ranging in depths from 20 to 50 cm were conducted at six of the sampled anvil locations within the Djouroutou chimpanzee research area (SOM Table S2). We excavated sites associated with each different nut species (*P. oleosa*, *C. edulis*, and *S. gabonensis)*. For each nut species, we conducted excavations at one stone anvil and one wooden anvil site. One 2 × 2 m trench and five 1 × 1 m trenches were hand excavated in 10 cm spits. The center of each excavation was located at the center of the anvil at each site. All lithic material from both surface and excavated contexts was hand mapped and collected, and the depth from the surface of all excavated lithics was recorded. Due to the remote nature of the field location and high level of foliage, it was impossible to use modern three-dimensional (3D) mapping systems such as a total station to record the excavations. Instead, the depth and position of all artifacts were recorded by hand using a grid system set out over the excavation. The depth of each artifact was measured using a tape measure and plumb from a known line datum with the plan of each artifact mapped by hand using measurement for both the x and y axes of the excavation. All excavated sediment was dry sieved to ensure the maximum retention of possible modified lithics. Plans and backwall sections of each excavation were digitized using QGIS v. 3.36.0 (QGIS Development Team, 2024).

To provide a temporal context, small quantities of charcoal were collected at varying depths during excavation. These are likely associated with localized forest fires caused by lightning strikes (Hart et al., 1996; Mercader, 2007). A total of six charcoal samples from five of the excavated sites were subjected to radiocarbon dating. These samples were taken either to date the surrounding sediment and provide a maximum age of excavation or to date associated lithic material. All samples were prepared at the 14CHRONO Centre (Queen's University Belfast). All samples were pretreated using an acid—alkali—acid treatment. Calibrations were carried out using CALIB v. 8.2 (Stuiver and Reimer, 1993) and using the IntCal20 dataset (Reimer et al., 2020). Due to time constraints, in the majority of cases, test trenches were excavated to a maximum depth of 0.5 m. In some cases, the maximum depth was less, when consolidated bedrock was encountered. In all cases, at a depth of 0.5 m, no lithics were recovered, the majority being found in the first tens of centimeters. In two trenches, excavation was stopped when anthropogenic archaeological material was encountered as this was beyond the scope of the research permit within the National Park.

2.3. *Lithic analysis*

Techno-typological analysis All recovered lithics were measured and weighed, with artifacts measuring >20 mm in their maximum dimension from both contemporary nut-cracking sites and excavations subjected to a full techno-typological analysis. The technological analysis and classification of lithic material follows the methods and classifications set out by de la Torre and Mora (2005), de la Torre et al. (2013), and (Arroyo et al., 2016). Although these methods were originally designed to study hominin percussive technology, they have also been successfully applied to the characterization of primate lithic material (Proffitt et al., 2016, 2018a). All lithics were classified into a range of typological groups based on a combination of morphology and the presence and location of percussive damage, with both absolute and relative frequencies reported. These include complete and fragmented hammerstones, anvils, natural unmodified stones, and a range of detached pieces from both hammerstones and anvils. These detached products are separated into eight groups: edge products (Group 1.1), corner products (Group 1.2), elongated pieces (Group 2.1), angular chunks, both with and without percussive damage (Group 2.2), detached pieces which resemble knapped flakes with and without percussive damage (Group 2.3), typical hammerstone flakes (Group 3), and angular fragments spontaneously detached from an inactive region of the hammerstone or anvil (Group 4). Artifacts measuring smaller than 20 mm possessing no percussive damage were classified as small debris (Group 5; Fig. 2).

Use-wear analysis All lithic artifacts measuring >20 mm in maximum length were visually examined for signs of percussive damage. Potential areas of damage were further investigated using low-power magnification (<100) using a Leica SAPO stereomicroscope equipped with an 18 objective lens and 10 eyepiece. Identification and characterization of percussive damage was undertaken following the criteria of Adams et al. (2009), which have been successfully used to characterize both hominin and nonhuman primate percussive damage (Arroyo and de la Torre, 2018; Proffitt et al., 2018a, 2018b; Arroyo et al., 2020, 2021).

The use-wear attributes identified in this study included the presence of crushing, impact points, grain removals, striations, flake detachments, depressions, fractures, and adhering residue. Furthermore, to determine whether excavated percussive tools more closely aligned to either hammerstones or anvils, they were compared to a sample of known modern hammers and anvils that have been previously published (Proffitt et al., 2022). This comparison included dimensions (maximum length, width, and thickness), as well as two-dimensional (2D) and 3D surface morphometric data associated with the macro use-wear patterns on each excavated artifact following the protocols set out in Proffitt et al. (2022). These data were then compared using a principal component analysis (PCA) to published examples of chimpanzee hammerstones and anvils of the same raw material from Djouroutou (Proffitt et al., 2022). The 2D data included the number of discreet use-wear areas, the total area (cm^2) of use-wear, the percentage area of use-wear (PA), the density of use-wear on the active surface of the artifact as a proportion of the total surface area of the active surface, maximum pit length and width (mm), the distance of the center of each pit to the active surface edge (DAE), and center of the active surface (DAC). The 3D surface morphometric attributes collected included minimum depth, maximum depth, mean depth, and standard deviation (SD) of the depth of each pitted region, and the minimum, maximum, mean, and SD of surface roughness and gradient of each pitted region. These attributes have been successfully used to characterize primate percussive damage on both hammerstones and anvils (de la Torre et al., 2013; Benito-Calvo et al., 2015; Proffitt et al., 2022).

2.4. *Statistical analysis*

To assess whether anvil type has an effect on the associated assemblage composition, as well as degree and type of percussive damage, both Chi-square tests and Fisher's exact test (the latter when counts were <5) were used to identify significant differences in categorical attributes associated with the lithic analyses, with subsequent calculations of adjusted residuals to identify the drivers behind any possible significant variation. Moreover, both Kruskal—Wallis (KW) and Mann—Whitney U tests were used to assess variation in dimensional properties (maximum length, width, thickness, and mass) of lithic material associated with different anvil types and post hoc pairwise comparisons using a Dunn's test with Bonferroni correction were used to identify the source of significant variation. Significant differences were determined using an α value of 0.05. The limitations of small sample sizes in some instances, including reduced statistical power and a higher risk of Type I and Type II errors, are acknowledged. Results of these statistical tests should be interpreted with caution, with the sample size noted as a study limitation. Additionally, to more clearly represent differences in the mass of artifacts in graphical form, all mass values were $\log_{10}$ transformed. However, all statistical comparisons were applied to the nontransformed data. All statistical tests were calculated in R v. 4.3 (R Core Team, 2021).

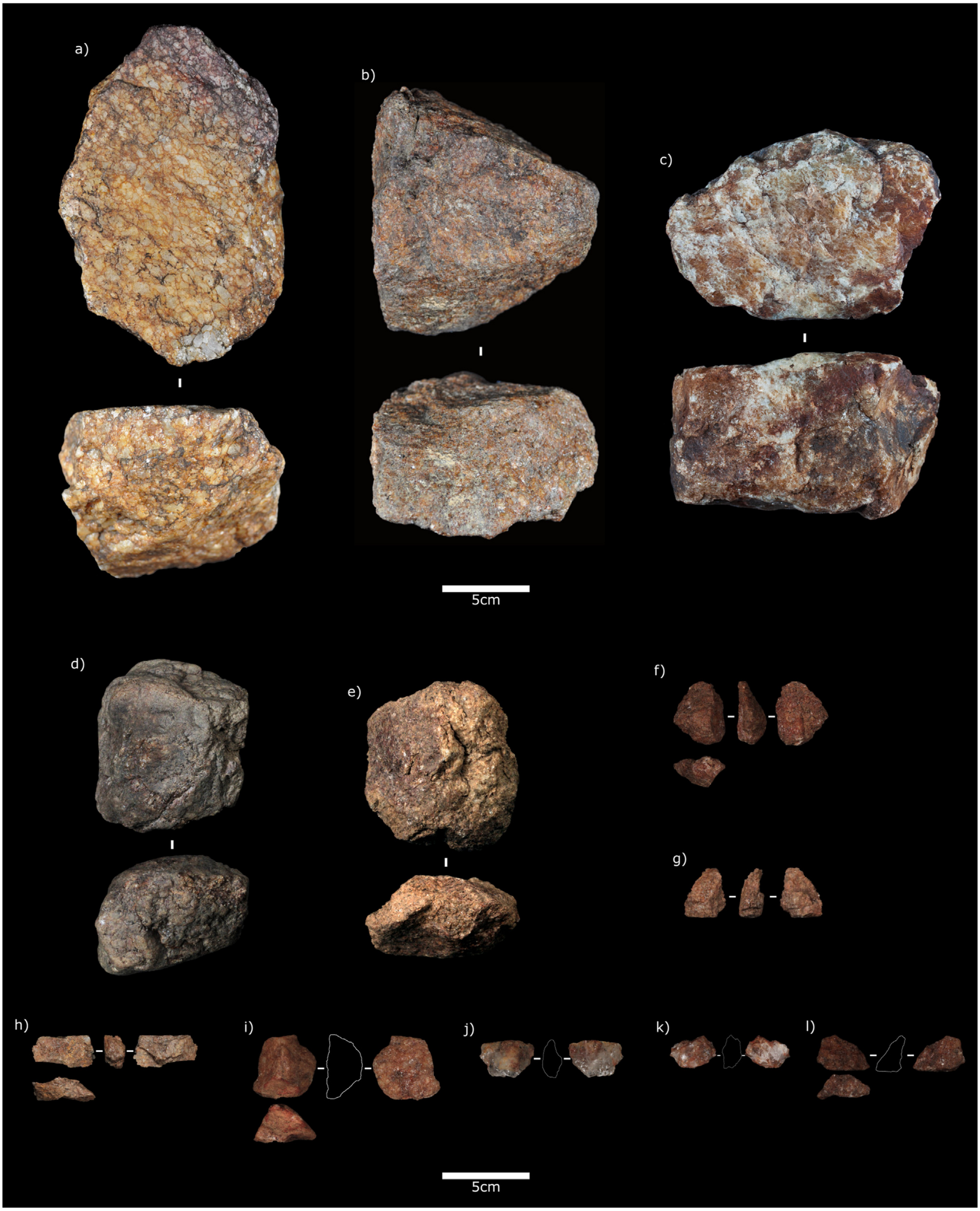

Figure 2. Examples of hammerstones associated with wood (a–c) and stone (d–e) anvils and detached percussive artifacts, including flake detachments (group 2.3; f–g), angular chunks (group 2.2, h–i), and edge products (group 1.1; j–l) associated with nut-cracking.

3. Results

3.1. The surface lithic material signature associated with wooden and stone anvil use

General frequencies A total of 161 lithic artifacts were recorded through surface collection at both stone anvil ($n = 141$, 87.6%) and wooden anvil ($n = 20$, 12.4%) sites. Four separate raw materials are represented within this assemblage: metamorphosed granite (mica-granite: $n = 92$, 57.1%) and quartzite ($n = 65$, 40.3%), along with lesser occurrences of granite ($n = 3$, 1.9%) and granodiorite ($n = 1$, 0.6%; SOM Fig. S1). Stone anvil sites exhibit a significantly greater frequency ($\chi^2 = 90.938$, df = 1, $p < 0.001$; adjusted residual = 9.54) and total mass (stone: 23.811 kg; wood: 13.944 kg; $\chi^2 = 8.715$, df = 1, $p = 0.003$) of lithic material than the wooden anvil sites (SOM Table S3). This difference corresponds to a clear difference in the density of lithic material accumulated at different anvil types. Stone anvils possess an average density of 10.6 artifacts per square meter (minimum [min] = 0.5; maximum [max] = 31, SD = 10.4) compared to an average density of three artifacts per square meter for wooden anvils (min = 0.75; max = 6, SD = 2). However, percussive artifacts found within both wooden anvil and stone anvil contexts are significantly larger in all dimensions and heavier than the unmodified natural stones that constitute the geological backdrop of these sites (SOM Table S4; SOM Fig. S1). Furthermore, a significant disparity exists in the frequencies of technological categories associated with each type of anvil ($\chi^2 = 28.498$, df = 2, $p < 0.001$), with complete hammerstones being significantly more prevalent at wooden anvils (adjusted residual = 5.31) as opposed to stone anvils and detached pieces being more prevalent at stone anvil sites (adjusted residual = 3.85; SOM Table S5; Fig. S2).

Stone anvils display a higher occurrence of lithics exhibiting at least one area of percussive damage ($n = 57$) than do wooden anvils ($n = 17$; SOM Table S6; Fig. S3). Nevertheless, when considering the proportion relative to the total assemblage of each anvil type, wooden anvils (85%) show a significantly greater relative frequency of lithics with percussive damage than do stone anvils (41.1%; Fisher's exact test: $p < 0.001$; SOM Table S6; Fig. S3).

Hammerstones and fragmented hammerstones The maximum dimensions and mass of both complete and fragmented hammerstones do not show a significant difference between stone and wooden anvils (SOM Table S7; Fig. S4). However, the extent of percussive damage on hammerstones varies between anvil types. The number of damaged surfaces is significantly higher (Fisher's exact test: $p = 0.045$) for hammerstones associated with stone anvils (mean = 3, min = 1, max = 6, SD = 1.9) than that found at wooden anvil sites (mean = 1.5, min = 1, max = 2, SD = 0.53). Moreover, the distribution of percussive damage differs significantly between anvil sites (Fisher's exact test: $p = 0.026$). Hammerstones at wooden anvils predominantly exhibit isolated areas ($n = 7$, 88%) of damage, whereas at stone anvils sites, a higher frequency of clustered damage patterns is observed ($n = 3$, 50%). Nevertheless, there is no significant distinction in the surface morphology where percussive damage is located (Fisher's exact test: $p = 0.654$). Most of the damage is situated on flat surfaces at both wooden anvil and stone anvil sites (SOM Table S8), suggesting that the manner in which hammers are used is not influenced by the anvil type.

Detached pieces A significantly greater frequency of detached pieces is associated with stone anvils ($\chi^2 = 94.053$, df = 1, $p < 0.001$; SOM Table S5). Despite this difference in absolute frequencies, there is no substantial variation in the relative frequencies of the different detached groups between anvil types ($\chi^2 = 10.167$, df = 6, $p = 0.117$). It is evident, however, that stone anvils are primarily characterized by angular chunks (Group 2.2) and small debris (Group 5; SOM Table S5). Additionally, there is no significant distinction in the dimensions of the detached pieces between anvil types (SOM Table S7). A limited number of detached pieces resembling knapping flakes (Group 2.3; Fig. 1) are associated with both anvil types; nevertheless, they are more frequent at stone anvils (SOM Table S5). Due to the small sample size of this group, meaningful statistical comparisons are not feasible. In general, however, detached flakes found at wooden anvil sites tend to be slightly larger than those from stone anvil sites (SOM Fig. S5). None of these flakes display indications of being detached through conchoidal fracture. Instead, forceful wedging initiations and fractures along internal cleavage planes are prevalent at both stone and wood anvil sites. All detached flakes from both anvil types feature cortical platforms with impact points located centrally. However, flakes at stone anvil locations are more likely to have fully cortical dorsal surfaces, whereas those at wooden anvil sites exhibit <50% cortical coverage. This corresponds to an increased frequency of dorsal scars on flakes detached at wooden anvil sites when compared to stone anvils (SOM Table S9).

Use-wear Use-wear damage was observed on a total of 75 lithics from both wooden anvil and stone anvil sites, accounting for 46.6% of the total surface lithics examined. A significantly higher frequency of artifacts with visible use-wear was found at stone anvils ($n = 58$, 77 %) than at wooden anvils ($n = 17$, 23%) ($\chi^2 = 22.414$, df = 1, $p < 0.001$). The majority of these lithics were made from mica-granite ($n = 47$, 63%) or quartzite ($n = 23$, 31%), with a notably smaller proportion of granatoid ($n = 5$, 6.7%) pieces. There is a significant difference in the representation of raw materials between anvil types ($\chi^2 = 18.306$, df = 2, $p < 0.001$), with a significantly higher proportion of granitoid (adjusted residual = 3.20) and quartzite (adjusted residual = 2.26) along with a lower proportion of mica-granite (adjusted residual = −3.80) identified at wooden anvil sites (SOM Table S10).

Among these lithics, the most prevalent artifact types displaying visible use-wear were detached pieces ($n = 41$, 55%) followed by fragmented hammerstones ($n = 20$, 27%), as well as all complete hammerstones (SOM Table S11). Despite stone anvils having a higher absolute frequency of lithics with percussive damage, there is a notably greater frequency of hammerstones with visible percussive damage ($\chi^2 = 12.056$, df = 2, $p = 0.002$; adjusted residual = 3.42) represented at wooden anvil sites than at stone anvil sites (SOM Table S11).

At a microscale level, the patterns of percussive damage on lithics generally exhibit few distinctions between stone and wooden anvils. A notable exception is the significant increase in occurrence of lithics with crushing at stone anvil sites (Fisher's exact test: $p = 0.043$) and the significantly greater frequency of residue on lithics from wooden anvils (Fisher's exact test: $p = 0.021$; SOM Table S12). Use-wear on lithics from both types of anvils is characterized by localized crushing and a sparse distribution of impact points, often accompanied by grain detachments. These areas of crushing and subsequent grain removal result in a noticeable alteration of surface coloration in contrast to undamaged areas (Fig. 3). Such characteristics aid in distinguishing damaged and undamaged regions of the lithic surfaces. Percussive damage is primarily located on flat surfaces ($n = 66$, 78.57%), as well as along ridges ($n = 15$, 17.85%) and convex surfaces ($n = 3$, 3.57%). There is no significant difference in the surface morphology bearing use-wear between anvil types (Fisher's exact test: $p = 0.179$; SOM Table S12). This is likely due to the general use of flat surfaces of hammerstones regardless of the anvil type used.

3.2. Nut-cracking-site excavations

CQQ3009 CQQ3009 is a 1 × 1 m excavation situated on the summit of a small hill, approximately 6 m west of a large *Coula* tree. At the

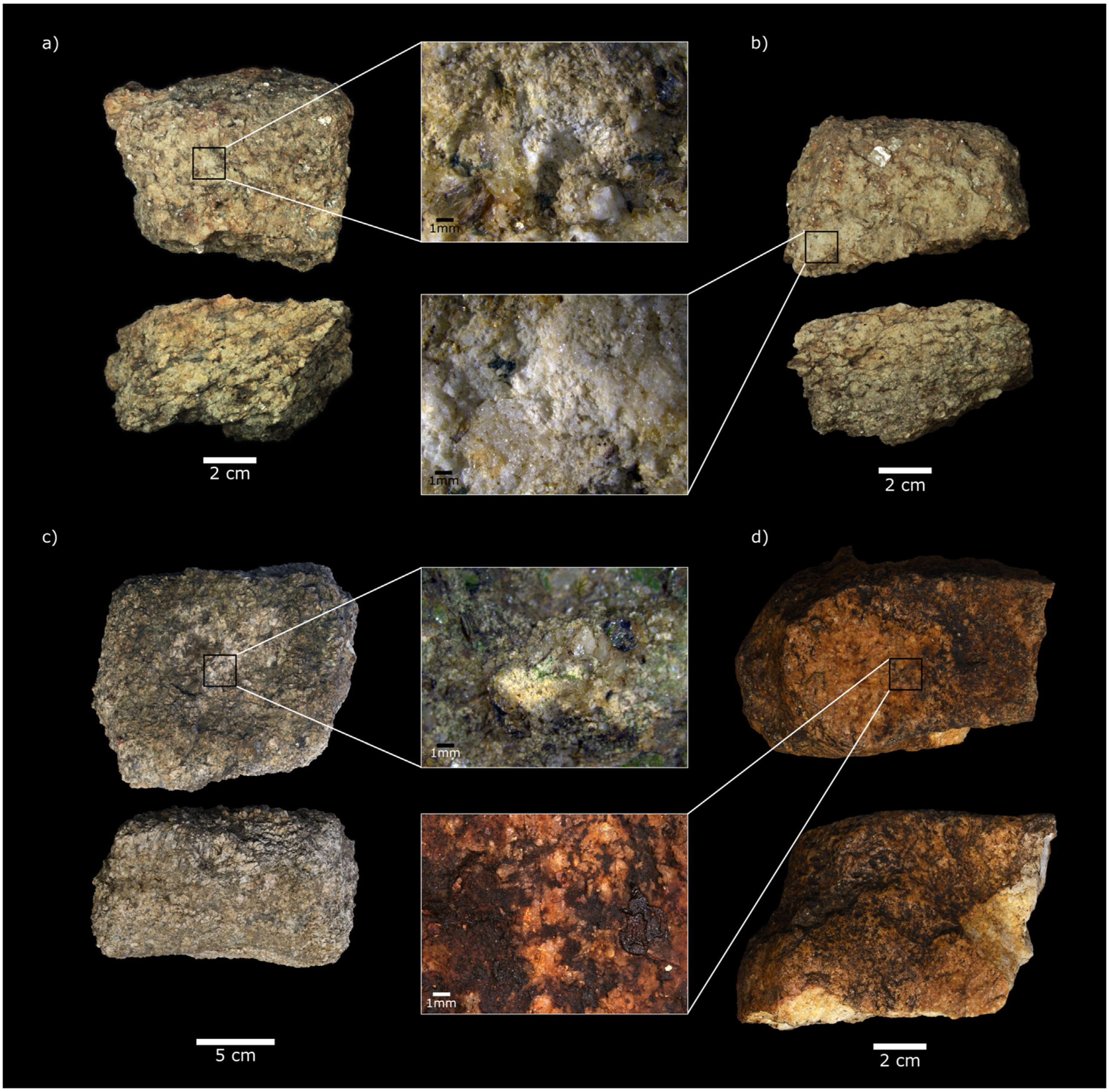

Figure 3. Examples of use-wear on the active surfaces of hammerstones used on stone (a–b) and wooden (c–d) anvils, resulting in crushing and discoloration of the surface (a–c) and the accrual of residue (d).

center of the excavation are two large, embedded quartzite anvils, surrounded by a substantial amount of lithic debris. Modern *Coula* nut remains were found around the anvil, along with a single *Panda* nut fragment, indicating that *Panda* nuts were occasionally transported to this nut-cracking site (Fig. 3a, b).

The excavation reached a maximum depth of 20 cm. All excavated artifacts were found within the top 5 cm of sediment, which consisted of sandy silt with frequent small laterite and quartz pebbles (1–15 mm in size). From 5 to 20 cm below the surface, the sediment was compacted silty sand with frequent laterite cobbles and blocks.

Most of the recovered lithics were natural, unmodified stones and showed no evidence of percussive damage. However, 12 stone artifacts with signs of percussive damage were found. Six were recovered from the surface, including a single quartzite hammerstone, three hammerstone fragments, and two embedded anvils. The other six lithics were found within 5 cm below the surface, comprising two hammerstones, two hammerstone fragments, and one broken and complete flake (Fig. 4c, d; SOM Table S13).

In addition to the lithics with clear percussive damage, several fragmented ceramic pieces were recovered from a depth of 4–6 cm. Most of these ceramic artifacts were found in the southern part of the excavation, situated at the interface between the topsoil and subsoil, indicating human occupation of this area before it was used as a chimpanzee nut-cracking site. A charcoal sample recovered from 7 cm below the surface, beneath all excavated lithics and ceramics, provides a maximum age of 328 (±20) BP for all the overlying artifacts (Fig. 4b; SOM Fig. S6; Table S14).

CCQ3010 CCQ3010 is a 1 × 1 m excavation situated 6 m south of CQQ3009, around a single *Coula* tree root used as a wooden anvil (Fig. 5a). On the surface, we identified a single quartzite

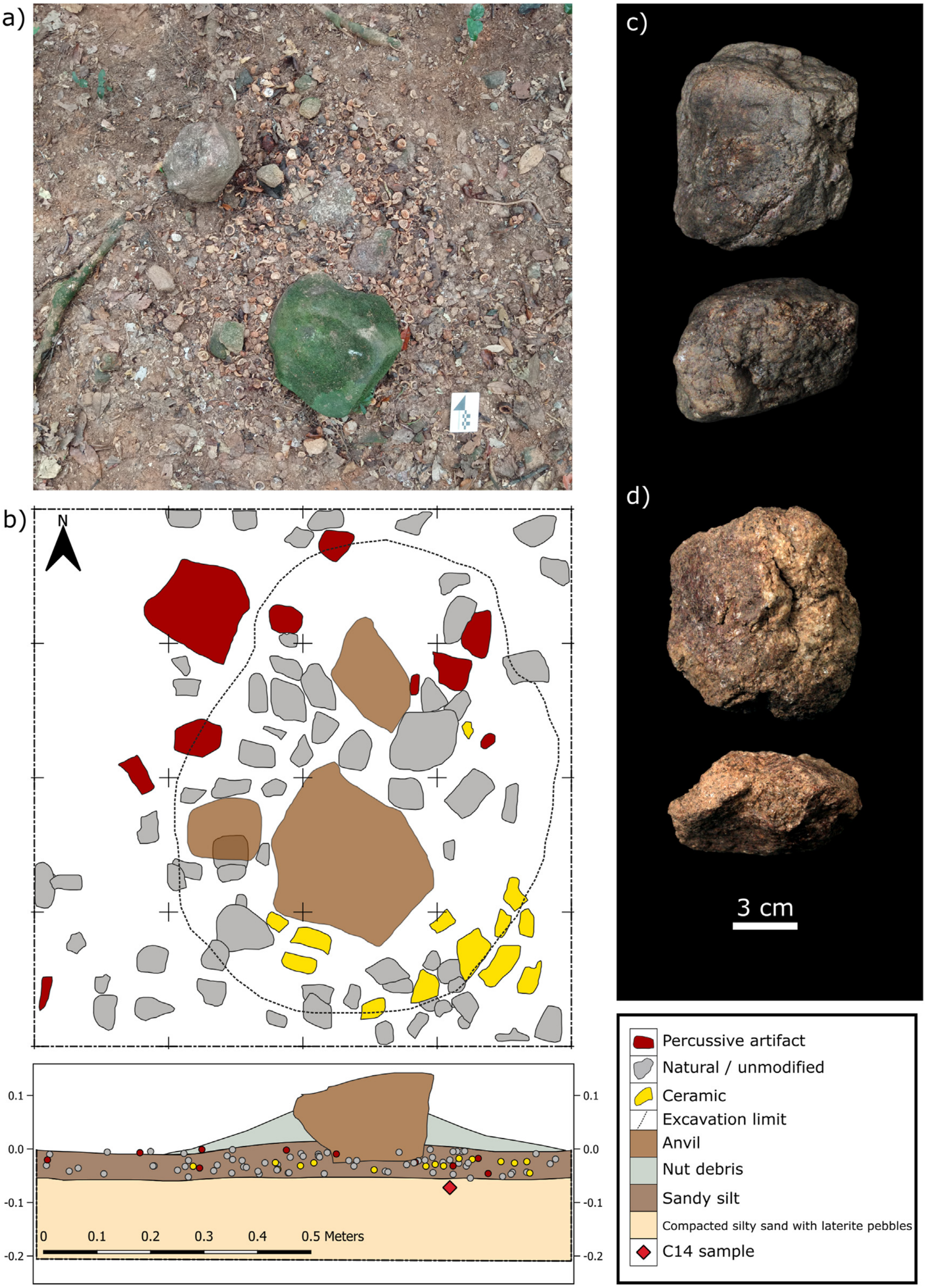

Figure 4. a) General view of the nut-cracking site at CQQ3009 and b) plan and section showing all archaeological material recovered, extent of the nut debris around the anvil, and the backwall stratigraphy. c–d) Example of two hammerstones recovered from CQQ3009 (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article).

hammerstone, a quartzite flake-like detachment, and an angular fragment. The excavation revealed a significant amount of nut debris, with a maximum depth of 5 cm concentrated directly around the anvil (Fig. 5a, b).

During excavation, two distinct stratigraphic layers were identified. The uppermost layer, situated directly beneath the nut debris, comprises a shallow, loosely consolidated, sandy silt, with a maximum depth of 7 cm. It features frequent roots and occasional small laterite and quartzite pebbles, extending 5–12 cm from the surface. Below this topsoil layer lies a moderately compacted reddish-brown sandy silt, also containing frequent laterite and quartzite pebbles (Fig. 5b).

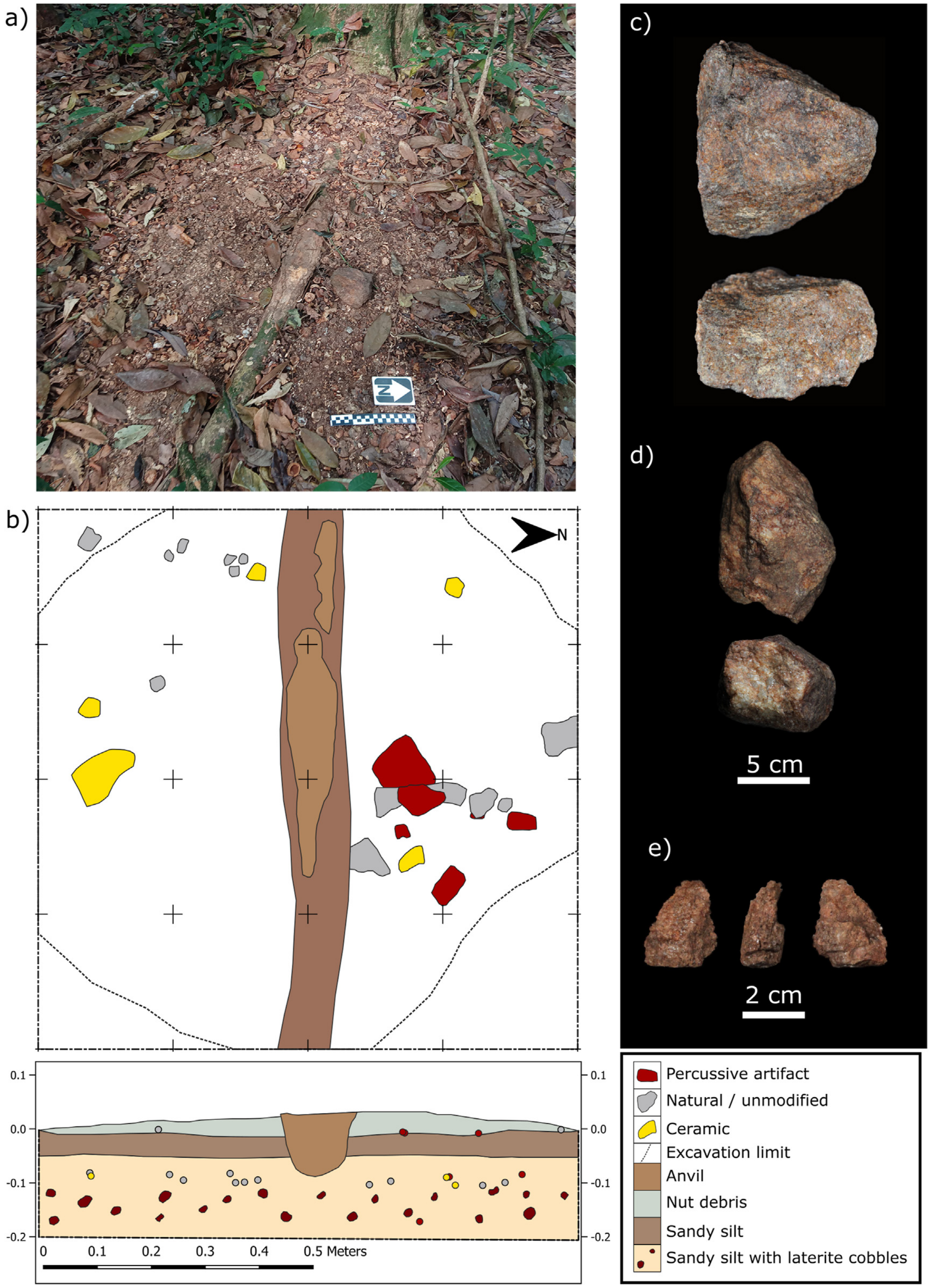

Figure 5. a) General view of the nut-cracking site at CCQ3010 and b) plan and section showing all archaeological material recovered, extent of the nut debris around the anvil, and the backwall stratigraphy. c) Example of a hammerstone, d) a hammerstone fragment, and e) flake-like detachments recovered from CCQ3010 (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article).

Two angular fragments without percussive damage were uncovered between 1 and 10 cm from the surface, and a single hammerstone fragment was identified at 17 cm below the surface (Fig. 4c–e). Additionally, at a depth of 10 cm, we unearthed three ceramic fragments. These ceramics correspond to a layer containing unmodified quartzite, laterite, and granodiorite pebbles and cobbles (Fig. 5b; SOM Table S13).

PPU3004 PPU3004 is a 1 × 1 m excavation with a maximum depth of 50 cm centered around a single large *Panda* tree root, which served as an anvil. Nut debris was located around the exposed anvil, extending to a maximum depth of 4 cm within the topsoil (Fig. 6a). The excavation revealed a small lithic assemblage both on the surface and in excavated contexts. To facilitate the recovery of large percussive artifacts found during excavation, the excavation area was expanded to 1.27 m^2 (Fig. 6b)

The topsoil extends to a maximum depth of 7.8 cm and consists of decomposing organic material. Below this is a thin layer of silty sand extending to around 10 cm in maximum depth. There are no clear stratigraphic horizons between 15 and 50 cm, which consist of a consolidated, fine-grained, clayey-silt with mica inclusions. There is an increase in mica inclusions between 42 and 50 cm from the surface. This increase is associated with in situ weathering of the underlying mica-granite bedrock in this area of Djouroutou.

The topsoil reaches a maximum depth of 7.8 cm and primarily comprises decomposing organic material. Beneath it lies a thin layer of silty sand, extending to approximately 10 cm in depth. Notably, there are no distinct stratigraphic horizons between 15 and 50 cm; instead, this interval consists of consolidated, fine-grained, clayey-silt with mica inclusions. There is an increase in mica inclusions between 42 and 50 cm from the surface. This is likely linked to in-situ weathering of the underlying micaceous granite bedrock in this area (Fig. 6b).

The associated lithic assemblage, composed exclusively of mica-granite, is relatively small. Most artifacts were recovered from the surface area around the wooden anvil. These include a hammerstone fragment, an angular fragment, a piece of small debris, and two detached pieces. Beyond the surface assemblage, two excavated artifacts—recovered from depths between 30–40 cm and 40–50 cm—are classified as hammerstones (SOM Table S13). These two large mica-granite boulders, measuring 260 × 220 × 160 mm and 410 × 310 × 210 mm, respectively (Fig. 6c, d), were found in the subsoil within a clayey-silt matrix devoid of other stones. Notably, each boulder exhibits depressions or pitted regions on their flat surfaces. Charcoal samples taken from stratigraphically above and below these hammerstones provide an estimated age range of 365 (±21) BP to 719 (±23) BP for these artifacts (Fig. 6b; SOM Fig. S6; Table S14).

Both excavated artifacts exhibit a broadly tabular morphology, featuring two opposing flat surfaces. Each artifact has a single flat surface marked by distinct depressions. Artifact 2200113 displays two pitted regions on its active surface (Fig. 6c). By contrast, the second artifact (2200108) is fragmented in half, with the fragmentation passing through the large central pitted region of its active plane (Fig. 6d).

The presence of centrally located pitted regions on these artifacts attests to their use as percussive tools. A Mann–Whitney U test shows no significant difference in either the length or width between the excavated artifacts and known hammers (length: $p = 0.666$, width: $p = 0.666$) or known anvils (length: $p = 0.428$, width: $p = 0.642$). However, when both excavated artifacts are grouped together, their maximum length and width closely resemble the dimensions of modern mica-granite hammerstones (SOM Fig. S7a, b). Interestingly, when separated, artifact 2200113 aligns more closely in both maximum length and width with the modern anvil samples (SOM Fig. S7c, d).

Given the small sample sizes involved in this comparison, further statistical comparisons are not feasible. There is no clear difference in the maximum length and width of pits between the excavated artifacts and known hammers and anvils. However, the total number of pits, total pit area, PA, density, DAE, and DAC all fall most closely within the range for known hammerstones compared to anvils (SOM Fig. S8a–h; Table S15). This clustering is evident from a PCA on the macro use-wear attributes (SOM Fig. S9; Table S16), which shows that the first three principal components (PC1, PC2, and PC3) account for 95% of the variation between categories. PC1 is negatively associated with use-wear density, mean DAC and DAE, the total use-wear area, and the number of use-wear areas. PC2 is positively associated with mean length and width as well as PA, whereas PC3 is negatively associated with mean length and width and positively associated with PA and density of use-wear.

Similarly, a PCA of the 3D surface morphometry attributes (SOM Fig. S10; Table S17) of pitted regions shows that the excavated artifacts cluster more closely with the modern hammerstone samples than with the more widely dispersed anvil samples. In this case, the first three PCs account for 79% of the total variation (SOM Fig. S10; Table S17).

Both the contextual data and the percussive damage data suggest that these artifacts can be considered as hammerstones.

PGG3005 PGG3005 is a 1 × 1 m excavation located along a micaceous granite ridge running in a southwest–northeast direction, a few meters south of PPU3004. During the excavation, a large micaceous granite block was uncovered, almost entirely buried, exhibiting clear evidence of multiple depressions—characteristics consistent with an anvil (Fig. 7a). Although no complete hammerstones were identified, a significant amount of micaceous granite debris with evident percussive damage was discovered around the anvil, along with a small number of *Panda* nut shells. The excavation reached a maximum depth of 39 cm, constrained by several micaceous granite boulders (Fig. 7b).

A total of 77 lithic artifacts associated with percussive stone tool use were identified either on the surface or within the first 10 cm of excavation, located in the topsoil and in the intersection/upper layer of the subsoil (Fig. 7c, d). The topsoil (0–6 cm in depth) consists of loosely compacted silty sand with frequent decomposing leaf litter and small roots, where nut remains were exclusively discovered. The subsoil (6–25 cm in depth) comprises moderately compacted sandy silt and lacks root action. Additionally, three lithic artifacts were identified at approximately 25-cm depth, where the sandy silt intersects with clayey silt. Beyond 25 cm, the sediment transitions to compacted clayey silt, containing frequent mica fragments and occasional small quartzite and laterite pebbles (1–2 cm maximum dimensions). Notably, no percussive artifacts were found beyond this depth. Furthermore, a charcoal sample recovered at a depth of 34 cm, located 5 cm above the underlying bedrock, provided an age estimate for the sediment at this location: 1489 (±23) BP (Fig. 7b; SOM Fig. S6; Table S14).

SSQ3001 SSQ3001 is a 2 × 2 m excavation located in a narrow, flat floodplain on the southern side of a small stream and is centered around a branching *Sacoglottis* root, which served as an anvil in three separate locations, two of which were identified during excavation (Fig. 8a). The excavation reached a maximum depth of 50 cm, revealing sediment composed of silty sands with occasional pebbles but lacking clear stratigraphic layers. The uppermost layer consisted of a 5-cm thick layer of loamy topsoil. Notably, modern nut debris was abundant up to a depth of 13 cm, covering the exposed anvils and filling gaps between them. However, beyond the immediate vicinity of the exposed anvils, the amount of nut debris decreased substantially. Although three stone hammers were found on the surface near the exposed anvils (Fig. 8c, d), no modified lithic artifacts were recovered from excavated contexts. A charcoal sample retrieved from the base of the excavation provided an estimated sediment age of 381 (±21) BP at a depth of 50 cm in this region of the Djouroutou forest (SOM Fig. S6; Table S14).

SQQ3003 SQQ3003 is a 1 × 1 m excavation situated on a gradual slope running north–south and surrounded by *Sacoglottis* nut debris (Fig. 9a). At the center of the excavation lies a large, coarse-grained quartzite anvil. The site was excavated to a maximum depth of 35 cm, where further excavation became impossible due to large quartzite boulders. The topsoil, approximately 10 cm deep,

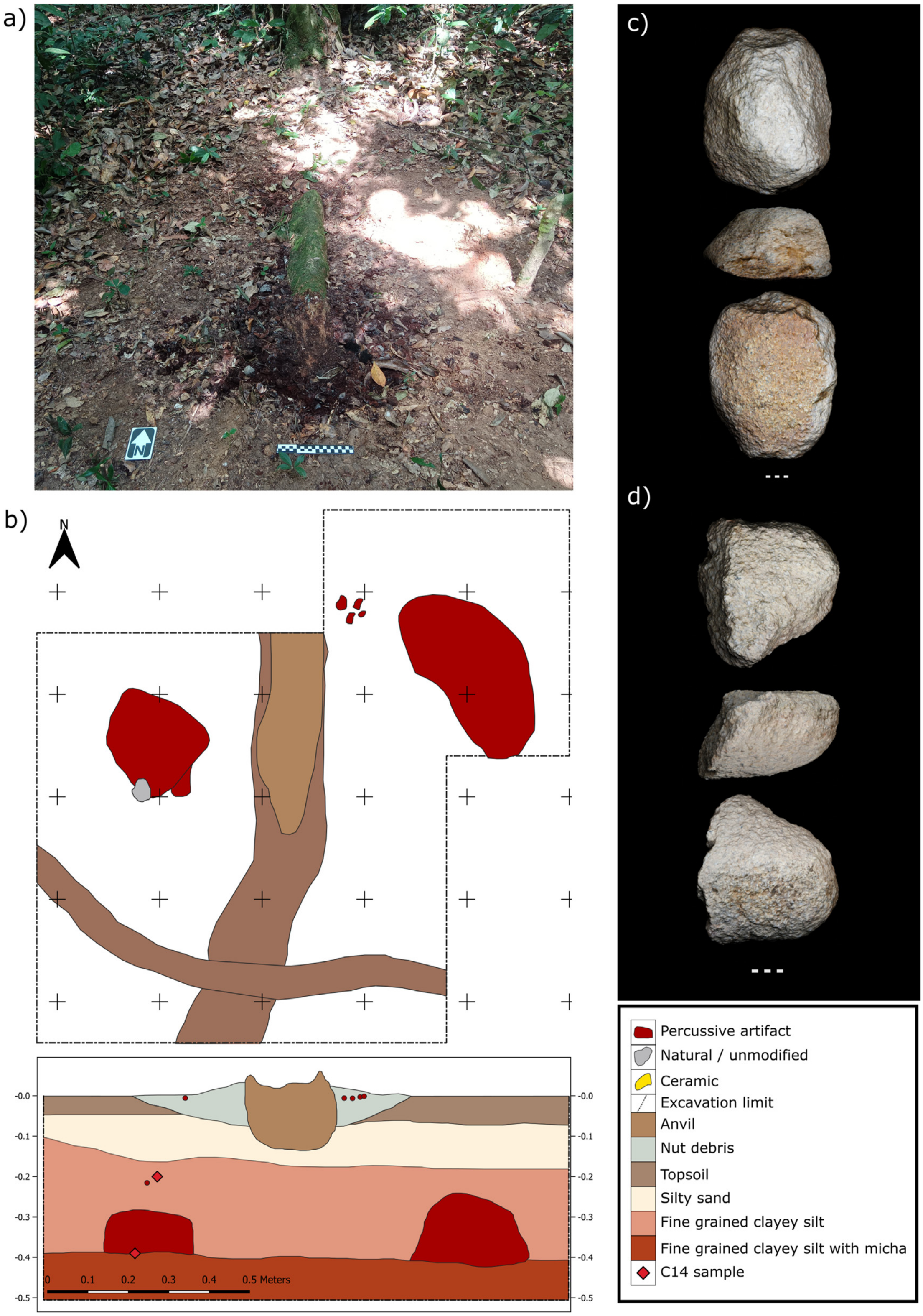

Figure 6. a) General view of the nut-cracking site at PPU3004 and b) plan and section showing all archaeological material recovered, extent of the nut debris around the anvil, and the backwall stratigraphy. Example of two hammerstones recovered from PPU3004 (c and d) (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article).

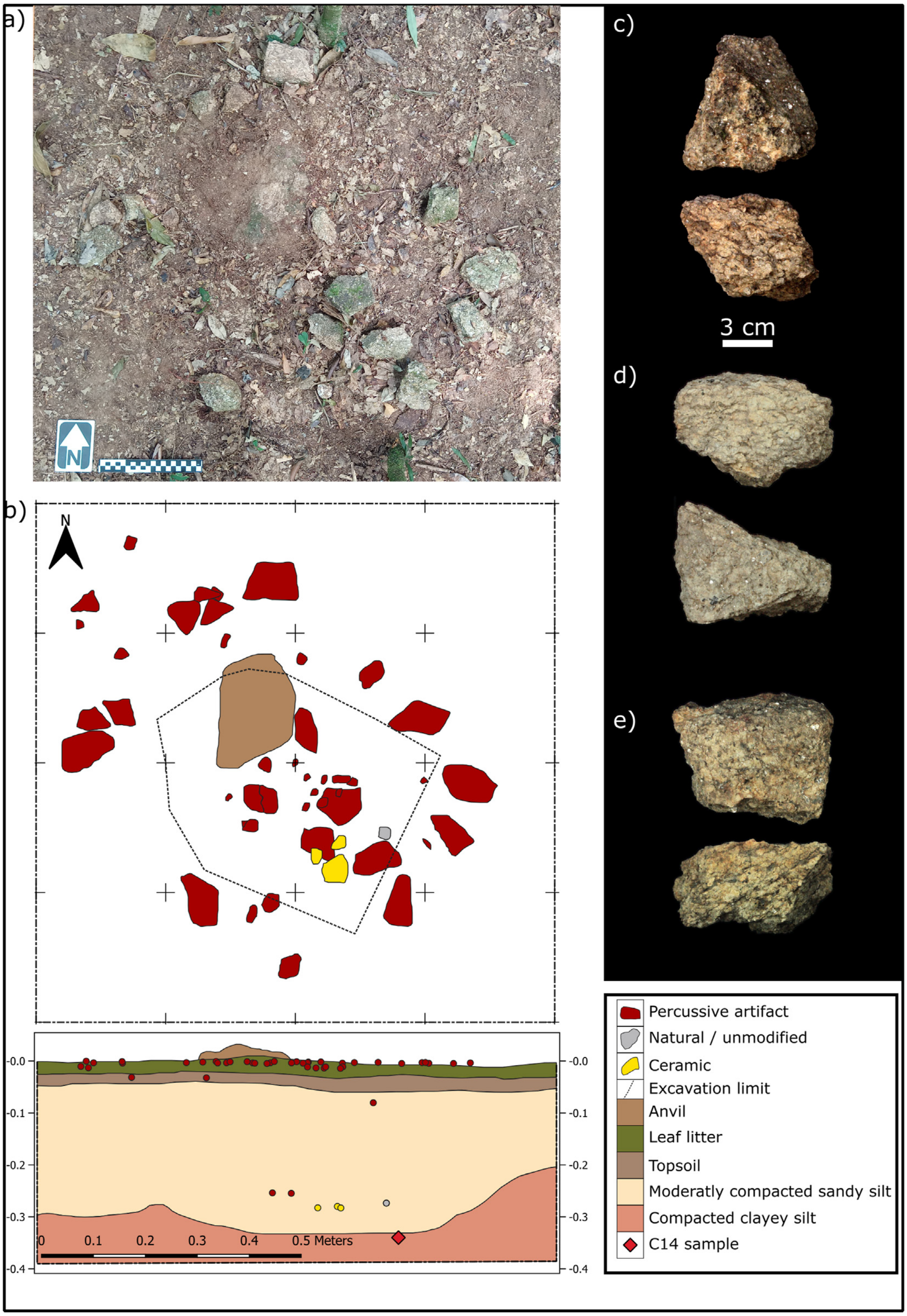

Figure 7. a) General view of the nut-cracking site at PGG3005 and b) plan and section showing all archaeological material recovered, extent of the nut debris around the anvil, and the backwall stratigraphy (b). Example of three hammerstone fragments recovered from PGG3005 (c–e) (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article).

consisted of frequent small pebbles, coarse-grained quartzite, and laterite gravel. Below the topsoil, no clear stratigraphic horizons were identified; instead, the sediment contained frequent large cobbles within a loosely consolidated matrix of sandy silt (Fig. 9b).

Ten quartzite lithic artifacts associated with percussive tool use were recovered. On the surface, two hammerstones were identified in close proximity to the anvil, along with another hammerstone fragment within the topsoil (5–10 cm from the surface). Additionally, a single hammerstone fragment and a piece of angular

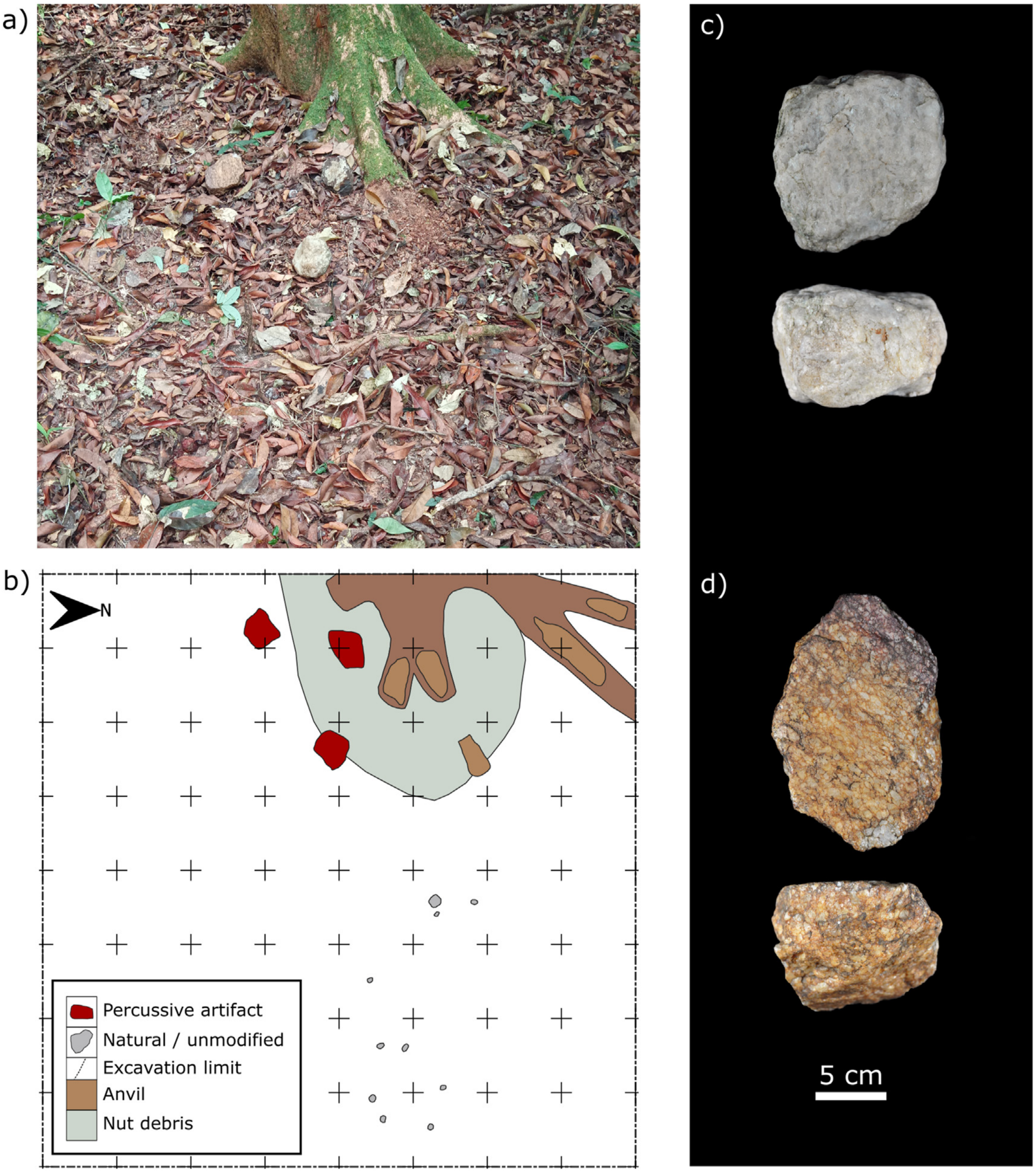

Figure 8. a) General view of the nut-cracking site at SSQ3001 and b) plan and section showing all archaeological material recovered, extent of the nut debris around the anvil, and the backwall stratigraphy (b). Example of two hammerstones recovered from SSQ3001 (c and d) (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article).

debris, along with five detached pieces were recovered from the depth of 10–20 cm. These artifacts consisted of a single wedge-initiated flake detachment, three edge detachments, and one angular chunk (Fig. 9c–g). Furthermore, a charcoal sample retrieved from a depth of 18 cm provides an age estimate of 586 (±25) BP for the artifacts uncovered within the 10- to 20-cm horizon (Fig. 8b; SOM Fig. S6; Table S14).

3.3. *Comparison between surface and excavated material signature at wooden anvil and stone anvil sites*

Excluding the three surface stone anvils at the three stone anvil sites, a total of 341 lithics were collected from both surface and excavated contexts from the six excavations at the DCP. Of these, 117 are classified as artifacts derived from percussive actions, whereas the remaining 224 were classified as naturally occurring unaltered stones (SOM Table S13).

Dating of the underlying sediments within these excavations provides a range of maximum dates for the excavated chimpanzee material at Djouroutou. The oldest of these dates are the two *Panda* nut excavations, with maximum ages of 1489 ± 23 BP and 719 ± 23 BP, with lithics from PPU3004 constrained to be between 719 ± 23 and 365 ± 21 BP by under and overlying C14 dates. The percussive lithics excavated from the *Coula* stone anvil site (CQQ3009) are younger than 328 ± 20 years, and the excavated lithics from the *Sacoglottis* stone anvil site are associated with a date of 586 ± 25BP (SOM Fig. S6; Table S14).

When all lithics from excavated and surface contexts are compared, the sites associated with stone anvils exhibited a significant difference in artifact frequency between surface and

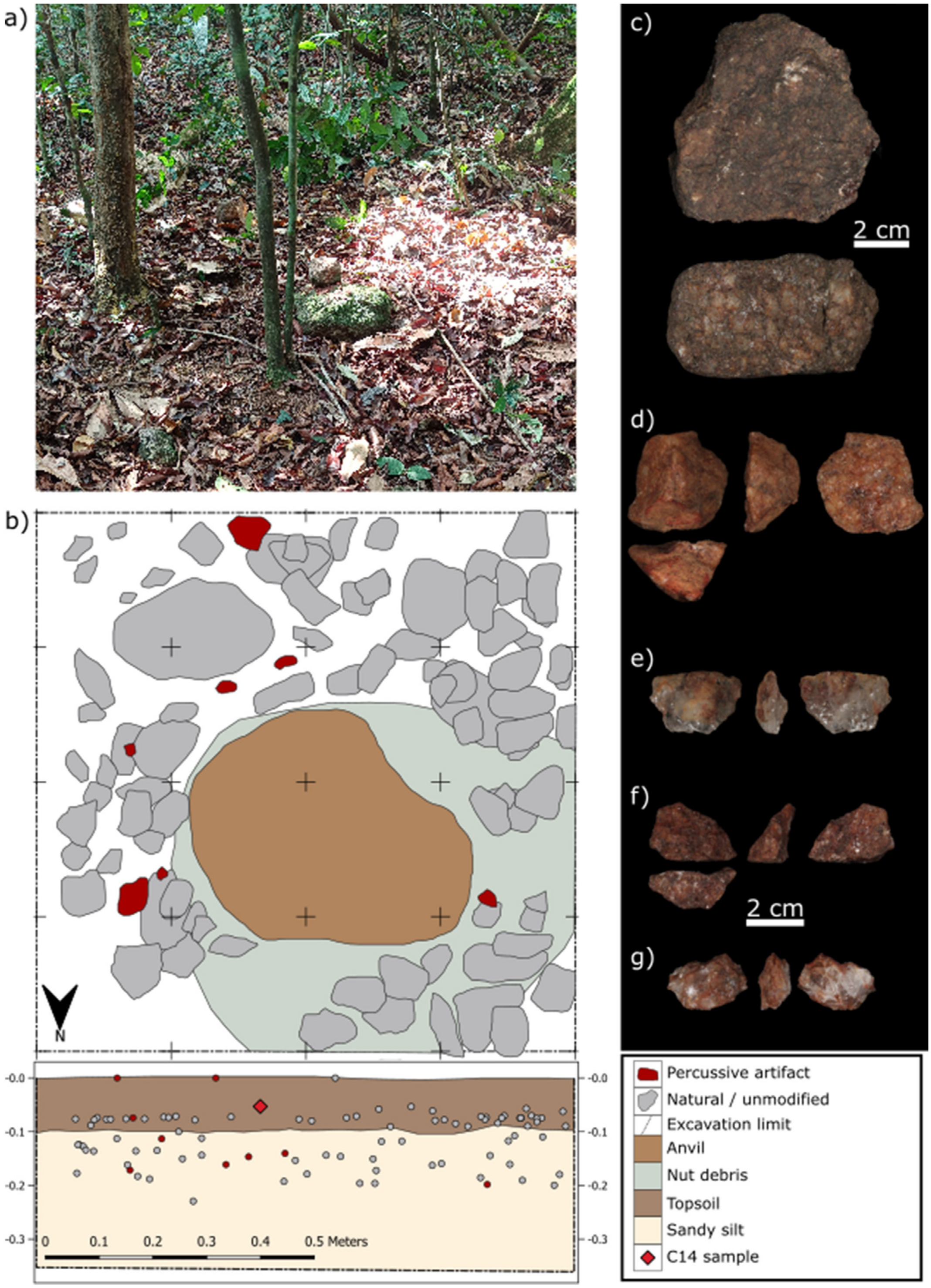

Figure 9. a) General view of the nut-cracking site at SQQ3003 and b) plan and section showing all archaeological material recovered, extent of the nut debris around the anvil, and the backwall stratigraphy (b). Examples of fragmented hammerstones (c), detached wedge-initiated flake (d), and edges pieces (e–g) from SQQ3003) (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article).

excavated contexts (χ^2 = 6.627, df = 1, p = 0.010), with more percussive lithics recovered from excavated contexts ($\underline{n}$ = 64; 62.7%; adjusted residual = 2.6; SOM Table S14). This difference between surface and excavated contexts, however, is not present at wooden anvil sites (χ^2 = 2.225, df = 1, p = 0.133; Fig. 10a). Conversely, the total mass of lithic material excavated from stone anvils is significantly lower than that of lithics recovered from surface contexts (KW: χ^2 = 18.834, df = 1, $p < 0.001$; Dunn's test: mean rank difference = −4.34, $p < 0.001$; SOM Table S19). This is indicative of a higher number of smaller lithics entering the archaeological record at stone anvil sites. However, this disparity is not observed at wooden anvil sites (KW: χ^2 = 2.339, df = 1, $p = 0.126$). Lithics found in excavated contexts at wooden anvil sites are significantly heavier than those from excavated contexts at stone anvil sites (KW: $\chi^2 = 11.11$, df = 1, $p < 0.001$; Dunn's test: mean rank difference = −3.33, $p < 0.001$; SOM Table S19). This difference persists regardless of including the two notably large percussive artifacts from excavated contexts of PPU3004 (KW: $\chi^2 = 5.88$, df = 1, $p = 0.015$; Dunn's test: mean rank difference = −2.43, $p = 0.008$; Fig. 10b).

When considering broad technological classifications, there is no significant difference in the frequency of detached pieces, hammerstones, and fragmented hammerstones between surface and excavated contexts at both stone anvil (Fisher's exact test: $p = 0.622$) and wooden anvil (Fisher's exact test: $p = 1.000$) sites. However, when considering specific percussive tool categories, there is a noticeable distinction between anvil types. There is a significantly higher frequency of small debris recovered from excavated contexts (adjusted residual = 4.63), along with a marked increase in the frequency of edge (adjusted residual = 2.55) and corner fragments (adjusted residual = 2.03) from surface contexts at stone anvil sites (Fisher's exact test: $p < 0.001$). No disparity was observed in the frequency of percussive artifact categories between surface and excavated contexts at wooden anvil sites (Fig. 11).

4. Discussion

Our ability to reconstruct past hominin behavior during the Plio-Pleistocene is largely confined to inferences derived from stone tools. In recent years, the role of percussive technology in the subsistence strategies of Plio-Pleistocene hominins (de la Torre and Hirata, 2015; de la Torre, 2019) and as a potential precursor to flake lithic technology (Rolian and Carvalho, 2017; Thompson et al., 2019; Luncz et al., 2022a) has been increasingly recognized. Although it has been suggested that wooden tools may have been used during the Plio-Pleistocene (Toth, 1985; Schick and Toth, 1994; Luncz et al., 2022a, 2022b), the low likelihood of preservation of this material remains a barrier for their identification in the

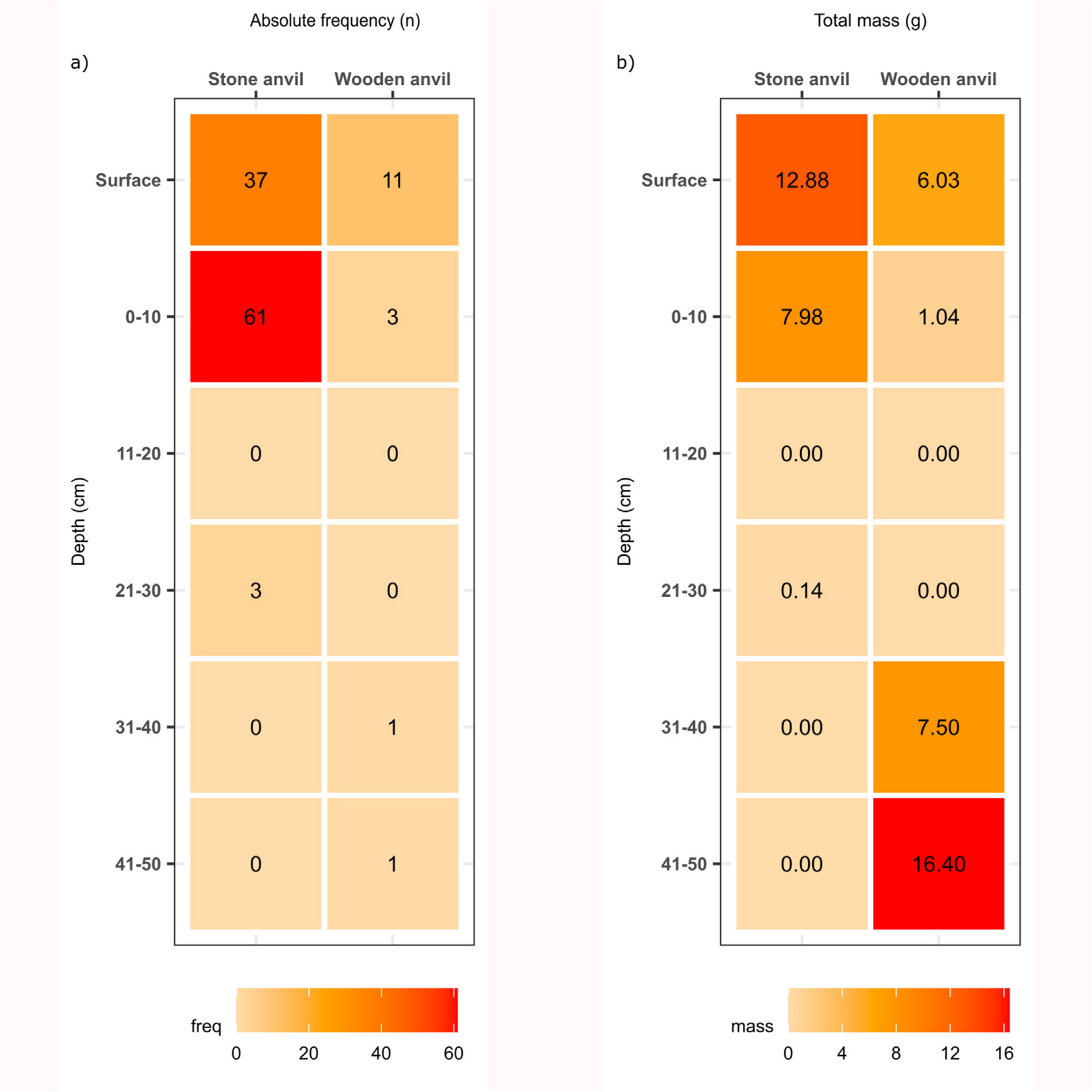

Figure 10. Density plots of a) the absolute frequency and (b) the total mass (g) of lithic artifacts recovered from surface and excavated contexts of stone and wooden anvil sites at Djouroutou (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article).

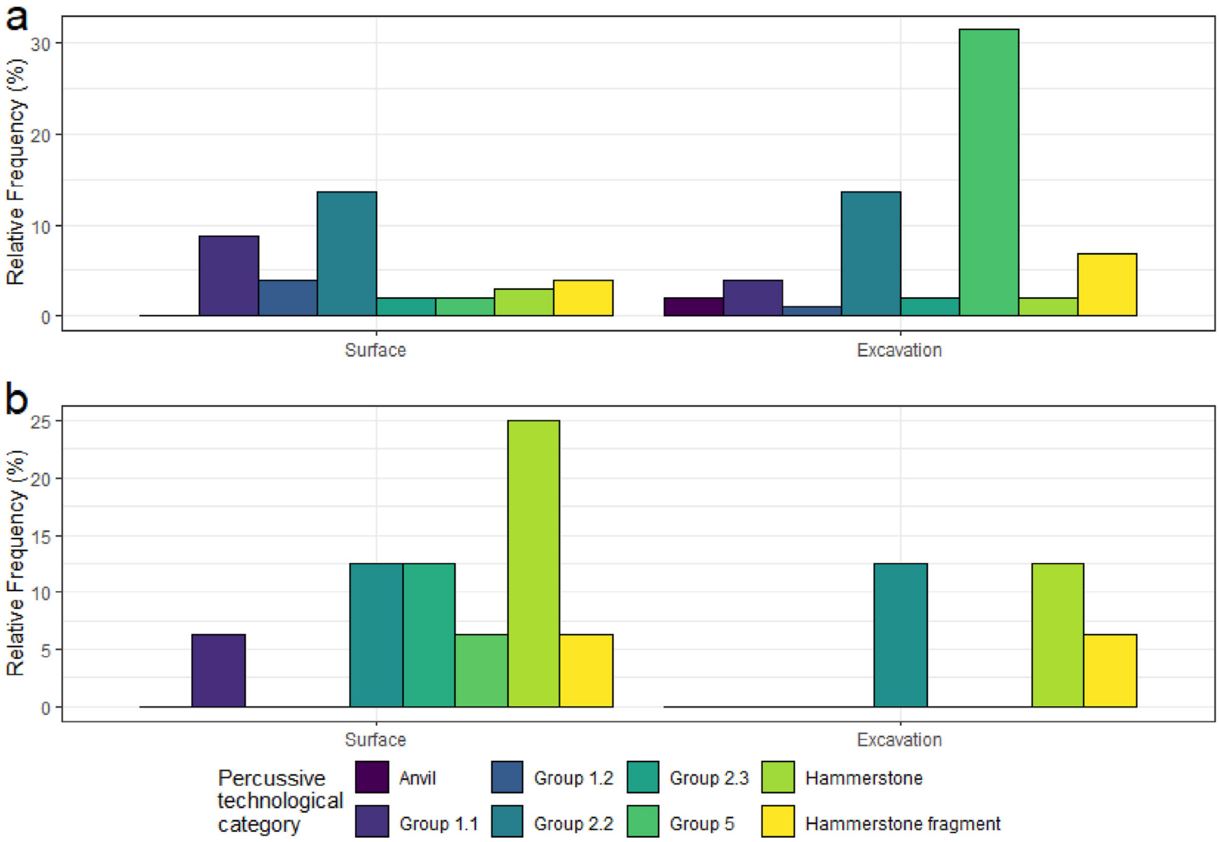

Figure 11. a) Relative frequency of artifact types at stone and b) wooden anvil sites, separated by stratigraphy. Artifact types include anvil, hammerstones, hammerstone fragments, edge products (Group 1.1), corner products (Group 1.2) elongated pieces (Group 2.1), angular chunks (Group 2.2), detached pieces (Group 2.3), typical hammerstone flakes (Group 3), angular fragments spontaneously detached from an inactive region of the hammerstone or anvil (Group 4), and artifacts measuring smaller than 20 mm (Group 5) (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article).

archaeological record. However, given the fact that modern extant primates as well as various modern and historical ethnographic groups use wooden tools widely in their percussive tool repertoire, it seems likely that this material was also used by hominins in the Plio-Pleistocene (Pascual-Garrido and Almeida-Warren, 2021; Luncz et al., 2022a, 2022b). Examining the variability in the material signature of chimpanzee percussive tool use and the factors that influence this record such as the use of multiple tool types (e.g., stone hammer and wooden anvil or vice versa) provides insights into the behaviors that may have influenced the hominin archaeological record. This contribution to the referential framework of archaeological signatures enhances our ability to infer such behaviors in the Plio-Pleistocene archaeological context (Panger et al., 2002; Harmand et al., 2015; Arroyo et al., 2016, 2021; Proffitt et al., 2016, 2018a, 2018b, 2022, 2023; Rolian and Carvalho, 2017; Thompson et al., 2019; Reeves et al., 2021; Luncz et al., 2022a).

4.1. What are the lithic material differences between stone and wooden anvil use?

Chimpanzees in the Taï National Park use both wooden and stone anvils for nut-cracking (Boesch, 2000; Soiret et al., 2015). Our study evaluates how anvil material can affect the resulting lithic archaeological signatures of this behavior. Comparative analyses of wooden anvil and stone anvil locations reveal distinct differences in the contemporary and archaeological material record produced on both anvil types (summarized in Fig. 12). Although there is a degree of overlap, the lithic record of stone anvil and wooden anvil use differs in the dimensions of associated artifacts. Artifacts from both anvil types are notably larger than the natural, unmodified stones found at the same locations. This is likely due to the transportation of larger stones to anvil locations as hammerstones (Luncz et al., 2016), resulting in larger fragments. The use of stone anvils leads to higher frequencies of hammerstone fragmentation, resulting in greater accumulations and densities of lithic material around the anvils. Stone anvil assemblages consist of complete and fragmented hammerstones, along with detached pieces both with and without percussive damage. Although some detached pieces are found at wooden anvil sites, these assemblages are predominantly composed of complete hammerstones. This material signature is heavily dependent on the relative hardness of the anvil material and the hardness/fragility of the hammerstone. Percussive damage on hammerstones and anvils results from a combination of miss-hits and follow-through hits during nut-cracking (Arroyo et al., 2016). While relative variation in density of wooden anvils depending on tree species may impact the likelihood that a hammerstone will fracture, when stone hammers are used against the relatively softer wooden anvils, there is an overall lower likelihood of fragmentation than when they are used on harder stone anvils. Although there is a higher frequency of complete tools (hammerstones) at wooden anvil sites, this may not necessarily translate into a more durable or identifiable archaeological signature. Hammerstones used by primates for nut-cracking are a part of an actively modified cultural landscape (Reeves et al., 2021; Almeida-Warren et al., 2022). These hammerstones are frequently transported between nut-cracking localities (Luncz et al., 2016). The identified hammerstones in surface contexts in this study represent only the current location of these tools within their use life and are

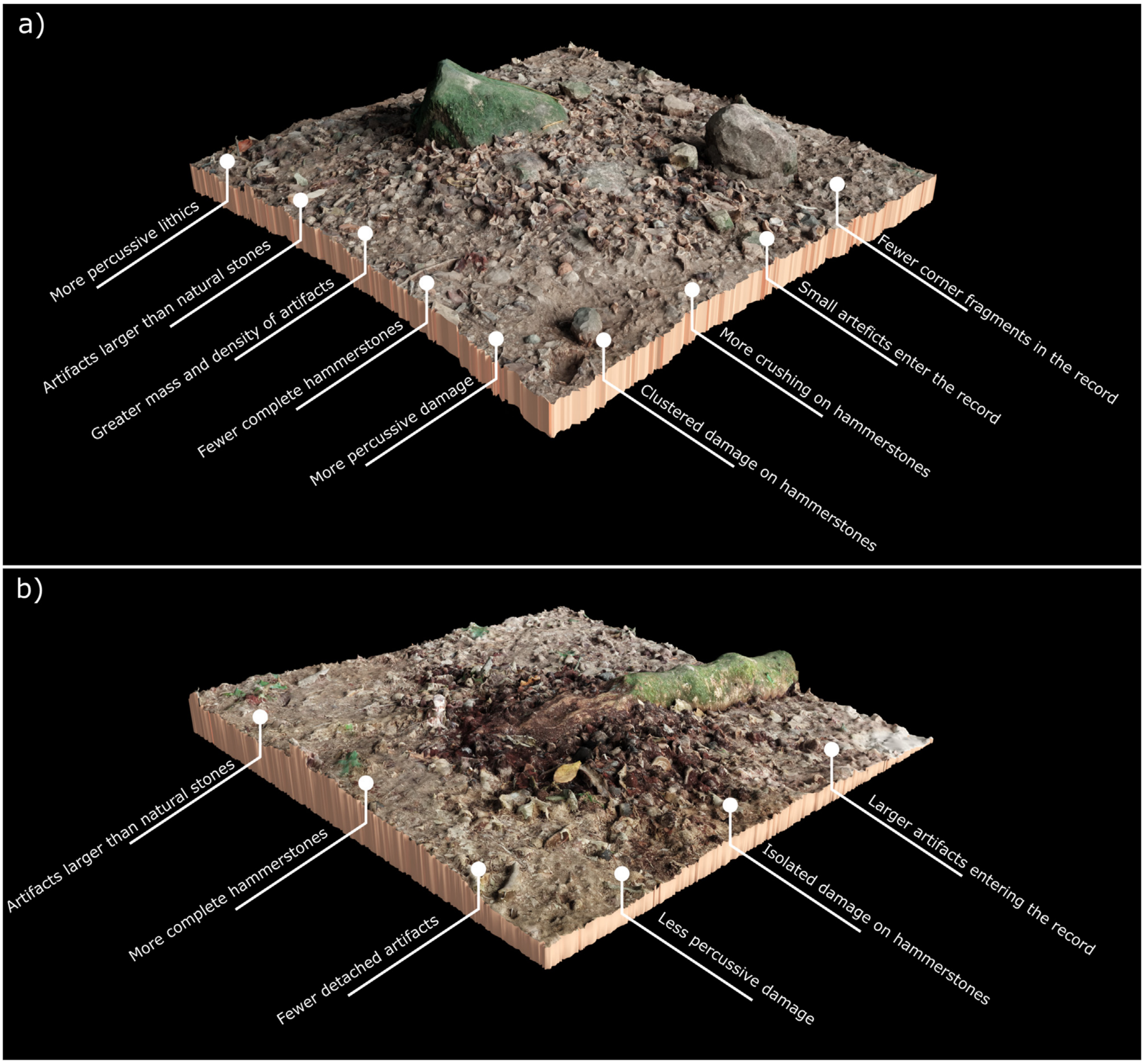

Figure 12. A comparison of the technological, use-wear, and archaeological differences of the lithic assemblages associated with (a) stone and (b) wooden anvils used for chimpanzee nut-cracking based on the results of this study.

less likely to enter the archaeological record at these locations (Proffitt et al., 2018a; Reeves et al., 2021). However, our excavations illustrate the potential for recovering complete tools at both wooden and stone anvil localities. The higher frequency and density of fragmented lithics identified at stone anvil sites, nonetheless, may represent a stronger archaeological signature of this behavior within the landscape compared to individual hammerstones. Regarding hammerstones, those found at stone anvil locations exhibit a greater degree and concentration of percussive damage. Although less frequent in the associated lithic assemblages, the damage patterns on these artifacts would likely be more identifiable in archaeological contexts.

When considering the second major technological category, detached pieces, significantly greater frequencies are recovered from stone anvils. However, this category mainly comprises angular and small debris than clearly identifiable techno-typological groups. Previous studies have shown that vast quantities of similar debris are often accumulated at chimpanzee nut-cracking sites (Proffitt et al., 2018a). While most of the angular and small debris in this study is associated with stone anvil use, when compared to other chimpanzee material records associated with wooden anvils (Mercader, 2002; Proffitt et al., 2018a), a similar pattern is clear. The wooden anvil site of Panda 100 is associated with large frequencies of small and angular debris and a lack of complete hammerstones (Proffitt et al., 2018a). One explanation for this similarity in material signatures despite the difference in anvil type might lie in locally available raw material variation. At the Panda 100 site, the dominant raw material present was granatoid, a highly fragmentary material with frequent internal fracture planes (Mercader, 2002; Proffitt et al., 2018a). Similarly, in our study, most of raw material found at stone anvil sites is mica-granite, which also fragments easily. Other factors such as time averaging of assemblages and the frequency and intensity of the behavior may also play a substantial role in the accumulation of dense lithic clusters around both wooden anvil and stone anvil sites. Given the high fragmentary nature of these raw materials, their use as hammerstones on a range of nut species, including the hard *Panda* nut, results in a substantial fragmentation of the hammer, regardless of the anvil material. While not directly investigated in this study, it is likely that the hardness of the underlying wooden anvil, potentially related to tree species, may have an effect on the degree of hammerstone fragmentation.

Additionally, both stone and wooden anvil sites yielded a small number of identifiable detached artifact types that closely resemble flakes. Although a higher frequency was identified at stone anvil sites, they constitute a larger relative proportion of the lithic material from wooden anvil sites. None of these flakes, however, exhibit features associated with conchoidal fracture. Similarly, low frequencies of detached pieces have been reported at other chimpanzee wooden anvil and stone anvil sites (Carvalho et al., 2008; Proffitt et al., 2018a). At the wooden anvil nut-cracking site of Panda 100, only a single flake accounting for 0.2% of the total assemblage has been identified (Proffitt et al., 2018a), with only two flakes identified at a stone anvil site at Diécké (Guinea; Carvalho et al., 2008). This supports previous observations that flake detachments resembling those often recovered from Stone Age contexts are very rare consequences of chimpanzee nut-cracking in wild settings. This can be explained by the low homogeneity and coarse-grained nature of the available raw material (Arroyo et al., 2016; Proffitt et al., 2018a, 2023). Moreover, the lithic assemblages at stone anvil sites display a higher degree of percussive damage than those from wooden anvil sites. This visible damage enhances the archaeological signature of this behavior, increasing the likelihood of interpreting this lithic material as associated with a percussive activity (Proffitt et al., 2018a). On the other hand, the lack of obvious percussive damage on lithics associated with wooden anvil use makes it difficult, but not impossible, to identify wooden anvil nut-cracking activities from the lithic remains alone in the archaeological record.

4.2. *How does anvil type affect the archaeological preservation and visibility of nut-cracking across time?*

The excavations at Djouroutou support the conclusion that nut-cracking using stone anvils demonstrate substantially higher archaeological visibility than wooden anvil use. Not only did the surface-material signature differ but so did the excavated material signature. The lithic material found at wooden anvil excavations was sparse or ephemeral, likely due to a reduced frequency of hammerstone fragmentation at these sites. However, notable were two large percussive artifacts, potentially hammerstones based on comparative analysis, recovered from the stratigraphy of a *Panda* nut wooden anvil site (PPU3004). This illustrates that, albeit infrequently, complete hammerstones do occasionally appear in the archaeological record. Yet, upon excluding these two artifacts from the sample, the fragmented assemblages identified within the excavations demonstrate that the use of stone anvils resulted in a more pronounced archaeological signature. In contrast, the fragmented assemblage recovered from wooden anvil excavations was smaller both in terms of total frequency of artifacts and material density.

The hypothesis that nut-cracking behaviors by hominins, similar to that of chimpanzees, would be difficult to discern in a Plio-Pleistocene context was proposed by Panger et al. (2002). It was suggested that although such behaviors may have been prevalent prior to the emergence of the Oldowan technocomplex, such artifacts must be identifiable and distinguishable from natural stone in the archaeological record. The data from the present study suggest that nut-cracking with stone anvils could be considerably more visible in the archaeological record than when undertaken on wooden anvils. Although complete hammerstones are unlikely to enter the archaeological record as either anvil type (Reeves et al., 2021; Proffitt et al., 2018a, 2018b), the archaeological footprint is more visible at stone anvil sites. Having said this, however, our analysis of surface and excavated material has shown that percussive behavior at wooden anvil sites is discernible both through the presence of tools and in the form of use-wear and residue adherence to hammerstones.

The visibility of nut-cracking behavior in the archaeological record of Djouroutou, however, is not solely determined by anvil material. For instance, both nut hardness and the underlying ecology of the region have the potential to affect material signature variation. Nut hardness has been shown to correlate with chimpanzee hammerstone mass, with larger hammers used for harder nuts. Given the scarcity of large stones at Djouroutou, it stands to reason that hammers used to crack the harder nuts (i.e., *Panda* and *Sacoglottis*) are more likely to be transported and reused once a nut-cracking tree is no longer producing nuts (Proffitt et al., 2018a). Additionally, processing these harder nuts is more likely to result in characteristic large central pitting on the active surface of the hammers and anvils (Proffitt et al., 2022). *Panda* nut trees are often found in areas where mica-granite is the predominant raw material (Reeves et al., 2021). The scarcity of these trees and the need for large tools as a result of the hardness of the nuts lead to mostly solitary nut-cracking behavior. The solitary nature of this behavior, which is driven by the wider ecology of the region (Boesch, 2012; Reeves et al., 2021), combined with the highly friable nature of the available raw material, results in stone anvils with identifiable percussive damage (Proffitt et al., 2022) distributed relatively sparsely within the landscape, possessing a dense lithic assemblage of broken hammers and fragments within their immediate vicinity. On the rare occasions when hammers are preserved undamaged, they are large and identifiable in the archaeological record. On the other hand, *Coula* nut-cracking sites present a different pattern. *Coula* trees typically grow in well-drained, higher elevations, where the sediment is rich in naturally occurring quartz pebbles and cobbles, providing more potential hammerstones. This leads to group foraging behavior, which, when undertaken on stone anvils, yields a high density of lithic material due to the increased levels of activity. However, when wooden anvils are used, the hard quartz hammerstones rarely fracture or develop significant percussive damage, beyond the adherence of residue, and are more likely to be moved due to the involvement of multiple chimpanzees in a foraging group (Boesch, 2000; Luncz et al., 2016). The *Sacoglottis* sites in this study were also located in areas where quartzite pebbles are the predominant raw material and as such are less likely to fragment when used on wooden anvils as observed with mica-granite hammerstones. This pattern is consistent with wider landscape studies of the Djouroutou region (Reeves et al., 2021).

The variable material signatures of nut-cracking on different anvil types have potential implications for our ability to search for such a behavioral record in Plio-Pleistocene archaeological contexts. While the archaeological signature associated with stone anvil use is stronger, our results corroborate previous studies that suggest in some cases it may be possible to identify percussive damage associated with wooden anvil use (Mercader, 2002; Proffitt et al., 2018a). However, this is likely dependent on raw material and wood type and the length of time a nut-cracking site is used. The largely ephemeral nature of the percussive damage identified on lithic material associated with wooden anvil use would likely result in an underrepresentation of this behavior in the archaeological record compared to the more clearly identifiable damage patterns at stone anvil sites.

The excavations at Djouroutou not only show that the variation in archaeological signatures associated with the two anvil materials is present across all nut species, but they also improve our understanding of the chronology of chimpanzee occupation in the area. Our findings indicate that chimpanzees have been living and using tools in the Djouroutou area for a minimum of 719 years BP. While previous studies have reported chimpanzee nut-cracking up to 4300 years ago in the North of the Taï Forest (Mercader, 2007), the species of nut processed remains unclear. Our excavations provide new evidence that nut-cracking has been long practiced by the chimpanzees of the Taï Forest. The material signature associated with the earliest chimpanzee archaeological record at Noulo (Mercader, 2007), consisting of angular debris and a lack of complete hammerstones, is notably similar to the lithic assemblages presented in this study. Given these material similarities and large chronological gap, it is likely that a chimpanzee archaeological record in the Taï Forest is widespread. The ability to track chimpanzee stone tool use into antiquity and across a landscape provides a potential new line of research to understand primate behaviors and past chronological and geographic variation of our closest living relatives.

5. Conclusions

Our study provides information on the lithic archaeological signature of nut-cracking behavior by chimpanzees who use two different anvil types. By comparing the lithic material record associated with stone and wooden anvils used for nut-cracking, we have shown that there are clear differences in the resulting assemblages. Wooden anvils result in a higher frequency of complete hammerstones; these are highly mobile objects and are unlikely to enter the archaeological record at the location of the behavior. Stone anvils, on the other hand, result in a higher frequency and density of fragmented stones that exhibit clear percussive damage and as such represent a clearer archaeological signature of nut-cracking on the landscape. These results show that the lithic signature of wooden anvil use for nut-cracking is less likely to result in a detectable archaeological record. These results represent a new referential framework which can contribute to our ability to search for and identify such activities associated with a pre-core and flake stage of hominin cultural evolution.

CRediT authorship contribution statement

Tomos Proffitt: Writing – original draft, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Serge Soiret Pacome:** Writing – original draft, Methodology, Investigation. **Jonathan S. Reeves:** Writing – original draft, Investigation. **Roman M. Wittig:** Writing – original draft, Project administration. **Lydia V. Luncz:** Writing – original draft, Supervision, Project administration, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no conflict of interest/competing interest.

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Appendix A. Supplementary Online Material

Supplementary Online Material to this article can be found online at https://doi.org/10.1016/j.jhevol.2024.103582.

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