Modelling the end of the Acheulean at global and continental levels suggests widespread persistence into the Middle Palaeolithic

Alastair J. M. Key1, Ivan Jarić2,3 & David L. Roberts4

The Acheulean is the longest cultural tradition ever practised by humans, lasting for over 1.5 million years. Yet, its end has never been accurately dated; only broad 300–150 thousand years ago (Kya) estimates exist. Here we use optimal linear estimation modelling to infer the extinction dates of the Acheulean at global and continental levels. In Africa and the Near East the Acheulean is demonstrated to end between 175 and 166 Kya. In Europe it is inferred to end between 141 and 130 Kya. The Acheulean’s extinction in Asia occurs later (57–53 Kya), while global models vary depending on how archaeological sites are selected (107–29 Kya). These models demonstrate the Acheulean to have remained a distinct cultural tradition long after the inception of Middle Palaeolithic technologies in multiple continental regions. The complexity of this scenario mirrors the increasingly dynamic nature of the Middle Pleistocene hominin fossil record, suggesting contemporaneous hominin populations to have practised distinct stone-tool traditions.
Introduction

Acheulean stone tools were produced for more than 1.5 million years. Such an extended period of production is well established, with an age bracket of ~1.75 to 0.15 million years ago (Mya) widely cited as ‘the Acheulean period’ (Gowlett, 2015; de la Torre, 2016; Shea, 2017; Galway-Whyman et al., 2019). Discoveries at Konso (Ethiopia), Olduvai Gorge (Tanzania), and West Turkana (Kenya) provide convincing evidence of the Acheulean’s origin in east Africa around 1.75 Mya (Lepre et al., 2011; Beyene et al., 2013; Diez-Martin et al., 2015). Multiple other sites support such an early occurrence in this region (de la Torre and Mora, 2014; de la Torre, 2016; Gallotti and Mussi, 2018), and no other countries claim evidence to the contrary (e.g. Dennell, 2018; Moncel and Ashton, 2018). The location and timing of the onset of the Acheulean therefore appears well supported.

In comparison, the end of the Acheulean is a relative unknown. No sites are widely recognised as displaying evidence of the ‘last Acheulean populations’, and no single region (nor continent) is convincingly argued to display the last stronghold of this technology. Instead, the Acheulean is broadly considered to have been replaced across the Old World between 0.3 and 0.15 Mya, but there is considerable debate on precisely when and where these transitions occurred, and how they varied between different regions (McBrearty and Tryon, 2006; Norton et al., 2009; Fontana et al., 2013; Shipton, 2016; Deino et al., 2018; Galway-Whyman et al., 2019; Scerri et al., 2019). Levallois and blade production techniques arrive with regionally dependent variation, and yet no matter when and where they first appear, changes to the cognition, anatomy, diet, and behaviour of hominins are inferred (e.g. Villa, 2006; Shipton, 2016; Picin, 2017; Akhilesh et al., 2018; Pappu and Akhilesh, 2019; Mathias et al., 2020; Moncel et al., 2020a; Meignen and Bar-Yosef, 2020).

Lithic culture is malleable and absorptive (Lycett and von Graevenitz, 2015; O’Brien and Buchanan, 2017), and we are in no doubt that later Acheulean populations likely combined known technologies with newly learnt or discovered ideas in diverse and chronologically variable ways (e.g. Mathias et al., 2020; Meignen and Bar-Yosef, 2020). However, refining our understanding of when hominin populations moved away from a purely ‘Acheulean’ technological way of thinking is important, and has implications for a multitude of cultural and biological factors in human origins research.

How, then, are we to seek better resolution on the end of the first global technological phenomenon without multiple well-dated sites being discovered across Africa and Eurasia? To start, any attempt to do so should account for imbalances and outliers concerning where late Acheulean sites have been found and dated (Fig. 1). Western Europe, Israel, and South Korea in particular have a relative abundance of sites dating to under <300 Kya compared to other regions and countries. We are not saying there are lots—far from it—but there are more than in other areas, and in turn, our temporal and geographic understanding of the later Acheulean is skewed to reflect this. Second, archaeological sites across 1.5 million years contribute to our view of the Acheulean as a global culture, and yet a paucity of data from the terminal end of this period limits debate to local or regional levels. Thus, there is a clear need to understand the end of the Acheulean as we currently recognise it during its peak; as a global cultural phenomenon displaying elements of unity and diversity, bound by shared functional necessities and the social transmission of tool-design concepts (Lycett and Gowlett, 2008; Wynn and Gowlett, 2018). However, at the moment we do not have the resolution to understand the end of the Acheulean at a localised level with any security, let alone how long it continued as a global or continental tradition.

Conservation science provides a route to more reliably define the end of the Acheulean both chronologically and geographically. No other discipline is more concerned with accurately predicting extinction dates based on fragmentary evidence. In the same way that handaxes and cleavers provide sporadic evidence of the presence of Acheulean populations, sightings, spoor and biological samples provide intermittent evidence of the presence of rare species. As species’ populations decrease and go extinct, these traces become more infrequent, geographically disconnected, and can be used as evidence of last-known populations. Optimal linear estimation (OLE) modelling was developed to reliably reconstruct the timing of species extinction dates using such traces (Roberts and Solow, 2003; Solow, 2005; Riva- deneira et al., 2009; Clements et al., 2013). Here, we use OLE to reconstruct the timing of the end of the Acheulean cultural
Methods

Defining the Acheulean. At its broadest, Acheulean assemblages are characterised by the presence of large bifacially flaked cutting tools (handaxes and cleavers, which do not occur prior to 1.75 Mya) and the absence of MP and MSA technologies (most notably Levallois hierarchical flaking) (Shea, 2017). There can be variation in biface form, alongside some technological differences (McNabb et al., 2004; Lycett and Gowlett, 2008; Sharon et al., 2011; Key, 2019; Shipton, 2020). As noted above, however, regional variation exists in how the Acheulean is defined; most notably through transitional cultural traditions that incorporate other technological elements.

For the present analyses we defined a site as belonging to the Acheulean cultural tradition based on two factors: (1) the presence of large bifacially flaked cutting tools (handaxes and cleavers) and an absence of Levallois technologies, and (2) the original authors describing a site also assigning it to the Acheulean. We are aware that not all individuals will be happy with this definition. Some sites could be excluded or included based on a researcher’s technological and typological predilections concerning the Acheulean, or debate over the accuracy of published dates. The analysis performed here is, however, designed to understand the extinction of the Acheulean cultural tradition at global and continental levels. In turn, it necessitated a broad definition to guarantee that sites feeding into each model were not unduly excluded based on individual pedagogy-based interpretations of the Acheulean (most notably our own). Simultaneously, we wanted to respect the interpretation of those individuals that know the relevant artefacts best, and the peer-review process in determining the accuracy of published dates (although also note the resampling procedures used in the section “OLE modelling methods”). Our definition of the Acheulean is not limited to stone artefacts. As with any discussion of the Acheulean, however, poor preservation rates in organic artefacts impede our ability to include them in our analyses (for example, Acheulean sites defined by bone handaxes/cleavers are included in our definition, but there are no examples late enough for inclusion).

We did not include sites (or assemblages/artefact layers) assigned to transitional cultures; although we do appreciate that the Acheulean ended in a technologically mosaic-like nature in some regions (e.g. Moncel et al., 2020b). Similarly, we do not distinguish between late Acheulean sites containing specific handaxe and cleaver forms (be it due to distinct evolutionary trajectories, or any other process). Application of this sampling procedure allows us to model the end of the Acheulean as a distinct cultural tradition, and thus, as it is recognised for the majority of its existence. An exception was made for the Fauresmith (which include blades and prepared cores alongside bifaces [McBrearty and Tryon, 2006; Porat et al., 2010; Herries, 2011]), where an additional ‘Sub-Saharan African’ model was run that incorporated these sites. Our intention was to demonstrate the impact of including transitional assemblages when inferring Acheulean extinction dates.

Site identification and model classifications. A comprehensive literature review was undertaken to identify ‘late’ or ‘final’ Acheulean sites across Africa and Eurasia. All of those assigned as late Acheulean on typological or morphological grounds alone were not considered (due to their subjective nature and requirements for absolute dates). Sites were then divided into four continental regions; Europe, Asia, Sub-Saharan Africa, and North Africa and the Near East (Table 1; Fig. 2). Only the most recent
(youngest) 10 sites in each region were required, as is generally recommended (Roberts and Solow, 2003; Solow, 2005; Rivadeneira et al., 2009). Indeed, OLE reconstructs extinction timings through the chronological spacing of the most recent records and the inclusion of additional older sites (i.e., greater numbers of sites further away from the last known occurrence) would have little impact on the result (or even could detrimentally impact it; see the section “Applying OLE modelling to the archaeological record”). As suggested by Solow (2005), overly large numbers of records used would risk invalidating the assumptions of the model.

Geographic biases in research focus mean that some countries have disproportionately greater numbers of late Acheulean sites compared to others. Such weighting results from historical and political biases unrelated to how Acheulean hominins are actually represented geographically and chronologically. Thus, there was potential for continental-level models to be overly influenced by individual countries. To counter this, each country was able to contribute a maximum of three sites to a continental model, meaning that at least four countries were represented in each. All continental models adhered to this except for Asia, as only three countries have dated sites from the terminal phase of the Acheulean (China, India and South Korea, with the latter contributing four sites). In addition, countries could only contribute one date from a localised region (for example, the Middle Son Valley [India]). This ensured that a heavy focus on localised regions could not disproportionately influence models. For these reasons, there will be some late Acheulean sites excluded from these models despite being younger than others that are included.

Two additional continental models were run (Table 1). First, we re-ran the Sub-Saharan African model but included sites assigned to the Fauresmith. This resulted in the four oldest sites in the original model being removed and replaced with younger Fauresmith alternatives. Second, we re-ran the Asian model after the removal of the five youngest sites in this region (i.e. n = 5). The five removed sites fit the criteria for inclusion in our models, however, they provide extremely late occurrences of large bifacial technology and are critical of their inclusion in the Acheulean (Shipston and Petraglia, 2011; Kuman et al., 2014; Lee, 2017; Bae, 2017; Li et al., 2018). The second Asian model therefore helps understand the extinction of the Acheulean cultural tradition in Asia irrespective of one’s perspective on these more recent artefacts.

Fig. 2 The four continental regions of the Acheulean world examined in the present study (Green = Sub-Saharan Africa, Yellow = North Africa and the Near East, Blue = Europe, Red = Asia). As indicated in Fig. 1, not all areas currently have strong or continued evidence of the Acheulean being present (e.g. Congo River Basin). Original satellite image credit: NASA Visible Earth Project.

Two models using intercontinental data were run to better understand the end of the Acheulean as a global cultural tradition (Table 1). Fauresmith sites were not included in either. In the first, the 10 youngest sites from those included in the continental models (n = 40), irrespective of their country of origin, were included. This meant that a country could contribute a maximum of three sites, but there were no limits on which continents these countries came from (i.e. individual continents could contribute heavily to the model). The second model included only one site per country, and a maximum of three sites per continental region (the youngest in each instance). This meant that all four continental regions contributed to the modelling process. For both, versions including and excluding the five debated young Asian sites were run.

We recognise that the dates assigned to some sites included in the models are subject to ongoing debate. However, it is not the role of this study to critique specific sites and their geochronology. If we were to remove every site subject to debate by a specific researcher or research group, then we would have very few sites available for inclusion (if any at all). Thus, we must go with the consensus view that appears in the literature and trust in the value of peer-review when assessing the reliability of a site’s published date. This does not discount the views of any individuals; simply, it is necessary for a standardised site sampling procedure to be used. If we were to make exceptions for individual researchers, then we would invalidate the integrity of the site-sampling procedure.

In total, 10 model classifications were examined. All sites and dates input into each model are available in Supplementary Material 1.

Applying OLE modelling to the archaeological record. Here we apply the optimal linear estimation (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). Although most regularly applied to model the extinction of faunal and floral species, the underlying assumptions of the OLE method are not specific to biological organisms. Instead, the method can readily be applied to diverse phenomena so long as they are characterised by sporadic observations through time prior to their extinction.

OLE uses the last known chronological occurrences, or ‘sightings’, of a given phenomenon to estimate how long it
Table 1 Definitions used in the 10 Acheulean extinction models.

| Model # | Model name | Definition |
|---------|------------|------------|
| 1       | Europe     | The 10 youngest Acheulean sites in the continent. A maximum of three sites per country. |
| 2       | North Africa & Near East | The 10 youngest Acheulean sites in the continental region. A maximum of three sites per country. |
| 3       | Sub-Saharan Africa | The 10 youngest Acheulean sites in the continental region. A maximum of three sites per country. |
| 4       | Sub-Saharan Africa (Fauresmith) | The 10 youngest Acheulean and Fauresmith sites in the continental region. A maximum of three sites per country. |
| 5       | Asia       | The 10 youngest Acheulean sites in the continent. A maximum of three sites per country. |
| 6       | Asia (n = 5) | The five youngest sites in the continent (not including the five debated sites). A maximum of three sites per country. |
| 7       | Global 1a  | The 10 youngest Acheulean sites from any of the continental models. |
| 8       | Global 1b  | The 10 youngest Acheulean sites from any of the continental models (not including the five debated Asian sites). |
| 9       | Global 2a  | The 10 youngest sites from any of the continental models. Only one site per country and a maximum of three sites per continental region. |
| 10      | Global 2b  | The 10 youngest sites from any of the continental models. Only one site per country and a maximum of three sites per continental region (not including the five debated Asian sites). |

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

\[
\hat{\nu} = \frac{1}{k-1} \sum_{i=1}^{k-2} \log \frac{T_i - T_k}{T_i - T_{i+1}}
\]

is an estimate of the shape parameter of the joint Weibull distribution of the \(k\) youngest sites date times. Following Solow (2005), an approximate one-sided upper bound of a \(1-\alpha\) confidence interval (CI) for \(\theta\) is

\[
S_U = \frac{T_1 - c(\alpha)T_k}{1 - c(\alpha)}
\]

where \(c(\alpha) = \left(\frac{1}{\log(k)}\right)^{-}\hat{\nu}\); note that in Solow (2005) 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 most recent records (in this case the youngest Acheulean sites), which obviated the need for including more ancient Acheulean sites in the analysis. We followed previous studies (Roberts and Solow, 2003; Solow, 2005; Rivadeneira et al., 2009; Clements et al., 2013; Boakes et al., 2015). The OLE method produces two types of estimates relevant to understanding the timing of extinctions. The first is \(T_E\), which here represents the estimated extinction date for the Acheulean in a given model. \(T_E\) is presented as years before present (BP). The second, \(T_{CI}\), is the upper bound of each model’s \(1-\alpha\) confidence interval. This is effectively the time beyond which the probability of the tradition still existing is below \(\alpha\). We chose \(\alpha = 0.05\) as the extinction threshold value (Roberts and Solow, 2003). The extinction date for each region was calculated using the R software package SExtinct (Clements, 2013). Since most dated Acheulean sites provide age ranges, mean values were used for the main analysis. Additionally, to address the uncertainty of some age estimates, 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
The end of the Acheulean: continental dates. The four continental regions returned dates spanning >120 Kya, demonstrating the Acheulean to end at different times across the world (Table 2; Fig. 3). Late Acheulean sites from North Africa and the Near East provide an extinction date estimated at 175 Kya. The Sub-Saharan African model returned similar dates, with the end of the Acheulean occurring 166 Kya. The Acheulean is predicted (57 Kya) to have ended slightly later in Europe, with the techno-complex’s demise happening between 141 and 130 Kya. The Asian OLE model predicted substantially later dates, with the end of the Acheulean occurring 57–56 Kya. As expected, the inclusion of the Fauresmth in the Sub-Saharan African model resulted in a later extinction date for this region (73–68 Kya). There was strong consistency in dates between the mean estimate and resampling methods (Table 2).

$T_{CI}$ values varied between the two methods, and provided diverse 95% confidence intervals between continental regions (Table 2). The sporadic nature of the archaeological record and the tens of thousands of years observed between some of the sites entered into each model explains this diversity. On occasion a negative value was returned, indicating a date in the future (from the present day). This is not meaningful, of course, as the Acheulean no longer exists, and instead reflects the aforementioned nature of the data.

The end of the Acheulean: global dates. Two sampling methods were used to identify sites for the global-level models (Table 1). The first (‘Global 1’) used the 10 youngest Late Acheulean sites from all continental regions, with no limit on where site contributions come from (bar the maximum of three per country). The second (‘Global 2’), which provided stricter limits on how the Acheulean was defined at a global level, required all four continental regions to contribute to the model. Date estimates based on the Global 1 OLE models varied between 52 and 50 Kya, but increased to 67–62 Kya when the five debated Asian sites were excluded (i.e. ‘Global 1b’). The further exclusion of Bhimbetka, India (another site debated by some), increased estimates to 107–105 Kya. A similar pattern exists for the Global 2 models, where Acheulean extinction estimates increase from between 29–32 Kya, to 56–45 Kya (Table 3; Fig. 4), and then 97–95 Kya with the removal of Bhimbetka.

Dates contributing to the Global 1 models were more tightly clustered around the most recent (i.e. ‘last seen’) records of the Acheulean at a global level, which resulted in a steeper incline of the model’s predictive slope after this occurrence. Effectively, this meant that the end of the cultural tradition was estimated to occur sooner after its final record, explaining why confidence intervals are less varied and remain positive for the Global 1 estimates (Table 3). As Global 2 estimates placed greater geographic limits on where sites contribute (data) came from, there was weaker clustering before the most recent record, which in turn resulted in greater confidence intervals.

### Table 2 Inferred extinction dates for the Acheulean in four continental regions.

| Model # | Model name                        | $T_E$ Mean estimates | $T_E$ Resampling | $T_{CI}$ Mean estimates | $T_{CI}$ Resampling |
|---------|-----------------------------------|----------------------|------------------|-------------------------|---------------------|
| 1       | Europe                            | 140,541              | 129,733          | 78,269                  | 52,125              |
| 2       | North Africa & Near East          | 175,892              | 174,938          | 143,176                 | 147,052             |
| 3       | Sub-Saharan Africa                | 166,212              | 169,590          | 18,475                  | 28,057              |
| 4       | Sub-Saharan Africa (Fauresmth)    | 68,006               | 72,678           | –83,156                 | –69,663             |
| 5       | Asia                              | 55,974               | 52,673           | 17,145                  | 12,592              |
| 6       | Asia (n = 5)                      | 56,214               | 57,014           | –208,890                | –207,653            |

Additional models were run for Sub-Saharan Africa and Asia. Included here are data derived from models using mean estimate and resampling procedure. $T_E$ is the estimated extinction date in years before present. $T_{CI}$ is the upper bound of the 95% confidence interval.
Discussion

The Acheulean lasted for over 1.5 million years, spreading widely across Africa and Eurasia. Our understanding of the period’s origin is relatively clear; multiple ~1.75 million-year-old sites support its emergence in East Africa (de la Torre, 2016), and little suggests otherwise. The end of the Acheulean, however, has always been more problematic, being limited to isolated dates from individual sites (e.g. Bates et al., 2014; Scerri et al., 2018) or broad 0.3–0.15 Mya statements drawn from overviews of the literature (McBrearty and Tryon, 2006; Stout, 2011; Fontana et al., 2013; Shea, 2017; Galway-Witham et al., 2019). Here, we use optimal linear estimation modelling and radiometric dates from 44 late Acheulean sites to provide the most accurate estimation yet of when the cultural tradition ended.

Continental-level models reveal broad consensus among estimates for Africa, Europe, and the Near East. North Africa and the Near East provided the oldest dates at 175 Kya, followed closely by Sub-Saharan Africa 170–166 Kya. European estimates are notably later, with its regional extinction estimated to be between 141 and 130 Kya. These dates are later than most statements in the literature concerning the end of the Acheulean in these regions (e.g. Bates et al., 2014; Scerri et al., 2018) or broad 0.3–0.15 Mya statements drawn from overviews of the literature (McBrearty and Tryon, 2006; Stout, 2011; Fontana et al., 2013; Shea, 2017; Galway-Witham et al., 2019). Here, we use optimal linear estimation modelling and radiometric dates from 44 late Acheulean sites to provide the most accurate estimation yet of when the cultural tradition ended.

Table 3 Predicted extinction dates for the Acheulean cultural tradition at a global level.

| Model # | Model name | $T_E$ | Resampling | $T_CI$ | Resampling |
|---------|------------|-------|------------|-------|------------|
| 7       | Global 1a  | 52,205| 50,451     | 10,595| 8077       |
| 8       | Global 1b  | 61,572| 66,818     | −63,770| −42,652    |
| 9       | Global 2a  | 31,969| 28,981     | −62,344| −68,838    |
| 10      | Global 2b  | 45,836| 55,982     | −130,035| −78,449    |

Included here are data derived from models using mean estimate and resampling procedures. $T_E$ is the estimated extinction date in years before present. $T_CI$ is the upper bound of the 95% confidence interval.

The inclusion of Fauresmith assemblages in the Sub-Saharan model decreased estimated dates considerably. This was not unexpected; Fauresmith artefacts are young compared to other Late Acheulean sites in this region (particularly Abdur Reef [Bruggemann et al., 2004]). The difference between the ‘last seen’ occurrence (i.e. Abdur Reef) and the estimated extinction date is, however, large (~55 Kya). Again, this is not surprising; few sites cluster around Abdur Reef’s late date, meaning that there is a long period without an Acheulean site prior to the last time the tradition is seen. This has the effect of increasing the predicted length of time that the Acheulean could have existed after the artefacts at Abdur Reef. This raises an important point concerning how the OLE method is impacted by the sporadic nature of archaeological finds, and whether an absence of dates immediately prior to a ‘last seen’ occurrence artificially decreases the tradition’s estimated end date. For example, had another site been found in Sub-Saharan Africa dating to 135 Kya (i.e. only 10 Kya older than Abdur Reef), it is likely that the model would have produced an older end date (see the North African and Near East model for an example of when chronologically tighter site clustering predicts a faster end to the tradition). Therefore, we want to stress that OLE estimates are only as accurate as the

![Fig. 4 Violin-boxplots detailing predicted dates for the end of the Acheulean at a global level, derived from 10,000 iterations of the random sampling method. Negative outliers in all models are not displayed.](https://doi.org/10.1057/s41599-021-00735-8)
radiometric dates and definitions available in existing literature. As new archaeological discoveries are made, it is possible that our inferences will not stand the test of time. Later instances of the Acheulean will push the extinction of the tradition even later, while other finds close to the ‘last seen’ occurrences used here could push it back in time (as described above). However, the present extinction inferences are robust in light of current archaeological knowledge.

It is also important to consider the varied definitions used for the Acheulean, and how this could have impacted the models. The Asian models highlight this predicament well. When all Acheulean sites in Asia are taken at face value, the tradition is predicted to end between 57 and 53 Kya. This appears to be due to a series of <100 Kya handaxe sites in South Korea and China. Yet, the inclusion of these assemblages in the Acheulean is controversial, both for their late occurrence and aspects of their form/production (Norton et al., 2006, 2009; Lycett and Gowlett, 2008; Shippton and Petraglia, 2011; Bae, 2017; Lee, 2017; Dennell, 2018; Li et al., 2018). Thus, while these sites adhere to standard technological definitions (see the section “Defining the Acheulean”), some would contest their inclusion. This is why we re-ran the Asian model but excluded the five controversial sites, such that the most recent Acheulean site in Asia was the 106 Kya Bhimbetka rockshelter III (India) (Bednarik et al., 2005; Petraglia et al., 2012). Even with the exclusion of the controversial younger sites, however, the Asian model predicted the Acheulean to end 57–56 Kya (with Bhimbetka removed as well the model still predicts an end 59–46 Kya). This suggests that, although positioned towards the extreme end of the tradition, handaxe assemblages from Houfang and Danjiangkou in China and Unjeong and Wolso in South Korea (among others) are not outside of the expected chronology for the Acheulean in this region. Future debate on their inclusion within the Acheulean cultural tradition should, therefore, focus on technological and morphological aspects (which includes their marked thickness and reduced elongation [Lee, 2017]).

The Acheulean as a global cultural tradition is demonstrated to end between 107 and 29 Kya. Some of this variation relates to the inclusion or removal of the aforementioned Asian sites. Equally, however, variation is driven by how the Acheulean as a global tradition is defined. If there are no geographic restrictions on the sites contributing to the model, then the Acheulean is predicted to end between 52 and 50 Kya (or 67–62 Kya, excluding the five Asian sites, and 107–105 Kya when also excluding Bhimbetka). When definitions are stricter, and incorporate all four continental regions on a broadly equal basis, the Acheulean is estimated to end between 29 and 32 Kya (or 56–45 Kya and 97–95 Kya, respectively, when excluding the Asian sites). This decrease pushes the end of the Acheulean further towards the end of the Middle Palaeolithic period. An explanation for this can be seen in how sites cluster around the youngest dates in each model. ‘Global 1’ models demonstrate tight clustering, while those in the ‘Global 2’ models extend over a greater period of time, resulting in a less sharp incline after the last seen date.

Both sampling methods have merit, however, we propose that an equal number of site contributions from each region is not necessary to define the Acheulean at a global level. Instead, if the Acheulean is present in two or more continental regions then we would argue that the tradition is still present at a global level. Thus, we favour the ‘Global 1’ estimates for when the Acheulean ended as a global cultural entity (i.e. between 107 and 50 Kya). Either way, the Acheulean is expected to continue on a global level after 100 Kya, most likely being restricted to smaller and more isolated geographic pockets within continental regions as time progresses. This would help to explain why some of the youngest sites exist in the extremes of the tradition’s range.

Overlap between the Acheulean and Middle Palaeolithic/Middle Stone Age. In all continental-level models, dates overlap with the emergence of MP and MSA technologies. The earliest MSA sites in Sub-Saharan Africa occur at Kathu Pan (South Africa), Florisbad (South Africa), and Olorgesailie (Kenya) (Kuman et al., 1999; Porat et al., 2010; Deino et al., 2018), and date to 291, 280, and 320 Kya (respectively). Thus, the Acheulean cultural tradition is demonstrated to overlap with MSA technological behaviours for over 110 Kya. The MP in the Near East displays similarly early dates (e.g. 335–240 Kya [Adler et al., 2014; Zaidner and Weinstein-Evron, 2020]), evidencing regional overlap of 160–70 Kya. France, Italy and the UK have early MP sites dating to between MIS 12 and MIS 8 (Déspriee et al., 2009; Moncel et al., 2020a), suggesting Acheulean and MP technological traditions to co-exist in Europe for over 250 Kya. Middle Palaeolithic assemblages in Asia date to as early as 380 Kya (Norton et al., 2009; Akhilesh et al., 2018), indicating an overlap of up to ~330 Kya years. We are not suggesting that there was constant cultural overlap; it would have been punctuated and dependent on population dynamics, extinction and colonisation events (Fig. 5).

Our results reveal that across the globe, the Acheulean overlapped with alternative stone tool cultures for substantial periods. As a result, a shift in how the Acheulean is defined at a chronological level is necessary. Either the Acheulean can no longer be considered exclusive to the Lower Palaeolithic (LP) period or Early Stone Age (ESA), or the LP (and ESA) as a technological entity persisted alongside the Middle Palaeolithic (and MSA). In both scenarios, populations practising Acheulean and Middle Palaeolithic (and MSA) technological behaviours would have coexisted. Definition of the Acheulean as both a LP and MP (or, ESA and MSA) cultural entity arguably provides greater consistency with existing techno-temporal frameworks.

Cultural overlap between the LP and MP is not a new suggestion (Isaac, 1972; Norton et al., 2009; Villa, 2009), and multiple research articles detail instances of the Acheulean continuing into the MP/MSA (McBrearty and Tryon, 2006; James and Petraglia, 2009; Norton et al., 2009; Hublin, 2009; Haslam et al., 2011; Fontana et al., 2013; Akhilesh et al., 2018; Mendez-Quintas et al., 2019, 2020). Santonja et al. (2016) have argued for such a scenario in the Iberian peninsula, even linking different technologies to the presence of different hominin populations. Scerri et al. (2018, p. 6) provide similar evidence at Saffaqah (Arabian Peninsula), where late Acheulean populations “overlap with an emerging Middle Palaeolithic”. What is provided here, however, is evidence of the strength of this overlap, and that irrespective of whether the Acheulean is considered at a continental or global level, it can no longer be restricted to a simple presence and absence dichotomy between the LP and MP (or ESA and MSA).

Implications for Late Acheulean hominin demography. Evidence of overlap between Acheulean and MP (and MSA) technologies indicates the co-existence of hominin populations practicing different stone tool behaviours. The widespread and extended overlap predicted here suggests that the arrival of MP technologies did not quickly replace its technological precursor in all instances. Rather, some populations continued to maintain Acheulean cultural traditions in spite of alternative technologies being practised elsewhere.

Potentially, the duration of technological overlap demonstrated in Africa, Europe and Asia (i.e. in the region of 300–100 Kya) is how long it took for these new technological ideas to permeate through social systems. Certainly, hominin populations were likely highly dispersed during the late Pleistocene (Dennell et al., 2011; Bocquet-Appel and Degioanni, 2013). However, given how
fast cultural information can be transmitted in human populations. We consider this unlikely. An alternative explanation is the existence of barriers limiting the spread of MP and MSA technologies (and in turn, the demise of the Acheulean) between hominin populations.

Physical and environmental barriers are known to prevent or mediate the spread of cultural information in non-human great apes and modern humans. Moreover, there are suggestions this occurred during the Mid-to-Late Pleistocene (Henshilwood and d’Errico, 2005; James and Petraglia, 2005; Lycett and Norton, 2010; Shea, 2017; Arroyo et al., 2019). Thus, it is plausible that on occasion, distance, mountain ranges, seas, and deserts created enough of a barrier to prevent the transmission of new technologies to Acheulean populations (particularly in north east Asia [Lycett and von Cramon-Taubadel, 2008; Lycett and Norton, 2010]). Climate change, mortality, and misfortune could have similarly influenced transmission (Dennell, 2018). However, given the substantial geographic and chronological peripheries discussed, such barriers could not have existed in all instances where overlap exists. Thus, two alternative scenarios can be suggested.

Potentially, the benefits conveyed by MP/MSA technologies were not strong enough to result in the consistent uptake of these new technologies when opportunities arose. Simply, individuals within Acheulean populations did not experience benefits enough to warrant spending time and energy learning new production techniques. Again, we consider this explanation unlikely given that MP/MSA technologies were adopted widely during this period (although we do not discount localised instances of this occurring) and multiple significant benefits have been demonstrated for MP technologies (e.g. Eren and Lycett, 2012; Shimelmitz and Kuhn, 2018).

Alternatively, it is possible that cognitive and anatomical barriers prevented the transmission of these new technologies, either through populations being unable to undertake more demanding tool production and use activities, or differences altering relevant cost benefit ratios. Indeed, hierarchical flaking is cognitively demanding (Stout, 2011), and Levallois tools have been suggested to indicate greater capabilities in MP/MSA species relative to those associated with the Acheulean (Foley and Lahr, 1997; McBrearty and Tryon, 2006; Sipton, 2016; Otte, 2019). We are not suggesting that transitioning between Acheulean and MP/MSA technologies always necessitates a cognitive leap. James and Petraglia (2009) discuss how Acheulean and MP technological overlap can reflect continuity of cognitive capabilities. Rather, cognitive differences between populations (perhaps species) may have prevented the uptake of MP/MSA technologies by some, even when opportunities for the transmission of these technologies occurred. The manual demands of Levallois flaking are not well understood and could also plausibly be greater than that required for Acheulean technologies (even if their use was not [Key et al., 2020]). Certainly, anatomical differences between Late Pleistocene hominin populations could have restricted lithic technological developments (Niewoehner, 2006; Marzke, 2013; Key and Lycett, 2018).

In recent years, fossil and genetic evidence has confirmed the co-existence of multiple hominin species during the later Middle Pleistocene of Africa and Eurasia. Evidence of admixture between some of these species confirms a degree of interaction (Browning et al., 2018; Villanea and Schraiber, 2019; Rogers et al., 2020), while anatomical comparisons highlight manipulative and cognitive differences varying in scale and nature (e.g. Tocheri et al., 2008; Holloway et al., 2018; Détroit et al., 2019; Galway-Whitam et al., 2019). Unfortunately, resolution on how these populations relate to the varying lithic technologies present during this time is often lacking. Nonetheless, it is not unreasonable to predict that the anatomical and cognitive differences observed between these species had the potential to result in the maintenance of different cultural traditions. Either through an inability to effectively use/produce some lithic technologies, or changes to relevant cost benefit ratios. Again, Asia provides a suitable (but not the only [e.g. Hawks and Berger, 2020]) example, with H. erectus (Rizal et al., 2020), H. floresiensis (Aiello, 2010), and H. luzonensis (Détroit et al., 2019) all displaying anatomy that could potentially limit their ability to produce and use MP technologies.

 Parsimony suggests the common ancestor of Neandertals and anatomically modern humans to be capable of producing MSA/MP technologies. In turn, it is logical to link the last known occurrences of the Acheulean with species that share a common ancestor with modern humans prior to our split with Neanderthals. Currently, this includes the aforementioned Asian Late
Pleistocene hominin species, along with *H. naledi*, and *H. heidelbergensis* (s.l.) populations separate to those that evolved into Neanderthals and modern humans. However, we again stress the dynamic nature of cultural and biological evolutionary pathways (Lycett and von Cramon-Taubadel, 2015; Scerri et al., 2019), and there is no specific reason that some Neanderthal, Denisovan and modern human populations could not also have reverted to or continued the Acheulean cultural tradition.

It is not our intention to discuss individual regions or species in detail. Nor is it within the scope of the paper to discuss precisely why regions transitioned away from the Acheulean at different times (although cultural, biological/species-related and ecological factors could be involved). Rather, we wish to stress that evidence of cultural overlap and increasing complexity in the distribution of late Middle Pleistocene lithic technologies is to be expected given increasing diversity in the fossil record (Wood and Boyle, 2016; Galway-Witham et al., 2019). Indeed, there is evidence of geographic and temporal overlap between multiple hominin species between 300 and 50 Kya (e.g. Dirks et al., 2017; Jacobs et al., 2019). The cultural scenario outlined here therefore mirrors the dynamic nature of the Middle Pleistocene hominin fossil record. Moreover, they are likely linked, with contemporaneous hominin species engaging in distinct stone-tool cultural practices in multiple regions around the world.

**Conclusion**

Presented here are the most accurate estimates yet for when the Acheulean cultural tradition ended. We do so using optimal linear estimation, a modelling technique often used to estimate the extinction of faunal species, but novel to archaeological research. In Africa and the Near East the Acheulean is predicted to end 175–166 Kya. In Europe, the Acheulean is predicted to end 141–130 Kya. These dates are only slightly younger than current understanding on the end of the tradition in these regions. Asian estimates, however, range between 57 and 53 Kya. Thus, the Acheulean continues in this region long after it has ended elsewhere, and for the majority of the MP. The Acheulean stopped being a global tradition between 107 and 29 Kya, although we favour an age bracket of between 107 and 50 Kya. These estimates suggest the Acheulean to have remained a distinct cultural tradition long after the inception of MP technologies in multiple continental regions. Persistence of the tradition in Europe and Asia may be linked to each region’s geographic isolation, relative to the rest of the Acheulean world. In line with the increasingly dynamic nature of the Middle Pleistocene hominin fossil record, contemporaneous hominin populations are demonstrated to have been practicing distinct stone-tool behaviours, potentially due to cognitive and anatomical differences.

**Data availability**

All data are available in the relevant Supplementary Information.

Received: 23 October 2020; Accepted: 10 February 2021; Published online: 02 March 2021

**References**

Adler DS, Wilkinson KN, Blockley S et al. (2014) Early Levallois technology and the Lower to Middle Palaeolithic transition in the Southern Caucasus. Science 345(6204):1609–1613

Aiello LC (2010) Five years of *Homo floresiensis*. Am J Phys Anthropol 142(2):167–179

Akholek K, Pappu S, Rajapara HM et al. (2018) Early Middle Palaeolithic culture in India around 385–172 ka refractions Out of Africa models. Nature 554:97–101

Arroyo A, Proffitt T, Key A (2019) Morphometric and technological analysis of Acheulean large cutting tools from Porzuna (Ciudad Real, Spain) and questions of African affinities. J Archaeol Sci Rep 27:101992

Bae K (2017) Paleolithic archaeology in Korea. In: Huba J, Lape P, Olsen J (eds) Handbook of East and Southeast Asian archaeology. Springer, New York, pp. 219–239

Bates MR, Wenban-Smith FF, Bello SM et al. (2014) Late persistence of the Acheulean in southern Africa in an MIS 8 interstadial: evidence from Harnham, Wiltshire. Quat Sci Rev 101:159–176

Bednarkim RG, Kumar G, Watchman A et al. (2005) Preliminary results of the EIP project. Rock Art Res 22(2):147–197

Beyene Y, Kotok S, WoldeGabriel G et al. (2013) The characteristics and chronology of the earliest Acheulean at Konso, Ethiopia. Proc Natl Acad Sci USA 110(5):1584–1591

Boakes EH, Rout TM, Colten B (2015) Inferring species extinction: the use of sighting records. Methods Ecol Evol 6(6):678–687

Bocquet-Appel JP, Degioanni A (2013) Neanderthal demographic estimates. Curr Anthropol 54(8):520–521

Brownie SR, Browning BL, Zhou et al. (2018) Analysis of human sequence data reveals two pulses of archaic Denisovan admixture. Cell 173(1):53–61

Brunner R, Aainer A (2017) The ‘Indian modern human’ handaxes from the Barkly Tabledland of northern Australia. Lithica 52:50–61

Clemens C (2013) eExtinct R Package. https://cran.rproject.org/src/contrib/Archive/eExtinct/ Accessed 16 Jul 2020

Clemens CF, Worsfold NT, Warren PH et al. (2013) Experimentally testing the accuracy of an extinction estimator: Solow’s optimal linear estimation model. J Anim Ecol 82:345–54

Corvinus G (2004) *Homo erectus* in East and Southeast Asia, and the questions of the age of the species and its association with stone artifacts, with special attention to handaxe-like tools. Quat Int 177(1):141–151

Deino AL, Behrensmeyer AK, Brooks AS et al. (2018) Chronology of the Acheulean to Middle Stone Age transition in eastern Africa. Science 360(6384):95–98

Dennell R (2009) The Palaeolithic settlement of Asia. Cambridge University Press, Cambridge

Dennell R (2018) The Acheulean assemblages of Asia: a review. In: Gallotti R, Musi M (eds) The emergence of the Acheulean in East Africa and beyond: contributions in Honor of Jean Chavaillon. Springer, Cham, pp. 195–214

Dennell RW, Martinon-Torres M, Bermudez de Castro J (2011) Hominin variability, climatic instability and population demography in Middle Pleistocene Europe. Quat Sci Rev 30(11–12):1511–1524

Désprie J, Voinchot P, Gageonnet R et al. (2009) Les vagues de peuplements dans la région Centre, France. Apports de l’anthropologie 133(1):125–137

Détroit F, Mijares AS, Corney J et al. (2019) A new species of Homo from the Late Pleistocene of the Philippines. Nature 568:181–186

Diez-Martín F, Yustos PS, Uribelarrea D et al. (2015) A new species of Homo from the Late Acheulean hominins at the Détroit F, Mijares AS, Corney J et al. (2019) A new species of Homo from the Late Pleistocene of the Philippines. Nature 568:181–186

Díez-Martin F, Yustos PS, Uribelarrea D et al. (2019) A new species of Homo from the Late Pleistocene of the Philippines. Nature 568:181–186

Dirks PHGM, Roberts ER, Hilbert-Wolf H et al. (2017) The emergence of the Acheulean in East Africa and beyond: contributions in Honor of Jean Chavaillon. Springer, Cham, pp. 195–214

Dennell RW, Martinon-Torres M, Bermudez de Castro J (2011) Hominin variability, climatic instability and population demography in Middle Pleistocene Europe. Quat Sci Rev 30(11–12):1511–1524

Eren MI, Lycett SJ (2012) Why Levallois? A morphometric comparison of experimental ‘preferential’ Levallois flakes versus debitage flakes. PLoS ONE 7(1):e29273

Foley R, Lahr MM (1997) Mode 3 technologies and the evolution of modern humans. Camb Archeol J 7(1):3–36

Fontana F, Moncel M-H, Nenziomi G et al. (2013) Widespread diffusion of technical innovations around 300,000 years in Europe as a reflection of anthropological and social transformations? New comparative data from the western Mediterranean sites of Orgnac (France) and Cave d’Ollio (Italy). J Archeol Anthropol 32(4):478–498

Gallotti R, Musi M (2018) The emergence of the Acheulean in East Africa and beyond: contributions in Honor of Jean Chavaillon. Springer, Cham

Galway-Witham J, Cole J, Stringer C (2019) Aspects of human physical and behavioural evolution during the last 1 million years. J Quat Sci 34(6):355–378

Gowlett JAJ (2015) Why the middle in the middle matters: the language of anthropological and social transformations? New comparative data from the western Mediterranean sites of Orgnac (France) and Cave d’Ollio (Italy). J Archeol Anthropol 32(4):478–498

Gallotti R, Musi M (2018) The emergence of the Acheulean in East Africa and beyond: contributions in Honor of Jean Chavaillon. Springer, Cham

Galway-Witham J, Cole J, Stringer C (2019) Aspects of human physical and behavioural evolution during the last 1 million years. J Quat Sci 34(6):355–378

Gowlett JAJ (2017) Why the middle in the middle matters: the language of comparative and direct in human evolution. Arch Pap Am Anthropol Assess 71(1):49–65

Gowlett JAJ (2015) Variability in an early hominin percussive tradition: the Acheulean versus cultural variation in modern chimpanzee artifacts. Philos Trans R Soc B 370(1682):20140358

Haslam M, Roberts RG, Shipman C et al. (2011) Late Acheulean hominins at the Marine Isotope Stage 6/5e transition in north-central India. Quat Res 75:670–682
Hawks J, Berger L (2020) On Homo naledi and its significance in evolutionary anthropology. In: Deane-Drummond C, Fuentes A (eds) Theory and evolution in anthropology. Routledge, Abingdon:107-123

Henshilwood C, d’Errico F (2005) Being modern in the Middle Stone Age: individuals and innovation. In: Gamble C, Poor M (eds) The Hominin individual and the question of social traditions. Current Anthropol 45(3):653–677

Meignen L, Bar-Yosef O (2020) Acheulo-Yabrudian and Early Middle Paleolithic at Hayonim Cave (Western Galilee, Israel): continuity or break? J Hum Evol 144:102735-3

Méndez-Quintas E, Demuro M, Arnold IJ et al. (2019) Insights into the late stages of the Acheulean technocomplex of Western Iberia from the Arbo site (Galicia, Spain). J Archaeol Sci Rep 27:101934

Méndez-Quintas E, Santonja M, Arnold IJ et al. (2020) The Acheulean technocomplex of the Iberian margin as an example of technology continuity through the Middle Pleistocene. J Palaeont Archæol https://doi.org/10.1007/s41982-020-00057-2

Michel V, Shen G, Valensi P et al. (2009) ESR dating of dental enamel from Middle Palaeolithic levels at Lazaret Cave, France. Quat Geochronol 4(3):233–240

Moncel MH, Ashton N (2018) From 800 to 500 Ka in Western Europe. The Oldest evidence of Acheulean in the technological, chronological, and geographic framework. In: Gallotti R, Musi M (eds) The emergence of the Acheulean in East Africa and beyond: contributions in Honor of Jean Chavaillon, Springer, Cham, pp. 215–235

Moncel MH, Ashton N, Arrarazelo M et al. (2020a) Early Levallois core technique between Marine Isotope Stage 12 and 9 in Western Europe. J Hum Evol 139:102735

Moncel MH, Biddittu I, Manzi G et al. (2020b) Emerging of regional cultural traditions during the Lower Palaeolithic: the case of Fosinoro-CEPTano basin (Central Italy) at the MIS 11-10 transition. Archaeol Anthropol Sci 12:185

Niewoehner WA (2006) Neandertal hands in their proper perspective. In: Hublin J-J, Harvati K, Harrison T (eds) Neandertals revisited: new approaches and perspectives. Springer, Dordrecht, pp. 157–190

Norton CJ, Bae K, Harris JWK et al. (2006) Middle Pleistocene handaxes from the Korean Peninsula. J Hum Evol 51(5):527–536

Norton CJ, Gao X, Feng X (2009) The East Asian Middle Paleolithic reexamined. In: Camps M, Chauhan PR (eds) Sourcebook of Palaeolithic transitions. Springer, New York, pp. 272–315

O’Brien MJ, Buchanan B (2017) Cultural learning and the Clovis colonization of Northeast North America. Evol Anthropol 26(6):270–284

Otte M (2019) Cognitive capabilities of the Neandertals. In: Nishiaki Y, Joris O (eds) Learning among Neandertals and Palaeolithic modern humans. Springer, New York, pp. 35–55

Pappu S, Akhilesh K (2019) Tools, trails and time: debating Acheulean group size at Attirampakkam, India. J Hum Evol 130:109–125

Pearse WD, Davis CC, Inouye DW et al. (2017) A statistical estimator for determining the limits of contemporary and historic phenology. Nat Ecol Evol 1:1876-1882

Petraglia MD, Ditchfield P, Jones S et al. (2012) The Toba volcanic super-eruption, environmental change, and hominin occupation history in India over the last 140,000 years. Quat Int 258:119–134

Picon A (2017) Technological adaption and the emergence of Levallois in Central Europe: new insights from the Markkleeberg and Zwochau open-air sites in Germany. J Quat Sci 33(3):300–311

Porta N, I, Chazan M, Schwarz V et al. (2002) Timing of the Lower to Middle Palaeolithic boundary: new dates from the Levant. J Hum Evol 43(1):107–122

Porta N, Chazan M, Grun R et al. (2010) New radiometric ages for the Fauresmith industry from Kathu Pan, southern Africa: implications for the Earlier to Middle Stone Age transition. J Archaeol Sci 37(2):269–283

Rivadeneira MM, Hunig G, Roy K (2009) The use of sighting records to infer species extinction: an evaluation of different methods. Ecology 90:1291–300

Rizal Y, Westaway KE, Zaim Y et al. (2020) Last appearance of Homo erectus at Ngandong, Java, 117,000-108,000 years ago. Nature 577:381–385

Robert DL, Solow AR (2003) When did the dodo become extinct? Nature 426:245–248

Roberts DL, Solow AR (2003) When did the dodo become extinct? Nature 426:245–248

Sanchez-Yuste P, Diez-Martín F, Domínguez-Rodrigo M et al. (2018) Acheulean without handaxes? Assemblage variability at FLK West (Lowermost Bed II, Olduvai, Tanzania). J Anthropol Sci 96:1–22

Santonja M, Perez-Gonzalez A, Panera J et al. (2016) The coexistence of Acheulean and ancient Middle Palaeolithic techno-complexes in the Middle Pleistocene of the Iberian Peninsula. Quat Int 411(Part B):367–377

Scher EML, Shipton C, Clark-Balzan L et al. (2018) The expansion of later Acheulean hominins into the Arabian Peninsula. Sci Rep 8:17165

Shipton C, Clark-Balzan L et al. (2018) The expansion of later Acheulean hominins into the Arabian Peninsula. Sci Rep 8:17165

Shipton C, Clark-Balzan L et al. (2018) The expansion of later Acheulean hominins into the Arabian Peninsula. Sci Rep 8:17165

Shea JJ (2017) Stone tools in human evolution. Cambridge University Press, New York
