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# Revisiting Panda 100, the first archaeological chimpanzee nut-cracking site

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ABSTRACT

Archaeological recovery of chimpanzee *Panda oleosa* nut cracking tools at the Panda 100 (P100) and Noulo sites in the Taï Forest, Côte d'Ivoire, showed that this behavior is over 4000 years old, making it the oldest known evidence of non-human tool use. In 2002, the first report on the lithic material from P100 was directly compared to early hominin stone tools, highlighting their similarities and proposing the name 'Pandan' for the chimpanzee material. Here we present an expanded and comprehensive technological, microscopic, and refit analysis of the late twentieth century lithic assemblage from P100. Our re-analysis provides new data and perspectives on the applicability of chimpanzee nut cracking tools to our understanding of the percussive behaviors of early hominins. We identify several new refit sets, including the longest (>17 m) hammerstone transport seen in the chimpanzee archaeological record. We provide detailed evidence of the fragmentation sequences of *Panda* nut hammerstones, and characterize the percussive damage on fragmented material from P100. Finally, we emphasize that the chimpanzee lithic archaeological record is dynamic, with the preservation of actual hammerstones being rare, and the preservation of small broken pieces more common. P100 – the first archaeological chimpanzee nut cracking lithic assemblage – provides a valuable comparative sample by which to identify past chimpanzee behavior elsewhere, as well as similar hominin percussive behavior in the Early Stone Age.


## 1. Introduction

Discussions of the evolution of tool use have historically centered on the hominin lineage: *Homo sapiens* and our ancestors since we split from the other apes (Leakey, 1971; Harmand et al., 2015). Hominin technological evolution is recorded in a durable record of stone tools, which provide detailed information about our cultural and cognitive development, extending back more than 3.3 million years (Harmand et al., 2015). In contrast, our understanding of the technological evolution of non-human primates is in its infancy. The emerging field of primate archaeology addresses this imbalance using modern archaeological techniques to understand the emergence and development of primate tool use, and to provide new comparative insights into the emergence of hominin lithic technology (Haslam, 2012; Haslam et al., 2017).

Owing to their close relatedness to humans, and their propensity to use a variety of tools, chimpanzees received the earliest and most intense attention as a potential model species for understanding early hominin stone tool use. Some West African chimpanzees (*Pan troglodytes verus*) use stone tools in the wild, to crack open different nut species. Two long-term study sites – Bossou in Guinea and the Taï National Park in Côte d'Ivoire – provide the majority of the research data on this behavior. In the Taï National Park, chimpanzees crack open five different nut species (*Panda oleosa, Parinari excelsa, Saccoglottis gabonensis, Coula edulis,* and *Detarium senegalensis*). To crack open the very hard *P. oleosa* nuts, chimpanzees use stone tools that vary in weight between 3 and 15 kg (Boesch and Boesch, 1984a), and mostly use tree roots for anvils. The uneven distribution of stone material throughout the forest means that chimpanzees need to transport hammerstones to *Panda* nut trees to use as tools (Boesch and Boesch, 1984a; Luncz

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et al., 2016). Conversely, the chimpanzees at Bossou do not crack *P. oleosa*, and instead primarily use lighter and smaller stone hammers and anvils to open the softer palm oil nut (*Elaeis guineensis*). Additional regional differences in the stone tool use between these two groups consist of the frequent use of transportable stone anvils and the rare reported use of stabilizing stones at Bossou (Carvalho et al., 2009).

In 2002, Mercader et al. published a pioneering study from the Taï Forest proving that inactive chimpanzee nut-cracking sites are identifiable in the archaeological record. For the first time, researchers demonstrated that a primate material record existed and could be traced, using archaeological techniques, into antiquity. In addition, Mercader et al. (2002) suggested that the chimpanzee artefactual record uncovered at their research site Panda 100 (P100) mimicked early hominin lithic technology. They compared the chimpanzee material with some Oldowan assemblages in terms of artefact densities, size ranges and general morphologies of flakes (Mercader et al., 2002). Specific attention was paid to its apparent similarities to Early Stone Age (ESA) lithic assemblages from Omo 123 (Chavaillon, 1970, 1976; de la Torre, 2004), the Shungura formation (FtJi1) (Merrick et al., 1973; Merrick and Merrick, 1976) and KBS Member (Koobi Fora, Kenya) (Isaac, 1976). This led to the suggestion that some lithic material from such Oldowan assemblages may derive from nut cracking behavior, or the processing of other hard-object foods. This first chimpanzee excavation contributed directly to the emergence of primate archaeology as a new discipline, combining both archaeological techniques and primate behavioral observations (Haslam et al., 2009, 2016a, 2016b, 2017; Visalberghi et al., 2013; Luncz et al., 2015; Proffitt et al., 2016). Here, we apply the latest primate archaeological methods to the P100 lithic assemblage, providing new insights into the relevance of this material for interpreting hominin behavior (Haslam, 2012).

## 2. Background

The P100 site was a known modern chimpanzee nut cracking location. The 100 square meter excavation at the site yielded a substantial artefactual record, including both lithics and organic remains in the form of abundant nut shells and wooden anvils. This study was joined by subsequent excavations at Noulo and Sacoglotis B, dated to over 4000 years ago, and located within a hundred meters of P100 (Mercader et al., 2007). The stones recovered from P100 were proposed as the 'Pandan' type assemblage, that is, the type assemblage against which future chimpanzee archaeological finds could be assessed (Mercader et al., 2002).

Although not explicitly stating that hominin-like conchoidal flake technology was represented at P100, Mercader et al. identified numerous pieces that they classified as 'flakes' within the assemblage, noting that 'panins may have been capable of producing assemblages that mimic some of the earliest hominin artifacts' (Mercader et al., 2002, p. 1455). The apparent similarity of the P100 lithic assemblage to Oldowan hominin stone tool technology has been discussed and contested by a number of researchers (de la Torre, 2004; Delagnes and Roche, 2005; Pelegrin, 2005; Schick and Toth, 2006; Harmand et al., 2015). They suggest that the intentionality and the 'know-how' associated with flake production is only clear in hominin lithic material (Pelegrin, 2005), including an understanding of conchoidal fracture. A recent re-analysis of the Omo Oldowan lithic assemblages has argued for the presence of relatively structured exploitation strategies there, including the structured production of fully conchoidal flakes (de la Torre, 2004). Both the quality and diminutive dimensions of the available raw material at Omo were a major factor in the apparently simple nature of the assemblages. De la Torre (2004) found that any similarity to the P100 lithic material was only in terms of dimensions. The lithic material produced by early hominins appeared qualitatively different to that identified at P100, and indeed to captive primate knapped artefacts (Delagnes and Roche, 2005; Pelegrin, 2005; Schick and Toth, 2006). Hominins showed intentional flake production through the application of consistent technical rules (Delagnes and Roche, 2005), which were detached with a high degree of precision and manual dexterity (de la Torre, 2004). These flakes possessed clear bulbs of percussion, striking platforms, dorsal flake scars and cores with impact points and flake negatives (Schick and Toth, 2006). Even when considering the earliest instances of hominin lithic technology, the Lomekwian (Harmand et al., 2015), the flakes produced are significantly larger than those reported by Mercader et al. (2002). Furthermore, even though it has been suggested that the Lomekwian is closer, in terms of technique, to primate nut cracking, the Lomekwian material indicates that hominins possessed the ability to intentionally strike cores with adequate accuracy and force to detach multiple flakes (Harmand et al., 2015).

The importance of percussive activities involving both an active hammerstone and a passive anvil has recently been highlighted in the human archaeological record at Olduvai (Mora and de la Torre, 2005; de la Torre et al., 2013; Arroyo and de la Torre, 2017 ), West Turkana (Harmand et al., 2015; Lewis and Harmand, 2016), and Gesher Benot Yaqov (Goren-Inbar et al., 2002, 2015). As the motions involved are similar, this technology may be a better candidate for hominin and chimpanzee comparative studies (de la Torre, 2010; Arroyo, 2015).

Research into percussive technology has focused on the Plio-Pleistocene archaeological record, particularly in East Africa, where percussive behaviors played an important role in the subsistence strategies of early hominins (de la Torre and Mora, 2005; Mora and de la Torre, 2005). To identify this type of behavior, a number of studies have developed referential datasets that characterize the archaeological signature of percussive activities (de la Torre et al., 2013; Caruana et al., 2014; Arroyo, 2015). These studies have either experimentally replicated percussion on the same raw materials identified in the archaeological record (de la Torre et al., 2013; Arroyo, 2015; Arroyo et al., 2016), or quantified the wear patterns associated with intentional percussive activities verses natural taphonomic damage (Caruana et al., 2014). For example, de la Torre et al. (2013) found that experimental activities such as nut cracking, bipolar knapping, meat tenderizing and plant processing produced a range of use-damage on the passive hammer (anvil) involved in the behavior. This damage included archaeologically identifiable detached pieces, corresponding with typical percussive anvil products identified in the archaeological record (de la Torre and Mora, 2005). More recently, the importance of primate percussive technology and behaviors for interpreting the hominin archaeological record has been highlighted using GIS analytical techniques on tools used in field experiments (Luncz et al., 2016) as well as microscopic characterization of percussive damage by captive and wild chimpanzees (Benito-Calvo et al., 2015; Arroyo et al., 2016).

Beyond chimpanzees, recent research with other tool-using primates provides insights into the emergence of hominin flake technology. For example, wild bearded capuchin monkeys in Serra da Capivara National Park (SCNP), Brazil, intentionally strike quartz cobbles together, possibly to obtain trace nutrients. By doing so, they unintentionally produced numerous fully conchoidal flakes (Proffitt et al., 2016), which were not subsequently used. The flakes, resulting from the only recorded behavior where wild primates deliberately strike stone tools on other stones, exhibit the same range of technological attributes commonly identified in hominin flaked assemblages. The identification of such artefacts in the primate record has relevance to the suggestion that hominin flaked technology may have initially emerged as a by-product of percussive behavior (McGrew, 1992) due to hammerstone mis-hits on stone anvils. This combination of new information regarding the technology of hominin percussive material in the East African archaeological record, and the identification of truly flaked primate (capuchin) artefacts, reaffirms the importance of the P100 lithic assemblage as a potentially valuable comparative dataset for the characterization and identification of percussive behavior in the archaeological record.

Here, we present a complete new technological analysis of the lithic material excavated from the P100 site. The combined technological, refit and microscopic analysis of this percussive material provides a finer grained characterization of the archaeological signature of wild chimpanzee nut cracking behavior than previously achieved. By renewing the analysis of the Panda 100 lithic material, this valuable primatological assemblage can be of further use to researchers in understanding the emergence of both West African chimpanzee and hominin percussive behavior.

## 3. Materials and methods

### 3.1. The Panda 100 site

The P100 site is located within the Taï Forest in the western region of the Ivory Coast (Fig. 1A) and lies between the confluence of two rainforest streams that frequently inundate the surrounding area. Mercader et al. (2002) addressed the degree of spatial and artefactual integrity of the lithic assemblage, noting that all material was identified in low energy sedimentary contexts, consisting of non-stratified clay, silt and sand sediments. Coupled with the presence of numerous nut shells and a high frequency of artefacts <20 mm ($n = 374$ of 479 pieces; 78%) in maximum dimension, these data suggest that post-depositional fluvial transportation of the assemblage was not a significant factor (Mercader et al., 2002). In addition, the vast majority of the lithic artefacts possess fresh fractured edges, with very little rounding of fractured surfaces, suggesting minimal fluvial effects.

P100 is in the immediate vicinity of a single *Panda* tree where chimpanzees were directly observed to crack nuts with stone tools. During the occupation of this site, from at least 1975, stone hammers were used in conjunction with wooden anvils, consisting of protruding tree roots. The site was eventually abandoned in 1996 (Boesch and Boesch, 1984a; Mercader et al., 2002; Boesch, 2012) when the *Panda* tree died and fell to the ground. The immediate area is devoid of adequate raw material sources for use as hammerstones, suggesting that all tools were actively carried to the vicinity of the *Panda* tree.

Archaeological excavation at P100 covered 59 $m^2$, excavated in arbitrary spits of 3 cm, concentrating on the regions immediately surrounding four visible anvils. In addition, an excavation of the wider area was conducted to a depth of 5 cm, resulting in the identification of two additional anvils. Fragmented lithic material was associated with all anvil areas and a total of 479 artefacts were recorded, consisting of four raw materials: granitoid, laterite, diorite, and quartzite. These were classified based on general morphology into hammer edges, cortical and non-cortical flakes, tabular products, angular shatter, amorphous shatter and microshatter (<20 mm) (Mercader et al., 2002). Of these artefact categories, Mercader et al. paid particular attention to the flakes, arguing that these shared similar dimensional, morphological and technological attributes to Oldowan flakes (Omo, Gona and Koobi Fora). They identified partially and non-cortical flakes, and a single example with a dihedral striking platform (Mercader et al., 2002). Seven refits (16 pieces) were also identified at two anvils, representing a maximum horizontal movement of stone pieces of between 0.05 and 1.60 m.

The P100 artefacts reported in 2002 (Mercader et al., 2002), which are the focus of the present re-analysis, were most likely deposited during the time of observed use of the P100 site by wild chimpanzees from 1979 to 1996 (Boesch and Boesch, 1984a). The P100 site, however, potentially preserves far older chimpanzee nut-cracking behavior (Mercader et al., 2007). There are currently five published radiocarbon dates for the Panda 100 site (Mercader et al., 2007) (Table 1), none of which are directly related to the lithic material dealt with in the current study These dates were obtained from excavations in 2003, which extended the P100 excavations into deeper (between 110 and 125 cm) and older sediments, and recovered three stone artefacts attributed to chimpanzee nut cracking. The deeper sediments returned uncalibrated radiocarbon ages of 2330–4280 BP (Mercader et al., 2007), which equate to 2182–4966 years BP when calibrated.

### 3.2. Technological analysis

For this study, all P100 lithic material was measured and weighed, with pieces >20 mm subjected to a full technological analysis (Supplementary Online Material [SOM] S1). In the original report of the P100 lithic material (Mercader et al., 2002), a brief analysis of the lithic material included typological classifications and dimensions of the artefacts as well as the range of raw materials present. Since that time a number of technological analyses have been conducted on both hominin and primate percussive lithic assemblages. Of these, de la Torre and Mora (2005, 2013) have outlined a comprehensive techno-typological classificatory scheme for the analysis of hominin lithic material derived from percussive behavior. This classification system was developed through the analysis of hominin passive anvils and their associated detached products, and the analysis presented here draws on these classification schemes in order to characterize the P100 lithic material. Mora and de la Torre (2005) set out five separate passive element percussive groups, based on both the morphological location from which a fragment is derived and its technological characteristics. These include edge products (Group 1.1), corner products (Group 1.2), elongated detached pieces from the anvil faces (Group 2.1), angular chunks (Group 2.2), and detached pieces that may resemble knapped flakes with a high degree of percussive damage (Group 2.3). Subsequently, Arroyo (Arroyo, 2015; Arroyo and de la Torre, 2016) expanded on this classificatory system, to include typical hammerstone flakes (Group 3), resembling knapping hammerstone unintentional detachments which possess a convex ventral surface with no clear impact point, and angular fragments detached spontaneously from an inactive region of the hammer or anvil (Group 4). In addition to these classifications, artefacts smaller than 20 mm in maximum dimensions that exhibited no clear percussive damage were classified as small debris (Group 5).

### 3.3. Refit analysis

A total of 471 artefacts underwent 40 h of refitting. All artefacts were subjected to refit analysis, using a raw material grouping as well as coordinate grouping. Initially artefacts from each anvil were grouped, followed by the grouping of all artefacts of each raw material. The vertical distance between refits may reflect a degree of time depth. As precise coordinates for each artefact are not available, the only way to assess vertical refit distance is through the variation in spits for each refit. Mercader et al. (2002) report that each spit was arbitrarily defined as 3 cm thick, with a total of six spits being excavated, as well as material being collected from the sub-surface.

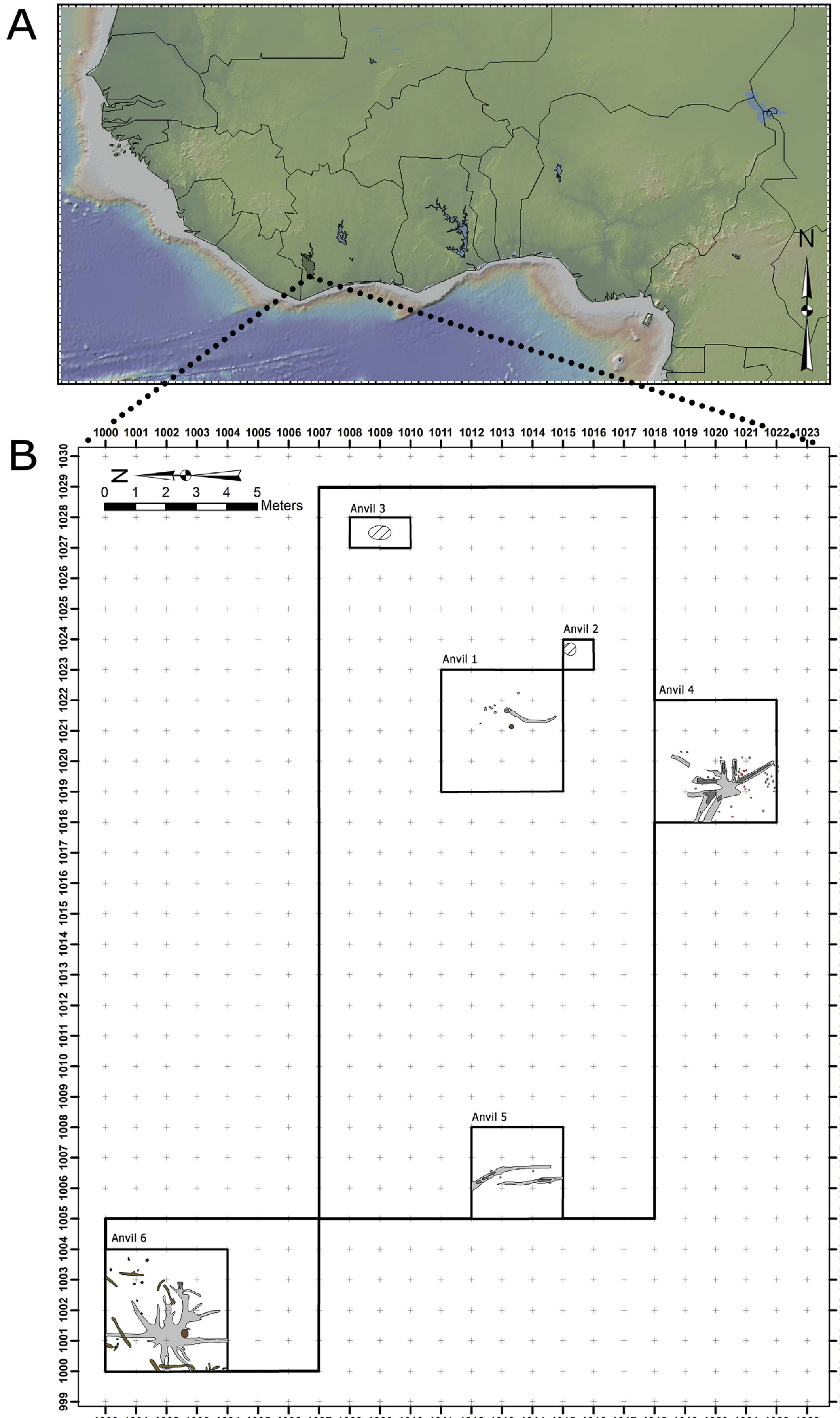


**Figure 1.** (A) Location map of Panda 100 (P100) site. (B) Excavation and refit map of P100 lithic assemblage (adapted from Mercader et al., 2002).

**Table 1**
Uncalibrated and calibrated radiocarbon ages from the Panda 100 site (Mercader et al., 2007), calibrated using OxCal 4.2 and the IntCal13 curve.

| Sample[a] | $\delta^{13}$C % | $^{14}$C age BP | Years BP (68.2%)[b] | Years BP (95.4%)[b] |
|---|---|---|---|---|
| Beta-172916 | −27.6 | 2330 ± 40 | 2420–2311 | 2485–2182 |
| Beta-164876 | −27.9 | 2440 ± 40 | 2684–2364 | 2705–2721 |
| Beta-164877 | −27.2 | 2440 ± 40 | 2684–2364 | 2705–2721 |
| Beta-172913 | −26.8 | 3750 ± 40 | 4218–3999 | 4235–3984 |
| Beta-164879 | −25 | 4280 ± 40 | 4871–4827 | 4966–4711 |

[a] Sample depths below the site surface are not provided in the original publication.
[b] 68.2% and 95.4% probability intervals.

An original refit study by Mercader et al. (2002) documented movement of artefacts at P100 over a distance of 0.05–1.6 m. To determine horizontal distance between refits, the original excavation hand drawn artefact maps were digitized using ArcMap and georeferenced to an internally coherent coordinate system (SOM S2). In most cases refitted pieces were correlated to drawn artefacts in the original notes, however, in a few cases ($n = 5$) either no artefacts or a single artefact in the refit set could not be identified in the original notes. To determine distance between refitted pieces, where possible, exact measurements were taken using ArcMap, however, where no correlation with hand drawn notes was possible, distance was calculated by taking the measurements from the center of associated grid references (we have distinguished between these two methods of measurement in Table 4). It is important to note that the distances reported in this study must be considered as minimum transportation distances, as hammerstone movement by chimpanzees is well documented by direct observation, and may consist of numerous individual transport events (Boesch and Boesch, 1984a; Luncz et al., 2016). In addition to horizontal measurements, the vertical distance between refitted pieces was calculated from spit designations.

**Table 2**
Absolute and relative frequency of technological artefact types for each raw material at Panda 100.

| | Diorite | | Granitoid | | Laterite | | Quartzite | | Total Assemblage | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | % | *n* | % | *n* | % | *n* | % | *n* | % |
| Group 1.1 | 1 | 11.1 | 13 | 3.5 | 0 | 0.0 | 0 | 0.0 | 14 | 3.0 |
| Group 1.2 | 3 | 33.3 | 25 | 6.6 | 1 | 1.3 | 0 | 0.0 | 29 | 6.2 |
| Group 2.1 | 0 | 0.0 | 1 | 0.3 | 0 | 0.0 | 1 | 16.7 | 2 | 0.4 |
| Group 2.2 | 0 | 0.0 | 26 | 6.9 | 7 | 8.8 | 0 | 0.0 | 33 | 7.0 |
| Group 2.3 | 1 | 11.1 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 1 | 0.2 |
| Group 3 | 3 | 33.3 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 3 | 0.6 |
| Group 4 | 0 | 0.0 | 18 | 4.8 | 7 | 8.8 | 0 | 0.0 | 25 | 5.3 |
| Group 5 | 1 | 11.1 | 293 | 77.9 | 65 | 81.3 | 5 | 83.3 | 364 | 77.3 |
| **Total** | **9** | **1.9** | **376** | **79.8** | **80** | **17.0** | **6** | **1.3** | **471** | **100** |

**Table 3**
Dimensional data for each percussive technological category at Panda 100.

| | | Diorite | | | | Granitoid | | | | Laterite | | | | Quartzite | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Min | Max | Mean | St. Dev | Min | Max | Mean | St. Dev | Min | Max | Mean | St. Dev | Min | Max | Mean | St. Dev |
| Group 1.1 | Length (mm) | 34.6 | 34.6 | 34.6 | – | 24.1 | 64.4 | 41.0 | 13.5 | – | – | – | – | | – | – | – |
| | Width (mm) | 15.9 | 15.9 | 15.9 | – | 17.5 | 53.3 | 31.9 | 11.1 | – | – | – | – | – | – | – | – |
| | Thickness (mm) | 9.0 | 9.0 | 9.0 | – | 11.0 | 49.9 | 26.4 | 10.9 | – | – | – | – | – | – | – | – |
| | Weight (g) | 7.8 | 7.8 | 7.8 | – | 5.3 | 108.4 | 38.5 | 34.8 | – | – | – | – | – | – | – | – |
| Group 1.2 | Length (mm) | 42.9 | 112.5 | 67.8 | 38.8 | 23.5 | 83.9 | 47.3 | 16.9 | 93.4 | 93.4 | 93.4 | – | – | – | – | – |
| | Width (mm) | 19.0 | 82.6 | 42.9 | 34.6 | 18.3 | 74.1 | 35.0 | 13.3 | 52.1 | 52.1 | 52.1 | – | – | – | – | – |
| | Thickness (mm) | 16.0 | 46.8 | 26.5 | 17.6 | 12.7 | 42.7 | 23.6 | 7.6 | 50.1 | 50.1 | 50.1 | – | – | – | – | – |
| | Weight (g) | 18.4 | 303.3 | 116.0 | 162.3 | 7.6 | 200.9 | 47.2 | 46.2 | 322.9 | 322.9 | 322.9 | – | – | – | – | – |
| Group 2.1 | Length (mm) | – | – | – | – | 36.8 | 36.8 | 36.8 | – | – | – | – | – | 77.0 | 77.0 | 77.0 | – |
| | Width (mm) | – | – | – | – | 26.3 | 26.3 | 26.3 | – | – | – | – | – | 44.9 | 44.9 | 44.9 | – |
| | Thickness (mm) | – | – | – | – | 16.9 | 16.9 | 16.9 | – | – | – | – | – | 31.4 | 31.4 | 31.4 | – |
| | Weight (g) | – | – | – | – | 16.0 | 16.0 | 16.0 | – | – | – | – | – | 124.9 | 124.9 | 124.9 | – |
| Group 2.2 | Length (mm) | – | – | – | – | 20.2 | 79.1 | 33.1 | 14.2 | 25.4 | 77.6 | 50.5 | 20.2 | – | – | – | – |
| | Width (mm) | – | – | – | – | 12.3 | 61.3 | 24.6 | 12.2 | 15.2 | 64.6 | 38.4 | 20.3 | – | – | – | – |
| | Thickness (mm) | – | – | – | – | 6.9 | 35.9 | 17.2 | 7.0 | 12.2 | 55.3 | 30.1 | 17.0 | – | – | – | – |
| | Weight (g) | – | – | – | – | 2.3 | 159.6 | 23.1 | 39.0 | 2.8 | 217.9 | 85.0 | 88.8 | – | – | – | – |
| Group .3 | Length (mm) | 39.2 | 39.2 | 39.2 | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | Width (mm) | 28.8 | 28.8 | 28.8 | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | Thickness (mm) | 8.9 | 8.9 | 8.9 | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | Weight (g) | 8.6 | 8.6 | 8.6 | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Group 3 | Length (mm) | 27.2 | 49.7 | 36.4 | 11.8 | – | – | – | – | – | – | – | – | – | – | – | – |
| | Width (mm) | 14.0 | 44.2 | 27.5 | 15.4 | – | – | – | – | – | – | – | – | – | – | – | – |
| | Thickness (mm) | 6.3 | 15.8 | 10.0 | 5.1 | – | – | – | – | – | – | – | – | – | – | – | – |
| | Weight (g) | 3.2 | 33.4 | 14.2 | 16.7 | – | – | – | – | – | – | – | – | – | – | – | – |
| Group 4 | Length (mm) | – | – | – | – | 12.5 | 67.7 | 25.3 | 12.5 | 17.1 | 58.6 | 39.1 | 14.0 | – | – | – | – |
| | Width (mm) | – | – | – | – | 9.6 | 60.1 | 19.2 | 11.2 | 15.8 | 43.6 | 32.7 | 10.1 | – | – | – | – |
| | Thickness (mm) | – | – | – | – | 4.9 | 31.5 | 12.4 | 5.7 | 6.5 | 27.5 | 19.4 | 8.0 | – | – | – | – |
| | Weight (g) | – | – | – | – | .8 | 117.5 | 10.8 | 26.8 | 2.1 | 48.6 | 25.9 | 18.2 | – | – | – | – |
| Group 5 | Length (mm) | 14.9 | 14.9 | 14.9 | – | 2.9 | 23.9 | 9.6 | 3.9 | 3.9 | 29.0 | 10.1 | 4.2 | 4.6 | 10.7 | 7.1 | 2.7 |
| | Width (mm) | 11.8 | 11.8 | 11.8 | – | 1.2 | 19.3 | 7.2 | 2.9 | 2.6 | 15.3 | 7.2 | 3.2 | 3.4 | 7.7 | 5.6 | 1.8 |
| | Thickness (mm) | 4.7 | 4.7 | 4.7 | – | 1.1 | 13.5 | 5.1 | 2.1 | 1.5 | 11.7 | 4.7 | 2.4 | 2.1 | 7.3 | 4.6 | 2.3 |
| | Weight (g) | .8 | .8 | .8 | – | .1 | 4.9 | .5 | .7 | .1 | 4.3 | .5 | .8 | .1 | .9 | .4 | .4 |

### 3.4. Microscopic analysis

All lithic artefacts >20 mm in maximum dimension were macroscopically screened for evidence of percussive damage. Potentially damaged areas were analyzed using a low-powered magnification (<100×) using a Leica S9APO stereo microscope equipped with a 1–8x objective lenses and a 10x eyepiece. Microscopic photographs were taken using a 3.1Mp EC3 digital microscope camera. Characterization of use-wear damage followed the criteria of Adams et al. (2009), which has been successfully applied to other primate battered lithics (Arroyo, 2015; Arroyo and de la Torre, 2016).

## 4. Results

### 4.1. Technological analysis

4.1.1. General frequencies The available lithic assemblage from Panda 100 consists of 473 artefacts, from five raw materials including granitoid ($n = 376$, 79.8%), laterite ($n = 80$, 17.0%), diorite ($n = 9$, 1.9%), quartzite ($n = 6$, 1.3%) (Table 2). Two pieces of weathered clast have been omitted from the following technological analysis as they are not mentioned in the original P100 report, may have entered the archaeological record through natural processes, and are not likely to have been utilized by chimpanzees as nut cracking hammerstones. In addition to this, all feldspar artefacts (originally reported as coming solely from Anvil 4), a single quartzite and a single diorite piece reported by Mercader et al. (2002) were not identified in this study, a mismatch of eight artefacts, resulting in a total assemblage of 471 artefacts.

The majority of the lithic assemblage is small debris ($n = 364$, 77.3%), angular chunks ($n = 34$, 7.2%) and angular fragments ($n = 25$, 5.3%). Techno-typological categories more frequently associated with percussive behavior in the archaeological record are represented in low frequencies, such as corner fragments ($n = 30$, 6.4%), edge fragments ($n = 14$, 3%), and typical hammerstone flakes ($n = 3$, 0.6%). Only one piece (0.2%) in the assemblage possesses a morphological similarity to detached flakes (Table 2).

4.1.2. Quartzite assemblage Six quartzite artefacts were recovered from the P100 excavations, two from the vicinity of Anvil 4, two from Anvil 3 and one each from Anvils 5 and 6. The quartzite is coarse-grained, however, it is relatively homogenous, with few internal fractures. Small debris makes up the majority of this sample ($n = 5$, 83.3%), with a mean length, width and thickness of 7.1 × 5.6 × 4.6 mm and a mean weight of 0.4 g (Table 3). The small debris does not show evidence of percussive damage, and as such may represent a background natural ‘noise’ of small quartzite fragments.

A single tabular quartzite edge fragment was also identified, measuring 77 × 44.9 × 31.4 mm and weighing 124.9 g (Table 3). This edge piece possesses a single impact point located on the intersection of a cortical horizontal plane and a newly fractured vertical plane. The fractured plane is clearly non-cortical and possesses sharp and fresh edges, indicating it to be a relatively recent breakage. Apart from the impact point that resulted in the fragmenting of the hammerstone, no repeated percussion marks are evident on either horizontal planes of the edge fragment. However, it has been shown that very little macro- and microscopic damage develops on quartzite during nut cracking activities (de la Torre et al., 2013), which may go some way to explaining the lack of visible percussive damage, coupled with the fact that softer organic anvils were used at this site. The thickness of this piece (31.4 mm) suggests that the original hammerstone was probably relatively thin.

4.1.3. Diorite assemblage The eight diorite artefacts have a total weight of 407.7 g. Almost all were found around Anvil 4 ($n = 7$, 87.5%), with a single fragment from Anvil 1. The diorite artefacts include corner ($n = 3$, 33.3%) and edge fragments ($n = 1$, 11.1%), typical hammerstone flakes (Group 3) ($n = 3$, 33.3%), a conchoidally fractured piece or positive base ($n = 1$, 11.1%), and a single piece of small debris (11.1%). Compared to the dominant granitoid raw material at P100, the diorite is relatively homogenous in structure, with no visible internal fissures or fractures and a fine-grained texture. The higher quality of this raw material helps explain the high percentages of fractured diorite pieces as opposed to angular chunks and small debris.

The single diorite edge fragment measures 34.6 × 15.9 × 9 mm (maximum dimensions) and weighs 7.8 g (Table 3), however when orientated technologically this fragment is relatively wide and thin in morphology (15.6 × 33.8 mm). All diorite corner fragments retain a portion of the active percussive plane, indicating that this surface was flat and cortical (Fig. 2B). In addition, Refit Set 2 (see below) is a distal fragmentation of a corner piece that retains both the active percussive plane and the opposed plane (Plane A2) suggesting that the diorite hammer had a tabular morphology. Coupled with the presence of typical hammerstone flakes (see below), two distinct morphologies of diorite hammerstone were used, tabular blocks and rounded cobbles. The majority of diorite percussive fragments possess a cortical dorsal surface, with only a single example possessing a fully non-cortical dorsal surface. This finding suggests that repeated fragmentation of individual diorite hammerstones was a rare occurrence.

Of particular interest amongst the diorite artefacts is the singular piece that resembles, morphologically, a percussive flake (Fig. 3). This piece possesses a clear non-cortical striking platform, although no distinct impact points are visible. The striking platform is relatively large, measuring 7.5 × 16.5 mm with a flat morphology. The flake possesses clearly delimitated dorsal and ventral surfaces and a diffuse bulb of percussion. The dorsal surface is >50% cortical, however it also retains evidence of three previous unidirectional, small dorsal removals. However, it is impossible to identify whether these removals were flake detachments or merely evidence of previous fragmentation.

Three of the diorite fragments can be considered stereotypical hammerstone detachments, two complete and one fragmented (Fig. 3). These possess convex cortical dorsal surfaces with highly concave ventral surfaces. No clear impact point is present and none possesses an area that could be considered a striking platform.

4.1.4. Laterite assemblage Eighty laterite fragments, weighting a total of 1131.9 g, were found at P100. Most of these are either small debris ($n = 65$, 81.3%) or angular chunks and fragments (Group 2.2 and Group 4) ($n = 14$, 17.6%), along with a corner fragment ($n = 1$, 1.3%), with no clear evidence of percussive behavior other than their fragmented state. Of note, the single corner fragment and an angular chunk were found to refit (Refit Set 9), which provides the only potential evidence of percussive behaviorr for this material and is described in detail below. A second refit (Refit Set 1) records the fracturing of a small laterite cobble. It is likely this was not used for successful *Panda* nut percussion, however, it may have been used by a juvenile (Boesch and Boesch, 1984b). The lack of macroscopic percussive damage on the majority of laterite artefacts does not in itself necessarily preclude laterite being used in percussive behavior. Their close association with organic anvils and nut shells, coupled with the fact that chimpanzees in Taï have been known to use this raw material, all increase the possibility of a percussive origin for these artefacts. However, based purely on percussive damage evidence in the P100 archaeological context this raw material would not be attributed to percussive behavior. These laterite pieces represent the fragmentation or splitting of relatively small cobbles, and they do not share the same morphology as detached corner fragments from a larger tabular block, as is seen with the diorite hammerstones.

4.1.5. Granitoid assemblage The 376 granitoid artefacts make up the majority of the P100 lithic assemblage. The P100 granitoid is quartz rich, consisting of quartz crystals in a groundmass dominated by small feldspars. Its internal structure has major fractures and fissures directly associated with regions of interior foliation that often grade into a highly irregular, coarse-grained internal structure.

The majority of the granitoid pieces are small debris ($n = 293$, 77.9%) (Fig. 2) with mean dimensions of 9.6 × 7.2 × 5.1 mm and a mean weight of 0.5 g (Table 3). The second most prevalent artefact types are angular chunks and angular fragments (including Groups 2.1, 2.2 and Group 4) ($n = 45$, 12%); these show no evidence of percussive damage but their highly fragmented state suggests a percussive origin. Of the identifiable percussive techno-morphological categories, corner fragments are the most frequent ($n = 25$, 6.6%), followed by edge fragments ($n = 13$, 3.5%). The presence of these technological morpho-types within the assemblage represents archaeologically visible evidence of percussive behavior, and in a number of cases these artefacts possess direct evidence of percussive impact.

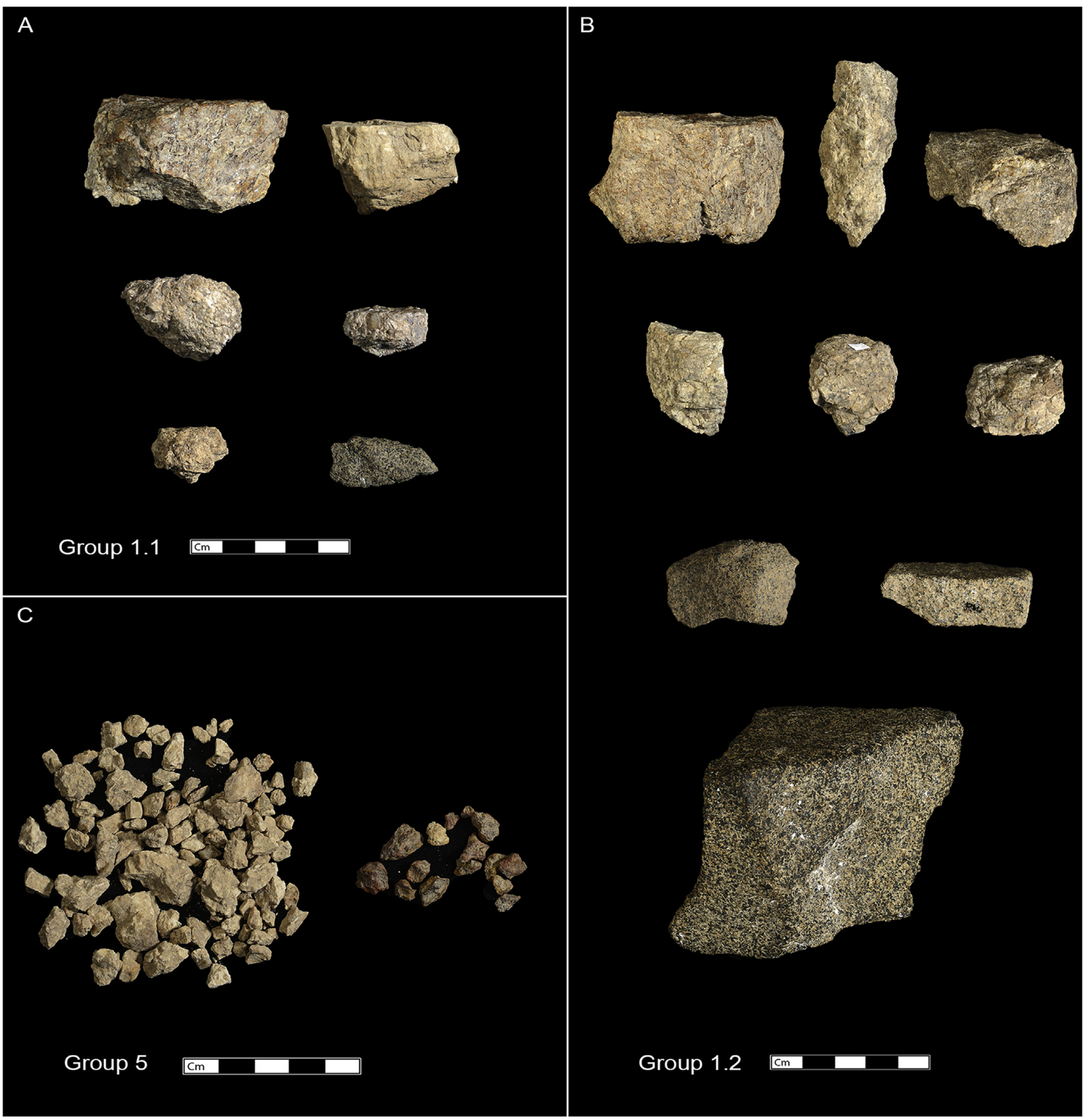


**Figure 2.** Examples of detached percussive products from lithic hammerstones at P100. A) Granitoid and diorite edge pieces (Group 1.1). B) Granitoid and diorite corner fragments (Group 1.2). C) Examples of granitoid and laterite small debris (<20 mm) (Group 5) (Scale = 5 cm).

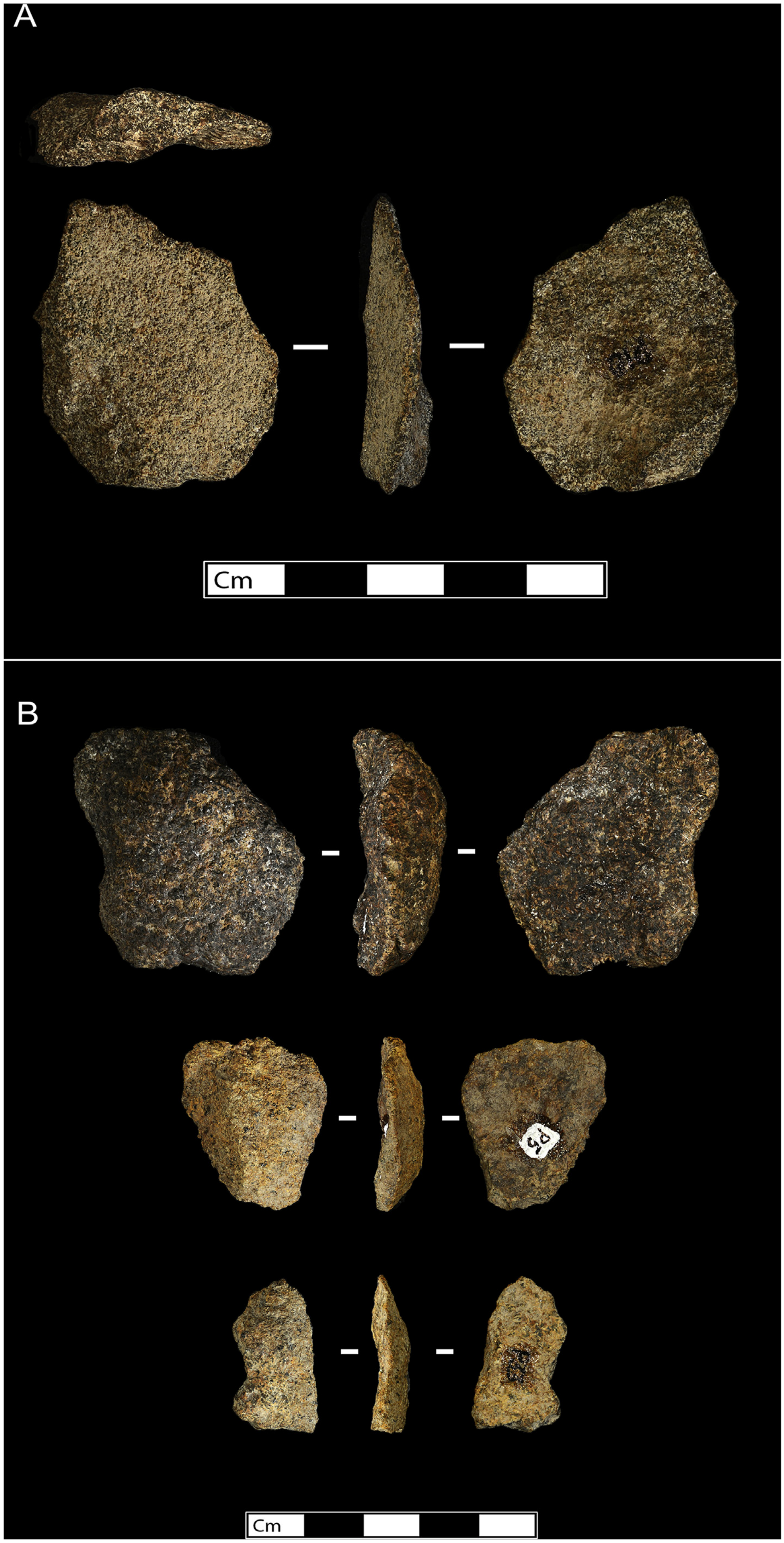


**Figure 3.** Examples of detached percussive artefacts from lithic hammerstones at P100. A) Detached diorite conchoidal flake (Group 2.3). B) Detached diorite typical hammerstone flakes (Group 3) (Scale = 5 cm).

**Table 4**
Refits identified in the current study of the Panda 100 lithic assemblage.

| Refit set | Raw material | Number of pieces | Piece numbers | Technological categories | Grid reference | Total horizontal distance (m) | Spit range |
|---|---|---|---|---|---|---|---|
| 1 | Laterite | 2 | P15 | 2.2 | R9 | 0.21 | 1–2 |
| | | | P16 | 2.2 | R9 | | |
| 2 | Diorite | 2 | P25 | 1.2 | S10 | 1–2* | 0–1 |
| | | | P7 | 1.1 | R11 | | |
| 3 | Granitoid | 4 | P28 | 1.2 | S10 | 9.54[a] | 1–2 |
| | | | P29 | 1.1 | S10 | | |
| | | | P39 | 1.1 | K7 | | |
| | | | P47 | 1.2 | K8 | | |
| 4 | Granitoid | 2 | P40 | 1.2 | K7 | 1–2* | 3 |
| | | | P53 | 1.1 | K8 | | |
| 5 | Granitoid | 2 | P18 | 2.2 | S10 | 1.27 | 0–1 |
| | | | P42 | 2.2 | R11 | | |
| 6 | Granitoid | 3 | P48 | 1.2 | T10 | 0.26 | 0 |
| | | | P52 | 1.2 | T10 | | |
| | | | P97 | 2.2 | T10 | | |
| 7 | Granitoid | 4 | P12 | 1.2 | S10 | 1.34 | 0–1 |
| | | | P30 | 1.1 | T10 | | |
| | | | P32 | 1.2 | ? | | |
| | | | P45 | 1.2 | S10 | | |
| 8 | Granitoid | 2 | P49 | 1.2 | T10 | 0.83 | 0 |
| | | | P51 | 1.1 | S10 | | |
| 9 | Laterite | 2 | P21 | 1.2 | N6 | 17.12[a] | 1 |
| | | | P33 | 2.2 | L23 | | |
| 10 | Granitoid | 5 | P6 | 1.1 | R10 | 16.59[a] | 0–1 |
| | | | P9 | 1.2 | K24 | | |
| | | | P22 | 2.2 | T10 | | |
| | | | P27 | 1.2 | R10 | | |
| | | | P56 | 4 | S10 | | |
| 11 | Granitoid | 2 | P1 | 1.2 | T10 | – | – |
| | | | P11 | 1.2 | ? | | |
| 12 | Granitoid | 5 | P24 | 1.1 | L8 | 1.49 | 1–3 |
| | | | P41 | 1.1 | K8 | | |
| | | | P58 | 2.2 | K8 | | |
| | | | P65 | 2.2 | K8 | | |
| | | | P88 | 4 | K8 | | |

*No direct measurement possible for entire refit sequence, distance was estimated based on grid reference.
[a] No direct measurement possible for a single piece in refit set, distance was estimated based on grid reference.

The corner fragments possess mean maximum measurements of 47.3 × 35 × 23.6 mm and a mean weight of 47.2 g (Table 3). When orientated technologically, however, they possess a mean length and width of 35.2 × 37.8 mm, presenting a roughly cuboid morphology. The preserved portion of the active percussive plane (platform) was identifiable in 92% ($n = 23$) of all corner fragments. The majority possessed cortical platforms ($n = 19$, 76%), however, a small number also possessed fully non-cortical platforms ($n = 3$, 12%). These platforms were relatively large (average length and width: 25.3 × 17.6 mm) and flat. Granitoid corner fragments possess relatively large external (mean = 122.7°) and interior (mean = 102.5°) platform angles, highlighting the forceful nature of their detachment. Corner fragments possessed either flat ($n = 13$, 52%) or irregular ($n = 10$, 40%) ventral surface morphologies, with only a very small proportion possessing concave morphologies. Dorsal surfaces were primarily >50% cortical (>50–100% cortex coverage) ($n = 21$, 84%), with only a few examples possessing <50% cortex coverage ($n = 4$, 16%) (Fig. 2). Only 12% ($n = 3$) possessed dorsal surface detachments, suggesting that corner fragment detachment often occurred as an initial breakage of the hammerstone. These fragments also typically possessed either a triangular ($n = 14$, 56%) or trapezoid ($n = 9$, 36%) transversal cross section.

Granitoid edge fragments possess mean maximum measurements of 41 × 31.9 × 26.4 mm and a mean weight of 38.5 g (Table 3). However, when technologically orientated they measure on average 28.6 × 32.5 mm, making them relatively wide and short in morphology. Almost all possess a fully cortical ($n = 12$, 92.3%) striking platform or the remnants of the active percussive plane, with only one example (7.7%) possessing a non-cortical platform. The platforms are relatively substantial and rectilinear in morphology, possessing a mean length and width of 28.2 × 21.4 mm. Edge fragments possessed a mean exterior platform angle of 117.7° and a mean interior platform angle of 98.5°. The dorsal surfaces of these fragments, representing the outer plane of the hammerstone, possess either triangular ($n = 5$, 38.5%) or trapezoid ($n = 8$, 61.5%) transversal cross section, and are rarely fully cortical ($n = 1$, 7.7%) or non-cortical ($n = 1$, 7.7%), possessing either >50% ($n = 7$, 53.8%) or <50% cortex coverage ($n = 4$, 30.8%) (Fig. 2). The presence of non-cortical regions on the dorsal surface, coupled with the identification of single dorsal extractions on four (30.8%) pieces, suggests that there is a repeated nature to the edge fragmentation of the P100 granitoid hammerstones.

### 4.2. Refit analysis

The original Panda 100 publication reported seven refit sets, totalling 16 refitted artefacts, and comprizing three raw materials: granitoid, laterite and diorite (Mercader et al., 2002). These refits revealed a maximum horizontal movement of 1.6 m and were identified at two of the six excavated anvil locations, Anvils 1 and 4. The original report did not identify the artefacts that contributed to these refit sets, with only one refit being identified via an illustration (Mercader et al., 2002, Fig. 2E). No technological analysis of the refitted material was presented.

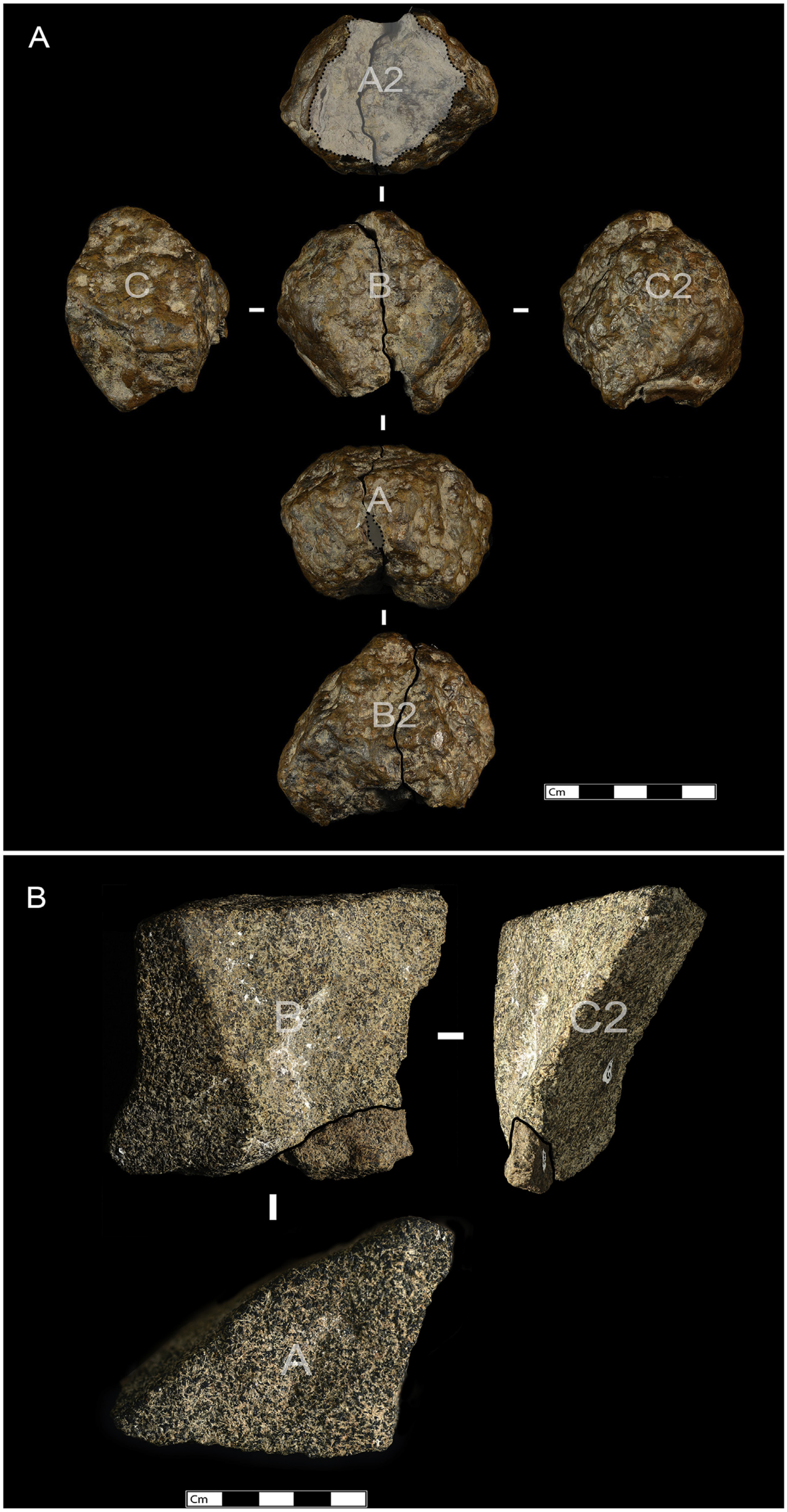


**Figure 4.** Refit Sets 1 and 2 from Panda 100. A) Refit Set 1: Two laterite angular chunks. B) Refit Set 2: Distally fractured, detached corner fragment of a diorite hammerstone (Scale = 5 cm).

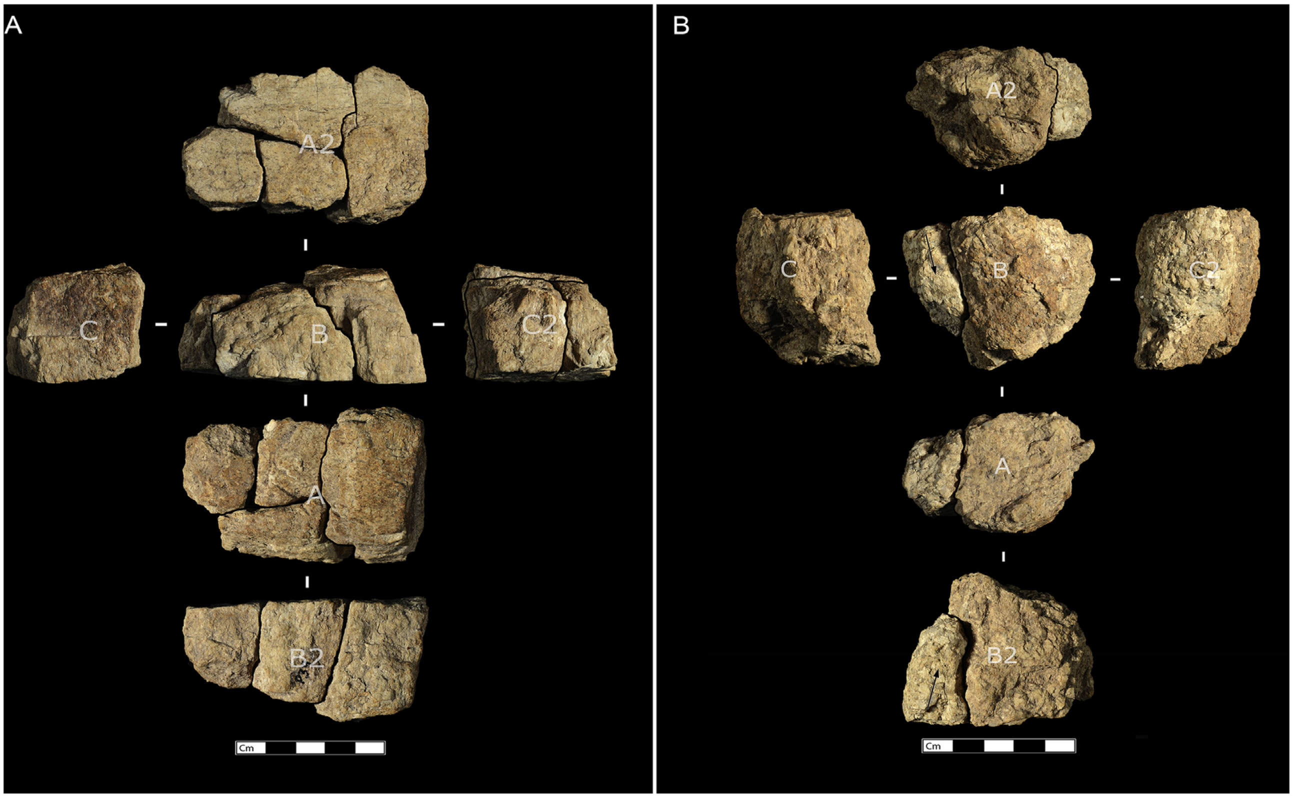


**Figure 5.** Refit Sets 3 and 4 from Panda 100. A) Refit Set 3: Four granitoid fragments, two edge fragments and two corner fragments. B) Refit Set 4: Two granitoid fragments representing a corner region of a hammerstone (Scale = 5 cm).

Our updated refit analysis of the Panda 100 lithic assemblage substantially increases the number of refits, and provides a detailed technological analysis of each refit set (SOM S3). A total of 35 artefacts were refitted (7.43% of the entire assemblage), increasing the total number of refit sets from seven to twelve (Table 4). Other than the illustrated example in Mercader et al. (2002), we do not know which of the refits identified in this study overlap with the ones described in the original report. The increased number of refit sets does, however, permit a number of new insights. First, refits are now represented at four separate anvil locations: while the majority are located within the vicinity of Anvil 4, refits are also identified at Anvils 1, 2, and 5. Second, three of the refit sets represent movement of hammerstones between anvil locations, with refitted fragments being identified between Anvil 4 and Anvils 1 and 5 as well as between Anvils 2 and 5.

The refits illustrate how hammerstones fragment during *Panda* nut cracking behavior (Figs. 4–8). The majority of the large fractures result from detachment of corner and edge fragments, often in tandem, with these pieces being detached consecutively or simultaneously. It is, however, possible to identify two primary fragmentation sequences within the P100 refits. The first sequence consists of small, non-invasive removals that detach a small portion of the intersection between the horizontal active plane and the vertical planes. This type of hammerstone fragmentation results in an increasingly rounded morphology of the hammerstone edges. The second fragmentation sequence is a more invasive 'slicing' of the hammerstone, whereby a large corner or edge fragment that retains remnants of both the active percussive surface, as well as the opposing plane of the hammerstone, is detached. This process results in a rapid loss of the volume of the hammerstone. Both of these fragmentation sequences are represented within the refit assemblage independently, as well as associated with each other in single refits sets. Furthermore, corner fragments appear to result from initial fragmentation of the hammerstone, followed either simultaneously or soon afterwards by detachments of short and wide edge fragments.

4.2.1. Spatial analysis: refitted data Just under half of the P100 refit sets ($n = 5$, 41%) are formed of pieces from two neighboring meter squares at the site, and therefore represent a horizontal movement of 1–2 m. A smaller number come from the fragmentation of a hammerstone within a single meter ($n = 3$, 25%), or a horizontal movement of <1 m. However, three (25%) refit sets record more substantial horizontal movement and inter-anvil transportation of hammerstones. In one instance, the hammerstone was transported 9.54 m between successive breakage events, and in two instances refitting pieces were found 16–17 m apart (Figs. 9 and 10).

Four refits (33%) record hammerstones that were likely broken at a single point in time, with examples found within the subsurface level and Spits 1 and 3, respectively. Another four refits were found between the subsurface level and Spit 1, with a further two (17%) examples being identified between Spits 1 and 2, representing a maximum vertical movement of 6 cm. A single refit (8%) was formed of pieces found in Spits 1–3, representing a maximum vertical movement of 9 cm. This vertical movement may be a result of an undulating original ground surface and, given that all pieces of this refit were found within an area of ~1 $m^2$, may represent a single hammerstone fragmentation.

### 4.3. Microscopic analysis

Microscopic damage was identified on 13 fragmented pieces (Table 5). Most of these were corner fragments ($n$ = 9, 69.2%), however, edge fragments ($n$ = 4, 30.8%) are also represented (Table 5). Granitoid is the prevalent raw material, making up eight of the 13 pieces with macroscopic visible percussive damage, whereas only a single diorite artefact possessed visible macroscopic percussive wear.

Undamaged cortical granitoid surfaces are light brown with frequent, large, intact quartz crystals. The natural granitoid surface morphology is either flat and levelled (with the quartz crystals showing worn dulled surfaces) or, conversely, highly irregular (with protruding quartz crystals representing high points on the surface). Percussive damage on granitoid hammerstone fragments is generally sparsely located on the active percussive surface. The impacts are either located towards the center of the percussive plane or immediately on the edge where the percussive plane intersects one or more vertical outer planes.

At a macroscopic level, percussive damage can be identified as a differentiation in color when compared to the unaltered cortical surface. At a microscopic level, percussive damage on these pieces is characterized by crushing of individual grains, resulting in a compacted or compressed morphology located around a single impact point. This crushing and compaction results in a discoloration or frosting of the cortical surface to a distinct white. When impacts are located close to the edge they present a characteristic V-shape in plan, whereas, when located in the center of the active plane on a relatively flat surface, they are characterized by an irregular plan shape. When located along an intersecting edge, impacts may also be associated with either a single large step-terminating removal or a series of smaller crushed step fractures, where individual quartz crystals have either detached or fragmented. Whole quartz crystals may be detached from the granitoid matrix, leaving behind characteristic, deep depressions surrounded by an area of crushed and compacted matrix. These characteristics either occur individually or as combinations, and appear to be influenced by the density of quartz crystals within the granatoid matrix (Figs. 11 and 12).

Percussive damage on the single diorite artefact is superficial and only identifiable through macroscopic visual inspection by a slight depression and roughening of the cortical surface. Under the microscope, few identifiable characteristics can be clearly contrasted to the non-damaged cortical surfaces. Two small impact points and areas of crushing of the quartz crystals can be identified


**Figure 6.** Refit Set 5, 6 and 7 from Panda 100. A) Refit Set 5: Two angular chunks representing the edge of a granitoid hammerstone. B) Refit Set 6: Two corner fragments and one angular chunk representing a corner detachment of a granitoid hammer. C) Refit Set 7: Corner refit of a tabular granitoid hammerstone consisting of three corner fragments and one edge fragment (Scale = 5 cm).

within the wider depressed area, however, these are not clearly related to percussive damage.

The issue of identifying percussive damage on diorite fragments at P100 is further complicated by the larger corner fragment from Refit Set 2. Originally illustrated in Mercader et al. (2002, Fig. 2E), this piece possesses a small visible depression on its horizontal active plane (Plane A) measuring 26 × 15 mm in maximum dimensions. This has been interpreted as pitting (Mercader et al., 2002), however, it is a natural undulation of the cortical surface. The lack of significant microscopic percussive traces within the depressed region of the active plane indicates that this area was not formed through active use. This is not to suggest that this artefact, and indeed the associated refit set, is not derived through chimpanzee percussive action, only that the previously identified pitted feature is a natural depression within the surface morphology of the hammerstone (Fig. 12).

## 5. Discussion and conclusions

Panda 100 was the first site to be archaeologically excavated to recover non-hominin tools. However, the site has much to offer beyond its historical significance. It provides the highest resolution data available on how non-human animals create an archaeologically durable assemblage, giving new insights into how wild chimpanzee stone tools break and move during their use under natural conditions.

The P100 artefacts demonstrate that archaeologically recovered lithic assemblages at *Panda* nut-cracking sites may not directly reflect the actual hammers used by chimpanzees to crack nuts. Instead of complete hammers being present throughout, the sequence is dominated by small fragmentary pieces, none of which could be considered as a complete modern hammerstone. P100 therefore preserves and supports evidence for an important behavioral observation made at Taï, namely that hammerstones are routinely removed from a site when a *Panda* tree becomes unproductive or dies (Boesch and Boesch, 1984a; Luncz et al., 2016). The P100 archaeological record has a primate mediated behavioral bias against tool preservation, and towards stone pieces that could not in themselves be used to crack *Panda* nuts. Given that the evolution of chimpanzee stone technology likely encompasses at least tens of thousands of years (Haslam, 2014), with tool use potentially reaching into the millions of years (Panger et al., 2003), the correct interpretation of partial behavioral evidence at sites like P100 is critical for reconstructing that long-term record.

The raw materials excavated at the P100 site – granitoid, laterite, diorite and quartzite – accurately reflect the materials that primatologists have observed chimpanzees using for *Panda* processing in the Taï Forest (Boesch and Boesch, 1983). Other than laterite, these stones do not occur naturally in the immediate vicinity of the site (Mercader et al., 2002), demonstrating that they were transported by chimpanzees. This kind of transport, essentially provisioning the *Panda* tree while it fruits, has also been well

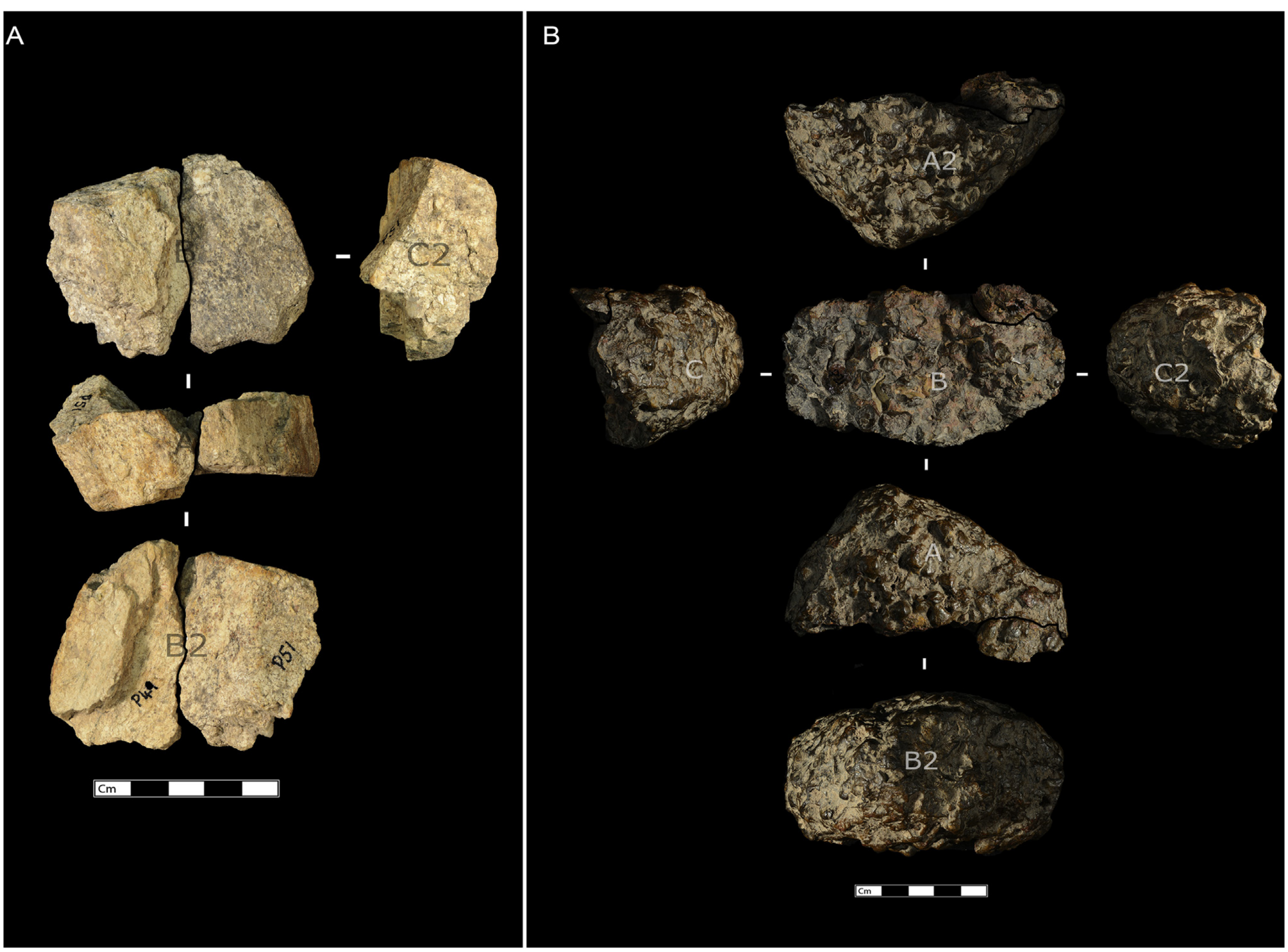


**Figure 7.** Refit Sets 8 and 9 from Panda 100. A) Refit Set 8: Edge fragment of a granitoid hammerstone consisting of one corner fragment and one edge fragment. B) Refit Set 9: Minor fragmentation of a laterite cobble (Scale = 5 cm).

documented at Taï (Boesch and Boesch, 1984a; Luncz et al., 2016). Currently, exact distances to the primary raw material sources within the national park can only be estimated (Luncz et al., 2016) and will require further raw material sourcing work (beyond the scope of this study) to correctly establish.

In themselves, therefore, the fragmented P100 artefacts permit reconstruction of such fundamental behavior as material selection and tool transport. From a primate archaeological perspective this is important as it allows the reconstruction (albeit at a low resolution) of primate behavior in antiquity. In addition, GIS mapping of artefacts to their grid reference shows that the highest concentrations of material are found within the immediate vicinity (<1 m) of anvils (Fig. 13).

Our technological analysis of the P100 artefacts is the most detailed yet performed for a wild chimpanzee lithic assemblage. It allows us to describe and interpret details of the unintentional reduction of stone tools by chimpanzee nut-cracking at a high resolution. This analysis found that two main fragmentation sequences dominate at P100, which may occur either independently, or concurrently. First, protruding corner regions of a hammerstone are removed through either direct impact or initiation of internal fracture planes. From behavioral observations, we know that such impacts are not deliberately aimed at the tool margins, but instead represent mis-hits or incidental blows, such as when the hammer contacts the anvil during nut-cracking (Boesch and Boesch-Achermann, 2000; Arroyo et al., 2016). Once corner elements are removed, edge fragments (the intersection of two planes) are then susceptible to breakage. These removals are non-invasive, and this process sequentially rounds the sharp edges and corners of an originally angular hammerstone, reducing its mass but not significantly reducing its overall size with each fragmentation event. This fragmentation may occur recurrently, as shown by non-cortical dorsal surfaces of detached edge fragments.

The second fragmentation sequence involves the wedging initiation or ‘slicing’ of tabular pieces, in which portions of both the active hammer surface and its opposing surface are removed at the same time. It occurs either because of excessive force used during the hammer strike (compared to the force required to simply

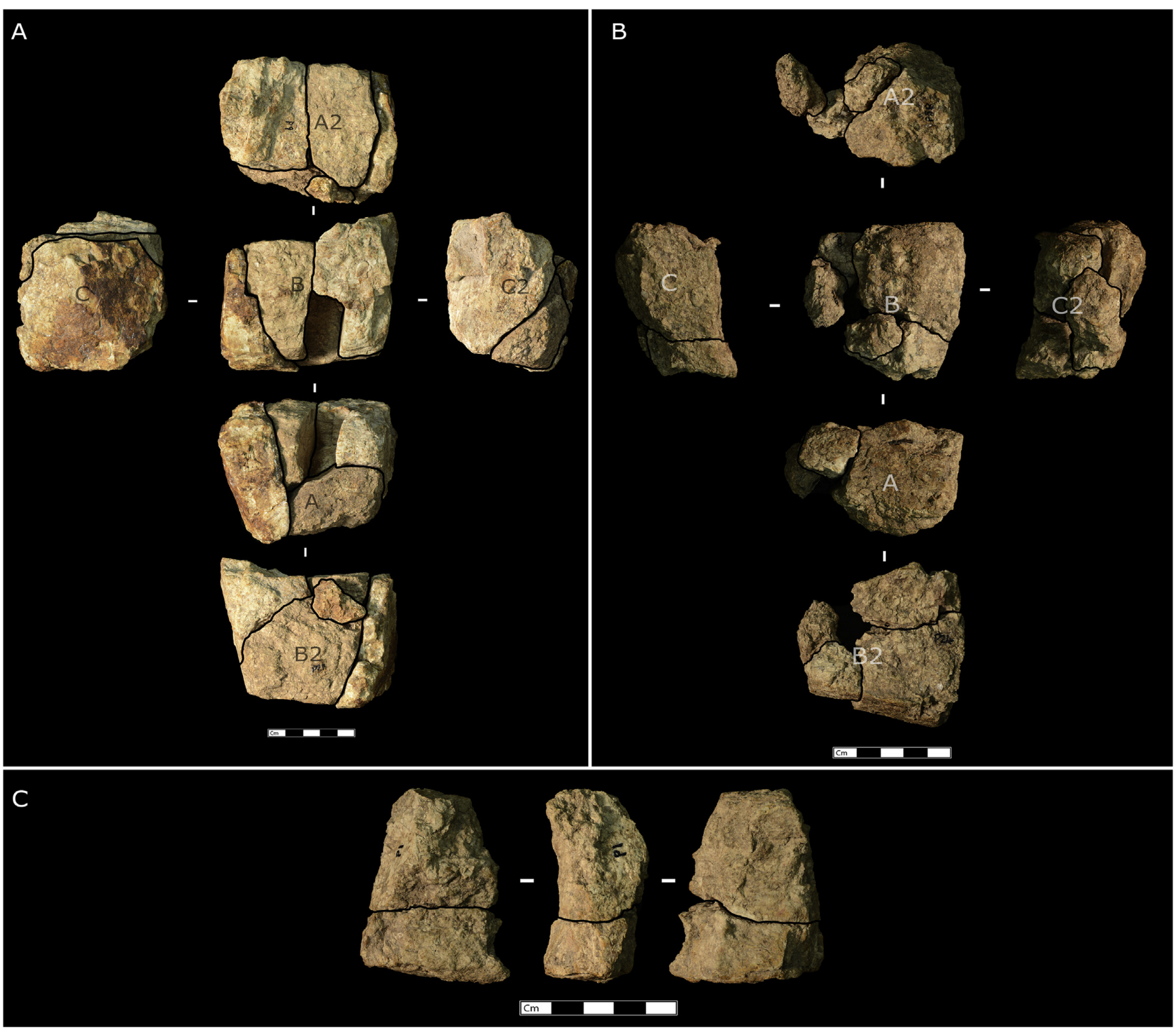


**Figure 8.** Refit Sets 10, 11, and 12 from Panda 100. A) Refit Set 10: Five granitoid fragments (three corner fragments, two angular chunks) representing an extensive fragmentation of a large hammerstone. B) Refit Set 12: Five granitoid fragments (two edge fragments, three angular chunks/fragments) of a larger hammerstone corner region. C) Refit Set 11: Edge fragment of a granitoid hammerstone consisting of one angular chunk and one edge fragment. (Scale = 5 cm).

remove a protruding corner or edge), or because of the presence of internal fracture planes. This process decreases both the mass and the size of a hammer, which, if continued, will reduce the stone to a form where it is no longer suitable for use as a *Panda* hammer. Further, this reduction sequence allows for an estimate of the original hammerstone thickness, because of the preservation of opposing hammer faces. Both of the main fragmentation sequences are present in the refit sets at P100, which means that they can be reconstructed in detail from the preserved archaeological evidence, even if direct observations were unavailable.

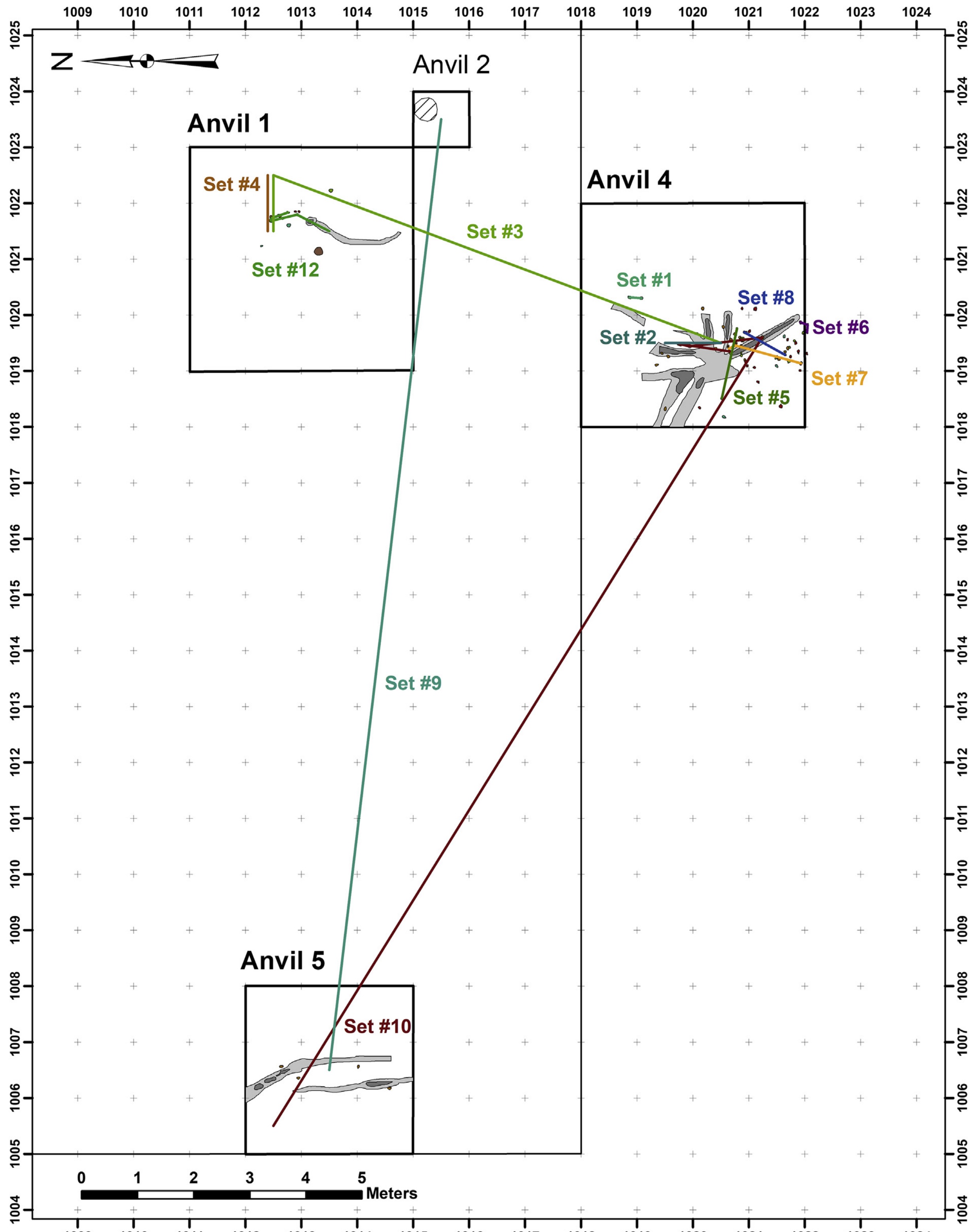


**Figure 9.** Spatial map of Panda 100 excavations highlighting all refit sets identified in this study.

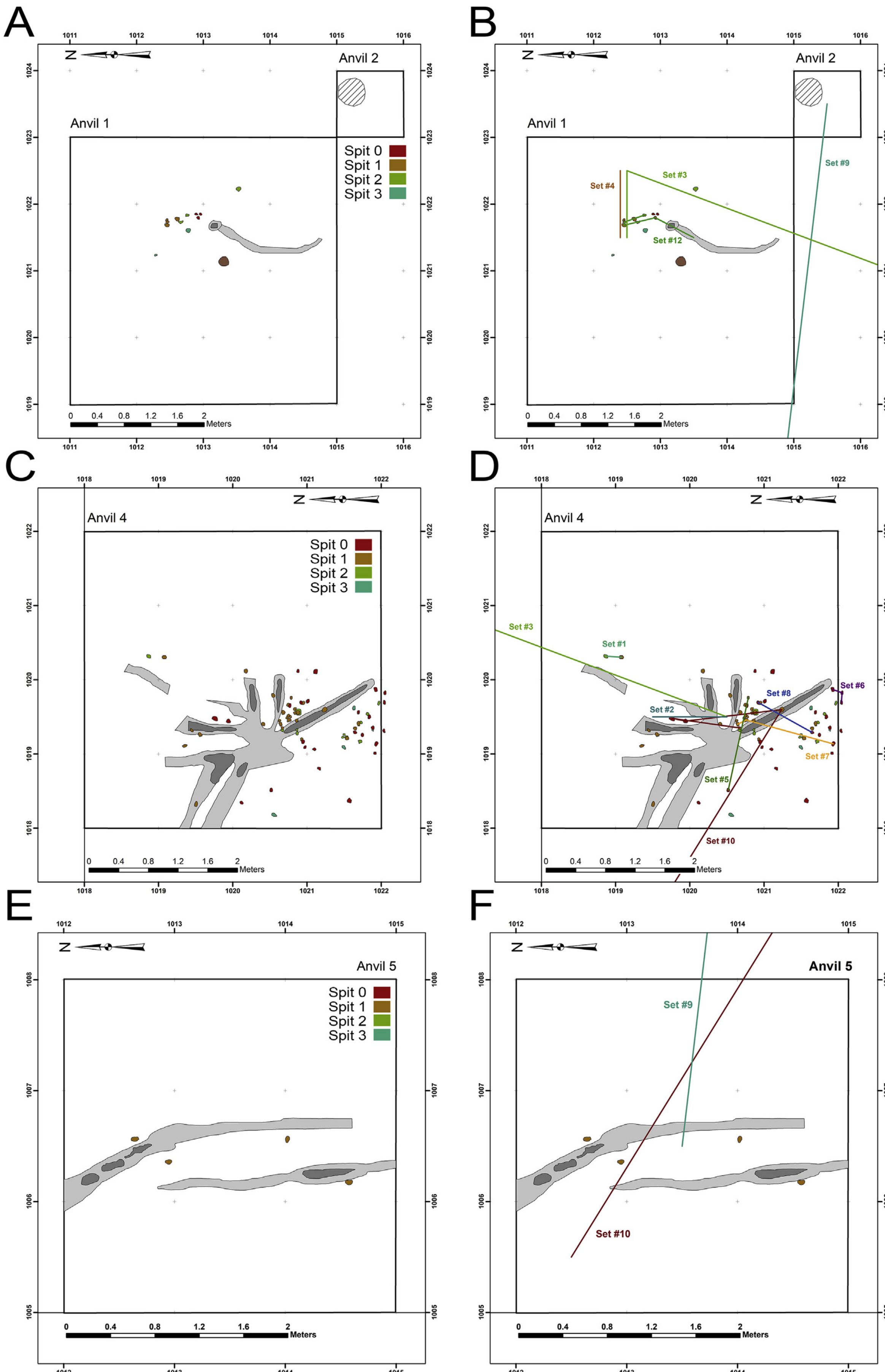


**Figure 10.** All mapped artefacts separated by spit with corresponding refit sets for each anvil location.

**Table 5**
Percussive damage identified on lithic artefacts from P100.

| Piece number | Raw material | Artefact category | Microscopic percussive damage |
|---|---|---|---|
| P13 | Granitoid | 1.2 | Crushing and levelling of individual crystals. The development of a frosted and irregular surface morphology. |
| P14 | Diorite | 1.2 | Isolated crushing and fracturing of individual quartz crystals. |
| P31 | Granitoid | 1.2 | Large area of intense crushing of quartz crystals and matrix. Development of large step scars and the detachment of individual crystals. |
| P37 | Granitoid | 1.2 | Small areas of crushing, and frosting of quartz crystals. Small step fractures within the crushed areas. |
| P38 | Granitoid | 1.2 | Crushing of quartz crystals and surrounding matrix. Detachment of individual crystals and the development of step scars. |
| P48 | Granitoid | 1.2 | V-shaped impact point in close association with intense crushing of quartz crystals. |
| P70 | Granitoid | 1.1 | V-shaped impact point. Intense crushing of quartz crystals and light crushing of matrix. Levelling of quartz crystals, resulting in an irregular surface morphology. |
| P80 | Granitoid | 1.2 | V-shaped impact point, associated with an area of crushing and levelling of quartz crystals. Detachment of individual crystals from the matrix, and the development of small step scars. |
| P91 | Granitoid | 1.2 | V-shaped impact points, associated with intense crushing of quartz crystals and matrix. Small step fractures. |
| P41 | Granitoid | 1.1 | Small area of crushed quartz crystals and matrix. |
| P24 | Granitoid | 1.1 | Isolated area of quartz crushing and slight pitting of the surface. |
| P39 | Granitoid | 1.1 | Small area of crushed quartz crystals and matrix. |
| P47 | Granitoid | 1.2 | Small area of crushed quartz crystals and matrix. |

As noted, the lack of complete hammerstones is the most striking feature of the P100 assemblage. This absence is remarkable considering that the assemblage consists of more than 400 artefacts, accumulated over a period of at least 21 years from a known *Panda* nut-cracking site. In some cases, usable hammers may have been completely fragmented, particularly if they were made of the more fragile granitoid and laterite materials. However, the extensive refitting efforts made in the current study, which almost doubled the number of known refits from P100, demonstrate that such a scenario is untenable for the large majority of recovered artefacts. The diorite assemblage is the most informative in this regard, as it is composed of a distinct and relatively fine-grained material that is easily recognized and allows for clear reconstruction of percussive activities – for example, the only conchoidal flake at P100 is a diorite piece. There are no diorite artefacts of sufficient size or mass to crack *Panda* nuts, which require hammerstones of 1–9 kg (Boesch and Boesch, 1983). The logical conclusion, therefore, is that any such tools have been moved offsite by the chimpanzees. Interestingly, at least part of this movement was completed by the chimpanzees in the relatively short five-year gap between the death of the *Panda* tree at P100 and its excavation. Furthermore, the exclusive recovery of small hammerstone fragments and the lack of complete or even substantial fragments of *Panda* nut hammerstones in the P100 record suggests that an exclusive focus on complete or broken hammerstones is not adequate when dealing with the behavioral prehistory of chimpanzee groups.

Chimpanzee tool transport is also recorded in the refit analysis. We have identified refitted pieces separated by 16–17 m at the time of excavation, representing the longest known instance of such movement in the excavated primate archaeological record. In addition, the present study found the first archaeological evidence of movement of a single hammerstone between two separate nut cracking locations. While this is unsurprising given the well-known chimpanzee transport of hammers in the Taï Forest (Boesch and Boesch, 1984a; Luncz et al., 2016), the fact that such behavior is preserved and recoverable from the primate archaeological record is promising for studies conducted at sites where animals are either unobserved or no longer present.

Wild chimpanzee hammerstone movement has been examined under experimental conditions by Carvalho et al. (2009) in Guinea. By observing and mapping the movement of hammerstones and portable anvils provided for the animals by human experimenters, it was shown that chimpanzee oil palm nut cracking hammerstones may undergo a number of different movement sequences within a local area (Carvalho et al., 2009). They noted, however, that the indirect record, i.e., the final resting place of a chimpanzee hammerstone, does not provide data on its previous use location(s). They suggest that hammerstone use-life can be better understood by using direct observational data derived from primatological studies. In contrast, the results of our current study show that sufficiently fine-grained archaeological data on hammerstone fragments, including spatial and technological analysis, offer a reliable additional means for reconstructing the minimum individual movements of a hammerstone within a chimpanzee nut cracking site. This finding has the potential to allow the tracing of diachronic behavioral variation through the primate archaeological record, including, potentially detailed hammerstone use sequences at a local and regional scale (Luncz et al., 2016). In addition, given sufficient sample size and differentiation between raw materials, it may be possible in future studies to identify a minimum number of hammerstones used at a given location.

In a wider context, since P100 was first published there have been excavations of stone tool activity areas for two more non-human primate species: Burmese long-tailed macaques (*Macaca fascicularis aurea)* in Thailand and bearded capuchin monkeys (*Sapajus libidinosus*) in Brazil (Proffitt et al., 2016; Haslam et al., 2016a, 2016b). Along with P100, these sites reveal a diversity of primate site formation processes, derived from both behavioral and environmental factors. For example, the rarity of suitable *Panda* hammerstones at Taï mirrors the situation for the wild capuchins at the Fazenda Boa Vista site (Visalberghi et al., 2009). In both cases, heavy but scarce hammers are required to crack tough nuts, and these hammers are not left at abandoned sites for a sufficient length of time to readily enter the archaeological record (Visalberghi et al., 2013). In contrast, wild capuchins at Serra da Capivara National Park (SCNP) (Haslam et al., 2016b) and wild macaques at Laem Son National Park (Haslam et al., 2016a) have abundant material suitable for use as hammerstones, with the result that these enter the archaeological record at a sufficient rate to enable later recovery.

Fragmentation of the Taï stone material occurs through a combination of large forces during nut-cracking and the natural weakness of the rock types employed by chimpanzees. The internal structure of the hammerstone may become more susceptible to fracturing due to the development of internal fracture planes, particularly evident in granitoid. Additionally, hammerstones most frequently fragment along the edges away from the primary use area, the center of mass (Boesch and Boesch, 1983). This combination creates an archaeological assemblage that is essentially

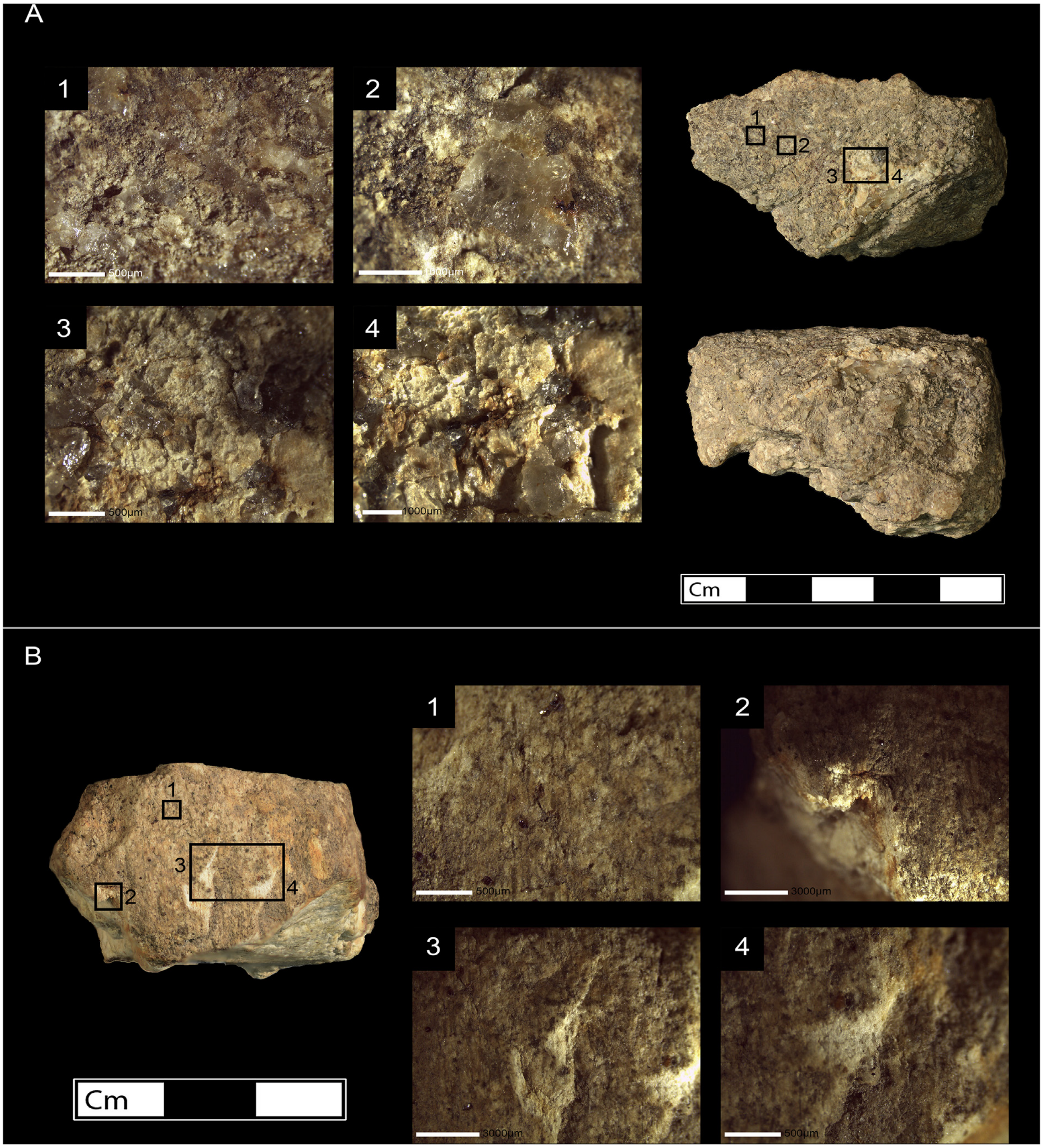


**Figure 11.** Microscopic damage of percussive artefacts at Panda 100. A) Granitoid corner fragment (Group 1.2) with clear percussive damage. 1 and 2. Cortical, undamaged areas, showing intact quartz crystals and flat smooth surface (scale = 500 μm and 1000 μm). 3 and 4. Impact point showing significant crushing and development of small steps along with detachment of quartz crystals (scale = 500 μm and 1000 μm). B) Granitoid edge fragment (Group 1.1). 1. Undamaged cortical surface (scale = 500 μm). 2, 3 and 4. V-shaped impact points along the edge and interior of the percussive surface (scale 3000 μm, 3000 μm and 500 μm).

exclusively fragments; a collection of abundant, small, fractured pieces that currently has no direct parallel in the nut-cracking sites of other wild primates or hominins.

The discovery of stone tool flaking behavior among the capuchins at SCNP (Proffitt et al., 2016) may provide a more suitable comparative dataset for the emergence of hominin flake technology. In the latter instance, capuchins pound quartzite stones directly onto other stones to break down the tool surface, producing many small flakes and angular pieces in the process. Despite potential similarities in debitage density between the SCNP and chimpanzee sites, however, there is an important difference, in that the capuchins regularly create conchoidally fractured, sharp-edged flakes, whereas the Taï chimpanzees do not. This difference is likely mediated in part by the difference in percussive behavior (stone-on-stone percussion vs nut cracking) and raw material availability and quality.

The P100 lithic material, and chimpanzee nut cracking behavior in general, has been argued to be of importance in understanding early hominin percussive activities (McGrew, 1992; Mercader et al., 2002, 2007; Panger et al., 2003). As discussed earlier, by comparing the dimensions of fragmented pieces to known Oldowan flakes and cores, Mercader et al. (2002) linked the lithic material produced at

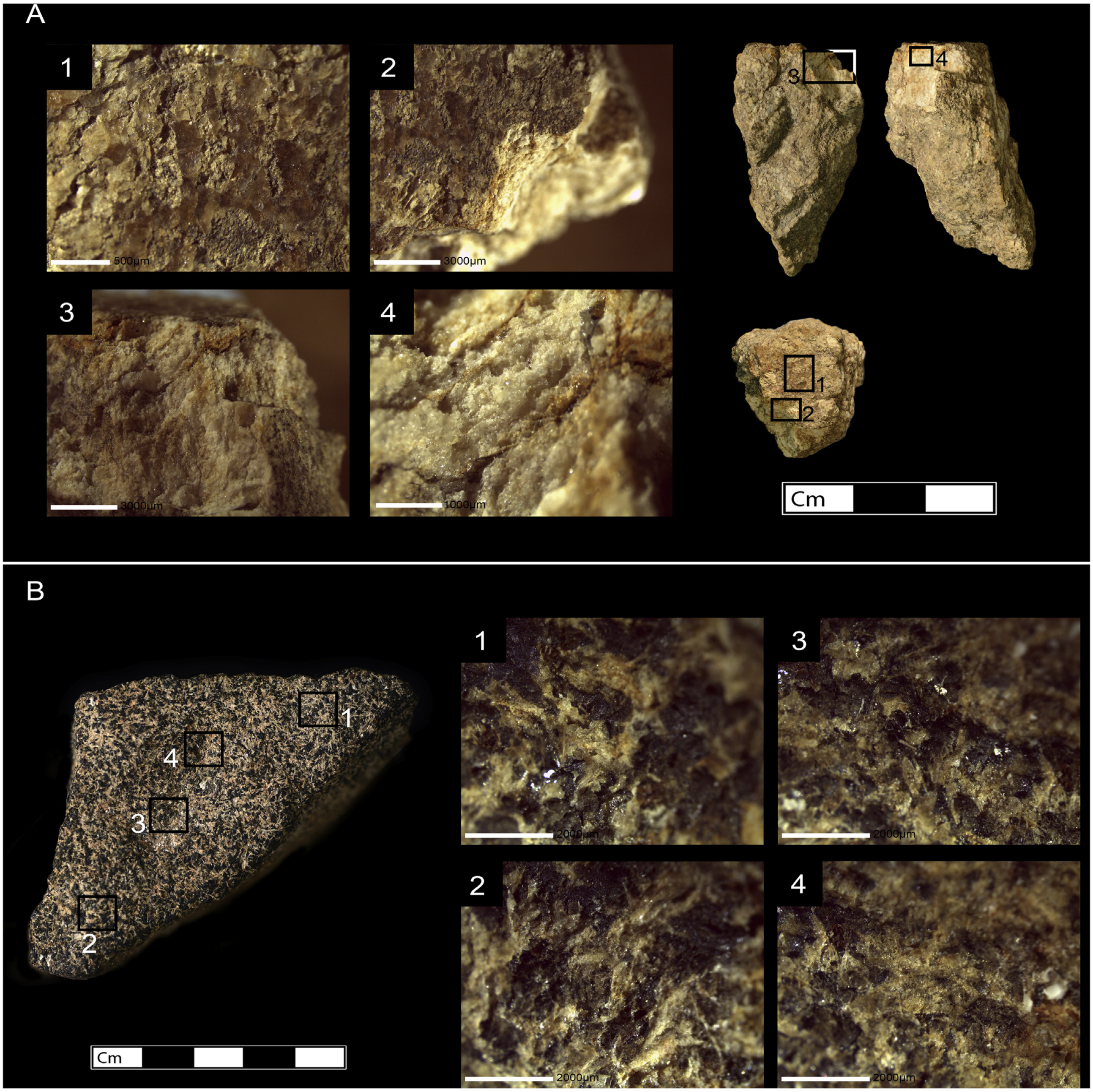


**Figure 12.** Microscopic damage of percussive artefacts at Panda 100. A) Granitoid corner fragment with clear percussive damage. 1. Cortical, undamaged surface (scale = 500 µm). 2. V-shaped impact point (scale 3000 µm). 3. Crushing and step fractures associated with impact point (scale = 3000 µm). 4. Impact point showing significant crushing of quartz crystals and matrix (scale = 1000 µm). B) Diorite corner fragment with possible pitted surface. 1 and 2. Cortical, undamaged surfaces preserving intact crystals and matrix. 3 and 4. Undamaged surface from within the pitted surface, showing intact crystals and matrix (scale = 2000 µm).

Panda 100 with the flaking technology of early hominins. Furthermore, similar comparisons have been made between chimpanzee technology and hominin flaking elsewhere (Kortlandt, 1986; McGrew, 1992; Marchant and McGrew, 2005).

Our analysis of the P100 hammerstone reduction sequences and the technological analysis of the detached products highlights their unsuitability for direct comparison with intentional hominin knapped assemblages (de la Torre, 2010). The earliest hominin stone tool technology (Lomekwian), as well as all Oldowan lithic assemblages, indicate the intentional, repeated production of conchoidally fractured flakes (Semaw et al., 1997; de la Torre, 2004; Delagnes and Roche, 2005; Harmand et al., 2015; Lewis and Harmand, 2016). For the Oldowan, associated cores retain evidence of both simple and highly structured exploitation strategies, often adhering to flaking rules. In addition to this, ESA knappers were able to identify and rectify simple accidents and maximize the number of flakes per core through directed hammerstone impacts and advantageous use of naturally occurring angles (Semaw, 2000; Delagnes and Roche, 2005; Stout et al., 2010). The rarity at P100 of conchoidal flakes (0.002%), coupled with the highly restricted and incidental range of fragmentation patterns prevent this assemblage from being directly comparable to even the simplest of Oldowan flaked assemblages. All detached pieces identified in this study are associated with the forceful and accidental interaction of the

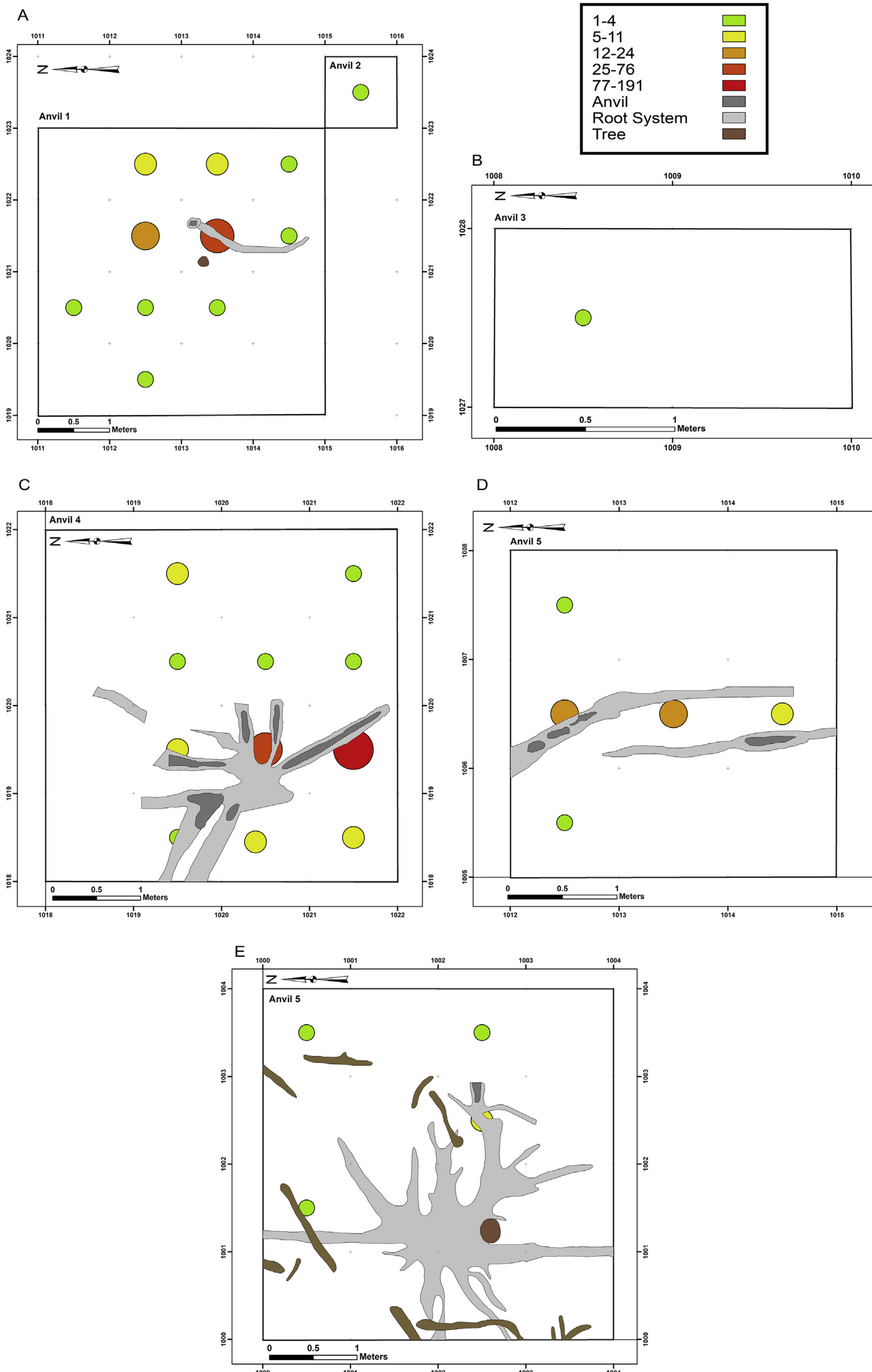


**Figure 13.** Density map of all artefacts at Panda 100 at each anvil location.

hammerstone with the passive anvil or the hard *Panda* nut target, with no instances of artefacts that resemble knapping cores.

To a large extent the degree of hammerstone fragmentation is dictated by the overall quality of the available raw material. Granitoid, for instance, is highly fragmentary with numerous internal fractures, resulting in a high frequency of shatter even when used against soft organic anvils. On the other hand, diorite hammerstones are far more homogenous, with fewer internal fractures, resulting in a significantly reduced fragmented assemblage. Having said this, however, diorite is brittle enough to develop fractures upon repeated impacts with organic anvils. Furthermore, the density of material in the excavated areas at P100, initially likened to the densities seen at ESA archaeological sites (Mercader et al., 2002), is largely mediated by the poor quality and highly fragmentary nature of the prevailing raw material, granitoid, whereas the density of Oldowan sites is the consequence of intentional repeated flake production. Having said this, however, the fragmentation of the Panda 100 assemblage offers an opportunity to develop testable hypotheses regarding the use of organic anvils in the archaeological record. Most of the chimpanzee material can be classified as small debris and percussive technological categories, which cluster within the immediate vicinity of a used wooden anvil. It may, therefore, be hypothesized that similar technological compositions and spatial clustering within the hominin archaeological record, where there is a lack of stone anvils, may have been a consequence of organic anvil use; an otherwise archaeologically invisible behavior.

The lack of viable hammerstones in the P100 archaeological record acts as a primate analogy for the high likelihood that both active hominin cores and hammerstones may not enter the archaeological record at the location of their use. This analogy applies directly to those stones that were still adequate for exploitation or percussive behavior. This study contributes to discussions of chimpanzee and wider primate stone tool transportation (Luncz et al., 2016). It has been shown that long distance transportation of stone hammers by chimpanzees, visible in the archaeological record, are often, in fact comprized of numerous smaller transportation events. The data presented in this study suggest that the death of a nut producing tree may be one of the reasons behind a hammerstone transportation event. The identification of numerous refits within this modern, archaeologically recovered, assemblage suggests that it may be possible to recover the original hammerstones that were transported from P100 within the immediate and wider area. Such analyses would provide high resolution data on hammerstone use sequences and transportation.

*Panda* nut trees are sparsely scattered within the Taï Forest (Boesch and Boesch, 1984a). In the vicinity of the Panda 100 location the average distance between Panda trees is around 100 m (Mercader et al., 2002). Whether or not these hammerstones were carried directly to another nut cracking site, or were instead moved in a more ad-hoc manner remains unknown. It is, however, known that chimpanzees have a remarkable understanding of the natural history of their environments and may use previously known nut cracking sites as raw material sources for new locations (Boesch and Boesch, 1984a). In this instance it can be hypothesized that the Panda 100 location, once depleted, may have been viewed as a new source of hammerstones within the landscape.

This chimpanzee behavior may provide insights into the behavioral processing underlying hominin transportation of artefacts and raw material (McNabb, 1998; de la Torre and Mora, 2005 ). It has been shown that hominins often transported raw materials for use as cores across significantly larger distances than has been identified for chimpanzees (Braun et al., 2008a). In the archaeological record these dynamic transportation events manifest as singular point to point movements. Often only the distance from the raw material source to the final deposition location is measurable. It has, however, been suggested that hominins were, in some instances, engaged in a far more dynamic system of raw material management across the landscape, possibly characterized by numerous short distance transportation and discard events based on raw material availability and quality (Braun et al., 2008a, 2008b, 2009). The chimpanzee material discussed in this study, as well as others (Luncz et al., 2016), offers a contemporaneous primate analogy of this additional behavioral step in hominin transportation of stone across the landscape.

Use wear and technological results of this study show that extensive percussive behavior may be reconstructed from fragmentary remains, and despite an almost complete absence of individual percussive tools. Future primate archaeological and archaeological percussive investigations should combine technological and microscopic use wear analyses with complementary experimental studies (de la Torre et al., 2013; Arroyo, 2015; Benito-Calvo et al., 2015; Arroyo et al., 2016). By identifying similar mechanical processes underlying percussive damage, we will be better able to identify and discriminate such behaviors in the ESA archaeological record. Ultimately, our study shows that a lack of complete stone hammerstones or anvils in the archaeological record does not necessarily preclude the presence of non-flaking percussive behavior.

The P100 lithic assemblage represents an important dataset for investigating hominin percussive behavior (Mora and de la Torre, 2005). Artefact categories previously associated with hominin percussive behavior in the ESA archaeological record (de la Torre and Mora, 2005; Mora and de la Torre, 2005; Arroyo and de la Torre, 2016) are represented at P100. This finding corroborates the technological validity and cross-species viability of this classification system, and suggests that these technological classificatory groupings are valid across different raw materials, and potentially raw material qualities. In addition, this study has shown that technological categories typically associated with anvil breakage may enter the archaeological record as a consequence of hammerstone breakage, and if identified should not be inherently associated with percussive anvil breakage. The issue of hammerstone breakage on organic (wooden) anvils has received little attention in the archaeological literature, and may require further investigation given its presence – albeit as a minority feature – in the primate tool use repertoire.

Our re-analysis of the first primate chimpanzee archaeological assemblages significantly updates our knowledge of both the material and behavior of which it is comprized. The importance of the P100 lithic collection – the 'Pandan' type assemblage (Mercader et al., 2002) – lies not only in its historical primacy among primate archaeological excavations, but also in the continued value of the Taï Forest material as a touchstone for comparisons with newly discovered hominin sites. Recent developments in the field of primate archaeology and human evolution suggest the need for more nuanced interpretations of chimpanzee percussive technology if we are to use it as an aid in understanding the tool use behavior of early hominins. Cross-taxa application of analytical methods, as emphasised here, is one of the simplest and clearest ways to improve our confidence in such analogies. Finally, we note that 16 years on from the seminal P100 publication, rigorous reports of additional excavations of chimpanzee sites are very rare. Both for the purpose of understanding how chimpanzee technology evolved, and how our own technology diverged so radically from that of other primates, further exploration of the chimpanzee archaeological record is essential.

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## Supplementary Online Material

Supplementary online material related to this article can be found at https://doi.org/10.1016/j.jhevol.2018.04.016.

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