



# Châtelperronian cultural diversity at its western limits: Shell beads and pigments from La Roche-à-Pierrot, Saint-Césaire

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Edited by Richard Klein, Stanford University, Stanford, CA; received April 7, 2025; accepted August 6, 2025

The timing and mechanisms underlying the gradual replacement of Neanderthal populations by *Homo sapiens* groups have elicited heated debate for decades. The Châtelperronian of France and northern Spain has figured prominently in these discussions. While the Neanderthal authorship of this techno-complex is far less certain than previously thought, the Châtelperronian is now generally accepted as being among the first genuine Upper Paleolithic industries in Eurasia rather than a “transitional” stone tool technology. Here, we report the first association of shell beads with Châtelperronian artifacts from new excavations at the site of La-Roche-à-Pierrot, Saint-Césaire (France), supported by a multiproxy spatial analysis that incorporates site formation processes. Similar types of personal ornaments are unknown from Middle Paleolithic contexts. Comparable examples have, however, been recovered from contexts penecontemporaneous with the Châtelperronian in south-eastern Europe and around the Mediterranean. This hitherto undocumented combination of an early Upper Paleolithic industry and shell beads provides insights into cultural variability in western Europe and raises the question as to whether the makers of the Châtelperronian were influenced by or formed part of the earliest dispersals of *H. sapiens* into the region.

Châtelperronian | shell beads | pigments | Saint-Césaire | Mousterian

Once considered a relatively straightforward, monolithic process involving the swift replacement of the final Neanderthals by dispersing *Homo sapiens* groups, the “Middle-to-Upper Paleolithic transition,” occurring 55 and 42 ka, now appears as a significantly more complex demographic and cultural process involving multiple waves of human populations bearing different stone tool technologies and material culture traditions (1). The Châtelperronian, now generally accepted as one of the first genuine Upper Paleolithic techno-complex in western Europe, features prominently in debates concerning the spread of modern human groups and the disappearance of the final Neanderthals (2–6). The emergence of the Châtelperronian appears to slightly postdate industries assigned to the Initial Upper Paleolithic, whose form and geographic coherence remains difficult to discern (7–10).

Whether the makers of these industries are Neanderthals, *H. sapiens*, or both also remains controversial (11–20). Currently, only the Initial Upper Paleolithic (IUP) levels at Bacho Kiro, in Bulgaria (9, but see 4 for discussion of the cultural attribution), the Neronian of Mandrin, southeastern France (3), a Lincombian–Ranisian–Jerzmanowician (LRJ) level at Ranis, in Germany (1, 7), the lowermost Châtelperronian level at the Grotte du Renne, Arcy-sur-Cure in France (21), and two Italian Uluzzian sites, Grotta del Cavallo and Rocca San Sebastiano (22–23), have produced *H. sapiens* remains, Upper Paleolithic stone tools, and occasionally, personal ornaments. While the Bacho Kiro and Ranis contexts are well documented, the integrity of the Grotte du Renne archeosequence remains contentious (12, 14, 20, 24) as do the find contexts of the Uluzzian human remains (6, 18 but see 25). Similarly, the association of a recently reported modern human tooth with the Neronian at Mandrin, in southeastern France, has also been questioned (4, 6). Contextual issues notwithstanding, these data nevertheless pose questions concerning the timing, geography, and mechanisms of modern human dispersal, the degree of interaction between these groups and the final Neanderthal populations, including potential implications for the disappearance of the latter (26–31).

One of the key material culture changes coincident with the emergence of the Upper Paleolithic in Eurasia is the near systematic presence of symbolic expressions, primarily in the form of personal ornaments and pigment use (32–37). Prior to the Middle-to-Upper

## Significance

The period between roughly 55 and 42 ka in Eurasia witnessed considerable biocultural changes, including the demic replacement of local Neanderthal populations by dispersing *Homo sapiens* groups. Once thought to be a rapid, monolithic process, new data have shown this demographic turnover to be far more complex, including a high degree of variability in stone tool technologies, symbolic expressions, including personal ornaments, and an earlier presence of *H. sapiens* in Eurasia than previously thought. Here, we present a robust, statistically supported spatial and site formation analysis of shell beads and pigments associated with Châtelperronian stone tools at La Roche-à-Pierrot, Saint-Césaire (France), and discuss their relevance for tracing Paleolithic cultural variability and the emergence of symbolic expressions.

The authors declare no competing interest.

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This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2508014122/-/DCSupplemental>.

Published September 22, 2025.

Paleolithic transition in Eurasia, personal ornaments are both limited and chronologically sporadic. Potential examples of Neanderthal personal ornaments include cut-marked eagle phalanges, potentially linked to talon extraction (38–40), claims for the exploitation of large bird feathers (41–42), and the discovery of a handful of naturally perforated or intact, pigment-stained shells (43–45). None of these artifacts bear clear functional evidence for their use as personal ornaments (see criteria in 46).

Mousterian pigment use is now well-documented and primarily concerns black shades (e.g., 47–50). Although considered largely utilitarian in nature (e.g., fire starting, coloring supple materials, tanning skins: 47, 50–52), a symbolic function cannot be ruled out. Red pigment use has equally been documented (53, 54), including debated claims for Middle Paleolithic cave art (55–57), but remains relatively limited (45, 53–58). Châtelperronian pigment use, while not significantly different from patterns observed in earlier periods in terms of color choice (34), may have increased in processing intensity, as potentially suggested by the Grotte du Renne record (59).

Here, we present data from a recently excavated archeostratigraphic unit at Saint-Césaire, which can be reliably correlated with the level originally attributed to the Châtelperronian (60) and discuss the first instance of shell beads associated with this techno-complex. This is demonstrated by a detailed study of site formation processes combined with a comprehensive statistically supported spatial analysis. This unprecedented artifact combination provides insights into early Upper Paleolithic cultural variability in western Europe and raises the question of whether the makers of the Châtelperronian were influenced by or formed part of the earliest dispersals of modern humans into western Europe.

## La Roche-à-Pierrot, Saint-Césaire

The site of La Roche-à-Pierrot, Saint-Césaire, plays a key role in discussions concerning the so-called “Middle-to-Upper Paleolithic transition”, given the 1979 discovery of a partial Neanderthal skeleton from what was described at the time as an “archaic” Châtelperronian level (61) (*SI Appendix, Supplementary Text S1*). However, a recent typo-technological, taphonomical, and spatial analysis of the level that produced the Saint-Césaire 1 Neanderthal skeletal remains showed it to contain a small number of diagnostic Châtelperronian artifacts mixed with the overwhelming Mousterian component, neither of which could be reliably associated with the human remains (19). Since 2013, renewed fieldwork and geoarchaeological investigations at La Roche-à-Pierrot, along with the reassessment of F. Lévêque’s faunal and lithic collections as well as field archives, have produced a much clearer understanding of site formation processes (62–64; see *SI Appendix, Supplementary Text S2*). The new excavations focus on an area of about 3 m<sup>2</sup> (lines J, K and bands 4, 5) situated near the apex of the sedimentary sequence and where the Middle and early Upper Paleolithic deposits are best preserved and expressed (64). Stratigraphic units (SU) 18 and 19—hereafter SU 18-19—identified within a single lithofacies (Unit 3, Facies 3a; 64) can be reliably correlated with the level originally attributed to the “Châtelperronian” (i.e., Lévêque’s EJOP sup; see *SI Appendix, Supplementary Text S2* for excavation methods and stratigraphic correlations). The heterogeneous, mixed composition of these units, including allochthonous sediment, limestone blocks, and abundant flint geofacts derived from the slope deposits above the site (64, *SI Appendix, Supplementary Text S2*), suggests that they form part of a paleotalus that developed in an open-air slope setting after the collapse of the overhang of the former rock shelter.

## Results

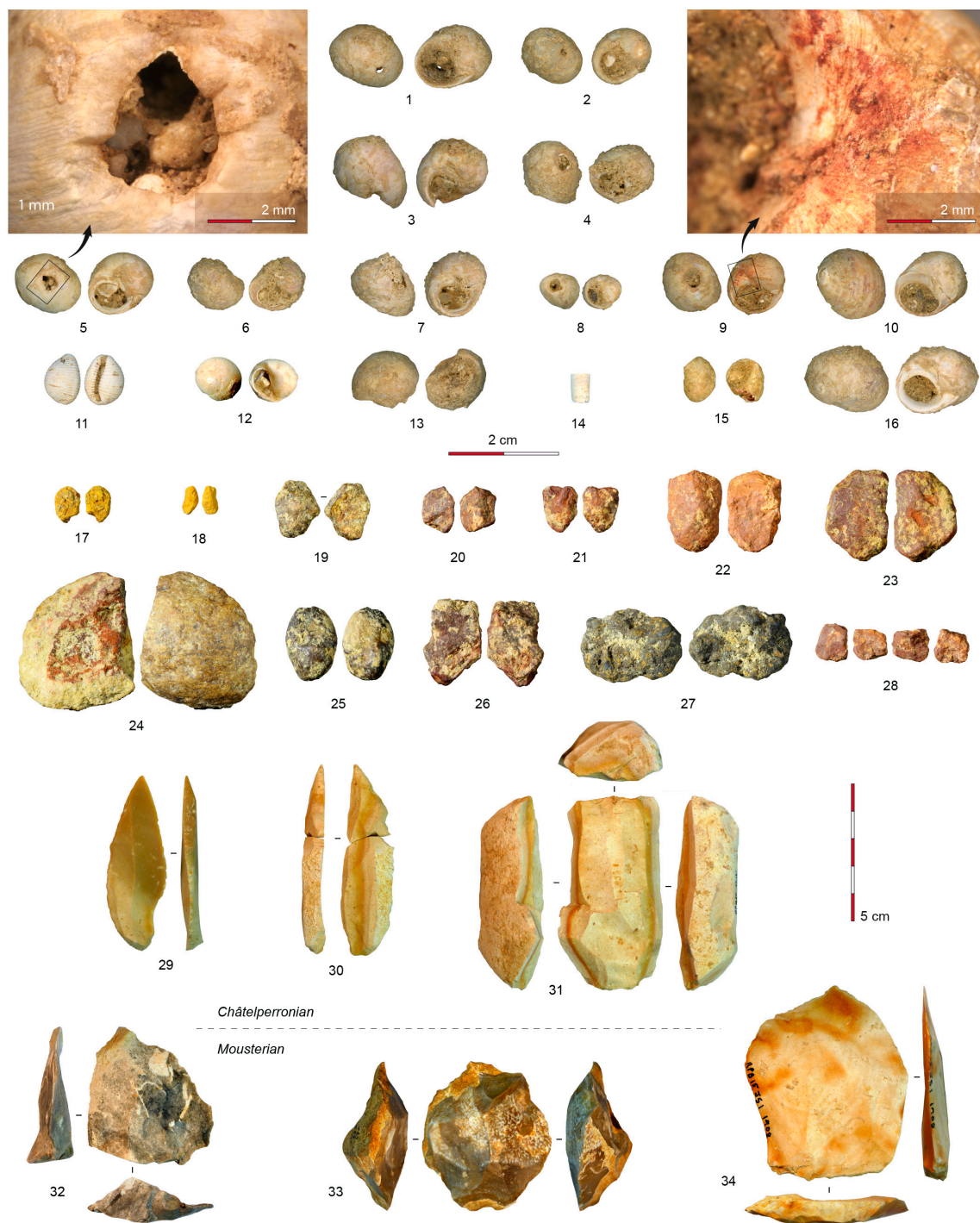
### The SU 18-19 Archeological Assemblage.

**Lithic industry and faunal spectrum.** The SU 18-19 lithic assemblage comprises 1,466 pieces larger than 2 cm. Like Lévêque’s EJOP sup, it contains two chrono-cultural elements, a dominant Middle Paleolithic component ( $n = 246$ , 87.9% of chronoculturally diagnostic material) accompanied by a small number ( $n = 37$ , 13.1% of chronoculturally diagnostic material) of typical Châtelperronian artifacts (Fig. 1 and *SI Appendix, Dataset S1*). The former is difficult to characterize, comprising primarily core-edge and centripetal flakes, pseudo-Levallois points, Levallois products, numerous scrapers, a smaller number of notches and denticulates. Due to the “mixed” character of the SU 18-19 lithic assemblage, it cannot be easily attributed to any of the now-well documented late Middle Paleolithic techno-complexes of south-western France (65–67). On the other hand, the Châtelperronian component is typical of this techno-complex, comprising retouched points, small blades, and bidirectional blade cores (e.g., 10, 68). Unlike the lithic assemblages recovered by Lévêque and the SU 18-19 Mousterian component, the Châtelperronian material from the new excavations is generally fresh and presents limited mechanical edge damage or heavily lustered surfaces (Fig. 1 and *SI Appendix, Supplementary Text S3*). The Châtelperronian artifacts are also more densely concentrated (12 pieces per m<sup>2</sup> compared to 2.8 per m<sup>2</sup> for the previous excavations). Importantly, a band of sterile rockfall separating SU 18-19 from the underlying SU 20 (*SI Appendix, Supplementary Text S2*), which also differs starkly in terms of lithic technology, effectively precludes the latter being the source of the Mousterian component in SU 18-19 (*SI Appendix, Supplementary Text S3*).

The SU 18-19 faunal assemblage primarily comprises reindeer (*Rangifer tarandus*) and bovid (*Bos/Bison*) remains, both species found in relatively equal proportions, followed by horse (*Equus ferus*), rhinoceros (*Coelodonta antiquitatis*), and mammoth (*Mammuthus primigenius*), accompanied by a few carnivore remains (*SI Appendix, Supplementary Text S4*). Of the latter, a single fox (*Vulpes* sp.) canine bears cut marks on the root consistent with extraction from a fresh carcass. Body part counts for reindeer show a markedly higher proportion of shed antlers in the upslope part of the excavation area (*SI Appendix, Supplementary Text S4*). The SU 18-19 faunal spectrum is comparable to that of Lévêque’s EJOP sup but, importantly, is markedly different from the underlying Mousterian in terms of species representation (Lévêque’s EGPF; 69–70). In terms of microfauna, two peaks in the density of remains potentially reflect the discontinuous nature of human occupations during the formation of SU 18-19 (62, see in *SI Appendix, Supplementary Text S4* and Fig. S21).

**Shell beads and pigments.** Pigments ( $n = 96$ ), in the form of red and yellow iron oxides, goethite, and different forms of hematite were recovered from SU 18-19 (Fig. 1 and *SI Appendix, Supplementary Text S5*). Earthy and oolitic hematites and goethite all derive from unidentified sources at least 40 km from the site (see *SI Appendix, Supplementary Text S5* for detailed geochemical information). Two pieces bear clear evidence of human modification in the form of impact points and percussion fractures (*SI Appendix, Supplementary Text S5*). Importantly, the pigments from SU 18-19 differ in terms of elementary and mineralogical composition from those recovered by Lévêque from the overlying Aurignacian levels as well as the pigments recovered from SU 16-17 (*SI Appendix, Supplementary Text S5*).

The SU 18-19 shell assemblage is dominated by the marine gastropods *Littorina obtusata*, followed by smaller numbers of *Littorina littorea*, a few *Dentalium* sp., and fragments of *Pecten* sp.



**Fig. 1.** Selection of characteristic artifacts from SU 18-19. Unmodified shells (10, 14, 16), broken shells (6, 12, 13, 15) and shell beads (1-9, 11); *L. obtusata* (1-10, 12, 13, 15, 16), *Trivia* sp. (11), *Dentalium* sp. (14); (1-#K5lc-Z204-206; 2-#K5ld-Z204-206; 3-#K5llla-Z206-208; 4-#4943; 5-#4579; 6-#5100; 7-#4591; 8-#J5llb-Z206-208; 9-#4908; 10-#5125; 11-#4934; 12-#J5lllb-Z206-208; 13-#5498; 14-#J5llla-Z206-208; 15-#3616; 16-#5363); 17 to 28 = pigments (17-#4148; 18-#J4ld-Z204-206; 19-#4589; 20-#4870; 21-#J5lllc-Z212-214; 22-#J5llla-Z210-212; 23-#4868; 24-#J5llld-Z206-208; 25-#4592; 26-#5270; 27-#J5lllb-Z202-204; 28-#5096); 29 to 30 = Châtelperronian points (#4431; #4681-4682); 31 = Châtelperronian core (#1487); 32 = core-edge flake (#1326); 33 = discoidal core (#270); 34 = typical Levallois flake (#167).

and *Trivia* sp. (Fig. 1 and see [SI Appendix, Supplementary Text S6](#) for a detailed description of the shell assemblage). While *Littorina obtusata* is well attested along the Atlantic coast throughout the Upper Pleistocene, its presence around the Mediterranean area is suspected only by its occurrence in a handful of archeological sites around south-eastern France (71). However, this species has never been reliably confirmed in Pleistocene beach deposits around the Mediterranean basin. The other species are more ubiquitous, present on both the Atlantic and Mediterranean coasts (72, 73).

In terms of human modifications, multiple complete ( $n = 30$ ) or fragmentary *Littorina* shells bear complete or partially preserved dorsal perforations on the last spire whorl. Fourteen shells are complete but unperforated, and only one shell bears use-wear. The heavy fragmentation of the perforated shells, the intact unperforated shells, and the near absence of use-wear are consistent with beads being manufactured on-site. The single example exhibiting use-wear suggests that it was suspended on a string prior to being discarded or lost ([SI Appendix, Supplementary Text S6 and Fig. S29](#)). Finally,

traces of red pigments embedded in concretions within a small number of shells or adhering to their surface likely result from postdepositional pedo-sedimentary soil transfer. Importantly, the diversity of mollusk species in the SU 18-19 shell assemblage differs from those recovered by Lévêque from the overlying Aurignacian levels, which comprise primarily non-*Littorina* species and perforated teeth (*SI Appendix, Supplementary Text S6*). No perforated shells were recorded in the previously excavated deposits adjacent to the newly excavated area nor in overlying SU 17.

**Spatial Patterning and Site Formation Processes.** The Mousterian and Châtelperronian lithics from SU 18-19 are not distributed uniformly across the excavated surface. Although indistinguishable from the Mousterian component stratigraphically, in plan, the Châtelperronian artifacts cluster primarily downslope in subsquares K5-III and J5-III and tend to be more numerous toward the summit of SU 18-19 (Fig. 2). These two subsquares equally produced the greatest quantities of pigments and shell beads. Notably, the only comparable shell bead recovered during Lévêque's excavations was found in a square neighboring the newly excavated area (Fig. 2). This pattern of Châtelperronian lithics clustering with the shell beads and pigments is equally borne out by a Kernel density analysis (Fig. 3 and *SI Appendix, Supplementary Text S7*). This association is further corroborated by a Ripley's K intertype function that shows a statistically significant spatial relationship uniquely between the distribution of Châtelperronian lithics, shell beads, and pigments (Fig. 3 and *SI Appendix, Supplementary Text S7*). Although statistically more frequent in the K5 and J5-II-III areas (*Supplementary Text S4*), shed reindeer antlers are not significantly associated with the latter three components. The same test shows Mousterian lithics to be spatially unrelated to the three previous components. On the other hand, the Mousterian lithics are statistically associated with the *Bos/Bison* remains, while no spatial association exists between the Châtelperronian and any of the five major prey species in the SU 18-19 faunal assemblage (Fig. 3 and *SI Appendix, Supplementary Text S7*).

The analysis of artifact orientations and dips (sediment fabric analysis) reveals three spatially segregated groups (*SI Appendix, Supplementary Text S7*). Downslope group 1 in square J5 shows a significant preferential orientation following the primary slope of the deposits. This would be consistent with the development of a small stone-banked solifluction lobe toward the base of SU 18/19 in this area (64). A second group concentrates upslope, toward the cliff in square K4, and may reflect reworked rock fall deposits (74). A third group of planar fabrics transects the group 1 and 2 fabrics and would be consistent with both shallow surface water runoff with low energy and relatively undisturbed lithic assemblages (74, 75). While fabric groups 1 and 3 overlap with the two areas with the highest density of Mousterian lithics and *Bos/Bison* remains, the Châtelperronian lithics, shell beads, and pigments largely coincide with the distribution of the group 2 fabrics. The upslope area equally contains the highest concentration of heavily mechanically edge-damaged lithics (*SI Appendix, Supplementary Text S7*) that also concentrate toward the summit of SU 18-19. The organization of the three fabric groups partially tracks the spatial patterning in artifact size distribution; the largest lithics cluster downslope in subsquare J5-IV with the group 1 fabrics and tend to concentrate upslope in subsquare K4-II with the group 3 fabrics (*SI Appendix, Supplementary Text S7*). The size-particle analysis of the lithic assemblages is equally consistent with these site formation processes (*SI Appendix, Supplementary Text S7*).

**The Chronology of SU 18-19.** Previously available radiometric data placed the end of the Mousterian (i.e., Lévêque's final Mousterian level EGPF, the equivalent of SU 20 from the new excavations)

at Saint-Césaire to between 44.6 and 41.8 ka cal BP (26). However, this model includes determinations with low collagen yields and a date obtained on a sample from a highly problematic, stratigraphically mixed downslope area of the site (19, 64).

Recently published OSL and radiocarbon dates show SU 18-19 to have accumulated between  $39.3 \pm 2.1$  ka and  $53.8 \pm 3.8$  ka (64). While the radiocarbon dates fall within the broader OSL range, they should be interpreted with caution due to diagenetic alterations and low collagen preservation (*SI Appendix, Supplementary Text S8*).

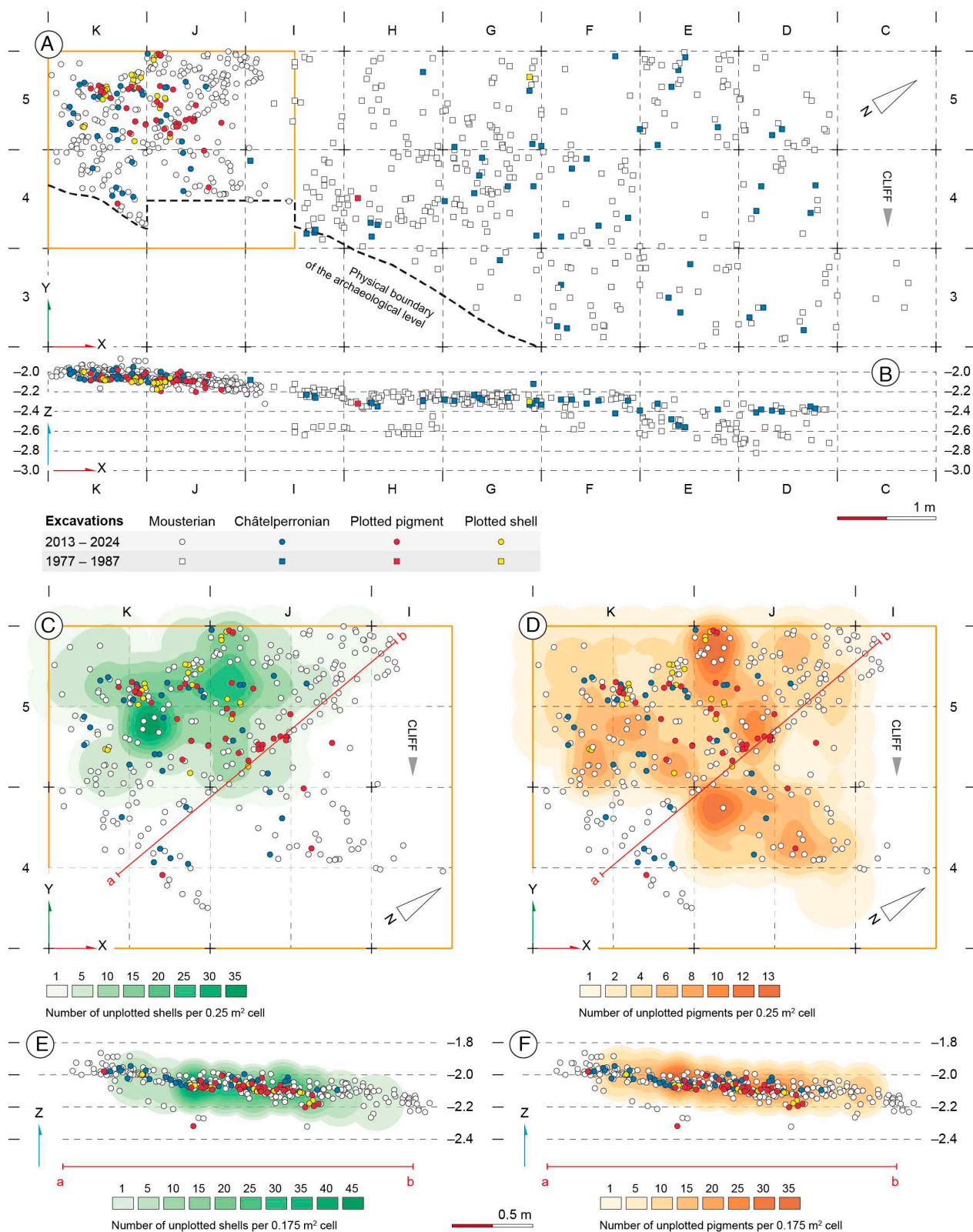
New radiocarbon analyses performed on five *Littorina* shells indicate that these mollusks lived before the radiocarbon dating range (~55 ka cal BP) (*SI Appendix, Supplementary Text S8*). To strengthen this conclusion, we applied a specific protocol with sequential acid leaching (76). Even if radiocarbon ages of marine carbonates are usually too old due to the marine reservoir effect (e.g., 77), these *Littorina* shells are still older than the currently accepted chronology for the Châtelperronian, as well as most of the other numerical ages for SU 18-19. This chronological discrepancy is best explained by humans having collected old shells from an exposed Upper Pleistocene deposit (e.g., 78). Modeling the Pleistocene coastline for the period between 65 to 40 ka indicates that thanatocenosis-bearing deposits would have been accessible along the Atlantic coast during the accumulation of SU 18-19 (*SI Appendix, Supplementary Text S6 and Fig. S33*). Lowered Pleistocene sea levels between 40 and 45 ka place the Atlantic coast at around 130 km from the site, and the western Mediterranean Sea only a few km further than current conditions (73, 79–82). This coastal paleogeography and the absence of inland fossil-bearing deposits around the site (*SI Appendix, Figs. S6 and S7 in Supplementary Text S6*) would imply that the SU 18-19 shell beads were either directly sourced or indirectly acquired via a relatively vast contact network.

The two most reliable ESR determinations on large bovid teeth produced ages ranging from 45 ka to 54 ka (*SI Appendix, Supplementary Text S8*), consistent with the OSL time range of Unit 3 (64) and their association with the Mousterian component of SU 18-19. This likelihood is equally borne out by the spatial association of these two elements (*SI Appendix, Supplementary Text S7*).

Finally, a Bayesian model combining OSL and radiocarbon ages was built with the open-source R package BayLum (83–85). Based on this model (*SI Appendix, Supplementary Text S8*), SU 18-19 accumulated between 41.6 and 48.4 ka, which is consistent with the currently understood chronology of its two components (5).

## Discussion

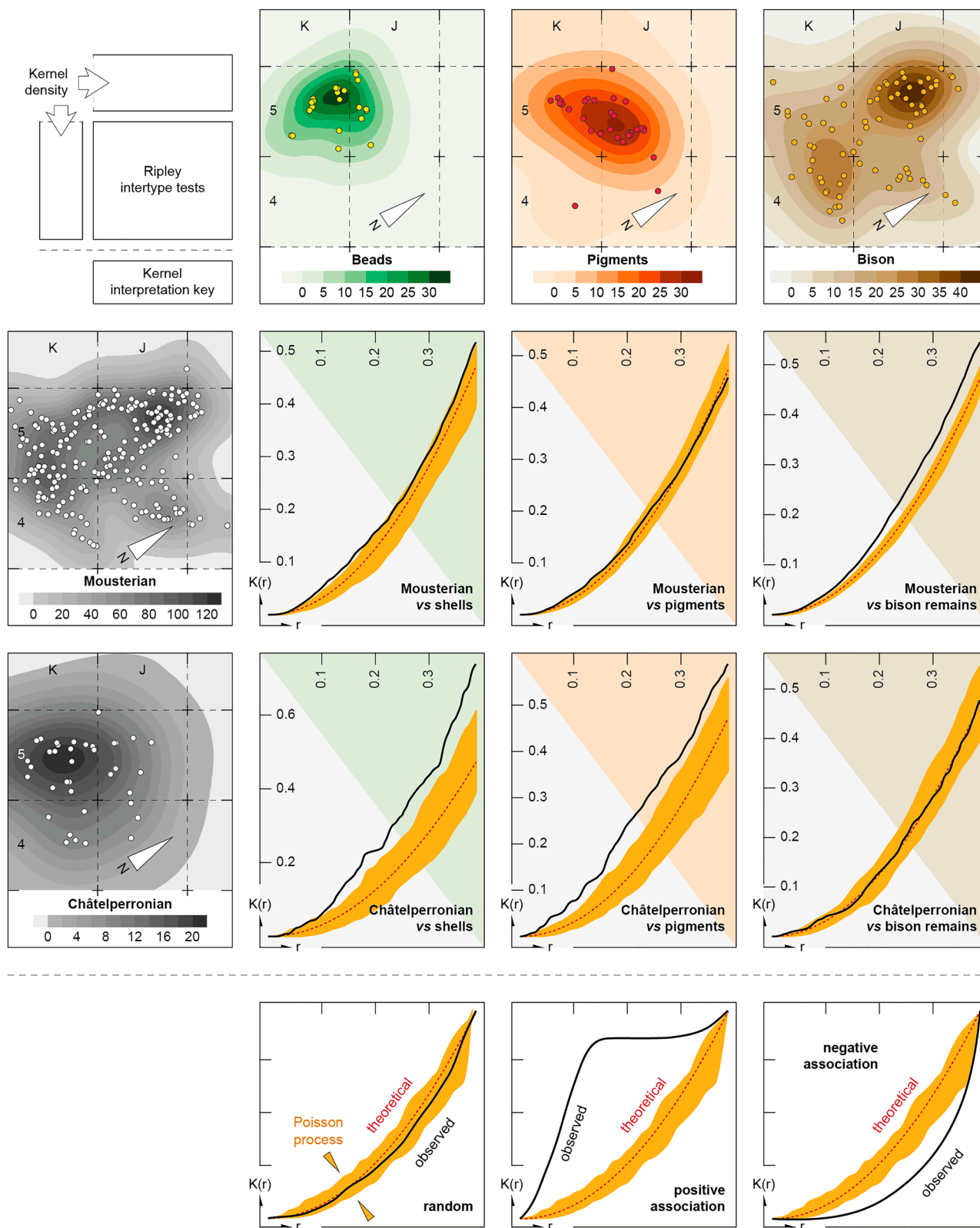
**A Three-Phase Model for the Formation of SU 18-19.** A three-phase model for the formation of SU 18-19 can be proposed based on archeological, spatial, and site formation processes data. After the collapse of a former rockshelter, an initial Mousterian occupation (Phase 1 in Fig. 4) focused on the processing of mid- and large-sized game, often *Bos/Bison*, occurred in the context of a stratified open-air slope deposit that formed, for the most part, under periglacial conditions. This included slow downslope mass movement, primarily solifluction, reworking both auto- and allochthonous sedimentary inputs. Once the solifluction lobe became inactive and fossilized, a Châtelperronian group set up a very localized area of technical activity, which included the maintenance of stone tools, the manufacture of shell beads and pigment use. This chronology is equally supported by the excellent preservation of the very fragile shell beads compared to the high numbers of edge-damaged and lustered Mousterian artifacts. This short occupation (Phase 2 in Fig. 4), typical of this



**Fig. 2.** Projection (Top) in plan (A) and section (B) of piece-plotted artifacts from the 1977–1987 (squares) and the new 2013–2024 (dots) excavations from lines 3 to 5. Blue dots/squares = Châtelperronian lithic artifacts; white dots/squares = Mousterian lithic artifacts; yellow dots/squares = shells; red dots/squares = pigments. Projection (Middle and Bottom) in plan view (C and D) and section (E and F) of the densities of unplotted shell and pigment fragments by 1/16 of a square meter in the newly excavated area appear, respectively, as green and orange shades.

techno-complex (86–88), cannot be reliably associated with any particular faunal component, which, of course, does not rule out Châtelperronian groups carrying out subsistence activities on-site. Phase 2 sedimentation is primarily dominated by low-energy

overland sheet flow on semiffat to gentle slopes, resulting in the good preservation of archeological material and relatively unaltered spatial associations between different artifact types. This is borne out by the recovery in close proximity (less than 5 cm) of two

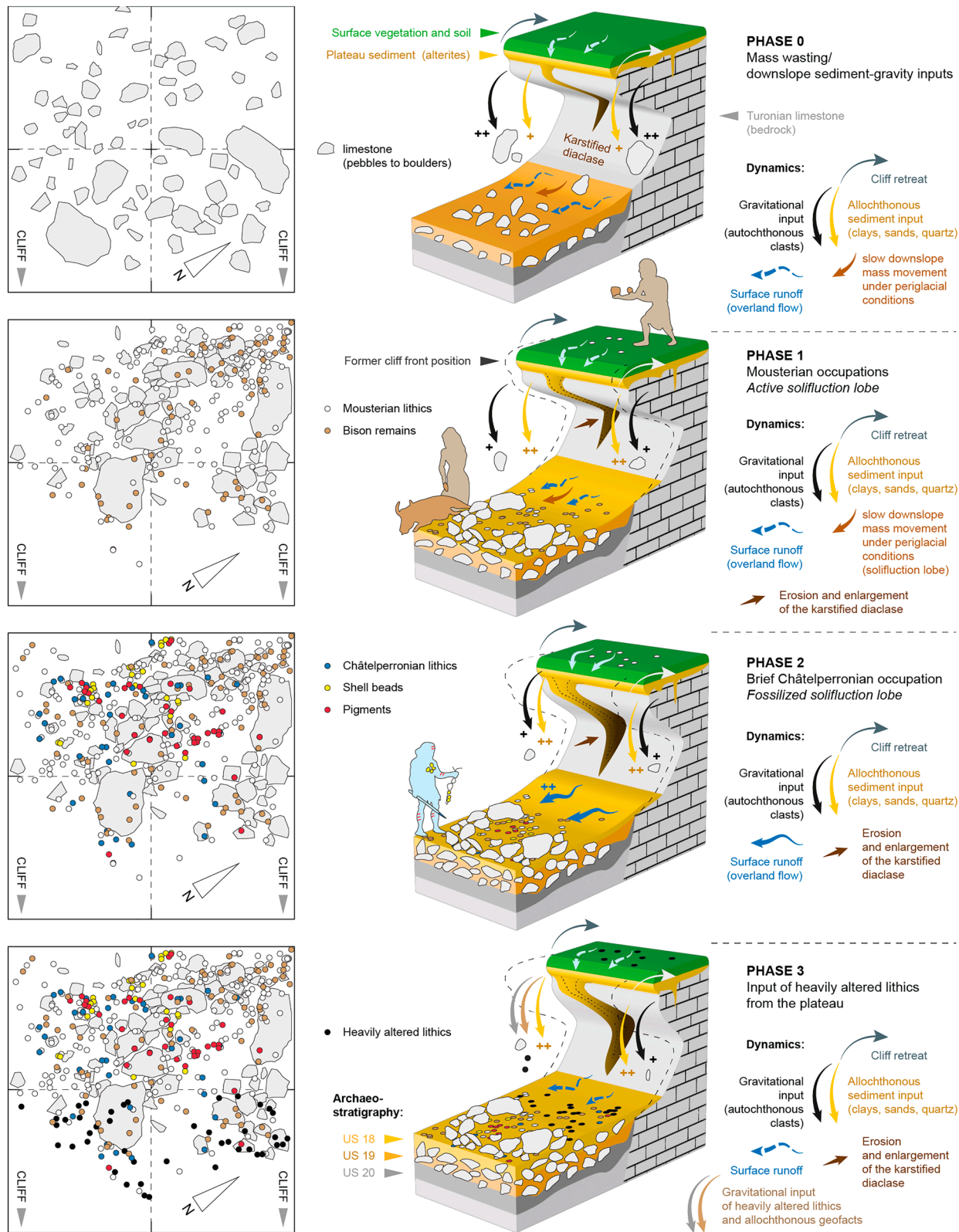


**Fig. 3.** Kernel density and Ripley intertype tests for the Châtelperronian and Mousterian lithic components, as well as the shell beads, the pigments, and the *Bos/Bison* remains.

conjoinable fragments of a Châtelperronian point broken during the retouching of the back (*SI Appendix, Supplementary Text S3 and Figs. S16 and S17*). As the karstified diaclose in the cliff expanded and the site was abandoned, exogenous sedimentation (Phase 3 in Fig. 4) from the overlying slopes introduced heavily altered Mousterian cultural material that clusters toward the cliff

and becomes mixed downslope with the phase 1 and phase 2 material.

**Uniqueness of the Saint-Césaire Châtelperronian Assemblage.** Châtelperronian lithic technology, while remarkably homogenous, does include some limited intersite variability likely linked to specific



**Fig. 4.** A three-phase model for the formation of SU 18-19. Left column = planar view of the excavated area; middle column = schematic representation of the hypothesized succession of occupations on the site; right column = geomorphological processes operating during each phase.

techno-economic activities (86, 89–91) and/or skill levels (92). Several specific symbolic elements are also generally shared features of Châtelperronian material culture. Pigment processing and use is well documented at, for example, Ormesson and the Grotte du Renne, while perforated tooth pendants, including fox canines, are currently known from Châtelperronian contexts at the Grotte du Renne (35,

93), Roc de Combe (94), and Quinçay (95). This latter type of personal ornament, together with the more frequent evidence for the exploitation of small and mid-sized carnivores for their skins and the production of bone tools in the IUP and early Upper Paleolithic contexts, has been interpreted as reflecting changes in human–carnivore interactions during the Middle-to-Upper Paleolithic

transition, when carnivores became a source of raw materials for symbolic expressions (96). The presence of pigments and potentially the cut-marked fox canine recovered from Saint-Césaire is additional evidence for this largely shared symbolic behavior.

On the other hand, the presence of marine shell beads in SU 18-19 at Saint-Césaire demonstrates a previously undocumented symbolic diversity expressed in nonutilitarian elements of Châtelperronian material culture. Additionally, these artifacts testify both to the diversity of activities carried out on-site and a degree of variability in site function. Moreover, the marine shell bead accumulation at Saint-Césaire differs from other occurrences of Châtelperronian personal ornaments, which are uniquely made from mammal bones and teeth (*SI Appendix, Supplementary Text S6 and Table S16*). It also contrasts with the Cova Foradada and Grotte du Renne records, which produced a single unperforated marine shell and a single *Dentalium* sp., respectively (35, 97). Shell beads are, however, documented eastward in the penecontemporaneous Uluzzian of southern Italy and Greece (32, but see discussion in 18) as well as in the IUP deposits of Ksar Akil, in Lebanon (98) and Üçağızlı Cave, in Türkiye (99). In these contexts, shell beads are made on multiple taxa, all of which originate from the Mediterranean Sea (*SI Appendix, Supplementary Text S6 and Table S16*). Bone and teeth ornaments are notably absent from these contexts. While the on-site manufacture of personal ornaments is typically associated with locally available raw material sources, the departure from this pattern underscores the originality of the shell accumulation at Saint-Césaire. Comparable long-distance transport and accumulation of unmodified marine shells has been documented in the late Upper Paleolithic site of Rochereil (100). The evidence from Saint-Césaire suggests that the manufacture of ornaments far from source areas may already reflect deliberate behavioral choices related to mobility, material transport, or social practices at the very onset of the Upper Paleolithic in western Europe. Cultural entities of this period were marked by discontinuities in economic and technical systems, yet showed a remarkable continuity in the culturalization of the body, accompanied by increasingly extensive symbolic networks over time (101). This pattern suggests that symbolic practices—particularly personal ornamentation—may have played a sustained role in strengthening social cohesion. Rather than reflecting a competitive or cognitive advantage, such practices likely constituted a significant cultural asset that facilitated the successful dispersal of human groups across diverse environments. The shell beads at Saint-Césaire reflect a local cultural innovation or, a westward expression of what is known from the more eastern Uluzzian, if not further afield (98, 102–103) but reinterpreted in a local raw material. This assemblage therefore potentially provides some of the earliest evidence for increased social cohesion at the very beginning of the Upper Paleolithic.

**Cultural Implications.** In terms of paleodemography, recent archeological and biological models have suggested several waves or pulses of *H. sapiens* dispersal into Eurasia. Associated with different initial or early Upper Paleolithic techno-complexes, during a period when Neanderthal groups were still present (i.e. between 55–42 ka) (1, 104–107), these events potentially involved intragroup interactions with varying degrees of intensity (1, 108, 109). Notably, the Bacho Kiro individuals had recent Neanderthal ancestors, while the Zlatý kůň and Ranis *H. sapiens* lineage, although roughly contemporaneous, lacks more recent introgression signals (1).

The successive incursions of biologically and culturally distinct populations into western Europe may have triggered variations in the types and frequency of personal ornaments during the period in question. Potential personal ornaments from Middle Paleolithic contexts are limited in number as is the range of raw materials used (38, 39–41, 42–43, 110, 111). Self-expression is manifested in a

broader range of media and becomes a generalized and consolidated behavior within the Eurasian Paleolithic record only with the arrival of *H. sapiens* groups. Multiple encounters between different human communities likely impacted how individuals perceived themselves and others, driving the need for intergroup- and self-identification materialized by new forms of personal ornamentation (112, see *SI Appendix, Supplementary Text S6*). For example, while the Uluzzian and Châtelperronian occupy the same chronology, they are culturally distinct in terms of lithic technology (113) but share the use of shell beads for personal ornamentation. Châtelperronian material culture diversity, as evidenced at Saint-Césaire, would appear to represent the western-most expression of this larger phenomenon. However, pre-Aurignacian Upper Paleolithic shell ornaments in Italy, Greece, and the eastern Mediterranean are dominated by local shell species (114–116; see *SI Appendix, Supplementary Text S6*), whereas Atlantic fossil shells were used at Saint-Césaire. This indicates that while the site's occupants adopted marine shells for ornamentation, species were selected based on local availability rather than reproducing Mediterranean stylistic patterns. The collection of fossil shells has been documented among Middle Paleolithic foragers (117), suggesting possible continuity or convergence in symbolic practices; however, such shells have never been reported as intentionally perforated. Furthermore, despite differences in shell bead composition between the Châtelperronian and Aurignacian at Saint-Césaire, taxa identified in the Châtelperronian recur throughout the Upper Paleolithic and later periods (100; 118–121), suggesting a degree of symbolic continuity in shell use that may be linked to long-distance cultural transmission, the increased need to signal social identity, or both (101; see *SI Appendix, Supplementary Text S6*).

This regional material culture patterning likely reflects a range of cultural and demographic processes, which is further complicated by the lack of secure evidence for who made the Châtelperronian and the fact that both *H. sapiens* and Neanderthal groups were present in Europe between 41.6 and 48.4 ka. Moreover, the Châtelperronian levels of Grotte du Renne (Arcy-sur-Cure) produced skeletal elements attributed to both populations (21, 122). If the Châtelperronian was produced by *H. sapiens*, the discovery of perforated shell beads at Saint-Césaire could indicate either 1) the presence of pioneer groups in western Europe whose use of marine shells for symbolic expression was opportunistic or formed part of Châtelperronian cultural diversity or 2) interactions between these *H. sapiens* groups and other culturally or biologically distinct Uluzzian and Initial Upper Paleolithic (IUP) populations. Conversely, if makers of the Châtelperronian were Neanderthals, these finds would contrast with what is currently known for these populations, suggesting that such innovations may have been stimulated by contact with *H. sapiens* groups. Disentangling these potential scenarios remains challenging in the absence of definitive evidence concerning the maker of the Châtelperronian. Nevertheless, the unique symbolic behavior of Châtelperronian groups brought to light at Saint-Césaire likely developed against the backdrop of a more diverse biocultural landscape. The complex interactions of multiple biological and culturally distinct groups could have triggered the onset of consolidated symbolic expressions during the European Upper Palaeolithic.

## Materials and Methods

New excavations at Saint-Césaire, begun in 2013, employ modern excavation and recording methods (see *SI Appendix, Supplementary Text S2* for details). Lithic and faunal analyses were carried out according to published criteria and methods (19, 70). The microwear analysis of lithic surface alterations was carried out with a Leica DMRM metallurgical reflected-light microscope equipped with

×10, ×20, ×50 lenses and observations at ×100 to ×500 magnifications (see [SI Appendix, Supplementary Text S3](#) for details). All complete and fragmented shells were examined at magnifications ranging between ×4 and ×40 and photographed using a motorized Leica Z6 APOA microscope equipped with a DFC420 digital camera. Eight gastropods were digitized at UMS 3626 PLACAMAT (University of Bordeaux) using a General Electric GE v|tome|x s X-ray microscanner, with a voxel size ranging from 12 to 23 μm ([SI Appendix, Supplementary Text S6](#)). All pigments from SU 18–19 were studied macroscopically. Twelve samples were selected for SEM-EDS and Raman analyses. ICP methods (ICP-MS & ICP-OES) were applied to seven archeological and thirteen geological samples ([SI Appendix, Supplementary Text S5](#)). Fabric and artifact size distributions analyses were adapted from published methods (74, 123), and a modified R script (124) ([SI Appendix, Supplementary Text S7](#)). The statistical analysis of spatial relationships between piece-plotted artifact types was carried out in the R package using kernel densities and Ripley's K intertype function ([SI Appendix, Supplementary Text S7](#)). Five *Littorina* shells were re-dated at CEREGE in Aix-en-Provence using a protocol that included sequential leaching to remove surface contaminants (80, see [SI Appendix, Supplementary Text S8](#)).

**Data, Materials, and Software Availability.** All study data are included in the article and/or supporting information.

**ACKNOWLEDGMENTS.** The Collective Research Project at La Roche-à-Pierrot is funded by the *Direction Régionale des Affaires Culturelles* (DRAC) of the *Région Nouvelle-Aquitaine* and by the *Département de Charente-Maritime* (CG 17), France. Fieldwork also benefited from financial support of the research project of the *Région Nouvelle-Aquitaine: Isotopes du calcium et anthropobiologie au Paléolithique moyen* (#2019-1R40208) and from logistical and material support from Archéosphère. Dating analyses were supported by the NeHos Project of the French National Research Agency (ANR-22-CE27-0016), and the Threads project « *Démêler les fils du changement culturel au cours du paléolithique supérieur en Europe: l'étude des objets de parure* » (#AAPR2024-2023-31912410). We are grateful to the *Service Régional d'Archéologie* (SRA) Nouvelle-Aquitaine, the *Conseil départemental de la Charente-Maritime*, and more specifically its *Service d'Archéologie* (SDA), the PACEA laboratory (UMR 5199), the University of Bordeaux and Paléosite (ALFRAN), for logistical support. This research equally benefited from the scientific framework of the University of Bordeaux's IdEx "Investments for the Future" program/GPR "Human Past." We would like to thank the three

anonymous reviewers and the PNAS editor for their constructive comments that helped improve the presentation of our research. Finally, we would like to thank all the volunteer excavators without whom this research would not have been possible.

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1. A. P. Sümer *et al.*, Earliest modern human genomes constrain timing of Neanderthal admixture. *Nature* **638**, 711–717 (2025).
2. J.-G. Bordes, N. Teyssandier, The upper Paleolithic nature of the Châtelperronian in south-western France: Archaeostratigraphic and lithic evidence. *Quat. Int.* **246**, 382–388 (2011).
3. L. Slimak, The three waves: Rethinking the structure of the first upper Paleolithic in Western Eurasia. *PLoS One* **18**, e0277444 (2023).
4. N. Teyssandier, Us and them: How to reconcile archaeological and biological data at the Middle-to-Upper Palaeolithic transition in Europe? *J. Paleolithic Archaeol.* **7**, 1 (2024).
5. I. Djakovic, M. Roussel, M. Soressi, Stone tools in shifting sands: Past, present, and future perspectives on the Châtelperronian stone tool industry. *J. Paleolit. Archaeol.* **7**, 29 (2024).
6. J. Zilhão, F. d'Errico, W. E. Banks, N. Teyssandier, A data-driven paradigm shift for the Middle-to-Upper Palaeolithic transition and the Neandertal debate. *Quat. Environ. Humans* **2**, 100037 (2024).
7. D. Mylopotamitaki *et al.*, *Homo sapiens* reached the higher latitudes of Europe by 45,000 years ago. *Nature* **626**, 341–346 (2024).
8. L. Slimak *et al.*, Modern human incursion into Neanderthal territories 54,000 years ago at Mandrin, France. *Sci. Adv.* **8**, eabj9496 (2022).
9. J.-J. Hublin *et al.*, Initial Upper Palaeolithic Homo sapiens from Bacho Kiro Cave, Bulgaria. *Nature* **581**, 299–302 (2020).
10. I. Djakovic, A. Key, M. Soressi, Optimal linear estimation models predict 1400–2900 years of overlap between *Homo sapiens* and Neandertals prior to their disappearance from France and northern Spain. *Sci. Rep.* **12**, 15000 (2022).
11. F. Caron, F. d'Errico, P. Moral, F. Santos, J. Zilhão, The reality of Neandertal symbolic behavior at the Grotte du Renne, Arcy-sur-Cure, France. *PLoS One* **6**, e21545 (2011).
12. T. Higham *et al.*, Chronology of the Grotte du Renne (France) and implications for the context of ornaments and human remains within the Châtelperronian. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 20234–20239 (2010).
13. T. Higham *et al.*, Chronology of the Grotte du Renne, Arcy-sur-Cure, France: A response to Zilhão *et al.* (this issue). *Before Farming* **3**, 1–5 (2011).
14. J.-J. Hublin *et al.*, Radiocarbon dates from the Grotte du Renne and Saint-Césaire support a Neandertal origin for the Châtelperronian. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 18743–18748 (2012).
15. P. Mellars, Neandertal symbolism and ornament manufacture: The bursting of a bubble? *Proc. Natl. Acad. Sci. U.S.A.* **23**, 20147–20148 (2010).
16. F. Welker *et al.*, Palaeoproteomic evidence identifies archaic hominins associated with the Châtelperronian at the Grotte du Renne. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 11162–11167 (2016).
17. J. Zilhão *et al.*, Analysis of Aurignacian interstratification at the Châtelperronian-type site and implications for the behavioral modernity of Neandertals. *Proc. Natl. Acad. Sci. U.S.A.* **103**, 12643–12648 (2006).
18. J. Zilhão, W. E. Banks, F. d'Errico, P. Gioia, Analysis of site formation and assemblage integrity does not support attribution of the Uluzzian to modern humans at Grotta del Cavallo. *PLoS One* **10**, e0131181 (2015).
19. B. Gravina *et al.*, No reliable evidence for a Neandertal-Châtelperronian association at La Roche-à-Pierrot. *Sci. Rep.* **8**, 15134 (2018).
20. B. Gravina, F. d'Errico, F. Bachellerie, "Disentangling Neandertal-modern human interactions in Western Europe: A heuristic odyssey" in *Archaeologies of Cultural Contact: At the Interface*, T. Clack, M. Brittain, Eds. (Oxford University Press, 2022), pp. 110–158.
21. A. Gicqueau *et al.*, Anatomically modern human in the Châtelperronian hominin collection from the Grotte du Renne (Arcy-sur-Cure, Northeast France). *Sci. Rep.* **13**, 112682 (2023).
22. S. Benazzi *et al.*, Early dispersal of modern humans in Europe and implications for Neandertal behaviour. *Nature* **479**, 525–528 (2011).
23. G. Oxilia *et al.*, Direct evidence that late Neandertal occupation precedes a technological shift in southwestern Italy. *Am. J. Biol. Anthropol.* **179**, 18–30 (2022).
24. O. Bar-Yosef, J.-G. Bordes, Who were the makers of the Châtelperronian culture? *J. Hum. Evol.* **59**, 586–593 (2010).
25. A. Maroni *et al.*, Grotta del Cavallo (Apulia - Southern Italy). The Uluzzian in the mirror. *J. Anthropol. Sci.* **96**, 1–36 (2018).
26. T. Higham *et al.*, The timing and spatiotemporal patterning of Neandertal disappearance. *Nature* **512**, 306–309 (2014).
27. C. Duarte *et al.*, The early Upper Paleolithic human skeleton from the Abrigo do Lagar Velho (Portugal) and modern human emergence in Iberia. *Proc. Natl. Acad. Sci. U.S.A.* **96**, 7604–7609 (1999).
28. C. S. Quilodrán, J. Rio, A. Tsoupas, M. Currat, Past human expansions shaped the spatial pattern of Neandertal ancestry. *Sci. Adv.* **9**, eadg9817 (2023).
29. S. Peyrégne *et al.*, Nuclear DNA from two early Neandertals reveals 80,000 years of genetic continuity in Europe. *Sci. Adv.* **5**, eaaw5873 (2019).
30. D. Reich *et al.*, Denisova admixture and the first modern human dispersals into Southeast Asia and Oceania. *Am. J. Hum. Genet.* **89**, 516–528 (2011).
31. J. C. Teixeira, A. Cooper, Using hominin introgression to trace modern human dispersals. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 15327–15332 (2019).

32. S. Arrighi *et al.*, Backdating systematic shell ornament making in Europe to 45,000 years ago. *Archaeol. Anthropol. Sci.* **12**, 59 (2020).
33. A. M. Byers, Symboling and the middle-upper palaeolithic transition: A theoretical and methodological critique. *Curr. Anthropol.* **35**, 369–399 (1994).
34. L. Dayet, F. d'Errico, R. García-Moreno, Searching for consistencies in Châtelperronian pigment use. *J. Archaeol. Sci.* **44**, 180–193 (2014).
35. M. Vanhaeren, F. d'Errico, M. Julien, C. Mourer-Chauviré, P. Lozouet, "Les objets de parure" in *Le Châtelperronien de la Grotte du Renne (Arcy-sur-Cure, Yonne, France)*, M. Julien, F. David, M. Girard, A. Robin-Jouve, Eds. (PALEO, 2019), pp. 259–285.
36. R. White, Rethinking the middle/upper paleolithic transition. *Curr. Anthropol.* **33**, 85–108 (1992).
37. J. Zilhão, The emergence of ornaments and art: An archaeological perspective on the origins of «Behavioural modernity». *J. Archaeol. Res.* **15**, 1–54 (2007).
38. E. Morin, V. Laroulandie, Presumed symbolic use of diurnal raptors by Neanderthals. *PLoS One* **7**, e32856 (2012).
39. D. Radović, A. O. Sršen, J. Radović, D. W. Frayer, Evidence for Neandertal jewelry: Modified white-tailed eagle claws at Krapina. *PLoS One* **10**, e0119802 (2015).
40. A. Rodríguez-Hidalgo *et al.*, The Châtelperronian Neanderthals of Cova Foradada (Calafell, Spain) used imperial eagle phalanges for symbolic purposes. *Sci. Adv.* **5**, eaax1984 (2019).
41. C. Finlayson *et al.*, Birds of a feather: Neanderthal exploitation of raptors and corvids. *PLoS One* **7**, e45927 (2012).
42. M. Peresani, I. Fiore, M. Gala, M. Romandini, A. Tagliacozzo, Late neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky B.P., Italy. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 3888–3893 (2011).
43. D. L. Hoffmann, D. E. Angelucci, V. Villaverde, J. Zapata, J. Zilhão, Symbolic use of marine shells and mineral pigments by Iberian Neandertals 115,000 years ago. *Sci. Adv.* **4**, eaar5255 (2018).
44. M. Peresani, M. Vanhaeren, E. Quaggiotto, A. Queffelec, F. d'Errico, An ochered fossil marine shell from the Mousterian of Fumane Cave. *Italy. PLoS One* **8**, e68572 (2013).
45. J. Zilhão *et al.*, Symbolic use of marine shells and mineral pigments by Iberian Neandertals. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 1023–1028 (2010).
46. S. Rigaud, F. d'Errico, M. Vanhaeren, C. Neumann, Critical reassessment of putative Acheulean Porosphaera globularis beads. *J. Archaeol. Sci.* **36**, 25–34 (2009).
47. M. Soressi, F. d'Errico "Pigments, gravures, parures: les comportements symboliques controversés des Néandertaliens" in *Les Néandertaliens. Biologie et Cultures*, B. Vandermeersch, B. Maureille, Eds. (Editions du CTHS, 2007), pp. 297–309.
48. D. Bonjean *et al.*, A new Cambrian black pigment used during the late Middle Palaeolithic discovered at Scladina Cave (Andenne, Belgium). *J. Archaeol. Sci.* **55**, 253–265 (2015).
49. L. Dayet *et al.*, Manganese and iron oxide use at Combe-Grenal (Dordogne, France): A proxy for cultural change in neanderthal communities. *J. Archaeol. Sci. Rep.* **25**, 239–256 (2019).
50. A. P. Marti *et al.*, Provenance, modification and use of manganese-rich rocks at Le Moustier (Dordogne, France). *PLoS One* **14**, e0218568 (2019).
51. P. J. Heyes *et al.*, Selection and use of manganese dioxide by Neanderthals. *Sci. Rep.* **6**, 1–9 (2016).
52. A.-C. Sorensen, Lucky strike: Testing the utility of manganese dioxide powder in Neandertal percussive fire making. *Archaeol. Anthropol. Sci.* **16**, 134 (2024).
53. W. Roebroeks *et al.*, Use of red ochre by early neandertals. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 1889–1894 (2012).
54. D. Álvarez-Alonso *et al.*, More than a fingerprint on a pebble: A pigment-marked object from San Lázaro rock-shelter in the context of Neandertal symbolic behavior. *Archaeol. Anthropol. Sci.* **17**, 1–21 (2025).
55. D. L. Hoffmann *et al.*, U-Th dating of carbonate crusts reveals Neandertal origin of Iberian cave art. *Science* **359**, 912–915 (2018).
56. R. White *et al.*, Still no archaeological evidence that Neanderthals created Iberian cave art. *J. Hum. Evol.* **144**, 102640 (2020).
57. D. L. Hoffmann *et al.*, Response to White *et al.*'s reply: 'Still no archaeological evidence that Neanderthals created Iberian cave art' [J. Hum. Evol. (2020) 102640]. *J. Hum. Evol.* **144**, 102810 (2020).
58. P. Bodu *et al.*, An open-air site from the recent middle palaeolithic in the Paris Basin (France): Les Bossats at Ormesson (Seine-et-Marne). *Quat. Int.* **331**, 39–59 (2014).
59. H. Salomon, "Les matières colorantes" in *Le Châtelperronien de la grotte du Renne (Arcy-sur-Cure Yonne, France, 2019)*, pp. 213–258.
60. F. Lévêque, A. M. Backer, M. Guilbaud, Eds., Context of a late Neandertal: Implications of Multidisciplinary Research for the Transition to Upper Palaeolithic Adaptations at Saint-Césaire, Charente-Maritime, France (Monographs in World Archaeology 16, Prehistory Press, 1993).
61. F. Lévêque, B. Vandermeersch, Découverte de restes humains dans un niveau castelperronien à Saint-Césaire (Charente-Maritime). *C. R. Acad. Sci. Paris* **291**, 187–189 (1980).
62. L. Lebreton *et al.*, The potential of micromammals for the stratigraphy and the timing of human occupations at La Roche-à-Pierrot (Saint-Césaire, France). *Quaternary* **4**, 33 (2021).
63. A. Couillet *et al.*, New visual analytics tool and spatial statistics to explore archeological data: The case of the Paleolithic sequence of La Roche-à-Pierrot, Saint-Césaire. France. *J. Comput. Appl. Archaeol.* **5**, 19–34 (2022).
64. D. Todisco *et al.*, A multiscale and multiproxy geoarchaeological approach to site formation processes at the Middle and Upper Palaeolithic site of La Roche-à-Pierrot, Saint-Césaire. France. *Quat. Sci. Rev.* **315**, 108218 (2023).
65. J. Jaubert, J.-G. Bordes, E. Discamps, B. Gravina "A new look at the end of the Middle Palaeolithic sequence in Southwestern France" in *Proceeding of the International Symposium "Characteristic features of the Middle to Upper Palaeolithic Transition in Eurasia: Development of Culture and Evolution of Homo Genus"*, A. P. Derevianko, M. Shunkov, Eds. (Department of the Institute of Archaeology and Ethnography SB RAS, Novosibirsk, 2011), pp. 102–115.
66. J.-P. Favre *et al.*, The contribution of lithic production systems to the interpretation of Mousterian industrial variability in south-western France: The example of Combe-Grenal (Dordogne, France). *Quat. Int.* **350**, 227–240 (2014).
67. J.-P. Favre, B. Gravina, L. Bourguignon, E. Discamps, A. Turq, Late middle palaeolithic lithic technocomplexes (MIS 5–3) in the northeastern Aquitaine Basin: Advances and challenges. *Quat. Int.* **433**, 116–131 (2017).
68. M. Roussel, M. Soressi, J.-J. Hublin, The Châtelperronian conundrum: Blade and bladelet lithic technologies from Quincy. *France. J. Hum. Evol.* **95**, 13–32 (2016).
69. E. Morin *et al.*, Bone refits in stratified deposits: Testing the chronological grain at Saint-Césaire. *J. Archaeol. Sci.* **32**, 1083–1098 (2005).
70. E. Morin, *Reassessing Paleolithic Subsistence. The Neandertal and Modern Human Foragers of Saint-Césaire* (Cambridge University Press, 2012).
71. J. Cataliotti-Valdina, Littorines quaternaires de Méditerranée. *Bull. Assoc. Fr. Etude Quat.* **21**, 211–219 (1984).
72. G. T. Poppe, Y. Goto, *European Seashells, Volume 1: Polyplacophora, Caudofoveata, Solenogastrea, Gastropoda* (Verlag Christa Hemmen, 1991).
73. G. T. Poppe, Y. Goto, *European Seashells, Volume 2: Scaphopoda, Bivalvia, Cephalopoda* (Verlag Christa Hemmen, 1993).
74. P. Bertran, A. Lenoble, Fabriques des niveaux archéologiques: Méthode et premier bilan des apports à l'étude taphonomique des sites paléolithiques. *PALEO* **14**, 13–28 (2002).
75. A. Lenoble, *Ruissellement et formation des sites préhistoriques: référentiel actualiste et exemples d'application au fossile* (British Archaeological Report International Series n° 1363, 2005).
76. E. Bard *et al.*, AixMICADAS, the accelerator mass spectrometer dedicated to <sup>14</sup>C recently installed in Aix-en-Provence, France. *Nucl. Instrum. Methods Phys. Res. B.* **361**, 80–86 (2015).
77. T. J. Heaton *et al.*, Marine20—the marine radiocarbon age calibration curve (0–55,000 cal BP). *Radiocarbon* **62**, 821–863 (2020).
78. T. C. Rick, R. L. Vellanoweth, J. M. Erlandson, Radiocarbon dating and the "old shell" problem: Direct dating of artifacts and cultural chronologies in coastal and other aquatic regions. *J. Archaeol. Sci.* **32**, 1641–1648 (2005).
79. J. Benjamin *et al.*, Late quaternary sea-level changes and early human societies in the central and eastern Mediterranean Basin: An interdisciplinary review. *Quat. Int.* **449**, 29–57 (2017).
80. K. Lambeck, T. M. Esat, E.-K. Potter, Links between climate and sea levels for the past three million years. *Nature* **419**, 199–205 (2002).
81. M. Siddall *et al.*, Smeed, Sea-level fluctuations during the last glacial cycle. *Nature* **423**, 853–858 (2003).
82. M. Medina-Elizalde, A global compilation of coral sea-level benchmarks: Implications and new challenges. *Earth Planet. Sci. Lett.* **362**, 310–318 (2013).
83. C. Christophe, A. Philippe, S. Kreutzer, G. Guérin, BayLum: Chronological Bayesian Models integrating optically stimulated luminescence and radiocarbon age dating (2017), <https://CRAN.R-project.org/package=BayLum>.
84. A. Philippe, G. Guérin, S. Kreutzer, BayLum—an R package for Bayesian analysis of OSL ages: An introduction. *Quat. Geochronol.* **49**, 16–24 (2019).
85. G. Guérin *et al.*, Towards an improvement of optically stimulated luminescence (OSL) age uncertainties: Modelling OSL ages with systematic errors, stratigraphic constraints. *Geochronology* **3**, 229–245 (2021).
86. F. Bachelierie, *Quelle unité pour le Châtelperronien? Apport de l'analyse taphonomique et techno-économique des industries lithiques de trois gisements aquitains de plein air: Le Basté, Bidart (Pyrénées-Atlantiques) et Canaule II (Dordogne)* (Université Bordeaux 1, Talence, 2011).
87. F. Bachelierie *et al.*, "La signature archéologique de l'activité de chasse appliquée à la comparaison des industries moustériennes, châtelperroniennes et aurignaciennes des Pyrénées: nature des équipements et fonctions des sites" in *Haltes de chasse en Préhistoire. Quelles réalités archéologiques?* F. Bon, S. Costamagno, N. Valdeyron, Eds. (Paléolithique 3, 2011), pp. 131–168.
88. M. Baillet, *Éclairage de la tracéologie lithique sur le système techno-économique nomade châtelperronien* (Université de Bordeaux, Pessac, 2017).
89. M. Roussel, *Normes et variations de la production lithique durant le Châtelperronien: la séquence de la Grande Roche de la Plématrie à Quincy (Vienne)* (Université Paris Ouest Nanterre-La Défense, Nanterre, 2011).
90. J. Pelegrin, *Technologie lithique: le Châtelperronien de Roc-de-Combe (Lot) et de la Côte (Dordogne) (Cahiers du Quaternaire 20)* (Editions du CNRS, 1995).
91. N. Connet, "La production lithique châtelperronienne de la grotte du Renne" in *Le Châtelperronien de la grotte du Renne (Arcy-sur-Cure Yonne, France, 2019)*, pp. 431–504.
92. J.-G. Bordes, F. Bachelierie, "Different skill levels and the structure of Early Upper Palaeolithic groups: the examples of Canaule II (Châtelperronian) and Corbiac-Vignoble II (Early Aurignacian)" in *L'apprenti préhistorique: appréhender l'apprentissage, les savoir-faire et l'expertise à travers les productions techniques des sociétés préhistoriques*, L. Klaric, Ed. (Dolní Věstonice Studies, 2018), pp. 52–76.
93. F. Caron, F. d'Errico, P. Moral, F. Santos, J. Zilhão, The reality of Neandertal symbolic behavior at the Grotte du Renne, Arcy-sur-Cure. France. *PLoS One* **6**, e21545 (2011).
94. F. Bordes, J. Labrot, La stratigraphie du gisement de Roc-de-Combe et ses implications. *Bull. Soc. Préhist. Fr.* **64**, 15–28 (1967).
95. J.-M. Granger, F. Lévêque, Parure castelperronienne et aurignacienne: Étude de trois séries inédites de dents percées et comparaisons. *C. R. Acad. Sci. Paris (Préhistoire)* **325**, 537–543 (1997).
96. W. Rendu *et al.*, Subsistence strategy changes during the Middle to Upper Paleolithic transition reveals specific adaptations of human populations to their environment. *Sci. Rep.* **9**, 15817 (2019).
97. J. Morales *et al.*, The middle-to-Upper Paleolithic transition occupations from Cova Foradada (Calafell, NE Iberia). *PLoS One* **14**, e0215832 (2019).
98. M. D. Bosch, F. P. Wesselingh, M. A. Mannino, The ksar 'akil (Lebanon) mollusc assemblage: Zooarchaeological and taphonomic investigations. *Quat. Int.* **390**, 85–101 (2015).
99. M. C. Stiner, S. L. Kuhn, G. Erksin, Early upper Paleolithic shell beads at Uçağızlı Cave I (Turkey): Technology and the socioeconomic context of ornament life-histories. *J. Hum. Evol.* **64**, 380–398 (2013).
100. S. Rigaud *et al.*, The management of symbolic raw materials in the Late Upper Paleolithic of South-Western France: a shell ornaments perspective. *Peer Community J.* **2**, e65 (2022).
101. F. Errico *et al.*, Multivariate analyses of Aurignacian and Gravettian personal ornaments support cultural continuity in the early upper Palaeolithic. *PLoS One* **20**, e0323148 (2025).
102. S. L. Kuhn, M. C. Stiner, D. S. Reese, E. Güleg, Ornaments of the earliest upper paleolithic: New insights from the Levant. *Proc. Natl. Acad. Sci. U.S.A.* **98**, 7641–7646 (2001).
103. K. Douka, C. A. Bergman, R. E. M. Hedges, F. P. Wesselingh, T. F. G. Higham, Chronology of Ksar Akil (Lebanon) and implications for the colonization of Europe by Anatomically Modern Humans. *PLoS One* **8**, e72931 (2013).
104. K. Douka *et al.*, Age estimates for hominin fossils and the onset of the Upper Palaeolithic at Denisova Cave. *Nature* **565**, 640–644 (2019).
105. Q. Fu *et al.*, Genome sequence of a 45,000-year-old modern human from western Siberia. *Nature* **514**, 445–449 (2014).
106. S. Talamo *et al.*, A 41,500-year-old decorated ivory pendant from Stajnia Cave (Poland). *Sci. Rep.* **11**, 22078 (2021).

107. L. Vallini *et al.*, Genetics and material culture support repeated expansions into Paleolithic Eurasia from a population hub out of Africa. *Genome Biol. Evol.* **14**, evac045 (2022).
108. M. Hajdinjak *et al.*, Initial upper palaeolithic humans in Europe had recent Neanderthal ancestry. *Nature* **592**, 253–257 (2021).
109. K. Prüfer *et al.*, A genome sequence from a modern human skull over 45,000 years old from Zlatý kůň in Czechia. *Nat. Ecol. Evol.* **5**, 820–825 (2021).
110. M. Romandini *et al.*, Neanderthal scraping and manual handling of raptors wing bones: Evidence from Fumane Cave. *Quat. Int.* **421**, 154–172 (2016).
111. S. Finlayson, G. Finlayson, F. G. Guzman, C. Finlayson, Neanderthals and the cult of the sun bird. *Quat. Sci. Rev.* **217**, 217–224 (2019).
112. S. Rigaud *et al.*, Symbolic innovation at the onset of the Upper Paleolithic in Eurasia shown by the personal ornaments from Tolbor-21 (Mongolia). *Sci. Rep.* **13**, 9545 (2023).
113. G. Marciani *et al.*, The Uluzzian and Châtelperronian: No technological affinity in a shared chronological framework. *J. Paleolithic Archaeol.* **8**, 1–30 (2025).
114. M. Stiner *et al.*, Klissoura cave 1 and the upper Paleolithic of Southern Greece in cultural and ecological contexts. *Eurasian Prehist.* **7**, 309–321 (2010).
115. S. Arrighi *et al.*, Bone tools, ornaments and other unusual objects during the Middle to Upper Palaeolithic transition in Italy. *Quat. Int.* **551**, 169–187 (2020).
116. D. E. Bar-Yosef Mayer, Early personal ornaments in early prehistory. Upper Paleolithic Explorers: The geographic sources of shell beads in early Upper Paleolithic assemblages in Israel. *PaleoAnthropology*, 105–115 (2019).
117. M.-H. Moncel *et al.*, Non-utilitarian lithic objects from the European Paleolithic. *Archaeol. Ethnol. Anthropol. Eur.* **40**, 24–40 (2012).
118. M. Vanhaeren, F. d'Errico, Aurignacian ethno-linguistic geography of Europe revealed by personal ornaments. *J. Archaeol. Sci.* **33**, 1105–1128 (2006).
119. Y. Taborin, *La parure en coquillage au Paléolithique (XXIX supplément à «Gallia Préhistoire»* (CNRS Éditions, 1993).
120. J. Baker *et al.*, Evidence from personal ornaments suggest nine distinct cultural groups between 34,000 and 24,000 years ago in Europe. *Nat. Hum. Behav.* **8**, 431–444 (2024).
121. S. Rigaud, F. d'Errico, M. Vanhaeren, Ornaments reveal resistance of north European cultures to the spread of farming. *PLoS One* **10**, e0121166
122. J. Henrion, J.-J. Hublin, B. Maureille, New neanderthal remains from the Châtelperronian-attributed layer X of the Grotte du Renne (Arcy-sur-Cure, France). *J. Hum. Evol.* **181**, 103402 (2023).
123. P. Bertran, J.-P. Texier, Fabric analysis: Application to Paleolithic sites. *J. Archaeol. Sci.* **22**, 521–535 (1995).
124. S. P. McPherron, Additional statistical and graphical methods for analyzing site formation processes using artifact orientations. *PLoS One* **13**, e0190195 (2018).