ANTHROPOLOGY

Wild macaques challenge the origin of intentional tool production

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Intentionally produced sharp-edged stone flakes and flaked pieces are our primary evidence for the emergence of technology in our lineage. This evidence is used to decipher the earliest hominin behavior, cognition, and subsistence strategies. Here, we report on the largest lithic assemblage associated with a primate foraging behavior undertaken by long-tailed macaques (*Macaca fascicularis*). This behavior results in a landscape-wide record of flaked stone material, almost indistinguishable from early hominin flaked pieces and flakes. It is now clear that the production of unintentional conchoidal sharp-edged flakes can result from tool-assisted foraging in nonhominin primates. Comparisons with Plio-Pleistocene lithic assemblages, dating from 3.3 to 1.56 million years ago, show that flakes produced by macaques fall within the technological range of artifacts made by early hominins. In the absence of behavioral observations, the assemblage produced by monkeys would likely be identified as anthropogenic in origin and interpreted as evidence of intentional tool production.

INTRODUCTION

The ability of humans and our ancestors to use complex technology is a defining aspect of our evolutionary trajectory (*1*). The onset of this uniqueness in our lineage is evident in ancient behaviors visible in the archaeological record in the form cores and sharp-edged flakes, which first appeared at 3.3 million years (Ma) (*2*, *3*) and more systematically from 2.6 Ma (*4*, *5*). These flakes, produced by striking two stones together, are often interpreted as cutting tools (*6*–*8*). A suite of attributes commonly associated with intentional tool production are often used to distinguish these artifacts from naturally fractured stones. The identification of core and flake technology in the archaeological record has been used to infer the degree of cognitive complexity (*9*–*14*), to suggest that hominins were able to select rock types with specific material properties (*2*, *3*, *15*–*17*), understand aspects of fracture mechanics (*2*, *5*), and exhibit precision and coordination in motor skills (*16*, *18*).

Traditionally, the ability to infer that stone flakes were intentionally produced artifacts has relied on the co-occurrence of a number of factors that rarely occur naturally together (*19*). These include the following: (i) An abundance of artifacts in a spatially discrete locale (*20*); (ii) the presence of specific rock types in archaeological assemblages in abundances that do not reflect the natural distribution of these materials (*21*, *22*); (iii) the repeated production of conchoidal flakes with distinct platforms and bulbs of percussion (*2*, *16*); (iv) flaked pieces (*23*) with repeated superimposed detachments on one or more faces (*24*, *25*); and (v) flakes and flaked pieces that exhibit selection of appropriate angles for flake detachments (*16*).

Studies of modern primates, unlike the archaeological record, allow direct observations of behaviors that produce a recognizable material record (*26*–*29*). Multiple primate taxa, including bearded capuchins (*Sapajus libidinosus*), chimpanzees (*Pan troglodytes verus*), white-faced capuchins (*Cebus capucinus*), and long-tailed macaques (*Macaca fascicularis*) are known to use stone tools for a range of percussive behaviors, which include nut cracking, seed processing, shellfish extraction, and digging (*30*–*33*). It is rare, however, for the material record of these behaviors to extend beyond individual hammerstones and anvils. One group of wild capuchin monkeys, in Brazil, however, has been the exception (*26*). The capuchins from Serra da Capivara National Park, Brazil, undertake a behavior (stone-on-stone percussion) that unintentionally fractures their stone tools. In doing so, the resulting flakes and flaked hammerstones share many features with hominin flaked stone tools (*26*). This type of direct stone-on-stone percussive behavior has no nutritional value and is not known in any other tool-using primate species. Percussive extractive foraging to access encased foods (i.e., nuts) is, however, suggested to have been within the behavioral repertoire of Plio-Pleistocene hominins (*34*–*37*). Among these, nut cracking using stone hammers and anvils is a shared behavior between stone-tool using humans (*38*, *39*), hominins (*34*), and non-human primates (*34*).

It is known that percussive stone tool use by chimpanzees, capuchins, and macaques all produce a durable archaeological record (*40*–*42*). This record often solely consists of stone hammers and anvils; however, in some cases, a wider fragmented record is produced (*41*, *43*, *44*). These fragmented lithic artifacts, however, lack the attributes commonly used to identify intentional stone flaking (*40*, *45*). Percussive behaviors such as nut cracking have, however, been suggested as a precursor to intentional stone flaking in the hominin lineage (*46*–*49*). Furthermore, anatomical changes that may be related to tool use (e.g., manual manipulative capabilities) evident in the Pliocene and even Miocene hominin fossil record suggest a potential earlier origin of tool use (*20*, *50*, *51*). The archaeological signature of this precursor percussive technology is currently, however, lacking and may differ from the known earliest archaeological record (*45*, *46*, *49*, *52*).

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Long-tailed macaques (*M. fascicularis*) in Phang Nga Bay (Phang Nga Province, Thailand) routinely crack nuts as part of their daily foraging (Fig. 1 and movie S1) (*53*). Here, we report that during this behavior, these macaques frequently and unintentionally produce conchoidal flakes, which share attributes that are routinely used for the identification and interpretation of intentionally produced sharp-edged flakes in the Plio-Pleistocene hominin archaeological record. Flakes produced by long-tailed macaques have not been observed to be subsequently used as tools. The archaeological signature of this behavior is widely distributed over the landscape (51,326.6 m^2) and represents the largest and clearest example of unintentional flaked lithic material associated with a non-human primate to date (Supplementary Text). Here, we assessed the similarities of this lithic record to Plio-Pleistocene archaeological material through comprehensive techno-typological analysis. Furthermore, we identified morphological overlap between unintentionally produced (macaque) material and those interpreted as intentional (Oldowan and Lomekwian). We conducted a comparative technological analysis between macaque nut-cracking flakes and flaked pieces and a selection of chronologically disparate Plio-Pleistocene lithic assemblages representing a time period from 3.3 to ~1.5 Ma ago. This comparative sample included sites from Tanzania (Olduvai Gorge: DK, FLK Zinj, FLK North, and HWKE), Kenya (Koobi Fora: FwJj20, FxJj1, FxJj10, FxJj18, FxJj20M, FxJj38, FxJj3, FxJj82, FxJj50; Nachukui: LOM3; Kanjera South), and Ethiopia (Ledi Geraru: BD1; for further details see the Supplementary Materials). Our analysis included direct statistical comparisons of technological and quantitative attributes. We also resampled the macaque and archaeological flake assemblages to identify the degree to which macaque flakes can be included within a Plio-Pleistocene flake assemblage before it becomes statistically different. Our results show that using current archaeological analytical criteria, flakes produced unintentionally from percussive behaviors may be misidentified and interpreted as intentional products if found in archaeological contexts.

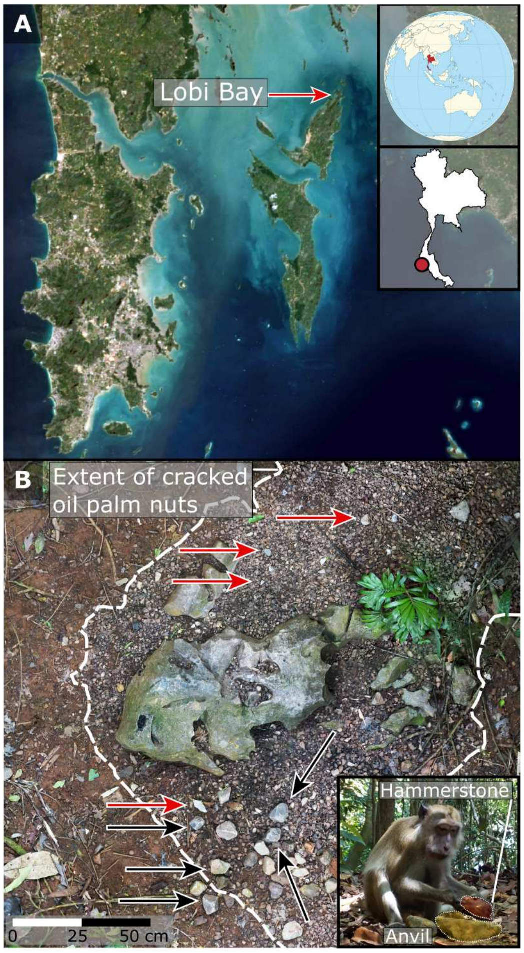

Fig. 1. The long-tailed macaques on Lobi Bay in Phang Nga Bay (Thailand) crack oil palm nuts using stone hammers and anvils, leaving a visible archaeological record of lithics and nut debris. Location of Lobi Bay (**A**) and example of long-tailed macaque nut-cracking site and associated behavior (**B**). Red arrows denote detached flakes, and black arrows denote hammerstones.

The importance of this macaque assemblage lies in its similarity to Plio-Pleistocene archaeological materials. Hence, we use a commonly used terminology for simple flaked tools that minimizes functional assumptions (*23*, *54*). By doing so, we focus exclusively on the resultant artifactual signature, which is directly linked to a known behavior—nut cracking. Oil palm cracking in wild macaques was first identified in this population in 2017 (*53*). As this group is not habituated, behavioral observations of nut cracking were assessed from camera trap footage (total of approximately 100 hours). Macaques generally place one nut on an anvil and strike it with a hammerstone, often shielding the nut with one hand to prevent it from flying off the anvil (see movie S1). Hammerstones identified in this study range in mass between 35 and 920 g.

RESULTS

Preferential selection of raw material

Long-tailed macaques at Lobi Bay crack oil palm nuts (*Elaeis guineensis*) with partially silicified, fine-grained limestone anvils and tabular or plano-convex hammerstones. The lithology of the flaked stone parallels the underlying geology of the region. Previous studies have shown that there is little evidence for preference of specific hammerstone morphologies, sizes, and weights (*53*) during nut cracking.

Abundance of artifacts in a spatially discrete locale

We collected a total of 1119 lithic percussive artifacts from 40 nut-cracking locations across the surveyed area, representing a density of 27.97 pieces per m^2. All material was found within 1 m^2 of a nut-cracking anvil (Supplementary Text). These assemblages include flaked pieces (flaked hammerstones) (Fig. 2, A to D), detached pieces (complete flakes, fragmented flakes, small debris, and angular debris) (Fig. 2, E to M), and percussive tools (hammerstones and anvils) (table S2). Hammerstones have damage patterns broadly corresponding with previously published descriptions for this behavior (*55*, *56*).

Repeated production of conchoidal flakes

Detached pieces [complete flakes (n = 133, 11.9% of 219 detached pieces) and fragmented flakes (n = 86, 7.7%)] represent a substantial artifact category in the macaque assemblage (n = 219, 19.6%) and are detached from both flaked pieces and larger anvils. Complete flakes [conchoidal, wedge or bending initiated (*57*, *58*)] are

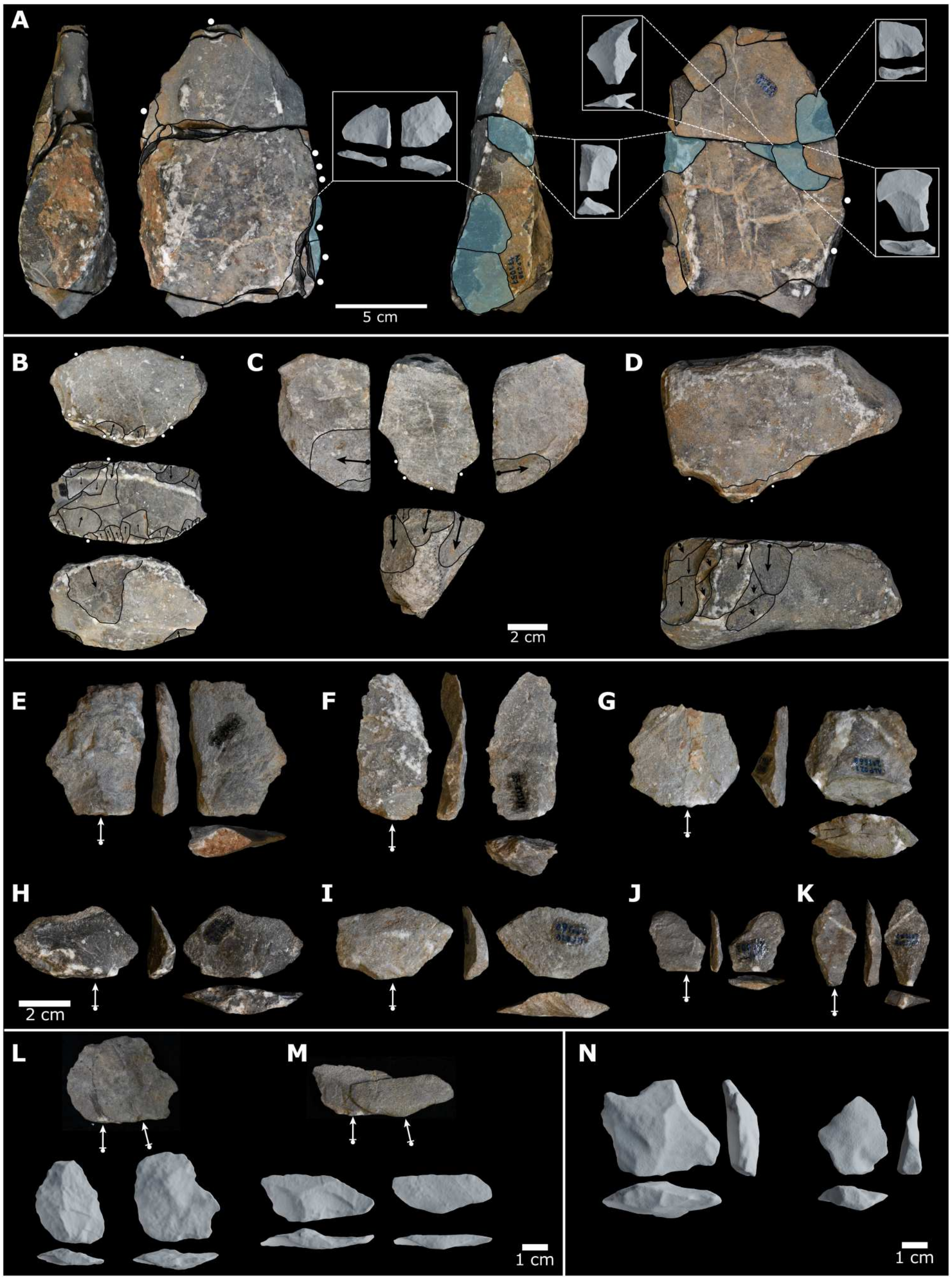

Fig. 2. Examples of limestone flakes and flaked pieces produced unintentionally during long-tailed macaque nut cracking. Selected examples of flaked pieces and complete flakes from Lobi Bay. (**A**) Refitted flaked hammerstone showing a total of 24 flake detachments during three separate phases of reduction and selected associated complete flakes. (**B** to **D**) Examples of flaked pieces with multiple superimposed flake detachments. (**E** to **K**) Examples of complete flakes with clear platforms and bulbs of percussion. (**L** to **M**) Dorsal-ventral flake refits illustrating recurrent unidirectional flake detachments. (**N**) Comparative Oldowan flakes from BD1 (*5*). White dots represent impact points associated with flake detachments; black arrows represent the directionality of a flake scar; and white arrows indicate the location of an impact point on a flake platform.

generally short and wide, ranging from 13 to 78.6 mm in maximum length (table S3 and movie S2).

In general, macaque flakes have clear bulbs of percussion ($n = 69$; 75.7%) and a mean external platform angle of <90° (81.3°, SD = 18.7°; Fig. 2 and fig. S5). Flake platforms are flat, wide, and thin with clear impact points located mostly centrally and with a general lack of percussive damage (Supplementary Text). Most flakes (73.7%) have one or more dorsal scars showing unidirectional, transversal, and opposed flaking patterns (Supplementary Text and table S4), with repeated flake production also evident in a number of flake refits (Fig. 2 and Supplementary Text). Dorsal surface battering is present on 37% ($n = 34$) of complete flakes. Quantitatively and technologically, macaque flakes fall within the range of variation observed for Pliocene and Early Pleistocene flake assemblages (Supplementary Text). The macaque flakes overlap substantially with the technological attributes of Oldowan flakes (Figs. 2N and 3A and movie S2). When a random sample of macaque flakes are incorporated into resampled Oldowan assemblages, a statistical overlap between the original Oldowan and the resampled combined macaque and Oldowan flake assemblage is observed (Supplementary Text). These results show that between 30 and 70% of an Oldowan assemblage can be replaced by macaque flakes before significantly changing the central tendency of the morphological and technological parameters of the original assemblage (for a detailed reporting of each comparative resampling test, see Supplementary Text).

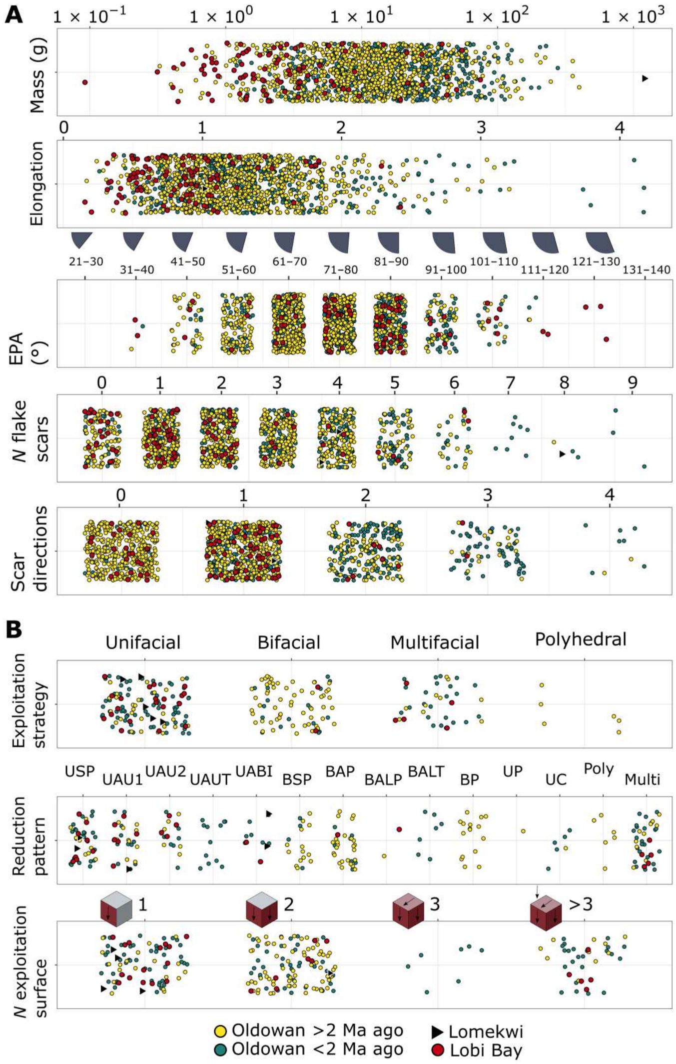

Fig. 3. Jitter plots showing the high degree of overlap in both dimensional and technological measures for both macaque flakes and flaked pieces when compared to Plio-Pleistocene assemblages. Comparative analysis of selected quantitative and technological attributes for Lobi Bay macaque, Oldowan and Lomekwian flakes (**A**) and flaked pieces (**B**). Note that all macaque datapoints fall within the range of variation for intentional hominin lithic technology. Mass is reported on a $\log_{10}$ scale. Abbreviations reported for reduction patterns are detailed in the Supplementary Materials. EPA, external platform angle.

Individual macaque flakes, in terms of quantitative and technological attributes, fall within the range of variation for Plio-Pleistocene flake assemblages (movie S3). Pairwise comparisons show that macaque flakes are significantly smaller and thicker than most Plio-Pleistocene flakes. Flake platform widths are similar between macaque and Plio-Pleistocene flakes. Platform depths on macaque flakes are significantly greater than flakes in half of the Plio-Pleistocene assemblages that were compared to the macaque materials. External platform angle does not significantly differ consistently between macaque and Plio-Pleistocene assemblages. Instead, no significant difference in external platform angles between the macaque and Plio-Pleistocene assemblages is identified for 5 of the 12 compared Oldowan assemblages. However, the macaque flakes show significantly lower ratios of cutting edge to mass compared to all sampled Plio-Pleistocene assemblages (Supplementary Text). Technologically, the macaque flake assemblage has significantly fewer platform facets compared to all sampled Plio-Pleistocene assemblages. However, in terms of the number of flake scars, and scar directions as well as dorsal cortex, there is no clear systematic difference between the macaque and archaeological assemblages (Supplementary Text).

Flaked pieces with repeated detachments along acute edges

Flaked pieces (n = 27, 2.4%) from Lobi Bay have clear flake scars, with discreet platforms and flaking surfaces (Fig. 2, A to D, and fig. S5). On the basis of the location and interaction of platforms and flaking surfaces, three repeated flaking patterns, unifacial (74%), multifacial (18.5%), and bifacial (7.4%), are evident. Most have some degree of percussive damage on one or more planes characterized by areas of battering and superimposed impacts. Percussive action resulted in numerous flake detachments (mean = 7, median = 6, and max = 21) (Fig. 2A), due to accidental impacts located along edges with natural angles of <90°. Multiple refits illustrate this reduction process (Supplementary Text and movies S4 to S7). In some cases, prolonged hammerstone use created surfaces and edges, which are battered and rounded (Fig. 2D). However, there are examples of percussive damage in discrete locations away from platforms (Fig. 2C and movie S5). It is possible therefore that these artifacts could be interpreted as being associated with intentional flaking as well as percussive activities.

Macaque flaked pieces also fall within the range of variation, both morphologically and technologically (number of exploitation surfaces, number of flake scars, reduction strategies, and exploitation types) for Plio-Pleistocene flaked pieces (Figs. 2 and 3B and Supplementary Text). Statistical comparison of both quantitative and technological attributes of Plio-Pleistocene flaked pieces and macaque flaked pieces highlights this overlap. Macaque flaked pieces are comparable in maximum dimensions and shape (elongation and flattening) to a number of Plio-Pleistocene flaked pieces (Supplementary Text); however, they have significantly reduced levels of reduction intensity to the majority of sampled Plio-Pleistocene assemblages (Supplementary Materials). Technologically, macaque flaked pieces differ significantly in terms of observed exploitation strategies and exploitation patterns to three (42.8%) of the compared archaeological assemblages. Furthermore, only two (of seven) of the archaeological assemblage that we used in our comparison showed significant differences in the number of exploited surfaces on flaked pieces. On an individual tool basis, the earliest archaeological examples of flaked pieces (>2 Ma) differ from those produced unintentionally by macaques in their linear maximum dimensions only (Supplementary Text).

DISCUSSION

Intentional stone flake technology represents our lineage's first definitive behavioral feature. Hence, our ability to recognize it in archaeological contexts is critical to our understanding of the emergence and evolution of hominin behavior.

The macaque nut-cracking assemblage from Lobi Bay represents the most extensive dataset of nonhuman primate percussive flakes and flaked stones to date. This archaeological record is produced unintentionally as a by-product of nut cracking using stone hammers and anvils. This is currently the only evidence of the creation of such an assemblage exclusively through a primate percussive behavior focused on food acquisition. This behavior leaves a durable landscape-wide archaeological record consisting of multiple conchoidal flakes and flaked pieces unparalleled in any other primate nut-cracking record currently known. These artifacts, in terms of quantifiable measures and technological attributes, fall within the range of variation of flakes and flaked pieces identified across Plio-Pleistocene archaeological sites (Fig. 3 and Supplementary Text). Furthermore, the fundamental technological criteria used to identify and interpret intentional anthropogenic flake production in Plio-Pleistocene contexts are found throughout this macaque lithic assemblage. These criteria include spatially associated flaked and detached pieces, evidence for repeated superimposed conchoidal flake production, and repeated exploitation patterns. The results of this study undermine the current notion of what constitutes an intentionally produced flake in the Early Stone Age.

The Oldowan techno-complex represents a novel adaptation associated with Plio-Pleistocene hominins, with evidence that some flakes were used for various cutting activities (*18*, *59*). Our analysis shows that, using measurements and attributes commonly associated with intentional hominin flake production, around 20 to 30% of an Oldowan assemblage can be substitutedby unintentionally produced flakes before statistical differences from the original Oldowan assemblage are evident. This comparison highlights the similarities, at an individual level, between flakes produced unintentionally by nonhuman primates through extractive foraging and those produced by hominins between 3.3 and 2.0 Ma ago. Given these similarities, it may be that some flakes and flaked stones from Plio-Pleistocene contexts are derived as a by-product of percussive behaviors (*60*) and may be easily misidentified as intentional products.

These data from Lobi Bay show that substantial similarities exist between intentionally produced sharp-edged conchoidal flakes and those derived unintentionally from primate nut cracking. In Plio-Pleistocene contexts, the stones from Lobi Bay would likely be interpreted as evidence of intentional flake production and as the use of anvils and hammerstones for various subsistence tasks (*2*, *5*, *35*). Tools with combined evidence of flaking and battering located away from tool edges are frequently attributed to multifunctional uses (*2*, *3*, *35*). It is likely that macaque flaked pieces would be diagnosed similarly if found in Plio-Pleistocene archaeological contexts. The quantity and quality of the Lobi Bay flakes and flaked pieces corroborate previously published evidence that flake production can be an unintentional by-product of percussive stone tool use (*26*, *28*, *61*). The evidence from primate archaeology indicates that this pattern should no longer be considered as purely anecdotal. Many Plio-Pleistocene archaeological assemblages have evidence of percussive activities in the form of anvils (*23*, *34*, *60*, *62*) and percussive damage on cores (*2*). On the basis of our data, the presence of flakes and flaked pieces in lithic assemblages that also have a percussive component should not be assumed to be exclusively the result of intentional flake production. Primates undertake percussive activities with no intention to produce nor use flakes. Analyzing these core and flake assemblages from the perspective of modern human intentionality risks misinterpreting or overlooking potentially distinct underlying behavioral variation.

The origins of stone tool use may extend considerably beyond the earliest known archaeological record (*2*, *45*, *46*, *52*). Evidence from the hominin fossil record and some Miocene apes potentially support this hypothesis (*20*, *50*, *51*, *63*). In recent years, ongoing research into the earliest hominin technology has increased the time depth associated with stone flake technology substantially from 2.6 Ma to older than 3 Ma ago (*2*, *3*, *8*). It has been argued that intentional flake production may have developed from a percussive behavior similar to modern primate nut cracking (*2*, *45*, *46*, *48*, *49*, *64*, *65*). Beyond their implications for known Plio-Pleistocene archaeological assemblages, our results show that durable landscape scale distributions of flakes and flaked pieces can be associated with percussive behavior. From this perspective, the percussive assemblage reported here, represents one possible, archaeologically identifiable signature of this hypothesized earliest stage of cultural evolution (*52*). Our results suggest that larger, more elongated flakes, with high cutting edge–to–mass ratios and more platform preparation are attributes associated with intentional flake production. However, measures such as external platform angle and platform dimensions, flake scar frequency, flake scar directionality and cortical coverage on flakes, as well as exploitation strategies and number of exploited surfaces on flaked pieces do not differ between nut cracking and intentionally produced assemblages.

As we explore the antiquity of hominin stone tool technology, the importance of various nonflaking percussive activities must be investigated further as a precursor to intentional flake production. Identifying the mechanisms that enabled our technological dependence will require a broadening of our understanding of the potential complexity and diversity of behaviors that may have contributed to the earliest archaeological records. Primate assemblages (*26*, *40*) can be used to recalibrate how we interpret the oldest hominin material records. This is especially pertinent when considering the increasingly simple nature of this archaeological record (*2*, *3*, *5*). Previous studies have relied on the aforementioned co-occurring attributes to infer intentional hominin tool production (*2*). Building on previous studies of primate flaked stone assemblages (*26*), this study shows that these criteria now occur repeatedly within multiple phylogenetically and geographically diverse nonhuman primate lineages (*26*).

The intentional production of stone tools represents an adaptive threshold that fundamentally altered the evolutionary trajectory of our lineage (*66*). The results of this study demonstrate that a fundamental reassessment of how we define and identify this uniquely hominin behavior in the archaeological record is still needed.

MATERIALS AND METHODS

Macaque data collection and technological analysis

The macaque lithic assemblage presented in this study consists of 1119 artifacts collected from 40 separate nut-cracking localities on Yao Noi Island in Lobi Bay, Phang Nga National Park, Thailand. All material was collected during two separate field seasons in 2017 and 2021 from the surface within a 1 m by 1 m square of each nut-cracking site. Hence, this assemblage represents a sample of the total detached lithic material associated with macaque nut cracking across this landscape. The total landscape scale lithic assemblage is, therefore, considerably greater in frequency and density.

All collected lithic material was classified into standard technological categories: flaked pieces, detached pieces, and pounded pieces (*67*). A full technological analysis was conducted on all complete flakes, fragmented flakes, hammerstones, and flaked hammerstones following commonly used technological attributes (*16*, *17*, *25*, *26*, *68*). The maximum linear dimensions and mass of all artifacts were recorded. Hammerstones that have at least one clear conchoidal flake detachment were analyzed as flaked pieces. The technological attributes recorded for flaked pieces include the number and dimensions of all flake extractions >10 mm, flake initiation type, core flaking accidents, degree of cortex coverage, and number of extractions. Each flaked piece was also classified into reduction types following classifications described by de la Torre (*24*, *25*) (table S1), which indicate the prevailing direction and angle of flake removals. In addition, a measure of reduction intensity for each flaked piece was calculated. Following the method set out by Caruana *et al.* (*69*), we use the measure of mass/total number of flake scars on flaked pieces as a measure of reduction intensity.

Complete flakes were defined as detached pieces, having clear ventral and dorsal surfaces separated by a sharp edge, as well as a complete platform and impact point. Flakes could be conchoidal, wedge or bending initiated following Andrefsky (*58*). In addition to linear maximum dimensions, a number of additional measurements were recorded. These included maximum dimensions (length, width, and thickness) (*58*) and technological dimensions (length and width) measured from the knapping platform to the distal end and the maximum measurement orthogonal to the technological length (*70*). Furthermore, technological width and thickness was recorded at 25, 50, and 75% of the total length of each flake. These dimensional measures were used to calculate additional shape variables including elongation (technological length/ technological width), flattening (thickness / technological width), area (maximum length × maximum width), and volume (maximum length × maximum width × maximum thickness). Platform depth and width were recorded and used to calculate platform area, and flattening. Last, both external platform angle and internal platform angles were recorded. The ratio of flake cutting-edge length to mass was used as a measure of flaking efficiency, following its successful application in multiple studies (*71*–*76*). This measure of flaking efficiency (mass/estimated edge length) was calculated following the method set out by Caruana *et al.* (*69*). Technological attributes recorded follow those set out by Mora *et al.* (*54*) and Proffitt (*77*) and include notable platform cortex (measured at 0, <50, >50, and 100%), platform morphology (platform, lineal, and puntiform), platform faceting (nonfacetd, unifaceted, bifaceted, and multifaceted), platform shape (flat, convex, concave, uni-angular, and irregular), bulb of percussion (marked, diffuse, fractured, and indeterminate), knapping accidents (step, hinge, and plunging terminations), presence of dorsal-surface step scars, transversal and sagittal cross-section shape, dorsal-surface cortex (measured the same as platform cortex), number of dorsal extractions, dorsal-extraction directionality (fig. S1), and flake categories following Toth (*13*). In addition to typical technological attributes, attributes related to percussion were also recorded, including the following: the presence or absence of dorsal surface and platform percussive damage and the number of percussive impacts on the dorsal surface.

For a full description and definition of the technological attributes used, see the Supplementary Materials. In addition, the assemblage was subjected to refit analysis, resulting in the refit of 70 (10.2%) individual pieces from 21 refit sets used to inform the technological analysis. All refits are summarized in full in the Supplementary Materials.

Comparative analysis with archaeological data

A comparative technological analysis between macaque nut-cracking flakes and flaked pieces and a selection of Plio-Pleistocene lithic assemblages representing a time period between 3.3 and ~1.5 Ma ago was undertaken to address the following questions: (i) Do the macaque flakes and flaked pieces fall within the range of variation for Plio-Pleistocene hominin artifacts? (ii) What proportion of macaque flakes can be included within a Plio-Pleistocene lithic assemblage before it becomes statistically distinct from the original purely Oldowan assemblage? (iii) Do macaque flakes and flaked pieces statistically differ in terms of quantitative and technological attributes to those identified in Plio-Pleistocene hominin assemblages?

Archaeological data were compiled from a combination of first-hand analyses and published data (*78*). Flake data were collected for 17 sites while data on flaked pieces were collected from 7 sites (tables S5 and S6). In addition, corresponding technological data were inferred from three three-dimensional models of Lomekwi flakes available online (*2*). Quantitative attributes for flakes include maximum dimensions, mass ($\log_{10}$ transformed), elongation ratio, flattening ratio, platform width, platform depth, and external platform angle. Technological data include percentage of cortex coverage, number of dorsal flake scars, number of platform facets, and the number of scar directions. Quantitative attributes compared for cores include maximum dimensions, mass ($\log_{10}$ transformed), elongation ratio, and flattening ratio. Technological data compared for cores include exploitation strategy, flaking pattern, and number of exploitation surfaces.

To address the first question, each variable compared was plotted onto the same axis to visually identify the degree of overlap with macaque unintentional flakes. The second question was address through a resampling exercise, which statistically tested the proportion of macaque flakes, which could be included within an Oldowan assemblage before becoming statistically different from the original Oldowan assemblages. To generate the Oldowan assemblage, flakes were randomly sampled from each Oldowan site (see below). To avoid error caused by sampling with replacement, the size of each resampled flake assemblage was limited to the smallest assemblage being compared. A mixed assemblage was then generated by substituting a proportion of Oldowan flakes from each site with a random sample of flakes from Lobi Bay. A Cramer test for the two-sample problem (*80*) was then used to statistically compare the differences between the two assemblages based on a series of commonly collected lithic attributes that are often associated with intentionality.

Attributes selected for this comparison are commonly collected during technological lithic analyses and correspond to various aspects of flake production typically associated with intentionality. External platform angle is directly linked to the detachment of conchoidal flakes (*81*), a hallmark of intentional flake production (*19*). Platform area is used here as a proxy for fine motor control during hammerstone use (*16*). The number of platform facets is related to the degree of core preparation associated with flake detachments. The number of dorsal scars indicates the degree of repeated flake production on a core (*2*, *25*). Dorsal scar directionality indicates the repeated patterns of removals from cores suggestive of intentional flake production (*2*, *25*). Last, percentage of dorsal-cortex coverage is commonly used to indicate the degree of reduction of cores (*13*).

To determine the proportion of macaque flakes that could be substituted before characteristics of the two assemblage became statistically distinguishable from each other, the proportion of substituted macaque flakes was systematically increased along the following intervals: 5% and, subsequently, at 10% intervals. The multivariate Cramer test for the two-sample problem was subsequently used to test the significant difference between each simulated assemblage and the original assemblage for each archaeological site. This process was reiterated 1000 times for each assemblage. The resulting range of *P* values indicate that the proportion of unintentional macaque percussive flakes can be embedded in a Plio-Pleistocene flake assemblage until the resampled assemblage becomes statistically significantly different to a purely hominin flake assemblage.

To address the third comparative question, both flakes and flaked pieces from the macaque assemblage were statistically compared to flakes and flaked pieces from each included archaeological assemblage. All quantitative measures were compared using a Mann-Whitney *U* test, with subsequent Bonferroni *P* value correction to account for multiple testing. Intersite variation of flake technological attributes was compared using a chi-square test and subsequent adjusted residual values were used to identify the source of any significant differences. All statistical analyses were conducted in R (v3.6.3, *82*).

Supplementary Materials

This PDF file includes:
Supplementary Text
Figs. S1 to S14
Tables S1 to S21
Legends for movies S1 to S7
References

Other Supplementary Material for this manuscript includes the following:
Movies S1 to S7

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