

Statistical Inference of Earlier Origins for the First Flaked Stone Technologies

Alastair J. M. Key ^{a,*}, David L. Roberts ^b, Ivan Jarić ^{c, d}

^a *School of Anthropology and Conservation, University of Kent, Canterbury, Kent, CT2 7NR, UK*

^b *Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Canterbury, Kent, CT2 7NR, UK*

^c *Biology Centre of the Czech Academy of Sciences, Institute of Hydrobiology, České Budějovice, Czech Republic*

^d *University of South Bohemia, Faculty of Science, Department of Ecosystem Biology, České Budějovice, Czech Republic*

Abstract

Identifying when hominins first produced Lomekwian, Oldowan and Acheulean technologies is vital to multiple avenues of human origins research. Yet, like most archaeological endeavors, our understanding is currently only as accurate as the artifacts recovered and the sites identified. Here we use optimal linear estimation (OLE) modelling to identify the portion of the archaeological record not yet discovered, and statistically infer the date of origin of the earliest flaked stone technologies. These models provide the most accurate framework yet for understanding when hominins first invented these tool types. Our results estimate the Oldowan to have originated 2.617 to 2.644 Ma, 36,000 to 63,000 years earlier than current evidence. The Acheulean's origin is pushed back further through OLE, by at least 55,000 years to 1.815 to 1.823 Ma. We were unable to infer the Lomekwian's date of origin using OLE, but an upper bound of 5.1 million years can be inferred using alternative nonparametric techniques. These dates provide a new chronological foundation from which to understand the emergence of the first flaked stone technologies, alongside their behavioral and evolutionary implications. Moreover, they suggest there to be substantial portions of the artifact record yet to be discovered.

Keywords: Lomekwian; Oldowan; Acheulean; Optimal linear estimation modelling; Early Stone Age; East African archaeology

1. Introduction

The invention of Lomekwian, Oldowan and Acheulean stone tool technologies during the late Pliocene and early Pleistocene represent major advances in early human adaptive behavior (Harmand et al., 2015; Toth, 1985; de la Torre, 2016). These technologies allowed hominins to access novel foods and increase the ease of resource acquisition (Key and Lycett, 2017), while also potentially conveying social and other benefits (e.g., Pope et al., 2006; Kuhn, 2012; Morgan et al., 2015). Each is technically more demanding than its immediate precursor (Roche et al., 1999; de la Torre and Mora, 2008; Braun et al., 2019; although see Sahle and Gossa [2019] for additional information on the Lomekwian-Oldowan transition), and is often associated with cognitive or anatomical change (Stout et al., 2010; Marzke, 2013; Lewis and Harmand, 2016; Key and Lycett, 2018). Together, these three stone technologies account for a substantial proportion of current knowledge on hominin behavior and evolution between 3.5–1.5 Ma.

Such is their importance, that their emergence can be considered “a momentous threshold in hominin evolution” (Hovers, 2012: 62). Yet, like most archaeological endeavors, our understanding of when hominins first started to produce novel lithic technologies is only as accurate as the artifacts recovered and the sites identified. Indeed, more so than any other archaeological field, Early Stone Age (ESA) archaeology suffers from a paucity of behavioral remains. This is mainly due to a unique combination of poor preservation, challenges in artifact identification, and the obstacles (e.g., cost, remoteness, politics) of undertaking fieldwork in East Africa (e.g., Isaac,

1984). It is for these reasons that the Lomekwian was only first described in 2015 (Harmand et al., 2015), and after 60+ years of ESA research the origin of the Acheulean was able to be pushed back by ~300,000 years in 2011 (Lepre et al., 2011).

Archaeology is not, however, alone in its quest to reconstruct behavioral and population data from temporally and geographically fragmented evidence. Nowhere is this felt more acutely than in conservation science. When an extant species becomes rarer, evidence demonstrating the existence of that species also decreases (McKelvey et al., 2008; Roberts et al. 2010; Brook et al. 2019). In turn, and in the quest to help preserve species from extinction, a considerable amount of effort has gone into developing techniques able to reconstruct the timing of past species extinctions, or calculate the rate of population decline in extant populations, from limited evidence (see reviews of the literature by Solow 2005; Rivadeneira et al. 2009; Clements et al. 2013; Boakes et al. 2015).

Optimal linear estimation (OLE) modelling (Roberts and Solow, 2003) has been shown to be a reliable method of inferring the timing of species extinctions based on last confirmed evidence of species presence (Rivadeneira et al. 2009; Clements et al., 2013). That is, the technique models the length of time a species is likely to have continued to survive after the last known evidence (e.g., spoor, photographs, museum specimens) for its existence. Here, we adapt the OLE method to work in reverse, to estimate the origin dates for the earliest human stone technologies in East Africa based on earliest confirmed records from current archaeological finds. The results of the models presented in this

study provide the most accurate estimates yet for when hominins invented the first flaked stone tool technologies.

2. Methods

2.1. Sampling procedure

As recommended for OLE modelling, ten dates were required for each model run (Solow, 2005; Rivadeneira et al., 2009). In this instance, we required the ten earliest archaeological occurrences of Lomekwian, Oldowan and Acheulean technologies (Fig. 1). A detailed literature review of African ESA sites was undertaken to identify these data. From each site, we collected the main estimated date and date range. The ten earliest occurrences of the Oldowan and Acheulean are detailed in Table 1. The Lomekwian is currently only known from one site (Harmand et al., 2015), and therefore it was not possible to use the OLE method to infer the origin date for this technology.

Our definitions of each technology follow widely accepted standards within the literature (Toth, 1985; Roche et al., 1999; Gowlett, 2006; Diez-Martín et al., 2015; Harmand et al., 2015), and our designation of sites to the Lomekwian, Oldowan or Acheulean follow those with first-hand experience of the assemblages (i.e., the authors of the associated research articles). To our knowledge the technological definitions applied to the 20 sites listed in Table 1 have broadly been accepted within the discipline.

Absolute dates were required in all instances, and we did not sample from sites dated using faunal or sedimentary evidence alone. Some ESA sites, such as Gona and Konso (both in Ethiopia), display multiple artifact-bearing layers that are chronologically close. In these instances, each layer was counted as a distinct datum entered into the models as long as their associated date ranges do not overlap. Konso, for example, contributes three distinct artifact dates to the Acheulean model. When overlap did occur, the oldest date was used. Subsequently, the next artifact level displaying no date range overlap with the first became the next date to be used. In addition, if two or more sites from a single localized area (within 5km in the same river valley or gorge, for example) displayed the same date, only one contributed to the model. Very occasionally there were assemblages older than those in Table 1 not included here as their date ranges overlapped with older alternatives from the same site, or they were from a site displaying an identical age to another from the same localized region (for example, EG12 and EG10 at Gona are only slightly younger than OSG-7, but because their date range overlaps with the latter they were not included). These sampling rules were implemented as OLE modelling assumes each datum to be a distinct 'observation' (Solow, 2005).

It is important to highlight that some of the sites included in this analysis are subject to ongoing debate. Of most relevance are discussions concerning their geochronology. As the oldest current occurrence of the Oldowan, the site of Ledi-Geraru provides a suitable and important example. Braun et al. (2019) provide an age of 2.581 Ma based on the overlaying sediment's normal geomagnetic polarity being assigned to the Gauss Chron, and thus after the known Gauss-Matuyama reversal. As highlighted by Sahle and

Gossa (2019), however, it remains to be proven beyond doubt that the Ledi-Geraru sediments do not reflect a later normal polarity from the Réunion subchron 2.14 Ma.

It is not, however, the intent of this study to critically appraise the geochronology of each archaeological site. Indeed, we only use archaeological sites from widely cited and accepted peer-reviewed sources, and as such their inclusion reflects the current state of understanding within the field as a whole. This does not discount the views of individuals who raise issue with a specific published date, but it is necessary for a standardized site sampling procedure to be used here, and as such we have to trust in the value of peer-review while simultaneously acknowledging ongoing debate. If we were to exclude sites because a specific researcher or research group raises issue with another teams' published interpretation, we would be left with no sites. If we were to make exceptions for some individuals' views but not others, we would invalidate the integrity of the site-sampling procedure. Thus, we acknowledge that some individuals' site sample preferences may be different to the one used here, but we also stress that these views will vary among individuals.

2.2. *Optimal Linear Estimation*

We applied the OLE method as proposed by Roberts and Solow (2003) for dating extinctions. The OLE method has proved to be robust in the inference of extinction under a variety of scenarios (Rivadeneira et al. 2009; Clements et al. 2013). We apply it here with the reverse temporal direction, with record age increasing towards the past, since

they are expressed as a number of years before present time, where $T_1 > T_2 > \dots > T_k$ are the k earliest records, ordered from the earliest record (with T_k being the most recent record in the dataset). Interest focuses on using this record of site dates to estimate the origin time, θ . In this context, the optimal linear estimation is based on the fact that the joint distribution of the k earliest sites has the same approximate 'Weibull form', regardless of the parent distribution of the complete record of dated sites.

The optimal linear estimator of θ (inferred time of origin, T_0) has the form of a weighted sum of the site date times (Roberts and Solow, 2003),

$$\hat{\theta} = \sum_{i=1}^k a_i T_i$$

where the vector of weights is

$$a = (e^t \Lambda^{-1} e)^{-1} \Lambda^{-1} e.$$

Here e is a vector of k 1's and Λ is the symmetric $k \times k$ matrix with typical element $\lambda_{ij} = (\Gamma(2\hat{\nu} + i)\Gamma(\hat{\nu} + j))/(\Gamma(\hat{\nu} + i)\Gamma(j))$, $j \leq i$, and where Γ is the standard gamma function.

Further,

$$\hat{\nu} = \frac{1}{k-1} \sum_{i=1}^{k-2} \log \frac{T_1 - T_k}{T_1 - T_{i+1}}$$

is an estimate of the shape parameter of the joint Weibull distribution of the k oldest sites date times.

Following Solow (2005), an approximate one-sided upper bound of a $1 - \alpha$ confidence interval (CI) for θ is

$$S_U = \frac{T_1 - c(\alpha)T_k}{1 - c(\alpha)},$$

where $c(\alpha) = \left(\frac{k}{-\log\alpha}\right)^{-\hat{\nu}}$; note that in Solow (2005) there is an error where the equation for $c(\alpha)$ was incorrectly inverted.

An advantage of the OLE method is that it takes into consideration the distribution of only the last existing records (in this case the oldest Oldowan and Acheulean sites), which obviated the need for including more recent archaeological sites in the analysis. We used the 10 (k) oldest sites for each region as suggested by Solow (2005) and Rivadeneira et al. (2009). However, as there is no specific start date for the time series, the 10th youngest site date was used as the beginning of the period. As the end point is non-independent to the time series records, k reduces by 1 (Solow 1993; Clements et al. 2013). The OLE method produces two types of estimates relevant to understanding the timing of extinctions. The first is T_0 , which here represents the estimated origin date for Oldowan and Acheulean technology in a given model. T_0 is presented as years before present (BP). The second, T_{CI} , represents the upper bound of each model's $1 - \alpha$ confidence interval. This is effectively the time beyond which the probability of the

technology already existing is below α . We used $\alpha = 0.05$ as the origin threshold value (Roberts and Solow, 2003). The origin date for each of the two technologies was calculated in R v. 3.4.4 using the R software package sExtinct (Clements 2013).

Artifact dates were taken from original research articles describing a site or assemblage. When only a date range was provided, we used the central point of this range. Additionally, to address the uncertainty of some age estimates within known date ranges, a resampling approach was also applied. Dates of each site were randomly drawn from a normal distribution, with the mean value represented by the mean of the age range, and standard deviation equal to the half of the difference between the mean value and range bounds. Such randomly generated datasets were consequently assessed with the OLE method, and the whole procedure was repeated 10,000 times, with results expressed as mean and median values across all iterations.

As stated earlier, multiple techniques able to estimate faunal extinction dates exist (e.g, McFarlane, 1999; Crees and Turvey, 2014; Du et al., 2020). Nevertheless, OLE is widely recognized as the most robust approach within a variety of extinction scenarios, and performs well under different sighting probabilities and trends, and different search effort intensities and trajectories (Rivadeneira et al. 2009; Clements et al. 2013), which obviates the need for using additional techniques. It is also important to emphasize that its underlying assumptions are not specific to biological organisms, and the method can readily be applied to diverse phenomena so long as they are characterized by sporadic observations through time prior to their extinction. It takes into

account the intervals between the last known observations of a phenomenon and their distribution, irrespective of whether it is applied to model the extinction of biological species or cultural traditions. OLE is based on the result that most recent (or oldest) sightings have the same 'Weibull form' regardless of the characteristics of the full record, its density and distribution (Roberts and Solow, 2003; Solow 2005).

3. Results

OLE modelling was used to infer the origin dates of Oldowan and Acheulean stone tool technologies based on current archaeological evidence. For each technology two models were run; one that relied on the main date assigned to each artifact occurrence (often a central range estimate), and an additional resampling approach drawing dates from associated date ranges. An upper and lower bound for each technology can be identified through the combination of these two dates.

The Oldowan is inferred to originate (T_0) between 2,616,897 and 2,644,446 years ago, with the upper bound resulting from the resampling technique (Fig. 2). The T_{CI} of each estimate, and thus the upper bound of each model's $1 - \alpha$ confidence interval is 2,749,452 and 2,831,069 (same technique order). This represents the date beyond which the probability of the Oldowan occurring prior to this is $<5\%$. The Acheulean's T_0 , and therefore estimated date of origin, is between 1,814,551 and 1,823,194 years ago. Its upper confidence interval (again, $\alpha = 0.05$) is estimated to be between 1,966,847 and

1,986,306 years ago. Earlier estimates again result from the resampling technique (Fig. 2).

4. Discussion and Conclusions

It is highly likely that the current oldest known Lomekwian, Oldowan, and Acheulean artifacts do not represent the earliest of their kind. To address this issue, we applied OLE modelling to statistically infer dates of origin for each technology, and thus identify the portions of the ESA archaeological record not yet discovered. This provides the most robust picture yet for understanding when hominins first produced these stone tool types. Moreover, it highlights that there are likely to be substantial portions of the artifact record waiting to be discovered.

Oldowan stone tools are inferred through OLE to have originated by 2.617 to 2.644 Ma, 36,000 to 63,000 years earlier than current evidence demonstrates (Semaw et al., 2003; Braun et al., 2019). The Acheulean's origin has been pushed back by a minimum of 55,000 years relative to current understanding (Lepre et al., 2011), with the OLE models inferring an origin date between 1.815 and 1.823 Ma. These dates push the origin of each technology beyond current known archaeological discoveries, opening up new time frames within which to discuss the evolution of human technological capabilities and associated dietary shifts.

A new date of origin for the Oldowan at least 2.617 Ma suggests hominins to have been practicing complex, effective stone tool production behaviors earlier than indicated

by current artifactual evidence. Indeed, the OLE models assume the Oldowan to have originated in the form we currently recognize at Ledi-Geraru, Gona, Lokalalei and elsewhere (e.g., Roche et al., 1999; Braun et al., 2019). Although it has been previously stated that the sites of Ledi-Geraru and OGS-7 may not represent the earliest instances of hominins producing Oldowan flake and core technologies (Semaw, 2000; Panger et al., 2002; Wynn et al., 2011; Hovers, 2012), it is only now that there is quantitative support for this widely held notion. In light of this new timeframe, the earliest members of the genus *Homo* (2.8–2.3 Ma) can still be considered primary candidates responsible for first producing Oldowan tools and the associated shift towards increased animal protein consumption (de Heinzelin et al., 1999; Antón, 2012; Villmoare et al., 2015). Although this does not, of course, rule out australopithecine species also using such flake technologies (e.g., Asfaw et al., 1999; Skinner et al., 2015).

An inferred origin of the Acheulean at least 1.815 Ma brings this technology in line with the earliest known occurrences of *Homo erectus*, supporting well established links between the two (de la Torre, 2016, Semaw et al., 2020). Recent discoveries at Drimolen (South Africa) have identified *H. erectus*-like cranial fossils 2.04–1.95 Ma (Herries et al., 2020), while longer-known east African sites confirm *H. erectus*' presence by 1.9–1.8 Ma (Antón, 2012). Although the species originated prior to the technology, this is not unexpected due to cognitive and anatomical thresholds needing to be reached in advance of handaxes and cleavers being produced or effectively used (Stout et al., 2015; Key and Lycett, 2018; Pargeter et al., 2020). What the OLE estimates have done, however, is

reduce the discontinuity between the two, bringing the origin of the Acheulean in-line with the lower date-ranges for *H. erectus*' appearance.

The Lomekwian is currently known from a single 3.3 million-year-old site in Kenya (Harmand et al., 2015) and it is not possible to run OLE modelling without additional discoveries. When this single date is combined with (contentious; see Domínguez-Rodrigo et al., 2010) evidence of hominin-made cut marks 3.39 Ma (McPherron et al., 2010), which could have been made with Lomekwian flake tools, it does, however, become possible to infer an upper bound date (T_{CI}) of 5.1 Ma. This is following Solow and Roberts' (2003) nonparametric method (which is not as robust as OLE), and infers the origin of Lomekwian technology to only have a 5% chance of preceding this date. Thus, this date is not the Lomekwian's inferred time of origin, and instead represents a maximum point of origin with 5% probability. Given recent discoveries concerning accidental stone flaking by nonhuman primates (Proffitt et al., 2016) and the cognitive and manual complexity of *Pan* tool-production and use strategies (Sanz et al., 2009; Gowlett, 2015; Neufuss et al., 2017; Musgrave et al., 2020), a Lomekwian origin up to 1.8 Ma prior to the current Lomekwi 3 artifacts would not be surprising. Current fossil evidence does not preclude this possibility, and an earlier origin to the Lomekwian would provide important implications for the cognitive, anatomical and behavioral evolution of hominins. However, we want to reemphasize that 5.1 Ma is an upper bound derived using debated cut-marked bones and nonparametric procedures. We look forward to further discoveries of Lomekwian technologies, to allow use of the OLE method in the future.

Although well established in other disciplines, OLE is new to archaeological science and it is our hope that the technique will be used widely in the future. Indeed, for a discipline heavily concerned with the chronology of human material culture and its linear expression through time, OLE has wide application across multiple subdisciplines. This includes through established routes, such as modelling the extinction of fauna and flora relevant to human prehistory, or new applications such as determining the terminus date of specific cultural expressions in the artifact record (e.g., Bicho et al., 2015; Manclossi et al., 2019; Shott, 2020). Indeed, OLE can be applied at any timescale and to any cultural tradition, from the very earliest stone artefacts (as demonstrated here) to historic organic material culture.

Our understanding of the earliest stone technologies is only as accurate as the artifacts discovered to date, and the same is true for the present models. As a result, it is possible that our inferences may not stand the test of time. New discoveries that push the origins of these technologies beyond the model's predictions would be welcome. However, the present origin dates are robust in light of current archaeological discoveries, and the close bracketing of current sites at 2.58 (Oldowan) and 1.75 (Acheulean) Ma supports this inference. Similarly, these estimates are based on 60+ years of archaeological discovery in East Africa conducted by numerous field teams; arguably a robust database from which to model origin dates for lithic technologies. Yet, as the West Turkana Archaeological Project and others have previously demonstrated, future archaeological finds that overhaul our understanding of ESA archaeology cannot be ruled

out. In such an event, renewed modelling will be able to provide additional insight into these discoveries.

References

Antón, S., 2012. Early *Homo*: Who, when, and where? *Curr. Anthropol.* 53, 278-298.

Asfaw, B., White, T., Lovejoy, O., Latimer, B., Simpson, S., Suwa, G., 1999. *Australopithecus garhi*: A new species of early hominid from Ethiopia. *Science* 284, 629-635.

Beyene, Y., Kato, S., WoldeGabriel, G., Hart, W.K., Uto, K., Sudo, M., Kondo, M., Hyodo, M., Renne, P.R., Suwa, G., Asfaw, B., 2013. The characteristics and chronology of the earliest Acheulean at Konso, Ethiopia. *Proc. Natl. Acad. Sci. USA* 110, 1584-1591.

Bicho, N., Marreiros, J., Cascalheira, J., Pereira, T., Haws, T., 2015. Bayesian modeling and the chronology of the Portuguese Gravettian. *Quat. Int.* 359-360, 499-509.

Boakes, E. H., Rout, T. M., Collen, B., 2015. Inferring species extinction: The use of sighting records. *Methods Ecol. Evol.* 6, 678-687.

Braun, D.R., Aldeias, V., Archer, W., Arrowsmith, J.R., Baraki, N., Campisano, C.J., Deino, A.L., DiMaggio, E.N., Dupont-Nivet, G., Engda, B., Feary, D.A., Garello, D.I., Kerfelew, Z., McPherron, S.P., Patterson, D.B., Reeves, J.S., Thompson, J.C., Reed, K.E., 2019. Earliest known Oldowan artifacts at >2.58 Ma from Ledi-Geraru, Ethiopia, highlight early technological diversity. *Proc. Natl. Acad. Sci. USA* 116, 11712-11717.

Brook, B.W., Buettel, J.C., Jarić, I., 2019. A fast re-sampling method for using reliability ratings of sightings with extinction-date estimators. *Ecology* 100, e02787.

Brown, F.H., Gathogo, P.N., 2002. Stratigraphic relation between Lokalalei 1A and Lokalalei 2C, Pliocene archaeological sites in West Turkana, Kenya. *J. Archaeol. Sci.* 29, 699-702.

Clements, C. sExtinct R Package; 2013. <https://cran.r-project.org/src/contrib/Archive/sExtinct/> (accessed Jul 16, 2020).

Clements C.F., Worsfold N.T., Warren P.H., Collen B., Clark, N., Blackburn, T.M., Petchey, O.L., 2013. Experimentally testing the accuracy of an extinction estimator: Solow's optimal linear estimation model. *J. Anim. Ecol.* 82, 345-54.

Crees, J.L., Turvey, S.T., 2014. Holocene extinction dynamics of *Equua hydruntinus*, a late-surviving European megafaunal mammal. *Quat. Sci. Rev.* 91, 16-29.

de Heinzelin, J., Clark, J.D., White, T., Hart, W., Renne, R., WoldeGabriel, G., Beyene, Y., Vrba, E., 1999. Environment and behavior of 2.5-million-year-old Bouri Hominids. *Science* 284, 625-629.

de la Torre, I., 2004. Omo revisited: Evaluating the technological skills of Pliocene hominids. *Curr. Anthropol.* 45, 439-465.

de la Torre, I., 2011. The Early Stone Age lithic assemblages of Gadeb (Ethiopia) and the developed Oldowan/early Acheulean in East Africa. *J. Hum. Evol.* 60, 768-812.

de la Torre, I., 2016. The origins of the Acheulean: Past and present perspectives on a major transition in human evolution. *Philos. Trans. R. Soc. Lond.* 371, 20150245.

de la Torre, I., Mora, R., Martinez-Moreno, J., 2008. The early Acheulean in Peninj (Lake Natron, Tanzania). *J. Anthropol. Archaeol.* 27, 244-264.

Delagnes, A., Roche, H., 2005. Late Pliocene hominid knapping skills: The case of Lokalalei 2C, West Turkana, Kenya. *J. Hum. Evol.* 48, 435-472.

Delagnes, A., Boisserie, J.-R., Beyene, Y., Chuiniaud, K., Guillemot, C., Schuster, M., 2011. Archaeological investigations in the Lower Omo Valley (Shungura Formation, Ethiopia): New data and perspectives. *J. Hum. Evol.* 61, 215-222.

Diez-Martín, F., Sánchez Yustos, P., UribeArrea, D., Baquedano, E., Mark, D.F., Mabulla, A., Fraile, C., Duque, J., Díaz, I., Pérez-González, A., Yravedra, J., Egeland, C.P., Organista, E., Domínguez-Rodrigo, M., 2015. The Origin of The Acheulean: The 1.7 million-year-old site of FLK West, Olduvai Gorge (Tanzania). *Sci. Rep.* 5, 17839.

Diez-Martín, F., Sánchez Yustos, P., de Luque, L., 2018. The East African early Acheulean of Peninj (Lake Natron, Tanzania). In: Gallotti, R., Mussi, M. (Eds.), *The Emergence of the Acheulean in East Africa and Beyond*. Springer, Cham. pp. 129-152.

Ditchfield, P.W., Whitfield, E., Vincent, T., Plummer, T., Braun, D., Deino, A., Hertel, F., Oliver, J.S., Louys, J., Bishop, L.C., 2019. Geochronology and physical context of Oldowan site formation at Kanjera South, Kenya. *Geol. Mag.* 156, 1190-1200.

Domínguez-Rodrigo, M., Pickering, T.R., Bunn, H.T., 2010. Configurational approach to identifying the earliest hominin butchers. *Proc. Natl. Acad. Sci. USA* 107, 20920-20934.

Du, A., Rowan, J., Wanh, S.C., Wood, B.A., Alemseged, Z., 2020. Statistical estimates of hominin origination and extinction dates: A case study examining the *Australopithecus anamensis-afarensis* lineage. *J. Hum. Evol.* 138, 102688.

Gallotti, R., Mussi, M., 2018. Before, during, and after the early Acheulean at Melka Kunture (Upper Awash, Ethiopia): A techno-economic comparative analysis. In: Gallotti, R., Mussi, M. (Eds.), *The Emergence of the Acheulean in East Africa and Beyond*. Springer, Cham. pp. 53-92.

Gibbon, R.J., Granger, D.E., Kuman, K., Partridge, T.C., 2009. Early Acheulean technology in the Rietputs Formation, South Africa, dated with cosmogenic nuclides. *J. Hum. Evol.* 56, 152-160.

Goldman-Neuman, T., Hovers, E., 2012. Raw material selectivity in Late Pliocene Oldowan sites in the Makaamitalu Basin, Hadar, Ethiopia. *J. Hum. Evol.* 62, 353-366.

Gowlett, J. A. J., 2006. The elements of design form in Acheulian bifaces: Modes, modalities, rules and language. In: Goren-Inbar, N., Sharon, G. (Eds.), *Axe Age: Acheulian tool-making from quarry to discard*. London, Equinox, pp. 203-221.

Gowlett, J.A.J., 2015. Variability in an early hominin percussive tradition: The Acheulean versus cultural variation in modern chimpanzee artefacts. *Philos. Trans. R. Soc. Lond.* 370, 20140358.

Granger, D.E., Gibbon, R.J., Kuman, K., Clarke, R.J., Bruxelles, L., Caffee, M.W., 2015. New cosmogenic burial ages for Sterkfontein Member 2 *Australopithecus* and Member 5 Oldowan. *Nature* 522, 85-88.

Harmand, S., Lewis, J.E., Feibel, C.S., Lepre, C.J., Prat, S., Lenoble, A., Boës, X., Quinn, R.L., Brenet, M., Arroyo, A., Taylor, N., Clément, S., Daver, G., Brugal, J.-P., Leakey, L., Mrtlock, R.A., Wright, J.D., Lokorodi, S., Kirwa, C., Kent, D.V., Roche, H., 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature* 521, 310–315.

Herries, A.I.R., Martin, J.M., Leece, A.B., Adams, J.W., Boshian, G., Joannes-Boyau, R., Edwards, T.R., Mallett, T., Massey, J., Murszewski, A., Neubauer, S., Pickering, R., Strait, D.S., Armstrong, B.J., Baker, S., Caruana, M.V., Denham, T., Hellstrom, J., Moggi-Cecchi, J., Mokobane, S., Penzo-Kajewski, P., Rovinsky, D.S., Schwartz, G.T., Stammers, R.C., Wilson, C., Woodhead, J., Mente, C., 2020. Contemporaneity of *Australopithecus*, *Paranthropus*, and early *Homo erectus* in South Africa. *Science* 386, eaaw7293.

Hovers, E., 2012. Invention, reinvention and innovation: The makings of Oldowan lithic technology. *Develop. Quat. Sci.* 16, 51-68.

Hovers, E., Gossa, T., Asrat, A., Niespolo, E.M., Resom, A., Renne, P.R., Ekshtain, R., Herzlinger, G., Ketema, N., Mertinez-Navarro, B., 2021. The expansion of the Acheulian to the Southeastern Ethiopian Highlands: Insights from the new early Pleistocene site-complex of Melka Wakena. *Quat. Sci. Rev.* 253, 106763

Isaac, G., 1984. The archaeology of human origins: Studies of the Lower Pleistocene in East Africa 1971-1981. In: Wendorf, F., Close, A. (Eds.), *Advances in Old World Archaeology*, vol. 3. Academic Press, New York. pp. 1-87.

Key, A.J.M., Lycett, S.J., 2017. Form and function in the Lower Palaeolithic: History, progress, and continued relevance. *J. Anthropol. Sci.* 95, 67-108.

Key, A.J.M., Lycett, S.J., 2018. Investigating interrelationships between Lower Palaeolithic stone tool effectiveness and tool user biometric variation: Implications for technological and evolutionary changes. *Archaeol. Anthropol. Sci.* 10, 989-1006.

Kibunja, M., 1994. Pliocene archaeological occurrences in the Lake Turkana basin. *J. Hum. Evol.* 27, 159-171.

Kimbel, W.H., Walter, R.C., Johanson, D.C., Reed, K.E., Aronson, J.L., Assefa, Z., Marean, C.W., Eck, G.G., Bobe, R., Hovers, E., Rak, Y., 1996. Late Pliocene *Homo* and Oldowan Tools from the Hadar Formation (Kada Hadar Member), Ethiopia. *J. Hum. Evol.* 31, 549-561.

Kuhn, S.L., 2012. Emergent patterns of creativity and innovation in early technologies. *Develop. Quat. Sci.* 16, 69-87.

- Kuman, K., Clarke, R.J., 2000. Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. *J. Hum. Evol.* 38, 827-847.
- Lepre, C.J., Roche, H., Kent, D.V., Harmand, S., Quinn, R.L., Brugal, J.-P., Texier, P.-J., Lenoble, A., Feibel, C.S., 2011. An earlier origin for the Acheulian. *Nature* 477, 82-85.
- Lewis, J.E., Harmand, S., 2016. An earlier origin for stone tool making: Implications for cognitive evolution and the transition to *Homo*. *Philos. Trans. R. Soc. Lond.* 371, 20150233.
- Manclossi, F., Rosen, S.A., Boeda, E., 2019. From stone to metal: The dynamics of technological change in the decline of chipped stone tool production. A case study from the Southern Levant (5th-1st Millennia BCE). *J. Arch. Meth. Theory* 26, 1276-1326.
- Marzke, M.W., 2013. Tool making, hand morphology and fossil hominins. *Philos. Trans. R. Soc. Lond.* 368, 20120414.
- McKelvey, K.S., Aubry, K.B., Schwartz, M.K., 2008. Using anecdotal occurrence data for rare or elusive species: The illusion of reality and a call for evidentiary standards. *BioScience* 58, 549-555.
- McFarlane, D.A., 1999. A comparison of methods for the probabilistic determination of vertebrate extinction chronologies. In: MacPhee, R.D.E. (Ed) *Extinction in Near Time*. Kluwer, New York. pp. 95-103.
- McHenry, L.J., Stanistreet, I.G., 2018. Tephrochronology of Bed II, Olduvai Gorge, Tanzania, and placement of the Oldowan-Acheulean transition. *J. Hum. Evol.* 120, 7-18.
- McPherron, S.P., Alemseged, Z., Marean, C.W., Wynn, J.G., Reed, D., Geraads, D., Bobe, R., Béarat, H.A., 2010. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466, 857-860.
- Morgan, T.J.H., Uomini, N.T., Rendell, L.E., Chouinard-Thuly, L., Street, S.E., Lewis, H.M., Cross, C.P., Evans, C., Kearney, R., de la Torre, I., Whiten, A., Laland, K.N., 2015. Experimental evidence for the co-evolution of hominin tool-making teaching and language. *Nat. Commun.* 6, 6029.
- Musgrave, S., Lonsdorf, E., Morgan, D., Prestipino, M., Bernstein-Kurtycz, L., Mundry, R., Sanz, C., 2020. Teaching varies with task complexity in wild chimpanzees. *Proc. Natl. Acad. Sci. USA* 117, 969-976.

- Neufuss, J., Humle, T., Cremanschi, A., Kivell, T.L., 2017. Nut-cracking behaviour in wild-born, rehabilitated bonobos (*Pan paniscus*): A comprehensive study of hand-preference, hand grips and efficiency. *Am. J. Primatol.* 79, e22589.
- Quade, J., Levin, N., Semaw, S., Stout, D., Renne, P., Rogers, M., Simpson, S., 2004. Paleoenvironments of the earliest stone toolmakers, Gona, Ethiopia. *Geol. Soc. Amer. Bull.* 116, 1529-1544.
- Roche, H., Delagnes, A., Brugal, J.-P., Feibel, C., Kibunjia, M., Mourre, V., Texier, P.-J., 1999. Early hominid stone tool production and technical skill 2.34 Myr ago in West Turkana, Kenya. *Nature* 399, 57-60.
- Pope, M., Russel, K., Watson, K., 2006. Biface form and structured behaviour in the Acheulean. *Lithics* 27, 44-57.
- Rivadeneira M.M., Hunt G., Roy K., 2009. The use of sighting records to infer species extinctions: An evaluation of different methods. *Ecology* 90, 1291–300.
- Roberts D.L., Solow A.R., 2003. When did the dodo become extinct? *Nature* 426, 245.
- Roberts, D.L., Elphick, C.S., Reed, J.M., 2010. Identifying anomalous reports of putatively extinct species and why it matters. *Conserv. Biol.* 24, 189-196.
- Panger, M.A., Brooks, A.S., Richmond, B.G., Wood, B., 2002. Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evol. Anthropol.* 11, 235-245.
- Pargeter, J., Khreisheh, N., Shea, J.J., Stout, D., 2020. Knowledge vs. know-how? Dissecting the foundations of stone knapping skill. *J. Hum. Evol.* 145, 102807.
- Proffitt, T., Luncz, L.V., Falótico, T., Ottoni, E.B., de la Torre, I., Haslam, M., 2016. Wild monkeys flake stone tools. *Nature* 539, 85-88.
- Sahle, Y., Gossa, T., 2019. More data needed for claims about the earliest Oldowan artifacts. *Proc. Natl. Acad. Sci. USA* 116, 20259-20260.
- Sahnouni, M., Pares, J.M., Duval, M., Caceres, I., Harichane, Z., van der Made, J., Perez-Gonzalez, A., Abdessadok, S., Kandi, N., Derradji, A., Meddig, M., Boulaghraif, K., Semaw, S., 2018. 1.9-million and 2.4-million-year-old artifacts and stone tool-cutmarked bones from Ain Boucherit, Algeria. *Science* 362, 1297-1301.

Sanz, C., Call, J., Morgan, D., 2009. Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biol. Lett.* 5, 293-296.

Shott, M.J., 2020. Toward a theory of the point. In: Groucutt, H.S. (Ed.) *Culture History and Convergent Evolution: Can We Detect Populations in Prehistory?* Springer, Cham. pp. 245-259.

Semaw, S., 2000. The world's oldest stone artefacts from Gona, Ethiopia: Their implications for understanding stone technology and patterns of human evolution between 2.6-1.5 million years ago. *J. Arch. Sci.* 27, 1197-1214.

Semaw, S., Rogers, M.J., Quade, J., Renne, P.R., Butler, R.F., Dominguez-Rodrigo, M., Stout, D., Hart, W.S., Pickering, T., Simpson, S.W., 2003. 2.6-Million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *J. Hum. Evol.* 45, 169-177.

Semaw, S., Rogers, M.J., Caceres, I., Stout, D., Leiss, A.C., 2018. The Early Acheulean ~1.6–1.2 Ma from Gona, Ethiopia: Issues related to the Emergence of the Acheulean in Africa. In: Gallotti, R., Mussi, M. (Eds.), *The Emergence of the Acheulean in East Africa and Beyond. Vertebrate Paleobiology and Paleoanthropology.* Springer, Cham. pp. 115-128.

Semaw, S., Rogers, M.J., Simpson, S.W., Levin, N.E., Quade, J., Dunbar, N., McIntosh, W.C., Caceres, I., Stinchcomb, G.R., Holloway, R.L., Brown, F.H., Butler, R.F., Stout, D., Everett, M., 2020. Co-occurrence of Acheulian and Oldowan artifacts with *Homo erectus* cranial fossils from Gona, Afar, Ethiopia. *Sci. Adv.* 6, eaaw4694.

Skinner, M.M., Stephens, N.B., Tsegai, Z.J., Foote, A.C., Nguyen, N.H., Gross, T., Pahr, D.H., Hublin, J.J., Kivell, T.L., 2015. Human-like hand use in *Australopithecus africanus*. *Science* 347, 395-399.

Solow A.R., 1993. Inferring extinction from sighting data. *Ecology* 74, 962–64.

Solow, A.R., 2005. Inferring extinction from a sighting record. *Math. Biosci.* 195, 47-55.

Solow, A.R., Roberts, D.L., 2003. A nonparametric test for extinction based on a sighting record. *Ecology* 84, 1329-1332.

Stanistreet, I.G., McHenry, L.J., Stollhofen, H., de la Torre, I., 2018. Bed II sequence stratigraphic context of EF-HR and HWK EE archaeological sites, and the Oldowan/Acheulean succession at Olduvai Gorge, Tanzania. *J. Hum. Evol.* 120,19-31.

Stollhofen, H., Stanistreet, I.G., Toth, N., Schick, K.D., Rodriguez-Cintas, A., Albert, R.M., Farrugia, P., Njau, J.K., Pante, M.C., Herrmann, E.W., Ruck, L., Bamford, M.K., Blumenshine, R.J. and Masao, F.T., 2012. Olduvai's oldest Oldowan. *J. Hum. Evol.* 150, 102910

Stout, D., Semaw, S., Rogers, M.J., Cauche, D., 2010. Technological variation in the earliest Oldowan from Gona, Afar, Ethiopia. *J. Hum. Evol.* 58, 474-491.

Stout, D., Hecht, E., Khreisheh, N., Bradley, B., Chaminade, T., 2015. Cognitive demands of Lower Paleolithic toolmaking. *PLoS One* 10, e0121804.

Tiercelin, J.-J., Schuster, M., Roche, H., Brugal, J.-P., Thuo, P., Prat, S., Harmand, S., Davtian, G., Barrat, J.-J., Bohn, M., 2010. New considerations on the stratigraphy and environmental context of the oldest (2.34 Ma) Lokalalei archaeological site complex of the Nachukui Formation, West Turkana, northern Kenya Rift. *J. Afr. Earth Sci.* 58, 157-184.

Toth, N., 1985. The Oldowan reassessed: A close look at early stone artifacts. *J. Archaeol. Sci.* 12, 101-120.

Villmoare, B., Kimbel, W.H., Seyoum, C., Campisano, C.J., DiMaggio, E.N., Rowan, J., Braun, D.R., Arrowsmith, J.R., Reed, K.E., 2015. Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. *Science* 347, 1352-1355.

Wynn, T., Hernandez-Aguilar, A., Marchant, L.F., McGrew, W.C., 2011. "An ape's view of the Oldowan" revisited. *Evol. Anthropol.* 20, 181-197.

Figure legends

Figure 1. The locations of the 20 stone tool assemblages contributing to the optimal linear estimation models, along with the only current known location of Lomekwian technology.

(1) LOM3, Lomekwi, (2) Ledi-Geraru, (3) OGS-7, Gona, (4) AB-Lw, Ain Boucherit, (5) AL 666, Hadar, (6) Lokalalei 1, (7) Omo 57 and 123, (8) Lokalalei 2C, (9) Member 5, Sterkfontein, (10) Kanjera South, (11) Trench 168, Western Olduvai Basin (12) Kokiselei 4, West Turkana, (13) KGA6-A1, Konso, (14) FLK West, Olduvai Gorge, (15) KGA4-A2, Konso, (16) Level D, Garba IV, (17) Val River, (18) OGS 12, Gona, (19) EF-HR, Olduvai, (20) KGA10-A11, Konso, (21) MW2-L3, Melka Wakena. Original satellite image credit: NASA Visible Earth Project.

Figure 2. Violin-boxplots detailing predicted origin dates for the Oldowan and Acheulean, derived from 10,000 iterations of the random sampling method.