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Research

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How and when did hominins move from the numerical cognition that we share with the rest of the animal world to number symbols? Objects with sequential markings have been used to store and retrieve numerical information since the beginning of the European Upper Palaeolithic (42 ka). An increase in the number of markings and complexity of coding is observed towards the end of this period. The application of new analytical techniques to a 44–42 ka old notched baboon fibula from Border Cave, South Africa, shows that notches were added to this bone at different times, suggesting that devices to store numerical information were in use before the Upper Palaeolithic. Analysis of a set of incisions on a 72–60 ka old hyena femur from the Les Pradelles Mousterian site, France, indicates, by comparison with markings produced by modern subjects under similar constraints, that the incisions on the Les Pradelles bone may have been produced to record, in a single session, homologous units of numerical information. This finding supports the view that numerical notations were in use among archaic hominins. Based on these findings, a testable five-stage scenario is proposed to establish how prehistoric cultures have moved from number sense to the use of number symbols.

This article is part of a discussion meeting issue 'The origins of numerical abilities'.

1. Introduction

The ability to use symbol systems for numbers is peculiarly human. Present-day lifestyle in developed societies is unthinkable without such symbolic systems. We use numbers in virtually every domain, from kitchen to high-tech science laboratories. Systems of notation, mainly in the form of tallies, have a remote history. So-called place-value systems developed in Mesopotamia only about 3.4 ka. Beneath human ability to implement symbolic systems for numbers, however, there are cognitive abilities that we share with several other animal species. A large body of experimental evidence shows that many non-human animal species are capable of processing numerical information [1–5]. These abilities mainly have to do with estimating magnitudes (length, duration, luminance, approximate amount of something, etc.) in an approximate manner. Many contributions to this special issue address this point and report about the cognitive and neural evidence that we share a 'number sense' [6] with other animal species.

When processing this kind of information, human and non-human animals are submitted to the same cognitive constraints predicted by the Weber law [7], which states, in short, that when comparing two different magnitudes, the chances of getting the difference right decrease with a reduction of the

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difference or proportion between the two stimuli [8]. For both humans [9] and non-human animals [10,11], non-symbolic numerical tasks are easier to perform when the difference between the numbers increases (distance effect) but harder when the magnitude of numbers increases (size effect). These similarities are suggestive of a shared, ancient, non-verbal numerical mechanism [10]. Therefore, uniquely human mathematical abilities seem to be based on a developmental and evolutionarily ancient 'number sense' [6].

These numerical competences do not depend on language or education, and are found in animals as well as in infants who are not able to count verbally. In adults, non-symbolic number comprehension can be assessed whenever the use of language is prevented [12]. Even in human cultures with very simple, language-based counting systems, the 'number sense' may be much richer than that allowed by the language-based systems in use [13]. From the neural viewpoint, adult humans, non-human primates and young children activate the same brain regions involved in approximate representation of magnitudes, and these regions are also related to the development of mathematical intelligence quotient from infancy to adulthood in educated human beings ([14,15] and references therein).

This indicates that the numerical cognition abilities that we share with other animals ([16] for review), and in particular with our extant evolutionary closest relatives, the chimpanzees (e.g. [17]), were already in place 8 Ma ago in our common ancestor [18–20]. However, there are essential differences in the way our species can deal with numerical information, especially as far as numerical symbol systems are concerned. These differences must have emerged during the evolution of our lineage and, although it can be reasonably argued that constitutive elements of number sense were already largely mastered by early hominins, at least three key challenges remains, i.e. (i) when verbal or gestural counting systems did arise in the history of humankind, (ii) when exosomatic devices, i.e. artificial memory systems (AMSs), were conceived and produced to store, process and/or transmit numerical information, and (iii) how they evolved to reach the symbolic systems of graphic marks that humans presently use for recording numbers. The first challenge is the hardest, as evidence about verbal or gestural counting systems is difficult to infer from the archaeological and palaeoanthropological record. We will not focus on this challenge in the present paper. As to the second and third challenges, which we address here, past material remains may provide more direct evidence. However, establishing how numeracy has evolved in our lineage is a largely unexplored field of study owing to the lack of specific heuristic tools to infer numeric knowledge from past material culture.

In trying to establish how numeracy evolved in our lineage, two points should be stressed. First, non-human animals lack the ability to externalize information and embody it in material objects and culture. Here, the emphasis is on the ability to produce objects bearing such information, and not just on the ability to perceive it in the surrounding environment. Many non-human animal species are able to attribute symbolic meaning to abstract representations. The use of symbols is not a human peculiarity. What is characteristic of all present-day human cultures is the ability to create and transmit symbolic material culture. The second point refers to the ability to treat and symbolize exact quantity (natural numbers at least) and not just approximate magnitudes. Here, the emphasis is on counting versus estimating.

Upper Palaeolithic (42–10 ka BP) archaeological sites from Europe have yielded numerous objects carrying sets of marks, produced with a variety of techniques, interpreted as systems of notation [21,22]. Challenged from a variety of perspectives, this interpretation has been proposed anew based on novel theoretical and analytical grounds [23–28]. On the one hand, a survey of AMSs presently in use in different human cultures worldwide individuated four distinct factors for information coding: (i) the number of marks, (ii) the accumulation of marks over extended periods of time, (iii) the spatial distribution and arrangement of marks, (iv) the morphology (or the different morphologies) of the marks (electronic supplementary material figure S1). On the other hand, the microscopic analysis of marks produced experimentally has identified criteria [23–26] to establish the technique used, the order in which markings were made, and to distinguish, for example, sets of marks produced by the same tool in a single session from sets representing an accumulation of marks made with different tools, probably at different times (electronic supplementary material, figure S2). The application of these criteria to Upper Palaeolithic objects bearing sequential markings has shown that a number of them can reasonably be interpreted as AMSs (electronic supplementary material, figures S3–S6). Evidence from earlier periods is however scant. In this paper, we apply this technological and experimental framework to study two key findings from Middle Palaeolithic and Middle Stone Age contexts. Results show that exosomatic devices to store numerical information were in use in Africa before the beginning of the European Upper Palaeolithic and that they may also have been in use among Neanderthals. These findings lead us to propose a testable five-stage scenario to establish how prehistoric cultures have moved from number sense to number symbols via a suite of cultural exaptations, i.e. co-options of existing cultural features for new purposes.

(a) Assessing degrees of intentionality from past material culture

Archaeologists face a challenge when they wish to address questions related to intentionality and the perceptive abilities of prehistoric populations, as they cannot interact with the makers of past material culture to assess the degree of divergence between the intended task to be carried out and the stimuli generated on the final product. They are only left with the latter. A strategy to overcome this problem consists in asking modern subjects to perform prescribed perceptual–motor tasks in which they are required to use the same technology and raw material, and to be submitted to the same neuromotor constraints to which past hominins were subjected. The underlying assumption is that both ancient hominins and experimenters possessed, as observed in a number of species, the cognitive building blocks required to estimate differences in the magnitude for different stimuli. Experiments can be conducted in conditions in which language is used or prevented [10,12]. The degrees of intentionality implicit in the archaeological productions are then evaluated by comparing the coefficients of variation (CV) [29–31] measured on these with those measured on the modern artefacts resulting from prescribed tasks. The first advantage of the CV lies in the fact that, being a scale-invariant parameter, it can capture meaningful differences in a number of behavioural domains [32]. The second advantage of this approach for the present study is that since the comparison is conducted at the perceptual–motor level only, it does not need to assume that prehistoric populations had or did not have symbolic representations, nor consider that modern subjects have them.

Application of this research philosophy to a notched raven bone from a Late Mousterian context has recently shown that the set of notches incised on this object falls well within the range of variation of regularly spaced experimental and Upper Palaeolithic sets of notches [33]. Apparently, the Neanderthal craftsman incised the raven bone with the intention of producing equidistant notches. The authors use their results to argue that Neanderthals were perceiving and discriminating equidistant from unequally spaced sequential marks in a way similar to us, and that their neuromotor control allowed them to master the techniques and motions necessary to obtain regularity when required.

2. Material and methods

(a) Archaeological context

(i) Les Pradelles

The site of Les Pradelles, also known as Marillac, is located near the village of Marillac-le-Franc, 20 km east of Angoulême in France. Discovered at the end of the nineteenth century, it was excavated between 1968 and 1980 by Bernard Vandermeersch, and between 2001 and 2013 by one of us (B.M.) and Alan Mann and co-workers [34]. The site is a collapsed gallery of a karstic system featuring a 7 m thick archaeological deposit. Twelve layers were identified during the first excavation campaigns. They have been reduced to eight main sedimentological lithofacies, not all recognized in the three loci composing the site (electronic supplementary material, figure S7). All facies, with the exception of the highest, contain lithics of Quina Mousterian and rich faunal assemblages. No Upper Palaeolithic artefacts were found at the site. The chronology of the locus East deposits, where the object analysed in the present work was found, is based on U–Th dating (81 960 ± 780 BP) of a stalagmite located within the sterile clay–lime deposits (lithofacies 1), which underlies the archaeo-sedimentological sequence, indicating that the karstic system was still active at the end of MIS 5A [35]. Unit 2a is tentatively assigned to MIS 4 (72–60 ka BP) based on the association of the Quina lithics and the abundance of reindeer remains typical of this period [36]. Thermoluminescence dating of a burned flint from the unit 2b provided a date of 58 000 ± 4800 BP. Based on their stratigraphic positions, units 4a, 4b and 5 are assigned to the beginning of MIS 3. Faunal remains above the collapsed roof at the top of the sequence provided AMS radiocarbon ages greater than 45 000 ^{14}C years BP for level 6 (MIS 3), and 33 320 ± 440 ^{14}C years BP for level 7.

The incised bone analysed in this article (M71 G10 c.10 # 53) was found in 1971 within layer 10, square G10, of the stratigraphy established during the 1965–1980 excavations. This layer corresponds to facies 2a of the more recent excavations. This facies yielded typical Quina Mousterian lithics [37] and abundant faunal remains interpreted as the remnant of a hunting camp specialized in reindeer exploitation [38,39]. According to Maureille *et al.* [34], faunal remains from lithofacies 2a bear traces left by both humans (28.4%) and carnivores (3.7%). Numerous Neanderthal remains found in this stratigraphic unit bear cut marks, percussion marks and fresh fractures, controversially interpreted as possible evidence of cannibalism [40,41].

(ii) Border Cave

Located in KwaZulu-Natal, 2 km north of the Ngwavuma River and 82 km west of the Indian Ocean, this large cave features a 4 m deep stratigraphic sequence that has experienced six excavation episodes (cf. [42,43] for a summary). It is currently under excavation by Lucinda Backwell, Lyn Wadley and one of us (F.d'E.). The stratigraphic sequence comprises eleven main alternating brown sand and white ash deposits [44] containing MSA 1, Howiesons Poort, Post-Howiesons Poort and Early Later Stone Age archaeological horizons (electronic supplementary material, table S1). The dating of archaeological layers with three techniques, electron spin resonance (ESR), amino acid decomposition and radiocarbon methods [42,45,46], has produced ages in broad agreement, indicating that the sequence spans from 227 to 24 ka BP (electronic supplementary material, table S1). Two recent studies have focused on archaeological material from layers 2WA to 2BS, attributed to the Post-Howiesons Poort, and 1WA to 1BS, attributed to the Early Later Stone Age [42,47]. These studies showed that novel cultural traits appear around 44–42 ka BP at Border Cave: digging sticks weighted with perforated stones, ostrich egg and marine shell beads, fine bone points for use as awls and poisoned arrowheads, wooden sticks decorated with incisions carrying residues of poison, lump of beeswax mixed with resin made from toxic *Euphorbia*, wrapped in vegetal twine, small pieces of stone to arm hunting weapons with resin residue still clinging to some of the tools, identified as a suberin produced from the sap of *Podocarpus*. ESR age estimates and Bayesian modelling of 40 calibrated radiocarbon ages indicate that layer 2WA accumulated at *ca* 60 ka and that 1WA and 1BS Lower B and C date between 44 and 42 ka BP. Four bones from Border Cave found in layers 2WA, 1WA and 1BS Lower B–C bear sets of notches produced by the to-and-fro movement of a lithic cutting edge. The object analysed in this article was discovered in square T18, layer 1BS Lower B–C, dated to *ca* 42.3–42.6 ka BP. A preliminary analysis of this object was conducted by d'Errico *et al.* [42].

(iii) The experimental incising

The experiment was conducted at the PACEA laboratory, Bordeaux University, and involved thirteen adult subjects, eleven right handed and two left handed, seven females and six males (electronic supplementary material, figure S8). Each subject was given a mesial fragment of *Bos taurus* rib, two *Ovis aries* metapodials and two replicates of Mousterian debitage flint flakes. The experiment was carried out in five phases. In the first phase, the subjects were asked to produce short incisions on the rib with the same technique used by the Neanderthals on the Les Pradelles bone, i.e. by incising the bone surface with a pointed edge of a flake. They were provided with a demonstration. This phase, which lasted 15 min, was aimed at getting the subjects familiar with the tasks that they were asked to perform in the following phases. In the second phase of the experiment, the subjects were instructed to produce a set of nine to 13 incisions on the lateral aspect of an *Ovis* metapodial; in the third phase, a set of nine to 13 parallel, equidistant and identical incisions was produced on the opposite side of the same metapodial. In the fourth phase, they were asked to produce, on the lateral aspect of the second metapodial, two subsets of five and four parallel, equidistant and identical marks, and precisely fit them in two spaces of 16 mm separated by a 4 mm empty slot, i.e. the same configuration in which these two subsets occur on the Les Pradelles bone. Each space beginning and end was

Figure 1. Fragment of a hyena femur from Les Pradelles, France, bearing a set of deep incisions; letters indicate subsets; numbers indicate incisions belonging to subsets *a* and *b*. Grey scale bar, 1 cm.

indicated on the lateral face of the *Ovis* metapodial with thin pencil lines, and the subjects were instructed to locate the first and last incisions for each subset on the corresponding lines. In the fifth phase of the experiment, identical to the fourth, the subjects were asked to produce the two subsets on the opposite aspect of the metapodial. No time restrictions were imposed to accomplish the tasks pertaining to the last four phases of the experiment. The experimental series of incisions were photographed. Metric data on incisions produced during the last four phases of the experiment were acquired with the ImageJ software from images taken with a NIKON D200 camera. The recorded variables included the length and width of the marks, the angle formed by each notch with the horizontal plane, and the top, middle and bottom distances between adjacent notches. The mean, standard deviation and CV were then calculated for each set, subset and variable.

(iv) Taphonomic analysis

A sample of 131 faunal remains from layer 10 were analysed in the framework of this study to identify the agents responsible for bone modification at Les Pradelles and compare natural and anthropogenic traces with incisions on specimen M71. We recorded for each bone remain information on context, species, anatomy, taxon and occurrence of bone modifications produced by abiotic processes (weathering, trampling, dissolution), carnivores (pitting, scoring, notching, furrowing, puncture, digestion) and humans (cut mark, impact, flake scar, use as a retoucher) according to criteria proposed by Binford [48], Fisher [49], Lyman [50] and Pokines & Symes [51]. Bone modifications were identified under a reflected light microscope and recorded with the same equipment used to study the incised object M71.

(v) Technological and morphometric analysis

The analytical methods applied to the analysis of Les Pradelles and Border Cave incised objects are specified in the electronic supplementary material, Text. Identification of marking techniques is based on the experimental reproduction and microscopic analysis of sequential marks produced with different tools and motions as well as blind tests aimed at verifying the pertinence of criteria to identify changes of tool in series of notches made by the back-and-forth displacement of retouched and unretouched lithic cutting edges [24,52–54].

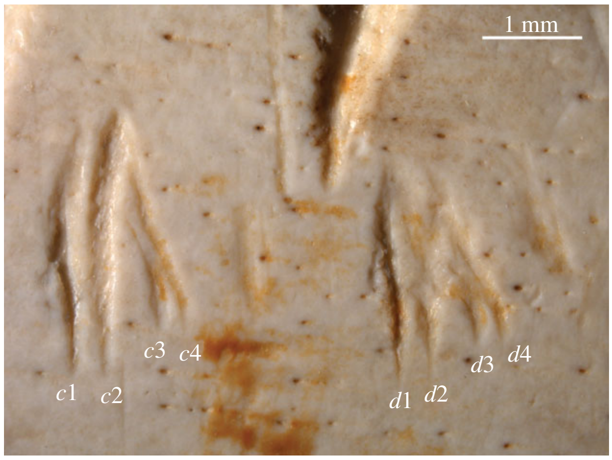

Figure 2. Photo of subsets *c* and *d* on the Les Pradelles specimen with numbers identifying individual incisions.

3. Results

(a) Les Pradelles

The incised limb shaft (figure 1; electronic supplementary material, figure S9) is identified as a mesio-distal fragment of the left femur of an adult *Crocuta crocuta spelaea* [55]. It has a length of 53.3 mm and a maximum diameter of 19.96 mm. The fractures are ancient. Their orientation, perpendicular to the bone main axis, irregular outlines and the presence of discontinuous, marginal flake scars suggest that the bone was not fresh when the breakage took place [56]. The bone surface presents a good state of preservation, apart from small areas of the anterior face showing traces of dissolution and recent scraping marks. Micrometric black deposits, probably of manganese, are scattered all over the periosteal surface. Nine parallel deep incisions are visible on the postero-mesial aspect of the shaft (figure 1). They are herein termed 1–9, from the proximal towards the distal end. A slight offset is observed between incisions 1–5, called herein subset *a*, and the following marks 6–9, called subset *b*. Two groups of superficial, partially overlapping incisions, called subsets *c* and *d*, are located at the bottom right of incisions 2 and 3, respectively (figure 2). They are very small but visible to the naked eye.

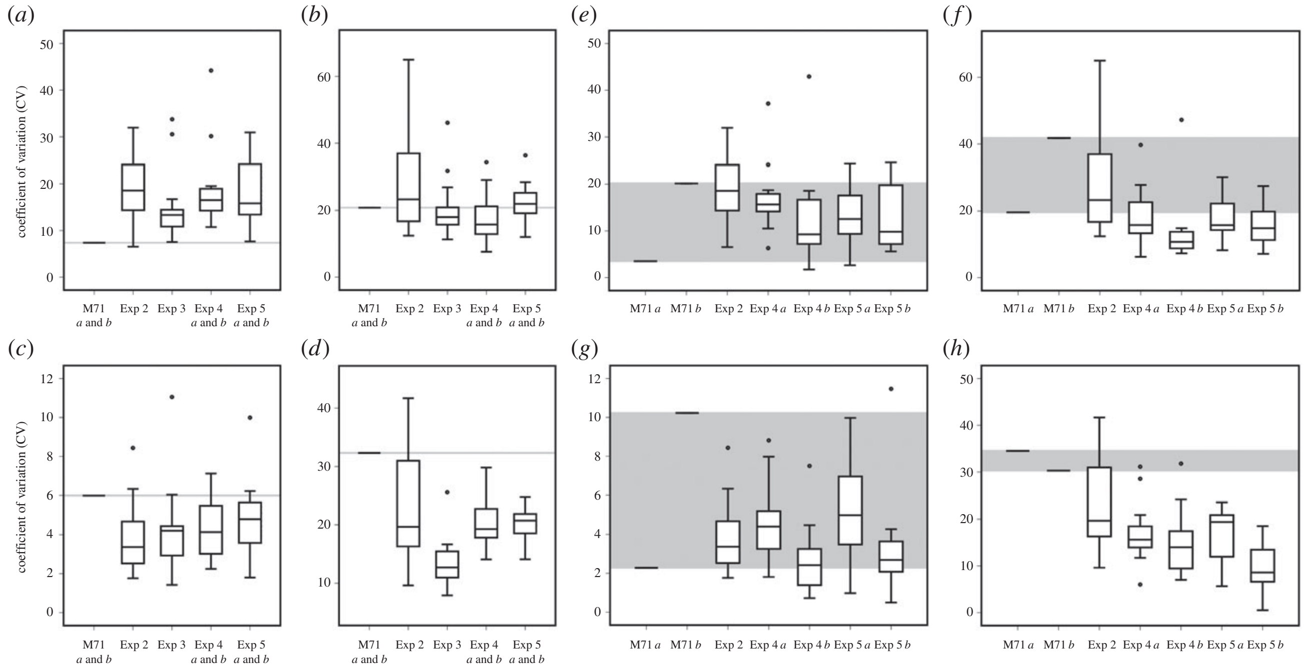

Figure 3. Coefficients of variation (CV) calculated for the incisions length (*a*,*e*), width (*b*,*f*) and angle (*c*,*g*) and distance between adjacent incisions (*d*,*h*) on Les Pradelles M71 and on sets of marks produced by modern subjects. Subsets *a* and *b* are considered jointly in plots (*a*–*d*) and separately in plots (*e*–*h*). Grey bands facilitate comparison between values obtained for archaeological and experimental sets. Results suggest that the Neanderthal was interested in producing marks that could be perceived as identical but not in creating a visual pattern relying on equidistance and, for a subset, parallelism.

Analysis of incisions 1–9 morphological features and sections indicate that they were made by a single stroke of the same robust lithic cutting edge during a single session (electronic supplementary material, figures S10 and S11 and table S2). Their outline indicates that they were engraved from the posterior towards the lateral aspect of the femur with the pointed end corresponding to exit of the tool. Their section and outline reveal they were juxtaposed from the proximal to the distal end of the skeletal element (i.e. from left to right). The technique used and the contemporaneity of the incisions are demonstrated by similarity in shape, termination, section and, in particular, by the presence of two identical grooves at the bottom of incisions 1–8, corresponding to the marks left by the displacement of two protruding areas of the same tool tip. Such consistency indicates that the incisions were done in rapid succession. The absence of these grooves in incision 9 and slight morphological differences between incisions 1–5 and 6–8 do not imply the use of a different tool or a time lag. They result from minor changes in the orientation of the tool when producing the last incisions of subset *b* and the offset between subsets *a* and *b*. The marked difference in morphology between incision 9 and the others is primarily due to it being more superficial and differently oriented. Its section, however, clearly shows that this last incision was also made by the point used for incisions 1–8 (electronic supplementary material, figure S10). Gradual increase in the size and depth from incisions 1 to 8 (electronic supplementary material, table S2) indicates that the engraver progressively applied more and more pressure before terminating the sequence with superficial incision 9.

Subsets *c* and *d* are both composed of two pairs of incisions (*c*1–4 and *d*1–4), slightly overlapping at their top (figure 2; electronic supplementary material, figures S10 and S12). The first four are well preserved; the beginnings of *d*2 and *d*3 are missing owing to a breakage of the bone surface, probably occurring during production of *d*2. The outline, sections and particularly terminations of *c*1, *c*2, *d*1 and *d*2 suggest they were made with the same tool edge; *c*3, *c*4, *d*3 and *d*4 were also made with the same point, possibly the same used for the *c*1, *c*2, *d*1 and *d*2 if the tool was tilted between their production. The incisions of all sets display fringed edges, rough internal morphology and internal fractures, suggesting that they were executed on a partially altered bone.

(b) Bone taphonomy

Modifications produced by a variety of taphonomic agents, including abiotic and biotic, are detected on the faunal remains from Les Pradelles, layer 10 (electronic supplementary material, table S3 and figures S13–S15), but none is comparable to the incisions on specimen M71. Human modifications are not found on hyena remains and, when present on other species, they considerably differ in morphology, arrangement and location from those on M71.

(c) Experimental results

The results from the first phase of the experiment were discarded as it was aimed at getting the subjects familiar with the task they were asked to perform in the following phases. When the CVs calculated from the experimental sample are compared with the values obtained for M71, it appears that the incisions on the hyena femur fall close to the lower limit of the range of modern variation for their length (figure 3*a*), within the range of modern variation for their width (figure 3*b*) and in the higher tail of modern variation for their angle and distance (figure 3*c*,*d*). When subsets *a* and *b* are considered separately (figure 3*e*–*h*), subset *a* falls at the lower limit of the modern variation for its length, within the modern range for its width and angle, and out of the modern range for the distance between incisions. Subset *b* is characterized by comparatively higher CVs, which fall in the higher tail of

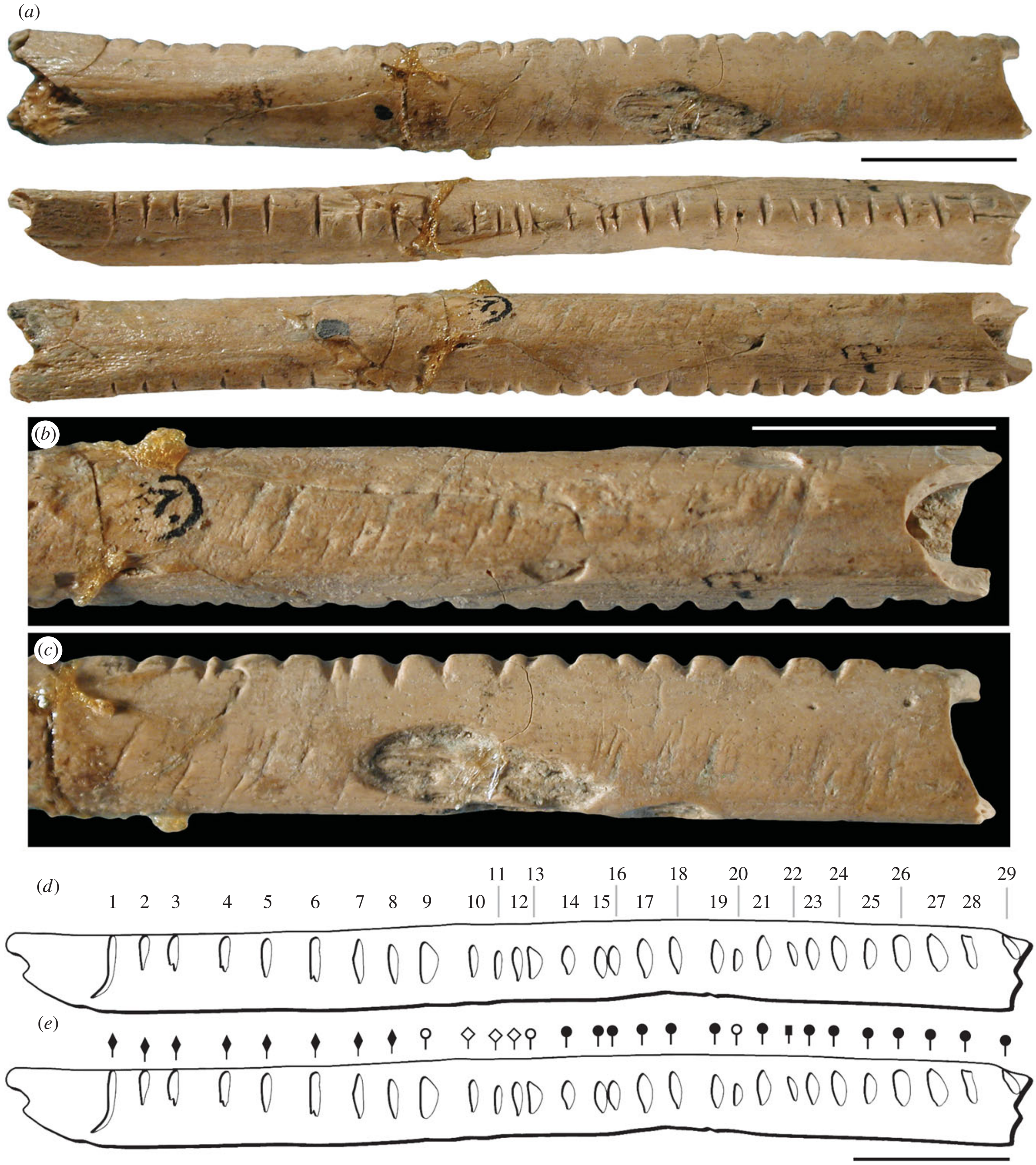

Figure 4. (*a*) Baboon fibula from Border Cave layer 1BS Lower B–C; (*b*,*c*) close-up view showing worn superficial incisions and the irregular sections of the notches; (*d*) tracing of the notched face with numbers identifying individual notches; (*e*) tracing indicating the notches made by the same tool with different symbols. Microscopic and morphometric analyses of the notches indicate that they were made by the back-and-forth movement of five different cutting edges, and that in two cases—notches 9, 13 and 20 on the one hand, and notch 22 on the other—new notches were added in between already carved notches. Scale bar, 1 cm.

modern variation for length and outside the modern variation for all other recorded variables. The first two components of a principal components analysis using the CVs for length, width, angle and spacing obtained on M71 subsets *a* and *b*, and the last two phases of the experiment (4 and 5) account for 77% of the variance (electronic supplementary material, figure S16). M71 subsets fall clearly outside the convex hulls containing the experimental subsets. This is due, as indicated by the variables' vectors, to the higher CVs for spacing and width recorded on the archaeological subsets.

(d) Border Cave

The object from layer 1BS Lower B–C is a diaphysis of a right baboon fibula presenting an incomplete sequence of 29 notches on the interosseous crest (figure 4*a*), and heavily worn oblique incisions on the proximal half of the other three aspects (figure 4*b*,*c*). Two-thirds of the notches are damaged to different degrees by flake scars and cracks or partially obliterated by encrusted sediment, residues of glues, and casting defects (electronic supplementary material, table S4). The surface of the object, and, in particular, the elevations between notches are heavily polished suggesting curation or long-term use. Damage, infilling and smoothing lowered the reliability of measurements, particularly on superficial notches (electronic supplementary material, figure S17). Microscopic and morphometric analyses of the notches nevertheless identify four, possibly five, sets of notches, each made by a different tool (electronic supplementary material, figures S18–S20). Starting from the distal end, the first set comprises eight consecutive notches 1–8. They are narrow, indicating the use of a sharp cutting edge, they have a profile slightly asymmetrical to the left, and four of them, notches 2–5, display at their bottom a distinct groove demonstrating the use of the same cutting edge (electronic supplementary material, figure S17 and table S4). The gradual increase in the angle formed by the notches' walls suggests that they were juxtaposed from the distal to the proximal end of the skeletal element. Microscopic features inside notches 1–8 are fresher than those on the remainder of the notches preserved on the bone indicating that this set was probably the last cut. The second set is composed of three closely spaced symmetrical broader notches 10–12, presenting similar steps at the top and middle of their left wall (electronic supplementary material, figure S17). The wide angle formed by the walls of notch 11 (electronic supplementary material, figure S18), quite different from that measured on notches 10 and 12, could be due to the shallowness of this notch and the heavy wear of its edges. The third set, composed of notches 14–19, 21 and 23–29, fills the remaining proximal half of the ridge and includes 14 notches. They are characterized by a cross-section asymmetrical to the left and rounded bottoms. Three additional notches, 9, 13 and 20, featuring extremely wide angles and sections heavily asymmetrical to the right are positioned between the first, notches 1–8, and the second set, notches 10–12, and in between notches of the third set. A last superficial notch 22 may have been made by the same cutting edge used for notches 9, 13 and 20, as suggested by its wide angle, or, more probably, by a fifth tool, as indicated by its symmetrical section and internal morphology. The widely and irregularly spaced location of the notches 9–13, and different orientation of notch 22, suggest that they were incised after completion of the first three sets.

4. Discussion

Our review of the evidence indicates that AMSs conveying numerical information have been in use since at least the beginning of the European Upper Palaeolithic (42 ka). They take the form of solid, long-lasting, transportable osseous artefacts bearing sequential markings produced with a variety of techniques and hand-motions. Although only a limited number of such devices has been studied exhaustively and formally identified [57], results obtained so far support the view that codes based on one or a combination of two, or possibly three factors (morphology, spatial distribution, accumulation over time of the markings) were already present at the beginning of the Upper Palaeolithic. Use wear and the markings' size and arrangement suggest that information was recovered, according to the objects, by tactual, visual or a combination of tactual and visual perception. A significant increase in the number of marks and distinct sets of marks, signalling an increase in the volume of stored information, is observed towards the end of this period (electronic supplementary material, figures S5 and S6). Such increase coincides with the use of marking techniques producing many marks on a reduced surface, and with a systematic application of visual perception in the process of recovering information.

The sophistication that characterizes the production of some of the earliest known AMSs, such as the Blanchard incised ivory spatula [57], suggests that these devices are several conceptual stages removed from the earliest origins. What kind of time-scale might we be looking at? The reappraisal of the set of notches on the Border Cave baboon fibula conducted with new analytical techniques in the framework of this work indicates that these marks were made by the back-and-forth movement of five different cutting edges, and that in two cases—notches 9, 13 and 20 on the one hand, and notch 22 on the other—new notches were added in between already carved notches. This observation, together with the heavily polished appearance of the bone surface (indicative of long-term handling and curation), and shifts in the inclination of the notches' cross sections (signalling changes in the orientation of the object between marking sessions) indicate that the sets of notches were added on the bone at different times. This bone is an ideal candidate for an AMS with accumulation of information over time as the single factor governing the AMS code. Apparently, between 1 and 14 homologous units of information were recorded in different sessions on the Border Cave bone. This implies, considering the age of the layer in which the bone was found (44–42 ka), that exosomatic devices to store numerical information are not an innovation strictly associated with the emergence of the European Upper Palaeolithic. Antecedents are found in Africa and similar or different devices may have been invented previously, in this same continent or elsewhere.

A number of sequentially marked bones, antlers, shells and stones are reported from Middle and Lower Palaeolithic sites [24,58–62]. Some were reinterpreted as the result of natural processes [63], few were studied in detail and many are unpublished. Our study of the Les Pradelles incised hyena femur demonstrates the need for such analyses. The nine main incisions on this bone are different from natural and human modifications recorded on the faunal assemblage recovered in the same layer. They are present on the wrong species and in the wrong place on the bone, incised with the wrong tool, a robust point, and are too regular to be interpreted as cut marks made during butchery activities. The marks are comparable in length and width to those produced by modern humans who had been asked to produce parallel, identical, equidistant marks with the same technique and in the same space on the type of bone available to the Neanderthal. However, they are significantly more variable in their spacing and, for those belonging to the second subset (*b*), in their orientation, than those produced under similar constraints by modern subjects. Apparently, the Neanderthal was interested in producing marks that could be perceived as identical but not in creating a visual pattern relying on equidistance and, for a subset, parallelism. This suggests that the aim of the markings was not that of producing a decoration visually striking for its regularity, as recently highlighted by the analysis of a Mousterian notched raven bone from Zaskalnaya [33]; rather, the aim seems to have been that of recording in a single session homologous units of information that could be retrieved visually or visually and tactilely.

Minute subsets *c* and *d* are puzzling and add a degree of complexity to the evidence. Microscopic analysis indicates that, in spite of their small size, the markings composing these sets were incised deliberately. The aim of their production may be independent from that of the main set or they may represent diacritical marks allowing identification of the incisions they point at, i.e. incisions 2 and 3. The latter is the more likely hypothesis as subsets *c* and *d* would have been barely perceivable in the absence of the main set and their small size may have been instrumental in distinguishing with no ambiguities information units from landmarks.

(a) Research perspectives

The sequential incisions on the Les Pradelles hyena femur fragment represent the earliest known possible example of a numerical notation for which such an interpretation is supported by a microscopic and morphometric study as well as by results of the analysis of a large sample of experimental alignments of incisions made under technological and neuromotor constraints similar to those at work when the Les Pradelles Neanderthal craftsman incised the bone. They support the view that numerical notations were in use among archaic hominins and, if these observations are corroborated in the future, contribute to filling the gap between the complexity that characterizes Upper Palaeolithic AMSs and the extent of numerical abilities that characterize the cognition of many non-human species. The approach that we have applied here should be adapted and expanded to other Lower and Middle Palaeolithic incised objects. This would allow us to distinguish those that best fit natural or utilitarian interpretations from those in which markings were intentionally carved. It should also allow us to distinguish, among the latter, those conforming to rules of equidistance and symmetry from those that, either because bearing markings produced in multiple sessions or, as at Les Pradelles, featuring homologous units of information recorded during a single session with no will to create a regular pattern, are more likely to represent numerical notations. These analyses may be useful to test scenarios for the emergence of number symbols out of the 'number sense' that humans share with other species. Systematic analysis of sequentially marked objects interpreted as recording numerical information could also establish whether, as at Les Pradelles, incisions were juxtaposed from left to right, which is consistent with data indicating that mental number line is arranged from left to right [4,64–66].

On the basis of available information on Upper Palaeolithic AMSs and results presented here, we may speculate that the invention of number symbols required at least five, not necessarily successive, stages or cultural exaptations, defined as the co-options of existing cultural features for new purposes (electronic supplementary material, figure S21). The first stage may have consisted in the production of cut marks. Contrary to other species, hominins have been marking bone with stone tools during butchery activities for at least the last 2.6 Myr [67–69]. Cut marks often take the form of sets of juxtaposed incisions. This utilitarian activity was certainly crucial for the development of the motor and cognitive skills necessary to produce durable and visible markings on this medium, and to enhance their perception.

A first 'cultural exaptation' may have occurred when visible parallel, equidistant, similar incisions, technically identical to cut marks, were purposely produced on bone or other materials. When doing so, hominins externalized and embodied in material culture regularities that they, like many other species, recognized when interacting with the outside world. These parallel marks, or marks organized in detectable abstract designs, were meaningful as a whole and may have played, according to the context, iconic, indexical or symbolic functions. Archaeological examples such as the engraved fresh-water shell from Trinil [59] and the pattern engraved on the Bilzingsleben mammoth bone [61] indicate that this means to record information was used by some populations at least 540 ka BP.

A following exaptation, exemplified by the pattern on the Les Pradelles bone, may have corresponded to a situation in which meaning was attributed to individual identical marks produced during the same session rather than to the whole pattern. This cultural exaptation is exemplified, archaeologically, by the identification of marks that are identical and recognizable individually but whose arrangement lacks equidistance, indicating that the craftsman was not interested in obtaining a visually consistent pattern. Results presented here suggest that this type of recording system was in use already 60 ka BP, and probably earlier.

A third exaptation occurred when, as with the Border Cave fibula, similar marks are added at different times, which gives the possibility of adding numerical information to an already existing pattern. The Border Cave notched bone, dated to 44–42 ka BP, is the earliest known example of such a notation.

A fourth exaptation occurred when the morphology of the marks, their spatial distribution, their number and their accumulation over time were individually or conjointly given a role in the code. The earliest known examples of such devices date back to 40–38 ka BP. This fourth exaptation contains most of the premises that did eventually allow some human populations to produce a further exaptation: the invention of the number symbols known historically and used at present. It is probably not by chance that the increased complexity of codes that we observe with the Upper Palaeolithic is paralleled by the use of a variety of personal ornaments. Personal ornament complexity reflects the multiplicity of codes that human societies can visually discriminate and transmit. Interestingly, in spite of its massive implications for our life and cognition, the invention of number symbols appeared very recently and has required no biological change. Our brain has not undergone specific adaptations in order to be able to use number symbols. This suggests that it is quite possible, and this is what we would argue, that these cultural exaptations have not required concomitant significant inheritable biological changes. They may have just occurred and become consolidated as the consequence of adapted teaching strategies and the brain plasticity that characterizes our genus.

Ethics. Subjects gave their explicit consent when participating in the experiment and signed a consent form.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. F.D., L.D. and I.C. wrote the first draft of the article; F.D. and L.D. conceived experiments and analysed results; F.D., G.G., A.Q. and E.L. conducted the microscopic and morphometric analysis of the archaeological specimens and the study of faunal remains; B.M. and B.V. directed the Les Pradelles excavations and provided information on the context and dating of the specimen from this site; all authors critically revised the article.

Competing interests. We have no competing interests.

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Supplementary Material

From number sense to number symbols.
An archaeological perspective

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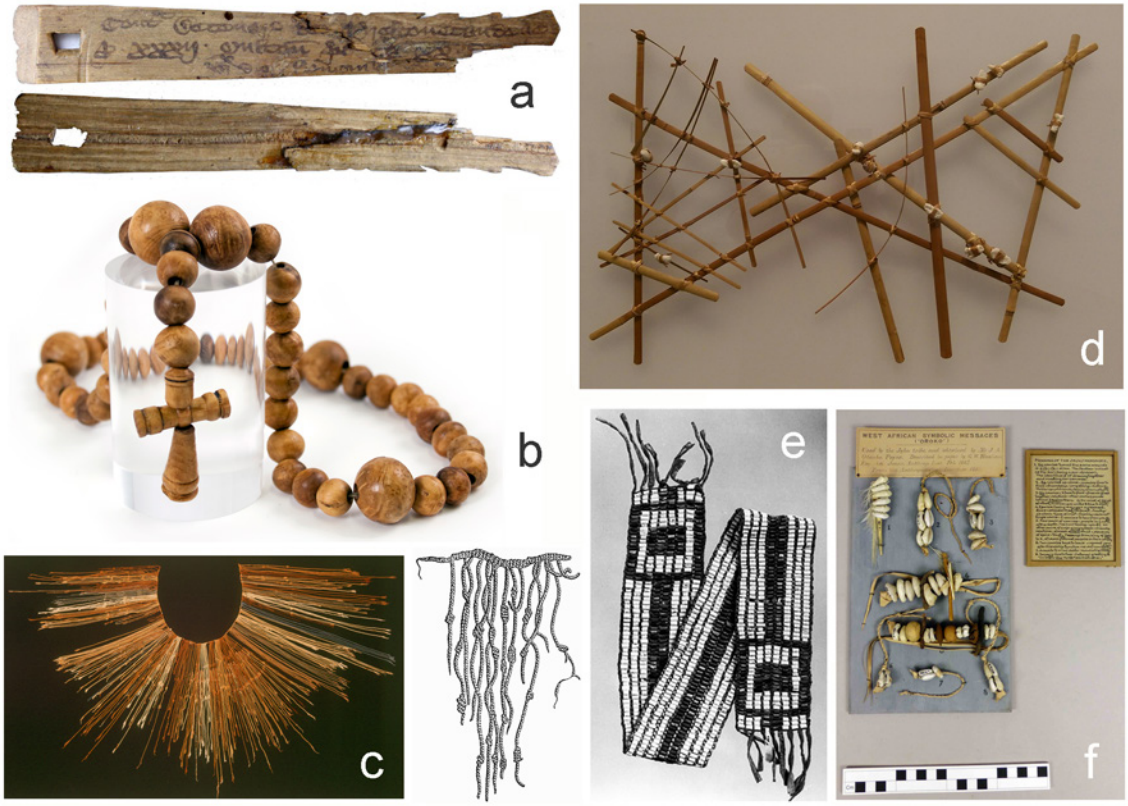
Supplementary Material - Text

Analytical Methods

The Les Pradelles bone was examined and photographed with a motorized Leica Z6 APOA, equipped with a DFC420 digital camera driven by LAS Montage and Leica Map DCM 3D computer software. Sections and 3D models of the incisions were obtained with the LAS Montage or by exporting depth maps obtained with the LAS Montage into the Leica Map DCM 3D. Accurate 3D reconstructions and sections of the incisions were also obtained using a STIL CHR 150 chromatic confocal microtopographer (STIL S.A., Aix-en-Provence, France) held at the C2RMF laboratory in Paris. This equipment allowed for a vertical and spatial resolution of 0,1 µm (44). Metric data recorded on experimental incisions were also collected on the Les Pradelles incised bone and the mean, standard deviation, and CV were calculated. Resin replicas of the incisions were produced by moulding them with Provil L dental elastomer (Bayer) and making casts with Araldite LY554 (Ciba Geigy). The replicas were metal coated and observed with a Leo 1430vp scanning electron microscope.

The Border Cave notched bone was studied at the McGregor Museum, Kimberley, South Africa, with an Olympus SZX16 Zoom Stereo Microscope. The notches were moulded with a Coltène® President light body high-resolution dental impression material. Transparent casts, obtained in M resin (Plastomax, South Africa), were analysed in reflected and transmitted light with the motorised Leica Z6 APOA, equipped with a DFC420 digital camera linked to a LAS Montage and Leica Map DCM 3D computer software. Sections and 3D reconstructions of the notches were obtained with the LAS Montage or by exporting depth maps obtained on a replica of the bone with the LAS Montage into the Leica Map DCM 3D. Accurate profiles of well-preserved notches were obtained on the resin cast of the notches with a Sensofar S-Neox confocal microscope driven by the SensoScan 6 software (Sensofar, Barcelona). Surface acquisitions were realized with the 20x objective (N.A. 0.45), green light illumination, measurement steps of 2 µm, and by stitching multiple fields of view. These parameters allow for a spatial sampling of 0.65 µm, a vertical resolution of ca. 0.60 µm, and an error of less than 8 nm. Data was processed with the SensoMap 7.4 software. Outliers were removed, rotation of the notch was applied if necessary to position it parallel to Y axis, and a mean profile calculated from a series of hundreds of profiles located on the X axis. Angles were measured between two best-fit lines adapted to the mean notch profile.

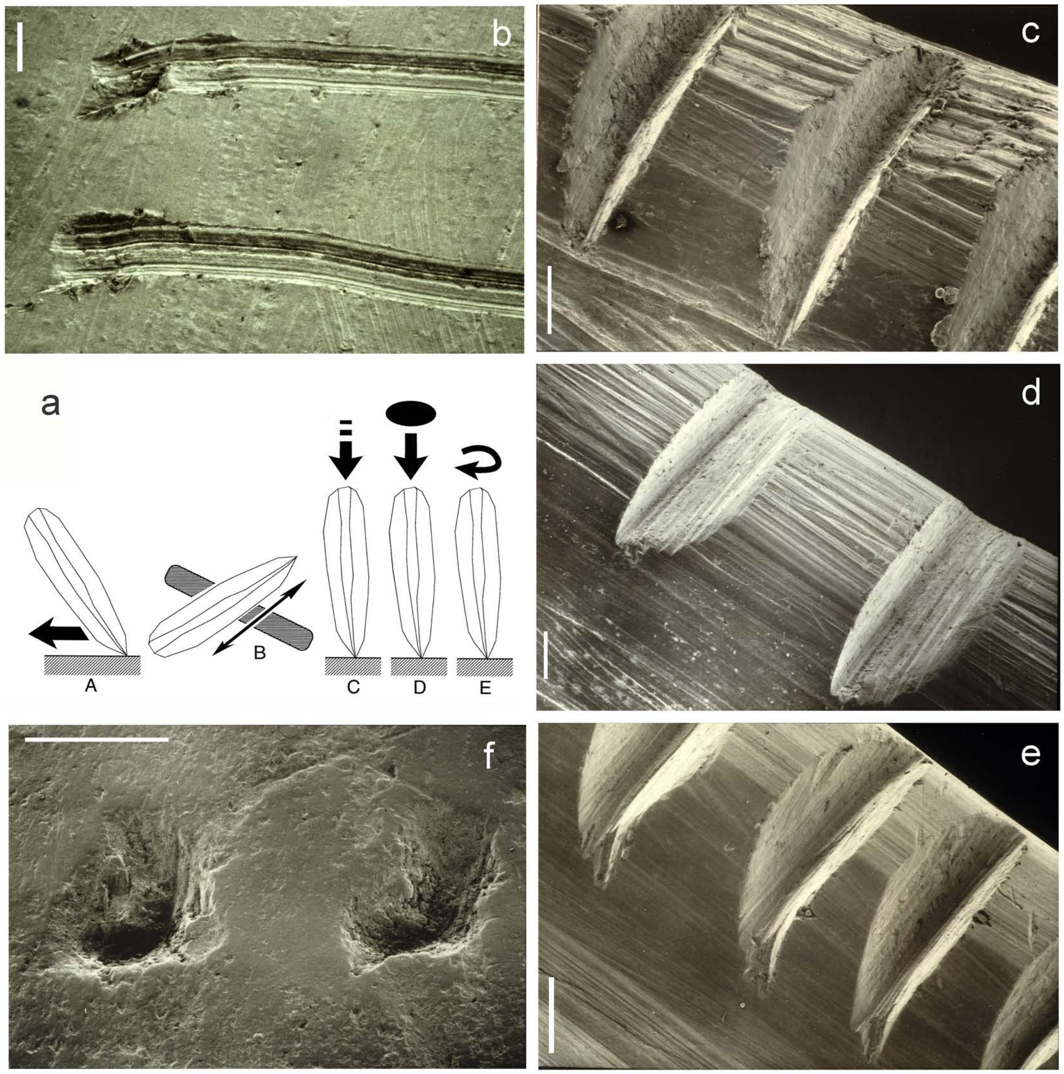
Supplementary Material - Figures
SM Figure 1



SM Figure 1. Artificial memory systems with different types of codes; a**:** Medieval English tally stick, made of wood, notched to record a debt owed to the rural dean of Preston Candover, Hampshire; b: wodden rosary found on board the carrack Mary Rose, XVI century; c: Quipu, a device consisting of knotted cotton or camelid strings used by the Incas to record and communicate numerical information on goods, tax obligations, and payments (1). The colour of the strings and the position and type of knot are the features used to store information; d: Micronesian navigational chart from the Marshall Islands, made of wood, sennit fiber and cowrie shells. Threads represent prevailing ocean surface wave-crests and the directions they take as they approached islands. Island locations are represented by shells tied to the framework or lashed junction of two or more sticks (2), e: Iroquois wampum belt made of shell and skin. Wampums were used by indigenous people of North America as cerimonial gifts and to record treaties and historical events (3, 4); f: mnemonic device used by the Yoruba of West Africa called Aroko. A message is conveied by sending an item, or group of items, with symbolic meaning to somebody else through a messenger. The information is given by the type and number of objects as well as by the way in which they are strung together (5, 6). The tally stick has a code based on the accumulation of information over time, the rosay, the micronesian navigational chart and the wampum on the morphology and spatial distribution of the elements bearing information. The Quipu code is based on the morphology (colour and types of knots), the spatial distribution (order of the strings and position of the knots), and the accumuation of information over time (by untying knots and tying them again at a different location). The code of the Aroko is based on the number, morphology and spatial distribution of the items conveing the information.

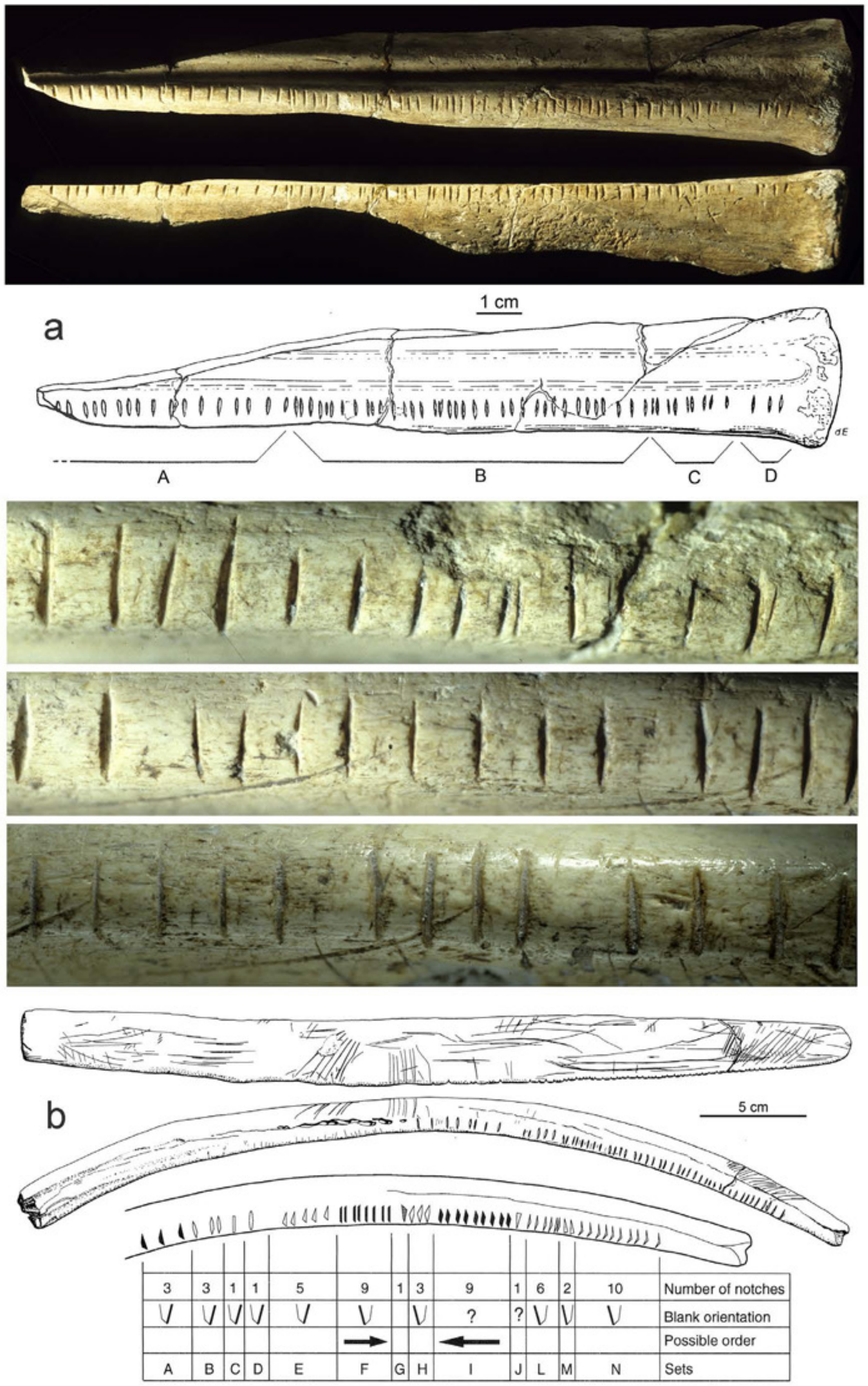
Credits. a: Winchester City Council Museums, modified after http://flickr.com/photos/106445670@N03/14169002135, Creative Commons Attribution-Share Alike 2.0 Generic license; b: photo Peter Crossman, Mary Rose Trust, licensed under the Creative Commons Attribution-Share Alike 3.0 Unported; c: Public Domain, https://commons.wikimedia.org/w/index.php?curid=123557; d: https://commons.wikimedia.org/w/index.php?curid=46844500; e: neg.# NC35-12972, courtesy University of Pennsylvania Museum of Archaeology and Anthropology, https://www.library.upenn.edu/exhibits/rbm/kislak/print/belt.html; f: Pitt Rivers Museum ; https://uoamuseums.wordpress.com/2016/04/02/zoom-in-on-yoruban-aroko/

SM Figure 2



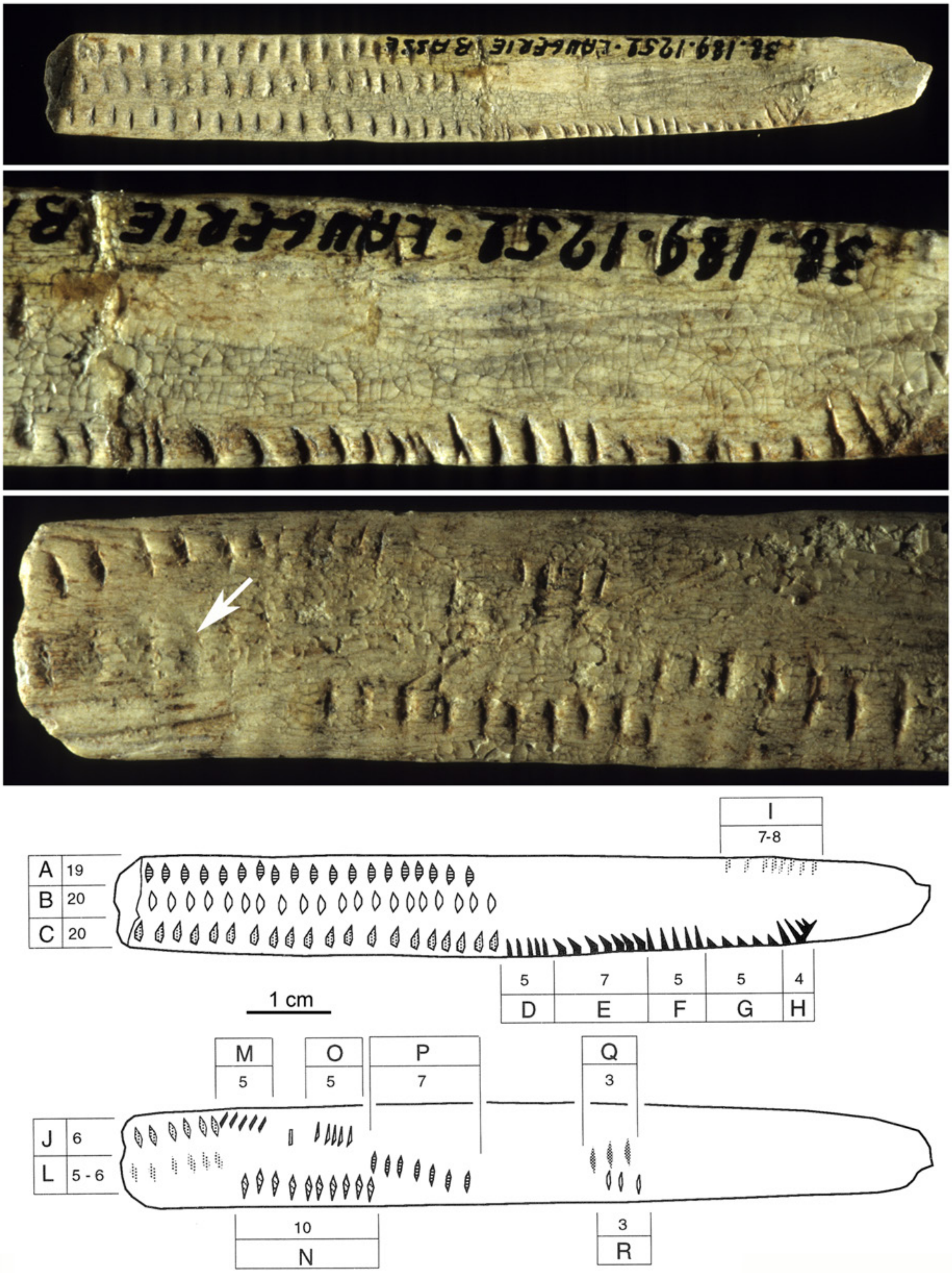
SM Figure 2. a: principal techniques used in the Upper Palaeolithic for marking bone, antler and ivory (A: incising; B: notching; C: puncturing by preassure; D: puncturing by indirect percussion; E: rotation under preassure); b: experimental single strokes line made by the same point; c-e: experimental sets of notches made by unretouched (c, e) and retouched (d) cutting edges; f: punctures on the La Marche antler produced by the preassure and incomplete rotation of a point. Notice features such as internal striations and section enabling the identification of the same tool. Scales = 1 mm. Modified after (7-9).

SM Figure 3



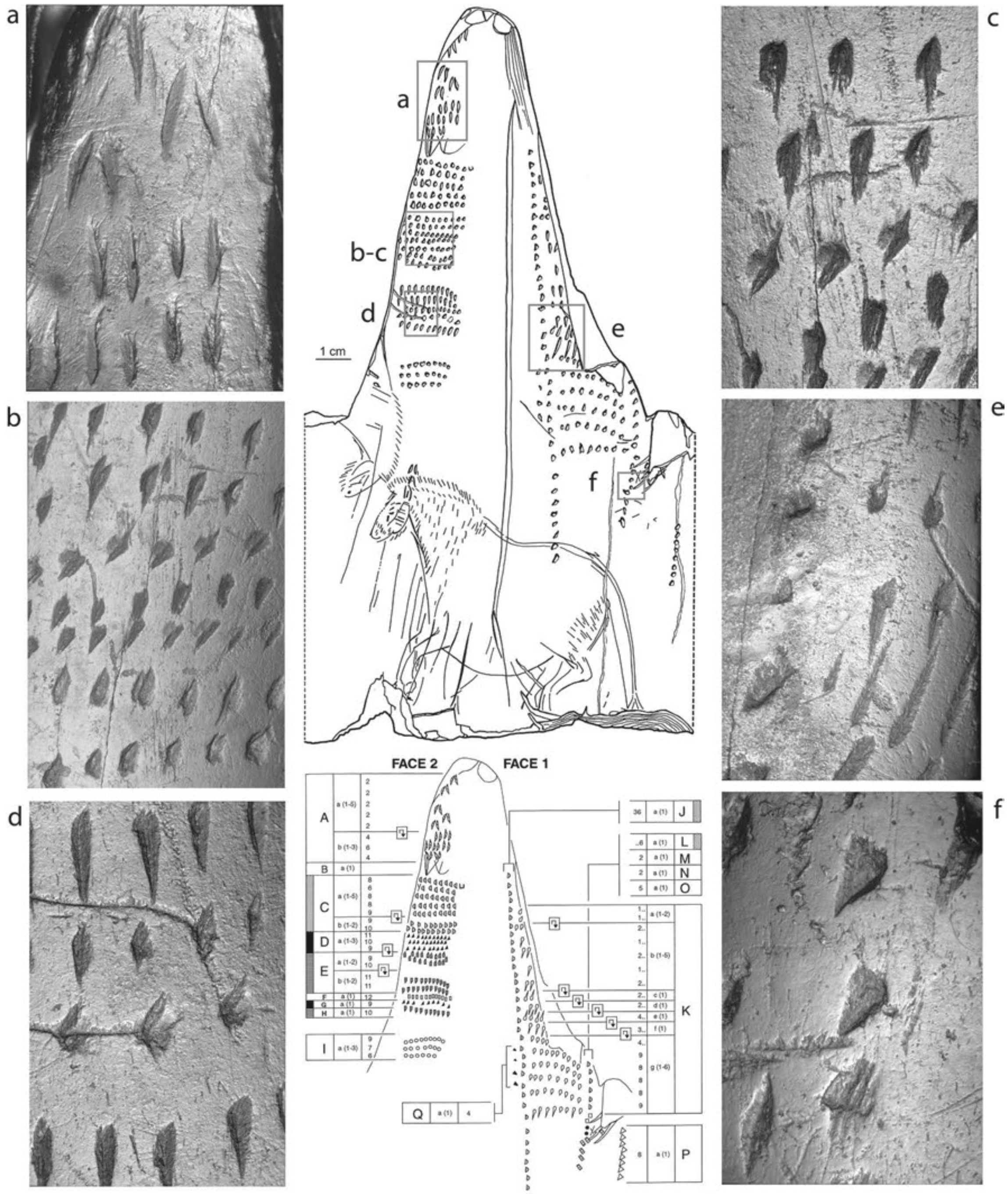
SM Figure 3. a: reindeer metapodial from the the Gravettian layers of the Labattut shelter, Dordogne, France, bearing 65 notches cut with three or four different tools, interpreted as an artificial memory system with a code based on the accumulation of marks over time; b: macrophotos of notches on a rib of a woolly rhinoceros from Solutré, Saône-et-Loire, France with its tracing and schematic rendering. The rib bears 53 notches produced by at least twelve different tools. Capital letters and patterns identify the sets of marks produced by the different tools. Tracings modified after (10).

SM Figure 4



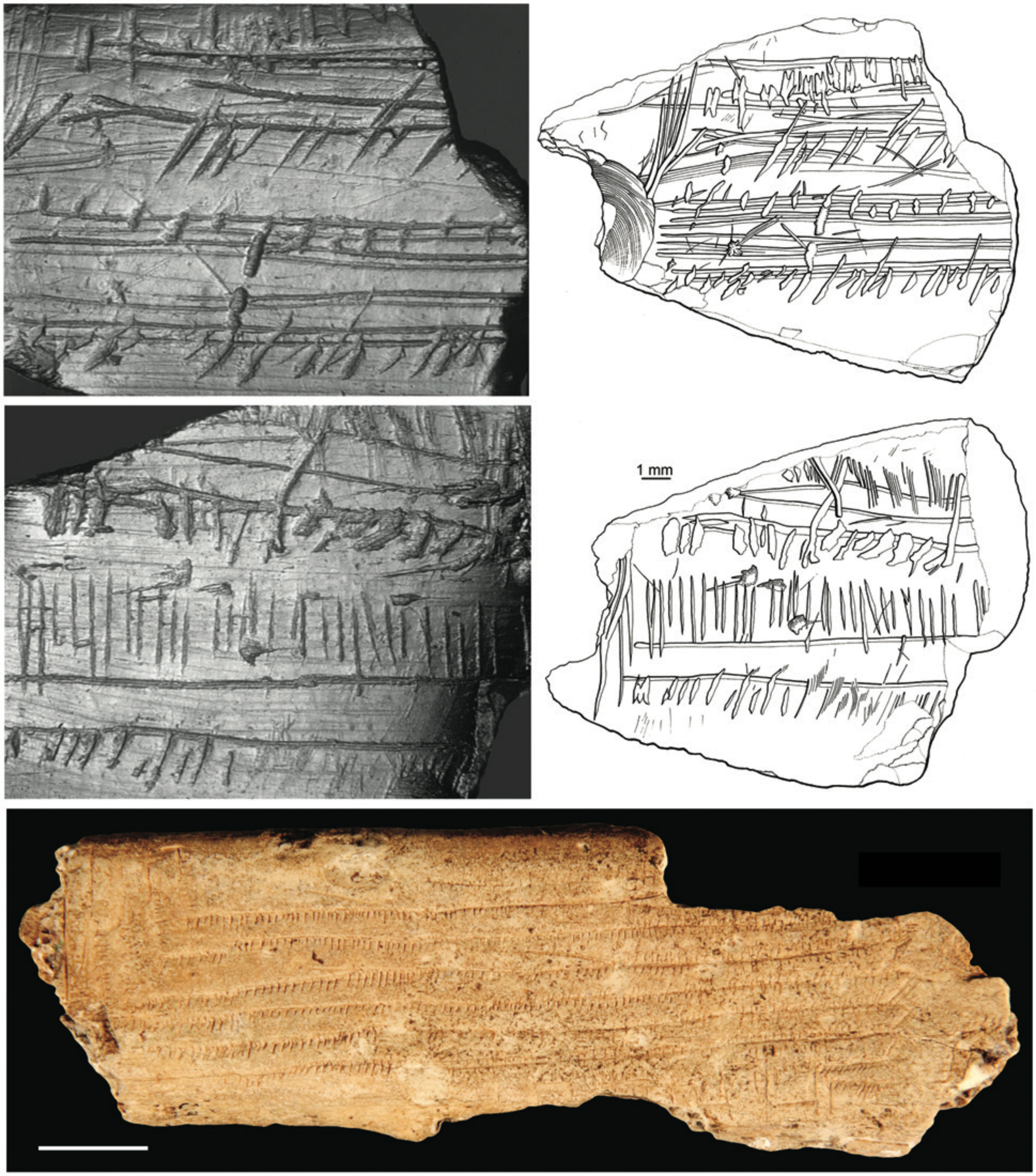
SM Figure 4. Rib from the Magdalenian layers of the Laugerie-Basse shelter, Dordogne, France, incised with more than 120 marks grouped in at least ten different sets. The code is possibly based on accumulation of markings over time, spatial organization of the markings, and their morphology. The object displays signs of deliberate obliteration of three sets of marks (arrow), which represents the earliest known evidence for a subtraction. Modified after (10).

SM Figure 5



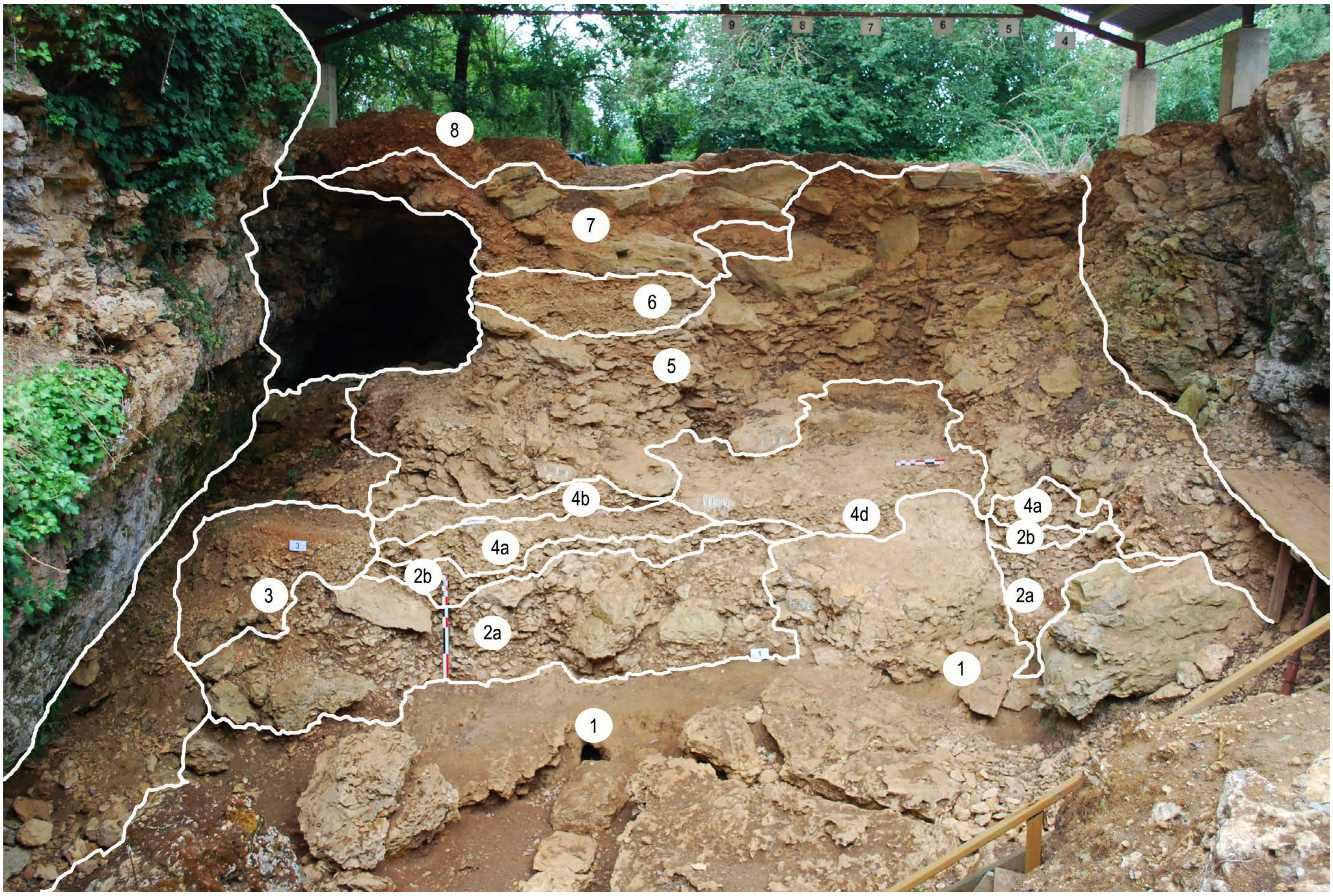
SM Figure 5. Tracing, schematic rendering and close-up views of the incised reindeer antler from the Magdalenian layers of the La Marche, Lussac-les-Châteaux, France. The object bears more than three hundred markings arranged in several sets. Each set is produced with a slightly different technique in order to create small but visually perceptible differences. Some “diacritic” marks are incised at the beginning of some sets, probably to provide additional information on the meaning of the set. The object is interpreted as an artificial memory system with a code based on both the spatial distribution and the morphology of the marks. Capital letters and patterns identify sets of marks produced by different tools and/or techniques. Modified after (7).

SM Figure 6



SM Figure 6. Top: photos and tracings of a fragmentary bone pendant from the Epipaleolithic site of Tossal de la Roca, Alicante, Spain. The object is engraved with eight sets of tiny marks, each made with a different technique or tool. It is interpreted as an artificial memory system with a code based on the spatial distribution of the elements bearing information, the elements' morphology and, possibly, the accumulation of marks over time. Bottom: incised rib from a Late Magdalenian layer of the Grotte du Taï, Drôme, France, bearing undred of incisions produced in multiple sessions. Scale bar = 1 cm. Modified after (11) and (12).

SM Figure 7



SM Figure 7. Eastern profile of Les Pradelles Locus East with indication of the limits between facies and sub-facies as established during the 2001-2003 excavation campaigns. The objet studied in this article comes from layer 10 of the stratigraphy proposed during excavations conducted between 1965 and 1980, correlated to new excavation’s sub-facies 2a.

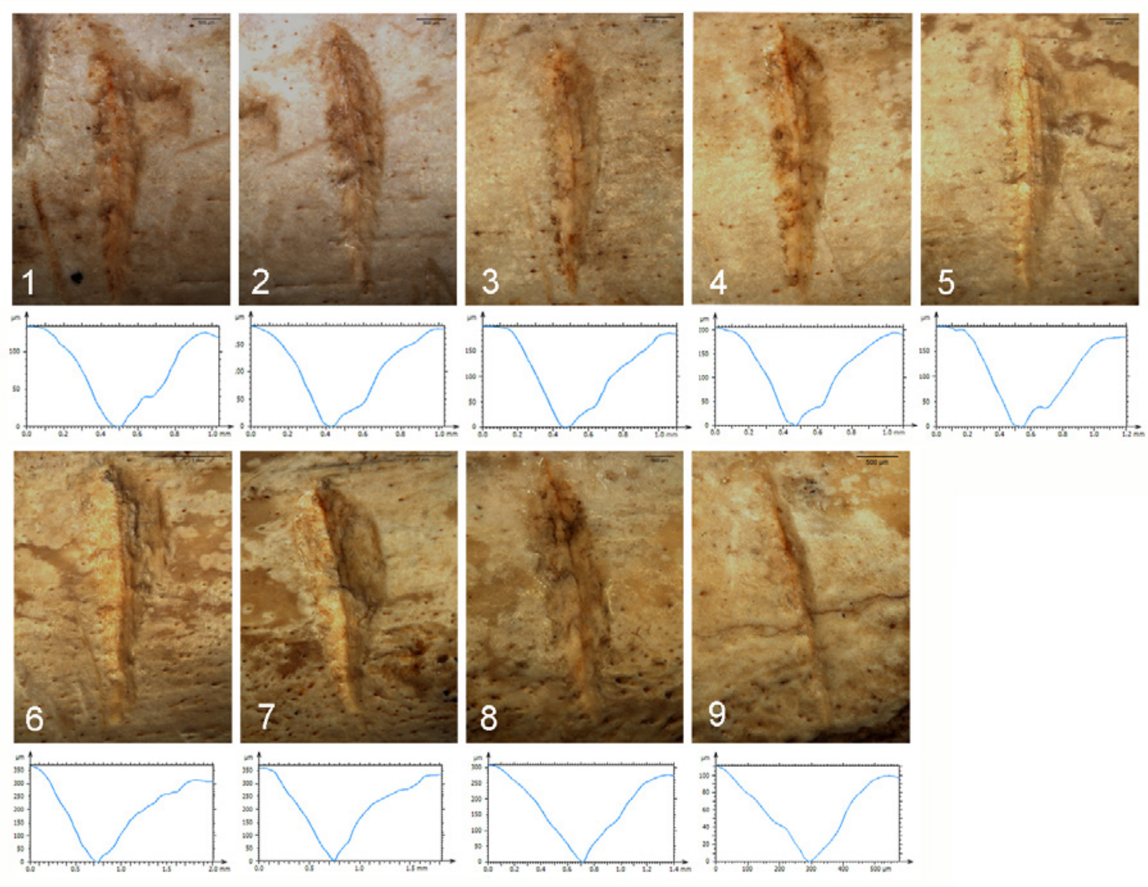
SM Figure 8

SM Figure 8. Subjects participating in the trial and three sets on incisions produced during the last two phases of the experiment. Scale = 1 cm.

SM Figure 9

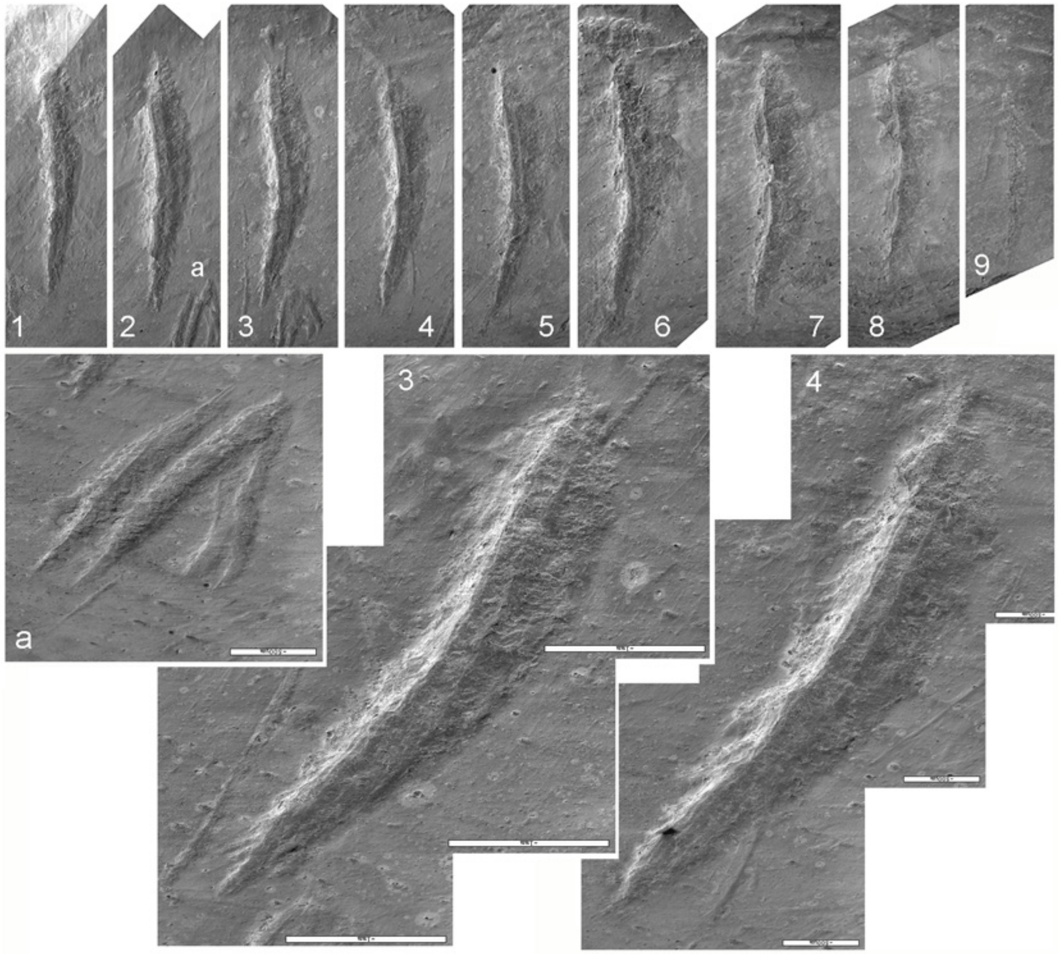
SM Figure 9. Mesio-distal fragment of the left femur of a *Crocuta crocuta spelaea* from the Les Pradelles Mousterian site bearing sequential incisions.

SM Figure 10



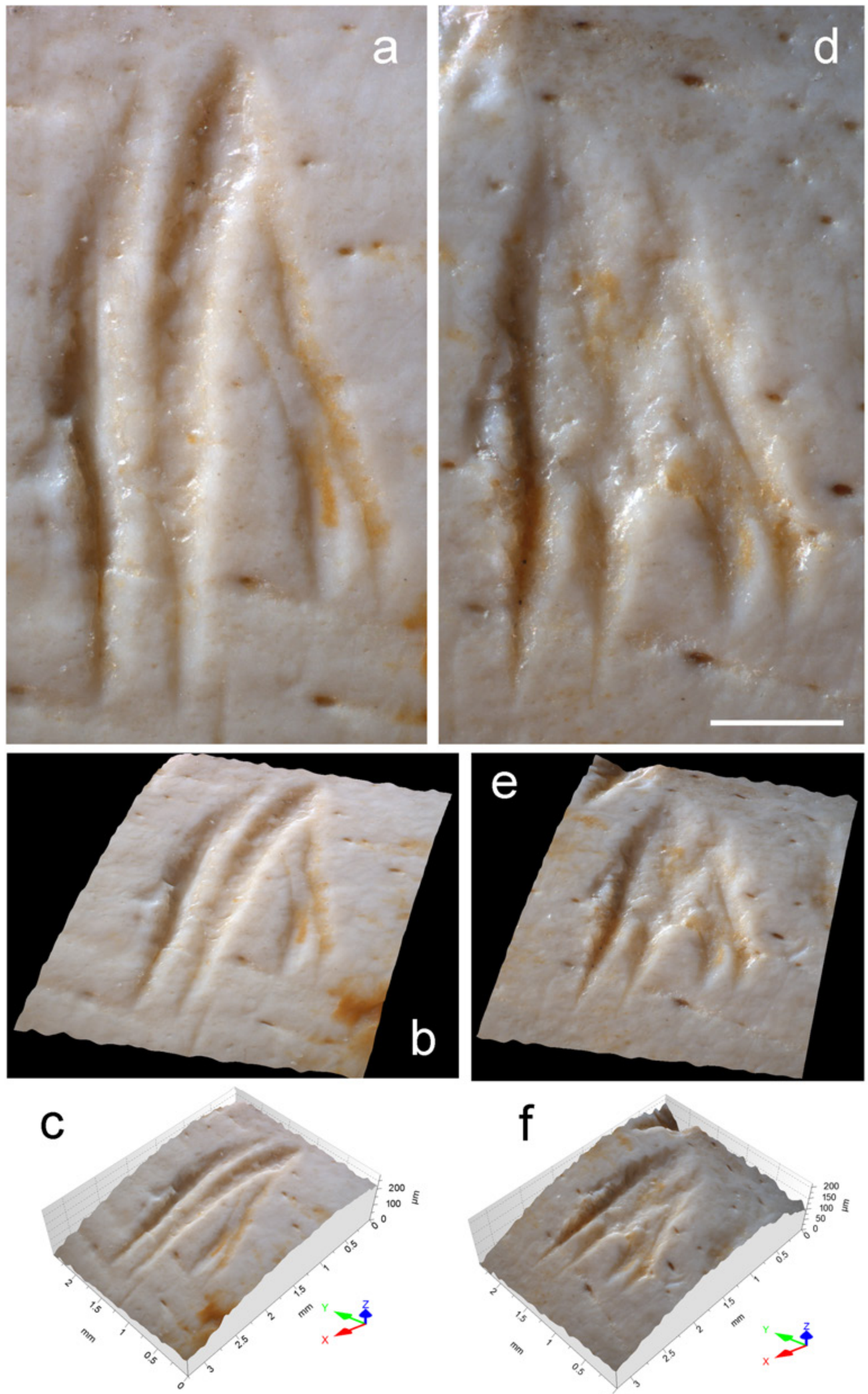
SM Figure 10. Photos and sections of the incisions on the Les Pradelles hyena femur.

SM Figure 11



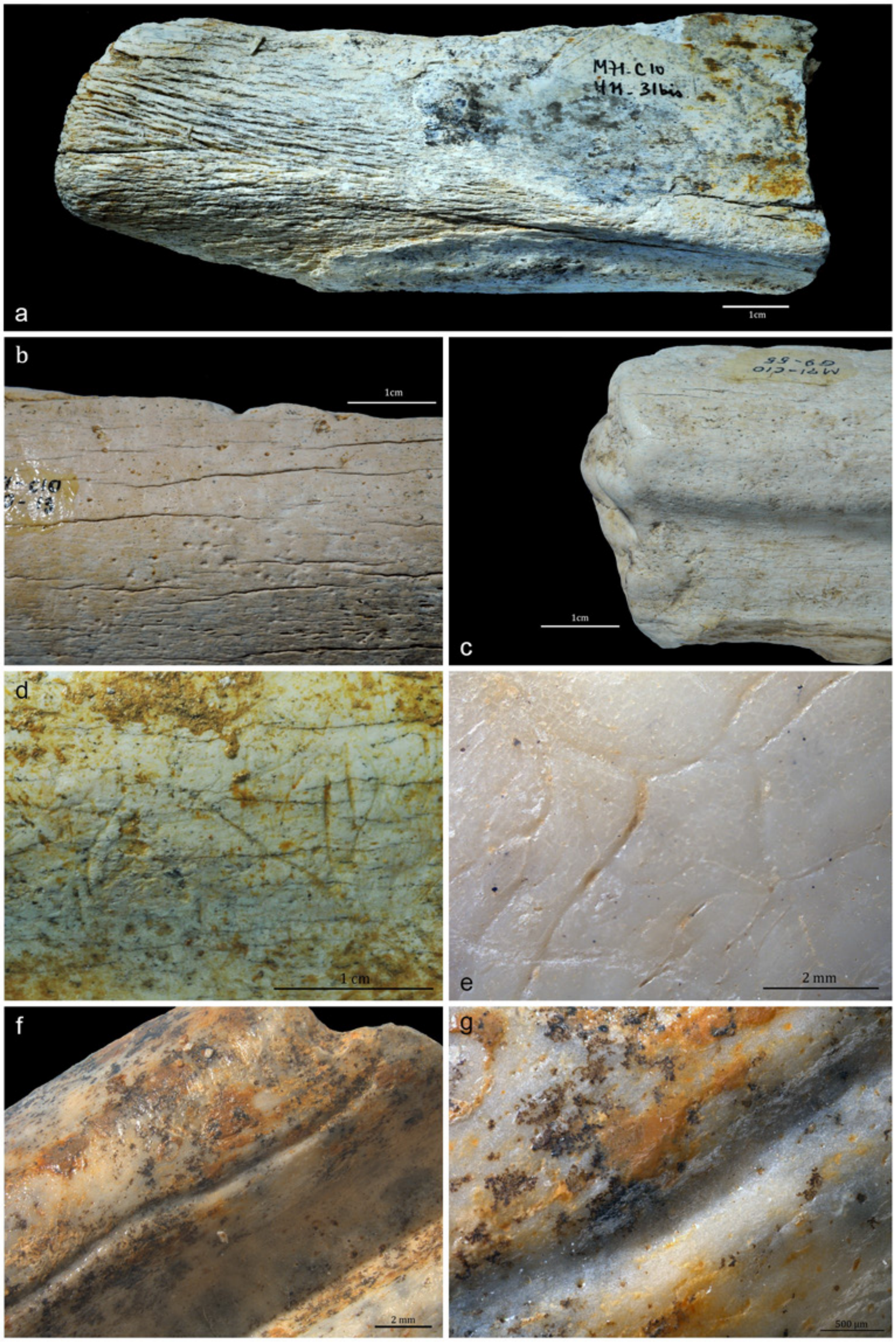
SM Figure 11. Scanning electron microscope micrographs of the incisions on the Les Pradelles specimen. Notice the similarity in shape and internal morphology indicating the use of the same point; a: close-up view of subset *c*.

SM Figure 12



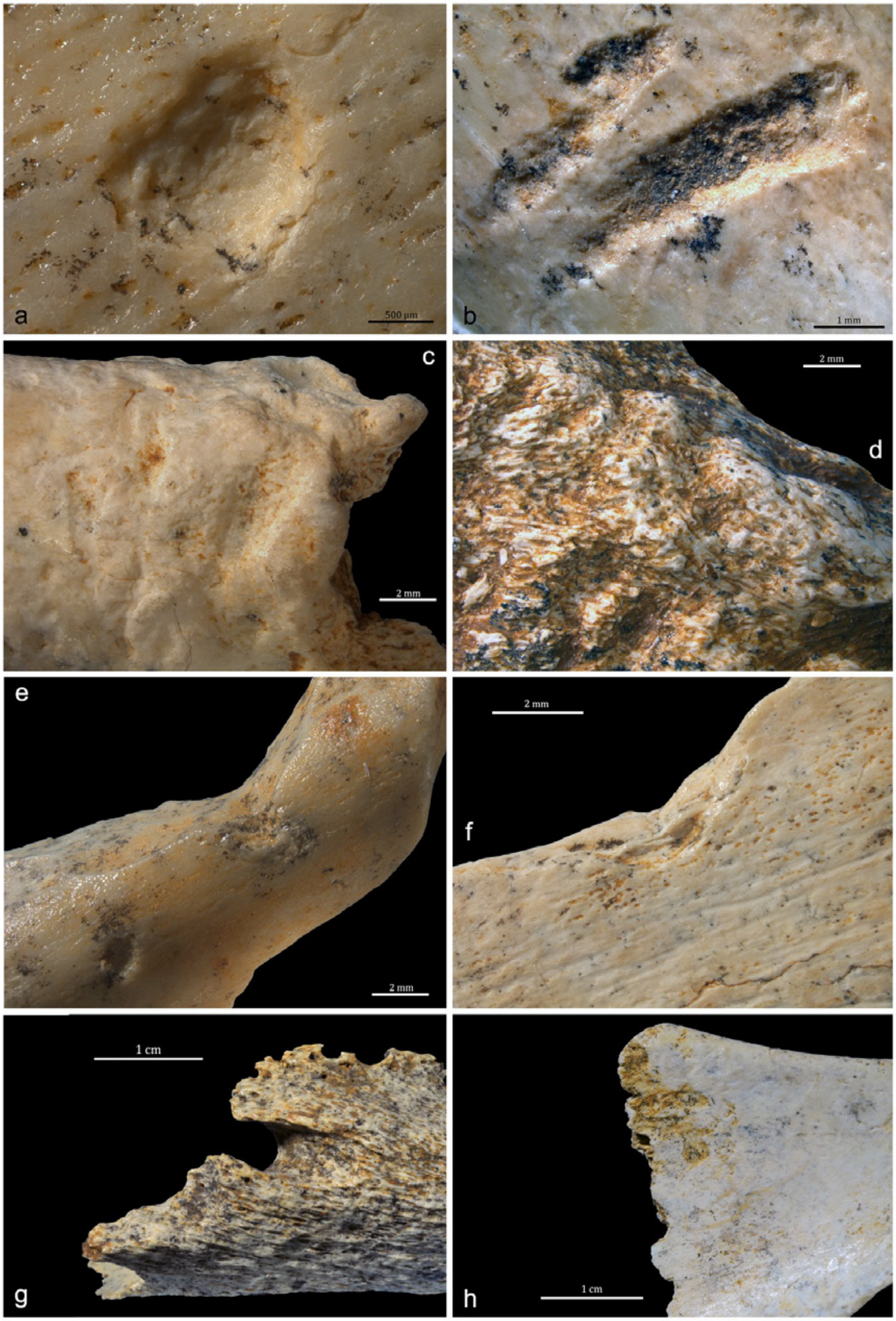
SM Figure 12. Microscopic photos of subsets *c* (a) and *d* (b) on the Les Pradelles femur and their 3D reconstruction (b, e) and volumetric rendering (c; f).

SM Figure 13



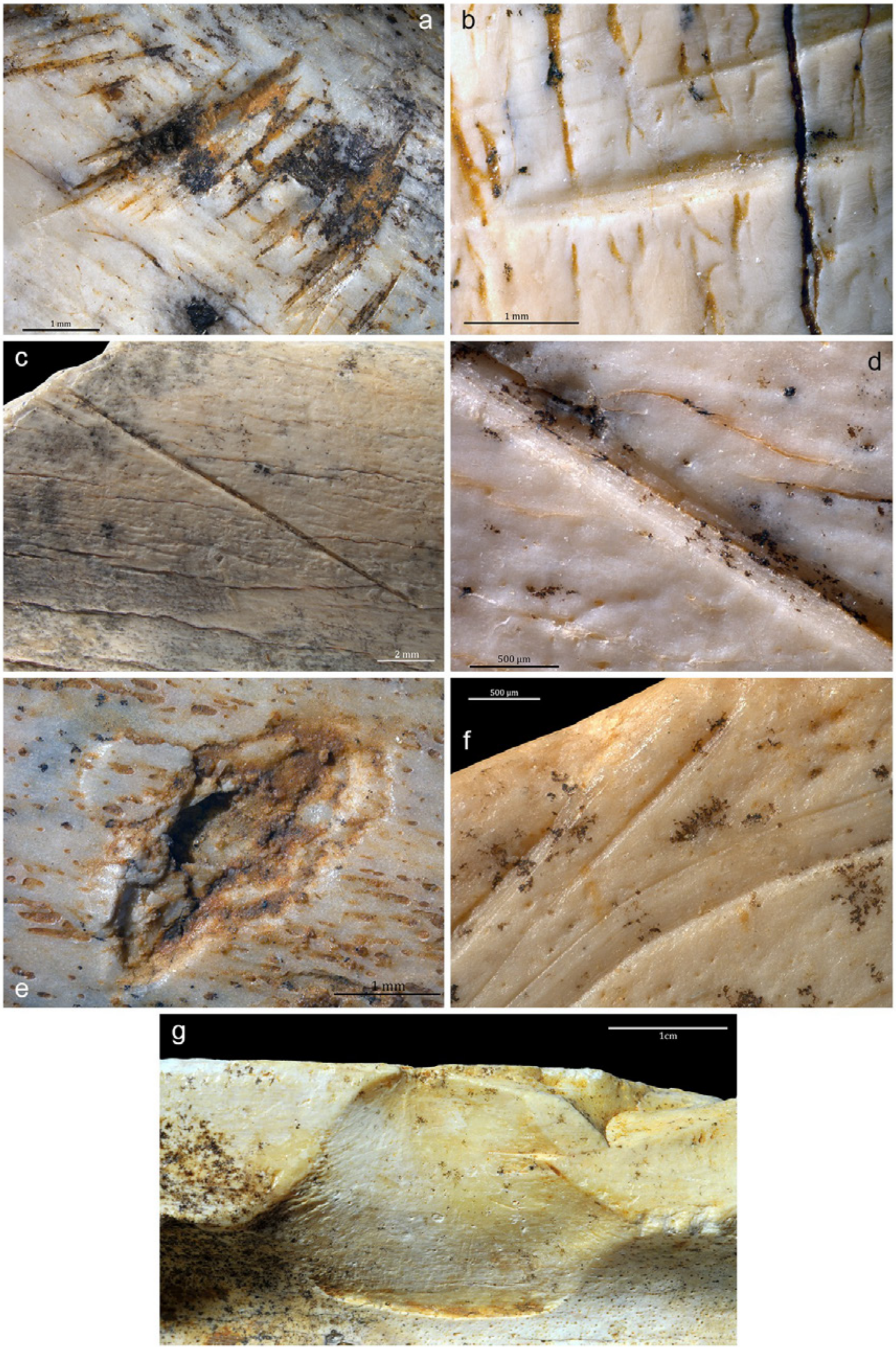
SM Figure 13. Natural modifications on faunal remains from Les Pradelles; a: weathering, b: weathering and dissolution, c: abrasion, d: trampling, e-g: impressions of vascular canal.

SM Figure 14



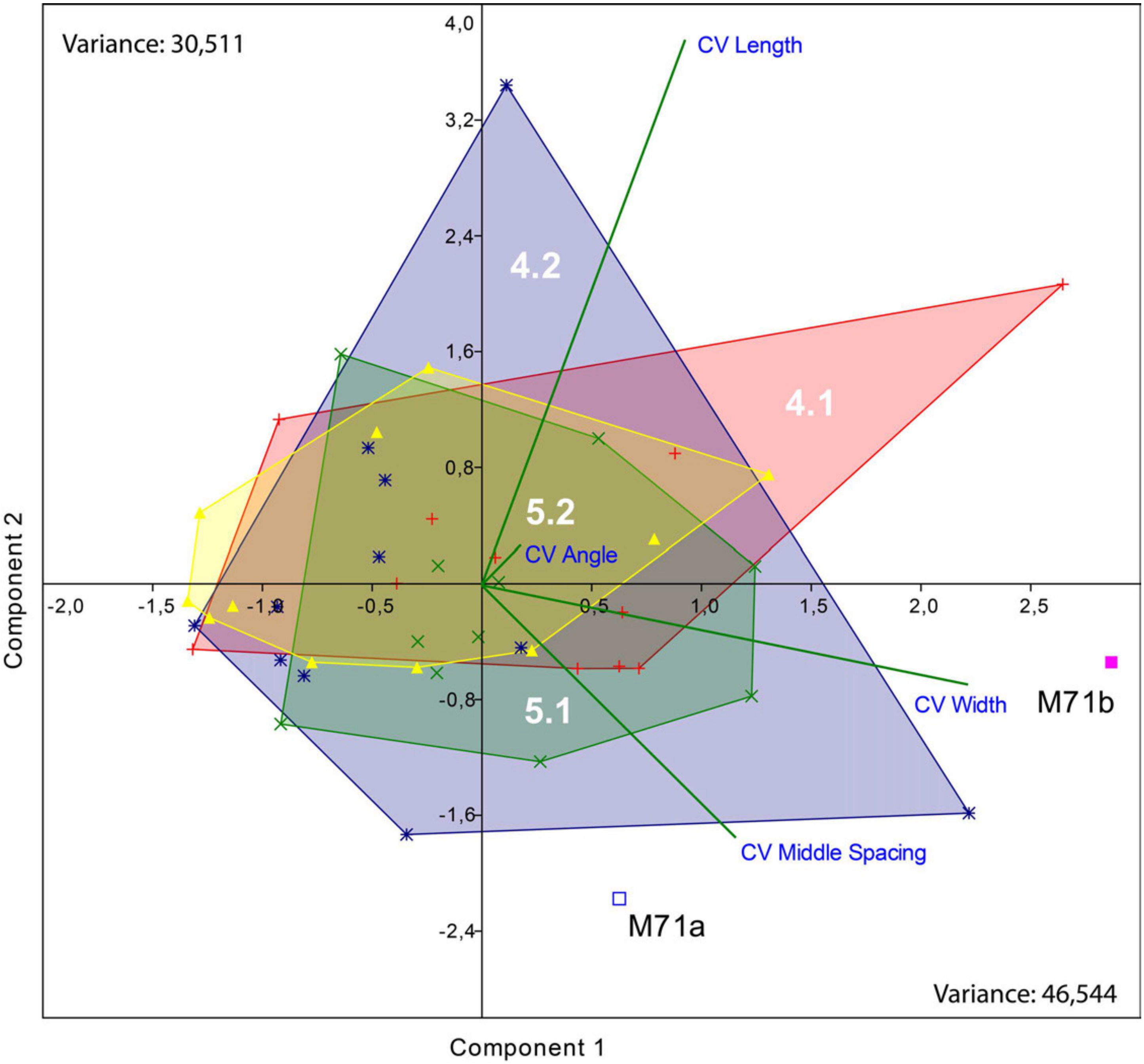
SM Figure 14. Modifications produced by carnivores on faunal remains from Les Pradelles; a: pit, b-c: scoring; e: chipping, f: chipping and crushing, g: regurgitated bone, h: crenulated edge.

SM Figure 15



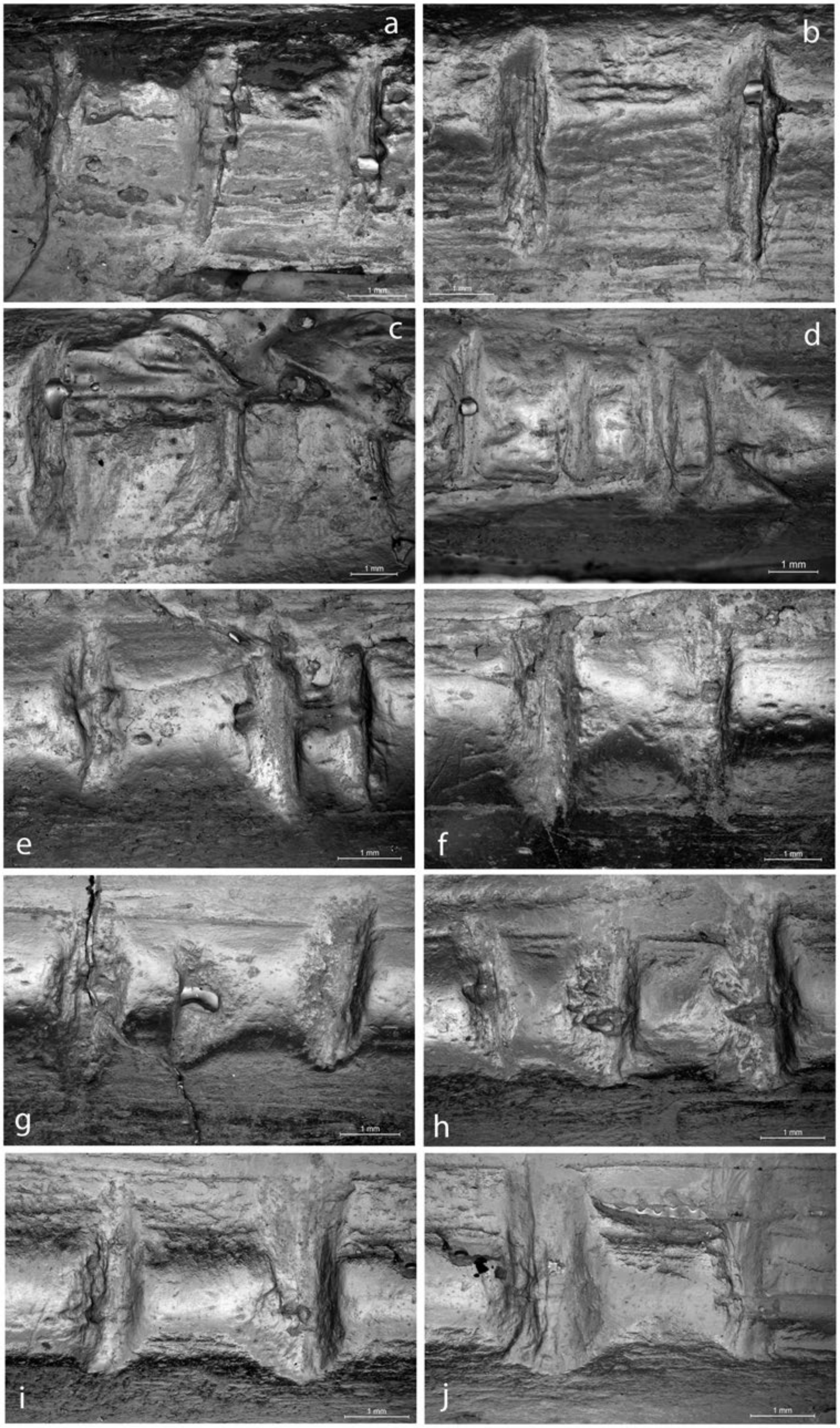
SM Figure 15. Human modifications on faunal remains from Les Pradelles; a-d: cutmarks; e: impact scar; f: scraping, g: flake-scar.

SM Figure 16



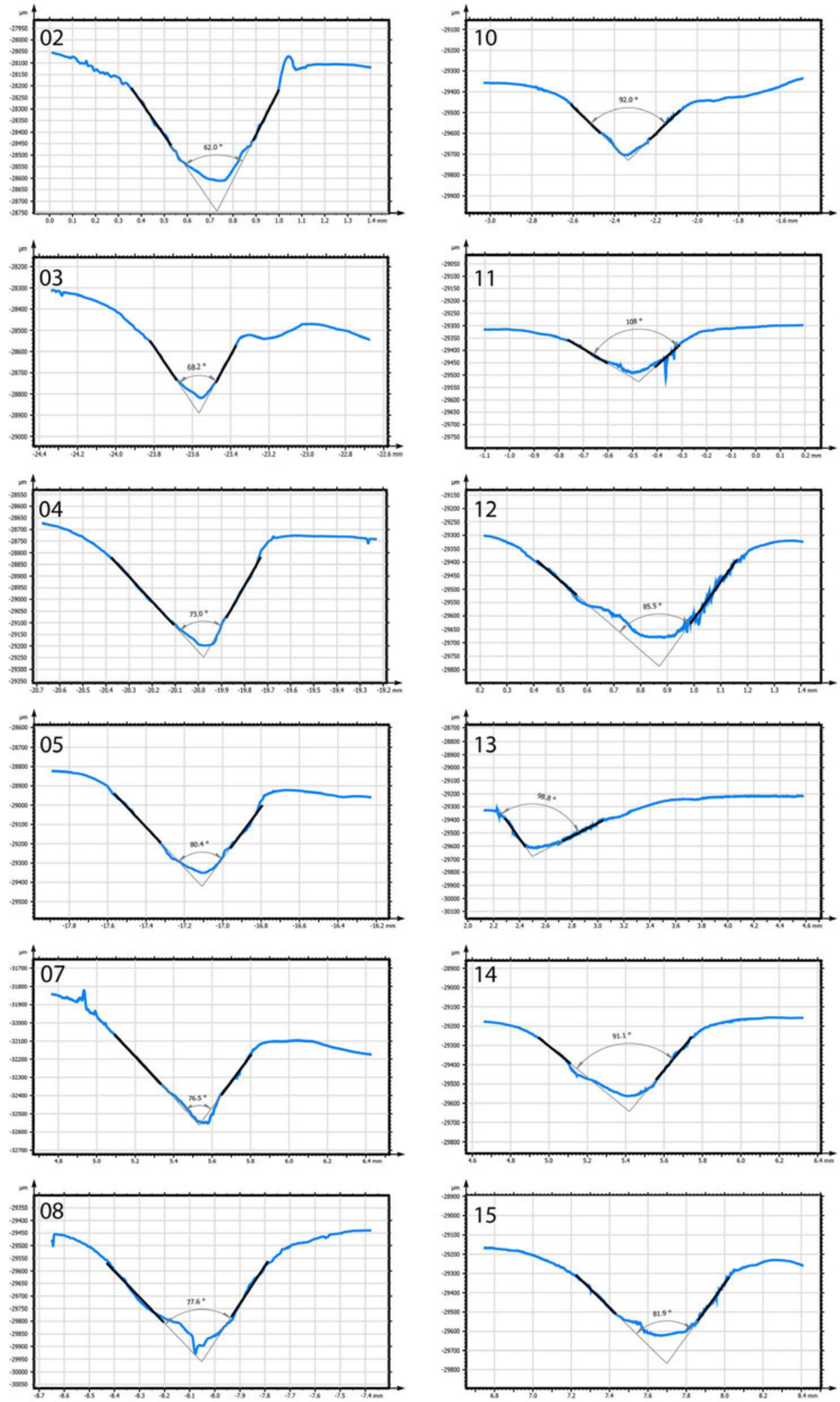
SM Figure 16. PCA scatter diagram of subsets of incisions produced by modern subjects during phase 4 and 5 of the experiment and subsets *a* and *b* incised on Les Pradelles M71 specimen.

SM Figure 17



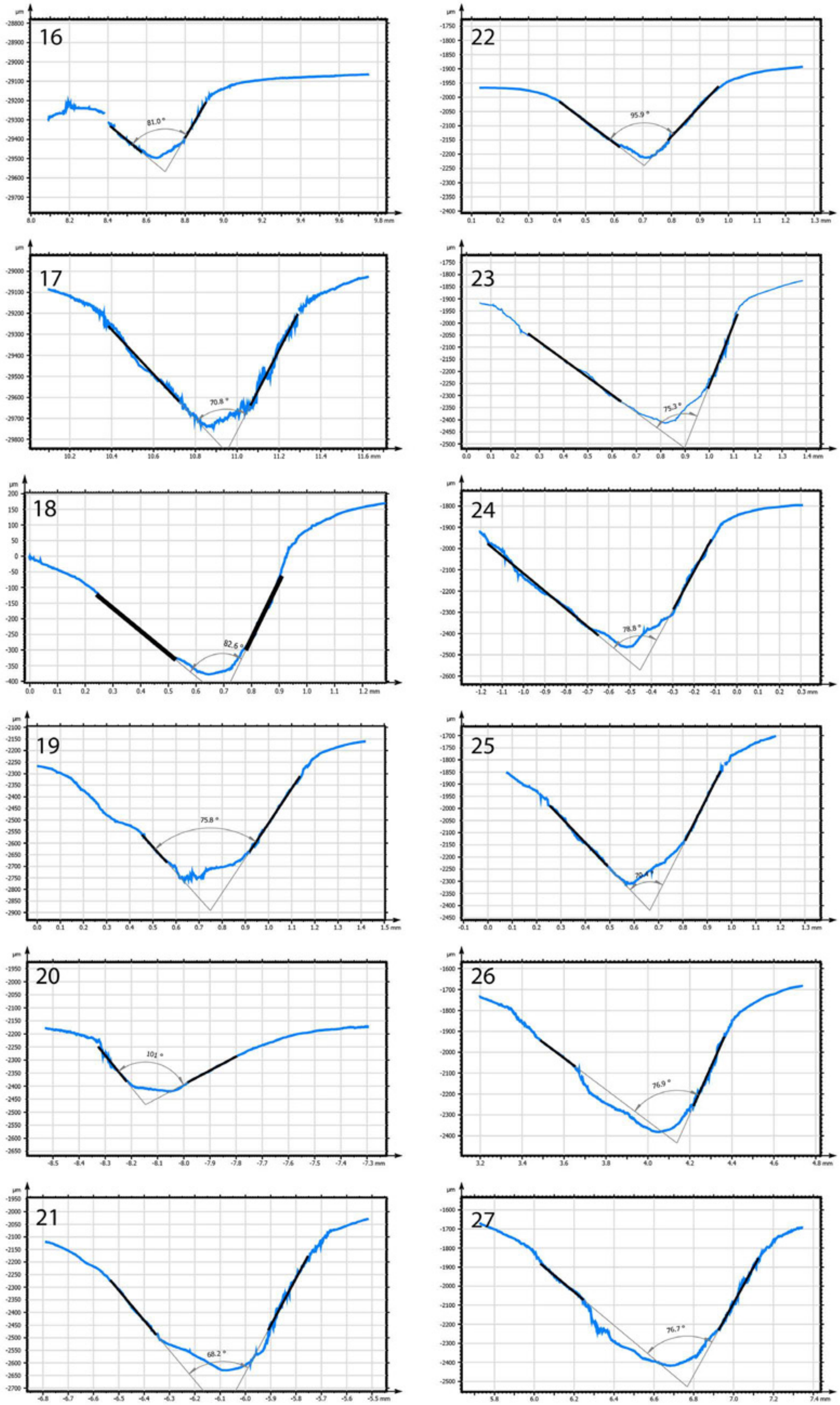
SM Figure 17. Notches on the Border Cave fibula; a: 1-3; b: 4-5; c: 6-8; d: 10-13; e: 14-16; f: 17-18; g: 19-21; h: 22-24; i: 25-26; j: 27-28.

SM Figure 18



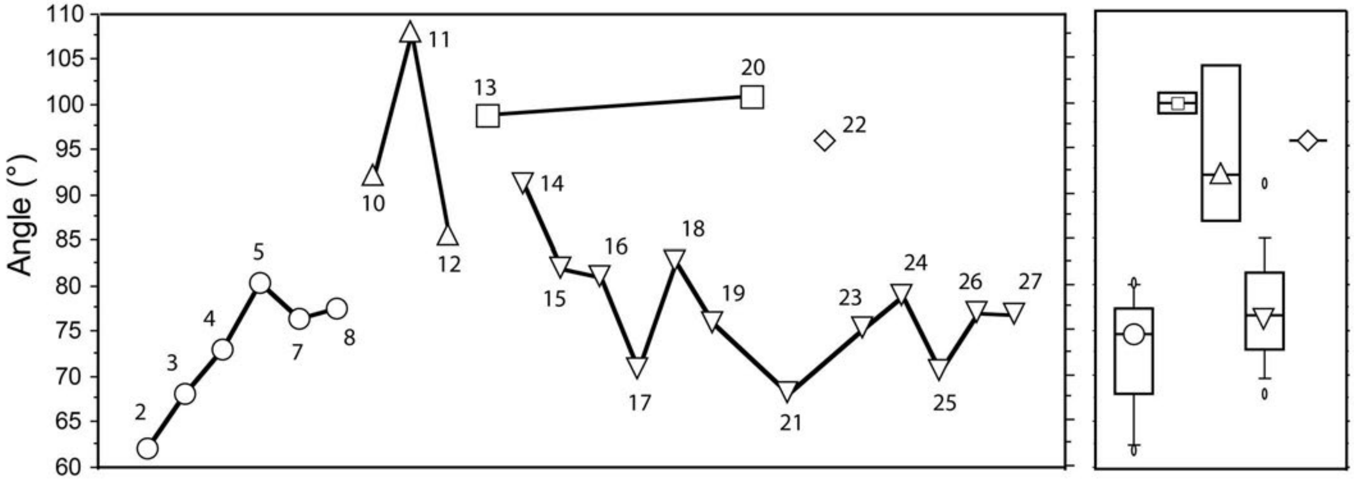
SM Figure 18. Cross-sections of notches 2-15 on the Border Cave baboon fibula with measured angles.

SM Figure 19



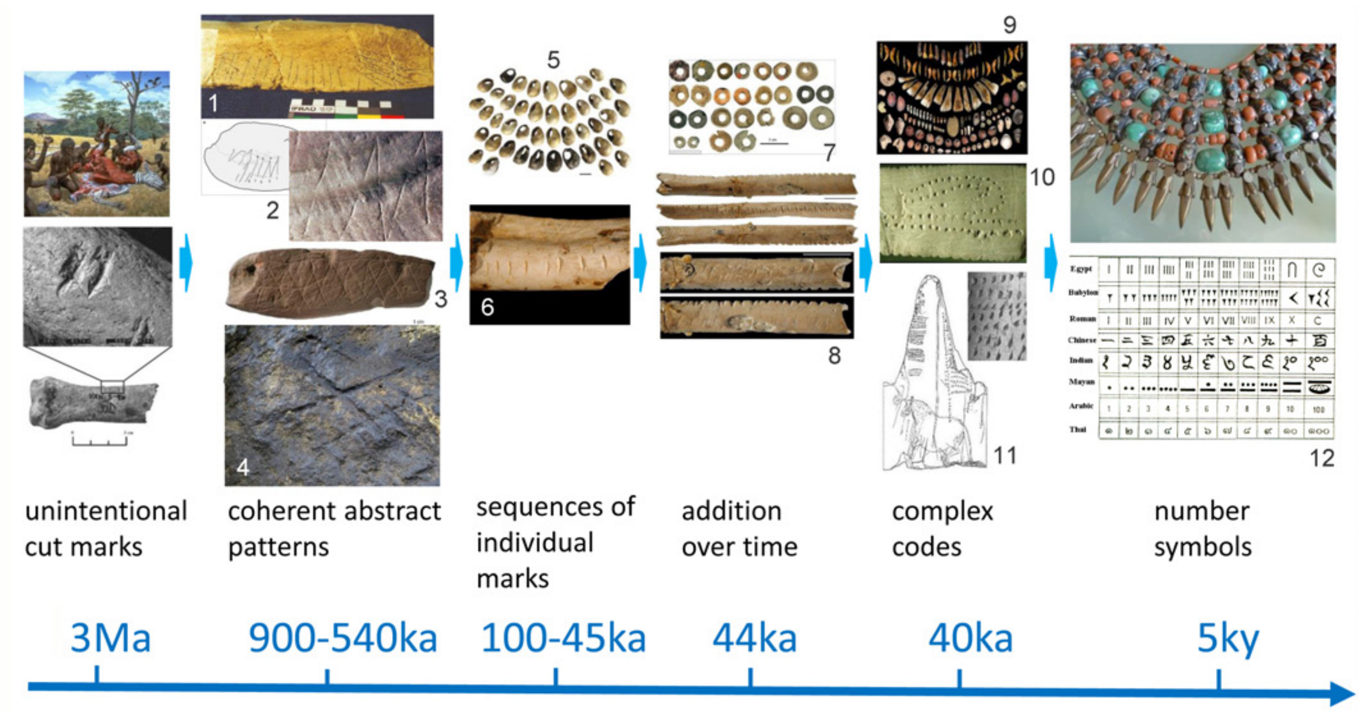
SM Figure 19. Cross-sections of notches 16-27 on the Border Cave baboon fibula with measured angles.

SM Figure 20



SM Figure 20. Variation in the angles of notches carved on the Border Cave baboon fibula. Symbols indicate notches attributed to the same tool.

SM Figure 21



SM Figure 21. Tentative five-stages scenario for the emergence of typically human numerical abilities (see text for explanation); 1: engraved mammoth bone from Bilzingsleben, Germany; 2: engraved freshwater mussel from Trinil, Java (540 kyr); 3: engraved ochre from Blombos Cave, South Africa (72 kyr); 4: engraving on the bedrock of Gorham's Cave, Gibraltar (40 kyr), 5: *Nassarius* shell beads from Blombos Cave, South Africa (72 kyr); 6: Les Pradelles incised hyena femur (72-60 kyr); 7: ostrich egg-shell beads from Border Cave, South Africa (44 kyr); 8: notched baboon fibula from Border Cave, South Africa (44 kyr); 9: personal ornaments from Upper Palaeolithic sites; 10: incisions on the Blanchard ivory spatula, France (36 kyr); 11: La Marche incised reindeer antler, France (15 kyr); 12: numeral systems.

Supplementary Material - Tables

SM Table 1

Layer	Sub-layer	Culture	Age BP	Dating method
1 BS	UP	ELSA	-	14C
	Lower A		41.5 - 24	14C
	Lower B		42.3	14C
	Lower C		42.6	14C
1 WA	UP	ELSA	43	14C
	2			14C
2 BS	UP	MSA 3	49.0 - 44.2	14C
	Lower A		49.0 - 60.0 *	14C
	Lower B			14C
	Lower C			14C
2 WA		MSA 3	60 ± 3 *	ESR
3 BS	1	HP	56 ± 2	ESR
	2		64 ± 3	ESR
	3		72 ± 4	ESR
3 WA		HP	64 ± 2	ESR
1 RGBS		HP	74 ± 4	ESR
4 BS		MSA 1	77 ± 2	ESR
4 WA	1	MSA 1	115 ± 8	ESR
	6		113 ± 5	ESR
	7		168 ± 5	ESR
5 BS	2	MSA 1	161 ± 10	ESR
	5		144 ± 11	ESR
5 WA	1	MSA 1	183 ± 20	ESR
	2		227 ± 11	ESR

SM Table 1. Chronology of Border Cave stratigraphic sequence. The notches baboon fibula comes form layer 1BS Lower B-C. Modified after 13.

SM Table 2

Notch	Shape	Concavity	Cross Section	Cross section orientation	Double Groove Bottom	Right step	Termination	Max Lenght (µm)	Max Width (µm)	Max Depth (µm)
1	CU	CLHS	V shape	AR	Yes	No	CTR	3950	640	147
2	CU	CLHS	V shape	AR	Yes	No	CTR	4330	910	165
3	CU	CLHS	V shape	AR	Yes	No	CTR	4130	910	215
4	CU	CLHS	V shape	AR	Yes	No	CTR	4210	1020	246
5	CU	CLHS	V shape	AR	Yes	No	CTR	4950	1020	244
6	CU	CLHS	V shape	AR	Yes	Yes	CTR	5400	1530	305
7	OB	ST	V shape	AR	Yes	Yes	CTR	4600	1490	351
8	OB	ST	V shape	SY	Yes	No	CTR	4690	1090	352
9	AC	ST	V shape	SY	No	No	ST	3390	260	118
CU: cuneate; CLHS: concave on the left left-hand side; ST: straight; AR: Asymmetrical to the right; SY: symmetrical;										
Asymmetrical to the left; CTR: pinched termination slightly curved to the right										

SM table 2. Technological and morphometric data on the Les Pradelles incisions.

SM Table 3

Carnivore damage							Natural mod.			Human modifications			
PU	N	CE	PI	S	F	D	W	MA	R	CM	RE	IM	SC
15	9	10	22	50	1	2	10	2	1	22	13	12	4

PU: puncture; N: notch; CE: crenulated edges; PI: pit; S: scoring; F: furrowing;
D: digested; W: weathering; MA: mechanical abrasion; CM: cutmarks;
RE: retoucher; IM: impacts; SC: scraping

SM table 3. Modifications on a sample of faunal remains from Les Pradelles layer 10.

SM Table 4

notch	preservation		morphology								size							tool
	complete	damage	cross section orientation	groove bottom	step center left	step center right	step bottom left	step bottom right	step top left	step top right	Max Lenght (mm)	Max Width (mm)	Width top (mm)	Width middle (mm)	Width bottom (mm)	Max Depth (µm)	Angle (°)	
1	yes	si	AL	na	no	no	no	no	no	no	2,6	0,9	0,48	0,84	0,75	251	na	1
2	yes		AL	yes	no	no	yes	no	no	no	3,45	1,4	0,72	0,98	0,72	471	62	1
3	yes	pe, ab	AL	yes	no	yes	yes	no	no	no	2,6	0,94	0,62	0,84	0,78	458	68,2	1
4	yes		AL	yes	no	yes	yes	yes	no	no	3,8	1,1	0,73	0,74	0,74	496	73	1
5	yes	ab	AL	yes	no	yes	no	no	no	no	3,85	0,91	0,84	0,9	0,67	463	80,4	1
6	yes	ab	AL	no	no	no	no	yes	no	no	4,2	1,4	0,82	1,2	0,86	583	na	1
7	no	gl	AL	no	no	yes	yes	yes	na	na	na	1,4	na	1,4	0,98	429	76,5	1
8	no	gl, si	AL	na	na	na	na	na	na	na	na	na	na	na	0,94	334	77,6	1
9	no	gl	AR	na	na	na	na	na	na	na	na	na	na	na	na	na	na	2
10	yes	pe, ab	SY	no	yes	no	no	no	yes	no	3	1,5	0,92	1,4	0,98	332	92	3
11	yes	gl	SY	no	yes	no	na	na	yes	no	2,6	1,4	0,75	1	0,92	576	108	3
12	yes	gl	SY	no	yes	no	no	no	yes	no	2,7	1,4	0,7	1,4	1,2	557	85,5	3
13	yes	cr, pe	AR	no	no	no	no	no	no	no	2,9	2	1,6	1,8	1,9	529	98,8	2
14	yes	cr	AL	no	no	no	no	no	yes	no	2,5	1,4	0,68	1,4	0,7	349	91,1	4
15	yes	cr, pe	AL	no	no	no	no	no	yes	no	2,6	0,94	0,78	0,84	0,78	574	81,9	4
16	yes	cr, pe	AL	no	no	no	no	no	no	no	2,5	0,74	0,69	0,7	0,68	463	81	4
17	yes		AL	no	no	no	no	no	yes	no	3,6	1,35	1,15	1,25	1,05	747	70,8	4
18	yes	pe	AL	no	no	no	no	no	yes	no	3,1	1,1	0,94	0,99	0,85	470	82,6	4
19	yes	cr	AL	no	yes	no	no	no	yes	no	2,65	1,44	1,1	1,25	1,1	520	75,8	4
20	yes	cr, pe, ab	AR	no	no	no	no	no	no	no	1,8	1,3	0,94	1,25	0,9	279	101	2
21	yes		AL	no	no	no	no	no	no	yes	2,85	1,18	1,04	1,17	1,05	542	68,2	4
22	yes		SY	no	no	no	no	no	no	no	2,25	0,77	0,74	0,7	0,72	183	95,9	4
23	yes	pe	AL	no	no	no	no	no	no	no	2,4	1,24	0,97	1,16	1,02	453	75,3	5 ?
24	yes	pe	AL	no	no	no	no	no	no	no	3	1,46	0,94	1,3	1,2	648	78,8	4
25	yes	pe	AL	no	yes	no	no	no	no	no	2,6	1,2	0,72	1,1	1,1	503	70,6	4
26	yes	pe	AL	no	yes	no	no	no	no	no	3,1	1,15	1,1	1	0,95	643	76,9	4
27	yes		AL	no	yes	no	no	no	no	no	3,45	1,68	1,25	1,3	1,6	747	76,7	4
28	no	cr	AL	no	yes	no	no	no	no	no	2,9	0,75	0,67	0,72	0,74	526	na	4
29	no	cr	na	na	no	no	na	na	na	na	na	na	na	na	na	na	na	4 ?

si: sediment infilling; cr: crack; pe: perforation; gl: glue; ab: air bubble in the replica; AR: Asymmetrical to the right; SY: symmetrical; AL: Asymmetrical to the left;

SM Table 4. Data on the notches carved on the Border Cave baboon fibula.

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