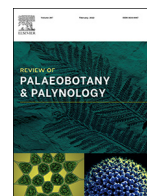




Contents lists available at ScienceDirect

## Review of Palaeobotany and Palynology

journal homepage: [www.elsevier.com/locate/revpalbo](http://www.elsevier.com/locate/revpalbo)

## New challenges in archaeopalynology: Pollen analysis on Roman bivalve shells from south-western Europe and North Africa

José Antonio López-Sáez <sup>a,\*</sup>, Darío Bernal-Casasola <sup>b</sup>, Sebastián Pérez-Díaz <sup>c</sup>, Reyes Luelmo-Lautenschlaeger <sup>d</sup>, José Juan Díaz-Rodríguez <sup>b</sup>, José Ángel Expósito-Álvarez <sup>b</sup>, Rafael Jiménez-Camino <sup>e</sup>, José Luis Portillo-Sotelo <sup>b</sup>, Fernando Villada-Paredes <sup>f</sup>, José Manuel Vargas-Girón <sup>g</sup>, Juan Jesús Cantillo-Duarte <sup>b</sup>

<sup>a</sup> Environmental Archaeology Research Group, Institute of History, CSIC, c/ Albasanz 26-28, 28037 Madrid, Spain

<sup>b</sup> Department of History, Geography and Philosophy, University of Cádiz, Avda. Dr. Gómez Ulla s.n., 11003 Cádiz, Spain

<sup>c</sup> Department of Geography, Urban and Regional Planning, University of Cantabria, Avda. de los Castros s/n, 39005 Santander, Spain

<sup>d</sup> CNRS- ISEM UMR 5554, 34090 Montpellier, France

<sup>e</sup> Department of Archaeology, City Hall of Algeciras, Paseo de Victoria Eugenia 17, 11207 Algeciras, Spain

<sup>f</sup> Consejería de Patrimonio Cultural, Edificio anexo al Teatro Revellín, c/ Ingenieros s/n, 51001 Ceuta, Spain

<sup>g</sup> Faculty of Education, University of Atlántico Medio, Carretera de Quilmes 37, 35017 Tafira Baja, Las Palmas de Gran Canaria, Spain

## ARTICLE INFO

## Article history:

Received 30 January 2023

Received in revised form 9 March 2023

Accepted 10 March 2023

Available online 15 March 2023

## Keywords:

Conchopalynology  
European flat oyster  
Roman times  
Southern Iberia  
Northern Africa

## ABSTRACT

The European flat oyster (*Ostrea edulis*) is a native species that was consumed as a luxurious product by the Romans. In the Strait of Gibraltar area, between southwest Iberia and North Africa, numerous oyster shells have been found in Roman archaeological sites located in both, the Atlantic Ocean and the Mediterranean Sea. The origin of these oysters is unknown, as so if they were farmed or harvested in the wild and/or even imported for consumption. This study presents the results of pollen analysis of oyster shells from six archaeological sites in the Strait of Gibraltar area dated between the 1st and 6th centuries AD. This is the first time that such research is undertaken in the Iberian Peninsula and North Africa; the second worldwide for a discipline rarely known until now: conchopalynology. Our study suggests that differences observed in pollen spectra could be used to identify the origin of the consumed specimens, i.e. where they were grown or harvested, discriminating whether oyster shells originated from the Mediterranean Sea or the Atlantic Ocean coastline.

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

## 1. Introduction

Human populations have long depended on coastal zones and the ecosystem services they provide; particularly in terms of food provision, transport, recreation and cultural activities (Madariaga, 1964; Davidson, 2002; Gibbs, 2004; Neumann et al., 2015; Mehvar et al., 2018). One of the most exploited natural resources in coastal areas since prehistoric times has been bivalve molluscs (e.g. Bayne, 1976; Thorpe et al., 2000; Bar-Yosef Mayer, 2005; Szabó and Quitmyer, 2008; Voultziadou et al., 2010; Thomas, 2015a). Since humans settled along the coasts thousands of years ago and exploited shallow marine resources, a vast number of bivalve shells are preserved in archaeological shell middens, i.e. ancient domestic waste deposits (Milner et al., 2007; Álvarez et al., 2011; Gutiérrez-Zugasti et al., 2011; Schöne and Surge, 2014; Thomas, 2015a).

Among them, oysters have played a singularly prominent role in Western Europe and the Mediterranean (Yonge, 1960; Stenzel, 1971; Colonese et al., 2011; Gutiérrez-Zugasti et al., 2011, 2016).

The most economically important native oyster species in Europe have been the European flat oyster (*Ostrea edulis*) and the Portuguese oyster (*Crassostrea angulata*); especially the first, with a long millennial tradition of consumption and cultivation (Bayne, 1976; Beck et al., 2011). Harvesting of flat oyster represented an important source of food for coastal communities in Europe, even during prehistoric times (Kristensen, 1997; Gercken and Schmidt, 2014), and in the 13th century it was one of the first commercially operated fisheries in Europe (Gibbs, 2004; Lotze, 2007). In the Iberian Peninsula this is confirmed by excavations of Palaeolithic, Mesolithic, Neolithic, Chalcolithic, Bronze and Iron Ages, Roman and Medieval archaeological sites, which contained traces of flat oyster shells (e.g. Moreno, 1995; Cortés-Sánchez et al., 2008; Colonese et al., 2011; Gutiérrez-Zugasti et al., 2011, 2016; Fernández-López de Pablo and Gabriel, 2016). The historical importance of oysters is also demonstrated by the fact that the Romans cultivated oysters to

\* Corresponding author at: Environmental Archaeology Research Group, Institute of History, CSIC, Albasanz 26-28, 28037 Madrid, Spain.

E-mail address: [joseantonio.lopez@cchs.csic.es](mailto:joseantonio.lopez@cchs.csic.es) (J.A. López-Sáez).

satisfy the huge demand for this delicacy (Günther, 1897; Yonge, 1960) which was consumed as a luxurious dish (Bernal-Casasola, 2011b; Bardot-Cambot, 2013; Mouchi et al., 2018).

The natural range of the European flat oyster stretches along the European Atlantic coastline from Norway to the Iberian Peninsula and south to Morocco (Díaz-Almela et al., 2004; Edwards, 2005; Airoldi and Beck, 2007; Lallias et al., 2007). In addition, localised remnant populations are found in the Mediterranean Sea, mainly along the northern coast and in the western part of the Black Sea to the Crimea peninsula (Gercken and Schmidt, 2014; Stagličić et al., 2020). This species once formed abundant and widespread beds and reefs along Europe's coastline during the Holocene (Lotze et al., 2011; Mautner et al., 2018), commonly occurring in the intertidal and subtidal coastal waters, but also in deeper waters and offshore down to 50–80 m depth (Pogoda, 2019), that constituted a highly significant resource for coastal populations and were probably a dominant ecological component (Gercken and Schmidt, 2014; Fariñas-Franco et al., 2018; Rodríguez-Pérez et al., 2019). However, although once widespread, flat oyster beds and reefs are now practically non-existent (Beck et al., 2011; Helmer et al., 2019; Pogoda, 2019; Stagličić et al., 2020). Oyster species are typically found in enclosed, wave-sheltered coastal and estuarine areas, settled on various types of hard intertidal and shallow subtidal substrates (Bianchi and Morri, 2000; Beck et al., 2011). Due to their long historical importance as a food source (Günther, 1897; Yonge, 1960; MacKenzie et al., 1997; Gercken and Schmidt, 2014; Voultsiadou et al., 2010), oysters are nowadays one of the most translocated marine species globally (Korringa, 1976; Ruesink et al., 2005; Bromley et al., 2016).

One of the characteristic features of the morphology of bivalve shells, as is the case of the European flat oyster, is the formation of a banded structure, originating from appositional growth, which produces growth increments and ensures that growth hysteresis is recorded within the hard carbonate shell (Andrus, 2011). Wide growth increments represent periods of fast growth (white bands), whereas narrow growth increments represent periods of slow growth (dark bands) (Nyström et al., 1995; Milner, 2002; Haag and Commens-Carson, 2008). The pattern of the banded structure is highly dependent on both growth and habitat conditions. In fact, bivalve shells have long been recognised to potentially represent excellent high-resolution (i.e. intra-annual) palaeoclimate archives (Hudson et al., 1976; Richardson, 2001; Bougeois et al., 2016; Mouchi et al., 2018, 2021). In addition, their generally large and thick calcitic shells promote good preservation of fossils such that oysters represent one of the most abundant macrofossil groups readily available in the sedimentary records (Stenzel, 1971). Structural analysis, sometimes in conjunction with geochemical analysis, of European flat oysters has been used to determine the season of death of the animal and the seasonality of use of midden (shell refuse) sites in Europe (Milner, 2001, 2002). These studies illustrate the potential of oyster shells to contribute to knowledge of past environments, from palaeoclimate, archaeological and ecological perspectives (Thomas, 2015b).

However, the provenance of these archaeological shells is usually unknown, except in those cases where they are associated with other characteristic taxa (epi-fauna) or with a specific substrate with endemic and unique characters identifiable by specialists (Mouchi et al., 2021). It is common in archaeology to use morphometric characters to determine the provenance of shells of various origins, even though such characteristics are not locality-specific but rather substrate-specific (Colonese et al., 2011). Different techniques have been developed to identify the provenance of fossil oyster shell remains, such as geochemical analyses (Mouchi et al., 2018, 2020a, 2020b, 2021). Provenance determination of archaeological remains is a valuable tool for reconstruction of past exchange networks. However, in the case of fossil oyster shells documented in Roman sites on the Iberian Peninsula, their provenance is still unknown.

In coastal systems, a mixture of organic particles from autochthonous and allochthonous origin contribute to the pool of particulate

organic matter (Savoie et al., 2012; Purroy et al., 2018). Bivalve molluscs, as filter-feeding organisms, are able to shift their diets along the year adapting to the available suspended material, e.g. following the magnitude and seasonality of primary production (Antonio et al., 2010). Bivalves mainly feed upon phytoplankton but other sources such as detritus, bacteria, microphytobenthos and zooplankton can also constitute an important component of their diet (Klaveness, 1990; Peharda et al., 2012). They also participate in the transfer of particulate organic matter between the water column and the surface sediment layer (Schubert and Calvert, 2001), being able to concentrate in their soft tissues various contaminants from ambient water due to the bioaccumulation process; foreign substances can be incorporated into shells during growth or through the passive adsorption on their surfaces from the extrapallial fluid and the water column. Bioaccumulation of various metals has been demonstrated in the literature for a number of species of bivalves (Zuykov et al., 2013) and even in oyster shells (Cariou et al., 2017). In this sense, it is logical to think that during their feeding oysters could incorporate pollen or other non-pollen microfossils dispersed in sea water, which will be incorporated and fossilised in their shells during the biomineralisation process related to their growth. These pollens would inform about the pollen rain corresponding to the time of life of the animal and therefore would have the potential to serve as markers of past vegetation. In short, the palynological analysis of fossil bivalve shells opens up new possibilities for palaeoenvironmental information in addition to other sedimentary archaeological contexts that are generally undervalued and little exploited, such as coprolites, bat and bird guano, dung and other biogenic deposits, and speleothems (McGarry and Caseldine, 2004; Dean, 2006).

In view of the above, it is therefore possible to study the pollen content of fossilised shells. To our knowledge, such studies have only been conducted in France on both mussel (*Mytilus edulis*) and oyster (*Ostrea edulis*) fossil shells from the Roman period, giving rise to a new archeopalynological discipline, the so-called “conchopalynology” (Argant, 2013, 2015). Although quantitatively the results were not very encouraging, qualitatively they were very interesting to determine the origin of the shells. The palynological study of fossil oysters would hardly allow any kind of palaeoenvironmental reconstruction, since their carbonated nature often poses an insurmountable problem for the conservation of the pollen contingent, and it is therefore to be expected that the amount of pollen preserved would be low (López-Sáez et al., 2003, 2006). Nevertheless, the preservation of pollen in fossil oyster shells - if those documented have some diagnostic character of the local vegetation - may shed light on the geographical location of oyster cultivation and/or fishing areas.

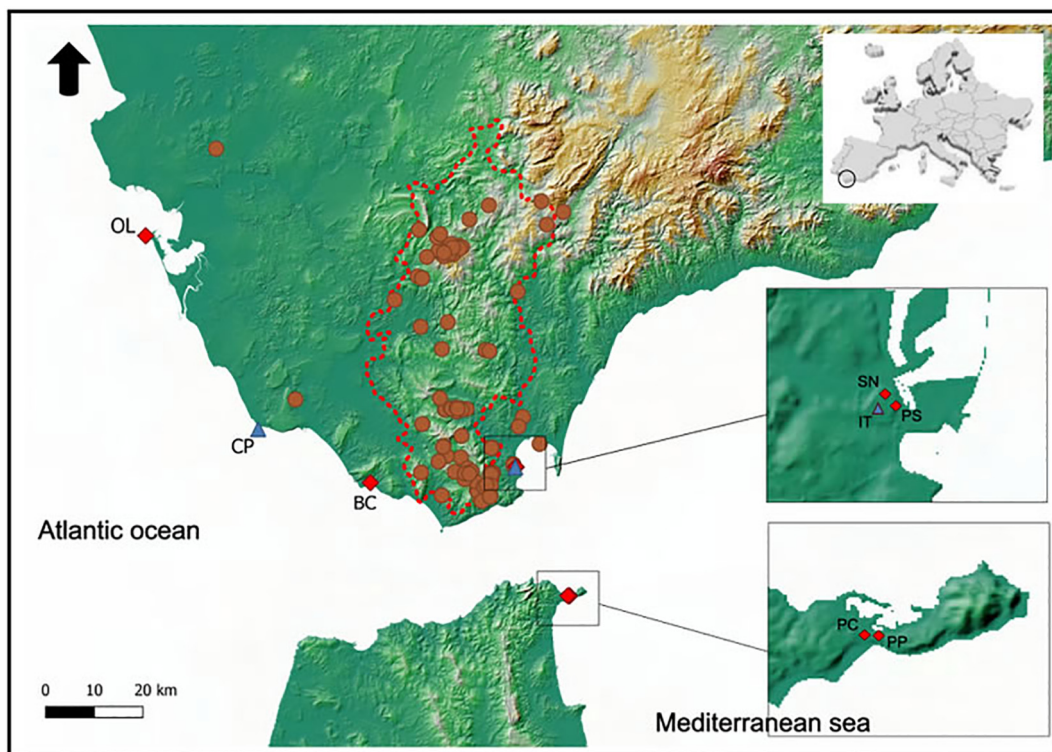
To test the possibilities of conchopalynology in the Iberian Peninsula and North Africa, we focused on the distribution of pollen in fossil shells of a bivalve, *Ostrea edulis*, collected at six Roman sites in the Strait of Gibraltar (Fig. 1). The objectives of this research are: i) to determine the potential of conchopalynology to reconstruct the vegetation of the past; ii) to try to discriminate specific pollen markers that inform about the origin of the oysters. So far, in the Strait of Gibraltar as a whole, there are only two known archaeological sites (Fig. 1) with evidence of oyster farming in Roman times (Bernal-Casasola et al., 2011, 2014, 2022a, 2022c): i) the Bay of Algeciras, specifically the Roman city of *Ivlia Tradvcta*, in contexts from the late Roman period (5th century AD); ii) a Roman maritime *villa* at Cape Trafalgar, in the municipality of Barbate, where a rock-hewn oyster nursery (*vivarium*) from the early Roman period (1st century AD) has been documented (Fig. 2).

## 2. Material and methods

### 2.1. Sampling archaeological sites

The fossil oyster specimens (*Ostrea edulis*) used in this study were collected between 2009 and 2021 from six Roman archaeological sites





**Fig. 1.** The Strait of Gibraltar region. Location of archaeological sites mentioned in the text where pollen analysis of fossil oysters was carried out (red diamonds): BC, *Baelo Claudia*; OL, El Olivillo; PC, *Puerta Califal*; PP, *Paseo de las Palmeras*; PS, *Parque Smith*; SN, *San Nicolás*. Archaeological sites with evidence of oyster farming in Roman times (blue triangles): CP, *Cape Trafalgar*; IT, *Ivliā Tradvcta*. The dashed red line indicates the boundaries of the Alcornocales Natural Park. The brown circles correspond to the quotations of *Rhododendrum ponticum* according to the international network "Global Biodiversity Information Facility"-GBIF (<https://www.gbif.org/>). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 2.** 3D Reconstruction of the Roman maritime villa at Cape Trafalgar and the associated oyster farm (redrawn from Bernal-Casasola et al., 2022c).



of Southern Iberia and Northern Africa (Spain). Separated by tens or hundreds of kilometres, the sites cover a representative territory in the Strait of Gibraltar (Fig. 1).

The first site, referred to as El Olivillo, corresponds to a large Roman dump or public landfill. It composed an artificial hill at the entrance of the outer harbour destined to contain the waste from fishing and canning industries of *Gades*, especially *garum* amphorae and archaeological ichthyofauna; the so-called *Haliotic Testaccio* of Roman *Gades* (Fig. 3). Five oyster specimens (OL1 to OL5) were selected from the stratigraphic unit (SU 2023, test pit 2) dated to the 1st century AD during the early Roman period (Bernal-Casasola et al., 2019). The second site corresponds to an abandoned residential area at the heart of the *Baelo Claudia* Roman city in the town of Tarifa (Fig. 4). Ten oyster shells (BC1 to BC10) were collected in the stratigraphic unit 1208 of the test pit 12, corresponding to the wasting food of a feast (*convivium*) dated to the 1st century AD (Bernal-Casasola et al., 2014, 2015).

Two other late Roman sites are located in the Algeciras town (the Roman *Ivlia Traducta*). In all the cases the oysters come from the fill of abandoned pools or associated strata (Fig. 5). At the first site, Parque Smith or Parque de las Acacias, six oysters were studied, three from the stratigraphic unit 124 (PS1 to PS3) dated between the end of the 3rd and the beginning of the 4th centuries AD, and three more from the stratigraphic unit 133 (PS4 to PS6) with an approximate chronology of the late 5th century AD (Jiménez-Camino et al., 2019; Bernal-Casasola et al., 2020). In the second site, known as San Nicolás, ten oysters were analysed (SN1 to SN10), five in each of the stratigraphic units 2006 and 2007. In both cases the analysed oysters have an estimated chronology around the 5th and the beginning of the 6th centuries AD (Bernal-Casasola and Jiménez-Camino, 2018).

Finally, the last two archaeological studied sites are located in Ceuta, in North Africa. The first site, known as Paseo de las Palmeras, gave two oysters (PP1 and PP2) from the stratigraphic unit 1766 of late Roman chronology (5th century AD). The second, known as Puerta Califal, one oyster (PC1) from the stratigraphic unit 033 dated to the 1st century AD was studied (Bernal-Casasola et al., 2022b).

## 2.2. Pollen and statistical analyses

Thirty-four fossil European flat oyster specimens were selected from the archaeological sites mentioned above, taking into account that they were in a good state of conservation and not fractured, and have a minimum size of 20 cm in length along its longest axis. We chose the upper shells of fossil oysters as they have shown the greatest potential to contain pollen (Argant, 2015). After isolation from the archaeological sediment, the fossil shells were separated from the host sediment using a chisel. Afterwards, the shell surface was cleaned using a needle under the binocular microscope to ensure that any potential contaminant pollen from post-depositional processes was removed, thorough cleaning of the shell's surface by brushing off loose material and rinsing with deionised water. Finally, each fossil oyster shell was individually weighed.

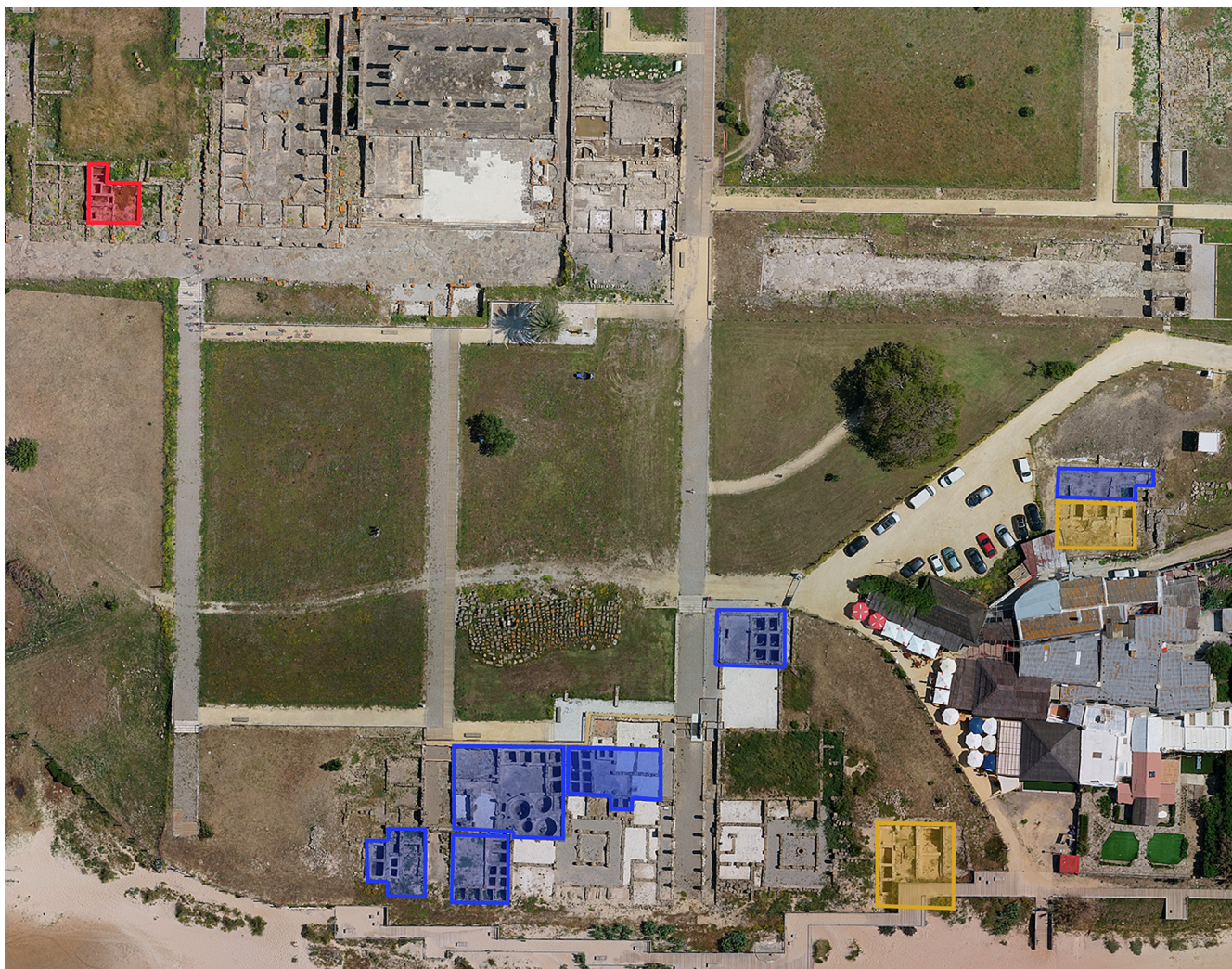
Shells of marine molluscs range from a simple to an ornate architecture, but all are constructed of a common chemical salt, calcium carbonate (Andrus, 2011). These shells are generally made up of three layers that are formed from conchiolin, a scleroprotein secreted by the mantle associated with carbonates extracted from the water filtered by the gills of the animals (Bowen and Tang, 1996). In order to analyse the pollen content, the oyster shells were ground in a porcelain mortar, washed in boiling water and dried to constant weight at 100 °C. The dry powder was decalcified in cold HCl (40%), added in small portions until all effervescence ceased, and then sieved through a 0.20 mm mesh and centrifuged (Coil et al., 2003). *Lycopodium* tablets were added to allow the calculation of pollen concentrations (Stockmarr, 1971). Later, all samples were ultrasonically rinsed with a Branson® S450 sonicating disruptor horn to agitate the sample, keeping the sample free from debris (Perrotti et al., 2018). After processing, samples were suspended in glycerine jelly prior to being mounted on slides.

Palynomorphs were identified at 400× and 1000× magnification to the lowest taxonomic level possible with a Nikon Eclipse 50i light-microscope. Identifications were based on the European and North African Atlas (Reille, 1999), and the pollen reference collection at the Institute of History (CSIC-Madrid). A minimum of 150 pollen grains were identified and counted for each sample. Pollen percentages were



Fig. 3. Recreation of the island strait of *Gades* with the *Haliotic Testaccio* of El Olivillo (redrawn from Bernal-Casasola et al., 2019).





**Fig. 4.** Abandoned residential area of the *Baelo Claudia* Roman city in the town of Tarifa (redrawn from Bernal-Casasola et al., 2015). The colours correspond to different archaeological excavation campaigns at the canneries.

calculated using a pollen sum excluding indeterminable pollen grains, and presented as bars in a pollen diagram, which was constructed using TGView (Grimm, 2004).

To estimate the relationships between pollen assemblages and pollen types we used ordination analysis. Principal component analysis (PCA) was used as a lineal interpretation method. A previously applied detrended correspondence analysis (DCA) pointed to a linear response (gradient length < 2 standard deviation of species turnover units) of pollen types (variables) instead of unimodal responses of taxa (ter Braak and Prentice, 1988). PCA was performed using square-root transformed percentage of pollen taxa and down-weighting of rare taxa with CANOCO version 4.5 (ter Braak and Šmilauer, 2002).

### 3. Results and discussion

A total of 20 pollen types were identified. The results of identification and counting are presented as a percentage diagram (Fig. 6). All of the samples are characterised by a poor pollen concentration (23–77 grains  $g^{-1}$ ) and abundant indeterminate pollen. This pollen concentration is much lower than that documented in the palynological study of different Pleistocene and Holocene coprolite assemblages in the Iberian Peninsula (Carrión et al., 2005, 2007). Due to poor concentration and preservation, the pollen counts involved all of the material obtained for each fossil shell.

Pollen spectra of fossil oysters from each archaeological site are very similar to each other when they correspond to the same chronology. This would support the chronological contemporaneity of fossil shells and their validity for the reconstruction of palaeovegetation.

In general, the pollen assemblages are dominated by anemophilous (wind-pollinated) taxa such as *Pinus pinea*, *Quercus suber*, *Q. ilex*, *Q. pyrenaica*, *Juniperus*, *Alnus*, *Olea*, *Pistacia lentiscus* and *Poaceae*, which account for more than 75% of the pollen sum. Nevertheless, the presence of entomophilous pollen taxa is also noteworthy, especially in the Algeciras's samples –*Erica arborea* and *Rhododendron ponticum*– and in all sites where there is evidence of human impact through the identification of anthropogenic-nitrophilous herbs such as *Asterioideae* and *Cichorioideae*. These data coincide with what is also documented in the pollen analysis of Quaternary Iberian coprolites, i.e. a dominance of anemophilous taxa over entomophilous taxa (González-Sampériz et al., 2003; Carrión et al., 2005, 2007).

Fig. 7 presents the PCA scatter plots for both samples (circles) and the most contributing pollen taxa into the PCA axis 1 and PCA axis 2, in which the contribution of axes 1 and 2 to the total variance are 66.0% and 15.2%, respectively. The PCA biplot of fossil oyster shells allows identifying two distinct groups. On the first axis (PCA axis 1) Mediterranean plant communities are separated from Atlantic ones. Many pollen taxa are discriminated along this axis; those displaying the highest species scores were typical of Mediterranean areas (negative





Fig. 5. Detail of the Roman salting pools at the Parque de las Acacias site.

values: e.g. *Rhododendron ponticum*, *Celtis australis*, *Frangula alnus*, *Salix*, *Myrtus communis*, *Erica arborea*, *Quercus suber*, *Q. pyrenaica*, *Pistacia lentiscus*) or from Atlantic ones (positive values: e.g. *Pinus pinea*,

*Juniperus*, *Quercus ilex*). The first group includes samples from Parque Smith and San Nicolás sites located in the Bay of Algeciras, while the second one includes samples from *Baelo Claudia* and El Olivillo located in

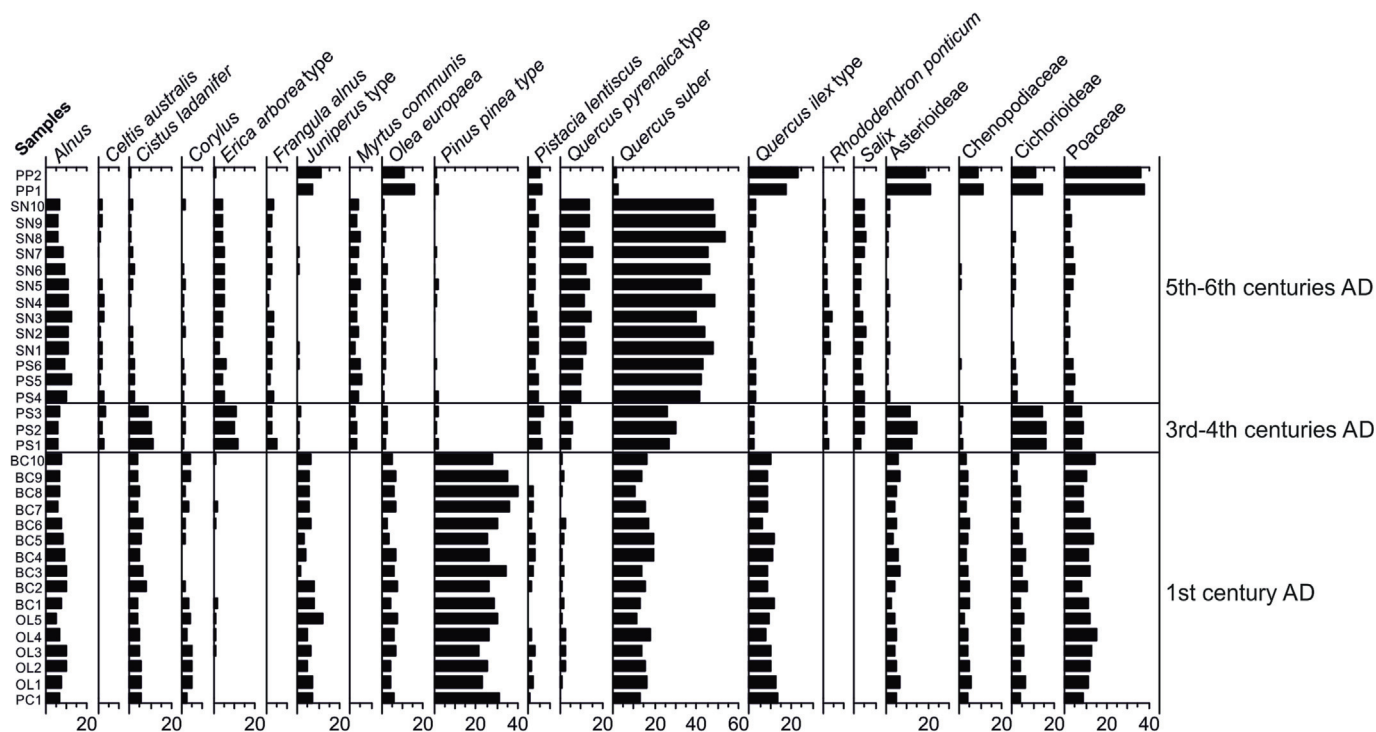


Fig. 6. Pollen diagram of 34 fossil oysters from six Roman sites in the Strait of Gibraltar (BC, *Baelo Claudia*; OL, El Olivillo; PC, Puerta Califal; PP, Paseo de las Palmeras; PS, Parque Smith; SN, San Nicolás).

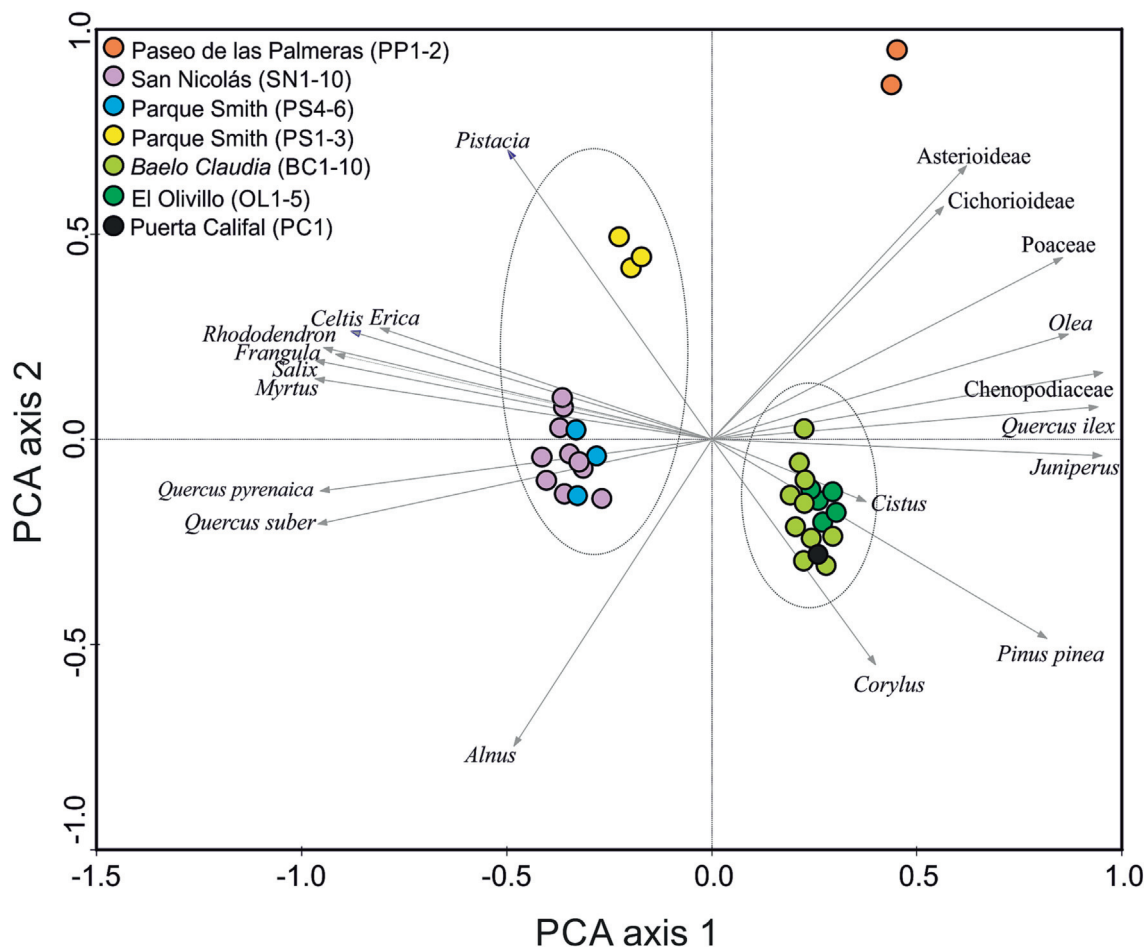


Fig. 7. Principal Component Analysis (PCA) ordination biplot of the 34 study fossil oyster shells (circles) and the dominant pollen taxa (arrows). Each sample is expressed by the archaeological site.

the Atlantic coast as well as one sample from Puerta Califal –located in Ceuta by the Mediterranean Sea– but whose oyster was probably cultivated in the oyster bed of Barbate or at some other hitherto unknown archaeological site with ostriculture. Samples from Paseo de las Palmeras site do not show good discrimination along this axis. The second principal component axis roughly separates the samples from Paseo de las Palmeras and Parque Smith sites with positive values, the latter dating from the late 3rd to the early 4th century AD, from those samples from Baelo Claudia, El Olivillo, Puerta Califal, San Nicolás and Parque Smith (samples dated to the end of the 5th century AD) sites with negative or almost zero values (Fig. 7). Asterioideae, Cichorioideae, Poaceae and Pistacia have the highest positive loading on the second principal component axis, whereas Alnus, Corylus and Pinus pinea pollen types have the highest negative loading on it. This indicates that the second component discriminates between pollen spectra (positive values) corresponding to highly anthropized landscapes with high percentages of anthropogenic-nitrophilous herbs, while those with negative values correspond to forested landscapes.

### 3.1. Provenance of Roman fossil oysters: A palaeopalynological approach

The exact origin of the oysters consumed in the Strait of Gibraltar during Antiquity is therefore still unknown. All samples with positive values in the first PCA axis (Fig. 7) are oysters from the Atlantic coast (Baelo Claudia, El Olivillo and Puerta Califal), while those with negative values are from the Mediterranean coast (Parque Smith and San Nicolás). Samples from Paseo de las Palmeras site have positive values

on PCA axis1, despite coming from the Mediterranean coast, which is possibly due to the high Quercus ilex, Juniperus and Olea europaea pollen percentages.

Pollen spectra of fossil oyster shells from Baelo Claudia (Fig. 6) closely resemble the palaeovegetation inferred at this Roman city site during the 1st century AD (Reicherter et al., 2022; López-Sáez et al., 2023; Fig. 8), as they are also dominated by Pinus pinea, evergreen Quercus, wild olives (Olea europaea), alder (Alnus), hazel (Corylus), junipers (Juniperus) and Poaceae. This vegetation of Mediterranean pine woods associated with stabilised dunes and sandy soils is characteristic of the Atlantic strip of the province of Cádiz, particularly the stretch between the Bolonia –where Baelo Claudia is located– and Barbate –location of the Roman maritime villa of Cape Trafalgar– inlets (Gómez-Serrano et al., 2009). These facts allow us to suggest two possibilities: i) the oysters consumed at Baelo Claudia would have come from the Cape Trafalgar oyster nursery (vivarium; Fig. 2), as the estimated chronology in both cases is the same and corresponds to the early Roman period (1st century AD) (Bernal-Casasola et al., 2011, 2022a); ii) the Baelo Claudia oysters were collected in situ in the Bolonia inlet, as the presence of Roman shellfish gatherers in the circle of the Strait of Gibraltar is well known (Bernal-Casasola, 2011a). However, the archaeomalacological study of the stratigraphic unit 1208 at Baelo Claudia revealed the remains of a highly diverse banquet or convivium primarily related to the consumption of oysters and wine (Bernal-Casasola et al., 2014), with 9 species identified, 6 of bivalves (Acanthocardia tuberculata, Cerastoderma edule, Glycymeris sp., Mytilus sp., Ostrea edulis, and Pecten maximus),



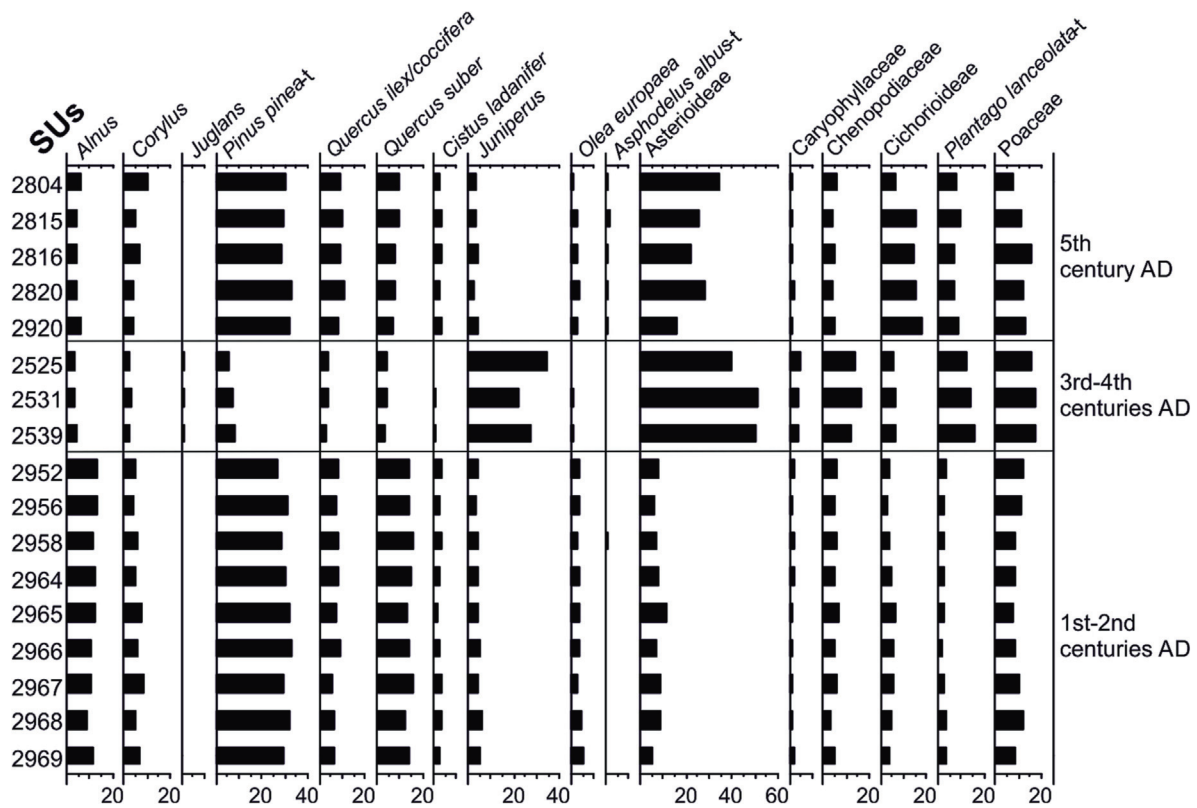


Fig. 8. Pollen diagram of the Baelo Claudia Roman city (redrawn from López-Sáez et al., 2023).

and 3 of gastropods (*Cymbula nigra*, *Patella intermedia*, and *P. ulysiponensis*). Of these, the most abundant mollusc was the European flat oyster, whose specimens showed relatively homogeneous sizes of large dimensions with no signs of having been subjected to induced growth such as ceramic adhesions (Fig. 9), charnelate outgrowths or through holes (Bernal-Casasola, 2011b), so that a priori it could be assumed that they would have been the result of collection in their natural environment (Bernal-Casasola et al., 2014).

Pollen spectra of fossil oysters from El Olivillo site closely resemble those of fossil shells from Baelo Claudia (Fig. 6), where the same pollen taxa are present in similar percentages during the early Roman period. However, there are remarkable differences between the pollen spectra

shown by Roman shells from El Olivillo and the one in the early Roman levels studied at the archaeological site itself (López-Sáez and Pérez-Díaz, 2019; Fig. 10): i) the percentages of *Pinus pinea* are higher in the fossil shells (24–31%) than in the site (<20%); and, ii) higher values of pollen taxa related to halophilic vegetation and coastal salt marshes are found in the site, case of Cyperaceae (absent in the fossil oysters) and Chenopodiaceae (30–40% in the archaeological site, <5% in the fossil shells).

El Olivillo site is related to a public landfill from Roman Gades (Bernal-Casasola et al., 2019), the present-day city of Cádiz (Fig. 3), in whose bay the most notable vegetation corresponds to extensive wetlands of coastal salt marshes and lagoons with halophilic species, although inland, as in Tarifa and Barbate, cork oak groves with wild olive trees and holm oak groves are also abundant, but no pine forests (Bejarano, 1997). It is therefore most likely that the oysters consumed in Gades and deposited in the public landfill at El Olivillo come from the Cape Trafalgar oyster bed in Barbate, or from other hitherto undocumented sites in the region. In fact, pollen spectra of fossil oysters from El Olivillo site are also very different from some fossil records from the late Holocene near Cádiz, such as Medina lake (Schröder et al., 2018, 2020), particularly due to the presence in the latter of floristic elements associated with lagoon environments such as *Tamarix*, *Ulmus*, Cyperaceae, *Myriophyllum*, Potamogetonaceae, as well as high percentages of Chenopodiaceae.

A similar case to the previous one occurs with the single fossil oyster analysed at the site of Puerta Califal in Ceuta, from the 1st century AD, whose pollen spectrum is totally concordant with the Baelo Claudia oysters' pollen record (Fig. 6). As in the previous case, it is most likely that the oysters consumed at this site came from the Cape Trafalgar oyster bed in Barbate, or from other unknown external sites.

The cluster composed of *Celtis australis*, *Myrtus communis*, *Pistacia lentiscus*, *Salix*, *Frangula alnus*, and *Rhododendron ponticum*, common to oyster samples from the late Roman sites of Parque Smith and San Nicolás in Algeciras (Fig. 6), represents a homogenous fingerprint.



Fig. 9. Oyster with attached fragment of Roman amphora from the archaeological site of San Nicolás.



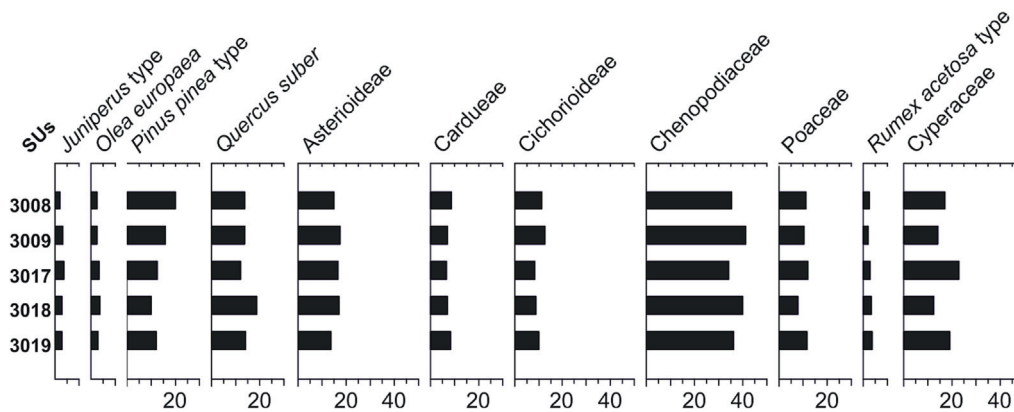


Fig. 10. Pollen diagram of the early Roman levels of El Olivillo site (redrawn from López-Sáez and Pérez-Díaz, 2019).

Among these pollen taxa, the constant presence in all samples of *Rhododendron ponticum* is very significant, as this species is part of the lauroid vegetation of the Alcornocales Natural Park (Fig. 1), typical of deep gorges, valley headwaters and high plateaus where cryptoprecipitation is abundant (Pérez-Latorre et al., 2000). The percentage of rhododendron is relatively low (0.6–3.7%) in the fossil oysters from Algeciras, which is justified given the zoophilous character of this species (Mejías et al., 1994). The presence of the aforementioned pollen taxa in the late Roman oysters from the Parque Smith and San Nicolás sites would suggest that all the oysters reached the Bay of Algeciras from the Alcornocales Natural Park. This Park is located ~25 km northwest of Algeciras, and is directly connected to the bay by a dense hydrographic network (Fig. 1). Therefore, it is most likely that the oysters from both sites came from the late Roman (5th century AD) oyster beds of the Roman city of *Ivlia Traducta* in the Bay of Algeciras (Fig. 11).

Finally, pollen spectra of the late Roman (5th century AD) site of Paseo de las Palmeras in Ceuta (North Africa) are very different from the rest of the studied sites (Fig. 6): percentages of *Pinus pinea* and *Quercus suber* are very low (<3%), while *Quercus ilex* (17–23%), *Olea europaea* (11–16%), *Juniperus* (7–11%), *Pistacia lentiscus* (5–6.5%) and *Poaceae* (37%) show quite high values. The identification of these floristic elements characteristic of the thermo-Mediterranean bioclimatic belt of North Africa (Charco, 1999) suggests that pollen data of these oysters represent the immediate environment of the coast of Ceuta. In fact, pollen spectra of the late Roman oysters from Paseo de las Palmeras site are very similar to those from other sites in Ceuta of the same chronology (Bernal-Casasola et al., 2022b). In short, these oysters were probably collected in situ near the site.



Fig. 11. Set of oysters from the late Roman factories at the San Nicolás site.

### 3.2. The potential of conchopalynology for reconstructing palaeovegetation

Obviously, the potential of conchopalynology to reconstruct vegetation history is conditioned by the provenance of fossil shells, being feasible as long as they were collected or cultivated in the immediate vicinity of a near-shore archaeological site. This would be the case of the *Baelo Claudia* and Paseo de las Palmeras sites. In the case of El Olivillo and Puerta Califal sites, as mentioned above, the fossil oysters probably come from the Cape Trafalgar oyster bed in Barbate (Fig. 2), so their pollen spectra would not be valid for reconstructing the palaeovegetation of Roman *Gades* or Ceuta but from the place of origin of the oysters. Considering that the coastal areas where the oysters were harvested or cultivated may receive water from the regional hydrological network, it is also possible that the pollen spectra of some fossil oysters reflect the regional palaeovegetation; this has been the case for Parque Smith and San Nicolás sites in the Bay of Algeciras.

During the 1st century AD, the local vegetation in the vicinity of the *Baelo Claudia* Roman city (Fig. 6), according to pollen spectra of ten fossil oysters, would consist mainly of open stone pine (*Pinus pinea* 25–38%) woods settled on stabilised fixed dunes, with thickets of beach juniper (*Juniperus phoenicea* subsp. *turbinata*) or maritime juniper (*Juniperus oxycedrus* subsp. *macrocarpa*) on coastal sandbanks (*Juniperus* 2–8%). These forest communities are now considered natural and autochthonous (Martínez and Montero, 2004; Mesa, 2016), and the presence of these pollen types in the studied oysters would corroborate their presence in Roman times in the area around the Bolonia inlet. Inland, on deeper soils –albeit sandy and decarbonated– and in shady areas, thermo-mediterranean cork oak groves of *Quercus suber* (10–19%) would develop, in which wild olive trees (*Olea europaea* 3–7%) would be frequent. In sunny areas, holm oak groves of *Quercus ilex* (6–12%) with an undergrowth of *Cistus ladanifer* (4–7%) would be dominant, while riparian woodlands would be represented by alders (*Alnus* 6–9%) accompanied by hazelnut trees (*Corylus* 0–4%). Anthropogenic-nitrophilous herbs (Asterioideae, Cichorioideae) are also present with low percentages (<6%), indicating some human impact on local ecosystems but not too important, while *Poaceae* (8–14%) would be indicative of open grassland areas. These data are in agreement with the palynological studies of the *Baelo Claudia* Roman city and the early Roman levels of El Olivillo site (López-Sáez and Pérez-Díaz, 2019; López-Sáez et al., 2023; Figs. 8 and 10), which show a completely concordant landscape during the 1st century AD and a very low human impact. These vegetation composition data are coherent with pollen spectra of fossil oysters from El Olivillo and Puerta Califal sites (Fig. 6), so the same conclusions can be drawn for the early Roman period.

The pollen record of fossil shells from two late Roman sites in Algeciras –Parque Smith and San Nicolás– (Fig. 6) are characterised by relatively high values of cork oak (*Quercus suber* 26–49%) and deciduous *Quercus* (*Q. pyrenaica* 5–15%), by the presence of termophilous

elements characteristic of the thermo-Mediterranean bioclimatic belt such as *Celtis australis* (0–4%), *Erica arborea* (3–12%), *Myrtus communis* (2–5%), *Olea europaea* (1–3%) and *Pistacia lentiscus* (3–7%), as well as by certain hygrophilic elements such as *Alnus* (6–12%), *Salix* (2–5%), *Frangula alnus* (1–5%) and *Rhododendron ponticum* (1–4%). These pollen spectra are fully consistent with the existing vegetation in the Alcornocales Natural Park (Pérez-Latorre et al., 1999). Thus, the fossil oysters from Algeciras would therefore represent the regional and local palaeovegetation existing between the meso- and thermo-Mediterranean bioclimatic belts between the Bay of Algeciras and the Alcornocales Natural Park. Both pollen records are in agreement with those known for the late Holocene in the Alcornocales Natural Park (Gutiérrez et al., 1996, 1997), where the pollen study of a peat bog shows the absence of pine pollen and high percentage values of other tree species such as cork oak (*Quercus suber*), hazelnut (*Corylus avellana*) and Mediterranean hackberry (*Celtis australis*), together with a large number of heathers (*Erica* sp.).

The 3rd- and 4th-century AD samples from the Parque Smith site (PS1 to PS3; Fig. 6) show relatively low values of *Quercus suber* (26–30%) and *Q. pyrenaica* (5–5.6%), but high percentages of shrub elements typical of the seral stages of the forests –*Erica arborea* 10–12% and *Cistus ladanifer* 9–11.5%– as well as anthropogenic-nitrophilous herbs such Asterioideae (11–15%) and Cichorioideae (14–16%), suggesting forest decline and high human impact in the Bay of Algeciras between the end of the 3rd and the beginning of the 4th centuries AD. A similar picture has been documented in the *Baelo Claudia* pollen record (Fig. 8) in the same chronological interval (López-Sáez et al., 2023), suggesting a strong anthropogenic impact in the first two centuries of the late Roman period in the Strait of Gibraltar area, which is in agreement with the known exploitation patterns that show a great intensification of agricultural, fishing and canning activities (Padilla, 2008).

During the 5th and 6th centuries AD the percentage of *Quercus suber* (>40%) and *Q. pyrenaica* increases notably in samples from Parque Smith (PS4 to PS6) and San Nicolás (SN1 to SN10) sites (Fig. 6), while the above-mentioned anthropogenic-nitrophilous herbs, heather and rockroses drastically reduced their values. These data would point to the progressive recovery of forests in the last centuries of the late Roman period, coinciding with a period of economic stagnation, fall of the production, and depopulation as a consequence of changes in the trading routes (Reynolds, 1995; Bernal-Casasola, 2000; Lagóstena, 2001). In North Africa, on the other hand, pollen data from Paseo de las Palmeras site (Fig. 6) in Ceuta indicate a highly anthropized environment –high percentages of Asterioideae and Cichorioideae– with a very low tree cover and large areas of grassland (Poaceae 37%), and it is even possible that olive trees were cultivated (*Olea europaea* 11–16%) during the 5th century AD.

Pollen samples from Paseo de las Palmeras and Parque Smith –PS1–PS3, late 3rd to early 4th century AD–, related to environments where human impact is higher (high percentages of Asterioideae and Cichorioideae and low tree cover) have the highest positive values on the PCA axis 2, while those where anthropisation is lower and tree cover higher have negative or almost zero values –*Baelo Claudia*, El Olivillo, Puerta Califal, San Nicolás and Parque Smith (PS4–PS6, end of the 5th century AD) sites– with negative or near zero values (Fig. 7). In short, PCA axis 2 is related to an increase in human impact, which manifests itself chronologically, so that the pollen study of Roman fossil oysters can be used to reconstruct the history of vegetation and anthropogenic dynamics in a diachronic sense.

#### 4. Conclusions

Our study provides the first results of a discipline practically unpublished in the palynological literature, conchopalynology, i.e. the study of the pollen content of fossil mollusc shells. It is the second study of this

type to be carried out worldwide and the first in the Iberian Peninsula. This research used palynological proxies for environmental reconstruction from thirty-four oyster shells (*Ostrea edulis*) on Roman archaeological specimens dated from the 1st century AD to the 6th century AD and found in archaeological sites in the Strait of Gibraltar area, between southwest Iberia and North Africa (Spain). Ordination of pollen samples indicated the existence of two characteristic groups, which can be assigned to the Mediterranean or Atlantic provenance of the fossil oysters. Pollen spectra of fossil oysters with different chronology have proven to be valid for reconstructing the vegetation history. This study has also made it possible to discriminate between those oysters that were harvested and those that were cultivated.

This approach can theoretically be extrapolated to other fossil mollusc shells, irrespective of the territory concerned. However, much more research is needed to determine whether other molluscs, beyond oyster and mussel, can also be used. It is also necessary to investigate further the taphonomic processes that have allowed the dispersal and subsequent preservation of the identified pollen taxa and those that are not present.

#### Data availability

Data will be made available on request.

#### Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Dario Bernal reports financial support, administrative support, and statistical analysis were provided by Spain Ministry of Science and Innovation.

#### Acknowledgements

This work was funded by the projects GARVM III (PID2019-108948RB-I00/AEI/10.13039/501100011033), ARQUEOSTRA (FEDER-UCA18-104415), ARQUEOFISH (P18-FR-1483, PAIDI 2020), and GARVMTRANSFER (PDC2021-121356-I00).

#### References

- Airoidi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe. *Oceanogr. Mar. Biol. Annu. Rev.* 45, 345–405.
- Álvarez, M., Briz Godino, I., Balbo, A., Madella, M., 2011. Shell middens as archives of past environments, human dispersal and specialized resource management. *Quat. Int.* 239, 1–7.
- Andrus, C.F.T., 2011. Shell midden sclerochronology. *Quat. Sci. Rev.* 30, 2892–2905.
- Antonio, E.S., Kasai, A., Ueno, M., Kurikawa, Y., Tsuchiya, K., Toyohara, H., Ishih, Y., Yokoyama, H., Yamashita, Y., 2010. Consumption of terrestrial organic matter by estuarine molluscs determined by analysis of their stable isotopes and cellulase activity. *Estuar. Coast. Shelf Sci.* 86, 401–407.
- Argant, J., 2013. La conchyliopalynologie: coquilles d'huitres et pollen. Le cas des huitres gallo-romaines de Cybele (Lyon, Rhône). In: Bardot-Cambot, A. (Ed.), *Les coquillages marins en Gaule romaine. Approche socio-économique et socioculturelle*. BAR International Series 2481, pp. 257–258 Oxford.
- Argant, J., 2015. Archéologie et paléoenvironnement. Contributions des apports ponctuels: palynologie des coprolithes et des coquillages. In: Bardot-Cambot, A., Tranoy, L. (Eds.), *L'environnement en mémoire. Marqueurs, outils et perspectives*. Presses universitaires de Rennes, Rennes, pp. 47–54.
- Bardot-Cambot, A., 2013. *Les coquillages marins en Gaule romaine. Approche socio-économique et socio-culturelle*. British Archaeological Reports International Series 2481, Oxford.
- Archaeomalacology. In: Bar-Yosef Mayer, D.E. (Ed.), *Molluscs in Former Environments of Human Behaviour*. Oxbow Books, Oxford.
- Bayne, B.L., 1976. Aspects of reproduction in bivalve molluscs. In: Wiley, M.L. (Ed.), *Estuarine Processes*. Academic Press, New York, pp. 432–448.
- Beck, M.W., Brumbaugh, R.D., Airoidi, L., Carranza, A., Coen, L.D., Crawford, C., Defeo, O., Edgar, G.J., Hancock, B., Kay, M.C., Lenihan, H.S., Luckenbach, M.W., Toropova, C.L., Zhang, G., Guo, X., 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience* 61, 107–116.
- Bejarano, R., 1997. *Vegetación y paisaje en la costa atlántica de Andalucía*. Universidad de Sevilla, Sevilla.



- Bernal-Casasola, D., 2000. La producción de ánforas en la Bética en el siglo III y durante el Bajo Imperio romano. Ex Baetica Amphorae. Conservas, aceite y vino en la Bética en el Imperio Romano. Editorial Gráficas, Écija, pp. 239–372.
- Bernal-Casasola, D., 2011a. Rastreado a los mariscadores romanos en las playas del círculo del Estrecho. Patélicos, burgaillos, mejillones y concheros poligénicos. In: Bernal-Casasola, D. (Ed.), *Pescar con arte. Fenicios y romanos en el origen de los aparejos andaluces*. Universidad de Cádiz, Cádiz, pp. 37–53.
- Bernal-Casasola, D., 2011b. Piscicultura y ostricultura en Baetica. Nuevos tiempos, nuevas costumbres. In: Bernal-Casasola, D. (Ed.), *Pescar con arte. Fenicios y romanos en el origen de los aparejos andaluces*. Universidad de Cádiz, Cádiz, pp. 137–159.
- Bernal-Casasola, D., Jiménez-Camino, R., 2018. Las cetariae de Iulia Traducta. Resultados de las excavaciones arqueológicas en la calle San Nicolás de Algeciras (2001–2006). Universidad de Cádiz, Cádiz.
- Bernal-Casasola, D., Alonso, C., Gracia, F.J., 2011. De la acuicultura en Baetica. A propósito de la posible piscina-vivero del yacimiento haliéutico del Cabo Trafalgar (Cádiz). *Zephyrus* 67, 145–160.
- Bernal-Casasola, D., Cantillo-Duarte, J.J., Arévalo-González, A., Muñoz-Vicente, A., 2014. Ostras y vino en la ciudad hispanorromana de Baelo Claudia. *Archaeofauna* 23, 89–103.
- Bernal-Casasola, D., Cantillo, J.J., Díaz, J.J., Expósito, J.A., Pascual, M.A., Durante, A.M., Hoyo, L., Blanco, E., Retamosa, J.A., 2015. Marisqueo en la Baelo Claudia Tardorromana. Contextos malacológicos de las termas marítimas. In: Gutiérrez-Zugasti, I., Cuenca-Solana, D., González-Morales, M.R. (Eds.), *La investigación arqueomalacológica en la Península Ibérica: nuevas aportaciones*. Santander, Nadir Ediciones, pp. 187–197.
- Bernal-Casasola, D., Vargas-Girón, J.M., Lara-Medina, M. (Eds.), 2019. 7 metros de la Historia de Cádiz... Arqueología en El Olivillo y en el Colegio Mayor Universitario. Universidad de Cádiz, Cádiz.
- Bernal-Casasola, D., Marlasca, R., Jiménez-Camino, R., Hernández, A., 2020. Un registro haliéutico poco habitual: Ictiofaunas arqueológicas y diversidad de modelos de pesca en las cetariae de Iulia Traducta. *Revista atlántica-mediterránea de prehistoria y arqueología social* 22, 169–188.
- Bernal-Casasola, D., Fantuzzi, L., Díaz, J.J., Cantillo, J.J., Portillo, J.L., Soriguer, M., 2022a. Ostras, mejillones y la piscina loculata de la villa marítima del Cabo Trafalgar (Barbate): nuevos desafíos. *Cuadernos de Prehistoria y Arqueología de la Universidad Autónoma de Madrid* 48, 289–321.
- Bernal-Casasola, D., Villada, F., Marlasca, R., Bustamante, M., Riquelme, J.A., Rodríguez, C.G., Soriguer, M.C., Cantillo, J.C., Ruiz-Zapata, B., Gil-García, M.J., Vargas, J.M., Lara, M., Portillo, J.L., 2022b. Economía y paleoambiente en Septem entre Juba II y Bizancio: desafíos interdisciplinarios de la puerta califal de Ceuta. In: Villada, F. (Ed.), (Coord.), *Puerta Califal de Ceuta. Génesis y evolución de la Muralla Real*. Instituto de Estudios Ceutíes, Ceuta, pp. 361–494.
- Bernal-Casasola, D., Díaz, J.J., Vijande, E., Expósito, J.A., Cantillo, J.J. (Eds.), 2022c. *Blue Archaeology in Trafalgar. From Research to Sustainable Tourism*. Universidad de Cádiz, Cádiz.
- Bianchi, C.N., Morri, C., 2000. Marine biodiversity of the Mediterranean Sea: situation, problems and prospects for future research. *Mar. Pollut. Bull.* 5, 367–376.
- Bougeois, L., de Rafélis, M., Reichart, G.J., Dupont-Nivel, G., 2016. Mg/Ca in fossil oyster shells as palaeotemperature proxy, an example from the Palaeogene of Central Asia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 441, 611–626.
- Bowen, C.E., Tang, H., 1996. Conchiolin-protein in aragonite shells of molluscs. *Comp. Biochem. Physiol.* 115A, 269–275.
- Bromley, C., McGonigle, C., Ashton, E.C., Roberts, D., 2016. Bad moves: pros and cons of moving oysters. A case study of global translocations of *Ostrea edulis* Linnaeus, 1758 (Mollusca: Bivalvia). *Ocean Coast. Manag.* 112, 103–115.
- Cariou, E., Guivel, C., La, C., Lenta, L., Elliot, M., 2017. Lead accumulation in oyster shells, a potential tool for environmental monitoring. *Mar. Pollut. Bull.* 125, 19–29.
- Carrión, J.S., Gil, G., Rodríguez, E., Fuentes, N., García-Antón, M., Arribas, A., 2005. Palynology of badger coprolites from central Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 226, 259–271.
- Carrión, J.S., Scott, L., Arribas, A., Fuentes, N., Gil-Romera, G., Montoya, E., 2007. Pleistocene landscapes in central Iberia inferred from pollen analysis of hyena coprolites. *J. Quat. Sci.* 22, 191–202.
- Charco, J., 1999. El bosque mediterráneo en el Norte de África. Biodiversidad y lucha contra la desertificación. A.E.C.I. Madrid.
- Coil, J., Korstanje, M.A., Archer, S., Hastorf, C.A., 2003. Laboratory goals and considerations for multiple microfossil extraction in archaeology. *J. Archaeol. Sci.* 30, 991–1008.
- Colonese, A.C., Mannino, M.A., Bar-Yosef Mayer, D.E., Fa, D.A., Finlayson, J.C., Lubell, D., Stiner, M.C., 2011. Marine mollusc exploitation in Mediterranean prehistory: an overview. *Quat. Int.* 239, 86–103.
- Cortés-Sánchez, M., Morales-Muñiz, A., Simón-Vallejo, M.D., Bergadà-Zapata, M.M., Delgado-Huertas, A., López-García, P., López-Sáez, J.A., Lozano-Francisco, M.C., Riquelme-Cantal, J.A., Roselló-Izquierdo, E., Sánchez-Marco, A., Vera-Peláez, J.L., 2008. Palaeoenvironmental and cultural dynamics of the coast of Málaga (Andalusia, Spain) during the Upper Pleistocene and early Holocene. *Quat. Sci. Rev.* 27, 2176–2193.
- Davidson, A., 2002. *Mediterranean Seafood*. Prospect Books, Devon.
- Dean, G.W., 2006. The science of coprolite analysis: the view from Hinds cave. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 237, 67–79.
- Díaz-Almela, E., Boudry, P., Launey, S., Bonhomme, F., Lapégué, S., 2004. Reduced female gene flow in the European flat oyster *Ostrea edulis*. *J. Hered.* 95, 510–516.
- Edwards, E., 2005. World shellfish production keeps growing. *Fish Farming Int.* 32, 1–38.
- Fariñas-Franco, J.M., Pearce, B., Mair, J.M., Harries, D.B., McPherson, R.C., Porter, J.S., Reimer, P.J., Sanderson, W.G., 2018. Missing native oyster (*Ostrea edulis* L.) beds in a European marine protected area: should there be widespread restorative management? *Biol. Conserv.* 221, 293–311.
- Fernández-López de Pablo, J., Gabriel, S., 2016. El Collado shell midden and the exploitation patterns of littoral resources during the Mesolithic in the Eastern Iberian Peninsula. *Quat. Int.* 407, 106–117.
- Gercken, J., Schmidt, A., 2014. Current Status of the European Oyster (*Ostrea edulis*) and Possibilities for Restoration in the German North Sea. Bundesamt für Naturschutz, Putbus.
- Gibbs, M.T., 2004. Interactions between bivalve shellfish farms and fishery resources. *Aquaculture* 240, 267–296.
- Gómez-Serrano, M.A., Sanjaume, E., Gracia-Prieto, F.J., 2009. 2270 Dunas con bosques de *Pinus pinea* y/o *Pinus pinaster*. Bases ecológicas preliminares para la conservación de los tipos de hábitat de interés comunitario en España. Ministerio de Medio Ambiente, y Medio Rural y Marino, Madrid, pp. 1–48.
- González-Sampériz, P., Montes, L., Utrilla, P., 2003. Pollen in hyena coprolites from Gabasa cave (northern Spain). *Rev. Palaeobot. Palynol.* 126, 7–15.
- Grimm, E.C., 2004. TGVView. Illinois State Museum, Research and Collection Center, Springfield.
- Günther, R.T., 1897. The oyster culture of the ancient Romans. *J. Mar. Biol. Assoc. UK* 4, 360–365.
- Gutiérrez, A., Nebot, M., Díez, M.J., 1996. Introducción al estudio polínico de sedimentos del Parque Natural de los Alcornocales. *Almoraima* 15, 87–90.
- Gutiérrez, A., Díez, M.J., Nebot, M., Celis, M., 1997. Nuevas aportaciones al estudio polínico de sedimentos del Parque Natural de los Alcornocales (Cádiz, Sur de España). *Acta Bot. Malacit.* 22, 123–130.
- Gutiérrez-Zugasti, I., Andersen, S.H., Araújo, A.C., Dupont, C., 2011. Shell midden research in Atlantic Europe: state of the art, research problems and perspectives for the future. *Quat. Int.* 239, 70–85.
- Gutiérrez-Zugasti, I., Cuenca-Solana, D., Colonese, A.C., Fernández-López de Pablo, J., 2016. Time for the tide. New perspectives on hunter-fisher-gatherer exploitation of intertidal resources in Atlantic Europe and Mediterranean regions. *Quat. Int.* 407, 2–5.
- Haag, W.R., Commens-Carson, A.M., 2008. Testing the assumption of annual shell ring deposition in freshwater mussels. *Can. J. Fish. Aquat. Sci.* 65, 493–508.
- Helmer, L., Farrell, P., Hendy, I., Harding, S., Robertson, M., Preston, J., 2019. Active management is required to turn the tide for depleted *Ostrea edulis* stocks from the effects of overfishing, disease and invasive species. *PeerJ* 7, e6431.
- Hudson, J., Shinn, E., Halley, R., Lidz, B., 1976. Sclerochronology: a tool for interpreting past environments. *Geology* 4, 361–364.
- Jiménez-Camino, R., Bernal-Casasola, D., Fernández, E., Moreno, M., López-Ruiz, U., Palomo, A., Blanco, M.E., Perles, B.D., Andrades, E.M., Garzón, E., Portillo, J.L., 2019. Excavación arqueológica en el Parque de las Acacias: la factoría de salazón, la necrópolis tardorromana y el cementerio castellano. *Almoraima* 51, 57–78.
- Klavness, D., 1990. Size structure and potential food value of the plankton community to *Ostrea edulis* L. in a traditional Norwegian “osterspoll”. *Aquaculture* 86, 231–247.
- Korringa, P., 1976. Farming the flat oysters of the genus *Ostrea* - a multidisciplinary treatise. *Dev. Aquac. Fish. Sci.* 3, 1–238.
- Kristensen, P.S., 1997. Oyster and mussel fisheries in Denmark. In: MacKenzie, C.L.J., Burrell, V.G.J., Rosenfield, A., Hobart, W.L. (Eds.), *The History, Present Condition, and Future of the Molluscan Fisheries of North and Central America and Europe*. U.S. Department of Commerce, NOAA Technical Report, NMFS 129, pp. 25–38.
- Lagóstena, L., 2001. La producción de salsas y conservas de pescado en la Hispania romana (II a.C. – VI d.C.). Universitat de Barcelona, Barcelona.
- Lallias, D., Lapegue, S., Haley, C., Heurtelise, S., Boudry, P., Beaumont, A., 2007. A preliminary genetic linkage map for the European flat oyster *Ostrea edulis*. *Aquaculture* 272, 281–282.
- López-Sáez, J.A., Pérez-Díaz, S., 2019. Palinología. El clima y la vegetación en Erytheia: el contexto de El Olivillo y del Colegio Mayor Universitario. In: Bernal, D., Vargas, J.M., Lara, M. (Eds.), *7 metros de la Historia de Cádiz... Arqueología en El Olivillo y en el Colegio Mayor Universitario*. Universidad de Cádiz, Cádiz, pp. 413–416.
- López-Sáez, J.A., López-García, P., Burjachs, F., 2003. Arqueopalinología: Síntesis Crítica. *Polen* 12, 5–35.
- López-Sáez, J.A., Burjachs, F., López-García, P., López-Merino, L., 2006. Algunas precisiones sobre el muestreo e interpretación de los datos en Arqueopalinología. *Polen* 15, 17–29.
- López-Sáez, J.A., Ruiz-Zapata, B., Gil-García, M.J., Val-Peón, C., 2023. Historia del paisaje y composición del garum de Baelo Claudia: una aproximación palinológica. In: Bernal Casasola, D., Expósito, J.A., Díaz, J.L. (Eds.), *Baelo Claudia y el Garum en la Antigüedad Tardía. Reflexiones interdisciplinarias sobre las actividades haliéuticas en el Círculo del Estrecho*. University of Hamburg, Hamburg (in press).
- Lotze, H.K., 2007. Rise and fall of fishing and marine resource use in the Wadden Sea, southern North Sea. *Fish. Res.* 87, 208–218.
- Lotze, H.K., Coll, M., Dunne, J.A., 2011. Historical changes in marine resources, food-web structure and ecosystem functioning in the Adriatic Sea, Mediterranean. *Ecosystems* 14, 198–222.
- MacKenzie, C.L.J., Burrell, V.G.J., Rosenfield, A., Hobart, W.L., 1997. The history, present condition, and future of the molluscan fisheries of North and Central America and Europe. U.S. Department of Commerce, NOAA Technical Report, NMFS 129.
- Madariaga, B., 1964. El mar y el hombre prehistórico. *Zephyrus* 15, 37–45.
- Martínez, F., Montero, G., 2004. The *Pinus pinea* L. woodlands along the coast of South-western Spain: data for a new geobotanical interpretation. *Plant Ecol.* 175, 1–18.
- Mautner, A.K., Gallmetzer, I., Haselmair, A., 2018. Holocene ecosystem shifts and human induced loss of Arca and Ostrea shell beds in the north-eastern Adriatic Sea. *Mar. Pollut. Bull.* 126, 19–30.
- McGarry, S.F., Caseldine, C., 2004. Speleothem Palynology: an undervalued tool in Quaternary studies. *Quat. Sci. Rev.* 23, 2389–2404.
- Mehvar, S., Filatova, T., Dastgheib, A., de Ruyter van Steveninck, E., Ranasinghe, R., 2018. Quantifying economic value of coastal ecosystem services: a review. *J. Mar. Sci. Eng.* 6, 5.

- Mejías, J.A., Ojeda, F., Arroyo, J., Marañoñ, T., 1994. *Biología y conservación de Rhododendron ponticum* subsp. *baeticum* en el campo de Gibraltar. *Almoraima* 11, 57–62.
- Mesa, M.A., 2016. Pinos autóctonos y conservación de bosques en Andalucía. *Investig. Geogr.* 65, 97–115.
- Milner, N., 2001. At the cutting edge: using thin sectioning to determine season of death of the European oyster, *Ostrea edulis*. *J. Archaeol. Sci.* 28, 861–873.
- Milner, N., 2002. Incremental Growth of the European Oyster *Ostrea edulis*. *Archaeopress, Oxford*.
- Milner, N., Craig, O.E., Bailey, G.N. (Eds.), 2007. *Shell Middens in Atlantic Europe*. *Oxbow Books, Oxford*.
- Moreno, R., 1995. Arqueomalacofaunas de la Península Ibérica: un ensayo de síntesis. *Complutum* 6, 353–382.
- Mouchi, V., Briard, J., Gaillot, S., Argant, T., Forest, V., Emmanuel, L., 2018. Reconstructing environments of collection sites from archaeological bivalve shells: case study from oysters (Lyon, France). *J. Archaeol. Sci. Rep.* 21, 1225–1235.
- Mouchi, V., Godbillot, C., Forest, V., Ulianov, A., Lartaud, F., de Rafélis, M., Emmanuel, L., Verrecchia, E.P., 2020a. Rare earth elements in oyster shells: provenance discrimination and potential vital effects. *Biogeosciences* 17, 2205–2217.
- Mouchi, V., Emmanuel, L., Forest, V., Rivalan, A., 2020b. Geochemistry of bivalve shells as indicator of shore position of the 2nd century BC. *Open Quat.* 6 (4), 1–15.
- Mouchi, V., Godbillot, C., Dupont, C., Vella, M.A., Forest, V., Ulianov, A., Lartaud, F., de Rafélis, M., Emmanuel, L., Verrecchia, E.P., 2021. Provenance study of oyster shells by LA-ICP-MS. *J. Archaeol. Sci.* 132, 195418.
- Neumann, B., Vafeidis, A.T., Zimmermann, J., Nicholls, R.J., 2015. Future coastal population growth and exposure to sea-level rise and coastal flooding – a global assessment. *PLoS One* 10, e0118571.
- Nyström, J., Lindh, U., Dunca, E., Mutvei, H., 1995. A study of *M. margaritifera* shells from the River Paulströmsån, S. Sweden. *Nucl. Instr. Meth. Phys. Res. B* 104, 612–618.
- Padilla, A., 2008. Aproximación a la ordenación territorial de la bahía de Cádiz durante el Imperio Romano tardío. *Revista atlántica-mediterránea de prehistoria y arqueología social* 10, 353–374.
- Peharda, M., Ezgeta-Balić, D., Davenport, J., Bojanić, N., Vidjak, O., Ninčević-Gladan, Ž., 2012. Differential ingestion of zooplankton by four species of bivalves (Mollusca) in the Mali Ston Bay, Croatia. *Mar. Biol.* 159, 881–895.
- Pérez-Latorre, A.V., Galán, A., Navas, P., Navas, D., Gil, Y., Cabezudo, B., 1999. Datos sobre la flora y vegetación del Parque Natural de los Alcornocales (Cádiz-Málaga, España). *Acta Bot. Malacit.* 24, 133–184.
- Pérez-Latorre, A.V., Galán, A., Cabezudo, B., 2000. La vegetación caracterizada por *Rhododendron ponticum* L. en Andalucía (España). Una complicada historia nomenclatural para una realidad fitocenológica. *Acta Bot. Malacit.* 25, 198–205.
- Perrotti, A.G., Siskind, T., Bryant, M.K., Bryant, V.M., 2018. Efficacy of sonication-assisted sieving on Quaternary pollen samples. *Palynology* 42, 466–474.
- Pogoda, B., 2019. Current status of European oyster decline and restoration in Germany. *Humanities* 8, 9.
- Purroy, A., Najdek, M., Isla, E., Župan, I., Thébault, J., Peharda, M., 2018. Bivalve trophic ecology in the Mediterranean: spatio-temporal variations and feeding behaviour. *Mar. Environ. Res.* 142, 234–249.
- Reicherter, K., Prados, F., Jiménez, H., García, I., Feist, L., Val-Peón, C., Höbig, N., Mathes-Schmidt, M., López-Sáez, J.A., Röth, J., Alexiou, S., Silva-Barroso, P.G., Cämmerer, C., Borau, L., Matthias May, S., Kraus, W., Brückner, H., Grützner, C., 2022. The Baelo Claudia tsunami archive (SW Spain) – archaeological deposits of high energy events. In: Álvarez-Martí-Aguilar, M., Machuca-Prieto, F. (Eds.), *Historical Earthquakes, Tsunamis and Archaeology in the Iberian Peninsula*. Springer Nature Singapore Pte Ltd, Singapore, pp. 313–344.
- Reille, M., 1999. *Pollen et spores d'Europe et d'Afrique du Nord*. 2nd edn. Laboratoire de Botanique Historique et Palynologie, Marseille.
- Reynolds, P., 1995. Trade in the western Mediterranean, AD 400–700: the ceramic evidence. *British Archaeological Reports International Series* 604, Oxford.
- Richardson, C., 2001. Molluscs as archives of environmental change. *Oceanogr. Mar. Biol. Annu. Rev.* 39, 103–164.
- Rodríguez-Pérez, A., James, M., Donnan, D.W., Henry, T.B., Møller, L.F., Sanderson, W.G., 2019. Conservation and restoration of a keystone species: understanding the settlement preferences of the European oyster (*Ostrea edulis*). *Mar. Pollut. Bull.* 138, 312–321.
- Ruesink, J.L., Lenihan, H.S., Trimble, A.C., Heiman, K.W., Micheli, F., Byers, J.E., Kay, M.C., 2005. Introduction of non-native oysters: ecosystem effects and restoration implications. *Annu. Rev. Ecol. Syst.* 36, 643–689.
- Savoye, N., David, V., Morisseau, F., Etcheber, H., Abril, G., Billy, I., Charlier, K., Oggian, G., Derriennic, H., Sautour, B., 2012. Origin and composition of particulate organic matter in a macrotidal turbid estuary: the Gironde Estuary, France. *Estuar. Coast Shelf Sci.* 108, 16–28.
- Schöne, B.R., Surge, D., 2014. Bivalve shells: ultra-high resolution paleoclimate archives. *Pages Magazine* 22, 20–21.
- Schröder, T., van't Hoff, J., López-Sáez, J.A., Viehberg, F., Melles, M., Reicherter, K., 2018. Holocene climatic and environmental evolution on the southwestern Iberian Peninsula: a high-resolution multi-proxy study from Lake Medina (Cádiz, SW Spain). *Quat. Sci. Rev.* 198, 208–225.
- Schröder, T., López-Sáez, J.A., van't Hoff, J., Reicherter, K., 2020. Unraveling the Holocene environmental history of south-western Iberia through a palynological study of Lake Medina sediments. *The Holocene* 30 (1), 13–22.
- Schubert, C., Calvert, S., 2001. Nitrogen and carbon isotopic composition of marine and terrestrial organic matter in Arctic Ocean sediments: implications for nutrient utilization and organic matter. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 48, 789–810.
- Stagličić, N., Šegvić-Bubića, T., Ezgeta-Balić, D., Bojanić Varezić, D., Grubišić, L., Žuvić, L., Lin, Y., Briski, E., 2020. Distribution patterns of two co-existing oyster species in the northern Adriatic Sea: the native European flat oyster *Ostrea edulis* and the non-native Pacific oyster *Magallana gigas*. *Ecol. Indic.* 113, 106233.
- Stenzel, H.B., 1971. Oysters. *Treatise Invertebr. Paleontol.* 3, 953–1184.
- Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. *Pollen Spores* 13, 614–621.
- Szabó, K., Quitmyer, I., 2008. Molluscs and other marine resources. *Archaeofauna* 17, 9–174.
- ter Braak, C.J.F., Prentice, I.C., 1988. A theory of gradient analysis. *Adv. Ecol. Res.* 18, 271–317.
- ter Braak, C.J.F., Šmilauer, P., 2002. *CANOCO Reference Manual and CanoDraw for Windows user's Guide: Software for Canonical Community Ordination*. Biometris, Wageningen.
- Thomas, K.D., 2015a. Molluscs emergent, part I: themes and trends in the scientific investigation of mollusc shells as resources for archaeological research. *J. Archaeol. Sci.* 56, 133–140.
- Thomas, K.D., 2015b. Molluscs emergent, Part II: themes and trends in the scientific investigation of molluscs and their shells as past human resources. *J. Archaeol. Sci.* 56, 159–167.
- Thorpe, J.P., Sole-Cava, A.M., Watts, P.C., 2000. Exploited marine invertebrates: genetics and fisheries. *Hydrobiologia* 420, 165–184.
- Voultsiadou, E., Koutsoubas, D., Achparaki, M., 2010. Bivalve mollusc exploitation in Mediterranean coastal communities: an historical approach. *J. Biol. Res. Thessalon.* 13, 35–45.
- Yonge, C.M., 1960. *Oysters*. Collins, London.
- Zuykov, M., Pelletier, M., Harper, D.A.T., 2013. Bivalve mollusks in metal pollution studies: from bioaccumulation to biomonitoring. *Chemosphere* 93, 201–208.