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From a marsh that was once sea: The geological evolution of Europe's largest biological reserve as told by its benthic foraminifera-a review

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ABSTRACT

This paper presents an updated list of benthic foraminifera found in brackish and marine (paleo-)environments of the Doñana National Park (SW Spain) from the Lower Pliocene to the present-day. This list, based on published records, includes ninety-four species whose autoecology and temporal distribution in surface sections and continuous sediment cores allow us to infer the palaeogeographic evolution of this Biosphere Reserve over the last millions of years. During the Lower Pliocene, this area was occupied by a wide shallow bay with *Nonion faba* and *Ammonia beccarii* as the most representative species. During the Upper Pliocene, there was a transition to terrestrial environments, later dominated by fluvial dynamics for much of the Pleistocene and devoid of these aquatic microorganisms. During the Upper Pleistocene and part of the Holocene, the park was flooded during the MIS-1 transgression and a large lagoon was formed and progressively silted up. At this stage, benthic foraminiferal assemblages were dominated by the brackish species *Ammonia* morphogroup *tepida* and *Haynesina germanica*, which were occasionally replaced by marine species (mainly miliolids) during high-energy events. Currently, benthic foraminifera are mainly represented by *Ammonia* morphogroup *tepida* in the temporary lagoons and distributary channels, while *Ammonia beccarii* is dominant in their marginal marine areas. In summary, there is a clear correspondence between the palaeogeographic evolution of the park and its benthic foraminiferal associations, a review of which contributes to increase the knowledge of its remarkable present and past faunal diversity.

1. Introduction

The Man and Biosphere (MAB) programme was started by UNESCO in 1971 as an environmentally-friendly initiative aimed at the conservation and enhancement of the natural resources of the biosphere. This programme includes the designation of Biosphere Reserves for areas where high biodiversity coexists with sustainable economic and social development of their environment, as well as with the maintenance of their cultural values (Panduragan, 2022). There are currently 748 biosphere reserves in 134 countries, of which 53 are in Spain (https://www.unesco.org/en/mab/map).

The Doñana National Park (DNP) is the largest ecological reserve in

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Europe, with a surface area of 54,251 ha located within the estuary of the Guadalquivir river (SW Spain) (Fig. 1, A). As pointed Green et al. (2016), biodiversity of DNP and the surrounding areas is unique in Europe, with over 1300 vascular plants, 300 different species of birds, 27 continental fish species and more than 110 species of aquatic Coleoptera, among others. DNP was created in 1969 and since then it has been recognised as UNESCO Biosphere Reserve (1980), Ramsar Site (1982), Special Protection Area for birds-SPA (1989), World Heritage Site (1994), Special Conservation Area (SAC) and IUCN Green List of Protected and Conserved Areas (2014).

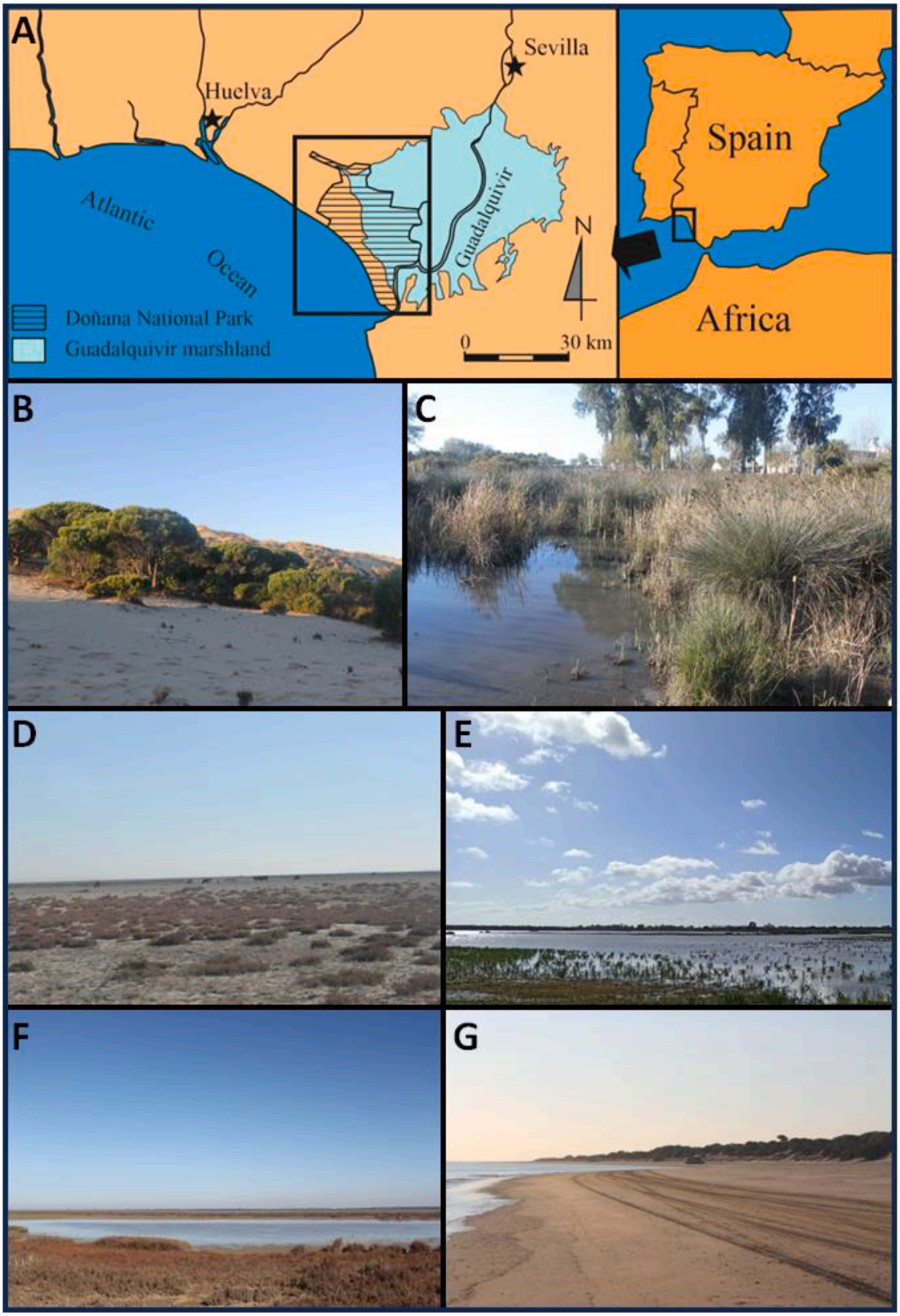

Fig. 1. A. Location of the Doñana National Park. B. Dune systems. C. Temporary pond. D. Dry marshland. E. Flooded marshland. F. Watercourse. G. Long beaches.

This biodiversity is distributed across the wide variety of ecosystems that constitute DNP, among which the following should be highlighted: i) an elongated sandy spit consisting of dune systems (Fig. 1, B) between which numerous temporary ponds are located in rainy years (Fig. 1, C); ii) an extensive silty-clayey marshland (~30,000 ha) that dries out frequently from June to October (Fig. 1, D) and is covered by a thin sheet of water during rainy periods (Fig. 1, E); iii) some former watercourses (Fig. 1, F) that have lost part of their tidal connection due to anthropogenic actions or siltation; and iv) the longest beaches in Spain (Fig. 1, G: 28 km). At present, this biodiversity depends on the availability of surface water, which is linked to the rainfall and the hydrogeology of the aquifer over which DNP is located.

The geological record of DNP has been reconstructed through the analysis of numerous sediment boreholes (e.g., Salvany and Custodio, 1995; Salvany et al., 2010, 2011), most of them obtained for hydrogeological purposes. The Doñana spit consists of Quaternary stabilised dune systems (Fig. 2, A: I to V) and Holocene dune systems deposited during three prograding phases (Fig. 2, A; H_2: 4200 BP-2600 BP; H_3: 2400 BP-800 BP; H_4: 500-Recent) (Zazo et al., 1994). In the innermost part of DNP, the most important geological formations are (Fig. 2, B):

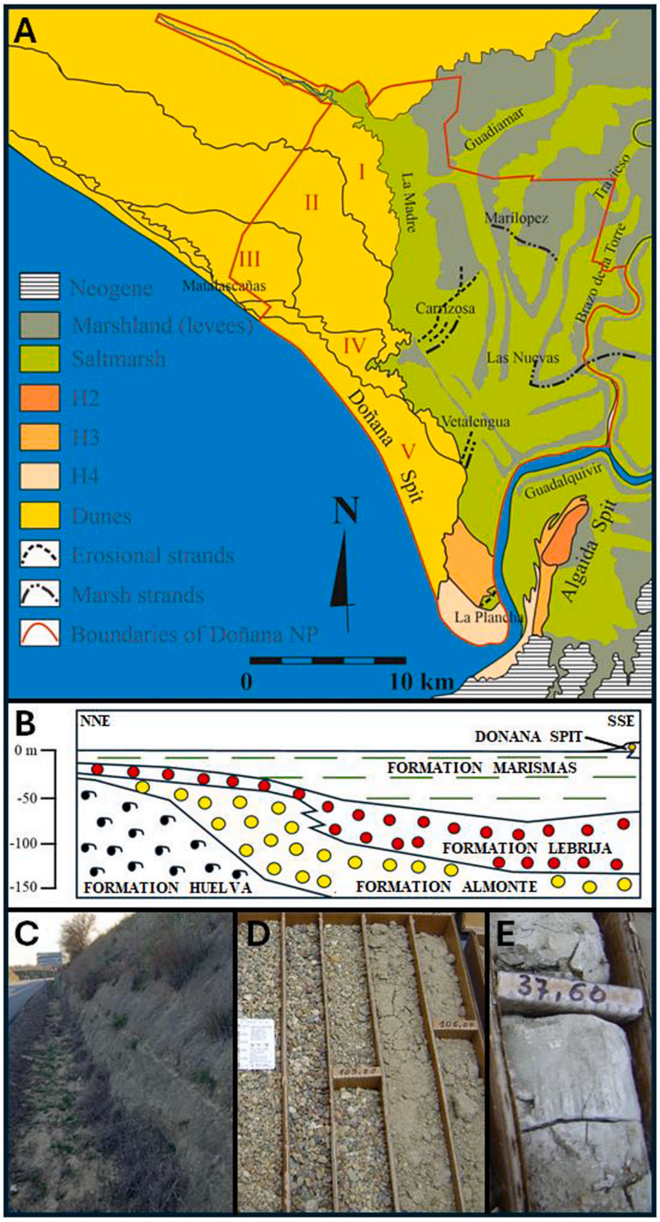

Fig. 2. A. Geomorphological map of the DNP. B. DNP: lithostratigraphic cross-section of the Plio-Quaternary formations (modified from Salvany et al., 2010); C. Surface section of the Formation Huelva, northwest of the DNP. D. Partial view of the Formation Lebrija in a sediment core. E. Partial view of the Formation Marismas in a sediment core.

i) Formation Huelva (Lower Pliocene; Civis et al., 1987), consisting of alternating layers of bioturbated sandy silt and bioclastic silty sands from the Lower Pliocene in surface sections west of DNP (Fig. 2, C) and at depths even deeper than 100 m within it due to its SE dip;
ii) Formation Almonte (Upper Pliocene-Lower Pleistocene; Salvany et al., 2011), made up of white to yellowish sandstones that may contain small, more clayey orange levels in the lower part and include thin levels of black clays with ferruginous nodules and carbonized plant remains in the upper part;
iii) Formation Lebrija (Lower Pleistocene-Upper Pleistocene; Salvany et al., 2011), formed by clays with ferruginous nodules and carbonized vegetal remains and yellowish sands (Fig. 2, D); and
iv) Formation Marismas (Upper Pleistocene-Recent; Salvany et al., 2011), with alternating greyish clayey silts (Fig. 2, E) and, to a lesser extent, black clays with abundant organic matter. This formation includes some tsunamigenic layers (e.g. Pozo et al., 2010; Ruiz et al., 2013).

This paper reviews the benthic foraminiferal record of the DNP from the Lower Pliocene to the present day through a literature review. The aim of this paper is mainly faunistic with additional biogeographical and paleoenvironmental tones, together with comments on selected species.

2. Material and methods

The first data on benthic foraminifera in DNP come from the micropalaeontological analysis of cores inventoried in the litholibrary of the Spanish Geological and Mining Institute. The explanatory reports of the geological maps on which they are found include references to the presence of these microorganisms in selected samples within their metadata (e.g. IGME, 1976). In the last twenty years, several multidisciplinary studies on short and long cores extracted in DNP include data on the distribution of the main benthic foraminiferal species from the Lower Pliocene to the present day (e.g. Carretero et al., 2002; Ruiz et al., 2004, 2005; Pozo et al., 2010; González-Regalado et al., 2020). For an exploration of the environmental factors related with the recent distribution of the benthic foraminífera in the area we recommend the papers by González-Regalado et al. (2019) or Guerra et al. (2020a).

In summary, this paper synthesises previous published results from seventeen long (over 100 m long in some cases) and short (1.5–3 m) cores, as well as from twenty-five surface samples from DNP (Fig. 3). In total, the distribution of benthic foraminifera in more than 300 sediment samples has been analysed. The taxonomy has been updated following the World Register of Marine Species (WoRMS).

The palaeogeographic reconstructions are based on: i) Martín et al. (2009) for the Pliocene; ii) the sea level changes inferred by Siddall et al. (2003) during the Upper Pleistocene; and iii) the inundation map of DNP during the Holocene transgressive maximum (~6.5 kyr BP; Zazo et al., 1994) carried out by Cáceres et al. (2024).

3. The foraminiferal record and evolution of DNP

Table 1 includes the taxonomic list of the ninety-four benthic foraminiferal species recorded in DNP and information on their corresponding habitat and age. Twenty-two of these have only been found in Pliocene sediments, while fourteen have been picked from the Pliocene to the present day, another thirty-six are restricted to the Holocene and a further sixteen have only been observed in current environments.

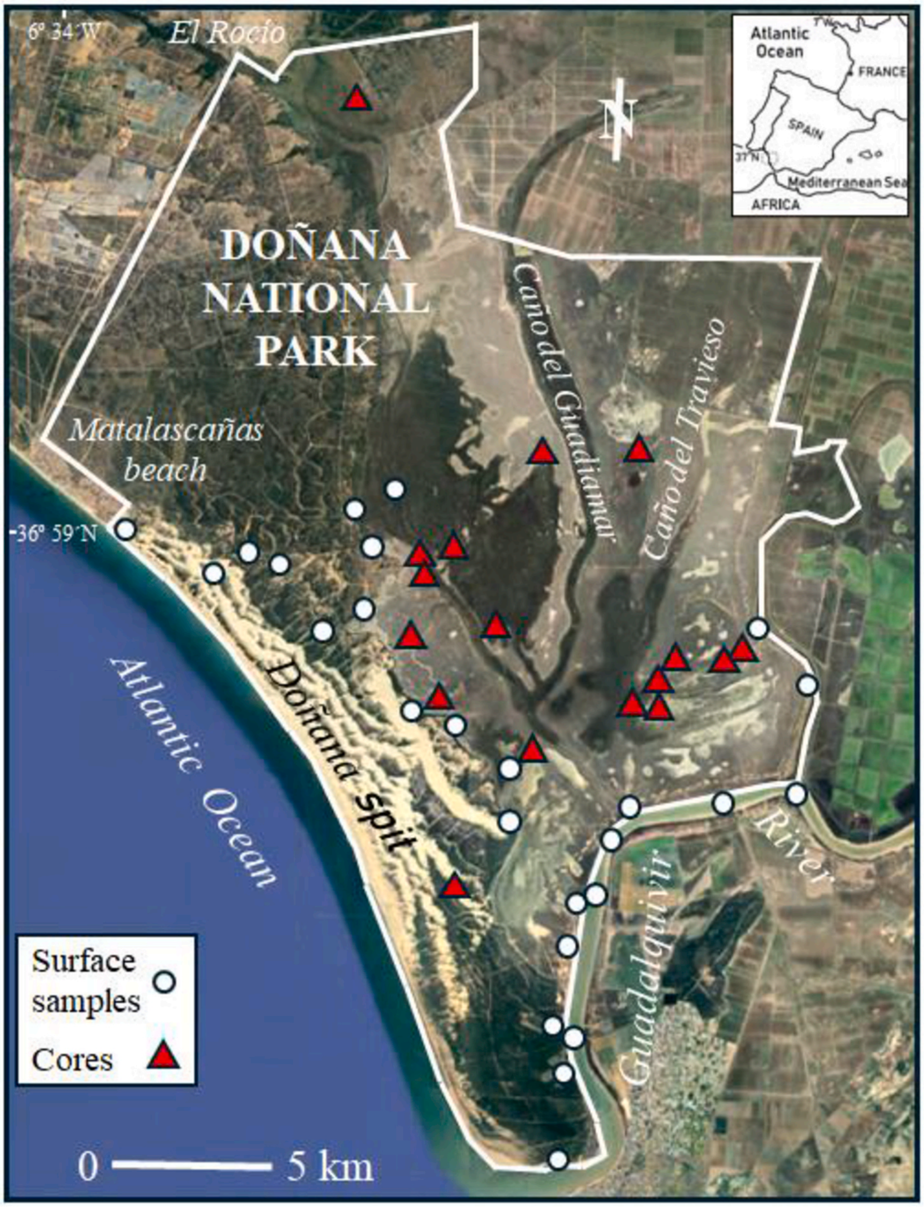

Fig. 3. Location of surface samples and sediment cores included in this study.

3.1. Lower Pliocene

During the Miocene, the connection between the Atlantic Ocean and the Mediterranean Sea was made through the northern North Betic Strait, which would occupy the southern part of today's Iberian Peninsula, and the Rifian Strait, which stretched across northern Morocco and Algeria. These straits disappeared at the end of this period and a wide bay was formed in the southwestern sector of the Iberian Peninsula, within which the current surface of DNP would be found (Fig. 4; Martín et al., 2009). The silty-sandy sediments of Formation Huelva were deposited in this shallow paleoenvironment, where storms caused the accumulation of several mollusc levels (González-Delgado et al., 2004, 2014). About one hundred species of benthic foraminifera have been reported from this formation (González-Regalado, 1989; González-Regalado and Ruiz, 1996).

Nonion faba (Fichtel & Moll, 1798) (Figs. 5, 7–9) is the most representative species during the Pliocene in the marine sediments of this formation, both in surface sections and in continuous cores obtained near or inside the DNP (as *Florilus boueanum* or *Nonion fabum*; IGME, 1976; González-Regalado, 1989; Pérez-Asensio et al., 2012), although it has also been cited in short Holocene cores from the park (Guerra et al., 2020b). This species currently lives in sediments of varying texture (muddy gravelly sands, gravelly mud, sandy mud, mud) at depths between 12 m and 40 m along the south Atlantic coast of the Iberian Peninsula (Mendes et al., 2004), although Milker and Schmiedl (2012) report the species as living in a deeper range (20–100 m) in the western Mediterranean Sea and Szarek (2001) considered it as an outer shelf - uppermost bathyal species. It has also been picked in the shallowest inner shelfs with high-energy gradients of the Bay of Bengal and Senegal (Redois and Debenay, 1999; Harikrishnan and Nathan, 2023), while it is frequent in sediments with high organic matter supplies close to the Rhone river (SE France) (Goineau et al., 2012). In southwestern Spain, this species has been reported from the Tortonian to the Pliocene in surface sections and continuous sediment cores obtained northwest of DNP (Baceta and Pendón, 1999; Pérez-Asensio et al., 2012).

During this period, this epifaunal to shallow infaunal species lived in the future DNP within: i) other epifaunal to shallow infaunal species, such as *Textularia agglutinans* d'Orbigny, 1839 (Figs. 5, 1–2) and

Table 1
Doñana National Park. List of benthic foraminifera with habitat and age.

Species	Habitat	Age (reworked)
Adelosina laevigata d'Orbigny, 1826	Marine	Recent
Adelosina longirostra (d'Orbigny, 1826) - as Adelosina longistrata in some previous papers-	Marine	(Holocene)
Adelosina pulchella (d'Orbigny, 1826)	Marine	Recent
Ammonia beccarii (Linnaeus, 1758)	Marine	Pliocene-Recent
Ammonia inflata (Seguenza, 1862)	Marine	Pliocene
Ammonia morphogroup tepida (Cushman, 1926)	Brackish to marine	Pliocene-Recent
Astigerinata mamilla (Williamson, 1858)	Marine	(Holocene)
Astrononion stelligerum (d'Orbigny, 1839)	Brackish	Holocene
Bolivina ordinaria Phleger and Parker, 1952	Marine	(Holocene)
Bolivina scalprata Schwager, 1883	Marine	Pliocene
Bolivina striatula Cushman, 1922	Marine	(Holocene)
Bulimina aculeata d'Orbigny, 1826	Marine	Pliocene-Recent
Bulimina buchiana d'Orbigny, 1846	Marine	Pliocene
Bulimina elongata d'Orbigny, 1846	Marine	(Holocene)
Bulimina gibba Fornasini, 1902	Marine	(Holocene)
Bulimina marginata d'Orbigny, 1826	Marine	(Holocene)
Bulimina minima -as Bulimina aculeata minima in some previous papers-	Marine	Pliocene
Bulimina striata d'Orbigny in Guerra et al., 2013*) -as Bulimina costata in some previous papers-*	Marine	Pliocene-Recent
Buliminella elegantissima d'Orbigny, 1839	Marine	(Holocene)
Cancris auricula (Fichtel & Moll, 1798)	Marine	Pliocene-(Recent)
Cassidulina carinata Silvestri, 1896 -as Cassidulina laevigata carinata in some previous papers-	Marine	Pliocene
Cassidulina laevigata (d'Orbigny, 1826)	Marine	Pliocene-(Holocene)
Cibicidoides pseudoungerianus (Cushman, 1922)	Marine	Pliocene
Cornuspira involvens (Reuss, 1850)	Marine	(Holocene)
Elphidium advena (Cushman, 1922) - as Elphidium advenum in some previous papers-	Brackish to marine	Holocene
Elphidium complanatum (d'Orbigny, 1839)	Brackish to marine	Pliocene-Holocene
Elphidium crispum (Linnaeus, 1758)	Brackish to marine	Pliocene-Recent
Elphidium cuvillieri Lévy, 1966	Brackish to marine	Holocene
*Elphidium decipiens (*Costa et al., 2022*)*	Marine	Pliocene
Elphidium macellum (Fichtel & Moll, 1798)	Brackish to marine	Recent
Elphidium oceanense (d'Orbigny, 1839 in Fornasini, 1904)	Brackish to marine	Holocene
Elphidium traslucens Natland, 1938	Marine	Holocene
Elphidium williamsoni Haynes, 1973	Brackish to marine	Holocene
Entzia macrescens (Brady, 1870) - as Jadammina macrescens in some previous papers-	Brackish	Holocene
Ehrenbergina alicantina Colom, 1950	Marine	Pliocene
Favulina squamosa (Montagu, 1803)	Marine	Pliocene
Fursenkoina complanata (Egger, 1893)	Marine	(Holocene)
Gavelinopsis praegeri (Heron-Allen and Earland, 1913)	Brackish	Recent
Hopkinsina atlantica Cushman, 1944	Marine	(Holocene)
Lagena sulcata (Walker & Jacob, 1798)	Marine	(Holocene)
Lobatula lobatula (Walker & Jacob, 1798) -as Cibicides lobatulus in some previous papers-	Marine	Pliocene-(Holocene)
Melonis padanus (Perconig, 1954) -as Nonion padanum in some previous papers-	Marine	Pliocene
Melonis pompiliodes (d'Orbigny, 1846) - as Melonis soldanii in some previous papers-	Marine	Pliocene-(Recent)
Miliammina fusca (Brady, 1870)	Brackish	Recent
Miliolinella circularis (Borneman, 1855)	Marine	Recent
Miliolinella subrotunda (Montagu, 1803)	Marine	(Holocene)
Neoconorbina terquemi (Rzehak, 1888)	Marine	Pliocene-Recent
Neoeponides antillarum (d'Orbigny, 1839) - as Eponides antillarum in some previous papers-	Marine	Pliocene-(Recent)
Neoeponides auberii (d'Orbigny, 1846) -as Neoeponides auderi in some previous papers-	Marine	Recent
Nonion commune (d'Orbigny, 1846)	Marine	Recent
Nonion faba (Fichtel & Moll, 1798) -as Florilus boueanum or Nonion boueanum in some previous papers -	Marine	Pliocene-(Holocene)
Nonionella stella Cushman and Moyer, 1930	Marine	(Holocene)
Oolina borealis Loeblich and Tappan, 1954 -as Lagena costata in some previous papers-	Marine	Recent
Oriodorsalis umbonatus (Reuss, 1851) -as Eponides umbonatus in some previous papers-	Marine	Pliocene
*Ortomorphina tenuicostata (*Costa et al., 2022*)*	Marine	Pliocene-(Recent)
Paracassidulina minuta (Cushman, 1933) -as Cassidulina minuta in some previous papers-	Marine	Recent
Planorbulina mediterranensis d'Orbigny, 1826	Marine	Pliocene-Recent
Planulina ariminensis d'Orbigny, 1826	Marine	Pliocene-Recent
Porosononion granosum (d'Orbigny, 1846) -as Elphidium granosum in some previous papers-	Brackish to marine	Holocene
Protoglobobulimina pupoides (d'Orbigny, 1846) -as Bulimina pupoides in some previous papers-	Marine	Pliocene
Pseudonodosaria aequalis (Reuss, 1863)	Marine	Recent
Pullenia bulloides (d'Orbigny, 1846)	Marine	Pliocene
Pyramidulina raphanus (Linnaeus, 1758) -as Nodosaria raphanus in some previous papers-	Marine	Recent
Quinqueloculina laevigata d'Orbigny, 1839	Brackish to marine	(Holocene)
Quinqueloculina seminulum (Linnaeus, 1758)	Brackish to marine	Holocene
Quinqueloculina slumbergeri (Wiesner, 1923) - as Miliolina schlumbergeri or Quinqueloculica stelligera in some previous papers-	Brackish to marine	(Holocene)
Quinqueloculina vulgaris d'Orbigny, 1826	Brackish to marine	(Holocene)
Rosalina bradyi (Cushman, 1915)	Marine	(Holocene)
Rosalina globularis d'Orbigny, 1826	Marine	Recent
Sphaeroidina bulloides d'Orbigny in Deshayes (1832)	Marine	Pliocene-(Recent)
Sphaeroidinella dehiscens (Parker and Jones, 1865)	Marine	Pliocene
Spirillina vivipara Ehrenberg, 1843	Marine	(Holocene)
Stainforthia fusiformis (Williamson, 1858) - as Bulimina fusiformis in some previous papers-	Marine	Pliocene
Textularia agglutinans d'Orbigny, 1839	Marine	Pliocene
Textularia sagittula Defrance, 1824 -as Textularia saggitula in some previous papers-	Marine	Recent
Trifarina bradyi Cushman, 1923	Marine	Pliocene

(*continued on next page*)

Table 1 (*continued*)

Species	Habitat	Age (reworked)	Species	Habitat	Age (reworked)
Globobulimina auriculata (Bailey, 1851)	Marine	(Holocene)	*Triloculina oblonga (Montagu, 1803) -as Quinqueloculina oblonga in some previous papers-*	Brackish to marine	Holocene
Globocassidulina subglobosa (Brady, 1881) -as Cassidulina subglobosa in some previous papers-	Marine	Pliocene	*Triloculina trigonula (Lamarck, 1804)*	Brackish to marine	Holocene
Gyroidinoides longispira (Tedeschi and Zanmatti, 1957)	Marine	Pliocene	*Trochammina inflata (Montagu, 1808)*	Brackish	Holocene
Hansenisca soldanii (d'Orbigny, 1826)	Marine	Pliocene-(Recent)	*Uvigerina auberiana d'Orbigny, 1839*	Marine	Pliocene
Haynesina depressula (Walker & Jacob, 1798)-as Nonion depressulum in some previous papers-	Brackish to marine	Pleistocene-Holocene	*Uvigerina mediterranea Hofker, 1932*	Marine	Recent
Haynesina germanica (Ehrenberg, 1840)	Brackish to marine	Holocene	*Uvigerina peregrina Cushman, 1923*	Marine	(Holocene)
Heterolepa bellincionii (Giannini and Tavani, 1960)	Marine	(Recent)	*Uvigerina pygmaea d'Orbigny, 1826*	Marine	Pliocene
Heterolepa praecincta (Karrer, 1868) -as Eponides praecintus in some previous papers-	Marine	Pliocene	*Uvigerina striatissima Perconig, 1955*	Marine	(Holocene)

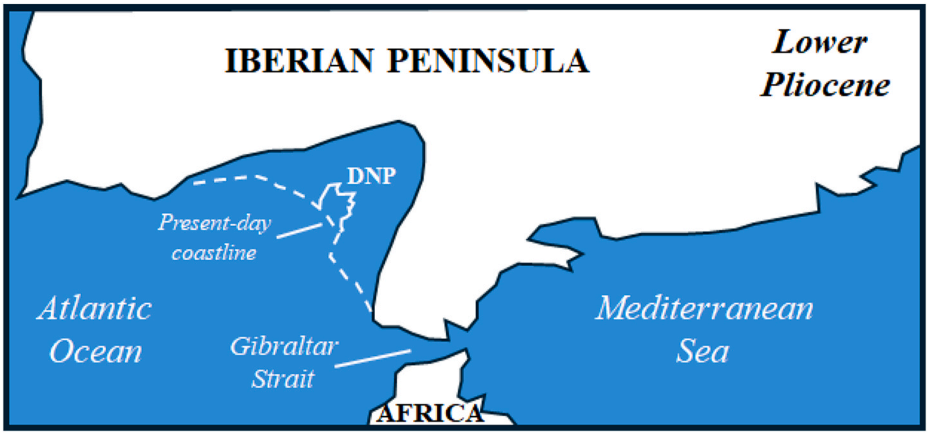

Fig. 4. Pliocene reconstruction of the southwestern Iberian Peninsula during the Lower Pliocene (modified from Martín et al., 2009). DNP: Doñana National Park.

Ammonia inflata (Seguenza, 1862) (Figs. 5, 3–4); ii) shallow infaunal species, such as *Cassidulina laevigata* (d'Orbigny, 1826) (Fig. 5 and 5–6), *Favulina squamosa* (Montagu, 1803) (Figs. 5 and 10), *Valvulineria bradyana* (Fornasini, 1900) (Figs. 5 and 11) and *Orthomorphina tenuicostata* (Costa et al., 2022) (Figs. 5 and 12); iii) intermediate to deep infaunal species, such as *Bulimina marginata* d'Orbigny, 1826 (Figs. 6 and 11) and *Bulimina elongata* d'Orbigny, 1846 (Figs. 6 and 12); and iii) encrusting or epifaunal species, such as *Rosalina bradyi* (Cushman, 1915) (Figs. 6, 3–6) and *Planorbulina mediterranensis* d'Orbigny, 1826 (Figs. 6–10). In addition, reworked species from deeper paleoenvironments are frequently present, such as *Uvigerina peregrina* Cushman, 1923 (Figs. 6, 1–2) (Diz et al., 2000; Fontanier et al., 2002; Mateu-Vicens et al., 2010; Spezzaferri et al., 2014).

3.2. Pleistocene to recent

A regressive cycle took place during the Upper Pliocene and Lower Pleistocene, with the transition from marine to continental environments represented by the Formation Almonte and the Formation Lebrija. The former involved the implantation of an alluvial system over Neogene marine sediments, while the latter includes distal alluvial sediments in its lower part that evolve into proximal alluvial environments towards its top (Salvany et al., 2011). Benthic foraminifera and other microorganisms, such as ostracods, have not been observed in these two formations (Ruiz et al., 2013).

During the Upper Pleistocene, the sea level underwent numerous oscillations as result of the succession of glacial and interglacial periods (Siddall et al., 2003) and the present-day continental shelf adjacent to DNP remained emerged during this period (Fig. 7). The lower part of the Formation Marismas was deposited on the future surface of this park, which marked the beginning of a transgressive cycle that also extended during the Holocene (Salvany et al., 2011). Brackish benthic foraminifera were frequent during this period, with abundant specimens of *Ammonia* morphogroup *tepida* (Cushman, 1926), *Haynesina* spp. and *Elphidium* spp. associated with brackish ostracods (e.g. *Cyprideis torosa* (Jones, 1850), *Loxoconcha elliptica* (Brady, 1868) in some samples deposited in a brackish marsh around 45–50 kyr BP (Zazo et al., 1999; Pozo et al., 2010).

Near the end of the Pleistocene, sea level was between −120 m and −130 m below present-day values during the Last Glacial Maximum (~26.5–19 kyr) (Clark et al., 2009). Subsequent deglaciation caused a progressive increase of marine influence in the DNP, leading to the creation of a large lagoon during the Holocene transgressive maximum around 6.5 kyr BP (Fig. 8; Zazo et al., 1994; Ruiz et al., 2010a; Cáceres et al., 2024). This lagoon became progressively filled over the next 5000–6000 years, due to fluvial inputs and the growth of the Doñana spit (e.g. Ruiz et al., 2004, 2005).

The main benthic foraminiferal assemblages of the DNP are very similar from the late Pleistocene to the present. *Ammonia* morphogroup *tepida* (Cushman, 1926) (Figs. 9, 10–13) and *Haynesina germanica* (Ehrenberg, 1840) (Figs. 9, 8–9) are the most abundant species in brackish (palaeo-)environments of the DNP during this period. These two species occur frequently together with *Elphidium* spp. and sometimes with the agglutinated species *Trochammina inflata* (Montagu,

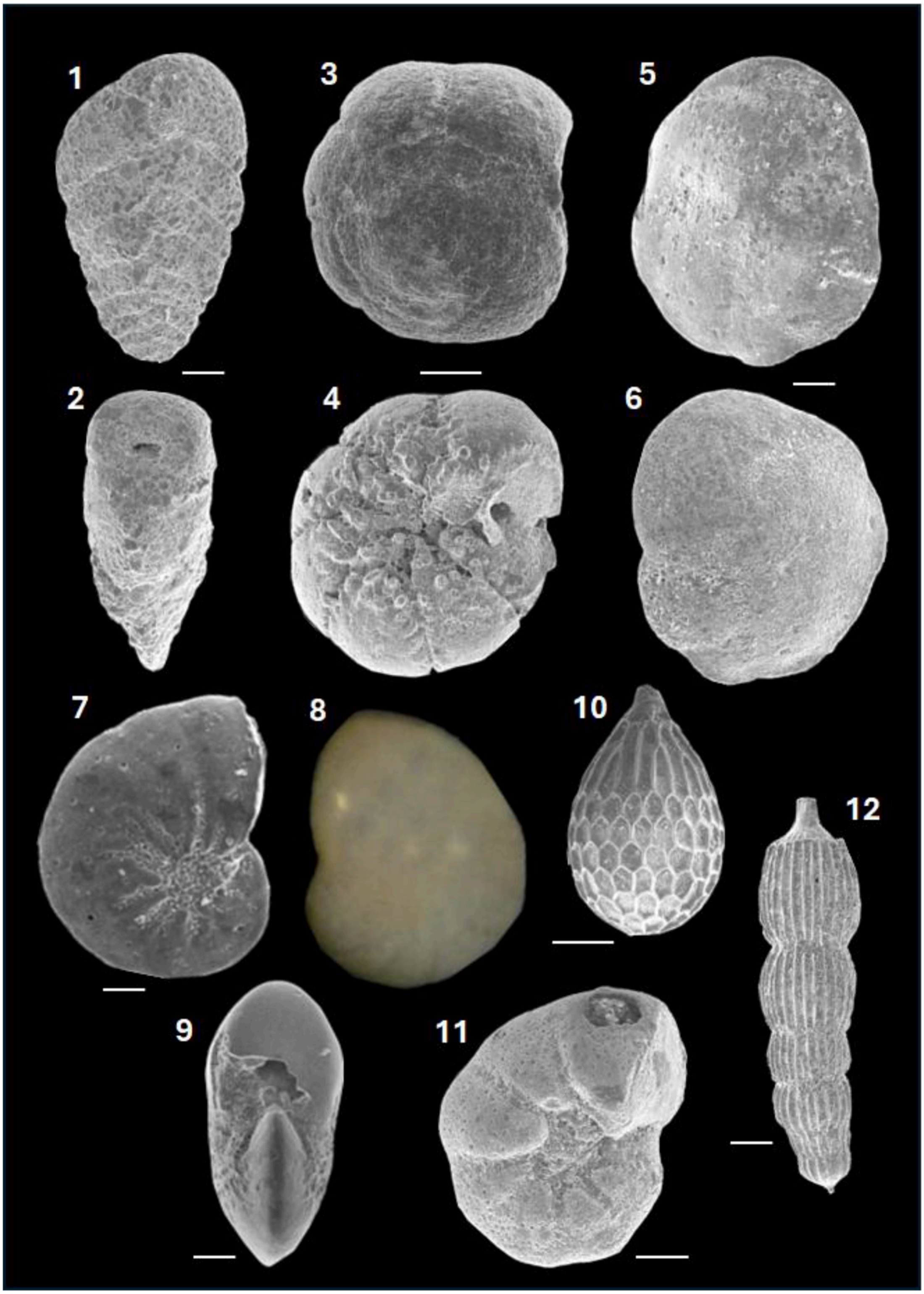

Fig. 5. Pliocene species. 1. *Textularia agglutinans.* 2. *Textularia agglutinans.* Apertural view. 3. *Ammonia inflata. Ammonia inflata.* 5–6. *Cassidulina laevigata.* 7–8. *Nonion faba.* 9. *Nonion faba.* Apertural view. 10. *Favulina squamosa.* 11. *Valvulineria bradyana.* 12. *Orthomorphina tenuicostata.* Scale: 100 μm.

1808) (Figs. 9, 1–3) and *Entzia macrecens* (Brady, 1870) (Figs. 9, 4–7) (e. g. Ruiz et al., 2004, 2005, 2010b; Pozo et al., 2010; González-Regalado et al., 2019; Guerra et al., 2020a, b, c).

Ammonia morphogroup *tepida* and *Haynesina germanica* are euryhaline species very frequent in surface sediments of tidal flats, marshes, lagoons or estuaries (Alve and Murray, 2001; Pascual et al., 2004; Debenay et al., 2006; Alday et al., 2013; Lintner et al., 2020). In these environments, *Ammonia* morphogroup *tepida* is abundant in the surface sediments (0–0.5 cm) of the main channels of estuaries, tributary tidal channels, intertidal mudflats, areas closer to the mouth of lagoons or shallow marine sediments (Jorissen, 1988; Blázquez, 2005; Frontalini et al., 2013), where this species feeds on detritus, algae or organic matter (Moodley et al., 2000; De Nooijer, 2007). Grain size does not play an important role in the distribution of this species (Debenay and

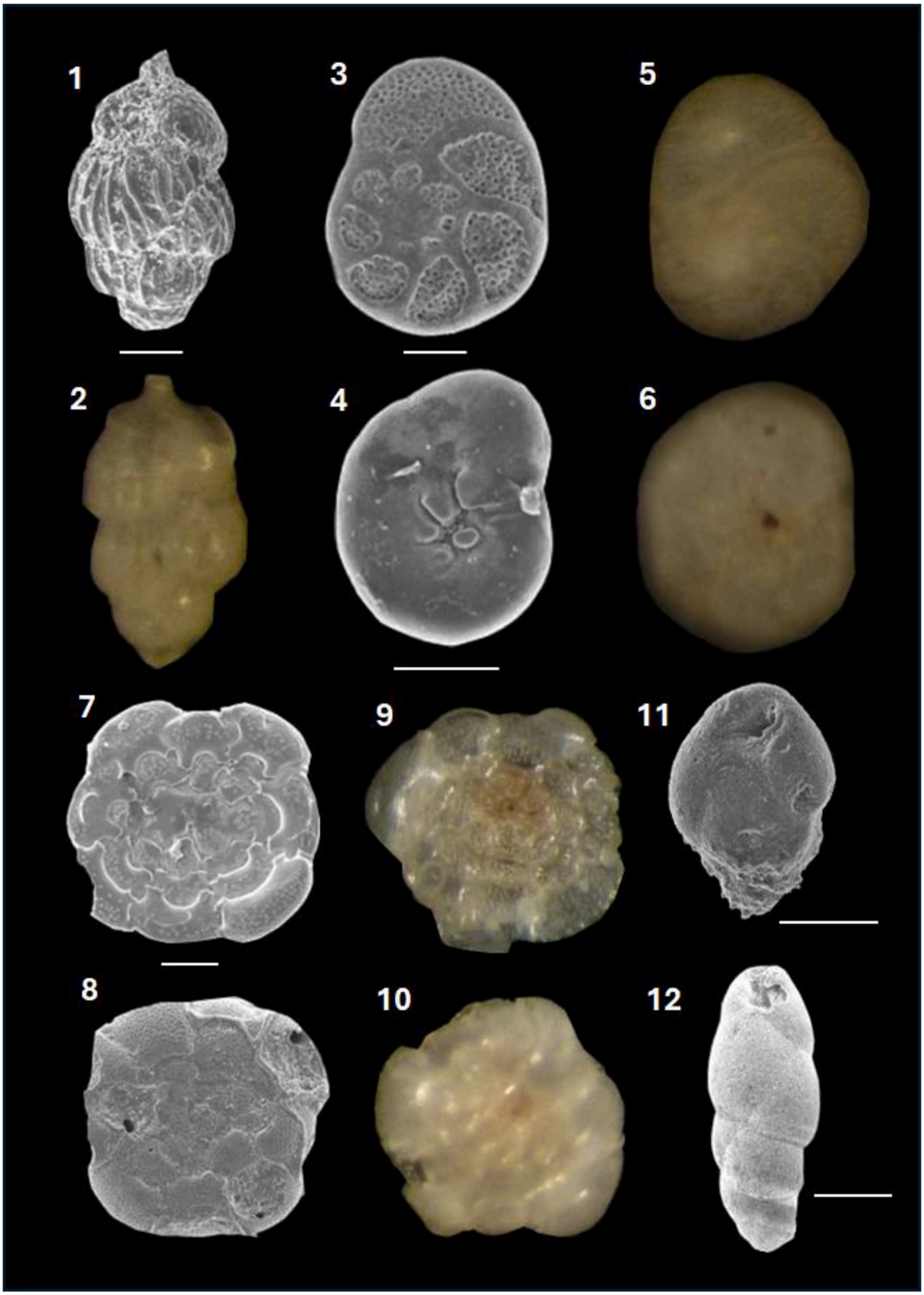

Fig. 6. Pliocene species (cont.). 1–2. *Uvigerina peregrina.* 3–5. *Rosalina bradyi.* 4–6. *Rosalina bradyi.* 7–9. *Planorbulina mediterranensis.* 8–10. *Planorbulina mediterranensis.* 11. *Bulimina marginata.* 12. *Bulimina elongata.* 2-5-6-9-10: direct photos with binocular magnifying glass. Scale: 100 μm.

Fernandez, 2009), although a greater affinity for sandy sediments has been occasionally described (Melis et al., 2017). *Haynesina germanica* (Ehrenberg, 1840) is an euryhaline and eurythermal species (0-32 °C; Murray, 1991) that is often a pioneer coloniser in brackish environments (Murray, 2006; Calvo-Marcilese and Langer, 2010). It is one of the fifteen species of benthic foraminífera that sequester chloroplasts (see review in Goldstein and Richardson, 2018). This species contributes to the reworking of intertidal sediments by bioturbating the first few centimetres of the sediments (Deldicq et al., 2023).

The most representative marine species of this period are *Ammonia beccarii* (Linnaeus, 1758) (Fig. 10, 1–2), *Elphidium crispum* (Linnaeus, 1758) (Figs. 10, 3–4), *Triloculina trigonula* (Lamarck, 1804) (Figs. 10,

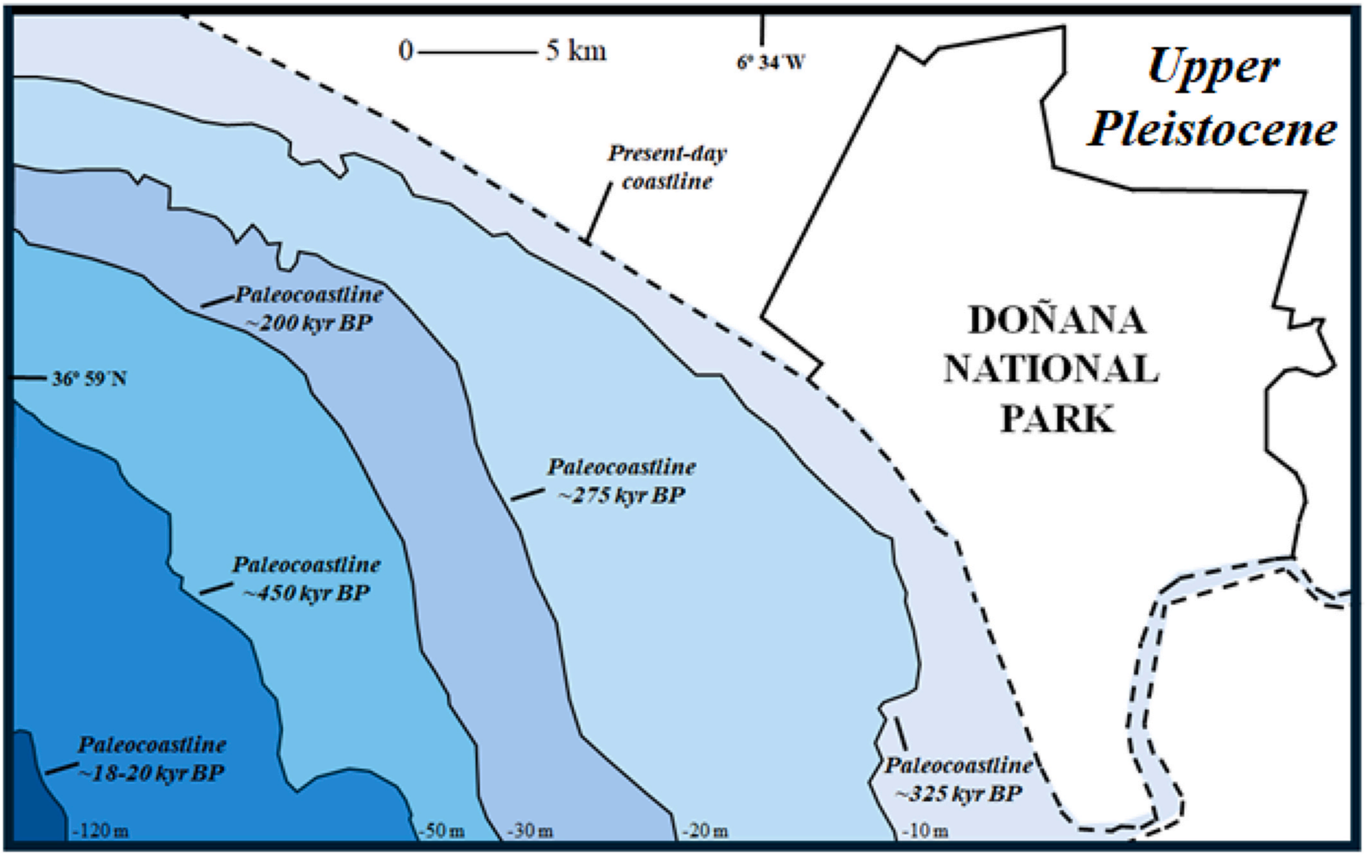

Fig. 7. Tentative reconstruction of paleocoastlines in the southwestern Iberian Peninsula during the Upper Pleistocene, according to the sea level changes deduced by Siddall et al. (2003).

Fig. 8. Palaeogeographical reconstruction of the DNP during the Holocene transgression maximum (~6.5 kyr BP; modified from Cáceres et al., 2024).

7–8) and *Quinqueloculina seminulum* (Linnaeus, 1758) (Figs. 10, 9–12), while *Elphidium oceanense* (d'Orbigny in Fornasini, 1904) (Figs. 10, 5–6) may be occasionally abundant (Pozo et al., 2010; González-Regalado et al., 2019; Guerra et al., 2020b, 2020c). *Ammonia beccarii* is one of the most widely distributed species in shallow marine environments around the world (for ecological parameters, see review in Walton and Sloan, 1990; Debenay et al., 1998; Murray, 2006). In the southwestern neritic zone of the Iberian Peninsula, *Ammonia beccarii* and *Elphidium crispum* are frequent in sandy sediments up to a water depth of 50 m (Mendes et al., 2004; Villanueva-Guimaraes and Canudo, 2008) and its distribution is influenced by river discharge (Mendes et al., 2012). In this area, *Ammonia beccarii*, *Elphidium crispum*, *Triloculina trigonula* and *Quiqueloculina seminulum* make up the most abundant assemblage of benthic foraminífera in the marine estuary of the main rivers, including the Guadalquivir mouth (González-Regalado et al., 2001, 2019). The same assemblage has been found in very shallow marine sediments (0–5 m depth) from southwest India (Gandhi and Rajamanickam, 2004).

In southern Europe and northern Africa, *Elphidium crispum* has been genetically distinguished in shallow waters with normal marine salinity from the coasts of Normandy to the Adriatic Sea and Algeria (review in Darling et al., 2016). It is an epifaunal species, preferring sandy substrates and often attached to rhizomes of sea-grasses (Murray, 2006). *Triloculina trigonula* is a cosmopolitan species preferentially found in shallow marine sediments but can be found even at a depth of 3250 m (review in Rajeshwara et al., 2018). *Quinqueloculina seminulum* shows similar preferences for infralittoral marine environments, as well as for the main channels of marine estuaries (Cearreta, 1988; Anbuselvan and Nathan, 2017).

The abundance of the main brackish species (*Ammonia* morphogroup *tepida* -AT-, *Haynesina germánica* -HG-) and some marginal, less euryhaline marine species (*Elphidium traslucens* Natland, 1938 -ET-, *Porosononion granosum* ((d'Orbigny, 1846)-PG-) has enabled Pérez-Asencio and Rodríguez-Ramírez (2020) to define a Benthic Foraminiferal Salinity (BFS) index in some cores of DNP, as follows:

$$\mathrm{BFS} = \frac{\%\,\mathrm{AT} + \%\,\mathrm{HG}}{\%\,(\mathrm{AT} + \mathrm{HG} + \mathrm{ET} + \mathrm{PG})}$$

so that 0 (higher salinity-higher marine influence) < BFS <1 (lower salinity-more restricted conditions). This new index has been applied to a Pleistocene lagoon in northern Italy (Barbieri and Vaiani, 2018) and a Pliocene coastal bay in southeastern Spain (Pérez-Asencio and Aguirre, 2010) with satisfactory results.

4. Benthic foraminifera as tracers of high-energy events

DNP is located very close to the boundary between the Eurasian and

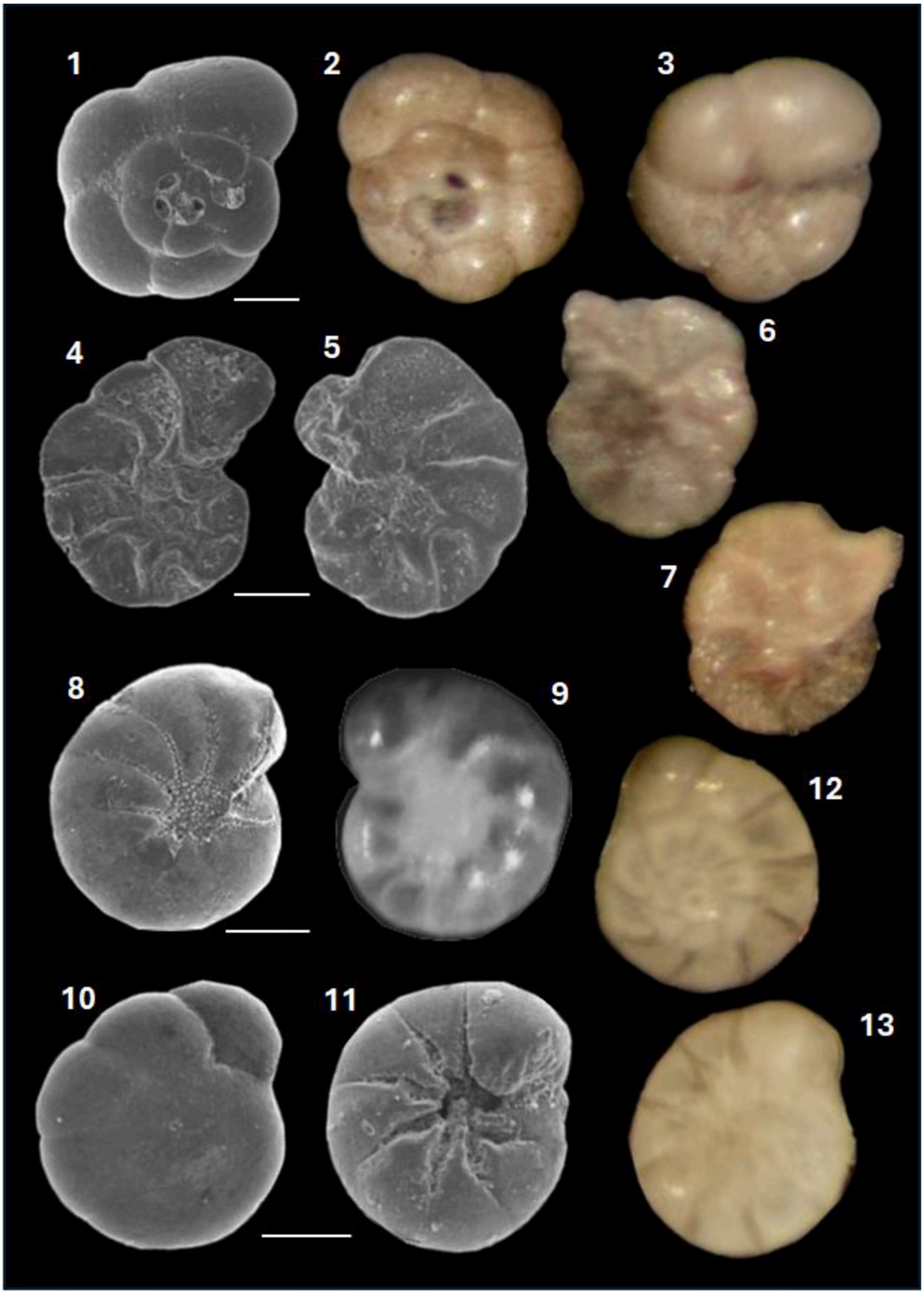

Fig. 9. Pleistocene to present-day brackish species. 1–2. *Trochammina inflata.* 3–4 *Trochammina inflata* 4-6- *Entzia macrescens*. 5–7. *Entzia macrescens*. 8–9. *Haynesina germanica.* 10–12. *Ammonia* morphogroup *tepida*. 11–13. *Ammonia* morphogroup *tepida*. 2-3-6-7-12-13: direct photos with binocular magnifying glass. Scale: 100 μm.

African plates, a tsunamigenic zone where one of the largest historical earthquakes occurred on 1 November 1755 and whose associated tsunami devastated the coasts of Portugal, Spain and Morocco (e.g. Blanc, 2009; Font et al., 2013; Costa et al., 2022). Similar events occurred in this area since at least 8000 years ago (Gracia et al., 2010) and the associated transport of marine sediments towards the coastal areas has been reflected in the DNP geological record, as well as in the benthic foraminiferal assemblages. Three different case studies can be distinguished from the benthic foraminiferal record (Fig. 11, A):

1. Erosión of the Doñana spit (Fig. 11, B; Ruiz et al., 2005). During the Upper Holocene, high-energy events eroded the Doñana spit, with the transport of its medium and fine sands into the ancient lagoon occupied by DNP during this period. These aeolian sandy sediments

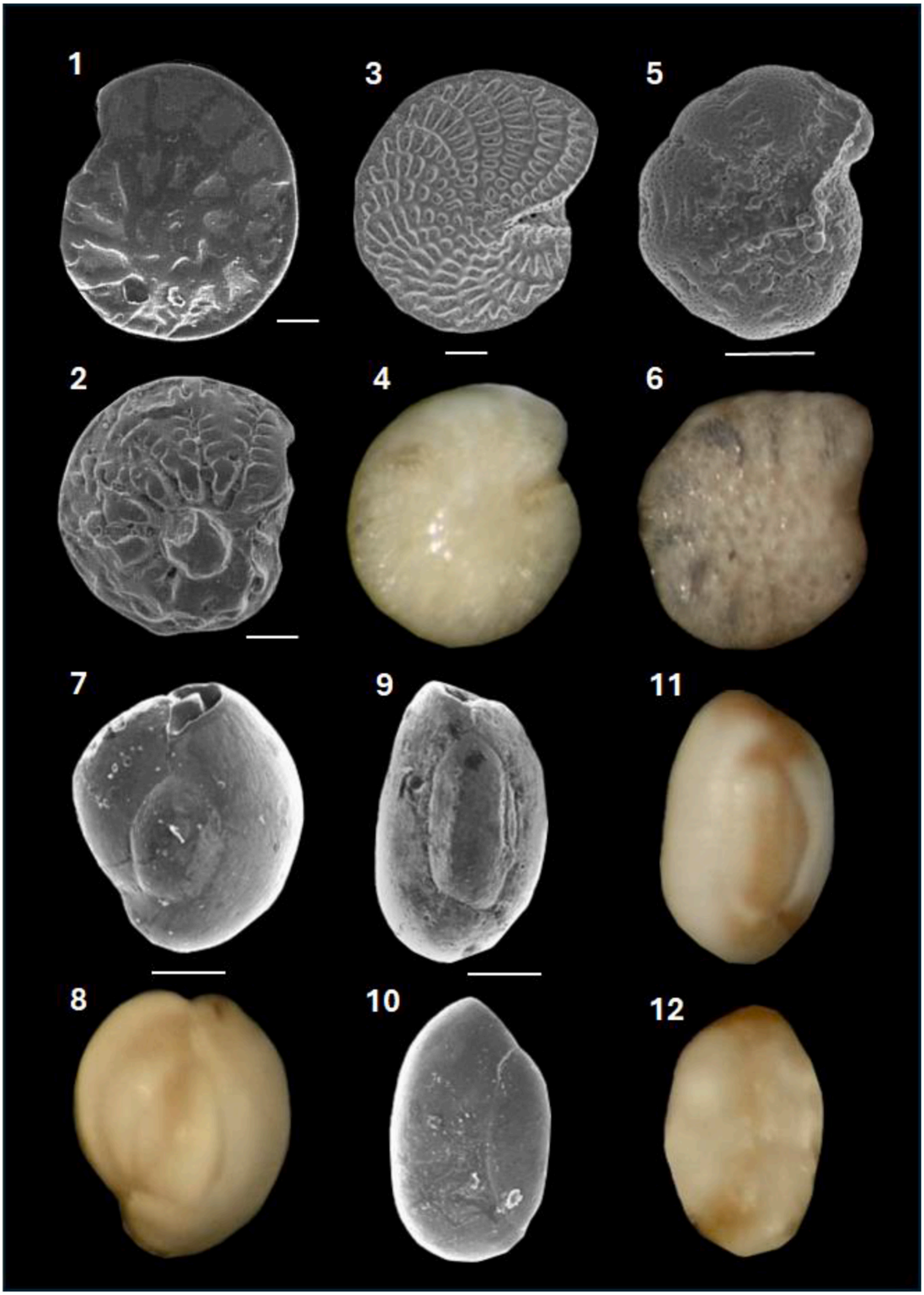

Fig. 10. Pleistocene to present-day marine species. 1. *Ammonia beccarii.* 2. *Ammonia beccarii.* 3–4. *Elphidium crispum*; 5–6. *Elphidium oceanensis*. 7–8. *Triloculina trigonula*. 9–12. *Quinqueloculina seminulum.* 4-6-8-11-12: direct photos with binocular magnifying glass. Scale: 100 μm.

are characterised by the absence of benthic foraminifera in contrast to the frequent occurrence of *Ammonia* morphogroup *tepida* in the underlying silty, lagoonal sediments.

2. Open lagoon (Fig. 11, C; Rodríguez-Ramírez et al., 2015). Between 4 kyr BP and 3 kyr BP, the current extent of DNP was still occupied by an open lagoon. In this scenario, high-energy events resulted in the deposition of thin sandy or silty-sandy layers characterised by the abundance of some of the marine species mentioned above (e.g. *Triloculina trigonula*, *Ammonia beccarii*, *Quinqueloculina seminulum*). These layers are also characterised by the presence of numerous marine molluscs (e.g. *Anomia ephippium*, *Tellina tenuis*, *Abra alba*, *Nassarius prismaticus*).
3. Restricted lagoon (Fig. 11, D; Guerra et al., 2020c). Between 2.4 kyr BP and 1.4 kyr BP, DNP was occupied by a relatively restricted

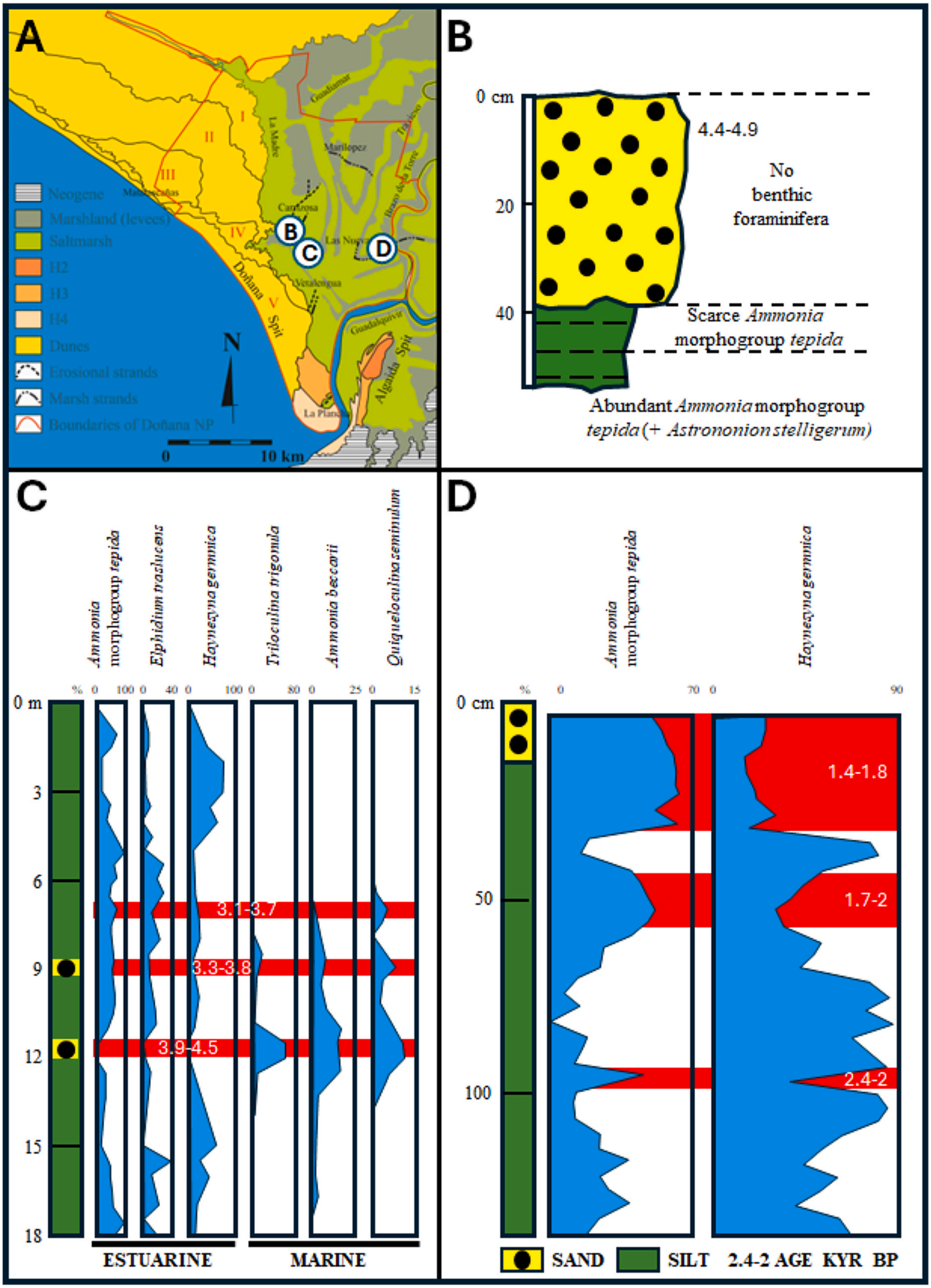

Fig. 11. High-energy events and benthic foraminifera. A. Location of high-energy layers; B. Erosion of Doñana spit (modified from Ruiz et al., 2005); C. Open lagoon (modified from Rodriguez-Ramírez et al., 2015); D. Restricted lagoon (modified from Guerra et al., 2020c).

lagoon due to progressive siltation by fluvial and, to a lesser extent, marine inputs (see review in Ruiz *et al.*, 2010). New high-energy events led to the deposition of new silty-sandy levels characterised by the transport of numerous shells of *Ammonia* morphogroup *tepida*, more abundant in the deeper main channels and the more open areas of the lagoon, towards the more restricted sectors, where *Haynesina germanica* was the dominant species. This replacement differentiates these layers, as well as the presence of numerous fragmentary specimens of marine bivalves and gastropods.

5. Summary

This paper is a contribution to the knowledge of the past and present biodiversity of the DNP, the largest biological reserve in southwestern Spain. Benthic foraminifera extracted from surface samples and continuous sediment cores testify to the transition from a Pliocene shallow bay to Pleistocene alluvial environments devoid of these microorganisms, and finally to the establishment of a progressively silted-up lagoon during the Holocene. This evolution, as well as the high-energy events that took place during the Holocene, is reflected in the assemblages of these microorganisms, which are confirmed as excellent palaeoenvironmental markers. Finally, the purpose of this paper is to show how this Biosphere Reserve has been shaped geologically, in order to make it even more valuable for its future preservation.

CRediT authorship contribution statement

María Luz González-Regalado: Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Liliana Guerra:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Francisco Ruiz:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Cristina Veiga-Pires:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Manuel Abad:** Writing – review & editing, Writing – original draft, Validation, Software, Methodology, Investigation, Conceptualization. **Tatiana Izquierdo:** Writing – review & editing, Visualization, Supervision, Software, Resources, Investigation, Conceptualization. **Joaquín Rodríguez Vidal:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Luis Miguel Cáceres:** Writing – review & editing, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Fernando Muñiz:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **María Isabel Carretero:** Writing – original draft, Methodology, Investigation, Formal analysis. **Josep Tosquella:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Adolfo Francisco Muñoz:** Writing – original draft, Validation, Supervision, Resources, Investigation, Funding acquisition, Conceptualization. **Manuel Pozo:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Juan Manuel Muñoz:** Writing – review & editing, Software, Investigation, Formal analysis, Data curation, Conceptualization. **Antonio Toscano:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Paula Gómez:** Writing – original draft, Methodology, Investigation, Formal analysis. **Verónica Romero:** Writing – original draft, Software, Investigation, Formal analysis, Conceptualization. **Gabriel Gómez:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

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

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Data availability

Data will be made available on request.

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