



Technological innovations and regional diversity in Western Europe at ca. the MIS 11 threshold: a cladistic approach

Valentin Rineau^{a,*}, Paula García-Medrano^{b,c,d,e}, Valery Zeitoun^a, René Zaragüeta^f, Nick Ashton^e, Marta Arzarello^g, Andreu Ollé^{d,h}, Agnes Lamotteⁱ, Carlo Peretto^g, Marie-Hélène Moncel^b

^a Sorbonne Université, MNHN, CNRS, Centre de Recherche en Paléontologie – Paris, CR2P, F-75252, Paris, France

^b UMR 7194, HNHP (MNHN-CNRS-UPVD), Département Homme et Environnement, Muséum National d'Histoire Naturelle, Paris, France

^c Centro Nacional de Investigación Sobre la Evolución Humana (CENIEH), Burgos, Spain

^d Institut Català de Paleoeologia Humana i Evolució Social (IPHES-CERCA), Tarragona, Spain

^e Department Britain, Europe and Prehistory, British Museum, London, United Kingdom

^f Sorbonne Université, MNHN, EPHE, CNRS, Université des Antilles, Institut de Systématique, Évolution, Biodiversité, ISYEB, 75005, Paris, France

^g Sezione di Scienze Preistoriche e Antropologiche, Dipartimento di Studi Umanistici, Università degli Studi di Ferrara, Italy

^h Dep. Història i Història de l'Art, Universitat Rovira i Virgili, Tarragona, Spain

ⁱ UMR 9028 Hartis University of Lille, France

ARTICLE INFO

Keywords:

Pleistocene
Cultural evolution
Europe
Ca. MIS 11
Cladistics
Lithic technology
Three-item analysis

ABSTRACT

The ca. Marine Isotope Stage (MIS) 11 interglacial is considered to be a threshold for behavioural innovations in Western Europe. Innovations both in technology and subsistence are observed, as well as the appearance of Neanderthal anatomical features. Core technologies and Large Cutting Tools reflect changes in behaviours and innovations, with for instance, the onset and diffusion of the iconic Levallois core technology associated with more complex and standardized debitage. Following the severe glacial event of MIS 12, the lithic assemblages yield evidence of both innovations, but the chronology of their appearance remains unclear. For tracking these innovations and generally characterizing the technological and typological features of this period of time, a large database of the available ca. MIS 11 assemblages (from MIS 12 to MIS 10) has been built including a revision of some of the assemblages. In order to unravel the relationship between sites of this period, we applied a cladistic approach using three-item analysis, considering the assemblages themselves as the object of analysis, with an emphasis on core technology. We show how three-item analysis is an efficient method capable of correctly analysing characters from lithic technologies that appear to be intrinsically hierarchical. Our results suggest that Levallois core technology survived during the glacial event of MIS 12 and diversified during the long interglacial of MIS 11. Our results also show the absence of cultural endemism, which may be linked to significant mingling between northern and southern Europe.

1. Introduction

From the point of view of hominin evolution, the long MIS (Marine Isotope Stage) 11 (including MIS 10 at some sites) stands out in Europe, where archaeological remains have highlighted this interglacial as a threshold period, not only in Western Europe, but also in Central Europe (e.g. Berger and Loutre, 2003; Bazin et al., 2013; Ashton et al., 2006, 2011, 2016; Blain et al., 2014, 2015, 2021; Kleinen et al., 2014; Combourieu-Nebout et al., 2015; Goñi et al., 2016; Hryniewicz and Winter 2016; Oliveira et al., 2016; Sadori et al., 2016; Kousis et al., 2018; Rivals

and Ziegler, 2018; Szymanek and Julien, 2018; Palumbo et al., 2019; Brandon et al., 2020; Limondin-Lozouet et al., 2015, 2020, 2025; Dabkowski et al., 2012; 2022; Górecki et al., 2022). Recent data indicate a rapid increase in temperature at the start of MIS 11 (e.g. Loutre and Berger, 2003; Candy et al., 2014; Sherriff et al., 2021; Stefaniak et al., 2022; Tzedakis et al., 2022; Sassoon et al., 2023). This interglacial and its relative stability deeply modified the size of the available territories for hominins (e.g. north-west of Western Europe) and possibly opened ways of dispersing and adapting to new animal and vegetational zones. The establishment of the Strait of Dover is dated to end of MIS 12,

* Corresponding author.

E-mail address: valentin.rineau@sorbonne-universite.fr (V. Rineau).

<https://doi.org/10.1016/j.qsa.2026.100314>

Received 11 July 2025; Received in revised form 16 January 2026; Accepted 21 January 2026

Available online 24 January 2026

2666-0334/© 2026 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

thereby reducing the land link to Britain from the continent to dryland across the southern North Sea Basin during MIS 11 (Gibbard, 2007; Gupta et al., 2007; Hijma et al., 2012). MIS 12 was a severe glacial period and is considered as a major challenge for hominins with an abrupt decrease of human evidence with gaps and hiatuses. The subsequent shrinking of coastal territories and new vegetational zones in the long interglacial of MIS 11 (424 ka to 374 ka), may have encouraged hominin occupation of the interior and mountainous regions, and with increased evidence of occupation in the north-west and south of Western Europe (Hérisson et al., 2016; Hosfield and Cole, 2018; López-García et al., 2018; Moncel et al., 2018a, 2018b; Antoine et al., 2021; Hosfield, 2022; Kot et al., 2022; Rodríguez et al., 2022). European vegetation was key in driving biomass availability for large herbivores and affecting the mobility of human groups and perhaps demographic expansion.

Current genetic data and anthropological analyses show that European Neanderthal characteristics emerged as a regional mosaic of anatomical features between 600 and 400 ka perhaps through local isolation of some groups (Green et al., 2008; Hublin, 2009; Martínón-Torres et al., 2012; Meyer et al., 2016; Demuro et al., 2019; Bergström et al., 2020; Lockey et al., 2022). However, the diversity of anatomical features, such as the Ceprano skull alongside other remains attributed to *Homo heidelbergensis*, suggests a complex European history with local diversification during MIS 11, which may have increased through the expansion of favourable territories for hominins (Manzi, 2016), prior to homogenisation of the Neanderthal metapopulation from MIS 5 (Condemi, 1985; Vandermeersch, 1989; Hublin, 1998).

The greater number of sites located in both north-western and southern parts of Europe (i.e. lithic assemblages with a clear stratigraphic context) helps investigation and description of evidence of new subsistence behaviours and technical innovations (e.g. core technologies and tool kits) (Limondin-Lozouet et al., 2010, 2015; Dabkowski et al., 2012; Wiśniewski, 2014; Mathias et al., 2017; García-Medrano et al., 2015, 2023; Hosfield and Cole, 2018; Moncel et al., 2016, 2018a, 2018b, 2020a, 2021a; 2021b; López-García et al., 2018; Davis and Ashton, 2019; White et al., 2019; De Lombera-Hermida et al., 2020).

For instance, the onset of Levallois core technology and increase in centripetal/discoidal-type debitage are now clearly recorded in different places and dated from the end of MIS 13 to MIS 12–11 (Moncel et al., 2021a,b). These new technologies are associated with the persistence of a diversity of various complex knapping methods depending on several aspects, such as the quality of the raw materials (Gagnepain and Gailard, 2003; Michel et al., 2013; Ollé et al., 2016; Peretto et al., 2016; Daura et al., 2017, 2018; Romagnoli, 2021; Bahain et al., 2022; Guibert-Cardin et al., 2022). Like biological lineages which can develop anatomical features which then disappear, some innovations can be occasionally rooted in the past, before MIS 12, possibly disappearing during the glacial event of MIS 12 and emerging again during MIS 11.

In some areas there is evidence of networks and of regionalization of traditions with possible regional mobility of human groups associated with specific land-use (Villa et al., 2016; Pereira et al., 2018; Biddittu et al., 2019; Moncel et al., 2020a, 2020b; Ravon et al., 2022; García-Medrano et al., 2022a, 2023). Raw material management and planning are observed in some sites, with not only gathering of local stones but fragmentation of the reduction sequences across the territory. Flint is the main raw material for north-west of Europe, while in the south industries are characterized by the use of various stones and it is admitted that the geological resources could have impacted the technological strategies and the tool kit. For instance, few cleavers are present in the north-west, possibly due to the main use of flint nodules while in the south various cobbles make for the easy production of large flakes (Mourre, 2003).

Bifaces ("Acheulean-type" industries) continue to be made, with origins prior to MIS 12, although some sites lack these tools. There is a diversity of traditions, some reflecting early Middle-Palaeolithic-type behaviours, while different activities (e.g. butchery sites) are proposed to explain the composition of some assemblages. There are changes in

shaping methods and morphological products with both thinner, symmetrical handaxes, sometimes resharpened, with a high degree of standardization, or sometimes crudely-made bifacial tools. Such variability could be due to the disruption of MIS 12, with possible local isolation of residual populations (Iovita et al., 2017; Moncel et al., 2018; Barsky et al., 2019; White et al., 2019; Méndez-Quintas et al., 2020; Nicoud et al., 2022; García-Medrano et al., 2023). Changes in subsistence behaviours are also recorded with improved hunting strategies, more complex management of carcasses and manufacturing of bone tools (Yravedra et al., 2010; Conard et al., 2015; Moigne et al., 2016; Rodríguez-Hidalgo et al., 2017; Parfitt et al., 2022; Venditti et al., 2022). These behavioural changes suggest increased cognition with new skills and social interactions that help the diffusion of innovations, and indicating a decrease in the constraints of raw material (Moncel et al., 2015; Shipton and White, 2020). Finally, early fire control (especially from MIS 11 and possible evidence from MIS 13) could have contributed to new hominin abilities to expand territories with behavioural adaptations for better survival in Northern and Central Europe (Kretzoi and Dobosi, 1989; Gowlett and Hallos, 2000; Preece et al., 2006; Lumley, 2015; Davis and Ashton, 2019; Sanz et al., 2020; Ravon et al., 2022; Davis et al., 2025).

This threshold in Western Europe, corresponding to the end of the Lower Palaeolithic (and Acheulean) and the beginning of the Middle Palaeolithic, is at present under-investigated, in particular in regard to why and how innovations appeared and were transmitted among populations (Dereux et al., 2016; Grove, 2016). The reasons underlying these behavioural changes, pushing back the roots of the Neanderthal world, have yet to be identified: was this behavioural evolution rooted in previous traditions and how is it possible to observe that in MIS 11 sites? Was it due to arrivals of new populations or the onset of Neanderthals from *Homo heidelbergensis* (and Middle Pleistocene hominins) with innovations? Is the higher number of sites reflective of increased population, rather than explained by taphonomy and better preservation? If so, was this conducive to early regional networks and the diffusion of innovations, or was it due to environmental adaptation to changes in climate?

Before we can answer these questions, we need to give a historical perspective to these technological changes by analysing the relationships between MIS 11 sites in order to reflect the cultural evolution of the period. Such a perspective raises questions on filiation, reinvention or introduction of new lithic strategies, loss or acquisition of technological behaviours or tools, and impact and constraints of environmental parameters such as the availability of raw materials and the role of geography. In order to resolve the general problem of the history of lithic innovations during MIS 11, several more specific sub-questions can be addressed:

- Evidence of Levallois core technology is dated to the transition of MIS 13/12 (i.e. Boëda, 1993, 1994; Moncel et al., 2020b; White et al., 2011, 2024) and exists in different assemblages during MIS 11 and MIS 10. If an early date is accepted, did this technology persist through to MIS 11, but is archaeologically difficult to identify due to the low population during MIS 12? Or was there reinvention (in situ?) after MIS 12? During MIS 11, as this technology is observed in different places, did it appear in one place and spread, or appear independently in several places?
- Discoid-type cores sensu lato (s.l.) and centripetal cores are often considered to be the origin of the Levallois method. As increased complexity is recorded in centripetal and discoid-type core technologies during MIS 11 (hierarchy in the debitage with bifacial discoid cores sensu stricto (s.s.), prepared platform, productivity), can we use these trends to estimate a degree of filiation and/or cultural evolution of human groups, and their roots in the past?
- For the heavy-duty component, can regional or chronologically constrained clusters of sites be identified, with relationships

recognized by the mode of “façonnage”, the intensity in shaping for some assemblages and the composition of the tool kit?

In this study, we use a cladistic approach based on the presence of technological innovations, to identify cultural groups and relationships between as many lithic assemblages as possible that broadly date to around MIS 11. A few sites from other periods were also added in order to discuss the temporality of the cladogram. The work is based on a large database of the most significant sites in Western Europe (SOM 1, 2) with chronological data, archaeological context, together with cultural data and technological details for each site. We apply a cladistic analysis using three-item analysis (3ia thereafter; Nelson and Platnick, 1991) on characters based on the technological data and innovations on both flaking methods, Large Cutting Tools (LCTs) and small tools, for each site. The principle of cladistic analysis is not to choose a priori one character that would be the only relevant one for reconstructing cladistic relationships. The process of bringing different types of characters into congruence is the procedure that makes it possible to show a posteriori that a given character is relevant for resolving the relationships between given sites, i.e. synapomorphic. This implies that a character may be relevant for certain relationships, but not all.

As a detailed discussion of typological terminology is beyond the scope of this paper, for the LCTs, we refer to the large shaped tools (sensu Kleindienst, 1962) using commonly accepted terms for the Lower Palaeolithic, such as choppers/chopping tools or pebble tools, as well as typical Acheulean forms such as bifacial handaxes, cleavers, picks, or knives (e.g., Bordes, 1961; Kleindienst, 1962; Leakey, 1971; Isaac and Isaac, 1977; Sharon, 2007).

Using a precise quantification of three-item statements (3is thereafter) and the computation of several analytical tools such as the retention index (Kitching et al., 1998) for character and character states using analytical tools (Rineau and Zaharias, 2025), the resulting cladogram is discussed to quantify the link between clades and characters in order to answer the question of the historical development of lithic innovations at the onset of MIS 11.

2. Materials and methods

2.1. Archaeological sites database

Our study is based on a large data set of 47 layers from 42 archaeological sites in Western Europe from France, Italy, Iberian Peninsula and England, to which we have added some sites from Germany, Ukraine and Hungary (see tables). The sites include various biomes and landscapes with open-air locations on the North European plain (southern England and northern France) and both open-air and cave sites in southern basins and valleys. The largest quantity of sites is however mostly located in Western Europe, explained by either better preservation of sites, historically more excavations or a higher density of human occupation in this part of the continent at this time. We are conscious of biases in this database due to the limited amount of qualitative and quantitative data published for some sites, and by variability in methods used to study them. These factors may affect the representativeness of the dataset and should be taken into account when interpreting the results.

The database is made of sub-datasets. The first informs on all the contextual and technological information on the archaeological sites and levels, using published and unpublished data, including some of our own reviews of the material. The main references are also listed on the database (SOM 1). The description lists the context of the occupations as primary, where remains are found within the sedimentary deposits, and secondary, when remains have been reworked and not in original deposits. Chronologically, we have focused on the ca. MIS 11 event and we have enlarged the database to key-sites from the end of MIS 13/beginning MIS 12 to MIS 10 (e.g. Cagny-la-Garenne I-II, TD10.1 Gran Dolina, Áridos I, Cueva del Ángel, Cueva de Bolomor, Ambrona, Torre in Pietra

and La Micoque) (Santonja et al., 1980, 2001; Fernández Peris et al., 2008; Yravedra et al., 2010; Méndez-Quintas et al., 2020). In order to test the hypothesis of past filiation of some innovations, we have included the French sites of Cagny-la-Garenne I and II dated to MIS 13/12 for the early Levallois evidence (Moncel et al., 2020b). Environmental proxies have been recorded to provide chronology (mammalian biostratigraphy, geology, malacology, palynology) and to reconstruct the climatic context (temperature - warm, mild, cool or cold).

For the location of each site, the geographical coordinates (longitude, latitude, altitude), topography (fluvial, fluvial without terrace information, hill, lake, mountain, plateau, lake-shore, valley, valley-edge), general location (inland, continental, coastal) and type of site (cave, open-air, shelter) have been recorded. Also included are data regarding the size of the excavations and density of the material, to help explain any biases in the record and the paucity of some assemblages.

A large corpus of data refers to the archaeological patterns: presence of fire and main features, human remains (number and types of remains), raw materials (types, distance - local, semi local and exogenous), lithic remains (number, main technological activity flaking and/or shaping, fragmented and/or complete operative chains), hard and/or soft hammerstones, function of the site (butchery site, camp, workshop), subsistence data, duration (long-term, short-term, seasonal) and faunal remains (herbivore and carnivore types). In this database, we have avoided cultural attribution, as for instance Clactonian, Acheulean and Middle Palaeolithic-type. These attributions are often questioned depending on the size of the excavated area, the type and date of the excavation (old surveys on open air surfaces) or the kinds of criteria selected, and are therefore not suitable for defining homologies in the context of cladistics (see Fig. 1).

This study is based on additional sub-databases, in which we have divided detailed technological patterns into two main fields: flaking (cores and flakes) and shaping processes (Large Cutting Tools-LCTs and small retouched tools on flake) (Figs. 2 and 3).

Core technology includes data on each raw material, (if known) number and ratio of various technological and metrical parameters, as for instance, core size, number of flaking faces (unifacial, bifacial, trifacial and multifacial), number and organization of removals. We have also included some features considered as marks of technological complexity such as hierarchical organization of removals and type/preparation of striking platform. Due to the diversity of approaches, the database has included first a long list of terminologies found in the literature for core structure. In order to simplify and harmonize, we have reduced the terminology to this following list: Unipolar, Bipolar, Alternate flaking (including S.D.D.A. “Surfaces de débitage alternées”- and “Clactonian” débitage), Orthogonal (orthogonal to multifacial, cores with more than two flaking surfaces), Centripetal, Discoid (s.l and s.s with pseudo-Levallois products) and Levallois (i.e. Boëda, 1993, 1994; Peresani, 2003; Baena et al., 2017; White et al., 2024). The definition of Levallois core technology is generally well-established (Boëda, 1993, 1994) despite the use of this term being sometimes questioned for early examples using proto-Levallois, pre-Levallois, prepared cores, or simple prepared cores (White and Ashton, 2003; Moncel et al., 2021a,b; White et al., 2024). It has been questioned as to whether Levallois evidence exists in the UK before MIS 9/8, a late arrival being related to a warming event (White et al., 2024), as is possibly the case in Central Europe (Wiśniewski, 2014). “Prepared core technology”, being sometimes related to Levallois, has also been called into question by White et al. (2024).

For products of débitage, we have recorded data by each raw material, and (if known) number of remains and ratios, sizes, type of flakes among the reduction processes, platform (prepared and/or non-prepared), number and organization of removals, and cortical extension.

The light-duty component (i.e. flake-tools) has been recorded (number and ratio) by each raw material, the type of flake-tool, type of support, size, type and extension of retouch.

Finally, the LCTs were described first in general with types of raw



Fig. 1. MIS 11 sites in Western Europe (©GörkemCenkYeşilova @IPHES-CERCA).

material and large categories (number and ratio). Then each category (handaxes, cleavers, picks, pebble tools, bifacial tools, “rabots”, crudely-made tools) was described for the size, support (flake, nodule, pebble and others), form, symmetry, extension of the shaping (number of removals and series) and cortex, final retouch, percussion and mode of shaping.

2.2. Cladistic analysis

The cladistic analysis using 3ia (Nelson and Platnick, 1991) was applied as a pilot study to lithic assemblages from several layers from the Italian site of Notarchirico (Rineau et al., 2023). The analyses made it possible to detect non-random cladistic structure supplementing the traditional technological analyses which had not shown any statistically significant differences between the studied assemblages (Moncel et al., 2020). The 3ia is a cladistic method that codes characters as inclusive hierarchies (Nelson and Platnick, 1981; Cao et al., 2007). The method only allows the terminals in the analysis to be grouped together on the basis of shared derived character states (Williams and Ebach, 2006). Using 3ia therefore prevents the formation of groupings supported by plesiomorphic states such as in parsimony, criticized as being a remnant of phenetics allowing entities to be grouped indifferently on the basis of absence and/or presence, unlike cladistic methods which only group entities on the basis of presence, i.e. derived states, i.e. evolutionary innovations. A summary of the relative merits of cladistic analysis and 3ia in the context of evolutionary archaeology has already been produced by Rineau et al. (2023).

Such an analysis was based directly on databases of lithic objects for

each layer. This method, which is useful for gathering homogeneous data from equivalent sites, was not possible here. In fact, the sites analyzed in this study had to be synthesized beforehand by literature review with additional data recorded by the project. From the initial database (see SOM), we have selected the most relevant sites due to the quantity and quality of the information, and the number of available materials to avoid disturbances in the comparison. The poor record of some assemblages would have led to problems in the analysis. The archaeological data did not allow us to distinguish between missing data that was due to a lack of sampling and a true absence, thus, coding poorly known sites would have led to errors. The inclusion of these sites would distort the analysis by using poor assemblages from which their lithic composition is more the result of a taphonomic bias or ancient excavations than a real distribution. Lademagne, Clacton, La Celle, Saint Acheul, Solana del Zamborino, Hitchin and Chadwell St Mary, were not included in the analysis due to the lack of too much important information that we have recorded or exists at these sites. This left, a total of 40 terminals representing lithic assemblages from 34 European sites making up the sampling.

We decided to analyse these sites directly from a synthetic matrix, which enabled us to skip directly the part of transforming homologies on lithic objects into characters on lithic assemblages (more detailed explanations of the protocol in Rineau et al., 2023). By directly producing the cladistic characters relating to the sites from a database designed specifically for this study of relationships between sites of MIS 11, we have nevertheless sought to code the sites in the most similar way possible in order to reflect the different behavioural acquisitions over time. Our approach, that aims at retrieving relationships between sites,

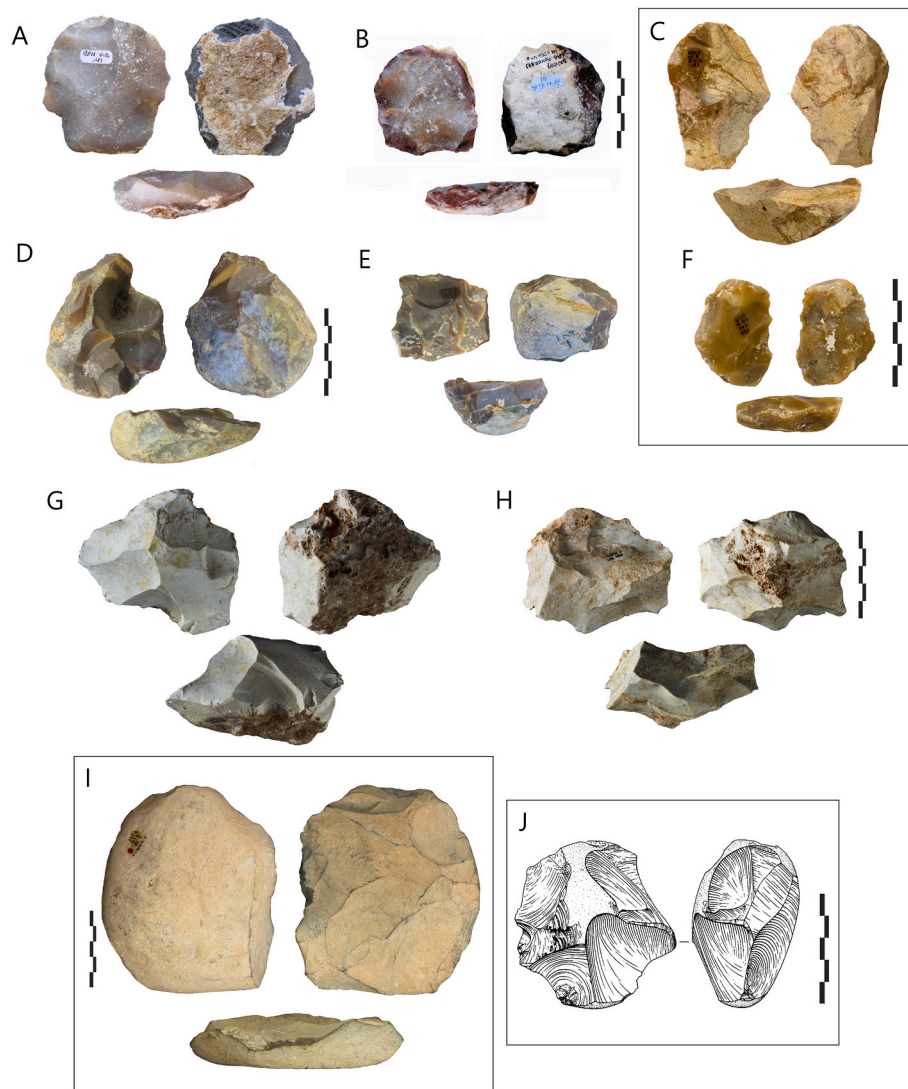


Fig. 2. Examples of cores from European MIS 11 sites: A-B, La Noira stratum a (France); C and F, Guado San Nicola (Italy); D-E, La Noira stratum a (France); G-H, La Cansaladeta Level J (Spain); I, Terra Amata (France); J, Elveden (UK).

is qualitative: the presence of a technological innovation on a site makes it possible to hypothesize the complete cultural acquisition of the innovation. There is therefore no need for a threshold number of objects in order to validate their evolutionary significance. In this way, the cladistic approach, essentially qualitative, avoids the problem of sites not being equivalent in terms of sampling effort. However, with single examples of a technology, it is dependent on inter-analyst consistency, and correct identification of more ambivalent examples, such as a chance preferential flake on a core, resembling Levallois.

Each character state can be understood as a hypothetical grouping. In the end, only four characters make up the analysis, but correspond to 24 derived states. We could have produced a matrix with 24 binary characters, for example absence/presence of Levallois. However, there is additional hierarchical information. For example, for the flaking methods, the centripetal, discoid and Levallois technologies can be grouped together in relation to the orthogonal technology since these three technologies involve a hierarchical organisation of removals. Furthermore, these four states can be grouped together as complex core technologies compared to unipolar, bipolar and alternate flaking technologies. As a result, the structure of information technologies is intrinsically hierarchical. The hierarchical structure of the characters means that the states can be directly coded hierarchically in 3ia (Faure-Brac et al., 2020). If it seems unusual to merge character states

like this, it is partly because combining numerous states tends to generate a lot of repetitions, which is equivalent to polymorphism in phylogenetics. However, we used the free-paralogy (Nelson and Ladiges, 1996) algorithm designed in Rineau et al., (2023) in order to cut character trees and eliminate repetitions while conserving the maximum amount of cladistic information. Following this protocol, we were able both to capture the intrinsic hierarchical information of lithic technologies and to remove the high number of repeated terminals without altering the original statements.

Three large sets of items, supplemented by a character derived from a statistical analysis of the relative proportions of lithic objects, were distinguished in order to produce four characters that were as informative and resolved as possible. Each resulting tree is displayed in Fig. 4. In each case, we indicate the title of the character and the corresponding hierarchy, i.e. the tree hypothesis (the character), in Newick format (see Cao et al., 2007). The brackets indicate the postulated relationships between states.

2.2.1. Character #FM: core flaking methods (0,(((1),(2),(3)),((4),((5),(6),((7),(8),(9))))))

Sites without cores are coded 0.

Presence of cores and types (((1),(2),(3)),((4),((5),(6),((7),(8),(9))))))

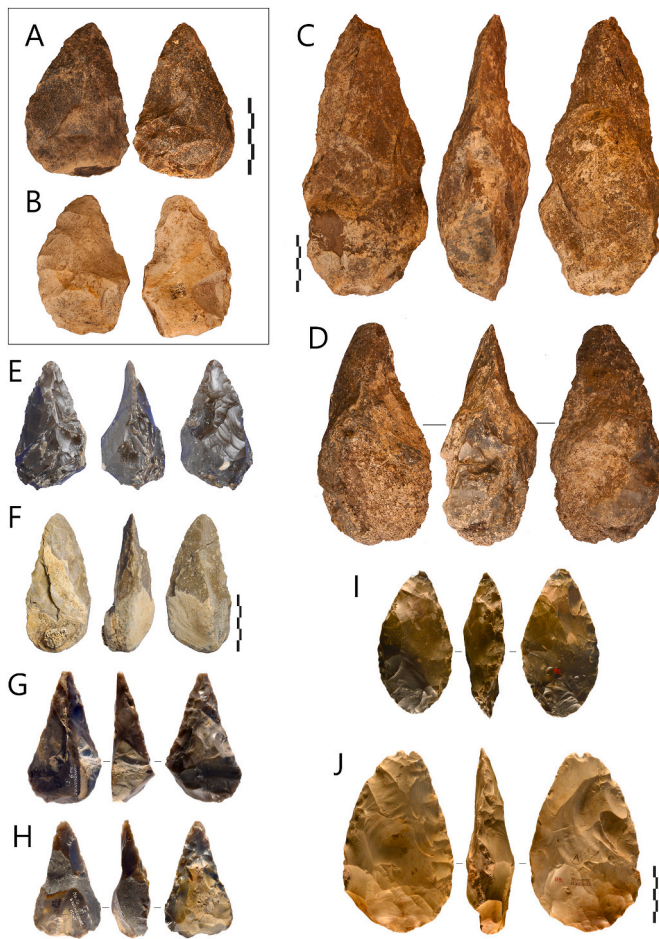


Fig. 3. Examples of Large Cutting Tools from European MIS 11 sites: A-F, Guado San Nicola (Italy); G-H, Swanscombe (UK); I-J, Elveden (UK).

Simple core technologies (1,2,3)

- Unipolar (1)
- Bipolar (2)
- Alternate flaking (3)

Complex core technologies (4,5,6)

- Orthogonal to multifacial (4)
- Centripetal (5)
- Discoidal (6)

Hierarchical organization of removals (7,8,9)

- Complex centripetal (7)
- Complex Discoidal (8)
- Levallois (9)

Comments – Character #FM allows extrapolation of potential relationships between lithic assemblages, based on core technologies, divided into simple and complex. All sites with unipolar cores include type A and type B of de Weyer et al. (2022). Sites with bipolar cores are grouped together. Sites with alternate flaking (two flaking surfaces) include type C and S.S.D.A. of Forestier (1993) and de Weyer et al. (2022). By the intensity or complexity of the core management, orthogonal to multifacial (more than two flaking surfaces), centripetal, discoidal (s.l. and s.s.), and Levallois technologies have also been considered to be informative characters, the three last above all being states close to each other. Finally, the increase of complexity due to the presence of both prepared striking platform and hierarchical organization of removals is also coded as informative, with three modalities (7–9). As many repetitions occur, such as complex discoidal appearing both in character states 6 and 8, we removed the redundancy by

applying the free-paralogy subtree following the procedure of Rineau et al. (2021). Such a coding is directly inspired from Faure-Brac et al. (2020) which faced the same issue.

2.2.2. Character #LCT: large cutting tools types (((0),(1)),(2,(3),(4))) Heavy duty tools s.l.

- Chopper and Chopping-tools (Pebble tools) (0)
- Picks (1)

Large Cutting Tools s.s.

- Handaxes (2)
- Pre-shapes and Proto-handaxes (3)
- Cleavers (4)

Comments – This second character is related to Large Cutting Tools s.l. (LCTs). Sites are gathered based on the presence of heavy-duty tools (Pebble-tools and picks) on the one side, and based on the presence of handaxes (LCTs s.s.) on the other side (bifaces, cleavers and crudely-made handaxes). The presence of some specific tools such as ‘rabots’ (large thick crudely-made scrapers) was not informative, as it does not allow the clustering of several sites.

2.2.3. Character #ST: small tools types ((0),(1,(2),(3),(4)),((5),(6),(7),(8)))

Marginal and isolated retouch.

- Notches (0)
- Continuous retouch (1)
- Marginal (2)
- Denticulates (3)
- Continuous retouch (scrapers) (4)

Other and special types.

- Endscrapers (5)
- Invasive and scaled retouch on scrapers (6)
- Convergent tools (7)
- Burins and others (8)

Comments – This third character concerns small tool types. Notches are isolated in a specific character state, as it is the only representative of the marginal and isolated retouch group. Sites are also lumped together by small tools with continuous retouch, and by the presence of special types of tools.

Most of the sites yield cores, LCTs, and small tools. However, although our approach is fundamentally qualitative and discrete, we also sought to capture potential quantitative information on the lithic assemblages. We therefore sought to discretize the relative proportions of cores, small tools, and LCTs. We used an agglomerative clustering using euclidean distances and a ward criterion to discretize two clusters that were coded as two potentially informative character states, allowing to obtain a qualitative treatment to quantitative data. Using visual inspection, no discretization of the distribution was obvious. Thus, we chose to limit to two the number of clusters generated to limit the amount of information in the form of three-taxon statements generated.

2.2.4. Character #clusters: lithic assemblages constitution ((0),(1))

- Cluster 1 (0)
- Cluster 2 (1)

A final type of data is likely to be able to provide information, but

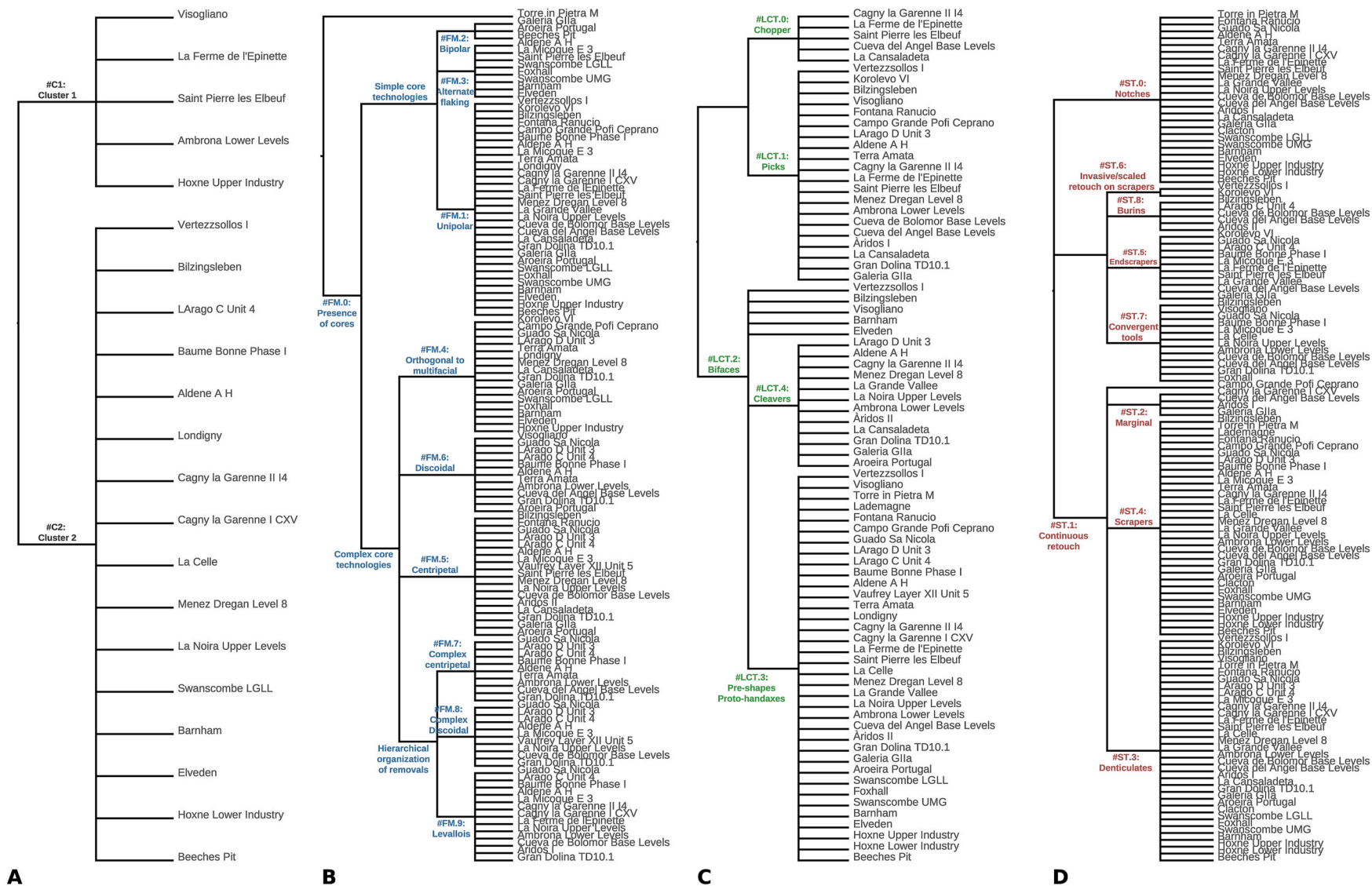


Fig. 4. The four trees representing the relationships between sites derived from the four characters based on relative proportions (A), flaking methods (B), large cutting tools (C), and small tools (D) before processing by free-paralogy subtree analysis to remove repeated terminals.

poses serious problems. This concerns the raw material used to produce lithic objects: chert/flint, limestones, quartzite, sandstone, volcanic rocks, etc. This characteristic may reflect a vertically transmitted behaviour, a specific interest in a particular raw material, the choice being the initial step of the “chaîne opératoire”. However, it might only reflect the real abundance of a raw material in the environment, an extrinsic character. If so, it is likely to alter the result of the cladistic analysis by grouping sites together not on the basis of shared constitutive elements, but on the basis of extrinsic factors, i.e. the presence of specific types of raw material in the immediate environment. In north-west Europe, flint was the main raw material due to its wide availability in sedimentary basins. In the South, a diversity of stones is collected by the environmental and mineral diversity. We have therefore chosen not to include any characters relating to raw materials after testing that there was no significant difference with or without this character in the analysis. The fact is that it cannot be demonstrated whether it is one case or the other. It is therefore on the basis of a precautionary principle that we had to avoid taking this criterion into account. However, it would be interesting to develop a methodology to extract behavioural similarities, in identifying whether or not there is a preferential choice of material, uncorrelated with the environment.

Thus, a first analysis of 40 lithic assemblages was coded in a matrix together with 26 character states grouped in four main characters, with the aim of establishing a tree linked showing technological and typological behaviour features. This was in order to identify the first signs of regionalization suggested with the development of Middle Palaeolithic diversity and spatial distribution of innovations. Due to the way the technological information was recorded in the database, there are more #FM character states (#FM.0-9) than any other. However, this also reflects the more easily identifiable hierarchical relationships with cores. It is acknowledged that this might downplay the role of handaxe variation, which is more suited to detailed technological analysis in combination with 3D Geometric Morphometrics (e.g. the WEAP Method; García-Medrano et al., 2022, 2023). But, as this paper is primarily seeking an understanding of innovation towards Middle Palaeolithic behaviours, as opposed to the origins of the Acheulean, this is best addressed through a deeper understanding of the chronological relationships between different core technologies.

2.3. Retention index

To complete the qualitative discussion of the cladogram, we quantitatively analyzed the results of the cladistic analysis by directly quantifying the amount of phylogenetic information contained in the characters and the amount of information involved in supporting the tree. To achieve this, we mainly used the retention index that was developed initially in parsimony and that is a central tool for 3ia (Kitching et al., 1998). For explanatory purposes, we needed to recall the definition of several terms that are specific to cladistic analysis. Note that if these terms are debated in cladistics (Göpel and Richter, 2023), 3ia is coherent with specific definitions that are presented below. In cladistics, it is necessary to distinguish between the *entities* to be analyzed and their *parts*. In order to understand the cladistic relationships between different entities (here, sites; in phylogeny, taxa), it is necessary to analyse the parts that make up these entities (here, sites are made up of lithic objects; in phylogeny, taxa can be divided into anatomical parts, for example).

Homology: a statement that several parts are the same related to others, based on vertical transmission (Nelson, 1994). Each level of sameness is called a homolog. Homology relates homologs, defined by Owen (1843: 379) as “the same organ in different animals under every variety of form and function”. Thus homology is a nested relationship of relative sameness among homologs.

Homoplasy: a rejected statement of homology after the cladistic analysis. The parts cannot be considered to be the same; hence, they cannot be explained by simple vertical transmission (De Pinna, 1991).

Character: a statement that different entities are related to others, extrapolated from homology. Each character-state corresponds to a homolog.

Synapomorphy: a character-state accepted after cladistic analysis that characterizes a clade of a cladogram. A synapomorphy statement links parts and entities.

The retention index has a particular history. It was simultaneously proposed by Archie (1989) and Farris (1989a, b) in the context of cladistic analysis using the parsimony method. Both propositions aimed to compute the proportion of extra-steps present in the hypotheses-set in relation to the maximum possible number of steps in either case. However, Archie applied the formula to matrices of characters whereas Farris calculated the retention index per character. Most interestingly, each author interpreted their index in a very different way. Archie called his index ‘Homoplasy Excess Ratio’ and considered it as a measurement of the complementarity of homoplasy. In cladistics, homoplasy is generally understood as the contrary of (secondary) homology (De Pinna, 1991), the primary homology being a hypothesis of grouping that can be accepted (secondary homology) or rejected (homoplasy). However, in parsimony analysis, homoplasy is considered more specifically as a quantity equivalent to the number of extra-steps. However, quantifying secondary homology as the contrary of a number of extra steps is of no meaning.

On his side, Farris considered his retention index as a measurement of the complementarity of the distortion, a coefficient he proposed in 1973 that was supposed to measure the disagreement among (phenetic) trees. Farris (1973) method produced a matrix of OTUS x Clusters. Each OTU was coded as ‘1’ if the OTU was present in the cluster in the source tree and ‘0’ if it was absent. Distortion measured how many times a cluster from the first phenogram appeared broken in the second one, in relation to the maximum number of possible fragments. In order to count the fragments, Farris used extra-steps using the parsimony method. Thus, distortion measured, at least operationally, the proportion of states included in a cluster characterized by another state. The retention index of Farris (1989a) is, indeed, calculated as the complementarity of the distortion formula. The distortion coefficient d is calculated as:

$$d = \frac{ES - ES_{\min}}{ES_{\max} - ES_{\min}}$$

Where ES is the number of observed extra-steps, $ES_{\max}$ is the maximum number of extra-steps on any tree, and $ES_{\min}$ is the minimum number of extra-steps (i.e. the number of character states – 1 in unordered characters). Finally, the retention index RI is defined $1 - d$, hence

$$RI_{\text{parsimony}} = \frac{ES_{\max} - ES}{ES_{\max} - ES_{\min}}$$

Farris (1989a,b) considered that the retention index measured ‘the fraction of apparent synapomorphy in the character that is retained as synapomorphy on the tree’. However, the Farris definition faces several problems. The first one, is that, in the parsimony method, both the character or the ensemble retention index are measured on unrooted trees, where both synapomorphy or homoplasy are not defined. A second one is illustrated by the following examples. Let’s take the tree $(a,b(c,(d,(e,(f,g)))))$ where c, d, e , and g bear the derived state ‘1’ of a binary character. This character has an extra-step and its RI = 0.5. Now, let’s take the same tree and character, with a third outgroup x , identical to the other two outgroups present in the first tree has been added which consequently does not bear the apomorphic state: $(x,a,b(c,(d,(e,(f,g)))))$. Obviously, neither the amount of homoplasy, i.e. extra-steps, or ‘fraction’ of synapomorphy has changed: the group (c,d,e,f,g) is monophyletic, its synapomorphy is the character-state ‘1’, and, because F shows the plesiomorphic character-state ‘0’, there is still an extra-step. However, the retention index changes from 0.5 to 0.67. The reason is that the proportion of distortion of the character has changed and, in the

parsimony method, this is what the retention index actually measures. Distortion may be measured on unrooted trees. Character-states partition taxa into several disjoint classes. Distortion measures how many instances of any character-state other than the one that defines a particular class are found in this particular class. The trees presented above have different potential distortion (but the same amount of homoplasy and synapomorphy as understood in the parsimony context) and have, as a consequence, different retention index values. The retention index is thus a measure of the complementarity of the distortion, a measurement whose utility can still be understood in the parsimony context.

In the context of 3ia, however, the retention index can be fruitfully redefined to circumvent the issues raised in parsimony. The 'fraction of apparent synapomorphy in the character that is retained as synapomorphy on the tree' can be quantified by using 3is. In 3ia, and, more generally, in the theory of phylogenetic systematics (Hennig, 1966), synapomorphy is a grouping hypothesis, and a 3is a minimal statement of grouping derived from the decomposition of a character. Each character state is a putative synapomorphy, any 3is can be understood as minimal fragment of synapomorphy hypothesis stating that two terminals are more closely related between them than to a third. For this reason, a 3is, as any hypothesis, can only be rejected or not. The retention index in 3ia is thus the proportion of hypotheses of grouping that are compatible with the general solution, i.e. the proportion of accepted 3is (Kitching et al., 1998). In other terms, the retention index of a character corresponds precisely to the proportion of 3is retained by the cladogram (Fig. 5):

$$RI_{\text{per character}} = \frac{T}{C}$$

C being the amount of 3is generated by the decomposition of the character, and T the number of 3is from C that are also present in the cladogram. A 3is rejected by the test is therefore simply a 3is incompatible with the optimal tree. Hence, we found here a complementarity between secondary homology that can be related to the amount of accepted 3is T, and homoplasy that can be related to the amount of rejected 3is C-T. Any variation of RI can be easily understood in terms of accepted and/or rejected 3is fluctuations. Finally, we note that the use of RI in 3is is made using solely rooted trees from the beginning to the end of the analysis, precluding the use of non-cladistic structures such as unrooted trees that cannot correctly represent cladistic groupings.

The ensemble retention index can also be soundly interpreted in the context of 3ia. It is a measure of the proportion of 3is that fits the cladogram. The global retention index is thus the optimality criterion of the 3ia and can be computed for any cladogram and for any $i \geq 1$ characters as

$$RI_{\text{total}} = \frac{\sum_{i=1}^n T_i}{\sum_{i=1}^n C_i}$$

Thereafter, we discuss both the Ri that represents the fraction of accepted statements, the values of C_i that quantify the weight of each character in the analysis, and T_i that represent the weight of each

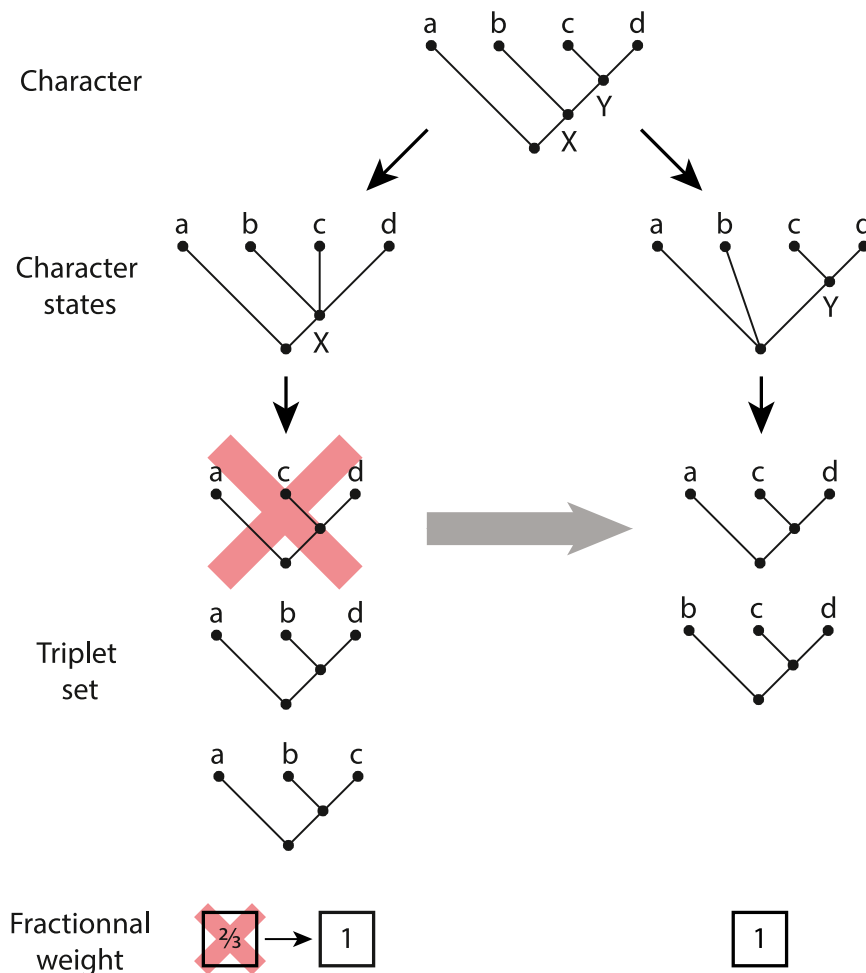


Fig. 5. Rationale of retention index in three-item analysis as a measure of congruence between a cladogram and one or several trees. The retention index is the ratio of three-item statements from a character tree that are in agreement with a cladogram.

character in supporting the final cladogram. In 3ia, the retention index really calculates the fraction of information contained in the character retained in the cladogram (Kitching et al., 1998). Here, the number of 3is independent of the character retained in the cladogram = the fraction of synapomorphy contained in a character. At 0, no information from the character is used to support the cladogram (no 3is retained). In supporting the cladogram (no 3is retained), whereas at 1, all the information contained in the character is used to support the cladogram (all the 3is are retained). Thus, optimal tree, i.e. the tree that maximizes compatibility is always the tree that maximizes the ensemble retention index.

Finally, a highly desirable property of 3ia is that it takes into account the information content of characters (Nelson and Ladiges, 1992), the fractional weight (FW) of each independent 3is into which a character is analyzed represents what might be called a minimal unit of cladistic information (Rineau et al., 2021). The amounts of 3is rescaled by their fractional weights might be used to remove issues of dependency amongst 3is. Due to the way the technological information was recorded in the database, there are more #FM character states (#FM.0-9) than #LCT character states (#LCT.0-4). However, this also reflects the more easily identifiable hierarchical relationships with cores. It is acknowledged that this might downplay the role of handaxe variation, which is more suited to detailed technological analysis in combination with 3D Geometric Morphometrics (e.g. the WEAP Method; García-Medrano et al., 2020; 2022, 2023). But, as this paper is primarily seeking an understanding of innovation towards Middle Palaeolithic behaviours, as

opposed to the origins of the Acheulean, this is best addressed through a deeper understanding of the chronological relationships between different core technologies.

3. Results

The hierarchical matrix (Cao et al., 2007; SOM 3) of 26 informative character states and 40 lithic assemblages analyzed with 3ia using Agatta software (Rineau and Zaharias, 2025) resulted in a single optimal tree. All character trees have been decomposed into three-taxon statements and weighted using fractional weighting (Rineau et al., 2021) to remove redundancy. Then, the retained optimal tree is the one in agreement with the maximal amount of statements. The optimal tree has been computed using heuristics algorithms of PAUP* (Swofford, 2003) and WQFM (Mahbub et al., 2021) modified for the specific use of 3ia. Repetitions were removed using the triplet maximisation (TMS) algorithm (Rineau et al., 2023). The cladogram shows a somewhat pectinate structure with an important division in two clades, one mostly britannic, and one continental. To allow a more precise discussion of the clades and their support, we interpreted the results with respect to the retention index (Kitching et al., 1998) and the information content of characters. We calculated the overall retention index for all the characters, the retention index per character and the retention index for each character state. We also calculated the total amount of information in terms of weighted 3is, and also amount of 3is supporting the optimal cladogram. These results are displayed in Table 1. Treatment of

Table 1

Table showing the repartition of cladistic information within the analysis in terms of sum of 3is for each character and character state. Line total represents the sum of all characters. Total information: sum of weighted 3is generated by the character/state. Retained information: sum of weighted 3is generated by the character/state that are in agreement with the cladogram. Total contribution: Total information of the character or state divided by the sum of all 3is generated by all characters. RI: retained information divided by total information.

Character codes	Character names	Retained Information	Total Information	Total contribution	RI
#Clusters		45.0667	130.00	0.01	0.3467
#FM		2456.6736	3658.00	0.25	0.6716
#LCT		781.8846	1456.00	0.10	0.537
#ST		960.3984	1954.00	0.14	0.4915
Total		8488.0466	14396.00	1.00	0.5896
Character codes	Character names	Retained Information	Total Information	Total contribution	RI
#Clusters.1		33.6	60.00	0.00	0.56
#Clusters.0		11.4667	70.00	0.00	0.1638
<i>Simple core technologies</i>					
#FM.1	Unipolar	123.2222	140.00	0.01	0.8802
#FM.2	Bipolar	27.3333	74.00	0.01	0.3694
#FM.3	Alternate flaking	109.00	224.00	0.02	0.4866
<i>Complex core technologies</i>					
#FM.4	Orthogonal to multifacial	139.75	360.00	0.03	0.3882
#FM.5	Centripetal	252.2353	368.00	0.03	0.6854
#FM.6	Discoidal	188.1429	338.00	0.02	0.5566
<i>Hierarchical organization of removals</i>					
#FM.7	Complex centripetal	223.1111	248.00	0.02	0.8996
#FM.8	Complex Discoidal	248.5455	290.00	0.02	0.8571
#FM.9	Levallois	281.7333	350.00	0.02	0.805
#LCT.0	Chopper and Chopping-tools	201.2	361.00	0.03	0.5573
#LCT.1	Picks	201.2	361.00	0.03	0.5573
#LCT.2	Bifaces	52.4571	136.00	0.01	0.3857
#LCT.3	Pre-shapes and Proto-handaxes	56.2941	165.00	0.01	0.3412
#LCT.4	Cleavers	160.3333	297.00	0.02	0.5398
<i>Marginal and isolated retouch</i>					
#ST.0	Notches	119.25	322.00	0.02	0.3703
#ST.1	Continuous retouch	156.5263	342.00	0.02	0.4577
#ST.2	Marginal	46.00	102.00	0.01	0.451
#ST.3	Denticulates	75.2903	210.00	0.01	0.3585
#ST.4	Continuous retouch (scrapers)	141.2414	252.00	0.02	0.5605
#ST.5	Endscrapers	131.6	252.00	0.02	0.5222
<i>Other and special types</i>					
#ST.6	Invasive and scaled retouch on scrapers	36.00	36.00	0.00	1.00
#ST.7	Convergent tools	173.6364	270.00	0.02	0.6431
#ST.8	Burins and others	46.8	132.00	0.01	0.3545

characters in 3ia, computation of fractional weights, removal of repetitions using TMS algorithm of free-paralogy subtree analysis, plus calculations of total information, retained information and retention index (global, per character, and per state) have all been made using Agatta Rineau and Zaharias, 2025) using the command: `agatta analysis filename.hmatrix -analysis = heuristic -chartest -consensus = strict -pdf -ri -software = paup -softpath = /paup-path/paup/paup4a168_u-buntu64`. The 3is information calculation and the retention index can also be calculated separately from the analysis using `ri Agatta` command.

4. Discussion

The aim of the cladistic analysis was to show whether a hierarchical structure could be highlighted on the basis of the technological patterns of each site and differential presence of lithic innovations between the different sites in our database, with a particular interest in core technologies. We justify the use of cladistics because of the congruence principle (Hennig, 1966). Indeed, the congruence principle implies that different, independent characters (here, technological strategies) all point in the same direction, towards a common history. Given that the characters in cladistic analysis are hierarchical, and represent grouping hypotheses, congruence between all the characters can only lead to obtaining an evolutionary scenario in the form of an inclusive hierarchy, i.e. a tree. Environmental parameters or horizontal transmission cannot generate congruence because they only concern specific characteristics and *ad hoc* events. Cultural diversification by vertical transmission and inheritance of innovations are the only mechanism that can generate congruence in cultural evolution, since all characters are supposed to be implied by this history. In the following section, we discuss the structure of the cladogram, and the hierarchical part of the history that it can tell us about at the threshold of MIS 11, bearing in mind that this is only the cladistic side of this period, the one that we can try to reconstruct using the principle of congruence. In the second part, we explain why this tree

was obtained regarding the characters and their congruence. Returning to the details of the characters we explain how they support this tree. To do this, we use the retention index and the quantification of 3is (total and accepted statements) to understand better how the characters are structured in relation to the tree and to each other. Finally, in the third part, we compare the cladogram obtained with environmental parameters that may have had an influence on cultural history during MIS 11.

4.1. Structure of the cladogram

The 3ia resulted in a single dichotomous cladogram highlighting the relationships between sites (Fig. 6), which shows a largely pectinate structure. Below we discuss more specifically a selection of clades that are thought to have particular significance because of the proposed groupings and the nature of their support. However, due to the absence of clear synapomorphies except “invasive and scaled retouch” (#ST.6), we discuss clades which gather the main occurrences of derived states, which is meaningful in terms of 3is, since these are the clades that are most locally supported by the characters.

4.1.1. Earlier dichotomies

Clade 1 (Fig. 6) groups together all sites except Torre in Pietra (Italy). The presence of the unipolar core technology (#FM.1) groups together most sites of the clade 1. At Torre in Pietra the series contains a high ratio of flake-tools and cores on flint with a hierarchical debitage, associated with limestone artefacts and LCTs (Villa et al., 2016; Grimaldi et al., 2020; Muttillio et al., 2021). However, Torre in Pietra does not contain any informative derived character state for cores (#FM.0), and only handaxes and proto-handaxes for LCTs (#LCT.2-3). Consequently, the 3ia rejects Torre in Pietra as a sister group of all other sites because of the very small number of derived states. Its cladistic position on the tree can therefore not be considered as artefactual due to the number of lithic objects found in it, leading to the conclusion that its position is due to a

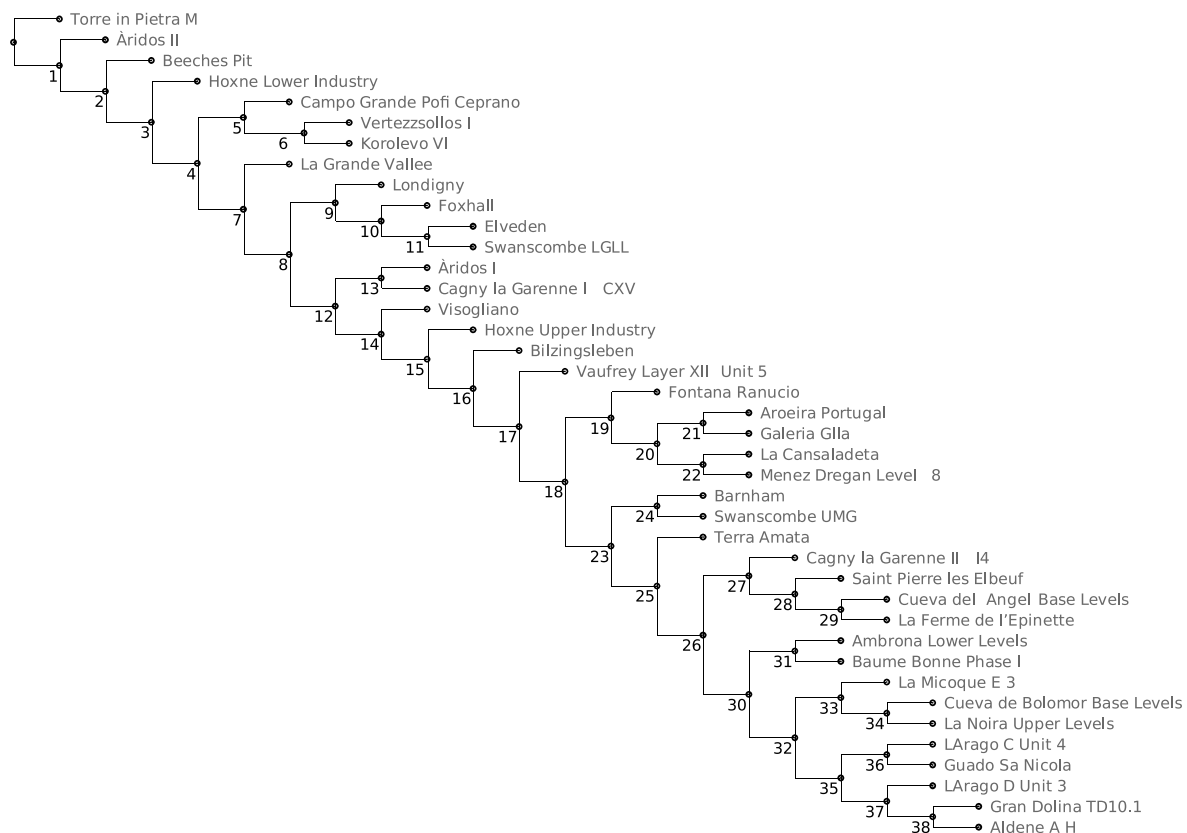


Fig. 6. Cladogram of sites obtained through the cladistic analysis of lithic technologies.

positive absence of some features and technological innovations (derived states). Within clade 1, Áridos II is the sister group of all other sites. Its position is due to a lack of many technological innovations, but this absence is probably due to a sampling bias, as only 34 items from a very small spot have been found. This hypothesis is confirmed by the high level of incongruence, because of similarities with phylogenetically highly distant sites: as the presence of centripetal debitage (#FM.5) links it to clade 16, the presence of cleavers (#LCT.4) links it to clade 18, and burins (#ST.8) to clade 26. We can estimate that if excavations continue in Áridos II, it is probable that the site would be included in clade 16 at least. Furthermore, Clade 4 is mainly supported by the presence of LCTs including choppers and chopping tools (#LCT.0), and picks (#LCT.1). Within this clade, we note the specific grouping of the sites of Korolevo (Ukraine) and Vertesszölos (Hungary) together (clade 6). This grouping confirms the existence of a specific Central European behaviour, east of the River Rhine, characterised by thick small tools, some being shaped (invasive and scaled retouch-type, #ST.6) and the lack of LCTs and bifaces (Kretzoi and Dobosi, 1989; Koulakovska et al., 2010; Usyk et al., 2023).

Regarding geography and in general, there is a complete absence of coherence when looking at the grouping of sites. Geographically distant sites appear to be cladistically linked. For example, clade 10 gathers three UK sites, and its sister group is to be found in France (Londigny). We also note the recurrence of clades with two sites, one in the north and one in the south: clade 13 group - Áridos I (Spain) and Cagny-la-Garenne CXV (France), clade 22 - Cansladeta (Spain) and Menez Dregan (France), clade 34 - Bolomor (Spain) and la Noira upper level (France), and clade 36 - Arago C (France) and Guado San Nicola (Italy). This recurrence of north/south clades implies an absence of endemism on a Western European scale despite the existence of significant geographical barriers such as the Alps, the Pyrenees, and the Strait of Dover. Somewhat differently, sites with contrasting assemblages are grouped, such as clade 11 with Elveden containing handaxes, but Swanscombe LGLL being a core and flake industry without handaxes. Equally, clade 24 with Swanscombe UMG has handaxes, but Barnham unit 5 is without. The sites within these clades emphasise that the cladistics analysis is focused on core technology, and the deep roots of that technology in Europe, rather than the presence or absence of handaxes.

4.1.2. Levallois core technology

The hierarchical structure of the characters used in this analysis results in a nesting of clades that makes it possible to discuss the way in which lithic innovations related to flaking methods starting from clade 14. Sites with discoid and centripetal cores are only present in clade 17 and 23, respectively. Clade 18 attests the existence of a cultural group, somewhat characterised by presence of cleavers (#LCT.4), typical of southern sites for all periods, but homoplastic, as it is not present in all sites of clade 18 and is also present in Áridos II (Spain) and la Grande Vallée (France). Within this clade, the main technological feature that appears in our cladogram is Levallois (#FM.9), which concerns sites within clade 23. They include both British sites (Barnham unit 5 and Swanscombe UMG, clade 24, with single examples each) and continental sites with this technology (clade 25). According to the cladistic analysis, the core technologies also explain why UK sites are scattered throughout the tree. The 'prepared core technology' described in UK, often related to a pre-Levallois concept, is younger, recognized mainly at the MIS 9/8 boundary. However, a recent unpublished revision of the core assemblages attributed some from Hoxne (upper and lower) and Elveden to discoid-types, and Levallois and discoid-type technology at Barnham unit 5 and Swanscombe UMG (Ashton et al., 1994, 2006, 2011, 2016, 2021; White and Ashton, 2003; White et al., 2019; Moncel et al., 2015, 2020a, 2020b; Ashton and Davis, 2021; García-Medrano et al., 2022, 2023). The increase of complexity in centripetal (clade 32, #FM.7) and discoid (clade 23, #FM.8) flaking methods seems related to Levallois in the tree. These core technologies are close together and technological relationships can be seen between an increase in

complexity in centripetal debitage and Levallois core technology (Peresani, 2003; Baena et al., 2017). Some sites show a higher hierarchical management of centripetal and discoid-type cores, considered as evidence of a higher complexity in this debitage (for instance Terra Amata, la Noira upper level) (Lumley, 2015). The proximity between these character states on the cladogram shows this technological proximity, and a possible threshold in cognition, even if the appearance of Levallois is not clearly nested in clades characterised by the appearance of complexity in discoid and or centripetal flaking methods, mainly because Áridos I and Cagny-la-Garenne I have Levallois but do not have discoid or centripetal cores (complex or not). If the cultural unit of clade 23 groups together sites on the basis of the presence of Levallois core technology (#FM.9), this state is homoplastic as it also characterizes these two sites. However, clade 13 grouping together Cagny-la-Garenne I CXV (North France, flint, with presence of LCTs) and Áridos I (Spain, quartzite, without LCTs) may be the consequence of both series being relatively small (Santonja et al., 1980, 2001; Yravedra et al., 2010; Tuffreau and Lamotte, 2010; Moncel et al., 2015; Lamotte and Tuffreau, 2016; Méndez-Quintas et al., 2020; García-Medrano et al., 2022). There is no clear synapomorphy, but the sites are grouped mainly by their diversity of light duty tools (especially scrapers with marginal retouch #ST.2) and by the presence of Levallois cores/flakes (#FM.9), even if these character states are homoplastic (Barsky et al., 2019; Rossoni-Notter et al., 2016). The cladistic analysis presented here rejects the hypothesis of a unique appearance of Levallois core technology in Western Europe (Santonja et al., 2001, 2014; Peretto et al., 2016, 2016b).

It is interesting to note that this division into two groups also divides the two areas of Cagny-la-Garenne I and II analyzed here. The technological association between Levallois on the one hand and complex discoid and centripetal on the other is not congruent and indicates at least two distinct and incompatible hypotheses of grouping. Thus discoid-type cores s.l. and centripetal cores currently cannot be considered as being the origin of the Levallois method in a historical sense. Another competing hypothesis would be that the homoplasy is due to missing data in Áridos I and Cagny-la-Garenne. Only a few cores have been found in Áridos I, and in Cagny-la-Garenne. It is clear that more artefacts are necessary to test more precisely the homology of Levallois in Western Europe, which does not appear in our analysis to be a synapomorphy (i.e. it does not characterise a single cultural clade), and of the technological link between Levallois and increased complexity of flaking methods.

We note, however, that clades 13 and 23, characterised by the presence of Levallois, include the Cagny-la-Garenne assemblages, which provides us information about the temporality of the development of cultural innovations. The increase in discoid complexity, centripetal, and the appearance of Levallois therefore occurred certainly before MIS 12. These technologies survived with human populations during the MIS 12 glacial event and were culturally diversified in MIS 11 (Moncel et al., 2021a,b; García-Medrano et al., 2023).

4.2. Character state contributions and retention index

The use of 3ia has the advantage of being able to explain how the optimal tree was found by measuring the fit between the cladogram and the 3is generated by the character decomposition. The analysis allows quantification of the overall contribution of each character and state to the analysis, and to quantify the total information content of each character (Table 1). In our analysis, there is a strong correlation between the total amount of information in each character state (and in each character as well) and the information retained, which contributes to the choice of the optimal tree. There is also a strong correlation between the information retained and the retention index. This correlation implies that the more informative a character is, the more likely it is to contribute in supporting clades within the optimal tree. A character with a lot of missing data will therefore have less influence than a character

with no missing data, since missing data reduces the number of 3is produced. In the same way, each character state being a clade hypothesis produces 3is accordingly. A character postulating two clade hypotheses will on average have a greater contribution than a character postulating only one clade (excluding the root).

Examination of the information content and retention index of the four characters reveals the high degree of heterogeneity in the information content of the characters. Character Cluster#1, splitting sites in two groups according to their relative proportions of lithic objects, is very poor and makes almost no contribution to the optimal tree (0.01). The fact that only two states were generated in order to downweigh the character is linked to the fact that there is no clear limit between the different proportions among sites. The low retention index of 0.35 clearly indicates that this character is highly incongruent with the others. With regard to lithic technologies, and while the large cutting tools and small tools are comparable in terms of total contribution, the small tools originally possessed more information, implying a lower retention index. Core technologies appear to be the decisive character in supporting the optimal cladogram, representing a total contribution equivalent to that of all the other characters combined. This is related to the high number of character states, leading to a higher contribution. However, the total retention index of 0.59 reveals a fairly low congruence, since such an index implies that 41 % of the total information encoded in the matrix has not been retained, which is relatively high – as the quantity of information accepted is symmetrical to the quantity of information rejected. Unlike parsimony, 3ia can be understood both as a method that minimizes homoplasy (minimizes the rejection of 3is) and maximizes homology (maximizes the retention of 3is). In parsimony, minimising transformation steps cannot be understood as the symmetric of maximizing homology.

When looking at information content for each state, we can compare more comparable things, since a state corresponds to a single clade hypothesis, whereas a character can contain a variable number of states. The total quantity of information generated is linked to the structure of the state, and the more symmetrical it is (i.e. same number of terminals possessing the state as terminals not possessing the state), the more informative it has (Nelson and Ladiges, 1992). We can see that the states corresponding to the ratio are the least informative of all, even at the state level. It should be noted that two character states, although they are very uninformative, have a very high retention index: continuous retouch (#ST.1, RI = 0.46) and “invasive and scaled retouch-type” (#ST.6, RI = 1). These values correspond to highly asymmetric character states corresponding to the least inclusive nodes, which were accepted during the analysis. The continuous retouch group is together in the matrix of all the sites except Áridos II, which explains its position in the tree, even though it is not directly the sister group of all the other sites, given the position of Torre in Pietra m. Moreover, the “invasive and scaled retouch Quina-type” is together with the two sites of Koroievo and Vertezsolos in an Eastern European clade.

When we look at the contribution of each character state to the analysis, we also note first that core technology has the most contributory states (4–9). Small tools, on the other hand, form character states that are generally poorly informative for the analysis. It would therefore seem that the information provided by small tools is of little use in reconstructing the relationships between sites, due to the higher rate of homoplasy they provide, implying an absence of hierarchical structure for these technologies. The LCTs are more heterogeneous, with scattered character states in terms of total contribution of information to the analysis. The presence of bifaces (#LCT.2) and crudely-made bifaces (#LCT.3) provides very little information for structuring the cladogram. Finally, we note that the most important character states for the analysis are those relating to the continental clade 12, i.e. pebble tools (#LCT.0), complex centripetal (#FM.8), discoid and complex discoid (#FM.6 and 7), and Levallois (#FM.9). It is these states, highly congruent between them, that seem to have structured the cladogram the most. These states correspond precisely to technological innovations in MIS 11.

4.3. Cladogram and the influence of extrinsic parameters

The type of raw material for LCTs (bifaces, cleavers and picks) is flint for British and northern French sites (nodules available in quantity), and variable for other continental sites, often depending on the size of the pebbles/nodules that allows production of large flakes in the south (e.g. De Lomberra-Hermida et al., 2020; García-Medrano et al., 2022). The flaking operational processes are either complete or fragmented with often local raw materials, a few sites with raw material from long-distances (la Noira upper level for flint, Caune de l'Arago C, D) (Barsky et al., 2019; Moncel et al., 2021a,b). The raw material for cores is on the principle stones, mainly local, often flint when available in the surroundings. The impact of the raw materials is thus not relevant and enough to explain the structure of the cladogram. We have tested the influence of raw material by considering it as an additional character in the cladistic analysis: (flint, chert, millstone, limestone, lidite: fine grained rocks/quartzite, quartz, sandstone: coarse-grained rocks and volcanic rocks). We have modified the matrix accordingly to test the cultural potential of raw material choices and reran the cladistic analysis. The addition of this character does not alter the structure of the important nodes in the cladogram. We conclude from this that the selection of raw material is not inherited but pragmatic and, in any way, has no effect on the appearance of technological innovations. The differential presence of flint is therefore not the cause of the dichotomy found in the tree, but can be explained by the use of distinct and regional technological strategies.

The control of fire has neither a special meaning, located both in the north (Beeches Pit, Barnham unit 6; Davis et al., 2025) and south (Terra Amata, Aroeira, Menez Dregan 8, Vertezsolos) (López-García et al., 2018; Ravon et al., 2022). In terms of the cladogram, the appearance of fire appears to be completely independent, with several appearances in very different cultural and technological contexts. As well, function of the sites or mobility patterns or fragmentation of the reduction sequences have no special meaning on the cladogram.

5. Conclusion

The cladistic analysis of the ca. MIS 11 sites has enabled us to reach several conclusions regarding the structuring of the history of lithic traditions from this period, the use of the 3ia, and the retention index within the framework of cultural cladistics.

From a methodological point of view, 3ia appears relevant in the framework of cultural histories both in reconstruction and for analyzing the resulting trees. By precisely quantifying the cladistic information of each character and each state, as well as the proportion of this information involved in supporting the tree, this method makes it possible to establish a link between the optimal tree obtained and the characters. In this respect, the retention index used in conjunction with the total informativity values provides essential information for understanding and analyzing the results of a cladistic analysis. It allows us to show that the character prepared core technologies is the most informative character given the structure of the databases used herein, almost equivalent in terms of absolute contributory value as all the other characters taken together (ratios, large cutting tools, and small tools).

With regard to the cladogram, a clear initial divide appears to exist between Western Europe (clade 12) and Central Europe (clade 9). However, within the Western Europe clade, many sites that are geographically very distant are sister groups in the cladogram. More specifically, four clades (13, 22, 34 and 38) highlight cladistic relationships between Spanish and French sites, which may be explained by a common technological background or dispersals of populations. Moreover, the clades seem mainly supported by discoid, centripetal, and Levallois core technologies. However, Levallois appears homoplastic, implying that the homology between the Levallois technologies with Áridos I and Cagny-la-Garenne II in relation to the other Levallois sites is rejected. These two sites do not have discoid cores and centripetal cores,

and are therefore rejected outside the main Levallois clade. This homoplasy could imply a technological threshold before the convergent appearance of Levallois independently, but could more likely be due to sampling from the Áridos I and Cagny-la-Garenne series. A bias is inherent in the direct study of sites by their lithic content, namely the rejection by most clades of sites poor in lithic artefacts, which find themselves in the position of a sister group to all the others. The study of assemblages does not allow us to distinguish the 'positive' absence of a technology from an absence due to a sampling problem. On the other hand, this sampling bias is easily revealed in this specific case by studying the structure of the tree and the number of objects found on the site. Sites with low number of items (or even unknown data) find themselves in the position of the sister group because the poverty of the series implies characters with few or no derived states. This is the case, for example, for Cagny-la-Garenne, or Áridos (I and II). In the specific case of Áridos I, cladistic analysis also has a predictive aspect by indicating which sites need to be excavated more in order to test hypotheses of a cladogram.

Overall, the tree and the clades suggest that Levallois core technology survived during the glacial event of MIS 12 and diversified during the long interglacial MIS 11.

Finally, we have shown that the 3ia method enabled us to obtain an optimal cladogram based on the lithic content of archaeological sites across Europe in MIS 11. This tree, obtained from the analysis of a synthetic database, enabled us to show the hierarchical structure of these sites, which may be interpreted historically as a vertical transmission of knowledge. Building this tree, instead of a classical comparison of lithic assemblages complements other approaches and allows another picture of the cultural European traditions, to propose hypotheses on their relationships over time and space.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The study has been performed in the frame of the ANR NEAND-ROOTS project (ANR-19-CE27-0011-01) directed by M.-H. Moncel. This work has been also possible thanks to the Spanish National Projects PID2024-156477NB-C31 and PID2024-156477NB-C32 financed by MICIU/AEI/10.13039/501100011033/FEDER, UE; the 2021SGR01239 project financed by the the Agència de Gestió d'Ajuts Universitaris i de Recerca; and the 2023PFR-URV-01239(1) project financed by the Universitat Rovira i Virgili. The IPHES-CERCA has received financial support through the "María de Maeztu" program for Units of Excellence (CEX2024-01485-M/funded by MICIU/AEI/10.13039/501100011033). N. Ashton received funding for the Pathways to Ancient Britain Project from the Calleva Foundation. Finally we would like to thank the editor Brian Chase, and one anonymous reviewer for their comments that enriched our paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.qsa.2026.100314>.

Data availability

all data are in supplementary

References

- Antoine, P., Coutard, S., Bahain, J.-J., Locht, J.-L., Herisson, D., Gonal, E., 2021. The last 750 ka in loess-palaeosols sequences from Northern France: environmental background and dating of the Western European Palaeolithic. *J. Quat. Sci.* <https://doi.org/10.1002/jqs.328>;hal-03164133.
- Archie, J.W., 1989. Homoplasy excess ratios : new indices for measuring levels of homoplasy in phylogenetic systematics and a critique of the consistency index. *Syst. Biol.* 38. <https://doi.org/10.2307/2992286>.
- Ashton, N., Davis, R., 2021. Cultural mosaics, social structure, and identity: the Acheulean threshold in Europe. *J. Hum. Evol.* 156, 103011.
- Ashton, N., McNabb, J., Irving, B., Lewis, S., Parfitt, S., 1994. Contemporaneity of Clactonian and Acheulean flint industries at Barnham, Suffolk. *Antiquity* 68 (260), 585–589.
- Ashton, N., Lewis, S.G., Parfitt, S., White, M., 2006. Riparian landscapes and human habitat preferences during the Hoxnian (MIS 11) Interglacial. *J. Quat. Sci.: Pub. Quaternary Res. Assoc.* 21 (5), 497–505.
- Ashton, N., Lewis, J.E., Hosfield, R., 2011. Mapping the human record: population change in Britain during the early Palaeolithic. In: Ashton, N., Lewis, J.E., Stringer, C. (Eds.), *The Ancient Human Occupation of Britain*. Quaternary Science, pp. 39–53.
- Ashton, N., Lewis, S.G., Parfitt, S.A., Davis, R.J., Stringer, C., 2016. Handaxe and non-handaxe assemblages during Marine Isotope Stage 11 in northern Europe: recent investigations at Barnham, Suffolk, UK. *J. Quat. Sci.* 31 (8), 837–843.
- Baena, J., Moncel, M.-H., Cuartero, F., Chacón, M.G., Rubio, D., 2017. late Middle Pleistocene genesis of Neanderthal technology in Western Europe. The case of Payre site (south-east France). *Quat. Int.* 436 (part A), 212–238.
- Bahain, J.-J., Valladas, H., Falguères, C., Mercier, N., Joron, J.-L., Froget, L., Masouidi, H., Moigne, A.-M., Comber, J., Moncel, M.-H., 2022. Reappraisal of the chronology of Orgnac III Lower-Middle Palaeolithic site (Ardèche, France), a regional key-sequence for the Middle Pleistocene of southern France. *J. Human Evolution. Humans Transition Special Issue*.
- Barsky, D., Moigne, A.M., Pois, V., 2019. The shift from typical Western European Late Acheulean to microproduction in unit 'D' of the late Middle Pleistocene deposits of the Caune de l'Arago (Pyrénées-Orientales, France). *J. Hum. Evol.* 135, 102650.
- Bazin, L., Landais, A., et al., 2013. An optimized multi-proxy, multi-site Antarctic ice and gas orbital chronology (AICC2012): 120–800 ka. *Clim. Past* 9 (4), 1715–1731.
- Berger, A., Loutre, M.F., 2003. Climate 4000,000 years ago, a key to the future? In: Droxler, A.W., Past, R.Z. (Eds.), *Interglacials Working Group of Pages, Interglacials of the last 800,000 years*, R. of Geop 54, 162–219.
- Bergström, A., McCarthy, S.A., Hui, R., Almarri, M.A., Ayub, Q., Danecek, P., et al., 2020. Insights into human genetic variation and population history from 929 diverse genomes. *Science* 367 (6484) eaay5012.
- Biddittu, I., Moncel, M.-H., Millic, S., Belluccia, L., Ruffoa, M., Saracinoa, B., Manzi, G., 2019. Stratigraphy, sedimentology, and archaeology of Middle Pleistocene localities near Ceprano, Campogrande area, Italy. *Quat. Res.* 93 (1), 155–171.
- Blain, H.A., Santonja, M., Pérez-González, A., Panera, J., Rubio-Jara, S., 2014. Climate and environments during Marine Isotope Stage 11 in the central Iberian Peninsula: the herpetofaunal assemblage from the Acheulean site of Áridos-1, Madrid. *Quat. Sci. Rev.* 94, 7–21.
- Blain, H.A., Lozano-Fernández, I., Ollé, A., Rodríguez, J., Santonja, M., Pérez-González, A., 2015. The continental record of Marine Isotope Stage 11 (Middle Pleistocene) on the Iberian Peninsula characterized by herpetofaunal assemblages. *J. Quat. Sci.* 30 (7), 667–678.
- Blain, H.A., Fagoaga, A., Ruiz-Sánchez, F.J., García-Medrano, P., Ollé, A., Jiménez-Arenas, J.M., 2021. Coping with arid environments: a critical threshold for human expansion in Europe at the Marine Isotope Stage 12/11 transition? The case of the Iberian Peninsula. *J. Hum. Evol.* 153, 102950.
- Boëda, É., 1993. Le débitage Discoïde et le débitage Levallois récurrent centripète. *Bull. Soc. Prehist. Fr.* 90 (6), 392–404.
- Boëda, É., 1994. Le Concept Levallois: Variabilité Des Méthodes. *Cnrs Éditions*, Paris, p. 280.
- Bordes, F., 1961. *Typologie Du Paléolithique Inférieur Et Moyen*. Institut de Préhistoire de l'Université de Bordeaux I, Bordeaux.
- Brandon, M., Landais, A., Duchamp-Alphonse, S., Favre, V., Schmitz, L., Abrial, H., et al., 2020. Exceptionally high biosphere productivity at the beginning of Marine isotopic Stage 11. *Nat. Commun.* 11 (1), 2112.
- Candy, I., Schreve, D.C., Sherriff, J., Tye, G.J., 2014. Marine Isotope Stage 11: palaeoclimates, palaeoenvironments and its role as an analogue for the current interglacial. *Earth Sci. Rev.* 128, 18–51.
- Cao, N., Zaragüeta Bagils, R., Vignes-Lebbe, R., 2007. Hierarchical representation of hypotheses of homology. *Geodiversitas* 29 (1), 5–15.
- Combouret-Nebout, N., Bertini, A., Russo-Ermolli, E., Peyron, O., Klotz, S., Montade, V., Fauquette, S., Allen, J., Fusco, F., Goring, S., Huntley, B., Joannin, S., Lebreton, V., Magri, D., Orain, R., Sadori, L., 2015. Climate changes in the central Mediterranean and Italian vegetation dynamics since the Pliocene. *R. of Palaeobotany Palynol.* 218, 127–147.
- Conard, N.J., Serangeli, J., Böhner, U., Starkovich, B.M., Miller, C.E., Urban, B., Van Kolschoten, T., 2015. Excavations at Schöningen and paradigm shifts in human evolution. *J. Hum. Evol.* 89, 1–17.
- Condemi, S., 1985. *Les Hommes Fossiles De Saccopastore (Italie) Et Leurs Relations Phylogénétiques*. Thèse de l'université de Bordeaux I, p. 232.
- Dabkowski, J., Limondin-Lozouet, N., 2022. Comparison of temperature and humidity during MIS 11 and MIS 5e interglacials with the Holocene using stable isotopes in tufa deposits from northern France. *Quat. Res.* 1–12.

- Dabkowski, J., Limondin-Lozouet, N., Antoine, P., Andrews, J., Marca-Bell, A., 2012. Climatic variations in MIS 11 recorded by stable isotopes and trace elements in a French tufa (La Celle, Seine valley). *J. Quat. Sci.* 27 (8), 790–799.
- Daura, J., Sanz, M., Arsuaga, J.L., Hoffmann, D.L., Quam, R.M., Ortega, M.C., et al., 2017. New middle Pleistocene hominin cranium from Gruta da Aroeira (Portugal). *Proc. Natl. Acad. Sci.* 114 (13), 3397–3402.
- Daura, J., Sanz, M., Deschamps, M., Matias, H., Igreja, M., Villaescusa, L., et al., 2018. A 400,000-year-old Acheulean assemblage associated with the Aroeira-3 human cranium (Gruta da Aroeira, Almonda karst system, Portugal). *C. R. Palevol* 17 (8), 594–615.
- Davis, R., Ashton, N., 2019. Landscapes, environments and societies: the development of culture in Lower Palaeolithic Europe. *J. Anthropol. Archaeol.* 56, 101107.
- Davis, R., Hatch, M., Hoare, S., et al., 2025. Earliest evidence of making fire. *Nature*. <https://doi.org/10.1038/s41586-025-09855-6>.
- De Lombera-Hermida, A., Rodríguez-Álvarez, X.P., Mosquera, M., Ollé, A., García-Medrano, P., Pedergrana, A., Terradillos-Bernal, M., López-Ortega, E., Bargalló, A., Rodríguez-Hidalgo, A., Saladié, P., Bermúdez de Castro, J.M., Carbonell, E., 2020. The dawn of the Middle Paleolithic in Atapuerca: the lithic assemblage of TD10.1 from Gran Dolina. *J. Hum. Evol.* 145, 102812.
- De Weyer, L., Pérez, A., Huguin, R., Forestier, H., Boëda, E., 2022. Temps, mémoire et altérité en technologie lithique: synthèse et perspectives de l'approche technogénétique française. *J. Lithic Stud.* 9 (1), 48.
- Demuro, M., Arnold, L.J., Aranburu, A., Sala, N., Arsuaga, J.L., 2019. New bracketing luminescence ages constrain the Sima de los Huesos hominin fossils (Atapuerca, Spain) to MIS 12. *J. Hum. Evol.* 131, 76–95.
- Dere, M., et al., 2016. Partial connectivity increases cultural accumulation within groups. *Proc. Natl. Acad. Sci. USA* 113, 2982–2987.
- Farris, J.S., 1973. On comparing the shapes of taxonomic trees. *Syst. Zool.* 22, 50–54. <https://doi.org/10.2307/2412378>.
- Farris, J.S., 1989a. The retention index and homoplasy excess. *Syst. Zool.* 38, 406–407.
- Farris, J.S., 1989b. The retention index and the rescaled consistency index. *Cladistics* 5, 417–419.
- Faure-Brac, M.G., Rineau, V., Bagils, R.Z., 2020. Rethinking Pleistocene (1995) characters under a hierarchical point of view. *bioRxiv*, 2020-10.
- Fernández Peris, J., Barciela, V., Blasco, R., Cuartero Monteagudo, F., Sañudo Die, P., 2008. El Paleolítico Medio en el territorio valenciano y la variabilidad tecnológica de la Cova del Bolomor. *Treballs arqueol.* (14), 141–169.
- Forestier, H., 1993. Le Clactonien: mise en application d'une nouvelle méthode de débitage s'inscrivant dans la variabilité des systèmes de production lithique du Paléolithique ancien. *Paléo. Revue d'Archéologie Préhistorique* 5 (1), 53–82.
- Gagnepain, J., Gaillard, C., 2003. La grotte de la Baume Bonne (Quinson, Alpes de Haute-Provence): synthèse chronostratigraphique et séquence culturelle d'après les fouilles récentes (1988–1997). In: *La Grotte de la Baume Bonne* (Quinson, Alpes de Haute-Provence): Synthèse Chronostratigraphique Et Séquence Culturelle D'Après Les Fouilles Récentes (1988–1997). John and Erica Hedges Ltd, pp. 73–86.
- García-Medrano, P., Ollé, A., Mosquera, M., Cáceres, I., Carbonell, E., 2015. The nature of technological changes: the Middle Pleistocene stone tool assemblages from Galería and Gran Dolina-subunit TD10.1 (Atapuerca, Spain). *Quat. Int.* 368, 92–111.
- García-Medrano, P., Despriée, J., Moncel, M.-H., 2022. Innovations in Acheulean Biface Production at La Noira (Centre France): Shift or Drift Between 700 and 450 Ka in Western Europe? *Anthropological and Archaeological Sciences*.
- García-Medrano, P., Shipton, C., White, M., Ashton, N., 2022. Acheulean diversity in Britain (MIS 15–MIS 11): from the standardization to the regionalization of technology. *Front. Earth Sci.* 10, 917207.
- García-Medrano, P., Moncel, M.-H., Maldonado-Garrido, R., Ollé, A., Ashton, N., 2023. The Western European Acheulean: reading variability at a regional scale. *J. Hum. Evol.* Humans in transition special issue. 179, 103357.
- Gibbard, P., 2007. Europe cut adrift. *Nature* 448, 259–260.
- Goni, M.S., Llave, E., Oliveira, D., Naughton, F., Desprat, S., Ducassou, E., et al., 2016. Climate changes in south western Iberia and Mediterranean outflow variations during two contrasting cycles of the last 1 Myrs: MIS 31–MIS 30 and MIS 12–MIS 11. *Global Planet. Change* 136, 18–29.
- Göpel, T., Richter, R., 2023. Homologues and homology and their related terms in phylogenetic systematics. *Cladistics* 39, 240–248. <https://doi.org/10.1111/ccla.12526>.
- Górecki, A., Żarski, M., Drzewicki, W., Pleśniak, L., Zalewska-Gałosz, J., Hryniewiecka, A., 2022. New climatic oscillations during MIS 11c in the record of the Skrzynka II site (Eastern Poland) based on palynological and isotope analysis. *Quat. Int.* 632, 4–20.
- Gowlett, J.A.J., Hallos, J., 2000. Beeches Pit: overview of the archaeology. *The Quaternary of Norfolk and Suffolk: Field Guide*, pp. 197–206.
- Green, Richard E., et al., 2008. A complete Neandertal mitochondrial genome sequence determined by high-throughput sequencing. *Cell* 134 (3), 416–426.
- Grimaldi, S., Santaniello, F., Angelucci, D.E., Bruni, L., Parenti, F., 2020. A Techno-Functional interpretation of the lithic assemblage from Fontana Ranuccio (Anagni, Central Italy): an insight into a MIS 11 human behaviour. *J. Paleolithic Archaeol.* 3 (4), 944–966.
- Grove, M., 2016. Population density, mobility, and cultural transmission. *J. Archaeol. Sci.* 74, 75–84. Bocquet-Appel, J.-P., Degioanni, A., 2013. Neanderthal demographic estimates. *Cur. Anth.* 54, S202–S213.
- Guibert-Cardin, J., Tourloukis, V., Thompson, N., Panagopoulou, E., Harvati, K., Nicoud, E., Beyries, S., 2022. The function of small tools in Europe during the Middle Pleistocene: the case of Marathousa 1 (Megalopolis, Greece). *J. Lithic Stud.* 9 (1).
- Gupta, S., Collier, J., Palmer-Felgate, A., et al., 2007. Catastrophic flooding origin of shelf valley systems in the English Channel. *Nature* 448, 342–345.
- Hennig, W., 1966. *Phylogenetic Systematics*. University of Illinois Press, Chicago, Illinois.
- Hérissou, D., Brenet, M., Cliquet, D., Moncel, M.H., Richter, J., Scott, B., et al., 2016. The emergence of the Middle Palaeolithic in north-western Europe and its southern fringes. *Quat. Int.* 411, 233–283.
- Hijma, M.P., Cohen, K.M., Roebroeks, J.W.M., Westerhoff, W.E., Busschers, F.S., 2012. Pleistocene Rhine-Thames landscapes: geological background for hominin occupation of the southern North Sea region. *J. Quat. Sci.* 27, 17–39.
- Hosfield, R., 2022. Variations by degrees: western European palaeoenvironmental fluctuations across MIS 13–11. *J. Hum. Evol.* 169, 103213.
- Hosfield, R., Cole, J., 2018. Early hominins in north-west Europe: a punctuated long chronology? *Quat. Sci. Rev.* 190, 148–160.
- Hryniewiecka, A., Winter, H., 2016. Palaeoclimatic changes in the Holsteinian Interglacial (Middle Pleistocene) on the basis of indicator-species method-palynological and macrofossils remains from Nowiny Żukowskie site (SE Poland). *Quat. Int.* 409, 255–269.
- Hublin, J.-J., 1998. Climatic changes, paleogeography, and the evolution of the Neandertals. In: Akazawa, T., Aoki, K., Bar-Yosef, O. (Eds.), *Neandertals and Modern Humans in Western Asia*. Plenum, New York, pp. 295–310.
- Hublin, J.J., 2009. The origin of Neandertals. *Proc. Natl. Acad. Sci. USA* 106 (38), 16022–16027.
- Iovita, R., Tuvi-Arad, I., Moncel, M.-H., Despriée, J., Voinchet, P., Bahain, J.-J., 2017. High handaxe symmetry at the beginning of the European Acheulean: the data from la Noira (France) in context. *PLoS One* 12 (5), e0177063.
- Isaac, G.L., Isaac, B., 1977. *Ologesalil: Archeological Studies of a Middle Pleistocene Lake Basin in Kenya* (No Title).
- Kitching, I.J., et al., 1998. In: *Cladistics: The Theory and Practice of Parsimony Analysis*, second ed. The Oxford University Press, Oxford.
- Kleindienst, M.R., 1962. Components of the East African Acheulean assemblage: an analytic approach. In: *Actes Du Ivéme Congres Panafricain De Préhistoire Et De L'Étude Du Quaternaire*, 40. Musée royal de l'Afrique centrale, Tervuren, pp. 81–105.
- Kleinen, T., Hildebrandt, S., Prange, M., Rachmayani, R., Müller, S., Bezrukova, E., et al., 2014. The climate and vegetation of Marine Isotope Stage 11—model results and proxy-based reconstructions at global and regional scale. *Quat. Int.* 348, 247–265.
- Kot, M., Berto, C., Krajcarz, M.T., Moskal-del Hoyo, M., Gryczewska, N., Szymanek, M., et al., 2022. Frontiers of the Lower Palaeolithic expansion in Europe: Tanel Wielki Cave (Poland). *Sci. Rep.* 12 (1), 16355.
- Koulikovska, L., Usik, V., Haesaerts, P., 2010. Early paleolithic of korolevo site (Transcarpathia, Ukraine). *Quat. Int.* 223, 116–130.
- Kousis, I., et al., 2018. Centennial-scale vegetation dynamics and climate variability in SE Europe during Marine Isotope Stage 11 based on a pollen record from Lake Ohrid. *Quat. Sci. Rev.* 90, 20–28.
- Kretzoi, M., Dobosi, T.V., 1989. *Vértesszőlös. Site, Man and Culture*. Akadémiai Kiadó.
- Lamotte, A., Tuffreau, A., 2016. Acheulean of the Somme basin (France): assessment of lithic changes during MIS 12 to 9. *Quat. Int.* 409, 54–72.
- Leakey, M.D., 1971. *Olduvai Gorge: Volume 3, Excavations in Beds I and II, 1960–1963*, 3. Cambridge University Press.
- Limondin-Lozouet, N., Nicoud, E., Antoine, P., Auguste, P., Bahain, J.-J., Dabkowski, J., et al., 2010. Oldest evidence of Acheulean occupation in the Upper Seine valley (France) from an MIS 11 tufa at La Celle. *Quat. Int.* 223–224, 299–311.
- Limondin-Lozouet, N., Dabkowski, J., Antoine, P., 2020. Palaeoenvironmental dynamics of the MIS 11 interglacial in north-western Europe based on the malacological succession from La Celle (Seine Valley, France): relationship with glacial refugia and palaeobiodiversity. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 560, 110044.
- Limondin-Lozouet, N., Dabkowski, J., Antoine, P., Bahain, J.-J., Voinchet, P., Penkman, K. E.H., White, D., Jolly-Saad, M.C., Auguste, P., Galeb, B., 2025. The 'La Celle interglacial': a key-record of MIS 11c palaeoenvironments and palaeoclimate in NW Europe. *Quat. Sci. Rev.* 370, 109667.
- Limondin-Lozouet, N., Antoine, P., Bahain, J.J., Cliquet, D., Coutard, S., Dabkowski, J., et al., 2015. North-West European MIS 11 malacological successions: a framework for the timing of Acheulean settlements. *J. Quat. Sci.* 30 (7), 702–712.
- Lockey, A.L., Rodríguez, L., Martín-Francés, L., Arsuaga, J.L., de Castro, J.M.B., Crété, L., et al., 2022. Comparing the Boxgrove and Atapuerca (Sima de los Huesos) human fossils: do they represent distinct paleodemes? *J. Hum. Evol.* 172, 103253.
- López-García, J.M., Blain, H.A., Sanz, M., Daura, J., Zilhão, J., 2018. Refining the environmental and climatic background of the Middle Pleistocene human cranium from Gruta da Aroeira (Torres Novas, Portugal). *Quat. Sci. Rev.* 200, 367–375.
- Louche, M.F., Berger, A., 2003. Marine Isotope Stage 11 as an analogue for the present interglacial. *Global Planet. Change* 36, 209–217.
- Lumley, H. de dir, 2015. *Terra Amata, nice, Alpes-Maritimes*. France. Tome IV. Fascicule 1. Les Industries Acheuléennes. Editions. CNRS, Paris, p. 806.
- Mahbub, M., Wahab, Z., Reaz, R., Rahman, M.S., Bayzid, M.S., 2021. wQFM: highly accurate genome-scale species tree estimation from weighted quartets. *Bioinformatics* 37 (21), 3734–3743.
- Manzi, G., 2016. Humans of the Middle Pleistocene: the controversial calvarium from Ceprano (Italy) and its significance for the origin and variability of Homo heidelbergensis. *Quat. Int.* 411, 254–261.
- Martínón-Torres, M., et al., 2012. Morphological description and comparison of the dental remains from Atapuerca-Sima de los Huesos site (Spain). *J. Hum. Evol.* 62 (1), 7–58.
- Mathias, C., Grégoire, S., Moncel, M.H., 2017. Nouvelles données sur l'assemblage lithique de la couche L2/3 de La Micoque (Les Eyzies-de-Tayac, Dordogne, France). *PALEO. Revue d'archéologie préhistorique* 28.
- Méndez-Quintas, E., Santonja, M., Arnold, L.J., Cunha-Ribeiro, J.P., da Silva, P.X., Demuro, M., et al., 2020. The Acheulean technocomplex of the Iberian Atlantic

- margin as an example of technology continuity through the Middle Pleistocene. *J. Paleolithic Archaeol.* 3 (4), 918–943.
- Meyer, Matthias, et al., 2016. Nuclear DNA sequences from the Middle Pleistocene Sima de los Huesos hominins. *Nature* 531 (7595), 504–507.
- Michel, V., Shen, G., Shen, C.C., Wu, C.C., Vérati, C., Gallet, S., et al., 2013. Application of U/Th and 40Ar/39Ar dating to Orgnac 3, a late acheulean and early middle Palaeolithic site in ardeche, France. *PLoS One* 8 (12), e82394.
- Moigne, Anne-Marie, Valensi, Patricia, Auguste, Patrick, García-Solano, José, Tuffreau, Alain, Lamotte, Agnes, Barroso, Cecilio, Moncel, Marie-Hélène, 2016. Bone retouchers from Lower Palaeolithic sites: Terra Amata, Orgnac 3, Cagny-l'Épinette and Cueva del Angel. *Quat. Int.* 409, 195–212.
- Moncel, M.-H., Ashton, N., Lamotte, A., Tuffreau, A., et al., 2015. The North-west Europe early Acheulian. *J. Anthropol. Archaeol.* 40, 302–331.
- Moncel, M.-H., Arzarello, M., et al., 2016. Editorial. The holstianian eldorado. *Quat. Int.* 409, 1–8.
- Moncel, M.-H., Arzarello, M., Boëda, E., Bonilauri, S., Chevrier, B., Gaillard, C., Forestier, H., Yinghua, Li, Sémah, F., Zeitoun, V., 2018a. In: Coppens, Y., Viallet, E. A. (Eds.), *The Assemblages with Bifacial Tools in Eurasia (First Part). What is Going on in the West? Data on Western and Southern Europe and the Levant, CR Palevol, Special Issue Eurasian Pleistocene*, 17, pp. 45–60, 1–2.
- Moncel, M.H., Landais, A., et al., 2018b. Linking environmental changes with human occupations between 900 and 400 ka in Western Europe. *Quat. Int.* 480, 78–94.
- Moncel, M.-H., Biddittu, I., Manzi, G., Saracino, B., Pereira, A., Nomade, S., Hertler, C., Voinchet, P., Bahain, J.-J., 2020a. Emergence of regional cultural traditions during the Lower Paleolithic: evidence of a network of sites at the MIS 11–10 transition in Central Italy (Frosinone-Ceprano basin). *Anthropological and archaeological. Sciences* 12 (8), 1–32.
- Moncel, M.-H., Santagata, C., Pereira, A., Nomade, S., Voinchet, P., Bahain, J.-J., et al., 2020b. The origin of early Acheulean expansion in Europe 700 ka ago: new findings at Notarchirico (Italy). *Sci. Rep.* 10 (1), 1–16. <https://doi.org/10.1038/s41598-020-68617-8>.
- Moncel, M.-H., Ashton, N., Arzarello, M., Fontana, F., Lamotte, A., Scott, B., Mutillo, B., Berruti, B., Nenzioni, G., Tuffreau, A., Peretto, C., 2021a. An early Levallois core technology between MIS 12 and 9 in Western Europe? *J. Hum. Evol.* 139, 102735.
- Moncel, M.-H., García Medrano, P., Despriée, J., Arnaud, J., Voinchet, P., Bahain, J.-J., 2021b. Tracking behavioral persistence and innovations during the Middle Pleistocene in Western Europe. Shift in occupations between 700 ka and 450 ka at la Noira site (Centre, France). *J. Hum. Evol.* 156, 103009. Humans in transition special issue.
- Mourre, V., 2003. Implications Culturelles De La Technologie Des Hachereaux, 10. Thèse de doctorat, Paris.
- Mutillo, B., Lembo, G., Gallotti, R., 2021. Lithic productions during the first half of the Middle Pleistocene (MIS 19–12) in the Italian Peninsula: an overview. *Alpine Mediterranean Quaternary* 34 (1), 33–54.
- Nelson, G., 1994. Homology and systematics. In: Hall, B.K. (Ed.), *Homology: the Hierarchical Basis of Comparative Biology*. Academic Press, pp. 101–149.
- Nelson, G., Ladiges, P.Y., 1992. Information content and fractional weight of three-item statements. *Syst. Biol.* 41, 490–494.
- Nelson, G.J., Ladiges, P.Y., 1996. Paralogy in cladistic biogeography and analysis of paralogy-free subtrees. *Am. Mus. Novit.* 3167.
- Nelson, G., Platnick, N., 1981. Systematics and Biogeography.
- Nelson, G., Platnick, N.I., 1991. Three-taxon statements: a more precise use of parsimony? *Cladistics* 7 (4), 351–366.
- Nicoud, E., Aureli, D., Pagli, M., Villa, V., Tomasso, A., Pereira, A., et al., 2022. Techno-economic behaviours during Middle Pleistocene: Valle Giumentina level ALB-42 (MIS 12b, Abbateggio, Central Italy). *Bull. Soc. Prehist. Fr.* 119 (3), 421–447.
- Oliveira, D., Desprat, S., et al., 2016. The diversity of millennial-scale cooling events in southwestern Europe during MIS 11. *Quat. Res.* 86 (3), 373–387.
- Ollé, A., Vergès, J.M., Rodríguez-Álvarez, X.P., Cáceres, I., Angelucci, D.E., Vallverdú, J., et al., 2016. The Middle Pleistocene site of La Cansaladeta (Tarragona, Spain): stratigraphic and archaeological succession. *Quat. Int.* 393, 137–157.
- Owen, R., 1843. *Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals, Delivered at the Royal College of Surgeons in 1843*. Longman, Brown, Green, and Longmans.
- Palumbo, E., Voelker, A.H., Flores, J.A., Amore, O.F., 2019. Surface-ocean dynamics during eccentricity minima: a comparison between interglacial Marine Isotope Stage (MIS) 1 and MIS 11 on the Iberian Margin. *Global Planet. Change* 172, 242–255.
- Parfitt, S.A., Lewis, M.D., Bello, S.M., 2022. Taphonomic and technological analyses of Lower Palaeolithic bone tools from Clacton-on-Sea, UK. *Sci. Rep.* 12 (1), 20222.
- Pereira, A., Nomade, S., Moncel, M.-H., Voinchet, P., Bahain, J.-J., Biddittu, I., Falguères, C., Giaccio, B., Manzi, G., Parenti, F., Scardia, G., Scao, V., Sottili, G., Vietti, A., 2018. Geochronological evidences of a MIS 11 to MIS 10 age for several pivotal Acheulian sites from the Frosinone province (Latium, Italy): archaeological implications. *Quat. Sci. Rev.* 187, 112–129.
- Peresani, M., 2003. Discoid lithic technology. Advances and implications. *BAR Int. Ser.* S1120, 276. Oxford.
- Peretto, C., et al., 2016. The Middle Pleistocene site of Guado San Nicola (Monteroduni, Central Italy) on the Lower/Middle Palaeolithic transition. *Quat. Int.* 411B, 301–315.
- Pinna, M.C., 1991. Concepts and tests of homology in the cladistic paradigm. *Cladistics* 7 (4), 367–394.
- Preece, R.C., Gowlett, J.A., Parfitt, S.A., Bridgland, D.R., Lewis, S.G., 2006. Humans in the Hoxnian: habitat, context and fire use at Beeches Pit, West Stow, Suffolk, UK. *J. Quat. Sci.: Pub. Quaternary Res. Assoc.* 21 (5), 485–496.
- Ravon, A.-L., García-Medrano, P., Moncel, M.-H., Ashton, N., 2022. Acheulean variability in Western Europe: the case of Menez-Dregan I (Plouhinec, Finistère, France). *J. Hum. Evol.*, 103103. Humans in transition special issue 162.
- Rineau, V., Zaharias, P., 2025. Agatta (Version 0.9.1). Github [Software]. <https://github.com/vrineau/Agatta>.
- Rineau, V., Zaragüeta, R., Bardin, J., 2021. Information content of trees: three-taxon statements, inference rules and dependency. *Biol. J. Linn. Soc.* 133 (4), 1152–1170.
- Rineau, V., Moncel, M.-H., Zeitoun, V., 2023. Revealing evolutionary patterns behind homogeneity: the case of the Palaeolithic assemblages from Notarchirico (Southern Italy). *J. Archaeol. Method Theor* 30, 203–238.
- Rivals, F., Ziegler, R., 2018. High-resolution paleoenvironmental context for human occupations during the Middle Pleistocene in Europe (MIS 11, Germany). *Quat. Sci. Rev.* 188, 136–142.
- Rodríguez, J., Willmes, C., Sommer, C., Mateos, A., 2022. Sustainable human population density in Western Europe between 560.000 and 360.000 years ago. *Sci. Rep.* 12 (1), 6907.
- Rodríguez-Hidalgo, A., Saladié, P., Ollé, A., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2017. Human predatory behavior and the social implications of communal hunting based on evidence from the TD10.2 bison bone bed at Gran Dolina (Atapuerca, Spain). *J. Hum. Evol.* 105, 89–122.
- Romagnoli, F., 2021. Changes in raw material selection and use at 400,000 years BP: a novel, symbolic relationship between humans and their world. Discussing technological, social and cognitive arguments. *Camb. Archaeol. J.* 31 (2), 325–336.
- Rossoni-Notter, E., Notter, O., Simone, S., Simon, P., 2016. Acheulean technical behaviors in Aldène cave (Cesseras, Hérault, France). *Quat. Int.* 409, 149–173.
- Sadori, L., Koutsodendris, A., Panagiotopoulos, K., Masi, A., Bertini, A., Combouirieu-Nebout, N., et al., 2016. Pollen-based paleoenvironmental and paleoclimatic change at Lake Ohrid (south-eastern Europe) during the past 500 ka. *Biogeosciences* 13, 1423–1437.
- Santonja, M., López Martínez, N., Pérez-González, A., 1980. Ocupaciones Achelenses En El Valle Del Jarama. Diputación Provincial de Madrid.
- Santonja, M., Pérez-González, A., Vega, G., Rus, I., 2001. Elephants and stone artifacts in the Middle Pleistocene terraces of the Manzanares river (Madrid, Spain). In: *The World of Elephants*, pp. 597–601. Roma.
- Santonja, M., Pérez González, A.J., Panera Gallego, J., Rubio Jara, S., Sesé Benito, C., Soto, E., Sanchez Romero, L., 2014. Ambrona and Torralba Archaeological and Paleontological Sites, Soria Province.
- Sanz, M., Daura, J., Cabanes, D., Égüez, N., Carrancho, Á., Badal, E., et al., 2020. Early evidence of fire in south-western Europe: the Acheulean site of Gruta da Aroeira (Torres Novas, Portugal). *Sci. Rep.* 10 (1), 12053.
- Sassoon, D., Lebreton, V., Combouirieu-Nebout, N., Peyron, O., Moncel, M.-H., 2023. Palaeoenvironmental Changes in the Southwestern Mediterranean (ODP site 976, Alboran Sea) during the MIS 12/11 transition and the MIS 11 interglacial and implications for Hominin populations. *Quat. Sci. Rev.* 304, 108010.
- Sharon, G., 2007. *Acheulian Large Flake Industries: Technology, Chronology, and Significance*. BAR Publishing.
- Sherriff, J.E., Schreve, D.C., Candy, I., Palmer, A.P., White, T.S., 2021. Environments of the climatic optimum of MIS 11 in Britain: evidence from the tufa sequence at Hitchin, southeast England. *J. Quat. Sci.* 36 (4), 508–525.
- Shipton, C., White, M., 2020. Handaxe types, colonization waves, and social norms in the British Acheulean. *J. Archaeol. Sci.: Reports* 31, 102352.
- Stefaniak, K., Kovalchuk, O., Marciszak, A., Stepanchuk, V., Rekovets, L., Van der Made, J., et al., 2022. Middle Pleistocene fauna and palaeoenvironment in the south of Eastern Europe: a case study of the Medzhybizh 1 locality (MIS 11, Ukraine). *Quat. Int.* 633, 103–117.
- Swofford, D.L., 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*And Other Methods). Sinauer Associates, Sunderland, Massachusetts. Version 4.
- Szymanek, M., Julien, M.A., 2018. Early and Middle Pleistocene climate-environment conditions in Central Europe and the hominin settlement record. *Quat. Sci. Rev.* 198, 56–75.
- Tuffreau, A., Lamotte, A., 2010. Oldest acheulean settlements in northern France. *Quat. Int.* 223 (224), 455.
- Tzedakis, P.C., Hodell, D.A., Nehrass-Ahles, C., Mitsui, T., Wolff, E.W., 2022. Marine isotope stage 11c: an unusual interglacial. *Quat. Sci. Rev.* 284, 107493.
- Usyk, V.I., Gerasimenko, N., Garba, R., Dambon, F., Nigst, P.R., 2023. Exploring the potential of the Middle and Upper Palaeolithic Site Korolevo II (Ukraine): new results on stratigraphy, chronology and archaeological sequence. *J. Paleolithic Archaeol.* 6 (1), 16.
- Vandermeersch, B., 1989. Homogénéité ou hétérogénéité des Néandertaliens. In: Giacobini, G. (Ed.), *Hominidae. Actes Du 2Ème Congrès International De Paléontologie Humaine*. Turin, 28 Septembre - 3 Octobre 1987. Jaca Book, Milan, pp. 311–317.
- Venditti, F., Rodríguez-Álvarez, B., Serangeli, J., Cesaro, S.N., Walter, R., Conard, N.J., 2022. Using microartifacts to infer Middle Pleistocene lifeways at Schöningen, Germany. *Sci. Rep.* 12 (1), 21148.
- Villa, P., Soriano, S., Grün, R., Marra, F., Nomade, S., Pereira, A., et al., 2016. The Acheulian and early Middle Palaeolithic in Latium (Italy): stability and innovation. *PLoS One* 11 (8), e0160516.
- White, M., Ashton, N., 2003. Lower Palaeolithic core technology and the origins of the Levallois method in north-western Europe. *Curr. Anthropol.* 44 (4), 598–609.
- White, M., Ashton, N., Scott, B., 2011. The emergence, diversity and significance of Mode 3 (prepared core) technologies. In: *Developments in Quaternary Sciences*, 14. Elsevier, pp. 53–65.
- White, M., Ashton, N., Bridgland, D., 2019. Twisted handaxes in Middle Pleistocene Britain and their implications for regional-scale cultural variation and the deep

- history of Acheulean hominin groups. In: *Proceedings of the Prehistoric Society*, 85. Cambridge University Press, pp. 61–81.
- White, M., Rawlinson, A., Foulds, F., Dale, L., Davis, R., Bridgland, D., et al., 2024. Making a U-turn on the purfleet interchange: stone tool technology in marine isotope stage 9 Britain and the emergence of the middle Palaeolithic in Europe. *J. Paleolithic Archaeol.* 7 (1), 13.
- Williams, D.M., Ebach, M.C., 2006. The data matrix. *Geodiversitas* 28 (3), 409–420.
- Wiśniewski, A., 2014. The beginnings and diversity of Levallois methods in the early Middle Palaeolithic of Central Europe. *Quat. Int.* 326, 364–380.
- Yravedra, J., Domínguez-Rodrigo, M., Santonja, M., Pérez-González, A., Panera, J., Rubio-Jara, S., Baquedano, E., 2010. Cut marks on the Middle Pleistocene elephant carcass of Áridos 2 (Madrid, Spain). *J. Archaeol. Sci.* 37 (10), 2469–2476.