# Neandertals made the first specialized bone tools in Europe

Marie Soressi<sup>a,b,c,d</sup>, Shannon P. McPherron<sup>c,1</sup>, Michel Lenoir<sup>e</sup>, Tamara Dogandžić<sup>c</sup>, Paul Goldberg<sup>f,g</sup>, Zenobia Jacobs<sup>h</sup>, Yolaine Maigrot<sup>i</sup>, Naomi L. Martisius<sup>j</sup>, Christopher E. Miller<sup>k</sup>, William Rendu<sup>l</sup>, Michael Richards<sup>c,m</sup>, Matthew M. Skinner<sup>c,n</sup>, Teresa E. Steele<sup>c, j</sup>. Sahra Talamo<sup>c</sup>, and Jean-Pierre Texier<sup>e</sup>

<sup>a</sup>Faculty of Archaeology, Leiden University, 2300 RA Leiden, The Netherlands; <sup>b</sup>Institut National de Recherches Archéologiques Préventives, Centre Archéologique d'Orléans, F-45590 Saint-Cyr-en-Val, France; <sup>c</sup>Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, D-04103 Leipzig, Germany; dentre National de la Recherche Scientifique, Unité Mixte de Recherche 7041-ArsScan/AnTet, and Unité Mixte de Recherche 8215–TRAJECTOIRES de la sédentarisation à l'État, Maison Archéologie et Ethnologie (MAE), F-92023 Nanterre Cedex, France; <sup>e</sup>Centre National de la Recherche Scientifique, Unité Mixte de Recherche 5199-de la Préhistoire à l'Actuel, Cultures, Environment, Anthropologie, Université Bordeaux 1, 33405 Talence Cedex, France; <sup>f</sup>Department of Archaeology, Boston University, Boston, MA 02215; <sup>g</sup>Role of Culture in Early Expansions of Humans (ROCEEH), Talence Cedex, France; <sup>f</sup>Department of Archaeology, Boston University, Boston, MA 02215; <sup>g</sup>Role of Culture in Early Expansions of Humans (ROCEEH), Talence Cedex, France; <sup>f</sup>Department of Archaeology, Boston University, Bosto Heidelberg Academy of Sciences and Humanities, 72070 Tübingen, Germany; hCentre for Archaeological Science, School of Earth and Environmental Sciences, University of Wollongong, Wollongong, NSW 2522, Australia; <sup>1</sup>Department of Anthropology, University of California, Davis, CA 95616; <sup>k</sup>Institute for Archaeological Sciences, University of Tübingen, 72070 Tübingen, Germany; <sup>1</sup>Centre National de la Recherche Scientifique, Travaux et Recherches Archéologiques sur les Cultures, les Espaces et les Sociétés-Unité Mixte de Recherche 5608, Université Toulouse-Le Mirail, 31058 Toulouse, France; <sup>m</sup>Department of Anthropology, University of British Columbia, Vancouver, BC, Canada V6T 1Z1; and <sup>n</sup>Department of Anthropology, University College London, WC1H 0BW London, United Kingdom

Edited by Erik Trinkaus, Washington University, St. Louis, MO, and approved May 22, 2013 (received for review February 12, 2013)

Modern humans replaced Neandertals ~40,000 y ago. Close to the time of replacement, Neandertals show behaviors similar to those of the modern humans arriving into Europe, including the use of specialized bone tools, body ornaments, and small blades. It is highly debated whether these modern behaviors developed before or as a result of contact with modern humans. Here we report the identification of a type of specialized bone tool, lissoir, previously only associated with modern humans. The microwear preserved on one of these lissoir is consistent with the use of lissoir in modern times to obtain supple, lustrous, and more impermeable hides. These tools are from a Neandertal context proceeding the replacement period and are the oldest specialized bone tools in Europe. As such, they are either a demonstration of independent invention by Neandertals or an indication that modern humans started influencing European Neandertals much earlier than previously believed. Because these finds clearly predate the oldest known age for the use of similar objects in Europe by anatomically modern humans, they could also be evidence for cultural diffusion from Neandertals to modern humans.

human evolution | Paleolithic archaeology | Middle Paleolithic

**S** pecialized bone technology first appears in Africa (1–5) and is widespread in Europe after the arrival of modern humans with the beginning of the Upper Paleolithic (6-8). Modern humans shaped bone by grinding and polishing to produce standardized or so-called formal tools that were used for specific functions (6, 9). Examples of Neandertal bone tools do exist (9– 15); however, most of these were made through percussion to mimic existing stone tools, such as handaxes, scrapers, and denticulates. Standardized bone tools in forms distinct from stone tools and shaped by grinding and polishing occur in the Châtelperronian (16) and Uluzzian (17), but (i) whether Neandertals made these assemblage types is debated and, furthermore, (ii) their late date means that Neandertals could have been influenced by modern humans already in Europe (18, 19). Examples with earlier dates are disputed (20). For example, the site of Saltzgitter-Lebenstedt yielded several mammoth ribs modified by percussion and then shaped by grinding (12). However, these ribs lack standardization, they do not match known bone-tool types, their intended use is unclear, and they are not repeated at other Neandertal sites. Similarly, the site of Grosse Grotte yielded a mammoth rib fragment with modifications reported as consistent with standardized bone tools (14). Although there are stone tools in the level associated with the rib, the majority of the fauna represents use of the cave by

cave bears, there are clear indications of carnivore modifications on the bones, and there are no other traces of human impact on the bones (e.g., cutmarks) (14). The problems with these two examples are illustrative of the difficulties demonstrating early Neandertal standardized bone tools. As a result, these bones are excluded from lists of Neandertal bone tool repertoires (17). Here we report four lissoir fragments that were recovered from recent excavations in three separate and radiometrically dated archaeological deposits at two Neandertal sites. Lissoirs (French: to make smooth, smoother) are a formal, standardized bone-tool type, made by grinding and polishing, interpreted as being used to prepare hides (6, 21-24), and previously only associated with modern humans. These bones are the earliest evidence of specialized bone tools associated with Neandertals.

### **Context of Discovery and Radiometric Age**

Two recently excavated Mousterian of Acheulian Tradition (MTA) sites, Pech-de-l'Azé I (Pech I) and Abri Peyrony, located ~35 km from each other on separate tributaries of the Dordogne river in southwest France (Fig. 1), yielded nearly identical fragments of bone with smoothed edges and a rounded tip (Fig. 2, Figs. S1–S4, and SI Appendix, Section S5). The three Abri Pevronv bones were recovered from two levels (3A and 3B) within layer L-3 (Fig. 1 A and B, and SI Appendix, Section S2). This layer is composed of limestone fragments and detritus derived from the backing cliff, and it rests on the bedrock. The layer was cemented during or shortly after deposition by calcium carbonate from a groundwater seep at the base of the cliffline. This cementation prevented postdepositional disturbance (e.g., bioturbation) from affecting the deposit, and an intact combustion feature in level L-3A demonstrates minimal postdepositional disturbance. The lithics from level L-3A include handaxe thinning flakes, cordiform handaxes, and backed knives typical of the MTA. The level L-3B lithics are very similar with regard to blank

Author contributions: M.S. and S.P.M. designed research: M.S., S.P.M., M.L., T.D., P.G., Z.J., Y.M., N.L.M., C.E.M., W.R., M.R., M.M.S., T.E.S., S.T., and J.-P.T. performed research; M.S., S.P.M., T.D., P.G., Z.J., Y.M., C.E.M., W.R., M.R., M.M.S., T.E.S., S.T., and J.-P.T. analyzed data; and M.S. and S.P.M. wrote the paper.

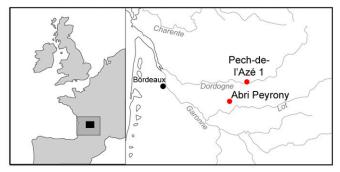
The authors declare no conflict of interest.

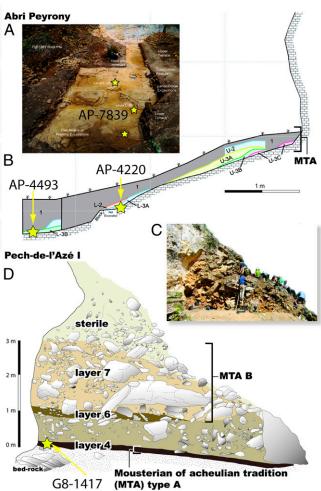
This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

<sup>1</sup>To whom correspondence should be addressed. E-mail: mcpherron@eva.mpg.de.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10. 1073/pnas.1302730110/-/DCSupplemental





**Fig. 1.** Map and stratigraphic sections of Abri Peyrony and Pech-de-l'Azé I. (A) View north of Abri Peyrony after 2010 excavation. (*B*) East section of Abri Peyrony with stars indicating the levels containing the reported bones. (C) View of the Pech I 3-m MTA section. (*D*) East section of Pech I with the star indicating the location (1 m from the drawn section) of the reported bone (more plans and photos in the *Si Appendix*). Only the MTA was discovered at both sites.

production and retouched tool types, including one backed knife and one partial bifacial piece. Bone preservation in both levels is good; 84% of the bones (number of specimens >2.5 cm = 930) preserve more than 50% of their cortical surfaces and only 3% have been strongly weathered. There is minimal evidence for carnivore damage on the bones (*SI Appendix*, Section S4.2). Above layer 3 is a thin deposit containing a small sample of Middle Paleolithic artifacts and a layer of backdirt. Two previous excavations also identified only the MTA (25, 26), and no Upper Paleolithic or later industries were identified in the recent or prior

excavations. Seven <sup>14</sup>C accelerator mass spectrometry age determinations on cut-marked bone from layer 3 provide a range of 47,710–41,130 Cal B.P. (*SI Appendix*, Section S3.3).

The Pech I bone, G8-1417, comes from layer 4 (Fig. 1 C and D, and SI Appendix, Section S1) at the base of the sequence. Layer 4 consists of stone artifacts, bones, including one juvenile Neandertal tooth (27), and ash (from hearths) in a clayey, sand matrix. These sands, deposited by run-off, are derived from underlying endokarstic fluvial sediments (28) (SI Appendix, Section S2). Minimal postdepositional disturbance is indicated by anatomical connections of a number of bones, spatial association of burned bone with ashes, artifacts broken in situ by rock fall, and a low percentage (<1%) of trampling fractures on bone (SI Appendix, Section 4.1). Bone preservation is good, with only 30% (number of specimens >2.5 cm = 2,632) affected by surface weathering and less than 8% being rounded. There is little evidence of carnivore impact on the assemblage, and carnivores seem to have had a very limited role in the assemblage formation. The stone artifacts include cordiform handaxes and backed knives typical of the MTA. No Upper Paleolithic or later period deposits have been found during four different excavations (27, 29), and layer 4 is below 3 m of undisturbed Middle Paleolithic deposits. Single-grain optically stimulated luminescence dating of three sediment samples from layer 4 gave a weighted mean age of 51.4  $\pm$  2.0 ka (SI Appendix, Section S3.2). This age is consistent with previously reported (30) conventional radiocarbon, electron-spin resonance, and coupled electron-spin resonance/uranium-series ages (SI Appendix, Section S3.1).

#### The Bone Artifacts

The four bones are rib fragments of medium-sized ungulates, likely red deer (Cervus elaphus) or reindeer (Rangifer tarandus). The unworked half of the most complete artifact, AP-7839 (Fig. 2A, Fig. S3, and SI Appendix, Section S5), preserves on one edge the unmodified rib; the opposite edge and the end were broken during excavation. The other half tapers gradually to a rounded tip. Spongy bone is exposed at and near the tip along both edges. Exposed vesicular structures testify to cortical thinning emanating from the tip (SI Appendix, Section 5). The three smaller artifacts (Fig. 2 B–I, Figs. S1, S2, and S4, and SI Appendix, Section 5) have one cortical face with a uniform shine and an opposite face of fresh, spongy bone. The artifacts also have polished cortical bone at the very tip and around the edges, and AP-4209 has polished spongy bone near the tip. The fragile spongy parts of these three show neither rounding nor striations indicative of postdepositional abrasion from the surrounding sediment. The four bones show no thinning of the edges or erosion of cortical bone as observed on bones exposed to hyena gastric acid (31). The majority of the bone surfaces do not exhibit traces of rootlet action, although AP-4493 has some root etching of the spongy part (32).

All four bones have a subrounded, ogival polished tip. A facet near the tip and along the edge of AP-4209 shows a set of parallel striations running obliquely to the edge (Fig. 2I) that is consistent with grinding against a coarse, hard material. The break on the three small fragments is typical of a bending fracture initiated on the underside of the bone, passing through the interface between cortical and spongy bone, and terminating at the cortical surface. This break type matches the pattern expected by a downward, longitudinal pressure on a fresh bone and in the direction of the tip (SI Appendix, Section 8). A break of this type on the most complete artifact, AP-7839, would have produced bone fragments nearly identical to the smaller fragments reported here. To make an originally complete example of these bone artifacts, the distal end of the rib, which flares to meet the sternum and is irregular in shape, was thinned and reshaped to form a smooth, ogival tip. This ogival tip is most effectively obtained by snapping the distal end or grinding the tip against a hard, coarse material. The facet on AP-4209 (Fig. 21) may preserve this stage of bone shaping.

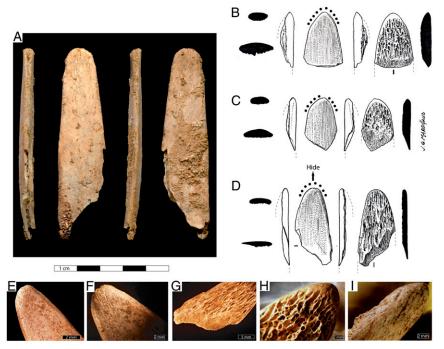


Fig. 2. Photographs and drawings of the Abri Peyrony (AP) and Pech-de-l'Azé I (PA I) bone tools. (A) AP-7839. (B) AP-4209. (C) AP-4493. (D) PA I G8-1417. (E and F) G8-1417 cortical side showing a uniform shine, rounding and slight crushing of the distal end. (G) G8-1417 trabecular bone with no rounding or striations and a bending fracture. (H) Close-up of tip polish on AP-4209 showing gradient from cortical bone to polished trabecular bone to fresh trabecular bone. (J) Close-up of facet on AP-4209. See also SI Appendix, Section S5.

#### **Use-Wear Pattern**

Once initially shaped, the uniform smoothness and rounded edges of the tips of these bones is the result of abrasive pressure, likely through use, against a softer material. Natural processes can produce pseudotools (20, 31). Thus, in analyzing function, observations at multiple scales and the use of explicit criteria and procedures are required to achieve stronger inferences (20). We combined evidence of the depositional context with analyses of the artifact's taphonomy and with the use of replicates (33) to distinguish between natural abrasion, predator or carnivores marks, and traces of digestion versus manufacturing marks and functional working edges (20). Under the stereoscopic microscope the distal end of the Pech I bone (G8-1417) shows rounding associated with a slight crushing of the bone (Fig. 2 D-F). The position and patterning of the striations do not match a pattern induced by fortuitous events, such as trampling (34). Under a metallographic microscope the distal end shows a homogeneous microtopography characterized by an intrusive polish affecting both the domes and the hollows and associated with numerous striations, some of which are long and shiny; others are shorter and finer (Fig. 3). Some linear microscratching is visible on the distal end (Fig. 3A) and on the lateral edges of the object. As one moves away from the tip, the surface topography gradually becomes more irregular and less domed, the patterns much less pronounced and the striations less frequent (Fig. 3).

The experimental bone tools were made from a medium size herbivore bone with a morphology and an active edge similar to the Pech I bone. These replicates were efficient for smoothing dry hide, and they exhibited similar damage, striations, and polish (35–40) on their active edge to the bone tool from Pech I (Fig. 3B). The combination of the Pech I bone's general morphology, edge morphology, damage, polish texture, polish distribution, and striations indicate that this bone was used on a soft material, such as dry hide with a repetitive motion transverse to the active edge (longitudinal to the long axis of the bone).

## **Discussion and Conclusion**

These bone tools are identical in outline, profile, and use-wear to *lissoirs* (Fig. 4 and *SI Appendix*, Section S6). *Lissoirs* are known from the early Upper Paleolithic of western Europe (6), including the Châtelperronian (16, 41), Proto-Aurignacian (42), and Aurignacian (22, 23), but are also found in the late Upper Paleolithic (24) through to historic and modern time periods (Fig. 4*E*). *Lissoirs* have a standardized shape and vary in size depending on the species used; they are an effective tool for producing and smoothly shifting pressure over a small area (21). This technique, when applied to animal skins, results in tougher, more impermeable, and lustrous hides (21). No other known artifact in the Middle or Upper Paleolithic toolkit could accomplish this task, meaning that these tools exploit specific properties of bone for shaping and use (21).

The bones reported here demonstrate that Middle Paleolithic Neandertals were shaping animal ribs to a desired, utilitarian form and, thus, were intentionally producing standardized (or formal) bone tools using techniques specific to working bone. These bones are the earliest evidence of this behavior associated with Neandertals, and they move the debate over whether Neandertals independently invented aspects of modern human culture to before the time of population replacement. In central Europe, artifact assemblages contemporaneous with the Pech I Neandertals but more comparable to assemblages from southwest Asia made by modern humans (19, 43) have such poor bone preservation that neither human fossils nor bone tools are known, and thus their influence on Neandertals cannot be evaluated. Thus, it remains to be determined whether MTA lissoirs are evidence that modern humans influenced Neandertals earlier and longer than previously suggested, whether these lissoirs represent independent invention and convergence, or whether, perhaps this time, Neandertals may have influenced subsequent Upper Paleolithic modern human populations in western Europe where lissoirs are common.

Soressi et al. PNAS Early Edition | 3 of 5

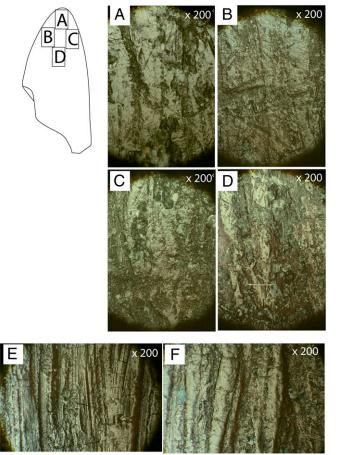


Fig. 3. Photomicrographs of the Pech I (G8-1417) bone showing details of the polish and striations (A-D). Use-wear traces on the upper side of an experimental bone lissoir used to soften dry hide with a longitudinal motion after 5 min of use (E) and after 10 min of use (F).

## Methods

On the archaeological material as well as experimental tools, we performed an initial observation with a stereoscopic microscope at low magnification (10× to 50×), followed by observation at high magnification (50× to 200×) with a metallographic microscope (44). Acetate cast replicas were photographed. Diagnostic characteristics were defined on the basis of restricted distribution on an element, distinction from the location and type of known natural agent damage, and similarity with experimental use-wear. Only the Pech I bone was subjected to microwear analysis because of the fragility of these objects during the casting process.

ACKNOWLEDGMENTS. C. Archambeau, N. Berrington, H. Dibble, B. Stec, S. Schwortz, and A. Turq assisted the field projects; L. Chiotti gave access to the Abri Pataud lissoir collection: C. Verna helped with the La Ouina research; H. Temming and P. Schönfeld scanned bones; B. Larmignat, C. Herold,

- 1. Yellen JE, Brooks AS, Cornelissen E, Mehlman MJ, Stewart K (1995) A middle stone age worked bone industry from Katanda, Upper Semliki Valley, Zaire. Science 268(5210): 553-556.
- 2. Henshilwood CS, d'Errico F, Marean CW, Milo RG, Yates RJ (2001) An early bone tool industry from the Middle Stone Age at Blombos Cave, South Africa: Implications for the origins of modern human behaviour, symbolism and language. J Hum Evol 41(6):631–678.
- 3. Feathers JK, Migliorini E (2001) Luminescence dating at Katanda—A reassessment. Quat Sci Rev 20:961-966.
- 4. Jacobs Z, Duller GAT, Wintle AG, Henshilwood CS (2006) Extending the chronology of deposits at Blombos Cave, South Africa, back to 140 ka using optical dating of single and multiple grains of quartz. J Hum Evol 51(3):255-273.
- 5. D' Errico F, Backwell LR, Wadley L (2012) Identifying regional variability in Middle Stone Age bone technology: The case of Sibudu Cave. J Archaeol Sci 39(7):2479–2495.
- 6. Leroi-Gourhan A (1968) Dictionnaire de la Préhistoire [Dictionary of Prehistory] (Presses Universitaires de France, Paris).

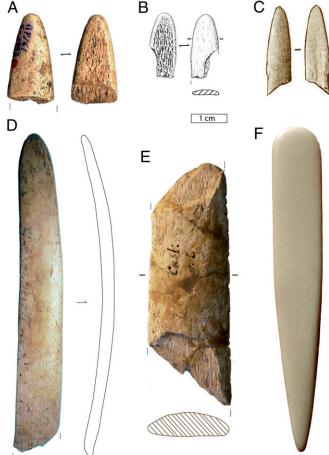


Fig. 4. Examples of Upper Paleolithic lissoirs. Distal fragment of a Gravettian lissoir from Abri Pataud (France) (45) (A). Distal fragment of a Proto-Aurignacian lissoir from La Grotte du Renne (France) (42) (B) and of a Magdalenian lissoir from La Grotte de la Vache (France) (24) (C). Almost complete Aurignacian lissoir from Gatzarria (France) (D) and mesial fragment (with typical scars of bending fractures at both ends) of a Aurignacian lissoir from Castanet-Nord (France) (46) (E). An unused modern lissoir (upper end) and plior (bottom end) use by leather craftsmen and made from a cow rib, purchased from the Internet, January 2013 (F). [(A) Collection MNHN, photo by C. Vercoutère; (C) Photo by E. Tartar; (D) Castanet project archives.]

and J.-G. Marcillaud helped with some the figures; and F. d'Errico, D. Liolios, and especially J.-J. Hublin gave helpful comments on the manuscript. Excavation permits and funding were provided by the Musée National de Préhistoire des Eyzies, the Service Régional de l'Archéologie d'Aquitaine, the Service Départemental de l'Archéologie de la Dordogne, the Commission Inter-régionale de la Recherche Archéologique d'Aquitaine, the Conseil Général de Dordogne, the Australian Research Council (DP1092438), and the Max Planck Society.

- 7. Bailey SE, Weaver TD, Hublin J-J (2009) Who made the Aurignacian and other early Upper Paleolithic industries? J Hum Evol 57(1):11-26.
- 8. Hublin J-J (2013) in The Origins of Modern Humans: Biology Reconsidered, eds Smith FH, Ahern JCM (Wiley-Blackwell).
- 9. Rosell J, et al. (2011) Bone as a technological raw material at the Gran Dolina site (Sierra de Atapuerca, Burgos, Spain). J Hum Evol 61(1):125-131.
- 10. Chase PG (1990) Tool-making tools and Middle Paleolithic behavior. Curr Anthropol 31(4):443-447.
- 11. Gaudzinski S, et al. (2005) The use of Proboscidean remains in every-day Palaeolithic life. Ouat Int 126-128:179-194.
- 12. Gaudzinski S (1999) Middle Palaeolithic bone tools from the open-air site Salzgitter-Lebenstedt (Germany). J Archaeol Sci 26(2):125-141.
- 13. Armand D, Delagnes A (1998) Economie Préhistorique: Les Comportements de Subsistance au Paléolithique [Prehistoric Economy: Paleolithic Subsistence Behaviors] (APDCA, Sophia Antipolis, France), pp 205-214.

- Weinstock J (1999) The Upper Pleistocene Mammalian Fauna from the Große Grotte near Blaubeuren (Southwestern Germany) (Staatliches Museum für Naturkunde, Stuttgart).
- Wagner E (1983) Das Mittelpaläolithikum der Grossen Grotte bei Blaubeuren (albdonau-kreis) [The Middle Paleolithic of Grossen Grotte near Blaubeuren (alb-donaukries)] (Komissionsverlag K. Theiss, Stuttgart).
- D'Errico F, Zilhão J, Julien M, Baffier D, Pelegrin J (1998) Neanderthal acculturation in Western Europe? A critical review of the evidence and its interpretation. Curr Anthropol 39(S1):S1–S44.
- D' Errico F, Borgia V, Ronchitelli A (2012) Uluzzian bone technology and its implications for the origin of behavioural modernity. Quat Int 259:59–71.
- Benazzi S, et al. (2011) Early dispersal of modern humans in Europe and implications for Neanderthal behaviour. Nature 479(7374):525–528.
- Hublin J-J (2012) The earliest modern human colonization of Europe. Proc Natl Acad Sci USA 109(34):13471–13472.
- Villa P, d'Errico F (2001) Bone and ivory points in the Lower and Middle Paleolithic of Europe. J Hum Evol 41(2):69–112.
- 21. Semenov SA (1964) Prehistoric Technology; An Experimental Study of the Oldest Tools
- and Artefacts from Traces of Manufacture and Wear (Cory, Adams & Mackay, London).
  22. Leroy-Prost C (1975) L'industrie ossseuse aurignacienne essai régional de classifica-
- 23. Leroy-Prost C (1979) L'industrie ossseuse aurignacienne essai régional de classification: Poitou, Charentes, Périgord (suite). *Gallia Préhistoire* 22(1):205–370.

tion: Poitou, Charentes, Périgord. Gallia Préhistoire 18(1):65-156.

- Averbouh A, Buisson D (2004) in La grotte de La Vache (Ariège). Fouilles Romain Robert. Tome I: Les Occupations du Magdalénien [La grotte de La Vache (Ariège). The Excavations of Romain Robert. Volume I: The Magdalenian Occupations], eds Clottes J, Delporte H (CTHS. Paris). pp. 309–324.
- Lenoir M, Dibble HL (1995) The Middle Paleolithic Site of Combe-Capelle Bas (France) (Univ of Pennsylvania Museum Press, Philadelphia, PA), pp 329–340.
- Peyrony D (1925) Le gisement préhistorique du haut de Combe-Capelle. Moustérien de Tradition Acheuléenne. Association Francaise pour l'Avancement des Sciences 49: 484–487.
- 27. Soressi M, et al. (2008) in Les Sociétés du Paléolithique dans un Grand Sud-Ouest de la France: Nouveaux Gisements, Nouveaux Résultats, Nouvelles Méthodes (Paleolithic Societies in the Greater Southwest of France: New Sites, New Results, and New Methods) eds Jaubert J, Bordes J-G, Ortega I (Société Préhistorique Française, Mémoire XLVII, Joué-Lès-Tours, France), pp 95–132.
- Texier J-P (2009) Histoire Géologique de Sites Préhistoriques Classiques du Périgord: Une Vision Actualisée [A Geological History of the Classic Prehistoric sites of the Périgord: An Updated View] (Éditions du Comité des Travaux Historiques et Scientifiques. Paris).
- Bordes F (1954) Les gisements du Pech de l'Azé (Dordogne). I. Le Mousterien de tradition acheuléenne I et suite, avec une note paleontologique de J.Bouchud [The sites of the Pech de l'Azé (Dordogne). I. The Mousterian of Acheulian Tradition I with a note on the paleontology by J Bouchud]. L'Anthropologie 58:401–432, 59:1–38.
- Soressi M, Jones HL, Rink WJ, Maureille B, Tillier A-M (2007) The Pech-de-l'Azé I Neandertal child: ESR, uranium-series, and AMS 14C dating of its MTA type B context. J Hum Evol 52(4):455–466.
- D'Errico F, Villa P (1997) Holes and grooves: The contribution of microscopy and taphonomy to the problem of art origins. J Hum Evol 33(1):1–31.
- 32. Binford LR (1981) Bones: Ancient Men and Modern Myths (Academic, New York).

- Backwell LR, d'Errico F (2001) Evidence of termite foraging by Swartkrans early hominids. Proc Natl Acad Sci USA 98(4):1358–1363.
- Fiorillo AR (1989) in Bone Modification, eds Bonnichsen R, Sorg H (Center for the Study of the First Americans, Institute for Quaternary Studies, Univ of Maine, Orono, ME), pp 61–71.
- 35. Peltier A, Plisson H (1986) in Outillage Peu élaboré en os et en Bois de Cervidés II (artefact 3) [Simple Bone and Cervid Antler Tools II (artifact 3)]. 3ème réunion du groupe de travail n° 1 sur l'industrie de l'os préhistorique, ed Patou M (CEDA, Paris), pp 69–80.
- Christidou R (1999) Outils en os néolithiques du Nord de la Grèce: Etude technologique [Neolithic bone tools from the north of Greece]. PhD Thesis, (Université de Paris X, Nanterre, France).
- Griffitts J (2001) in Crafting Bone: Skeletal Technologies Through Time and Space.
   Proceedings of the second meeting of the (ICAZ) Worked Bone Research Group,
   Budapest, 31 August 5 September, eds Choyke AM, Bartosiewicz L (BAR International series, Oxford), pp 185–195.
- 38. Maigrot Y (2003) Etude technologique et fonctionnelle de l'outillage en matières dures animales. La station 4 de Chalain (Néolithique final, Jura, France) [Technological and Functional Study of Tools made of Hard Animal Materials. Station 4 of Chalain (Final Neolithic, Jura, France)). PhD Thesis (Université de Paris I, France).
- Van Gjin A (2005) in From Hooves to Horns, from Mollusc to Mammoth, Manufacture and Use of Bone Artefacts from Prehistoric Times to the Present, Fourth meeting of the ICAZ WBRG, Muinasaja Teadus, 15, eds Luik H, Choyke AM, Batey CE, Lõugas L (Tallinn Book Printers, Tallinn, Estonia), pp 47–66.
- 40. Clemente I, Gyria EY (2003) Analiz orudii iz reber losya so stoyanki Zamostje 2 (7 sloi, raskopki 1996-97 gg.). Arkheologicheskie Vesti 10:47–59.
- Baffier D, Julien M (1990) in Paléolithique Moyen Récent et Paléolithique Supérieur Ancien en Europe [The Recent Middle Paleolithic and Early Upper Paleolithic of Europe], eds Farizy C, Combier J (Mémoires du Musée de Préhistoire d'Ile de France, No. 3), pp 329–334.
- Julien M, Baffier D, LioLios D (2002) in L'Aurignacien de la Grotte du Renne. Les Fouilles d'André Leroi-Gourhan à Arcy-sur-Cure (Yonne) [The Aurignacian of La Grotte du Renne. The Excavations of André Leroi-Gourhan at Arcy-sur-Cure (Yonne)], XXXIVème supplément à Gallia Préhistoire, ed Schmider B (CNRS, Paris), pp 217–250.
- 43. Müller UC, et al. (2011) The role of climate in the spread of modern humans into Europe. *Quat Sci Rev* 30:273–279.
- Plisson H, Lompré A (2008) Prehistoric Technology: 40 Years Later. Functional Studies and the Russian Legacy, eds Longo L, Skakun N (BAR International Series, Oxford).
- 45. Vercoutère C (2004) Utilisation de l'animal comme ressource de matières premières non-alimentaires: Industrie osseuse et parure. Exemple de l'abri Pataud (Dordogne, France) [The Utilization of Animals as a non-food Material Resource: Bone and ornamental industry. The Example of Abri Pataud (Dordogne, France)] PhD Thesis (Institut de Paléontologie Humaine, Paris, France).
- 46. Tartar E (2009) De l'os à l'outil. Caractérisation technique, économique et sociale de l'utilisation de l'os à l'aurignacien ancien. Etude de trois sites: L'abri Castanet (secteurs nord et sud), Brassempouy (grotte des Hyènes et abri Dubalen) et Gatzarria [From Bone to Tool. Technical, Economic, and Social Characterization of the use of bone in the Early Aurignacian. A study of Three Sites: L'abri Castanet (sectors north and south), Brassempouy (grotte des Hyènes and abri Dubalen) and Gatzarria] PhD Thesis (Université de Paris I, Paris, France).

Soressi et al. PNAS Early Edition | 5 of 5