Corrections

PHARMACOLOGY
Correction for “Selective activation of the M1 muscarinic acetylcholine receptor achieved by allosteric potentiation,” by Lei Ma, Matthew Seager, Marion Wittmann, Marlene Jacobson, Denise Bickel, Maryann Burno, Keith Jones, Valerie Kuzmick Graufelds, Guanping Xu, Michelle Pearson, Alexander McCampbell, Renee Gaspar, Paul Shughrue, Andrew Danziger, Christopher Regan, Rose Flick, Danette Pascarella, Susan Garson, Scott Doran, Constantine Kreatsoulas, Lone Veng, Craig W. Lindsley, William Shipe, Scott Kuduk, Cyrille Sur, Gene Kinney, Guy R. Seabrook, and William J. Ray, which appeared in issue 37, September 15, 2009, of Proc Natl Acad Sci USA (106:15950–15955; first published August 26, 2009; 10.1073/pnas.0900903106).

The authors note that the author name Matthew Seager should have appeared as Matthew A. Seager. The online version should have appeared as Matthew A. Seager. The corrected author line, affiliation line, and a related footnote appear below.

Lei Ma1, Matthew A. Seager1, Marion Wittmann1, Marlene Jacobson, Denise Bickel, Maryann Burno, Keith Jones, Valerie Kuzmick Graufelds, Guanping Xu, Michelle Pearson, Alexander McCampbell, Renee Gaspar, Paul Shughrue, Andrew Danziger, Christopher Regan, Rose Flick, Danette Pascarella, Susan Garson, Scott Doran, Constantine Kreatsoulas, Lone Veng, Craig W. Lindsley, William Shipe, Scott Kuduk, Cyrille Sur, Gene Kinney, Guy R. Seabrook, and William J. Ray

Author contributions: L.M., M.A.S., and M.W. contributed equally to this work.

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ANTHROPOLOGY

The authors note that Abdeljalil Bouzouggar should be credited for designing and performing the research. The corrected author contributions footnote appears below.


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PERSPECTIVE
Correction for “Feeding aquaculture in an era of finite resources,” by Rosamond L. Naylor, Ronald W. Hardy, Dominique P. Bureau, Alice Chiur, Matthew Elliott, Anthony P. Farrell, Ian Forster, Delbert M. Gatlin, Rebecca J. Goldberg, Katherine Hua, and Peter D. Nichols

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APPLIED PHYSICAL SCIENCES

The authors note that, due to a printer’s error, on page 15227, right column, the equation on lines 14 and 15 of the first full paragraph appeared incorrectly. This error does not affect the conclusions of the article. The corrected equation appears below.

\[ E = \int_{0}^{t_{m}} GV(t)/S \ dt \]

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Additional evidence on the use of personal ornaments in the Middle Paleolithic of North Africa

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Recent investigations into the origins of symbolism indicate that personal ornaments in the form of perforated marine shell beads were used in the Near East, North Africa, and SubSaharan Africa at least 35 ka earlier than any personal ornaments in Europe. Together with instances of pigment use, engravings, and formal bone tools, personal ornaments are used to support an early emergence of behavioral modernity in Africa, associated with the origin of our species and significantly predating the timing for its dispersal out of Africa. Criticisms have been leveled at the low numbers of recovered shells, the lack of secure dating evidence, and the fact that documented examples were not deliberately shaped. In this paper, we report on 25 additional shell beads from four Moroccan Middle Paleolithic sites. We review their stratigraphic and chronological contexts and address the issue of these shells having been deliberately modified and used. We detail the results of comparative analyses of modern, fossil, and archaeological assemblages and microscopic examinations of the Moroccan material. We conclude that Nassarius shells were consistently used for personal ornamentation in this region at the end of the last interglacial. Absence of ornaments at Middle Paleolithic sites postdating Marine Isotope Stage 5 raises the question of the possible role of climatic changes in the disappearance of this hallmark of symbolic behavior before its reinvention 40 ka ago. Our results suggest that further inquiry is necessary into the mechanisms of cultural transmission within early Homo sapiens populations.


The authors declare no conflict of interest.

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Recent investigations into the origins of symbolism indicate that personal ornaments in the form of perforated marine shell beads were used in the Near East, North Africa, and SubSaharan Africa at least 35 ka earlier than any personal ornaments in Europe. Together with instances of pigment use, engravings, and formal bone tools, personal ornaments are used to support an early emergence of behavioral modernity in Africa, associated with the origin of our species and significantly predating the timing for its dispersal out of Africa. Criticisms have been leveled at the low numbers of recovered shells, the lack of secure dating evidence, and the fact that documented examples were not deliberately shaped. In this paper, we report on 25 additional shell beads from four Moroccan Middle Paleolithic sites. We review their stratigraphic and chronological contexts and address the issue of these shells having been deliberately modified and used. We detail the results of comparative analyses of modern, fossil, and archaeological assemblages and microscopic examinations of the Moroccan material. We conclude that Nassarius shells were consistently used for personal ornamentation in this region at the end of the last interglacial. Absence of ornaments at Middle Paleolithic sites postdating Marine Isotope Stage 5 raises the question of the possible role of climatic changes in the disappearance of this hallmark of symbolic behavior before its reinvention 40 ka ago. Our results suggest that further inquiry is necessary into the mechanisms of cultural transmission within early Homo sapiens populations.

Cruccial questions in the debate on the origin of quintessential human behaviors are whether modern cognition and associated innovations are unique to our species and whether they emerged abruptly or gradually. A related question is to what extent behavioral innovations developed in Africa may have favored the spread of our species out of that continent. Three scenarios have been proposed to account for the origin of cultural modernity. The first argues that modern cognition is unique to our species and the consequence of a genetic mutation that took place 50 ka in Africa among anatomically modern humans (AMH) (1). The second posits that cultural modernity emerged gradually in Africa starting 200 ka and is directly linked to the origin of our species on that continent (2). Used pigments at sites dated to at least 160 ka (3), abstract engravings on ochre and bone (4) and personal ornaments dated to between 100 and 70 ka (5–9) support this view. The third scenario states that innovations indicative of modern cognition are not restricted to our species and appear and disappear in Africa, Europe, and the Near East between 200 and 40 ka before becoming fully consolidated (10–13). The main driving force in this last scenario is long-term climatic variability and its effect on population dynamics (14).
a few beads, and that the reported beads are not deliberately shaped (1). In addition, criticisms have been leveled at the Taforalt evidence. It has been argued that beach abrasion makes the shell beads from this site less compelling than those from Blombos and that their archaeological context is only “weakly described” (1).

In this paper, we report on 25 additional shell beads from four Moroccan Middle Paleolithic (MP) sites. Analyses of these beads, conducted with a variety of methods (SI Text), and their stratigraphic and chronological contexts contradict the idea that the occurrence of shell beads at MP sites in North Africa and the Levant is accidental or the result of idiosyncratic behavior. The evidence demonstrates that *Nassarius* (*Na*) were consistently used as personal ornaments in this region at the end of the last interglacial. Absence of ornaments at MP sites postdating Marine Isotope Stage (MIS) 5 supports the hypothesis (14, 23–25) that climatic changes and consequent impacts on demography played a key role in the disappearance of this and other hallmarks of modern behavior before their re-appearance 50–40 ka ago. This pattern reinforces a scenario linking a single or multiple (26) Out-of-Africa dispersal to demographic increases.

Archaeological Context and Dating of the New Shell Beads. Taforalt. Grotte des Pigeons is a large cave situated in eastern Morocco near the village of Taforalt, 40 km from the Mediterranean coast (Fig. 1). At the cave, a 10-m thick archaeological sequence containing Iberomaurusian (Upper Paleolithic) and Aterian MP artifacts was identified (27). Excavations conducted since 2003 by Barton and Bouzouggar have reinvestigated a 2.5-m portion (Fig. S1) of this sequence, which they have divided into five principal units (A, B+C, D, E, and F), each of which is bracketed by a significant shift in sediment type (8). MP occupation horizons have been recorded in Units C–F. Unit E is characterized by Aterian tools including tanged artifacts, bifacial foliates, side scrapers, and small radial Levallois cores. The paleoenvironmental context is documented by the presence of arid plant and small mammal species indicating a drier climate than the present. Thirteen *Ng* shells already have been reported from this unit (8), which consists of multiple interdigitated ash lenses indicating major combustion zones. The presence of 2 beads in the overlying layers is attributed to reworking due to human activity. Three other shells were found in the fill of burrows intersecting the thick ashy lenses; the last was recovered during screening. Of the 19 shells reported in the present paper (Fig. 2 and Table S1), 14 were found in situ and come from Unit E. Two other shells came from burrows, and three came from reworked sediments. Eight of the shells came from the same contiguous 6 m² (Fig. S1) that previously yielded such objects (M13–14, N13, and P13). Ten shells came from neighboring squares (N14, P12, and L15). A single specimen came from a more distant square (I14), where no perforated shells have been recovered previously. ¹⁴C AMS determinations on charcoal provided ages ranging between 11–23 ka for the upper part of the archaeological sequence (A–C). The lower layers, including the

![Fig. 1](image1.png)  
**Fig. 1.** Location of Middle Paleolithic sites from Mediterranean regions that have yielded shell beads (●) and modern and fossil reference collections (*) (see SI Text); The designated sites are: 1, Dar es-Soltan I; 2, Contrebandiers; 3, Ifri n’Ammar; 4, Rhafas; 5, Taforalt (Grotte des Pigeons); 6, Oued Djebbana; 7, Monastir; 8, Djerba; 9, Haifa; 10, Yafo; 11, Nahariyya; 12, Skhul; 13, Qafzeh.

![Fig. 2](image2.png)  
**Fig. 2.** Marine shells found at Moroccan Middle Paleolithic sites and modern shells of the same species. Shells are from: 1–19, Taforalt (Grotte des Pigeons); 20–24, Rhafas; 25, Contrebandiers; 26 and 27, Ifri n’Ammar; 28, modern *Nassarius gibbosulus*; 29 and 30, modern *Nassarius circumcinctus*; 31, modern *Columbella rustica* (see Table S1 for contextual information and analytical data).
shell-bearing Unit E, were dated by multiple- and single-grain optically stimulated luminescence (OSL) methods, thermoluminescence (TL) determinations obtained on heated flint artifacts, and U-Series isotopic measurements on flowstone samples (8). The upper portion of Unit E (Raynal’s Levels 18–21) is dated by OSL to 60,100 ± 3,900 and 73,300 ± 5,700 B.P., whereas the lower portion of Unit E (Raynal’s Levels 23 and 25) is attributed an age ranging between 84,500 ± 4,400 (OSL date of the overlying Layer 22) and 85,500 ± 8,100 (OSL date for the underlying Layer 26). A Bayesian age model, based on the obtained age estimates, constrained Layer 21 (the upper portion of Unit E) to between 73,400 and 91,500 years ago with a likely age of 82,500 years B.P.

Rhabaf. Rhabaf is a small cave, located 50 km from the Mediterranean coast, with a 4.5-m stratigraphic sequence (28) (Fig. 1). The base of the sequence consists of a deep series of MP levels, the uppermost being Level 3b. The overlying Level 3a is Proto-Aterian and Level 2 is Aterian. The Neolithic Level 1 caps the sequence. Four chalcedony lithics from Level 3a and six from Level 3b were TL dated to between 92 ± 10 ka and 62 ± 7 ka for the end of the MP and between 76 ± 8 ka and 60 ± 5 ka for the Proto-Aterian (29). Excavations have confirmed the cultural designations for Levels 6–3. These excavations have produced five Na shells: One from a good context and the remaining four from site cleaning and disturbed or unclear contexts (Fig. 2 and Table S1). The in situ example, D12–145, was found in Layer 3a ~40 cm below the surface and ~20 cm below the contact with the overlying Level 1. The presence in this same level of tanged pieces supports its attribution to the Aterian. Based on the TL determinations for this level, the conservative age range is between 80–60 ka, although Mercier et al. (29) suggest a likely age range of 80–70 ka.

Ifni n’Ammar. Located 59 km from the Mediterranean coast, close to Hassi Ouenza, Ifni n’Ammar (Fig. 1) is a cave excavated between 1997 and 2005 by the Institut National des Sciences de l’Archéologie et du Patrimoine (INSAP) and the German Archaeological Institute (DAI) to a depth of 7 m. The sequence features, from top to bottom (30), an Iberomaurusian layer, a 1-m thick Aterian layer with tanged tools and uni- and bifacial foliates (Layer MP-A), and a 0.7-m thick Middle Paleolithic layer (Layer MP-B) lacking Aterian industries. Separated from MP-B by 0.7 m of almost sterile sediment, the 0.3-m thick Layer MP-C contains a MP industry with tanged points. After another 0.2-m thick layer of mostly sterile calcite, the lowermost 1-m thick MP Layer MP-D contains a Middle Paleolithic industry lacking Aterian tanged tools. Radiocarbon determinations of 39,700 ± 1,320/–1,130 for Layer MP-A, and 38,740 ± 2,290/–1,780, and 51,480 ± 1,470/–1,240 for Layer MP-B (31) are interpreted as minimum ages because they are at the fringes of the method, and samples have been contaminated by exogenous carbon (32). Weighted TL average ages of 83.3 ± 5.6 ka and 130 ± 7.8 ka have been proposed for Layers MP-A and MP-B, respectively (32). Two perforated marine shells were recovered within Layer MP-A: a Na sp. and a worn undetermined shell (33) (Fig. 2 and Table S1).

Contrebandiers. Also called El Mnasra I, this cave is located 17 km south of Rabat, next to the ocean (Fig. 1). Previous and recent excavations have identified a sequence with 16 layers (34, 35). Layers 1–5 contain Neolithic occupations, Layer 6 is sterile, and Layers 7–11 contain Iberomaurusian assemblages. Layers 8–11 are Aterian and Layers 11–14 are either Aterian or Middle Paleolithic without tanged tools. Layers 15 and 16 are sterile. Attempts to date the Aterian layers have been unsuccessful. Radiocarbon determinations for Layers 8–12 range between 12.5 ka and ≥40 ka and reveal no stratigraphic consistency (36). U-Th series provide ages of ~137 ka for the same layers (36). The perforated Na described here (Fig. 2 and Table S1) was found in 2005, while the section was sampled for OSL dating and environmental studies, and comes from a disturbed context, possibly attributable to Layer 9, 10, or 11.

Results

Taxonomic Identification. Three of the 19 Na from Taforalt and one of the four from Rhabaf (Table S1) present morphological features indicating that they may belong to the species circumcinctus (Nc) rather than Ng. Modern Ng and Nc differ in their morphology and color pattern (SI Text and Fig. 2). Most archaeological specimens have lost their original color, are fragmentary, and display a muted shell sculpture, making it difficult to identify ambiguous specimens to the species level. The morphology of Ng has also changed through time. Pleistocene specimens are larger and present a thicker parietal shield (7, 8). Modern Ng are on average significantly bigger than Nc, and their size ranges overlap only slightly (Fig. S2). Well-preserved specimens from a Thyrrenian fossil beach near Monastir (Tunisia) dated to 126 ± 7 ka (37) follow the same trend but are comparatively wider than their modern counterparts.

Complete Ng from archaeological sites are significantly larger (P < 0.0001) than modern specimens. The few possible Nc also plot at the upper edge of their modern size range. Finally, it is worth noting that Ng and Nc from Rhabaf found out of context and the isolated specimen from Contrebandiers are as large as specimens recovered in Aterian in situ layers at this site and contemporary sites and present morphological features (thick parietal shield extending over the apex) that support their Pleistocene attribution. Ng is today only present in the eastern Mediterranean and westward to the Sicilian Channel, and Nc is restricted to the coasts of the Near East (36). One of the two shells from the Aterian layers of Ifni n’Ammar and a specimen found out of context at Rhabaf most likely belong to the species Columbella rustica.

Shell Provenance, Modification, and Use. Analysis of the shells from Rhabaf, Ifni n’Ammar, Contrebandiers, and the specimens from Taforalt reinforces the conclusion that they were transported to these sites by humans during the Aterian and used for symbolic purposes. The shells do not derive from the bedrock in which these cave sites are formed. Both Ng and Nc live exclusively in sandy habitats in the infralittoral zone (ca. 2–27 m depth) (38). Ifni n’Ammar and Rhabaf are respectively 59 and 50 km from the present day coastal line, which is even more than Taforalt (40 km). This distance would have been similar to or greater than the present-day distance during the period in which the shells were deposited at these sites (39), a distance too great for natural processes known to carry marine shells inland as transport agents (7, 9). The absence of Nassarius in all overlying layers at the four sites and at all other Upper (Iberomaurusian), Epipaleolithic (Capsian), and Neolithic sites from Morocco (SI Text) argues against the possibility that the Nassarius derive from younger layers.

As already observed on the first discovered Na from Taforalt, the specimens from this site and the other sites show features indicating that they were collected already dead on the shore and cannot be interpreted as the remains of subsistence-related activities (Table S1). These observations reinforce, rather than weaken, the argument for their symbolic use. All of the specimens present a muted shell sculpture with smoothing of the apex typical of a mechanical abrasion on the shore. Half of them feature perforations made by gastropod predators, beach gravel and shell fragments stuck inside the shell, and nets of micro pits left by boring sponges of the family Clionidae (40) on the surface of the aperture (Fig. S3). The archaeological Na, however, are not the result of a random collection of dead shells on a shoreline. In such an instance one should find, by comparison to the perforation patterns recorded on modern and fossil taphocoenoses, a very large proportion of unperforated shells and...
few shells with a hole on the dorsal side at the center of the body whorl (Fig. 3, type f). The opposite is observed archaeologically, suggesting that the shells with a perforation on the dorsal side were either deliberately collected or perforated by humans. One Ng from Taforalt in situ layers bears direct evidence of human involvement in the production of the perforations (Fig. S4), consisting of two groups of parallel striations radiating from the edge of the perforation in the area close to the siphonal canal. With reference to known diagnostic criteria of stone tool generated marks, the morphology, composite nature, and location of the marks suggest that each group was made by a robust lithic point. Unsuccessful attempts to perforate shells of the same genus by punching the outer surface of the body whorl with a lithic point (5) produced similar striations when the lithic point slipped on the curved shell surface. A mark produced by a lithic point on the dorsal side of an unperforated Ng from the in situ layers of Taforalt may have been produced by the same action (Fig. S4).

Direct evidence for the use of the shells as beads comes from the identification on eighteen Na from Taforalt and the five shells from Rhafas of a use-wear pattern different from that recorded on modern biocoenoses, modern and fossil thanatocoenoses, as well as on unperforated specimens from Taforalt. The parietal shields of Ng collected while alive present a glass-like texture with rare superficial micropits (Fig. S4), that of Ng from modern thanatocoenoses is covered with deep subcircular micropits 20–80 μm in diameter (Fig. S4). A similar texture, enriched by few randomly oriented striations, is observed on unperforated Ng from Taforalt (Fig. S4). In contrast, well-preserved perforated Ng from Taforalt and Rhafas have their surface covered by a palimpsest of 5–10 μm wide, randomly oriented striations, and a few worn residual micropits (Fig. S4). These striations are responsible for the shine that covers all prominent well-preserved areas of the perforated shells (Table S1 and Fig. S5). Considering its appearance and location, this wear pattern was produced by sorted abrasive particles scratching the shell surface in a situation in which the shell was relatively free to move. Two other types of wear patterns, absent in natural collections and likely related to the stringing of the shells, are recorded on most of the discovered specimens (Table S1 and Fig. S5). These patterns take the form of intense smoothing observed on the edge of the perforation and on the spiral whorl. Also, wear facets absent on unperforated shells from Taforalt and modern biocoenoses are present on the lip, the parietal wall, and the upper and lower edges of perforations (Table S1, Fig. S5, and Fig. S6). The only specimen that we were unable to examine directly, the Ng from Ifri n’Ammar, presents a shine on its outer surface and a smoothing of the perforation edges (Fig. S7) very similar to that observed on the best preserved Taforalt specimens.

Eight Na from Taforalt, Rhafas, and Ifri n’Ammar present evidence of heating. This process has produced a dark brown coloring and, at the microscopic scale, exfoliations and microcracks on the outer surface (Table S1 and Fig. S7). Heating shell with the temperature of an open fire in an oxidizing environment produces the gradual loss of the shell organic content, the conversion of aragonite into calcite at approximately 520°C, the oxidation of the carbon content, and in the end, the destruction of the shell and the production of sulfur-rich ash. During this process the shell progressively loses its natural coloring to become white, porous, and fragile. Shells become black or dark brown, as observed at Taforalt, Rhafas, and Ifri n’Ammar, and to some extent keep their integrity, only when they are heated progressively, at relatively high temperatures, in a reductive atmosphere and in the presence of organic material (41). This last ingredient is needed to transfer to the shell the carbon responsible for the darkening of the shell surface and inner degraded amorphous calcite. Shell heating at the three sites under study cannot be interpreted as evidence for cooking as they were collected dead. This observation is further confirmed by the presence of a marine shell belonging to another species stuck into one of the burnt specimens from Taforalt (Fig. S7). The darkening of the shell beads can have either resulted from the accidental heating of lost or discarded ornaments buried in organic–rich cave sediment or a deliberate and controlled process to change their color. The aim, in the latter case, would arguably be that of making beadworks composed by ornaments of different colors. A well-preserved dark shell from Taforalt shows evidence that the heating took place before the use of the shell as a bead (Fig. S7): The microcracks opened by the heating around the first suture and on the edge of the perforation appear to be smoothed by the use wear, suggesting that, in this case at least, a shell blackened by heating was subsequently used as a bead.

**Pigment.** Elemental and mineralogical analysis of residues from one Ng from Taforalt and the Ifri n’Ammar specimen (8, 33) demonstrate the pigmented nature of the red particles adhering to the perforated shells from these sites. Both analyses have revealed a high content of iron oxide, probably in the form of hematite. Similar residues were recorded on thirteen of the shells from Taforalt and two from Rhafas (Table S1 and Fig. S5).

![Fig. 3. Perforation types (Upper) recorded on the dorsal and the ventral side of Nassarius shells and their frequency (Lower) in modern (*), fossil (**), and the archaeological specimens.](image-url)
organized exchange networks, and value is ascribed to their available only in distant regions, their acquisition depends on essential symbolic items. A peculiarity of these objects is that when the natural world and the meaning attributed to them, quintessential elements of the natural word (feathers, shells, bone, teeth, shell beads. Many ethnographically documented beadworking modification observed on the vast majority of Upper Paleolithic (10, 11). As in North Africa, a single perforation bearing no beginning of the Upper Paleolithic in the Mediterranean region traditions are exclusively or almost exclusively represented by here. A number of archaeologically recognized beadworking and recent human societies and in light of the results presented evidence because they are not manufactured is difficult to accept consistent with the wear patterns. Diagenesis of these sediments, let alone how such oxide could have been deposited on the shells at any point during the diagno

In five cases red pigment is trapped in the groove between the lip and the body whorl (Fig. S8). In the others, it fills pits left by bioeroders (Fig. S3 and Fig. S8), the broken apex, variously located microconcrations, or adheres to the columella. One Ng from Taforalt represents a special case in that its entire outer surface is covered with red pigment residues (Fig. S8). Because the shells from Taforalt, Rhafas, and Ifrí n’Ammar do not derive from ochred layers, and no detected postdepositional processes can account for the presence of pure iron oxide on these objects, this presence must be due to fact that they were covered with ochre while in use, that they were continuously rubbing against an ochred material, or their thread was impregnated with ochre. These three possibilities are not mutually exclusive. The presence of pigment in microcracks located on the perforation edge, where the thread was rubbing the surface, suggests the thread was ochred (Fig. S8). On the other hand, the discovery among the shells of a specimen fully covered with ochre strongly suggests that the beadwork in which the shells were integrated was covered with pigment.

Conclusion

Evidence presented here contradicts the view that instances of symbolic mediated behavior dated before 50 ka should be discarded due to the paucity of sites with shell beads, provenance, and deficient modifications of the latter, limited dating evidence, and inadequate contextual information. Our results and already published data indicate that marine shells were used as personal ornaments in North and South Africa and in the Near East during the last interglacial. The data presented here raises to at least nine the number of MP sites that have yielded personal ornaments made of marine shells, raises to several dozen the number of recovered perforated shells, and raises to five the number of shell species used. Even if the number of beads recovered at some of the sites from North Africa is admittedly low, behavioral and chronological consistencies suggest the evidence will inevitably grow, qualitatively and quantitatively, to encompass more sites, types of beads, and, possibly, a wider geographic area. The view that these beads represent negligible evidence because they are not manufactured is difficult to accept in the light of what we know about personal ornament use in past and recent human societies and in light of the results presented here. A number of archaeologically recognized beadworking traditions are exclusively or almost exclusively represented by marine shells. This situation is observed, for example, at the beginning of the Upper Paleolithic in the Mediterranean region (10, 11). As in North Africa, a single perforation bearing no other compelling evidence of human intervention is the only modification observed on the vast majority of Upper Paleolithic shell beads. Many ethnographically documented beadworking traditions exclusively use unmodified beads or minimally modified elements of the natural world (feathers, shells, bone, teeth, etc.) (42). Whether used in isolation or integrated into complex arrangements, ornaments made of slightly modified natural objects often represent, by the direct link they establish between the natural world and the meaning attributed to them, quintessential symbolic items. A peculiarity of these objects is that when available only in distant regions, their acquisition depends on organized exchange networks, and value is ascribed to their possession. Such networks are instrumental in the trade of other items, as well as genetic and cultural exchange. It is striking in this respect: three of the Moroccan sites yielding Na beads are located 40–60 km inland; the only site reported in Algeria, Oued Djebbana, is 190 km from the sea; the number of recovered beads is often relatively small; and at Taforalt unperforated shells are also documented. This pattern is precisely what one would expect if the presence of Na at inland sites was the archaeological signature of networks linking coastal areas and inland regions. A supplementary reason for discounting the lack of manufacture argument is based on the observations presented here that suggest that MP shell beads were deliberately perforated. The anthropogenic origin of the perforations on MP shells has so far been inferred from the rarity in natural assemblages of the perforation types recorded on the archaeological shells and the results of experimental piercing of the shell (5) that produced, with some techniques, perforations comparable in location, size, shape, and position of microchipping to those observed on archeological specimens. The marks recorded on two Na from Taforalt confirm what was previously suggested based on the inner position of the microchipping, that is, that the perforations on these Na were made by vigorously punching the body whorl with a robust lithic point.

Analysis of the amount, spatial distribution and degree of alteration by heating of other categories of burnt items found in the same layers (lithics, bone, and land snails) is necessary to verify the hypothesis that Na were intentionally heated to change their color. Identification of use-wear posterior to heating indicates that intentional heating is a viable hypothesis that requires further investigation.

The presence of pigment residues on many well-preserved shell beads from MP sites links bead and pigment use, further reinforcing the argument for their interconnected symbolic value (5). Intensely developed use-wear suggests beads were used for a long period although the length of use and the way they were strung remain to be determined.

Despite uncertainties associated with TL, OSL, and U/Th dating, a clear consistency appears when considering the ages and cultural attribution of MP Moroccan sites that have yielded perforated shell beads. According to available data, in every instance in which Na shells have been recovered in stratigraphic context, they are associated with Aterian lithic artifacts and were used as beads 82–85 ka ago at Taforalt, 82 ka ago at Ifrí n’Ammar (32), and 80–70 ka ago at Rhafas. The specimen from Contrebandiers is of unknown age but given its morphology and size is most likely of Pleistocene age and possibly contemporaneous with the three better dated sites. A further element suggesting a certain degree of contemporaneity is the presence of bifacial foliates and tanged tools in the layers yielding Na beads at Taforalt, Ifrí n’Ammar, and Rhafas. At Ifrí n’Ammar, no perforated shells were recovered either in the Mousserian layer underlying the Aterian layer with shell beads or in the Aterian layer beneath the Mousterian. This pattern may indicate, if we fix the beginning of the Aterian at approximately 110 ka (43), that shell bead use may have arisen or spread during the later part of MIS 5, after the Aterian had become established in NW Africa. The dating of Skhul Layer B with perforated Na to approximately 135–100 ka and those of Qafzeh with perforated Glycymeris to 90–100 ka may indicate a temporal gap between the Near East and the Moroccan early shell beads. The same applies when one compares the Moroccan ages with those of the bead layers from Blombos (~75 ka) and Sibudu (~70 ka). It is probably too soon, based on these ages, to conclude that there are three different and independent origins of beadworking. Rather the use of the same genus, Na, supports an opposing hypothesis that we are observing an interrelated, if not peri-contemporaneous, phenomenon across a broad region and covering a substantial time span. Although the duration of shell bead use in North Africa is difficult to evaluate, results presented here reveal that Na beads were lost or discarded.
at Taforalt throughout most of the deposition of Group E. Considering the stratigraphic consistency of the ages obtained within a number of dating methods, Group E may represent a time span that covers thousands of years. The identification of similar beads at a number of sites also argues for a relatively long duration. One would expect that if bead use was spatially or temporally limited then the chances of detecting it archaeologically would be significantly diminished. Its identification at a number of sites and over a large area supports the hypothesis that it had an extended duration.

An equally important question concerns the end of this phenomenon. Evidence presented here strengthens the view that such ornaments become obsolete after 70 ka in Africa and the Near East. This observation and the different appearance of ornaments used after 40 ka in Eurasia, Africa, and Australia support the view that major discontinuities in cultural transmission of innovations occurred 70 ka ago. Other cultural innovations arose during the last interglacial such as the production of formal bone tools (44), abstract engravings (16, 45), bifacial shaping of projectile points (45), and all disappear from the archaeological record before reappearing in different forms between 10 ka and 30 ka later (45). The long and intense climatic deterioration that occurred in both hemispheres during MIS 4 (46), between 73 and 60 ka, has been proposed by a number of authors as a good candidate to explain the rise and fall of these innovations (14, 23–25). In particular, by applying computer simulation Shennan (14) has shown that patterns of innovation during the last climatic cycle are accounted for by expected population size and contact range variation. In such a context, marine shell beads may have been instrumental in creating and maintaining exchange networks between coastal and inland areas during a period of demographic growth toward the end of MIS 5. The arrival of harsher conditions at the onset of MIS 4 and its negative impact on population size may have disrupted these networks through the depopulation of some areas, thereby isolating hunter-gatherer populations to the extent that social and exchange networks became untenable. Following this scenario, the reemergence after 60 ka of cultural innovations and the spread out of Africa of AMH reflect a new phase of population growth probably associated to previously unseen innovations allowing a more effective exploitation of a variety of environments.

In conclusion, the evidence presented here demonstrates a widespread use of beads, during the second half of the last interglacial, that disappeared soon after its termination. Such a use represents one of the most fascinating cultural experiments in human history that must be explored further, and the broad implications of which may shed light on the mechanisms of cultural transmission associated with early Homo sapiens populations.

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