



## What can microshells tell us? A case-study from the Palaeolithic site of Riparo Bombrini (Balzi Rossi, NW Italy)

Silvia Gazzo<sup>a</sup>, Fabio Negrino<sup>a,\*</sup>, Julien Riel-Salvatore<sup>b</sup>, Stefano Schiaparelli<sup>c</sup>

<sup>a</sup> Department of Antiquities, Philosophy, History (DAFIST), University of Genoa, Via Balbi, 2, 16126, Genoa, Italy

<sup>b</sup> Department of Anthropology, University of Montreal, 2900 Edouard Montpetit Blvd, Montreal, QC, H3T 1N8, Canada

<sup>c</sup> Department of Earth, Environment and Life Sciences (DISTAV), University of Genoa, C.so Europa 26, I-16132, Genoa, Italy

### ARTICLE INFO

#### Keywords:

Marine molluscs  
Taphonomy  
Microshells  
Mousterian  
Protoaurignacian

### ABSTRACT

The exploitation of marine molluscs during the Middle and Upper Palaeolithic is a topic that has been extensively investigated over the last few years, shedding light on human adaptation in coastal environments. However, such studies mainly focus on the role of marine molluscs in the subsistence practices of the hunter-fisher-gatherers of the Mediterranean Basin.

Although small, non-dietary gastropods found in archaeological deposits have the potential to provide important clues regarding past human activities, their role is still little investigated. This research explores the question of whether taphonomy could be useful for the interpretation of these less conspicuous “incidental” shell remains found in archaeomalacological assemblages.

In this paper we present the results of a taphonomic study carried out on a total of 314 *Bittium* shells recovered in the Mousterian and Protoaurignacian levels of Riparo Bombrini, a collapsed rockshelter in the Balzi Rossi Palaeolithic site complex (NW Italy). How did these small, non-dietary gastropods come to be deposited? Are they an unintentional by-product of certain harvesting techniques, or the result of a deliberate gathering? Or, could natural factors be responsible for their presence at the site? To answer these questions, different types of taphonomic processes were considered. Comparing the Bombrini archaeomalacological remains and modern shells accumulated on beaches leads us to propose that the most likely cause of their presence at the site is a correlation between *Bittium* shells and small sea pebbles, rather than the accidental transport of these shells with algae and seagrasses that could have been brought back to the site.

### 1. Introduction

The role of marine molluscs in prehistoric Mediterranean subsistence practices and symbolic material culture has generated much debate among archaeologists over the last decade. However, most of the debate is focused on large-sized species (i.e., macromolluscs) to examine past human subsistence strategies, economy, land use practices and aspects of social organization, as well as paleoenvironmental conditions and impacts on littoral areas. Particularly, numerous works focused on Early Upper Palaeolithic shell beads and their key role in understanding symbolic behaviour, ethnocultural identities, and exchange networks of the first Anatomically Modern Humans (e.g., Newell et al., 1990; Taborin, 1993; Fritz and Simonnet, 1996; White, 1999; Álvarez-Fernández, 2001; Stiner, 2003; Vanhaeren and d’Errico, 2003;

Vanhaeren et al., 2004; Vanhaeren and d’Errico, 2005, 2006, 2013).

Non-dietary marine micromolluscs found in Palaeolithic archaeological sites have received far less attention. This is partly because their presence in shell assemblages may have been underestimated – especially in older collections – due to the poor quality of early excavation methods that often did not allow the retrieval of such small objects. As a result, possible explanations for their presence in archaeological deposits have rarely been considered in detail, and simplistic interpretations have been favoured.

Micromolluscs are defined as shelled molluscs with the greatest dimension of their shell being less than 10 mm at full adult size (Beu and Maxwell, 1990). When found in archaeological sites, they represent an important tool for paleoenvironmental reconstructions and provide important clues regarding littoral ecosystems and their transformation

\* Corresponding author.

E-mail addresses: [silvia.gazzo@edu.unige.it](mailto:silvia.gazzo@edu.unige.it) (S. Gazzo), [fabio.negrino@unige.it](mailto:fabio.negrino@unige.it) (F. Negrino), [julien.riel-salvatore@umontreal.ca](mailto:julien.riel-salvatore@umontreal.ca) (J. Riel-Salvatore), [stefano.schiaparelli@unige.it](mailto:stefano.schiaparelli@unige.it) (S. Schiaparelli).

<https://doi.org/10.1016/j.qsa.2023.100104>

Received 25 March 2023; Received in revised form 30 May 2023; Accepted 18 July 2023

Available online 19 July 2023

2666-0334/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

over time. Remains of small cerithiids belonging to the genus *Bittium* (Gray, 1847) have been identified in archaeological contexts dated as far back as the Lower Palaeolithic, in the Acheulean occupation level of Grotte du Lazaret (French Côte-d'Azur) (Barrière, 1969; de Lumley et al., 2004; Valensi et al., 2007). Small gastropod shells, including *Bittium*, were also found in Upper Palaeolithic deposits at Grotta della Serratura (Marina di Camerota, Salerno) (Colonese and Wilkens, 2005; Martini et al., 2005), Grotta dell'Addaura (Monte Pellegrino, Palermo) (Mannino et al., 2011), Grotta d'Oriente (Favignana, Trapani) (Colonese et al., 2018), Grotta del Cavallo (Nardò, Lecce) (Arrighi et al., 2020), Grotta della Cala (Marina di Camerota, Salerno) (Fiocchi, 1998), Grotta di Fumane (Western Lessini Mountains, Verona) (Peresani et al., 2019) and Riparo Mochi (Balzi Rossi, Imperia) (Stiner, 1999) in the Italian Peninsula; Cueva Foradada (Xàbia, Spain) in Mediterranean Iberia (Casabó i Bernad, 1997; Verdún-Castelló and Casabó i Bernad, 2020); and Franchthi Cave, on the Argolid Peninsula of the Peloponnese (Greece) (Douka et al., 2011).

Since members of the genus *Bittium* live shallow benthic marine habitats in association with sea grasses (e.g., *Zostera*, *Posidonia*), seaweeds (e.g., *Cystoseira*) and algae (D'Angelo and Gargiulo, 1978; Fretter and Graham, 1981; Urra et al., 2013), some authors suggested that these small gastropods with no nutritional value to humans reached the sites unintentionally, mixed in algae, kelp or seagrass, brought to the settlements by Palaeolithic hunter-fisher-gatherers (Martini et al., 2005; Valensi et al., 2007; Colonese et al., 2018; Verdún-Castelló and Casabó i Bernad, 2020). However, human use of marine organisms such as seagrasses and seaweeds has been inferred indirectly and a systematic taphonomic study to better understand the introduction of these small-sized taxa into occupation layers has never been carried out. It is suggested that marine algae and plants have been harvested by human groups as bedding material and fuel for fires (de Lumley et al., 2004) or as food resources – roughly 150 species of seaweeds are considered edible with some species boasting mineral contents higher than many land plants (Kumar et al., 2008). Additionally, ethnobotanical studies reveal substantial and varied uses of marine plants (both living and dead) by traditional coastal communities worldwide, including the production of cordage, nets, basketry and medicine (Scagel, 1961; Turner and Bell, 1973; McRoy and Helfferich, 1980; Connolly et al., 1995; Vellanoweth et al., 2003; Mouritsen, 2013; Milchakova et al., 2014; Ainis et al., 2019).

From an archaeological point of view, early direct evidence of human use of marine plants dates back to the Early Holocene, when seagrasses were collected to produce cordage and other artefacts (Connolly et al., 1995; Vellanoweth et al., 2003).

The present article assesses the importance of marine micromolluscs found in archaeological records by presenting proper taxonomic and taphonomic analyses carried out on *Bittium* shell remains from Mousterian and Protoaurignacian levels of Riparo Bombrini, Italy. This research also considers their inclusion in the assemblage and the significance of their presence.

## 2. Riparo Bombrini: archaeological setting

Riparo Bombrini is a collapsed rock shelter that is part of well-recognized Balzi Rossi archaeological complex within an iron-stained cliff formation of Upper Jurassic dolomitic limestone, in Western Liguria (Imperia province, NW Italy) (Fig. 1a–b) (Holt et al., 2019).

Initially tested in 1938, Riparo Bombrini was first properly investigated using controlled recovery and documentation methods by G. Vicino in 1976, ahead of partial destruction due to the construction of a walkway built to facilitate access to other sites at Balzi Rossi. A quarter century later, excavations led by the University of Pisa resumed at the site (lasting from 2002 to 2005) to elucidate the timing and behavioural aspects of the region's Middle-Upper Paleolithic transition. In 2015, renewed excavations at the site began under the direction of two of the authors (F.N. and J.R.-S.) (Fig. 1c). The most recent phase of fieldwork,

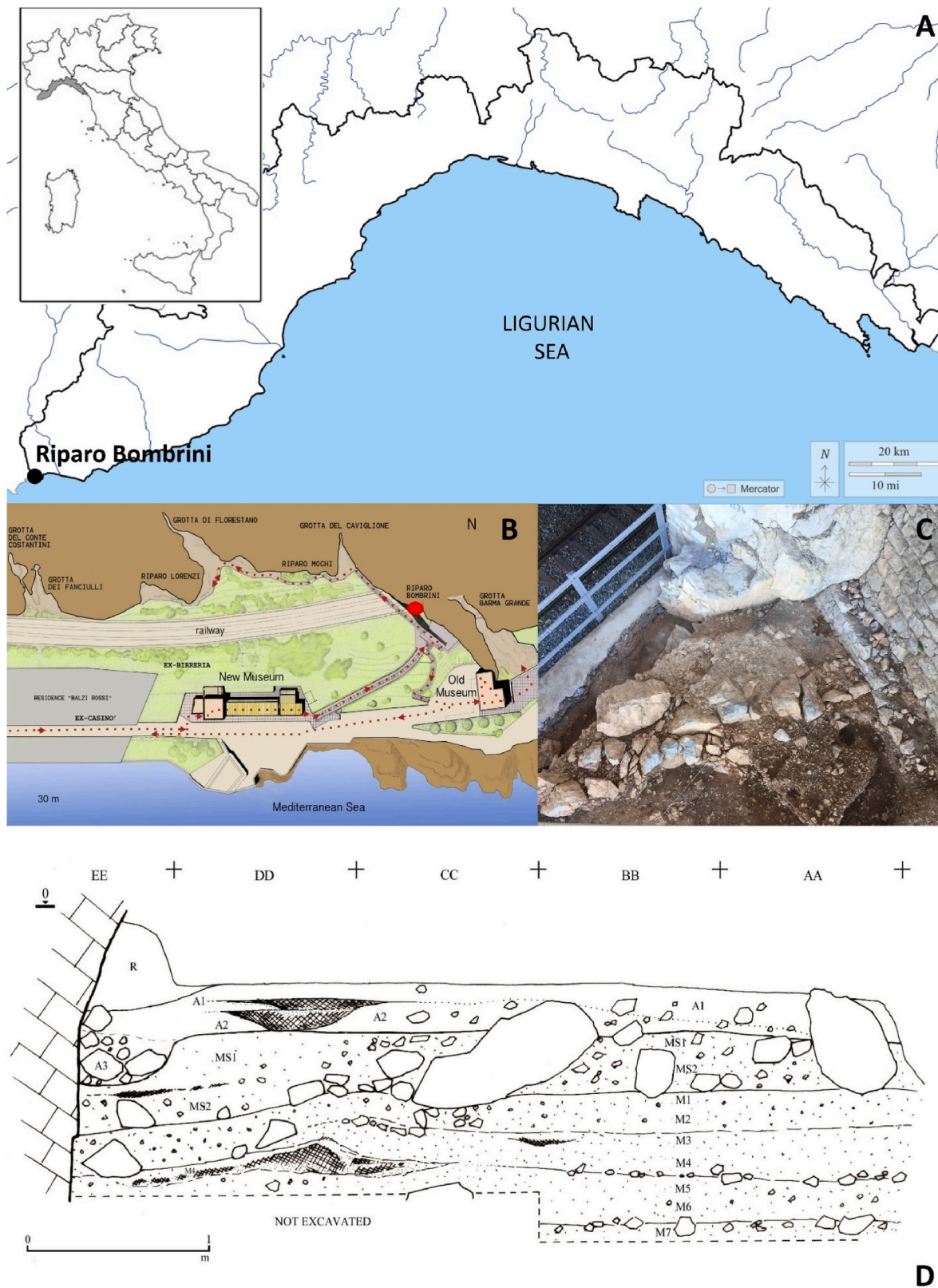
which concluded in 2022, applied new analytical methods to document the transition over a more extensive area (Negrino et al., 2016; Negrino and Riel-Salvatore, 2018; Riel-Salvatore and Negrino, 2018a). These methods included, among other techniques, the large-scale implementation of a ZooMS program to identify faunal remains at the site (Pothier-Bouchard et al., 2019, 2020). This research also involved integrating the collections and documentation collected since 1976 into an updated dataset to permit a fine-grained understanding of diachronic shifts in human occupation. This has permitted detailed analyses of Mousterian and Protoaurignacian chronology, lithic technology, spatial organization, and faunal exploitation strategies at the site, as well as determination of the spatial context of the deciduous *H. sapiens* incisor recovered from the Protoaurignacian level A2 in 1976 (Benazzi et al., 2015). It has also allowed the integration of data from Bombrini in recent syntheses of the lithic, faunal, and symbolic dimensions of the Middle-Upper Paleolithic transition in Italy (Arrighi et al., 2020; Marciani et al., 2020; Romandini et al., 2020).

More than ten years of excavation have allowed the distinction of three macro-units of human occupation at Riparo Bombrini (Fig. 1d; S1; S2; S3). The first macro-unit comprises Protoaurignacian levels A1, A2 and A3. Level A3 is present only as a strip of relict deposits against the site's back wall and almost completely devoid of artefacts. These levels consist of a yellowish clayey loam deposit 10–20 cm thick that accumulated over large blocks of roof collapse in the immediately underlying level of the Final Mousterian. The Protoaurignacian macro-unit has been dated using radiocarbon analysis of charcoal to ca. 41–36.5 ka cal. BP (Holt et al., 2019).

The below macro-unit is separated from the Protoaurignacian by an erosional horizon and consists of the 'semi-sterile' Final Mousterian deposits (divided into levels MS1–2) dated between ca. 43–42 ka cal. BP. Levels MS1 and MS2 consist of several large blocks of roof fall and coarse bedrock clasts in a clayey loam matrix with a total thickness of 30–40 cm. They are characterized by scant traces of human activity and the presence of carnivore coprolites, suggesting the shelter was frequented sporadically at a time when Neanderthals occupied Liguria as a contracting refugium (Riel-Salvatore et al., 2022). The third macro-unit comprises Late Mousterian deposits, which accumulated between ca. 45–43 ka cal. BP; this incorporates levels M1–7 that have been excavated over a depth of about 70 cm and contain an abundance of roof spall throughout. The sediments increase in redness and clay content with depth.

Preliminary analyses have demonstrated the presence of concentrated combustion zones and distinct activity areas across all Mousterian levels. Furthermore, despite their technological differences, variable land-use and mobility strategies can be identified in both the Protoaurignacian and the Mousterian (Riel-Salvatore, 2010; Negrino et al., 2016, 2018; Negrino and Riel-Salvatore, 2018; Riel-Salvatore and Negrino, 2018b). The Mousterian levels have yielded abundant remains of fauna and malacofauna, as well as lithic artefacts made mainly from local and circum-local raw materials. The Protoaurignacian, on the other hand, is characterized by a significant presence of bladelets, transformed into retouched Dufour-type bladelets and made from raw materials obtained from very distant outcrops, including flints from western Provence region (south-eastern France) or from the Adriatic area (Marche region, Italy); also present are awls and needles on bone, as well as abundant red ochre and several decorative elements, including perforated sea shells, steatite pendants and fossil belemnites (Holt et al., 2019).

Both Mousterian and Protoaurignacian faunal assemblages are dominated by large cervids (mainly red deer - *Cervus elaphus* - and roe deer - *Capreolus*). However, other taxa like bovines (*Bos/Bison*), caprids (*Capra*) and wild boar (*Sus*) were also regularly hunted (Holt et al., 2019; Pothier-Bouchard et al., 2020). Zooarchaeological analysis of large mammal species from macro-unit MS indicates a very similar faunal composition, with an overall dominance of cervids (23%) (Riel-Salvatore et al., 2022). The faunal assemblages are similar across cultural



**Fig. 1.** a) Location of Riparo Bombrini, in the region of Liguria (NW Italy). b) Map of the Balzi Rossi (Ventimiglia, Italy) with archaeological sites indicated and Riparo Bombrini highlighted (modified from Holt et al., 2019). c) Excavation area of Riparo Bombrini. d) Stratigraphic profile of Riparo Bombrini with Protoaurignacian (A1-A3), Final Mousterian (MS1-MS2), and Late Mousterian (M1-M7) levels indicated.



horizons; however, bovids, mountain goats (*Capra ibex*) and chamois (*Rupicapra rupicapra*) are more frequent in the Upper Palaeolithic levels, implying that the Protoaurignacian assemblages were accumulated under slightly colder conditions. Also, the presence of remains of rhinoceros and equids in level A2 points to the presence of an open plain ecosystem between the Balzi Rossi cliffs and the coastline (Holt et al., 2019; Pothier-Bouchard et al., 2020).

### 3. *Bittium* shells: ecological aspects

*Bittium* (Gray, 1847) is a common genus of small (usually less than 10 mm) sea snails generally occurring in seagrasses meadows (Fretter and Graham, 1981), where it represents a quantitatively dominant, although not exclusive, fraction of the whole fauna (Pérès, 1967). It can also be found in association with seaweeds (Fretter and Graham, 1981) or on rock surfaces, and in crevices (Laubier, 1966). As *Bittium* species are typically found in shallow sublittoral zones, they may be used as an ecological indicator for benthic habitats of the phytal zone. Gastropods of this genus forage on a variety of food items, ranging from sponges, foraminifera, and small molluscs. *B. reticulatum* (da Costa, 1778) was reported by Starmühlner (1956) to feed on diatoms. *Bittium latreillii* (Payraudeau, 1826) is one of the most dominant species living on *Posidonia oceanica* leaves (Russo and Terlizzi, 1998), but its life history, ecology, and feeding mechanism are still little investigated (Russo et al., 2002). *Bittium* are very common on the coasts of Liguria, where mostly dead specimens can be found on its shores.

## 4. Materials and methods

### 4.1. Archaeological sample

A total of 381 micromollusc remains (314 *Bittium*) were collected from the site (field season: 1976, 2002 to 2005, 2015 to 2019 and 2022) and analysed for this paper. The retrieval of microshells was achieved by the water-sieving of sediment bulks through 2 mm mesh sieves. Shells were then sorted dry using tweezers. Specimens were identified to the lowest taxonomic level based on shape, colour, size, and ornamentation using reference collections held at the Paleoethnology Laboratory of the Department of Antiquities, Philosophy, History (DAFIST) at the University of Genoa, and supported by standard taxonomic literature (e.g., D'Angelo and Gargiulo, 1978; Poppe and Goto, 1993; Doneddu and Trainito, 2010; Cossignani and Ardovini, 2011). The nomenclature of the species listed was assigned following the updated online *World Register of Marine Species* (WoRMS, 2023). Specimens were quantified using the Number of Identified Specimens (NISIP) and the Minimum Number of Individuals (MNI). The MNI was estimated for each taxonomic designation and level using the highest number of whole individuals and the diagnostic parts of shells (i.e., apex and aperture). Since *Bittium* fall within the shell category with apical and basal remains, in each case we added complete remains plus the apical or basal, whichever was more abundant, following Gutiérrez-Zugasti (2011). Biometric measurements taken for *Bittium* shells are as follows: length (SL), from the apex to the base of the peristome; width (SW), taken at the widest part of the shell, usually that of the last whorl; aperture length (AL), and aperture width (AW) (Fig. S4).

### 4.2. The taphonomic study

Taphonomic analysis was performed using an OPTIKA SZN-6 Stereo Microscope with Parfocal achromatic zoom 0.67X – 4.5X.

The taphonomy of the analysed microshells was explored with a particular focus on pre-depositional processes related to the marine environment (i.e., effects of marine abrasion, fragmentation, encrustation and bioerosion). Anthropogenic modifications of archaeological remains (i.e., signs of burning and traces of mineral pigments) and post-depositional natural alterations (i.e., decalcification, and post-

depositional cracks) were also considered in this study.

We identified three different categories of preservation for *Bittium* remains: (1) intact shells with complete anatomical elements; (2) partially incomplete shells with more than 50% anatomical integrity; and (3) incomplete shells with less than 50% of anatomical integrity containing one or more diagnostic elements. Fragmentation index was calculated for each category after dividing the assemblage into complete and incomplete shells, using the formula MNI/NISP. We also considered shell breakage that occurred during rinsing and sieving the samples, even though these procedures were carried out very carefully.

To photograph the shells, we used a Dino-Lite Edge Digital Microscope (10X-140X magnification) supported with DinoCapture 2.0 software, while the low-vacuum TM3030Plus tabletop Scanning Electron Microscope (SEM) was used to photograph a representative sample of predation holes and areas of the shell surface from which optical and digital microscopes could not obtain information due to depth of field (Ollé et al., 2016; García-Argudo et al., 2020). SEM images were captured by Deirdre D. Ryan at the Department of Earth Sciences of the University of Pisa (Italy).

### 4.3. Modern sample

Since the study of taphonomic processes in present-day environments is a particularly useful tool for elucidating taphonomic patterns in archaeological assemblages, a sampling of recently (modern) dead *Bittium* shells was conducted in April 2016 and February 2022 along the coast of Sestri Levante, Levante Ligure (44° 16' 23" N, 9° 23' 48" E), approximately 40 km southeast of Genoa (Italy). The environmental setting is a narrow strip of pebble beach containing shells and shell debris of a mixed sublittoral-intertidal origin. Larger specimens were systematically collected by hand, while the smaller ones were recovered from sieving the sediments. Specimens were picked out using tweezers, examined, and the species were identified. In total, we collected about 2000 small gastropods, some of which were later identified as *Cerithiopsis* sp. and excluded from the present study.

We randomly selected 400 modern adult-sized *Bittium* shells of different species as a modern comparative. These were microscopically analysed and compared with the archaeological specimens. Live-collected shells from the reference collection were also used as a comparative sample.

## 5. Results

### 5.1. Archaeological materials

A total of 22 different taxa of small gastropods predominantly (sometimes exclusively) associated with seaweeds and seagrasses, were identified, accounting for a total of 381 shell remains. The most dominant genus is *Bittium* (NISIP 314), while other taxa such as *Melarhaphe neritoides* (NISIP 34), *Alvania* sp. (NISIP 8), *Rissoa* sp. (NISIP 7), *Cerithiopsis* sp. (NISIP 6), *Alvania mamillata* (NISIP 2), are only sporadically represented (Fig. 2).

Taxonomic analysis of *Bittium* shells reveals high taxonomic richness, the most common species being *Bittium reticulatum* (14.6%) and *Bittium latreillii* (13.4%) in both periods (Table 1). Unsurprisingly, many specimens (61.8%) were not identified to species level (*Bittium* sp.) due to fragmentation, decalcification, and fading of the diagnostic natural shell markings.

In general, the degree of fragmentation is quite low and similar across the two assemblages, probably due to the morpho-structural features of shells.

Excavations of the Protoaurignacian levels A1, A2, A1-A2 and A3 yielded a total of 2645 mollusc remains, including micromolluscs and larger shellfish taxa known to be of dietary value, as well as shell beads made for ornamental purposes. A total of 138 *Bittium* shells belonging to different species (Table 2) were identified in these levels. Although level



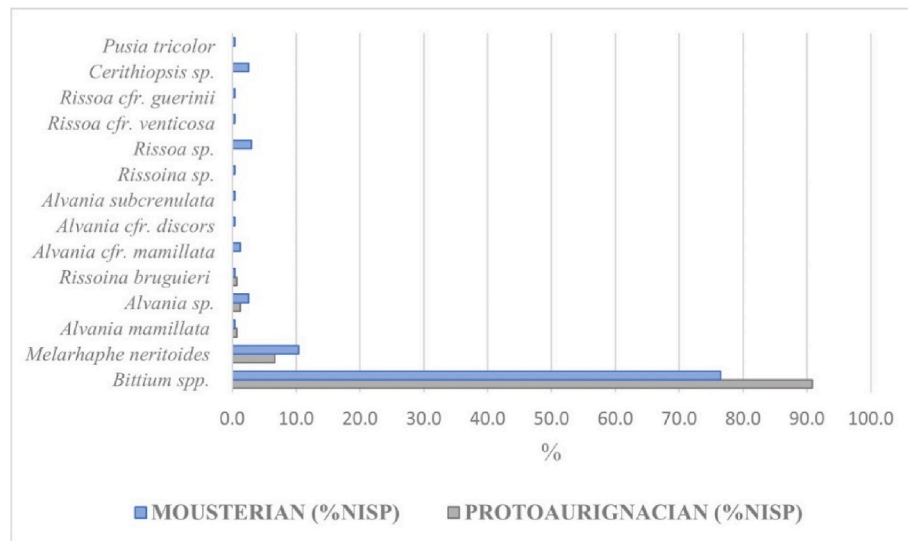


Fig. 2. %NISP of micromolluscs retrieved from Mousterian and Protoaurignacian levels at Riparo Bombrini.

Table 1

Taxonomic composition of *Bittium* shell assemblages (NISP and %NISP) in archaeological levels and in the modern sample.

TAXA	Protoaurignacian		Mousterian		Modern	
	NISP	%	NISP	%	NISP	%
<i>Bittium latreillii</i>	12	8.7	30	17.0	208	52.0
<i>Bittium cfr. latreillii</i>	4	2.9	4	2.3	13	3.3
<i>Bittium reticulatum</i>	24	17.4	22	12.5	83	20.8
<i>Bittium cfr. reticulatum</i>	3	2.2	3	1.7	4	1.0
<i>Bittium lacteum</i>	1	0.7	–	–	1	0.3
<i>Bittium cfr. lacteum</i>	2	1.4	1	0.6	–	–
<i>Bittium simplex</i>	6	4.3	1	0.6	–	–
<i>Bittium cfr. simplex</i>	5	3.6	–	–	3	0.8
<i>Bittium jadertinum</i>	–	–	1	0.6	–	–
<i>Bittium cfr. incile</i>	1	0.7	–	–	–	–
<i>Bittium sp.</i>	80	58.0	114	64.8	88	22.0
<b>TOT.</b>	<b>138</b>	<b>100.0</b>	<b>176</b>	<b>100.0</b>	<b>400</b>	<b>100.0</b>

Table 2

*Bittium* species abundance (NISP and MNI) in the Protoaurignacian levels of Riparo Bombrini.

TAXA	A1		A1-A2		A2		A3	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
<i>Bittium reticulatum</i>	1	1	1	1	16	15	6	6
<i>Bittium cfr. reticulatum</i>	1	1	–	–	2	2	–	–
<i>Bittium latreillii</i>	4	4	–	–	8	8	–	–
<i>Bittium cfr. latreillii</i>	–	–	2	2	2	2	–	–
<i>Bittium simplex</i>	3	3	–	–	1	1	2	2
<i>Bittium cfr. simplex</i>	4	4	1	1	–	–	–	–
<i>Bittium lacteum</i>	1	1	–	–	–	–	–	–
<i>Bittium cfr. lacteum</i>	2	2	–	–	–	–	–	–
<i>Bittium cfr. incile</i>	1	1	–	–	–	–	–	–
<i>Bittium sp.</i>	23	19	4	3	35	31	18	17
<b>TOT.</b>	<b>40</b>	<b>36</b>	<b>8</b>	<b>7</b>	<b>64</b>	<b>59</b>	<b>26</b>	<b>25</b>

A2 is the one that yielded a largest number of specimens (46.4%), we can observe a general homogeneity in *Bittium* distribution along the whole Protoaurignacian sequence. Remains of *Bittium* shells are mainly

distributed in squares located inside the rock shelter – especially in EE2 and FF3 – while only few specimens were retrieved from the exterior area (Table S1).

Mousterian levels MS1, MS2, MS1-2, M1, M1-M2, M2, M3, M4, M5, M6 and M7 yielded a total of 1600 shell remains, almost exclusively represented by fragments of large edible mussels, *Mytilus galloprovincialis*, and top snails, *Phorcus turbinatus*. Micromolluscs are documented as well, and the genus *Bittium* is the best represented (NISP 176).

As shown in Table 3, level MS1 yielded most of the *Bittium* remains, accounting 57.4% of the specimens retrieved from Mousterian. Spatial distribution of *Bittium* remains in Middle Palaeolithic levels is similar to the one observed in the uppermost Protoaurignacian levels, with a greater concentration in the interior area (squares EE2, EE3, DD2 and CC2) (Table S2).

In Protoaurignacian levels, most of the remains are complete (37%) or partially complete (45.7%), while only 17.4% are fragmented. A very similar pattern can be observed in Mousterian levels, where 20.5% of *Bittium* remains are fragmented, suggesting that pre-depositional and/or post-depositional breaks occurred very similarly in shells from the two assemblages. Partially complete shells represent 49.4% of the Mousterian assemblage, while 30.1% are complete (Fig. S5).

Most partially complete shells have lost their last (aperture) or first (apex) body whorl, indicating that the thin structure of these anatomical parts makes them especially prone to fracture. The fragmentation index (MNI/NISP) reveals an excellent overall preservation in all levels, especially in Protoaurignacian, where the rate of fragmentation is very low (Fig. S6).

Biometric data (maximum length sizes) (Fig. S7) reveals that most complete shells range between 7–8 and 8–9 mm, while 14.4% are >10 mm.

Pre-depositional processes indicating that shells reached the site post-mortem are well documented in both Protoaurignacian and Mousterian levels (Fig. 3; Table S3). The best represented taphonomic process related to the marine environment is erosion caused by natural abrasive action resulting in shell discoloration, loss of natural markings and sometimes natural holes on the shell surface.

We identified natural erosion on 37.9% of the shells, of which 31% bear a natural hole with thinned margins. In Protoaurignacian levels, marine abrasion affects 48.6% of the remains (Fig. 4a–b), while it is less common (29.5%) in Mousterian materials (Fig. 4c).

Traces of predated gastropods were distinguished from dwelling burrows of the boring sponge *Cliona*. Small and diffused holes produced by boring sponges were mainly noted in the Protoaurignacian levels,

**Table 3**  
*Bittium* species abundance (NISP and MNI) in the Mousterian levels of Riparo Bombrini.

TAXA	MS1		MS 1-2		MS2		M1		M1-M2		M2		M3		M4		M5		M6		M7	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
<i>Bittium reticulatum</i>	15	15	3	3	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1
<i>Bittium</i> cfr. <i>reticulatum</i>	2	2	-	-	-	-	-	-	-	-	-	-	1	1	1	1	-	-	-	-	-	-
<i>Bittium latreillii</i>	14	13	2	2	1	1	1	1	1	1	1	4	4	2	2	2	5	4	1	1	1	1
<i>Bittium</i> cfr. <i>latreillii</i>	1	1	-	-	-	-	-	-	-	-	-	3	3	3	3	-	-	-	-	-	-	-
<i>Bittium</i> cfr. <i>simplex</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-
<i>Bittium</i> cfr. <i>lacteum</i>	-	-	-	-	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-
<i>Bittium jaderitium</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-
<i>Bittium</i> sp.	69	52	3	3	4	4	7	5	1	1	4	2	4	3	15	9	6	3	-	-	1	1
<b>TOT.</b>	<b>101</b>	<b>83</b>	<b>8</b>	<b>8</b>	<b>7</b>	<b>7</b>	<b>7</b>	<b>5</b>	<b>1</b>	<b>1</b>	<b>6</b>	<b>4</b>	<b>12</b>	<b>11</b>	<b>19</b>	<b>13</b>	<b>13</b>	<b>9</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>

where they occur in 20.3% of the remains. Gastropod predation affects 6.5% of the shells from the Protoaurignacian levels, while only two specimens (1.1%) from the Late Mousterian levels (M3 and M5) show perfectly rounded holes caused by predators (Fig. 4d-e).

Anthropogenic modifications are quite uncommon in the analysed assemblages, supporting the idea of an unintentional minimal human intervention. Thermal alteration affects only five specimens distributed in Protoaurignacian levels A1, A2 and A3 (Fig. 5a). Furthermore, shell structures are well preserved, suggesting that the heat exposure may have been of short duration or the temperature relatively low. The presence of a small portion of non-dietary mollusc remains altered by exposure to heat would be interpreted as an unintentional action if the remains were previously in the place where a hearth was built (Bosch et al., 2015). Unsurprisingly, most of the *Bittium* shells bearing traces of burning damages were retrieved not far from the two hearths of level A1 and the large hearth of level A2.

Two specimens of *B. latreillii*, distributed in levels A1 and M3, in the internal area of the rock shelter, are covered with small dots of red ochre (Fig. 5b). Since dots of mineral pigment are very localised and cover some calcareous concretions on the shell, it is likely that this dotting is simply the result of the proximity of the shells to ochre fragments present in the sediment, as also suggested for some faunal remains found in Protoaurignacian levels (Pothier-Bouchard et al., 2020).

Post-depositional traces of diagenesis, including decalcification and manganese staining, were observed in the archaeological record. In the Protoaurignacian levels, 39.1% of the shells are affected by decalcification, of which 57.4% are distributed in level A2 (Fig. 5c). A slightly higher degree of decalcification was observed in Mousterian levels, where 55.1% of the remains – mainly distributed in level MS1 – show typical traces of decalcification. Manganese staining resulting in black-blue stains is observed on 47.1% of the remains from Protoaurignacian levels, mostly distributed in levels A1 and A2, while in Mousterian levels, more than half of the shells (64.2%) are affected by manganese oxide coating, a large number of them (65.5%) being distributed in level MS1 (Fig. 5d). No evidence of root and microorganism etching was found.

During different field campaigns, we noted the presence of several small sea pebbles along the sequence (Fig. S8). The identified pebbles – characterized by a flat or rounded shape produced by abrasion during water conveyance – were counted, classified by metrics (maximum length), and microscopically analysed. Table 4 shows the distribution of *Bittium* shells (NISP 42) and sea pebbles (n = 780) retrieved from Mousterian levels (MS2, M1, M2, M3, M4, and M5) investigated in 2022. The identified pebbles – of which 52.1% range from 50 to 100 mm – were retrieved from squares BB2, CC2, DD2, and EE2.

The Pearson correlation coefficient was calculated to establish if a correlation between *Bittium* shells and sea pebbles existed. As a result, the investigated levels show a significant positive correlation in both levels ( $R = 0.86$ ,  $p = 0.0263974$ ) and squares ( $R = 0.99$ ,  $p = 0.012154$ ), revealing that the two elements might have reached the site together (Fig. S9).

## 5.2. Taphonomic processes in modern *Bittium* shells

Taphonomic signatures, such as shell-size distribution, fragmentation, traces of drilling organisms, encrustations, and abrasion were identified on *Bittium* shells from present-day environments (Fig. 6a).

*B. latreillii* and *B. reticulatum* were found to dominate the accumulations of mollusc microfauna at the pebble-dominated beach of Sestri Levante. It was not possible to identify the species of 88 shells, due to fragmentation and/or the presence of encrustations (Table 1).

Complete shells represent 54.5% of the sample, while fragmentation affects 16.8% of the total sample. Nearly a third (28.8%) of specimens have less than 50% of their shell surface broken (Fig. S6).

Shell-size distribution is right-skewed, with most of the specimens (32.6%) ranging from 5 to 6 mm, while no specimen is longer than 9 mm

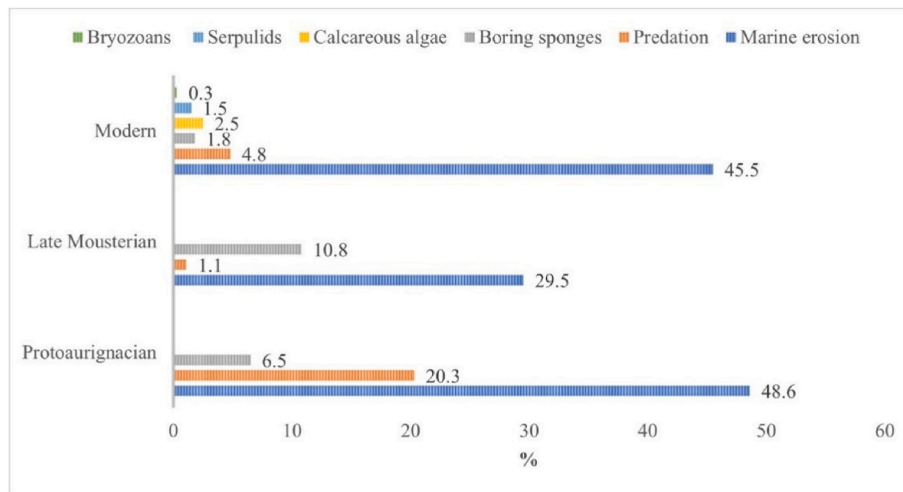


Fig. 3. Pre-depositional natural damage (%NISP) in the archaeological record and in the modern sample.

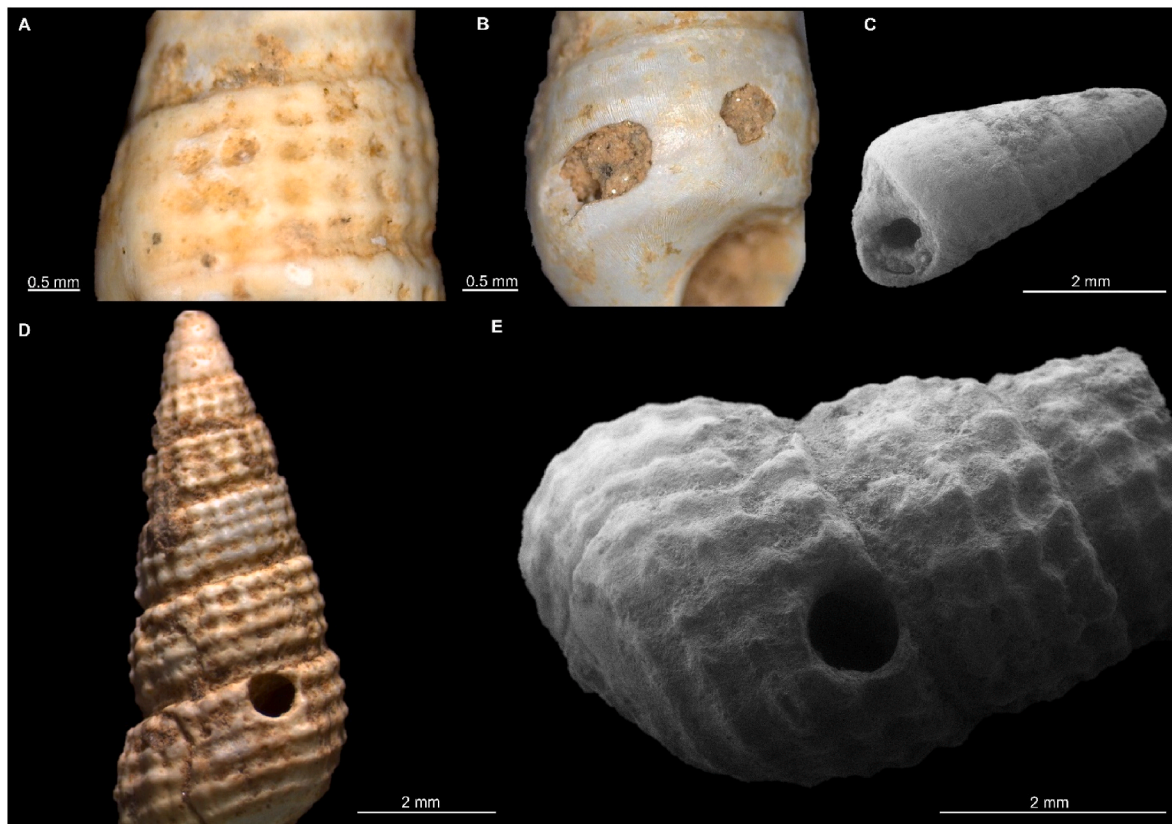


Fig. 4. Different degrees of marine abrasion (a, b, c). a) *Bittium* sp. from level A2. Abraded, glossy surface. The natural ornamentation is partially visible. b) *Bittium* sp. from level A1. Intense abrasion resulting in holes and loss of the natural shell ornamentation. c) *Bittium* sp. from level M1. SEM images allows a better identification of the polished surfaces (magnification 30X). Predation hole on *Bittium latreillii* from level A1 (d, e). d) vision under a stereomicroscope. e) vision under SEM (magnification 30X). SEM photos by Deirdre D. Ryan.

(Fig. S7).

While there is a great number of marine abrasions (45.5%), bioerosion related to marine organisms is quite scarce (10.5%). The primary organisms responsible for the perforations identified in our sample are carnivorous gastropods (3.5%). They drill shells in exposed or weak areas, either near the apex or on central whorls (Fig. 6b). To a lower degree, there are also micro-holes caused by clionid sponges (1.8%), encrustations of calcareous algae (2.5%), serpulid skeletons (1.3%) (Fig. 6c), and bryozoan encrustation (Fig. 6d) (0.5%).

Marine abrasion is evident on shells that were exposed to external environmental conditions and that were in contact with particles that abraded and polished the surfaces. The shells display varying degrees of abrasion, ranging from specimens with a slight thinning of the natural ornamentation to almost white, very eroded shells (Fig. 7). Approximately 30% of the collected shells display perforations produced as a consequence of natural erosion.

No wave-induced alteration can be noted in shells collected alive from vegetated sea bottoms, whose “fresh” appearance results in the



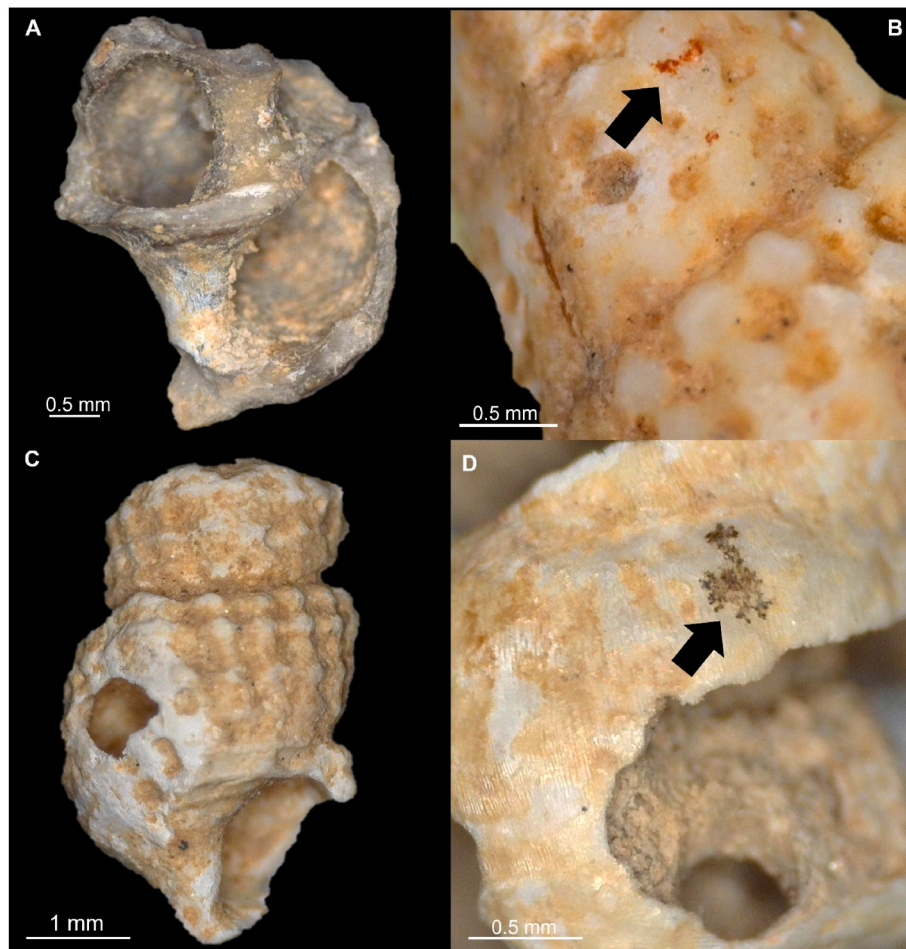


Fig. 5. Anthropogenic modifications (a, b). a) Last whorl of *Bittium* sp. from level A1. Burning damage. b) *Bittium latreillii* covered with dots of red ochre, from level M3. Natural post-depositional traces (c, d). c) *Bittium reticulatum* from level A3. Decalcification. d) *Bittium* sp. from level A1. Manganese coloration.

Table 4

Distribution of small sea pebbles (n = 780) and *Bittium* shells (NISP 42) in Mousterian levels and squares investigated in 2022.

LEVELS	SQUARES					
	Small pebbles					
	BB2	CC2	DD2	EE2	TOT	%
M52	22	10	–	–	32	4.1
M1	46	19	–	–	65	8.3
M2	43	101	21	24	189	24.2
M3	–	27	48	60	135	17.3
M4	–	167	98	33	298	38.2
M5	–	34	9	18	61	7.8
TOT.	111	358	176	135	780	100.0
%	14.2	45.9	22.6	17.3	100	
	<i>Bittium</i> shells (NISP)					
M52	2	–	–	–	2	4.8
M1	3	2	–	–	5	11.9
M2	1	3	–	1	5	11.9
M3	–	–	4	4	8	19.0
M4	–	13	2	1	16	38.1
M5	–	2	2	2	6	14.3
TOT. NISP	6	20	8	8	42	100.0
%	14.3	47.6	19.0	19.0	100	

preservation of the original colour, shell sculpture and ornamentation (Fig. 8).

## 6. Discussion

When examining possible reasons for bringing molluscs to archaeological sites, it seems reasonable to assume that medium to large molluscs were brought for subsistence purposes, while small, intentionally modified shells were collected for ornamental and symbolic purposes (e.g., Taborin, 1993; Vanhaeren and d'Errico, 2006; Vanhaeren, 2010). However, little is known about small, non-dietary, unmodified shells (however, see Aini et al., 2014), which are the focus of our attention in this paper. Our detailed analysis provides new information on small, unmodified micromollusc, specifically small gastropod found in Palaeolithic sites and the ways in which they might have deposited in the Protoaurignacian and the Mousterian levels of Riparo Bombrini.

From a paleoenvironmental point of view, the presence of a large number of *Bittium* spp. together with *Cerithiopsis* sp., *Alvania* spp., and other molluscan grazers normally associated with seaweeds and other marine plants of the shallow benthic zone, denote the presence of vegetated environments on the sea floor near the Balzi Rossi area during the Middle and Upper Palaeolithic. A similar marine environment is currently observed on the seabed that characterizes the Mortola Natural Marine Park (Imperia, Italy), where today meadows of *P. oceanica* sea-grass stretch from the Balzi Rossi complex to Latte. Spatial analysis reveals a patterned distribution of *Bittium* shells at the Bombrini site, with a concentration inside the rock shelter, especially close to large hearths, where various human activities are well documented. Here, different



Fig. 6. Modern sample. a) Dead *Bittium* spp. collected from the beach. b) *Bittium latreillii* with a predation hole on the first whorls. c) *Bittium reticulatum* with serpulids inside the aperture. d) *Bittium* sp. covered with bryozoan encrustation.

materials such as faunal remains, lithic artefacts, shell beads, as well as fragments of large shells interpreted as food debris were retrieved, suggesting that the analysed small gastropods were placed in the same areas where human groups lived and performed their activities. As we see no possible natural, depositional, or post-depositional explanation (e.g., wave action and tides) for the presence of a large sample of such small gastropods, it is likely that their presence in the studied assemblages is the result of human intervention. To test this hypothesis, we considered different possible mechanisms that may have caused the introduction of these tiny shells at the site, focusing on their taphonomic history.

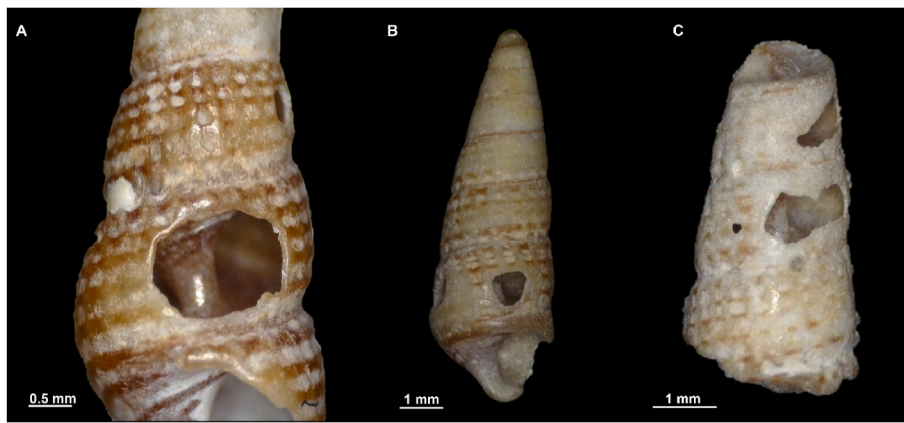
The analysed *Bittium* shells were never deliberately perforated or

directly modified by humans, although extensive polishing by waves left holes in the surface of many. The high incidence of marine abrasion in the archaeological assemblage indicates that shells remained within the marine environment for a long time before reaching the rock shelter. Thus, they are considered non-food taxa, which is unsurprising since they are very small.

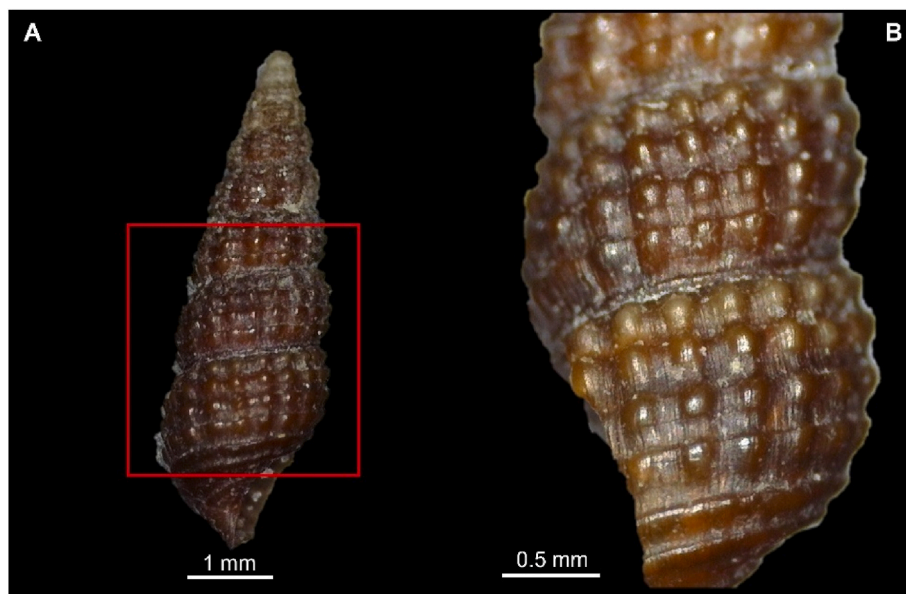
Marine erosion was observed with similar frequencies in both the Protoaurignacian and Mousterian levels, suggesting comparable modalities of introduction over time. Similarly, the presence of bioerrosive agents such as *Cliona* sponges and predatory gastropod drillings confirm that *Bittium* shells reached the site when the animal was already dead.

The comparison to modern assemblages turned out to be a useful tool





**Fig. 7.** Different degrees of marine abrasion on modern *Bittium* shells collected from the beach. a) *Bittium reticulatum*. Abraded, glossy surface. The natural ornamentation is still partially visible. b) *Bittium latreillii*. Intense abrasion resulting in holes and loss of the natural shell ornamentation. c) *Bittium* sp. fragment completely abraded.



**Fig. 8.** Modern *Bittium reticulatum* live-collected between green algae (Llança, Girona, Spain, 0.5 m deep, Mar. 2016). a) general aspect. b) detail of the shell sculpture and ornamentation. From the reference collection.

for our understanding of the taphonomic events that occurred in the archaeological record, allowing analogies to be drawn between observable processes in the present and those that happened in the past. Fragmentation occurs in a similar proportion in the archaeological materials, supporting the hypothesis that some shells from Riparo Bombrini probably reached the site when they were already fragmented. Although bioerosion is observed in a similar percentage in both the archaeological and the modern assemblage, encrustations of calcareous algae, serpulids and bryozoans are only documented on the surface of modern shells. Their lack on archaeological shells might be due to both taphonomic processes and natural factors related to the marine environment. The incidence of marine abrasion observed on the archaeological materials is an almost perfect match for the modern specimens found on the seashore.

The presence of many modern shells being <4 mm and, in comparison, their near absence in the archaeological record, may be due to a variety of factors. The decrease in shell size could represent the combined effect of local environmental conditions (e.g., habitat types), seawater temperature, and anthropic pressure. Furthermore, there is a possibility that smaller specimens are underrepresented in

archaeological contexts due to post-depositional processes. The rock shelter was never far from the shore, due to the steep coastal morphology of the Balzi Rossi coast. However, given the presence of a larger open plain between the base of the cliff and the shoreline at that time (Holt et al., 2019), we reject the hypothesis that small, beach-worn shells, including *Bittium*, are the result of high tides and/or storms having deposited beach debris. For the same reasons, we also reject the hypothesis of wind-blown micromolluscs.

Among the anthropogenic factors, we considered the hypothesis that *Bittium* shells and other small gastropods found at the site might be by-products of collecting other marine resources. For example, swallowing-feeding fishes usually swallow prey directly without chewing it into smaller pieces, frequently ingesting micromolluscs and other microorganisms lying on the seabed. Thus, it is conceivable that some of the shells reached the site as materials stuck in the digestive tracts of fish, as a result of fishing activities. However, there is no clear evidence of systematic fishing activities at the site that could explain such a large quantity of microshells.

The site of Riparo Mochi – located about 20 m north-west of Riparo Bombrini – yielded a large number of small gastropods belonging to



*Cerithiopsis tubercularis*, particularly abundant in the Gravettian layer D (Stiner, 1999). Since this taxon lives in close proximity to sponges, the author interpreted these small horn shells as an accidental by-product of sponge collection. However, a reinspection of the illustrations makes it clear that at least some of the shells identified as *C. tubercularis* in that study (Stiner, 1999, Fig. 5, p. 743) are instead cerithiids of the genus *Bittium*. That is because some of the illustrated shells have four spiral cords of natural ornamentation as opposed to the three displayed by *C. tubercularis* and lack the elongated protoconch characteristic of *C. tubercularis*. Taphonomic analysis performed on these small shells reveals a high co-occurrence of beach polish caused by wave action (24% on average) (Stiner, 1999), implying that microshells found at Riparo Mochi reached the site post-mortem. Considering the proximity of the two rock shelters, as well as their similarities in taphonomic processes affecting micromolluscs, it is reasonable to hypothesize that a comparable event caused the deposition of small, wave-worn gastropods at the two sites.

Another hypothesis explaining the presence of microshells in archaeological contexts was proposed by de Lumley et al. (2004), albeit without the support of taphonomic analyses to support their case. They suggest that small gastropods living in vegetated marine environments (including *B. reticulatum*) and retrieved from the Acheulean stratigraphic complex C of Grotte du Lazaret are indirect evidence of a human introduction of seaweed or *P. oceanica* leaf blades, possibly used as fuel for hearths or bedding. As mentioned above, taphonomic conditions observed on *Bittium* shells from Riparo Bombrini prove that they reached the rock shelter when the animal was already dead. Thus, we can also reject the hypothesis of an unintentional introduction of the analysed specimens with marine plants or algae, from which shells detach after the death of the mollusc (Russo and Terlizzi, 1998). We analysed both dead *P. oceanica* mat and green leaves accumulated on the beaches of different areas of the Ligurian coast, including the seashore currently located in front of the Balzi Rossi cliff (Fig. S10) and no *Bittium* was identified mixed in the *P. oceanica* samples.

Small gastropods may be interpreted as materials having been introduced at sites along with shells collected for ornamental purposes, especially in Upper Palaeolithic deposits. The proximity of shells in shore thanatocoenoses usually allow smaller shells to become lodged inside the aperture of larger specimens (Fig. 9). This should be considered, especially in the case of inland sites such as Grotta di Fumane –

located at an altitude of 350 masl in the Monti Lessini (Venetian Pre-Alps, north-eastern Italy) – where some sporadic remains of small gastropods, including *B. latreillii* and *B. reticulatum*, were retrieved from the Early Upper Palaeolithic levels (Peresani et al., 2019). Considering that the cave sits today in a pre-Alpine environment (currently ca.100 km away from the coastline) and also that sea levels were even lower during the Upper Palaeolithic exposing a wide plain extending as far south as the modern town of Ancona, it is extremely unlikely that these shells reached the cave mixed with marine resources such as algae, seagrasses, or fish. It is more likely that *Bittium* shells and other tiny molluscs arrived at the cave attached to species used as ornaments materials, which are well documented at the Venetian site.

In the case of Riparo Bombrini, the presence, along the sequence, of small pebbles unsuitable for tool production caught our attention. Their shapes (mainly spheres and discs) indicate that they are beach pebbles (Williams and Stepanova, 2013), which is also suggested by their worn, abraded aspect, probably as a result of water transport. Similarities (in shape and size) can be noted with the sea pebbles from the so-called “Spiaggia delle Uova” (Egg Beach), a little beach located below the Balzi Rossi cliff, and covered by egg-shaped pebbles. Studies demonstrate that although the modern shorelines of Western Liguria have been altered by decades of human modification for touristic purposes, beaches of the Pleistocene were probably of similar composition (Bozzano et al., 2006; Rovere et al., 2011; Gravel-Miguel et al., 2017). Also, “Tyrrhenian” fossil beaches (MIS 5) documented at the Balzi Rossi sites of Ex-Casinò, Ex Birreria, Barma Grande, Grotta dei Fanciulli and Prince Cave (Leonardi, 1934, 1935; Simone, 1970; Vicino, 1972, 1974; Cremaschi et al., 1991; Negrino and Tozzi, 2008; Tozzi and Negrino, 2008) contains rolled pebbles similar to those observed in both the modern beaches and the archaeological assemblage. Since the presence of such pebbles is not imputable to the natural site geomorphology, we hypothesize transportation (intentional or unintentional) of marine sediment to the rock shelter as a possible explanation for the presence of small beach-worn shells in archaeological levels, leaving open the hypothesis of whether beach sediments might have served for specific functional activities that are still unknown, or little investigated by archaeologists (e.g., using sediments to put out fires or to level the floor).

In future research, we believe it could be interesting to also consider symbolic aspects that may be associated with the presence of micromolluscs in Palaeolithic contexts. Although we do not have objective evidence to support the hypothesis of deliberate harvesting of these objects, the innate characteristics of the human species including attention to aesthetics must be considered when studying the possible role of non-utilitarian objects during the Palaeolithic. Small, non-dietary gastropods unearthed at the sites may have attracted the attention of human groups by their aesthetic traits and were thus selected, collected from the beach, and brought in without any utilitarian intention. It is in fact possible that small shells were identified and collected by children as simple actions of playful delight or curiosity, reflecting a basic human activity (Meert et al., 2013). In this light, the presence of very small shells could be the result of conscious, purposeful decisions, reflecting aesthetic and visual choices, which are parts of a rich cultural world only slightly known to us (Assaf, 2018).

## 7. Conclusion

This paper demonstrates the types of data that can be obtained from the taphonomic analysis of small, non-dietary shells incorporated in archaeological records and suggests tentative implications for further investigation. The data provided by the study of *Bittium* shell remains from the Protoaurignacian and Mousterian levels of Riparo Bombrini provide new insights regarding marine resource management at the site. The discovery of specimens with clear non-human modifications caused by bioeroders, as well as traces of abrasion related to beach environments or undertows demonstrates the introduction of the shells post-mortem, for non-food purposes that cannot be specified, but only



Fig. 9. *Bittium* sp. lodged inside the aperture of a specimen of *Ocenebra edwardsii*, from level A1.

hypothesized.

Here, we suggest the intentional or unintentional transport of marine sediments – including small beach-worn specimens and sea pebbles – into the site as a hypothesis to explain the recurrent presence of abraded *Bittium* shells in the investigated levels. Also, we cannot exclude that some small-sized shells were deliberately collected by human groups, potentially resulting from their eye-catching characteristics appealing to the hunter-gatherer populations living along the Mediterranean shorelines.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

Data will be made available on request.

### Acknowledgments

Thanks to Ana B. Marín-Arroyo and Marta Moreno-García for inviting us to contribute this paper to the special issue on Quaternary Taphonomy. We are grateful to Ermanno Quaggiotto for his help in taxonomic classification of shells. Thanks are also due to Dr. Deirdre D. Ryan, who provided SEM images of *Bittium* shells. Research at Riparo Bombrini is coordinated by the University of Genoa (F.N.) and Université de Montréal (J.R.S.) and supported by FRQSC grant 2016-NP-193048 (J.R.S.), the Direction des affaires internationales UdeM (J.R.S.), SSHRC Insight Grant 435-2017-1520 (J.R.S. & F.N.), Canadian Foundation for Innovation JELF grant # 37754 (J.R.S.) and the ERC Horizon 2020 grant 724046 (SUCCESS, to Stefano Benazzi, University of Bologna - Italy). Fieldwork was conducted under authorization of the Ministero della Cultura (MiC) with local supervision by the Soprintendenza Archeologia, Belle Arti e Paesaggio per le province di Imperia e Savona, with logistical support from the Istituto Internazionale di Studi Liguri (Bordighera), the Direzione regionale Musei Liguria and the Museo preistorico dei “Balzi Rossi” e zona archeologica. We wish to acknowledge the very useful comments of two anonymous reviewers. Their comments helped improve the clarity of some of the arguments presented in this study.

### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.qsa.2023.100104>.

### References

- Ainis, A.F., Vellanoweth, R., Lapeña, Q.G., Thornber, C.S., 2014. Using non-dietary gastropods in coastal shell middens to infer kelp and seagrass harvesting and paleoenvironmental conditions. *J. Archaeol. Sci.* 49, 343–360. <https://doi.org/10.1016/j.jas.2014.05.024>.
- Ainis, A.F., Erlandson, J., Gill, K., Graham, M., Vellanoweth, R., 2019. The potential use of seaweeds and Marine plants by native Peoples of Alta and Baja California: implications for ‘Marginal’ Island ecosystems. In: Gill, K.M., Erlandson, J.M., Fauvel, M. (Eds.), *An Archaeology of Abundance: Reevaluating the Marginality of California’s Islands*. University Press of Florida, Gainesville, FL, USA, pp. 135–170. <https://doi.org/10.5744/florida/9780813056166.003.0005>.
- Álvarez-Fernández, E., 2001. L’axe Rhin-Rhône au Paléolithique supérieur récent: l’exemple des mollusques utilisés comme objets de parure. *L’Anthropologie* 105, 547–564.
- Arrighi, S., Bortolini, E., Tassoni, L., Benocci, A., Manganeli, G., Spagnolo, V., Foresi, L. M., Bambini, A.M., Lugli, F., Badino, F., Aureli, D., Boschin, F., Figus, C., Marciani, G., Oxilia, G., Silvestrini, S., Cipriani, A., Romandini, M., Peresani, M., Ronchitelli, A., Moroni, A., Benazzi, S., 2020. Backdating systematic shell ornament making in Europe to 45,000 years ago. *Archaeol. Anthropol. Sci.* 12 (2) <https://doi.org/10.1007/s12520-019-00985-3>.
- Assaf, E., 2018. Paleolithic aesthetics: collecting colorful flint pebbles at Middle Pleistocene Qesem cave, Israel. *Journal of Lithic Studies* 5 (1). <https://doi.org/10.2218/jls.2616>.
- Barrière, J., 1969. Les coquilles marines découvertes sur le sol de la cabane acheuléenne du Lazaret. In: de Lumley, H. (Ed.), *Une cabane Acheuléenne dans la Grotte du Lazaret (Nice)*. Mémoires de la Société Préhistorique Française, Tome, vol. 7, pp. 117–118.
- Benazzi, S., Slon, V., Talamo, S., Negrino, F., Peresani, M., Bailey, S.E., Sawyer, S., Panetta, D., Vicino, G., Starnini, E., Mannino, M.A., Salvadori, P., Meyer, M., Pääbo, S., Hublin, J., 2015. The makers of the Protoaurignacian and implications for Neandertal extinction. *Science* 348 (6236), 793–796. <https://doi.org/10.1126/science.aaa2773>.
- Beu, A.G., Maxwell, P.A., 1990. Cenozoic mollusca of New Zealand. *N. Z. Geol. Surv. Paleontol. Bull.* 58, 518.
- Bosch, M.D., Wesselingh, F.P., Mannino, M.A., 2015. The Ksâr ‘Akil (Lebanon) mollusc assemblage: zooarchaeological and taphonomic investigations. *Quat. Int* 390, 85–101. <https://doi.org/10.1016/j.quaint.2015.07.004>.
- Bozzano, A., Corradi, N., Fanucci, F., Ivaldi, R., 2006. Late Quaternary deposits from the Ligurian continental shelf (NW Mediterranean): a response to problems of coastal erosion. *Chem. Ecol.* 22 (1), S349–S359. <https://doi.org/10.1080/02757540600688036>.
- Casabó i Bernad, J., 1997. L’excavació: anàlisi preliminar de la informació arqueològica. *Aguaites* 13–14, 63–75.
- Colonese, A., Wilkens, B., 2005. The malacofauna of the Upper Palaeolithic levels at Grotta della Serratura (Salerno, southern Italy), preliminary data. In: Bar Yosef, D. (Ed.), *Archaeomalacology: Molluscs in Former Environments of Human Behaviour*. Oxbow Books, Oxford, pp. 63–70.
- Colonese, A.C., Lo Vetro, D., Landini, W., Di Giuseppe, Z., Hausmann, N., Demarchi, B., d’Angelo, C., Leng, M.J., Incarbona, A., Whitwood, A.C., Martini, F., 2018. Late Pleistocene-Holocene coastal adaptation in central Mediterranean: Snapshots from Grotta d’Oriente (NW Sicily). *Quat. Int.* 493, 114–126. <https://doi.org/10.1016/j.quaint.2018.06.018>.
- Connolly, T.J., Erlandson, J.M., Norris, S.E., 1995. Early basketry and cordage from Daisy cave, San Miguel Island, California. *Am. Ant.* 60 (2), 309–318. <https://doi.org/10.2307/282142>.
- Cossignani, T., Ardovali, R., 2011. *Malacologia Mediterranea- Atlante delle conchiglie del Mediterraneo*. L’Informatore Piceno, Ancona.
- Crevaschi, M., Del Lucchese, A., Negrino, F., Ottomano, C., Wilkens, B., 1991. Ventimiglia (Imperia). Località Balzi Rossi. Nuovi dati sulla successione stratigrafica del ciclo interglaciale-glaciale-postglaciale. *Scavi 1990. Bollettino di Archeologia* 8, 47–50.
- da Costa, E.M., 1778. *Historia naturalis testaceorum Britanniae, or the British Conchology*. Containing the descriptions and other particulars of natural history of the shells of Great Britain and Ireland. illustrated with figures. London.
- D’Angelo, G., Gargiulo, S., 1978. Guida alle conchiglie mediterranee. In: Conoscerle, Cercarle, Collezionarle. Fabbri, Milano.
- De Lumley, H., Echassoux, A., Bailon, S., Cauche, D., de Marchi, M.P., Desclaux, E., El Guennouni, K., Khatib, S., Lacomat, F., Roger, T., Valensi, P., 2004. Le solle d’occupation acheuléenne de l’unité archéostratigraphique UA 25 de la grotte du Lazaret. *Alpes-Maritimes, Aix-en-Provence, Edisud, Nice*.
- Doneddu, M., Trainito, E., 2010. *Conchiglie del Mediterraneo: guida ai molluschi conchigliati*. Il Castello, Milano.
- Doutka, K., Perlès, C., Valladas, H., Vanhaeren, M., Hedges, R., 2011. Franchthi cave revisited: the age of the Aurignacian in south-eastern Europe. *Antiquity* 85 (330), 1131–1150. <https://doi.org/10.1017/S0003598X00061962>.
- 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. Ph.D. Thesis. Universities of Bologna, Ferrara and Parma, Italy.
- Fretter, V., Graham, A., 1981. The prosobranch molluscs of Britain and Denmark. Part 6 - Cerithiacea, Strombacea, Hipponicacea, Calyptraea, Lamellariacea, Cypraeaacea, Naticacea, Tonnacea, Heteropoda. *J. Molluscan Stud. Suppl.* 9, 285–363.
- Fritz, C., Simonnet, R., 1996. Du geste à l’objet: le s contours découpés de Labastide: résultats préliminaires. *Techne* 3, 63–77.
- García-Argudo, G., Fernández-Marchena, J.L., Vergés, J.M., Fullola, J.M., 2020. Contributions of microscopy to the study of the Upper Paleolithic *Homalopoma sanguineum* shell beads. *Quat. Int.* 569–570, 23–38. <https://doi.org/10.1016/j.quaint.2020.08.049>.
- Gravel-Miguel, C., Riel-Salvatore, J., Maggi, R., Martino, G., Barton, C., 2017. The breaking of ochred pebble tools as part of Funerary ritual in the Arene Candide Epigravettian Cemetery. *Camb. Archaeol. J.* 27 (2), 331–350. <https://doi.org/10.1017/S0959774316000640>.
- Gray, J.E., 1847. The classification of the British Mollusca by W.E. Leach, M.D. *Ann. Mag. Nat. Hist.* 20, 267–273. <https://doi.org/10.1080/037454809496042>.
- Gutiérrez-Zugasti, F.I., 2011. Shell fragmentation as tool for quantification and identification of taphonomic processes in archaeomalacological analysis: the case of the Cantabrian region (Northern Spain). *Archaeometry* 53, 614–630.
- Holt, B., Negrino, F., Riel-Salvatore, J., Formicola, V., Arellano, A., Arobba, D., Boschian, G., Churchill, S.E., Cristiani, E., Di Canzio, E., Vicino, G., 2019. The Middle-upper Paleolithic transition in Northwest Italy: new evidence from Riparo Bombrini (Balzi Rossi, Liguria, Italy). *Quat. Int* 508, 142–152. <https://doi.org/10.1016/j.quaint.2018.11.032>.
- Kumar, C.S., Ganesan, P., Suresh, P.V., Bhaskar, N., 2008. Seaweeds as a source of nutritionally beneficial compounds: a review. *J. Food Sci. and Technol.* 45 (1), 1–13.
- Laubier, L., 1966. *Le coralligène des Albères, Monographie biocénotique*. Ann. Inst. Oceanogr. 43 (2), 137–316.

- Leonardi, P., 1934. Fauna malacologica della Barma Grande di Grimaldi (scavi dell'Istituto Italiano di Paleontologia Umana). *Atti della Società Italiana per il Progresso delle Scienze* 22, 111–113.
- Leonardi, P., 1935. I Molluschi pleistocenici della Barma Grande. In: Istituto Italiano di Paleontologia Umana. *Faune*, pp. 5–34.
- Mannino, M.A., di Salvo, R., Schimmenti, V., di Patti, C., Incarbona, A., Sineo, L., Richards, M.P., 2011. Upper palaeolithic hunter-gatherer subsistence in Mediterranean coastal environments: an isotopic study of the diets of the earliest directly-dated humans from Sicily. *J. Archaeol. Sci.* 38 (11), 3094–3100. <https://doi.org/10.1016/j.jas.2011.07.009>.
- Marciani, G., Ronchitelli, A., Arrighi, S., Badino, F., Bortolini, E., Boscato, P., Boschin, F., Crezzini, J., Delpiano, D., Falucci, A., Figus, C., Lugli, F., Oxilia, G., Romandini, M., Riel-Salvatore, J., Negrino, F., Peresani, M., Spinapolice, E.E., Moroni, A., Benazzi, S., 2020. Lithic techno-complexes in Italy from 50 to 39 thousand years BP: an overview of lithic technological changes across the Middle-Upper Palaeolithic boundary. *Quat. Int.* 551, 123–149. <https://doi.org/10.1016/j.quaint.2019.11.005>.
- Martini, F., Colonese, A.C., Wilkens, B., 2005. Grotta della Serratura (Marina di Camerota - Salerno). La malacofauna dei livelli gravettiani ed epigravettiani. *Considerazioni paleoecologiche*. In: Malerba, G., Visentini, P. (Eds.), *Atti della IV Convegno Nazionale di Archeozoologia*, pp. 87–96. Pordenone, 13-15 novembre 2003.
- McRoy, C.P., Helfferich, C., 1980. Applied aspects of seagrasses. In: Phillips, R.C., McRoy, C.P. (Eds.), *Handbook of Seagrass Biology: an Ecosystem Perspective*. Garland Publishing, New York, pp. 297–344.
- Meert, K., Pandelaere, M., Patrick, V.M., 2013. Taking a shine to it: how the preference for glossy stems from an innate need for water. *J. Consum. Psychol.* 24 (2), 195–206. <https://doi.org/10.1016/j.jcps.2013.12.005>.
- Milchakova, N.A., Böer, B., Boyko, L.I., Mikulich, D.V., 2014. The chemical composition and technological properties of seagrasses a basis for their use (a review). In: Ajmal Khan, M., Böer, B., Öztürk, M., Al Abdessalaam, T.Z., Clüsener-Godt, M., Gul, B. (Eds.), *Sabkha Ecosystems, Tasks for Vegetation Science*. Springer Netherlands, pp. 313–323.
- Mouritsen, O.G., 2013. *Seaweeds: Edible, Available and Sustainable*. The University of Chicago Press, Chicago.
- Negrino, F., Bertola, S., Riel-Salvatore, J., Simon, P., Laliberté, A., Nicora, A., 2018. Discarded bladelets – preliminary analysis of the Protoaurignacian retouched bladelets from Riparo Bombrini (Ventimiglia, Imperia). In: Arzarello, M., Fontana, F., Peresani, M., Peretto, C., Thun Hohenstein, U. (Eds.), *IV Annual Meeting IPPP, Application of emerging technologies to Italian Palaeolithic and Mesolithic case-studies*, Abstract book, *Annali dell'Università degli Studi di Ferrara - Museologia Scientifica e Naturalistica*, vol. 13, pp. 19–20.
- Negrino, F., Riel-Salvatore, J., Bertola, S., 2016. Colonization dynamics and the diffusion of the Protoaurignacian in Italy and southern France. In: *The Rhone-Marche Corridors and its Chrono- Cultural Implications*, Abstract Book, *Proceedings of the Human Society of Human Evolution*, vol. 5, p. 172.
- Negrino, F., Riel-Salvatore, J., 2018. From Neanderthals to anatomically Modern humans in Liguria (Italy): the current state of knowledge. In: Borgia, V., Cristiani, E. (Eds.), *Palaeolithic Italy. Advanced Studies on Early Human Adaptations in the Apennine Peninsula*. Sidestone Press Academics, Leida, pp. 161–182.
- Negrino, F., Tozzi, C., 2008. Il Paleolitico in Liguria. *Bull. Musee Anthropol. Prehist. Monaco* 48, 21–28.
- Newell, R.R., Kielman, D., Constandse-Westermann, T.S., van der Sanden, W.A.B., van Gijn, A., 1990. An Inquiry into the Ethnic Resolution of Mesolithic Regional Groups: the Study of Their Decorative Ornaments in Time and Space. Brill, Leyden.
- Ollé, A., Pedergnana, A., Fernandez-Marchena, J.L., Martin, S., Borel, A., Aranda, V., 2016. Microwear features on vein quartz, rock crystal and quartzite: a study combining Optical Light and Scanning Electron Microscopy. *Quat. Int.* 424, 154–170. <https://doi.org/10.1016/j.quaint.2016.02.005>.
- Peresani, M., Forte, M., Quaggiotto, E., Colonese, A.C., Romandini, M., Cilli, C., Giacobini, G., 2019. Marine and freshwater shell exploitation in the early upper Palaeolithic: Re-examination of the assemblages from Fumane cave (NE Italy). In: *PaleoAnthropology, Special Issue: Personal Ornaments in Early Prehistory*, pp. 64–81. <https://doi.org/10.4207/PA.2019.ART124>.
- Payraudeau, B.C., 1826. *Catalogue descriptif et méthodique des Annelides et des Mollusques de l'île de Corse*. Béchot, Paris. <https://doi.org/10.5962/bhl.title.12944>.
- Péres, J.M., 1967. Les bioconoses benthiques dans le système phytal. *Rec. Trav. Stat. mar. Endoume. Fr* 42 (58), 3–113.
- Poppe, G.T., Goto, Y., 1993. *European Seashells*, vol. 2. Verlag Christa Hemmen, Wiesbaden.
- Pothier-Bouchard, G., Mentzer, S.M., Riel-Salvatore, J., Hodgkins, J., Miller, C.E., Negrino, F., Wogelius, R., Buckley, M., 2019. Portable FTIR for on-site screening of archaeological bone intended for ZooMS collagen fingerprint analysis. *J. Archaeol. Sci. Rep.* 26 (101862). <https://doi.org/10.1016/j.jasrep.2019.05.027>.
- Pothier-Bouchard, G., Riel-Salvatore, J., Negrino, F., Buckley, M., 2020. Archaeozoological, taphonomic and ZooMS insights into the Protoaurignacian faunal record from Riparo Bombrini. *Quat. Int.* 551, 243–263. <https://doi.org/10.1016/j.quaint.2020.01.007>.
- Riel-Salvatore, J., 2010. A niche construction perspective on the Middle-Upper Palaeolithic Transition in Italy. *J. Archaeol. Method Theor* 17, 323–355. <https://doi.org/10.1007/s10816-010-9093-9>.
- Riel-Salvatore, J., Negrino, F., 2018a. Human adaptations to climatic change in Liguria across the Middle-upper Palaeolithic transition. *J. Quat. Sci.* 33, 313–322.
- Riel-Salvatore, J., Negrino, F., 2018b. Proto-Aurignacian lithic technology, mobility, and human niche construction: a case study from Riparo Bombrini. In: Robinson, E., Sellet, F. (Eds.), *Lithic Technological Organization and Paleoenvironmental Change: Global and Diachronic Perspectives*. Springer, pp. 163–187.
- Riel-Salvatore, J., Negrino, F., Bouchard, G., Vallerand, A., Costa, S., Benazzi, S., 2022. The 'semi-sterile Mousterian' of Riparo Bombrini: evidence of a late-lasting Neanderthal refugium in Liguria. *J. Quat. Sci.* 37 (2), 268–282. <https://doi.org/10.1002/jqs.3411>.
- Romandini, M., Crezzini, J., Bortolini, E., Boscato, P., Boschin, F., Carrera, L., Nannini, N., Tagliacozzo, A., Terlato, G., Arrighi, S., Badino, F., Figus, C., Lugli, F., Marciani, G., Oxilia, G., Moroni, A., Negrino, F., Peresani, M., Riel-Salvatore, J., Ronchitelli, A., Benazzi, S., 2020. Macromammal and bird assemblages across the late Middle to Upper Palaeolithic transition in Italy: an extended zooarchaeological review. *Quat. Int.* 551, 188–223. <https://doi.org/10.1016/j.quaint.2019.11.008>.
- Rovero, A., Vacchi, M., Firpo, M., Carobene, L., 2011. Underwater geomorphology of the rocky coastal tracts between Finale Ligure and Vado Ligure (western Liguria, NW Mediterranean sea). *Quat. Int.* 232 (1-2), 187–200. <https://doi.org/10.1016/j.quaint.2010.05.016>.
- Russo, G.F., Terlizzi, A., 1998. Structural patterns in the Molluscs assemblages of *Posidonia oceanica* beds: methodologic, edaphic or biogeographic product? *Boll. Malacol.* 33, 89–94.
- Russo, G.F., Fraschetti, S., Terlizzi, A., 2002. Population ecology and production of *Bitium latreilii* (Gastropoda, Cerithiidae) in a *Posidonia oceanica* seagrass bed. *Ital. J. Zool.* 69, 215–222. <https://doi.org/10.1080/1125000209356462>.
- Scagel, R.F., 1961. Marine plant resources of British Columbia. *Fish. Res. Board Can.* Bull. 127.
- Simone, S., 1970. Les formations de la mer du Mindel-Riss et les brèches à ossements rissiens de la Grotte du Prince (Grimaldi, Ligurie italienne). *Bull. Musee Anthropol. Prehist. Monaco* 15, 5–90.
- Starmühlner, F., 1956. Zur Molluskenfauna des Felsitorals und submariner Höhle am Capo di Sorrento (I Teil). *Österreichischer Zoologischer Zeitschrift* 6, 147–249.
- Stiner, M.C., 1999. Palaeolithic mollusc exploitation at Riparo Mochi (Balzi Rossi, Italy): food and ornaments from the Aurignacian through Epigravettian. *Antiquity* 73, 735–754.
- Stiner, M.C., 2003. "Standardization" in upper Paleolithic ornaments at the coastal sites of Riparo Mochi and Üçağlızli cave. In: d'Errico, F., Zilhao, J. (Eds.), *The Chronology of the Aurignacian and of the Transitional Complexes. Dating, Stratigraphies, Cultural Implications*. *Trabalhos de Arqueologia*, vol. 33, pp. 49–59.
- Taborin, Y., 1993. *La parure en coquillage au Paléolithique*. CNRS Éditions, Paris.
- Tozzi, C., Negrino, F., 2008. Nouvelles données sur les cultures moustériennes des grottes de Grimaldi. In: de Lumley, H., Hurel, A. (Eds.), *Histoire et actualité de l'œuvre scientifique de S.A.S. Le Prince Albert 1er de Monaco – 1895-2005: bilan et perspectives des connaissances sur les peuplements néandertaliens et les premiers hommes modernes de l'Europe méditerranéenne*, Archives de l'Institut de Paléontologie Humaine, vol. 39. Mémoire, Paris, pp. 101–107.
- Turner, N.J., Bell, M.A.M., 1973. The ethnobotany of the southern Kwakiutl Indians of British Columbia. *Econ. Bot* 27 (3), 257–310.
- Urra, J., Ramirez, A., Marina, P., Salas, C., Gofas, S., Rueda, J.L., 2013. Highly diverse molluscan assemblages of *Posidonia oceanica* meadows in northwestern Alboran Sea (W Mediterranean): Seasonal dynamics and environmental drivers. *Estuar. Coast Shelf Sci.* 117, 136–147. <https://doi.org/10.1016/j.ecss.2012.11.005>.
- Valensi, P., Bailon, S., Michel, V., Desclaux, E., Rousseau, L., Onorati, G., Genty, D., Blamart, D., de Lumley, H., 2007. Cadre climatique et environnemental des acheuléens de la grotte du Lazaret, à Nice. *Données paléontologiques, biogéochimiques et radiométriques établies sur les faunes de vertébrés et d'invertébrés*. *ArchéoSciences* 31, 137–150. <https://doi.org/10.4000/archeosciences.844>.
- Vanhaeren, M., 2010. *Les fonctions de la parure au paléolithique supérieur: de l'individu à l'unité culturelle*, Éditions Universitaires Européennes, Saarbrücken.
- Vanhaeren, M., d'Errico, F., 2003. Childhood in the Epipalaeolithic. What do personal ornaments associated to burials tell us? In: Larsson, L., Kindgren, H., Knutsson, K., Loeffler, D., Akerlund, A. (Eds.), *Mesolithic on the Move*. Oxbow Monographs, Oxford, pp. 494–505.
- Vanhaeren, M., d'Errico, F., Billy, I., Grousset, F., 2004. Tracing the source of Upper Palaeolithic shell beads by strontium isotope dating. *J. Archaeol. Sci.* 31, 1481–1488.
- Vanhaeren, M., d'Errico, F., 2005. Grave goods from the Saint-Germain-la-Rivière burial: evidence for social inequality in the Upper Palaeolithic. *J. Anthropol. Archaeol.* 24, 117–134.
- Vanhaeren, M., d'Errico, F., 2006. Aurignacian ethno-linguistic geography of Europe revealed by personal ornaments. *J. Archaeol. Sci.* 33 (8), 1105–1128.
- Vanhaeren, M., d'Errico, F., 2013. Thinking strings: additional evidence for personal ornament use in the Middle Stone Age at Blombos Cave, South Africa. *J. Hum. Evol.* 64, 500–517.
- Vellanoweth, R.L., Lambright, M., Erlandson, J.M., Rick, T.C., 2003. Early New World maritime technologies: sea grass cordage, shell beads, and a bone tool from Cave of the Chimneys, San Miguel Islands, California, USA. *J. Archaeol. Sci.* 30, 1161–1173. [https://doi.org/10.1016/S0305-4403\(03\)00013-X](https://doi.org/10.1016/S0305-4403(03)00013-X).
- Verdún-Castelló, E., Casabó i Bernad, J., 2020. Shellfish consumption in the early upper palaeolithic on the Mediterranean coast of the Iberian Peninsula: the example of Foradada cave. *J. Archaeol. Sci. Rep.* 29 (102035). <https://doi.org/10.1016/j.jasrep.2019.102035>.
- Vicino, G., 1972. Incisioni rupestri paleolitiche ai Balzi Rossi. *Riv. St. Lig* 38, 5–26.
- Vicino, G., 1974. La spiaggia tirreniana dei Balzi Rossi nei recenti scavi della zona dell'ex-casino. *Atti della XVI Riunione Scientifica (Istituto Italiano di Preistoria e Protostoria)*, pp. 75–95.
- White, R., 1999. Intégrer la complexité sociale et opérationnelle: la construction matérielle de l'identité sociale à Sungir. In: Camps-Faber, H. (Ed.), *Préhistoire d'os*.



Recueil d'études sur l'industrie osseuse préhistorique. Publications de l'Université de Provence, Aix-en-Provence, pp. 319–331.

Williams, A.T.W., Stepanova, K., 2013. In: Pebble Origin and Beach Zone Differentiation. 3rd International Geography Symposium - GEOMED, vol. 2013, p. 255, 64.

WoRMS, 2023. World register of Marine species. <https://www.marinespecies.org>. (Accessed 24 March 2023).