



Holocene molluscan successions from southeastern Spain (Galera, Andalusia): a palaeoenvironmental framework and a palaeobiogeographic resource of the Granada UNESCO Geopark

Quentin Wackenheim, Christiane Richter, Nicole Limondin-Lozouet, Daniel Wolf, Francisco Juan García-Tortosa, Elisa Marzin, Luise Hofmann, Julie Dabkowski, Dominik Faust

► To cite this version:

Quentin Wackenheim, Christiane Richter, Nicole Limondin-Lozouet, Daniel Wolf, Francisco Juan García-Tortosa, et al.. Holocene molluscan successions from southeastern Spain (Galera, Andalusia): a palaeoenvironmental framework and a palaeobiogeographic resource of the Granada UNESCO Geopark. *Journal of Molluscan Studies*, 2023, 89 (1), 10.1093/mollus/eyac033 . hal-03940286

HAL Id: hal-03940286

<https://hal.science/hal-03940286>

Submitted on 6 Feb 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Holocene molluscan successions from southeastern Spain (Galera, Andalusia): a palaeoenvironmental framework and a palaeobiogeographic resource of the Granada UNESCO Geopark

Quentin Wackenheim^{1,2}, Christiane Richter³, Nicole Limondin-Lozouet¹, Daniel Wolf³, Francisco Juan García-Tortosa⁴, Elisa Marzin³, Luise Hofmann³, Julie Dabkowski¹ and Dominik Faust³

¹Laboratoire de Géographie Physique, UMR 8591 CNRS-Univ. Paris 1-UEPEC, Thiais, France;

²Trajectoires, UMR 8215 CNRS & Univ. Paris 1, Paris, France;

³Institute of Geography, Technische Universität Dresden, Helmholtzstr., Dresden, Germany; and

⁴Geology Department, Universidad de Jaén, Campus Las Lagunillas, 23071 Jaén, Spain

Correspondence: Q. Wackenheim; e-mail: quentin.wackenheim@gmail.com

(Received 13 June 2022; editorial decision 28 September 2022)

ABSTRACT

In Spain, Holocene deposits are widespread, and although they have been extensively investigated by quaternarists for several decades, their malacological content has remained scarcely studied. In the framework of a German–French–Spanish collaboration, alluvial and tufa sequences in the Baza Basin, Andalusia, Spain are analysed with a multidisciplinary approach, including the analysis of the molluscan successions. Holocene fossil molluscs of the studied sequences reveal a rich assemblage of 53 species, among which 33 are terrestrial. Between 10,000 and 9,000 cal. yr BP, the Galera succession indicates strong river dynamics that prevented the establishment of adjacent terrestrial habitats. The Early to Middle Holocene transition reflects the continuity of humid environments. The Middle Holocene fauna reveals a decrease in humidity accompanied by slight evidence of drier habitats in the near periphery of the floodplain/tufa deposits from 5,900 cal. yr BP onwards. Late Holocene deposits (around 3,000 to 300 cal. yr BP) point to dry and open biotopes indicated by the appearance of xero-resistant and mesophilous gastropods. The palaeoenvironmental reconstruction inferred from the malacocenoses allows discussing local to regional responses of the malacofauna to environmental changes and is consistent with past regional environmental and climatic trends identified in southeastern Spain. The fossil record at Galera offers new evidence to question and clarify the modern range of endemic taxa whose distributions are fragmented. By following a ‘conservation paleobiology’ approach, the analysis of the mollusc fossil record at Galera provides (1) baselines to determine the natural variability of ecosystems and their response to environmental changes, (2) data to discuss and clarify species distribution evolution and (3) arguments to support conservation priorities.

INTRODUCTION

The Iberian Peninsula is recognized as a Mediterranean biodiversity hotspot (Médail & Quézel, 1999; Médail *et al.*, 2019) and is home to a high diversity of freshwater and land molluscs (Arconada & Ramos, 2003; Cadeval & Orozco, 2016). The distribution of the rich modern Iberian fauna has been shaped by a combination of climatic and geological parameters since the end of the Cenozoic (Sacchi, 1965; Andre, 1984; Giusti & Manganelli, 1984). In the Mediterranean Basin, land snail species inhabit very contrasting environments and are adapted to a wide range of climatic and ecological conditions (Martin & Sommer, 2004; Juříčková *et al.*, 2008; Moreno-Rueda, 2014; Bros, Torre & Santos, 2016; Schweizer, Triebkorn & Köhler, 2019).

Within the Iberian Peninsula, Andalusia is considered a particularly complex and composite geographical region due to its orographic configuration (Martin-Serrano, 2005), the diversity of climates (Hidalgo-Muñoz *et al.*, 2011; Gómez-Zotano *et al.*, 2016), and its unique and rich vegetation (Blanca *et al.*, 2011; Moreno-Said *et al.*, 2019). This region shares characteristics with northern West Africa regarding biological communities, which led Médail & Quézel (1999) to designate it as the ‘Baetic–Rifan complex’ based on a study of endemic plants. Modern Andalusian and northwestern African nonmarine molluscs, which exhibit similar distributional features, support the biogeographical connection between both areas (Pallary, 1922; Sacchi, 1965; Giusti & Manganelli, 1984). To date, however, fossils of terrestrial molluscs have been poorly utilized to question and discuss the

biogeographical history of the western Mediterranean Basin, despite their common preservation in a variety of calcareous Quaternary deposits. Fossil shells provide unique opportunities to investigate past environments and climate evolution across various scales (Ložek, 1986; Goodfriend, 1992; Preece, 1997; Juričková *et al.*, 2014; Granai *et al.*, 2020; Horsák *et al.*, 2020; Richter *et al.*, 2020; Magnin, Bonnet & Cençon-Salvayre, 2022). Furthermore, Quaternary nonmarine mollusc fossil records provide crucial material to better understand the diversity and distribution of modern European molluscs (Preece, 1998; Limondin-Lozouet & Preece, 2014; Kowalewski, 2017; Limondin-Lozouet, 2020).

In the western Mediterranean Basin, Holocene sedimentary archives reveal a strong spatial and temporal variability in the response of continental ecosystems to environmental and climatic changes (Jalut *et al.*, 2000; Pérez-Obiol *et al.*, 2011; Fletcher, Debret & Goñi, 2012; Fletcher & Zielhofer, 2013; Faust & Wolf, 2017; Morellón *et al.*, 2018; Di Rita *et al.*, 2022). Although land snail shells are common in Quaternary deposits in Spain, they have been underexploited in this area albeit being promising biological proxies to discuss the environmental variability during the Holocene. As Spain is home to many archaeological archives of cultural and historical importance, it appears valuable to develop the aspect of related environmental changes over time. Indeed, only few studies on fossil Holocene malacofauna comprise—often partial—inventories from archaeological or palaeontological sites (e.g. Jodot, 1958; Madurga, 1973; Moreno Nuño, 1995a; Lloveras *et al.*, 2011; Gutiérrez Zugasti, Cuenca Solana & Gonzales Morales, 2015).

While the earliest studies on Pliocene and Lower Pleistocene continental molluscs in Andalusia were carried out in the Guadix–Baza depression in the vicinity of Granada (Robles, 1989; Bandel *et al.*, 2000; Albasa & Robles, 2020), the first inventory of Holocene snails was done by Madurga (1973) for the Alfacar and Padul fossil sites. Recently, we discovered rich Holocene shell deposits near Galera, which provide a new palaeontological resource for the UNESCO Geopark of Granada. Our aims are first to offer a state-of-the-art assessment of Spanish Holocene nonmarine mollusc sequences and, secondly, to present new molluscan successions from southeastern Spain in order to (1) examine the responses of malacofauna to environmental changes, (2) discuss palaeoenvironmental reconstructions at local and regional scales, and (3) investigate Andalusian biogeography based on molluscan records. In synthesis, our approach shows how the historical perspective inferred from the Holocene successions in the Galera River valley improves and questions our understanding of the extant Andalusian malacofauna.

MATERIAL AND METHODS

Study site

The Galera River is a tributary of the Guadiana Menor River, which drains the Guadix–Baza Basin. The Galera River valley is located in Andalusia (province of Granada, southeastern Spain), 100 km north of the city of Almería, between Castellérjar and Galera, in the UNESCO Geopark of Granada (Rosillo *et al.*, 2017). The Guadix–Baza Basin is an intermontane depression located in the Betic Cordillera and filled by Neogene and Quaternary deposits that had been strongly dissected by the hydrological system during the Middle and Late Quaternary period (Peña, 1985; Martín-Serrano, 2005; Pla-Pueyo, 2011; El Hamouti & Gibert, 2012). The modern Andalusian climate is characterized by strong seasonality with cold and wet winters and warm and dry summers. The local steppe conditions are cold and semiarid with a mean annual precipitation of 423 mm and an average annual temperature of 14.4 °C.

The incision of the Galera River led to the exposure of a diversity of Pleistocene and Holocene fluvial terraces across the valley.

Wolf *et al.* (2021) conducted stratigraphic and sedimentological analyses on eight profile sections along the river that are named Galera I (GA-I) to VIII (GA-VIII) (Fig. 1). Radiocarbon ages and stratigraphic correlations provide a chronological framework of the Galera River deposits covering the Early to Late Holocene period. Figures 2–4 present sections in proximal positions of the river valley (GA-I, GA-II and GA-VII) and in a more distal position on the fringe (GA-IB) of the valley where malacological data was obtained (Fig. 1). In the entire spectrum from coarser fluvial to fine silty units, the Galera River succession comprises mainly carbonated deposits that favour the preservation of mollusc shells. Among these deposits, tufa layers that mainly precipitated during the mid-Holocene in the Galera Valley constitute a particularly suitable sedimentary context for the study of fossil land snail assemblages. This study is mostly based on the stratigraphic information provided by Wolf *et al.* (2021), while a new detailed stratigraphic framework for the section GA-IB is shown in the Supplementary Material.

Literature review

Our literature review regarding Holocene nonmarine molluscs was based on publications in Spanish and English. In Spain, most of the available postglacial malacological data come from old and limited palaeontological inventories (e.g. Jodot, 1958; Madurga, 1973) or from the description of archaeological sites (e.g. Moreno Nuño, 1995a, b; Aparicio, 2001; Lloveras *et al.*, 2011; Gutiérrez Zugasti *et al.*, 2015), lacking extensive palaeoenvironmental analyses. The faunal lists of Jodot (1958) and Madurga (1973) are examined from a biogeographical perspective, taking into consideration their imprecise chronological assignment. A few studies of sedimentary sequences provide palaeoenvironmental results (Collado & Robles, 1983; Porras & Díaz del Olmo, 1997; Taylor *et al.*, 1998; Roqué Pau, Buxó & Olmo, 2001; Murelaga *et al.*, 2012). Preece (1991a) provides a well-dated molluscan sequence that records most of the Holocene period. During the last decade, several works based on oxygen and carbon stable isotopes of land snail shells have contributed to reliable climatic and environmental records (Yanes *et al.*, 2011, 2012, 2013a, b; Colonese *et al.*, 2013; Murelaga *et al.*, 2012). Among those studies, some focused on Andalusia, such as a study of a single Upper Pleistocene–Holocene sequence from Sevilla Province (Porras & Díaz del Olmo, 1997) and two isotopic studies made in an archaeological context from Granada and Jaen provinces (Yanes *et al.*, 2011, 2013a). The most relevant sites that are of malacological interest were selected from our literature review. They were then divided into sites with and without archaeological context and mapped for further biogeographical discussion.

Fossil mollusc sampling

The mollusc samples have been taken following stratigraphic units of the natural outcrops studied (Fig. 1). The sampling interval is 10 cm on average and reaches 20 cm for the coarser layers. Malacological sampling is discontinuous in GA-I, GA-II and GA-VIII sections, where each sample reaches a constant volume of 10 l (Figs 2, 4). As the calcareous nature of the tufa provides particularly good preservation conditions for fossil shells, a smaller volume of sediment is needed (Preece, 1991b; Frodllova, Hájková & Horsák, 2018). Accordingly, the GA-IB tufa section comprises two continuous sampling columns of 5 l per sample (Fig. 3). A total of 88 malacological samples were wet-sieved on a 500- μ m mesh, and the residues were sorted under a microscope to extract shells. Shells and identifiable fragments have been counted to identify the minimum number of individuals for each sample (see Evans, 1972; Limondin-Lozouet, 2002).

The sampling of geological sections was conducted from 2014 to 2019 during the research programme ‘Galera Valley’ funded by the German Research Foundation (DFG) (grant nos FA 239/22–1 and FA 239/24–1) and supervised by Dr Dominik Faust (Technische

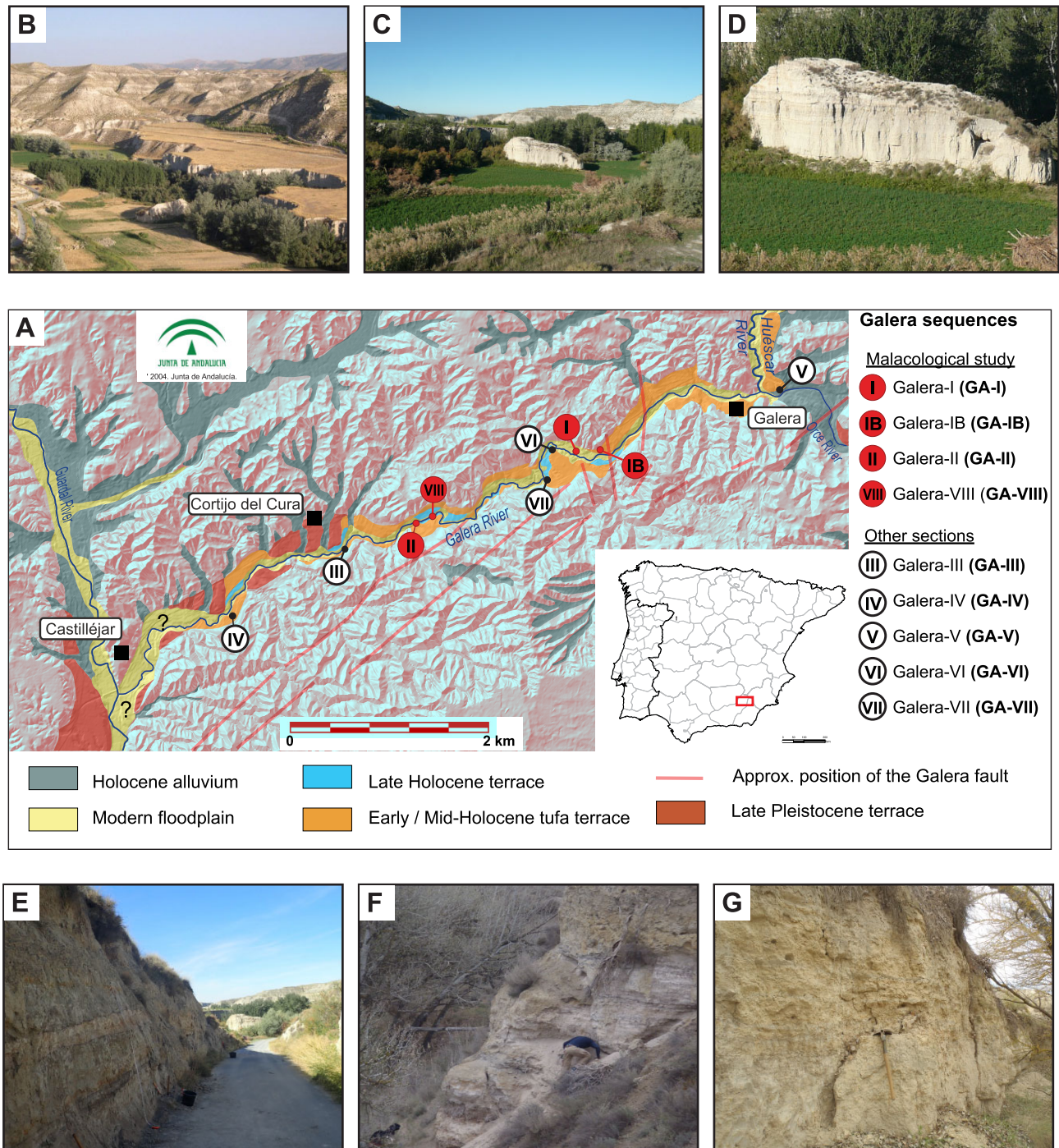


Figure 1. A. Map of the studied sections in the Galera Valley (modified from Wolf *et al.*, 2021). B–F. Views of the Galera floodplain (A, B) and the Holocene sedimentary succession of Galera-I (C), Galera-IB (D), Galera-II (E) and Galera-VIII (F).

Universität, Dresden) who is a member of the scientific committee of the UNESCO Geopark ‘Valles Norte de Granada’. The shell material we collected will be deposited at the Museo Arqueológico de Galera, Galera, Granada, Spain.

Mollusc identification

Identification guides and atlases for the European fauna (Kerney, Cameron & Bertrand, 1999; Welter-Schultes, 2012; Gloer, 2019, 2022a,b) and specific works on the Iberian Peninsula

(Altonaga *et al.*, 1994; Puente, 1994; Arrébola, 1995; Martínez-Ortí, 1999; Ruiz Ruiz *et al.*, 2006; Arconada, Delicado & Ramos, 2007; Martínez-Ortí, 2008; Arrébola *et al.*, 2012; Cadeval & Orozco, 2016) were used to identify land and freshwater snails.

The identification of taxa to species level was achieved in most cases. However, the identification of fossil shells occasionally remained challenging due to poor preservation conditions, taxonomic issues or the necessity to rely on anatomical features to identify species. The latter applies to the highly diverse Hydrobiids. Seven taxa of the family Hydrobiidae were distinguished in the Holocene mollusc assemblages of this study. They include three morphologi-

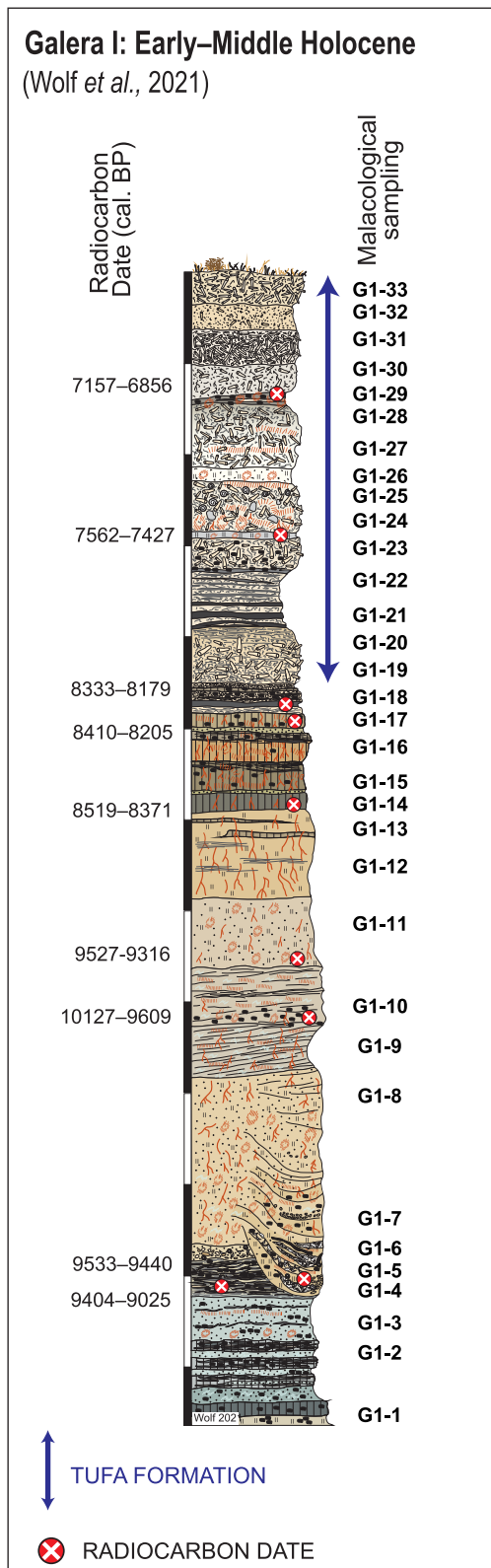


Figure 2. Chronostratigraphic framework of sampled Galera profile I. Radiocarbon dates are presented with 2σ interval (see Table 5). See Wolf et al. (2021) for detailed stratigraphy.

cally homogeneous groups of gastropods classified as Hydrobiidae sp. 1 (Fig. 5U), Hydrobiidae sp. 2 (Fig. 5S, T) and Hydrobiidae sp. 3 (Fig. 5W–Y). Additionally, specimens of *Mercuria* Boeters, 1971 and *Corrosella* Boeters, 1970 could not be identified to the species level, as species delimitations in both taxa require anatomical and, in some cases, even genetic analyses (Miller, 2021; Delicado & Ramos, 2012). Although *Mercuria similis* (Draparnaud, 1805) is the most common extant taxon in Iberia, the identification of fossil material is limited to *Mercuria* sp., and the taxa of *Corrosella* are designated as *Corrosella* sp. 1 (Fig. 5V). Based on shell morphology and malleated protoconch microsculpture, a 1-mm-long valvatiform hydrobiid found in considerable abundance was determined as the endemic taxon *Iberhoratia morenoi* (Arconada, Delicado & Ramos, 2007) (Fig. 5Z–BB). Identifying modern specimens belonging to the genera *Radix* and *Stagnicola* remains tricky even when considering anatomical features (Jackiewicz, 1998; Schniebs et al., 2013; Vinarski, Aksenova & Bolotov, 2020). Today, *Radix labiata* (Ross-mässler, 1835), *Radix balthica* (Linnaeus, 1758), *Stagnicola fuscus* (Pfeiffer, 1821) and *Stagnicola palustris* (Müller, 1774) occur in Spain (Soler et al., 2006; Welter-Schultes, 2012; Lopez Soriano, Quiñero Salgado & Glöer, 2016; Glöer, 2019). Consequently, fragmented fossil material from the Galera Valley could not be identified more precisely than *Radix* sp. and *Stagnicola* sp.

An abundant Orculidae was identified as the endemic species *Orculella aragonica* (Westerlund, 1897) (Arrébola et al., 2012) (Fig. 5P–R). *Microxeromagna lowei* (Potiez & Michaud, 1835) and *Xerotracha conspurcata* (Draparnaud, 1801) are two xerothermic geomitrids whose conchological distinction is based on the length and density of periostracum hairs (Martinez-Orti, 2008; Cadeval & Orozco, 2016). As this feature is undetectable in fossil shells, all specimens that could be attributed to one or the other species were grouped under the designation *Microxeromagna lowei/Xerotracha conspurcata* (Fig. 5J–L) (see Magnin & Bonnet, 2014; Magnin et al., 2022). Among Geomitridae, *Xerotracha zujarensis* (Ortiz de Zárate López, 1950) (Fig. 5G–I) was identified. Geomitrid shells of morphologically homogeneous groups were designated as Geomitridae sp. 1 (Fig. 5D–F), and some very fragmented shells were designated as Geomitridae indet. Similarly, due to the poor preservation and the rarity of available specimens, identifications were limited to family level for some taxa (Helicidae indet.) and genus level for others (*Theodoxus* sp., *Planorbis* sp., *Pisidium* sp., *Truncatellina* sp., *Oxychilus* sp., *Cepaea* sp.).

Ecological classification

Palaeoecological interpretations are based on ecological groups defined by Puisségur (1976), as well as the known habitat requirements of the species extracted from the literature (see Supplementary Material Tables S1–S3). The xerothermic assemblage includes xerothermic molluscs that are able to live in open, sometimes rocky, and well-exposed terrain. Slugs are considered a separate group as their internal shells do not enable identification to the species level. The paludal assemblage groups together taxa that live in marshes and near banks, and whose occurrence is necessarily linked to the presence of water. Hygrophilous land snails require moist habitats but are not necessarily restricted to the aquatic domain. The mesophilous taxa correspond to land snails able to adapt to a wide variety of habitats. Puisségur's classification was amended by including additional taxa, whose ecological affiliations are detailed in the following paragraph.

Orculella aragonica is assigned to the 'hygrophilous' group as it lives in humid and calcareous biotopes and commonly near wetlands or springs (Garrido, Arrébola & Bertrand, 2005; Arrébola et al., 2012; Cadeval & Orozco, 2016). *Microxeromagna lowei/Xerotracha conspurcata*, *Theba pisana* (Müller, 1774), *Pseudotachea splendida* (Draparnaud, 1801), *Rumina decollata* (Linnaeus, 1758), *Granopupa granum* (Draparnaud, 1801), *Cernuella virgata* (Da Costa, 1778), *Xerosecta cespitum* (Draparnaud, 1801) and *Cochlicella barbara* (Linnaeus, 1758)

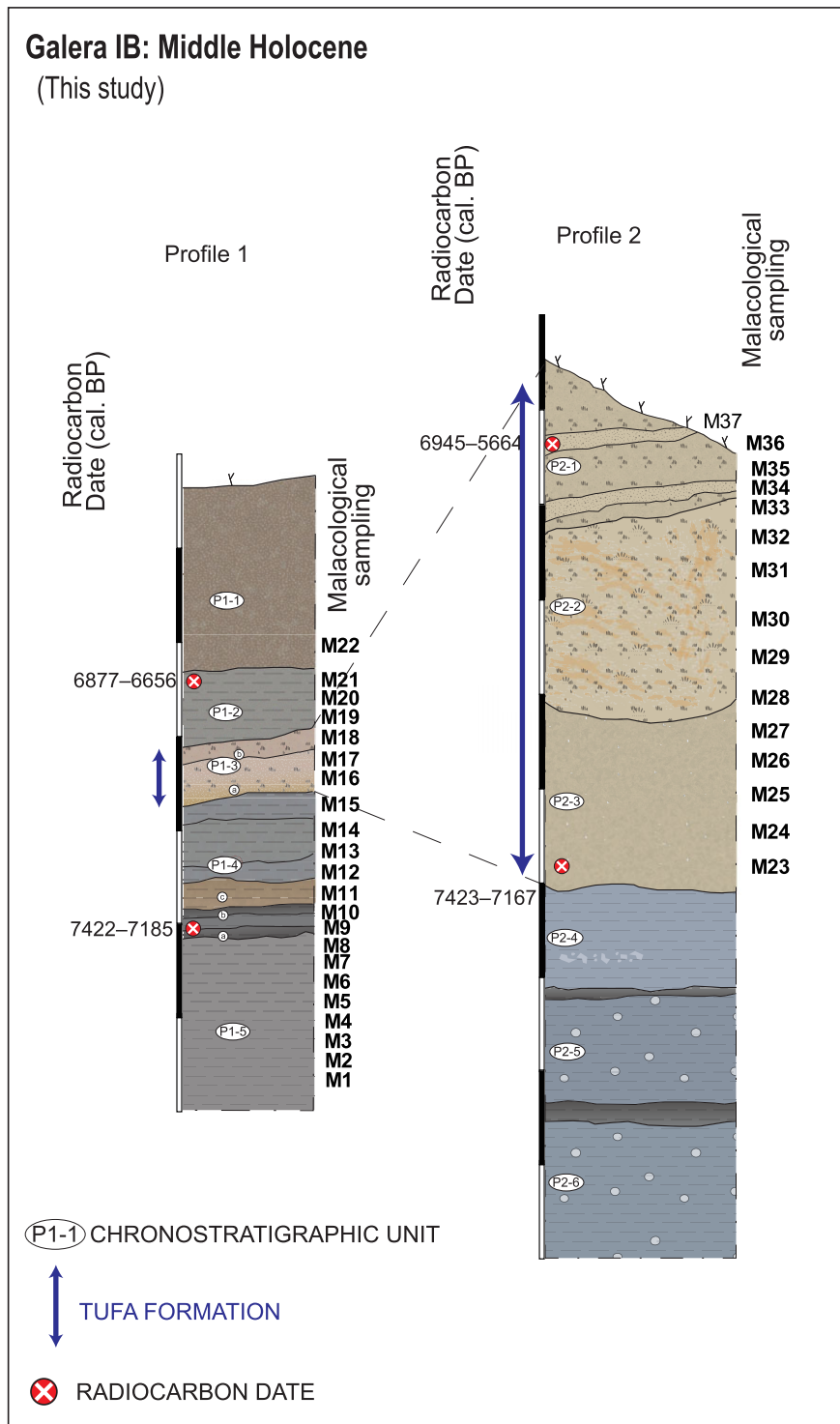


Figure 3. Chronostratigraphic framework of sampled Galera profile IB, profiles 1 and 2. Radiocarbon dates are presented with 2σ interval (see Table 5). Detailed stratigraphy is described in the Supplementary Material.

represent typical components of the dry Mediterranean fauna that predominantly inhabit a variety of open and sclerophyllous environments (Giusti, Manganelli & Schembri, 1995; Kerney *et al.*, 1999; Puente, 1994; Welter-Schultes, 2012). The southern Spanish endemic *Xerotracha zujarensis* is dwelling up to 700 m in ruderal, rupestral habitats in the matorral (Puente, 1994; Arrébola, 1995). Consequently, these taxa are affiliated with the xerothermic group.

The broad ecological tolerance of oxychilids allows them to adapt to a range of very different habitats and justifies the allocation of *Mediterranea hydatina* (Rossmässler, 1838) and *Oxychilus* sp. to the mesophile association (Germain, 1911; Kerney *et al.*, 1999; Welter-Schultes, 2012). *Jaminia quadridens* (Müller, 1774) prefers dry and sunny environments, such as the matorral (Welter-Schultes, 2012; Cadeval & Orozco, 2016). Although Puisségur (1976)

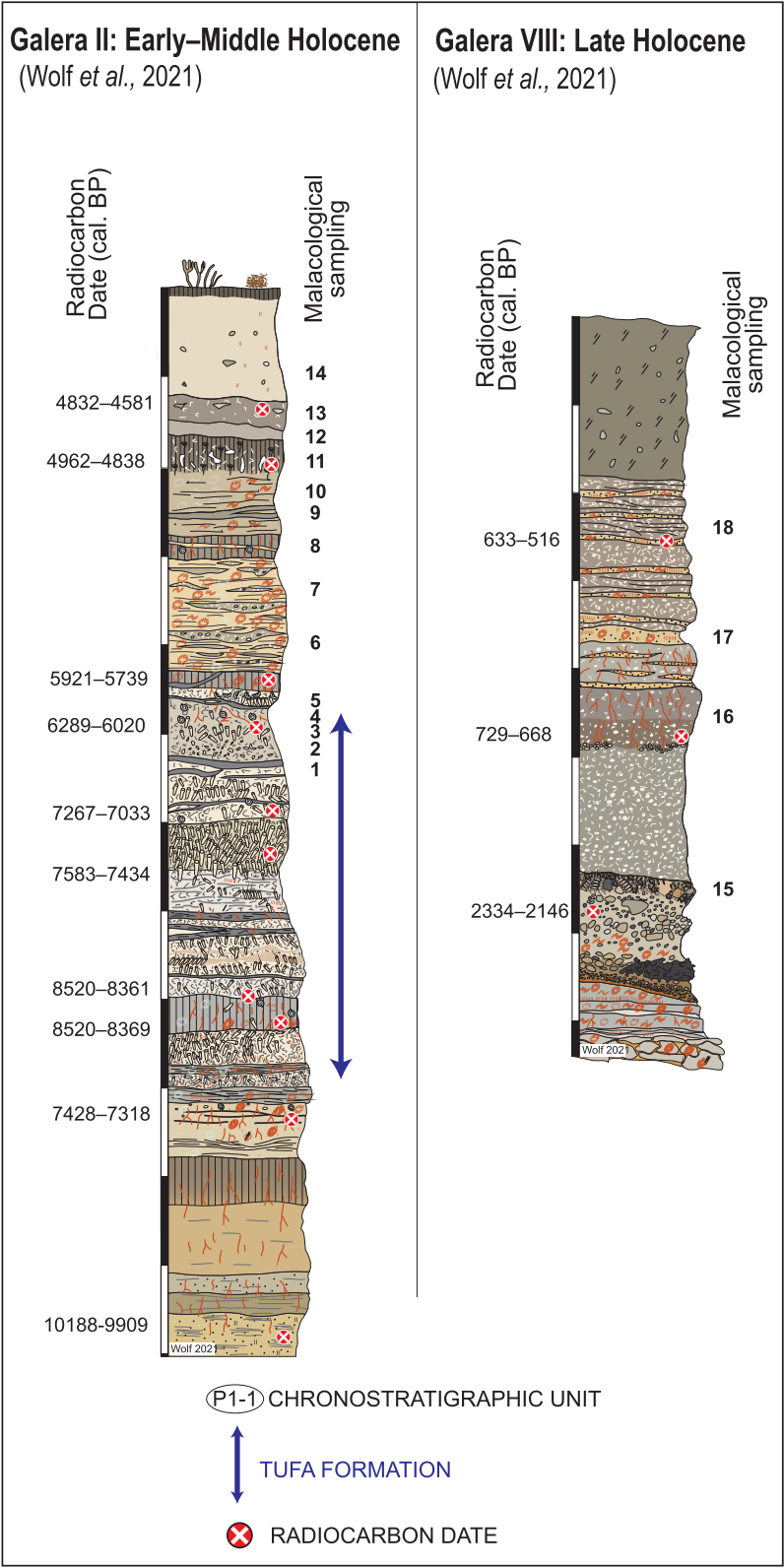


Figure 4. Chronostratigraphic framework of sampled Galera profiles II and VII. Radiocarbon dates are presented with 2σ interval (see Table 5). See Wolf et al. (2021) for detailed stratigraphy.

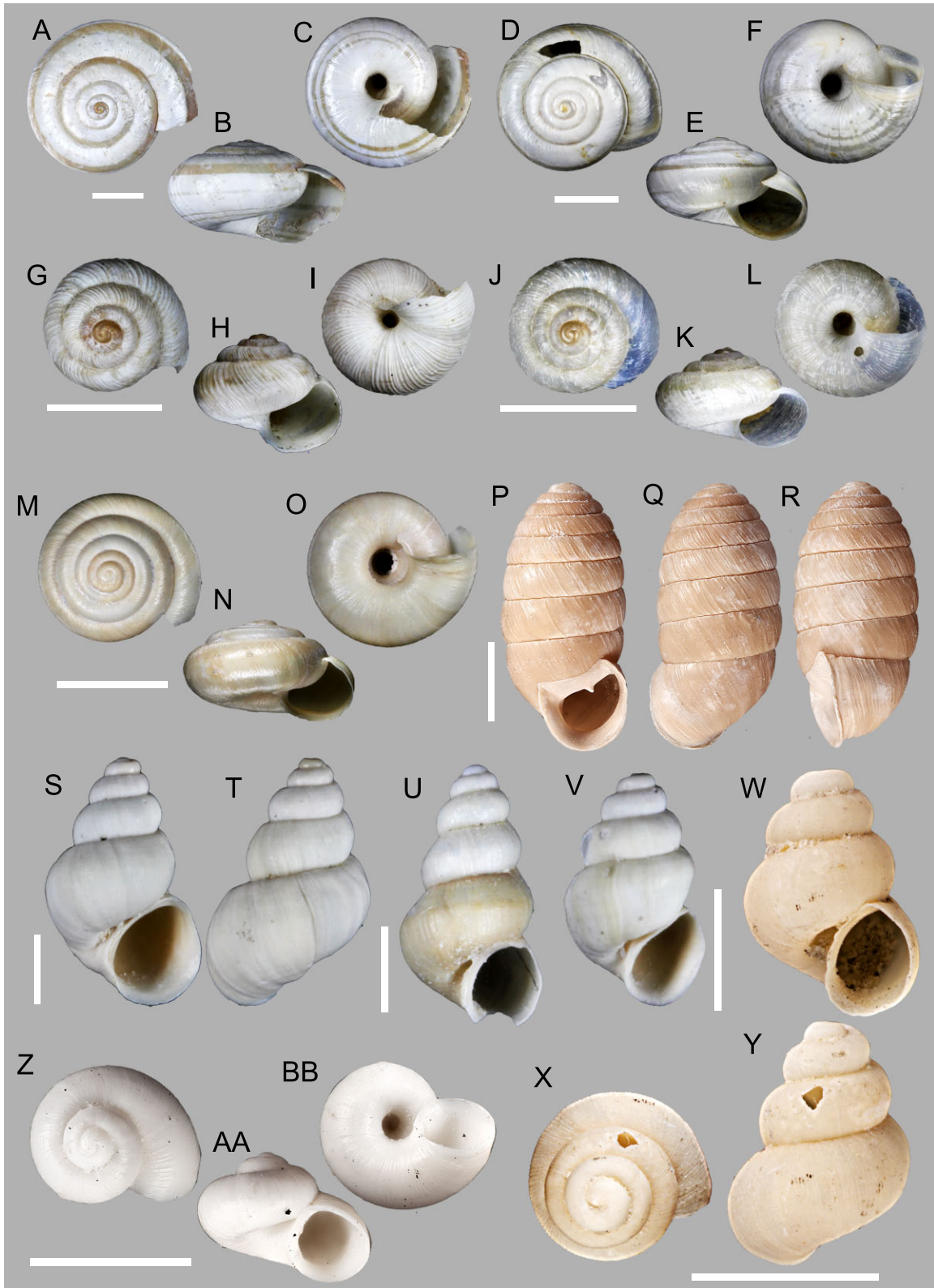


Figure 5. Holocene molluscs from Galera. **A–C.** *Xerosecta cespitum*. **D–F.** Geomitridae sp. 1. **G–I.** *Xerotracha ziyarensis*. **J–L.** *Microxeromagna lowei*/*Xerotracha conspurcata*. **M–O.** *Trochulus hispidus*. **P–R.** *Orculella aragonica*. **S, T.** Hydrobiidae sp. 3. **U.** Hydrobiidae sp. 1. **V.** *Corrosella* sp. 1. **W–Y.** Hydrobiidae sp. 2. **Z–BB.** *Iberhoratia morenoi*. Scale bars: **A–R,** 5 mm; **S–BB,** 1 mm.

considered it a steppic taxon, it has been allocated to the xerothermic group in the Mediterranean context. Occurrences of *Cecilioides acicula* (Müller, 1774) are excluded from the ecological analysis and the calculation of specific frequencies because its endogenous habits do not ensure the *in situ* stratigraphic position of the shells (Vandel, 1964; Evans, 1972). Its abundance is presented in specific frequency diagrams. Malacological data was implemented using the software Psimpoll v. 4.27 (Bennett, 2009) to obtain frequency histogram diagrams and analyses based on ecological groups. The zonation module of the Psimpoll software was applied to perform the cluster analysis using the CONISS method on all successions except GA-VIII, which includes only four samples. The zonation obtained is illustrated in the specific frequency diagrams.

Extant modern mollusc fauna

To document present-day faunas and compare them with the fossil records, a survey of modern gastropod species was conducted in the river valley (37°44'14.64"N, 2°34'25.89"O). In addition, for the screening, 1 l of flood debris was scanned under the microscope. The list of taxa identified is presented in Table 1.

Chronology

Twenty-two radiocarbon ages were acquired on charcoals and discussed by Wolf *et al.* (2021) for GA-I, GA-II and GA-VIII sections (Table 2, Figs 2, 3). GA-IB chronology is based on three radiocarbon ages obtained on nonmarine shells and one on charcoal (Table 2). In order to avoid the reservoir effect of old carbonate ingestion, the selection of the tiny hygrophilous species *Vertigo antivertigo* (Draparnaud, 1801) was favoured (Pigati *et al.*, 2013; Forman *et al.*, 2021; Granai & Wackenheim, 2022). *Vertigo* shells were cleaned using an ultrasonic bath and carefully examined under the microscope to avoid contamination. The dates were calibrated using the IntCal20 calibration curve (Reimer *et al.*, 2020) with OxCal 4.4 software (Ramsey, 2009). The phase of tufa precipitation in GA-IB, during the first part of the Middle Holocene, is consistent with the chronostratigraphic scheme obtained from other Galera sequences (Wolf *et al.*, 2021).

RESULTS

Holocene studies using nonmarine molluscs as an environmental proxy

Holocene studies based on nonmarine molluscs have focused on the geochemical analysis of geological or archaeological sites that are irregularly distributed throughout Spain and mapped in Figure 6. Sequences where the sedimentary context is reliable and well dated by a strong chronological framework are scarce. Sedimentary sequences studied for their molluscan content are located in the eastern half of the Iberian Peninsula: Torreblanca (Castellón province), El Jardín/Alcaraz (Albacete province), Bardenas Reales (Navarre province), Río Ter (Gerone province) and Constantina (Seville province) (Fig. 6). The Baides molluscan succession in central Spain represents one of the most complete and well-dated continuous palaeomalacological studies in Spain (Fig. 6). Although there are numerous archaeological sites for which a list of continental molluscs is available, only the largest species are studied, and detailed palaeoecological analyses are often lacking. Except for Bardenas Reales, geochemical analyses of snail shells have not been combined with a palaeoenvironmental study of the mollusc assemblages.

Overview of Holocene and current Galera malacofauna

The occurrences of modern and fossil taxa are presented in Table 1. For the four malacological profiles of the Holocene Galera river deposit, shells and shell fragments of 94,685 individuals were

extracted and allocated to 53 taxa, including 33 terrestrial species. The modern Galera malacofauna comprises 22 terrestrial and 4 freshwater species. In the fossil record, hygrophilous species such as *Vertigo antivertigo*, *Vallonia enniensis* (Gredler, 1856), *Carychium minimum* Müller, 1774, *Oxyloma elegans* (Risso, 1826) and *Orculella aragonica* are the most abundant taxa and remain rather persistent over the molluscan successions. Profiles GA-II and GA-VIII contain a higher diversity of xerothermic land snails. In the aquatic species, the endemic *Iberhoratia morenoi* and *Mercuria* are notably common and rich in most profiles. No living population of *Iberhoratia morenoi* has been reported in Galera, whereas *Mercuria* is still present. The taxa *Vallonia enniensis*, *Succinella oblonga* (Draparnaud, 1801), *Euconulus fulvus* (Müller, 1774), *Trochulus hispidus* (Linnaeus, 1758) and *Orculella aragonica* appear in all the Galera sections but have not been recorded as extant species in the valley. *Vertigo antivertigo* has been identified as a few old shells in the valley flood debris without any evidence of a living population, while the fossil population totals over 9,000 individuals. *Lauria cylindracea* (da Costa, 1778), *Truncatellina calliocratis* (Scacchi, 1833), *Merdigera obscura* (Müller, 1774), *Cecilioides veneta* (Strobel, 1855), *Oligolimax annularis* (Studer, 1820), *Oxychilus draparnaudi* (Beck, 1837), *Xerosecta* sp., *Potamopyrgus antipodarum* (Gray, 1843), *Cochlicella acuta* (Müller, 1774) and *Oestophora* sp. constitute 10 taxa living in the valley at present but absent from the fossil record.

Holocene molluscan successions

Molluscan successions were divided into malacozones based on ecological patterns (Figs 7–10) of the occurrence, extension and disappearance of taxa (Figs 11–15) and supported by constrained cluster analysis (CONISS). The zonation obtained by CONISS is consistent with the major environmental phases identified empirically by Galera's ecological and specific frequency diagrams. The two methods provided slightly different results for one or two offset samples from GA-IB. The largest differences observed are concentrated in GA-I, where abundances are very inconsistent and nearly half of the samples are not significant due to low numbers of shells extracted. The zonation of the Galera I (GA-I) sequence follows the frequency diagram only, as ecological diagrams could not be produced. Malacozones are identified with the name of the sequence (GA-I, GA-IB, GA-II and GA-VIII) and numbered (MZ1 to n).

Galera I (GI)

For the section GI, we identified two zones (GI-MZ1 and GI-MZ2) (Fig. 11). GI-MZ2 was further divided into three subzones (GI-MZ2a, GI-MZ2b and GI-MZ2c).

Malacozone GI-MZ1: GI-1 to GI-12: In the malacozone GI-MZ1, molluscs are scarce and not very diverse except for sample GI-6, which includes a high number of opercula from *Bithynia tentaculata* (Linnaeus, 1758) and eight other aquatic species (Fig. 11). Although the extreme poverty of the assemblages does not allow any detailed analysis to be carried out, some palaeoecological trends could be highlighted. The malacological assemblage is dominated by the freshwater taxa *Mercuria* sp., *Iberhoratia morenoi* and *Bithynia tentaculata* (Fig. 11). Sporadic occurrences of paludal molluscs *Zonitoides nitidus* (Müller, 1774), *Carychium minimum* and *Vallonia enniensis*, slugs, open terrain taxa (*Vallonia pulchella*) and two xerothermic species (*Geomitridae* sp. 1 and *Granopupa granum*) supplement the sequence.

The high abundance of opercula but the absence of corresponding shells of *Bithynia tentaculata* in sample GI-6 implies an allochthonous contribution of shell remains and indicates a reworking of the stratigraphic unit. The species assemblage indicates the former existence of a damp valley floor (hygrophilous, palustrine and aquatic molluscs predominate), but with a dynamic water regime that caused reworking and prevented the preservation of shells or the establishment of suitable terrestrial biotopes, respectively.

Table 1. Modern *vs* fossil species at Galera.

	Molluscan taxa	Holocene				Modern
		GA-I	GA-IB	GA-II	GA-VIII	
Freshwater	<i>Mercuria</i> sp.	X	X	X	X	X
	<i>Anisus spirorbis</i> (Linnaeus, 1758)	X	X	X	X	X
	<i>Pisidium casertanum</i> (Poli, 1791)	X	X			X
	<i>Theodoxus</i> sp.	X	X	X	X	
	<i>Melanopsis</i> sp.	X	X	X	X	
	<i>Iberhoratia morenoi</i> Arconada, Delicado & Ramos, 2007	X	X	X	X	
	<i>Radix</i> sp.	X	X	X	X	
	<i>Stagnicola</i> sp.	X	X	X	X	
	<i>Galba truncatula</i> (Müller, 1774)		X	X	X	
	Hydrobiidae sp. 2	X			X	
	Hydrobiidae sp. 3	X			X	
	<i>Pisidium</i> sp.			X	X	
	<i>Ancylus fluviatilis</i> Müller, 1774	X	X			
	Lymnaeidae indet.	X				
	<i>Bithynia tentaculata</i> (Linnaeus, 1758)	X				
	<i>Corrosella</i> sp. 1	X				
	<i>Gyraulus crista</i> (Linnaeus, 1758)	X				
	<i>Planorbis</i> sp.		X			
	<i>Pisidium subtruncatum</i> (Malm, 1855)		X			
	Hydrobiidae sp. 1		X			
	<i>Potamopyrgus antipodarum</i> (Gray, 1843)					X
Terrestrial	<i>Carychium minimum</i> Müller, 1774	X	X	X	X	X
	<i>Oxyloma elegans</i> (Risso, 1826)	X	X	X	X	X
	<i>Vertigo antivertigo</i> (Draparnaud, 1801)	X	X	X	X	X
	<i>Granopupa granum</i> (Draparnaud, 1801)	X	X	X	X	X
	<i>Rumina decollata</i> (Linnaeus, 1758)		X	X	X	X
	<i>Cochlicella barbara</i> (Linnaeus, 1758)		X	X	X	X
	<i>Theba pisana</i> (Müller, 1774)			X	X	X
	<i>Vallonia pulchella</i> (Müller, 1774)	X	X			X
	<i>Cecilioides acicula</i> (Müller, 1774)		X			X
	<i>Vallonia costata</i> (Müller, 1774)				X	X
	<i>Cernuella virgata</i> (Da Costa, 1778)				X	X
	<i>Mediterranea hydatina</i> (Rossmässler, 1838)				X	X
	<i>Vallonia enniensis</i> (Gredler, 1856)	X	X	X	X	
	<i>Succinella oblonga</i> (Draparnaud, 1801)	X	X	X	X	
	<i>Euconulus fulvus</i> (Müller, 1774)	X	X	X	X	
	<i>Microxeromagna lowei</i> (Potiez & Michaud, 1835)/ <i>Xerotricha conspurcata</i> (Draparnaud, 1801)	X	X	X	X	
	Geomitridae sp. 1	X	X	X	X	
	<i>Trochulus hispidus</i> (Linnaeus, 1758)	X	X	X	X	
	<i>Orculella aragonica</i> (Westerlund, 1897)	X	X	X	X	
	<i>Cepaea</i> sp.	X	X		X	
	<i>Zonitoides nitidus</i> (Müller, 1774)	X	X	X		
	Geomitridae indet.		X	X	X	
	Unidentified slug		X		X	
	<i>Cochlicopa lubrica</i> (Müller, 1774)		X			
	<i>Jamina quadridens</i> (Müller, 1774)		X			
	<i>Oxychilus</i> sp.		X			
	Helicidae indet.		X			
	<i>Xerosecta cespitum</i> (Draparnaud, 1801)			X		
	<i>Truncatellina</i> sp.			X		
	<i>Vitrea contracta</i> (Westerlund, 1871)				X	
	<i>Cornu aspersum</i> (Müller, 1774)				X	
	<i>Pseudotachea splendida</i> (Draparnaud, 1801)				X	
	<i>Lauria cylindracea</i> (da Costa, 1778)					X
	<i>Truncatellina callicratis</i> (Scacchi, 1833)					X

Table 1. Continued.

Molluscan taxa	Holocene				Modern
	GA-I	GA-IB	GA-II	GA-VIII	
<i>Merdigera obscura</i> (Müller, 1774)					X
<i>Cecilioides veneta</i> (Strobel, 1855)					X
<i>Oligolimax annularis</i> (Studer, 1820)					X
<i>Oxychilus draparnaudi</i> (Beck, 1837)					X
<i>Microxeromagna lowei</i> (Potiez & Michaud, 1835)					X
<i>Xerosecta</i> sp.					X
<i>Cochlicella acuta</i> (Müller, 1774)					X
<i>Oestophora</i> sp.					X
Total number of species	30	35	28	34	25

Taxa have been classified according to their occurrence in the profiles and the modern survey. Taxa recorded only as fossils are indicated by bold font.

Table 2. Radiocarbon ages for the Galera sequence.

	Lab code	Sample position	Material	Radiocarbon date (yr BP)	IntCal20-calibrated	Publication
					radiocarbon date (2σ calyr BP)	
GA-I	Beta-404764	SU-4	Charcoal	6,100 \pm 30	7,157–6,856	Wolf et al. (2021)
	Beta-485046	SU-4	Charcoal	6,580 \pm 30	7,562–7,427	Wolf et al. (2021)
	Beta-404762	SU-4	Charcoal	7,420 \pm 30	8,333–8,179	Wolf et al. (2021)
	Beta-485045	SU-3	Charcoal	7,530 \pm 40	8,410–8,205	Wolf et al. (2021)
	Beta-485044	SU-3	Charcoal	7,630 \pm 40	8,519–8,371	Wolf et al. (2021)
	Beta-499012	SU-2	Charcoal	8,230 \pm 50	9,404–9,025	Wolf et al. (2021)
	Beta-485043	SU-2	Charcoal	8,410 \pm 30	9,527–9,316	Wolf et al. (2021)
	Beta-404760	SU-2	Charcoal	8,460 \pm 30	9,533–9,440	Wolf et al. (2021)
	Beta-378613	SU-2	Charcoal	8,800 \pm 40	10,127–9,609	Wolf et al. (2021)
GA-IB	Beta-561782	M9	Charcoal	6,390 \pm 30	7,422–7,185	This study
	Poz-141018	M21C	<i>Vertigo antivertigo</i> shell	5,920 \pm 40	6,877–6,656	This study
	Poz-141031	M23C	<i>V. antivertigo</i> shell	6,370 \pm 50	7,423–7,167	This study
	Poz-141032	M37C	<i>V. antivertigo</i> shell	5,510 \pm 270	6,945–5,664	This study
GA-II	Beta-485036	SU-7	Charcoal	4,170 \pm 30	4,832–4,581	Wolf et al. (2021)
	Beta-499008	SU-6	Charcoal	4,320 \pm 30	4,962–4,838	Wolf et al. (2021)
	Beta-486033	SU-5	Charcoal	5,090 \pm 40	5,921–5,739	Wolf et al. (2021)
	Beta-485029	SU-4	Charcoal	5,400 \pm 30	6,289–6,020	Wolf et al. (2021)
	Beta-485028	SU-4	Charcoal	6,270 \pm 30	7,267–7,033	Wolf et al. (2021)
	Beta-485027	SU-3	Charcoal	6,460 \pm 30	7,428–7,318	Wolf et al. (2021)
	Beta-485031	SU-4	Charcoal	6,660 \pm 30	7,583–7,434	Wolf et al. (2021)
	Beta-485026	SU-2	Charcoal	7,620 \pm 40	8,520–8,361	Wolf et al. (2021)
	Beta-499007	SU-2	Charcoal	7,630 \pm 40	8,520–8,369	Wolf et al. (2021)
GA-VIII	Beta-485037	SU-2	Charcoal	8,920 \pm 30	10,188–9,909	Wolf et al. (2021)
	Beta-499009	SU-9	Charcoal	550 \pm 30	633–516	Wolf et al. (2021)
	Beta-485035	SU-9	Charcoal	770 \pm 30	729–668	Wolf et al. (2021)
	Beta-485034	SU-8	Charcoal	2,220 \pm 30	2,334–2,146	Wolf et al. (2021)

Radiocarbon ages previously obtained from Wolf et al. (2021) were recalibrated using the recent IntCal20 calibration curve (Reimer et al., 2020).

Malacozone GI-MZ2: G1-13 to G1-33: The assemblages of the second malacozone GI-MZ2 are more diversified and abundant in shells. They still include a significant proportion of freshwater molluscs, with 11 taxa in total (Fig. 11). *Mercuria* sp., *Radix* sp., *Iberhoratia morenoi* and *Pisidium casertanum* (Poli, 1791) represent the most common freshwater species. Furthermore, there are occurrences of *Ancylus fluviatilis* Müller, 1774, *Stagnicola* sp., *Theodoxus* sp., *Corrosella* sp. 1 and Hydrobiidae sp. 3 (Fig. 11). The presence and progressive expansion of the paludal taxa *Oxyloma elegans*, *Vertigo antivertigo*, *Zonitoides nitidus* and *Vallonia enniensis* characterizes the lower part of the zone. *Orculella aragonica* is recorded occasionally (Fig. 11). The mesophilic species *Euconulus fulvus* is commonly presented within G1-MZ2, while *Oxychilus* sp. and *Trochulus hispidus* occur sporadi-

cally (Fig. 11). Occurrences of the open field taxon *Vallonia pulchella* (Müller, 1774) and slugs are relatively constant.

GI-MZ2 can be divided into three subzones based on variations in abundance and proportions of ecological groups: GI-MZ2a (G1-13 to G1-22), GI-MZ2b (G1-23 to G1-26) and GIMZ2c (G1-27 to G1-33). The first subzone, GI-MZ2a, is characterized by the clear expansion of aquatic, paludal, mesophilous taxa and *Vallonia pulchella*. The vallonid *Vallonia pulchella* is absent from GI-MZ2b, which appears to be less rich and less diversified (Fig. 11). These ecological groups are recorded as well in the last part of the zone (i.e. G1-MZ2c), but paludal species appear less diversified, and the occurrences of *Vallonia pulchella* and mesophilous taxa (*Euconulus fulvus*, *Oxychilus* sp. and *Trochulus hispidus*) are rare.

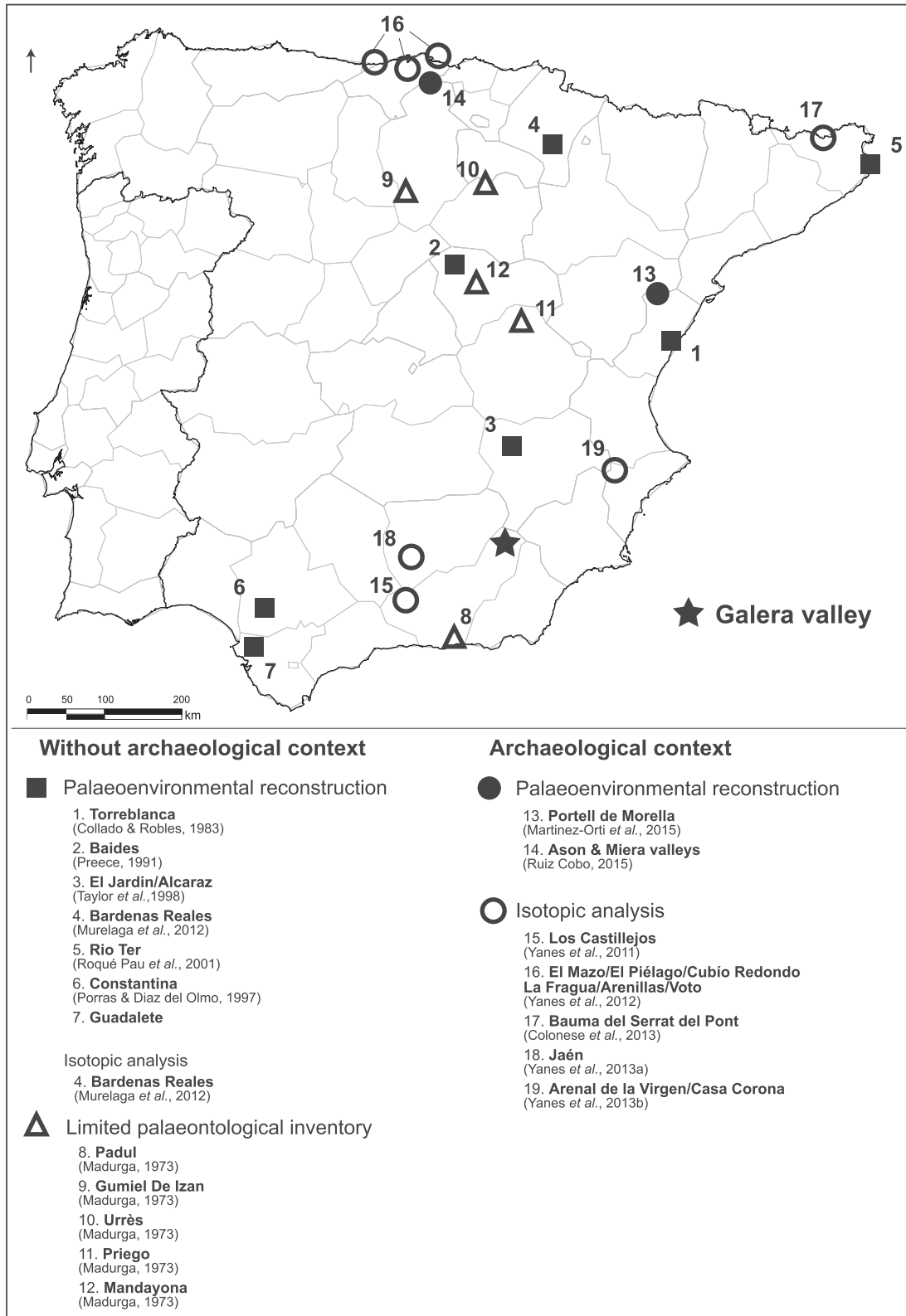


Figure 6. State of the art on Holocene paleomalocology in Spain: palaeoenvironmental studies and limited palaeontological inventories cited in the paper.

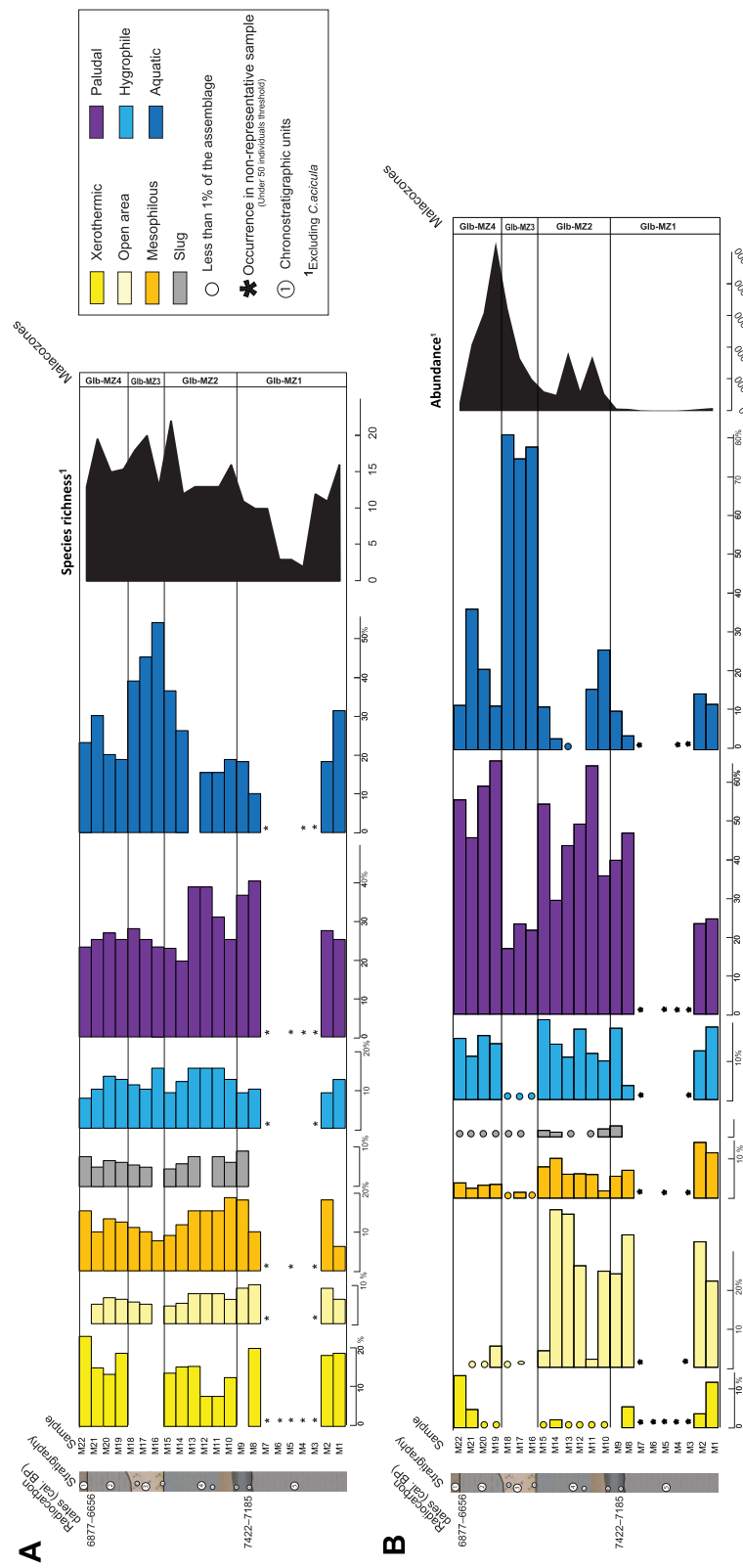


Figure 7. Ecological diagrams of the profile 1 of Galera IB. **A.** Species distribution according to ecological groups (%) and species diversity. **B.** Individual distribution in ecological groups for assemblages (%) and shell abundance.

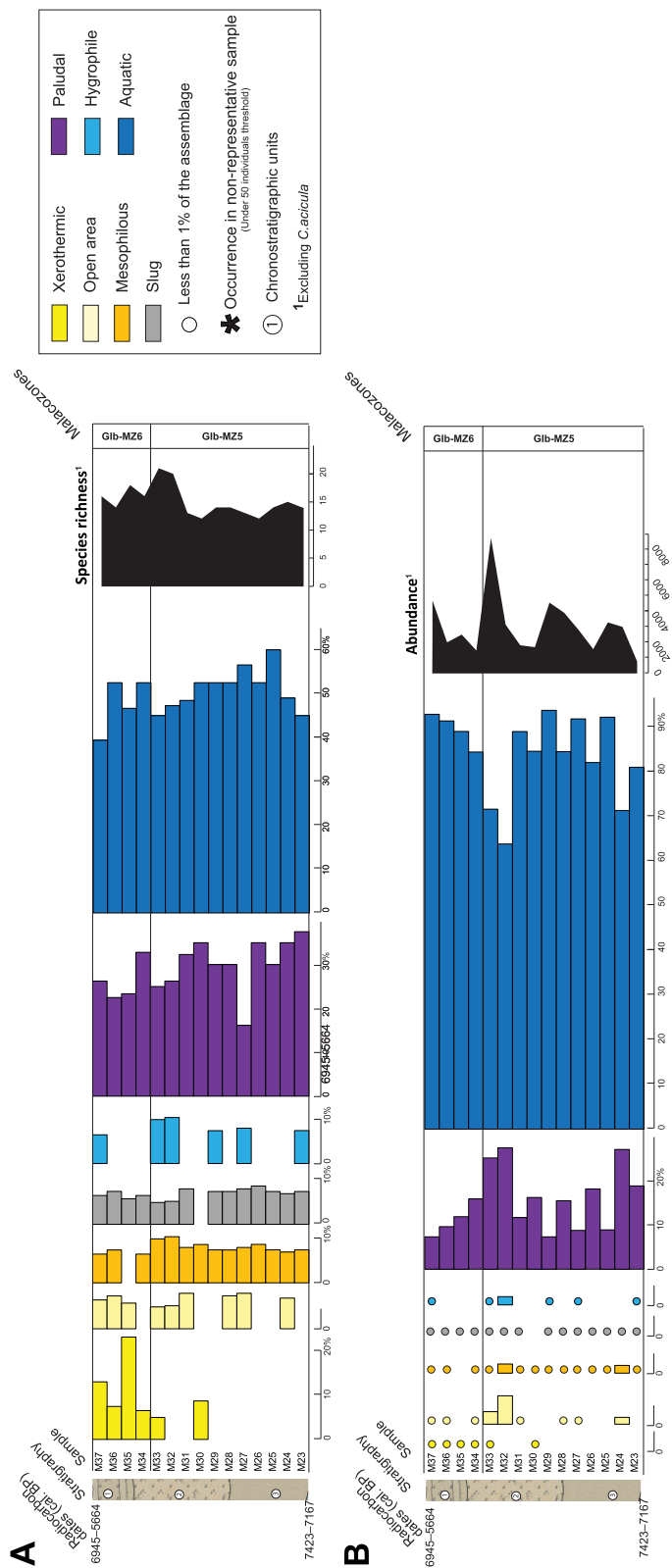


Figure 8. Ecological diagrams of the profile 2 of Galera IB. **A.** Species distribution according to ecological groups (%) and species diversity. **B.** Individual distribution in ecological groups for assemblages (%) and shell abundance.

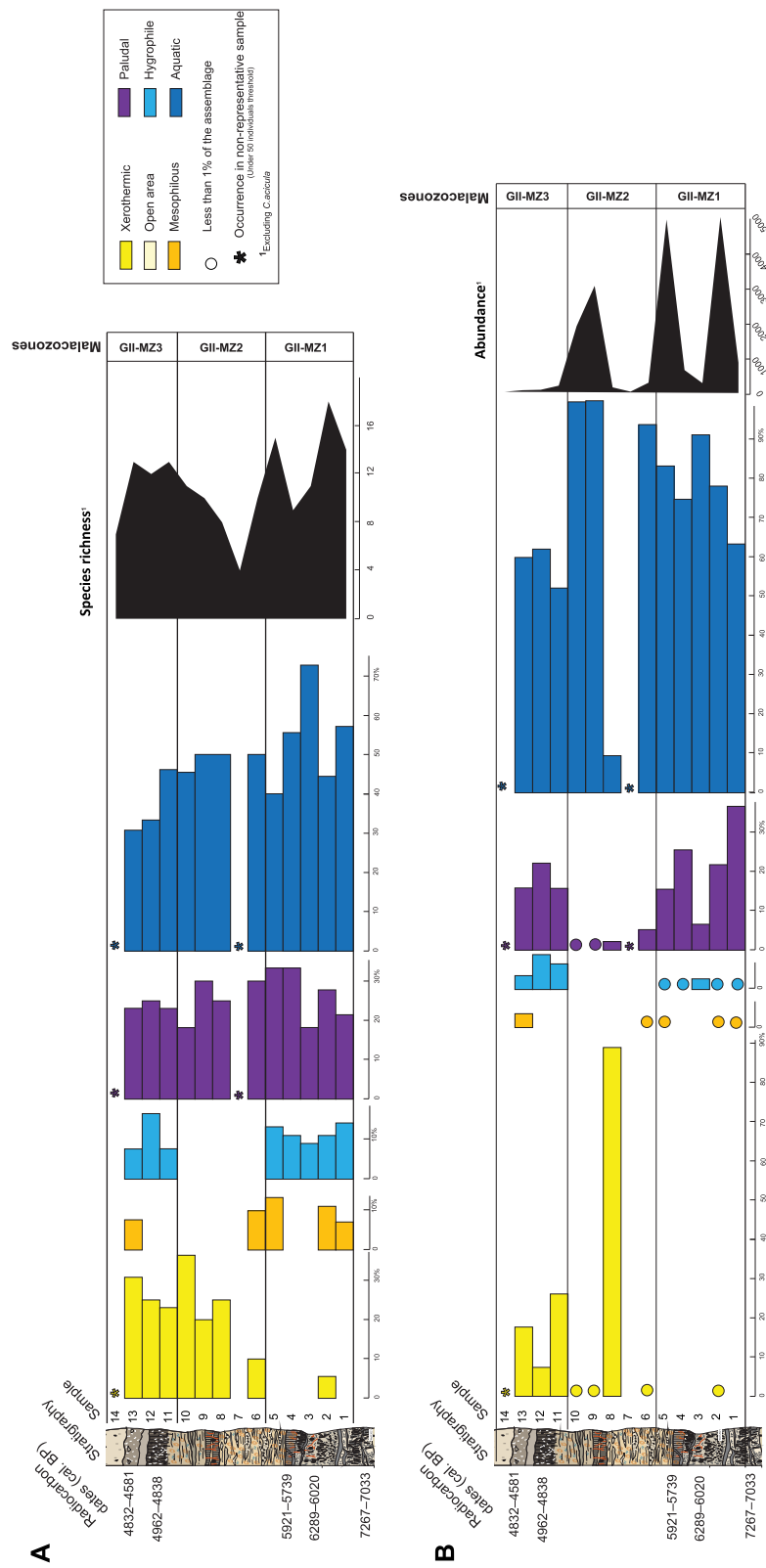


Figure 9. Ecological diagrams of Galera II. **A.** Species distribution according to ecological groups (%) and species diversity. **B.** Individual distribution in ecological groups for assemblages (%) and shell abundance.

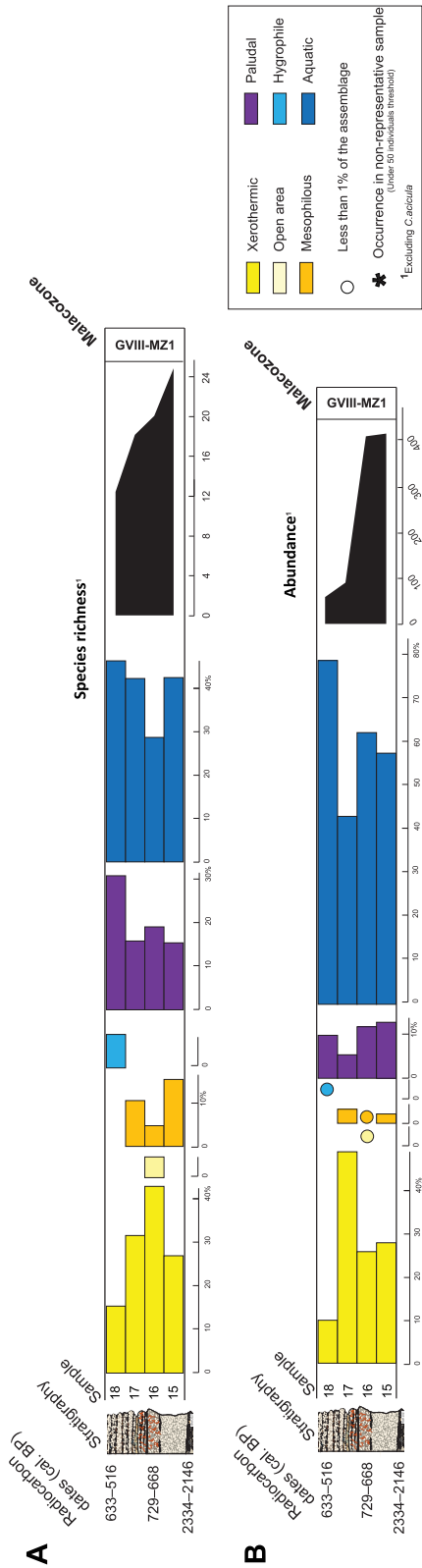


Figure 10. Ecological diagrams of Galera VIII. **A.** Species distribution according to ecological groups (%) and species diversity. **B.** Individual distribution in ecological groups for assemblages (%) and shell abundance.



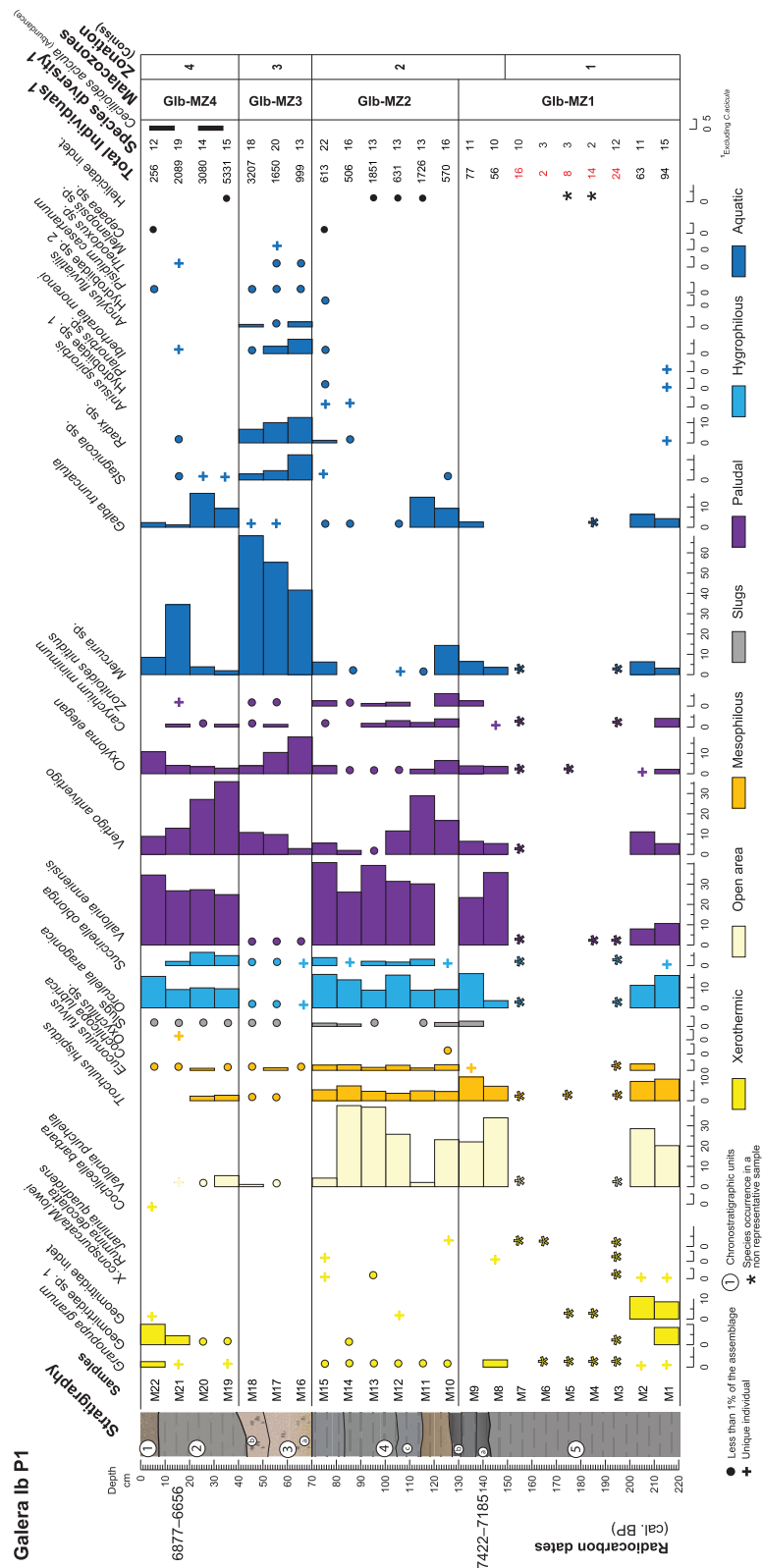
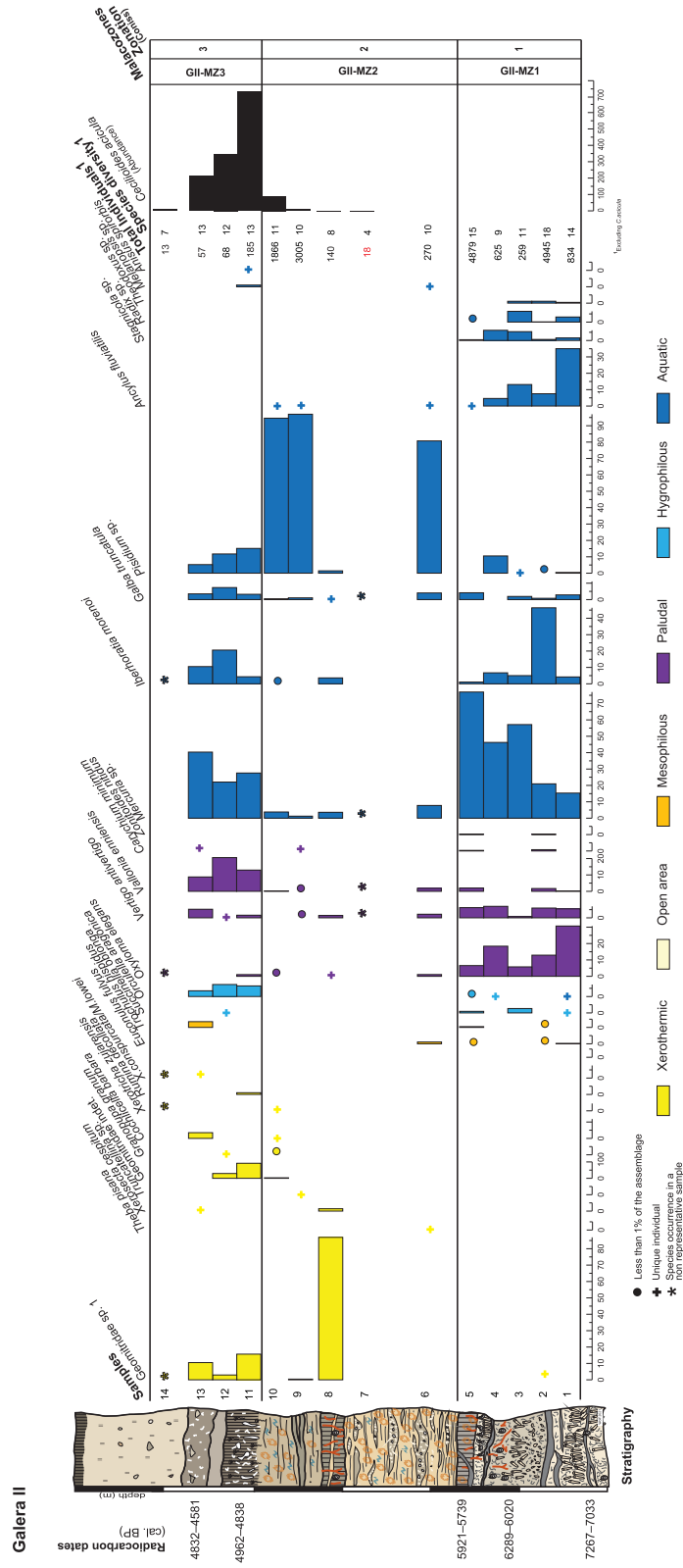


Figure 12. Percentage frequency histogram of Galera IB profile 1. Individuals of nonsignificant samples with abundances below 50 individuals are in red.





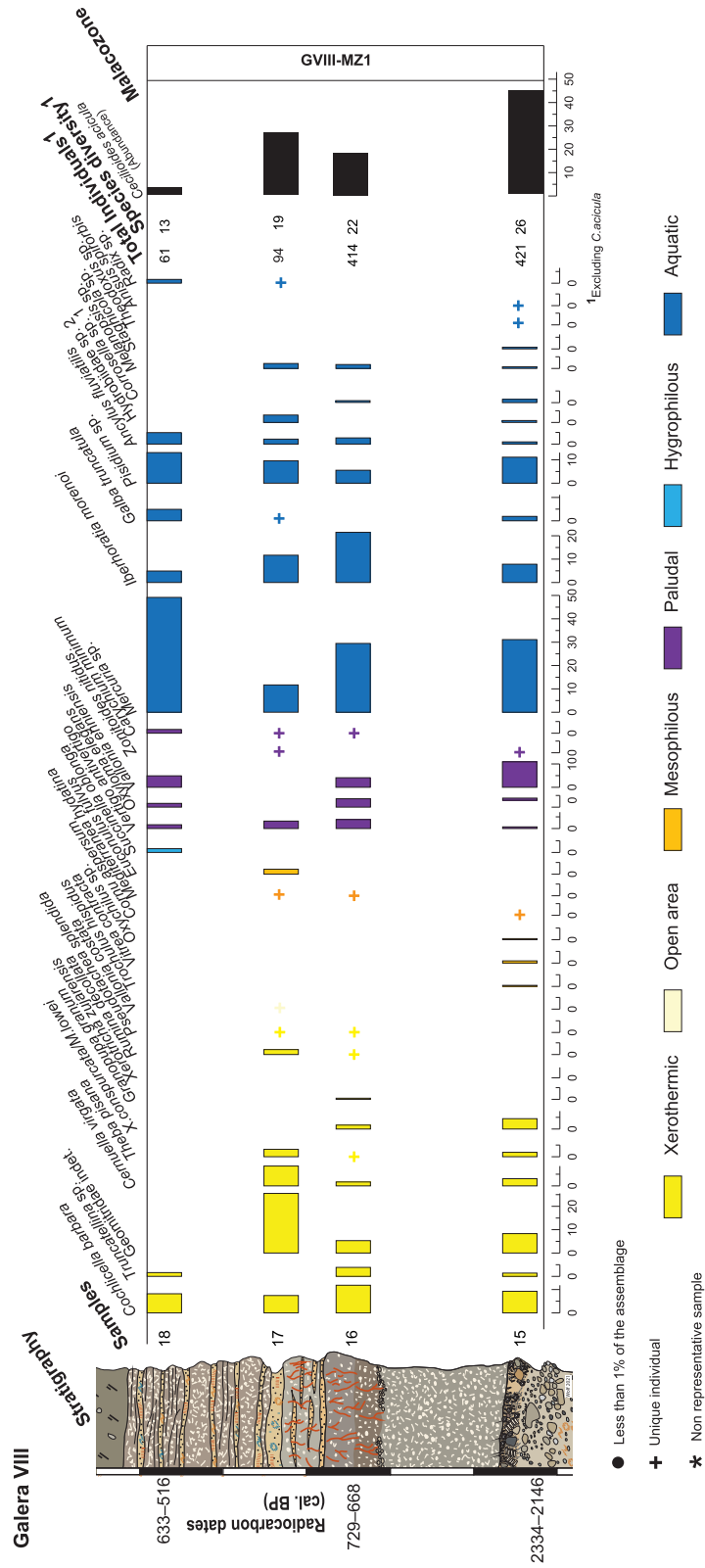


Figure 15. Percentage frequency histogram of Galera VIII.

The malacocenoses of this zone indicate the presence of a rather dynamic aquatic environment in the vicinity of which calmer water body with paludal vegetation. Subzone GI-MZ2b shows a more dynamic episode, after which the marshy habitats are slightly less expanded than in the lower part of the zone (GI-MZ2a).

Galera IB (GIB)

Six malacozones have been identified in both profiles (profile 1: GIB-MZ1 to GIB-MZ4; profile 2: GIB-MZ5 and GIB-MZ6) (Figs 12, 13).

Malacozone GIB-MZ1: M1 to M9 (profile 1): In the GIB-MZ1, molluscs are rare and no sample reaches the representativeness threshold of 200 individuals. For this reason, a detailed analysis of its malacological content is not considered. However, some palaeoecological patterns can be described. The zone presents an assemblage mainly characterized by xerothermic and paludal taxa (Fig. 7A, B). Seven xerothermic taxa occur throughout the zone, namely *Granopupa granum*, the Geomitridae, *Microxeromagna lowei*/*Xerotracha conspurcata*, *Rumina decollata* and *Jamnia quadridens* (Fig. 12). Marshland gastropods comprise five species (*Vertigo antiwertigo*, *Vallonia enniensis*, *Oxyloma elegans*, *Carychium minimum* and *Zonitoides nitidus*) and occur irregularly (Fig. 12). Aquatic, hygrophilous, mesophilous and open country taxa are present only in small numbers. Few individuals of slugs are preserved at the top of the malacozone (Fig. 12).

The environmental conditions indicated by this malacocenose imply a relative instability of the vegetation cover for samples M3 to M7, which are dominated by xerothermic vegetation with limited, temporary and poorly developed wetlands.

Malacozone GIB-MZ2: M10 to M15 (profile 1): In malacozone GIB-MZ2, the number and diversity of molluscs increase (Fig. 7A, B) and reflect higher habitat stability. Paludal gastropods dominate the assemblage and represent on average 40% of the species and almost 50% of individuals (Fig. 7A, B). The frequency of *Vallonia enniensis* slightly increases, while the frequency of other molluscs preferring swamp habitats remains constant. Aquatic, hygrophilous, open ground and xerothermic molluscs represent between c. 10 and 20% of the species assemblage. In the upper part of the zone (samples M14 and M15), the aquatic species richness increases and *Radix* sp., Hydrobiidae sp. 1 and *Planorbis* sp. re-occur, while *Iberhoratia morenoi*, Hydrobiidae sp. 2 and *Anisus spirorbis* (Linnaeus, 1758) are recorded for the first time (Fig. 12). *Vallonia pulchella* is the only open ground taxon present in GIB. In GIB-MZ2, the frequency of *Vallonia pulchella* increases slightly to c. 30% (Fig. 12). *Orculella aragonica* is an Oriculidae that favours wet biotopes, such as the banks of water bodies or plant cover in marshy areas. Within malacozone GIB-MZ2, the proportion of *Orculella aragonica* is constant, varying between 10 and 15%. Except for *Granopupa granum*, the occurrences of xerothermic taxa remain low (Fig. 12).

The malacocenoses reflect the establishment of a stable, well-supplied marshy area with adjacent hygrophilous and rather open vegetation.

Malacozone GIB-MZ3: M16 to M18 (profile 1): The abundance curve shows that the mollusc population size increases along GIB-MZ3 (Fig. 7B). The malacological assemblage is characterized by the absence of xerothermic and hygrophilous taxa in favour of aquatic taxa whose numbers increase (Fig. 7A, B). Freshwater taxa represent nearly 40–50% of species and more than 70% of individuals (Fig. 7A, B). *Theodoxus* sp., *Pisidium casertanum* and *Melanopsis* sp. are recorded and the number of aquatic species increases. *Mercuria* sp. expands and represents almost 50% of the total abundance. The proportion of paludal and mesophilous species slightly decreases to 20 and 10% of the species assemblage, respectively. The average proportion of paludal individuals is around 15% (Fig. 7B). A declin-

ing abundance of *Vallonia enniensis* implies a change in the wetland, resulting in the vegetation being slightly more open (Fig. 12).

Malacozone GIB-MZ3 indicates an environmental shift towards dynamic aquatic habitats with marshy margins dominating the landscape.

Malacozone GIB-MZ4: M19 to M22 (profile 1): Malacozone GIB-MZ4 is characterized by a high abundance of terrestrial molluscs and a limited occurrence of freshwater species (Fig. 7A, B). Xerothermic taxa reappear (20% of the species assemblage) at the expense of freshwater gastropods, which only represent 20% of species (Fig. 7A, B). Within the aquatic group, *Mercuria* sp. and *Galba truncatula* are the dominant components. Xerothermic taxa comprise Geomitridae sp. 1, *Granopupa granum* and *Cochlicella barbara* (Fig. 12). The share of other ecological groups that are paludal, mesophilous, open ground and hygrophilous remains constant. Marshland species comprise more than 50% by abundance for all assemblages in all samples (Fig. 7B).

The environmental conditions inferred from the malacological association show the new development of a marshy area with lower water input. The assemblages point to wetland banks with well-developed hygrophilous and paludal vegetation, as well as an increase in open and xerothermic plant formations in the vicinity of the swamp.

Malacozone GIB-MZ5: M23 to M33 (profile 2): The molluscan assemblage in malacozone GIB-MZ5 is characterized by the predominance of aquatic molluscs. They represent almost half of species and 70–90% of individuals (Fig. 8D). *Mercuria* sp. and *Iberhoratia morenoi* dominate the freshwater species: they sometimes account for nearly 70% of individuals. Their specific frequencies are negatively correlated. When the frequency of *Mercuria* is low, that of *Iberhoratia morenoi* is high and vice versa (Fig. 13). The paludal element represents on average 30% of the gastropods in the assemblages of MZ5 (Fig. 8C). The frequencies of *Vertigo antiwertigo*, *Oxyloma elegans*, *Carychium minimum* and *Vallonia enniensis* are constant. The other ecological groups are represented by less than 10% of individuals (Fig. 8C). Geomitridae sp. 1 is the only xerothermic species within this malacozone and appears in the upper part of the unit.

The environmental conditions suggested by the malacocenoses correspond to dynamic and well-established wetland conditions and point to the presence of marshy vegetation in habitats adjacent to the water body.

Malacozone GIB-MZ6: M34 to M37 (profile 2): Malacozone GIB-MZ6 differs from the previous one by the greater abundance of xerothermic taxa (Fig. 13). The proportion of freshwater molluscs increases, while that of marshland molluscs remains constant. Freshwater molluscs represent 40% of the total abundance and 25% of species on average (Fig. 8C, D). The proportion of individuals from aquatic taxa remains high (80–90%). However, the frequency of *Iberhoratia morenoi* decreases significantly, accompanied by the appearance of the bivalve *Pisidium subtruncatum* (Malm, 1855) (Fig. 13). In GIB-MZ6, the proportion of xerothermic species varies between 10 and 20%. Geomitridae sp. 1, *Granopupa granum*, *Microxeromagna lowei*/*Xerotracha conspurcata* and *Rumina decollata* are dominant among the xerophilous taxa. The proportion of mesophilous and open-ground gastropods remains constant. Hygrophilous taxa occur less frequently and comprise just a single occurrence of *Orculella aragonica* at the top of the zone.

The malacocenoses indicate a reduction in water supply from adjacent marshy areas and the development of drier, exposed habitats.

Galera II (GII)

Three zones, GII-MZ1, GII-MZ2 and GII-MZ3, were identified in the Galera II section (Fig. 14).

Malacozone GII-MZ1: samples 1–5: Molluscs in GII-MZ1 are abundant and dominated by aquatic taxa, which constitute 50–60% of species (Fig. 9A). *Mercuria* sp., *Ancylus fluviatilis*, *Pisidium* sp. and the crenophilous species *Iberhoratia morenoi* are the predominant freshwater snails. Marshland taxa (*Oxyloma elegans*, *Vertigo antiver-tigo*, *Vallonia enniensis* and *Carychium minimum*; Fig. 14) supplement the malacological assemblage and constitute one quarter of the total species diversity (Fig. 9A) and 20% of all shells (Fig. 9B). The hygrophilous species *Succinella oblonga* and *Orculella aragonica* occasionally occur at the basis of the succession (samples 1–5). The catholic *Trochulus hispidus* and the humid mesophilous *Euconulus fulvus* occur irregularly (Fig. 14). They represent less than 10% of the species assemblage in these samples (Fig. 9A).

The molluscan assemblage reflects the aquatic environment of a channel with a dynamic water regime partially supplied by spring water. The mollusc record points to river banks with slightly stabilized areas, where marsh developed. The very low abundance and diversity in sample 7 suggest local environmental stress, which characterizes the lower part of GII-MZ2.

Malacozone GII-MZ2: samples 5–10: In malacozone GII-MZ2, mollusc abundance fluctuates across samples, but the species richness remains constant (Fig. 9A, B). Freshwater taxa comprise 40–50% of species (Fig. 9A) and reach over 80% of individuals in some samples (Fig. 9B). The variation in aquatic species can partially be explained by two peaks of *Pisidium* sp. that reach 1,000 individuals in sample 9 and 2,000 individuals in sample 10 (Supplementary Material Table S3). The malacological assemblage is supplemented by marsh taxa that are more restricted in distribution and occur irregularly. They represent 20% of the species and less than 20% of all individuals (Fig. 9B). Xerothermic land snails consist mainly of Geomitridae sp. 1 and *Granopupa granum*, with *Cochlicella barbara* and *Xerotricha zu-jarensis* appearing in the upper part of the zone (Fig. 14).

The malacocenoses reflect the development of aquatic habitats with adjacent rather open vegetation.

Malacozone GII-MZ3: samples 11–14: In malacozone GII-MZ3, molluscan abundance is lower than in the rest of the succession, but the species-level diversity remains stable (Fig. 9A, B). The development of aquatic (*Mercuria* sp. and *Iberhoratia morenoi*), and palustrine (*Vertigo antiver-tigo* and *Vallonia enniensis*) taxa (Fig. 14) and the reappearance of the hygrophilous *Orculella aragonica* (Fig. 14) are significant features of the zone. Freshwater taxa comprise 30–40% of the species assemblage (Fig. 9A) and paludal gastropods reach an average of 20% of species (Fig. 9A). In contrast to GII-MZ1, xerothermic species occur and reach 25% of the total species (Fig. 9A). The xero-resistant species Geomitridae sp. 1 is constantly recorded, whereas *Truncatellina* sp., *Xerosecta cespitum*, *Cochlicella barbara*, *Xerotricha zu-jarensis* and *Rumina decollata* are sporadic (Fig. 14). From sample 11 onwards, the burrowing taxon *Cecilioides acicula* is very abundant, sometimes reaching several hundreds of individuals (Supplementary Material Table S3). The occurrence of *Cecilioides acicula* probably postdates the deposition of the lithological unit.

The environmental conditions deduced from the malacocenoses indicate a drier habitat than in malacozone GI-MZ1 and GII-MZII. The malacozone GII-MZ3 indicates the presence of wetlands in the valley, while the river banks and the surrounding vegetation remained rather open and dry.

Galera VIII (GVIII)

A single consistent malacozone (GVIII-MZ1) was designed for the sequence Galera VIII (Fig. 11).

Malacozone GVIII-MZ1: samples 15–18: In malacozone GVIII-MZ1, aquatic taxa represent 30 to 40% of species (Fig. 10C). *Mercuria* sp., *Iberhoratia morenoi*, *Ancylus fluviatilis* and *Pisidium* sp. appear through-

out the GVIII sequence (Fig. 15). Xerothermic gastropods comprise 30% of species (Fig. 10C). *Cochlicella barbara*, *Truncatellina* sp., *Cer-nuella virgata* and *Theba pisana* occur constantly, whereas *Granopupa granum*, *Xerotricha zu-jarensis*, *Rumina decollata* and *Pseudotachea splendida* are intermittently recorded (Fig. 15). Marsh taxa constitute 20% of the species assemblage. *Trochulus hispidus*, *Vitrea contracta*, *Cornu aspersum*, *Euconulus fulvus* and *Mediterranea hydatina* are mesophilous snails that appear sporadically. *Succinella oblonga* (hygrophilous) and the open-ground taxa *Vallonia costata* (Müller, 1774) occur occasionally in the upper part of the sequence.

The malacological assemblages suggest the presence of a partial spring-supplied channel with limited marshy areas along its banks. The vegetation cover near the banks and surrounding areas was rather dry and open.

DISCUSSION

In the Mediterranean Basin, Holocene terrestrial palaeoenvironmental archives show spatial and temporal variability in relation to environmental and climatic changes (Jalut et al., 2000; Pérez-Obiol et al., 2011; Fletcher et al., 2012; Fletcher & Zielhofer, 2013; Faust & Wolf, 2017; Morellón et al., 2018; Di Rita et al., 2022). According to the chronostratigraphic data, the molluscan successions in the Galera Valley cover a period from 10,000 to 5,500 cal. yr BP, along with two later snapshots from the Late Holocene, from c. 3,000 to 300 cal. yr BP, respectively (Fig. 16). The first part of our discussion aims to examine the response of the Galera malacofauna to environmental and climatic change from a broad perspective (i.e. both local and regional). In the context of the increased aridification of the Mediterranean Basin, understanding the long-term evolution of continental mollusc distribution is a key conservation issue. The second part of the discussion explores the significance of comparing data from the fossil record with the modern distributional ranges of both sensitive and less vulnerable species; it relies on a biogeographical approach to do so.

Palaeoenvironmental reconstruction for the Galera Valley from a regional perspective

The Early Holocene and the transition to the Middle Holocene: The Early Holocene phase recorded at the base of the section Galera I (i.e. Malacozone GI-MZ1) is poor in shells and has to be treated with caution, as there are strong signs of reworking (i.e. indicated by the abundance of allochthonous *Bithynia tentaculata* opercula, as well as stratigraphic features indicating river channel aggradation; Fig. 2). Between 10,000 and 9,000 cal. yr BP, the malacofaunal palaeoenvironmental reconstruction is consistent with the fluvial sedimentation period identified by Wolf et al. (2021) and suggests strong river dynamics that prevented the establishment of adjacent terrestrial environments, such as marshes (Fig. 16).

Palaeoenvironmental archives from southern Spain provide a very heterogeneous pattern for the Early Holocene period. From 10,000 to 8,000 cal. yr BP, lake level fluctuations in the southeastern part of the Iberian Peninsula and pollen data from the Padul site reflect frequent humid conditions (Ortiz et al., 2004; Morellón et al., 2018; Ramos-Roman et al., 2018) that are consistent with the modelling of past regional precipitation (Ilvonen et al., 2022). In contrast, the pollen record from Lake Siles shows arid conditions for this period and this is indicated by an increase in xerophytic vegetation (Jalut et al., 2000; Carrión, 2002). With respect to the mollusc assemblages of the Galera Valley, terrestrial environments were unstable and rather open during the Early Holocene. However, in contrast to sedimentological indications, no clear evidence of aridity is indicated by the mollusc record. In the Early to mid-Holocene transition, the malacological record suggests an environmental continuum of humid habitats. Based on a high-resolution

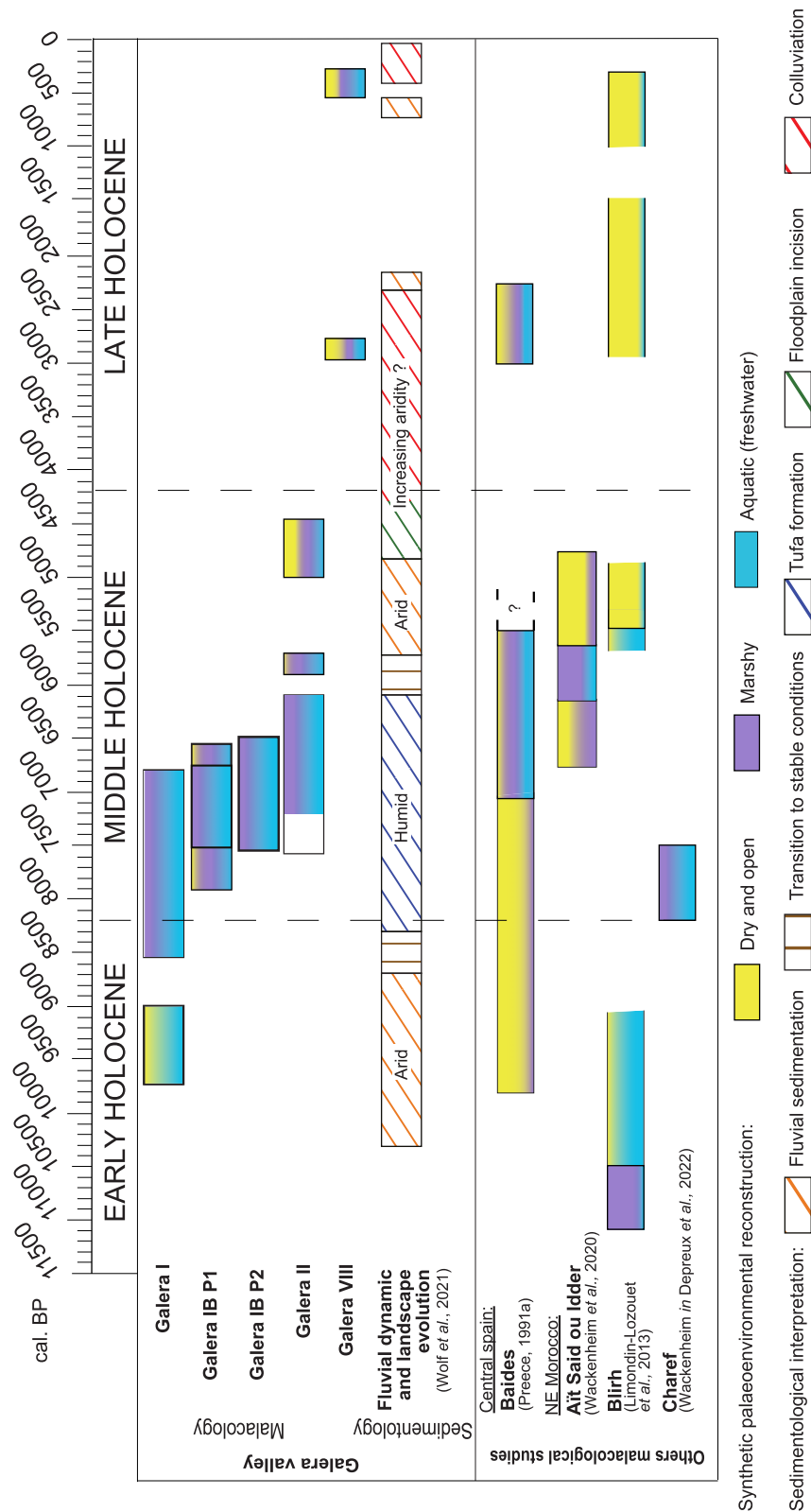


Figure 16. Synthetic palaeoenvironmental reconstruction based on the Galera mollusc data, Galera floodplain dynamics (Wolf et al., 2021) and synthetic malacological data from Spain (Preece, 1991a) and northeastern Morocco (Limondin-Lozouet et al., 2013; Wackenheim et al., 2020; Depreux et al., 2022).

isotopic record from a speleothem of Victoria's cave, an increased seasonality has been highlighted by Budsky *et al.* (2019) between 9,700 and 7,800 cal. yr BP. The existence of moister conditions during winter and autumn could have led to the following: (1) natural selection within the hygrophilous land snail assemblage, favouring taxa whose life cycle and activity are better adapted to hot summer temperatures and droughts (Arad, 1993; Schweizer *et al.*, 2019); (2) seasonal resilience of the wetlands in the Galera Valley that supports the maintenance of humid zones with a rich assemblage of freshwater species (*Mercuria* sp., *Iberhoratia morenoi*, *Ancylus fluviatilis* and *Pisidium casertanum*) and several marsh-living taxa (*Vertigo antiverigo*, *Vallonia enniensis* and *Carychium minimum*). Molluscan assemblages with *Vertigo antiverigo*, *Vallonia enniensis* and *Iberhoratia morenoi* from the end of the Early Holocene to the beginning of the Middle Holocene (between 8,500 and 8,000 cal. yr BP) indicate homogeneous conditions and stable biotopes with freshwater habitats and marshy vegetation.

The Middle Holocene. The first half of the Middle Holocene is well covered by Galera I, IB, and II sequences and allows us to discuss the variability of records. Malacocenoses present rich assemblages of hygrophilous species (*Orculella aragonica*, *Vallonia enniensis*, *Vertigo antiverigo*, *Succinella oblonga*, *Oxyloma elegans* and *Iberhoratia morenoi*), which imply the establishment of calm and well-developed marshland between 8,200 and 6,000 cal. yr BP. In the sections located in the valley bottom (GI and GII; Fig. 1), dynamic fluvial phases are sporadically identified. In contrast, section GIB, situated at the fringe of the valley, reveals a continuous evolution of terrestrial environments, comprising abundant and rich fauna that could be more sensitive to local variations. In the uppermost part of section GIB P1, the few pieces of evidence for a drying up of the wetland seem to reflect a local feature (perhaps related to local slope dynamics), which is not evident in the other sequences. In Galera I, IB and II, the high abundance of the stygobitic snail *Iberhoratia morenoi*, which is consistent with the sustained input of groundwater, strongly supports humid environmental conditions in the valley. Humid conditions, as deduced from the molluscan assemblage of the first part of the Middle Holocene (until 6,000 cal. yr BP), are consistent with tufa formation and the stability of habitats in the Galera Valley (Wolf *et al.*, 2021).

Likewise, numerous palaeoenvironmental and palaeoclimatic studies in southern Spain indicate typically humid conditions during the first half of the Middle Holocene, corresponding to the development of mesophytic vegetation (Carrión, 2002; Carrión *et al.*, 2003, 2010; Anderson *et al.*, 2011; Pérez-Obiol *et al.*, 2011; Fletcher *et al.*, 2012; Mesa-Fernández *et al.*, 2018; Morellón *et al.*, 2018; Ramos-Román *et al.*, 2018; Gil-García *et al.*, 2022; Ilvonen *et al.*, 2022). From 5,900 cal. yr BP, the appearance of xero-resistant species in the upper part of Galera II section is a reliable feature that suggests an environmental transition to drier habitats and fits with the scheme of landscape evolution developed by Wolf *et al.* (2021). The first evidence of this mid-Holocene transition towards arid conditions appeared around 300 years earlier in the Galera Valley than in northeastern Morocco, as highlighted by the molluscan succession of Ait Said ou Idder (Fig. 15; Wackenheim *et al.*, 2020). The strong aridification in southern Spain started between 5,500 and 5,000 cal. yr BP, depending on the records examined, and was characterized by the xerophytisation of the vegetation (Carrión *et al.*, 2010; Pérez-Obiol *et al.*, 2011; Ilvonen *et al.*, 2022). This environmental shift coincided with the end of the African Humid Period (deMenocal *et al.*, 2000) and to a rapid climate change interval identified between 6,000 and 5,000 yr BP (Mayewski *et al.*, 2004), when mesophytic forests declined (Carrión, 2002) and numerous data indicate of regional aridification (Reed, Stevenson & Juggins, 2001; Combourieu Nebout *et al.*, 2009; Carrión *et al.*, 2010; Anderson *et al.*, 2011; Vannière *et al.*, 2011). Furthermore, the mid-Holocene transition was characterized by an increase in the human population in southeastern Spain (Lillios *et al.*, 2016; Fyfe *et al.*, 2019;

Schirmacher *et al.*, 2020) that could have fragmented vegetation habitats and increased the effects of aridification (Carrión *et al.*, 2010).

Late Holocene: Late Holocene reconstructions are based on a small amount of data that have been obtained from four malacological samples from the section GVIII (Fig. 15). Malacocenoses show a diversified assemblage of catholic and xero-resistant species (*Cochlicella barbara*, *Truncatellina* sp., *Theba pisana* and *Xerotracha zujarensis*). The environmental conditions inferred from the mollusc records indicate the occurrence of a limited wetland area with extensive dry and open habitats.

As Late Holocene reconstructions from mollusc records in the Galera Valley involve only two short time periods, any comparison with other regional studies must be carried out cautiously. The Late Holocene represents a period of global aridification in the western Mediterranean, also highlighting a strong anthropogenic impact on vegetation (Combourieu Nebout *et al.*, 2009; Vannière *et al.*, 2011; Bellin, Vanacker & De Baets, 2013; Schirmacher *et al.*, 2020). In central Spain, environmental reconstructions based on molluscan sequences (Preece, 1991a) seem consistent with the regional trends as well as the Galera Valley record, whereas Late Holocene conditions appear drier in northeastern Morocco (Fig. 16). However, further data from the Galera Valley are needed to provide a more in-depth record for this period.

From Holocene to current faunas—answers and questions

Species selected for the purpose of biogeographic inferences include: (1) hygrophilous taxa that are widespread in Europe and common in the fossil record, but rarer in Spain today (*Vallonia enniensis*, *Vertigo antiverigo*, *Succinella oblonga* and *Euconulus fulvus*); (2) taxa that are less vulnerable but whose distribution in Spain are still to be documented (*Trochulus hispidus* and *Mediterranea hydantina*); and (3) species endemic to Spain for which our study represents the first record of fossil occurrence (*Iberhoratia morenoi* and *Xerotracha zujarensis*) or for which we provide further data of fossil occurrence (*Orculella aragonica*).

In Europe, as in the Iberian Peninsula, occurrences of *Vallonia enniensis* are rare (Gittenberger, 1998; Kerney *et al.*, 1999; Welter-Schultes, 2012; Cadeval & Orozco, 2016) and distributional data to assess its conservation status are inadequate (Bragado, Araujo & Aparicio, 2010) (Fig. 17). In southeastern Spain, a considerable investment in mollusc surveys has revealed several new populations of *V. enniensis* in Andalusia (Torres, Vázquez & Ripoll, 2020, Fig. 17); these dates strongly support the habitat fragmentation of this Palearctic taxon, a factor that causes difficulties in the location of the populations. However, in the Galera Valley, *Vallonia enniensis* occurred almost continuously from the Early to Late Holocene (Figs 11, 14, 15). Furthermore, in Holocene records, *Vallonia enniensis* is very common from Spain (Preece, 1991a; Taylor *et al.*, 1998) to Morocco (Limondin-Lozouet *et al.*, 2013; Wackenheim *et al.*, 2020; Depreux *et al.*, 2021; Depreux *et al.*, 2022), which indicates a wider Holocene distribution of the species compared to the modern biogeographic range. Reviewing and considering fossil data from *Vallonia enniensis* would overcome the deficient modern data to assess its status and argue for conservation measures.

Vertigo antiverigo is a hygrophilous Holarctic vertiginid that occurs throughout the Iberian Peninsula (Welter-Schultes, 2012; Cadeval & Orozco, 2016) but whose populations appear localized and dispersed (Altonaga *et al.*, 1994; Martínez-Orti, 1999; Bragado *et al.*, 2010) (Fig. 17). In the southern half of Spain, living populations are quite rare (Gasull, 1975; Arrébola, 1995; Ruiz Ruiz *et al.*, 2006), whereas *Vertigo antiverigo* is a very common taxon in the Spanish Holocene fossil successions (Madurga, 1973; Preece, 1991a; Taylor *et al.*, 1998) (Fig. 17). The large fossil population in the Galera Valley, which totals nearly 9,400 individuals, indicates that the environmental conditions were sufficiently humid and suitable for this

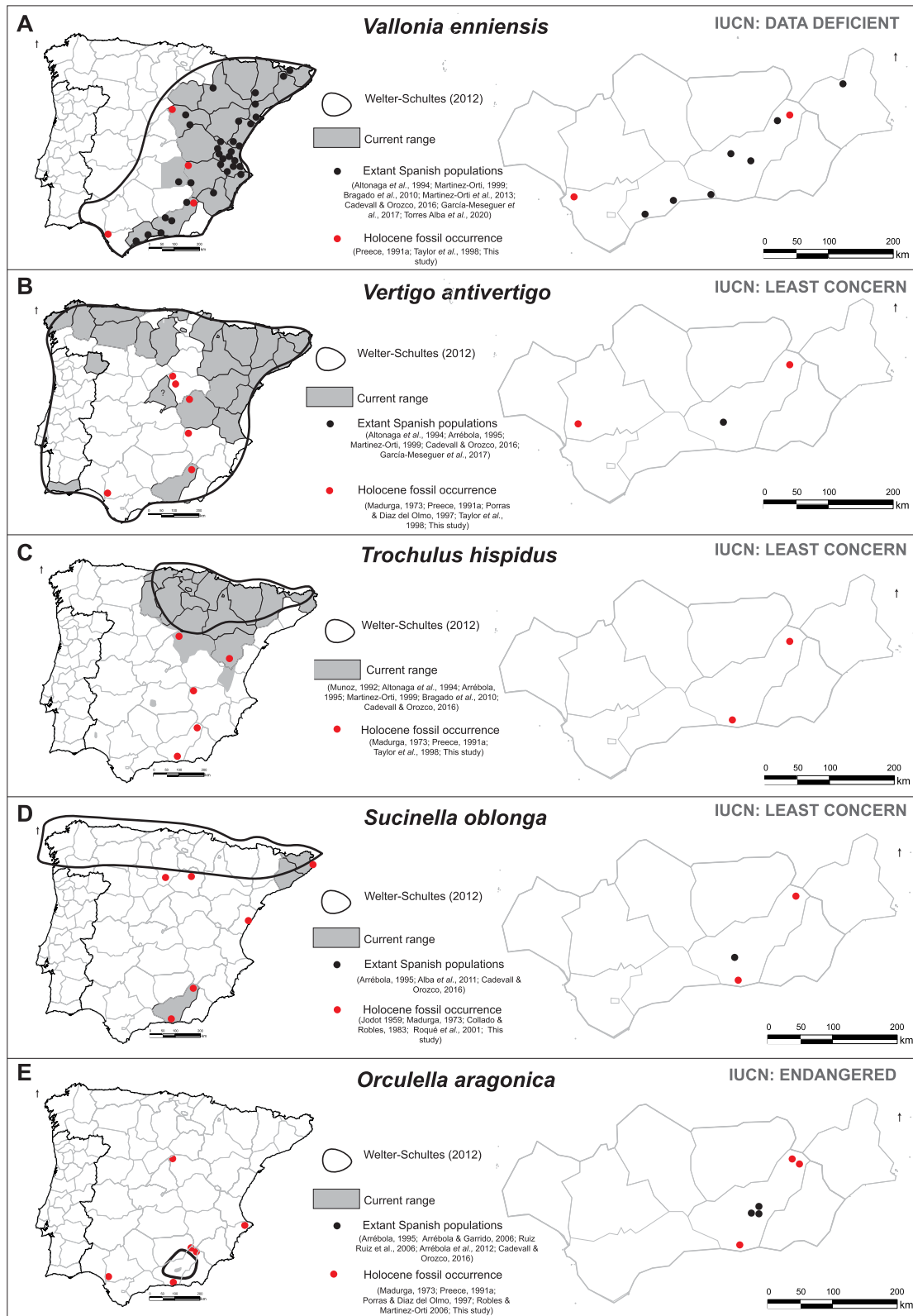


Figure 17. Modern distribution and Holocene occurrences in the Iberian Peninsula of *Vallonia enniensis* (A), *Vertigo antivertigo* (B), *Trochulus hispidus* (C), *Succinella oblonga* (D) and *Orculella aragonica* (E). Extant populations are mapped for southern Iberia. For *Vallonia enniensis*, we reviewed the distribution for Spain. Distribution maps and occurrence records are based on the literature mentioned within the figure.

taxon in Andalusia during the Holocene. The population growth of this taxon is particularly significant during the wet phase of the Middle Holocene (Figs 11–14), and *Vertigo antiveritigo* was still present during the Late Holocene (Fig. 15). In modern times, increased aridification and anthropization in this part of Spain have led to fragmentation and destruction of wetland habitats, making populations of *Vertigo antiveritigo* rare.

Succinella oblonga is relatively rare in the Galera Valley fossil record, with the exception of profile 1 of section GA-IB, where its co-occurrence with *Orculella aragonica* (Fig. 12) suggests that they share the same ecological hygrophilous requirements. However, *Succinella oblonga* appears in several Spanish Holocene deposits (Madurga, 1973). In the Iberian Peninsula, *Succinella oblonga* is a rare succineid (Cadevall & Orozco, 2016) and has been recorded from only a single location in Andalusia, in the Province of Granada (Arrébola, 1995; Ruiz Ruiz et al., 2006) (Fig. 17). The fossil presence of this taxon during the Middle Holocene wet period in the periphery of wetlands in the Galera Valley is consistent with the ecological sensitivity of this taxon in the Mediterranean context in which the temperature could represent a limiting factor. A rare occurrence of this taxon during the Late Holocene is identified at the top of GA-VIII section (Fig. 15). In contrast, *Oxyloma elegans* is very common in the fossil record and its modern distribution is more widespread (Welter-Schultes, 2012; Cadevall & Orozco, 2016). However, its populations are more restricted, especially in southern Spain (Arrébola, 1995; Ruiz Ruiz et al., 2006; Soler et al., 2006). Shells of *Oxyloma elegans* were found in the flood leach and confirm the presence of this species in the vicinity of Galera, whereas *Succinella oblonga* was not detected.

Euconulus fulvus is a Holarctic species occurring in a wide range of habitats but preferring rather humid conditions (Puisségur, 1976). Although this taxon is widespread across the Iberian Peninsula (Cadevall & Orozco, 2016), populations appear restricted and particularly rare in southern Spain (Arrébola, 1995; Martínez-Orti, 1999; Ruiz Ruiz et al., 2006) (Fig. 17). The expansion of this taxon occurred during the first half of the Middle Holocene (Fig. 11), but its presence is much more sporadic during the Late Holocene in the Galera Valley (Fig. 15). Further malacological surveys of modern populations are needed to establish the extent to which its distribution has been fragmented.

At present, *Trochulus hispidus* is widely distributed in the northern half of Iberia (Altonaga et al., 1994; Puente, 1994; Cadevall & Orozco, 2016) (Fig. 17). However, data on its extension in the southern part of Spain seem insufficient because it occurs sporadically in central Spain (Bragado et al., 2010), and a few occurrences, which are considered as introductions, are reported in the province of Huelva (Muñoz, 1992; Arrébola, 1995) (Fig. 17). The population in the Galera Valley from the Middle to the Late Holocene, and fossil occurrences at Padul, Baides and Alcaraz (Fig. 17; Madurga, 1973; Preece, 1991a; Taylor et al., 1998), suggest that the modern distribution of *Trochulus hispidus* in southern Iberia results from the fragmentation of a much larger area of Quaternary extension. Further malacological surveys of modern populations are needed to clarify the current range of the species.

The records of *Mediterranea hydatina* from the Galera Late Holocene sediments (Fig. 15) appear to be from outside the modern range of this species, which includes the more western provinces of Andalusia (Arrébola, 1995). The distribution of this circum-Mediterranean taxon (Fig. 18; Giusti et al., 1995; Welter-Schultes, 2012) is probably poorly known in this part of Andalusia because this species is known to occasionally burrow into the ground (Germain, 1911) and its identification is difficult (Kerney et al., 1999). The discovery of modern shells in the flood debris confirms the presence of *Mediterranea hydatina* in the province of Granada.

Among Hydrobiidae, *Iberhoratia morenoi* is the most abundant species, with a total of more than 15,000 shells collected (GI: 2,107; GIB: 11,641; GII: 2,478; GVIII: 136). In common with numer-

ous hydrobiids (Bole & Velkovrh, 1986; Gloër, 2022a, b), *Iberhoratia morenoi* seems to be a stygobiont species that lives near springs and in adjacent water bodies (Arconada, 2000; Arconada & Ramos, 2003; Arconada et al., 2008). Its occurrence from the Early to the Late Holocene of the Galera Valley successions represents the first fossil record of this endemic snail. Its modern distribution is fragmented and limited to Andalusia, where it occurs in Cádiz, Sevilla, Málaga, Almería and Huelva provinces (Arconada, 2000) (Fig. 18). From a palaeoecological perspective, this taxon, which is assigned a 'vulnerable' status due to its sensitivity to habitat disturbance (Arconada et al., 2008), provides an excellent indicator species of a sustained groundwater supply and a sustained wetland habitat. The several thousand shells extracted from the GIB profile suggest a close connection to the spring. This indication is consistent with the tufa sedimentary facies of section GIB, where groundwater input may have favoured tufa construction. The presence of dozens of shells in Late Holocene deposits, around 500–300 cal. yr BP, questions the current presence of this species in the Galera Valley and requires further investigations to clarify whether *Iberhoratia morenoi* has a continued presence in the area. Its fossil occurrences in the Galera Valley correspond to a more northerly distribution as compared with the modern range (Fig. 18). The negative correlation between *Iberhoratia morenoi* and *Mercuria* sp. frequencies is clearly identified in profile 2 of section GIB (Fig. 13) and distinguishable in GI and GII (basis of GII-MZ1, upper part of GII-MZ2 (Fig. 14) and GI-MZ2a (Fig. 11)); this raises the question of interspecific competition between these two species. Arconada (2000) postulated that both species can be found in the same habitat. However, regarding ecological adaptation, *Mercuria* species tolerate a wide diversity of aquatic habitats (Gloër, Boeters & Walther, 2015; Boeters & Falkner, 2017; Miller, 2021), whereas *Iberhoratia morenoi* prefers muddy habitats and is restricted to the vicinity of springs (Arconada, 2000). Fluctuation in the intensity of groundwater input and the position of springs could locally modify habitat conditions and impact the population dynamics of *Iberhoratia morenoi*. Furthermore, interspecific competition and the role of predators in the population dynamics of freshwater gastropods are irregularly documented, while species that are c. 1 mm in size or less are traditionally not examined (Covich, 2010; Goeppner et al., 2020). Characterizing the position and the relationships of freshwater molluscs in the food web is a prerequisite to examine their ecological niche. The fossil record does not provide extended arguments to test whether this hypothesis can explain temporal variations in malacocenoses.

The currently threatened endemic species *Orculella aragonica* was represented by a fossil population of more than 1,700 individuals throughout profile 1 of section GIB, which covers a time interval of c. 500 years (Supplementary Material Table S2). Its distribution is more scattered in profile 2 of GIB and in GI and GII (Supplementary Material Tables S1, S3). The spatial variation in the occurrence of *Orculella aragonica* suggests the reliance of this species on hygrophilous vegetation in the adjacent spring habitat and confirms its narrow ecological tolerance (Arrébola et al., 2012; Cadevall & Orozco, 2016). *Orculella aragonica* was more widespread in Spain during the Holocene, but its modern distribution is restricted to a few localities, with this species being considered to be recently extinct at two of these (Arrébola, 1995; Robles & Martínez-Orti, 2009) (Fig. 17). The Galera Valley is located 75 km northeast of the last existing populations (Arrébola & Garrido, 2008). However, this orculid was rare during the second half of the Middle Holocene (Fig. 14) and was not recorded during the Late Holocene. The fossil record suggests that from the Middle Holocene onwards, this taxon was no longer present in the Galera Valley, and the absence of shells from the flood debris argues for its modern absence. The Galera population of *Orculella aragonica* provides additional evidence of a much wider range in the Holocene as compared with the modern distribution, and this supports its categorization as endangered in the IUCN Red List of Threatened Species (Arrébola & Garrido, 2008; Robles & Martínez-Orti, 2009).

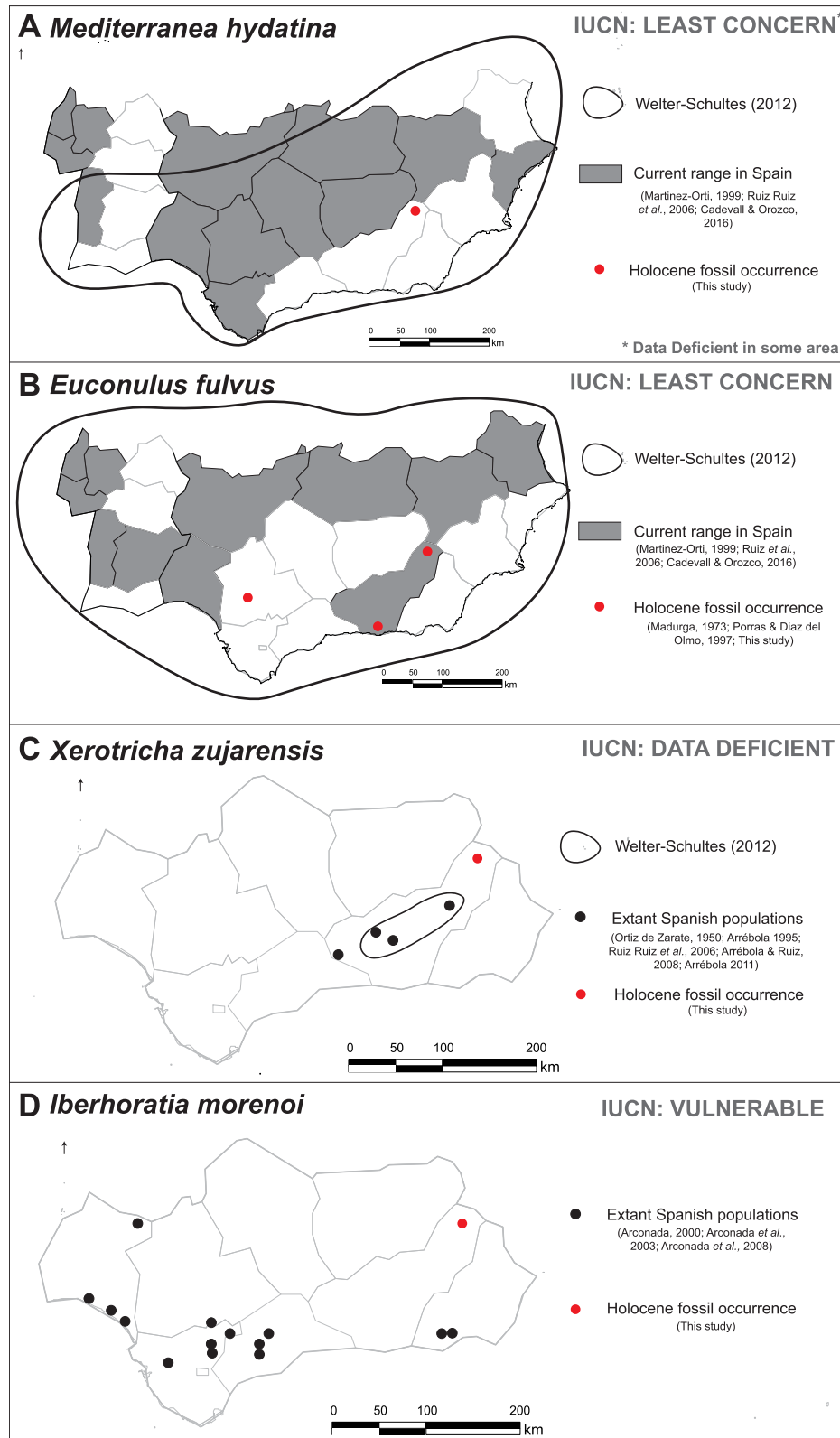


Figure 18. Modern distribution and Holocene occurrences in the southern Iberian Peninsula of *Meditteranea hydatina* (A), *Euconulus fulvus* (B), *Xerotracha zujarensis* (C) and *Iberhoratia morenoi* (D). Distribution maps and occurrence records are based on the literature mentioned within the figure.

The occurrence of *Xerotracha zujarensis* during the second half of the MidHolocene at Galera (Fig. 14) represents the first fossil record of this endemic Andalusian geometrid, whose type locality is located 30 km to the northeast, at Monte Jabalcón (Ortiz de Zarate Lopez, 1950). The modern distribution of *Xerotracha zujarensis* is restricted to four stations in the province of Granada (Arrébola, 1995) in which no living population have been observed since the 1990s (Arrébola & Ruiz Ruiz, 2008; Arrébola, 2011) (Fig. 18). The fossil occurrence in the Galera Valley indicates that its Holocene range was slightly larger than today (Fig. 18). The search for this taxon in fossil deposits could be an opportunity to overcome the lack of data related to its current distribution and to clarify its conservation status.

In summary, the environmental reconstructions inferred from the Galera palaeomalacocenoses are consistent with regional environmental and climatic trends in southeastern Spain. Our comprehensive reconstruction of the Middle Holocene makes it possible to discuss the variability of the records and provides valuable information on hygrophilous species (*Iberhoratia morenoi*, *Orculella aragonica*, *Vallonia enniensis*, *Vertigo antiveritigo* and *Succinella oblonga*) that are now rare in the region. Indeed, the climatic and environmental change across the Holocene at Galera offers insights into the palaeobiogeographic history of terrestrial molluscs prior to the aridification trends and the strong anthropogenic impact on ecosystems. The rich Middle Holocene wet mollusc assemblage at Galera shows strong similarities with faunas of the same period from Morocco (Wackenheim et al., 2020; Depreux et al., 2021; Depreux et al., 2022). However, in Morocco, the modern distribution of faunas has been less studied than in Spain and is therefore not suitable for an extensive palaeobiogeographical discussion. Biostratigraphic information about species occurrences over time offers a valuable basis for discussing and refining the range of the modern fauna and highlights new opportunities for assessing the conservation status of certain species.

CONCLUSIONS

The study of fossil shell assemblages in the Galera Valley revealed valuable information about the ecological response of ecosystems to environmental changes. Molluscan analyses indicate strong river dynamics between 10,000 and 9,000 cal. yr BP, leading to a high stress level and instability of adjacent environments. The transition from the Early to Middle Holocene reflects an environmental continuum of humid conditions (between 8,500 and 8,000 cal. yr BP). Middle Holocene faunas revealed moister conditions with strong development of wetlands, although slight evidence of adjacent drier habitats is recorded from 5,900 cal. yr BP onwards. The taxonomic composition of the mid-Holocene malacofauna, which includes ecologically tolerant and hygrophilous taxa (*Vertigo antiveritigo*, *Zonitoides nitidus* and *Oxyloma elegans*) as well as humidity-sensitive species (*Vallonia enniensis*, *Orculella aragonica*, *Iberhoratia morenoi* and *Succinella oblonga*), underlies the discussion about the micro-local to local variations of habitats. The Late Holocene snapshots from around 3,000 and 300 cal. yr BP indicate rather dry and open biotopes, which are characterized by the appearance of xero-resistant and mesophilous gastropods (*Cochlicella barbara*, *Truncatellina* sp., *Theba pisana* and *Xerotracha zujarensis*). The Holocene palaeoenvironmental scheme deduced from Galera malacocenoses is consistent with the interpretation of sedimentological and stratigraphic data from the valley and with several regional studies. Although rarely used in Spain, these results reinforce the value and reliability of molluscs as a strong palaeoenvironmental proxy to reconstruct Mediterranean landscapes and emphasize their complementary nature with other biological proxies such as pollen.

Holocene fossil nonmarine molluscs represent a strong and promising instrument for a 'palaeobiology conservation' approach. Fossil occurrences from the Galera Valley, for example, of *Xerotracha zujarensis*, *Vertigo antiveritigo*, *Vallonia enniensis*, *Succinella oblonga*, *Euconulus fulvus* and *Orculella aragonica*, shed new light on the past ranges

of these molluscs and aid in the understanding of their fragmented modern distribution. Our study clearly demonstrates that the fossil record is crucial to guide future malacological research in the region and to focus survey efforts on particular species. Compared with their currently restricted and fragmented distribution in Spain, the past distributions of taxa such as *Vallonia enniensis* and *Succinella oblonga* suggest that conservation measures are urgently needed for these hygrophilous taxa whose habitats are increasingly threatened.

Continental molluscs represent a sensitive and widespread group of invertebrates for exploring long-term biogeographical evolution, prior to human impact, which is particularly pronounced in Mediterranean ecosystems. This Andalusian study area is a relevant case example of this approach, as the palaeoenvironmental scheme inferred from fossil malacocenoses provides a striking contrast to the fauna associated with the modern Andalusian environments. The mid-Holocene historical perspective provides a critical point of view to understand how the modern malacofauna of southern Spain has been shaped by environmental and climatic changes. Overall, the fossil mollusc record of the Galera Valley provides the following: (1) crucial baselines for determining the natural variability of ecosystems and their response to environmental changes, (2) data to discuss and clarify the evolution of species distributions and (3) information that can be used for setting conservation priorities (Louys, 2012; Dielt et al., 2015; Barnosky et al., 2017). The fossil mollusc content of the Holocene Galera River sediments constitutes a significant palaeontological resource for the UNESCO Geopark of Granada. By providing an excellent basis for palaeoenvironmental reconstruction and a highly informative benchmark for understanding the distribution and vulnerability of modern faunas, this work highlights the importance of continuing palaeomalacological studies in Spain.

ACKNOWLEDGEMENTS

Q.W. thanks Jonathan Miller for valuable feedback and information on the Spanish Hydrobiidae and Sebastian Torres Alba for providing modern material on Spanish species and helpful information about the Andalusian fauna. Many thanks to Pierre Lozouet for his skilful help with shell photography. Fieldwork and analyses in the Galera Valley were funded by the German Research Foundation (DFG) (grant nos FA 239/22-1 and FA 239/24-1). The authors thank two anonymous reviewers and Michal Horsák for their helpful remarks and Dinarzarde Raheem for her extensive and detailed editing of the MS. Finally, Q.W. is grateful to Florian Jabbour for proofreading and correcting the English.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

AUTHORS' CONTRIBUTIONS

Q.W., N.L.L., C.R., F.J.G.T., D.W., D.F., E.M. and L.H. conducted the fieldwork in Andalusia. Q.W. performed the malacological analyses for GA-IB, C.R. for GA-I, and L.H. and E.M. for GA-II and GA-VIII with the guidance of C.R., D.W. and D.F. Q.W. checked all species identifications and synthesized data analyses and interpretations from all sections. The manuscript was written by Q.W. under the supervision of N.L.L. and J.D., with contributions from all coauthors.

REFERENCES

- ALBESA, J. & ROBLES, F. 2020. Contribución al conocimiento de los moluscos del Pleistoceno Inferior del yacimiento de Barranco León (Cuenca de Guadix-Baza). *Spanish Journal of Palaeontology*, **35**: 125–146.

- ALTONAGA, K., GOMEZ, B., MARTIN, R., PRIETO, C.E., PUENTE, A.I. & RALLO, A. 1994. *Estudio Faunístico y Biogeográfico de los Molluscos terrestres del Norte de la Península Ibérica*. Eusko Legebiltzarra, Vitoria-Gasteiz.
- ANDERSON, R.S., JIMÉNEZ-MORENO, G., CARRIÓN, J.S. & PÉREZ-MARTÍNEZ, C. 2011. Postglacial history of alpine vegetation, fire, and climate from Laguna de Río Seco, Sierra Nevada, southern Spain. *Quaternary Science Reviews*, **30**: 1615–1629.
- ANDRE, J. 1984. Biogeographical studies on the terrestrial molluscs of the bioclimatological region of the Mediterranean parts of the Iberian Peninsula and France. Preliminary results. In: *Worldwide snails. Biogeographical studies on non-marine Mollusca* (A. Solem & A. C. van Bruggen, eds), pp. 207–223. Arch Brill, Leiden.
- APARICIO, M.T. 2001. Malacofauna terrestre del Yacimiento de Cubio Redondo (Matienzo, Cantabria). *Munibe. Antropología-Arkeología*, **53**: 61–66.
- ARAD, Z. 1993. Effect of desiccation on the water economy of terrestrial gastropods of different phylogenetic origins: a prosobranch (*Pomatias glaucus*) and two pulmonates (*Sphincterochila cariosa* and *Helix engaddensis*). *Israel Journal of Zoology*, **39**: 95–104.
- ARCONADA, B. 2000. *Contribución al conocimiento sistemático y filogenético de la familia Hydrobiidae (Mollusca, Prosobranchia) de la Península Ibérica*. Universidad Autónoma de Madrid, Madrid.
- ARCONADA, B., DELICADO, D. & RAMOS, Á.M. 2007. A new genus and two new species of Hydrobiidae (Mollusca, Caenogastropoda) from the Iberian Peninsula. *Journal of Natural History*, **41**: 2007–2035.
- ARCONADA, B. & RAMOS, M.D. 2003. The Ibero-Balearic region: one of the areas of highest Hydrobiidae (Gastropoda, Prosobranchia, Rissoidea) diversity in Europe. *Graellsia*, **59**: 91–104.
- ARCONADA, B., RAMOS, M.A., DELICADO, D. & MORENO, D. 2008. *Iberhoratia morenoi* Arconada, Delicado y Ramos 2007. In: *Libro Rojo de los Invertebrados de Andalucía* (J.M. Barea-Azcón, E. Ballesteros-Duperón & D. Moreno, eds), pp. 508–511. Consejería de Medio Ambiente, Sevilla.
- ARRÉBOLA, J.R. 1995. *Caracoles terrestres (Gastropoda, Stylommatophora) de Andalucía, con especial referencia a las provincias de Sevilla y Cádiz*. Universidad de Sevilla, Sevilla.
- ARRÉBOLA, J.R. 2011. *Xerotracha zujarensis*. The IUCN Red List of Threatened Species 2011: e.T9799A13017655. Available at: <https://www.iucnredlist.org/species/9799/13017655>. Last accessed 18 May 2022.
- ARRÉBOLA, J.R. & GARRIDO, J.A. 2008. *Orculella bulgarica* (Hesse, 1915). In: *Libro Rojo de los invertebrados de Andalucía*. (J. M. Barea-Azcón, E. Ballesteros-Duperón & D. Moreno, eds), pp. 601–603. Consejería de Medio Ambiente, Sevilla.
- ARRÉBOLA, J., RAZKIN, O., GÓMEZ-MOLINER, B. & PÁLLGERGELY, B. 2012. Redescription of *Orculella aragonica* (Westerlund 1897), an Iberian species different from *O. bulgarica* (Hesse 1915) (Gastropoda: Pulmonata: Orculidae). *North-Western Journal of Zoology*, **8**: 292–299.
- ARRÉBOLA, J.R. & RUIZ RUIZ, A. 2008. *Helicella* (?) *zujarensis* Ortiz de Zárate. In: *Libro Rojo de los Invertebrados de Andalucía* (J. M. Barea-Azcón, E. Ballesteros-Duperón & D. Moreno, eds), pp. 1308 Consejería de Medio Ambiente, Sevilla.
- BANDEL, K., REICHERTER, K., DYRSSEN, U. & REISS, S. 2000. Late Neogene lacustrine sedimentary facies and gastropod assemblages (Granada Basin, southern Spain). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, **84**: 111–130.
- BARNOSKY, A.D., HADLY, E.A., GONZALEZ, P., HEAD, J., POLLY, P.D., LAWING, A.M., ERONEN, J.T., ACKERLY, D.D., ALEX, K., BIBER, E., BLOIS, J., BRASHARES, J., CEBALLOS, G., DAVIS, E., DIETL, G.P., DIRZO, R., DOREMUS, H., FORTELIUS, M., GREENE, H.W., HELLMANN, J., HICKLER, T., JACKSON, S.T., KEMP, M., KOCH, P.L., KREMEN, C., LINDSEY, E.L., LOOY, C., MARSHALL, C.R., MENDENHALL, C., MULCH, A., MYCHAJLIV, A.M., NOWAK, C., RAMAKRISHNAN, U., SCHNITZLER, J., DAS SHRESTHA, K., SOLARI, K., STEGNER, L., STEGNER, M.A., STENSETH, N.C., WAKE, M.H. & ZHANG, Z. 2017. Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science*, **355**: eaah4787.
- BELLIN, N., VANACKER, V. & DE BAETS, S. 2013. Anthropogenic and climatic impact on Holocene sediment dynamics in SE Spain: a review. *Quaternary International*, **308–309**: 112–129.
- BENNETT, K.D. 2009. PSIMPOLL 4.27 and PSCOMB 1.03. C programs for plotting pollen diagrams and analysing pollen data. 4.27 Edn. Available at: <http://chrono.qub.ac.uk>. Last accessed 17 March 2022.
- BLANCA, G., CABEZUDO, B., CUETO, M., SALAZAR, C. & MORALES, T.O.R.R.E.S.C. 2011. *Flora Vascular de Andalucía Oriental*. Universidades de Almería, Granada.
- BOLE, J. & VELKOVIRH, F. 1986. Mollusca from continental subterranean aquatic habitats. In: *Stygofauna mundi. A faunistic, distributional and ecological synthesis of the world fauna inhabiting subterranean waters* (L. Botosaneanu, ed.), pp. 177–208. E.J. Brill, Leiden.
- BUDSKY, A., SCHOLZ, D., WASSENBURG, J.A., MERTZ-KRAUS, R., SPÖTL, C., RIECHELMANN, D.F.C., GIBERT, L., JOCHUM, K.P. & ANDREAE, M.O. 2019. Speleothem $\delta^{13}\text{C}$ record suggests enhanced spring/summer drought in south-eastern Spain between 9.7 and 7.8 ka—a circum-western Mediterranean anomaly? *Holocene*, **29**: 1113–1133.
- BOETERS, H.D. & FALKNER, G. 2017. The genus *Mercuria* Boeters, 1971 in France (Gastropoda: Caenogastropoda: Hydrobiidae). West-European Hydrobiidae, part 13. *Zoosystema*, **39**: 227–261.
- BRAGADO, M.D., ARAUJO, R. & APARICIO, M.T. 2010. *Atlas y libro rojo de los moluscos de Castilla-La Mancha*. Organismo Junta de Comunidades de Castilla-La Mancha, Guadalajara.
- BROS, V., TORRE, I. & SANTOS, X. 2016. Uncovering the environmental factors that influence diversity patterns of Mediterranean terrestrial Gastropod communities: a useful tool for conservation. *Ecological Research*, **31**: 39–47.
- CADEVAL, J. & OROZCO, A. 2016. *Caracoles y Babosas de la Península Ibérica y Baleares*. Omega, Barcelona.
- CARRIÓN, J.S. 2002. Patterns and processes of late quaternary environmental change in a montane region of southwestern Europe. *Quaternary Science Reviews*, **21**: 2047–2066.
- CARRIÓN, J.S., FERNÁNDEZ, S., JIMÉNEZ-MORENO, G., FAUQUETTE, S., GIL-ROMERA, G., GONZÁLEZ-SAMPÉRIZ, P. & FINLAYSON, C. 2010. The historical origins of aridity and vegetation degradation in southeastern Spain. *Journal of Arid Environments*, **74**: 731–736.
- CARRIÓN, J.S., SÁNCHEZ-GÓMEZ, P., MOTA, J.F., YLL, R. & CHAÍN, C. 2003. Holocene vegetation dynamics, fire and grazing in the Sierra de Gádor, southern Spain. *Holocene*, **13**: 839–849.
- COLLADO, M.Á. & ROBLES, F. 1983. Estudio de las asociaciones de moluscos de la turbera holocena de Torreblanca (Castellón). *Mediterranea*, **1**: 105–140.
- COLONESE, A.C., ZANCHETTA, G., FALLICK, A.E., MANGANELLI, G., SAÑA, M., ALCADÉ, G. & NEBOT, J. 2013. Holocene snail shell isotopic record of millennial-scale hydrological conditions in western Mediterranean: data from Bauma del Serrat del Pont (NE Iberian Peninsula). *Quaternary International*, **303**: 43–53.
- COMBOURIEU NEBOUT, N., PEYRON, O., DORMOY, I., DESPRAT, S., BEAUDOUIN, C., KOTTHOFF, U. & MARRET, F. 2009. Rapid climatic variability in the west Mediterranean during the last 25 000 years from high resolution pollen data. *Climate of the Past*, **5**: 503–521.
- COVICH, A.P. 2010. Winning the biodiversity arms race among freshwater gastropods: competition and coexistence through shell variability and predator avoidance. *Hydrobiologia*, **653**: 191–215.
- DELICADO, D., MACHORDOM, A. & RAMOS, M.A. 2012. Underestimated diversity of hydrobiid snails. The case of *Pseudamnicola* (Corrosella) (Mollusca: Caenogastropoda: Hydrobiidae). *Journal of Natural History*, **46**: 25–89.
- DELICADO, D. & RAMOS, M.A. 2012. Morphological and molecular evidence for cryptic species of springsnails genus *Pseudamnicola* (Corrosella) (Mollusca, Caenogastropoda, Hydrobiidae). *ZooKeys*, **190**: 55–79.
- DEMENOCAL, P., ORTIZ, J., GUILDERSON, T., ADKINS, J., SARN-THAIN, M., BAKER, L. & YARUSINSKY, M. 2000. Abrupt onset and termination of the African humid period. *Quaternary Science Reviews*, **19**: 347–361.
- DEPREUX, B., BERGER, J.F., LEFÈVRE, D., WACKENHEIM, Q., PONEL, V.A., VINAI, S., DEGEAI, J.P., HARRADJI, A.E., BOUDAD, L., LALIBERTÉ, S.S., MICHEL, K. & LOZOUET, N.L. 2022. First fluvial archive of the 8.2 and 7.6–7.3 ka events in North Africa (Charef River, High Plateaus, NE Morocco). *Scientific Reports*, **12**: 1–15.

- DEPREUX, B., LEFÈVRE, D., BERGER, J.F., SEGAOUI, F., BOUDAD, L., EL HARRADJI, A., DEGEAI, J.P. & LIMONDIN-LOZOUET, N. 2021. Alluvial records of the African Humid Period from the NW African highlands (Moulouya basin, NE Morocco). *Quaternary Science Reviews*, **255**: 106807.
- DIETL, G.P., KIDWELL, S.M., BRENNER, M., BURNEY, D.A., FLESSA, K.W., JACKSON, S.T. & KOCH, P.L. 2015. Conservation paleobiology: leveraging knowledge of the past to inform conservation and restoration. *Annual Review of Earth and Planetary Sciences*, **43**: 79–103.
- DR RITA, F., MICHELANGELI, F., CELANT, A. & MAGRI, D. 2022. Sign-switching ecological changes in the Mediterranean Basin at 4.2 ka BP. *Global and Planetary Change*, **208**: 103713.
- EL HAMOUTI, N. & GIBERT, L. 2012. Contribution to the plio-Pleistocene paleolimnology of the Baza basin (SE Spain) using diatoms. *Quaternaire*, **23**: 253–260.
- EVANS, J.G. 1972. *Land snails in archaeology. With special reference to the British Isles*. Seminar Press, London.
- FAUST, D. & WOLF, D. 2017. Interpreting drivers of change in fluvial archives of the Western Mediterranean—a critical view. *Earth-Science Reviews*, **174**: 53–83.
- FLETCHER, W.J., DEBRET, M. & GOÑI, M.E.S. 2012. Mid-Holocene emergence of a low-frequency millennial oscillation in western Mediterranean climate: implications for past dynamics of the North Atlantic atmospheric westerlies. *Holocene*, **23**: 153–166.
- FLETCHER, W.J. & ZIELHOFER, C. 2013. Fragility of Western Mediterranean landscapes during Holocene rapid climate changes. *Catena*, **103**: 16–29.
- FORMAN, S.L., HOCKADAY, W., LIANG, P. & RAMSEY, A. 2021. Radiocarbon age offsets, ontogenetic effects, and potential old carbon contributions from soil organic matter for pre-bomb and modern detritivorous gastropods from central Texas, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **583**: 110671.
- FRODOVÁ, J., HÁJKOVÁ, P. & HORSÁK, M. 2018. Effect of sample size and resolution on palaeomalacological interpretation: a case study from holocene calcareous-fen deposits. *Journal of Quaternary Science*, **33**: 68–78.
- FYFE, R.M., WOODBRIDGE, J., PALMISANO, A., BEVAN, A., SHENAN, S., BURJACHS, F., LEGARRA HERRERO, B., GARCÍA PUCHOL, O., CARRIÓN, J.S., REVELLES, J. & ROBERTS, C.N. 2019. Prehistoric palaeodemographics and regional land cover change in eastern Iberia. *Holocene*, **29**: 799–815.
- GARCÍA-MESEGUER, A.J., ESTEVE, M.A., ROBLEDANO, F. & MIÑANO, J. 2017. *Atlas y Libro Rojo de los Moluscos Continentales de la Región de Murcia*. Comunidad Autónoma de la Región de Murcia, Murcia.
- GARRIDO, J.A., ARRÉBOLA, J.R. & BERTRAND, M. 2005. Extant populations of *Orbulella bulgarica* (Hesse, 1915) in Iberia. *Journal of Conchology*, **38**: 653–662.
- GASULL, L. 1975. Fauna malacológica terrestre del sudeste ibérico. *Bolletí de la Societat d'Història Natural de les Balears*, **16**: 23–83.
- GERMAIN, L. 1911. Biospeologica XVIII. Mollusques. *Archives de Zoologie Expérimentale et Générale*, **5**: 229–256.
- GIL-GARCÍA, M.J., RUIZ RUIZ-ZAPATA, B., ORTIZ, J.E., TORRES, T., ROS, M., RAMALLO, S., LÓPEZ-CILLA, I., GALÁN, L.A., SÁNCHEZ-PALENCIA, Y., MANTECA, I., RODRÍGUEZ-ESTRELLA, T., BLÁZQUEZ, A. & GÓMEZ-BORREGO, Á. 2022. Paleoenvironmental variability and anthropic influence during the last 7300 years in the western Mediterranean based on the pollen record of Cartagena Bay, SE Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **589**: 110839.
- GIL-ROMERA, G., CARRIÓN, J.S., MCCLURE, S.B., SCHMICH, S. & FINLAYSON, C. 2009. Holocene vegetation dynamics in Mediterranean Iberia: historical contingency and climate-human interactions. *Journal of Anthropological Research*, **65**: 271–285.
- GITTENBERGER, E. 1998. Once more on the range of *Vallonia enniensis*. *Journal of Conchology*, **33**: 185–186.
- GIUSTI, F. & MANGANELLI, G. 1984. Relationships between geological land evolution and present distribution of terrestrial gastropods in the western Mediterranean area. In: *World-wide snails. Biogeographical studies on non-marine Mollusca* (A. Solem & A. C. van Bruggen, eds), pp. 70–90. E.J. Brill, Leiden.
- GIUSTI, F., MANGANELLI, G. & SCHEMBRI, P.J. 1995. *The non-marine molluscs of the Maltese Islands*. Monografie di Museo Regionale di Scienze Naturali, Torino.
- GLOËR, P. 2019. *The freshwater gastropods of the West-Palaearctis. Vol. 1. Fresh- and brackish waters except spring and subterranean snails*. Peter Glöer ed., Hetlingen.
- GLÖER, P. (ed.) 2022a. *The freshwater gastropods of the West-Palaearctis. Vol. 2. Moitessieridae, Bythinellidae, Stenothyridae*. Biodiversity Research Lab, Hetlingen, Germany.
- GLOËR, P. (ed.) 2022b. *The freshwater gastropods of the West-Palaearctis. Vol. 3. Hydrobiidae*. Biodiversity Research Lab, Hetlingen, Germany.
- GLÖER, P., BOETERS, H.D. & WALTHER, F. 2015. Species of the genus *Mercuria* Boeters, 1971 (Caenogastropoda: Truncatelloidea: Hydrobiidae) from the European Mediterranean region, Morocco and Madeira, with descriptions of new species. *Folia Malacologica*, **23**: 279–291.
- GOEPPNER, S.R., ROBERTS, M.E., BEATY, L.E. & LUTTBEG, B. 2020. Freshwater snail responses to fish predation integrate phenotypic plasticity and local adaptation. *Aquatic Ecology*, **54**: 309–322.
- GÓMEZ-ZOTANO, J., ALCÁNTARA-MANZANARES, J., MARTÍNEZ-IBARRA, E. & OLMEDO-COBO, J.A. 2016. Applying the technique of image classification to climate science: the case of Andalusia (Spain). *Geographical Research*, **54**: 461–470.
- GOODFRIEND, G.A. 1992. The use of land snail shells in paleoenvironmental reconstruction. *Quaternary Science Reviews*, **11**: 665–685.
- GRANAI, S., DABKOWSKI, J., HÁJKOVÁ, P., NATON, H.G. & BROU, L. 2020. Holocene palaeoenvironments from the Direndall tufa (Luxembourg) reconstructed from the molluscan succession and stable isotope records. *Holocene*, **30**: 982–995.
- GRANAI, S. & WACKENHEIM, Q. 2022. La datation radiocarbone sur coquilles de mollusques continentaux: quelles limites et quels usages? *Bulletin de l'APRAB*, **8**: 21–33.
- GUTIÉRREZ ZUGASTI, F.I., CUENCA SOLANA, D. & GONZALES MORALES, M.R. 2015. *La investigación arqueomalacológica en la Península Ibérica: nuevas aportaciones*. Ediciones Universidad Cantabria, Santander.
- HIDALGO-MUÑOZ, J.M., ARGÜESO, D., GÁMIZ-FORTIS, S.R., ESTEBAN-PARRA, M.J. & CASTRO-DÍEZ, Y. 2011. Trends of extreme precipitation and associated synoptic patterns over the southern Iberian Peninsula. *Journal of Hydrology*, **409**: 497–511.
- HORSÁK, M., LIMONDIN-LOZOUET, N., GRANAI, S., DABKOWSKI, J., DIVÍŠEK, J. & HÁJKOVÁ, P. 2020. Colonisation dynamic and diversity patterns of Holocene forest snail fauna across temperate Europe: the imprint of palaeoclimate changes. *Quaternary Science Reviews*, **240**: 106367.
- ILVONEN, L., LÓPEZ-SÁEZ, J.A., HOLMSTRÖM, L., ALBA-SÁNCHEZ, F., PÉREZ-DÍAZ, S., CARRIÓN, J.S., RAMOS-ROMÁN, M.J., CAMUERA, J., JIMÉNEZ-MORENO, G., RUHA, L. & SEPPÄ, H. 2022. Spatial and temporal patterns of Holocene precipitation change in the Iberian Peninsula. *Boreas*, **51**: 776–792.
- JACKIEWICZ, M. 1998. European species of the family Lymnaeidae (Gastropoda: Pulmonata: Basommatophora). *Genus*, **9**: 1–93.
- JALUT, G., ESTEBAN AMAT, A., BONNET, L., GAUQUELIN, T. & FONTUGNE, M. 2000. Holocene climatic changes in the Western Mediterranean, from south-east France to south-east Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **160**: 255–290.
- JODOT, P. 1958. *Les faunes des mollusques continentaux réparties dans le sud-est de l'Espagne entre le Miocene supérieur et le Quaternaire*, Vol. 17. Memorias y Comunicaciones del Instituto Geológico, Barcelona.
- JURIČKOVÁ, L., HORSÁK, M., CAMERON, R., HYLANDER, K., MÍKOVCOVÁ, A., HLAVÁČ, J.Č. & ROHOVEC, J. 2008. Land snail distribution patterns within a site: the role of different calcium sources. *European Journal of Soil Biology*, **44**: 172–179.
- JURIČKOVÁ, L., HORSÁK, M., HORÁČKOVÁ, J., ABRAHAM, V. & LOŽEK, V. 2014. Patterns of land-snail succession in Central Europe over the last 15,000 years: main changes along environmental, spatial and temporal gradients. *Quaternary Science Reviews*, **93**: 155–166.
- KERNEY, M.P., CAMERON, R.A.D. & BERTRAND, A. 1999. *Guide des escargots et limaces d'Europe*. Delachaux et Nieslé, Paris.
- KOWALEWSKI, M. 2017. The youngest fossil record and conservation biology: holocene shells as eco-environmental recorders. In: *Conservation*

- paleobiology: using the past to manage for the future*, Vol. 15 (G. P. Dielt & K. W. Flessa, eds), pp. 7–29. University of Chicago Press, Chicago.
- LILLIOS, K.T., BLANCO-GONZÁLEZ, A., DRAKE, B.L. & LÓPEZ-SÁEZ, J.A. 2016. Mid-late Holocene climate, demography, and cultural dynamics in Iberia: a multi-proxy approach. *Quaternary Science Reviews*, **135**: 138–153.
- LIMONDIN-LOZOUET, N. 2002. Les mollusques continentaux. In: *Géologie de la Préhistoire* (J.-C. Miskovsky, ed.), pp. 773–784. GEOPRE, Perpignan.
- LIMONDIN-LOZOUET, N. 2020. Diversité et répartition des faunes de mollusques continentaux de France : l'héritage du Quaternaire. *Naturae*, **8**: 131–141.
- LIMONDIN-LOZOUET, N., HADDOUMI, H., LEFÈVRE, D., GHAMIZI, M., AOURAGHE, H. & SALEL, T. 2013. Holocene molluscan succession from NE Morocco: palaeoenvironmental reconstruction and biogeographical implications. *Quaternary International*, **302**: 61–76.
- LIMONDIN-LOZOUET, N. & PREECE, R.C. 2014. Quaternary perspectives on the diversity of land snail assemblages from northwestern Europe. *Journal of Molluscan Studies*, **80**: 224–237.
- LLOVERAS, L., NADAL, J., ARGÜELLES, P.G., FULLOLA, J.M. & ESTRADA, A. 2011. The land snail midden from Balma del Gai (Barcelona, Spain) and the evolution of terrestrial gastropod consumption during the late Palaeolithic and Mesolithic in eastern Iberia. *Quaternary International*, **244**: 37–44.
- LOPEZ SORIANO, J., QUIÑONERO SALGADO, S. & GLÖER, P. 2016. Presence of *Radix lagotis* (Schrank, 1803) (Gastropoda: Lymnaeidae) in the NE Iberian Peninsula. *Spira*, **6**: 89–90.
- LOUYS, J. 2012. *Paleontology in ecology and conservation* (J. Louys, ed.). Springer, Berlin.
- LOŽEK, V. 1986. Mollusca analysis. In: *Handbook of Holocene palaeoecology and palaeohydrology* (B. E. Berglund, ed.), pp. 729–740. Wiley, Chichester.
- MADURGA, M.C. 1973. Los gasterópodos dulceacuícolas y terrestres del Cuaternario español. *Boletín de la Real Sociedad Española de Historia Natural. Sección Geológica*, **71**: 43–165.
- MAGNIN, F. & BONNET, S. 2014. Une succession malacologique du pléniglaciaire moyen et du postglaciaire à Aix-en-Provence (France): éléments de datation, taphonomie des assemblages et paléoenvironnements. *Quaternaire*, **25**: 163–185.
- MAGNIN, F., BONNET, S. & CENZON-SALVAYRE, C. 2022. Land snail fauna and Holocene environmental changes in Mediterranean France: a digest from three representative sedimentary sequences. *Quaternary Science Reviews*, **276**: 107303.
- MARTIN, K. & SOMMER, M. 2004. Effects of soil properties and land management on the structure of grassland snail assemblages in SW Germany. *Pedobiologia*, **48**: 193–203.
- MARTIN-SERRANO, A. 2005. *Mapa Geomorfológico de España y del Margen Continental a escala 1: 1.000. 000*. Instituto Geológico y Minero de España, Madrid.
- MARTÍNEZ-ORTÍ, A. 1999. *Moluscos terrestres testáceos de la Comunidad Valenciana*. Universitat de València, València (digital version by Proquest LLC 2014).
- MARTÍNEZ-ORTÍ, A. 2008. Taxonomical clarification of the Iberian endemic *Helicella (Xerotricha) mariae* Gasull, 1972 (Gastropoda, Pulmonata Hygromiidae). *Basteria*, **72**: 147–154.
- MARTINEZ-ORTI, A., PEREZ FERRER, A., LOPEZ-ALABAU, A. & ARCO, M.C. 2013. Nuevos hallazgos de poblaciones de *Vertigo moulinsiana* (Dupuy, 1849) (Pulmonata: Vertiginidae) en las provincias de Castellón, Cuenca y Teruel (España). *Noticiario SEM*, **59**: 60–63.
- MARTÍNEZ-ORTÍ, A., RUIZ RUIZ-SÁNCHEZ, F.J., MANSINO, S. & ROBLES, F. 2015. Fauna de moluscos y mamíferos de un nivel fosilífero en las inmediaciones del yacimiento mesolítico-neolítico de Cingle del Mas Cremat (Portell de Morella, Castellón). In: *Preses petites i grups humans en el passat. II Jornades d'arqueozoologia* (A. Sanchis Serra, J.L. Pascual Benito & J.E. Aura Tortosa, eds), pp. 245–260. Museu de Prehistòria de València, València.
- MAYEWSKI, P.A., ROHLING, E.E., STAGER, J.C., KARLÉN, W., MAASCH, K.A., MEEKER, L.D., MEYERSON, E.A., GASSE, F., VAN KREVELD, S., HOLMGREN, K., LEE-THORP, J., ROSQVIST, G., RACK, F., STAUBWASSER, M., SCHNEIDER, R.R. & STEIG, E.J. 2004. Holocene climate variability. *Quaternary Research*, **62**: 243–255.
- MÉDAIL, F., MONNET, A.C., PAVON, D., NIKOLIC, T., DIMOPOULOS, P., BACCHETTA, G., ARROYO, J., BARINA, Z., ALBASSATNEH, M.C., DOMINA, G., FADY, B., MATEVSKI, V., MIFSUD, S. & LERICHE, A. 2019. What is a tree in the Mediterranean basin hotspot? A critical analysis. *Forest Ecosystems*, **6**: 1–19.
- MÉDAIL, F. & QUEZÉL, P. 1999. Biodiversity hotspots in the Mediterranean Basin: setting global conservation priorities. *Conservation Biology*, **13**: 1510–1513.
- MESA-FERNÁNDEZ, J.M., JIMÉNEZ-MORENO, G., RODRIGO-GÁMIZ, M., GARCÍA-ALIX, A., JIMÉNEZ-ESPEJO, F.J., MARTÍNEZ-RUIZ RUIZ F., SCOTT ANDERSON, R., CAMUERA, J. & RAMOS-ROMÁN, M.J. 2018. Vegetation and geochemical responses to holocene rapid climate change in the Sierra Nevada (southeastern Iberia): the Laguna Hondera record. *Climate of the Past*, **14**: 1687–1706.
- MILLER, J. 2021. *Systematics, biogeography and evolutionary patterns of the Hydrobiidae family (Mollusca: Caenogastropoda)*. Universidad Autónoma de Madrid, Madrid.
- MORELLÓN, M., ARANBARRI, J., MORENO, A., GONZÁLEZ-SAMPÉRIZ, P. & VALERO-GARCÉS, B.L. 2018. Early Holocene humidity patterns in the Iberian Peninsula reconstructed from lake, pollen and speleothem records. *Quaternary Science Reviews*, **181**: 1–18.
- MORENO NUÑO, R. 1995a. Arqueomalacofaunas de la Península Ibérica: un ensayo de síntesis. *Complutum*, **6**: 353–382.
- MORENO NUÑO, R. 1995b. Catálogo de malacofaunas de la península Ibérica. *Archaeofauna*, **4**: 143–272.
- MORENO-RUEDA, G. 2014. Distribution of arid-dwelling land snails according to dryness. *Journal of Arid Environments*, **103**: 80–84.
- MORENO SAIZ, J.C., IRIONDO ALEGRÍA, J.M., MARTÍNEZ GARCÍA, F., MARTÍNEZ RODRÍGUEZ, J. & SALAZAR MENDÍAS, C. 2019. *Atlas y Libro Rojo de la Flora Vascular Amenazada de España*. Adenda 2017. SEBicoP, Madrid.
- MUÑOZ, A.B. 1992. *Gasterópodos terrestres (Mollusca, Gastropoda, Pulmonata) de Cáceres, Badajoz y Huelva*. Universidad Complutense de Madrid, Madrid.
- MURELAGA, X., ORTEGA, L.A., SANCHEZ, C., MUÑOZ, A., OSÁCAR, C. & LARRAZ, M. 2012. Succession and stable isotope composition of gastropods in Holocene semi-arid alluvial sequences (Bardeas Reales, Ebro Basin, NE Spain): palaeoenvironmental implications. *Holocene*, **22**: 1047–1060.
- ORTIZ DE ZARATE Y LOPEZ, A. 1950. Observaciones anatómicas y posición sistemática de varios helicidos españoles III. *Boletín de la Real Sociedad Española de Historia Natural. Sección Biológica*, **48**: 21–84.
- ORTIZ, J.E., TORRES, T., DELGADO, A., JULIÀ, R., LUCINI, M., LLAMAS, F.J., REYES, E., SOLER, V. & VALLE, M. 2004. The palaeoenvironmental and palaeohydrological evolution of Padul Peat Bog (Granada, Spain) over one million years, from elemental, isotopic and molecular organic geochemical proxies. *Organic Geochemistry*, **35**: 1243–1260.
- PALLARY, P. 1922. Notes de zoogéographie-nord-Africaine. *Bulletin de la Société Géologique de France*, **21**: 247–252.
- PEÑA. 1985. La depresión de Guadix-Baza. *Estudios Geológicos*, **41**: 33–46.
- PÉREZ-OBOL, R., JALUT, G., JULIÀ, R., PÉLACHS, A., IRIARTE, M.J., OTTO, T. & HERNÁNDEZ-BELOQUI, B. 2011. Mid-holocene vegetation and climatic history of the Iberian Peninsula. *Holocene*, **21**: 75–93.
- PIGATI, J.S., MCGEEHIN, J.P., MUHS, D.R. & BETTIS, E.A. 2013. Radiocarbon dating late quaternary loess deposits using small terrestrial gastropod shells. *Quaternary Science Reviews*, **76**: 114–128.
- PLA-PUEYO, S., VISERAS, C., SORIA, J.M., TENT-MANCLÚS, J.E. & ARRIBAS, A. 2011. A stratigraphic framework for the pliocene-Pleistocene continental sediments of the Guadix Basin (Betic Cordillera, S. Spain). *Quaternary International*, **243**: 16–32.
- PORRAS CREVILLEN, A.I. & DIAZ DEL OLMO, F. 1997. Malacofauna del travertino de Constantina: primeros datos paleoambientales. *Estudios de Geografía Física*, **26**: 111–113.
- PREECE, R.C. 1991a. Radiocarbon-dated molluscan successions from the Holocene of Central Spain. *Journal of Biogeography*, **18**: 409.

- PREECE, R.C. 1991b. Mapping snails in time: the prospect of elucidating the historical biogeography of the European malacofauna. In: *Proceedings of the Tenth International Malacological Congress*, 477–479, Tübingen.
- PREECE, R.C. 1997. The spatial response of non-marine Mollusca to past climate changes. In: *Past and future rapid environmental changes* (B. Huntley, W. Cramer, A.V. Morgan, H.C. Prentice & J.R.M. Allen, eds), pp. 163–177. Springer, Berlin.
- PREECE, R.C. 1998. Molluscan conservation: the importance of the fossil record. *Journal of Conchology*, **2**: 155–164.
- PUENTE, A.I. 1994. *Estudio taxonómico y biogeográfico de la superfamilia Helicoidea Rafinesque, 1815 (Gastropoda: Pulmonata: Stylommatophora) de la Península Ibérica e Islas Baleares*. Sarriena Auzoa Universidad del país Vasco.
- PUISSÉGUR, J.J. 1976. *Mollusques continentaux quaternaires de Bourgogne*. Mémoires géologiques de l'université, Dijon.
- RAMOS-ROMÁN, M.J., JIMÉNEZ-MORENO, G., CAMUERA, J., GARCÍA-ALIX, A., SCOTT ANDERSON, R., JIMÉNEZ-ESPEJO, F.J., SACHSE, D., TONEY, J.L., CARRIÓN, J.S., WEBSTER, C. & YANES, Y. 2018. Millennial-scale cyclical environment and climate variability during the Holocene in the western Mediterranean region deduced from a new multi-proxy analysis from the Padul record (Sierra Nevada, Spain). *Global and Planetary Change*, **168**: 35–53.
- RAMSEY, C.B. 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon*, **51**: 337–360.
- REED, J.M., STEVENSON, A.C. & JUGGINS, S. 2001. A multi-proxy record of holocene climatic change in southwestern Spain: the Laguna de Medina, Cádiz. *Holocene*, **11**: 707–719.
- REIMER, P.J., AUSTIN, W.E.N., BARD, E., BAYLISS, A., BLACKWELL, P.G., BRONK RAMSEY, C., BUTZIN, M., CHENG, H., EDWARDS, R.L., FRIEDRICH, M., GROOTES, P.M., GILDERSON, T.P., HAJDAS, I., HEATON, T.J., HOGG, A.G., HUGHEN, K.A., KROMER, B., MANNING, S.W., MUSCHELER, R., PALMER, J.G., PEARSON, C., VAN DER PLICHT, J., REIMER, R.W., RICHARDS, D.A., SCOTT, E.M., SOUTHON, J.R., TURNEY, C.S.M., WACKER, L., ADOLPHI, F., BÜNTGEN, U., CAPANO, M., FAHRNI, S.M., FOGTMANN-SCHULZ, A., FRIEDRICH, R., KÖHLER, P., KUDSK, S., MIYAKE, F., OLSEN, J., REINIG, F., SAKAMOTO, M., SOOKDEO, A. & TALAMO, S. 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon*, **62**: 725–757.
- RICHTER, C., WOLF, D., WALTHER, F., MENG, S., SAHAKYAN, L., HOVAKIMYAN, H., WOLPERT, T., FUCHS, M. & FAUST, D. 2020. New insights into Southern Caucasian glacial-interglacial climate conditions inferred from quaternary gastropod fauna. *Journal of Quaternary Science*, **35**: 634–649.
- ROBLES, F. 1989. Moluscos continentales del Plio-Pleistoceno de la cuenca de Guadix-Baza. *Trabajos Neógeno-Cuaternario*, **11**: 127–138.
- ROBLES, F. & MARTÍNEZ-ORTÍ, A. 2009. Moluscos continentales de los alrededores de Molina de Aragón (Guadalajara, España), con notas sobre *Orculella bulgarica* (Hesse, 1915) (Gastropoda, Orculidae). *Iberus*, **27**: 99–105.
- ROQUÉ PAU, C., BUXÓ, L.P. & DÍAZ DEL OLMO, F. 2001. El Holoceno medio palustre de la llanura litoral del río Ter (Baix Empordà, Girona). *Revista C&G*, **15**: 87–101.
- ROSILLO, J.F., GUILLÉN-MONDÉJAR, F., ALIAS, M.A., ARRUFAT, L. & SÁNCHEZ, A. 2017. Lugares de interés geológico y usos tradicionales de la geodiversidad en la Comarca de Huéscar (Granada), como base para nuevas propuestas de espacios naturales protegidos y geoparques. In: *Patrimonio geológico, gestionando la parte abiótica del patrimonio natural* (I. Carcavilla, J.D. Macías, J. Giménez, A.H. Orús, M.M. Ganuzas, J. Vegas & A. Rodríguez, eds), pp. 345–351. Instituto Geológico y Minero de España, Madrid.
- RUIZ RUIZ, A., CÁRCABA POZO, Á., PORRAS CREVILLEN, A.I. & ARRÉBOLA BURGOS, J.R. 2006. *Caracoles terrestres de Andalucía. Guía y manual de identificación. Consejería de Medio Ambiente de la Junta de Andalucía*. Fundación Gypaetus, Sevilla.
- RUIZ RUIZ-COBO, J. 2015. Gasterópodos continentales en yacimientos arqueológicos de los valles Asón y Miera (Cantabria) durante el Holoceno: aspectos paleo-ecológicos. In: *La Investigación Arqueomalacológica en la Península Ibérica: Nuevas Aportaciones* (I. G. Zugasti, D. C. M. Solana & M. R. González, eds), pp. 43–53.
- SACCHI, C.F. 1965. Ecological and historical bases for a study of the Iberian terrestrial mollusca. In: *Proceedings of the First European Malacologists Congress*, pp. 243–257, London.
- SCHIRRMACHER, J., KNEISEL, J., KNITTER, D., HAMER, W., HINZ, M., SCHNEIDER, R.R. & WEINELT, M. 2020. Spatial patterns of temperature, precipitation, and settlement dynamics on the Iberian Peninsula during the Chalcolithic and the Bronze Age. *Quaternary Science Reviews*, **233**: 106220.
- SCHNIEBS, K., GLOËR, P., VINARSKI, M.V. & HUNSDOERFER, A.K. 2013. Intraspecific morphological and genetic variability in *Radix balthica* (Linnaeus 1758) (Gastropoda: basommatophora: lymnaeidae) with morphological comparison to other European *Radix* species. *Journal of Conchology*, **82**: 55–68.
- SCHWEIZER, M., TRIEBSKORN, R. & KÖHLER, H.R. 2019. Snails in the sun: strategies of terrestrial gastropods to cope with hot and dry conditions. *Ecology and Evolution*, **9**: 12940–12960.
- SOLER, J., MORENO, D., ARAUJO, R. & RAMOS, M.A. 2006. Diversidad y distribución de los moluscos de agua dulce en la Comunidad de Madrid (España). *Graellsia*, **62**: 201–252.
- TAYLOR, D.M., PEDLEY, H.M., DAVIES, P. & WRIGHT, M.W. 1998. Pollen and mollusc records for environmental change in central Spain during the mid- and late holocene. *Holocene*, **8**: 605–612.
- TORRES ALBLA, J.S., VÁZQUEZ, F. & RIPOLL, J. 2020. Nuevas citas de distribución de gasterópodos continentales para Andalucía. *Elona*, **2**: 36–42.
- VANDEL, A. 1964. *Biospéologie. La biologie des animaux cavernicoles*. Gauthier-Villars, Paris.
- VANNIÈRE, B., POWER, M.J., ROBERTS, N., TINNER, W., CARRIÓN, J., MAGNY, M., BARTLEIN, P., COLOMBAROLI, D., DANIAU, A.L., FINSINGER, W., GIL-ROMERA, G., KALTENRIEDER, P., PINI, R., SADORI, L., TURNER, R., VALSECCHI, V. & VESCOVI, E. 2011. Circum-mediterranean fire activity and climate changes during the mid-Holocene environmental transition (8500–2500 cal. BP). *Holocene*, **21**: 53–73.
- VINARSKI, M.V., AKSENOVA, O.V. & BOLOTOV, I.N. 2020. Taxonomic assessment of genetically-delineated species of radicine snails (Mollusca, Gastropoda, Lymnaeidae). *Zoosystematics and Evolution*, **96**: 577–608.
- WACKENHEIM, Q., LIMONDIN-LOZOUET, N., DABKOWSKI, J., BOUDAD, L. & BERGER, J.F. 2020. Reconstructing mid-holocene palaeoenvironmental dynamic in the middle atlas (Morocco) inferred from non-marine molluscs succession of the Ait Said ou Idder tufa sequence. *Quaternaire*, **31**: 145–164.
- WELTER-SCHULTES, F. 2012. *European non-marine molluscs, a guide for species identification*. Planet Poster, Göttingen.
- WOLF, D., GARCÍA-TORTOSA, F.J., RICHTER, C., DABKOWSKI, J., ROETTIG, C.B. & FAUST, D. 2021. Holocene landscape evolution in the Baza Basin (SE-Spain) as indicated by fluvial dynamics of the Galera River. *Quaternary Science Advances*, **4**: 100030.
- YANES, Y., RIQUELME, J.A., CÁMARA, J.A. & DELGADO, A. 2013a. Stable isotope composition of middle to late holocene land snail shells from the Marroquíes archeological site (Jaén, southern Spain): paleoenvironmental implications. *Quaternary International*, **302**: 77–87.
- YANES, Y., GÓMEZ-PUCHE, M., ESQUEMBRE-BEBIA, M.A. & FERNÁNDEZ-LÓPEZ-DE-PABLO, J. 2013b. Younger Dryas – early Holocene transition in the south-eastern Iberian Peninsula: insights from land snail shell middens. *Journal of Quaternary Science*, **28**: 777–788.
- YANES, Y., ROMANEK, C.S., MOLINA, F., CÁMARA, J.A. & DELGADO, A. 2011. Holocene paleoenvironment (~7200–4000 cal BP) of the Los Castillejos archaeological site (SE Spain) inferred from the stable isotopes of land snail shells. *Quaternary International*, **244**: 67–75.
- YANES, Y., GUTIÉRREZ-ZUGASTI, I. & DELGADO, A. 2012. Late-glacial to Holocene transition in northern Spain deduced from land-snail shelly accumulations. *Quaternary Research*, **78**: 373–385.