A systematic review of animal predation creating pierced shells: implications for the archaeological record of the Old World

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ABSTRACT

Background. The shells of molluscs survive well in many sedimentary contexts and yield information about the diet of prehistoric humans. They also yield evidence of symbolic behaviours through their use as beads for body adornments. Researchers often analyse the location of perforations in shells to make judgements about their use as symbolic objects (e.g., beads), the assumption being that holes attributable to deliberate human behaviour are more likely to exhibit low variability in their anatomical locations, while holes attributable to natural processes yield more random perforations. However, there are non-anthropogenic factors that can cause perforations in shells and these may not be random. The aim of the study is compare the variation in holes in shells from archaeological sites from the Old World with the variation of holes in shells pierced by mollusc predators.

Methods. Three hundred and sixteen scientific papers were retrieved from online databases by using keywords, (e.g., ‘shell beads’; ‘pierced shells’; ‘drilling predators’); 79 of these publications enabled us to conduct a systematic review to qualitatively assess the location of the holes in the shells described in the published articles. In turn, 54 publications were used to assess the location of the holes in the shells made by non-human predators.

Results. Almost all archaeological sites described shells with holes in a variety of anatomical locations. High variation of hole-placement was found within the same species from the same site, as well as among sites. These results contrast with research on predatory molluscs, which tend to be more specific in where they attacked their prey. Gastropod and bivalve predators choose similar hole locations to humans.

Discussion. Based on figures in the analysed articles, variation in hole-location on pierced shells from archaeological sites was similar to variation in the placement of holes created by non-human animals. Importantly, we found that some predators choose similar hole locations to humans. We discuss these findings and identify factors researchers might want to consider when interpreting shells recovered from archaeological contexts.
INTRODUCTION

The adornments of prehistoric people play an important role in our understanding of the evolution of human behaviour (Bednarik, 2001; Szabo, Brumm & Bellwood, 2007; Gutiérrez-Zugasti & Cuenca-Solana, 2013) because they can indicate evolutionary changes in the ethno-linguistic diversity of early humans (Vanhaeren & D'Errico, 2006; Schick & Toth, 2013; Stiner, 2014). These findings help anthropologists to construct a picture of the life of prehistoric human groups, and can give insights into their social status (Bednarik, 1998; Stiner, 1999; Vanhaeren & D'Errico, 2005), group membership, age or marital status (Kuhn et al., 2001). Molluscs are among the most robust material remains. Shells fashioned into personal adornments survive well in most sedimentary contexts (Bar-Yosef-Mayer & Beyin, 2009; Lombardo et al., 2013) and can be interpreted in various ways, depending on the context of the find. Usually the deposits are associated with graves (Vanhaeren et al., 2004; Vanhaeren & D'Errico, 2005), human shelters (Kuhn et al., 2001) and hearths (Douka et al., 2014). Some of the earliest forms of body adornment are shell beads that date back to ~75 Kya (Henshilwood et al., 2004) and ~82 Kya (Bouzouggar et al., 2007), possibly even 100–130 Kya (Vanhaeren et al., 2006) or earlier (Bednarik, 2015). However, some researchers argue that this “modern behaviour” was probably established earlier than is reflected in the archaeological record, and is simply not visible due to taphonomic processes (Bowdler & Mellars, 1990; Noble & Davidson, 1996; Botha, 2008; Botha, 2010).

Teasing apart pre-depositional effects in mollusc remains, however, can be made more difficult because predators can produce modifications which are similar to those produced by humans through their ability to make holes in shells.

Researchers use detailed analyses of adornments, radiometric dates and stratigraphic information to explain innovations in shell beads and the spread of cultural traditions (Kuhn et al., 2001). The location of piercings in shells can provide information on the placement of the shell bead within the finished adornment (e.g., a necklace; Baysal, 2013; Stiner, Kuhn & Güleç, 2013). Indications of human manipulation can also be detected, such as striations indicating rotary drilling by a tool (Zilhão et al., 2010), notches close to the perforation that might indicate the presence of a suspension system (e.g., cord) and the direction the traction was exerted (Cristiani, 2012). Researchers also use experiments to understand shell anatomy (e.g., mineralogy and structure) and the processes involved in the production of piercings (e.g., Beyin, 2010; Nigra & Arnold, 2013; Tátá et al., 2014; Joordens et al., 2015). Microscopy can provide evidence of the shape of the tools used for piercing shells, as well as other tell-tale signs of human activity (D’Errico et al., 2005; Nigra & Arnold, 2013). For example, piercings are often examined for the presence of residues, such as ochre or polishing by the cord (D’Errico et al., 2005; D’Errico et al., 2009; Stiner, Kuhn & Güleç, 2013). Similarly, microscopic analyses of naturally made holes in molluscs provide insight (e.g., Li, Young & Zhan, 2011; Gorzelak et al., 2013).
Based upon this kind of painstaking evidence-gathering, experts make judgements as to whether perforations in shells from archaeological sites are anthropogenic in origin or formed by natural processes (D’Errico et al., 2005), such as those made by hole-boring predators or parasites (Kowalewski, 2004; Li, Young & Zhan, 2011) or taphonomic processes (e.g., water erosion, crushing, diagenesis; Peacock et al., 2012; Gorzelak et al., 2013). While the location and type of the perforation is only part of a raft of evidence that indicates an operational chain (starting with the collection of the raw material, followed by the manufacture and use, and ending with its discard), some researchers have proposed that the anatomical locations of holes pierced in shells by humans exhibit low variability whereas holes made by non-human animals yield more random perforations (Stiner, 1999; Bouzouggar et al., 2007).

In the Palaeolithic, beads made from molluscs were desirable for body adornments (e.g., necklaces, headdresses), which likely varied due to decorative traditions of prehistoric human groups (Stiner, 2014). Although there is only rare evidence of shell bead arrangements from the Palaeolithic, we might expect beads strung in different arrangements to require differently placed piercings for the shells to hang according to a predetermined design. The evidence indicates that prehistoric people were adept at piercing holes in shells, but also made use of natural perforations when possible (Bar-Yosef Mayer, Vandermeersch & Bar-Yosef, 2009), suggesting that perforation location may also have varied based on opportunistic natural hole placements.

People also appear to have preferred mollusc species with vivid markings and that vary in size and shape (Stiner, 2014). Inter-specific morphological differences in shell size and shape also encompass variations in shell thickness that impacts the ease with which a piercing can be made. All these factors have influenced the attraction of humans to particular species of mollusc and likely contributed to the variability of hole placement in shells, hence, the assumption that humans pierce shells in consistent places, may not be borne out (D’Errico et al., 2005; Kuhn et al., 2009; Stiner, Kuhn & Güleç, 2013).

Furthermore, animal predation on mollusc populations is a widespread phenomenon (Quensen & Woodruff, 1997; Rosin et al., 2011). Such behaviours have been observed for many hole-boring predators, such as naticids, muricids, octopuses, crabs and birds (Grey, Lelievre & Boulding, 2005; Grey, 2005; Rosin et al., 2011; Li, Young & Zhan, 2011). Moreover, predators can be specific in where they attack molluscs because shell strength and location of internal organs can be important in prey selection (Hagadorn & Boyajian, 1997; Dodge & Scheel, 1999; Rosin et al., 2013). For instance, birds usually choose to perforate the part of the gastropod shell near the apex, which is less resistant to crushing than, for example, the labium (Rosin et al., 2013). In contrast, octopuses and predatory snails choose areas close to the bivalve umbo, which tends to be thicker than other areas of the shell, but is near to the heart. This strategy appears to be a compromise between the time taken to pierce the shell and the effectiveness of the injected toxin (Dodge & Scheel, 1999).

Recent evidence also indicates that holes in shells can be made without the action of predators or humans. In a set of shell-rolling experiments that imitate the action of the waves and tides, Gorzelak and co-workers (2013) showed that abrasive action of rolling
shells together can create holes in predictable locations that coincide with the holes of predators. It is therefore possible that abrasion may also imitate human actions.

Considering that pierced shells can not only be produced by humans for making Palaeolithic jewellery, but can also be produced by natural processes, we examined if the range of variability of hole location in shells made by humans is less than the variability in hole location in shells made by non-human animals (Stiner, 1999; Bouzouggar et al., 2007). We discuss these findings with a focus on the actions of mollusc predators, and consider factors researchers might want to consider when interpreting shells recovered from archaeological contexts.

**MATERIALS & METHODS**

The first part of this research assessed the variability of hole placement in shell beads made by humans. For this purpose we reviewed information within 316 publications including articles, PhD theses and chapters in books about malacological findings in archaeological contexts (Supplemental Information 3). Most of the gathered literature was written in English, with only a few papers published in other language (e.g., French or Spanish). We searched for these using Google Scholar and SCOPUS, and using keywords such as: shell beads, pierced shells, beads, shells, mollusc, Gastropoda, bivalves, pendant, shell midden, ornaments, shell ornaments, predators. Once the publications were selected, their references (backward search) and citation records (forward search) were analysed to find other articles that could provide relevant data (Table 1). Gathered literature was published between the 1966 and the first quarter of 2015. From these articles we selected papers which contained figures and information about the perforated shells. Related articles, which included the same figures of shells, were rejected. This approach ensured that site data was only assessed once (i.e., data were not replicated). We were able to select 79 papers from 316 gathered scientific articles.

Information from all 79 papers was assessed for the following information: (1) mollusc species from which the shell beads were made; (2) name and country of the archaeological site where the perforated shells were found; (3) period from which the shell beads came; (4) hole location in the shell beads (Table 1). We made the assumption that analyses performed by experts correctly interpreted holes in shells as human made (i.e., the pierced shells were not predator-made intrusions).

Next, we created a classification of hole location in shell beads which helped us analyse gathered data from the literature (Fig. 1). As an example of shell shape we used species from genus *Nassarius*, *Patella*, *Pecten* and *Antalis* which are relatively common in the archaeological findings. Then, we assessed hole location in shells found in the archaeological literature (i.e., holes made by humans), based on the figures in each article. Our estimation was based on the figures within the publications, thus the analysis is not quantitative, but qualitative.

In the second part of the research we analysed variation of hole location in shells made by non-human animals. Thus, we searched for information on hole-making predators for each mollusc species recovered from each archaeological site with putative shell beads.
| Mollusc species (Class) | Country       | Site (N)                  | Date                     | References                                                                 | HT (n) |
|-------------------------|---------------|---------------------------|--------------------------|-----------------------------------------------------------------------------|--------|
| Acanthocardia tuberculata (Bivalvia) | Cyprus        | Shillourokambus (1)       | 9.000–8.000 BP           | Serrand, Vigne & Guilaine (2005)                                           | 9 (1)  |
|                         | France        | Balauzerie (1)            | 40.000–28.000 BP         | Barge (1983)                                                               | 9 (1)  |
|                         |               | Régismont (1)             | 40.000–28.000 BP         | Fiocchi (1998)                                                             | 9 (1)  |
|                         |               | Tournal (1)               | 40.000–28.000 BP         | Fiocchi (1998)                                                             | 9 (1)  |
|                         | Italy         | Fanciulli (1)             | 40.000–28.000 BP         | Barge (1983)                                                               | 9 (1)  |
|                         |               | Riparo Mochi (1)          | 34.870–32.280 BP         | Barge (1983)                                                               | 9 (1)  |
|                         | Spain         | Cueva de los Aviones (1)  | 50.000 BP                | Zilhão et al. (2010), Vanhaeren & D’Errico (2011)                         | 9 (1)  |
|                         |               |                           |                          |                                                                            |        |
|                         |               | Cova de l’Or (4)          | 6.720–6.265 BP           | Zilhão et al. (2010)                                                      | 9 (4)  |
|                         |               | Cova del Parpallo (2)     | 50.000–10.000 BP         | Zilhão et al. (2010)                                                      | 9 (1), 10 (1) |
|                         | Turkey        | Üçağızli (1)              | 41.000–39.000 BC         | Stiner, Kuhn & Güleç (2013)                                               | 10 (1) |
| Antalis sp. (Scaphopoda) | Italy         | Fumane (1)                | 41.000–38.000 BP         | Bertola et al. (2013)                                                     | 5 (1)  |
|                         | Portugal      | Vale Boi (4)              | 20.570–18.859 BP         | Tátá et al. (2014)                                                        | 5 (4)  |
|                         | Spain         | El Cuco (30)              | 29.000–22.000 ka         | Gutiérrez-Zugasti & Cuenca-Solana (2013)                                   | 5 (30) |
|                         |               | Guilanya (5)              | 14.160–9.500 BP          | Martinez-Moreno, Mora & Casanova (2010)                                    | 5 (5)  |
|                         |               | Tito Bustillo (1)         | 18.000–10.000 ka         | Avezuela (2014)                                                            | 5 (1)  |
| Bolinus brandaris      (Gastropoda) | Cyprus        | Shillourokambus (1)       | 9.000–8.000 BP           | Serrand, Vigne & Guilaine (2005)                                           | 4 (1)  |
| Buccinum undatum       (Gastropoda) | Italy         | Riparo Tagliente (1)      | 14.600–11.500 BC         | Fontana et al. (2009)                                                     | 4 (1)  |
| Cerastoderma sp.       (Bivalvia)  | Spain         | Cova del Parpallo (8)     | 50.000–10.000 BP         | Zilhão et al. (2010)                                                      | 9 (4), 10 (4) |
| Cerithium sp. (Gastropoda) | Italy         | Riparo Mochi (1)          | 34.870–32.280 BP         | Kuhn & Stiner (1998)                                                      | 7 (1)  |
|                         |               | Riparo Tagliente (1)      | 14.600–11.5000 BC        | Fontana et al. (2009)                                                     | 6 (1)  |
|                         | Jordan        | Wadi Mataha (1)           | 15.579–11.042 BP         | Jantetski & Bar-Yosef (2005)                                              | 2 (1)  |
| Chlamys sp. (Bivalvia) | Italy         | Riparo Mochi (1)          | 34.870–32.280 BP         | Kuhn & Stiner (1998)                                                      | 10 (1) |
| Clanculus corallines   (Gastropoda) | Greece        | Klisoura (1)              | 41.000–38.000 BP         | Stiner (2010)                                                              | 6 (1)  |
|                         | Italy         | Cala (1)                  | 40.000–28.000 BP         | Fiocchi (1998)                                                            | 4 (1)  |
|                         |               | Riparo Mochi (3)          | 34.870–32.280 BP         | Kuhn & Stiner (1998)                                                      | 4 (3)  |
| Columbella sp. (Gastropoda) | Austria      | Krems-Hundsteig (10)      | 40.000–28.000 BP         | Fiocchi (1998), Wild et al. (2008)                                        | 2 (5), 3 (5) |
|                         | Croatia       | Zala cave (N10)           | 11.070–10.500 BP         | Komio & Vukosavljević (2011)                                              | 3 (4), 4 (5), 7 (1) |
|                         | Cyprus        | Shillourokambus (3)       | 9.000–8.000 BP           | Serrand, Vigne & Guilaine (2005)                                          | 4 (3)  |
|                         | Greece        | Klisoura (1)              | 41.000–38.000 BP         | Stiner (2010)                                                              | 4 (1)  |

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| Mollusc species (Class) | Country | Site (N) | Date       | References                          | HT (n) |
|-------------------------|---------|----------|------------|-------------------------------------|--------|
| Conus sp. (Gastropoda)  | Australia | Mandu Mandu Creek rock-shelter (1) | 35.200–30.900 BP | Morse (1993), Balme & Morse (2006) | 8 (1)  |
|                         | Cyprus   | Shillourokambus (2) | 9.000–8.000 BP | Serrand, Vigne & Guilaine (2005) | 8 (2)  |
| Conus sp. (Gastropoda)  | Italy    | Cala (1) | 40.000–28.000 BP | Fiocchi (1998) | 4 (1)  |
| Conus sp. (Gastropoda)  | Italy    | Riparo Mochi (1) | 34.870–32.280 BP | Kuhn & Stiner (1998), Stiner (1999) | 2 (1)  |
| Conus sp. (Gastropoda)  | Oman     | Sumhuram (1) | 4.000–1.000 BP | Wilkens (2005) | 8 (1)  |
| Conus sp. (Gastropoda)  | Turkey   | Uçagızlı (1) | 41.000–39.000 BC | Kuhn, Kuhn & Güleç (2013) | 8 (1)  |
| Cyclope sp. (Gastropoda)| France   | Abri Peyrony (13) | 40.000–28.000 BP | Vanhaeren & D’Errico (2011) | 1 (1), 3 (6), 4 (1), 11 (3) |
| Cyclope sp. (Gastropoda)| Germany  | Andernach-Martinsberg (4) | 13.200–12.820 BP | Zilhão (2007), Langley & Street (2013) | 1 (1), 2 (3) |
| Cyclope sp. (Gastropoda)| Greece   | Klisoura (1) | 41.000–38.000 BP | Stiner (2010) | 6 (1)  |
| Cyclope sp. (Gastropoda)| Italy     | Fumane (1) | 41.000–38.000 BP | Bertola et al. (2013) | 4 (1)  |
| Cyclope sp. (Gastropoda)| Spain     | Riparo Tagliente (2) | 9.000–7.000 BP | Cristiani (2012) | 1 (1)  |
| Cyclope sp. (Gastropoda)| Spain     | Riparo Mochi (25) | 34.870–32.280 BP | Kuhn & Stiner (1998), Stiner (1999) | 1 (25) |
| Cypraea sp. (Gastropoda)| Cyprus    | Shillourokambus (1) | 9.000–8.000 BP | Serrand, Vigne & Guilaine (2005) | 6 (1)  |
| Cypraea sp. (Gastropoda)| India     | Deccan region (3) | 2.300–900 BC | Deshpande-Mukherjee (2005) | 5 (3)  |
| Dentalium sp. (Scaphopoda) | Austria | Krems-Hundsteig (1) | 40.000–28.000 BP | Fiocchi (1998), Neugebauer-Maresch (1999) | 5 (1)  |
| Dentalium sp. (Scaphopoda) | Austria | Langmannersdorf (5) | 40.000–28.000 BP | Hahn (1972) | 5 (5)  |
| Dentalium sp. (Scaphopoda) | Austria | Senftenberg (1) | 40.000–28.000 BP | Hahn (1972) | 5 (1)  |

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| Mollusc species (Class) | Country | Site (N) | Date | References | HT (n) |
|------------------------|---------|----------|------|------------|-------|
| **Cyprus**             |         |          |      |            |       |
| Willendorf (1)         |         |          | 28.000–22.000 BP | Kozlowski (1996) | 5 (1) |
| Shillourokambus (2)    |         |          | 9.000–8.000 BP | Serrand, Vigne & Guilaine (2005) | 5 (2) |
| **France**             |         |          |      |            |       |
| Abri Peyrony (600)     |         |          | 40.000–28.000 BP | Vanhaeren & D’Errico (2011) | 5 (600) |
| Blanchard (2)          |         |          | 34.000–32.000 BP | Taborin (1993) | 5 (2) |
| Caminade Est (1)       |         |          | 37.200–32.140 BP | Taborin (1993) | 5 (1) |
| Castanet (1)           |         |          | 34.000–32.000 BP | Taborin (1993) | 5 (1) |
| Cellier (1)            |         |          | 40.000–28.000 BP | Taborin (1993) | 5 (1) |
| Lauzoua (1)            |         |          | 40.000–28.000 BP | Fiocchi (1998) | 5 (1) |
| Pecheurs (1)           |         |          | 28.000–22.000 BP | Barge (1983) | 5 (1) |
| Rochette (1)           |         |          | 40.000–28.000 BP | Movius (1995) | 5 (1) |
| Rothschild (2)         |         |          | 40.000–28.000 BP | Zilhão (2011) | 5 (2) |
| **Greece**             |         |          |      |            |       |
| **Italy**              |         |          |      |            |       |
| Saint-Germain-la-Rivière (1) |         |          | 15.570 BP | Vanhaeren & D’Errico (2005) | 5 (1) |
| Salpetriere (1)        |         |          | 22.000–18.000 BP | Barge (1983) | 5 (1) |
| Tournal (1)            |         |          | 40.000–28.000 BP | Fiocchi (1998) | 5 (1) |
| Tuto de Camalhot (1)   |         |          | 40.000–28.000 BP | Taborin (1993) | 5 (1) |
| Vachons (1)            |         |          | 40.000–28.000 BP | Taborin (1993) | 5 (1) |
| Klisoura (1)           |         |          | 41.000–38.000 BP | Stiner (2010) | 5 (1) |
| Cala (1)               |         |          | 40.000–28.000 BP | Fiocchi (1998) | 5 (1) |
| Grotta del Cavallo (1) |         |          | 31.000–21.000 BP | Cesnola & Mallegr (1996) | 5 (1) |
| Grotta di Pozzo (4)    |         |          | 85.000–60.000 BP | Mussi et al. (2000) | 5 (4) |
| Fanciulli (1)          |         |          | 40.000–28.000 BP | Barge (1983) | 5 (1) |
| Fumane (1)             |         |          | 41.000–38.000 BP | Fiocchi (1998) | 5 (1) |
| Riparo Mochi (3)       |         |          | 34.870–32.280 BP | Kuhn & Stiner (1998) | 5 (3) |
| Riparo Tagliente (1)   |         |          | 14.600–11.5000 BC | Fontana et al. (2009) | 5 (1) |
| **Jordan**             |         |          |      |            |       |
| Wadi Mataha (6)        |         |          | 15.579–11.042 BP | Janetksi & Bar-Yosef (2005) | 5 (6) |
| **Near East Spain**    |         |          |      |            |       |
| Ksar Akil (1)          |         |          | 41.000–39.000 BP | Douka (2013) | 5 (1) |
| Beneito (1)            |         |          | 40.000–28.000 BP | Soler-Major (2001) | 5 (1) |
| Cingle Vermell (1)     |         |          | 9.760 BP | Oliva & Yll (2010) | 5 (1) |
| Cova del Parco (2)     |         |          | 13.175–12.460 BP | Estrada et al. (2010), Mangado et al. (2010) | 5 (2) |
| **Turkey**             |         |          |      |            |       |
| Cova del Reclau Viver (53) |         |          | 39.000–29.000 BP | Avezuela Arisú & Álvarez-Fernández (2012) | 5 (53) |
| Nerja Cave (2)         |         |          | 25.000–21.000 BP | Jordà Pardo et al. (2010) | 5 (2) |
| Roc del Migdia (4)     |         |          | 8.800–8.190 BP | Oliva & Yll (2010) | 5 (4) |
| Çatalhöyük (5)         |         |          | 7.200–6.000 BP | Bar-Yosef Mayer, Gümüs & Isamoğlu (2010) | 5 (5) |
| Pınarbaşı (2)          |         |          | 8.5000–8.000 BC | Baysal (2013) | 5 (2) |
| Boncuklu Höyük (3)     |         |          | 9.000–8.000 BC | Baysal (2013) | 5 (3) |

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Table 1 (continued)

| Mollusc species (Class) | Country | Site (N) | Date                  | References                                      | HT (n) |
|-------------------------|---------|----------|-----------------------|-------------------------------------------------|--------|
| *Engina mendicaria*     | Eritrea | Red Sea Coast (3) | 7.330–5.385 BP     | Bar-Yosef-Mayer & Beyin (2009)                  | 4 (3)  |
| *Euthria cornea*        | Turkey  | Üçâğızlı (1) | 41.000–39.000 BC     | Stiner, Kuhn & Güleç (2013)                    | 4 (1)  |
| *Gibbula* sp. (Gastropoda) | Italy  | Fumane (2) | 41.000–38.000 BP     | Bertola et al. (2013)                           | 4 (2)  |
|                         |         | Üçâğızlı (1) | 41.000–39.000 BC     | Stiner, Kuhn & Güleç (2013)                    | 4 (1)  |
| *Glycymeris* sp. (Bivalvia) | Cyprus | Shillourokambus (1) | 9.000–8.000 BP | Serrand, Vigne & Guilaine (2005)                | 9 (1)  |
|                         | France  | Figuiier (1) | 40.000–28.000 BP     | Taborin (1993)                                 | 9 (1)  |
|                         | Israel  | Qafzeh cave (1) | 90.000 y BP     | Taborin (1993)                                 | 9 (1)  |
|                         | Italy   | Fumane (6) | 41.000–38.000 BP     | Vanhaeren & D’Errico (2011), Bertola et al. (2013) | 9 (6)  |
| *Homalopoma sanguineum* | Germany | Andernach-Martinsberg (54) | 13.200–12.820 BP | Álvarez-Fernández (2009), Langley & Street (2013) | 1 (1), 3 (1), 4 (21), 8 (8) |
| *Lithoglyphus* sp. (Gastropoda) | Greece | Klisoura (1) | 41.000–38.000 BP     | Stiner (2010)                                   | 6 (1)  |
|                         | Italy   | Fumane (1) | 41.000–38.000 BP     | Bertola et al. (2013)                           | 4 (1)  |
|                         | Spain   | Cova del Parco (7) | 50.000–10.000 BP | Mangado et al. (2010)                          | 11 (1) |
|                         |         | Cueva de los Aviones (2) | 50.000 BP | Álvarez Fernández (2006)                       | 4 (1), 8 (1) |
| *Littorina obtusata*    | Croatia | Pupiçina Cave (1) | 11.070–10.500 BP | Komšo & Vukosavljević (2011)                   | 6 (1)  |
|                         |         | Zala cave (20) | 11.070–10.500 BP     | Komšo & Vukosavljević (2011)                   | 1 (9), 4 (11) |
|                         | Italy   | Riparo Biarzo (7) | 12.000–7.000 BP     | Cristiani (2012)                                | 3 (3), 7 (4) |
| *Littorina littorea*     | France  | Gargas Cave (1) | 26.910–23.590 BP     | Juan-Foucher & Foucher (2008)                  | 1 (1)  |
|                         | Spain   | Hautes-Pyrénées (3) | 21.000–10.000 BP | Cattelain (2012)                               | 1 (1), 2 (1), 4 (1) |
|                         |         | El Cuco (1) | 29.000–22.000 ka     | Gutiérrez-Zugasti & Cuenca-Solana (2013)       | 2 (1)  |
|                         |         | Tito Bustillo (1) | 18.000–10.000 ka | Álvarez Fernández (2006)                       | 4 (1)  |
|                         | Spain   | Hautes-Pyrénées (97) | 10.000–6.000 BP     | Cattelain (2012)                               | 1 (1), 2 (10), 4 (11) |
|                         |         | Rothschild (1) | 40.000–28.000 BP     | Zilhão (2011)                                  | 1 (1)  |
|                         |         | Cueto de La Mina (1) | 50.000–10.000 BP | Cáceres, Marcos & Díez (2008)                  | 4 (1)  |
|                         |         | El Cuco (2) | 29.000–22.000 ka     | Gutiérrez-Zugasti & Cuenca-Solana (2013)       | 2 (1), 3 (1) |

(continued on next page)
| Mollusc species (Class) | Country          | Site (N) | Date               | References                                      | HT (n) |
|-------------------------|------------------|----------|--------------------|-------------------------------------------------|--------|
| *Littorina* sp. (Gastropoda) | Italy            | Fumane (1) | 41.000–38.000 BP   | Bertola et al. (2013)                           | 4 (1)  |
|                         |                  | Riparo Mochi (1) | 34.870–32.280 BP   | Stiner (2010)                                   | 8 (1)  |
|                         | France           | Saint-Jean-De-Verges (6) | 40.000–28.000 BP   | Vezian & Vezian (1966)                          | 1 (2), 4 (2) |
| Portugal                | Vale Boi (9)     | 20.570–18.859 BP | 70.000–60.000 BP   | Táta et al. (2014)                              | 1 (2), 4 (7), 8 (3) |
| South Africa            | Sibudu Cave Middle Stone (3) | 14.600–11.5000 BC | 35.000 BP              | Vanhaeren & D’Errico, Vanhaeren & Wadley (2008) | 1 (2), 4 (1) |
| *Melanopsis* sp. (Gastropoda) | Turkey          | Üçâğızlı (1) | 41.000–39.000 BC   | Stiner, Kuhn & Güleç (2013)                     | 3 (1)  |
| *Mitra corniculata* (Gastropoda) | Italy           | Riparo Mochi (1) | 34.870–32.280 BP   | Kuhn & Stiner (1998)                            | 4 (1)  |
| *Monodonta* sp. (Gastropoda) | Greece           | Klisoura (1) | 41.000–38.000 BP   | Stiner (2010)                                   | 4 (1)  |
| *Nassarius* circumcintus (Gastropoda) | Spain           | Moroccan cave (1) | 83.000–60.000 BP   | D’Errico et al. (2009)                         | 4 (1)  |
|                         | Italy            | Fumane (1) | 41.000–38.000 BP   | Bertola et al. (2013)                            | 4 (1)  |
|                         |                   | Riparo Tagliente (1) | 14.600–11.5000 BC   | Fontana et al. (2009)                           | 4 (1)  |
| *Nassarius* gibbosulus (Gastropoda) | Algeria         | Oued Djebbanna (1) | 35.000 BP             | Vanhaeren & D’Errico (2006), Douka (2013)       | 2 (1)  |
|                         | Cyprus           | Shillourokambus (6) | 9.000–8.000 BP      | Serrand, Vigne & Guilaine (2005)                | 6 (6)  |
|                         | France           | Blanchard (1) | 34.000–32.000 BP   | Taborin (1993)                                  | 4 (1)  |
|                         | Rothschild (1)   | 40.000–28.000 BP   | Zilhão (2011)                                 | 4 (1), 11 (1) |
|                         | Israel           | Skhul (2) | 110.000 BP            | Vanhaeren & D’Errico (2006)                  | 1 (1), 2 (1) |
|                         | Italy            | Fumane (1) | 41.000–38.000 BP   | Vanhaeren & D’Errico (2011)                    | 3 (1)  |
| Morocco                 | Riparo Mochi (1) | 40.000–28.000 BP   | Kuhn & Stiner (1998), Stiner (1999)              | 4 (1)  |
|                         | Grotte des Contrebandiers (1) | 40.000–12.500 BP   | Vanhaeren & D’Errico (2011)                   | 4 (1)  |
|                         | Grotte des Pigeons, Taforalt (13) | 83.000–81.000 BP | 1 (1), 2 (5), 3 (1), 4 (4), 6 (1), 11 (1) | Vanhaeren & D’Errico (2011), Elias (2012), Douka (2013) |
| Near East               | Ksar Akil (2)    | 41.000–39.000 BP   | 1 (1), 4 (1)                  | Douka et al. (2012), Douka (2013)              | 4 (1)  |
|                         | Sefunim (1)      | 41.000–15.000 BP   | Bar-Yosef (1996b)                | 1 (1), 4 (1)                  | 4 (1)  |
| Spain                   | Moroccan cave (17) | 83.000–60.000 BP   | D’Errico et al. (2009)              | 2 (4), 3 (3), 4 (8), 11 (2) | (continued on next page) |
| Mollusc species (Class) | Country | Site (N) | Date               | References                                                                 | HT (n) |
|------------------------|---------|----------|--------------------|---------------------------------------------------------------------------|--------|
|                        | Turkey  | Üçagızlı (11) | 41.000–39.000 BC | *Kuhn et al. (2001)*, *Stiner, Kuhn & Güleç (2013)*                      | 1 (1), 2 (1), 3 (2), 4 (6), 7 (2), 8 (1) |
| Nasarius incrassatus   | Italy   | Fumane (2)  | 41.000–38.000 BP  | *Vanhaeren & D’Errico (2011)*, *Bertola et al. (2013)*                   | 2 (2)  |
| (Gastropoda)           | Spain   | Riparo Mochi (1) | 34.870–32.280 BP | *Kuhn & Stiner (1998)*                                                   | 4 (1)  |
|                        |         | Riparo Tagliente (1) | 14.600–11.500 BC | *Fontana et al. (2009)*                                                  | 4 (1)  |
|                        |         | Cingle Vermell (1) | 9.760 BP          | *Oliva & Yll (2010)*                                                    | 1 (1)  |
|                        |         | El Horno (1)  | 12.862–12.481 BP  | *Fano & Alvarez-Fernández (2010)*                                       | 3 (1)  |
|                        |         | Roc del Migdia (7) | 8.800–8.190 BP   | *Oliva & Yll (2010)*                                                    | 4 (7)  |
| Nasarius kraussianus   | South Africa | Blombos Cave (2) | 78.000–75.600 BP | *D’Errico et al. (2005)*, *Douka (2013)*, *Vanhaeren et al. (2013)* | 1 (1), 3 (1) |
| (Gastropoda)           |         | Border Cave (2) | 44.000–22.000 BP  | *D’Errico et al. (2012)*                                                | 3 (1), 4 (1), 11 (2) |
| Nasarius mutabilis     | France  | Rothschild (1) | 40.000–28.000 BP  | *Zilhão (2011)*                                                          | 4 (1)  |
| (Gastropoda)           | Italy   | Fumane (2)  | 41.000–38.000 BP  | *Vanhaeren & D’Errico (2011)*, *Bertola et al. (2013)*                   | 2 (1), 4 (1) |
| Spain                  | Tito Bustillo (1) | 18.000–10.000 ka | *Álvarez Fernández (2006)* |                                                                 | 1 (1)   |
| Nasarius reticulates   | Turkey  | Üçagızlı (11) | 41.000–39.000 BC | *Stiner, Kuhn & Güleç (2013)*                                            | 3 (9), 11 (5) |
| (Gastropoda)           | Italy   | Fumane (1)  | 41.000–38.000 BP  | *Bertola et al. (2013)*                                                 | 3 (1)  |
| France                 | Rothschild (1) | 40.000–28.000 BP | *Zilhão (2011)* |                                                                 | 3 (1)   |
| Russia                 | Mezmaiskaya Cave (1) | 36.000–28.510 BP | *Golovanova, Doronichev & Cleghorn (2010)* |                                                                | 2 (1), 11 (1) |
| Spain                  | El Horno (1)  | 12.862–12.481 BP | *Fano & Alvarez-Fernández (2010)* |                                                                 | 3 (1)   |
|                        | Tito Bustillo (1) | 18.000–10.000 ka | *Avezuela (2014)* |                                                                 | 1 (1)   |
| Nasarius sp. (Gastropoda) | Italy  | Fumane (1)  | 41.000–38.000 BP  | *Bertola et al. (2013)*                                                 | 4 (1)  |
|                        | Riparo Mochi (1) | 34.870–32.280 BP | *Kuhn & Stiner (1998)* |                                                                 | 4 (1)   |
|                        | Jordan  | Wadi Mataha (2) | 15.579–11.042 BP | *Janetski & Bar-Yosef (2005)*                                            | 3 (2)  |
| Morocco                | Grotte des Contrebandiers (1) | 40.000–12.500 BP | *D’Errico et al. (2009)* |                                                                 | 4 (1), 11 (1) |
| Spain                  | Cova del Parco (1) | 13.175–12.460 BP | *Mangado et al. (2010)* |                                                                 | 4 (1)   |
| Turkey                 | Boncuklu Höyük (1) | 9.000–8.000 BC | *Baysal (2013)* |                                                                 | 11 (1)  |
|                        | Pınarbaşı (2)  | 8.5000–8.000 BC | *Baysal (2013)* |                                                                 | 4 (2)   |
| Naticea sp. (Gastropoda) | Italy  | Fumane (1)  | 41.000–38.000 BP  | *Vanhaeren & D’Errico (2011)*                                            | 3 (1)  |
|                        | Spain   | Cova del Parco (1) | 13.175–12.460 BP | *Mangado et al. (2010)*                                                 | 3 (1)  |
| Naticarius sp. (Gastropoda) | Turkey | Üçagızlı (2)  | 41.000–39.000 BC | *Stiner, Kuhn & Güleç (2013)*                                            | 1 (2), 8 (1) |

(continued on next page)
### Table 1 (continued)

| Mollusc species (Class) | Country    | Site (N)                  | Date               | References                                      | HT (n) |
|-------------------------|------------|---------------------------|--------------------|-------------------------------------------------|--------|
| *Neritina picta* (Gastropoda) | France     | Hautes-Pyrénées (1)       | 21.000–10.000 BP   | Cattelain (2012)                                | 10 (3) |
|                         |            | Abri Peyrony (99)         | 40.000–28.000 BP   | Vanhaeren & D’Errico (2011)                    | 1 (1)  |
|                         |            | Gargas Cave (1)           | 26.910–23.590 BP   | Juan-Foucher & Fouche (2008)                   | 1 (1)  |
| *Nucella lapillus* (Gastropoda) | France     | Hautes-Pyrénées (2)       | 21.000–10.000 BP   | Cattelain (2012)                                | 1 (1)  |
|                         |            | Gargas Cave (2)           | 26.910–23.590 BP   | Juan-Foucher & Fouche (2008)                   | 1 (2)  |
|                         |            | Rothchild (1)            | 40.000–28.000 BP   | Zilhão (2007)                                  | 4 (1)  |
|                         |            | Saint-Germain-la-Rivière (1) | 15.570 BP         | Vanhaeren & D’Errico (2005)                    | 4 (1)  |
|                         | Greece     | Klisoura (1)              | 41.000–38.000 BP   | Stiner (2010)                                  | 4 (1)  |
|                         | Spain      | La Garma A (1)            | 29.000–22.000 ka   | Avezuela Aristu & Álvarez-Fernández (2012)     | 4 (1)  |
| *Ocinebrina edwardsii* (Gastropoda) | Spain      | Cueto de la Mina (1)      | 18.000–10.000 ka   | Sella (1916)                                   | 2 (1)  |
|                         |            | Riparo Mochi (7)          | 34.870–32.280 BP   | Kuhn & Stiner (1998), Stiner (1999)             | 4 (7)  |
| *Oliva bulbosa* (Gastropoda) | Oman       | Sumhuram (9)              | 4.000–1.000 BP     | Wilkens (2005)                                 | 8 (9)  |
| *Patella vulgata* (Gastropoda) | France     | Hautes-Pyrénées (3)       | 21.000–10.000 BP   | Cattelain (2012)                                | 10 (3) |
|                         | Spain      | La Garma A (1)            | 29.000–22.000 ka   | Avezuela Aristu & Álvarez-Fernández (2012)     | 10 (1) |
|                         |            | Maltravieso cave (1)      | 40.000–10.000 BP   | Rodríguez Hidalgo et al. (2010)                 | 10 (1) |
| *Pecten sp.* (Bivalvia) | France     | Gargas Cave (1)           | 26.910–23.590 BP   | Juan-Foucher & Fouche (2008)                   | 10 (1) |
|                         | Spain      | Rothschild (1)           | 40.000–28.000 BP   | Zilhão (2007)                                  | 1 (1)  |
|                         |            | Cueva Anton (1)           | 38.440–36.810 BP   | Zilhão et al. (2010)                           | 4 (1)  |
|                         |            | Riparo Mochi (1)          | 40.000–28.000 BP   | Stiner (1999)                                  | 4 (1)  |
| *Persicula terveriana* (Gastropoda) | Eritrea    | Red Sea Coast (1)         | 7.330–5.385 BP     | Bar-Yosef-Mayer & Beyin (2009)                  | 4 (1)  |
| *Pirenella plicata* (Gastropoda) | France     | Hautes-Pyrénées (1)       | 21.000–10.000 BP   | Cattelain (2012)                                | 2 (1)  |
| *Theodoxus fluviatilis* (Gastropoda) | France     | Gargas Cave (1)           | 26.910–23.590 BP   | Juan-Foucher & Fouche (2008)                   | 1 (1)  |
|                         | Portugal   | Hautes-Pyrénées (1)       | 21.000–10.000 BP   | Cattelain (2012)                                | 1 (1)  |
|                         | Russia     | Rothschild (1)           | 40.000–28.000 BP   | Zilhão (2007)                                  | 1 (1)  |
|                         | Spain      | Vale Boi (5)              | 20.570–18.859 BP   | Táta et al. (2014)                             | 4 (5)  |
|                         |            | Kostienki 14 (4)          | 36.500–32.600 BP   | Sinitsyn (2003)                                | 2 (2)  |
|                         |            | Cova del Parco (2)        | 13.175–12.460 BP   | Estrada et al. (2010), Mangado et al. (2010)   | 1 (1)  |
|                         |            | Nerja Cave (4)            | 25.000–21.000 BP   | Jordá Pardo et al. (2010)                      | 4 (4)  |
| *Theodoxus sp.* (Gastropoda) | Greece     | Klisoura (3)              | 41.000–38.000 BP   | Stiner (2010)                                  | 6 (3)  |
|                         | Italy      | Riparo Biarzo (2)         | 12.000–7.000 BP    | Cristiani (2012)                               | 1 (1)  |
|                         | Turkey     | Uçağızlı (1)              | 41.000–39.000 BC   | Stiner, Kuhn & Güleç (2013)                    | 4 (1)  |

(continued on next page)
| Mollusc species (Class) | Country  | Site (N)          | Date          | References                                               | HT (n) |
|------------------------|----------|-------------------|---------------|----------------------------------------------------------|--------|
| *Trivia* sp. (Gastropoda) | France   | Gargas Cave (3)   | 26.910–23.590 BP | Juan-Foucher & Foucher (2008)                           | 3 (3), 11 (2) |
|                        |          | Hautes-Pyrénées (2) | 21.000–10.000 BP | Cattelain (2012)                                        | 1 (2)  |
|                        |          | Rothschild (1)    | 40.000–28.000 BP | Zilhão (2011)                                           | 3 (1)  |
|                        |          | Saint-Germain-la-Rivière (3) | 15.570 BP | Vanhaeren & D’Errico (2005)                              | 5 (3)  |
|                        | Italy    | Fumane (1)        | 41.000–38.000 BP | Bertola et al. (2013)                                   | 11 (1) |
|                        |          | Riparo Mochi (1)  | 34.870–32.280 BP | Kuhn & Stiner (1998), Stiner (1999)                     | 3 (1)  |
|                        | Portugal | Vale Boi (4)      | 20.570–18.859 BP | Tánta et al. (2014)                                     | 5 (1), 8 (3) |
|                        | Spain    | Cingle Vermell (2) | 9.760 BP                  | Oliva & Yll (2010)                                      | 5 (2)  |
|                        |          | El Horno (1)      | 12.862–12.481 BP | Fano & Álvarez-Fernández (2010)                         | 5 (1)  |
|                        |          | La Fragua (1)     | 12.960 BP                  | Zugasti (2010.)                                         | 5 (1)  |
|                        |          | La Pena de Estebanvela (4) | 12.000–9.000 BP | Avezuela (2014)                                         | 5 (2)  |
|                        |          | Los Canes (6)     | 7.930–7.580 BP                  | Álvarez-Fernández (2010)                                | 3 (6)  |
|                        |          | Nerja Cave (1)    | 25.000–21.000 BP | Jordà Pardo et al. (2010)                               | 3 (1)  |
|                        |          | Tito Bustillo (1) | 18.000–10.000 ka         | Avezuela (2014)                                         | 5 (1)  |
| *Trophon muricatus* (Gastropoda) | Russia  | Mezmaiskaya Cave (1) | 36.000–28.510 BP | Golovanova, Dornichev & Cleghorn (2010)                     | 11 (1) |
| *Turritella* sp. (Gastropoda) | Italy    | Fumane (1)        | 41.000–38.000 BP | Bertola et al. (2013), Taborin (1993)                     | 2 (1)  |
|                        | France   | Abri Peyrony (25) | 40.000–28.000 BP | Vanhaeren & D’Errico (2011)                              | 2 (6), 3 (19) |
|                        | Spain    | Cova del Reclau Viver (1) | 39.000–29.000 BP | Avezuela Aristu & Álvarez-Fernández (2012)                | 3 (1), 11 (1) |
|                        |          | El Horno (4)      | 18.000–10.000 ka         | Álvarez Fernández (2006)                                | 2 (4)  |

Notes.

* N, the number of mollusc species; n, the number of shells with appropriate hole type; HT, hole type.

(Table 2). For this purpose, we gathered information on the location of holes in the shells made by mollusc predators from 54 scientific articles. To be clear, these articles were not associated with archaeological finds. Next, we assessed hole locations in shells made by hole-boring predators using the same classification that was used for the human-made holes in shell beads (Fig. 1). This part of the research was also based on the figures within the publications. We made the assumption that analyses by experts correctly interpreted holes in shells as naturally made and not made by humans (i.e., the shells were pierced by predators).

Next, we analysed separately the types of hole location in shell beads made by human and non-human animals for normality by using the Shapiro Wilk test, and for homogeneity of variances by using Levene’s test; all were non-significant (P < 0.05). Analysed material did not fulfil the criterion of normality, thus data were log or square root transformed.
and tested again for normality (Sokal & Rohlf, 1981). After these transformations the data were still not normally distributed; we therefore used nonparametric sign test to analyse variation and differences in types of hole location between shells perforated by humans and non-human animals within mollusc species.

In order to analyse the strength of the differences between holes locations made by human and non-human animals we calculated size of the effect using the following equation: $d = (M_1 - M_2)/SD_{pooled}$, where $d$ is the Cohen-d index, $M_1$ is the mean of the first group, $M_2$ is the mean of the second group and $SD_{pooled}$ is the pooled standard deviation.

**Figure 1** Graphical representation of hole location types in shells.
Table 2  Drilling predators for mollusc species used as a shell bead by prehistoric human groups.

| Mollusc species recovered from archaeological sites (Class) | Predators class | Predator | References | HT (n) |
|-----------------------------------------------------------|-----------------|----------|------------|--------|
| Acanthocardia tuberculata (Bivalvia)                      | Gastropoda      | Naticarius hebraeus | Calvet (1992) | 4 (1), 9 (1) |
| Antalis sp. (Scaphopoda)                                  | No data         |          |            |        |
| Bolinus                                                   | Cephalopoda     | Octopus vulgaris    | Nixon & Maconnachie (1988), No data | |
| brandaris (Gastropoda)                                   | Gastropoda      | Naticidae         | Passini & Garassino (2012) | |
| Buccinum undatum (Gastropoda)                            | Gastropoda      | Euspira macilenta | Sawyer (2010) | No data |
| Cerastoderma sp. (Bivalvia)                              | Gastropoda      | Polinices pulchellus Hexaplex trunculus | Kingsley-Smith, Richardson & Seed (2003), Morton, Peharda & Harper (2007) | 1 (1), 4 (1), 10 (1) |
| Cerithium sp. (Gastropoda)                               | Gastropoda      | Euspira macilenta | Turra, Denadai & Leite (2005), Sawyer & Zuschin (2010), Coleman (2010), Gorman, Sikinger & Turra (2015) | 3 (1) |
| Chlamys sp. (Bivalvia)                                   | Asteroidea      | Pycnopodia helianthoides | Guerrero & Reynen (1988), Farren & Donovan (2007), Chattopadhyay & Dutta (2013) | 2 (1), 10 (1) |
| Clanculus corralinus (Gastropoda)                        | No data         |          |            |        |
| Cylindrocallista sp. (Gastropoda)                        | Cephalopoda     | Octopus vulgaris    | Nixon & Maconnachie (1988) | No data |
| Cytheria macilenta                                       | Gastropoda      | Euspira macilenta | Kohn & Arua (1999), Sawyer & Zuschin (2010) | 4 (2), 8 (1), 11 (3) |
| Cypraea sp. (Gastropoda)                                 | Cephalopoda     | Natica carinata Neverita duplicata Oichnus sp. | Yochelson, Dockery & Wolf (1983), Sawyer & Zuschin (2010), Li, Young & Zhan (2011) | 4 (25), 8 (1) |
| Cypraea sp. (Scaphopoda)                                 | Gastropoda      | Euspira macilenta | Nixon & Maconnachie (1988), Nixon & Young (2003) | 4 (2) |
| Dentalium sp. (Scaphopoda)                               | Cephalopoda     | Octopus vulgaris    | Guerra & Nixon (1987), Mowles, | 4 (1) |
| Dentalium sp. (Scaphopoda)                               | Gastropoda      | Euspira macilenta | | |
| | | Euspira obliquata | | |
| | | Natica carinata | | |
| | | Neverita duplicata | | |
| | | Oichnus sp. | | |
| Dentalium sp. (Scaphopoda)                               | Malacostraca    | Cancer pagurus  | Calvet (1992), Ramsay, Richardson & Kaiser (2001), Amano (2006), Sawyer & Zuschin (2010) | 4 (1), 9 (1) |
| (continued on next page)
Table 2 (continued)

| Mollusc species recovered from archaeological sites (Class) | Predators class | Predator | References | HT (n) |
|----------------------------------------------------------|-----------------|----------|------------|-------|
| Hexaplex trunculus (Gastropoda)                           | Cephalopoda     | Octopus vulgaris | McQuaid (1994), Sawyer & Zuschin (2010), Passini & Garassino (2012) | 4 (1), 11 (1) |
| H. trunculus (Gastropoda)                                  | Gastropoda      | Naticidae |            |       |
| Homalopoma sanguineum (Gastropoda)                        | No data         |          |            |       |
| Lithoglyphus sp. (Gastropoda)                              | No data         |          |            |       |
| Littorina littorea (Gastropoda)                            | Asteroidea      | Pisaster straceatus | Pechenk & Lewis (2000), Harley et al. (2013) | 11 (1) |
| Littorina obtusata (Gastropoda)                            | Aves            | Calidris canutus | Alerstam, Gudmundson & Johannesson (1992), Edgell et al. (2008), Edgell & Rochette (2009) | No data |
| L. littorea (Gastropoda)                                   | Malacostraca    | Carcinus maenas |            |       |
| Mellanopsis sp. (Gastropoda)                               | Malacostraca    | Carcinus maenas | Reimchen (1982) | 1 (1), 4 (1) |
| Melanopsis sp. (Gastropoda)                                | Gastropoda      | Gastropoda | Kowalewski, Rosa & Marcheno (2009) | No data |
| Mitella corniculata (Gastropoda)                           | Gastropoda      | Euspira macilenta | Sawyer & Zuschin (2010), Cardoso & Dias Coelho (2012) | 4 (1) |
| Monodonta sp. (Gastropoda)                                 | Aves            | Haematopodidae Laridae | Tongiorgi et al. (1981), Harris (1984) | 4 (1) |
| Nassarius circumcintus                                     | Malacostraca    | Carcinus maenas | Stenzler & Atema (1977), Kohn & Arua (1999), Sawyer & Zuschin (2010) | 8 (1), 11 (1) |
| Nassarius gibbosulus                                      | Gastropoda      | Euspira macilenta Lunatiaheros, Natica tecta |            |       |
| Nassarius incrassatus                                     | Gastropoda      | Euspira macilenta Lunatiaheros, Natica tecta |            |       |
| Nassarius kraussianus                                     | Gastropoda      | Euspira macilenta Lunatiaheros, Natica tecta |            |       |
| Nassarius mutabilis                                       | Gastropoda      | Euspira macilenta Lunatiaheros, Natica tecta |            |       |
| Nassarius reticulates                                     | Gastropoda      | Euspira macilenta Lunatiaheros, Natica tecta |            |       |
| Nassarius sp. (Gastropoda)                                | Gastropoda      | Euspira macilenta Lunatiaheros, Natica tecta |            |       |
| Natica sp. (Gastropoda)                                   | Gastropoda      | Euspira macilenta Naticidae, Muricidae | Arua (1989), Zlotnik (2001), Sawyer (2010), Das, Mondal & Bardhan (2013) | 4 (1), 11 (37) |
| Naticarius sp. (Gastropoda)                               | Asteroidea      | Asterina sarasini | Sawyer (2010) | No data |
| Neritina picta (Gastropoda)                               | Gastropoda      | Acteocina Muricidae | Zagvai & Demeter (2008) | 4 (2), 8 (4), 11 (1) |
| Nerita lapillus (Gastropoda)                              | No data         |          |            |       |
| Ocinebrina edwardsii (Gastropoda)                         | No data         |          |            |       |
| Oliva bulbosa (Gastropoda)                                | Gastropoda      | Naticidae | Kohn & Arua (1999), Passini & Garassino (2012) | 11 (1) |
| Patella vulgaris (Gastropoda)                              | Aves            | Haematus ostrelegus | Coleman et al. (1999), Kohn & Arua (1999), Smith (2003), Silva et al. (2008), Silva et al. (2010), Sawyer (2010) | 10 (1) |
| Patella vulgaris (Gastropoda)                              | Cephalopoda     | Octopus vulgaris |            |       |
| Patella vulgaris (Gastropoda)                              | Gastropoda      | Euspira macilenta |            |       |
| Patella vulgaris (Gastropoda)                              | Malacostraca    | Cancer pagurus, Carcinus maenas, Necora puber, Pachygrapsus marmoratus, |            |       |
Table 2 (continued)

| Mollusc species recovered from archaeological sites (Class) | Predators class | Predator | References | HT (n) |
|-----------------------------------------------------------|-----------------|----------|------------|--------|
| *Pecten* sp. (Bivalvia)                                   | Asteroidea      | *Asteria rubens* | Jonkers (2000), Sawyer (2010), Magnesen & Redmond (2011) | 4 (2), 10 (1) |
|                                                           | Asteroidea      | *Marthasterias glacialis* |                          |        |
|                                                           | Asteroidea      | *Euspira macilenta* |                          |        |
| *Persicula terveriana* (Gastropoda)                      | Cephalopoda     | *Octopus insularis* | Leite, Haimovic & Mather (2009) | No data |
| *Pirenella plicata* (Gastropoda)                         | Gastropoda      | *Naticidae*       | Taraschewski & Paperna (1982) | No data |
| *Theodoxus* sp. (Gastropoda)                             | Malacostraca    | *Macrobrachium* sp. | Arpad (1993), Zagyvai & Demeter (2008) | 4 (2), 8 (4), 11 (1) |
| *Theodoxus* sp. (Gastropoda)                             | Gastropoda      | *Muricidae*       | Sadhukhan & Raghunathan (2013) | No data |
| *Trivia* sp. (Gastropoda)                                | Asteroidea      | *Asterina sarasini* | Gordillo & Archuby (2014) | 11 (1) |
| *Trophon muricatus* (Gastropoda)                         | Gastropoda      | *Naticidae*       | Allmon, Nieh & Norris (1990), Hagadorn & Boyajian (1997), Filipesca & Popa (2001), Sawyer (2010) | 4 (3) |

Notes.

\(n\), the number of shells with appropriate hole type; HT, hole type.

deviation (Cohen, 1988). To interpret \(d\) values we used the following criteria for effect sizes: \(d \geq 0.1\), small; \(d \geq 0.3\), medium; \(d \geq 0.5\), large (Cohen, 1988).

RESULTS

Human made holes in shells

Table 1 shows hole assessment in 49 taxa of Mollusca perforated by humans from archaeological sites. Anthropogenically modified shells come from 21 countries of the Old World, with most archaeological sites located in Spain and France (Table 3). Twenty-seven taxa exhibited more than one type of hole location in their shells, while shells from 22 taxa were classified as having only one type of hole (Fig. 2A). However, 15 taxa from the latter group were recovered at one archaeological site alone.

The number of hole location types was diverse amongst mollusc species (Fig. 2A). Bivalves were more diverse in terms of hole location than Scaphopoda with most species exhibiting more than one type of hole location (Table 3). Gastropoda was the most numerous and diverse class in terms of hole location. *Nassarius gibbosulus* was the most variable species in terms of hole location among all archaeological sites (1, 2, 3, 4, 6, 7, 8 and 11) (Table 1; Fig. 2A). Moreover, shells of *Nassarius gibbosulus* from Üçağızlı (Turkey) and Grotte des Pigeons (Morocco) had the most variable hole location from single archaeological site (Table 3). Compared to other mollusc species, which are more frequently found at archaeological sites, but are less variable in terms of types of hole location, high variation in hole location in *Nassarius gibbosulus* does not appear to be a consequence of the relative abundance of this species.
Table 3  Summary class differences for hole location of Scaphopoda, Bivalvia and Gastropoda.

| Country   | Site                          | Bivalvia | Gastropoda | Scaphopoda | Summary |
|-----------|-------------------------------|----------|------------|------------|---------|
|           |                               | N        | HT         | N          | HT      | N  | n |
| Algeria   | Oued Djebbanna                 | 1        | 2          | 1          | 1       | 1  |   |
| Australia | Mandu Mandu Creek rock-shelter | 1        | 8          | 1          | 1       | 1  |   |
| Austria   | Krems-Hundsteig                | 1        | 2, 3       | 1          | 5       | 2  | 3 |
|           | Langmannersdorf                |          |            | 1          | 5       | 1  | 1 |
|           | Senftenberg                    | 1        | 5          | 1          | 1       | 1  |   |
|           | Willendorf                     | 1        | 5          | 1          | 1       | 1  |   |
| Croatia   | Pupićina Cave                  | 1        | 6          | 1          | 1       | 1  |   |
|           | Zala cave                      | 2        | 1, 3, 4, 7 | 2          | 4       | 2  |   |
| Cyprus    | Shillourokambus                | 2        | 9          | 6          | 4, 6, 8 | 9  | 5 |
| Eritrea   | Red Sea Coast                  | 2        | 4          | 2          | 1       | 2  |   |
| France    | Abri Peyrony                   | 3        | 1, 2, 3, 4, 11 | 1       | 5       | 4  | 6 |
|           | Balauzerie                     | 1        | 9          | 1          | 1       | 1  |   |
|           | Blanchard                      | 1        | 4          | 1          | 5       | 2  | 2 |
|           | Caminade Est                   | 1        | 5          | 1          | 1       | 1  |   |
|           | Castanet                       | 1        | 5          | 1          | 1       | 1  |   |
|           | Cellier                        | 1        | 5          | 1          | 1       | 1  |   |
|           | Figuier                        | 1        | 9          | 1          | 1       | 1  |   |
|           | Gargas Cave                     | 1        | 10         | 7          | 1, 3, 4, 11 | 8  | 5 |
|           | Hautes-Pyrénées                | 8        | 1, 2, 4, 10, 11 | 1       | 5       | 8  | 5 |
|           | Laouza                         |          |            | 1          | 5       | 1  | 1 |
|           | Pecheurs                       |          |            | 1          | 5       | 1  | 1 |
|           | Régismont                      | 1        | 9          | 1          | 1       | 1  |   |
|           | Rochette                       |          |            | 1          | 5       | 1  | 1 |
|           | Rothschild                     | 1        | 1          | 8          | 1, 3, 4, 11 | 1  | 5  | 10 | 5 |
|           | Saint-Germain-la-Rivière       | 2        | 4, 5       | 1          | 5       | 3  | 2 |
|           | Saint-Jean-De-Verges           | 1        | 1, 4       | 1          | 2       | 1  |   |
|           | Salpetriere                    |          |            | 1          | 5       | 1  | 1 |
|           | Tournal                        | 1        | 9          | 1          | 5       | 2  | 2 |
|           | Tuto de Camalhot               | 1        | 5          | 1          | 1       | 1  |   |
|           | Vachons                        | 1        | 5          | 1          | 1       | 1  |   |
| Germany   | Andernach-Martinsberg          | 2        | 1, 3, 4, 8 | 2          | 4       | 2  |   |
| Greece    | Klisoura                       | 7        | 4, 6       | 1          | 5       | 8  | 3 |
| India     | Deccan region                  | 1        | 5          | 1          | 1       | 1  |   |
| Israel    | Qafzeh cave                    | 1        | 9          | 1          | 1       | 1  |   |
|           | Skhul                          | 1        | 1, 2       | 1          | 2       | 1  |   |
| Italy     | Cala                           | 3        | 2, 4       | 1          | 5       | 4  | 3 |
|           | Fanciulli                      | 1        | 9          | 1          | 5       | 2  | 2 |
|           | Fumane                         | 1        | 9          | 13         | 2, 3, 4, 11 | 2  | 5  | 16 | 6 |
|           | Grotta del Cavallo             | 1        | 5          | 1          | 1       | 1  |   |
|           | Grotta di Pozzo                | 1        | 4          | 1          | 5       | 2  | 2 |

(continued on next page)
Table 3

| Country  | Site                          | Bivalvia | | Gastropoda | | Scaphopoda | | Summary |
|----------|-------------------------------|----------|----------|-----------|----------|-----------|----------|----------|
|          |                               | N  | HT      | N  | HT      | N  | HT      | N  | n  |
|          |                               |     |         |     |         |     |         |     |     |
| Riparo Biarzo |                            | 4 | 1, 3, 4, 6, 7, 8 | 4 | 6 |
| Riparo Mochi   |                            | 12| 1, 2, 3, 4, 7, 8 | 1 | 5 | 16    | 9    |
| Riparo Tagliente |                          | 6 | 1, 4, 6 | 1 | 5 | 7     | 4    |
| Jordan       | Wadi Mataha                  | 2 | 2, 3 | 1 | 5 | 3     | 3    |
| Morocco      | Grotte des Contrebandiers   | 2 | 4, 11 | 2 | 2 |
|             | Grotte des Pigeons, Taforalt | 1 | 1, 2, 3, 4, 6, 11 | 1 | 6 |
| Near East   | Ksar Akil                     | 2 | 1, 3, 4, 7, 11 | 1 | 5 | 3     | 6    |
|             | Sefunim                       | 2 | 4 | 2 | 1 |
| Oman        | Sumhuram                      | 2 | 8 | 2 | 1 |
| Portugal    | Gruta do Caldeirao            | 1 | 4 | 1 | 1 |
|             | Vale Boi                      | 3 | 1, 4, 5, 8 | 1 | 5 | 4     | 4    |
| Russia      | Kostienki 14                  | 2 | 2, 3 | 2 | 2 |
|             | Mezmaiskaya Cave              | 2 | 2, 11 | 2 | 2 |
| South Africa| Blombos Cave                  | 1 | 1, 3 | 1 | 2 |
|             | Border Cave                   | 1 | 3, 4, 11 | 1 | 3 |
|             | Sibudu Cave Middle Stone      | 1 | 1, 4 | 1 | 2 |
| Spain       | Benoite                       | 1 | 5 | 1 | 1 |
|             | Botiqueria de Los Moros       | 1 | 4, 8, 11 | 1 | 3 |
|             | Cingle Vermell                | 3 | 1, 5 | 1 | 5 | 4     | 2    |
|             | Cova de l’Or                  | 2 | 9 | 2 | 1 |
|             | Cova del Parco                | 4 | 1, 3, 4, 11 | 1 | 5 | 5     | 5    |
|             | Cova del Parpallo             | 3 | 9, 10 | 3 | 2 |
|             | Cova del Reclau Viver         | 1 | 3, 11 | 1 | 5 | 2     | 3    |
|             | Cueto de La Mina              | 2 | 2, 4 | 2 | 2 |
|             | Cueva Anton                   | 1 | 4 | 1 | 1 |
|             | Cueva de los Aviones           | 2 | 9 | 2 | 1 |
|             | El Cuco                       | 2 | 2, 3 | 1 | 5 | 3     | 3    |
|             | El Horno                      | 5 | 1, 2, 3, 5 | 5 | 4 |
|             | Guilanya                      |     | 1 | 5 | 1 | 1 |
|             |                               |     |     |     |     |     |     |
| La Fragua   |                              | 1 | 5 | 1 | 1 |
| La Garma A  |                              | 3 | 1, 4, 8, 10, 11 | 3 | 5 |
| La Pena de Estebanvela |            | 2 | 1, 4, 5 | 2 | 3 |
| Los Canes   |                              | 1 | 3 | 1 | 1 |
| Maltravieso cave |                           | 2 | 1, 10 | 2 | 2 |
| Moroccan cave |                            | 2 | 2, 3, 4, 11 | 2 | 4 |
| Nerja Cave  |                              | 4 | 1, 3, 4 | 1 | 5 | 5     | 4    |
| Roc del Migdia |                            | 1 | 4 | 1 | 5 | 2     | 2    |
| Tito Bustillo |                            | 6 | 1, 4, 5, 8 | 1 | 5 | 7     | 4    |
| Turkey      | Boncuklu Hoyuk                | 1 | 11 | 1 | 5 | 2     | 2    |
|             | Cat�hoyuk                     | 1 | 5 | 1 | 1 |
|             | Pinarbaşt                    | 2 | 4, 8 | 1 | 5 | 3     | 3    |
|             | Uçağıziz                     | 1 | 10 | 8 | 1, 2, 3, 4, 7, 8, 11 | 9 | 8 |

Notes.

N, the number of mollusc species; n, the number of hole types; HT, hole type.
Bivalves were the least common taxa found in archaeological assemblages and are characterised by hole locations 4, 9 and 10 (Table 3). Scaphopoda were more common than Bivalvia, but much less diverse in terms of types of hole location. Shell beads belonging to Scaphopoda had two holes, one in the anterior and the second one in the posterior of the shell (type number 5, Fig. 2A). In turn, gastropod shell beads were recovered at almost all archaeological sites and mostly showed more than one type of hole location.

Fumane (Italy) was the most diverse in context of number of gastropod species (13 taxa, Table 3), while Üçağızlık (Turkey) was characterised by the greatest number of types of hole location in gastropod shells at single archaeological site. Across all species, the most variable placed holes in shells were found at the site of Riparo Mochi (Italy) dated to the earliest Aurignacian (Kuhn & Stiner, 1998; Stiner, 1999).

**Predator made holes in shells**

Table 2 shows that almost all mollusc taxa recovered from the analysed archaeological sites are preyed upon by hole-making predators (41 taxa). Among these taxa we were able to
Table 4  Descriptive statistics and results of Kruskal–Wallis test for mollusc classes.

| Class                  | N  | Mean | SD  | Min | Max | N   | P    | Z    | d  |
|------------------------|----|------|-----|-----|-----|-----|------|------|----|
| Human made holes in shells |    |      |     |     |     |     |      |      |    |
| Scaphopoda             | 2  | 1.00 | 0.00| 1   | 1   |     |      |      |    |
| Bivalvia               | 5  | 2.00 | 0.63| 1   | 3   |     |      |      |    |
| Gastropoda             | 42 | 2.72 | 1.93| 1   | 8   |     |      |      |    |
| Non-human made holes in shells |  |      |     |     |     |     |      |      |    |
| Scaphopoda             | 1  | 2.00 | 0.00| 2   | 2   | 60  | 0.398| −0.845| 0.14|
| Bivalvia               | 5  | 2.20 | 0.40| 2   | 3   |     |      |      |    |
| Gastropoda             | 30 | 1.71 | 0.68| 1   | 3   |     |      |      |    |

Notes.

N, the number of mollusc taxa; SD, standard deviation; Min, minimal number of hole location types at archaeological site; Max, maximal number of hole location types at archaeological site; n, the total number of compared taxa; Z, result of sign test (P < 0.05).

Assess the hole location in the shells made by non-human animals in 30 mollusc species. Most of the assessed species exhibited two types of hole location in their shells, while only four species were classified as having three types of hole (Fig. 2B).

All species from the Bivalvia have predators that make holes in shells (Table 2). Species from this mollusc class are usually associated with more than one predator. Gastropoda is the class with the most numerous predators (nine species), then the Asteroidea (three species) and then Malacostraca with only one predator (Table 2). Almost all taxa from the Gastropoda have non-human predators that attack the prey by piercing holes in the mollusc’s shell.

Assessment of hole location types in shells made by predators was possible only for one Scaphopoda species (Dentalium sp., Table 2). Dentalium sp. can be attacked by five species of the Gastropoda and is pierced by gastropod predators in two places: in the middle or at the apex of the shell. Bivalvia is more diverse than Scaphopoda in terms of the placement of holes made by non-human predators. Gastropoda, Asteroidea and Malacostraca make holes in bivalves in the following locations: 1, 2, 3, 9 and 10 (Fig. 1). In turn, gastropods have predators that usually pierce holes in only one or two locations in particular species (Table 2, Fig. 2B).

Comparison of hole locations made by humans and predators

The number of hole location types per scaphopod and bivalve species were higher for hole-boring predators than for anthropogenically modified shells. In turn, holes in gastropod shells made by humans were characterised by slightly greater variation than holes in shells pierced by non-human predators (Table 4). However, the sign test revealed no significant difference in types of hole location between shells perforated by humans and non-human animals within mollusc species (Table 4, P = 0.398). The result of the sign test was supported by value of the Cohen-d index. For differences between human made and non-human made holes in shell, the Cohen’s d value was small (d = 0.14, Table 4).
DISCUSSION

In this study we examined the assertion that the anatomical locations of holes in mollusc shells pierced by prehistoric human groups have lower variability compared to predator made holes, which have been said to be more randomly placed (Stiner, 1999; Bouzouggar et al., 2007). We found that holes in shells reported to have been pierced by humans were as variable as those made by predators. Furthermore, predators and humans pierced shells in similar locations (Fig. 3).

Holes in the shells of Gastropoda

Among molluscs, species within the Gastropoda were found to be the most varied in terms of hole locations in shell beads made by humans (Fig. 2A, Table 4). This may be associated with natural morphological variation (shape, size and shell thickness) among species in this mollusc class (Stiner, 2014). Different styles of Palaeolithic bead adornments using ornate shells (Stiner, 2014) may also increase the variability of hole placements in the analysed shells.
Almost all gastropod taxa reported from archaeological sites are also vulnerable to hole-boring predators (e.g., Fig. 2B). In most cases, the predators belong to the class Gastropoda or Malacostraca (Table 2). The rest belong to Aves, Asteroidea, Cephalopoda and Polychaeta (Table 2). Despite the numerous predators, gastropod taxa had lower variation in the types of hole location per species made by non-human species than by humans (Table 4). These findings are supported by other research which shows that anatomical locations selected by predators of gastropods are not randomly selected, but are strategically located (Arpad, 1993; Zagyvai & Demeter, 2008). For example, in Neritina picta, access to the apex of the shell is preferred as a strategic location by predators belonging to Asteroidea, Muricidae, or Polychaeta (Zagyvai & Demeter, 2008). In turn, Theodoxus sp. usually exhibit a muricid (predatory sea snail) borehole that is often located close to the umbilicus (Arpad, 1993).

**Holes in the shells of Scaphopoda**

Scaphopoda was the least diverse mollusc class in terms of variation in hole location in shell beads made by humans (Table 4), which is probably a consequence of their characteristic anatomy (tusk shaped). All shell beads belonging to this class have two anatomical holes, one in the anterior (allowing the burrowing foot and captacula to protrude) and a second one in the posterior part of the shell (responsible for respiration; Reynolds, 2002). As such, these shells can be threaded onto a cord without being pierced.

Mean variation of hole location in shells pierced by predators of scaphopods was greater than in shells modified by humans (Table 4). Klompmaker (2011) found that predators pierced holes in the shells of Miocene scaphopods in the middle section of the shell, which is the thickest part. Whereas we found that Dentalium sp. was pierced in two places: in the middle or at the posterior part of the shell. However, we were only able to assess predator made holes in one species of Scaphopoda (Dentalium sp.), therefore results for this class should be interpreted with caution.

**Holes in the shells of Bivalvia**

Holes pierced by humans in bivalves were slightly more diverse than in scaphopods, but were less variable than in gastropods (Table 4). According to Carter (2008) bivalves in South America were rarely used as beads or pendants due to their size and weight and it is possible that most perforations could be attributed to predation or taphonomic processes. Other evidence, based upon context and use-wear analysis of shells from Palaeolithic sites, suggests the presence of bivalves can often be attributed to utilitarian purposes (e.g., food, receptacles for pigments) rather than as body adorning (Harper, 2005; Bar-Yosef-Mayer, 2007; Rogalla & Amler, 2007; Douka et al., 2014). Zilhão et al. (2010) suggest that for most species of bivalves recovered from archaeological sites, anthropogenic modifications can be confirmed when (i) the weathering stage and perforation patterns do not agree with those seen in natural death assemblages; (ii) a tool was involved in the perforation, or (iii) the hole is associated with artificial modification of the shell’s geometry.

Predators of bivalves are also diverse and belong to Asteroidea, Gastropoda or Malacostraca. This variation in predators might be associated with higher variations in types
of hole placement per species, which is slightly greater than reported in anthropogenically modified shells (Table 4). For example, variation in hole location is very low in Chlamys sp., with naticid and muricid predators usually choosing the region near the adductor muscle (corresponding to number 2 in Fig. 1), which may facilitate access to the viscera (Chattopadhyay & Dutta, 2013). Similar behaviour to non-human predators has been noted in the fossil bivalve Pseudodon in which 33% of holes were made near the anterior adductor muscle by Homo erectus at Trinil (Joordens et al., 2015). In this mollusc species, the adductor muscles are placed near the 1 and 6 of the hole location types (Fig. 1). Location of the holes made by H. erectus may vary from the data presented in our study because Pseudodon shells at Trinil, although engraved, appear to have been perforated in order to open the shells to access the meat rather than to be used as body adornments.

Evidence from the study of bivalve species from the early and middle Pleistocene, indicate that shells were most often pierced by non-human predators close to the umbo or near the centre (Amano, 2006). Only few examples of piercings near the adductor muscle have been described, and these could have been caused by the incomplete drill holes in prey which continue to grow after the attack changing the relative position of the incomplete hole (Chattopadhyay & Dutta, 2013).

### Pierced shells; factors to consider

Our results show that within the analysed sample, there were no significant differences between the placement of holes made by non-human animals and those made by humans; both pierce shells in the same locations in most classes of molluscs (Table 4; Fig. 3). For example in Euthria cornea, Gibbula sp. and Mitra corniculata we observed that humans and non-human predators made holes in the same location (type number 4). Similarly, in Glycymeris sp. humans and predators pierced the same part of the shell (types number 4 and 9; Tables 1 and 2). However, for some mollusc species selection of hole location was only partial. For example in Littorina sp. we observed that humans and non-human animals made holes in the centre of shell (type number 4) and near apex (type number 8), but this species is also perforated by humans near the outer lip (type number 1; Tables 1 and 2).

The non-random piercing of holes by the mollusc predators is widely reported (e.g., Johannesson & Ekendahl, 2002; Kingsley-Smith, Richardson c A & Seed, 2003; Dietl & Kelley, 2006; Gorzelak et al., 2013) and it can be associated with shell thickness of prey which varies across the body, probably due to differential age of the shell whorls and predatory pressure on snails (Rosin et al., 2013). In molluscs with ornamental shells, up to five times more force can be required to make a hole (Dalziel & Boulding, 2005). Predatory gastropods can spend between three to twenty minutes locating a piercing site on their prey’s shell surface and, once the location is fixed, it may take from several hours to several days to pierce the shell, depending on the thickness (Hagadorn & Boyajian, 1997). The variation in shell thickness within and between mollusc species may be linked to why holes in shells most often occur near the lip and in the centre (e.g., types number 1, 2, 3 and 4; Fig. 1) and why humans and non-human predators choose similar locations to pierce shells of Bivalvia and Gastropoda (Fig. 3) However, results for scaphopods deviated from this pattern, with
humans and non-human predators piercing holes in different locations (type 8 and 4 versus type 5, respectively; Fig. 1). Similarity in the choice of hole location made by humans and non-human predators in most species of mollusc could cause researchers to wrongly assign shell perforations as anthropogenically manipulated because they believe predator made holes are less likely to be pierced in suitable locations for threading (D’Errico et al., 2005; Bouzouggar et al., 2007).

Bicho & Haws (2008) have suggested that the larger biomass of molluscs in the Palaeolithic likely meant that mollusc gathering formed part of hunter-gatherers’ regular foraging behaviour in Portugal. Furthermore, predator drill frequency in gastropods and bivalves has been estimated to range between 2.8%–50.0% and 8.6%–34.1%, respectively. In contrast, scaphopods were pierced at a much lower rates (0.9% in Dentalium sp.; Taraschewski & Paperna, 1982; Yochelson, Dockery & Wolf, 1983; Hagadorn & Boyajian, 1997; Zagyvai & Demeter, 2008; Sawyer, 2010). It is possible that prehistoric people that regularly foraged for molluscs, were more likely exposed to a greater numbers of naturally perforated shells than we might expect. As such, the likelihood of finding shells with predator-made holes in locations suitable for threading could be higher than researchers believe.

Beads made from shells with holes made by natural processes have been identified at archaeological sites, for example, the perforated bead of Antalis sp. from the Early Upper Paleolithic site in El Cuco (Spain; Gutiérrez-Zugasti & Cuenca-Solana, 2013). Some researchers claim that shell beads from the Middle and Lower Palaeolithic could have been perforated by natural processes. For example, Bednarik (2015) proposed that predators and parasitic organisms commonly perforate mollusc shells and that it should be expected that naturally perforated shells were used as beads and pendants. Hahn (1972) emphasized that the signs of human manipulation in shells from Aurignacian sites such as Kremshundssteig, Willendorf, Kostienki 1 and Sjuren, are not always present and that some holes could have been made by predators. It is possible that before tools were used to bore holes, finding shells with holes in favourable positions for threading into ornate jewellery may have increased their importance or value. Similarly the natural apertures in fish vertebrae or crinoid discs may have made them attractive as items for threading (e.g., see Mussi, 2002).

Finally we would like to draw attention to the common assumption that predator-made holes are mostly made by chemical processes and tend to be round in outline, while shells pierced by humans have elliptical or irregular outlines (Stiner, 1999; Komšo & Vukosavljević, 2011). We would argue, however, that this statement is probably an overgeneralisation because many predators form holes in their prey which range in shape from nearly perfect circles to ellipsoids (Zagyvai & Demeter, 2008). For example, muricids, naticids and cephalopods use their radula to bore into mollusc shells and they can adapt the size and shape of the pierced hole to the morphology of their prey, as a result, bore holes can differ in shape (Walker & Brett, 2002). Bird beaks can also cause cracks and chips to the shells that imitate stone tool use (Ingolfsson & Estrella, 1978; Harper, 2005; Shumaker, Walkup & Beck, 2011). Thus, detailed analytical methods remain critical to identifying the tell-tale signs of anthropogenic manipulation of shells recovered from archaeological sites.
CONCLUSIONS

Some researchers have argued that holes in shells made by predators vary more than holes made by humans. However, our findings show that the variation in hole location on shell beads recovered from archaeological sites did not significantly differ from the locations of predator-made holes. Our assessment of hole location was based on figures from the published literature only, so it is possible that the true level of variation from beads recovered from archaeological sites might be higher (i.e., in collections not described in the literature).

This study highlights how the placement of holes on the shells made by predators can potentially be similar to human activity. Moreover, the likelihood of finding shells with holes made by predators in locations suitable for threading is probably higher than researchers believe. These findings emphasise the importance of the battery of tests currently used to identify whether piercings in shells are made naturally or are anthropogenic modifications. Dispelling assumptions about human and non-human predator hole placements in shells and providing information on the patterns of predation on molluscs can augment these tests in order to contribute to more realistic scenarios of the social and cultural expressions of prehistoric people.

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Author Contributions
• Anna Maria Kubicka conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
• Zuzanna M. Rosin wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
Piotr Tryjanowski analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper.

Emma Nelson conceived and designed the experiments, wrote the paper, reviewed drafts of the paper.

Data Availability
The following information was supplied regarding data availability:

The raw data has been supplied as a Supplemental File.

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REFERENCES

Alerstam T, Gudmundsson G, Johannesson K. 1992. Resources for long distance migration: intertidal exploitation of Littorina and Mytilus by Knots Calidris Canutus in Iceland. Oikos 65:179–189 DOI 10.2307/3545008.

Allmon W, Nich J, Norris R. 1990. Drilling and peeling of Turritelline gastropods since the late Cretaceous. Palaeontology 33:595–611.

Álvarez Fernández E. 2006. The use of Columbella rustica (class: gastropoda) in the Iberian peninsula and Europe during the Mesolithic and the early Neolithic. In: Hernandez-Perez M, Soler Diaz J, Lopez Padilla J, eds. IV congreso del neolítico peninsular. Alicante: Museo Arqueológico de Alicante—MARQ, 103–111.

Álvarez-Fernández E. 2007. La explotación de los moluscos marinos en la Cornisa Cantábrica durante el Gravetiense: primeros datos de los niveles E Y F De La Garma A (Omoño, Cantabria). Zephyrus 60:43–58.

Álvarez-Fernández E. 2009. Magdalenian personal ornaments on the move: a review of the current evidence in Central Europe. Zephyrus 63:45–59.

Álvarez-Fernández E. 2010. Shell beads of the last hunter-gatherers and earliest farmers in south-western Europe. Munibe. Antropologia-Arkeologia 61:129–138.

Amano K. 2006. Temporal pattern of naticid predation on Glycymeris Yessoensis (Sowerby) during the Late Cenozoic in Japan. Palaios 21:369–375 DOI 10.2110/palo.2005.P05-37e.

Arpad D. 1993. Trace fossils on molluscs from the Molluscan Clay (Late Oligocene, Egerian)—a trace fossils between two localities (Wind Brickyard, Eger, and Nyárjas Hill Novaj, NE Hungary). Scripta Geologica 2:75–82.

Arua I. 1989. Gastropod predators and their dietary preference in an eocene molluscan fauna from Nigeria. Palaeogeography, Palaeoclimatology, Palaeoecology 72:283–290 DOI 10.1016/0031-0182(89)90148-X.

Avezuela B. 2014. The personal ornaments made from molluscs at the Middle-Late Magdalenian site of La Peña de Estebanvela (Segovia, Spain). In: Álvarez-Fernández E, Carcajal-Contreras D, eds. Not only food. Marine, terrestrial and freshwater molluscs
in archaeological sites. Proceedings of the 2nd meeting of the ICAZ archaeomalacology working group (Santander, February 19th–22nd 2008). Gipuzkoa: Aranzadi Zientzia Elkartea, 265–282.

Avezuela Aristu B, Álvarez-Fernández E. 2012. Los objetos de adorno-colgantes durante el Solutrense en la Península Ibérica. Solutrean personal ornaments in the Iberian Peninsula. Espacio, Tiempo y Forma Serie I, Nueva época Prehistoria y Arqueología 5:323–332.

Baeta M, Ramón M. 2013. Feeding ecology of three species of Astropecten (Asteroidea) coexisting on shallow sandy bottoms of the northwestern Mediterranean Sea. Marine Biology 160:2781–2795 DOI 10.1007/s00227-013-2270-0.

Balme J, Morse K. 2006. Shell beads and social behaviour in Pleistocene Australia. Antiquity 80:799–811 DOI 10.1017/S0003598X0009436.

Bar-Yosef O. 1996a. The middle/upper Palaeolithic transition: a view from the Eastern Mediterranean. In: Carbonell E, Vaquero M, eds. The last neanderthals, the first anatomically modern humans: a tale about human diversity. cultural change and human evolution: the crisis at 40 ka BP. Tarragona: Servei de Publicacions, 79–94.

Bar-Yosef O. 1996b. The walls of Jericho: an alternative explanation. Current Anthropology 27:157–162.

Bar-Yosef-Mayer D. 2007. Archaeomalacological research in Israel: the current state of research. Israel Journal of Earth Sciences 56:191–206 DOI 10.1560/IJES.56.2-4.191.

Bar-Yosef-Mayer DE, Beyin A. 2009. Late stone age shell middens on the red sea coast of eritrea. The Journal of Island and Coastal Archaeology 4:108–124 DOI 10.1080/15564890802662171.

Bar-Yosef Mayer DE, Gümüs BA, Islamoglu Y. 2010. Fossil hunting in the neolithic: shells from the Taurus Mountains at Çatalhöyük, Turkey. Geoarchaeology 25:375–392 DOI 10.1002/gea.20311.

Bar-Yosef Mayer DE, Vandermeersch B, Bar-Yosef O. 2009. Shells and ochre in Middle Paleolithic Qafzeh Cave, Israel: indications for modern behavior. Journal of Human Evolution 56:307–314 DOI 10.1016/j.jhevol.2008.10.005.

Barge H. 1983. Essai sur les parures du Paléolithique supérieur dans le sud de la France la faune malacologique aurignacienne de l’abri Rothschild (Cabrières, Hérault). Bulletin du Musée d’Anthropologie Préhistorique de Monaco Monaco 27:69–83.

Baysal E. 2013. A tale of two assemblages: early Neolithic manufacture and use of beads in the Konya plain. Anatolian Studies 63:1–15 DOI 10.1017/S006615461300001X.

Bednarik RG. 1998. The archaeological significance of beads and pendants. Man and Environment 23:87–99.

Bednarik RG. 2001. Beads and pendants of the pleistocene. Anthropos 96:545–555.

Bednarik RG. 2015. The significance of the earliest beads. Advances in Anthropology 5:51–66 DOI 10.4236/aa.2015.52006.

Bertola S, Broglio A, Cristiani E, De Stefani M, Gurioli F, Negrino F, Romandini M, Vanhaeren M. 2013. La diffusione del primo Aurignaziano a sud dell’arco alpino. Preistoria Alpina 47:123–152.
Beyin A. 2010. Use-wear analysis of obsidian artifacts from Later Stone Age shell midden sites on the Red Sea Coast of Eritrea, with experimental results. *Journal of Archaeological Science* 37:1543–1556 DOI 10.1016/j.jas.2010.01.015.

Bicho N, Haws J. 2008. At the land’s end: marine resources and the importance of fluctuations in the coastline in the prehistoric hunter-gatherer economy of Portugal. *Quaternary Science Reviews* 27:2166–2175 DOI 10.1016/j.quascirev.2008.08.011.

Blanco-Libreros JF, Arroyave-Rincón A. 2009. Predator damage and shell size on the diadromous snail Neritina virginea (Gastropoda: Neritidae) in the Mameyes River, Puerto Rico. *Revista de Biología Tropical* 57:1069–80.

Botha R. 2008. Prehistoric shell beads as a window on language evolution. *Language and Communication* 28(3):197–212 DOI 10.1016/j.langcom.2007.05.002.

Botha R. 2010. On the soundness of inferring modern language from symbolic behaviour. *Cambridge Archaeological Journal* 20(3):345–356 DOI 10.1017/S0959774310000454.

Bouzouggar A, Barton N, Vanhaeren M, D’Errico F, Collcutt S, Higham T, Hodge E, Parfitt S, Rhodes E, Schwenninger J-L, Stringer C, Turner E, Ward S, Moutmir A, Stambouli A. 2007. 82,000-year-old shell beads from North Africa and implications for the origins of modern human behavior. *Proceedings of the National Academy of Sciences of the United States of America* 104(24):9964–9969 DOI 10.1073/pnas.0703877104.

Bowdler S, Mellars P. 1990. *The emergence of modern humans: an archaeological perspective*. Edinburgh: Edinburgh University Press.

Cáceres M, Marcos G, Diez G. 2008. Upper Paleolithic ornament seashell from Sala de las Chimeneas, Maltravieso cave (Cáceres, Spain). In: Álvarez-Fernández E, Carcajal-Contreras D, eds. *Not only food. Marine, terrestrial and freshwater molluscs in archaeological sites. Proceedings of the 2nd meeting of the ICAZ archaeomalacology working group (Santander, February 19th–22nd 2008)*. Gipuzkoa: Aranzadi Zientzia Elkartea, 19–22.

Calvet C. 1992. Borehole site-selection in *Naticarius hebraeus* (Chemnitz in Karsten, 1769) (Naticidae: Gastropoda). *Orsis* 7:57–64.

Cardoso JL, Dias Coelho M. 2012. The marine malacological remains from the chalcolithic fortified settlement at Outeiro Redondo (Sesimbra): collection strategies used by a sedentary community from the 3rd millennium BC on the portuguese coast. *Zephyrus* 70:85–111.

Carter BP. 2008. Technology, society and change: shell artifact production among the Manteno (A.D. 800–1532) of coastal ecuador. D. Phil. thesis, University in St. Louis, Washington.

Cattelain P. 2012. La parure de Cro-Magnon à Clovis. In: Cattelain P, Bozet N, Di Stazio G, eds. *Les Parures au Paléolithique et au Mésolithique: coquillages, dents, os, ivoire et pierres*. Treignes: Editions Du Cedarc, 7–35.

Cesnola AP, Mallegni F. 1996. *Le Paléolithique inférieur et moyen en Italie*. Grenoble: Editions Jérôme Millon.
Chattopadhyay D, Dutta S. 2013. Prey selection by drilling predators: a case study from Miocene of Kutch, India. *Palaeogeography, Palaeoclimatology, Palaeoecology* **374**:187–196 DOI 10.1016/j.palaeo.2013.01.016.

Cohen J. 1988. *Statistical power analysis for the behavioral sciences*. New Jersey: Routledge.

Coleman HM. 2010. Complex species interaction in tropical backreef communities. *Journal of Experimental Marine Biology and Ecology* **393**(1–2):124–129 DOI 10.1016/j.jembe.2010.07.013.

Coleman R, Goss-Custard J, Dit Durell S, SJ H. 1999. Limpet *Patella* spp. consumption by oystercatchers *Haematopus ostralegus*: a preference for solitary prey items. *Marine Ecology Progress Series* **183**:253–261 DOI 10.3354/meps183253.

Cristiani E. 2012. Ornamental traditions of the Late Pleistocene and the Early Holocene Foragers in the Eastern Alps: the Case of Riparo Biarzo. *Geologia, Paleontologia, Paletnologia* **34**:89–102.

Dalziel B, Boulding EG. 2005. Water-borne cues from a shell-crushing predator induce a more massive shell in experimental populations of an intertidal snail. *Journal of Experimental Marine Biology and Ecology* **317**(1):25–35 DOI 10.1016/j.jembe.2004.11.015.

Das A, Mondal S, Bardhan S. 2013. A note on exceptionally high confamilial naticid drilling frequency on Natica gualteriana from the Indian subcontinent. *Historical Biology* **26**(6):758–764 DOI 10.1080/08912963.2013.841684.

D’Errico F, Backwell L, Villa P, Degano I, Lucejko JJ, Bamford MK, Higham TFG, Colombini MP, Beaumont PB. 2012. Early evidence of San material culture represented by organic artifacts from Border Cave, South Africa. *Proceedings of the National Academy of Sciences of the United States of America* **109**:13214–13219 DOI 10.1073/pnas.1204213109.

D’Errico F, Henshilwood C, Vanhaeren M, Van Niekerk K. 2005. *Nassarius kraussianus* shell beads from Blombos Cave: evidence for symbolic behaviour in the Middle Stone Age. *Journal of Human Evolution* **48**(1):3–24 DOI 10.1016/j.jhevol.2004.09.002.

D’Errico F, Vanhaeren M, Barton N, Bouzouggar A, Mienis H, Richter D, Hublin JJ, McPherron SP, Lozouet P. 2009. Additional evidence on the use of personal ornaments in the Middle Paleolithic of North Africa. *Proceedings of the National Academy of Sciences of the United States of America* **106**(38):16051–16056 DOI 10.1073/pnas.0903532106.

D’Errico F, Vanhaeren M, Wadley L. 2008. Possible shell beads from the middle stone age layers of Sibudu Cave, South Africa. *Journal of Archaeological Science* **35**(10):2675–2685 DOI 10.1016/j.jas.2008.04.023.

Deshpande-Mukherjee A. 2005. Marine shell utilisation by the Chalcolithic societies of the western Deccan region of India. In: Bar-Yosef-Mayer D, ed. *Archaeomalacology. Molluscs in former environments of human behaviour*. Oxford: Oxbow Books, 174–184.

Dietl G, Kelley P. 2006. Can naticid gastropod predators be identified by the holes they drill? *Ichnos* **13**(3):103–108 DOI 10.1080/10420940600848889.
Dodge R, Scheel D. 1999. Remains of the prey—recognizing the midden piles of Octopus dofleini (Wülker). *The Veliger* 42:260–266.

Douka K. 2013. The chronology of the middle to the upper paleolithic transition in the Northern Levant. *Mitteilungen der Gesellschaft Urgeschichte* 22:11–40.

Douka K, Bergman CA, Hedges REM, Wesselingh FP, Higham TFG. 2013. Chronology of Ksar Akil (Lebanon) and implications for the colonization of Europe by anatomically modern humans. *PLOS ONE* 8:e72931 DOI 10.1371/journal.pone.0072931.

Douka K, Higham TFG, Wood R, Boscolo P, Gambassini P, Karkanas P, Peresani M, Ronchitelli AM. 2014. On the chronology of the Uluzzian. *Journal of Human Evolution* 68:1–13 DOI 10.1016/j.jhevol.2013.12.007.

Edgell T, Brazeau C, Grahame J, Rochette R. 2008. Simultaneous defense against shell entry and shell crushing in a snail faced with the predatory shorecrab *Carcinus maenas*. *Marine Ecology Progress Series* 371:191–198 DOI 10.3354/meps07698.

Edgell TC, Rochette R. 2009. Prey-induced changes to a predator’s behaviour and morphology: implications for shell–claw covariance in the northwest Atlantic. *Journal of Experimental Marine Biology and Ecology* 382(1):1–7 DOI 10.1016/j.jembe.2009.10.004.

Elias S. 2012. *Origins of human innovation and creativity: breaking old paradigms*. Amsterdam: Elsevier.

Estrada A, Tejero JM, Mangado X, Petit MA, Fullola JM, Esteve X, Bartroli R. 2010. From the Mediterranean sea to the Segre river: manipulated shells from Magdalenian levels of Parco’s cave (Alós de Balaguer, Lleida Spain). In: Álvarez-Fernández E, Carcajal-Contreras D, eds. *Not only food. Marine, terrestrial and freshwater molluscs in archaeological sites. Proceedings of the 2nd meeting of the ICAZ archaeomalacology working group (Santander, February 19th–22nd 2008)*. Donostia: Aranzadi Zientzia Elkartea, 70–77.

Fano MÁ, Álvarez-Fernández E. 2010. Magdalenian marine shells from El Horno Cave (Ramales , Cantabria , Spain) in the regional context. In: Alvarez-Fernandez E, Carvajal-Contreras DR, eds. *Not only food. Marine, terrestrial and freshwater molluscs in archaeological sites. Proceedings of the 2nd meeting of the ICAZ archaeomalacology working group (Santander, February 19th–22nd 2008)*. Santander: Munibe, 58–68.

Farren HM, Donovan DA. 2007. Effects of sponge and barnacle encrustation on survival of the scallop *Chlamys hastata*. *Hydrobiologia* 592(1):225–234 DOI 10.1007/s10750-007-0743-1.

Filipescu S, Popa M. 2001. Biostratigraphic and paleoecologic significance of the macro- and microfossil assemblages in the Borod Formation (eastern Borod Depression, north-west Romania). *Acta Palaeontologica Romaniae* 3:135–148.

Fiocchi C. 1998. Contributo alla conoscenza del comportamento simbolico di Homo sapiens sapiens. Le conchiglie marine nei siti del Paleolitico superiore europeo: strategie di approvvigionamento, reti di scambio, utilizzo. D. Phil. Thesis, Università degli Studi di Bologna.
Fontana F, Cilli C, Cremona MG, Giacobini G, Guirìolo F, Liagre J, Malerba G, Rocci Ris A, Veronese C, Guerreschi A. 2009. Recent data on the Late Epigravettian occupation at Riparo Tagliente, Monti Lessini (Grezzana, Verona): a multidisciplinary perspective. Preistoria Alpina 44:49–57.

Golovanova LV, Doronichev VB, Cleghorn NE. 2010. The emergence of bone-working and ornamental art in the Caucasian Upper Paleolithic. Antiquity 84(324):299–320 DOI 10.1017/S0003598X0006659X.

Gordillo S, Archuby F. 2014. Live-live and live-dead interactions in marine death assemblages: the case of the Patagonian clam Venus antiqua. Acta Palaeontologica Polonica 59:429–442.

Gorman D, Sikinger CE, Turra A. 2015. Spatial and temporal variation in the predation risk for hermit crabs in a subtropical bay. Journal of Experimental Marine Biology and Ecology 462:98–104 DOI 10.1016/j.jembe.2014.10.009.

Gorzelań P, Salamon MA, Trzęsiok D, Niedzwiedź R. 2013. Drill holes and predation traces versus abrasion-induced artifacts revealed by tumbling experiments. PLOS ONE 8:e58528 DOI 10.1371/journal.pone.0058528.

Grey M. 2005. Shape differences among boreholes drilled by three species of Naticid Gastropods. Journal of Molluscan Studies 71(3):253–256 DOI 10.1093/mollus/eyi035.

Grey M, Lelievre PG, Boulding EG. 2005. Selection for prey shell thickness by the Naticid Gastropod Euspira lewisii (Naticidae) on the Bivalve Protothaca staminea (Veneridae). The Veliger 48:6–11.

Guerra A, Nixon M. 1987. Crab and mollusc shell drilling by Octopus vulgaris (Mollusca: Cephalopoda) in the Ria de Vigo (north-west Spain). Journal of Zoology 211(3):515–523 DOI 10.1111/j.1469-7998.1987.tb01549.x.

Guerrero S, Reyment R. 1988. Predation and feeding in the Naticid Gastropod Naticarius Intrica Toides (Hidalgo). Palaeogeography, Palaeoclimatology, Palaeoecology 68(1):49–52 DOI 10.1016/0031-0182(88)90015-6.

Gutiérrez-Zugasti I, Cuenca-Solana D. 2013. The role of shellfish in hunter-gatherer societies during the Early Upper Palaeolithic: a view from El Cuco rockshelter, northern Spain. Journal of Anthropological Archaeology 32(2):242–256 DOI 10.1016/j.jaa.2013.03.001.

Hagadorn JW, Boyajian GE. 1997. Subtle changes in mature predator-prey systems: an example from neogene turritella (Gastropoda). Palaios 12(4):372–379 DOI 10.2307/3515336.

Hahn J. 1972. Aurignacian signs, pendants and art objects in Central and Eastern Europe. World Archaeology 3(3):252–266 DOI 10.1080/00438243.1972.9979508.

Harley CDG, Anderson KM, Lebreton CA-M, Mackay A, Ayala-Diaz M, Chong SL, Pond LM, Amerongen Maddison JH, Hung BHC, Iversen SL, Wong DCM. 2013. The introduction of Littorina littorea to British Columbia, Canada: potential impacts and the importance of biotic resistance by native predators. Marine Biology 160(7):1529–1541 DOI 10.1007/s00227-013-2206-8.

Harper EM. 2005. Fossils explained 50. Recognizing predator–prey interactions in the fossil record. Geology Today 21(5):191–196 DOI 10.1111/j.1365-2451.2005.00529.x.
Harris L. 1984. Tested studies for laboratory teaching. In: Proceedings of the 35th workshop/conference of the association for biology laboratory education (ABLE). Alberta: University of Calgary, 134.

Henshilwood C, D’Errico F, Vanhaeren M, Van Niekerk K, Jacobs Z. 2004. Middle stone age shell beads from South Africa. *Science* **304**(5669):404 DOI 10.1126/science.1095905.

Ingolfsson A, Estrella B. 1978. The development of shell-cracking behavior in Herring Gulls. *Auk* **95**:577–579.

Inizan M-L. 1978. Coquillages de Ksar-‘Aqil: éléments de parure? *Paléorient* **4**(1):295–306 DOI 10.3406/paleo.1978.4232.

Janetski JC, Bar-Yosef ED. 2005. Shifts in Epipaleolithic marine shell exploitation at wadi Mataha, southern Jordan. In: Bar-Yosef Mayer D, ed. * Archaeomalacology*. *Molluscs in former environments of human behaviour*. Oxford: Oxbow Books, 149–158.

Johannesson K, Ekendahl A. 2002. Selective predation favouring cryptic individuals of marine snails (Littorina). *Biological Journal of the Linnean Society* **76**(1):137–144 DOI 10.1111/j.1095-8312.2002.tb01720.x.

Jonkers HA. 2000. Gastropod predation patterns in Pliocene and Recent pectinid bivalves from Antarctica and New Zealand. *New Zealand Journal of Geology & Geophysics* **43**(2):247–254 DOI 10.1080/00288306.2000.9514884.

Joordens J, D’Errico F, Wesselingh F, Munro S, De Vos J, Wallinga J, Ankjægaard C, Reimann T, Wijbrans J, Kuiper K, Mümker H, Coqueugniot H, Prié V, Joosten I, Van Os B, Schulp A, Panuel M, Van der Haas V, Lustenhouwer W, Reijmer J, Roebroeks W. 2015. *Homo erectus* at Trinil on Java used shells for tool production and engraving. *Nature* **518**:228–231.

Jordá Pardo J, Aura Tortosa JE, Martín C, Avezuela B. 2010. Archaeomalacological remains from the Upper Pleistocene. Early Holocene record of the Vestíbulo of Nerja Cave (Malaga, Spain). In: Álvarez-Fernández E, Carcajal-Conrreras D, eds. *Not only food. Marine, terrestrial and freshwater molluscs in archaeological sites. Proceedings of the 2nd meeting of the ICAZ archaeomalacology working group (Santander, February 19th–22nd 2008)*. Donostia: Aranzadi Zientzia Elkarteas, 78–87.

Juan-Foucher C, Foucher P. 2008. Marine shell beads from the Gravettian at Gargas cave (Hautes- Pyrenees, France): cultural and territorial markers. In: Álvarez-Fernández E, Carcajal-Conrreras D, eds. *Not only food. Marine, terrestrial and freshwater molluscs in archaeological sites. Proceedings of the 2nd meeting of the ICAZ archaeomalacology working group (Santander, February 19th–22nd 2008)*. Donostia: Aranzadi Zientzia Elkarteas, 28–35.

Kingsley-Smith PPR, Richardson CAC, Seed R. 2003. Stereotypic and size-selective predation in *Polinices pulchellus* (Gastropoda: Naticidae) Risso 1826. *Journal of Experimental Marine Biology and Ecology* **295**(2):173–190 DOI 10.1016/S0022-0981(03)00294-6.

Klompmaker AA. 2011. Drilling and crushing predation on scaphopods from the Miocene of the Netherlands. *Lethaia* **44**:429–439.
Kohn AJ, Arua I. 1999. An early pleistocene molluscan assemblage from Fiji: gastropod faunal composition, paleoecology and biogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology* 146(1–4):99–145 DOI 10.1016/S0031-0182(98)00135-7.

Komšo D, Vukosavljević N. 2011. Connecting coast and inland: perforated marine and freshwater snail shells in the Croatian Mesolithic. *Quaternary International* 244(1):117–125 DOI 10.1016/j.quaint.2011.05.033.

Kowalewski M. 2004. Drill holes produced by the predatory gastropod *Nucella Lamellosa* (Muricidae): palaeobiological and ecological implications. *Journal of Molluscan Studies* 70:359–370 DOI 10.1093/mollus/70.4.359.

Kowalewski M, Rosa M, Mancheno M. 2009. Drill hole in freshwater Gastropods from the Pleistocene of the Southeastern Spain: evidence for drilling predation (or parasitism) in freshwater ecosystems? *Journal of Molluscan Studies* 70:359–370.

Kozłowski J. 1996. Cultural context of the last Neanderthals and early modern humans in central-eastern Europe. In: Bar-Yosef O, Cavalli-Sforza L, March R, Piperno M, eds. The lower and middle Paleolithic, the colloquia of the XIII international congress of prehistoric and protohistoric sciences. Abaco: Forli, 205–218.

Kuhn S, Stiner M. 1998. The earliest Aurignacian of Riparo Mochi (Liguria, Italy). *Current Anthropology* 39(1):175–189 DOI 10.1086/204710.

Kuhn SL, Stiner MC, Güleç E, Ozer I, Yilmaz H, Baykara I, Açikkol A, Goldberg P, Molina KM, Unay E, Suata-Alpaslan F. 2009. The early Upper Paleolithic occupations at Uçağızli Cave (Hatay, Turkey). *Journal of Human Evolution* 56(2):87–113 DOI 10.1016/j.jhevol.2008.07.014.

Kuhn SL, Stiner MC, Reese DS, Güleç E. 2001. Ornaments of the earliest Upper Paleolithic: new insights from the Levant. *Proceedings of the National Academy of Sciences of the United States of America* 98(13):7641–7646 DOI 10.1073/pnas.121590798.

Langley MC, Street M. 2013. Long range inland-coastal networks during the Late Magdalenian: evidence for individual acquisition of marine resources at Andernach-Martinsberg, German Central Rhineland. *Journal of Human Evolution* 64(5):457–465 DOI 10.1016/j.jhevol.2013.01.015.

Leite TS, Haimovici M, Mather J. 2009. *Octopus insularis* (Octopodidae), evidences of a specialized predator and a time-minimizing hunter. *Marine Biology* 156(11):2355–2367 DOI 10.1007/s00227-009-1264-4.

Li R-Y, Young HR, Zhan R-B. 2011. Drilling predation on scaphopods and other molluscs from the Upper Cretaceous of Manitoba, Canada. *Palaeoworld* 20(4):296–307 DOI 10.1016/j.palwor.2011.04.001.

Lombardo U, Szabo K, Capriles JM, May JH, Amelung W, Hutterer R, Lehndorff E, Plotzki A, Veit H. 2013. Early and middle Holocene hunter-gatherer occupations in Western Amazonia: the hidden shell middens. *PLOS ONE* 8:e72746.

Magnesen T, Redmond KJ. 2011. Potential predation rates by the sea stars *Asterias rubens* and *Marthasterias glacialis*, on juvenile scallops, Pecten maximus, ready for sea ranching. *Aquaculture International* 20:189–199.

Mangado X, Tejero JM, Fullola JM, Petit MA, García-Argüelles P, García M, Soler N, Vaquero M. 2010. Nuevos territorios, nuevos grafismos: una visión del Paleolítico...
superior en Cataluña a inicios del siglo XXI. El Paleolítico Superior Peninsular. Novedades Del Siglo XXI 8:63–83.

Martínez-Moreno J, Mora F, Casanova J. 2010. Lost in the mountains? Marine ornaments in the Mesolithic of the northeast of the Iberian Peninsula. In: Álvarez-Fernández E, Carcajal-Contreras D, eds. Not only food. Marine, terrestrial and freshwater molluscs in archaeological sites. Proceedings of the 2nd meeting of the ICAZ archaeomalacology working group (Santander, February 19th–22nd 2008). Donostia: Aranzadi Zientzia Elkartea, 100–109.

Mather JA, O’Dor RK. 1991. Foraging strategies and predation risk shape the natural history of juvenile Octopus vulgaris. Bulletin of Marine Science 49:256–269.

McQuaid CD. 1994. Feeding behaviour and selection of bivalve prey by Octopus vulgaris Cuvier. Journal of Experimental Marine Biology and Ecology 177(2):187–202 DOI 10.1016/0022-0981(94)90236-4.

Morse K. 1993. Shell beads from Mandu Mandu Creek rock-shelter, Cape Range peninsula, Western Australia, dated before 30,000 b.p. Antiquity 67(257):877–883 DOI 10.1017/S0003598X00063894.

Morton B, Peharda M, Harper E. 2007. Drilling and chipping patterns of bivalve prey predation by Hexaplex trunculus (Mollusca: Gastropoda: Muricidae). Journal of the Marine Biological Association of the UK 87(4):187–202 DOI 10.1017/S0025315407056184.

Movius HL. 1995. Inventaire analytique des sites aurignaciens et périgordiens de Dordogne. Paris: Éditions de la Maison des Sciences de l’Homme.

Mowles SL, Rundle SD, Cotton PA. 2011. Susceptibility to predation affects trait-mediated indirect interactions by reversing interspecific competition. PLOS ONE 6:e23068 DOI 10.1371/journal.pone.0023068.

Mussi M. 2002. Fully Equipped Hunter-Gatherers. In: Mussi M, ed. Earliest Italy. An Overview of the Italian Paleolithic and Mesolithic. Boston: Kluwer Academic Publishers, 219–282.

Mussi M, Coubray S, Giraudi C, Mazzaella G, Tonietti P, Wilkens T, Zampetti D. 2000. L’exploitation des territoires de montagne dans les Abruzzes (Italie centrale) entre le Tardiglaciaire et l’Holocène ancien. Actes de la Table Ronde “Epipaléolithique et Mésolithique” 81:277–284.

Neugebauer-Maresch C. 1999. Le Paléolithique en Autriche. Bulletin de la Société Préhistorique Française 97:313–314.

Nigra BT, Arnold JE. 2013. Explaining the monopoly in shell-bead production on the Channel Islands: drilling experiments with four lithic raw materials. Journal of Archaeological Science 40(10):3647–3659 DOI 10.1016/j.jas.2013.04.021.

Nixon M, Maconnachie E. 1988. Drilling by Octopus vulgaris (Mollusca: Cephalopoda) in the Mediterranean. Journal of Zoology 216(4):687–716 DOI 10.1111/j.1469-7998.1988.tb02466.x.

Nixon M, Young JZ. 2003. The brains and lives of cephalopods. Oxford: OUP Oxford.

Noble W, Davidson I. 1996. Human evolution, language and mind a psychological and archaeological inquiry. Cambridge: Cambridge University Press.
Oliva M, Yll R. 2010. The use of marine shell in Cingle Vermell and Roc del Migdia (Vilanova de Sau, Barcelona, Spain), two prehistoric sites in the western Mediterranean. First approach. In: Álvarez-Fernández E, Carcajal-Contreras D, eds. Not only food. Marine, terrestrial and freshwater molluscs in archaeological sites. Proceedings of the 2nd meeting of the ICAZ archaeomalacology working group (Santander, February 19th–22nd 2008). Donostia: Aranzadi Zientzia Elkartea, 138–145.

Passini G, Garassino A. 2012. Naticid gastropod and octopodid cephalopod predatory traces: evidence of drill holes on the leucosid crab Ristoria plicocaenica (Ristori, 1891), from the Pliocene of the “La Serra” quarry (Tuscany, Italy). Atti della società italiana di scienze naturali e del museo civico di storia naturale di Milano 153:257–266.

Peacock E, Randklev CR, Wolverton S, Palmer R, Zaleski S. 2012. The “cultural filter,” human transport of mussel shell, and the applied potential of zooarchaeological data. Ecological Applications 22(5):1446–1459 DOI 10.1890/11-1943.1.

Pechenik JA, Lewis S. 2000. Avoidance of drilled gastropod shells by the hermit crab Pagurus longicarpus at Nahant, Massachusetts. Journal of Experimental Marine Biology and Ecology 253(1):17–32 DOI 10.1016/S0022-0981(00)00234-3.

Quensen J, Woodruff D. 1997. Associations between shell morphology and land crab predation in the land snail cernion. Functional Ecology 11(4):464–471 DOI 10.1046/j.1365-2435.1997.00115.x.

Ramsay K, Richardson C, Kaiser M. 2001. Causes of shell scarring in dog cockles Glycymeris glycymeris L. Journal of Sea Research 45(2):131–139 DOI 10.1016/S1385-1101(01)00050-8.

Reimchen TE. 1982. Shell size divergence in Littorina mariae and L. obtusata and predation by crabs. Canadian Journal of Zoology 60(4):687–695 DOI 10.1139/z82-098.

Reynolds PD. 2002. The scaphopoda. Advances in Marine Biology 42:137–236.

Rodríguez Hidalgo AJ, Canals A, Saladié P, García AB, García Diez M. 2010. Upper Paleolithic ornament seashells from Sala de las Chimeneas, Maltravieso cave (Cáceres, Spain). In: Álvarez-Fernández E, Carcajal-Contreras D, eds. Not only food. Marine, terrestrial and freshwater molluscs in archaeological sites. Proceedings of the 2nd meeting of the ICAZ archaeomalacology working group (Santander, February 19th–22nd 2008). Donostia: Aranzadi Zientzia Elkartea, 36–46.

Rogalla NS, Amler MRW. 2007. Statistic approach on taphonomic phenomena in shells of Glycymeris glycymeris (Bivalvia: Glycymeridae) and its significance in the fossil record. Paläontologische Zeitschrift 81:334–355 DOI 10.1007/BF02990183.

Rosin ZM, Kobak J, Lesicki A, Tryjanowski P. 2013. Differential shell strength of Cepaea nemoralis colour morphs—implications for their anti-predator defence. Naturwissenschaften 100(9):843–851 DOI 10.1007/s00114-013-1084-8.

Rosin ZM, Olborska P, Surmacki A, Tryjanowski P. 2011. Differences in predatory pressure on terrestrial snails by birds and mammals. Journal of Biosciences 36(4):691–699 DOI 10.1007/s12038-011-9077-2.

Sadhukhan K, Raghunathan C. 2013. Feeding ecology of Asterina sarasini in reef communities of Andaman and Nicobar islands. International Journal of Plant, Animal and Environmental Sciences 3:137–144.
Sawyer J. 2010. Quantitative studies of drilling predation on Cenozoic and recent marine molluscs from Europe. D. Phil. thesis, University of Vienna.

Sawyer JA, Zuschin M. 2010. Intensities of drilling predation of molluscan assemblages along a transect through the northern Gulf of Trieste (Adriatic Sea). *Palaeogeography, Palaeoclimatology, Palaeoecology* 285(3–4):152–173 DOI 10.1016/j.palaeo.2009.11.007.

Schick K, Toth N. 2013. The origins and evolution of technology. In: Begun DR, ed. *A companion to paleoanthropology*. Oxford: Blackwell Publishing Ltd, 265–290.

Sella VD. 1916. *Paleolitico de cueto de la Mina (Austrias)*. Madrid: Junta para Ampliación de Estudios e Investigaciones Científicas, Museo Nacional de Ciencias Naturales.

Serrand N, Vigne J, Guilaine J. 2005. Early Preceramic Neolithic marine shells from Shillourokambos, Cyprus (late 9th–8th mill. cal BC): a mainly-ornamental set with similarities to mainland PPNB. In: Bar-Yosef-Mayer D, ed. *Archaeomalacology. Molluscs in former environments of human behaviour*. Oxford: Oxbow Books, 122–129.

Shumaker RW, Walkup KR, Beck BB. 2011. *Animal tool behavior: the use and manufacture of tools by animals*. New York: Johns Hopkins University Press.

Silva ACF, Hawkins SJ, Boaventura DM, Thompson RC. 2008. Predation by small mobile aquatic predators regulates populations of the intertidal limpet *Patella vulgata* (L.). *Journal of Experimental Marine Biology and Ecology* 367(2):259–265 DOI 10.1016/j.jembe.2008.10.010.

Silva A, Hawkins S, Clarke K, Boaventura D, Thompson R. 2010. Preferential feeding by the crab *Necora puber* on differing sizes of the intertidal limpet *Patella vulgata*. *Marine Ecology Progress Series* 416:179–188 DOI 10.3354/meps08777.

Sinitsyn A. 1993. Les niveaux Aurignaciens de Kostienki 1. In: Pavúk J, ed. *Actes du XII congrès international des sciences préhistoriques et préhistoriques* (Bratislava, 1–7 sept., 1991). Bratislava: Institut d’archéologie de l’Académie slovaque des sciences, 242–259.

Sinitsyn A. 2003. A Palaeolithic “Pompeii” at Kostenki, Russia. *Antiquity* 77(295):9–14 DOI 10.1017/S0003598X00061299.

Smith CD. 2003. Diet of *Octopus vulgaris* in false bay, South Africa. *Marine Biology* 143(6):1127–1133 DOI 10.1007/s00227-003-1144-2.

Sokal RR, Rohlf FJ. 1981. *Biometry: the principles and practice of statistics in biological research*. New York: W.H. Freeman and Company.

Soler-Major N. 2001. Adorno, imagen y comunicación. In: Villaverde Bonilla V, ed. *De Neandertals a Cromanyons. El inicio del poblamiento humano en las tierras valencianas*. Valencia: Servei de l’Àrea Cultural de la Universitat de València, 367–376.

Stenzler D, Atema J. 1977. Alarm response of the marine mud snail, *Nassarius obsoletus*: specificity and behavioral priority. *Journal of Chemical Ecology* 3(2):159–171 DOI 10.1007/BF00994143.
Stiner MC. 1999. Paleolithic mollusc exploitation at riparo mochi (Balzi Rossi, Italy): food and ornaments from the aurignacian through epigravettian. *Antiquity* 73:735–754.

Stiner M. 2010. Shell ornaments from the Upper Paleolithic and Mesolithic layers of Klissoura Cave 1 by Prosymnia, Greece. *Eurasian Prehistory* 7:287–308.

Stiner MC. 2014. Finding a common bandwidth: causes of convergence and diversity in paleolithic beads. *Biological Theory* 9(1):51–64 DOI 10.1007/s13752-013-0157-4.

Stiner MC, Kuhn SL, Güleç E. 2013. Early Upper Paleolithic shell beads at Uçagızlı Cave I (Turkey): technology and the socioeconomic context of ornament life-histories. *Journal of Human Evolution* 64(5):380–398 DOI 10.1016/j.jhevol.2013.01.008.

Szabo K, Brumm A, Bellwood P. 2007. Shell artefact production at 32,000–28,000 BP in Island Southeast Asia: thinking across media? *Current Anthropology* 48(5):701–723 DOI 10.1086/520131.

Taborin Y. 1993. *La parure en coquillage au Paléolithique*. Paris: Editions du C.N.R.S.

Taraschewski H, Paperna I. 1982. Trematode infections in *Pirenella conica* in three sites of a mangrove lagoon in Sinai. *Zeitschrift für Parasitenkunde* 67(2):165–173 DOI 10.1007/BF00928112.

Tátá F, Casaçalheira J, Marreiros J, Pereira T, Bicho N. 2014. Shell bead production in the Upper Paleolithic of Vale Boi (SW Portugal): an experimental perspective. *Journal of Archaeological Science* 42:29–41 DOI 10.1016/j.jas.2013.10.029.

Tongiorgi P, Nardi P, Galleni L, Nigro M, Salghetti U. 1981. Feeding habits of ocinebrina edwardsi (Mollusca: Prosobranchia) a common mussel drill of the Italian coasts. *Marine Ecology* 2(2):169–180 DOI 10.1111/j.1439-0485.1981.tb00270.x.

Turra A, Denadai MR, Leite FPP. 2005. Predation on gastropods by shell-breaking crabs: effects on shell availability to hermit crabs. *Marine Ecology Progress Series* 286:279–291 DOI 10.3354/meps286279.

Vanhaeren M, D’Errico F. 2005. Grave goods from the Saint-Germain-la-Rivière burial: evidence for social inequality in the Upper Palaeolithic. *Journal of Anthropological Archaeology* 24(2):117–134 DOI 10.1016/j.jaa.2005.01.001.

Vanhaeren M, D’Errico F. 2006. Aurignacian ethno-linguistic geography of Europe revealed by personal ornaments. *Journal of Archaeological Science* 33(8):1105–1128 DOI 10.1016/j.jas.2005.11.017.

Vanhaeren M, D’Errico F. 2011. L’emergence du corps paré. *Civilisations* 59:59–86.

Vanhaeren M, D’Errico F, Billy I, Grousset F. 2004. Tracing the source of Upper Palaeolithic shell beads by strontium isotope dating. *Journal of Archaeological Science* 31(10):1481–1488 DOI 10.1016/j.jas.2004.03.011.

Vanhaeren M, D’Errico F, Stringer C, James SL, Todd JA, Mienis HK. 2006. Middle Paleolithic shell beads in Israel and Algeria. *Science* 312(5781):1785–1788 DOI 10.1126/science.1128139.

Vanhaeren M, D’Errico F, Van Nierkerk KL, Henshilwood CS, Erasmus RM. 2013. Thinking strings: additional evidence for personal ornament use in the Middle Stone Age at Blombos Cave, South Africa. *Journal of Human Evolution* 64(6):500–517 DOI 10.1016/j.jhevol.2013.02.001.
Vezian J, Vezian J. 1966. Les gisements de la grotte de Saint-Jean-de-Verges (Ariège). *Gallia Préhistoire* 9(1):93–130 DOI 10.3406/galip.1966.1260.

Walker SE, Brett CE. 2002. Post-paleozoic patterns in marine predation post-paleozoic patterns in marine predation: was there a mesozoic and cenozoic marine predatory revolution? *Paleontological Society Papers* 8:119–194.

Wild EM, Neugebauer-Maresch C, Einwögerer T, Stadler P, Steier P, Brock F. 2008. 14C dating of the Upper Paleolithic site at Krems-Hundssteig in Lower Austria. *Radiocarbon* 50(1):1–10 DOI 10.1017/S0033822200043332.

Wilkens B. 2005. The use of marine shells at Sumhuram, Oman. In: Bar-Yosef-Mayer D, ed. *Archaeomalacology. Molluscs in former environments of human behaviour*. Oxford: Oxbow Books, 159–165.

Yochelson E, Dockery D, Wolf H. 1983. Predation on sub-holocene scaphopod mollusks from Southern Louisiana. Washington: Geological Survey Professional Paper, 1282.

Zagyvai Á, Demeter G. 2008. Tracing prey-predatory interactions in the Early Sarmatian (Mid-Miocene) shelly community from Rollsdorf Formation, Waldhof, Austria based on bioerosional observations. *Acta Geographica a Geologica et Meteorologica Debrecina* 3:51–60.

Zilhão J. 2007. The emergence of ornaments and art: an archaeological perspective on the origins of “behavioral modernity”. *Journal of Archaeological Research* 15(1):1–54 DOI 10.1007/s10814-006-9008-1.

Zilhão J. 2010. Neanderthals are us: genes and culture. *Radical Anthropology* 4:4–15.

Zilhão J. 2011. Aliens from outer time? Why the human revolution is wrong, and where do we go from here? In: Condemi S, Weniger G-C, eds. *Continuity and discontinuity in the peopling of Europe. Vertebrate paleobiology and paleoanthropology*. Dordrecht: Springer Netherlands, 331–366.

Zilhão J, Angelucci DE, Badal-García E, D’Errico F, Daniel F, Dayet L, Douka K, Higham TFG, Martínez-Sánchez MJ, Montes-Bernárdez R, Murcia-Mascarós S, Pérez-Sirvent C, Roldán-García C, Vanhaeren M, Villaverde V, Wood R, Zapata J. 2010. Symbolic use of marine shells and mineral pigments by Iberian Neandertals. *Proceedings of the National Academy of Sciences of the United States of America* 107(3):1023–1028 DOI 10.1073/pnas.0914088107.

Zlotnik M. 2001. Size-related changes in predatory behaviour of naticid gastropods from the Middle Miocene Korytnica Clays, Poland. *Acta Palaeontologica Polonica* 46:87–97.

Zugasti FIG. 2010. Exploitation of molluscs and other littoral resources in the Cantabrian region during the late Pleistocene and the early Holocene. Paris: Universidad de Cantabria.