



## **BENTHIC DIATOMS AND FORAMINIFERA AS INDICATORS OF COASTAL WETLAND HABITATS: APPLICATION TO PALAEOENVIRONMENTAL RECONSTRUCTION IN A MEDITERRANEAN DELTA**

**Xavier Benito Granell**

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Benthic diatoms and foraminifera as indicators of coastal wetland habitats:  
application to palaeoenvironmental reconstruction in a Mediterranean delta

# Benthic diatoms and foraminifera as indicators of coastal wetland habitats: application to palaeoenvironmental reconstruction in a Mediterranean delta



Ph.D. Thesis

Xavier Benito Granell 2016



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**Ph.D. Thesis**

**Universitat Rovira i Virgili**



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MEDITERRANEAN DELTA**

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WE STATE that the present study, entitled “BENTHIC DIATOMS AND FORAMINIFERA AS INDICATORS OF COASTAL WETLAND HABITATS: APPLICATION TO PALAEOENVIRONMENTAL RECONSTRUCTION IN A MEDITERRANEAN DELTA”, presented by Xavier Benito Granell for the award of the degree of Doctor with European mention, has been carried out under my supervision at the Aquatic Ecosystems Program (IRTA) and the Centre for Climate Change (Department of Geography, URV).

Tortosa, 4 de Desembre de 2015

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*A la meva petita família, amb vosaltres les distàncies s'escurcen;*

*i a la Sara, per tot i més*



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Foto inferior: Llacuna del Garxal*



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## ***Abstract***

Deltas such as the Ebro are highly dynamic ecosystems of great ecological and economic importance. The Ebro Delta (NW Mediterranean) has been the focus of many ecological studies since the 70s but little is known about its recent and historical environmental changes. The present PhD thesis investigates, first, the utility of benthic diatoms and foraminifera as ecological indicators of modern Ebro Delta habitats, where the species–environment relationships have been evaluated qualitatively (through Indicator Species Analysis) and quantitatively (through transfer functions). Second, environmental change has been examined, in which the modern ecology of the benthic assemblages is applied in reconstructing past deltaic habitats at two different temporal scales: millennial (Holocene epoch) and decadal–centennial (human impacts). And third, the potential distribution of the natural habitats in the Delta has been modelled using multivariate Generalized Additive Models (GAM) coupled with Geographic Information Systems (GIS).

The results showed that, in the Ebro Delta, the distribution of benthic diatoms and foraminifera is mostly related to environmental gradients of conductivity (as a proxy of salinity), water depth (shallowness), and sediment characteristics (including the proportions of sand and organic matter). From these results, conductivity and water depth were identified as the single environmental variables most structuring diatom and foraminiferal assemblages respectively, and therefore, realistic diatom-based conductivity and foraminifera-based water depth transfer functions could be derived. On the other hand, GAM-based models showed that potential habitat distributions could be predicted by ecogeographical variables (elevation and ‘distances’ predictors). Then, habitat maps were constructed, illustrating where coastal and inland habitats could potentially exist across the whole deltaic plain, to inform future environmental restoration as a function of scenarios of sea level rise and coastal retreat.

Different habitats within the whole range of the Delta environments (i.e. from the deltaic plain to the adjacent marine area) were characterized using diatoms and foraminiferal assemblages. Benthic diatoms identified a total of five habitat types, namely salt marshes, brackish marshes, brackish coastal lagoons and bays, coastal lagoons with fresher conditions, and nearshore open sea. Benthic foraminifera (living and dead assemblages) identified four habitat types: salt and brackish marshes, coastal lagoons and inner bays, nearshore and outer bays, and offshore. For each of the habitat types identified, diatom and foraminiferal indicator species were recognised, which complemented pretty well habitat characterisation obtained using transfer functions (i.e. conductivity and water depth). Dead foraminiferal assemblages which integrate seasonal and post-depositional (taphonomic) effects on the modern assemblages, were found to be similar



enough to the living ones to allow the modern assemblages to be used for the interpretation of buried foraminiferal assemblages. Concerning diatoms, unfortunately no well-preserved valves were found in sediments below *ca* 10 cm depth, so that it was impossible to infer past environmental conditions based on this indicator. Thus, for past reconstructions, the thesis focused on foraminiferal assemblages, which were well preserved (including both agglutinated and calcareous tests) and therefore allowed us to reconstruct palaeoenvironmental changes registered in the Ebro Delta sediments.

A total of seven sedimentary sequences from the Ebro Delta were analysed on the basis of foraminiferal content and sediment proxies (sand content and organic matter): these were obtained from two boreholes and five short cores. The two boreholes (Carlet and Sant Jaume, *ca* 20 m depth both) were radiocarbon-dated and provided a fine-grained habitat reconstruction. First, it was shown that the Ebro Delta had already undergone a major development in the early Holocene (7500 yr BP), since the Carlet borehole already recorded close modern analogues of deltaic plain habitats (i.e. coastal lagoons) at this time. These findings rejected hypotheses that the Ebro Delta was an estuary prior to the Roman period, as previously suggested by some authors. Second, the Sant Jaume borehole (younger and located nearer the present coastline than Carlet) allowed identification for the first time of a differential progradation of the last three Ebro Delta lobes (Riet Vell, Riet de Zaida and Mijorn), using micropalaeontological evidences, and also placed such lobes in a more accurate chronological framework.

The five shorter sediment cores (*ca* 80 cm depth) were also dated via a  $^{210}\text{Pb}$ -based chronology. The down-core foraminiferal assemblages revealed clear habitat shifts during the last 150 years, as a result of the introduction of intensive rice cultivation in the Ebro Delta. The foraminiferal record showed a replacement of calcareous-dominated assemblages by agglutinated-dominated ones, this change being significantly correlated with the increase of sediment organic matter due to inputs of agricultural runoff. Overall, the identification of these habitat changes provides a management tool not only for assessing baseline environmental conditions but also for habitat restoration in the context of ongoing climate change impacts in the Ebro Delta (i.e. sea level rise, sediment deficit).

## *Resum*

Els deltes com el del riu Ebre són ecosistemes molt dinàmics d'una gran importància ecològica i econòmica. Tot i que el Delta de l'Ebre (Mediterrani occidental) ha estat objecte de nombrosos estudis ecològics des de els anys 70, es coneixen poc els canvis ambientals ocorreguts en el passat. En primer lloc, aquesta tesi doctoral investiga la utilitat de les comunitats de diatomees i foraminífers bentònics com a indicadors ecològics dels hàbitats del Delta de l'Ebre, a través de tècniques qualitatives (espècies indicadores) i quantitatives (funcions de transferència). En segon lloc, s'han estudiat els canvis ambientals registrats als sediments del Delta de l'Ebre, on l'ecologia moderna de les comunitats bentòniques s'ha aplicat en la reconstrucció dels hàbitats deltaics passats a dues escales de temps diferents: milenis (Holocè) i decades-segles (impactes humans). I en tercer lloc, s'ha modelitzat la distribució potencial dels hàbitats naturals al Delta utilitzant Models Aditius Generalitzables (GAM) conjuntament amb Sistemes d'Informació Geogràfica (SIG).

Els resultats van mostrar que, al Delta de l'Ebre, la distribució de les diatomees i foraminífers bentònics es troba majoritàriament determinada per gradients ambientals de conductivitat (com a indicador de salinitat), de profunditat de l'aigua (superficialitat) i de les característiques del sediment (incloent-hi les proporcions de arena i matèria orgànica). A partir d'aquests resultats, es van identificar la conductivitat i la profunditat de l'aigua com les variables ambientals que de forma estadísticament significativa i individual són més importants per estructurar les comunitats de diatomees i foraminífers, respectivament. Per tant, es van desenvolupar funcions de transferència realistes per les variables de conductivitat (mitjançant diatomees) i profunditat de l'aigua (mitjançant foraminífers). D'altra banda, els models GAM van mostrar que la distribució potencial dels hàbitats es podria predir a partir de variables ecogeogràfiques (elevació i un conjunt de 'distàncies'). Aleshores es van construir mapes d'hàbitat potencial, els quals van il·lustrar on existirien els hàbitats costaners i els hàbitats terrestres al llarg de tota la plana deltaica per tal d'informar futurs plans de restauració ambiental en funció dels escenaris d'augment del nivell del mar i retrocés de la costa.

Mitjançant les comunitats de diatomees i foraminífers es van caracteritzar diferent tipus d'hàbitats dins de tot el rang d'ambients del Delta (és a dir, des de la plana deltaica fins els ambients marins adjacents). Així, les diatomees bentòniques van identificar un total de cinc hàbitats: aiguamolls salins, aiguamolls salobres, llacunes costaneres i badies salobres, llacunes costaneres més dolces, i mar obert costaner. Els foraminífers bentònics (ambdues comunitats vives i mortes) van identificar quatre tipus d'hàbitats: aiguamolls salins i salobres, llacunes costaneres i badies interiors, mar obert costaner i badies externes, i mar obert lluny de la costa. Per cadascun d'aquests tipus d'hàbitat, es van identificar diferent grups d'espècies indicadores de diatomees i foraminífers, les quals van complementar força bé la caracterització ambiental

dels hàbitats obtinguda amb les funcions de transferència (és a dir, conductivitat i profunditat de l'aigua). Les comunitats de foraminífers morts, els quals combinen els efectes estacionals i *post-mortem* (tafonòmics) de les associacions modernes, van resultar ser suficientment similar a les associacions vives en quan a la composició d'espècies i abundància, i per tant, l'ús de les comunitats actuals es pot aplicar per la interpretació de les comunitats de foraminífers enterrats en el sediment. Pel que fa a les diatomees, desafortunadament, no es van trobar valves ben conservades als sediments per sota de 10 cm aprox. de profunditat, i per tant, no va ser possible reconstruir les condicions ambientals del passat a partir d'aquest indicador. En el seu lloc, la tesi es va centrar en les comunitats de foraminífers com a indicadors paleoambientals, els quals estaven ben conservats, tant espècies amb paret de tipus aglutinant com calcària, permetent així reconstruir l'evolució dels hàbitats del Delta de l'Ebre.

A partir del registre de foraminífers bentònics i característiques del sediment (contingut de arena i matèria orgànica), es van analitzar un total de set seqüències sedimentàries del Delta de l'Ebre, incloent-hi dos testimonis profunds (20 metres aprox. de profunditat) i cinc testimonis més curts (80 cm aprox. de profunditat). Els resultats dels dos testimonis profunds datats amb la tècnica del carboni 14 (Carlet i Sant Jaume) van proporcionar una reconstrucció paleoambiental precisa dels hàbitats deltaics. En primer lloc, van indicar que el Delta de l'Ebre ja tenia un desenvolupament important en l'Holocè primerenc (fa 7500 anys), tal i com el testimoni de Carlet va demostrar amb la presència d'anàlegs moderns d'hàbitats de plana deltaica (llacuna costanera) durant aquell temps. Aquests resultats han permès rebutjar la hipòtesi sobre l'origen i evolució del Delta de l'Ebre, en la qual diversos autors afirmen que el Delta era un estuari abans de l'època romana (és a dir fa uns 2000 anys). En segon lloc, l'anàlisi del testimoni de Sant Jaume (més jove i en una posició més pròxima a l'actual línia de costa que Carlet) va permetre identificar per primera vegada la progradació diferencial dels últims tres lòbuls del Delta de l'Ebre (Riet Vell, Riet de Zaida i Mijorn) utilitzant evidències micropaleontològiques. A la vegada, aquests resultats van permetre contextualitzar aquests tres lòbuls en un marc cronològic més precís, ja que estudis previs suggerien un desenvolupament més actual.

Els cinc testimonis més curts van ser datats mitjançant l'isòtop  $^{210}\text{Pb}$ . Els foraminífers enterrats van indicar canvis d'hàbitat des de els últims 150 anys, moment en que el cultiu d'arròs va començar de forma intensiva al Delta de l'Ebre. Els resultats mostren un canvi de comunitats de foraminífers dominades per espècies calcàries amb una elevada diversitat cap a comunitats dominades per espècies aglutinants amb una baixa diversitat. A més, aquest canvi es va correlacionar significativament amb l'increment de matèria orgànica al sediment, degut a les aportacions d'aigua procedents dels arrossars. En general, la identificació d'aquests canvis d'hàbitat no només proporcionen una eina de gestió per l'avaluació de les condicions de referència als aiguamolls estudiats, sinó també per a la restauració de l'hàbitat en el context dels impactes actuals i futurs del canvi climàtic al Delta de l'Ebre (és a dir, augment del nivell del mar amb dèficit de sediments).



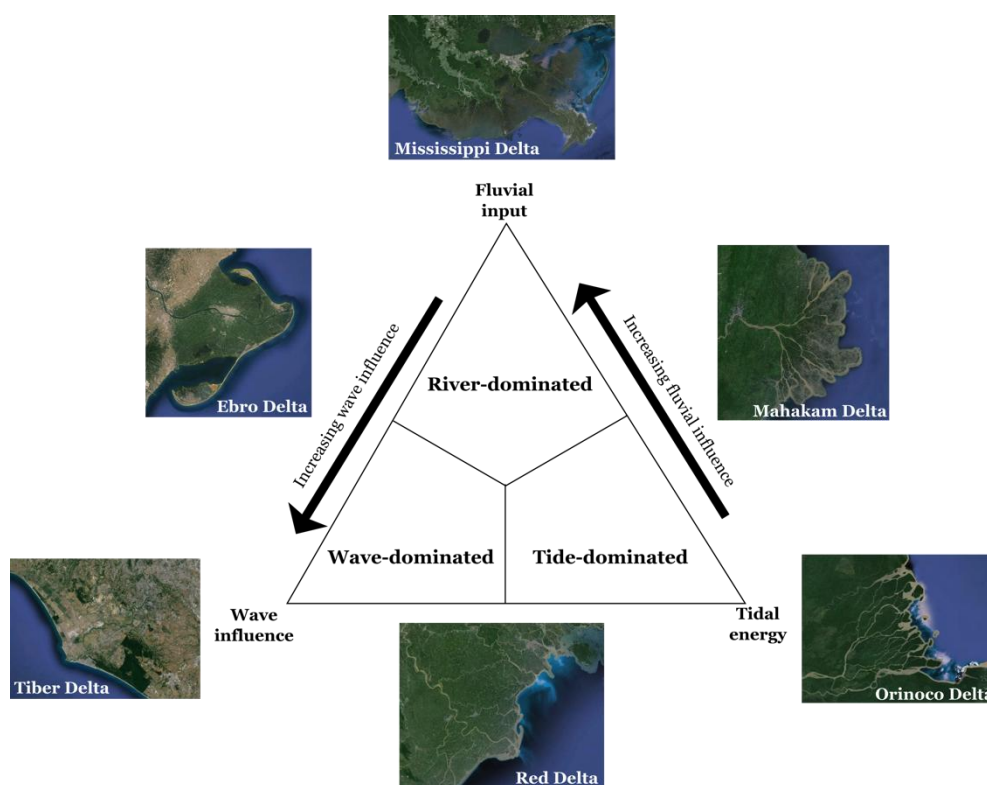




## General introduction

### Mediterranean deltas: definition, structure and dynamics

Deltas are considered to be the largest coastal landforms in the world. They are assemblies of environments such as rivers, bays, lagoons, marshes, and nearshore open sea (Goodbred 2009). Deltas are the result of strong interactions between river and sea forces. Rivers deliver sediment into the coast, and the sea molds the resulting deposits (Coleman and Wright 1975). In most cases, especially in microtidal settings such as the Mediterranean Sea or Gulf of Mexico, deltas protrude well into the sea, where the river forms distributaries that each construct their own deltaic lobes. Mediterranean deltas are usually classified as river- or wave-dominated systems according to the dominant processes (i.e. sediment delivery and dispersal or wave influence respectively) (Galloway 1975) (Fig. 1). The largest wetland areas in the Mediterranean and Black Sea are concentrated in deltas such as Ebro (Spain), Rhône (France), Po (Italy), Nile (Egypt) and Danube (Romania).



**Figure 1** Diagram showing the traditional delta's classification as a function of fluvial inputs and wave and tides energy (adapted from Galloway 1975).

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Mediterranean deltas, as other world deltas, comprise three main environments. These (progressing from deeper to shallower areas) are the prodelta, the delta front and the deltaic plain (Bhattacharya 2003). The prodelta comprises widespread subaqueous muddy deltaic sediments, grading into sand toward nearshore and into clay offshore (> 10 m depth) (Maldonado and Murray 1975). The delta front is situated nearshore and it is a high-energy sandy environment that includes the 'delta coastal fringe'. Beaches and spits occupy the outer edge of the delta plain, and they are usually built by sand derived from the delta front due to longshore currents or erosion of the abandoned deltaic lobes (Maldonado and Murray 1975). Within the deltaic plain, fluvial levées have the highest elevation above mean sea level (> 3 m). Most of the deltaic plain however, is located near mean sea level (< 0.5 m) and will, in its natural state, contain large areas of marshes and lagoons. The marine area (prodelta and delta front) is a highly dynamic environment due to riverine discharges and bottom currents, but the deltaic plain environments are spatially and temporally even more dynamic, basically because they are influenced by many factors (winds, marine and river influences, rainfall, etc.). This dynamism is the result of the fluctuation and interaction of environmental parameters with broad ranges (salinity, nutrients, oxygen, substrates, water level, etc). Mediterranean deltas and associated wetlands are therefore clear examples of fluctuating systems with a patchy distribution (Ibáñez et al. 2000, Trobajo et al. 2004).

Mediterranean deltas are in constant change. Their dynamics depend mainly on the fluxes of water and sediments delivered by rivers and sea and are driven by different pulsing events (Table 1) (Day et al. 1995). Among these is river switching, which affects large parts of the deltaic plain by cycles of delta lobe extension and abandonment with a periodicity of about 1000 yr (Edmonds et al. 2009). Over shorter periods of a few centuries, the most powerful river floods lead to major episodes of deposition and result in large-scale habitat changes (i.e. formation of new wetlands). As the time scale decreases, the frequency of pulsing events increases, but the spatial scale of impact decreases (Table 1).

Over longer periods and affecting the whole deltaic system, sea level changes occur as a result of eustatic (global) sea level rise and local subsidence. These control the overall morphological evolution of the delta. Natural subsidence (land sinking due to compaction of sediments) can cause relative sea level rise (RSLR) to be much greater than eustatic rate (Day et al. 2011). However, RSLR can be compensated for by vertical accretion in the deltaic plain (Jerolmack 2009). In turn, accretion rates depend on fluvial sediment inputs and sea level rise through complex feed-back mechanisms (Ibáñez et al. 2014). In that context, short-term pulsing events can also play an important role by enhancing sediment and hydrologic exchanges between wetlands and adjacent water bodies (Table 1) (Day et al. 1995, Kirwan and Temmerman 2009).

**Table 1** Temporal scale and impact of pulsing events in deltas (adapted from Day et al. 1995)

Event	Time scale	Impact
River switching	1000 yr	Deltaic lobe formation Net advance of deltaic land masses Major habitat changes
Major river floods	100 yr	Channel switching Formation of new wetlands
Major storms	10–20 yr	Major deposition Enhanced production
Average river floods	Annual	Sediment and nutrients inputs Freshening (lower salinity)
Normal storms (low pressure events)	Annual	Enhanced deposition Net transport

Sea level changes along last glacial cycles have special relevance due to its strong link with formation and growth of world deltas in general, and Mediterranean deltas in particular (Pirazzoli et al. 2005, Anthony et al. 2014). Since the Last Glacial Maximum (LGM, i.e. around 21 kyrs BP), the Mediterranean Sea level has experienced a succession of rises and periods of relative stability following the retreat of the ice sheets, from a low of *ca* –130 m during the glacial maximum to its present level (Zazo et al. 2008). For the northwestern Mediterranean area, Lambeck and Purcell (2005) have indicated a rapid sea-level rise until 6000 yr BP, followed by a gradual increase in sea level with a slight deceleration during the last 1500 yrs, and stabilization for the last 500 yrs. Existing bibliography shows that modern deltas were initiated during the early-middle Holocene, i.e. 8000 and 6000 yr ago, when sea level stabilized near the current level and inputs of fluvial sediment began to accumulate along the coast (Stanley and Warne 1994). Since then, Mediterranean deltas have undergone river switching to create successive delta lobes, later abandoned and partially eroded by wave action (present high-stand deltas, Ibáñez et al. 2014).

### **Human impacts on Mediterranean deltas**

Mediterranean deltas, including their watersheds, have been severely impacted by human activities (Anthony et al. 2014). Perhaps one of the most studied impacts is the significant reduction of water and sediments along watersheds due to dam constructions intended for

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intensive agriculture and water consumption purposes (Ibáñez et al. 1997, Walling 2006, Syvitski and Kettner 2011). In most Mediterranean deltas, drastic sediment load reductions (> 80%) have been reported following the building of dams (Anthony et al. 2014). Moreover, the transformation of the original landscape of a river basin can either increase or reduce the sediment load, through land clearing or reforestation respectively, and will ultimately determine delta morphology (Mikhailova 2003). Nevertheless, the connection between sediment dynamics at the basin scale and delivery at the river mouth (i.e. progradation) is not always strong or direct (Walling 2006). It is also to be expected that river discharges will vary with climate (e.g. rainfall), especially in the Mediterranean region (Moreno et al. 2012, Xing et al. 2014, Benito et al. 2015), further hampering efforts to distinguish human impacts on river sediment supply from the effects of background climate changes.

Despite the high variety of Mediterranean deltas and associated wetlands, these systems have suffered similar trajectories of change since the last centuries (Halpern et al. 2008). Human impacts in deltaic plains range from land use changes to hydromorphological and ecological disruptions. Besides the obvious destruction of natural wetland surface through agriculture and urbanization (Cardoch et al. 2002), human impacts on delta wetlands include, among others, hydrological alterations (i.e. salinity reduction, water levels: Marco-Barba et al. 2013, Prado et al. 2014), nutrient and pollutant enrichment (Pérez-Ruzafa et al. 2005), habitat degradation (Soria 2006), and suppression of hydrological connectivity (i.e. dikes, canals) (Day et al. 1995).

At the same time, Mediterranean deltas are highly sensitive to increasing risks arising from climate change (Ibáñez 2009). For instance, coastal retreat, salt intrusion and sea level rise, coupled with sediment retention, threaten the sustainability of deltas (Day et al. 2011, Giosan et al. 2013). Worldwide, average sea-level rise is currently (1993-2010) *ca.* 3.0 mm/year (Hay et al. 2015) and this is projected to increase over the next 100 years (IPCC 2014). Deltas will be especially badly affected because of land subsidence (Ibáñez et al. 2010) and there is therefore especial concern among scientists and managers to address and if possible mitigate the worst effects of change. Therefore, a strategy to further develop scientifically-based methods for sustainable management of deltas is of paramount importance and such a strategy can only be achieved by understanding the natural and anthropogenic processes that have moulded these ecosystems on a range of time scales.



### **Palaeoecology in deltaic environments**

Palaeoecology is broadly defined as the ecology of the past (Birks and Birks 1980) and it is based on the principle of “uniformitarianism”. This means that natural processes operating nowadays are assumed to be basically the same as those that have operated in the past, although intensity and rates can change through time (Delcourt and Delcourt 1991). Importantly, palaeoecological techniques allow ecological and geological approaches to be combined across space and time. Analysing deltaic sedimentary environments has value from a geological point of view because it can provide information about the position of the palaeocoastline under natural conditions associated with Holocene sea-level changes (e.g. Stanley and Warne 1994). It is also valuable from an ecological point of view because represent marine-to-continental water transition, providing a background to study species’ responses to different types of natural and anthropogenic stressors (e.g. Debenay and Guillou 2002).

Reconstructing deltaic environments has proven to be complex, basically because of their multiple environmental controls (Goodbred 2009, Ibáñez et al. 2014). Nevertheless, the sediments beneath deltaic plains represent a potential record of environmental changes driven by continental and marine processes, climate change or human impacts (Phillips and Slattery 2006, Sarti et al. 2015). At scales of thousands of years, palaeoenvironmental reconstructions of deltas have been usually approached using geological methods (e.g. stratigraphy, sedimentology, geochemistry)(Somoza et al. 1998, Amorosi et al. 2003, Amorosi et al. 2005, Boyer et al. 2005, Vella et al. 2005, Stefani et al. 2005). However, application of palaeoecological techniques using biological proxies is becoming more frequent, and can be adapted to address different environmental issues at a range of temporal scales (Saunders and Taffs 2009). Table 2 summarizes the common biological proxies used in coastal and estuarine palaeoecological studies.

The study of modern analogues has been an important tool in the interpretation of past environments (Jackson and Williams 2004). The rationale of the method is to infer past conditions by identifying the modern assemblages that are most similar to the fossil ones, based on a similarity measure (e.g. squared chord distance, Overpeck et al. 1985) (Birks 2003). The reliability of such reconstruction is highly dependent on the variety of environments studied (Rull and Vegas-Vilarrúbia 1999). This aspect is specially significant when past inferences do not cover the whole range of environments that modern Mediterranean deltas harbour, since most palaeoenvironmental studies carried out in these systems have only used modern analogues from the open marine environments, i.e. prodelta and delta front (Amorosi et al. 2008, Rossi and Horton 2009, Dinelli et al. 2012, Amorosi et al. 2013). Despite some promising attempts in deltas from the Mediterranean (Scrutton 1969 in the Ebro Delta, Spain, and

Vangerow 1974 in the Rhône Delta, France), Asian (Lambert 2003 in the Mahakam Delta, Indonesia, and Melis and Violanti 2006 in Mae Khlong Delta, Thailand) and Gulf of Mexico (Lankford 1959 in the Mississippi Delta, USA) modern analogues from the deltaic plain environments have not been studied in detail. To our knowledge, this thesis is the first palaeoenvironmental reconstruction of a Mediterranean delta using modern analogues of delta plain habitats, giving therefore the possibility for a new and sounder interpretation of deltaic sedimentary sequences.

**Table 2** Common biological proxies used in coastal palaeoecological studies. The environmental topics and temporal scales are also shown, together with some references of examples.

<b>Proxy</b>	<b>Environmental topic</b>	<b>Temporal scale</b>	<b>Examples</b>
Chironomids	Eutrophication	10s–100s	Luoto and Ojala 2014
Chrysophytes	Sea-level	1000s	García-Rodríguez et al. 2010
Diatoms	Water physico-chemistry, sea-level	10s–1000s	Gaiser et al. 2001, Ryves et al. 2004, Weckström 2006, Saunders et al. 2007, Hassan et al. 2009, Wachnicka et al. 2013, Ferreira 2013
Foraminifera	Salinity, sea-level	10s–1000s	Brewster-Wingard and Ishman 1999, Horton and Edwards 2005, Leorri et al. 2008, Rossi and Horton 2009, Milker et al. 2011, Amorosi et al. 2013
Ostracods	Water physico-chemistry	10s–100s	Marco-Barba et al. 2013, Mischke et al. 2014
Pollen	Landscape	1000s	Byrne et al. 2001, Hofmann 2002, Watson et al. 2011
Testate amoebae	Sea-level	1000s	Charman et al. 2010

### **Foraminifera and diatoms as biological proxies**

Foraminifera (unicellular protists) and diatoms (unicellular algae) have been widely used as indicators of present and past environmental conditions due to their highly sensitive and quick responses to numerous environmental factors. Foraminifera are distributed among marine and coastal environments (lagoons, marshes, bays) (Scott et al. 2001), whereas diatoms are present

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in continental, coastal and marine waters and often represent a major component of primary producer communities (Smol and Stoermer 2010). These micro-organisms live in the plankton and the benthos, but benthic communities dominate in coastal wetlands in terms of abundance and diversity (Patterson et al. 2005). All benthic diatoms and many foraminifera form a resistant cell wall, which are made of silica (diatoms) and calcium carbonate (“calcareous” foraminifera, i.e. hyaline and porcellaneous, though not the “agglutinated” foraminifera, which their wall is made of cemented detrital material). Their remains can be preserved in the sediments as fossils or subfossils, giving extraordinary potential as palaeoenvironmental indicators. In this sense, perhaps no other fossilizable groups of benthic microorganisms are so well documented in terms of environmental requirements of their present-day assemblages (Murray 1991, Battarbee et al. 2001).

Many works have studied the ecology and distribution of contemporary diatoms and foraminiferal assemblages to reconstruct past environmental conditions from fossil assemblages (e.g. Cooper et al. 2001, Murray 2006). One of the most widely used palaeoecological techniques is statistical calibration between selected environmental variables and modern species distributions to infer quantitatively past environmental variables (i.e. the use of transfer functions) (Birks 2003). However, while quantitative reconstructions have been successfully applied in several coastal ecosystems using diatoms (Australian estuaries: Saunders et al. 2007, Logan and Taffs 2011; Argentinean estuaries: Hassan et al. 2009; Sub-tropical bays: Wachnicka et al. 2013) and foraminifera (Atlantic marshes and estuaries: Leorri and Cearreta 2009, Kemp et al. 2013, García-Artola et al. 2015; Australian embayments: Horton et al. 2007, Woodroffe 2009), reconstructions in Mediterranean coastal wetlands have been mainly qualitative and always using autoecological data from other areas (Usera et al. 2002, Flower et al. 2001, Zalat and Vildary 2007). Although the ecological meaning of diatoms and foraminifera can be obtained from the literature (e.g. Vos and de Holf 1993, Murray 1991), it is of paramount importance for palaeoenvironmental reconstructions to investigate post-depositional changes (i.e. living and dead assemblages), which only species data in their source communities can provide (Juggins 1992, Duchemin et al. 2005).

The detail and accuracy of palaeoenvironmental reconstructions will inevitably increase with strong correlations between the species or assemblage and the target environmental factor(s) (Murray 2001). However, most diatoms and foraminiferal species inhabiting estuarine ecosystems (marshes, lagoons) have been documented as having a broad range of tolerance for a high number of factors; hence they are able to occupy different environments (eurytopic species) (Battarbee et al. 2001, Scott et al. 2001). In this case, the identification of groups of indicator species rather than their individual abundances, could better reflect the specific habitat

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conditions (Wachnicka et al. 2010, Rovira et al. 2012a). Besides the use of diatoms and foraminifera as individual indicators, multiproxy approaches can provide multifaceted insights into modern environments (Birks and Birks 2006). In Mediterranean deltas and associated wetlands, however, these two indicators have been used so far independently, without matching results obtained by each of them (foraminifera: Zaninetti 1984, Albani et al. 2007, Coccioni et al. 2009; diatoms: Flower et al. 2001, Trobajo et al. 2004, Zalat and Vildary 2005, Della Bella et al. 2007). The reliability of palaeoenvironmental reconstructions can be improved by identifying weakness and enhancing the strengths of the proxies used (Gehrels et al. 2005, Kemp et al., 2009, Hassan et al. 2012)

Studies of benthic foraminifera and diatoms can also make significant contributions to monitoring coastal ecosystems and can therefore assist management decisions in the context of future restoration projects. However, before trying to implement realistic management strategies, it is essential also to achieve a good understanding of how environmental conditions have varied through time and what the background conditions were (Smol 2010). One of the greatest challenges in assessing the onset, causes and magnitude of environmental changes in coastal ecosystems is the lack of long-term monitoring data (>20 years), and the high influence of human activities. Hence, it is not possible to identify baseline conditions (i.e. with no or minor human disturbance); consequently, the most reliable approach to objectively determine pre-impact conditions is analysis of the sediment record (Andersen et al. 2004).

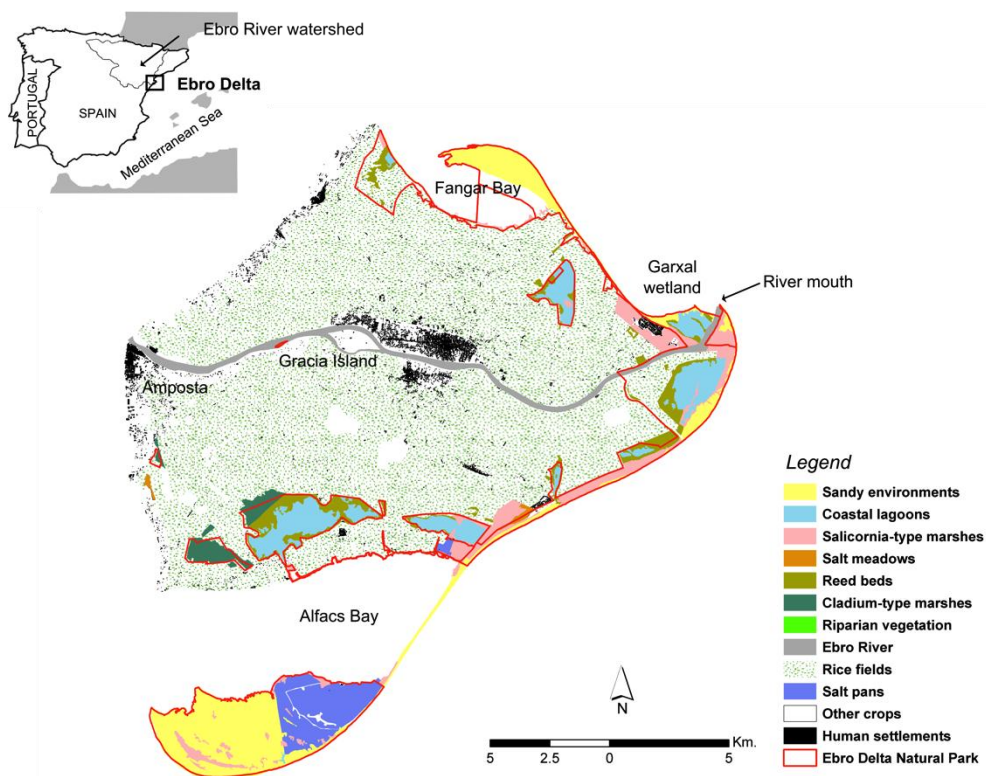
Palaeoecological approaches are currently being used to address water quality and ecosystem condition issues in order to be integrated into environmental assessments such as the Water Framework Directive (WFD) (e.g. Bennion and Battarbee 2007). For example, the WFD requires the degree of deviation from undisturbed conditions to be documented using hydrological, physicochemical, and biological quality elements. Although the use of diatoms and foraminifera is not required by the WFD (Annex V) as biological quality elements for monitoring coastal and transitional waters, their fossil remains in estuarine and marine sediments have been used to assess deviations from pre-impacted conditions (diatoms: Weckström 2006, Saunders et al. 2008, Logan and Taffs 2011; foraminifera: Alve et al. 2009, Bouchet et al. 2012, Dolven et al. 2013, Dijkstra et al. 2013). To date, similar use of diatoms and foraminifera has not been made in Mediterranean coastal wetlands.

### Study context: the Ebro Delta

The Ebro Delta is situated on the NE Iberian Peninsula (Fig. 3) and is one of the largest coastal wetlands in the Western Mediterranean, extending over an area of about 330 km<sup>2</sup>. The Delta is irrigated by the Ebro River, which is the longest river in Spain (928 km) and has the largest water discharge (*ca.* 400 m<sup>3</sup> s<sup>-1</sup>). The drainage of the Ebro River is 85,550 km<sup>2</sup>, representing 15% of the total area of Spain (Maldonado and Murray 1975). Within the Delta, natural wetland habitats occupy about 25% of the total surface. All of them are included in and protected by the Ebro Delta Natural Park and Natura 2000 network (EU). These natural areas support important economic activities associated with agriculture (mainly rice), aquaculture, hunting and tourism, with a total annual economic value of about €120 million (SEO/BirdLife 1997). Although rice cultivation has transformed and removed most of original wetland surface of the Delta (65% of the deltaic plain) (Cardoch et al. 2002), rice fields provide significant ecosystem services, such as habitat for migratory birds, prevention of saline intrusion or nutrient removal (Martínez-Vilalta 1995).

Despite the ecological, economic and geologic importance of the Ebro Delta, its origin remains controversial. The pioneering work of Maldonado (1972) suggested that the present Delta initiated its progradation about 8000 yr BP as a consequence of slowing of postglacial sea-level rise. Later, in 1998, the comprehensive stratigraphical study by Somoza et al. (based on peat material radiocarbon dated by Arasa, 1994) indicated that the main progradation of the Delta began at around 6900 yr BP. Furthermore, Canicio and Ibáñez (1999) showed through radiocarbon dated palaeoshorelines that the present Delta had an important development *ca.* 6000 yr ago, and that the river mouth was then already located around the present fluvial island of Gracia (see Fig. 3 for the location of the Gracia Island). In contrast, wrong interpretations of documentary records and the lack of scientific data led some authors to state that the present Ebro Delta initiated during the Roman period (*ca.* 2000 yr ago) following an intense deforestation period within the Ebro's watershed (Guillén and Palanques 1997, Serra 1997, Palanques and Guillén 1998, Maselli and Trincardi 2013, Somoza and Rodríguez-Santalla 2014). All these studies have also stated that the late Holocene sea level rise led the Delta to become an estuary with the coastline located as far inland as the town of Amposta (see Fig. 3 for the location of Amposta). This erroneous idea began with a personal interpretation of Roman texts by Bayerri (1934), who considered the presence of a “sea port” in Roman times to be proof for the existence of an estuary up to the town of Tortosa (12 km upstream from Amposta). The concept of “sea port”, however, could also refer to fluvial ports that harbour marine vessels.

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**Figure 3** Geographical location of the Ebro Delta. The distribution of the natural habitats and land uses (modified from Catalonia Habitats Map 1:50,000) is also shown.



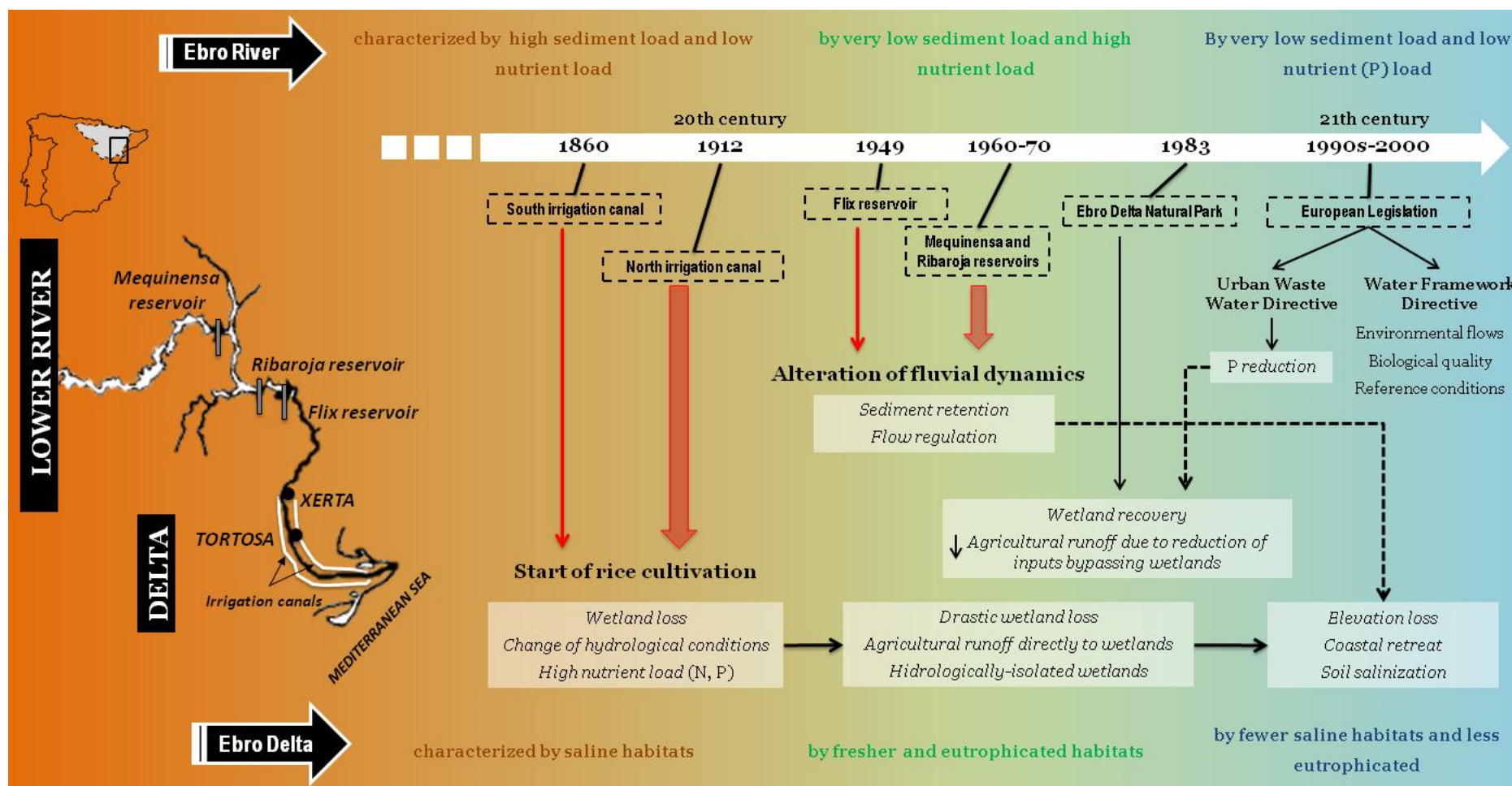
**Figure 4** Examples of natural habitats of the Ebro Delta: A) *Salicornia* marshes, B) *Phragmites* marshes (reed beds), C) Coastal lagoons, D) shallow inner bay, E) *Juncus* marshes, F) *Cladium* marshes, G) Salt meadows, H) Microbial mats, I) Sandy environments.

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The recent history of the Ebro Delta can be summarized as consisting of three periods, which reflect variation in human impacts on the Delta itself and the lower Ebro River (100 km from the mouth) (Ibáñez et al. 1997, SEO/BirdLife 1997):

- i. The first period lasting until the first half of 19<sup>th</sup> century, prior to rice cultivation in the Delta, when the transformation was minor and its natural features preserved; was characterized by large floods with high sediment inputs. This produced high accretion rates ( $> 0.5$  cm/ yr, Ibáñez et al. 1997), and large areas of saline wetlands were preserved.
- ii. The second period began in 1860, with the construction of the south irrigation canal derived from the river, and later in 1912, with the construction of the north irrigation canal. These two canals allowed the rice cultivation in the southern and northern hemideltas, respectively. Intensive rice agriculture was further developed between 1910 and 1960 to the detriment of natural habitats, which reduced from 88% to 33% (Mañosa et al. 2001). The irrigation and drainage system was progressively expanded to bring freshwater into the rice paddies. Remaining natural habitats received persistently variable amounts of agricultural runoff, becoming fresher and eutrophicated (Comín et al. 1991).
- iii. In the third period, beginning in the 1960s and lasting until the present, the fluvial regime of the lower Ebro River has been altered due to dam constructions. The Mequinença-Ribaroja-Flix dam system has caused drastic reductions of mean annual flow (28%) and sediment load (99%) (Ibáñez et al. 1996, Batalla et al. 2004, Vericat and Batalla 2006). Consequently, large river floods have been prevented and accretion rates have decreased dramatically. Transformation of wetlands to rice fields and eutrophication increased markedly since 1960, stopping only in the 1990s, when the Ebro Delta Natural Park was created (1983). Figure 5 summarises the general chronology of the main human activities in the Delta and the lower Ebro River since the second half of the 19<sup>th</sup> century and their main effects on deltaic ecosystems.





**Figure 5** Chronology of main human activities impacting on the lower Ebro River and its Delta since the middle of 19th century and their main effects on deltaic ecosystems.

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Since the beginning of the 80's, limnological and biological research has been performed in the Ebro Delta and its salt-wedge estuary (i.e. the last 40 km of the river occupying the Delta). These studies describe the main ecological processes and assess the human impacts on their functioning (Comín et al. 1987, Delgado 1987, Comín et al. 1991, Capítulo et al. 1994, Curcó et al. 1995, Ibáñez et al. 1996, Mañosa et al. 2001, Suarez-Serrano et al. 2010, Prado et al. 2012, Calvo-Cubero et al. 2013, Rodríguez-Climent et al. 2013). However, few studies investigated the benthic communities and to date, none were based on palaeoenvironmental reconstructions. For instance, Prado et al. (2014) studied the macrobenthos of some Ebro Delta coastal lagoons, and Rovira et al. (2012a,b) and Nebra et al. (2011, 2014) described the benthic communities of diatoms and macroinvertebrates inhabiting the Ebro estuary, respectively; only the pioneering work by Scrutton (1969) analyzed quantitatively the benthic foraminiferal assemblages living off the Ebro Delta, but the study of deltaic plain habitats was very limited. Moreover, all of these studies were carried out once intensive rice agriculture was already operating in the Delta (from 1960' to present), so it is not possible to discern how deviated the present conditions are when compared to pre-rice period.

The Ebro Delta is a very dynamic coastal system, where geological processes occur at human scale and where the interaction between biotic and abiotic elements is intense and complex. With all this in mind, the whole range of habitats of the Ebro Delta, i.e. from the deltaic plain to the adjacent marine area (Fig. 4) are integrated in the present thesis, which uses benthic assemblages of diatoms and foraminifera as indicators of present and past environmental change.

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## Objectives

The main aims of the present PhD thesis are twofold: i) To investigate the applicability of benthic diatoms and foraminifera as ecological indicators to identify and characterise modern habitats in a Mediterranean delta, and ii) To develop palaeoenvironmental reconstructions in the Ebro Delta using one of these indicators (foraminifera).

To achieve these aims, the following specific objectives were formulated:

1. To identify the main environmental factors that structure the distributions of benthic diatoms (*Chapter 1*) and benthic foraminifera (*Chapter 2*) in the Ebro Delta
2. To compare the performance of benthic diatoms and foraminifera as indicators of coastal wetland habitats in the Ebro Delta (*Chapter 2*)
3. To investigate the role of benthic diatoms and foraminifera as (paleo)indicators of habitats using qualitative and quantitative approaches (*Chapter 1* and *2*)
4. To reconstruct the Holocene evolution of the Ebro Delta using fossil foraminiferal assemblages (*Chapter 3*)
5. To document habitat changes that intensive human transformation had on the Ebro Delta wetlands during the last 150 years (*Chapter 4*)
6. To determine the potential distribution of the different wetland habitats under a scenario of no human disturbance (*Chapter 5*)





## ***Chapter 1***

### **Benthic diatoms in a Mediterranean delta: ecological indicators and a conductivity transfer function for paleoenvironmental studies**

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*Chapter 1: Benthic diatom assemblages*

# Benthic diatoms in a Mediterranean delta: ecological indicators and a conductivity transfer function for paleoenvironmental studies

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**Abstract** The contemporary distribution of benthic diatoms and their use as ecological indicators were examined in a coastal wetland, the Ebro Delta, as a representative of environmental conditions in Mediterranean coastal wetlands. A total of 424 diatom taxa were identified across 24 sites encompassing a wide range of wetland habitat types (coastal lagoons, salt and brackish marshes, shallow bays, microbial mats and nearshore marine waters) and conductivities. Canonical correspondence analysis showed that water conductivity and water depth were the main factors structuring the diatom assemblages. Cluster analysis identified five habitat types according to the similarity in diatom species composition: salt

marshes, brackish marshes, brackish coastal lagoons and bays, coastal lagoons with fresher conditions, and nearshore open sea. For each wetland habitat, diatom indicator species were identified. Partial canonical correspondence analysis showed that water conductivity, a proxy for salinity, was the most statistically significant and independent variable for explaining the distribution of benthic diatoms in the study area. A transfer function, using a weighted average regression model, was developed for conductivity and displayed reasonable performance ( $r^2 = 0.64$ ; RMSEP =  $0.302 \log_{10}$  mS/cm). Our study in the Ebro Delta provides a basis for using diatom assemblages to make quantitative conductivity inferences, and for using diatom indicator species to identify wetland habitats. These approaches are complementary and may be valuable for paleoenvironmental studies of (1) effects of large-scale, natural changes in the Delta (e.g. sea-level fluctuations), and (2) impacts of short-term anthropogenic changes, such as the introduction and development of rice agriculture.

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## Introduction

Diatoms are used extensively to study present and past environmental conditions in aquatic ecosystems

worldwide because (1) their species react in a rapid and sensitive way to environmental changes and (2) they preserve in sediments for a long time because of their resistant cell wall, which is made of silica (Smol and Stoermer 2010). Knowledge of the modern ecology of diatoms is needed to interpret what conditions were like when past assemblages existed. In contemporary freshwater systems such information is abundant, but by no means complete. Studies of the ecological preferences of diatoms in transitional waters (e.g. estuaries, coastal wetlands, deltas), however, are scarce, despite the fact that these systems are ecologically and economically very important (Costanza et al. 1997), by virtue of the many ecosystem goods and services they provide, e.g. nutrient cycling, productivity, pollutant binding, etc.

In the Mediterranean Sea region, deltas and coastal wetlands have been greatly affected by environmental changes, both natural and anthropogenic. At a local scale, for instance, hydrological impacts caused by intensive agriculture have in some cases led to a decline in water salinity and an increase in nutrient concentrations (Comín et al. 1991), as well as a loss of habitats via human settlement (Hollis 1992). At the same time, deltas have been modified by a broad range of natural factors, such as sea-level fluctuations (Ibáñez et al. 2014) or changes in fluvial sediment discharge (Xing et al. 2014). Given the lack of historical records of past environmental conditions and poor knowledge of their natural variability, a comprehensive understanding of how historical processes have structured deltaic habitats is important to support better management of these vulnerable systems. Such knowledge can be acquired through paleoecological methods (Smol 2002).

Quantitative assessments of diatom–environment relationships (i.e. transfer functions) are frequently used to reconstruct past environmental changes in aquatic environments, particularly changes in salinity (Hassan et al. 2009), pH (Battarbee et al. 2005), and total phosphorus (Cooper et al. 1999). Of these variables, salinity (or its proxy, conductivity) seems to be especially relevant for tracking environmental changes at the land–sea interface in coastal wetlands, where freshwater and marine interactions are inherently dynamic and intense. If there is good preservation of diatom valves in dated sediment cores, the diatom fossil record can be used to reconstruct salinity changes, for instance, during Holocene sea-level

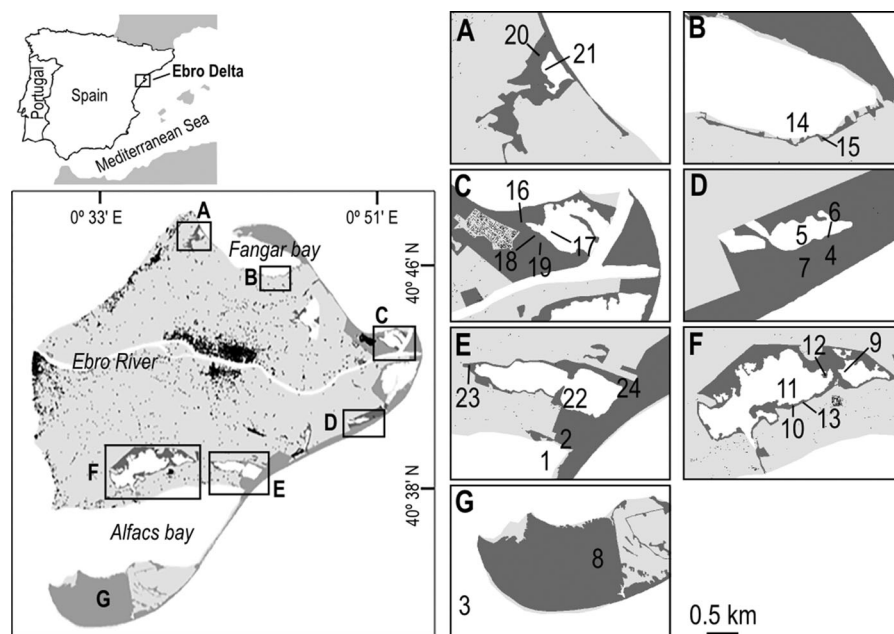
fluctuations (Castro et al. 2013). Such processes are essential for delta evolution (Giosan and Goodbred 2007; Ibáñez et al. 2014).

Another useful approach is the one pioneered by Wachnicka et al. (2010, 2011) in Florida Bay and the Everglades, who used diatoms as indicators of coastal wetland habitats, to complement use of transfer functions. To our knowledge, no work of this kind has been done outside Florida coastal environments, and certainly not in Mediterranean coastal wetlands, where several distinct wetland habitats (e.g. marshes, lagoons, sandflats, bays) occur in a patchy distribution over a relatively small area, as in the Ebro Delta (Ibáñez et al. 2000).

Our study had three main aims: (1) to determine the main ecological factors that affect the distribution of benthic diatom assemblages in the Ebro Delta, NE Iberian Peninsula, (2) to identify indicator species for the main habitat types, and (3) to develop a diatom-based conductivity transfer function for the Ebro Delta. With results from the present study (conductivity transfer function and indicator species for the main habitat types), we should be able to improve predictions made in an earlier study (Benito et al. 2014), in which we used a GIS approach to model actual and potential habitat distributions, under scenarios of no human disturbance, in the Ebro Delta. It is our hope that this approach will help establish benchmark or reference conditions for deltaic habitats to support environmental policies (e.g. Water Framework Directive) and better define restoration targets.

#### Study area

The study was performed in the Ebro Delta (330 km<sup>2</sup>, Fig. 1), which is one of the largest coastal wetlands in the NW Mediterranean. The deltaic plain contains diverse ecosystems, is extremely important for biodiversity (e.g. it is the second most important “Special Protection Area” for birds in Spain), and has considerable economic value (e.g. agricultural, fisheries, aquaculture and tourism activities provide about €120 million annually) (SEO/BirdLife 1997). The Delta is a micro-tidal system with an astronomical tidal range of about 20–30 cm, though meteorological tides can exceed 1 m. In the last ca. 150 years, large parts of the Ebro Delta have been transformed for agricultural purposes (Cardoch et al. 2002). Despite intensive use of the Delta for agriculture, it still contains a high



**Fig. 1** Regions within the Ebro Delta (a–g) and the locations of the 24 sampling sites (1–24). a Olles; b Fangar; c Garxal; d Aufacada; e Tancada–Alfacs; f Encanyissada–Clot; g Banya. For detailed information about the 24 sampling sites see ESM Table 2

diversity of natural aquatic ecosystems, such as coastal lagoons, marshes, mudflats and shallow bays, which are included in the Ebro Delta Natural Park (EDNP) and in the Natura 2000 Network, and all represent good examples of Mediterranean wetland habitats.

## Materials and methods

### Sampling

Twenty-four sites were selected in nine different regions within the EDNP [Fig. 1; Table 1 and Electronic Supplementary Material (ESM) Table 2] to encompass the main environmental gradients (e.g. salinity, nutrients) and habitat types in the study area. Specifically, the coastal habitats selected for this study were: coastal lagoons, salt marshes (i.e. *Salicornia* and *Juncus* marshes), brackish marshes (i.e. *Phragmites* marshes), microbial mats, semi-enclosed shallow bays, and nearshore marine waters.

Sampling of sediment and overlying water, and in situ measurement of selected environmental variables, were performed in November 2012, April 2013 and August 2013 to evaluate the contribution (if any) of seasonal variation in the time-averaged diatom

communities sampled. The surface sediment layer, which provides a spatially and temporally integrated sample at each site, was collected using a 5.7-cm-diameter corer (Beeker-type sampler), except at the nearshore open-sea site, where a grab sampler was needed because of the depth of the overlying water. The corer was pressed into the sediment to ~30 cm depth to ensure the top layer was collected. The sediment was then carefully extruded to expose the top 0.5 cm of the core, which was transferred to a vial. This process was repeated three times at each site to cover spatial variability of diatom assemblages and the three samples were merged in a single vial and preserved with 4 % formalin. Samples were taken near the edges of coastal lagoons and bays, whereas in marshes samples were collected within the marsh, far from nearby lagoons or bays. In a few cases sampling was not possible because the site had dried. Thus, we obtained a total dataset of 61 samples. Simultaneous with sediment sampling, and taking care to avoid sediment resuspension, we collected water samples by hand from near the bottom of the water column and stored them on ice for transport to the laboratory. Inorganic dissolved nutrients ( $\text{NO}_3^-$ -N,  $\text{NO}_2^-$ -N,  $\text{NH}_4^+$ -N,  $\text{PO}_4^{3-}$ -P and  $\text{SiO}_4^{4-}$ -Si) were measured in filtered samples, following Grasshoff et al. (1983). Seston chlorophyll *a* and pheophytin *a* were

**Table 1** Sampling scheme showing selected habitats within the Ebro Delta

Delta region	Habitats					Historical impacts	Current status	
	Nearshore open sea	Semi-enclosed bay	Microbial mat	Coastal lagoon	<i>Salicornia</i> marsh			<i>Juncus</i> marsh
Olles	-	-	-	X	-	-	X	The ecological status of the lagoon and adjacent wetlands is poor, with accumulation of organic matter in the sediment
Clot	-	-	-	X	-	-	-	The ecological status is quite good, but far from reference conditions because of freshwater inputs
Garxal	-	-	-	X	X	X	X	The ecological status is good because of its undisturbed status, though it receives nitrogen inputs from the Ebro river
Aufacada	-	-	-	X	X	X	X	The lagoon is undergoing restoration that is leading to improvement of its ecological status
Encanyissada	-	-	-	X	X	X	X	Since the beginning of the 1990s the lagoon's ecological status has improved because of construction of channels to prevent direct freshwater discharges coming from rice fields
Tancada	-	-	-	X	X	-	X	Since the beginning of the 1990s the lagoon's ecological status has improved because of construction of channels to prevent direct freshwater discharges coming from rice fields

**Table 1** continued

Delta region	Habitats					Historical impacts			Current status
	Nearshore open sea	Semi-enclosed bay	Microbial mat	Coastal lagoon	<i>Salicornia</i> marsh	<i>Juncus</i> marsh	<i>Phragmites</i> marsh		
Fangar	-	X	-	-	X	-	-	Freshwater inputs coming from rice field drainage waters led to lower salinity and eutrophication	The ecological status has improved in the last decades because of better rice farming practices and better water quality in the Ebro River
Alfacs	-	X	-	-	X	-	-	Freshwater inputs coming from rice field drainage waters led to lower salinity and eutrophication	The ecological status has improved in the last decades because of better rice farming practices and better water quality in the Ebro River
Banya	X	-	X	-	-	-	-	Sand spit with salt marsh habitat and nearby marine waters with no significant human alterations	The ecological status is good, given its pristine condition

Brief description of the historical impacts and current status of each Delta region are also given

extracted with 90 % acetone after filtration, measured with a fluorometer, and calculated using the Lorenzen formula (Lorenzen 1966). Additionally, electrical conductivity EC<sub>25</sub> (mS/cm), hereafter referred to as conductivity, temperature (°C), dissolved oxygen (DO, %), water level (cm) and pH were measured in situ with a YSI 556 multiprobe. Furthermore, in one sample campaign (April 2013), two additional sediment samples (top 1 cm of the sediment layer) were taken from each site to estimate the following sediment properties: (1) the sediment fraction >0.063 mm referred to here as percent sand, determined by the wet sieving method (Facca and Sfriso 2007) and, (2) organic matter content, as loss on ignition (LOI at 450 °C for 4 h) (Dean 1974).

### Diatom processing and identification

For diatom analysis, sediment subsamples (~10 mL of slurry) were cleaned using 30 % H<sub>2</sub>O<sub>2</sub> and 37 % HCl to remove organic material and carbonates, respectively, and then rinsed several times with deionised water (Renberg 1990). After complete homogenization, ~0.5 mL of cleaned material was air dried on cover slips and permanently mounted in Naphrax (refractive index 1.74). Diatom slides were examined at 1000×, using a Zeiss Axio A.1 light microscope equipped with differential interference contrast. Light micrographs were taken using a Canon digital camera. At least 400 diatom valves were counted per sample along transects. All identifications were made to species level when possible, mainly using diatom floras by Krammer and Lange-Bertalot (1986a, b) and Witkowski et al. (2000), but also many other taxonomic and floristic works, including Tomàs (1988) and Álvarez-Blanco and Blanco (2014).

### Multivariate ordinations

Diatom abundances, expressed as relative abundances, were square root transformed to stabilize their variance. To reduce the effect of rare species in the multivariate space, only taxa with a relative abundance >3 % in at least one sample and occurring in >2 samples, were included in the analyses. Environmental variables, including water physico-chemical data and sediment properties, were checked for skewness and transformed (log<sub>10</sub> + 1) to improve linearity and homoscedasticity.

Diatom data were analysed by means of cluster and ordination analyses. First, to group samples according to their species composition similarity, we performed a hierarchical cluster analysis based on Bray–Curtis similarity, with flexible beta as the linkage method (Dufrière and Legendre 1997). Diatom data were also analysed with detrended correspondence analysis (DCA). As an indirect ordination method, DCA allows the major patterns of variation in the diatom data to be determined without incorporating environmental variables. Both methods (i.e. cluster analysis and DCA) are complementary and helped identify groups of diatom samples having similar species (cluster analysis) and provided information about the pattern of variation within and between groups in ordination space (DCA).

DCA ordination was also used to estimate the length of the gradient. Axis lengths  $>2$  standard deviation (SD) units mean a complete turnover of species (Legendre and Legendre 1998) and therefore a unimodal species response can be assumed for the species data. DCA with downweighting for rare species was applied to the diatom data and a gradient length of 3.88 SD was obtained, indicating that unimodal models were adequate for our data. Consequently, canonical correspondence analysis (CCA) was used to relate the structure of the diatom assemblages to measured environmental variables.

A preliminary CCA, including all measured environmental variables, was performed to identify collinear variables, based on the inspection of variance inflation factors (VIF). All environmental variables with VIFs  $>20$  were removed for subsequent CCAs. Next, a series of CCAs was performed using a single environmental variable at a time. This was done to quantify the explanatory power of each environmental variable on the diatom data set (i.e. marginal effects), as well as to obtain a full suite of individually significant variables, including the most powerful environmental predictors. The variables that did not explain a significant contribution based on 999 Monte Carlo permutation tests were excluded from the following analyses. Then, a series of partial CCAs was applied using the previously selected variables individually, with the remaining ones as covariables. This was employed to determine which variable made independent contributions to explaining the total variation in the diatom species data (i.e. unique effects), as well as the contribution of interactions

between variables. The statistical significance of environmental variables was assessed by 999 Monte Carlo permutation tests at  $p < 0.05$ .

#### Indicator species analyses

Indicator species analyses (IV) (Dufrière and Legendre 1997) were used to identify diatom species that are indicators of the diatom assemblages derived from cluster analyses and CCA. The rationale of the method is that the indicator value of a given species will be maximal (IndVal varies between 0 and 100) if all the individuals are found in a single group (high specificity) and they are present in all samples of that group (high fidelity). The statistical significance of the indicator taxa was assessed using a randomization method involving 999 permutations.

#### Diatom-based inference model

The ratio of the first eigenvalue from the CCA-constrained axis ( $\lambda_1$ ) to the first eigenvalue from the unconstrained axis ( $\lambda_2$ ) was used to choose which environmental variable was most suitable for modelling species' response to the selected variable. Ideally, the ratio  $\lambda_1/\lambda_2$  should be  $>1$  (Juggins 2013) or at least not lower than 0.5 (Kingston et al. 1992), as this will ensure that the variable of interest explains a significant and independent portion of the variation in the biological data. Additionally, detrended canonical correspondence analysis (DCCA) was used to check whether a linear or unimodal response model is most appropriate for building the diatom inference model (Birks 1998).

Weighted averaging (WA) with classical and inverse deshrinking (also known as simple WA), and with/without tolerance downweighting, was used as a transfer function statistical technique. Weighted averaging partial least squares (WA-PLS) was also used to determine if this method led to a substantial improvement over WA when long environmental gradients and low noise affect the dataset (Juggins and Birks 2012). All models were built using  $\log_{10}$  transformed conductivity and square-root transformed species data. Leave-one-out (LOO, also termed jack-knifing) and leave-one-site-out (LOSO) were chosen as cross-validation methods (Birks 1998). The latter takes into account the effect of potential spatial autocorrelation on model performance, and is considered more



appropriate for clustered data sets (Payne et al. 2012). The performance (predictive ability) of each model was determined by evaluating different parameters: correlation between observed and inferred conductivities ( $r_{\text{LOO/LOSO}}^2$ ), root mean square error of prediction ( $\text{RMSEP}_{\text{LOO/LOSO}}$ ), and maximum bias $_{\text{LOO/LOSO}}$ . The criteria to choose the preferred model were high  $r^2$ , low RMSEP and low maximum bias, following Birks (1998). To correct the possible bias in RMSEP estimation caused by uneven sampling along the environmental gradient of interest, we applied the segment-wise RMSEP approach (Telford and Birks 2011). All models were initially built using a screened diatom data set (137 diatom taxa). However, effects of (1) including all diatom taxa (424) and (2) removing outlier samples, following Reed (1998), were also assessed to see if there was any improvement in the transfer functions.

Most multivariate analyses were performed using R version 3.0.1 (R Development Core Team 2010). C2 version 1.6.8 (Juggins 2003) was used to calculate all transfer functions. Finally, CANOCO version 4.5 (Ter Braak and Smilauer 2002) was used to carry out DCCA.

## Results

### Environmental gradients

A summary of the environmental variables measured for each of the 24 study sites is in ESM Table 2. The sites covered a wide range of conductivity (1.13–107.67 mS/cm),  $\text{NO}_3^-$ -N (0.6–1233.7  $\mu\text{g/L}$ ),  $\text{PO}_4^{3-}$ -N (2.5–201.4  $\mu\text{g/L}$ ),  $\text{NH}_4^+$ -N (2.5–358.1  $\mu\text{g/L}$ ), sand proportion (0–93.3 %) and organic matter content (0.9–97.0 %). According to the sediment properties, a clear pattern was observed. Sites with low sand proportion had high organic matter content, whereas those with higher sand proportions had lower organic matter content.

### Diatom assemblages and relationships with environmental variables

A total of 424 diatom taxa, representing 85 genera, were identified in the study sites (ESM Table 1), out of which 137 taxa occurred in more than two samples and

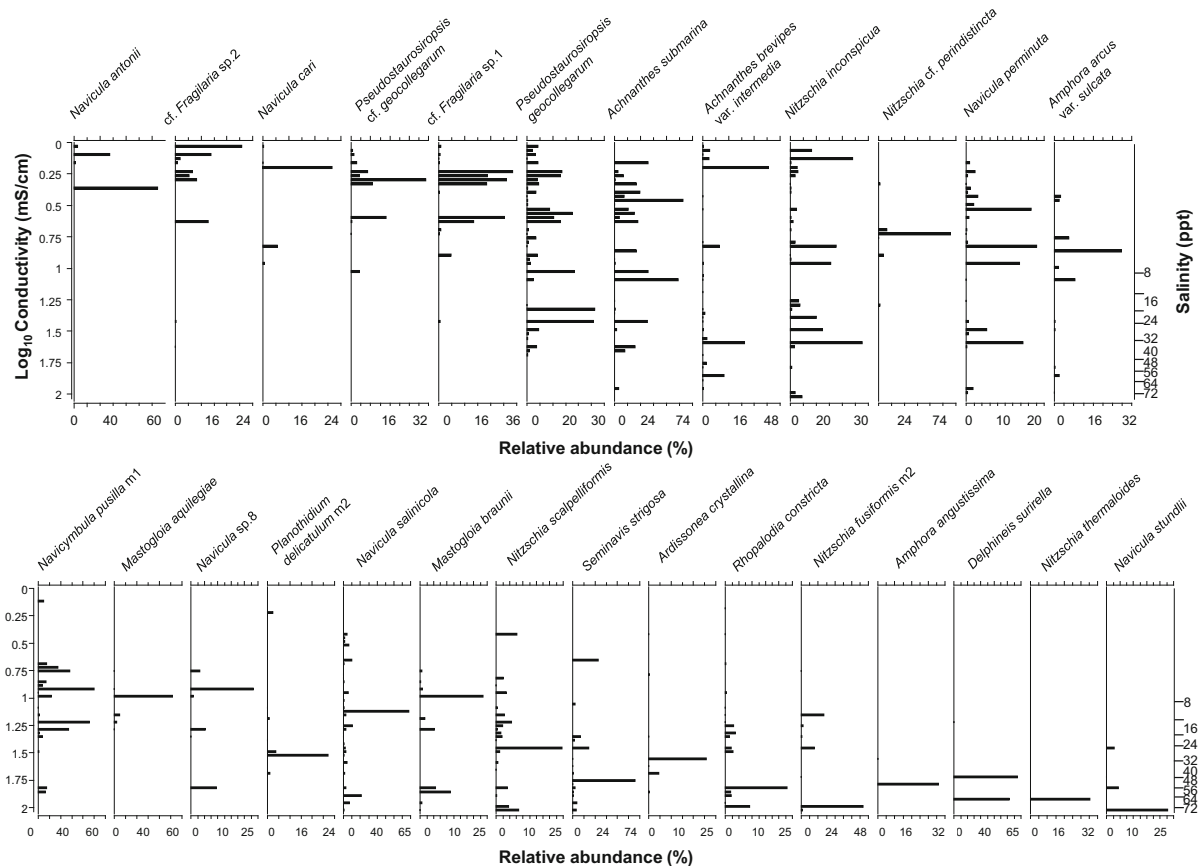
had a relative abundance  $>3$  %, and were the ones principally used in the statistical analyses. Species richness ranged from 9 to 58, with an average of 36. Most of the species identified were benthic (96.4 %). Twenty-seven species were abundant (relative abundance  $\geq 20$  % in at least one sample) across the study sites (Fig. 2). Among these, *Achnanthes submarina*, *Pseudostaurosiropsis geocollegarum* and *Navicula salinicola* were also widespread (i.e. occurring in  $\geq 50$  % of the samples), together with *Nitzschia constricta* and *Cocconeis placentula* var. *placentula*. The relationship between some of these abundant diatoms and conductivity showed a clear trend of species turnover along the conductivity gradient (Fig. 2).

Cluster analyses identified five diatom groups according to the similarity in species composition (ESM Fig. 1). The environmental characteristics of each cluster group are shown in Fig. 3. Cluster 1 (17 samples) comprised salt marsh samples (i.e. *Salicornia* and *Juncus* marshes: Fig. 1, sampling sites 2, 4, 7, 15, 24) and the two microbial mat samples (sampling site 8). All samples of this group had high sand proportion ( $\geq \sim 60$  %) and either medium ( $\sim 21$  mS/cm) or high (up to  $\sim 75$  mS/cm) conductivity. Cluster 2 (13 samples) mainly comprised samples from brackish marshes (i.e. *Phragmites* marshes: Fig. 1, sampling sites 6, 10, 12, 13, 21, 23), with the exception of four salt marsh samples from the Encanyissada region (Fig. 1, sampling sites 10, 13), which had especially high organic matter content in their sediment. This group, 2, clustered samples with a wide range of water conductivity, from freshwater to as much as  $\sim 42$  mS/cm. There was also a wide variation in sediment sand proportion, but the overall average was lower than any other cluster except cluster 5 (nearshore open sea). Cluster 3 (15 samples) was composed of brackish coastal lagoon samples, with medium or high conductivities averaging  $\sim 44$  mS/cm (i.e. from Encanyissada and Tancada lagoons: Fig. 1, sampling sites 11 and 22), and the bay samples (i.e. from Alfacs and Fangar Bays: Fig. 1, sampling sites 1 and 14). In contrast, cluster 4 (14 samples) comprised samples from coastal lagoons with fresher conditions, i.e. with conductivities averaging  $\sim 10$  mS/cm and never exceeding 20 mS/cm (from Aufacada, Garxal, Olles and Clot Lagoons: Fig. 1, sampling sites 5, 9, 17, 20), together with brackish marsh samples from a coastal lagoon that is

directly connected to the Ebro River mouth (Garxal Lagoon: Fig. 1, sampling site 18). Samples of this cluster displayed a wide range of  $\text{NO}_3^-$ -N and  $\text{NO}_2^-$ -N content, as well as sediment sand and organic matter percentages. Finally, cluster 5 consisted only of the two samples from the nearshore open sea, with high conductivity, the greatest water depth and rather low sand proportion; indeed visual inspection revealed a muddy sediment (Fig. 1, sampling site 3).

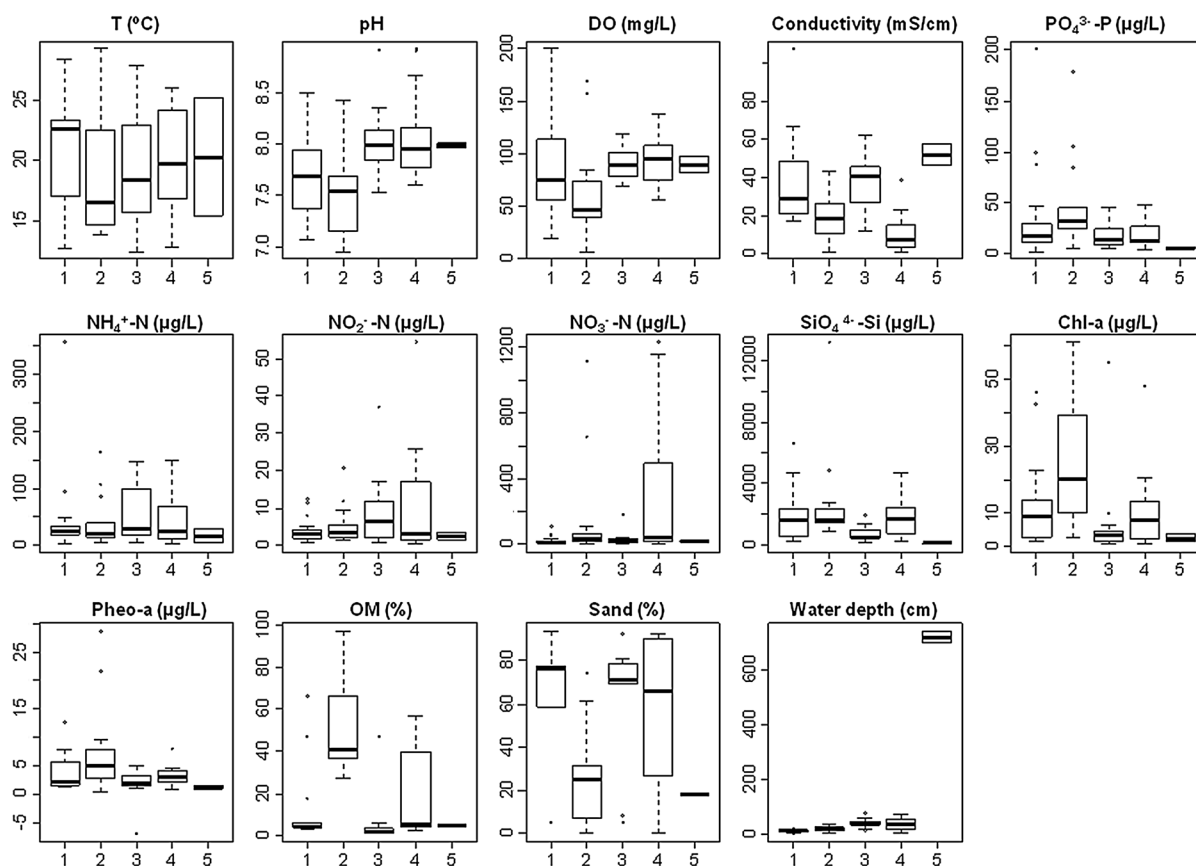
The gradient lengths (3.88 and 5.04 SD) revealed by the DCA confirmed the suitability of unimodal constrained ordination methods (CCA) to explore the relationship between diatom assemblages and the main environmental variables. The first two axes of an initial CCA performed with all 14 measured environmental variables and 137 taxa (those with a relative abundance  $>3\%$  in at least one sample and occurring

in  $>2$  samples), explained 12.3 % of the variance in the diatom data. The CCA eigenvalues ( $\lambda_{1\text{CCA}} = 0.42$ ;  $\lambda_{2\text{CCA}} = 0.36$ ) were similar to those of the DCA ( $\lambda_{1\text{DCA}} = 0.53$ ;  $\lambda_{2\text{DCA}} = 0.44$ ), thus indicating that the measured environmental variables have a significant influence on the diatom species distribution. There was no significant collinearity between environmental variables because all variance inflation factors were  $<10$  and therefore all environmental variables were subsequently retained. Among the 14 environmental variables measured, 10 accounted for significant portions of the total variance ( $p < 0.05$ ) in the diatom species data and were selected for further analyses. These variables were (from higher to lower explained marginal variance): conductivity (5.57 %), water depth (5.34 %), organic matter content (4.40 %), sand proportion (3.42 %),



**Fig. 2** Relative abundances of the most abundant diatom species ( $\geq 20\%$  in at least one sample) in the Ebro Delta dataset along the  $\log_{10}$  conductivity gradient. Species are ordered according to their  $\log_{10}$  conductivity optimum

(estimated using weighted average regression). Samples are arranged by increasing  $\log_{10}$  conductivity (mS/cm), from low (*top*) to high conductivities (*bottom*)



**Fig. 3** Ranges of the measured environmental variables (*box plots*) for the diatom groups defined by cluster analysis. 1, salt marshes; 2, brackish marshes; 3, brackish coastal lagoons and bays; 4, coastal lagoons with fresher conditions; 5, nearshore open sea. *T* temperature, *pH*, *DO* dissolved oxygen saturation, *conductivity* conductivity,  $PO_4^{3-}-P$  orthophosphate–

phosphorus,  $NH_4^+-N$  ammonium–nitrogen,  $NO_2^- -N$  nitrite–nitrogen,  $NO_3^- -N$  nitrate–nitrogen,  $SiO_4^{4-}-Si$  orthosilicate–silicon, *Chl-a* seston chlorophyll *a*, *Pheo-a* pheophytin *a*, *OM* organic matter content, *Sand* sand proportion. The *boxes* represent the 25th and 75th percentiles, and the median (*middle line* inside each *box*)

$NO_3^- -N$  (2.78 %),  $NO_2^- -N$  (2.61 %), *pH* (2.61 %),  $SiO_4^{4-}-Si$  (2.59 %), seston chlorophyll *a* (2.53 %) and  $PO_4^{3-}-P$  (2.37 %). Partial CCAs determined that conductivity, water depth, organic matter content, sand proportion,  $NO_2^- -N$  and  $NO_3^- -N$  independently explained significant portions of the variance in the diatom data (ESM Table 3). Interestingly, water depth was also selected as significant even after the two nearshore open sea samples were removed, these two being anomalous in our data set because they were collected at depths >7 m.

The first two axes of the CCA, with the reduced set of environmental variables, explained 11.5 % of the diatom variance, with conductivity explaining the greatest variance (4.6 %) once the effect of the other variables had been taken into account (ESM Table 3).

The CCA ordination performed with conductivity, water depth, organic matter content, sand proportion,  $NO_2^- -N$  and  $NO_3^- -N$  (the six variables selected by the reduced environmental data set that accounted for independent and significant unique effects) and with 137 diatom species, supported the cluster division of samples according to diatom composition (Fig. 4). CCA axis 1 (6.3 % of the explained variance) arranged samples from predominantly brackish/marine habitats (salt marshes; brackish coastal lagoons and bays; and nearshore open sea, i.e. clusters 1, 3 and 5, respectively) to fresher habitats (*Phragmites* marshes and those coastal lagoons with lower conductivity, i.e. clusters 2 and 4, respectively). Thus, this axis is principally a conductivity gradient. CCA axis 2 (5.2 % of the explained variance) separated the marshes that

have very shallow waters (i.e. *Salicornia*, *Juncus* and *Phragmites* marshes, and microbial mats), from the coastal lagoons, bays and nearshore open sea habitats. Therefore, CCA axis 2 can be considered a shallowness (water depth) gradient.

### Indicator species

Indicator species for the five diatom groups identified in the Ebro Delta were recognised through indicator species analysis (IV). Thirty-nine species (Fig. 5) showed statistically significant ( $p < 0.05$ ) indicator values (IV) and had high IV ( $>50\%$ ) and could therefore be considered good indicator species (Table 2). Interestingly, for clusters 1–3, the indicator species showing full specificity (100%) are also the ones showing the lowest fidelity values ( $\leq 40\%$ ), indicating they are only present in particular samples within the group. Thus, within the salt marshes group, *Mastogloia aquilegiae* and *Amphora* cf. *roettgeri* occurred only in *Juncus* marshes and in microbial mats, respectively. In the group of brackish coastal lagoons and bays, *Navicula viminoides* and *Navicula* cf. *hansenii* were recorded only in Encanyissada Lagoon, whereas *Ardissonea crystallina* and *Navicula* sp. 7 were found only in Tancada Lagoon.

### Diatom-based conductivity model

Results of partial CCAs confirmed that conductivity explained the largest and most significant amount of variability in the diatom species data. DCCA axis-1 indicated a gradient length of 3.2 SD units, supporting the use of unimodal methods (WA and WA-PLS). Conductivity showed the highest ratio of the first (constrained) CCA axis ( $\lambda_1$ ) to the first unconstrained axis ( $\lambda_2$ ) ( $\lambda_1/\lambda_2 = 0.80$ ) (ESM Table 3), indicating that conductivity is an ecologically important determinant of the distribution of diatoms in the Ebro Delta, and therefore we proceeded on the basis that a realistic diatom-based conductivity transfer function could be developed.

Simple WA with classical deshrinking, performed with all diatom species (424 taxa) and samples (61), resulted in the best-performing diatom-conductivity model, with the highest  $r_{\text{LOO}}^2$  (0.64), lowest  $\text{RMSEP}_{\text{LOO}}$  (0.241  $\log_{10}$  mS/cm) and lowest maximum bias (0.305  $\log_{10}$  mS/cm) (ESM Table 4). The performance

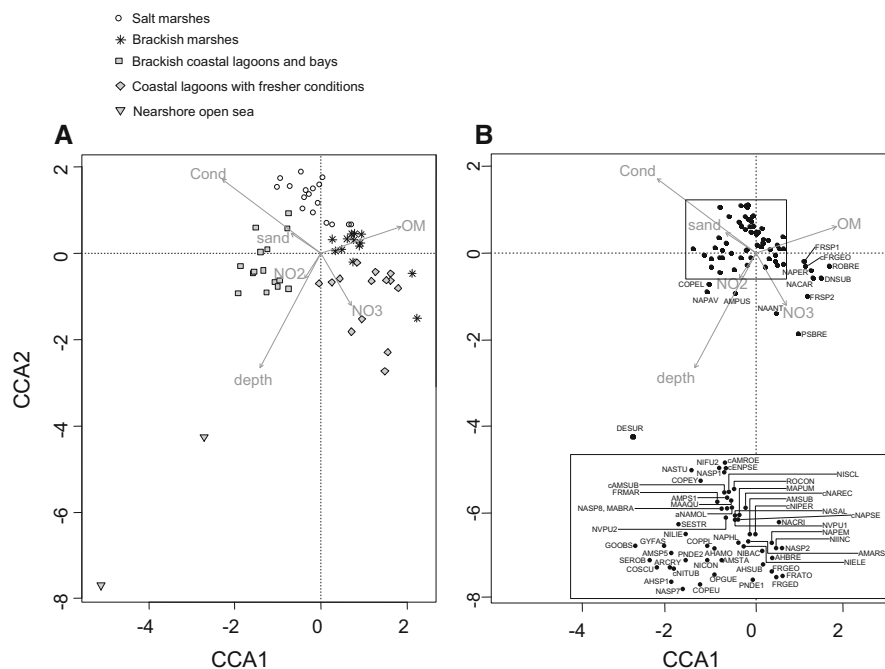
parameters based on WA-PLS methods did not show a significant improvement over simple WA in terms of  $r^2$  and  $\text{RMSEP}$  (results not presented). Segment-wise  $\text{RMSEP}$  under the two cross validation methods (LOO/LOSO) was higher (0.302  $\log_{10}$  mS/cm) than model  $\text{RMSEP}_{\text{LOO}}$ , indicating that  $\text{RMSEP}$  values were biased because of (1) uneven sampling of the conductivity gradient and, (2) clustered samples (ESM Table 4). Following Reed (1998), outliers can be identified as those samples that have a jack-knifed residual  $>25\%$  of the conductivity range (conductivity range = 1.71  $\log_{10}$  mS/cm; 25% of the conductivity range = 0.427  $\log_{10}$  mS/cm). Applying such a criterion, two potential outliers were identified: a *Phragmites* marsh sample from the Encanyissada region collected in November 2012 (jack-knifed residual = 0.658  $\log_{10}$  mS/cm) and a sample of Olles Lagoon from April 2013 (jack-knifed residual = 0.545  $\log_{10}$  mS/cm). The deletion of these outliers resulted in an improvement of the WA model performance in terms of  $r^2$  ( $r_{\text{LOO}}^2 = 0.70$ ). Regardless of this improvement, segment-wise  $\text{RMSEP}_{\text{LOSO}}$  revealed a decrease in the model performance, and therefore, we decided to keep these two potential outliers in the WA model.

The preferred WA-based model had an  $r_{\text{LOSO}}^2 = 0.64$  and a  $\text{RMSEP}_{\text{LOSO}} = 0.27 \log_{10}$  mS/cm (Fig. 6a, b). Note that the simple WA-based model performed better (in terms of all performance parameters:  $r_{\text{LOO/LOSO}}^2$ ,  $\text{RMSEP}_{\text{LOO/LOSO}}$  and maximum bias $_{\text{LOO/LOSO}}$ ) when all diatom taxa ( $n = 424$ ) were used for the calibration of the transfer function than when only the screened diatom data ( $n = 137$  taxa) were used (ESM Table 4).

## Discussion

### Diatom–environment relationships

The environmental variables identified as important for structuring the diatom distributions explained  $\sim 12\%$  of the total variance, which is low when compared with the total variance explained in many freshwater systems (Schönfelder et al. 2002; Leira and Sabater 2005), but is not dissimilar to the total variance explained in previous works dealing with the ecology of diatoms in coastal habitats ( $\sim 7\text{--}25\%$ :



**Fig. 4** Canonical correspondence analysis (CCA) diagram showing the relationships of **a** samples and **b** species with the selected environmental variables. Species reaching  $\geq 10\%$  maximum relative abundance in at least one sample are shown. Only the six environmental variables that accounted for statistically significant unique effects are shown (*Cond*

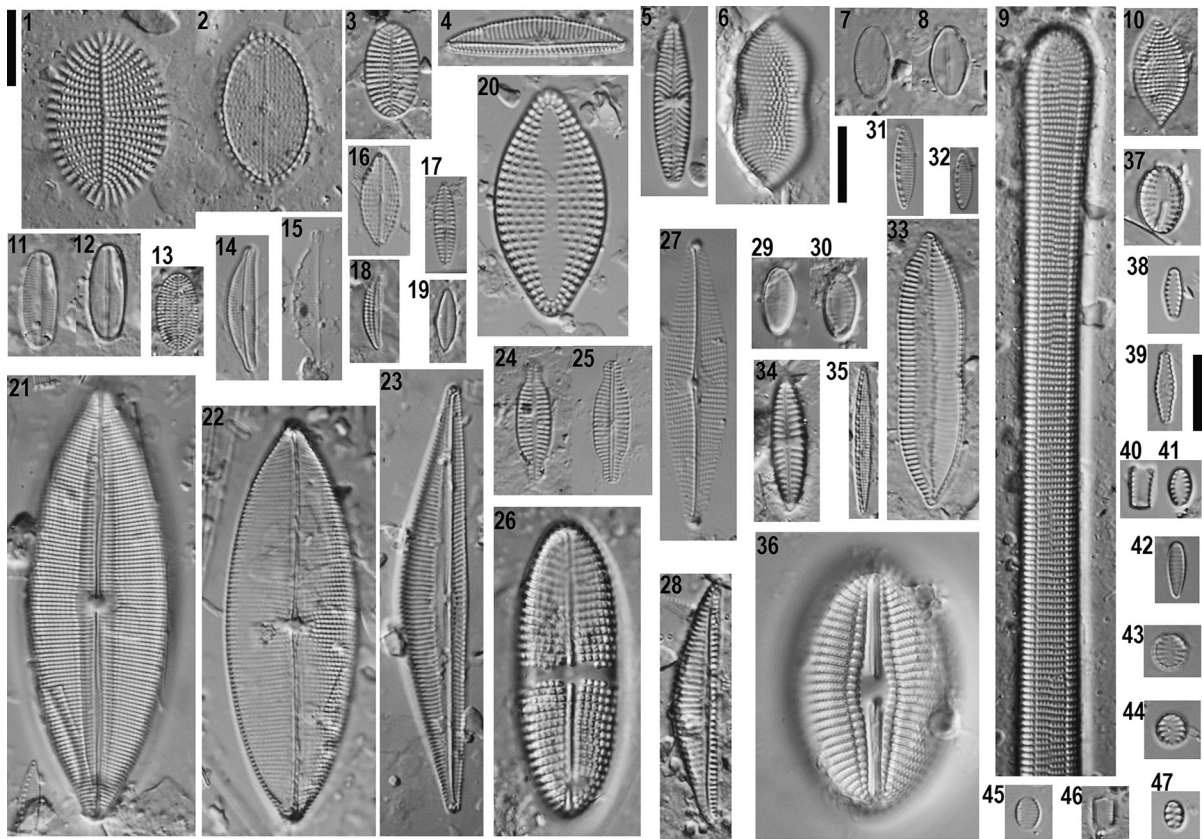
conductivity, *depth* water depth, *OM* organic matter content, *sand* sand proportion, *NO<sub>2</sub>* nitrite–nitrogen, *NO<sub>3</sub>* nitrate–nitrogen). The sample *symbols* correspond to the diatom groups defined by cluster analysis (see text). For full species names see ESM Table 1. Species scores located at the centre of the diagram are shown separately in the bottom part of **b**

Sullivan 1978; Trobajo et al. 2004). Such relatively low values are not surprising because of the particularly dynamic nature of these coastal environments (wetlands and lagoons, deltas, estuaries, etc.), which exacerbates the problem of “potential mismatches between time-integrated sedimentary assemblages compared to ‘spot’ measurements of environmental variables” (Saunders 2011), especially when environmental measures are taken from the water column. There is also the problem, shared with freshwater ecosystems, that large biological datasets often contain many species and many zero values (Weckström and Juggins 2005).

Conductivity and shallowness (water depth) emerged as the main environmental gradients affecting the benthic diatom community in the Ebro Delta. Of course, conductivity itself does not affect the physiology of diatoms. Rather, it is a proxy for the overall amounts of salts present in water (salinity), which have long been known to have a major effect on diatom distributions. Thus, although there have not

been many works similar to ours in Mediterranean deltas, Zalat and Vildary (2005) being one of the few exceptions, in other Mediterranean coastal environments salinity has, not surprisingly, been shown to be of paramount importance for the diatom assemblages (Tomàs 1988; Trobajo et al. 2004 in Spanish Mediterranean coastal wetlands). However, it is also known that in these types of systems, i.e. estuaries, salt marshes, coastal lagoons, etc., conductivity usually co-varies with other environmental variables that also influence diatom distribution, such as nutrients (Thornton et al. 2002), and therefore the role of conductivity (as a proxy for salinity) may be overestimated unless its real effect, attributable solely to conductivity, is actually distinguished. Partial canonical correspondence analyses shows that, of all the measured variables, conductivity (representing salinity) has the highest unique effect on the diatom distribution. Moreover, single-variable CCA (constrained to conductivity) revealed that conductivity also explains a statistically significant amount of the





**Fig. 5** Diatom indicator species under LM. Light microphotographs were taken under differential interference contrast (DIC), all at the same magnification. Scale bar represents 10  $\mu\text{m}$ . 1, *Cocconeis scutellum* (raphe valve); 2, *Cocconeis scutellum* (rapheless valve); 3, *Cocconeis peltoides* (rapheless valve); 4, *Navicymbula pusilla* m1; 5, *Navicula microcari*; 6, *Nitzschia coarctata*; 7, *Achnanthes fogedii* (rapheless valve); 8, *Achnanthes fogedii* (raphe valve); 9, *Ardissonaea crystallina*; 10, *Nitzschia pararostrata*; 11, *Achnanthes* sp.1 (rapheless valve); 12, *Achnanthes* sp.1; 13, *Cocconeis* cf. *neothumensis* var. *marina* (rapheless valve); 14, *Amphora* sp. 1; 15, *Amphora* cf. *roettgeri*; 16, *Navicula vimineoides*; 17, *Navicula perminuta*; 18, *Amphora* sp.5; 19, *Navicula* sp.7; 20, *Delphineis surirella*;

21, *Mastogloia braunii*; 22, *Mastogloia aquilegiae*; 23, *Seminavis robusta*; 24, *Achnanthes amoena* (rapheless valve); 25, *Achnanthes amoena* (raphe valve); 26, *Achnanthes brevipes* var. *intermedia*; 27, *Navicula gregaria*; 28, *Seminavis strigosa*; 29, 30, *Planothidium deperditum* (frustule); 31, 32, *Nitzschia inconspicua*; 33, *Nitzschia constricta*; 34, *Navicula* cf. *hansenii*; 35, *Nitzschia liebethuthii*; 36, *Diploneis smithii*; 37, *Fragilaria* cf. *neoe elliptica*; 38, *Pseudostaurosira* cf. *geocollegarum*; 39, *Pseudostaurosira* cf. *geocollegarum*; 40, cf. *Fragilaria* sp.1 (frustule); 41, cf. *Fragilaria* sp.1; 42, *Fragilaria gedanensis*; 43, *Fragilaria* cf. *sopotensis*; 44, cf. *Fragilaria* sp.2; 45, *Fragilaria atomus*; 46, *Fragilaria atomus* (frustule); 47, cf. *Opephora* sp.1

total species variance ( $\lambda_1/\lambda_2$  for conductivity = 0.80). Therefore, we are confident that salinity, as a single factor, is very likely the overriding environmental variable that influences diatom assemblages in the Ebro Delta.

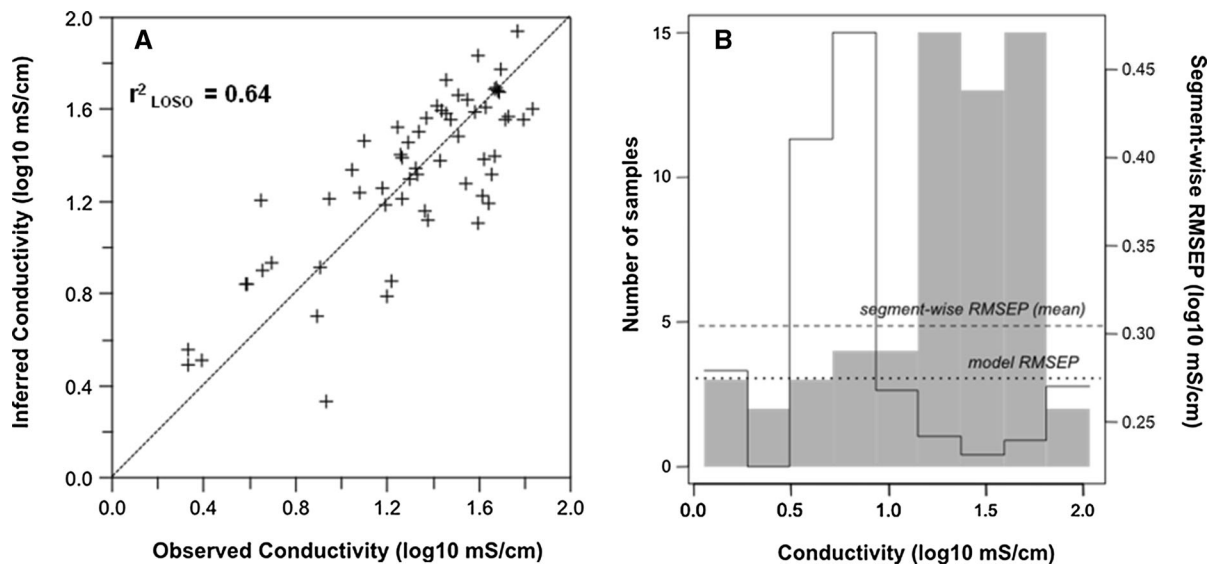
Partial CCAs also revealed significant unique effects of water depth on diatom assemblage distribution, even when the two samples from open sea habitats were removed, these effects being only slightly lower than those accounted for by conductivity (ESM Table 3). Water depth has also been found

to be an important variable affecting diatom distributions in other coastal habitats (Ryves et al. 2004). The way water depth affects the diatom communities of the Ebro Delta, however, is probably much more complex than salinity. For instance, greater water depth provides the opportunity for planktonic communities to develop, as has been pointed out by several authors (Weckström and Juggins 2005). In the Ebro Delta, this effect can only make a limited contribution because benthic diatom species dominate the samples at all depths, even at the two nearshore, open sea sites

**Table 2** Indicator values (IV) of diatom indicator species of each habitat group identified by cluster analysis (see text)

Diatom species	Code	S	F	IV	<i>p</i> value
Salt marshes (cluster 1: <i>Salicornia</i> , <i>Juncus</i> marshes, and microbial mats)					
<i>Navicymbula pusilla</i> m1	NVPU1	89.1	64.7	75.9	0.024
<i>Amphora</i> sp.1	AMSP1	82.5	58.8	69.7	0.013
<i>Mastogloia braunii</i>	MABRA	92.8	41.2	61.8	0.044
<i>Mastogloia aquilegiae</i>	MAAQU	100	35.3	59.4	0.037
<i>Amphora</i> cf. <i>roettgeri</i>	cAMROE	100	29.4	54.2	0.028
Brackish marshes (cluster 2: <i>Phragmites</i> marshes)					
<i>Achnanthes brevipes</i>	AHBRE	81.0	84.6	82.8	0.018
<i>Navicula perminuta</i>	NAPER	90.0	61.5	74.4	0.009
<i>Diploneis smithii</i>	DISMI	88.2	61.5	73.7	0.015
<i>Navicula microcari</i>	NAMIC	91.1	53.8	70.1	0.018
<i>Nitzschia inconspicua</i>	NIINC	77.6	69.2	73.3	0.040
<i>Fragilaria</i> cf. <i>neoe elliptica</i>	cFRNEO	87.2	46.2	63.4	0.046
Brackish coastal lagoons and bays (cluster 3)					
<i>Cocconeis scutellum</i>	COSCU	93.2	80.0	86.4	0.011
<i>Achnanthes</i> sp.1	AHSP1	99.2	73.3	85.3	0.014
<i>Seminavis strigosa</i>	SESTR	81.9	80.0	80.9	0.017
<i>Cocconeis</i> cf. <i>neothumensis</i> var. <i>marina</i>	cCONEM	95.1	66.7	79.6	0.019
<i>Nitzschia pararostrata</i>	NIPAR	91.1	60.0	73.9	0.019
<i>Achnanthes amoena</i>	AHAMO	76.1	66.7	71.3	0.019
<i>Amphora</i> sp.5	AMSP5	67.8	73.3	70.5	0.033
<i>Nitzschia constricta</i>	NICON	59.8	80.0	69.2	0.048
<i>Seminavis robusta</i>	SEROB	99.4	46.7	68.1	0.012
<i>Nitzschia liebetruthii</i>	NILIE	85.6	53.3	67.6	0.017
<i>Planothidium deperditum</i>	PLDEP	95.4	46.7	66.7	0.023
<i>Cocconeis peltoides</i>	COPEL	82.1	53.3	66.2	0.012
<i>Navicula vimineoides</i>	NAVIM	100	40.0	63.2	0.018
<i>Navicula</i> cf. <i>hansenii</i>	cNAHAN	100	40.0	63.2	0.018
<i>Ardissonea crystallina</i>	ARCRY	97.4	33.3	57.0	0.045
<i>Navicula</i> sp.7	NASP7	94.9	33.3	56.3	0.043
Coastal lagoons with fresher conditions (cluster 4)					
Cf. <i>Fragilaria</i> sp.1	FRSP1	96.2	78.6	86.9	0.007
<i>Fragilaria atomus</i>	FRATO	93.5	78.6	85.7	0.005
<i>Pseudostaurosiropsis geocollegarum</i>	FRGEO	67.2	100	82.0	0.002
<i>Pseudostaurosiropsis</i> cf. <i>geocollegarum</i>	cFRGEO	98.7	64.3	79.7	0.008
<i>Fragilaria</i> cf. <i>sopotensis</i>	cFRSOP	84.4	71.4	77.6	0.029
<i>Navicula gregaria</i>	NAGRE	61.4	92.9	75.5	0.027
<i>Fragilaria gedanensis</i>	FRGED	87.9	64.3	75.2	0.034
Cf. <i>Fragilaria</i> sp.2	FRSP2	96.9	57.1	74.4	0.015
Cf. <i>Opephora</i> sp.1	OPSP1	89.1	50.0	66.8	0.025
<i>Achnanthes fagedii</i>	AHFOG	76.1	57.1	66.0	0.043
Nearshore open sea (cluster 5)					
<i>Delphineis surirella</i>	DESUR	99.2	100	100	0.001
<i>Nitzschia coarctata</i>	NICOA	57.3	100	75.7	0.019

*p* value denotes the statistical significance of IV based on Monte Carlo tests (999 permutations). Values of specificity (S) and fidelity (F) are also shown



**Fig. 6** **a** Scatter plot showing the observed log<sub>10</sub> conductivity (mS/cm) against the diatom-inferred log<sub>10</sub> conductivity (mS/cm) for weighted averaging with classical deshrinking model (WA-CLA) and **b** comparison of overall RMSEP and segment-

wise RMSEP under LOSO cross validation method. Grey bars are the number of samples within the ten equal groups of log<sub>10</sub> conductivity values

(>7 m depth). Water depth can also affect diatom communities through light availability and how it buffers the effect of wind-induced turbulence and wave action; the recurrent dominant NW winds in the study area can exceed 100 km/h (Curcó et al. 2002). Hence CCA axis 2 is defined as a shallowness gradient—an integrative factor, including water depth, but also other unmeasured variables like light availability, physical habitat instability, etc.—and could be regarded as the expression of how energy enters into the system and is dissipated through it.

#### Diatom assemblages as ecological indicators of the Ebro Delta habitats

Results of this study illustrate that the five wetland habitats identified in the Ebro Delta can be characterized using diatom indicator species. Most diatom indicator species ( $p < 0.05$  and  $IV > 50$ ) showed high specificity and high fidelity to their habitat; however, interestingly, a few exhibited a combination of full specificity (100 %) and relatively low fidelity ( $\leq 40$  %), very likely indicating a preference for particular conditions or sites within the habitat type. For instance, in the salt marsh group (cluster 1), *Mastogloia aquilegiae* and *Amphora* cf. *roettgeri* were

exclusively found in *Juncus* marsh samples and microbial mat samples, respectively, and may therefore be indicators of these two environments. Again, within brackish coastal lagoons and bays (cluster 3), *Navicula viminoides* and *Navicula* cf. *hanseni*, which are small motile diatoms considered to be epipsammic, brackish-marine species (Witkowski et al. 2000), were only found in Encanyissada Lagoon (in all samples), whereas *Ardissonea crystallina* and *Navicula* sp. 7 were restricted to Tancada Lagoon (some samples), and this could reflect the different salinity regimes present in these two lagoons. Both lagoons receive freshwater from surrounding rice fields during the rice-flooding season (April–December), but Encanyissada (mesohaline) shows more freshwater influence than Tancada Lagoon (polyhaline) (Prado et al. 2012). Our results highlight the usefulness of considering not only the overall indicator value, but also the combination of specificity and fidelity values, to understand what the presence of a particular indicator species means (Rovira et al. 2012).

Distributions of some abundant diatom taxa along the conductivity gradient (Fig. 2) can serve to identify potential indicators of conductivity (as a proxy for salinity) in the Delta habitats. For instance, *Navicula stundlii* and *Nitzschia thermaloides* are only present at



the upper end of the conductivity gradient and might be indicators of saline environments. Similarly, species only present at the lower end of the gradient, such as *Navicula antonii* and *Navicula cari*, could be used as indicators of freshwater conditions.

#### Diatom-conductivity model

Performance of the model looks reasonable ( $r_{\text{LOSO}}^2 = 0.64$ ) when compared with other salinity/conductivity models developed for similar environments, such as South American estuaries (Hassan et al. 2009:  $r_{\text{jack}}^2 = 0.75$ ), Australian coastal waters (Saunders et al. 2008:  $r_{\text{jack}}^2 = 0.54$ ) and South Florida coastal wetlands (Wachnicka et al. 2011:  $r_{\text{jack}}^2 = 0.85$ ). However, application of the transfer function presented here to similar environments elsewhere might need to be done with caution, because the sampled sites come from only one Mediterranean wetland region, the Ebro Delta, and might therefore be biased by particular site-specific natural or human-driven processes. To overcome this potential problem, future research should span a wider range of Mediterranean coastal wetlands, such as the Nile Delta and salt marshes and lagoons along the African coast of the Mediterranean (Gasse et al. 1995; Flower et al. 2001), or geographically adjacent areas such as Spanish coastal wetlands (Trobajo et al. 2004) and endorheic salt lake basins (Reed 1998), to develop a combined diatom-conductivity training set.

#### Application to paleoenvironmental reconstruction

Most Mediterranean deltas and other coastal wetlands have been severely influenced by intensive agriculture, upstream catchment water use and sediment retention, eutrophication, etc., and in the future will likely be affected by sea-level rise associated with global climate change (Day et al. 2011). For example, global average sea-level rise is currently (1993–2010)  $\sim 3.0$  mm/year (Hay et al. 2015) and projected to increase (IPCC 2013), which is greater than the current sediment accretion rate in some coastal habitats of the Ebro Delta (Ibáñez et al. 2010). However, the economic and ecological value of estuaries and coastal wetlands is among the highest of any biome (on an area basis) according to the global analysis of Costanza et al. (1997). Therefore, a strategy for

sustainable management of deltas is of paramount importance and such a strategy can only be achieved by understanding the natural and anthropogenic processes that have moulded these ecosystems on a range of time scales. In the absence of long-term environmental and historical records (certainly poor for many Mediterranean coastal wetlands), paleoecological approaches are perhaps the only way to investigate how these dynamic ecosystems have been structured as a result of natural processes, together with human impacts.

Results of our study show that present-day delta diatom assemblages can be used to determine past conductivity and habitat conditions because (1) there is a significant quantifiable relationship between diatoms and present-day water conductivity, as shown by the transfer function and, (2) the most representative Delta habitat types have been successfully classified via diatom indicator species. As noted in the Introduction, whereas reconstruction of salinity has often been undertaken using changes in diatom communities, the use of diatoms as indicators of the presence of particular coastal wetland habitats is unusual, with the exception of e.g. Wachnicka et al. (2010, 2011). This aspect adds a valuable extra dimension to the study, because conductivity (as a proxy for salinity) is not the only factor structuring Ebro Delta habitats. Thus, even if the exact conductivity could be inferred for a particular site at some time in the past, we would not necessarily know which habitat was present. For instance, for a conductivity  $\sim 40$  mS/cm, both *Salicornia* marsh and coastal lagoon could be possible. The diatom indicator species approach allows the main coastal wetland habitats to be characterized and identified in adequately preserved fossil assemblages, assuming of course that sufficiently similar habitat types were present in the past, i.e. assuming uniformitarianism (Birks 2003). In the shorter term (100–150 years) this assumption seems safe for the greater part of the Ebro Delta, because the major factor involved in creating the modern appearance of the Delta, intensive rice cultivation, has operated since ca. 1860 (Comín et al. 1991). The main consequence of rice cultivation for the remaining Delta ecosystems has been alteration of the natural hydrological regime, making the period spring–summer (April–September) fresher than before, because of the rice-growing season (Prado et al. 2012). We therefore think our dataset not only covers

the most representative habitat types, but is suitable for detecting changes caused by human activities during the last 150 years. Furthermore, lagoons, salt marshes, bays and nearshore marine environments have always existed in the Delta and so both the conductivity transfer function and our indicator approach should also be useful over a longer period for tracing the evolution of the Delta and how it has been affected by historical (Iberian, Roman, mediaeval) events, taking appropriate caution because some habitats and communities may have no modern analogues. Although dense human settlement of the Delta is comparatively recent and accompanied development of intensive rice agriculture during the last 150 years, the Delta has long been used for ranching and exploited for its rich resources of wild game, fish and salt, soda manufacture, etc. (SEO/BirdLife 1997).

## Conclusions

This study presents the first dataset from a Mediterranean delta that provides a basis for inferring past habitat changes from diatom communities. Not surprisingly, the conductivity (salinity) gradient explains a significant proportion of differences among diatom assemblages and a transfer function for reconstructing water conductivity can therefore be developed. In addition, our indicator species analysis provides a basis for identifying the major wetland habitat types in the Delta from the diatoms. These tools are important given the lack of data about environmental change in the Delta, including the hydrological alterations that accompanied intensive rice cultivation and earlier changes that may have been caused by more subtle exploitation. Diatoms, together with other biological proxies (e.g. benthic foraminifera), may allow the reconstruction of changes in habitat condition across space and time in the Ebro Delta wetlands.

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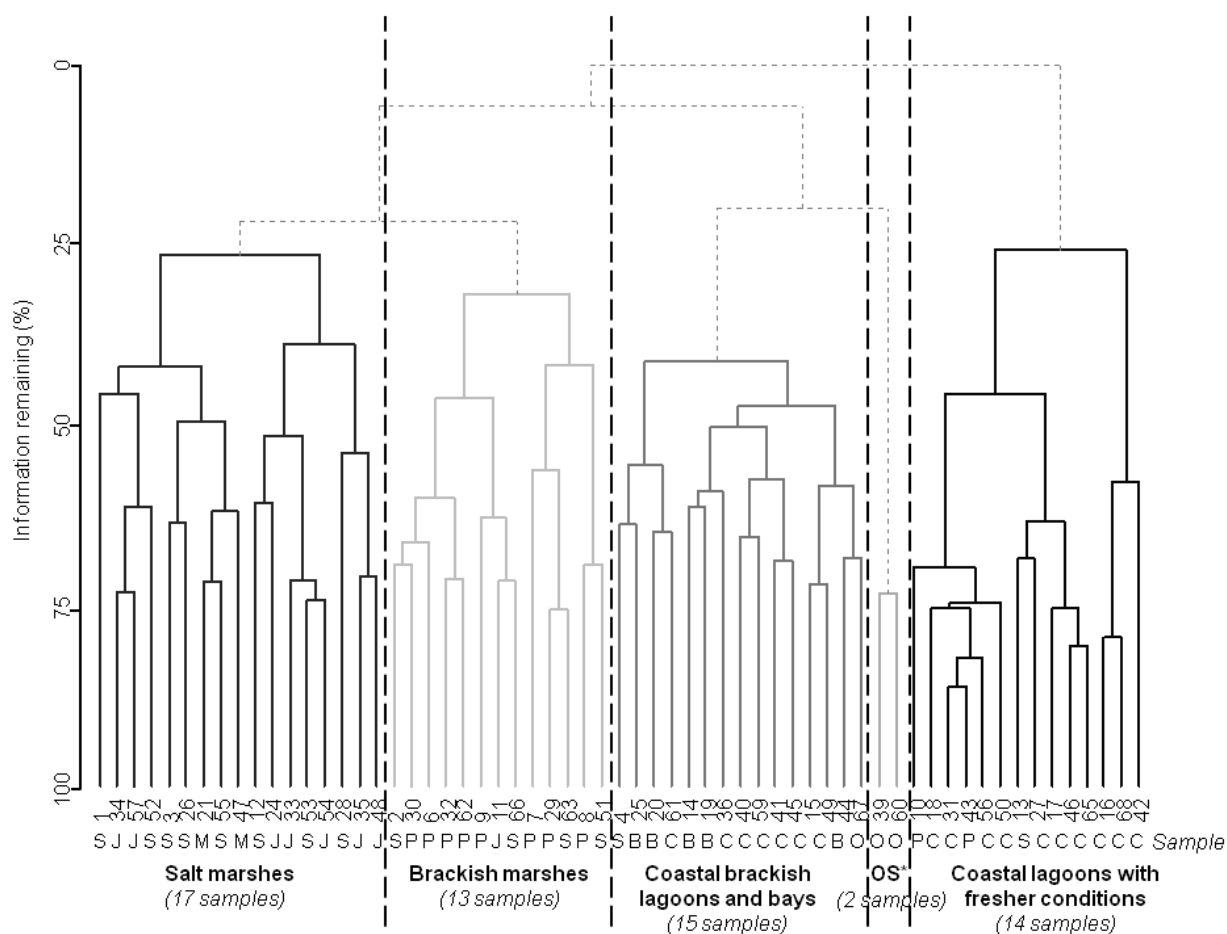
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**Supplementary material**

**Supplementary Figure 1.** Dendrogram of the Ebro Delta samples showing the five habitat types (OS: nearshore open sea) identified according to similarity in diatom species composition (number of samples per group in brackets). Sample provenances: O = nearshore open sea; M = microbial mat; B = semi-enclosed bays; C = coastal lagoons; S = *Salicornia* marshes; J = *Juncus* marshes; P = *Phragmites* marshes



**Supplementary Table 1** List of diatom taxa found in the Ebro Delta samples with their corresponding codes (see Appendix I)

**Supplementary Table 2** Mean and standard deviation (in italics) of the measured environmental variables from the 24 studied sites in the Ebro Delta. Abbreviations: n = number of samples for each site. T = temperature; DO = dissolved oxygen saturation; Cond = conductivity (EC<sub>25</sub>); Sand = sand proportion; OM = organic matter content; Chl-a = Seston chlorophyll *a*; Pheo = Pheophytin *a*

Site	Delta region	Habitats	n	T °C	pH	DO %	Cond mS/cm	Sand %	OM %	Depth cm	PO <sub>4</sub> <sup>3-</sup> -P µg/L	NH <sub>4</sub> <sup>+</sup> -N µg/L	NO <sub>2</sub> <sup>-</sup> -N µg/L	NO <sub>3</sub> <sup>-</sup> -N µg/L	SiO <sub>4</sub> <sup>4-</sup> -Si µg/L	Chl-a µg/L	Pheo-a µg/L
1	Alfacs	Bay	3	18.5	8.09	92.4	43.97	69.3	1.1	42	14.6	43.4	7.6	27.4	628	3	2
				<i>5.4</i>	<i>0.15</i>	<i>12.4</i>	<i>5.81</i>	<i>0</i>	<i>0</i>	<i>4</i>	<i>9.6</i>	<i>51.0</i>	<i>5.9</i>	<i>13.1</i>	<i>197</i>	<i>2</i>	<i>1</i>
2	Alfacs	<i>Salicornia</i>	3	18.8	7.97	122.3	44.71	5.0	5.9	8	16.2	40.2	5.6	20.7	488	5	2
				<i>5.1</i>	<i>0.13</i>	<i>29.64</i>	<i>8.88</i>	<i>0</i>	<i>0</i>	<i>4</i>	<i>9.2</i>	<i>48.2</i>	<i>4.2</i>	<i>19.6</i>	<i>126</i>	<i>4</i>	<i>1</i>
3	Banya	Sea	2	20.3	7.99	89.4	51.84	18.5	4.9	720	5.9	16.9	2.5	17.8	107	3	1
				<i>6.9</i>	<i>0.04</i>	<i>11.46</i>	<i>7.93</i>	<i>0</i>	<i>0</i>	<i>28</i>	<i>1.2</i>	<i>17.2</i>	<i>1.3</i>	<i>2.2</i>	<i>81</i>	<i>2</i>	<i>0</i>
4	Aufacada	<i>Juncus</i>	3	18.3	7.45	60.93	20.16	77.5	3.8	12	12.3	19.4	2.9	15.7	2,083	7	5
				<i>5.3</i>	<i>0.4</i>	<i>30.06</i>	<i>2.59</i>	<i>0</i>	<i>0</i>	<i>3</i>	<i>8.5</i>	<i>14.0</i>	<i>2.0</i>	<i>11.7</i>	<i>2,346</i>	<i>6</i>	<i>3</i>
5	Aufacada	Lagoon	3	19.8	8.12	93.47	15.06	89.8	3.7	52	13.3	12.1	7.4	42.6	1,865	7	3
				<i>5.2</i>	<i>0.48</i>	<i>16.82</i>	<i>7.47</i>	<i>0</i>	<i>0</i>	<i>5</i>	<i>10.2</i>	<i>9.2</i>	<i>8.3</i>	<i>42.9</i>	<i>135</i>	<i>4</i>	<i>1</i>
6	Aufacada	<i>Phragmites</i>	2	15.2	7.2	44.35	17.11	25	36.7	20	22.1	8.7	7.8	63.6	2,122	21	5
				<i>0.9</i>	<i>0.1</i>	<i>5.02</i>	<i>4.21</i>	<i>0</i>	<i>0</i>	<i>14</i>	<i>7.0</i>	<i>5.3</i>	<i>5.6</i>	<i>63.7</i>	<i>956</i>	<i>26</i>	<i>4</i>
7	Aufacada	<i>Salicornia</i>	3	18.7	7.46	37.8	29.27	58.8	2.8	11	16.5	37.0	1.7	25.5	3,517	9	3
				<i>5.1</i>	<i>0.19</i>	<i>17.41</i>	<i>1.96</i>	<i>0</i>	<i>0</i>	<i>8</i>	<i>9.5</i>	<i>11.5</i>	<i>1.1</i>	<i>28.1</i>	<i>2,650</i>	<i>12</i>	<i>2</i>
8	Banya	Microbial mat	2	21.4	8.02	99.6	73.18	76.3	5.8	3	37.0	32.0	3.6	20.6	461	6	2
				<i>8.9</i>	<i>0.03</i>	<i>20.22</i>	<i>48.76</i>	<i>0</i>	<i>0</i>	<i>3</i>	<i>14.0</i>	<i>1.6</i>	<i>0.6</i>	<i>25.6</i>	<i>224</i>	<i>5</i>	<i>1</i>
9	Clot	Lagoon	1	16.9	7.82	75.2	2.9	0	26.6	55	48.2	150.0	15.1	642.7	1,613	5	4
				-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	Encanyissada	<i>Juncus</i>	3	22.1	7.55	117.77	36.4	73.9	66.3	19	40.0	22.8	6.1	34.6	2,027	25	3
				<i>6.6</i>	<i>0.52</i>	<i>99.53</i>	<i>28.37</i>	<i>0</i>	<i>0</i>	<i>18</i>	<i>40.5</i>	<i>7.3</i>	<i>5.4</i>	<i>19.1</i>	<i>495</i>	<i>17</i>	<i>3</i>
11	Encanyissada	Lagoon	4	20.3	8.01	91.1	28.74	76.8	0.9	56	25.6	37.0	2.2	54.2	1,107	16	-1

Site	Delta region	Habitats	n	T °C	pH	DO %	Cond mS/cm	Sand %	OM %	Depth cm	PO <sub>4</sub> <sup>3-</sup> -P µg/L	NH <sub>4</sub> <sup>+</sup> -N µg/L	NO <sub>2</sub> <sup>-</sup> -N µg/L	NO <sub>3</sub> <sup>-</sup> -N µg/L	SiO <sub>4</sub> <sup>4-</sup> -Si µg/L	Chl-a µg/L	Pheo-a µg/L
				5.4	0.35	17.93	16.15	2.8	0	17	20.0	18.3	2.3	87.4	689	26	4
12	Encanyissada	<i>Phragmites</i>	3	22.7	7.88	100.03	25.89	7.2	96.9	16	35.2	23.5	5.2	227.7	5,573	22	10
				5.6	0.2	63.27	19.68	0	0	6	9.2	4.9	3.8	373.7	6,610	24	11
13	Encanyissada	<i>Salicornia</i>	3	21.4	7.73	92.07	24.83	61.2	56.6	19	51.8	56.5	2.8	36.3	2,370	32	5
				7.5	0.64	69.73	14.22	0	0	11	47.0	45.9	0.5	31.4	2,356	26	1
14	Fangar	Bay	2	19.5	8.47	109.5	22.12	92.3	1.8	30	16.6	20.0	19.5	23.4	310	4	4
				3.4	0.63	14.57	7.98	0	0	14	8.5	8.0	25.1	20.9	232	2	2
15	Fangar	<i>Salicornia</i>	2	25.5	7.68	53.6	56.93	80.5	46.8	17	48.8	229.4	9.1	8.1	1,318	4	3
				3.4	0.23	48.22	6.75	0	0	1	55.4	182.0	3.5	3.7	922	1	2
16	Garxal	<i>Juncus</i>	2	21.7	7.33	62.25	18.8	93.4	3.9	11	55.6	18.5	2.7	7.1	2,471	14	2
				6.7	0.09	5.16	2.27	0	0	1	61.9	0.2	1.0	5.6	306	3	0
17	Garxal	Lagoon	3	19.1	8.22	82.73	8.88	92.1	2.3	27	11.2	26.1	1.7	16.8	1,461	7	2
				6.7	0.59	43.84	6.03	0	0	3	1.1	17.4	1.4	13.8	1,470	6	2
18	Garxal	<i>Phragmites</i>	3	20.1	8.39	102.7	8.37	65.8	39.8	8	13.2	32.8	1.3	47.9	1,949	7	4
				6.3	0.46	37.39	5.83	0	0	5	2.2	28.6	1.0	39.2	2,382	5	3
19	Garxal	<i>Salicornia</i>	1	23.9	8.5	106.8	17.27	92.3	3.2	10	11.7	24.8	2.4	2.6	293	10	3
				-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	Olles	Lagoon	3	19.9	7.88	96.97	3.39	26.8	5.6	56	28.0	91.2	32.6	963.5	2,091	24	5
				5.5	0.23	18.96	3.63	0	0	15	14.3	27.7	19.4	403.9	858	23	3
21	Olles	<i>Phragmites</i>	2	17.6	7.62	51.3	1.98	0	40.6	18	34.2	46.7	11.4	570.8	2,009	9	3
				5.4	0.09	32.39	1.18	0	0	11	13.8	55.1	13.3	770.2	518	5	0
22	Tancada	Lagoon	4	18.1	7.79	80.88	39.55	55.2	3.3	46	19.5	100.5	11.2	21.8	758	5	3
				5.22	0.24	15.88	9.73	31.0	0	13	17.1	54.9	6.1	15.2	409	4	2
23	Tancada	<i>Phragmites</i>	3	18.4	7.24	44.97	27.94	31.9	27.2	9	75.1	66.6	3.5	15.2	1,033	28	15
				4.4	0.28	4.43	12.99	0	0	5	91.9	85.0	1.8	24.4	143	14	12

*Chapter 1: Benthic diatom assemblages*

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<b>Site</b>	<b>Delta region</b>	<b>Habitats</b>	<b>n</b>	<b>T</b>	<b>pH</b>	<b>DO</b>	<b>Cond</b>	<b>Sand</b>	<b>OM</b>	<b>Depth</b>	<b>PO<sub>4</sub><sup>3-</sup>-P</b>	<b>NH<sub>4</sub><sup>+</sup>-N</b>	<b>NO<sub>2</sub><sup>-</sup>-N</b>	<b>NO<sub>3</sub><sup>-</sup>-N</b>	<b>SiO<sub>4</sub><sup>4-</sup>-Si</b>	<b>Chl-a</b>	<b>Pheo-a</b>
				°C		%	mS/cm	%	%	cm	µg/L	µg/L	µg/L	µg/L	µg/L	µg/L	µg/L
24	Tancada	<i>Salicornia</i>	1	13.4	7.33	62.1	26.52	63.7	17.8	14	201.4	3.3	3.2	113.4	1,286	46	13

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**Supplementary Table 3** Results of Canonical Correspondence Analysis (CCA) of diatom-environment relationships for the Ebro Delta samples. **a)** Marginal effects indicate the variance explained by each variable considered alone. **b)** Unique effects indicate percentage of variance explained by each environmental variable, with the remaining variables treated as covariables.  $\lambda_1$ : eigenvalue of the constrained axis 1;  $\lambda_1/\lambda_2$ : ratio of the constrained axis 1 to the unconstrained axis 1. In bold are those variables initially selected by the CCAs. In bold and highlighted in gray colour are the final variables selected by the partial CCAs. T: temperature (°C); pH; DO: dissolved oxygen saturation (%); Sand = sand proportion; OM = organic matter content;  $\text{PO}_4^{3-}$ -P: orthophosphate-phosphorus ( $\mu\text{g/L}$ );  $\text{NH}_4^+$ -N: ammonium-nitrogen ( $\mu\text{g/L}$ );  $\text{NO}_2^-$ -N: nitrite-nitrogen ( $\mu\text{g/L}$ );  $\text{NO}_3^-$ -N: nitrate-nitrogen ( $\mu\text{g/L}$ );  $\text{SiO}_4^{4-}$ -Si: orthosilicate-silicon ( $\mu\text{g/L}$ ); Chl-a: seston chlorophyll *a* ( $\mu\text{g/L}$ ); Pheo-a: pheophytin *a* ( $\mu\text{g/L}$ )

a) CCAs (marginal effects)

Variable	% variance explained	<i>p</i> value
<b>Conductivity</b>	<b>5.47</b>	<b>0.005</b>
<b>Depth</b>	<b>5.34</b>	<b>0.005</b>
<b>OM</b>	<b>4.40</b>	<b>0.005</b>
<b>Sand</b>	<b>3.42</b>	<b>0.005</b>
<b><math>\text{NO}_3^-</math>-N</b>	<b>2.78</b>	<b>0.01</b>
<b><math>\text{NO}_2^-</math>-N</b>	<b>2.61</b>	<b>0.01</b>
<b>pH</b>	<b>2.61</b>	<b>0.01</b>
<b><math>\text{SiO}_4^{4-}</math>-Si</b>	<b>2.59</b>	<b>0.01</b>
<b>Chl-a</b>	<b>2.53</b>	<b>0.01</b>
<b><math>\text{PO}_4^{3-}</math>-P</b>	<b>2.37</b>	<b>0.01</b>
Pheo-a	2.09	0.14
$\text{NH}_4^+$ -N	1.89	0.12
DO	1.57	0.43
T	1.33	0.77

b) Partial CCAs (unique effects)

Variable	% variance explained	<i>p</i> value	$\lambda_1$	$\lambda_1/\lambda_2$
<b>Conductivity</b>	<b>4.58</b>	<b>0.005</b>	<b>0.294</b>	<b>0.80</b>
<b>Depth</b>	<b>4.08</b>	<b>0.005</b>	<b>0.262</b>	<b>0.70</b>
<b>OM</b>	<b>2.56</b>	<b>0.005</b>	<b>0.164</b>	<b>0.44</b>
<b>Sand</b>	<b>2.28</b>	<b>0.005</b>	<b>0.147</b>	<b>0.39</b>
<b><math>\text{NO}_2^-</math>-N</b>	<b>2.16</b>	<b>0.015</b>	<b>0.138</b>	<b>0.37</b>
<b><math>\text{NO}_3^-</math>-N</b>	<b>1.82</b>	<b>0.05</b>	<b>0.113</b>	<b>0.31</b>
pH	1.82	0.07	0.110	0.30
$\text{PO}_4^{3-}$ -P	1.74	0.13	0.111	0.29

SiO <sub>4</sub> <sup>4-</sup> -Si	1.21	0.71	0.077	0.21
Chl-a	1.11	0.91	0.069	0.18
Sum unique effects	23.3			
Intercorrelations	4.1			
Total variance explained	27.4			

**Supplementary Table 4** Model performances for the diatom-based conductivity transfer functions (WA-INV, WA-CLA, WATOL-INV, WATOL-CLA). All models were cross-validated using the leave-one-out method (LOO, also called jack-knifing) and leave-one-site-out (LOSO), and were built on square root transformed species data and log<sub>10</sub> transformed conductivity. Abbreviations: WA = Weighted-Averaging; INV = Inverse deshrinking; CLA = Classical deshrinking; WATOL = Weighted-Averaging with tolerance downweighted. The model preferred is highlighted in bold and gray colour

Model	$r^2$	RMSEP (log <sub>10</sub> mS/cm)	Max Bias (log <sub>10</sub> mS/cm)	Mean segment RMSEP (log <sub>10</sub> mS/cm)
Diatom dataset: n samples = 61, n taxa = 424				
LOO (leave-one-out)				
WA-INV	0.63	0.24	0.38	0.32
WA-CLA	0.64	0.24	0.30	0.30
WATOL-INV	0.48	0.29	0.72	-
WATOL-CLA	0.48	0.29	0.70	-
LOSO (leave-one-site-out)				
WA-INV	0.62	0.26	0.39	0.33
<b>WA-CLA</b>	<b>0.64</b>	<b>0.27</b>	<b>0.32</b>	<b>0.30</b>
WATOL-INV	0.43	0.31	0.74	-
WATOL-CLA	0.43	0.31	0.72	-
Diatom dataset: n samples = 61, n taxa = 137				
LOO (leave-one-out)				
WA-INV	0.58	0.25	0.42	0.33
WA-CLA	0.59	0.28	0.33	0.31
WATOL-INV	0.53	0.27	0.46	-
WATOL-CLA	0.54	0.29	0.36	-
LOSO (leave-one-site-out)				

<b>Model</b>	$r^2$	<b>RMSEP</b> ( $\log_{10}$ mS/cm)	<b>Max Bias</b> ( $\log_{10}$ mS/cm)	<b>Mean segment</b> <b>RMSEP (<math>\log_{10}</math></b> <b>mS/cm)</b>
WA-INV	0.59	0.25	0.43	0.34
WA-CLA	0.60	0.27	0.33	0.32
WATOL-INV	0.48	0.29	0.47	-
WATOL-CLA	0.49	0.30	0.45	-
<hr/>				
Diatom dataset: n samples = 59, n taxa = 413				
LOO (leave-one-out)				
WA-INV	0.69	0.28	0.39	0.34
WA-CLA	0.70	0.21	0.33	0.32
WATOL-INV	0.53	0.27	0.64	-
WATOL-CLA	0.53	0.27	0.61	-
LOSO (leave-one-site-out)				
WA-INV	0.70	0.21	0.38	0.35
WA-CLA	0.70	0.29	0.32	0.32
WATOL-INV	0.53	0.27	0.65	-
WATOL-CLA	0.53	0.27	0.61	-
<hr/>				
Diatom dataset: n samples = 59, n taxa = 137				
LOO (leave-one-out)				
WA-INV	0.64	0.23	0.38	0.36
WA-CLA	0.65	0.25	0.29	0.36
WATOL-INV	0.62	0.24	0.40	-
WATOL-CLA	0.63	0.25	0.37	-
LOSO (leave-one-site-out)				
WA-INV	0.65	0.23	0.36	0.36
WA-CLA	0.66	0.24	0.27	0.35
WATOL-INV	0.63	0.24	0.38	-
WATOL-CLA	0.63	0.25	0.38	-

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BENTHIC DIATOMS AND FORAMINIFERA AS INDICATORS OF COASTAL WETLAND HABITATS: APPLICATION TO PALAEOENVIRONMENTAL RECONSTRUCTION

Xavier Benito Granel

## ***Chapter 2***

### **Benthic foraminifera as ecological indicators and development of a water-depth transfer function in a Mediterranean delta**

Benito, X., Trobajo, R., Cearreta, A. and Ibáñez, C.

*Estuaries and Coasts* (under review)



## **Benthic foraminifera as ecological indicators and development of a water-depth transfer function in a Mediterranean delta**

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## Chapter 2: Benthic foraminiferal assemblages

### Abstract

The modern ecology of benthic foraminiferal assemblages and their use as ecological indicators were analyzed in the Ebro Delta (NW Mediterranean Sea). Foraminiferal distributions were based upon our own data and those in an unpublished PhD dissertation, altogether comprising 191 sediment surface samples covering a wide range of deltaic habitats and adjacent open sea areas. According to similarity in species composition, cluster analysis identified four habitat types: (1) offshore, (2) nearshore and outer bays, (3) coastal lagoons and inner bays, and (4) salt and brackish marshes. Canonical Correspondence Analysis showed that water depth, salinity and sand content were the main environmental factors structuring living foraminiferal assemblages. As revealed by partial Canonical Correspondence Analysis, water depth emerged as the most statistically significant variable affecting the distribution of modern foraminifera in the Ebro Delta. Thus, a transfer function for water depth using Weighted Average Partial Least Squares regression was developed. The resulting model ( $r^2 = 0.89$ ; RMSEP =  $0.32 \log_{10}$  m) assessed by cross validation (leave-one-site-out, LOSO) has provided a potentially useful tool for water-depth reconstructions in the Ebro Delta. In addition, a multiproxy approach (foraminifera plus diatoms) was used for the Delta plain habitats, showing that the relationship between salinity and species was strong, but not better than using diatom assemblage alone. The results of this work indicated the potential role of modern foraminifera as quantitative indicators of water depth and habitat types in the Ebro Delta. This integrated approach (transfer function and indicator species) will allow reconstruction of the palaeoenvironmental changes that have occurred in the Ebro Delta, based on Holocene foraminiferal analysis.

Keywords: Ebro Delta; Coastal wetlands; Multiproxy; Palaeoecology; Diatoms; Indicator Species



## **1. Introduction**

Among benthic micro-organisms, foraminifera and diatoms are of great importance in aquatic ecosystems worldwide because i) their species react in a rapid and sensitive way to environmental changes in water bodies, and ii) they preserve in sediments for a long time due to their shells, which are made mainly of calcium carbonate (i.e. hyaline and porcellaneous foraminifera) or silica (diatoms) (Scott et al. 2001; Smol and Stoermer 2010). If the modern ecology of these organisms is known, then the composition of fossil assemblages can be used for palaeoenvironmental reconstructions and palaeoecological indication (Debenay et al. 2000; Birks 2003), including studies of transitional ecosystems (e.g. estuaries, coastal lagoons, deltas). These kind of environments are of paramount importance because provide more goods and services than other biomes for the same unit area (e.g. productivity, nutrient removal, sediment retention, etc.) (Costanza et al. 1997; Bouchet et al. 2012; Schönfeld et al. 2012).

In Mediterranean coastal wetlands, present-day habitat distributions have been determined by both natural and anthropogenic-driven changes. Human impacts include, among others, alteration of hydrological cycles and loss of habitats, caused mostly by intensive agriculture (Comín et al. 1991; Hollis 1992). Key natural factors affecting Mediterranean deltas include sea-level fluctuations (Ibáñez et al. 2014), changes in fluvial sediment discharge (Xing et al. 2014) and, at the marine interface, wave action (Jiménez et al. 1995). In the context of the high complexity of coastal ecosystems and poor knowledge of their intrinsic variability, and given that there is a lack of written historical records in many cases, palaeoecological approaches can play a crucial role in providing enough temporal scale to disentangle natural from human-related changes (Smol 2002).

In shallow coastal marine environments, benthic foraminiferal assemblages are controlled by a wide range of environmental conditions (Murray 2001). If a statistical significant relationship exists between species and the variable of interest, quantitative assessment of foraminifera–environment relationships can provide useful tools for reconstructing changes in these ecosystems. Foraminifera transfer functions have been published for various physical and chemical parameters, such as sea surface temperature (Sejrup et al. 2004), salinity (Leorri and Cearreta 2009), surface elevation (Horton and Edwards 2006; Callard et al. 2010; Leorri et al. 2010; Kemp et al. 2013) and water depth (Hayward 2004; Horton et al. 2007; Rossi and Horton 2009; Milker et al. 2011). Water depth and elevation would be useful parameters to estimate from fossil assemblages in deltas, giving valuable information about the evolution of the delta and past sea-level changes. Although the depth-related niche of a species may vary depending on local physiographic conditions (Herkat and Ladjal 2013), correlations between water depth and foraminiferal assemblages have already been shown to reflect both the direct effects of this variable (from hydrostatic pressure, in the deeper parts of the continental shelf: Gooday 2003)

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and also the indirect effects on benthic foraminiferal distributions in the Mediterranean Sea (e.g. from organic matter and oxygen concentrations in the surface sediments: Mojtahid et al. 2010; Goineau et al. 2011; López-Belzunce et al. 2014). Specifically, a pioneering study by Scrutton (1969) in the shallow marine area off the Ebro Delta revealed that foraminiferal distributions are closely related with bathymetry.

Another method used by palaeoecologists to reconstruct past environments is the indicator species approach (Birks 2003). Although the use of diatoms as indicators of coastal ecosystems is relatively common (Wachnicka et al. 2011; Rovira et al. 2012; Nodine and Gaiser 2014; Benito et al. 2015), only two studies have previously applied such an approach together with foraminifera. One of these cases is Goineau et al. (2011), who studied the offshore foraminiferal assemblages in the Rhone prodelta (NW Mediterranean), and the other one is Baldi and Hohenegger (2008), who applied an indicator approach to a sedimentary sequence from Austria. To our knowledge, however, no study of this kind has been done in coastal wetlands, where different habitats (e.g. marshes, lagoons, sandflats, bays) are present in small patches due to the micro-tidal setting (as in the case of the Ebro Delta: Ibáñez et al. 2000).

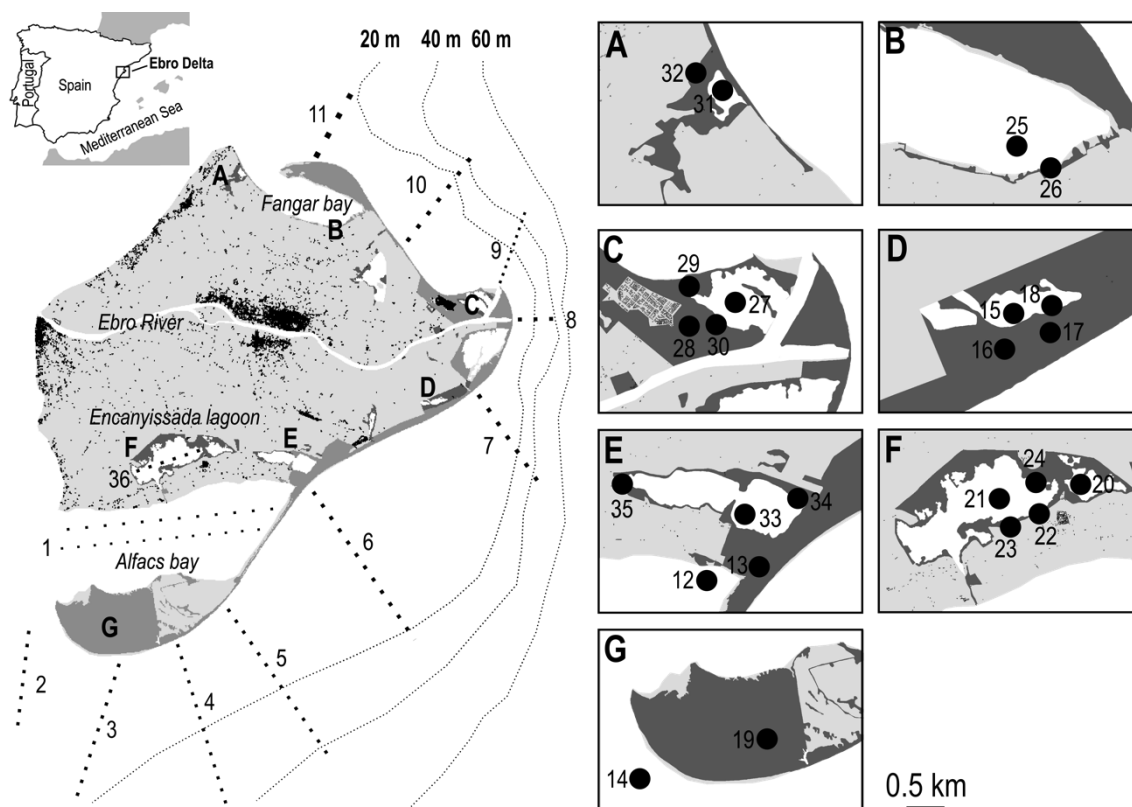
The principal aims of our study are (1) to identify the main environmental factors structuring living foraminiferal assemblages of the Ebro Delta (NE Iberian Peninsula), (2) to identify indicator species for the main habitat types, and (3) to develop a water-depth transfer function based on modern distribution of foraminifera in the Delta plain and its surrounding marine areas. An additional aim was to compare a multiproxy analysis (foraminifera plus diatoms) with the results obtained in a previous study, in which diatom assemblages were used as indicators of the Ebro Delta habitat types (Benito et al. 2015). The tools developed here were designed for use in analysing the fossil foraminiferal content in dated sediment cores collected at different sites on the Delta plain. The objective is to provide reliable evidence to assess the palaeoenvironments and evolution of the Delta during the Holocene, and to document environmental changes since the beginning of intensive human settlement in the Ebro Delta (i.e. in the last *c.* 200 years). It is hoped that this study will help to provide data for supporting environmental policies in the context of future restoration projects.

### **2. Study area**

The Ebro Delta is located on the Mediterranean coast of the Iberian Peninsula (Fig. 1). The Delta is one of the largest coastal wetlands in the NW Mediterranean and is irrigated by the Ebro River, which has the highest mean annual flow of any Spanish river and drains 15% of the area of Spain (85,550 km<sup>2</sup>) (Romaní et al. 2010). Nowadays, however, the Delta receives only a small fraction of the water and sediments it would have carried naturally, because of the dam

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constructions (started mid 1960s) and intensive use of water for agriculture. Before intensive human activities, xerophytic Mediterranean woodlands were the most dominant land use in the basin. Nowadays, irrigated cropland and pasture with fragmented vegetation patches dominate the landscape of the Ebro Basin. However, though these land cover changes increased the suspended sediment load at the river mouth, the final result is still considerably lower than the sediment load naturally transported by the river (Xing et al. 2014).



**Fig. 1** Location of Scrutton's transects (1–11 and 36, back dots) and our sampling sites (12–35, filled circles) within the Delta plain regions (A–G). Transects shown in detail: 1: South bay, 2: Las Casas, 3: Vinaroz, 4: South faro, 5: Salinas, 6: South platform, 7: South channel, 8: Cabo Tortosa, 9: River mouth, 10: North platform, 11: North faro, 36: Encanyissada lagoon. Different areas within the Delta shown in detail: A: Olles; B: Fangar; C: Garxal; D: Aufacada; E: Tancada–Alfacs; F: Encanyissada–Clot; G: Banya.

The deltaic plain has a subaerial surface of 330 km<sup>2</sup> while its submerged area (pro-delta) has an estimated surface of 2,2 km<sup>2</sup> (Rodríguez et al. 2010). The plain is extremely flat, reaching a maximum altitude of 3–4 m above sea level only near the inner border of the Delta. The Ebro Delta is a micro-tidal system, with an astronomical tidal range of around 20–30 cm. However, meteorological tides resulting from changes in atmospheric pressure can sometimes exceed 1 m. Coastal processes operating in the Delta include longshore currents towards the south and wave

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action. These affect the deltaic fringe generating sediment erosion and transportation. Fine sediment is transported by offshore (i.e. prodelta, >10 m water depth) and longshore currents to form spits at the north and south of the Delta (see Fig. 1). These sandy spits constitute two semi-enclosed shallow bays with marine salinities and sandy-mud substrates. The freshwater river discharge forms a surface layer *ca.* 3 m thick on the denser seawater and does not influence depths greater than 10 m (Maldonado and Murray 1975). Within deltaic plain, salinity can vary from almost freshwater (< 3 ppt) to brackish-marine (16–30 ppt) or hypersaline (~70 ppt) depending on factors such as elevation, inputs of upland runoff, marine influence or soil drainage.

A typical Mediterranean littoral climate characterises the Ebro Delta, with mean temperatures ranging from 26°C during July and August to 10°C in January. Maximum precipitation is recorded mainly during autumn (37% of the total) with annual mean of 525 mm (Curcó 2006).

As with deltas in other parts of the world, the formation of the Ebro Delta has been complex, as a result of changes in river flow and sea level, together with coastal reshaping by the sea. The evolution of the Ebro Delta during the late Holocene (i.e. in the last few millennia) has been recognized by avulsions in the course of the main river channel, which have in turn caused the development of successive delta lobes, later abandoned and partially eroded (Maldonado and Riba 1971; Canicio and Ibáñez 1999; Somoza and Rodríguez-Santalla 2014). In the last millennium the Ebro Delta prograded significantly due to the development of three main deltaic lobes: the Riet Vell, Riet Zaida and Migjorn lobes (Ibáñez et al. 1997). This last active lobe is the result of a new river switching event that took place around the year 1666 close to the Gracia Island as a consequence of a man-made excavation in the outer levee of a pronounced meander (Ribas 1996). At present, relative sea-level rise and coastal erosion by wave action cannot be compensated by river sediment input (Ibáñez et al. 1997). A series of dams were built along the Ebro River during the 1960s to support a variety of intensive water uses. These dams are responsible of a 30% decrease in the water discharge and retain approximately 99% of the sediment input that partially should be deposited in the Ebro Delta, creating a severe sediment deficit (Ibáñez et al. 1996). As a result, the Delta has ceased to grow, erosive processes have become dominant and the area has changed from a progradational to a storm wave-dominated coast that is being morphologically reshaped.

The Ebro Delta is a diverse area in terms of wetland habitat types and has high ecological (e.g. it is the second most important “Special Protection Area” for birds in Spain) and economic value (e.g. third largest producer of rice in Europe) (Fatoric and Chelleri 2012). In the last 150 years, the Delta has been largely transformed into rice fields, which now cover 70% of the total area (Cardoch et al. 2002) and have both direct and indirect effects on the ecology of the area. The main impact is obviously the destruction of natural habitats, but even the remaining deltaic

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ecosystems have been affected by rice production, through alteration of the natural hydrological cycle as a result of freshwater inputs during the rice growing season (April to September). In addition, large amounts of nutrients and pesticides are delivered for the fertilization and care of the rice paddies (Forés 1992). Nevertheless, the remaining natural habitats represent good examples of Mediterranean coastal wetlands.

### 3. Material and methods

#### 3.1 Sampling

A total of 70 surface sediment samples from 24 different sites within the Delta plain were collected in order to encompass environmental gradients and habitat types present in the study area (sites 12–35D, Fig. 1 and Table 1). Specifically, the natural habitats selected were: coastal lagoons, salt marshes (i.e. *Salicornia* and *Juncus* marshes), brackish marshes (i.e. *Phragmites* marshes), microbial mats, semi-enclosed shallow bays, and nearshore marine waters. In order to cover the possible seasonal variability of foraminiferal assemblages, samplings were performed in November 2012, April 2013 and August 2013, except for site 32D (Olles), 14D (Alfacs), 20D (Clot) and 28D (Garxal) that could not be sampled three times due to technical problems and because during some campaigns they were dried (Table 1). We collected the top surface of the sediment at each sampling site using a 5.7 cm diameter corer (Becker-type sampler), except at the nearshore open-sea site, where a grab sampler was needed due to the water depth. The corer was pressed down into the sediment to *c.* 10 cm depth and the top 1 cm of sediment contained in it was then carefully placed in a bottle containing an equal volume of ethanol. This process was repeated three times at each site to cover spatial variability of the patchy foraminiferal distribution (very common in marginal marine environments like deltas or estuaries as a result of different reproduction pulses among successive years: Buzas et al. 2002), and the three samples were merged and placed in the same bottle, resulting in a single sample representing *c.* 78 cm<sup>3</sup>. Samples were taken near the edges of coastal lagoons and bays, while marsh samples were collected well within the marsh, away from any nearby lagoon or bay. At each sampling site, water samples were collected by hand near the bottom, taking care to avoid sediment resuspension, and stored on ice until transported to the laboratory for analysis. In the laboratory, inorganic dissolved nutrients (NO<sub>3</sub><sup>-</sup>-N, NO<sub>2</sub><sup>-</sup>-N, NH<sub>4</sub><sup>+</sup>-N, PO<sub>4</sub><sup>3-</sup>-P and SiO<sub>4</sub><sup>4-</sup>-Si) were measured from filtered samples following Grasshoff et al. (1983). Seston chlorophyll *a* was extracted with 90% acetone after filtration and measured with a fluorimeter using the Lorenzen formula (Lorenzen 1966). Salinity (ppt: parts per thousand), temperature (°C), dissolved oxygen (DO, mg/L), water depth (cm) and pH were measured *in situ* with a YSI 556 multiprobe. Depths at each sample are referred to Spanish national ordenance datum (mean sea level at Alicante

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recorded between 1870-1882 CE). Furthermore, in one campaign (April 2013), two additional sediment samples (top 1 cm of the sediment layer) were taken from each site to estimate: i) the sediment fraction  $>0.063\text{mm}$  determined by the wet sieving method (Facca and Sfriso 2007), which is referred to here as the percentage of sand; and ii) the organic matter content, as loss on ignition (LOI) (Dean 1974).

We also used the foraminiferal dataset created for the Ebro Delta by Scrutton (1969), who focused mainly on marine areas (sites 1–11M, Fig. 1 and Table 1), though he also sampled the Encanyissada lagoon (site 36D, Fig. 1 and Table 1). Scrutton's dataset consists of 121 sediment samples collected along transects off and perpendicular to the Delta coast, which covered the outer bay, delta front and prodelta areas (Fig. 1 and Table S1). At most of the twelve different transects performed by Scrutton (1969), samples were collected in three different periods: April 1967, August 1967 and July 1968 (Tables 1 and S1). Transects 2M (Las Casas) and 8M (Cabo Tortosa) were only sampled once (April 1967 and August 1967, respectively) due to technical problems with the boat (Scrutton 1969 and Table 1). Samples of  $\sim 50\text{ cm}^3$  were obtained with a small grab by slicing off the top 1–2 cm of surface sediment. Each sediment sample was transferred into a bottle and preserved in 98% alcohol. At most sampling sites, water depth (m), salinity (ppt), sediment sand proportion ( $>0.076\text{ mm}$ ) and water temperature ( $^{\circ}\text{C}$ ) were measured. Water depth was recorded at each site by means of an echo-sounder, and it was referred to mean sea level in Alicante datum (MSLA). Salinity was determined indirectly by first measuring the chlorinity with the standard silver nitrate method and then applying the Salinity formula of Sverdrup et al. (1942). The sediment sand proportion was obtained by washing through a  $>0.076\text{ mm}$  mesh sieve.

**Table 1** Detail of the sampling sites with descriptive statistics (mean, with the standard deviation in italics) of some of the environmental variables. Each N samples corresponded to the three subsamples mixed together at any sampling site. D = deltaic plain; M = marine adjacent area. 1M-11M = data from Scrutton (1969), 12D-35D = data obtained in this study. 36D = Encanyissada lagoon transect from Scrutton (1969). Sampling campaigns performed in each sampling site are also detailed.

M/D	Site	Habitat	n samples	Season	Water depth (m)	Sand (%)	Salinity (ppt)	Assemblage available
1M	South bay	marine	25	April67', August67', July68'	5.1 <i>1.2</i>	26.92 <i>24.49</i>	38.10 <i>0.63</i>	Foraminifera
2M	Las Casas	marine	8	April67'	8.0 <i>1.8</i>	12.75 <i>18.95</i>	39.00 <i>0.14</i>	Foraminifera
3M	Vinaroz	marine	11	April67', August67'	11.2 <i>3.3</i>	32.09 <i>37.34</i>	38.70 <i>0.68</i>	Foraminifera
4M	South faro	marine	14	April67', August67', July68'	22.3 <i>12.7</i>	28.85 <i>39.55</i>	38.53 <i>0.48</i>	Foraminifera
5M	Salinas	marine	14	April67', August67', July68'	15.7 <i>11.7</i>	51.50 <i>37.72</i>	38.89 <i>0.75</i>	Foraminifera
6M	South platform	marine	12	April67', August67'	12.4 <i>3.9</i>	43.36 <i>37.04</i>	38.12 <i>0.73</i>	Foraminifera
7M	South channel	marine	7	April67', August67'	18.3 <i>15.9</i>	55.57 <i>45.95</i>	38.03 <i>0.75</i>	Foraminifera
8M	Cabo Tortosa	marine	3	August67'	8.5 <i>3.8</i>	44.67 <i>46.11</i>	38.30	Foraminifera
9M	River mouth	marine	10	April67', August67'	25.9 <i>14.8</i>	3.20 <i>2.30</i>	38.64 <i>0.15</i>	Foraminifera
10M	North platform	marine	7	April67', August67', July68'	14.4 <i>9.8</i>	56.57 <i>43.99</i>	38.27 <i>0.21</i>	Foraminifera

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M/D	Site	Habitat	n samples	Season	Water depth (m)	Sand (%)	Salinity (ppt)	Assemblage available
11M	North faro	marine	4	August67', July68'	8.6	57.00	38.70	Foraminifera
					5.1	36.94		
12D	Alfacs	Inner bay	3	November12', April13', August13'	0.4	69.28	32.92	Foraminifera plus diatoms
					0.3	0.00	2.77	
13D	Alfacs	<i>Salicornia</i>	3	November12', April13', August13'	0.9	4.96	33.13	Foraminifera plus diatoms
					0.4	0.00	4.04	
14D	Alfacs	Nearshore	2	April13', August13'	7.2	18.51	37.93	Foraminifera plus diatoms
					0.3	0.00	0.25	
15D	Aufacada	Coastal lagoon	3	November12', April13', August13'	0.5	89.77	10.37	Foraminifera plus diatoms
					0.3	0.00	2.77	
16D	Aufacada	<i>Salicornia</i>	3	November12', April13', August13'	0.1	58.77	20.93	Foraminifera plus diatoms
					0.3	0.00	4.04	
17D	Aufacada	<i>Juncus</i>	3	November12', April13', August13'	0.1	77.45	14.24	Foraminifera plus diatoms
					0.2	0.00	0.18	
18D	Aufacada	<i>Phragmites</i>	3	November12', April13', August13'	0.2	25.00	11.98	Foraminifera plus diatoms
					0.4	0.00	3.49	
19D	Banya	Microbial mat	3	November12', April13', August13'	0.3	76.30	52.42	Foraminifera plus diatoms
					0.6	0.00	0.47	
20D	Clot	Coastal lagoon	1	November12'	0.6	45.63	1.81	Foraminifera plus diatoms
					0.0	0.00	0.00	
21D	Encanyissada	Coastal lagoon	4	November12', April13', August13'	0.6	76.81	20.07	Foraminifera plus diatoms
					0.2	2.81	12.31	



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M/D	Site	Habitat	n samples	Season	Water depth (m)	Sand (%)	Salinity (ppt)	Assemblage available
22D	Encanyissada	<i>Salicornia</i>	3	November12', April13', August13'	0.2	61.21	16.24	Foraminifera plus diatoms
					0.1	0.00	9.91	
23D	Encanyissada	<i>Juncus</i>	3	November12', April13', August13'	0.2	73.88	23.51	Foraminifera plus diatoms
					0.2	0.00	17.47	
24D	Encanyissada	<i>Phragmites</i>	3	November12', April13', August13'	0.2	7.17	16.18	Foraminifera plus diatoms
					0.6	0.00	12.44	
25D	Fangar	Inner bay	3	November12', April13', August13'	0.3	92.25	23.01	Foraminifera plus diatoms
					0.1	0.00	14.39	
26D	Fangar	<i>Salicornia</i>	3	November12', April13', August13'	0.2	80.50	31.16	Foraminifera plus diatoms
					0.01	0.00	10.90	
27D	Garxal	Coastal lagoon	3	November12', April13', August13'	0.4	92.12	5.51	Foraminifera plus diatoms
					0.1	0.00	3.26	
28D	Garxal	<i>Salicornia</i>	2	November12', April13'	0.1	92.34	13.82	Foraminifera plus diatoms
					0.01	0.00	4.84	
29D	Garxal	<i>Juncus</i>	3	November12', April13', August13'	0.1	93.96	10.20	Foraminifera plus diatoms
					0.02	0.00	3.13	
30D	Garxal	<i>Phragmites</i>	3	November12', April13', August13'	0.1	65.80	5.14	Foraminifera plus diatoms
					0.04	0.00	3.28	
31D	Olles	Coastal lagoon	3	November12', April13', August13'	0.6	26.75	1.93	Foraminifera plus diatoms
					0.1	0.00	2.02	
32D	Olles	<i>Phragmites</i>	2	November12', August13'	0.2	37.58	1.2	Foraminifera plus diatoms

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M/D	Site	Habitat	n samples	Season	Water depth (m)	Sand (%)	Salinity (ppt)	Assemblage available
33D	Tancada	Coastal lagoon	4	November12', April13', August13'	0.1 0.5	0.00 55.18	0.6 29.45	Foraminifera plus diatoms
34D	Tancada	<i>Salicornia</i>	4	November12', April13', August13'	0.1 0.3	31.03 61.23	7.00 25.26	Foraminifera plus diatoms
35D	Tancada	<i>Phragmites</i>	3	November12', April13', August13'	0.2 0.1	2.82 31.89	3.59 20.32	Foraminifera plus d diatoms
36D	Encanyissada	Coastal lagoon	6	July68'	0.6 1.29 0.46	0.00 1.25 0.90	10.26 20.33 20.20	Foraminifera

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### 3.2 Foraminiferal analysis

The methodology used for the analysis of the foraminiferal samples collected for this study was the same as that used by Scrutton (1969), including rose Bengal staining and flotation technique with trichloroethylene. The unique exception was the sieve mesh size: we used a 0.063 mm sieve and Scrutton (1969) a 0.076 mm sieve.

Each sediment sample was wet sieved through 1 mm and 0.063 mm sieves (to remove first large organic fragments, then silt and clay). The washed sand fraction retained in the sieve was transferred into a ceramic bowl and an equal volume of rose Bengal stain was added (1 g rose Bengal/L deionised water) following Walton's protocol (1952). After one hour, samples were then wet sieved again in order to remove the excess of stain and dried overnight at 50°C. Rose Bengal stains protoplasm bright red, allowing to identify foraminifera considered to be alive at the time of sampling (i.e. stained forms). Only tests with the last few chambers completely red stained were considered living at the time of collection (Murray and Alve 2000; Horton and Edwards 2006; Milker et al. 2015). Foraminiferal tests were concentrated using a flotation technique with trichloroethylene (Alve and Murray 1999). Each sample was then gently brushed off into a container. For each sample, separate dead and living specimens were picked from representative splits containing approximately 300 tests (dead and alive specimens), or at least 100 if it was impossible to find 300 (Fatela and Taborda 2002). Foraminifera were examined under a Leica M165C binocular stereomicroscope using reflected light. Photographs were taken using a digital camera. Identifications were made to species level when possible, using mainly Murray (1971), Colom (1974), Cimerman and Langer (1991), Guillem (2007) and Milker and Schmiedl (2012).

Use of staining to reveal which foraminifera had been alive in each sample allowed us to distinguish between autochthonous and allochthonous species. Following Leorri and Cearreta (2009), we considered as autochthonous those species with relative abundances >1% and regularly found among the living assemblages. On the other hand, dead species absent in the living assemblages or with relative abundances <0.3% and occurring only occasionally in the live component were considered as allochthonous.

In order to preserve taxonomic consistency between Scrutton's identifications and those made in the present study, several varieties and species of *Ammonia* were grouped into "*Ammonia beccarii* agg". In the deltaic plain sites, *Ammonia tepida* was the principal taxon of the *A. beccarii* group, while other forms different from *A. tepida* were abundant in the marine sites (e.g. *A. beccarii beccarii*, *A. beccarii* var. *batavus*, *A. beccarii* var. 1, *A. beccarii* var. 2 and *A. beccarii* var. 3).

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Fisher's  $\alpha$  index was calculated for foraminiferal samples with >100 tests (Murray 2006), in order to explore the diversity of living assemblages. Based on the  $\alpha$  values, a clear boundary can be drawn between normal marine environments ( $\alpha > 5$ ) and restricted marginal marine environments ( $\alpha < 5$ ) (Debenay 1987).

The similarity index of Rogers (1976), which ranges from 0 to 100%, was used to compare living and dead assemblages for each sample in order to assess what percentage of microfauna is common to both assemblages. For each species common to both assemblages, the lower of the two percentage values is taken. Then, the percentage of similarity corresponds to the sum of the lowest percentage of each species occurring in both assemblages. In addition, to assess seasonal changes in the assemblages, the spring (April) and summer (August) foraminiferal contents were also compared for both living and dead assemblages. Similarity values >70% are usually considered to indicate that a given pair of samples are very similar (Cearreta 1988; Rodríguez-Lázaro et al. 2013).

Living foraminiferal data were used to relate the assemblage composition to measured environmental variables, whereas dead assemblages were used to develop the transfer function model. This is based on the assumption that dead assemblages are time-averaged assemblages, which directly derive from production and post-mortem changes (e.g. transport, destruction of tests) of the living ones. Therefore, dead assemblages are considered to give better analogues (than living) of fossil samples in a particular area for palaeoenvironmental reconstructions (Murray 1991; Horton et al. 1999).

### 3.3 Multivariate ordinations

Foraminiferal relative abundances were square root transformed to stabilize their variance. Environmental variables were checked for skewness and transformed ( $\log_{10} + 1$ ) to improve linearity and homoscedasticity.

The 121 foraminiferal samples of Scrutton (1969) were combined with the 70 samples collected for the present study to produce an enlarged dataset of 191 samples (Table S1). After removing samples with less than 100 tests, living (stained) foraminifera assemblages were represented by 155 samples, and dead (unstained) assemblages by 115 samples. The six foraminiferal samples collected by Scrutton from the Encanyissada lagoon collected in July 1968 (samples from 36M-116 to 36M-121: Table S1) were considered to be extreme outliers (because at that time the lagoon was managed as a freshwater body) and they were therefore excluded from the combined dataset prior to statistical analyses. Fifty of the remaining 149 samples did not contain full environmental data (water depth, salinity, sand content) and were excluded from the multivariate analysis. Thus, a total of 99 samples with full environmental data were used to

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explore the structure of living foraminiferal assemblages (Table S1). Only those species with a relative abundance >2% in at least one sample were included in the analysis.

Living foraminiferal assemblages were analyzed by cluster and ordination analyses. Hierarchical cluster analysis was first used to group samples according to their similarity in species composition using Bray–Curtis distance and flexible beta as the linkage method (Dufrêne and Legendre 1997). Second, DCA ordination was performed to determine whether unimodal or linear species responses should be assumed. By estimating the length of the gradient, a unimodal species response can be assumed if lengths are greater than 2 standard deviation (SD) units. In our case, DCA with downweighting for rare species revealed a gradient length of 5.82 SD, indicating that unimodal models were adequate in this case. Consequently, Canonical Correspondence Analysis (CCA) was used to relate the structure of the living foraminiferal assemblages to measured environmental variables.

A preliminary CCA was performed using all measured environmental variables in order to identify collinear variables, based on the inspection of Variance Inflation Factors (VIF). All collinear variables with VIFs > 20 were removed for the subsequent CCAs. Next, a series of CCAs were performed using a single environmental variable at a time. Here, the purpose was to quantify the marginal effects (i.e. explanatory power of each environmental variable on the foraminiferal data set), as well as to obtain a full suite of individually significant variables, including the most powerful environmental predictors. The variables that did not explain a significant contribution based on 999 Monte Carlo permutation tests were excluded for the subsequent analyses. Then, a series of partial CCAs were applied using the previously selected variables individually and the remaining ones as covariables. This was done to determine which environmental variable made independent and statistically significant contributions to explain the total variation in the foraminiferal species data (i.e. unique effects), and to quantify the interactions between variables. Monte Carlo permutation test (999 permutations) was carried out to estimate the statistical significance of environmental variables at  $p < 0.05$ .

### 3.4 Indicator species

Indicator Species Analysis (Dufrêne and Legendre 1997) was used to identify species that are indicators of the foraminiferal groups derived from cluster analysis. The rationale of the technique is that the indicator value (IV) of a given species will be maximal (IV varies between 0 and 100) if all the individuals are found in a single group (high specificity) and they are present in all the samples of that group (high fidelity). The statistical significance of the indicator taxa was assessed using a randomization method involving 999 permutations.

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### 3.5 Multiproxy analysis (foraminifera plus diatoms)

A multiproxy analysis combining foraminiferal and diatom data was performed. The foraminiferal data were based upon the dead assemblages obtained in this study. Diatom data were obtained from the same 24 sites as the foraminifera and consisted of 61 surface sediment samples (Benito et al. 2015) (Fig. 1 and Table 1). The multiproxy dataset comprised 70 samples, all with full environmental data (water physicochemical data and sediment properties). It contained 140 diatom species and 29 foraminiferal species with a relative abundance >2% in at least one sample, and occurring in > 3 samples (169 species in total). First, DCA was used to show whether unimodal ordination models were more appropriate for the multivariate analysis. Then, a series of partial CCA's, using 14 environmental variables, one at time (salinity, water depth, organic matter, sand content, pH, temperature, dissolved oxygen,  $\text{NO}_3^-$ -N,  $\text{NO}_2^-$ -N,  $\text{NH}_4^+$ -N,  $\text{PO}_4^{3-}$ -P,  $\text{SiO}_4^{4-}$ -Si, seston chlorophyll *a* and pheophytin *a*) were applied to determine the unique contribution of individual environmental variables to microorganism distributions.

### 3.6 Transfer function development

The ratio of the first eigenvalue from the CCA constrained axis ( $\lambda_1$ ) to the first eigenvalue from the unconstrained axis ( $\lambda_2$ ) was used to choose which environmental variable was most suitable for modelling species' response to the selected variable. According to Juggins (2013), the ratio  $\lambda_1/\lambda_2$  should be >1, although a ratio  $\lambda_1/\lambda_2$  not lower than 0.5 could be sufficient (Kingston et al. 1992; Dixit et al. 1993), since this will ensure that the variable of interest explains a significant and independent portion of the variation in the biological data. Additionally, Detrended Canonical Correspondence Analysis (DCCA) was used to check whether a linear or unimodal response model was the most appropriate for building the transfer function (Birks, 1998).

We used Weighted Averaging (WA) and Weighted Averaging Partial Least Square (WA-PLS) as transfer function models. WA-PLS is an extension of the unimodal-based WA, which represents a substantial improvement when long environment gradients and low noise are affecting the dataset (Juggins and Birks 2012). A WA-PLS model results in five components. The selection of a "useful" component depends upon the principle of parsimony, i.e. choosing the component that gives a reduction of the root mean squared error of prediction (RMSEP) of  $\geq 5\%$  of the previous component (Birks 2003). All models were built using square-root transformed species data. We used the leave-one-site-out (LOSO) as a cross validation method (Payne et al. 2012). This method is considered adequate when the effects of spatial autocorrelation (i.e. clustered samples) may introduce bias in model performance. Each model was evaluated on the basis of its predictive ability by calculating three different parameters: correlation between observed and predicted values ( $r^2$ ), root mean squared error of prediction (RMSEP), and maximum bias. Following Birks (1998), the criteria to choose the preferred

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model were to have high  $r^2$ , low RMSEP and low maximum bias, assessed by LOSO cross validation. However, root mean squared error of prediction (RMSEP) values can be biased if some parts of the environmental gradient are not evenly sampled. To correct this, we applied the segment-wise RMSEP approach (Telford and Birks 2011). We did not screen any species from the dataset and so all species were used in the transfer functions. Following Reed's (1998) criteria, we removed outlier samples based on their jack-knifed residuals to check any improvement in the transfer functions. Analyses were run for the foraminiferal dataset (dead assemblages) and for the multiproxy dataset separately.

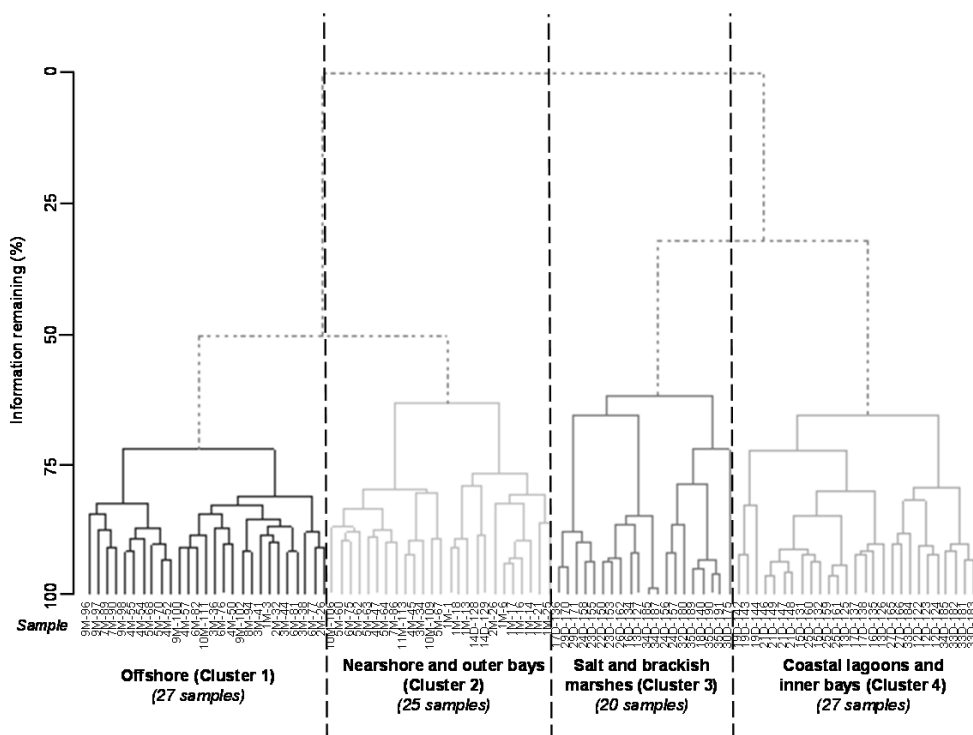
Most multivariate analyses were performed using R version 3.0.1 (R Development Core Team 2010), including the packages vegan (Oksanen et al. 2013) and rioja (Juggins 2014). Finally, CANOCO version 4.5 (Ter Braak and Smilauer 2002) was used to carry out DCCA.

## 4. Results

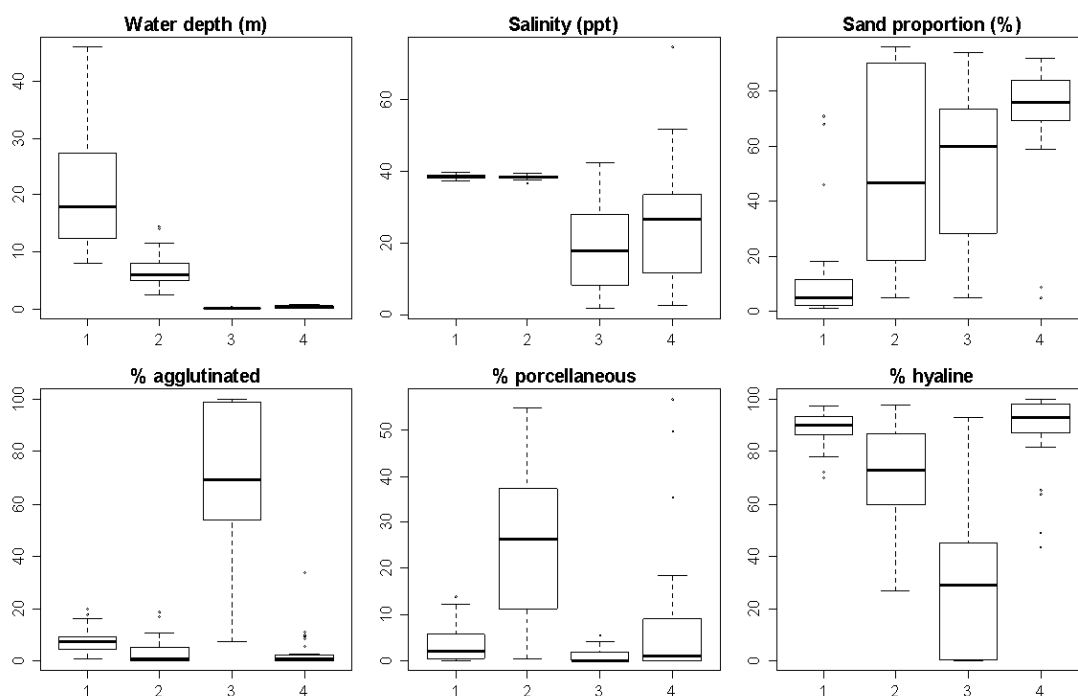
### 4.1 Environmental gradients

A summary of the measured environmental variables for the study sites (deltaic plain and adjacent marine area) are shown in Tables 1 and S1. The measured water depth ranges from 0.13 to 51.50 m, water salinity from 0.74 to 74.63 ppt, and sand content from 1.0 to 100%. Sites with the highest water depths were recorded off the Delta (marine sites) and showed low variability in environmental parameters, while sites sampled in the deltaic plain covered a wide range of sediment organic matter (ranged from 0.89 to 96.99%),  $\text{NO}_3^-$ -N (0.59–1233.69  $\mu\text{g/L}$ ),  $\text{PO}_4^{3-}$ -P (2.48–201.39  $\mu\text{g/L}$ ) and pH (6.96–9.07).

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**Fig. 2** Dendrogram of the Ebro Delta (D) and marine adjacent areas (M) samples showing the four habitat groups identified according to similarity in species composition.



**Fig. 3** Box plots of measured environmental variables and wall type for the foraminiferal groups defined by cluster analysis. 1: Offshore; 2: Nearshore and outer bays; 3: Salt and brackish marshes; 4: Coastal lagoons and inner bays. *Boxes* represent the 25th and 75th percentiles, and the median (middle line inside each box).



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### 4.2 Foraminiferal assemblages and environmental relationships

Altogether, 138 living foraminiferal species were identified in the study area, including the Delta plain and marine sites. A total of 87 living foraminiferal species had relative abundances higher than 2% in at least one sample, and therefore these were the species selected for statistical analyses. Living species richness (S) and diversity (Fisher's  $\alpha$ ) increased from the Delta plain sites (mean S = 7; mean  $\alpha$  = 1.50) to marine sites (mean S = 25; mean  $\alpha$  = 7.05). The living foraminiferal assemblages of the deltaic plain sites were dominated by the hyaline species *A. beccarii* agg. ( $36 \pm 33\%$ ; mean  $\pm$  SD), *Haynesina germanica* ( $10 \pm 18\%$ ) and *Trichohyalus aguayoi* ( $8 \pm 18\%$ ), and the agglutinated species *Trochammina inflata* ( $15 \pm 25\%$ ) and *Jadammina macrescens* ( $8 \pm 17\%$ ). On the other hand, the living foraminiferal assemblages of the marine sites were mostly represented by the hyaline species *A. beccarii* agg ( $15 \pm 19\%$ ), *Nonionoides scaphus* ( $11 \pm 13\%$ ), *Bolivinellina pseudopunctata* ( $9 \pm 7\%$ ), and *Nonion laevigatum* ( $5 \pm 8\%$ ), together with the porcellaneous *Quinqueloculina stelligera* ( $7 \pm 11\%$ ).

In general, the dead assemblages of the deltaic plain sites were composed of the same dominant species as the living assemblages, namely *A. beccarii* agg ( $37 \pm 33\%$ ), *T. inflata* ( $15 \pm 23\%$ ), *H. germanica* ( $10 \pm 19\%$ ), *T. aguayoi* ( $9 \pm 16\%$ ) and *J. macrescens* ( $7 \pm 15\%$ ). In contrast, the composition of the dead assemblages from the marine sites off the Delta was slightly different from that found in the living assemblages. Thus, unidentified miliolids ( $15 \pm 10\%$ ), *A. beccarii* agg ( $14 \pm 13\%$ ) and *Q. stelligera* ( $11 \pm 14\%$ ) dominated the dead assemblages, with *Eggerelloides scaber* ( $5 \pm 6\%$ ) and *Asterigerinata* sp.1 ( $4 \pm 6\%$ ) as secondary species.

In agreement with the frequencies of the dominant species, similarity indices (Rogers index, %) indicated a relatively high resemblance between the living and dead foraminiferal assemblages of the deltaic plain sites (mean similarity = 72.9%), but much lower similarities at the marine sites off the Delta (mean similarity = 35.1 %) (Table 2). Comparison of the sampled sites between spring and summer campaigns (April 2013/August 2013 and April 1967/ July 1967 for the present study and for Scrutton's dataset, respectively) revealed higher average similarity values for the dead assemblages (65.1%) than for the living assemblages (52.9 %), indicating that the dead foraminifera assemblages showed less seasonal variation (Table 2).

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**Table 2** Roger's similarity index for the marine sites (1M-11M from Scrutton 1969) and for the deltaic sites (12D-35D, own data) between spring and summer foraminiferal assemblages and living and dead foraminiferal assemblages. *n.d.* = no data.

M/D	Site	Habitat	Living/Dead (Spring)	Spring/Summer: living	Spring/Summer: dead
1M	South bay	marine	26.6	63.8	68.3
2M	Las Casas	marine	23.9	49.7	33.6
3M	Vinaroz	marine	36.4	47.8	22.8
4M	South faro	marine	44.3	20.5	62.4
5M	Salinas	marine	28.9	43.2	70.5
6M	South platform	marine	n.d.	57.2	70.5
7M	South channel	marine	29.8	45.5	88
8M	Cabo Tortosa	marine	n.d.	38.2	70.8
9M	River mouth	marine	34.6	38.1	40
10M	North platform	marine	49.9	23.6	92.3
11M	North faro	marine	n.d.	17.1	91.8
12D	Alfacs	Inner bay	77.8	76.1	89.3
13D	Alfacs	<i>Salicornia</i>	63.1	48.1	n.d.
14D	Alfacs	Nearshore	61.1	52.8	74.1
15D	Aufacada	Coastal lagoon	76.8	89.2	89.3
16D	Aufacada	<i>Salicornia</i>	65.8	21.8	24.5
17D	Aufacada	<i>Juncus</i>	87.8	77.4	89.4
18D	Aufacada	<i>Phragmites</i>	87	n.d.	2.6
19D	Banya	Microbial mat	54.2	56.6	68.6
20D	Clot	Coastal lagoon	n.d.	n.d.	n.d.
21D	Encanyissada	Coastal lagoon	90.3	n.d.	95.6
22D	Encanyissada	<i>Salicornia</i>	95.4	91.3	64.1
23D	Encanyissada	<i>Juncus</i>	47.3	37.7	33.9
24D	Encanyissada	<i>Phragmites</i>	85.5	52.8	47.6
25D	Fangar	Inner bay	95.5	92.2	90.4
26D	Fangar	<i>Salicornia</i>	67	n.d.	78.4
27D	Garxal	Coastal lagoon	69.4	n.d.	70.1
28D	Garxal	<i>Salicornia</i>	45	n.d.	n.d.
29D	Garxal	<i>Juncus</i>	80.2	n.d.	67.6
30D	Garxal	<i>Phragmites</i>	57.5	n.d.	13.9
31D	Olles	Coastal lagoon	65	n.d.	98.6
32D	Olles	<i>Phragmites</i>	n.d.	n.d.	n.d.
33D	Tancada	Coastal lagoon	75.7	39.8	85.4
34D	Tancada	<i>Salicornia</i>	82.3		n.d.
35D	Tancada	<i>Phragmites</i>	62.8	90.1	58.2
		<b>Mean marine sites</b>	35.1	41.5	65.4
		<b>Mean deltaic sites</b>	72.9	64.4	64.9
		<b>Mean all sites</b>	62.2	52.9	65.1

**Table 3** Indicator values (IV) of foraminiferal indicator species of each habitat group identified by cluster analysis (see text). *p* value denotes the statistical significance of IV based on Monte Carlo tests (999 permutations). Values of Specificity (S) and Fidelity (F) are also shown. Ecological requirements of the main foraminiferal indicator species marked in bold (i.e. those having >10% relative abundance in at least one sample) and the references where this information was obtained are also indicated.

Foraminifera species	Code	S	F	IV	<i>p</i> value	Ecological requirements	References
<b>Offshore (cluster 1)</b>							
<i>Bulimina aculeata</i>	BUACU	89.5	100	94.6	0.001	Infaunal, inner shelf marine species with preferences for clayey silt sediments	Blázquez 2001
<i>Nonionoides scaphus</i>	NOSCA	79.2	100	89.0	0.001	Infaunal, shelf marine species. Affinities for muddy sediments close to river mouths areas	Avnaim-Katav et al. 2015; Mojtahid et al. 2010
<i>Ammosphaeroidina sphaeroidiniforme</i>	AMMSPH	85.7	81.5	83.6	0.001		
<i>Bulimina gibba</i>	BUGIB	87.8	77.8	82.6	0.001		
<i>Textularia calva</i>	TECAL	100	66.7	81.6	0.001		
<i>Elphidium matagordanum</i>	ELMAT	85.2	77.8	81.4	0.001	Infaunal, shallow marine species (<10 m). Affinities for sandy sediments	Murray 1991
<i>Elphidium incertum</i>	ELINC	87.7	74.1	81.4	0.001	Infaunal, shallow marine species linked to deltaic-marine transitions with preferences for a wide range of substrates (clay, silt, sand)	Mojtahid et al. 2010
<i>Valvulineria bradyana</i>	VABRA	100	63.0	79.3	0.001	Epifaunal, outer shelf marine species (>20 m) linked to river mouth areas with fine sediments	Colom 1974; Mojtahid et al. 2010
<i>Bolivinellina pseudopunctata</i>	BLPSE	62.8	100	79.2	0.001	Infaunal, inner shelf marine species commonly found in water depths <15 m and muddy substrates	Blázquez 2001

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Foraminifera species	Code	S	F	IV	p value	Ecological requirements	References
<i>Haplophragmoides canariensis</i>	HACAN	91.5	66.7	78.1	0.001		
<i>Uvigerina</i> sp. 1	UVSP1	99.3	59.3	76.7	0.001		
<i>Reussella aculeata</i>	REACU	97.3	59.3	75.9	0.001		
<i>Criboelphidium selseyensis</i>	ELSEL	57.1	92.6	72.7	0.001	Infaunal, marine species with very narrow water depth range (10-15 m). Affinities for sandy mud sediments. Usually reported as a ecophenotype of <i>C. excavatum</i>	Murray 1991; Usera et al. 2002
<i>Gavelinopsis praegeri</i>	GAPRA	90.6	55.6	70.9	0.001		
<i>Elphidium</i> cf. <i>flexuosum</i>	eELFLE	73.2	59.3	65.9	0.001		
<i>Eggerelloides scaber</i>	EGSCA	60.6	70.4	65.3	0.001		
<i>Cassidulina laevigata</i>	CALAE	95.1	44.4	65.0	0.001	Infaunal, shelf marine species with preferences for sandy mud sediments and sea grass beds. Observed in water depths between 25 and 800 m	Mojtahid et al. 2010
<i>Elphidium advenum</i>	ELADV	56.6	74.1	64.8	0.001		
<i>Reophax subfusiformis</i>	RESUB	100	40.7	63.8	0.001		
<i>Elphidium</i> sp. 2	ELSP2	97.6	40.7	63.1	0.001		
<i>Planorbulina mediterraneensis</i>	PLMED	94.4	40.7	62.0	0.001		
<i>Elphidium crispum</i>	ELCRI	98.6	37.0	60.4	0.001	Epifaunal, innermost shelf species (0–25 m) with preferences for a wide range of substrates: seagrass beds, muds and sands	Avnaim-Katav et al. 2015
<b>Nearshore and outer bays (cluster 2)</b>							
<i>Quinqueloculina stelligera</i>	QUSTE	91.5	84.0	87.7	0.001	Epifaunal, shallow marine species (<10 m). Typical from marine to hypersaline lagoonal environments. High affinities for sandy substrates and linked to turbulent zones off deltaic fringes.	Blázquez 2001

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Foraminifera species	Code	S	F	IV	p value	Ecological requirements	References
<i>Triloculina</i> sp. 1	TRSP1	87.8	68.0	77.3	0.001	Epifaunal, shallow marine species (<10 m) with preferences for marine and hypersaline marginal environments. Affinities for sandy sediments	Avnaim-Katav et al. 2015
Miliolid undetermined	MIUND	57.6	92.0	72.8	0.001		
<i>Nonionella atlantica</i>	NOATL	85.0	60.0	71.4	0.001	Infaunal, open marine species. Affinities for muddy sediments linked to pro-delta areas	Mojtahid et al. 2010 (referred as <i>N. turgida</i> )
<i>Epistominella vitrea</i>	EPVIT	97.0	52.0	71.0	0.001	Epifaunal, shelf marine species (10–40 m). Common in muddy sediments	Milker et al. 2009
<i>Asterigerinata</i> sp. 1	ASSP1	81.0	60.0	69.7	0.001	Epifaunal, innermost shelf species. Abundant in nearshore sandy environments, from 4 to 11 m	Milker et al. 2009
<i>Buliminella elegantissima</i>	BUELE	70.8	68.0	69.4	0.001		
<i>Nonion laevigatum</i>	NOLAE	69.3	68.0	68.6	0.001	Infaunal, shelf marine species. Frequent in sandy sediments from shallow waters of deltaic front	Avnaim-Katav et al. 2015
<i>Brizalina striatula</i>	BRSTR	70.9	60.0	65.2	0.001	Infaunal, open marine species commonly found in sandy and muddy substrates. From shallow to nearshore environments	Blázquez 2001
<b>Salt and brackish marshes</b> (cluster 3: <i>Salicornia</i> , <i>Juncus</i> marshes, and <i>Phragmites</i> marshes)							
<i>Trochammina inflata</i>	TRINF	94.8	95.0	94.9	0.001	Epifaunal or infaunal, euryhaline marsh species with preferences for muddy substrates	Usera et al. 2002
<i>Jadammina macrescens</i>	JAMAC	97.1	85.0	90.8	0.001	Epifaunal, euryhaline marsh species. High affinities for muddy and sandy substrates rich in organic matter	Blázquez 2001; Usera et al. 2002
<i>Trichohyalus aguayoi</i>	TRAGU	94.5	70.0	81.3	0.001	Infaunal, euryhaline species inhabiting marsh and coastal lagoons. High affinities for muddy sediments	Blázquez 2001; Usera et al. 2002

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Foraminifera species	Code	S	F	IV	p value	Ecological requirements	References
<i>Haplophragmoides wilberti</i>	HAWIL	99.7	45.0	67.0	0.001	Infaunal, low-salinity marsh species with high tolerance to organic-rich sediments	Debenay and Guillou 2002
<b>Coastal lagoons and inner bays (cluster 4)</b>							
<i>Haynesina germanica</i>	HAGER	84.7	85.2	84.9	0.001	Infaunal, brackish species very common in coastal lagoons and estuaries, although it can live in hypersaline environments. Preferences for muddy sand substrates	Blázquez 2001; Usera et al. 2002
<i>Ammonia beccarii</i> agg	AMBEagg	62.3	100	78.9	0.001	Epifaunal, cosmopolitan eurhyhaline species inhabiting marshes and coastal lagoons ( <i>A. tepida</i> ), although it can live in open sea ( <i>A. beccarii</i> ). Affinities for sandy substrates	Usera et al. 2002
<i>Quinqueloculina jugosa</i>	QUJUG	99.3	40.7	63.6	0.001	Epifaunal, shallow marine species inhabiting coastal lagoons and estuaries. Preferences for sandy substrates	Murray 1991
<i>Criboelphidium oceanensis</i>	CROCE	96.0	40.7	62.5	0.001	Infaunal, brackish specie inhabiting shallow coastal lagoons with muddy sand substrates	Usera et al. 2002
<i>Quinqueloculina seminula</i>	QUSEM	81.1	40.7	62.5	0.001	Epifaunal, shallow marine species. Preferences for coastal lagoons and estuaries with normal salinities, although it can also live in nearshore environments. High affinities for sandy substrates	Blázquez 2001

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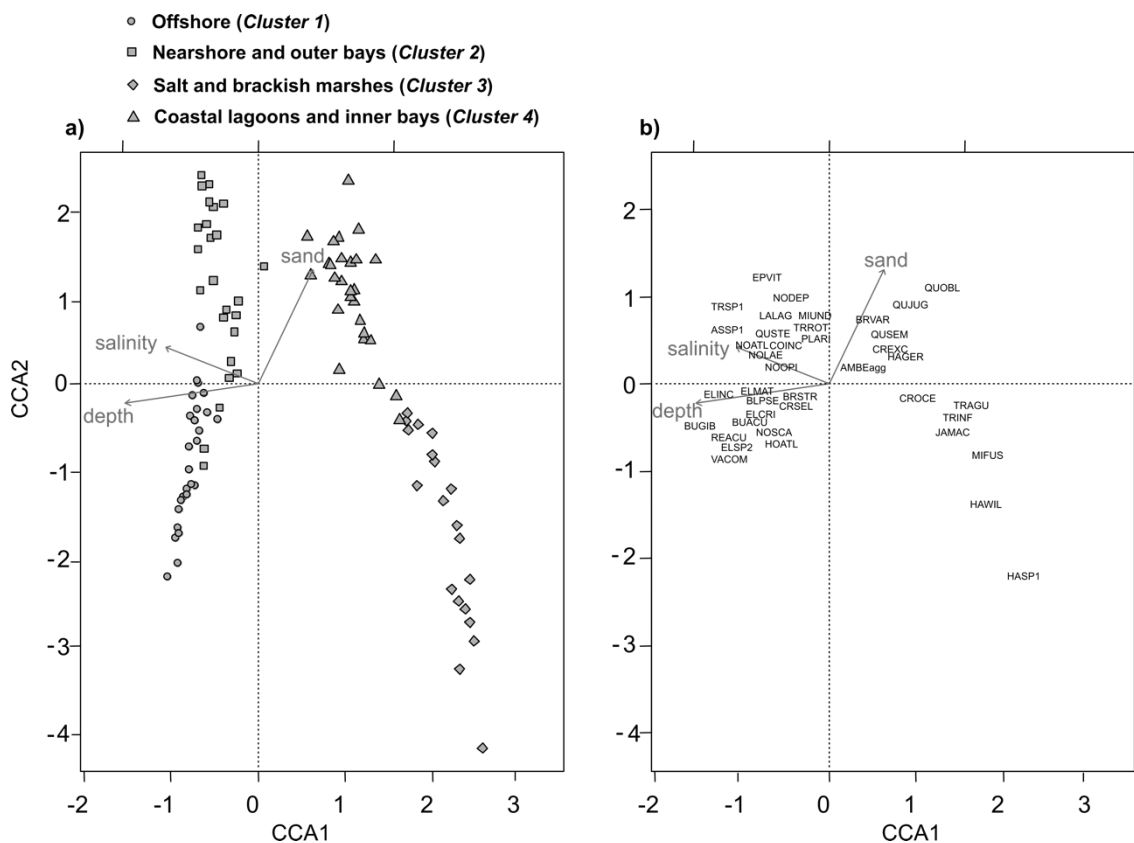
Cluster analyses identified four living foraminiferal groups according to similarities in species composition (Fig. 2). For each cluster, the main environmental characteristics and the relative abundances of the three wall types of foraminifera (agglutinated, porcellaneous, hyaline) are shown by boxplots in Figure 2. Cluster 1 (27 samples) and cluster 2 (25 samples) comprised samples from the marine sites off the Ebro Delta, which had the greatest water depths (cluster 1:  $21.85 \pm 9.8$  m; cluster 2:  $7.01 \pm 3.02$  m) and normal marine salinities (cluster 1:  $38.58 \pm 0.63$ ; cluster 2:  $38.26 \pm 0.58$ ). Most of the samples from cluster 1 were from offshore sites and had a very low sand content ( $12.07 \pm 18.12$  %). Cluster 2 grouped the nearshore and outer bay samples and had a higher sand content than cluster 1 ( $52.3 \pm 24.8$  %); it also contained the highest proportion of porcellaneous species of any of the four clusters. Cluster 3 (20 samples) and cluster 4 (27 samples) were composed of deltaic plain samples. In both groups, samples exhibited a wide variation in salinity, from near fresh-brackish (2.23 ppt) to hypersaline conditions (74.63 ppt). Samples of clusters 3 and 4 were also alike in coming from very low water depths (cluster 3:  $0.14 \pm 0.09$  m; cluster 4:  $0.40 \pm 0.19$  m), and in exhibiting a wide range of sediment sand content (cluster 3:  $49.57 \pm 29.74$  %; cluster 4:  $69.91 \pm 24.93$  %). Cluster 3 was mainly composed of samples from salt- (i.e. *Salicornia* and *Juncus* marshes) and brackish marshes (i.e. *Phragmites* marshes), and here relative abundance of agglutinated foraminifera was particularly high ( $70.0 \pm 31.7$  %). All samples of this group had high organic matter content ( $39.08 \pm 30.1\%$ ) compared to samples from cluster 4. Cluster 4 comprised coastal lagoon, inner bay and microbial mat samples, which had a particularly high sand content ( $70.0 \pm 23.9\%$ ) and a high proportion of hyaline species ( $89.0 \pm 15.2$  %).

Gradient lengths of the first DCA axis (5.82 SD) revealed a high species turnover, confirming the use of unimodal constrained ordination techniques for exploring the relationship between foraminiferal assemblages and measured environmental variables (salinity, water depth, sand content and temperature). An initial CCA with 87 foraminiferal species (>2% relative abundance in at least one sample) revealed that salinity, water depth and sand content explained 23.1 % of the variance within the species data. Temperature was excluded from the subsequent CCAs ( $p = 0.35$ ). The very similar eigenvalues of this initial CCA ( $\lambda_{1\text{CCA}} = 0.704$ ;  $\lambda_{2\text{CCA}} = 0.240$ ) and those of the DCA ( $\lambda_{1\text{DCA}} = 0.758$ ;  $\lambda_{2\text{DCA}} = 0.279$ ) suggested that the measured environmental variables capture a significant proportion of the variance of the foraminiferal distribution. Partial CCAs showed that water depth, sand content and salinity independently explained significant portions ( $p < 0.05$ ) of the variance in the species distribution (Table S2).

The first two CCA axes of the reduced set of environmental variables explained 20.9% of the foraminiferal variance, with water depth explaining the greatest proportion (8.7%) once the effect of the other variables had been taken into account (Table S2). The CCA ordination with the three variables that accounted for independent and significant unique effects (i.e. water

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depth, sand content and salinity), and with 87 foraminiferal species, separated groups of samples that were in agreement with those from the cluster analysis (Fig. 4). CCA axis 1 (16.1% of the explained variance) grouped samples from the Delta plain sites (clusters 3 and 4) together and clearly separated them from the marine samples (clusters 1 and 2). CCA axis 2 (4.8% of the explained variance) arranged samples following sediment characteristics (% sand content).



**Fig. 4** Canonical Correspondence Analysis (CCA) diagram showing the relationships of **a** samples and **b** species with the selected environmental variables. The species plotted have  $\geq 10\%$  maximum relative abundance in at least one sample. Environmental variables accounting statistically significant unique effects are shown (depth: water depth; salinity; sand: sand content). The sample symbols correspond to the foraminiferal groups defined by cluster analysis (see text). For full species names see Appendix A.

#### 4.3 Indicator species

Indicator species were recognised through Indicator Species Analysis for the four foraminiferal groups obtained with cluster analysis. A total of 41 foraminiferal species showed statistically significant and high indicator values (IV,  $>60\%$ ) and therefore could be considered as good indicator species (Table 3) (Fig. S1). In general, the specificity of all indicator species was high ( $>65\%$ ), and indeed some of them showed very high specificity values ( $>96\%$ ). Among these highly specific foraminifera were *Criboelphidium oceanensis* and *Quinqueloculina jugosa* for



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the coastal lagoons and inner bays group (cluster 4), and *Haplophragmoides wilberti* for the salt- and brackish marshes group (cluster 3). Interestingly, these three species with highest specificity also showed low fidelity values ( $\leq 40\%$ ) (Table 3).

### 4.4 Foraminifera-based water depth transfer function

Results of partial CCAs showed that water depth explained the largest and independent proportion of variance in the foraminiferal species data. DCCA of the dataset with water depth as the only constraining variable indicated a gradient length of 2.49; it therefore confirmed the unimodal response of foraminiferal species with respect to water depth and also supported the use of WA and WA-PLS methods. Water depth showed a ratio of 0.75 between the first constrained CCA axis and the first unconstrained axis ( $\lambda_1/\lambda_2$ ), indicating that this variable is an ecologically important factor determining the distribution of foraminiferal assemblages in the Ebro Delta.

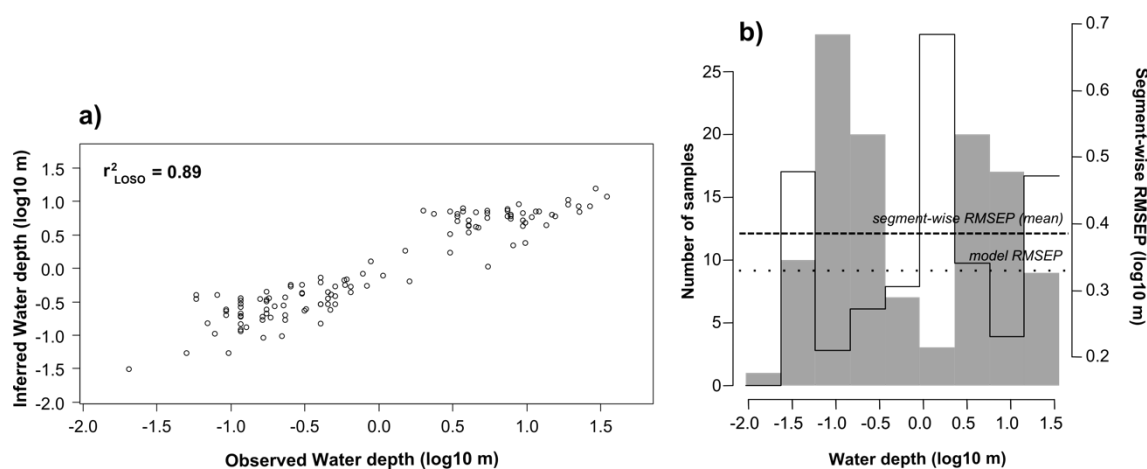
The two-component WA-PLS model (WA-PLS-2) performed with dead foraminiferal assemblages ( $n$  samples = 115,  $n$  species = 155 species, Table S6) resulted in the best performing foraminifera–water depth inference model, since it showed the highest  $r^2_{\text{LOSO}}$  (0.82), lowest RMSEP<sub>LOSO</sub> (0.41 log<sub>10</sub> m), and lowest maximum bias<sub>LOSO</sub> (1.06 log<sub>10</sub> m) (Table S3). Segment-wise RMSEP<sub>LOSO</sub> showed a decrease in the model performance (0.50 log<sub>10</sub> m), indicating uneven sampling along the water depth gradient (Fig. 5). A total of seven samples had residuals exceeding 25% of the water depth range (0.84 log<sub>10</sub> m) and were considered as potential outliers. The deletion of these seven samples (4M–47, 5M–64, 5M–65, 7M–86, 9M–95, 13D–125, 18D–141) resulted in an improvement of WA-PLS component 2. Thus, the preferred transfer function with this screened data set (108 samples and 151 species) had a higher  $r^2_{\text{LOSO}}$  of 0.89 and a lower segment-wise RMSEP<sub>LOSO</sub> of 0.40 log<sub>10</sub> m (Fig. 5 and Table S3).

### 4.5 Multiproxy analysis (foraminifera plus diatoms)

DCA axis 1 (3.124 SD) from the multiproxy dataset supported the use of unimodal constrained ordination techniques to examine species–environment relationships. Partial CCAs revealed that salinity (4.22%), water depth (3.47%), organic matter (2.38%), pH (2.40%), NO<sub>2</sub><sup>-</sup>-N (2.03%) and sand content (1.86%) accounted for independent and significant portions ( $p < 0.05$ ) of the variance in the species data (Table S4). The first two axes of the CCA with these six environmental variables explained 13.19% of the variance, with salinity identified as the most important variable (explaining 4.22% of the variance within the species data).

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The CCA ordination plot from the multiproxy dataset showed that Ebro Delta habitat samples were arranged very similarly to the ordination obtained when diatoms alone were analysed (Fig. S2 and Benito et al. 2015). Thus, shallowness and salinity appeared as the main gradients affecting species distribution. CCA axis 1 from the multiproxy data set predominantly separated samples from brackish and salt marshes with very shallow water and organic-rich sediments (i.e. *Phragmites*, *Salicornia* and *Juncus* marshes, and microbial mat), from the coastal lagoons, inner bays and nearshore open sea habitats. CCA axis 2 the multiproxy analysis distinguished habitats with fresher conditions (i.e. coastal lagoons and associated *Phragmites* marshes with lower salinities) from habitats characterized by brackish/marine conditions (*Salicornia* and *Juncus* marshes; brackish coastal lagoons and inner bays; nearshore open sea).



**Fig. 5 a** Scatter plot showing the observed  $\log_{10}$  water depth (m) against the foraminifera-inferred  $\log_{10}$  water depth (m) for the two-component Weighted Averaging Partial Least Squares model (WA-PLS-2) and **b** comparison of the overall RMSEP and segment-wise RMSEP under LOSO cross validation method. Grey bars are the number of samples within the ten equal groups of  $\log_{10}$  water depth values.

### 4.6 Multiproxy salinity-based transfer function

Salinity made the highest unique contribution (4.22%) to explaining the variance of the multiproxy dataset (foraminifera plus diatoms). Salinity also had the highest  $\lambda_1/\lambda_2$  ratio (0.70) (Table S5), indicating the ecological importance of this variable in explaining species distributions. Therefore, a transfer function was developed for salinity using the multiproxy dataset. All species (dead foraminifera and diatoms,  $n = 511$ ) were included in the initial transfer function. The results showed that WA with classical deshrinking resulted in the best performing salinity model, with the highest  $r^2_{\text{LOSO}}$  (0.63), lowest RMSEP (0.28  $\log_{10}$  ppt) and lowest maximum bias (0.45  $\log_{10}$  ppt). However, the multiproxy salinity transfer function was

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only slightly better in terms of statistical performance than a conductivity (a proxy of salinity) model using diatoms alone ( $r^2_{\text{LOSO}} = 0.64$ ; RMSEP =  $\log_{10} 0.27$  mS/cm; maximum bias =  $\log_{10} 0.32$  mS/cm) (Table S5).

### 5. Discussion

#### 5.1 Living foraminiferal assemblages

The living assemblages of the two areas studied in the Ebro Delta (i.e. deltaic plain and adjacent marine areas) can be characterized by means of different biocenotic parameters. Firstly, a clear distinction can be made between the low-diversity habitats ( $\alpha$  range = 0.32–6.96) of the deltaic plain (i.e. coastal lagoons and marshes) and the high-diversity habitats ( $\alpha$  range = 2.04–16.97) of the open sea (i.e. nearshore and offshore habitats). A very similar difference has been observed between tidal estuaries and the neighbouring shelf area in the Gulf of Cadiz, Southern Iberian Peninsula (Mendes et al. 2012), while Cearreta (1988) showed that the diversity of living foraminiferal assemblages increased from the upper ( $\alpha$  range = 1–3.5) to the lower parts ( $\alpha$  range = 1–4.5) of the Santoña estuary in northern Spain. Secondly, the deltaic plain and marine adjacent areas can also be distinguished by the proportions of different foraminiferal wall types. The agglutinated species are more abundant in shallow marsh habitats (i.e. cluster 3), and the hyaline and porcellaneous species in subtidal environments (i.e. clusters 1, 2 and 4) (Fig. 3). This agrees with the general trend found in estuaries (e.g. Weiss 1976; Debenay and Guillou 2002), where a gradual change has been observed from agglutinated-dominated assemblages upstream to calcareous-dominated assemblages (hyaline + porcellaneous) downstream.

Within the Delta plain habitats, the living and dead foraminiferal assemblages show high similarity, well above the critical value of 70% identified by Cearreta (1988) and Rodríguez-Lázaro et al. (2013), indicating very restricted marine conditions and limited post-mortem changes (Murray 1991). Also, the low proportion of allochthonous foraminifera found in the Delta plain samples (average 25.1%) supported the hypothesis that the dead foraminiferal assemblages are derived basically from the living ones. However, major differences between the living and dead assemblages were evident in the adjacent marine habitats (average similarity 35.1%). These may reflect accidental bias due to the limited number of dead samples processed by Scrutton (1969), but they could also be explained by i) post-mortem changes such as transport by wave action and currents, and ii) living population dynamics, which include species-specific reproduction rates and population densities in response to environmental fluctuations (Mendes et al. 2012). A better example of differences between living and dead assemblages is provided in outer bay samples from the Scrutton's transects of Vinaroz and Las

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Casas (Fig. 1). Relatively high percentages of *Asterigerinata* sp.1 and *E. scaber* were found as dead forms, which could have been redistributed by currents to sheltered areas at the ends of and behind the sand spits, since these two species were very abundant in the living assemblages of the vicinity sites. But they might be also reflecting a change in the environmental conditions that was detrimental for the growth of these two species, because in the specific case of *E. scaber*, it may be too large to be transported as living form. Therefore, dead populations are a reflection of the living population as it used to be.

In relation to seasonality, the similarity index showed that the living foraminiferal assemblages of spring and summer are different. This is because living communities are strongly dependent on environmental conditions at the moment of sampling (Duchemin et al. 2005), and are also subject to different reproduction rates for each species (Jorissen and Wittling 1999). Dead assemblages, however, represent the successive accumulation of living assemblages over time, and their seasonal (and spatial) variations tend to be integrated into the dead assemblages (Murray 1991). Evidence of this was also found in our study, where the comparison of dead assemblages between spring and summer seasons indicates higher similarities than those obtained for the living assemblages. Thus, dead assemblages were more homogenous from a seasonality point of view, and may be more useful for the interpretation of palaeoenvironments in the Ebro Delta.

### 5.2 The relation of foraminifera to water depth

Water depth emerged as the main environmental gradient structuring living foraminiferal assemblages in the study area. In the microtidal Mediterranean Sea, other studies have also shown water depth zonation of foraminifera near river deltas (for instance, Frezza and Carboni (2009), Rossi and Horton (2009) in the Po Delta; or Goineau et al. (2011) in the Rhône Delta). Water depth *per se* probably never affects foraminiferal distributions directly. However, many abiotic (e.g. oxygen, food availability, substrate) and biotic (e.g. competition) factors covary with depth that do determine foraminiferal distributions, especially in nearshore marine waters (<20 m depth) (Jorissen et al. 1992; De Rijt et al. 2000; Morigi et al. 2005) thus producing a bathymetric zonation and allowing estimation of palaeodepth from fossil assemblages (Rossi and Horton 2009; Milker et al. 2011; Avnaim-Katav et al. 2015). A better example is provided in the Ebro Delta. Substrate type (sand content) is a significant factor affecting species composition, suggesting the direct influence of bottom currents in sorting sand fractions in shallower nearshore areas, and mud fractions in deeper, prodelta environments. This may indicate the indirect effect of water depth, which resulted in a bathymetric zonation of the benthic foraminifera in the Ebro Delta.

### 5.3 Foraminifera–water depth model

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The transfer function performance looks reasonable ( $r^2_{\text{LOSO}} = 0.89$ ) when compared with previously published water depth models, for instance in Mediterranean deltas (Rossi and Horton 2009:  $r^2_{\text{jack}} = 0.95$ ), in the westernmost Mediterranean (Alboran) Sea (Milker et al. 2011:  $r^2_{\text{jack}} = 0.83$ ), or in Australian embayments (Horton et al. 2007:  $r^2_{\text{jack}} = 0.90$ ). Although the transfer function appears to be statistically robust for palaeowater depth estimations in the Ebro Delta, its application should be done cautiously since the water depth gradient has been unevenly covered, with a small number of samples from intermediate depths (Fig. 5a, b). Therefore, future research should focus on more intermediate depths as well as to span a wider range of Mediterranean deltas in order to develop an enlarged foraminifera-water depth training set for palaeo-sea level reconstructions in similar deltas.

### 5.4 Foraminiferal assemblages as ecological indicators

In general, most of the indicator species ( $IV > 60$ ;  $p < 0.05$ ) for each habitat group (i.e. offshore; nearshore and outer bays; coastal lagoons and inner bays; salt and brackish marshes) showed high specificity and fidelity values to the group. However, some indicator species require special attention, due to their particular combination of very high specificity (>96%) and low fidelity ( $\leq 40\%$ ), suggesting a preference for particular conditions or sites within the habitat group. This is the case for *C. oceanensis* and *Q. jugosa* which, although they emerge as indicator species of the coastal lagoons and inner bays environments (cluster 4), are restricted to the Garxal and Tancada coastal lagoons (*C. oceanensis*) and the inner Alfacs bay (*Q. jugosa*). It may be, therefore, that *C. oceanensis* is an indicator of a particular subset of brackish lagoonal conditions, while the miliolid *Q. jugosa* probably indicates shallow environments with normal marine salinities. Similarly, within the salt and brackish marsh habitats (cluster 3), *H. wilberti* is only found in *Phragmites* marshes, likely indicating the lower salinity conditions of these marshes compared to *Salicornia* and *Juncus* marshes (Hayward et al. 1999). The same type of ecological indication was also found for these three species in studies of similar Mediterranean coastal lagoons and marshes (e.g. in the Rhône Delta: Vangerow et al. 1974, and Venice lagoon: Serandrei-Barbero et al. 2011). Likewise, most the indicator species of our marine habitat groups (see Table 3) were also found to be characteristic of inner shelf environments elsewhere in the Mediterranean Sea: off other parts of the Spanish coast (Blázquez 2001; Colom 1974; Milker et al. 2009; Usera et al. 2002), in the Gulf of Lyon (Mojtahid et al. 2010) and off the coast of Israel (Avnaim-Katav et al. 2015).

On the other hand, within the offshore habitat group (Table 3) there are species with very high fidelities but relatively low specificity (i.e. they are also found along other habitat groups). These species include *Cribrorhynchium selseyensis* and *B. pseudopunctata* which, according to Murray (1991) and Blázquez (2001), are associated with muddy sand substrates and shallow environments. However, our results suggest wider ecological ranges, since these species are

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characteristic of offshore habitats (i.e. deeper and muddy), but also thrive in the nearshore and outer bays habitat (i.e. shallower and sandier). Therefore, our findings highlight the usefulness of considering not only the overall indicator value but also the combination of specificity and fidelity values in order to explain what the presence of a particular foraminiferal indicator species means. Previous studies dealing with diatom indicator species have yielded similar conclusions (Rovira et al. 2012; Benito et al. 2015).

### 5.5 Implications of multiproxy analysis (foraminifera plus diatoms)

The multiproxy approach reinforces the environmental characterization of the Ebro Delta habitats (CCA) and the salinity prediction (transfer function) obtained using benthic diatoms solely (Benito et al. 2015). Some previous studies of transitional environments have also investigated whether a combination of different benthic micro-organism groups can improve the environmental information provided by each of them individually (e.g. for foraminifera, diatoms and testate amoebae by Gehrels et al. 2001; for foraminifera, diatoms and macrophytes by Patterson et al. 2005; and for foraminifera and testate amoebae by Vázquez Riveiros et al. 2007). The conclusion of those works combining foraminifera and diatoms are very similar to ours: i.e. that combining datasets offers minimal statistical improvement. This may be because foraminiferal microfaunas are less diverse and exhibit lesser compositional changes of their assemblages between sites. Diatoms, on the other hand, have more diverse assemblages than foraminifera and tend to be more compositionally different between sites (Kemp et al. 2009). Thus, in the Delta plain, habitats with distinctly different salinities (e.g. salt/brackish vs. freshwater) were clearly identified and defined using the diatom assemblages (Fig. S2) but not using foraminifera. This could be explained by the dominance of a few euryhaline foraminiferal species in most of the salt/brackish habitats of the Delta, as has been shown in marginal marine environments elsewhere (Scott et al. 2001; Murray, 2006).

The usefulness of one type of indicator or the other (e.g. benthic foraminifera, benthic diatoms), or a combination of both microorganisms, should be assessed not only by the amount of environmental information gained but also the time needed to obtain it. From the regression analyses, it is clear that foraminifera and diatoms, considered separately, are good indicators of water depth and salinity of the Ebro Delta respectively, and therefore complementary when analysed individually. However, there is no information gained about salinity when foraminifera and diatoms are analysed together. On the other hand, for the identification and description of the Delta plain habitats, diatoms alone discriminated up to five habitat types (i.e. salt marshes, brackish marshes, brackish coastal lagoons and bays, coastal lagoons with fresher conditions, nearshore open sea: see Benito et al. 2015), while foraminifera detected three (i.e. salt and brackish marshes, coastal lagoons and bays, nearshore open sea, in this study); and four habitat types when Scrutton's data (1969) are included in the analyses (this study). The habitat types

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recognised when diatom and foraminifera are analysed together are the same as with diatoms alone. Therefore, since the analysis of benthic foraminifera is more cost-effective (e.g. easier taxonomy and less diverse communities), this group seems to be the most suitable when a coarse grained habitat reconstruction is all that is required. However, if a more detailed habitat reconstruction is needed then diatoms should be the proxy to use. Concerning quantitative reconstructions, the choice of the indicator group depends entirely on the parameter one wants to predict (i.e. foraminifera for water depth and diatoms for salinity).

### 5.6 Implications for palaeoenvironmental reconstructions

In Mediterranean deltas, the severe impact caused by humans (e.g. through intensive agriculture, upstream catchment water use, sediment retention) is a major environmental concern (Giosan et al. 2013; Anthony et al. 2014). Moreover, the consequences of increased relative sea-level rise associated with global warming put deltas and their coastal wetlands at risk (e.g. from submergence, coastal retreat, salinization: Day et al. 2011; Ibáñez et al. 2014). In order to plan for this and take effective measures for mitigation and/or adaptation, it is crucial to obtain reliable quantitative estimates of the pristine and current status of deltaic ecosystems, and to determine how and why changes have occurred. In the absence of long-term monitoring data, palaeoecological approaches are irreplaceable for evaluating how natural and human-driven processes have affected the functioning and development of deltas at different temporal scales. In the specific case of the Ebro Delta, both natural changes (i.e. shifts of the river mouth) and human-made changes (resulting mainly from extensive rice cultivation and sediment and water retention by upstream dams) have determined the evolution of the Delta during the last centuries (Canicio and Ibáñez 1999; Somoza and Rodriguez-Santalla 2014). It is clear from previous studies that the Ebro Delta has experienced major human impacts, such as wetland surface reduction and degradation (Mañosa et al. 2001; Cardoch et al. 2002), nutrient enrichment (Comín et al. 1991), salinity modification (Prado et al. 2012) and changes in catchment land use (Xing et al. 2014), together with the regional impacts of climate change (Ibáñez 2009). However, the extent to which these impacts have affected natural habitats and their timescale of change are largely unknown. Application of the approaches developed in this paper should provide valuable insights in this respect. Furthermore, over a longer time scale, our foraminiferal dataset will be useful for tracking the natural evolution of the Ebro Delta during the Holocene (Cearreta et al. under review), and therefore for determining the intrinsic variability of the system, which is essential for being able to disentangle natural from anthropogenic-related changes.

The use of benthic foraminifera as ecological indicators requires a good knowledge of modern assemblages (live and dead) and their relationships with present-day environmental conditions. Our study has shown that modern foraminiferal assemblages can be used to predict past water

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depths and habitat conditions because i) foraminifera show a significant quantifiable relationship to water depth (i.e. transfer function), ii) the most representative habitat types of the deltaic plain and its adjacent marine areas have been successfully characterized using foraminiferal indicator species. Interestingly, the indicator species approach has proved to be a complementary improvement for quantitative palaeoreconstructions, as also found with diatoms (Benito et al. 2015). For instance, in the Ebro Delta, for a water depth (inferred from the fossil foraminifera) around c. 3 m ( $\pm 1.5$  m), two distinct subtidal habitats could be possible (i.e. coastal lagoon, and nearshore/ outer bay habitats). Because coastal lagoon, bays, nearshore and offshore habitats have always existed in the Delta, this complementary approach allows main habitats to be characterized and identified in adequately preserved fossil assemblages.

### **6. Conclusions**

Modern (living and dead) foraminiferal assemblages have been characterized along environmental gradients of the Ebro Delta, resulting in the definition of four distinct habitat groups. Although the spatial and seasonal distributions of living assemblages fluctuate, the occurrence of distinct indicator species for each habitat type provides useful information about the Delta ecosystem. An integrative approach via quantitative water-depth estimates and indicator species will improve the resolution of palaeoenvironmental interpretations.

In the Ebro Delta, tests of a multiproxy approach (foraminifera plus diatoms) have reinforced environmental characterization of the habitats. Furthermore, each indicator individually has value, foraminifera for quantitative predictions of water depth and diatoms for prediction of salinity.

These results are currently being used to interpret fossil foraminifera assemblages in order to i) establish reference conditions in these coastal wetland habitats before significant human intervention had place, and ii) reconstruct the evolution of the Delta over the Holocene epoch (last 11,700 years).



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**Appendix A** Taxonomic list of all foraminiferal species identified in this study. Legend: SD = Samples Deltaic plain, SM = Samples Marine area; L = living, D = dead.

Code	Specie
ADLAE	<i>Adelosina laevigata</i> (d'Orbigny) = <i>Quinqueloculina laevigata</i> d'Orbigny, 1939 (SD;SM;L;D)
AMBAL	<i>Ammobaculites balkwilli</i> Haynes, 1973 (SD;L;D)
cAMARE	<i>Ammobaculites</i> cf. <i>arenaria</i> Natland, 1938 (SM;L;D)
AMSP1	<i>Ammobaculites</i> sp.1 (SD;L;D)
AMBEagg	<i>Ammonia beccarii</i> agg (Linné) = <i>Nautilus beccarii</i> Linné, 1758 (Variants included in this taxon) (SD;SM;L;D)
AMMSP1	<i>Ammosphaeroidina</i> sp.1 (SD;L;D)
AMSPH	<i>Ammosphaeroidina sphaeroidiniforme</i> (Brady) = <i>Haplophragmium sphaeroidiniforme</i> Brady, 1884 (SM;L;D)
cATSAL	<i>Ammotium</i> cf. <i>salsum</i> (Cushman and Brönniman) = <i>Ammobaculites salsum</i> Cushman and Brönniman, 1948 (SD;SM;L;D)
AMSCA	<i>Amphicoryna scalaris</i> (Batsch) = <i>Nautilus scalaris</i> Batsch, 1791 (SM;L;D)
ARMEX	<i>Arenoparella mexicana</i> (Kornfeld) = <i>Trochammina inflata</i> var. <i>mexicana</i> Kornfeld, 1931 (SD;L)
ASMAM	<i>Asterigerinata mamilla</i> (Williamson) = <i>Rotalia mamilla</i> Williamson, 1858 (SD;SM;L;D)
ASSP1	<i>Asterigerinata</i> sp.1 (SM;L;D)
AUPER	<i>Aubignyna perlucida</i> (Heron-Allen and Earland) = <i>Rotalia perlucida</i> Heron-Allen and Earland, 1913 (SD;SM;L;D)
BODIL	<i>Bolivina dilatata</i> Reuss, 1850 (SD;L)
BOPSE	<i>Bolivina pseudoplicata</i> Heron-Allen and Earland, 1930 (SD;SM;L;D)
BOSTR	<i>Bolivina striatula</i> (Cushman) = <i>Brizalina striatula</i> Cushman, 1922 (SD;SM;L;D)
BOSUB	<i>Bolivina subaenariensis</i> (Cushman) = <i>Brizalina subaenariensis</i> Cushman, 1922 (SD;L)
BLPSE	<i>Bolivinellina pseudopunctata</i> (Höglund) = <i>Bolivina pseudopunctata</i> Höglund, 1947 (SD;SM;L;D)
cBRAEN	<i>Brizalina</i> cf. <i>aenariensis</i> (Costa) = <i>Bolivina</i> cf. <i>aenariensis</i> Costa, 1856 (SM;L;D)
BRSPA	<i>Brizalina spathulata</i> (Williamson) = <i>Textularia variabilis</i> Williamson var. <i>spathulata</i> Williamson, 1858 (SD;SM;L;D)
BRVAR	<i>Brizalina variabilis</i> (Williamson) = <i>Textularia variabilis</i> Williamson, 1859 (SD;L;D)
BCGRA	<i>Buccella granulata</i> (di Napoli Alliata) = <i>Eponides frigidus</i> var. <i>granulatus</i> di Napoli Alliata, 1952 (SD;SM;L;D)
BUACU	<i>Bulimina aculeata</i> d'Orbigny, 1926 (SM;L;D)
BUELO	<i>Bulimina elongata</i> d'Orbigny, 1926 (SD;SM;L;D)
BUGIB	<i>Bulimina gibba</i> Fornasini, 1902 (SD;SM;L;D)
BUMAR	<i>Bulimina marginata</i> d'Orbigny, 1826 (SM;L;D)
BUSP1	<i>Bulimina</i> sp. 1 (SM;L;D)
BMELE	<i>Buliminella elegantissima</i> (d'Orbigny) = <i>Bulimina elegantissima</i> d'Orbigny, 1939 (SD;SM;L;D)
CAAUR	<i>Cancriis auricula</i> (Fichtel and Moll) = <i>Nautilus auricula</i> Fichtel and Moll, 1798 (SD;D)
cCACRA	<i>Cassidulina</i> cf. <i>crassa</i> d'Orbigny, 1939(SM;L;D)
CALAE	<i>Cassidulina laevigata</i> d'Orbigny, 1826 (SM;L;D)

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Code	Specie
CIBRA	<i>Cibicidoides bradyi</i> (Trauth) = <i>Truncatulina bradyi</i> Trauth, 1918 (SM;L;D)
CILOB	<i>Cibicides lobatulus</i> (Walker and Jacob) = <i>Nautilus lobatulus</i> Walker and Jacob, 1798 (SM;D)
CLOBS	<i>Clavulina obscura</i> Chaster, 1982 (SM;L;D)
COINC	<i>Cornuspira incerta</i> (d'Orbigny) = <i>Cyclogyra incerta</i> d'Orbigny, 1939 (SM;L;D)
CYINV	<i>Cornuspira involvens</i> (Reuss) = <i>Operculina involvens</i> Reus, 1850 (SD;L)
CREXC	<i>Cribrulphidium excavatum</i> (Terquem) = <i>Polystomella excavatum</i> Terquem, 1875 (SD;SM;L;D)
CRMAG	<i>Cribrulphidium magellanicum</i> (Heron-Allen and Earland) = <i>Elphidium magellanicum</i> Heron-Allen and Earland, 1932 (SD;D)
CROCE	<i>Cribrulphidium oceanensis</i> (d'Orbigny) = <i>Polystomella oceanensis</i> d'Orbigny, 1826 (SD;SM;L;D)
CRSEL	<i>Cribrulphidium selseyensis</i> (Heron-Allen and Earland) = <i>Elphidium selseyensis</i> Heron-Allen and Earland, 1911 (SD;SM;L;D)
CRSP1	<i>Cribrulphidium</i> sp.1 (SD;L;D)
CRWIL	<i>Cribrulphidium williamsoni</i> (Haynes) = <i>Elphidium williamsoni</i> Haynes, 1973 (SD;L;D)
DECOM	<i>Delosina complexa</i> (Sidebottom) = <i>Polymorphina complexa</i> Sidebottom, 1907 (SM;L;D)
EGADV	<i>Eggerella advena</i> (Cushman) = <i>Verneuilina advena</i> Cushman, 1921 (SD;SM;L;D)
EGSCA	<i>Eggerelloides scaber</i> (Williamson) = <i>Bulimina scabra</i> Williamson, 1858 (SD;SM;L;D)
ELADV	<i>Elphidium advenum</i> (Cushman) = <i>Polystomella advenum</i> Cushman, 1922 (SD;SM;L;D)
cELERL	<i>Elphidium</i> cf. <i>earlandi</i> Cushman, 1936 (SD;L;D)
cCRPOE	<i>Cribrulphidium</i> cf. <i>poeyanum</i> (d'Orbigny) = <i>Polystomella poeyana</i> d'Orbigny, 1839 (SD;D)
cELFLE	<i>Elphidium</i> cf. <i>flexuosum</i> (d'Orbigny) = <i>Polystomella flexuosa</i> d'Orbigny, 1936 (SM;L;D)
cELSMI	<i>Elphidium</i> cf. <i>schmitti</i> Cushman and Wickenden, 1929 (SM;L;D)
ELCRI	<i>Elphidium crispum</i> (Linné) = <i>Nautilus crispus</i> Linné, 1758 (SD;SM;L;D)
ELINC	<i>Elphidium incertum</i> (Williamson) = <i>Polystomella umbilicatulata</i> var. <i>incerta</i> Williamson, 1858 (SD;SM;L;D)
ELLID	<i>Elphidium lidoense</i> Cushman, 1936 (SM;L;D)
ELMAR	<i>Elphidium margaritaceum</i> (Cushman) = <i>Elphidium advenum</i> var. <i>margaritaceum</i> Cushman, 1930 (SD;D)
ELMAT	<i>Elphidium matagordanum</i> (Kornfeld) = <i>Nonion depressula</i> (Walker and Jacob) var. <i>matagordana</i> Kornfeld, 1931 (SM;L;D)
ELSP1	<i>Elphidium</i> sp.1 (SM;L;D)
ELSP2	<i>Elphidium</i> sp.2 (SM;L;D)
EPVIT	<i>Epistominella vitrea</i> Parker, 1953 (SM;L;D)
FILUC	<i>Fissurina lucida</i> (Williamson) = <i>Entosolenia marginata</i> (Montagu) var. <i>lucida</i> Williamson, 1848 (SD;SM;L;D)
FISP1	<i>Fissurina</i> sp.1 (SM;L;D)
cFUFUS	<i>Fursenkoina</i> cf. <i>fusiformis</i> (Williamson) = <i>Bulimina pupoides</i> d'Orbigny var. <i>fusiformis</i> Williamson, 1858 (SD;L;D)
cFUCOM	<i>Fursenkoina</i> cf. <i>complanata</i> (Egger) = <i>Virgulina schreibersiana</i> Czjzek var. <i>complanata</i> Egger, 1893 (SM;L;D)
FUSCH	<i>Fursenkoina schreibersiana</i> (Czjzek) = <i>Virgulina schreibersiana</i> Czjzek, 1848

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Code	Specie
	(SM;L;D)
FSP1	<i>Fursenkoina</i> sp.1 (SM;L;D)
cGARUD	<i>Gaudryina</i> cf. <i>rudis</i> Wright, 1900 (SD;L)
GAPRA	<i>Gavelinopsis praegeri</i> (Heron-Allen and Earland) = <i>Discorbina praegeri</i> Heron-Allen and Earland, 1913 (SD;SM;L;D)
HASP1	<i>Haplophragmoides</i> sp.1 (SD;L;D)
HACAN	<i>Haplophragmoides canariensis</i> (d'Orbigny) = <i>Nonionina canariensis</i> d'Orbigny, 1839 (SM;L;D)
HAWIL	<i>Haplophragmoides wilberti</i> Anderson, 1953 (SD;L;D)
cHAGER	<i>Haynesina</i> cf. <i>germanica</i> (Ehrenberg) = <i>Nonionina</i> cf. <i>germanica</i> Ehrenberg, 1840 (SM;L;D)
HADEP	<i>Haynesina depressula</i> (Water and Jacob) = <i>Nautilus depressulus</i> Walker and Jacob, 1798 (SD;SM;L;D)
HAGER	<i>Haynesina germanica</i> (Ehrenberg) = <i>Nonionina germanica</i> Ehrenberg, 1840 (SD;SM;L;D)
HOPAC	<i>Hopkinsina pacifica</i> Cushman, 1933 (SD;SM;L;D)
JAMAC	<i>Jadammina macrescens</i> (Brady) = <i>Trochammina inflata</i> (Montagu) var. <i>macrescens</i> Brady, 1870 (SD;SM;L;D)
cLASEM	<i>Lagena</i> cf. <i>semistriata</i> (Williamson) = <i>Lagena striata</i> Walker var. <i>semistriata</i> Williamson, 1848 (SM;L;D)
LASUB	<i>Lagena substriata</i> Williamson, 1848 (SM;L;D)
LASUL	<i>Lagena sulcata</i> (Walter and Jacob) = <i>Serpula sulcata</i> Walter and Jacob, 1798 (SD;SM;L;D)
LATEN	<i>Lagena tenuis</i> (Börneman) = <i>Ovulina tenuis</i> Börneman, 1855 (SM;L;D)
LAVUL	<i>Lagena vulgaris</i> Williamson, 1858 (SM;L;D)
LADIF	<i>Lagenammina difflugiformis</i> (Brady) = <i>Reophax difflugiformis</i> Brady, 1879 (SM;L;D)
LALAG	<i>Lagenammina laguncula</i> Rhumbler, 1911 (SM;L;D)
LESCO	<i>Leptohalysis scottii</i> (Chaster) = <i>Reophax scotti</i> Chaster, 1892 (SM;L;D)
MASEC	<i>Massilina secans</i> (d'Orbigny) = <i>Quinqueloculina secans</i> d'Orbigny, 1826 (SM;L;D)
MEPOM	<i>Melonis pompilioides</i> (Fitchel and Moll) = <i>Nautilus pompilioides</i> Fitchel and Moll, 1798 (SM;L;D)
MUFUS	<i>Miliammina fusca</i> (Brady) = <i>Quinqueloculina fusca</i> Brady, 1870 (SD;SM;L;D)
MIUND	Miliolid undetermined (SD;SM;L;D)
NODEN	<i>Nodulina dentaliniformis</i> (Brady) = <i>Reophax dentaliniformis</i> Brady, 1844 (SM;SD;L;D)
NOAST	<i>Nonion asterizans</i> (Fichtel and Moll) = <i>Riminopsis asterizans</i> Fichtel and Moll, 1798 (SM;L;D)
NOLAE	<i>Nonion laevigatum</i> (d'Orbigny) = <i>Nonionina laevigata</i> d'Orbigny, 1826 (SM;L;D)
NOATL	<i>Nonionella atlantica</i> Cushman, 1947 (SD;SM;L;D)
NOOPI	<i>Nonionella opima</i> Cushman, 1947 (SD;SM;L;D)
cNOJAP	<i>Nonionoides</i> cf. <i>japonicum</i> (Asano) = <i>Florilus</i> cf. <i>japonicum</i> Asano, 1938 (SM;L;D)
NOSCA	<i>Nonionoides scaphus</i> (Fitchel and Moll) = <i>Florilus scaphus</i> Fitchel and Moll, 1798 (SM;L;D)
NOPOL	<i>Nouria polymorphides</i> Heron-Allen and Earland, 1914 (SM;L;D)
PACOR	<i>Patellina corrugata</i> Williamson, 1858 (SM;L;D)
PLMED	<i>Planorbulina mediterraneensis</i> d'Orbigny, 1826 (SM;L;D)

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Code	Specie
POLAT	<i>Poroepionides lateralis</i> (Terquem) = <i>Rosalina lateralis</i> Terquem, 1878 (SM;L;D)
PRCLA	<i>Procerolagena clavata</i> (d'Orbigny) = <i>Lagena clavata</i> d'Orbigny, 1826 (SM;L;D)
PSBOW	<i>Psammosphaera bowmani</i> Heron-Allen and Earland, 1912 (SM;L)
PYINO	<i>Pyrgo inornata</i> (d'Orbigny) = <i>Biloculina inornata</i> d'Orbigny, 1846 (SM;L;D)
QUDEP	<i>Quinqueloculina depressa</i> d'Orbigny, 1852 (SM;L;D)
QUJUG	<i>Quinqueloculina jugosa</i> (Cushman) = <i>Quinqueloculina seminula</i> var. <i>jugosa</i> Cushman, 1944 (SD;L;D)
QULAT	<i>Quinqueloculina lata</i> Terquem, 1876 (SD;L;D)
QULON	<i>Quinqueloculina longirostra</i> d'Orbigny, 1826 (SM;L;D)
QUOBL	<i>Quinqueloculina oblonga</i> (Montagu) = <i>Vermiculum oblongum</i> Montagu, 1893 (SD;L;D)
QURUG	<i>Quinqueloculina rugosa</i> d'Orbigny, 1839 (SM;L;D)
QUSEM	<i>Quinqueloculina seminula</i> (Linné) = <i>Serpula seminulum</i> Linné, 1758 (SD;SM;L;D)
QUSP1	<i>Quinqueloculina</i> sp.1 (SM;L;D)
QUSTE	<i>Quinqueloculina stelligera</i> Schlumberger, 1893 (SD;SM;L;D)
cRECOM	<i>Rectuvigerina</i> cf. <i>compressa</i> (Cushman) = <i>Uvigerina compressa</i> Cushman, 1925 (SM;L;D)
cREFUS	<i>Reophax</i> cf. <i>fusiformis</i> (Williamson) = <i>Proteonina fusiformis</i> Williamson, 1858 (SM;L;D)
RECYL	<i>Reophax cylindrica</i> Brady, 1884 (SM;L;D)
REMON	<i>Reophax moniliformis</i> Siddall, 1886 (SD;SM;L;D)
RENAN	<i>Reophax nana</i> Rhumbler, 1913 (SM;L;D)
RESCO	<i>Reophax scorpiurus</i> Montfort, 1808 (SM;L;D)
RESUB	<i>Reophax subfusiformis</i> Earland, 1933 (SM;L;D)
REACU	<i>Reussella aculeata</i> Cushman, 1945 (SM;L;D)
ROARC	<i>Robertina arctica</i> d'Orbigny, 1846 (SM;L;D)
ROANO	<i>Rosalina anomala</i> Terquem, 1875 (SD;L;D)
ROBUL	<i>Rosalina bulbosa</i> (Parker) = <i>Discorbis bulbosa</i> Parker, 1954 (SM;L;D)
cROMED	<i>Rosalina</i> cf. <i>mediterraneensis</i> Brady, 1826 (SM;L;D)
cROVAL	<i>Rosalina</i> cf. <i>valvulata</i> d'Orbigny, 1826 (SM;L;D)
ROGLO	<i>Rosalina globularis</i> d'Orbigny, 1826 (SD;SM;L)
ROIIR	<i>Rosalina irregularis</i> (Rhumbler) = <i>Discorbina irregularis</i> Rhumbler, 1906 (SD;L;D)
SAATL	<i>Saccammina atlantica</i> (Cushman) = <i>Proteonina atlantica</i> Cushman, 1944 (SM;L;D)
SVSP1	<i>Svratkina</i> sp.1 (SD;D)
TEBOC	<i>Textularia bocki</i> Höglund, 1947 (SD;L;D)
TECAL	<i>Textularia calva</i> Lalicker, 1935 (SM;L;D)
TETEN	<i>Textularia tenuissima</i> Earland, 1933 (SM;L;D)
TESP1	<i>Textularia</i> sp.1 (SM;L;D)
TEXUN	Texturalid undetermined (SD;L;D)
TRCON	<i>Tretomphalus concinnus</i> (Brady) = <i>Discorbina concinna</i> Brady, 1884 (SM;L;D)
TRAGU	<i>Trichohyalus aguayoi</i> (Bermudez) = <i>Discorinopsis aguayoi</i> Bermudez, 1935 (SD;L;D)
TRANG	<i>Trifarina angulosa</i> (Williamson) = <i>Uvigerina angulosa</i> Williamson, 1858

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<b>Code</b>	<b>Specie</b>
	(SM;L;D)
TRDUB	<i>Triloculina dubia</i> d'Orbigny, 1826 (SM;L;D)
TRMAR	<i>Triloculina marioni</i> Schlumberger, 1893 (SM;L;D)
TRROT	<i>Triloculina rotunda</i> d'Orbigny, 1939 (SM;L;D)
TRSP1	<i>Triloculina</i> sp.1 (SD;SM;L;D)
TRINF	<i>Trochammina inflata</i> (Montagu) = <i>Nautilus inflatus</i> Montagu, 1808 (SD;L;D)
cTRADV	<i>Trochammina</i> cf. <i>advena</i> Cushman, 1922 (SM;L;D)
TRLOB	<i>Trochammina lobata</i> Cushman, 1944 (SM;L;D)
UVSP1	<i>Uvigerina</i> sp.1 (SM;L;D)
VABRA	<i>Valvulineria bradyana</i> (Fornasini) = <i>Discorbina bradyana</i> Fornasini, 1899 (SD;SM;L;D)
INDET	Unidentified forms (SD;SM;L;D)

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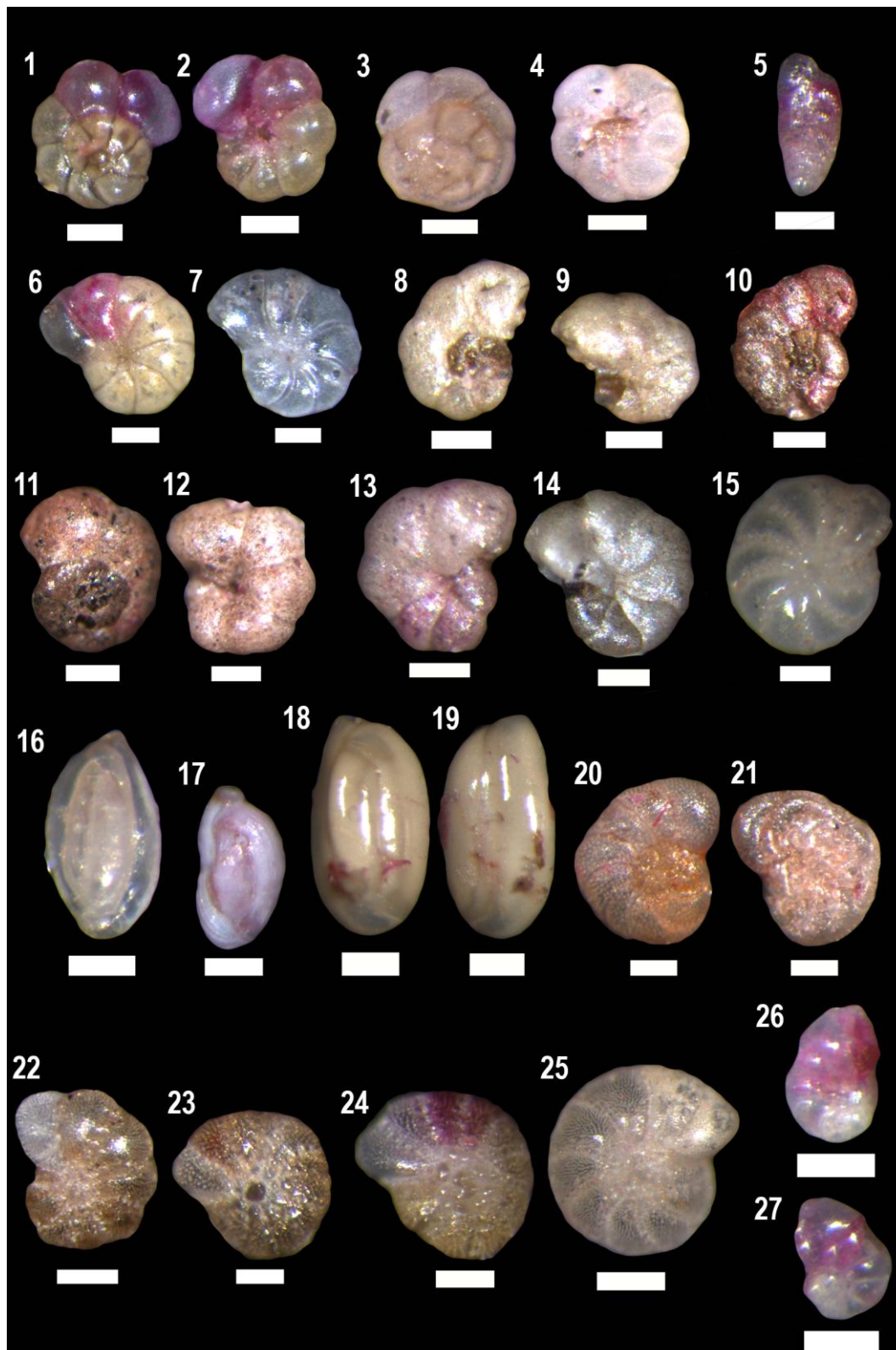
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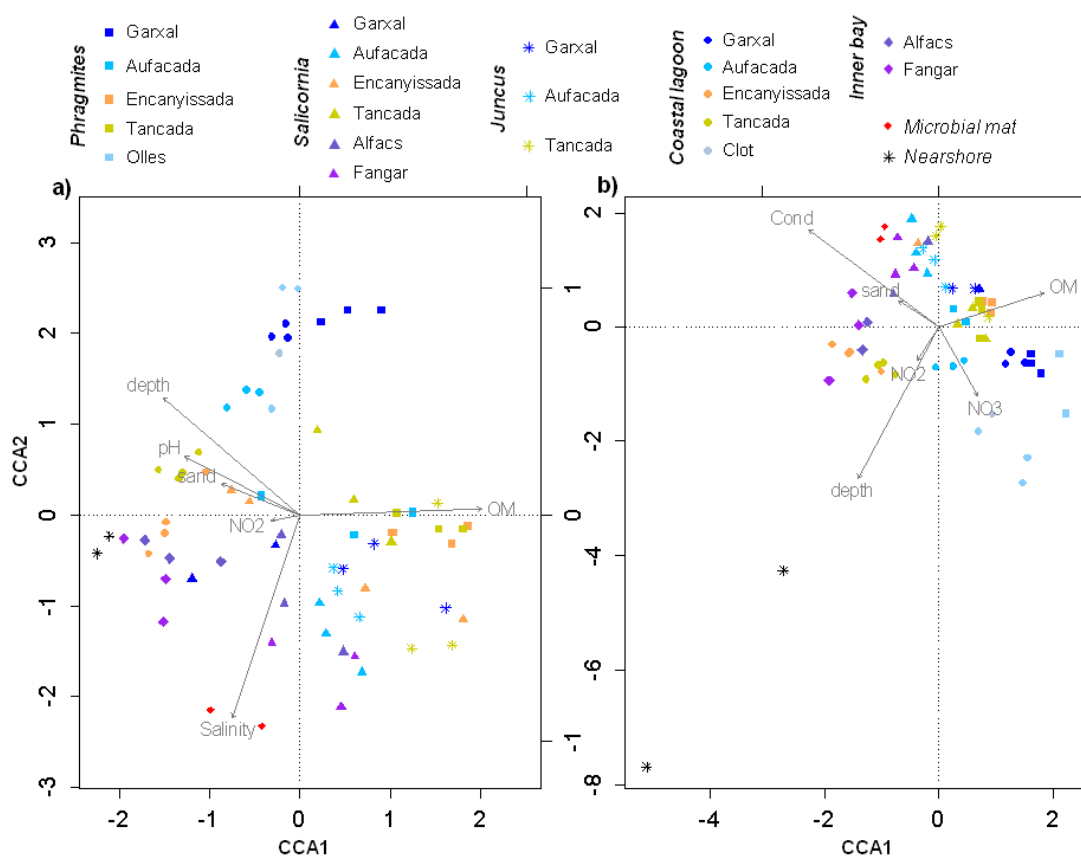
Supplementary material



**Supplementary Fig. S1** Foraminiferal indicator species of the Ebro Delta under binocular stereomicroscope. Scale bar represents 100  $\mu\text{m}$ , except when specified. Legend: L = living (stained) test, D = dead (unstained) test. 1-4: *Ammonia tepida* (in text referred as *Ammonia*

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*beccarii* agg). 1: spiral view, L. 2: umbilical view, L. 3: spiral view, D. 4: umbilical view, D; 5: *Bolivina striatula*, general view, D; 6-7: *Haynesina germanica*. 6: general view, L. 7: general view, D; 8-10: *Jadammina macrescens*, 8: spiral view, D. 9: umbilical view, D. 10: spiral view, L; 11-12: *Trochammina inflata*, 11: spiral view, L. 12: umbilical view, L; 13-14: *Haplophragmoides wilberti*, 13: general view, L. 14: general view, D; 15: *Elphidium advenum*, general view, D; 16: *Quinqueloculina stelligera*, general view, D; 17: *Quinqueloculina jugosa*, general view, L; 18-19: *Quinqueloculina seminula*, general view, D; 20-21: *Trichoyalus aguayoi* (scale bar = 500  $\mu$ m), 20: spiral view, D. 21: umbilical view, D; 22: *Criboelphidium excavatum* general view, D; 23-24: *Criboelphidium oceanensis*, 23: general view, D. 24: general view, L; 25: *Criboelphidium selseyensis* general view, D; 26-27: *Nonionella atlantica*, 26: umbilical view, L. 27: spiral view, L.



**Supplementary Fig. S2** Canonical Correspondence Analysis (CCA) diagram showing the relationships of samples with selected environmental variables for (a) multiproxy (foraminifera plus diatom) dataset and (b) diatom dataset.

## Supplementary Table S1

Dataset of 191 samples (1M-11M = data from Scrutton (1969), 12D-35D = data obtained in this study). D = deltaic dataset, M = marine dataset. 36D = Encanyissada lagoon transect from Scrutton (1969). T = temperature; DO = dissolved oxygen; Sand = sand proportion; OM = organic matter content; Chl-a = Seston chlorophyll *a*; NA: No data obtained from marine dataset. Samples in bold (n = 99) contained >100 living (stained) foraminiferal tests and full environmental data (water depth, sand and salinity) and therefore were included in the statistical analysis. All measured environmental variables in the deltaic dataset (D) were used as potential predictors for multiproxy-environment relationships (foraminifera plus diatoms).

Sample	Site	Habitat	Period	Water depth m	Sand %	Salinity ppt	OM %	T °C	pH	DO %	PO <sub>4</sub> <sup>3-</sup> -P µg/L	NH <sub>4</sub> <sup>+</sup> -N µg/L	NO <sub>2</sub> <sup>-</sup> -N µg/L	NO <sub>3</sub> <sup>-</sup> -N µg/L	SiO <sub>4</sub> <sup>4-</sup> -Si µg/L	Chl-a µg/L	PO <sub>4</sub> <sup>3-</sup> -P µg/L
<b>1M-1</b>	<b>South bay</b>	<b>marine</b>	<b>APR67'</b>	<b>6.0</b>	<b>20.00</b>	<b>38.90</b>	<b>NA</b>	<b>16.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
1M-2	South bay	marine	JUL68'	6.0	25.00	NA	NA	16.50	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>1M-3</b>	<b>South bay</b>	<b>marine</b>	<b>JUL68'</b>	<b>8.0</b>	<b>8.00</b>	<b>37.60</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
1M-4	South bay	marine	JUL68'	3.5	94.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1M-5	South bay	marine	AUG67'	4.5	49.00	NA	NA	23.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>1M-6</b>	<b>South bay</b>	<b>marine</b>	<b>AUG67'</b>	<b>5.0</b>	<b>47.00</b>	<b>38.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
1M-7	South bay	marine	AUG67'	5.0	21.00	NA	NA	13.50	NA	NA	NA	NA	NA	NA	NA	NA	NA
1M-8	South bay	marine	AUG67'	6.0	19.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>1M-9</b>	<b>South bay</b>	<b>marine</b>	<b>APR67'</b>	<b>6.0</b>	<b>11.00</b>	<b>37.80</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
1M-10	South bay	marine	AUG67'	6.0	16.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1M-11	South bay	marine	APR67'	6.0	11.00	NA	NA	14.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
1M-12	South bay	marine	APR67'	6.0	3.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>1M-13</b>	<b>South bay</b>	<b>marine</b>	<b>APR67'</b>	<b>6.0</b>	<b>11.00</b>	<b>38.30</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>1M-14</b>	<b>South bay</b>	<b>marine</b>	<b>AUG67'</b>	<b>4.5</b>	<b>43.00</b>	<b>38.20</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
1M-15	South bay	marine	AUG67'	5.0	8.00	NA	NA	13.50	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>1M-16</b>	<b>South bay</b>	<b>marine</b>	<b>AUG67'</b>	<b>5.0</b>	<b>8.00</b>	<b>38.40</b>	<b>NA</b>	<b>27.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>1M-17</b>	<b>South bay</b>	<b>marine</b>	<b>AUG67'</b>	<b>6.0</b>	<b>9.00</b>	<b>38.40</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>1M-18</b>	<b>South bay</b>	<b>marine</b>	<b>APR67'</b>	<b>5.0</b>	<b>5.00</b>	<b>38.40</b>	<b>NA</b>	<b>26.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
1M-19	South bay	marine	AUG67'	5.5	9.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1M-20	South bay	marine	APR67'	5.0	10.00	NA	NA	26.00	NA	NA	NA	NA	NA	NA	NA	NA	NA

*Chapter 2: Benthic foraminiferal assemblages*

Sample	Site	Habitat	Period	Water depth m	Sand %	Salinity ppt	OM %	T °C	pH	DO %	PO <sub>4</sub> <sup>3-</sup> -P µg/L	NH <sub>4</sub> <sup>+</sup> -N µg/L	NO <sub>2</sub> <sup>-</sup> -N µg/L	NO <sub>3</sub> <sup>-</sup> -N µg/L	SiO <sub>4</sub> <sup>4-</sup> -Si µg/L	Chl-a µg/L	PO <sub>4</sub> <sup>3-</sup> -P µg/L
<b>1M-21</b>	<b>South bay</b>	<b>marine</b>	<b>JUL68'</b>	<b>2.5</b>	<b>59.00</b>	<b>36.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
1M-22	South bay	marine	JUL68'	3.0	62.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1M-23	South bay	marine	JUL68'	3.0	39.00	NA	NA	24.50	NA	NA	NA	NA	NA	NA	NA	NA	NA
1M-24	South bay	marine	JUL68'	3.5	44.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>1M-25</b>	<b>South bay</b>	<b>marine</b>	<b>JUL68'</b>	<b>3.5</b>	<b>70.00</b>	<b>38.10</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>2M-26</b>	<b>Las Casas</b>	<b>marine</b>	<b>APR67'</b>	<b>11.0</b>	<b>5.00</b>	<b>39.10</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
2M-27	Las Casas	marine	APR67'	9.0	4.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2M-28	Las Casas	marine	APR67'	8.0	7.00	NA	NA	16.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
2M-29	Las Casas	marine	APR67'	6.0	2.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2M-30	Las Casas	marine	APR67'	5.0	58.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2M-31	Las Casas	marine	APR67'	9.0	4.00	NA	NA	27.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>2M-32</b>	<b>Las Casas</b>	<b>marine</b>	<b>APR67'</b>	<b>8.5</b>	<b>4.00</b>	<b>38.90</b>	<b>NA</b>	<b>26.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
2M-33	Las Casas	marine	APR67'	7.0	18.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>3M-34</b>	<b>Vinaroz</b>	<b>marine</b>	<b>AUG67'</b>	<b>8.0</b>	<b>69.00</b>	<b>39.30</b>	<b>NA</b>	<b>15.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
3M-35	Vinaroz	marine	APR67'	5.0	89.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>3M-36</b>	<b>Vinaroz</b>	<b>marine</b>	<b>APR67'</b>	<b>8.0</b>	<b>16.00</b>	<b>39.40</b>	<b>NA</b>	<b>14.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
3M-37	Vinaroz	marine	AUG67'	9.0	100.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>3M-38</b>	<b>Vinaroz</b>	<b>marine</b>	<b>APR67'</b>	<b>15.0</b>	<b>2.00</b>	<b>38.80</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
3M-39	Vinaroz	marine	APR67'	14.0	6.00	NA	NA	15.50	NA	NA	NA	NA	NA	NA	NA	NA	NA
3M-40	Vinaroz	marine	APR67'	14.6	6.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>3M-41</b>	<b>Vinaroz</b>	<b>marine</b>	<b>AUG67'</b>	<b>14.0</b>	<b>4.00</b>	<b>38.10</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
3M-42	Vinaroz	marine	AUG67'	13.5	5.00	NA	NA	26.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
3M-43	Vinaroz	marine	AUG67'	11.5	10.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>3M-44</b>	<b>Vinaroz</b>	<b>marine</b>	<b>APR67'</b>	<b>11.0</b>	<b>46.00</b>	<b>37.90</b>	<b>NA</b>	<b>26.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>4M-45</b>	<b>South faro</b>	<b>marine</b>	<b>APR67'</b>	<b>4.5</b>	<b>96.00</b>	<b>38.40</b>	<b>NA</b>	<b>15.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
4M-46	South faro	marine	APR67'	10.0	33.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>4M-47</b>	<b>South faro</b>	<b>marine</b>	<b>AUG67'</b>	<b>10.5</b>	<b>96.00</b>	<b>37.90</b>	<b>NA</b>	<b>26.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
4M-48	South faro	marine	AUG67'	5.0	97.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
4M-49	South faro	marine	JUL68'	5.0	96.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA



*Chapter 2: Benthic foraminiferal assemblages*

Sample	Site	Habitat	Period	Water depth m	Sand %	Salinity ppt	OM %	T °C	pH	DO %	PO <sub>4</sub> <sup>3-</sup> -P µg/L	NH <sub>4</sub> <sup>+</sup> -N µg/L	NO <sub>2</sub> <sup>-</sup> -N µg/L	NO <sub>3</sub> <sup>-</sup> -N µg/L	SiO <sub>4</sub> <sup>4-</sup> -Si µg/L	Chl-a µg/L	PO <sub>4</sub> <sup>3-</sup> -P µg/L
<b>4M-50</b>	<b>South faro</b>	<b>marine</b>	<b>APR67'</b>	<b>18.0</b>	<b>13.00</b>	<b>39.20</b>	<b>NA</b>	<b>15.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
4M-51	South faro	marine	APR67'	27.0	4.00	NA	NA	16.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>4M-52</b>	<b>South faro</b>	<b>marine</b>	<b>APR67'</b>	<b>33.0</b>	<b>1.00</b>	<b>38.90</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
4M-53	South faro	marine	APR67'	38.0	2.00	NA	NA	15.50	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>4M-54</b>	<b>South faro</b>	<b>marine</b>	<b>APR67'</b>	<b>43.0</b>	<b>1.00</b>	<b>38.80</b>	<b>NA</b>	<b>15.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>4M-55</b>	<b>South faro</b>	<b>marine</b>	<b>JUL68'</b>	<b>34.5</b>	<b>2.00</b>	<b>38.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
4M-56	South faro	marine	APR67'	28.0	3.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>4M-57</b>	<b>South faro</b>	<b>marine</b>	<b>AUG67'</b>	<b>22.0</b>	<b>7.00</b>	<b>38.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
4M-58	South faro	marine	AUG67'	17.0	20.00	NA	NA	25.50	NA	NA	NA	NA	NA	NA	NA	NA	NA
5M-59	Salinas	marine	APR67'	14.0	43.00	NA	NA	15.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>5M-60</b>	<b>Salinas</b>	<b>marine</b>	<b>APR67'</b>	<b>14.0</b>	<b>90.00</b>	<b>39.10</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
5M-61	Salinas	marine	APR67'	10.0	40.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>5M-62</b>	<b>Salinas</b>	<b>marine</b>	<b>AUG67'</b>	<b>14.5</b>	<b>77.00</b>	<b>38.80</b>	<b>NA</b>	<b>25.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>5M-63</b>	<b>Salinas</b>	<b>marine</b>	<b>AUG67'</b>	<b>8.0</b>	<b>96.00</b>	<b>37.50</b>	<b>NA</b>	<b>26.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>5M-64</b>	<b>Salinas</b>	<b>marine</b>	<b>AUG67'</b>	<b>6.0</b>	<b>30.00</b>	<b>38.60</b>	<b>NA</b>	<b>26.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
5M-65	Salinas	marine	JUL68'	12.0	97.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5M-66	Salinas	marine	AUG67'	10.5	88.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>5M-67</b>	<b>Salinas</b>	<b>marine</b>	<b>JUL68'</b>	<b>5.0</b>	<b>96.00</b>	<b>38.80</b>	<b>NA</b>	<b>21.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>5M-68</b>	<b>Salinas</b>	<b>marine</b>	<b>APR67'</b>	<b>39.5</b>	<b>2.00</b>	<b>39.70</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
5M-69	Salinas	marine	APR67'	33.5	2.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>5M-70</b>	<b>Salinas</b>	<b>marine</b>	<b>AUG67'</b>	<b>28.0</b>	<b>3.00</b>	<b>39.70</b>	<b>NA</b>	<b>15.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
5M-71	Salinas	marine	AUG67'	19.0	32.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5M-72	Salinas	marine	JUL68'	10.0	19.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
6M-73	South platform	marine	AUG67'	4.5	99.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
6M-74	South platform	marine	AUG67'	8.0	76.00	NA	NA	26.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>6M-75</b>	<b>South platform</b>	<b>marine</b>	<b>APR67'</b>	<b>10.0</b>	<b>82.00</b>	<b>37.70</b>	<b>NA</b>	<b>21.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>6M-76</b>	<b>South platform</b>	<b>marine</b>	<b>APR67'</b>	<b>17.5</b>	<b>68.00</b>	<b>38.90</b>	<b>NA</b>	<b>13.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>6M-77</b>	<b>South platform</b>	<b>marine</b>	<b>APR67'</b>	<b>12.0</b>	<b>6.00</b>	<b>37.20</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
6M-78	South platform	marine	AUG67'	12.0	22.00	NA	NA	15.50	NA	NA	NA	NA	NA	NA	NA	NA	NA

## Chapter 2: Benthic foraminiferal assemblages

Sample	Site	Habitat	Period	Water depth m	Sand %	Salinity ppt	OM %	T °C	pH	DO %	PO <sub>4</sub> <sup>3-</sup> -P µg/L	NH <sub>4</sub> <sup>+</sup> -N µg/L	NO <sub>2</sub> <sup>-</sup> -N µg/L	NO <sub>3</sub> <sup>-</sup> -N µg/L	SiO <sub>4</sub> <sup>4-</sup> -Si µg/L	Chl-a µg/L	PO <sub>4</sub> <sup>3-</sup> -P µg/L
6M-79	South platform	marine	APR67'	34.5	2.00	NA	NA	25.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
6M-80	South platform	marine	AUG67'	12.0	79.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>6M-81</b>	<b>South platform</b>	<b>marine</b>	<b>AUG67'</b>	<b>13.0</b>	<b>18.00</b>	<b>38.80</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>6M-82</b>	<b>South platform</b>	<b>marine</b>	<b>APR67'</b>	<b>17.5</b>	<b>5.00</b>	<b>38.00</b>	<b>NA</b>	<b>20.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
6M-83	South platform	marine	AUG67'	16.0	3.00	NA	NA	21.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
6M-84	South platform	marine	APR67'	14.0	19.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
7M-85	South channel	marine	AUG67'	5.0	95.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>7M-86</b>	<b>South channel</b>	<b>marine</b>	<b>AUG67'</b>	<b>8.0</b>	<b>91.00</b>	<b>38.00</b>	<b>NA</b>	<b>26.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
7M-87	South channel	marine	APR67'	11.5	94.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
7M-88	South channel	marine	AUG67'	8.0	89.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>7M-89</b>	<b>South channel</b>	<b>marine</b>	<b>APR67'</b>	<b>27.0</b>	<b>5.00</b>	<b>38.80</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>7M-90</b>	<b>South channel</b>	<b>marine</b>	<b>APR67'</b>	<b>18.5</b>	<b>14.00</b>	<b>37.30</b>	<b>NA</b>	<b>13.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
7M-91	South channel	marine	AUG67'	50.0	1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
8M-92	Cabo Tortosa	marine	AUG67'	5.0	97.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
8M-93	Cabo Tortosa	marine	AUG67'	8.0	27.00	NA	NA	35.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>8M-94</b>	<b>Cabo Tortosa</b>	<b>marine</b>	<b>AUG67'</b>	<b>12.5</b>	<b>10.00</b>	<b>38.30</b>	<b>NA</b>	<b>25.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
9M-95	River Mouth	marine	APR67'	51.5	2.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>9M-96</b>	<b>River Mouth</b>	<b>marine</b>	<b>APR67'</b>	<b>33.5</b>	<b>4.00</b>	<b>38.80</b>	<b>NA</b>	<b>13.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>9M-97</b>	<b>River Mouth</b>	<b>marine</b>	<b>APR67'</b>	<b>22.0</b>	<b>6.00</b>	<b>38.80</b>	<b>NA</b>	<b>13.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
<b>9M-98</b>	<b>River Mouth</b>	<b>marine</b>	<b>AUG67'</b>	<b>46.0</b>	<b>1.00</b>	<b>38.60</b>	<b>NA</b>	<b>25.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
9M-99	River Mouth	marine	AUG67'	31.5	1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>9M-100</b>	<b>River Mouth</b>	<b>marine</b>	<b>AUG67'</b>	<b>20.0</b>	<b>2.00</b>	<b>38.50</b>	<b>NA</b>	<b>26.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
9M-101	River Mouth	marine	AUG67'	14.0	4.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>9M-102</b>	<b>River Mouth</b>	<b>marine</b>	<b>AUG67'</b>	<b>10.0</b>	<b>2.00</b>	<b>38.50</b>	<b>NA</b>	<b>26.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
9M-103	River Mouth	marine	AUG67'	7.0	2.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
9M-104	River Mouth	marine	AUG67'	23.0	8.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
10M-105	North platform	marine	JUL68'	13.5	4.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>10M-106</b>	<b>North platform</b>	<b>marine</b>	<b>APR67'</b>	<b>5.5</b>	<b>26.00</b>	<b>38.10</b>	<b>NA</b>	<b>13.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
10M-107	North platform	marine	JUL68'	11.0	99.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

## Chapter 2: Benthic foraminiferal assemblages

Sample	Site	Habitat	Period	Water depth m	Sand %	Salinity ppt	OM %	T °C	pH	DO %	PO <sub>4</sub> <sup>3-</sup> -P µg/L	NH <sub>4</sub> <sup>+</sup> -N µg/L	NO <sub>2</sub> <sup>-</sup> -N µg/L	NO <sub>3</sub> <sup>-</sup> -N µg/L	SiO <sub>4</sub> <sup>4-</sup> -Si µg/L	Chl-a µg/L	PO <sub>4</sub> <sup>3-</sup> -P µg/L
10M-108	North platform	marine	AUG67'	5.5	100.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>10M-109</b>	<b>North platform</b>	<b>marine</b>	<b>JUL68'</b>	<b>11.5</b>	<b>92.00</b>	<b>38.20</b>	<b>NA</b>	<b>22.00</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
10M-110	North platform	marine	JUL68'	33.5	4.00	NA	NA	25.50	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>10M-111</b>	<b>North platform</b>	<b>marine</b>	<b>JUL68'</b>	<b>20.0</b>	<b>71.00</b>	<b>38.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
11M-112	North faro	marine	JUL68'	11.0	28.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>11M-113</b>	<b>North faro</b>	<b>marine</b>	<b>JUL68'</b>	<b>6.0</b>	<b>23.00</b>	<b>38.70</b>	<b>NA</b>	<b>13.50</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>
11M-114	North faro	marine	JUL68'	3.0	96.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
11M-115	North faro	marine	AUG67'	14.5	81.00	NA	NA	13.50	NA	NA	NA	NA	NA	NA	NA	NA	NA
36D-116	Encanyissada	Lagoon	JUL68'	1.0	22.00	2.60	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
36D-117	Encanyissada	Lagoon	JUL68'	1.5	60.00	NA	NA	24.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
36D-118	Encanyissada	Lagoon	JUL68'	2.0	7.00	0.80	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
36D-119	Encanyissada	Lagoon	JUL68'	1.5	7.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
36D-120	Encanyissada	Lagoon	JUL68'	1.0	13.00	0.90	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
36D-121	Encanyissada	Lagoon	JUL68'	0.8	13.00	0.70	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>12D-122</b>	<b>Alfacs</b>	<b>Inner bay</b>	<b>NOV12'</b>	<b>0.46</b>	<b>69.28</b>	<b>31.30</b>	<b>1.10</b>	<b>13.23</b>	<b>7.97</b>	<b>8.12</b>	<b>24.41</b>	<b>5.29</b>	<b>6.37</b>	<b>38.36</b>	<b>525.48</b>	<b>1.13</b>	<b>1.12</b>
<b>12D-123</b>	<b>Alfacs</b>	<b>Inner bay</b>	<b>APR13'</b>	<b>0.40</b>	<b>69.28</b>	<b>36.11</b>	<b>1.10</b>	<b>18.37</b>	<b>8.04</b>	<b>7.86</b>	<b>5.23</b>	<b>101.31</b>	<b>14.03</b>	<b>31.02</b>	<b>502.51</b>	<b>1.99</b>	<b>1.35</b>
<b>12D-124</b>	<b>Alfacs</b>	<b>Inner bay</b>	<b>AUG13'</b>	<b>0.40</b>	<b>69.28</b>	<b>31.34</b>	<b>1.10</b>	<b>23.93</b>	<b>8.26</b>	<b>5.58</b>	<b>14.12</b>	<b>23.45</b>	<b>2.52</b>	<b>12.90</b>	<b>854.50</b>	<b>4.97</b>	<b>2.40</b>
<b>13D-125</b>	<b>Alfacs</b>	<b>Salicornia</b>	<b>NOV12'</b>	<b>0.14</b>	<b>4.96</b>	<b>28.95</b>	<b>5.95</b>	<b>13.00</b>	<b>7.86</b>	<b>7.78</b>	<b>24.90</b>	<b>10.70</b>	<b>7.98</b>	<b>43.08</b>	<b>482.26</b>	<b>1.14</b>	<b>1.62</b>
<b>13D-126</b>	<b>Alfacs</b>	<b>Salicornia</b>	<b>APR13'</b>	<b>0.10</b>	<b>4.96</b>	<b>37.01</b>	<b>5.95</b>	<b>20.57</b>	<b>7.94</b>	<b>10.37</b>	<b>6.50</b>	<b>95.75</b>	<b>8.03</b>	<b>12.89</b>	<b>365.08</b>	<b>6.53</b>	<b>2.84</b>
<b>13D-127</b>	<b>Alfacs</b>	<b>Salicornia</b>	<b>AUG13'</b>	<b>0.06</b>	<b>4.96</b>	<b>33.43</b>	<b>5.95</b>	<b>22.67</b>	<b>8.12</b>	<b>9.62</b>	<b>17.13</b>	<b>14.12</b>	<b>0.77</b>	<b>6.23</b>	<b>617.60</b>	<b>8.34</b>	<b>1.52</b>
<b>14D-128</b>	<b>Alfacs</b>	<b>Nearshore</b>	<b>APR13'</b>	<b>7.40</b>	<b>18.51</b>	<b>37.75</b>	<b>4.94</b>	<b>15.31</b>	<b>8.01</b>	<b>7.76</b>	<b>5.02</b>	<b>4.75</b>	<b>3.36</b>	<b>16.26</b>	<b>49.46</b>	<b>3.98</b>	<b>1.40</b>
<b>14D-129</b>	<b>Alfacs</b>	<b>Nearshore</b>	<b>AUG13'</b>	<b>7.00</b>	<b>18.51</b>	<b>38.11</b>	<b>4.94</b>	<b>25.19</b>	<b>7.96</b>	<b>5.39</b>	<b>6.72</b>	<b>29.09</b>	<b>1.58</b>	<b>19.37</b>	<b>164.36</b>	<b>1.62</b>	<b>0.83</b>
15D-130	Aufacada	Lagoon	NOV12'	0.56	89.77	16.63	3.70	16.73	7.75	8.66	24.22	2.51	16.88	91.83	1783.37	9.70	3.27
<b>15D-131</b>	<b>Aufacada</b>	<b>Lagoon</b>	<b>APR13'</b>	<b>0.54</b>	<b>89.77</b>	<b>10.23</b>	<b>3.70</b>	<b>16.82</b>	<b>7.94</b>	<b>6.81</b>	<b>4.03</b>	<b>13.04</b>	<b>3.96</b>	<b>13.40</b>	<b>1791.57</b>	<b>8.20</b>	<b>2.74</b>
<b>15D-132</b>	<b>Aufacada</b>	<b>Lagoon</b>	<b>AUG13'</b>	<b>0.47</b>	<b>89.77</b>	<b>4.26</b>	<b>3.70</b>	<b>25.70</b>	<b>8.66</b>	<b>8.53</b>	<b>11.68</b>	<b>20.77</b>	<b>1.48</b>	<b>22.69</b>	<b>2020.47</b>	<b>2.76</b>	<b>1.64</b>
16D-133	Aufacada	Salicornia	NOV12'	0.04	58.77	22.46	2.84	13.20	7.37	1.9	17.56	26.54	0.48	57.93	2415.77	2.24	1.41
<b>16D-134</b>	<b>Aufacada</b>	<b>Salicornia</b>	<b>APR13'</b>	<b>0.08</b>	<b>58.77</b>	<b>20.00</b>	<b>2.84</b>	<b>19.79</b>	<b>7.34</b>	<b>3</b>	<b>6.47</b>	<b>49.33</b>	<b>2.49</b>	<b>10.18</b>	<b>1595.14</b>	<b>3.02</b>	<b>2.02</b>
<b>16D-135</b>	<b>Aufacada</b>	<b>Salicornia</b>	<b>AUG13'</b>	<b>0.20</b>	<b>58.77</b>	<b>20.34</b>	<b>2.84</b>	<b>23.18</b>	<b>7.68</b>	<b>4.23</b>	<b>25.37</b>	<b>35.04</b>	<b>2.12</b>	<b>8.28</b>	<b>6540.55</b>	<b>23.12</b>	<b>5.64</b>
<b>17D-136</b>	<b>Aufacada</b>	<b>Juncus</b>	<b>NOV12'</b>	<b>0.10</b>	<b>77.45</b>	<b>18.09</b>	<b>3.84</b>	<b>12.70</b>	<b>7.07</b>	<b>2.51</b>	<b>16.82</b>	<b>3.36</b>	<b>1.60</b>	<b>23.77</b>	<b>1334.03</b>	<b>5.21</b>	<b>5.69</b>

## Chapter 2: Benthic foraminiferal assemblages

Sample	Site	Habitat	Period	Water depth m	Sand %	Salinity ppt	OM %	T °C	pH	DO %	PO <sub>4</sub> <sup>3-</sup> -P µg/L	NH <sub>4</sub> <sup>+</sup> -N µg/L	NO <sub>2</sub> <sup>-</sup> -N µg/L	NO <sub>3</sub> <sup>-</sup> -N µg/L	SiO <sub>4</sub> <sup>4-</sup> -Si µg/L	Chl-a µg/L	PO <sub>4</sub> <sup>3-</sup> -P µg/L
<b>17D-137</b>	<b>Aufacada</b>	<b><i>Juncus</i></b>	<b>APR13'</b>	<b>0.15</b>	<b>77.45</b>	<b>11.71</b>	<b>3.84</b>	<b>18.89</b>	<b>7.41</b>	<b>6.46</b>	<b>17.44</b>	<b>25.56</b>	<b>5.22</b>	<b>2.31</b>	<b>202.72</b>	<b>13.97</b>	<b>7.85</b>
<b>17D-138</b>	<b>Aufacada</b>	<b><i>Juncus</i></b>	<b>AUG13'</b>	<b>0.10</b>	<b>77.45</b>	<b>12.91</b>	<b>3.84</b>	<b>23.27</b>	<b>7.87</b>	<b>6.49</b>	<b>2.48</b>	<b>29.27</b>	<b>1.79</b>	<b>21.11</b>	<b>4712.35</b>	<b>1.62</b>	<b>1.18</b>
18D-139	Aufacada	<i>Phragmites</i>	NOV12'	0.30	25.00	14.85	36.70	15.79	7.27	4.34	27.04	4.99	11.82	108.62	1445.90	3.11	1.68
<b>18D-140</b>	<b>Aufacada</b>	<b><i>Phragmites</i></b>	<b>APR13'</b>	<b>0.10</b>	<b>25.00</b>	<b>10.46</b>	<b>36.70</b>	<b>14.59</b>	<b>7.13</b>	<b>3.89</b>	<b>17.19</b>	<b>12.49</b>	<b>3.85</b>	<b>18.56</b>	<b>2797.60</b>	<b>39.43</b>	<b>7.52</b>
18D-141	Aufacada	<i>Phragmites</i>	AUG13'	0.15	25.00	10.62	36.70	25.81	7.95	0.71	5.45	67.11	6.47	16.02	4429.28	37.79	-0.10
<b>19D-142</b>	<b>Banya</b>	<b>Microbial mat</b>	<b>NOV12'</b>	<b>0.01</b>	<b>76.30</b>	<b>31.14</b>	<b>5.80</b>	<b>15.06</b>	<b>8</b>	<b>7.1</b>	<b>27.13</b>	<b>30.83</b>	<b>3.18</b>	<b>38.70</b>	<b>619.45</b>	<b>9.18</b>	<b>2.01</b>
<b>19D-143</b>	<b>Banya</b>	<b>Microbial mat</b>	<b>APR13'</b>	<b>0.05</b>	<b>76.30</b>	<b>74.63</b>	<b>5.80</b>	<b>27.71</b>	<b>8.04</b>	<b>5.91</b>	<b>46.89</b>	<b>33.08</b>	<b>3.99</b>	<b>2.47</b>	<b>302.20</b>	<b>2.70</b>	<b>1.19</b>
<b>19D-144</b>	<b>Banya</b>	<b>Microbial mat</b>	<b>AUG13'</b>	<b>0.02</b>	<b>76.30</b>	<b>51.48</b>	<b>5.80</b>	<b>24.71</b>	<b>9.07</b>	<b>13.57</b>	<b>14.43</b>	<b>30.39</b>	<b>1.47</b>	<b>7.49</b>	<b>626.05</b>	<b>0.94</b>	<b>0.49</b>
20D-145	Clot	Lagoon	NOV12'	0.55	45.63	1.81	26.62	16.87	7.82	7.21	48.20	149.98	15.09	642.73	1613.01	4.92	4.42
<b>21D-146</b>	<b>Encanyissada</b>	<b>Lagoon</b>	<b>NOV12'</b>	<b>0.77</b>	<b>78.21</b>	<b>8.48</b>	<b>0.89</b>	<b>14.15</b>	<b>8.35</b>	<b>11.36</b>	<b>40.20</b>	<b>59.33</b>	<b>0.64</b>	<b>184.52</b>	<b>1368.16</b>	<b>55.12</b>	<b>-7.05</b>
<b>21D-147</b>	<b>Encanyissada</b>	<b>Lagoon</b>	<b>APR13'</b>	<b>0.60</b>	<b>78.21</b>	<b>29.45</b>	<b>0.89</b>	<b>19.49</b>	<b>7.58</b>	<b>6.54</b>	<b>9.91</b>	<b>42.40</b>	<b>5.63</b>	<b>24.26</b>	<b>686.86</b>	<b>2.76</b>	<b>1.93</b>
<b>21D-148</b>	<b>Encanyissada</b>	<b>Lagoon</b>	<b>APR13'</b>	<b>0.40</b>	<b>72.59</b>	<b>31.88</b>	<b>0.89</b>	<b>20.21</b>	<b>7.88</b>	<b>5.6</b>	<b>6.94</b>	<b>29.82</b>	<b>1.01</b>	<b>7.56</b>	<b>421.48</b>	<b>0.82</b>	<b>1.50</b>
<b>21D-149</b>	<b>Encanyissada</b>	<b>Lagoon</b>	<b>AUG13'</b>	<b>0.45</b>	<b>78.21</b>	<b>10.45</b>	<b>0.89</b>	<b>27.24</b>	<b>8.23</b>	<b>6.63</b>	<b>45.41</b>	<b>16.47</b>	<b>1.61</b>	<b>0.59</b>	<b>1949.98</b>	<b>3.57</b>	<b>1.48</b>
<b>22D-150</b>	<b>Encanyissada</b>	<b><i>Salicornia</i></b>	<b>NOV12'</b>	<b>0.31</b>	<b>61.21</b>	<b>7.35</b>	<b>56.63</b>	<b>14.22</b>	<b>7.16</b>	<b>1.81</b>	<b>106.02</b>	<b>108.43</b>	<b>2.16</b>	<b>67.57</b>	<b>1965.54</b>	<b>20.57</b>	<b>6.03</b>
22D-151	Encanyissada	<i>Salicornia</i>	APR13'	0.10	61.21	26.92	56.63	20.76	7.61	7.69	26.51	21.49	3.07	4.80	242.52	14.20	3.31
22D-152	Encanyissada	<i>Salicornia</i>	AUG13'	0.15	61.21	14.45	56.63	29.26	8.43	11.11	22.95	39.70	3.07	36.64	4901.76	61.26	4.29
<b>23D-153</b>	<b>Encanyissada</b>	<b><i>Juncus</i></b>	<b>NOV12'</b>	<b>0.40</b>	<b>73.88</b>	<b>7.80</b>	<b>66.29</b>	<b>15.18</b>	<b>6.96</b>	<b>0.67</b>	<b>84.87</b>	<b>17.37</b>	<b>2.61</b>	<b>34.09</b>	<b>1468.82</b>	<b>24.42</b>	<b>0.46</b>
23D-154	Encanyissada	<i>Juncus</i>	APR13'	0.10	73.88	20.41	66.29	22.81	7.78	11.22	6.35	31.08	12.37	53.93	2200.22	9.31	2.87
<b>23D-155</b>	<b>Encanyissada</b>	<b><i>Juncus</i></b>	<b>AUG13'</b>	<b>0.08</b>	<b>73.88</b>	<b>42.32</b>	<b>66.29</b>	<b>28.40</b>	<b>7.92</b>	<b>12.27</b>	<b>28.65</b>	<b>20.04</b>	<b>3.33</b>	<b>15.66</b>	<b>2411.93</b>	<b>42.44</b>	<b>6.28</b>
<b>24D-156</b>	<b>Encanyissada</b>	<b><i>Phragmites</i></b>	<b>NOV12'</b>	<b>0.19</b>	<b>7.17</b>	<b>2.22</b>	<b>96.99</b>	<b>16.41</b>	<b>7.9</b>	<b>8.08</b>	<b>45.56</b>	<b>18.38</b>	<b>9.44</b>	<b>659.21</b>	<b>2046.03</b>	<b>5.73</b>	<b>5.05</b>
<b>24D-157</b>	<b>Encanyissada</b>	<b><i>Phragmites</i></b>	<b>APR13'</b>	<b>0.10</b>	<b>7.17</b>	<b>26.08</b>	<b>96.99</b>	<b>24.49</b>	<b>7.67</b>	<b>12.22</b>	<b>32.15</b>	<b>28.21</b>	<b>2.10</b>	<b>5.64</b>	<b>1474.43</b>	<b>10.10</b>	<b>2.30</b>
<b>24D-158</b>	<b>Encanyissada</b>	<b><i>Phragmites</i></b>	<b>AUG13'</b>	<b>0.20</b>	<b>7.17</b>	<b>20.23</b>	<b>96.99</b>	<b>27.18</b>	<b>8.07</b>	<b>3.31</b>	<b>27.88</b>	<b>23.91</b>	<b>4.16</b>	<b>18.28</b>	<b>13198.19</b>	<b>49.64</b>	<b>21.81</b>
<b>25D-159</b>	<b>Fangar</b>	<b>Inner bay</b>	<b>NOV12'</b>	<b>0.20</b>	<b>92.25</b>	<b>11.59</b>	<b>1.83</b>	<b>17.09</b>	<b>8.02</b>	<b>8.93</b>	<b>22.61</b>	<b>25.69</b>	<b>37.22</b>	<b>38.15</b>	<b>474.25</b>	<b>2.37</b>	<b>5.17</b>
<b>25D-160</b>	<b>Fangar</b>	<b>Inner bay</b>	<b>APR13'</b>	<b>0.20</b>	<b>92.25</b>	<b>39.17</b>	<b>1.83</b>	<b>25.67</b>	<b>8.3</b>	<b>7.21</b>	<b>6.10</b>	<b>21.08</b>	<b>1.54</b>	<b>9.36</b>	<b>187.25</b>	<b>2.38</b>	<b>1.15</b>
<b>25D-161</b>	<b>Fangar</b>	<b>Inner bay</b>	<b>AUG13'</b>	<b>0.40</b>	<b>92.25</b>	<b>18.27</b>	<b>1.83</b>	<b>21.93</b>	<b>8.91</b>	<b>9.44</b>	<b>10.62</b>	<b>14.31</b>	<b>1.68</b>	<b>8.67</b>	<b>146.16</b>	<b>4.76</b>	<b>2.38</b>
<b>26D-162</b>	<b>Fangar</b>	<b><i>Salicornia</i></b>	<b>NOV12'</b>	<b>0.16</b>	<b>80.50</b>	<b>18.71</b>	<b>46.79</b>	<b>17.11</b>	<b>7.24</b>	<b>0.63</b>	<b>224.40</b>	<b>2.96</b>	<b>2.68</b>	<b>87.95</b>	<b>671.72</b>	<b>2.38</b>	<b>4.14</b>
26D-163	Fangar	<i>Salicornia</i>	APR13'	0.16	80.50	38.98	46.79	27.87	7.84	5.53	9.66	100.71	6.56	10.73	666.08	4.84	4.19
26D-164	Fangar	<i>Salicornia</i>	AUG13'	0.17	80.50	35.80	46.79	23.13	7.52	1.35	87.97	358.08	11.54	5.48	1969.58	3.05	1.37
<b>27D-165</b>	<b>Garxal</b>	<b>Lagoon</b>	<b>NOV12'</b>	<b>0.25</b>	<b>92.12</b>	<b>5.25</b>	<b>2.26</b>	<b>12.74</b>	<b>7.8</b>	<b>5.68</b>	<b>11.34</b>	<b>7.79</b>	<b>0.34</b>	<b>32.41</b>	<b>749.46</b>	<b>0.91</b>	<b>0.88</b>

## Chapter 2: Benthic foraminiferal assemblages

Sample	Site	Habitat	Period	Water depth m	Sand %	Salinity ppt	OM %	T °C	pH	DO %	PO <sub>4</sub> <sup>3-</sup> -P µg/L	NH <sub>4</sub> <sup>+</sup> -N µg/L	NO <sub>2</sub> <sup>-</sup> -N µg/L	NO <sub>3</sub> <sup>-</sup> -N µg/L	SiO <sub>4</sub> <sup>4-</sup> -Si µg/L	Chl-a µg/L	PO <sub>4</sub> <sup>3-</sup> -P µg/L
<b>27D-166</b>	<b>Garxal</b>	<b>Lagoon</b>	<b>APR13'</b>	<b>0.25</b>	<b>92.12</b>	<b>2.39</b>	<b>2.26</b>	<b>18.69</b>	<b>7.97</b>	<b>5.47</b>	<b>12.11</b>	<b>42.30</b>	<b>3.18</b>	<b>12.02</b>	<b>481.36</b>	<b>6.30</b>	<b>1.67</b>
27D-167	Garxal	Lagoon	AUG13'	0.30	92.12	8.90	2.26	26.00	8.9	10.29	10.04	28.17	1.48	5.99	3151.19	13.79	3.95
28D-168	Garxal	<i>Salicornia</i>	NOV12'	0.08	92.34	17.24	3.15	15.40	8.4	7.64	21.93	11.57	0.69	84.64	990.52	8.88	0.91
28D-169	Garxal	<i>Salicornia</i>	APR13'	0.10	92.34	10.39	3.15	23.98	8.5	8.48	11.65	24.79	2.40	2.55	293.21	10.03	3.05
<b>29D-170</b>	<b>Garxal</b>	<b>Juncus</b>	<b>NOV12'</b>	<b>0.07</b>	<b>93.96</b>	<b>6.59</b>	<b>3.86</b>	<b>13.83</b>	<b>7.68</b>	<b>7.64</b>	<b>43.95</b>	<b>85.65</b>	<b>20.76</b>	<b>1115.36</b>	<b>1642.72</b>	<b>5.77</b>	<b>2.76</b>
<b>29D-171</b>	<b>Garxal</b>	<b>Juncus</b>	<b>APR13'</b>	<b>0.10</b>	<b>93.96</b>	<b>12.18</b>	<b>3.86</b>	<b>16.97</b>	<b>7.39</b>	<b>5.27</b>	<b>11.83</b>	<b>18.38</b>	<b>3.40</b>	<b>11.07</b>	<b>2254.42</b>	<b>15.80</b>	<b>2.21</b>
29D-172	Garxal	<i>Juncus</i>	AUG13'	0.11	93.96	11.83	3.86	26.36	7.26	4.97	99.43	18.60	1.96	3.21	2687.78	11.88	2.00
30D-173	Garxal	<i>Phragmites</i>	NOV12'	0.14	65.80	4.93	39.81	13.09	8.09	6.41	14.56	65.64	0.29	57.93	871.46	2.30	2.07
30D-174	Garxal	<i>Phragmites</i>	APR13'	0.15	65.80	1.97	39.81	21.70	8.16	9.4	14.40	19.29	2.21	81.11	297.43	7.70	2.39
<b>30D-175</b>	<b>Garxal</b>	<b>Phragmites</b>	<b>AUG13'</b>	<b>0.07</b>	<b>65.80</b>	<b>8.52</b>	<b>39.81</b>	<b>25.46</b>	<b>8.92</b>	<b>10.71</b>	<b>10.62</b>	<b>13.46</b>	<b>1.29</b>	<b>4.59</b>	<b>4679.33</b>	<b>12.03</b>	<b>7.99</b>
31D-176	Olles	Lagoon	NOV12'	0.72	26.75	0.73	5.61	13.65	7.77	8.3	32.18	122.76	25.90	1157.49	1108.68	2.57	2.24
31D-177	Olles	Lagoon	APR13'	0.50	26.75	4.26	5.61	24.08	8.14	9.65	12.14	80.15	54.49	1233.69	2687.78	20.66	3.94
31D-178	Olles	Lagoon	AUG13'	0.45	26.75	0.79	5.61	21.97	7.73	8.1	39.77	70.75	17.42	499.17	2477.70	47.78	7.94
32D-179	Olles	<i>Phragmites</i>	NOV12	0.25	37.58	0.74	40.55	13.03	7.41	6.02	20.32	12.70	0.90	25.87	1496.11	3.24	2.30
<b>32D-180</b>	<b>Olles</b>	<b>Phragmites</b>	<b>AUG13'</b>	<b>0.10</b>	<b>37.58</b>	<b>1.58</b>	<b>40.55</b>	<b>21.42</b>	<b>7.55</b>	<b>2.49</b>	<b>24.50</b>	<b>7.69</b>	<b>1.93</b>	<b>26.21</b>	<b>2375.75</b>	<b>12.19</b>	<b>2.84</b>
<b>33D-181</b>	<b>Tancada</b>	<b>Lagoon</b>	<b>NOV12'</b>	<b>0.50</b>	<b>70.69</b>	<b>20.77</b>	<b>3.28</b>	<b>12.40</b>	<b>7.99</b>	<b>9.77</b>	<b>44.76</b>	<b>98.66</b>	<b>17.24</b>	<b>39.40</b>	<b>1058.80</b>	<b>6.37</b>	<b>1.04</b>
<b>33D-182</b>	<b>Tancada</b>	<b>Lagoon</b>	<b>APR13'</b>	<b>0.60</b>	<b>70.69</b>	<b>35.03</b>	<b>3.28</b>	<b>17.66</b>	<b>7.65</b>	<b>5.97</b>	<b>8.73</b>	<b>147.66</b>	<b>14.52</b>	<b>27.47</b>	<b>356.77</b>	<b>1.36</b>	<b>3.82</b>
<b>33D-183</b>	<b>Tancada</b>	<b>Lagoon</b>	<b>APR13'</b>	<b>0.30</b>	<b>8.64</b>	<b>35.22</b>	<b>3.28</b>	<b>17.44</b>	<b>7.53</b>	<b>5.38</b>	<b>9.14</b>	<b>131.61</b>	<b>9.48</b>	<b>16.32</b>	<b>457.37</b>	<b>10.18</b>	<b>4.43</b>
<b>33D-184</b>	<b>Tancada</b>	<b>Lagoon</b>	<b>AUG13'</b>	<b>0.45</b>	<b>70.69</b>	<b>26.77</b>	<b>3.28</b>	<b>25.07</b>	<b>8</b>	<b>5.14</b>	<b>15.21</b>	<b>23.97</b>	<b>3.39</b>	<b>3.99</b>	<b>1158.53</b>	<b>3.87</b>	<b>2.09</b>
<b>34D-185</b>	<b>Tancada</b>	<b>Salicornia</b>	<b>NOV12'</b>	<b>0.32</b>	<b>58.78</b>	<b>23.69</b>	<b>59.27</b>	<b>13.03</b>	<b>7.34</b>	<b>5.95</b>	<b>200.46</b>	<b>131.90</b>	<b>5.88</b>	<b>21.46</b>	<b>1532.43</b>	<b>30.90</b>	<b>13.76</b>
<b>34D-186</b>	<b>Tancada</b>	<b>Salicornia</b>	<b>NOV12'</b>	<b>0.14</b>	<b>63.67</b>	<b>21.43</b>	<b>17.82</b>	<b>13.35</b>	<b>7.33</b>	<b>5.68</b>	<b>201.39</b>	<b>3.25</b>	<b>3.18</b>	<b>113.40</b>	<b>1285.53</b>	<b>46.20</b>	<b>12.61</b>
<b>34D-187</b>	<b>Tancada</b>	<b>Salicornia</b>	<b>APR13'</b>	<b>0.14</b>	<b>63.67</b>	<b>29.81</b>	<b>17.82</b>	<b>12.37</b>	<b>7.69</b>	<b>3.35</b>	<b>18.55</b>	<b>13.05</b>	<b>1.34</b>	<b>7.13</b>	<b>159.67</b>	<b>18.00</b>	<b>6.08</b>
34D-188	Tancada	<i>Salicornia</i>	APR13'	0.50	58.78	26.12	59.27	15.83	8	6.82	119.34	9.66	5.17	1.43	522.95	6.53	2.84
<b>35D-189</b>	<b>Tancada</b>	<b>Phragmites</b>	<b>NOV12'</b>	<b>0.08</b>	<b>31.89</b>	<b>17.50</b>	<b>27.19</b>	<b>13.74</b>	<b>7.15</b>	<b>3.72</b>	<b>179.15</b>	<b>14.24</b>	<b>1.62</b>	<b>43.38</b>	<b>1177.12</b>	<b>22.86</b>	<b>28.77</b>
<b>35D-190</b>	<b>Tancada</b>	<b>Phragmites</b>	<b>APR13'</b>	<b>0.05</b>	<b>31.89</b>	<b>31.69</b>	<b>27.19</b>	<b>18.88</b>	<b>7.02</b>	<b>3.74</b>	<b>40.76</b>	<b>20.87</b>	<b>5.31</b>	<b>1.06</b>	<b>891.60</b>	<b>17.81</b>	<b>9.50</b>
<b>35D-191</b>	<b>Tancada</b>	<b>Phragmites</b>	<b>AUG13'</b>	<b>0.15</b>	<b>31.89</b>	<b>11.76</b>	<b>27.19</b>	<b>22.53</b>	<b>7.55</b>	<b>3.76</b>	<b>5.23</b>	<b>164.64</b>	<b>3.42</b>	<b>1.05</b>	<b>1029.53</b>	<b>44.51</b>	<b>7.88</b>

**Supplementary Table S2**

Results of Canonical Correspondence Analysis (CCA) of foraminifera-environment relationships. a) Marginal effects indicate the variance explained by each variable considered alone. b) Unique effects indicate percentage variance explained by each environmental variable with the remaining treated as covariables.  $\lambda_1$ : eigenvalue of the constrained axis 1;  $\lambda_1/\lambda_2$ : ratio of the constrained axis 1 to the unconstrained axis 1. Those variables selected by initial series of CCA including all individual variables are emboldened, while variables finally selected by partial CCAs are emboldened and highlighted in gray color.

a) CCAs (marginal effects)				
Variable	% variance explained	p value		
<b>Water depth</b>	<b>15.51</b>	<b>0.005</b>		
<b>Salinity</b>	<b>8.86</b>	<b>0.005</b>		
<b>Sand proportion</b>	<b>6.44</b>	<b>0.005</b>		
Temperature	1.72	0.35		
b) Partial CCAs (unique effects)				
Variable	% variance explained	p value	$\lambda_1$	$\lambda_1/\lambda_2$
<b>Water depth</b>	<b>8.66</b>	<b>0.005</b>	<b>0.380</b>	<b>0.75</b>
<b>Sand proportion</b>	<b>4.33</b>	<b>0.005</b>	<b>0.191</b>	<b>0.37</b>
<b>Salinity</b>	<b>3.12</b>	<b>0.005</b>	<b>0.137</b>	<b>0.26</b>
Sum unique effects	16.11			
Intercorrelations	6.74			
Total variance explained	22.85			

**Supplementary Table S3**

Model performances for the foraminifera-based water depth transfer functions (WA-INV, WA-CLA, WA-PLS). All models were cross-validated using leave-one-site-out method (LOSO), and were built on square root transformed species data and  $\log_{10}$  transformed water depth (m). Abbreviations: WA = Weighted-Averaging; INV = Inverse deshrinking; CLA = Classical deshrinking; WA-PLS = Weighted-Averaging Partial Least Squares. The model preferred is highlighted in bold and gray colour.

<b>Model</b>	$r^2_{\text{LOSO}}$	<b>RMSEP</b> LOSO ( $\log_{10}$ <b>m)</b>	<b>Max Bias</b> LOSO ( $\log_{10}$ m)	<b>% improvement</b> <b>in RMSEP</b>	<b>Mean segment</b> <b>RMSEP</b> <sub>LOSO</sub> ( $\log_{10}$ m)
Foraminiferal dataset: n samples = 115, n taxa = 155					
WA-INV	0.76	0.46	1.68		0.72
WA-CLA	0.76	0.51	0.62		0.74
WA-PLS-1	0.76	0.46	1.62		0.70
WA-PLS-2	0.82	0.41	1.06	9.91	0.50
WA-PLS-3	0.80	0.42	0.99	-0.83	0.49
Foraminiferal dataset: n samples = 108, n taxa = 151					
WA-INV	0.84	0.36	1.41		0.61
WA-CLA	0.84	0.39	1.36		0.61
WA-PLS-1	0.84	0.37	1.43		0.61
<b>WA-PLS-2</b>	<b>0.89</b>	<b>0.31</b>	<b>0.77</b>	<b>12.23</b>	<b>0.40</b>
WA-PLS-3	0.88	0.32	0.74	-0.93	0.35

**Supplementary Table S4**

Results of Canonical Correspondence Analysis (CCA) of combined foraminifera-diatom dataset and relationships with the measured environmental variables for the Ebro Delta samples. a) Marginal effects indicate the variance explained by each variable considered alone. b) Unique effects indicate percentage variance explained by each environmental variable with the remaining treated as covariables.  $\lambda_1$ : eigenvalue of the constrained axis 1;  $\lambda_1/\lambda_2$ : ratio of the constrained axis 1 to the unconstrained axis 1. Those variables selected by initial series of CCA including all individual variables are emboldened, while variables finally selected by partial CCAs are emboldened and highlighted in gray color.

a) CCAs (marginal effects)				
Variable	% variance explained	p value		
<b>OM</b>	<b>5.49</b>	<b>0.005</b>		
<b>Salinity</b>	<b>5.46</b>	<b>0.005</b>		
<b>Water depth</b>	<b>5.35</b>	<b>0.005</b>		
<b>pH</b>	<b>3.57</b>	<b>0.005</b>		
<b>SiO<sub>4</sub></b>	<b>3.57</b>	<b>0.005</b>		
<b>Chl-a</b>	<b>3.35</b>	<b>0.005</b>		
<b>Sand</b>	<b>3.03</b>	<b>0.005</b>		
<b>Feopig-a</b>	<b>2.55</b>	<b>0.01</b>		
<b>NO<sub>2</sub><sup>-</sup>-N</b>	<b>2.32</b>	<b>0.015</b>		
<b>NO<sub>3</sub><sup>-</sup>-N</b>	<b>2.23</b>	<b>0.03</b>		
<b>PO<sub>4</sub><sup>3-</sup>-P</b>	<b>2.16</b>	<b>0.032</b>		
NH <sub>4</sub> <sup>+</sup> -N	1.62	0.34		
DO	1.48	0.43		
T	1.33	0.61		

b) Partial CCAs (unique effects)				
Variable	% variance explained	p value	$\lambda_1$	$\lambda_1/\lambda_2$
<b>Salinity</b>	<b>4.22</b>	<b>0.005</b>	<b>0.176</b>	<b>0.70</b>
<b>Water depth</b>	<b>3.47</b>	<b>0.005</b>	<b>0.145</b>	<b>0.57</b>
<b>OM</b>	<b>2.38</b>	<b>0.005</b>	<b>0.099</b>	<b>0.40</b>
<b>pH</b>	<b>2.40</b>	<b>0.005</b>	<b>0.099</b>	<b>0.39</b>
<b>NO<sub>2</sub><sup>-</sup>-N</b>	<b>2.03</b>	<b>0.005</b>	<b>0.085</b>	<b>0.34</b>
<b>Sand</b>	<b>1.86</b>	<b>0.019</b>	<b>0.078</b>	<b>0.31</b>
SiO <sub>4</sub> <sup>4-</sup> -Si	1.71	0.06	0.071	0.28
PO <sub>4</sub> <sup>3-</sup> -P	1.56	0.07	0.065	0.26



NO <sub>3</sub> <sup>-</sup> -N	1.49	0.11	0.062	0.25
Chl-a	1.09	0.63	0.046	0.18
Feopig-a	1.07	0.75	0.045	0.18
Sum unique effects	16.36			
Intercorrelations	5.06			
Total variance explained	21.42			

### Supplementary Table S5

Performance statistics for multiproxy-salinity and diatom-conductivity transfer functions (WA-INV, WA-CLA, WATOL-INV, WATOL-CLA). Multiproxy model was based on dead foraminifera and diatom assemblages. All models were cross-validated using leave-one-site-out (LOSO), and were built on square root transformed species data and log<sub>10</sub> transformed salinity (ppt), and log<sub>10</sub> transformed conductivity (mS/cm). Abbreviations: WA = Weighted-Averaging; INV = Inverse deshrinking; CLA = Classical deshrinking; WATOL = Weighted-Averaging with tolerance downweighted. The models preferred are highlighted in bold and gray colour.

Variable	Model	$r^2_{\text{LOSO}}$	RMSEP <sub>LOSO</sub>	Max Bias <sub>LOSO</sub>	Mean segment RMSEP <sub>LOSO</sub>
Salinity (log <sub>10</sub> ppt)	Multiproxy dataset: n samples = 70, n taxa = 511				
	WA-INV	0.62	0.28	0.053	0.36
	<b>WA-CLA</b>	<b>0.63</b>	<b>0.28</b>	<b>0.045</b>	<b>0.32</b>
	WATOL-INV	0.51	0.27	0.75	
	WATOL-CLA	0.51	0.28	0.78	
Conductivity (log <sub>10</sub> mS/cm)	Diatom dataset: n samples = 61, n taxa = 424				
	WA-INV	0.62	0.26	0.39	0.33
	<b>WA-CLA</b>	<b>0.64</b>	<b>0.27</b>	<b>0.32</b>	<b>0.30</b>
	WATOL-INV	0.43	0.31	0.74	-
	WATOL-CLA	0.43	0.31	0.72	-

### Supplementary Table S6 Relative abundances of living and dead foraminifera.

The data table can be found online at the XXX website <http://XXX>.



## ***Chapter 3***

### **Holocene palaeoenvironmental evolution of the Ebro Delta (Western Mediterranean Sea): Evidence for an early construction based on the benthic foraminiferal record**

Cearreta, A., Benito, X., Ibáñez, C., Trobajo, R. and Giosan, L.

*The Holocene* (under review)

*Chapter 3: Holocene Ebro Delta evolution*

## **Holocene palaeoenvironmental evolution of the Ebro Delta (Western Mediterranean Sea): Evidence for an early construction based on the benthic foraminiferal record**

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### **Abstract**

Major Mediterranean deltas began to develop within a period between 8000 and 6000 yr BP as the rate of fluvial sediment input overtook the declining rate of sea-level rise. However, different authors have considered that the Ebro Delta formed mostly during the Late Middle Ages as a consequence of increased anthropogenic pressure on its river basin and supported by the scarcity of previous geological studies and available radiocarbon dates. In order to reconstruct the environmental evolution of the Ebro Delta during the Holocene, we used micropalaeontological analysis of continuous boreholes drilled in two different locations of the central delta plain (Carlet and Sant Jaume). Different lithofacies distributions and associated environments of deposition were defined based on diagnostic foraminiferal assemblages and the application of a palaeowater-depth transfer function. The more landward Carlet sequence shows an older and more proximal progradational delta with a sedimentary record composed of inner bay, lagoonal, and beach materials deposited after 7600 yr BP until >2000 yr BP under sea-level rising and highstand conditions. This phase was followed by a series of delta-plain environments reflected in part by the Carlet deposits before 2000 yr BP. The Sant Jaume borehole is located nearer the present coastline and contains a much younger sequence accumulated in the last 2.0 ka during the development of three different deltaic lobes under highstand sea-level conditions. Results of the present study reinforce the idea that the Ebro Delta dates back to the early Holocene as other large Mediterranean deltas.

### **Keywords**

Ebro Delta, sedimentary sequences, benthic foraminifera, environmental evolution, Mediterranean Sea, Holocene

## **Introduction**

Deltas are the largest coastal landforms in the world (Evans, 2012). They are coastal depositional environments resulting from the interaction between river and marine forces. The strength of both elements determines the dominant processes governing the evolution of the deltaic systems through time (Jiménez et al., 1997). The morphology and sedimentary architecture of deltas depend on the relative magnitude of tides, waves and currents (Wright and Coleman, 1973; Galloway, 1975). The morphological evolution of a delta is also controlled by relative sea-level changes depending, in turn, on the eustatic sea-level rise and local subsidence or uplift (Galloway, 1975). Subsidence results naturally from compaction of deltaic sediments, degassing of peats and growth faults developed at the base of deltaic sediments, but can be additionally increased by human activities such as extraction of groundwater. However, relative sea-level rise (RSLR) can be compensated by vertical accretion processes taking place in the delta plain and in turn accretion rates depend on fluvial sediment inputs and sea-level rise itself through feedback mechanisms (Day et al., 2011; Ibáñez et al., 2014).

Deltas are considered to be highly vulnerable to even minor changes in relative sea level, particularly because most modern deltas are actively subsiding and their sediment supply has been curtailed (Giosan et al., 2014; IPCC, 2014). Moreover, global warming is accelerating sea-level rise, which intensifies coastal erosion and land loss due to marine inundation (Fatorić and Chelleri, 2012). In order to implement science-based coastal protection measures in these sensitive areas, a precise definition of the relation between sea-level change and delta evolution is critical, and consequently it is essential to understand the relation between delta development and sea-level change during the Holocene (Stanley and Warne, 1994). Under natural conditions, deltas have mechanisms to enhance vertical accretion and land gain as a response to RSLR, specially the increased river avulsion and delta lobe formation in shallow areas, and increased accretion in coastal marshes and beaches connected to marine environments (Ibáñez et al., 2014). This suggests that river-dominated deltas can be resilient to changes in sea level.

Previous analysis of major modern deltas in the Mediterranean Sea showed that these environments started to build between 8000 and 6000 yr BP. Overlapping fluvial upper Pleistocene gravels, Holocene deltaic deposits consist of variable aggradational and progradational lithologies (Stanley and Warne, 1994, 1997; Vella et al., 2005; Anthony et al., 2014). These previous works showed that the deceleration in sea-level rise was the key to initiation of deltas and that Holocene deltaic sequences began to accumulate as the rate of fluvial sediment input overtook the declining rate of sea-level rise along coasts. For the northwestern Mediterranean area, Lambeck and Purcell (2005) and Pirazzoli (2005) indicated a rapid sea-level rise until 6.0 ka, followed by a more gradual increase in sea level with a slight deceleration during the last 1.5 ka, and stabilization for the last 0.5 ka.

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Recently, Maselli and Trincardi (2013) supported the idea that the onset of the northern Mediterranean deltas followed an ancestral phase dominated by estuary fill and relatively slow delta growth, around 6000 yr BP. Furthermore they suggested that these deltas formed almost synchronously during two short intervals of enhanced anthropogenic pressure on landscapes, respectively during the Roman Empire and the Little Ice Age.

Mediterranean deltas contain a widespread and generally consistent Holocene stratigraphic succession composed of peat, lagoonal, and other organic-rich facies that accumulated as delta plain deposits at or near sea level (Stanley and Warne, 1994). These resource-rich ecosystems were used by humans soon after their development. Documented archaeological sites dated to 7000 yr BP or earlier are positioned on or adjacent to deltas as the Rhône and the Nile (Stanley and Warne, 1997).

Benthic foraminifera have been long and widely used as indicators of past environmental conditions (i.e., salinity, temperature, oxygen content, etc.) of open marine and coastal areas (Murray, 2006), and are a valuable tool, in combination with the stratigraphical sequence and other palaeontological and geochemical proxies, for palaeoenvironmental reconstruction. However, the use of foraminifera for an accurate reconstruction of coastal habitats is not straightforward due to the enormous complexity and variability of these ecosystems. This is of paramount importance in the case of deltas, since a small delta plain such as the Ebro (320 km<sup>2</sup>) contains at least four different habitats with their particular foraminiferal assemblages (Benito et al. (2006) and Tables 1 and 2). Moreover, the existing literature shows that previous palaeoenvironmental reconstructions of Mediterranean deltaic sequences have used modern analogues from the open marine environments only (Amorosi et al., 1999, 2013; Rossi and Horton, 2009; Curzi et al., 2006; Carboni et al., 2010; Dinelli et al. 2012; Milli et al., 2013) but not from the delta plain habitats (coastal lagoons, inner bays, salt marshes, etc.). Thus, the present study represents the first palaeoreconstruction based on both open marine and delta plain assemblages, giving therefore the possibility for a new and sounder interpretation of the fossil record in deltaic sedimentary sequences.

#### *Previous work*

Earlier geological studies of the Ebro Delta and its Holocene sedimentary archives and evolution are scarce and most of them based on just a few radiocarbon dates, especially initial works carried out in 1960s and 1970s (e.g., Solé et al., 1961; Macau, 1961; Maldonado and Riba, 1971; Maldonado, 1972). According to Maldonado and Murray (1975), and based on sedimentological and palaeontological comparison between borehole depositional sequences and recent environments, after a temporary stabilization of sea level at *ca.* -10 m extensive deltaic progradation started and delta plain formed over the last 8.0 ka (based on peat material radiocarbon dated by Solé et al. (1965) at 7680 yr BP). Fluvial supply of sediments was sufficient to prevent extensive transgression of the delta



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plain during this time interval concurrent with the slowing of the sea-level rise. Maldonado and Murray (1975) concluded that the entire development of the Ebro Delta was governed mainly by the interaction between the rate of sea-level rise and the rate of sediment delivery by the river. Other factors, such as river floods and coastal processes caused the diversion of the distributaries as well as changes in the delta morphology, with river avulsions being responsible of an evolution based on the sequential progradation and abandonment of different deltaic lobes subsequently being modified by rapid subsidence. Thus, the geometry of Ebro Delta was created by the advance of successive deltaic lobes that prograded radially seawards from an avulsion point usually located close to the Gracia Island (Maldonado and Riba, 1971). These processes were studied by Maldonado (1977) who found evidence for five different major avulsions during the last centuries (Díaz et al., 1990).



**Figure 1.** Geographical location of the Ebro Delta in the western Mediterranean Sea, boreholes and places referred to in the text. Dashed line represents the approximate morphology and position of the two ancient deltaic lobes (from Maldonado, 1972). Images taken from Google Earth.

The Holocene deposits of the delta present a thickness ranging from 20 m at the landward side to 52 m at the delta front (Maldonado, 1972; Maestro et al., 2002). Radiocarbon ages indicate that deposition of the prodelta on the shelf began at about 11,000-10,000 yr BP (Díaz et al., 1990). After the pioneering work of Maldonado (1972), Somoza et al. (1998) published the most comprehensive study of the Holocene depositional units of the Ebro Delta based on high-resolution seismic profiles and analysis of 11 existing boreholes (20-60 m long) drilled on the modern delta (3 in the alluvial valley, 7 in the delta plain and 1 in the prodelta). The Holocene deposits of the delta were interpreted as a depositional sequence being composed of a transgressive systems tract (TST), formed mainly of a basal mollusc-shell lag and marine gray or black clays overlapping the upper Pleistocene gravels, and a highstand systems tract (HST). The top of the maximum flooding surface (MFS) separating the TST

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from the HST was dated at 6900 yr BP based on peat material from the inner delta area published previously by Arasa (1994), as they did not obtain any direct dates from their sedimentary sequences. The HST, which overlies the MFS, is reported to include a total of five progradational units made of prodelta clays, sandy delta fronts and silty sands of delta-plain deposits depending on location within the deltaic three-dimensional architecture. Only their ITGE-6 borehole was drilled in the central area of the delta plain near the Gracia Island (Figure 1). The ITGE-6 borehole was around 30 m long, of which about 27 m were of Holocene age. The Holocene stack was interpreted to be composed of five progradational units (with assigned ages in Somoza and Rodríguez-Santalla, 2014): basal unit d0 made of bioclastic coarse sand containing marine mollusks and deposited during the TST before 7000 yr BP; units d1 and d2 composed of coarse and medium sands, accumulated above the MFS and dated between 6150 and 3600 yr BP. These three lower units are considered as delta-front and nearshore deposits; and finally, units d3 and d4 characterized by sands with scattered pebbles and silty sands are defined as delta-plain deposits younger than 2700 yr BP. These progradational units were interpreted to have been deposited as a succession of prograding delta lobes with frequencies of thousand-year magnitude.

Canicio and Ibáñez (1999) identified several coastal barriers separating thick peat bodies in the landward limit of the present delta plain dated  $3050 \pm 45$  radiocarbon years old in the northern hemidelta and  $5745 \pm 50$  radiocarbon years old in the southern hemidelta, and concluded that the orientation of the barriers suggests that about 6000 yr BP the mouth of the delta was around the present fluvial island of Gracia (Figure 1).

Recently, in contrast to the above mentioned studies, Maselli and Trincardi (2013) supported the idea that Amposta, a town now located at the inland margin of the delta, had a marine harbour during Roman times. This erroneous idea began with a personal interpretation of Roman texts by Bayerri (1934) who considered the mention of a “sea port” in Tortosa (12 km upstream of Amposta; Figure 1) to be proof for the existence of an estuary. The concept of “sea port”, however, could also refer to fluvial ports that harbour marine vessels. As pointed out by Canicio and Ibáñez (1999), the same misinterpretation led some other authors to consider that the Ebro Delta formed very recently (mostly during the Islamic Period, 14th and 15th centuries) and that during Roman times it was an estuary. For example, Guillén and Palanques (1997) and Palanques and Guillén (1998) considered that the Holocene sea-level rise caused the flooding of the river mouth, which became an estuary that evolved into a delta only during the last 2.0 ka. Some publications even concluded that the delta plain began to form during the 12th century downstream from the town of Amposta (Serra, 1997; Somoza and Rodríguez-Santalla, 2014).

Differential delta lobe progradation has been identified during the last millennium in the Ebro Delta through the recognition of three main lobes: the Riet Vell, Riet de Zaida and Migjorn lobes (Ibáñez et al., 1997) (Figure 1). The oldest map showing a relatively detailed and reliable

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configuration of the Ebro Delta is the Mercator-Hondius Atlas, which dates from 1580 CE (Ibáñez et al., 1997). The southeastern Riet Vell lobe was the main active mouth of the delta in 1149 CE and was probably abandoned in 1362 CE (Somoza and Rodríguez-Santalla, 2014). Modern bathymetric configuration suggests that marine partial destruction of this abandoned lobe provoked an 8 km retreat of the old headland and the subsequent growth of the southern La Banya spit (Canicio and Ibáñez, 1999). After this period, the main mouth of the Ebro Delta moved northward to the Riet de Zaida lobe that was already active in 1575 CE (Somoza and Rodríguez-Santalla, 2014). This lobe was separated from the old Riet Vell lobe by a large palaeobay (Port Fangós), and it developed from the proximal zone of the delta, suggesting that it was built by the switching of the river near the Gracia Island (Figure 1). This new channel, shorter and with more hydraulic gradient to the sea, provoked a quick decay of the old Riet Vell main channel. The next detailed maps include a navigation chart of the Ebro Delta coast (Plan Des Rades de Sausa, 1733 CE) and the map of Miguel Marín (1749 CE) (Canicio and Ibáñez, 1999). The main differences with the previous situation at the end of the 16th century were the complete filling of the palaeobay that separated the two previous deltaic lobes and the rapid progradation of a new and central Migjorn lobe. This last active lobe is the result of a new river switching event that took place around the year 1666 CE at a location called La Cava close to the Gracia Island area (Figure 1) as a consequence of a reported anthropogenic excavation in the outer levee of a pronounced meander (Ribas, 1996). The retreat of the Riet de Zaida lobe by marine erosion conducted to the subsequent development of the Fangar spit that started to form around 1739 CE, as indicated on the Miguel Marín map (Canicio and Ibáñez, 1999). Modern maps show a rapid progradation of the central Migjorn lobe until 1880 CE due to the infill of the shallow inner palaeobay of Port Fangós, followed by a relative stabilisation of the delta mouth during the first half of the 20th century and a quick retreat during the last decades due to sediment retention in the various dams located along the Ebro River watercourse (Ibáñez et al., 1997).

Another controversial issue related to the hypothesis of a recent and rapid growth of the Ebro Delta is the impact of land use changes in the river basin on the progradation rates. The 13th century is considered to be the beginning of an intense deforestation of the Ebro basin caused by the change in land use, from forest to agricultural activities. These changes favoured sediment erosion and may have caused an important progradation of the Ebro River mouth (Palanques and Guillén, 1998; Maselli and Trincardi, 2013; Somoza and Rodríguez-Santalla, 2014). However, a recent study modelling sediment transport in the Ebro River during the last 4.0 ka (Xing et al., 2014) shows that sediment load was already high (30.5 Mt yr<sup>-1</sup>) before any human significant intervention and that the increase in sediment load due to land use change was up to a maximum of 47.2 Mt yr<sup>-1</sup>.

Modern foraminifera (live and dead assemblages) off the Ebro Delta were studied extensively by Scrutton (1969), who defined quantitatively the different species that characterized mainly the open marine environments; in contrast, the study of delta plain habitats was very limited (only 6

samples from a coastal lagoon). Afterwards, Maldonado (1972) published qualitative results on the presence of benthic foraminifera in several surface (total assemblages) and borehole samples from the Ebro Delta (from both delta plain and open marine environments). More recently, an exhaustive analysis of delta plain and nearshore foraminiferal assemblages of the Ebro Delta was carried out by the authors (see Tables 1 and 2), which complements very well the study by Scrutton (1969). Data from both studies are the base for the palaeoreconstruction carried out in the present paper, in combination with the interpretation of stratigraphic sequences and radiocarbon dates. Geological analysis of continuous borings in deltas and their lateral correlation can define the associated environments of deposition. Such analyses provide a context for interpreting both regional palaeogeography and site-specific environmental settings.

### **Objectives**

The present work is focused on the methodological contribution of the foraminiferal assemblages to reconstructing the sequence of palaeoenvironments that characterize the Holocene evolution of the central Ebro Delta plain. We supply new data to pinpoint the age of the delta as it has been questioned during recent years (Maselli and Trincardi, 2013). We contribute substantial new environmental and chronological information to complete and improve previous interpretations (e.g., Somoza et al., 1998).

The main aim of the current work is to provide new insights into the Holocene evolution of the Ebro Delta using micropalaeontological proxies (benthic foraminifera) based on modern analogues covering the whole range of deltaic environments (from the inner delta plain to the outer prodelta).

The combination of the fossil foraminiferal data obtained from two new boreholes with the available geological knowledge (mainly published by Somoza et al, 1998) and the existing data of modern foraminifera allowed a more precise reconstruction of deltaic environments and their evolution through time in the central delta-plain area. From this knowledge, a new understanding on some controversial points regarding the origin and evolution of the delta has been obtained. In addition, numerous radiocarbon dates allowed a detailed chronology of the deltaic succession at the two boreholes to be made.

### **Materials and methods**

#### *Study area*

The Ebro Delta is one of the largest modern deltas in the Mediterranean after those of the Nile, Rhône and Po (Barnolas et al., 1996). It is located on the western Mediterranean coast, about 200 km southwest of Barcelona, and it extends over an area of 320 km<sup>2</sup>, has an outer sandy shoreline of 50

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km length and an estimated sedimentary volume of 28 km<sup>3</sup> (Figure 1). The maximum tidal amplitude is 0.25 m (astronomical) and 1 m (meteorological) (Sánchez-Arcilla et al., 1996; Somoza and Rodríguez-Santalla, 2014).

The main morphological features of this microtidal delta are two spits, Fangar and La Banya, which partially close two adjacent bays, Fangar and Alfacs (Figure 1). Most of the surface area of the modern Ebro Delta is devoted to agriculture since the construction in 1860 CE of the first irrigation canal which transformed most wetlands and some lagoons into rice fields which occupy 65% of the delta plain (Cardoch et al., 2002; Ibáñez et al., 2010; Roca and Villares, 2012). Delta natural habitats account for only 20% of the surface area and include freshwater, brackish and saline lagoons, salt marshes and coastal and sandy dune systems (Valdemoro et al., 2007). Several national and international designations (RAMSAR, Natura 2000 and Natural Park) currently protect the natural delta habitats.

At present, RSLR and coastal erosion by wave action cannot be compensated by river sediment input (Ibáñez et al., 1997; Jiménez et al., 1997). A series of dams were built along the Ebro River watercourse mainly in the 1960s to support a variety of intensive water uses (Ibáñez and Prat, 2003). Irrigation and damming are responsible of a 30% decrease in the water discharge and reservoirs retain approximately 99% of the sediment input that partially should be deposited in the Ebro Delta, creating a severe sediment deficit (Ibáñez et al., 1996). As a result, the delta has ceased to grow, erosive processes are dominant and it has changed from progradational to a storm wave-dominated coast that is being morphological reshaped (Guillén and Palanques, 1992; Jiménez and Sánchez-Arcilla, 1993; Jiménez et al., 1997).

At different temporal scales, Somoza et al. (1998) estimated subsidence rates of approximately 1.75 mm/yr for the Ebro Delta during the last 7.0 ka, and Ibáñez et al. (1997) considered a subsidence of 2 mm/yr for the last 0.3 ka and recent subsidence rates to be 1-3.2 mm/yr. Recent research combining subsidence and sea-level rise data on the Ebro Delta coast estimate a variable RSLR ranging between 2 and 6 mm/yr (Jiménez et al., 1997), and from 4 to 6 mm/yr (Ibáñez et al., 1997).

#### *Sampling*

Carlet and Sant Jaume boreholes were drilled in 2011 in reclaimed areas of the central modern delta plain (Figure 1): X 303479/Y 4508218, about 18 km from the modern delta mouth, Z 2.33 m above national ordnance datum, 19.27 m long; and X 310438/Y 4508070, about 10.5 km from the modern delta mouth, Z 1.02 m above national ordnance datum, 21.95 m long respectively. Depths are referred always to the Spanish national ordnance datum (mean sea level at Alicante recorded between 1870-1882 CE). The boreholes did not reach the basal Pleistocene gravels, although some gravels were recovered in Carlet suggesting their proximity. They were drilled using a percussion/rotary drill that produced a core approximately 8 cm in diameter. The cores comprise alternating sands, sandy muds,

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muddy sands and muds with plant remains and mollusk-shell fragments in the muddy and sandy intervals.

**Table 3.** Radiocarbon dates from the Carlet and Sant Jaume boreholes (Ebro Delta).

Sample	Publication code	Altitude (cm)	Material	Method	Conventional C-14 age BP	$\delta^{13}\text{C}$ (‰)	Calendar calibrated age BP	2 $\sigma$ calibrated BP
Carlet-250	Beta-380015	-17	shells	AMS	2340±30	-8.7	2350	2360-2330
Carlet-261	Beta-380016	-28	shells	AMS	2230±30	-7.8	2305 2225 2205	2335-2150
Carlet-282	Beta-348511	-49	shells	AMS	3680±30	-9.2	4060 4050 3990	4140-4130 4090-3960 3950-3920
Carlet-284	Beta-380017	-51	shells	AMS	2130±30	-8.9	2120	2295-2270 2155-2035 2025-2005
Carlet-291	Beta-380018	-58	shells	AMS	3540±30	-7.7	3835	3895-3815 3800-3720
Carlet-307	Beta-348512	-74	shells	AMS	1560±30	-9.1	1410	1530-1380
Carlet-350	Beta-348513	-117	shells	AMS	2150±30	-9.6	2140	2300-2240 2180-2170 2160-2060
Carlet-377	Beta-380019	-144	shells	AMS	1600±30	-9.0	1525	1555-1410
Carlet-406	Beta-380020	-173	shells	AMS	1630±30	-8.6	1535	1570-1515 1490-1485 1460-1415
Carlet-416	Beta-348514	-183	shells	AMS	1700±30	-8.5	1600 1580 1570	1700-1540
Carlet-423	Beta-348515	-190	shells	AMS	1770±30	-8.4	1700	1770-1760 1740-1610
Carlet-440	Beta-380021	-207	shells	AMS	2540±30	-7.3	2720	2745-2695 2635-2615 2595-2500
Carlet-448	Beta-348516	-215	shells	AMS	2490±30	-7.5	2700 2640 2620 2590 2540 2530 2520	2720-2460
Carlet-611	Beta-348517	-378	wood	AMS	2000±30	-	1950	2000-1880
Carlet-1251	Beta-380023	-1018	shells	AMS	370±30	-9.4	465	505-420 405-315
Carlet-1256	Beta-348518	-1023	wood	AMS	06.3±0.3 pMC*	-	-	-
Carlet-1261	Beta-380024	-1028	shells	AMS	2670±30	-8.3	2765	2840-2825 2795-2750
Carlet-1274	Beta-354495	-1041	wood	AMS	2980±30	-	3200 26.5 3190 3160	3260-3070
Carlet-1368	Beta-380025	-1135	shells	AMS	4032±42**	-2.5	4065	4155-3930
Carlet-1405	Beta-380026	-1172	shells	AMS	4252±42**	-0.7	4385	4445-4240

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Sample	Publication code	Altitude (cm)	Material	Method	Conventional C-14 age BP	$\delta^{13}\text{C}$ (‰)	Calendar calibrated age BP	2 $\sigma$ calibrated BP
Carlet-1411	Beta-380027	-1178	shells	AMS	4062±42**	+0.2	4085	4220-3970
Carlet-1435	Beta-380028	-1202	shells	AMS	4162±42**	NA	4230	4375-4125
Carlet-1596	Beta-380030	-1363	shells	AMS	6262±50**	NA	6715	6835-6615
Carlet-1706	Beta-354496	-1473	shells	AMS	7270±50**	-1.6	7720	7830-7630
Carlet-1731	Beta-354497	-1498	shells	AMS	1710±40**	+2.1	1260	1320-1200
Carlet-1741	Beta-380031	-1508	shells	AMS	7432±42**	-1.4	7915	7965-7815
Carlet-1751	Beta-380032	-1518	shells	AMS	7402±42**	-1.3	7865	7945-7785
Carlet-1798	Beta-380033	-1565	shells	AMS	7422±50**	+1.3	7905	7970-7785
Carlet-1843	Beta-380034	-1610	shells	AMS	7502±42**	-4.0	7955	8020-7900
Carlet-1910	OS-90972	-1677	shells	AMS	7620±35**	-	7955	8043-7866
StJaume-528	Beta-354498	-426	shells	AMS	560±40**	-0.7	240	280-80 post-1950 CE
StJaume-626	Beta-354499	-524	shells	AMS	680±40**	-2.6	300	420-260
StJaume-651	Beta-354500	-549	shells	AMS	870±40**	-2.7	490	530-440
StJaume-	Beta-373725	-1026	shells	AMS	890±40**	+0.4	500	545-460
StJaume-	Beta-373726	-1159	shells	AMS	1120±40**	0.0	665	730-630
StJaume-	Beta-373727	-1415	shells	AMS	1250±40**	+2.8	780	895-700
StJaume-	Beta-373728	-1425	shells	AMS	1360±40**	+0.9	910	970-820
StJaume-	Beta-373729	-1482	shells	AMS	1310±40**	-3.0	880	925-765
StJaume-	Beta-373730	-1552	shells	AMS	1870±40**	+0.6	1400	1515-1325
StJaume-	Beta-373731	-1745	shells	AMS	1240±40**	+1.8	775	890-690
StJaume-	Beta-354501	-1751	shells	AMS	1730±40**	+2.9	1280	1340-1220
StJaume-	Beta-373732	-1847	shells	AMS	1760±40**	+0.3	1295	1370-1255

\* pMC: percent modern carbon; the material was living about the last 60 years or so.

\*\* adjusted for marine reservoir with a local deltaR correction of 120 years.

NA: sample too small to provide a  $^{13}\text{C}/^{12}\text{C}$  ratio on the original material.

### Analyses

*Foraminifera*. Samples for micropalaeontological analysis were taken along the boreholes at approximately 25 cm (Carlet) and 20 cm (Sant Jaume) intervals. They were dried in an oven at 50°C and then weighed. The target weight was 70 g per sample. Samples were wet sieved through 63-microns and 2-mm meshes in order to retain sands and gravels respectively, dried, and weighed again to determine the proportion of sand. The foraminifera were concentrated using trichloroethylene. Samples were split into fractions using a splitter and tests were picked until a representative amount of more than 300 individuals for each assemblage was obtained. Otherwise, all the available tests were picked and studied under a stereoscopic binocular microscope using reflected light. Only assemblages with more than 100 tests were used for calculations. Altogether, 143 samples were studied (Table S1), and more than 21,850 foraminifera grouped in 113 different species were identified (Appendix A).

The species were divided into deltaic and marine forms based on modern distribution and abundance of living foraminiferal assemblages in the Ebro Delta environments studied quantitatively by Scrutton (1969) and our own data (Table 1). Dead foraminiferal assemblages were also

characterised from modern samples and their results used as modern analogues for the interpretation of the fossil foraminiferal record (Table 2).

*Radiocarbon dating.* Thirty nine samples of shell fragments and three of wood were radiocarbon dated. Radiometric analyses were carried out by Beta Analytic Inc. (Miami, USA) and NOSAMS (Woods Hole, USA) using Accelerator Mass Spectrometry (AMS). The radiocarbon ages of shells were adjusted for the marine reservoir with a local  $\delta R$  correction, and conversion of all dates into calendar years was also performed using 2013 calibration databases (Reimer et al., 2013) (Table 3).

*Statistical analyses.* Fisher's alpha index was calculated for foraminiferal assemblages with >100 tests (Murray, 2006) in order to explore their diversity. Based on the alpha values, a clear boundary can be drawn between normal marine environments (alpha >5) and restricted marginal marine environments (alpha <5).

A Detrended Correspondence Analysis (DCA) was used to determine whether fossil foraminiferal assemblages were represented by the modern Ebro Delta habitats. This was done by passively plotting onto the same unconstrained ordination space modern (dead) foraminiferal samples along with borehole samples. Analyses were performed using the 'vegan' package of R (Oksanen et al., 2013).

Linear Discriminant Function (LDF) was used to statistically assign each fossil sample to the most likely modern habitat group. A total of four modern habitat groups based on cluster analyses of dead foraminiferal samples were identified in the Ebro Delta: 1) offshore, 2) nearshore and outer bays, 3) coastal lagoons and inner bays, and 4) salt and brackish marshes. LDFs estimated the probability (0–1) that borehole samples should be classified to each of the four modern habitat groups by means of discriminant functions. Relative abundances of foraminiferal data were square root transformed prior analyses to stabilize their variance. Following Kemp et al. (2012), samples with probability >0.95 are considered exclusive of one habitat group, whereas with probability <0.95 samples can be assigned to more than one group. LDFs analyses were carried out using the 'MASS' package of R (Venable and Ripley, 2002).

The Modern Analogue Technique (MAT) was used to test the reliability of the palaeowater depth reconstructions based on the transfer function developed by the authors. This technique evaluates the degree of similarity (or dissimilarity) in the foraminiferal assemblages between each fossil sample and the modern ones. The squared chord distance (SCD) was used as dissimilarity coefficient. By using the largest dissimilarity coefficient among all modern foraminiferal samples as a critical threshold (Woodroffe, 2009) we identified fossil samples with close modern analogues. Samples with  $SCD \leq 0.271$  were considered similar. MAT analyses were calculated using the 'analogue' package of R (Simpson and Oksanen, 2014).



*Chapter 3: Holocene Ebro Delta evolution***Results**

Based on general sedimentological features (sand content), foraminiferal test abundance, and species diversity and dominance, the microfossil assemblages present in the two boreholes can be divided into different depth intervals (DIs). Table 4 and Figures 2 and 3 summarize the main borehole and microfaunal data. Interpretation of these DIs in terms of different habitats or subenvironments that evolved through time in this central area of the Ebro Delta is based on a palaeowater-depth transfer function developed by the authors which compares these buried Holocene assemblages with dead foraminiferal-assemblages composition in various settings of the modern delta obtained previously by Scrutton (1969) and our own data (Table 2 and Figure 4).

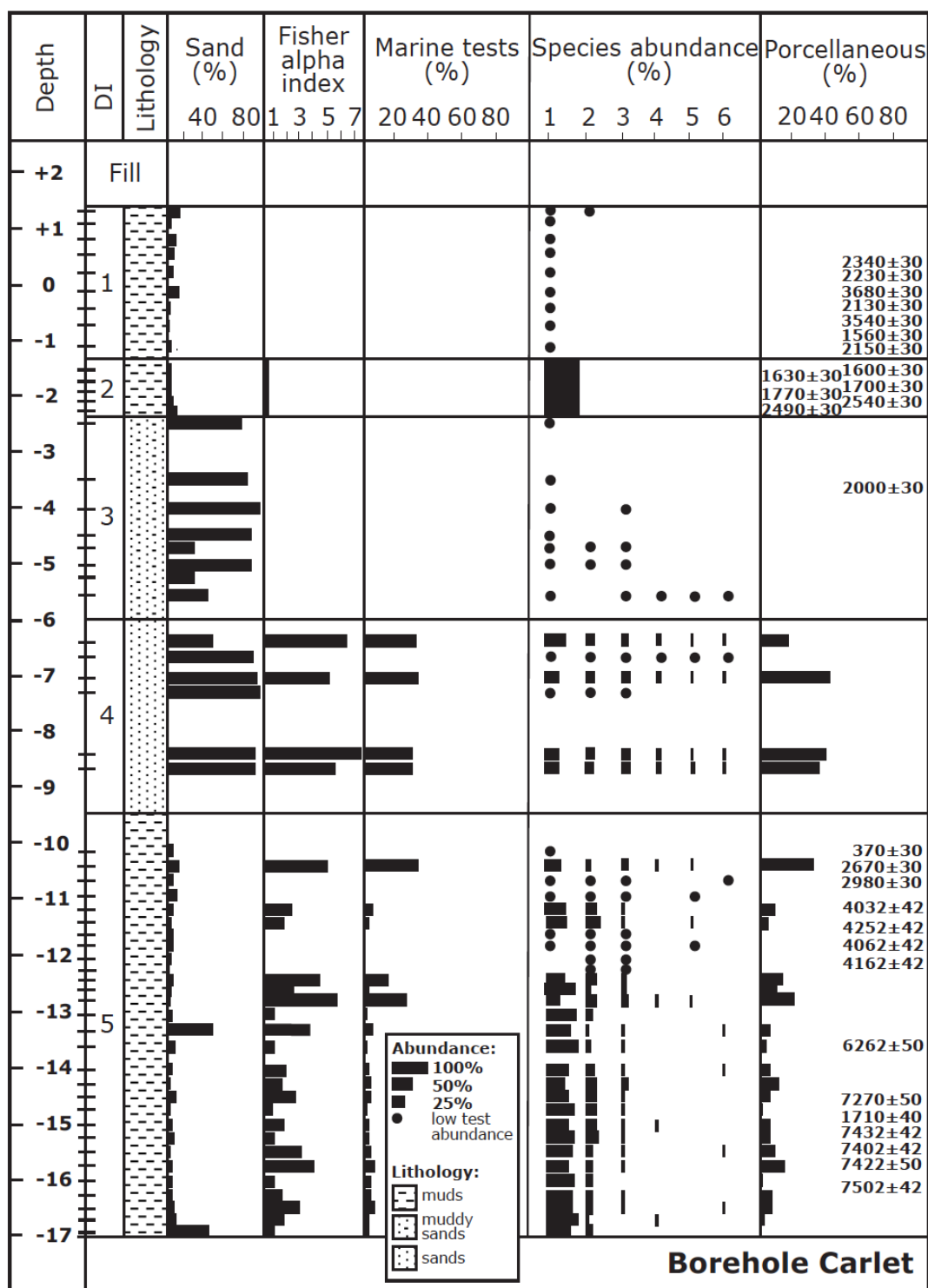
**Table 1.** Living foraminiferal species found in and off the Ebro Delta. Above: Quantitative summary of living foraminiferal assemblages composition in different environmental settings of the modern Ebro Delta. Figures represent relative abundance (%) unless otherwise indicated. The single value represents the average and those in parentheses give the range; Below: Reference list of marine species found in the modern foraminiferal assemblages of the Ebro Delta.

Living assemblages (own data)					
<i>Phragmites</i> marsh	<i>Juncus</i> marsh	<i>Salicornia</i> marsh	Lagoon	Inner bay	Nearshore
9 samples	7 samples	10 samples	12 samples	6 samples	2 samples
141 (65-197) standing crop (10 cm <sup>3</sup> )	150 (65-197) standing crop (10 cm <sup>3</sup> )	117 (71-201) standing crop (10 cm <sup>3</sup> )	133 (69-222) standing crop (10 cm <sup>3</sup> )	217 (197-236) standing crop (10 cm <sup>3</sup> )	196 (186-205) standing crop (10 cm <sup>3</sup> )
5 (2-9) species	6 (4-7) species	5 (2-7) species	7 (4-12) species	9 (5-14) species	23 (20-26) species
1 (0.3-0.9) Fisher alpha index	1 (0.7-1.3) Fisher alpha index	1 (0.3-1.5) Fisher alpha index	1.5 (0.7-2.4) Fisher alpha index	1.8 (0.9-3) Fisher alpha index	5.9 (4.8-7) Fisher alpha index
86.2 (48-100) agglutinated	25.6 (7-91) agglutinated	51 (0.9-100) agglutinated	1.7 (0-8.6) agglutinated	0.2 (0-1.5) agglutinated	0.8 (0.4-1.3) agglutinated
0.4 (0-2) porcellaneous	1.3 (0-5.4) porcellaneous	1.6 (0-5.2) porcellaneous	1.7 (0-12.4) porcellaneous	9.2 (0.3-17.6) porcellaneous	14.8 (12.8-16.8) porcellaneous
13.4 (0-50.1) hyaline	73.1 (9-93) hyaline	47.4 (0-99.1) hyaline	96.6 (87.4-100) hyaline	90.5 (82.4-99.7) hyaline	84.4 (82.8-86) hyaline
<i>T. inflata</i> 43.3 (0-88)	<i>T. aguayoi</i> 39.9 (4-79.3)	<i>A. beccarii</i> 30.8 (0-90.6)	<i>A. beccarii</i> 56 (10.8-87.4)	<i>A. beccarii</i> 68.7 (33.2-96.4)	<i>A. beccarii</i> 27.8 (19.7-36)
<i>H. wilberti</i> 23.3 (8.1-60.4)	<i>A. beccarii</i> 33 (2.3-86.2)	<i>J. macrescens</i> 28.3 (0-61.4)	<i>H. germanica</i> 21.7 (3.6-66.2)	<i>H. germanica</i> 12.6 (0.6-24.9)	<i>Q. telligera</i> 12.6 (10.8-14.4)
<i>M. fusca</i> 11.9 (0-87.0)	<i>T. inflata</i> 18.4 (2.2-68)	<i>T. inflata</i> 22.5 (0.9-57.9)	<i>C. oceanensis</i> 9.5 (0-48.6)	<i>Q. jugosa</i> 4.4 (0-10.8)	<i>B. striatula</i> 10.1 (1.4-18.8)
<i>T. aguayoi</i> 10.1 (0-36)	<i>J. macrescens</i> 4.2 (0-18.4)	<i>H. germanica</i> 13.5 (0-84.6)	<i>C. excavatum</i> 4 (0-22.4)	<i>Q. seminula</i> 3.7 (0-7.5)	<i>B. pseudopunctata</i> 9.4 (5.7-13)
<i>J. macrescens</i> 4.9 (0-18.4)	<i>M. fusca</i> 2.3 (0-12)	<i>T. aguayoi</i> 2.9 (0-14.5)	<i>C. selseyense</i> 3 (0-14.8)	79.3 (57.3-95.5) similarity L/D	<i>N. opima</i> 8.7 (5.1-12.3)
<i>A. beccarii</i> 3.4 (0-29.1)	73.8 (36.4-95.5) similarity L/D	73.3 (53-94.4) similarity L/D	75.7 (52.6-91) similarity L/D		<i>H. depressula</i> 6.5 (3.5-9.5)
69.2 (31.8-87) similarity L/D					<i>A. mamilla</i> 1.3 (0.7-1.9)
					<i>R. irregularis</i> 0.9 (0.3-1.4)
					59.1 (57.1-61.1) similarity L/D
List of marine species (Scrutton (1969) and own data)					
<i>Adelosina laevigata</i>	<i>Cassidulina laevigata</i>	<i>Fursenkoina</i> cf <i>fusiformis</i>	<i>Massilina secans</i>	<i>Quinqueloculina longirostra</i>	<i>Textularia bocki</i>
<i>Ammobaculites</i> cf <i>arenaria</i>	<i>Cibicidoides bradyi</i>	<i>Fursenkoina</i> cf <i>complanata</i>	<i>Melonis pompilioides</i>	<i>Quinqueloculina rugosa</i>	<i>Textularia calva</i>
<i>Ammosphaeroidina sphaeroidiniforme</i>	<i>Clavulina obscura</i>	<i>Fursenkoina schreibersiana</i>	<i>Nodulina dentaliniformis</i>	<i>Quinqueloculina</i> sp.1	<i>Textularia tenuissima</i>
<i>Amphicoryna scalaris</i>	<i>Cornuspira incerta</i>	<i>Fursenkoina</i> sp.1	<i>Nonion asterizans</i>	<i>Rectuvigerina</i> cf <i>compressa</i>	<i>Textularia</i> sp.1
<i>Asterigerinata</i> sp.1	<i>Delosina complexa</i>	<i>Gaudryina</i> cf <i>rudis</i>	<i>Nonion laevigatum</i>	<i>Reophax</i> cf <i>fusiformis</i>	<i>Tretomphalus concinnus</i>
<i>Aubignyina perlucida</i>	<i>Eggerella advena</i>	<i>Gavelinopsis praegeri</i>	<i>Nonionella atlantica</i>	<i>Reophax cylindrica</i>	<i>Trifarina angulosa</i>
<i>Brizalina</i> cf <i>aenariensis</i>	<i>Elphidium advenum</i>	<i>Haplophragmoides canariensis</i>	<i>Nonionoides</i> cf <i>japonicum</i>	<i>Reophax nana</i>	<i>Triloculina dubia</i>
<i>Brizalina spathulata</i>	<i>Elphidium</i> cf <i>flexuosum</i>	<i>Haynesina depressula</i>	<i>Nonionoides scaphus</i>	<i>Reophax scorpiurus</i>	<i>Triloculina marioni</i>
<i>Brizalina variabilis</i>	<i>Elphidium</i> cf <i>schmitti</i>	<i>Hopkinsina pacifica</i>	<i>Nouria polymorphides</i>	<i>Reophax subfusiformis</i>	<i>Triloculina rotunda</i>
<i>Buccella granulata</i>	<i>Elphidium crispum</i>	<i>Lagena</i> cf <i>semistriata</i>	<i>Patellina corrugata</i>	<i>Reussella aculeata</i>	<i>Triloculina</i> sp.1
<i>Bulimina aculeata</i>	<i>Elphidium incertum</i>	<i>Lagena substriata</i>	<i>Planorbulina mediterraneensis</i>	<i>Robertina arctica</i>	<i>Trochammina</i> cf <i>advena</i>
<i>Bulimina elongata</i>	<i>Elphidium lidoense</i>	<i>Lagena sulcata</i>	<i>Poroepionides lateralis</i>	<i>Rosalina anomala</i>	<i>Trochammina lobata</i>
<i>Bulimina gibba</i>	<i>Elphidium matagordanum</i>	<i>Lagena tenuis</i>	<i>Procerolagena clavata</i>	<i>Rosalina bulbosa</i>	<i>Uvigerina</i> sp.1
<i>Bulimina marginata</i>	<i>Elphidium</i> sp.1	<i>Lagena vulgaris</i>	<i>Psammospaera bowmani</i>	<i>Rosalina</i> cf <i>mediterraneensis</i>	<i>Valvulineria bradyana</i>
<i>Bulimina</i> sp. 1	<i>Elphidium</i> sp.2	<i>Lagenammina difflugiformis</i>	<i>Pyrgo inornata</i>	<i>Rosalina</i> cf <i>valvulata</i>	
<i>Buliminella elegantissima</i>	<i>Epistominella vitrea</i>	<i>Lagenammina laguncula</i>	<i>Quinqueloculina depressa</i>	<i>Saccammina atlantica</i>	
<i>Cassidulina</i> cf <i>crassa</i>	<i>Fissurina</i> sp.1	<i>Leptohalysis scottii</i>	<i>Quinqueloculina lata</i>	<i>Svratkina</i> sp.1	

**Table 2.** Dead foraminiferal species found in and off the Ebro Delta. Quantitative summary of dead foraminiferal assemblages composition in different environmental settings of the modern Ebro Delta. Figures represent relative abundance (%) unless otherwise indicated. The single value represents the average and those in parentheses give the range.

Dead assemblages (own data)					
<i>Phragmites</i> marsh	<i>Juncus</i> marsh	<i>Salicornia</i> marsh	Lagoon	Inner bay	Nearshore
13 samples	9 samples	18 samples	18 samples	6 samples	2 samples
Water depth 0.1 (0.05-0.2) m	Water depth 0.1 (0.07-0.4) m	Water depth 0.2 (0.04-0.5) m	Water depth 0.5 (0.3-0.8) m	Water depth 0.3 (0.2-0.5) m	Water depth 7 (7-7.4) m
Sand 33 (7-66)	Sand 82 (74-94)	Sand 58 (5-81)	Sand 67 (9-92)	Sand 81 (69-92)	Sand 19 (19)
8 (5-10) species	8 (5-16) species	9 (5-15) species	7 (2-11) species	11 (8-16) species	34 (30-38) species
Fisher alpha index 1.8 (0.8-3.6)	Fisher alpha index 1.6 (0.8-3.5)	Fisher alpha index 1.9 (0.8-4.6)	Fisher alpha index 1.2 (0.3-2.1)	Fisher alpha index 2.2 (1.5-3.3)	Fisher alpha index 9 (7.4-10.7)
7 (0-50) marine tests	1 (0-7) marine tests	3 (0-13) marine tests	1 (0-6) marine tests	3 (1-6) marine tests	60 (57-62) marine tests
58 (1-99.5) agglutinated	30 (2-93) agglutinated	29 (0-94) agglutinated	0.6 (0-3) agglutinated	0.4 (0-0.9) agglutinated	4 (2-6) agglutinated
0.1 (0-0.8) porcellaneous	1 (0-5) porcellaneous	4 (0-28) porcellaneous	0.4 (0-3) porcellaneous	12 (3-22) porcellaneous	22 (22) porcellaneous
42 (0.5-99) hyaline	69 (8-98) hyaline	67 (6-99) hyaline	99 (97-100) hyaline	88 (78-97) hyaline	74 (72-77) hyaline
<i>A. beccarii</i> 27.1 (0-92.5)	<i>A. beccarii</i> 34.6 (2.2-84.6)	<i>A. beccarii</i> 45 (2-92.2)	<i>A. beccarii</i> 51.5 (16.9-85.7)	<i>A. beccarii</i> 77.8 (62.2-92.9)	<i>A. beccarii</i> 32.1 (26.9-37.4)
<i>H. wilberti</i> 23.5 (1-78.5)	<i>T. aguayoi</i> 32.8 (2.6-75.5)	<i>J. macrescens</i> 20.7 (0-70.9)	<i>H. germanica</i> 27.9 (5.3-59.3)	<i>Q. jugosa</i> 6 (0.9-12.7)	<i>Q. stelligera</i> 15.1 (14.8-15.4)
<i>T. inflata</i> 19.3 (0-60.1)	<i>T. inflata</i> 21.2 (0.6-70.3)	<i>H. germanica</i> 15.8 (0.3-62.8)	<i>C. oceanensis</i> 10.7 (0-32.9)	<i>H. germanica</i> 5.1 (2.8-7.4)	<i>H. depressula</i> 12.7 (11.8-13.7)
<i>M. fusca</i> 7.5 (0-80.8)	<i>J. macrescens</i> 4 (0-17.2)	<i>T. inflata</i> 7 (0-23.9)	<i>C. excavatum</i> 6.1 (0-28.7)	<i>Q. seminula</i> 5 (0.9-11.4)	<i>A. mamilla</i> 4.7 (3.4-6)
<i>H. germanica</i> 5.4 (0-36.5)	<i>H. wilberti</i> 3.8 (0-17.8)	<i>T. aguayoi</i> 3.1 (0-28.7)			<i>A. perlucida</i> 3.6 (2.5-4.8)
<i>J. macrescens</i> 4 (0-11.9)		<i>Q. seminula</i> 2.7 (0-20.9)			<i>B. pseudopunctata</i> 3.6 (2.5-4.8)
<i>T. aguayoi</i> 3.4 (0-15.8)					<i>Q. seminula</i> 3.6 (3.6)
					<i>R. irregularis</i> 2.8 (1.7-3.8)
Dead assemblages (Scrutton, 1969)					
Lagoon	Lake ("Bay")	Transition	Deltaic marine	Inner shelf	Outer shelf
2 samples	9 samples	3 samples	5 samples	15 samples	17 samples
Water depth 1 (1-1.5) m	Water depth 5.5 (2.5-9) m	Water depth 8 (6-11) m	Water depth 29 (7-51) m	Water depth 9 (3-17) m	Water depth 23 (5-50) m
Sand 37 (13-60)	Sand 23 (4-59)	Sand 12 (5-25)	Sand 4 (1-6)	Sand 59 (4-100)	Sand 15 (1-97)
3 (3-4) species	27 (16-41) species	29 (27-30) species	31 (19-40) species	32 (20-49) species	41 (22-56) species
42 (33-50) marine tests	72 (56-82) marine tests	58 (52-63) marine tests	74 (68-81) marine tests	68 (60-78) marine tests	67 (59-73) marine tests
15 (5-24) agglutinated	6 (1-13) agglutinated	9 (5-12) agglutinated	16 (3-21) agglutinated	8 (2-15) agglutinated	15 (5-24) agglutinated
20 (5-53) porcellaneous	43 (10-69) porcellaneous	29 (5-58) porcellaneous	12 (5-25) porcellaneous	42 (16-42) porcellaneous	20 (5-53) porcellaneous
65 (37-83) hyaline	51 (28-79) hyaline	62 (37-83) hyaline	72 (54-84) hyaline	50 (35-73) hyaline	65 (37-83) hyaline
<i>A. beccarii</i> 48 (36-60)	<i>A. beccarii</i> 21.9 (0-46)	<i>Q. stelligera</i> 10.5 (0.7-28.2)	<i>A. beccarii</i> 16.5 (0.7-64.4)	<i>Q. stelligera</i> 23.8 (1.1-62.5)	<i>A. beccarii</i> 8.5 (1.7-25.2)
<i>H. germanica</i> 43.5 (30.4-56.6)	<i>Q. stelligera</i> 9.7 (0-24.9)	<i>A. beccarii</i> 9.7 (6.9-11.1)	<i>E. scaber</i> 6.7 (2.7-11.5)	<i>A. beccarii</i> 15.1 (6.3-26.8)	<i>Q. stelligera</i> 6.1 (0-36.4)
	<i>T. rotunda</i> 5.7 (0-22.8)	<i>Asterigerinata</i> sp.1 9.1 (1.4-22)	<i>V. complanata</i> 6 (0.7-21.9)	<i>Asterigerinata</i> sp.1 8.2 (1.6-30)	<i>N. opima</i> 5.3 (0-13.3)
	<i>E. scaber</i> 5.4 (0-12)	<i>E. advenum</i> 8.3 (5.3-13.2)	<i>B. aculeata</i> 5.5 (0-10.8)	<i>N. depressulus</i> 5.6 (1.5-10.2)	Miliolid 13 (3.4-34)
	Miliolid 23.2 (0.8-40.2)	<i>Elphidium</i> sp.1 5.9 (1.4-11.1)	<i>N. opima</i> 5.3 (0-10.5)	<i>E. scaber</i> 5.2 (0-17.5)	
		Miliolid 15.3 (1.0-24.4)	Miliolid 8.3 (2.4-18.5)	<i>E. lidoense</i> 5.1 (0-14.4)	
				Miliolid 21.8 (13.6-38.5)	

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**Figure 2.** Sedimentary sequence, sand content, general micropalaeontological data, distribution and relative abundance of the main foraminiferal species (1: *A. beccarii*; 2: *C. selseyense*; 3: *Q. seminula*; 4: *R. anomala*; 5: *T. marioni*; 6: *C. lobatulus*), and porcellaneous wall type content with depth (m) in the borehole Carlet (Ebro Delta). Foraminiferal depth intervals (DIs), radiocarbon dates (conventional years BP) and sample levels are also indicated. Black dots indicate presence of the species in assemblages with less than 100 foraminiferal tests.

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In the Carlet borehole, DI5 at the base with at least 7.5 m of muds is characterized by an assemblage highly dominated by *Ammonia beccarii* (average 74%) and *Criboelphidium selseyense* (13%) with minor *Quinqueloculina seminula* (4%). The number of species is moderate (average 10), and the contents of marine and porcellaneous tests are low (average 7% and 8% respectively). Comparison with modern assemblages suggests a lagoonal or shallow inner bay environment (0.5-1.5 m depth) for this interval that developed during a long time lapse from 7600 to 2600 yr BP. Above, DI4 is made of 3.5 m of sands with irregular abundance of foraminifera, and a high number of species (21), marine tests (34%) and porcellaneous forms (35%). Assemblages are composed mainly by *A. beccarii* (36%), *Q. seminula* (18%) and *C. selseyense* (13%) with secondary *Rosalina anomala* (6%), *Triloculina marioni* (6%) and *Cibicides lobatulus* (4%). All these features indicate a sandy environment with a mixture of deltaic (inshore) and marine (offshore) species similar to a beach or back-barrier setting around the deltaic fringe. The transfer function did not find a close modern analogue for the assemblages in this interval although indicated very shallow palaeowater depths (c. 0–1 m). No date has been obtained in this DI4 but comparison with radiocarbon dates from the below and above intervals suggests its development after 2600 and before 2000 yr BP, and the consequent presence of the coastline close to this location around that time. The following 3.7 m of muddy sands (DI3) contain very scarce foraminiferal tests and could indicate the shift to a higher elevation and less flooded habitat (alluvial environment closer to the river levee) in the area of Carlet around 2000 yr BP. These new conditions suggest the presence of a fresh to brackish marsh environment (less than 0.5 m depth) at about 1700 yr BP that deposited 1 m of muddy sediments (DI2) characterized exclusively by an abundant *A. beccarii* assemblage. The presence of terrestrial gastropods and oogonia of characeae algae is indicative of very low salinity conditions in this area. Finally, DI1 with 2.7 m of muds presents also terrestrial gastropods and characeae oogonia but the foraminiferal content is very scarce (only few tests of *A. beccarii*) suggesting a lacustrine environment. Radiocarbon dates show a great variety of ages and inverted dates. This reinforces the idea that during the last 2.0 ka (DI2-1) this area was a fresh to brackish aquatic environment located close to the river and thus with a relatively high elevation and occasional marine flooding conditions.

On the other hand, the Sant Jaume borehole shows much more recent and deeper materials than the Carlet borehole. The lower part of the sequence initiates with DI5 and more than 3 m of muds containing an irregular abundance of foraminifera characterized by a high number of species (22), marine tests (43%) and porcellaneous forms (24%). The assemblage is composed mainly by *C. selseyense* (18%), *A. beccarii* (13%) and *Q. seminula* (11%), together with *Criboelphidium poeyanum* (6%), *Brizalina variabilis* (5%), *Bulimina gibba* (4%), *Valvulineria bradyana* (3%) and *Rosalina irregularis* (3%). A radiocarbon date of 1760 yr BP for the upper part of this interval indicates that in this period the sediment was accumulated in the nearshore environment (around 7 m depth). The following unit (DI4) is represented by 6.3 m of muddy sediment deposited in an inshore



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more proximal setting (lagoon or shallow inner bay environment; 0.5-1.5 m depth) dominated by *A. beccarii* (65%) and *C. selseyense* (19%) with *Q. seminula* (3%) and *C. poeyanum* (3%). The number of species is moderate (13) and the marine tests (8%) and porcellaneous content (5%) are low. This interval developed between 1700 and 1100 yr BP. Above, 3.4 m of sandy muds with an irregular abundance of foraminiferal tests exhibit an increase in the number of species (18), and marine (34%) and porcellaneous (16%) tests (DI3). An assemblage made of *A. beccarii* (38%), *C. selseyense* (18%) and *Asterigerinata mamilla* (11%) with minor *Quinqueloculina oblonga* (3%), *Q. seminula* (3%) and *Haynesina germanica* (3%) suggests a sandier nearshore habitat (about 7 m depth) developed around 1.0 ka ago. The following interval DI2 (4 m of muds) shows a decrease in the open marine influence (15% marine tests and 5% porcellaneous forms), a moderate number of species (14) and the dominance of more deltaic (inshore) forms as *A. beccarii* (52%), *H. germanica* (11%), *Criboelphidium oceanensis* (11%) and *C. selseyense* (8%) with *B. variabilis* (6%). These features are indicative of a lagoonal or shallow inner bay environment (0.5-1.5 m depth) developed in this area between 900-600 yr BP. The final 3.3 m of sandy muds (DI1) are younger than 0.5 ka, contain few foraminiferal tests (*A. beccarii*, *H. germanica* and *C. selseyense*) and could represent an emerged fresh-water environment with occasional marine flooding located in a delta plain.

**Table 4.** Summary of core and microfaunal data from the Carlet and Sant Jaume boreholes (Ebro Delta). Figures represent relative abundance (%) unless otherwise indicated. The single value represents the average and those in parentheses give the range.

Carlet	Sant Jaume
DI 1	DI 1
Elevational range +1.44-1.29 m	Elevational range 0.73-4.04 m
Thickness 2.73 m	Thickness 3.31 m
Sand 9 (0.9-16.8)	Sand 17.3 (0.1-98.2)
Radiocarbon age 1560±30, 2130±30, 2150±30, 2230±30, 2340±30, 3540±30, 3680±30 BP	Age < 500 BP
Few tests of <i>A. beccarii</i>	Few foraminifera
Terrestrial gastropods	
Oogonia of Characeae algae	
DI 2	DI 2
Elevational range 1.29-2.27 m	Elevational range 4.04-8.16 m
Thickness 0.98 m	Thickness 4.12 m
Sand 3 (0.4-10.6)	Sand 1 (0.1-5.3)
Radiocarbon age 1600±30, 1630±30, 1700±30, 1770±30, 2490±30, 2540±30 BP	Radiocarbon age 560±40, 680±40, 870±40 BP
Very abundant tests	Very abundant tests
1 (1-2) species	14 (6-28) species
Fisher alpha index 0.2 (0.1-0.3)	Fisher alpha index 3 (1.2-6.8)
0 (0-0) marine tests	15 (0.6-52.5) marine tests
0 (0-0) agglutinated	0.1 (0-0.9) agglutinated
0 (0-0) porcellaneous	5 (0.5-20.9) porcellaneous
	95 (78.7-99.5) hyaline

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Carlet	Sant Jaume
100 (100-100) hyaline	<i>A. beccarii</i> 52 (27.3-67.7)
<i>A. beccarii</i> 99 (94.9-100)	<i>H. germanica</i> 11 (0.4-40)
Terrestrial gastropods	<i>C. oceanensis</i> 11 (0-48.1)
Oogonia of Characeae algae	<i>C. selseyense</i> 8 (0-21)
	<i>B. variabilis</i> 6 (0-20.7)
DI 3	DI 3
Elevational range 2.27-5.94 m	Elevational range 8.16-11.56 m
Thickness 3.67 m	Thickness 3.4 m
Sand 67 (28.1-98.2)	Sand 10 (0.1-80.1)
Radiocarbon age 2000±30 BP	Radiocarbon age 890±40 BP
Few foraminifera	Irregular abundance of tests
	18 (10-28) species
	Fisher alpha index 4.6 (1.4-7.9)
	34 (3.8-60.1) marine tests
	0.5 (0-2.3) agglutinated
	16 (1.2-32.6) porcellaneous
	84 (65.1-98.8) hyaline
	<i>A. beccarii</i> 38 (11.6-74.9)
	<i>C. selseyense</i> 18 (3.1-72.4)
	<i>A. mamilla</i> 11 (0-36.7)
	<i>Q. oblonga</i> 3 (0-11.9)
	<i>Q. seminula</i> 3 (0-10.7)
	<i>H. germanica</i> 3 (0.4-7.8)
DI 4	DI 4
Elevational range 5.94-9.48 m	Elevational range 11.56-17.81 m
Thickness 3.54 m	Thickness 6.25 m
Sand 86 (47.7-95.6)	Sand 1 (0.3-2.5)
Irregular abundance of tests	Radiocarbon age 1120±40, 1240±40, 1250±40,
21 (17-24) species	1310±40, 1360±40, 1730±40 1870±40 BP
Fisher alpha index 6.1 (5.6-7.7)	Irregular abundance in the upper 2.7 m
34 (32-37.1) marine tests	13 (4-22) species
0.7 (0-1.4) agglutinated	Fisher alpha index 3.3 (1-5.8)
35 (18.7-41.6) porcellaneous	8 (0-17.7) marine tests
65 (58-79.9) hyaline	0.3 (0-1.8) agglutinated
<i>A. beccarii</i> 36 (31.5-41.5)	5 (1-10.7) porcellaneous
<i>Q. seminula</i> 18 (9.5-21.1)	95 (89.3-99) hyaline
<i>C. selseyense</i> 13 (10-16)	<i>A. beccarii</i> 65 (40.2-92.4)
<i>R. anomala</i> 6 (1.6-9.2)	<i>C. selseyense</i> 19 (2.3-35.9)
<i>T. marioni</i> 6 (2-11.9)	<i>Q. seminula</i> 3 (0-9.2)
<i>C. lobatulus</i> 4 (3.1-5.6)	<i>C. poeyanum</i> 3 (0-7.7)
DI 5	DI 5
Elevational range 9.48-16.94 m	Elevational range 17.81-20.93 m
Thickness 7.54 m	Thickness 3.12 m
Sand 7 (0.4-52.2)	Sand 5 (0.2-19.1)
Radiocarbon age 370±30, 1710±40, 2670±30,	Radiocarbon age 1760±40 BP
2980±30, 4032±42, 4062±42, 4162±42,	Irregular abundance of tests
4252±42, 6262±50, 7270±50, 7402±42,	22 (10-35) species
7422±50, 7432±42, 7502±42, 7620±35 BP	Fisher alpha index 7.6 (2.4-12.4)
Irregular abundance in the upper 2.7 m	43 (26.5-69.5) marine tests
10 (4-17) species	1 (0-6.5) agglutinated
Fisher alpha index 2.4 (0.8-5.8)	24 (3.4-38.9) porcellaneous



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Carlet	Sant Jaume
7 (0.3-37.5) marine tests	75 (61.1-96.6) hyaline
0.1 (0-1.2) agglutinated	<i>C. selseyense</i> 18 (0-47.4)
8 (0-36.5) porcellaneous	<i>A. beccarii</i> 13 (4.5-22.2)
92 (63.5-100) hyaline	<i>Q. seminula</i> 11 (2-25.2)
<i>A. beccarii</i> 74 (29.9-97.3)	<i>C. poeyanum</i> 6 (0-22.1)
<i>C. selseyense</i> 13 (0.3-35.4)	<i>B. variabilis</i> 5 (0-13.4)
<i>Q. seminula</i> 4 (0-14.6)	<i>B. gibba</i> 4 (0-10.7)
	<i>V. bradyana</i> 3 (0-17.3)
	<i>R. irregularis</i> 3 (0-13.4)

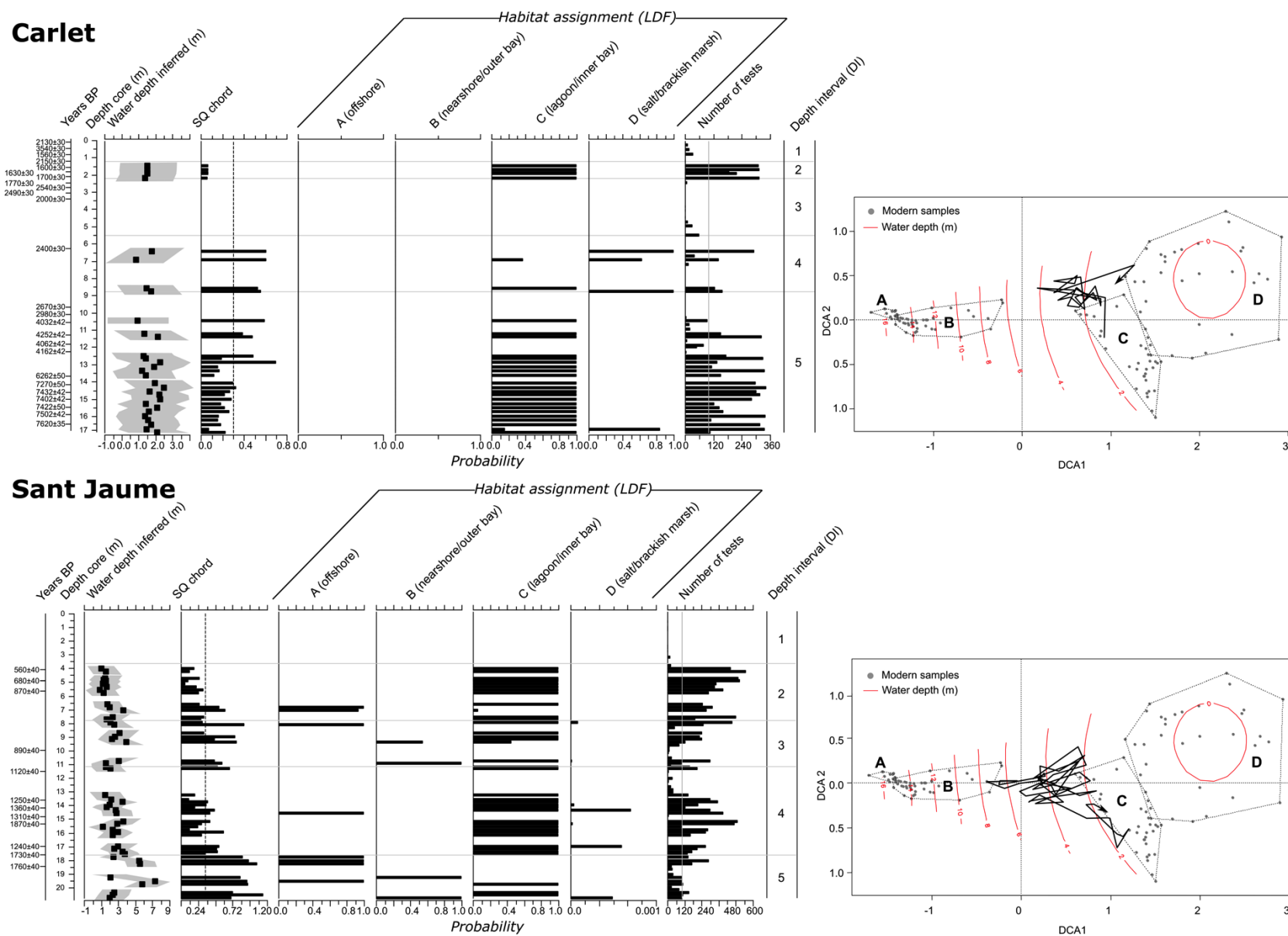
**Discussion**

*Palaeoenvironmental evolution of the Ebro Delta*

Comparison of materials, microfossil assemblages, radiocarbon ages and palaeoenvironmental evolution between both boreholes clearly indicates that sandier, older and more continental conditions are characteristic of the more landward Carlet sedimentary sequence, whereas the Sant Jaume geological record exhibits muddier, younger and more marine environmental conditions characteristic of a more seaward setting within the Holocene architecture of the Ebro Delta. These distinctive stratigraphic and foraminiferal sequences with an older and more proximal progradational record on one side and a younger and more distal progradational record on the other side is also found in other Mediterranean deltas such as the Rhône (France) and Po (Italy) (Amorosi et al., 2005, 2013; Boyer et al., 2005; Rossi and Vaiani, 2008; Dinelli et al., 2012). However, the interpretation of the environments in some cases is different when compared to the present study due to the fact that here a wider range of foraminiferal assemblages, including open marine and delta plain environments, is considered (see discussion on this topic in the following section).

The palaeoenvironmental interpretation of the sedimentary sequences in the Carlet and Sant Jaume boreholes based on diagnostic foraminiferal assemblages is shown in Figure 5. At Carlet, apart of the lowermost part of DI5 deposited before 7.0 ka during TST under sea-level rise conditions, the muddy interval DI5 at the base and sandy DI4 are interpreted mainly as part of a sequence made of inner bay-lagoonal-beach deposits in this central area under sea-level highstand conditions between 7000 and ~2000 yr BP. Then, further sediment accumulation led to the formation of a series of non-marine deposits represented during the last 2.0 ka initially represented by continental sands in DI3. It was followed by an occasionally marine flooded and very-low-salinity marsh environment at about 1700 yr BP (DI2) that was finally replaced by a fresh-water muddy environment (higher elevation, closer to the river levee) containing a mixture of materials with variable radiocarbon ages (DI1).

Comparison of the Carlet results with the previous ITGE-6 borehole sequence of Somoza et al. (1998) indicates in our record the partial absence of the most basal terms of the Holocene sequence deposited under rapid sea-level rise conditions (TST) (Figure 5). There are similarities but also



**Figure 4.** Reconstruction of palaeowater-depth (associated errors as grey envelope) and different environmental settings through time in the Carlet and Sant Jaume boreholes (Ebro Delta) based on the transfer function developed by the authors. Habitat assignments using Linear Discriminant Functions (LDFs) are also shown. The foraminiferal depth intervals (DIs), number of tests and radiocarbon dates (conventional years BP) are also indicated. On the right, core trajectories projected onto DCA along with modern (dead) foraminiferal assemblages are shown. Dashed lines in DCA plots encompass modern habitat samples of each habitat type identified in the Ebro Delta: A) offshore; B) nearshore and outer bays, C) coastal lagoons and inner bays; and D) salt and brackish marshes. Water depth (m) intervals are marked for each DCA plot.

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important quantitative and qualitative differences between both records in terms of palaeoenvironmental reconstruction and temporal control of events. The lower part of our muddy DI5 interval (deposited between 7.6 and 7.0 ka) could be assimilated to the muddy aggradational (a1) unit of ITGE-6 (deposited as the transgressive wedge h1 before 7.0 ka) and represents the final record of the TST. After the MFS suggested by Somoza and Rodríguez-Santalla (2014) to occur around 6900 yr BP, the rest of muddy DI5 and sandy DI4 intervals (deposited between 6.9 and 2.5 ka) could be assimilated to the sandy units d1 and d2 (delta front/nearshore) of ITGE-6 (deposited between 6.1 and 3.6 ka under sea-level highstand conditions). Then, the identification of a series of delta-plain deposits (sandy and muddy intervals DI3-DI1) during the last 2.5 ka in Carlet very likely correspond to the sandy and silty d3 and d4 delta-plain units considered younger than 2.7 ka in the ITGE-6 sequence. However, the information given by the foraminiferal assemblages in our study (absent in the work by Somoza et al., 1998) suggests that the maximum of the Holocene marine transgression did not reach the inner part of the Ebro Delta as open sea but rather via lagoon and/or shallow bay development. This is an important difference with the interpretation provided by Somoza et al. (1998) in relation to the existence of a transgressive wedge (h1) with marine clayey sediments corresponding to the maximum flooding surface (MFS). Our results clearly show the existence of restricted and brackish environments, which is more compatible with the presence of fresh-water peat deposits in the innermost part of the delta during that time (Solé et al., 1961; Arasa, 1994), since fresh-water peat cannot form during high-salinity conditions. This reasoning also applies to the other highstand sea-level events (h2, h3, h4) postulated by Somoza et al. (1998) in the innermost part of the delta (upstream the city of Amposta, in the alluvial valley) and next to the Ebro River, in which each period of fresh-water peat accumulation would coincide with the presence of the salt-water conditions. We do not find any evidence for this interpretation and an alternative explanation is a succession of fresh-water peat deposits and alluvial or lagoonal deposits as a function of the changing distance of the borehole location to the Ebro River through time (due to migration of the river course), as well as changes in the frequency and magnitude of river floods.

This alternance of peat and alluvial or lagoonal clay deposits is also found in the innermost part of other large Mediterranean deltas. In the Po delta plain, Amorosi et al. (2005) describe a similar sequence in the innermost boreholes (204-S17, 204-S5, 204-S6) with the presence of peat layers in the middle of fresh-water (swamp) clays or brackish-water (lagoonal) clays, whereas the marine (bay) clays are only found in the outermost boreholes (204-S7, 205-S5) and never coinciding with peat layers. This study also included the analysis of microfossils (foraminifera and ostracoda) and similar foraminiferal assemblages (Ba-Bd) with few species that were interpreted as low-energy brackish-water back-barrier environments. In the Rhône Delta, Boyer et al. (2005) also describe the presence of clay (including layers of alluvial sand) with brackish to fresh-water fauna in the innermost boreholes

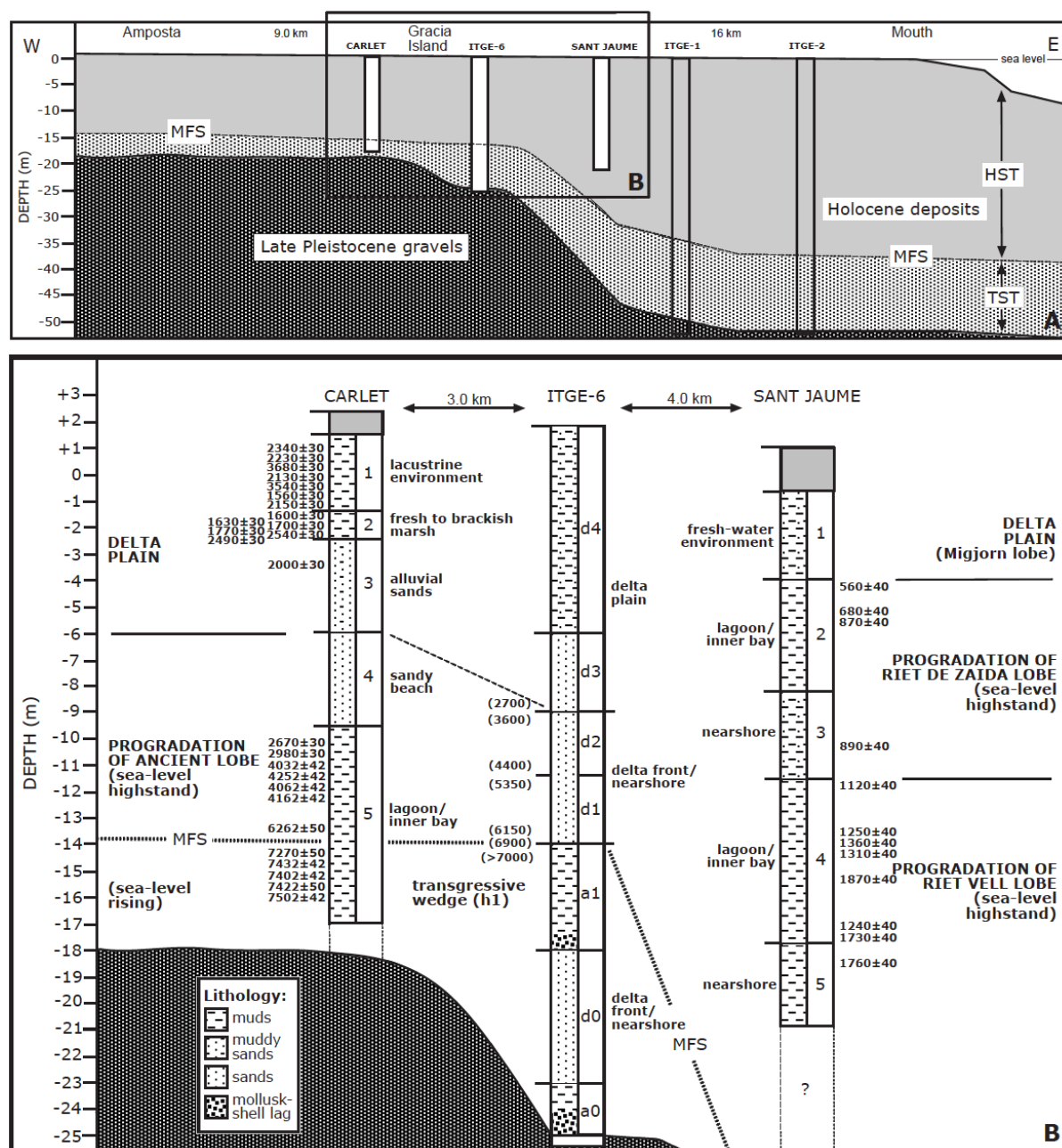
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(109, 108, 126), whereas clays with marine fauna are only found in the outermost boreholes (125 to 106).

The Sant Jaume borehole is located in a more seaward position than Carlet and contains a longer, deeper and much younger sequence accumulated during the last 2.0 ka. Thanks to available historical data mentioned above, it is possible to interpret its sedimentary record as deposited during the formation and development of three different deltaic lobes under highstand sea-level conditions. Muddy intervals DI5 and DI4 represent a partial record of the formation and development of the Riet Vell lobe that prograded towards the southeast and deposited progressively shallower (from nearshore to more proximal inner bay) materials in this area between 2000 and 1100 yr BP. Then deposition of a new muddy progradational shallowing-upward succession between 1100 and 500 yr BP, represented by DI3 and DI2, characterizes the development of a new deltaic lobe (Riet de Zaida) that developed towards the northeast and deposited in this area nearshore-inner bay-lagoonal sediments. A new switch in the river course due to human intervention made possible the newest delta lobe (Migjorn) represented by lacustrine (fresh-water) deposition (DI1) in this area during the last 0.5 ka.

Two external boreholes (ITGE-1 and ITGE-2; Figure 1) were studied by Somoza et al. (1998) although their descriptions are less detailed than central ITGE-6 borehole. Both sedimentary successions reached the Pleistocene gravels and were about 50 m thick including TST and HST deposits. The HST was composed of four progradational units (d1, d2, d3 and d4) and three aggradational units (a2, a3 and a4). The boreholes were located at the apices of two main delta lobes identified in historical records: ITGE-1 over the Riet Vell lobe, and ITGE-2 over the most recent Migjorn lobe. Their final progradational unit (d4) corresponds to the formation of their respective deltaic lobes but no information on the origin, sedimentary characteristics and chronology of the other preceding progradational units is presented. Our Sant Jaume borehole is located in the central delta plain at the confluence area of the last three delta lobes: Riet Vell, Riet de Zaida and Migjorn (Figure 1). Distinct marine and delta plain habitat successions have characterized the formation and development of those three lobes that in turn were associated to particular foraminiferal palaeoassemblages. Firstly, Riet Vell lobe progradation (2.0-1.1 ky) that shows progressively shallower muddy environments from nearshore (DI5) to more proximal inner bay (DI4). Then, Riet de Zaida lobe (1.1-0.5 ky) that exhibits a similar environmental succession with nearshore (DI3) and inner bay-lagoonal sediments (DI2). Finally, the most recent Migjorn lobe (0.5 ka) represented here by a fresh-water environment (DI1) in a delta plain setting.

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**Figure 5.** A. General location of the analyzed boreholes in the framework of the Ebro Delta architecture proposed by Somoza et al (1998) for the Late Quaternary; B. Palaeoenvironmental interpretation of the Carlet and Sant Jaume boreholes based on foraminiferal assemblages. Foraminiferal depth intervals (DIs), lithology and radiocarbon dates (conventional years BP) are also indicated. Interpretation of the ITGE-6 borehole is from Somoza et al (1998) with indication of the aggradational marine (a units) and progradational deltaic (d units) deposits. Dates in parentheses were assigned by Somoza and Rodríguez-Santalla (2014) but were not obtained from materials of this borehole.

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As we have seen, there is an important difference on resolution scale between the Carlet and Sant Jaume boreholes. Carlet provides information at a geological scale of resolution of thousands of years, while San Jaume is providing data at historical scale. Almost the same thickness of sediments represents 7.6 ka in Carlet against circa 2 ka in San Jaume. Carlet borehole correlates with the progradational d1, d2, d3 and d4 of Somoza et al. (1998) which correspond to four different 5th-order cycles. On the other side, the entire record of the San Jaume borehole can be assimilated to the prograding portion of one complete cycle of higher rank, corresponding to the last d4 unit of the historical lobes Riet Vell, Riet de Zaida and partially d5 of Migjorn. Beyond the processes of compaction, preservation and possible time-averaging experienced by the older Carlet sedimentary sequence, the shorter time interval and deeper environments represented by the longer Sant Jaume sedimentary sequence can be understood as a consequence of the greater accommodation space available in the delta from the Gracia Island in a seaward direction. As it is shown in Figure 5A, the geometry of the Holocene materials has a thickness ranging from 20 m at the landward side (Amposta) to 52 m at the delta front. The erosional unconformity between the late Pleistocene gravels and the Holocene deposits exhibits a more pronounced slope in the external delta just after the Gracia Island, and formed initially by marine erosion during rapid sea-level rise at the first stages of the Holocene transgression (Maestro et al., 2002). These authors also indicated the presence of extensional tectonics that affects the Quaternary deltaic deposits with formation of large-scale faulting that generates differential subsidence beneath the Ebro Delta and increases the slope angle. The principal process involved in fault development is considered to be differential compaction resulting from the prograding deltaic lobes that overlie aggradational clay deposits. Growth faults increase subsidence, which in turn generates accommodation space for subsequent prograding deltaic sediment. This arc-shaped topographic depression acted as a trap for distributary channels meandering over the delta plain, like the abandoned Riet Vell and Riet de Zaida (Maestro et al., 2002).

#### *Implications for the Holocene evolution of Mediterranean deltas*

In terms of their palaeoenvironmental significance, when modern foraminiferal assemblages from the delta plain habitats are included in the analysis, the interpretation is more robust compared with other studies only considering open marine (offshore) assemblages. Existing literature shows that foraminiferal assemblages living in coastal marginal environments, such as coastal lagoons, bays or salt marshes, differ greatly from those in adjacent offshore habitats (Murray, 2006); and this also applies in the case of some world and Mediterranean deltas such as the Mississippi, USA (Lankford, 1959), Mahakam, Indonesia (Lambert, 2003), Rhône, France (Vangerow, 1974; Fanget et al., 2012), Nile, Egypt (Arbouille and Staney, 1991) or Ebro, Spain (Scrutton, 1969). Previous studies often interpreted the occurrence of shallow brackish-marine species, such as *Ammonia* spp. (*A. tepida*, *A. beccarii*, *A. parkinsoniana*), *Criboelphidium* spp. and/or *H. germanica*, as indicators of past offshore habitats within Holocene deltaic sequences (Amorosi et al., 2008, 2013; Rossi and Vaiani, 2008; Milli

### *Chapter 3: Holocene Ebro Delta evolution*

et al., 2013). However it is well known that these species are mainly indicative of particular marginal coastal habitats, unless other ecological requirements based on the study of their living populations are actually identified (Usera et al., 2002; Guillem, 2007). Otherwise, the lack of close modern analogues may lead to weaker interpretations of the foraminiferal fossil record.

The present study has demonstrated the similarity between most of modern and fossil samples in the Ebro Delta by applying the modern analogue technique (MAT) and Linear Discriminant Functions (LDFs); hence, a finer-grained habitat reconstruction can be done. The interpretation of results would have been different if foraminifera from deltaic (inshore) environments would have not been included, especially for the Carlet sequence that shows the presence of shallower habitats typical from delta plain environments, in comparison with the Sant Jaume sequence showing deeper environments typical from the prodelta and delta front. To our knowledge, this is the first approach in including modern samples from both delta plain (coastal lagoons, marshes and inner bays) and open marine (prodelta and delta front) habitats of a Mediterranean delta to provide adequate analogues for all borehole samples. Thus, the Ebro Delta data set could be used in other Mediterranean deltas with the aim to provide new interpretations of their depositional environments since all of them share a similar Holocene evolution (Stanley and Warne, 1994).

The application of a water depth transfer function to fossil foraminiferal assemblages has complemented the palaeoenvironmental reconstruction of the Ebro Delta. The only comparable work is by Rossi and Horton (2009), who applied the Northern Adriatic Transfer Function (NATF) to reconstruct the evolution of the Holocene palaeobathymetry of the Po Delta. These authors concluded the existence of a shallowing upward trend following the progradational succession of this delta during the last 5.5 ka. In turn, palaeowater depths were considered reliable according to MAT results. For the Ebro Delta, very similar results were found in the Sant Jaume sequence, where two deeper-to-shallower successions were detected (DI5-4 and DI3-2) with inferred water depths from 7 to 1 m (Figure 5). These findings suggest the progradation of delta lobes in this distal part of the delta during the last centuries, although some samples did not contain close modern analogues. On the other hand, the palaeowater depths of the Carlet sequence revealed very shallow conditions throughout all depositional environments recorded, ranging between 1–2 m of water depth. The validity of these reconstructions is supported by MAT and LDFs results, although palaeowater depths must be taken with caution because of the complex relationship between water depth and foraminiferal distribution, particularly in highly dynamic systems like deltas. Further research on modern foraminiferal assemblages of inshore habitats of other Mediterranean deltas could allow a more reliable interpretation of their Holocene evolution.

## **Conclusions**

The scarcity of previous geological studies and the few available radiocarbon dates from its Holocene sedimentary archives, together with misinterpretations of historical documents, have permitted the idea that the present Ebro Delta plain formed mostly during the 14th-15th centuries and that during Roman times it was an estuary. Our results support an early Holocene start for the Ebro Delta proving a deltaic depositional system was present all through the Holocene, and thus the Ebro Valley never became an estuary. This brings the Ebro evolution story in line with other major deltas of the Mediterranean Sea and worldwide, which were initiated 8.0-6.0 ka ago when the rate of fluvial sediment input overtook the decreasing rate of sea-level rise.

The palaeoenvironmental evolution of the central plain of the Ebro Delta during the Holocene was reconstructed using micropalaeontological analysis of two continuous boreholes (Carlet and Sant Jaume). Diagnostic foraminiferal assemblages and the application of a palaeowater-depth transfer function allowed the definition of various lithofacies and associated environments of deposition. The geometry of the Ebro Delta was created by the advance of successive deltaic lobes, which prograded radially across the inner shelf up to 25 km seaward during the Holocene time. Avulsion and channel abandonment processes are considered to be the main delta constructional processes with the resulting deposits subsequently being modified by rapid subsidence.

Similarity between most of modern and fossil samples in the Ebro Delta has been demonstrated by applying the modern analogue technique (MAT) and Linear Discriminant Functions (LDFs), allowing a much better habitat reconstruction to be done. The importance of extensive characterization of modern foraminiferal assemblages from both deltaic inshore and offshore environments in order to provide adequate analogues for the interpretation of borehole samples is demonstrated particularly by the more landward Carlet sequence which only contains shallow and inshore deltaic habitats. The palaeowater depths revealed very shallow conditions throughout all depositional environments, ranging between 1–2 m during the last 7.6 ka under salty, brackish and fresh-water conditions.



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## Appendix A. Foraminiferal reference list.

### Agglutinated forms

*Eggerelloides scaber* (Williamson) = *Bulimina scabra* Williamson, 1858

*Haplophragmoides wilberti* Anderson, 1953

*Jadammina macrescens* (Brady) = *Trochammina inflata* (Montagu) var. *macrescens*  
Brady, 1870

*Textularia agglutinans* d'Orbigny, 1839

*Textularia bocki* Höglund, 1947

*Textularia calva* Lalicker, 1935

*Textularia* sp.

*Trochammina inflata* (Montagu) = *Nautilus inflatus* Montagu, 1808

### Porcellaneous forms

*Adelosina bicornis* (Walker and Jacob) = *Serpula bicornis* Walker and Jacob, 1798

*Adelosina laevigata* (d'Orbigny) = *Quinqueloculina laevigata* d'Orbigny, 1939

*Adelosina mediterraneensis* (Le Calvez and Le Calvez) = *Quinqueloculina mediterraneensis* Le Calvez and Le Calvez, 1958

*Adelosina striata* d'Orbigny, 1826

*Adelosina* sp.

*Cornuloculina* sp.

*Cornuspira incerta* (d'Orbigny) = *Operculina incerta* d'Orbigny, 1839

*Cornuspira involvens* (Reuss) = *Operculina involvens* Reus, 1850

*Lachlanella undulata* (d'Orbigny) = *Quinqueloculina undulata* d'Orbigny, 1852

*Massilina secans* (d'Orbigny) = *Quinqueloculina secans* d'Orbigny, 1826

*Miliolinella subrotunda* (Montagu) = *Vermiculum subrotundum* Montagu, 1803

*Miliolinella webbiana* (d'Orbigny) = *Triloculina webbiana* d'Orbigny, 1839

*Pyrgo inornata* (d'Orbigny) = *Biloculina inornata* d'Orbigny, 1846

*Pyrgo* sp.

*Quinqueloculina berthelotiana* d'Orbigny, 1839

*Quinqueloculina depressa* d'Orbigny, 1852

*Quinqueloculina lata* Terquem, 1876

*Quinqueloculina longirostra* d'Orbigny, 1826

*Quinqueloculina oblonga* (Montagu) = *Vermiculum oblongum* Montagu, 1893

*Quinqueloculina seminula* (Linné) = *Serpula seminulum* Linné, 1758

*Quinqueloculina stelligera* Schlumberger, 1893



*Quinqueloculina vulgaris* d'Orbigny, 1826

*Quinqueloculina* sp.1

*Quinqueloculina* sp.2

*Siphonaperta quadrata* (Nørvang) = *Quinqueloculina quadrata* Nørvang, 1945

*Triloculina dubia* d'Orbigny, 1826

*Triloculina marioni* Schlumberger, 1893

*Triloculina rotunda* d'Orbigny, 1939

*Triloculina trigonula* (Lamarck) = *Miliolites trigonula* Lamarck, 1804

### Hyaline forms

*Acervulina inhaerens* Schulze, 1854

*Ammonia beccarii* (Linné) = *Nautilus beccarii* Linné, 1758 (Variants included in this taxon)

*Astacolus crepidulus* (Fichtel and Moll) = *Nautilus crepidula* Fichtel and Moll, 1798

*Asterigerinata mamilla* (Williamson) = *Rotalia mamilla* Williamson, 1858

*Aubignyna hamblensis* Murray, Whittaker and Alve, 2000

*Aubignyna perlucida* (Heron-Allen and Earland) = *Rotalia perlucida* Heron-Allen and Earland, 1913

*Bolivina difformis* (Williamson) = *Textularia variabilis* var. *difformis* Williamson, 1858

*Bolivina dilatata* Reuss, 1850

*Bolivina pseudoplicata* Heron-Allen and Earland, 1930

*Bolivina striatula* (Cushman) = *Brizalina striatula* Cushman, 1922

*Bolivinellina pseudopunctata* (Höglund) = *Bolivina pseudopunctata* Höglund, 1947

*Brizalina spathulata* (Williamson) = *Textularia variabilis* Williamson var. *spathulata* Williamson, 1858

*Brizalina variabilis* (Williamson) = *Textularia variabilis* Williamson, 1859

*Buccella granulata* (di Napoli Alliata) = *Eponides frigidus* var. *granulatus* di Napoli Alliata, 1952

*Bulimina aculeata* d'Orbigny, 1926

*Bulimina elongata* d'Orbigny, 1926

*Bulimina gibba* Fornasini, 1902

*Bulimina marginata* d'Orbigny, 1826

*Buliminella elegantissima* (d'Orbigny) = *Bulimina elegantissima* d'Orbigny, 1939

*Cassidulina carinata* Silvestri, 1896

*Cassidulina obtusa* Williamson, 1858

*Cibicides lobatulus* (Walker and Jacob) = *Nautilus lobatulus* Walker and Jacob, 1798

*Cibicides* sp.

*Criboelphidium excavatum* (Terquem) = *Polystomella excavatum* Terquem, 1875

*Criboelphidium magellanicum* (Heron-Allen and Earland) = *Elphidium magellanicum*  
Heron-Allen and Earland, 1932

*Criboelphidium oceanensis* (d'Orbigny) = *Polystomella oceanensis* d'Orbigny, 1826

*Criboelphidium poeyanum* (d'Orbigny, 1826) = *Polystomella poeyana* d'Orbigny, 1826

*Criboelphidium selseyense* (Heron-Allen and Earland) = *Elphidium selseyensis* Heron-Allen and Earland, 1911

*Criboelphidium williamsoni* (Haynes) = *Elphidium williamsoni* Haynes, 1973

*Discorbis* sp.

*Elphidium advenum* (Cushman) = *Polystomella advenum* Cushman, 1922

*Elphidium crispum* (Linné) = *Nautilus crispus* Linné, 1758

*Elphidium erlandi* Cushman, 1936

*Elphidium flexuosum* (d'Orbigny) = *Polystomella flexuosa* d'Orbigny, 1936

*Elphidium gerthi* Van Voorthuysen, 1957

*Elphidium incertum* (Williamson) = *Polystomella umbilicatula* var. *incerta* Williamson,  
1858

*Elphidium macellum* (Fichtel and Moll) = *Nautilus macellus* Fichtel and Moll, 1798

*Elphidium margaritaceum* Cushman, 1930

*Elphidium* sp.

*Epistominella vitrea* Parker, 1953

*Favulina melo* (d'Orbigny) = *Oolina melo* d'Orbigny, 1839

*Fissurina lucida* (Williamson) = *Entosolenia marginata* (Montagu) var. *lucida*  
Williamson, 1848

*Fissurina marginata* (Montagu) = *Vermiculum marginatum* Montagu, 1803

*Fissurina* sp.

*Fursenkoina schreibersiana* (Czjzek) = *Virgulina schreibersiana* Czjzek, 1848

*Gavelinopsis praegeri* (Heron-Allen and Earland) = *Discorbina praegeri* Heron-Allen  
and Earland, 1913

*Globobulimina* sp.

*Gyroidina* sp.

*Haynesina depressula* (Walker and Jacob) = *Nautilus depressulus* Walker and Jacob,  
1798

*Haynesina germanica* (Ehrenberg) = *Nonionina germanica* Ehrenberg, 1840

*Lagena semistriata* (Williamson) = *Lagena striata* Walker var. *semistriata* Williamson,  
1848

## Chapter 3: Holocene Ebro Delta evolution

- Lagena sulcata* (Walter and Jacob) = *Serpula sulcata* Walter and Jacob, 1798
- Lagena vulgaris* Williamson, 1858
- Nonionella atlantica* Cushman, 1947
- Nonionella opima* Cushman, 1947
- Nonionoides boueanum* (d'Orbigny) = *Nonionina boueana* d'Orbigny, 1846
- Nonionoides turgida* (Williamson) = *Nonionina turgida* Williamson, 1858
- Patellina corrugata* Williamson, 1858
- Planorbulina mediterraneensis* d'Orbigny, 1826
- Rectuvigerina compressa* (Cushman) = *Uvigerina compressa* Cushman, 1925
- Reussella aculeata* Cushman, 1945
- Reusoolina laevis* (Montagu) = *Vermiculum laeve* Montagu, 1803
- Rosalina anomala* Terquem, 1875
- Rosalina globularis* d'Orbigny, 1826
- Rosalina irregularis* (Rhumbler) = *Discorbina irregularis* Rhumbler, 1906
- Rosalina valvulata* d'Orbigny, 1826
- Rosalina williamsoni* (Chapman and Parr) = *Discorbis williamsoni* Chapman and Parr, 1932
- Rosalina* sp. 1
- Rosalina* sp. 2
- Spirillina vivipara* Ehrenberg, 1843
- Svratkina* sp.
- Tretomphaloides concinnus* (Brady) = *Discorbina concinna* Brady, 1884
- Trichohyalus aguayoi* (Bermudez) = *Discorinopsis aguayoi* Bermudez, 1935
- Trifarina angulosa* (Williamson) = *Uvigerina angulosa* Williamson, 1858
- Uvigerina peregrina* Cushman, 1923
- Valvulineria bradyana* (Fornasini) = *Discorbina bradyana* Fornasini, 1899

**Supplementary material**

**Table S1.** Foraminiferal census data from the Carlet and Sant Jaume boreholes (Ebro Delta). The data table can be found online at the XXX website <http://XXX>.

## ***Chapter 4***

### **Benthic foraminifera as indicators of habitat change in anthropogenically impacted coastal wetlands of the Ebro Delta (NE Iberian Peninsula)**

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BENTHIC DIATOMS AND FORAMINIFERA AS INDICATORS OF COASTAL WETLAND HABITATS: APPLICATION TO PALAEOENVIRONMENTAL RECONSTRUCTION

Xavier Benito Granel



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# Benthic foraminifera as indicators of habitat change in anthropogenically impacted coastal wetlands of the Ebro Delta (NE Iberian Peninsula)

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### ABSTRACT

Present-day habitats of the Ebro Delta, NE Iberian Peninsula, have been ecologically altered as a consequence of intensive human impacts in the last two centuries (especially rice farming). Benthic foraminiferal palaeoassemblages and sediment characteristics of five short cores were used to reconstruct past wetland habitats, through application of multivariate DCA and CONISS techniques, and dissimilarity coefficients (SCD). The timing of environmental changes was compared to known natural and anthropogenic events in order to identify their possible relationships. In deltaic wetlands under altered hydrological conditions, we found a decrease in species diversity and calcareous-dominated assemblages, and a significant positive correlation between microfaunal changes and organic matter content. Modern analogues supported palaeoenvironmental interpretation of the recent evolution of the Delta wetlands. This research provides the first recent reconstruction of change in the Ebro Delta wetlands, and also illustrates the importance of benthic foraminifera for biomonitoring present and future conditions in Mediterranean deltas.

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## 1. Introduction

Coastal ecosystems (e.g. deltas, wetlands, estuaries) are both naturally and artificially subject to many and varied environmental changes (Elliott and Quintino, 2007). Due to their location at the land–sea interface, these transitional waters have a strong intrinsic dynamism and pronounced environmental gradients (e.g. salinity, nutrients, sediment types, oxygen levels) (LePage, 2011). Some of these natural gradients, however, are often drastically modified by human activities, particularly in deltas, which are often densely populated and heavily farmed (Syvitski et al., 2009). Among human impacts in Mediterranean coastal wetlands, changes in land and water uses and demand for agricultural purposes have caused the largest serious modifications of their natural ecological functioning. These changes have altered wetland habitat structure across a variety of spatial and temporal scales, mainly by artificial freshwater inputs and eutrophication (Margalef and Mir, 1973; Pérez-Ruzafa et al., 1991; Marco-Barba et al., 2013; Prado et al., 2014). Furthermore, intensive agricultural and human settlements have

eliminated most of the original distribution of coastal wetland habitats (Benito et al., 2014; Halpern et al., 2008).

Given the accepted ecological and economic importance of coastal wetlands (Costanza et al., 1997), well-informed and climate-resilient management is essential to maintain the proper functioning of the remaining natural ecosystems, while allowing exploitation for agriculture, tourism and/or industry. Unfortunately, due to the lack of long-term monitoring data, palaeoecological information is the only archive to document past environmental changes (Smol, 2002; Willis and Birks, 2006).

Existing literature shows that benthic foraminifera (unicellular protists) are widely used to study both present and past environmental conditions in many coastal ecosystems around the world (Horton et al., 2007; Pruitt et al., 2010; Cheng et al., 2012; Takata et al., 2014). Their fossil remains are commonly used in climate reconstruction but they also allow tracking environmental changes due to human impacts over last hundreds years (Cearreta et al., 2002; Debenay and Fernandez, 2009). Numerous ecological studies have employed different multivariate statistical techniques for interpreting modern foraminifera–environment relationships, and then for applying those into dated sediment cores (Vance et al., 2006; Kemp et al., 2012, 2013; Narayan et al., 2015). Benthic foraminifera living in coastal marshes respond to a broad range of biotic and abiotic factors that result in complex interactions in space and time (Debenay and Guillou, 2002). Moreover, palaeoenvironmental reconstructions should demonstrate the similarity

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between modern and buried microfaunas to provide accurate inferences (Guilbault et al., 1996). In this context, combined approaches are required, using modern foraminiferal analyses coupled with palaeoecological information and independent sediment proxies (e.g. organic matter).

The proportion of transitional waters that can be considered to have “high ecological status” (i.e. reference conditions) is very limited but important for management purposes. Successful management requires good understanding of ecosystem structure and functioning under pre-impacted conditions in order to set realistic restoration goals. The Water Framework Directive (WFD) requires the degree of deviation from these reference conditions to be documented using hydromorphological, physicochemical, and biological quality elements (European Communities, 2003). As other authors have highlighted, reference conditions should preferably be assessed *in situ*, rather than comparing the area in question with similar systems elsewhere (if any) that have not been altered by human activities (Blanchet et al., 2008; Alve et al., 2009). This is particularly relevant in the case of transitional ecosystems, due to the great heterogeneity of ecological conditions within them (Alve, 1995; Bald et al., 2005). Palaeoecological approaches can allow objective assessment of local “reference conditions” for any type of water body (river, lake, coastal waters) (Andersen et al., 2004).

Down-core benthic foraminiferal assemblages have recently been used to determine whether human activities have changed “baseline” conditions in marginal marine environments (Tsujiimoto et al., 2008; Martínez-Colón et al., 2009; Alve et al., 2009; Bouchet et al., 2012; Dolven et al., 2013). Benthic foraminifera are not required by the WFD (Annex V) as biological quality elements for monitoring transitional waters and have rarely been used as ecological indicators of anthropogenic disturbances in Mediterranean coastal environments (Carboni et al., 2009), with the exception of the Venice lagoon (Donnici et al., 1997; Serandrei-Barbero et al., 1999, 2011; Albani et al., 2007; Coccioni et al., 2009). Another group of unicellular benthic eukaryotes, the diatoms, are widely used in biomonitoring (indeed, their use is required by the WFD for assessing some water bodies, e.g. rivers, though not transitional waters) and proved

valuable as ecological indicators in an earlier study of the Ebro Delta (Benito et al., 2015). However, the lack of well-preserved diatom remains in some Delta sediments led us to focus instead on foraminifera in the present study.

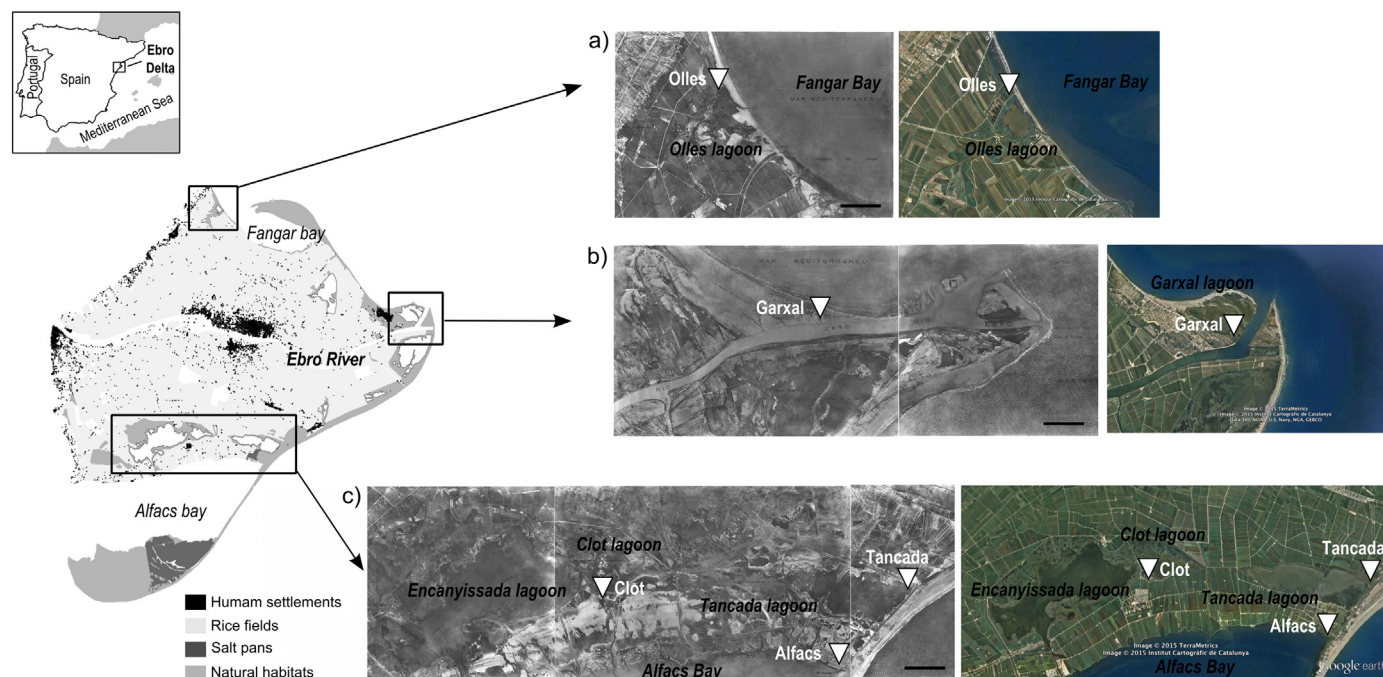
The present paper represents the first study using benthic foraminiferal palaeoecology within a Mediterranean delta. The main objective was to examine the effects that intensive human settlement has had on the habitats of the Ebro Delta during the last two centuries. We aimed to document the effects of rice field expansion and hydrological changes by studying the buried foraminiferal assemblages preserved in five short sediment cores. An additional aim was to compare the recent evolution of two contrasted wetland types within the Delta represented by four sites under altered hydrological conditions, and one site under a natural brackish hydrological regime.

## 2. Material and methods

### 2.1. Study area

The Ebro Delta is one of the largest coastal wetlands in the Western Mediterranean, extending over an area of about 330 km<sup>2</sup>, and is situated in the NE Iberian Peninsula (Fig. 1). The Delta is irrigated by the Ebro River, which is the largest river in Spain in terms of mean annual flow (c. 400 m<sup>3</sup> s<sup>-1</sup>). The drainage area of the Ebro River is 85,550 km<sup>2</sup>, representing 15% of the total area of Spain (Maldonado and Murray, 1975). Nowadays a large amount of the water that the river would have carried under natural conditions is extracted for irrigation and other purposes. Consequently, the amount of water and sediment reaching the Delta has been drastically reduced, particularly between 1940 and 1970, when nearly 200 dams were built (Ibáñez et al., 1996).

From an ecological point of view, the Ebro Delta is important due to its high diversity of Mediterranean coastal wetlands concentrated in a small area (Ibáñez et al., 2000). This is in part due to the micro-tidal nature of the Delta (with an astronomical range of only 20–30 cm), which allows high spatial heterogeneity of wetland habitats structured in small patches (Ibáñez et al., 2000). The Ebro Delta is also economically important, with two thirds of the area devoted to rice crop, but also



**Fig. 1.** Location of the Ebro Delta. The positions of the cores (white triangles) are shown in both historical (1927, left side) and modern (2015, right side) aerial photographs; a) Olles; b) Garxal; c) Clot, Alfacs and Tancada. Scale bar represents 1 km. Historical photographs were obtained from the Ebro Water Authority ([www.chebro.es](http://www.chebro.es)).



with other activities such as tourism, aquaculture or hunting that contribute to the total annual economic value of about €120 million (Fatoric and Chelleri, 2012).

During the last two centuries, most of the deltaic plain has been reclaimed for rice cultivation. Agriculture was poorly developed in the Delta until the 19th century, when intense landscape transformation began (in the 1860s) with the construction of the south irrigation channel derived from the Ebro River, and rose drastically from 1912, when the construction of the north irrigation channel was completed (Rovira and Ibáñez, 2007). Even so, at the beginning of the 20th century, natural habitats still covered 80% of the total deltaic area (Mañosa et al., 2001). Outside the area of rice cultivation, human activities were based on subsistence economy (farming, salt production, fishing and hunting), which did not cause widespread transformation of the area. The period between 1910 and 1960 saw rapid development of rice farming in the Delta, which resulted in a drastic loss of fresh, brackish and salt marshes, and lagoons as they were converted to paddy fields (Cardoch et al., 2002). Transformation for rice cultivation started from the inner part of the Delta and areas adjacent to river levees (which were naturally more elevated and had less saline soils) and advanced progressively seaward. Altogether, the surface area occupied by natural habitats reduced from 80% to 33% between 1910 and 1960 (Mañosa et al., 2001). Transformation continued during the next two decades (1960–1980), stopping only in the 1980s, when the Ebro Delta Natural Park was created (1983). The area still covered by marshes and coastal lagoons amounts to just 25% of the deltaic plain, but this contains good examples of a diversity of Mediterranean coastal wetlands, including salt and brackish marshes, coastal lagoons, sand dunes, freshwater marshes, ponds and bays. Most of these habitats are protected by European Directives (e.g. the Habitat Directive and Bird Directive) and regional environmental laws (for the Ebro Delta Natural Park).

Rice field cultivation necessitates large-scale control of water inputs and outputs and so an extensive system of irrigation and drainage canals has been constructed in the Delta. From the 1860s to the late 1980s, runoff from the rice paddies was drained directly into the remaining lagoons during the rice growing season (i.e. from April to September), and then from these systems into the sea (in the Alfacs and Fangar bays: Fig. 1). The main consequence has been the alteration of the natural hydrological cycles of the coastal lagoons and surrounding marshes (Prado et al., 2012, 2014; Rodríguez-Climent et al., 2013) and the bays (Llebot et al., 2011). These freshwater inputs also carry nutrients and pesticides, altering further the ecology of the habitats. Moreover, the construction of infrastructures such as canals, dikes and roads has contributed to the isolation of the remaining natural habitats from the Ebro River and Mediterranean Sea (Ibáñez et al., 1997), with the exception of the Garxal wetland located at the river mouth area and the marshes located along the outermost edges of the Delta.

## 2.2. Core sampling and chronology

Five short sediment cores, two placed in the northern hemidelta (Olles and Garxal, Fig. 1) and three in the southern one (Tancada, Alfacs and Clot, Fig. 1), were retrieved from sites well within marshes in April 2014. The locations were chosen to cover a range of different environments affected historically by natural and human factors (Table 1 and Appendix B). Each core was collected to a depth of 65–106 cm (depending on marsh soil thickness) using a hand-operated Beeker-type corer of 5.7-cm diameter, which allows recovery of undisturbed sediments.

The five cores collected in 2014 were taken at exactly the same locations as some short cores (50 cm length) collected in 2009, which were dated with  $^{210}\text{Pb}$  (Table 1).  $^{210}\text{Pb}$  is a natural radionuclide with a half-life of 22.3 years, and is continuously introduced into the aquatic systems by atmospheric deposition, after radioactive decay of  $^{222}\text{Rn}$ . Core samples for determining  $^{210}\text{Pb}$  activities were sliced into 4 cm sections. Each sample was first homogenized in a mortar and then dried at 60 °C. Dried samples were placed in 65 cm<sup>3</sup> Petri dishes, and then counted for 20 to 90 h in the CRIL-RAD laboratory (France). Determination of  $^{210}\text{Pb}$  activities was carried out using a gamma hyperpure germanium “N” type detector (EGG/ORTEC, Type GMX) coupled to a multichannel analyser (type NUCLEUS) and calibrated by a pitchblende gamma multiray source.

The chronology was tentatively inferred on average sediment accumulation rate (cm/year) using the exponential-type decline of  $^{210}\text{Pb}_{\text{excess}}$  with depth (Fig. S1 and Table S1). The model applied (Constant Initial Concentration, CIC) assumes that the initial  $^{210}\text{Pb}_{\text{excess}}$  concentration into the accumulated sediment is the same regardless of changes in the sediment accumulation rate in depth (Appleby, 2001). Note that the  $^{210}\text{Pb}$  methods do not provide absolute ages but rather gives sedimentation rates that can be indirectly used to determine how much time has elapsed between samples at different depths (Augustinus et al., 2006). We assume that the estimated chronology from these dated cores is also applicable to the five cores studied in the present study.

## 2.3. Foraminiferal analysis

Cores were sliced at 5-cm intervals in the field, and part of each, corresponding to a target weight of about 120 g of wet sediment was retained for foraminiferal analysis. The remaining material from each segment was used to estimate the organic matter content, as loss on ignition (LOI at 450 °C for 4 h) (Dean, 1974). The foraminiferal samples were wet washed through 1 mm and 0.063 mm sieves (to remove first large organic fragments, then silt and clay), and dried at 50 °C for 12 h. Foraminifera were concentrated by flotation in trichloroethylene (Alve and Murray, 1999). For each sample, foraminiferal tests were picked on representative splits containing at least 300 tests under a Leica M165C stereomicroscope, using reflected light. Otherwise, all the tests present in the sample were picked. Only those samples with at least 100 tests were used for numerical analyses (Fatela and Taborda,

**Table 1**

Summary of the five cored sites in the Ebro Delta: surface elevation, average sedimentation rates using the  $^{210}\text{Pb}$  method, main habitat, and brief description of historical impacts. The habitat evolution for each site is also indicated according to the present study.

Site	Elevation (cm)	$^{210}\text{Pb}$ sedimentation rate (cm/yr)	Habitat	Historical human impacts	Habitat evolution
Olles	6.2	0.24	<i>Phragmites</i> marsh	Freshwater inputs and high nutrient levels coming from rice field drainage channels and urban waste water	From coastal lagoon/inner bay to brackish marsh
Tancada	13.6	0.17	<i>Salicornia</i> marsh	Drainage waters coming from rice fields caused a strong decrease of salinity and high nutrient loads	From coastal lagoon/inner bay to salt marsh
Alfacs	1.1	0.37	<i>Salicornia</i> marsh	Freshwater inputs from rice field drainage waters provoked a decrease in salinity and high nutrient loads	From inner bay to salt marsh (backshore)
Clot	1.3	0.70	<i>Phragmites</i> marsh	Persistent freshwater inputs from the Ebro river and irrigation channels lead to low salinity	From coastal lagoon/inner bay to brackish marsh
Garxal	9.9	0.21	<i>Phragmites</i> marsh	Natural brackish conditions due to its direct connection to the Ebro river since the last recent mouth change (60 years ago)	From coastal lagoon/inner bay to coastal lagoon

2002). Altogether, 82 samples and around 25,400 foraminifera were examined for the five cores. Taxonomic identifications were based on foraminiferal works from the W Mediterranean, including Murray (1971), Colom (1974), Cimerman and Langer (1991) and Milker and Schmiel (2012).

The palaeoenvironmental interpretation of the foraminiferal record was based on the modern (living and dead) distributions of species in the Ebro Delta. Benito et al. (under review) recognized four habitat types based on species composition. These habitats cover a wide range of modern analogues from both the deltaic plain and the adjacent marine area and comprise: 1) offshore, 2) nearshore and outer bays, 3) coastal lagoons and inner bays, and 4) salt and brackish marshes. In addition, foraminiferal species regularly found in living assemblages (i.e. those foraminifera that got stained after treated with rose Bengal, see Walton (1952) for method details) of the modern samples of Ebro Delta habitats were considered as autochthonous (living and reproducing within the delta plain), whereas those found only as dead tests (i.e. unstained) were considered to be allochthonous species transported from the adjacent marine area (Murray, 2006; Cearreta et al., 2013; Rodriguez-Lazaro et al., 2013, Benito et al., under review).

#### 2.4. Data analysis

We calculated the relative abundance (RA) of foraminiferal species for each core sample. Foraminiferal relative abundances were square root transformed prior to statistical analyses in order to stabilize their variances. Only those species with >2% of relative abundance in at least one sample were used in the analyses.

To analyse changes in the foraminiferal assemblages throughout the cores, depth intervals (DIs) were defined by stratigraphically constrained cluster analyses (CONISS) and the squared chord distance to the species data. Clusters were constrained by stratigraphic order, and the statistical significance of each cluster was determined using the “broken stick” method (Bennett, 1996).

A Detrended Correspondence Analysis (DCA) was used to visualize the trajectory of change of each core through unconstrained ordination space in which modern (dead) foraminiferal samples were also passively plotted (Benito et al., under review). The same multivariate ordination was used further to determine whether buried foraminiferal samples were represented by the modern Ebro Delta habitats. In order to aid interpretation of DCA ordination axes, environmental variables (water depth, salinity and sand content) from modern dataset (Benito et al., under review) were fitted using the ‘envfit’ function within R’s vegan package with 999 permutations. The ‘envfit’ function provides information about the statistical relationship of the environmental vectors to the DCA axes. Thus, the length of each vector is proportional to the correlation between the ordination axes and environmental variables. Finally, for each sediment core, we calculated statistical correlations between DCA axis scores and organic matter content using Pearson *r* coefficient.

To check the degree of dissimilarity (or similarity) in the foraminiferal assemblages between each buried sample and the modern ones, we calculated the squared chord distance (SCD) as a dissimilarity coefficient (Overpeck et al., 1985). We chose the largest dissimilarity coefficient among all modern foraminiferal samples as a critical threshold to determine whether the buried samples had “close” modern analogues (Woodroffe, 2009). Samples with SDC < 0.271 were considered similar.

All the numerical analyses were performed using R version 3.0.1 (R Development Core Team, 2010), including the packages vegan (Oksanen et al., 2013), rioja (Juggins, 2014) and analogue (Simpson and Oksanen, 2014).

### 3. Results

A total of 81 benthic foraminiferal species (range 4–24 species per sample) were identified from 82 samples derived from the five cores

analysed in this study (Appendix A and Table S1). Of these species, 31 had a relative abundance >2% in at least one sample and were retained for statistical analysis. The sediment cores were mainly composed of grey muddy sand (10–80% sand content) with sandier layers (>90% sand content) generally increasing downwards in the cores.

#### 3.1. Olles

Two distinct depth intervals (DI) were identified within the Olles core (Fig. 2 and Table 2). The basal D2 (32–70 cm depth) was characterized by the dominance of hyaline foraminifera, with *Ammonia beccarii* (average relative abundance [RA] 54%) and *Haynesina germanica* (average RA 39%) as the dominant species. The allochthonous hyaline *Brizalina variabilis*, *Criboelphidium selseyensis* and *Asterigerinata mamilla* appeared in this zone as secondary species, with average RA of 1–5%. DI2 was also characterized by a gradual decrease of organic matter content with depth. The following DI1 (0–32 cm depth) was characterized by a shift to an agglutinated-dominant assemblage, with *Haplophragmoides wilberti* as the most abundant form (average RA 82%). This DI1 showed a reduction of species richness and relatively high organic matter content (average 31%).

#### 3.2. Tancada

Three distinct DI were identified within the Tancada core (Fig. 2 and Table 2). The basal DI3 (67–106 cm depth) was characterized by a mixture of hyaline (average RA 91%) and porcellaneous foraminifera (average RA 9%). *A. beccarii* and *H. germanica* were the dominant species within DI3. Overlying DI3, the second depth interval (DI2, 12–67 cm depth) showed a very similar species composition, with *A. beccarii* and *H. germanica* as the dominant species, and *Criboelphidium oceanensis* and *Criboelphidium* sp.1 as secondary species. This DI2 was also characterized by the presence of *Quinqueloculina seminula* and other miliolids, with a peak of abundance around 40–45 cm depth. The topmost DI1 (0–12 cm depth) showed an abrupt shift in the foraminiferal assemblages: the calcareous species disappeared, and the foraminiferal assemblages were entirely dominated by the agglutinated *Jadammina macrescens* and *Trochammina inflata* (Fig. 2). Species richness was low (average 6) and organic matter content was high (average 49%, range 37–59%).

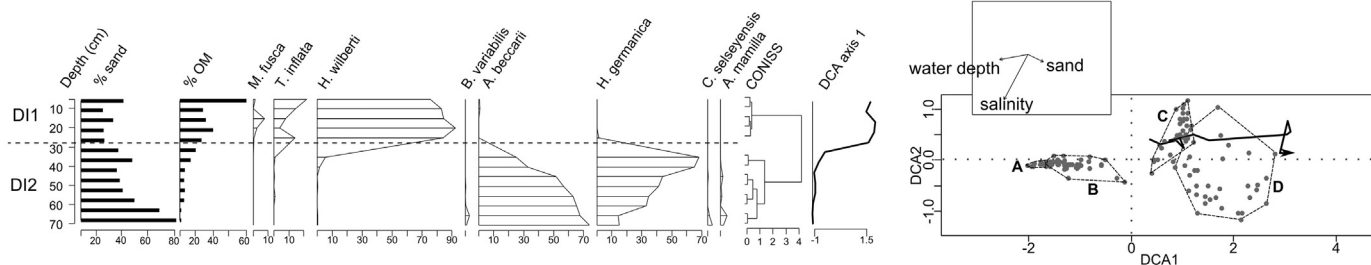
#### 3.3. Alfacs

Three distinct DI were distinguished within the Alfacs core (Fig. 2 and Table 2). The basal DI3 (37–65 cm depth) was characterized by the presence of the hyaline marine species *Buccella granulata*, *Aubygnina* cf. *perlucida*, *A. mamilla* and *Tretomphalus* cf. *concinus*. The overlying DI2 (12–37 cm depth) was marked by an increase of porcellaneous foraminifera (average RA 49%). There was also an increase of other marine species such as *Haynesina depressula* and *Criboelphidium* sp.1, and sand content in relation with underlying DI3. The topmost DI1 (0–12 cm depth) was dominated by agglutinated species *J. macrescens* and *T. inflata* (average RA 54%), with a minor contribution of *A. beccarii* and miliolids. DI1 also showed the highest organic matter content of the core (Fig. 2). The species richness was slightly lower than in DI2 and D3.

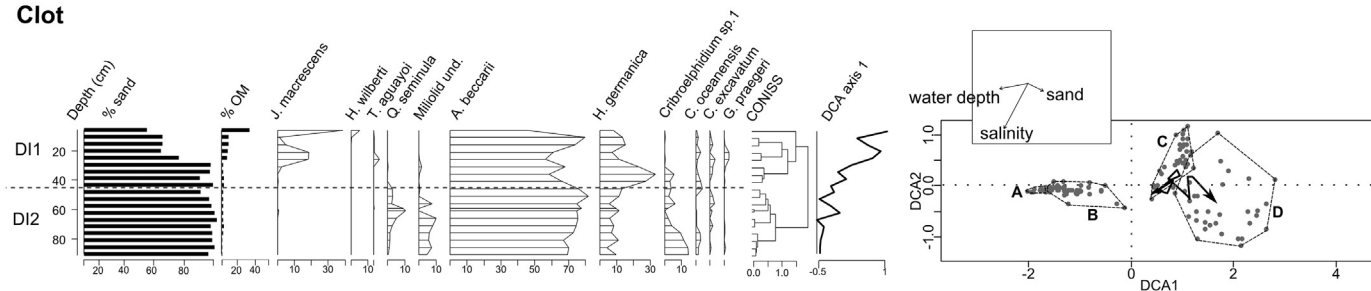
#### 3.4. Clot

The Clot core was divided into two distinct DIs (Fig. 2 and Table 2). The basal DI2 (42–90 cm depth) had high relative abundances of *A. beccarii* (average 74%). This interval showed also an average of 13 allochthonous species, in particular *Q. seminula*, *Criboelphidium* sp.1 and miliolids appeared at 60 cm depth. The sand content was very high throughout this DI2 (average 92.7%). The overlying DI1 (0–42 cm depth) was characterized by a mixture of hyaline and agglutinated

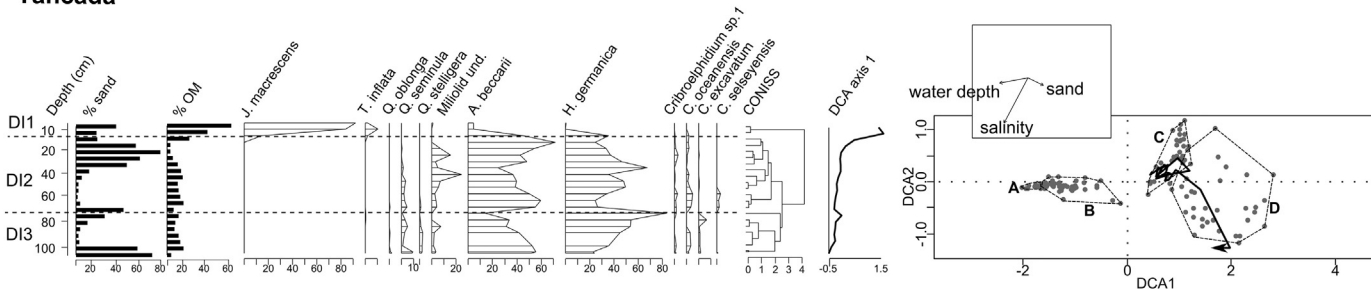
**Olles**



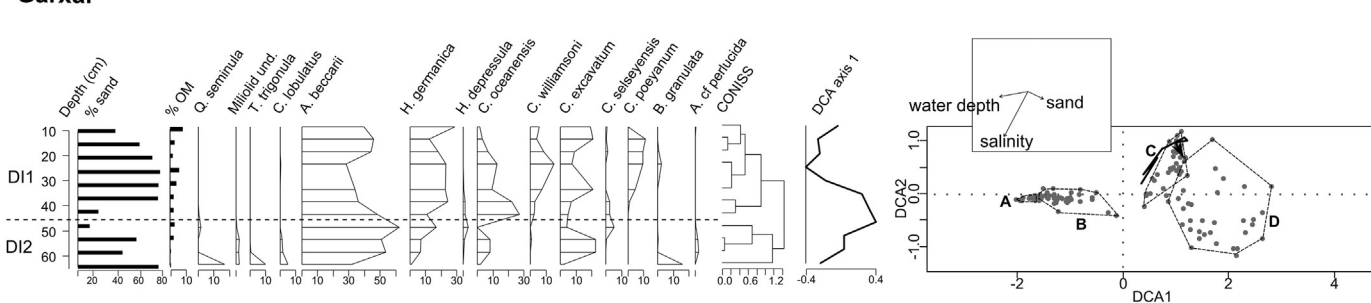
**Clot**



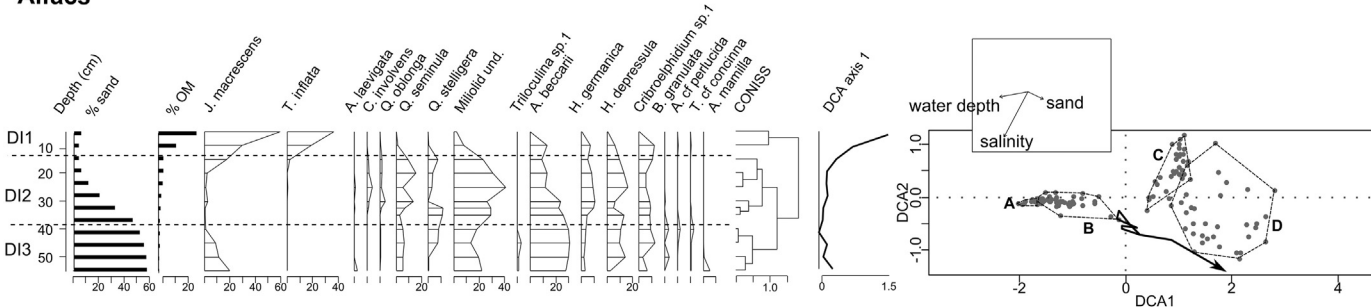
**Tancada**



**Garxal**



**Alfacs**



**Fig. 2.** Stratigraphic diagrams of the five studied cores in the Ebro Delta: sand content (%), organic matter content (%), main foraminiferal species (>2% RA at least in one sample), DCA axis 1, CONISS cluster analysis, and core trajectories projected onto the DCA along with modern samples. Dashed lines in DCA plots encompass modern habitat samples of each habitat type identified in the Ebro Delta according to Benito et al. (under review): A) offshore; B) nearshore and outer bays, C) coastal lagoons and inner bays, and D) salt and brackish marshes. Environmental vectors are fitted on top of each DCA plot. Notice that the DCA axis 1 scale differs among each diagram.

**Table 2**  
Summary of estimated periods and foraminiferal assemblages from the Ebro Delta studied cores. The single value represents the mean and the range is represented between parentheses.

	OLLES	TANCADA	ALFACS	CLOT	GARXAL
Depth core (cm)	70	106	65	90	70
	<i>DI1</i>	<i>DI1</i>	<i>DI1</i>	<i>DI1</i>	<i>DI1</i>
Elevational range (cm)	1.2 to -23.8	8.6 to -1.4	-3.9 to -13.9	-3.7 to -43.7	4.9 to -25.1
Tests	285 (144–344)	234 (163–304)	333 (325–341)	335 (304–379)	317 (178–421)
Species	4 (4–5)	6 (6–6)	13 (7–18)	11 (7–15)	13 (9–16)
Estimated period	1930s–present	1970s–present	1980s–present	1960s–present	1900s–present
Allochthonous %	0.06 (0–0)	0.8 (0–1)	16.8 (3–30)	5.1 (0–10)	25.9 (9–41)
Agglutinated %	99.5 (99–100)	94.5 (94–95)	72.4 (48–96)	12.1 (0–46)	1.0 (0–3)
Porcellaneous %	0	0.3 (0–1)	6.52 (3–10)	0.3 (0–2)	0.1 (0–0)
Hyaline %	0.5 (0–1)	5.2 (5–6)	21.1 (1–41)	87.6 (54–100)	98.9 (97–99)
	<i>DI2</i>	<i>DI2</i>	<i>DI2</i>	<i>DI2</i>	<i>DI2</i>
Elevational range (cm)	-23.8 to -63.8	-1.4 to -61.4	-13.9 to -38.9	-43.7 to -88.7	-25.1 to -60.1
Tests	322 (199–415)	362 (323–406)	393 (350–440)	357 (316–386)	256 (100–344)
Species	10 (4–21)	9 (7–13)	19 (18–20)	8 (5–12)	18 (17–20)
Estimated period	Before 1900s	Middle 1800s–1970s	1900s–1980s	Before 1960s	Before 1900s
Allochthonous %	3.9 (0–16)	10.4 (2–27)	61.0 (49–73)	12.8 (1–24)	23.1 (9–48)
Agglutinated %	1.4 (0–7)	1.5 (0–16)	4.6 (1–19)	0.1 (0–1)	0.7 (0–1)
Porcellaneous %	0.1 (0–1)	8.1 (0–26)	49.0 (44–55)	8.5 (3–16)	10.6 (3–34)
Hyaline %	99.5 (93–100)	90.4 (74–100)	46.5 (36–55)	91.4 (84–97)	88.6 (65–97)
		<i>DI3</i>	<i>DI3</i>		
Elevational range (cm)		-61.4 to -92.4	-38.9 to -63.9		
Tests		340 (314–379)	237 (150–355)		
Species		10 (7–15)	19 (16–24)		
Estimated period		Before 1800s	Before 1900s		
Allochthonous %		8.2 (2–13)	51.4 (44–60)		
Agglutinated %		0.1 (0–1)	11.5 (2–21)		
Porcellaneous %		9.1 (1–16)	31.0 (27–34)		
Hyaline %		90.8 (84–99)	57.6 (48–64)		

foraminifera, with *A. beccarii* (average RA 63%), *H. germanica* (18%) and *J. macrescens* (11%). This DI2 showed a gradual decrease of the allochthonous component and an increase of the organic matter content towards the top.

### 3.5. Garxal

Two distinct DIs were recognized in the Garxal core (Fig. 2 and Table 2). The basal DI2 (32–70 cm depth) was characterized by a mixture of hyaline (average 89%) and porcellaneous (average 11%) foraminifera. The mean allochthonous content through this DI2 interval was 23%, with the appearance of different marine foraminifera, such as *H. depressula*, *B. granulata* and *Cibicides lobulatus*. The top DI1 (0–32 cm depth) showed an increase of hyaline foraminifera (average 99%), with *A. beccarii*, *H. germanica*, and several *Criboelphidium* species (e.g. *C. excavatum*, *C. oceanensis* and *C. poeyanum*) as dominant species. The proportion of allochthonous foraminifera was slightly higher than in DI2, where the average was 26%.

### 3.6. Core trajectories and analogue matching

Core trajectories, illustrated in Fig. 2, showed that Olles, Tancada and Clot indicated a clear habitat shift from coastal lagoons and inner bays to salt and brackish marshes. Alfacs showed a trajectory from nearshore habitats to salt and brackish marshes (Fig. 2). On the other hand, the core trajectory of Garxal showed that this site did not experience significant habitat change, since its whole trajectory lay within the coastal lagoon and inner bay habitat (Fig. 2).

The buried foraminiferal samples, when plotted passively onto DCA ordination with the modern samples, also showed that Olles, Clot and Alfacs cores were arranged along DCA axis 1, but Tancada and Garxal cores mainly along axis 2 (Fig. 2). Salinity was significantly correlated with both ordination axes ( $r^2 = 0.57$ ,  $p < 0.001$ ). There was also

significant relationship between the first two DCA axes and water depth ( $r^2 = 0.31$ ,  $p < 0.001$ ) and sand content ( $r^2 = 0.10$ ,  $p < 0.001$ ). Organic matter content was significantly and positively correlated with DCA axis 1 scores (Pearson  $r > 0.80$ ,  $p < 0.01$ ), except for the Garxal core.

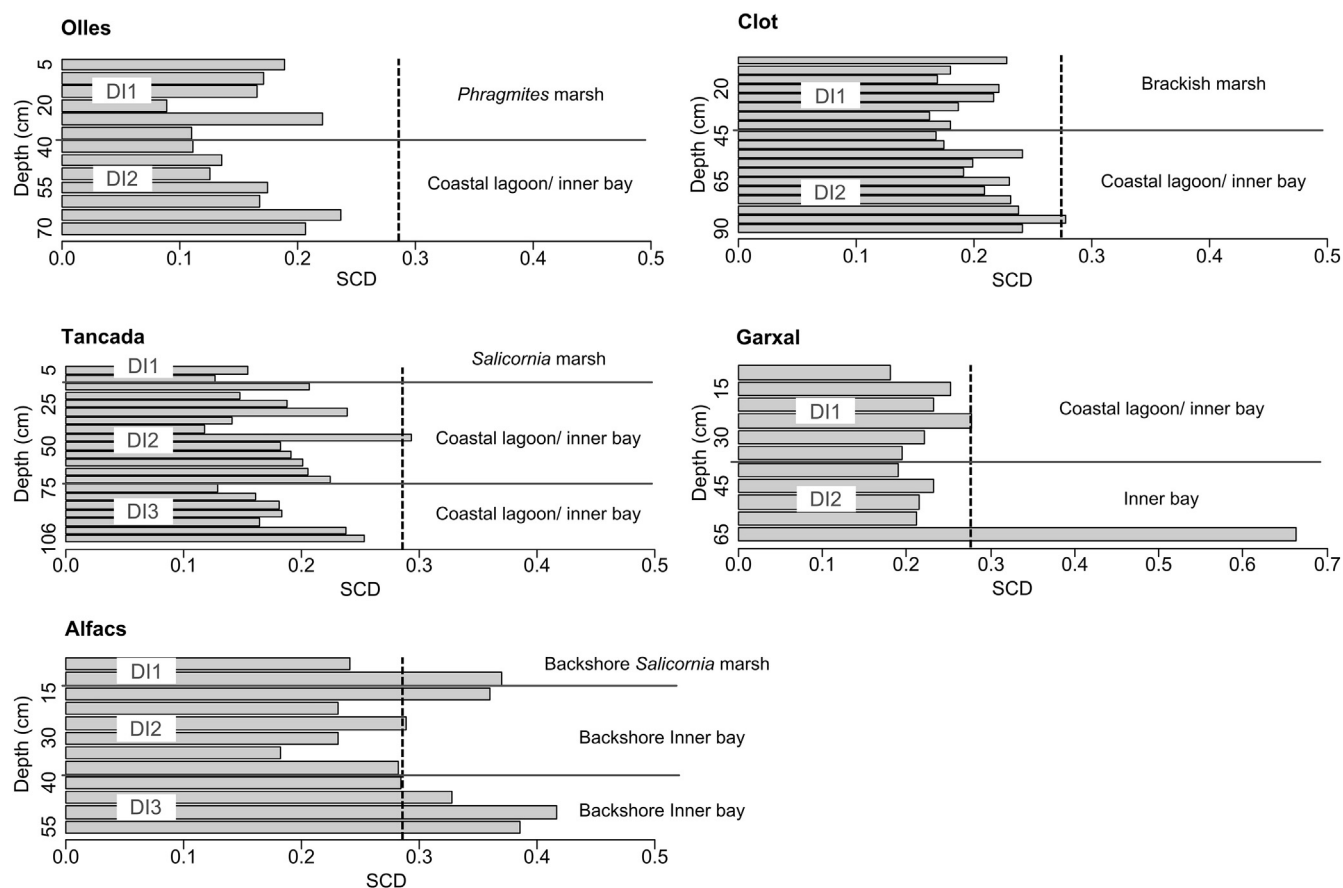
Most of the core samples from Olles, Clot, Tancada and Garxal showed low dissimilarity distances from the modern data set (SCD < 0.271), implying that they have “close” modern analogues (Fig. 3). High dissimilarity distances (SCD > 0.39) were observed in two samples of the Alfacs core, one in DI3 and the other in DI1, where relatively high average RAs (i.e. 10–30%) of marine species were found. Very similar results were found in one sample of Garxal core (DI2) (Fig. 3).

## 4. Discussion

Detailed knowledge of modern foraminiferal distributions and ecology in the Ebro Delta (Benito et al., under review) was used to reconstruct environmental changes in the five studied cores. As in similar microtidal systems elsewhere (Alve and Murray, 1999; Serandrei-Barbero et al., 2011), the dead foraminiferal assemblages of the Ebro Delta have proved to be a good reflection of the living ones, with a mean similarity of 72.9% based on Rogers index (Benito et al., under review). Although calcareous and agglutinated foraminifera can be prone to dissolution once buried in the sediments (Boltovskoy and Wright, 1976; Murray and Alve, 1999), in the present study foraminiferal tests were abundant in almost all samples and very well preserved. Therefore, because of the positive performance of these two factors (i.e. similarity between living and dead assemblages, and good test preservation) modern and buried assemblages can be properly compared in order to interpret the palaeoenvironmental changes recorded in the Ebro Delta cores.

The core assemblages show that present-day environmental conditions in the Ebro Delta wetlands differ greatly from those at the end of





**Fig. 3.** Barplots of square chord distance (SCD) between buried and modern (dead) foraminiferal samples for each of the five studies cores. The vertical dashed line indicates the largest dissimilarity coefficient (SCD = 0.271). Depth intervals (DIs) defined by CONISS analyses and analogue habitat types are also shown for each core.

the 1800s and in the early 1900s. The assemblages at the base of the Olles core (DI2, i.e. before the 1900s) were characterized by relatively few allochthonous components and a hyaline dominated assemblage, suggesting shallow subtidal lagoonal conditions (Murray, 2006). The habitat shift recorded in DI1, when agglutinated *H. wilberti* became dominant, correlates well with the wetland transformation for rice cultivation that began in the northern hemidelta in 1912, with the construction of the north irrigation channel derived from the Ebro River. Olles wetland was then largely isolated from the Mediterranean Sea (Fangar Bay, see Fig. 1), and began to receive enhanced inputs of drainage and sewage waters. A comparable assemblage occurs nowadays in the *Phragmites* marshes of the Ebro Delta (Benito et al., under review), which occupy the littoral zones around fresh-brackish coastal lagoons. These marshes are rich in nutrients and organic matter and are fresher than they were originally, due to freshwater inputs coming from rice field drainage. Debenay and Guillou (2002) also indicate the preference of *H. wilberti* for organic-rich sediments in Mediterranean coastal wetlands.

The different locations of the Alfacs and Tancada cores may explain the differences in habitat conditions recorded before the 1970s–1980s: DI3 and DI2 of Alfacs are interpreted as inner bay with high marine influence due to its near connection with the bay through a backshore marsh, whereas DI3 and DI2 of Tancada are interpreted as coastal lagoon/inner bay environment with much less hydrologic connectivity with the sea (i.e. further away from the bay, see Fig. 1). This interpretation is supported by the dominance of allochthonous foraminifera in DI3 and DI2 of Alfacs, and autochthonous foraminifera in both DI3 and DI2 of Tancada (Table 2). A higher marine influence in Alfacs is further supported by the very high dissimilarity distances in DI3 compared to those in DI3 of the Tancada core. However, although originally rather different, the Tancada and Alfacs biotopes

evolved towards a similar end-point (i.e. *Salicornia* marsh). This habitat transition was accompanied by an abrupt microfaunal change, revealed by DCA axis 1 (Fig. 2), and by the clear dominance of agglutinated species in both DI1 intervals (Table 2). These results could be related to agricultural runoff that these two areas began to receive recently (1970s–1980s) due to water management practises: input of freshwater from rice drainage to the corner of Alfacs bay (near Alfacs site, see Fig. 1) and to the eastern side of the Tancada lagoon (near Tancada site, see Fig. 1). Environmental changes will have not only decreased salinity but also lowered pH, since rice-field runoff is generally acid (Comoretto et al., 2008). More acidic conditions are known to be favourable for agglutinated foraminifera (Alve, 1995; Scott et al., 2005; Tsujimoto et al., 2006). The dominance of agglutinated foraminifera in surface sediments at Tancada and Alfacs is comparable to that observed in the salt marshes in the Mekong Delta, where *T. inflata* and *J. macrescens* became dominant due to artificial freshwater inflows for shrimp and rice farming (Luan and Debenay, 2005).

The foraminiferal assemblages revealed that habitat changes were smaller in the Clot core than in the cores from Olles, Tancada and Alfacs, with a lesser decline in the calcareous assemblage in DI1, even though rice cultivation has developed similarly in all four areas. The reason for this may be the recent restoration of Clot lagoon that took place in 1991 (Comín et al., 1991). Since then, the freshwater inputs to Clot have mainly been direct from the river (via the irrigation canals, and therefore of better quality; Ibáñez et al., 2012), rather than from rice-field drainage. Lower pH, associated with the high organic content of the rice field runoff, decreases the availability of  $\text{CaCO}_3$  and it is known to affect calcareous foraminifera (Greiner, 1969). Interestingly, Clot is also set apart from the other three sites (Olles, Tancada and Alfacs) by the fact that it has recovered its natural macrophyte vegetation during the last 20 years, since the change to riverine water supply (Forés et al., 2002).

Although two distinct foraminiferal assemblages were found in the Garxal core, the habitat shift observed here was much less pronounced than those observed in the four other study sites, comprising only a slight decline in marine influence within the same habitat type (i.e. coastal lagoon/inner bay). This decline is very likely related to the natural change in the river mouth that took place at the beginning of 20th century. Between 1907 and 1937 exceptional river floods (up to  $23,000 \text{ m}^3 \text{ s}^{-1}$ ; Somoza and Rodríguez-Santalla, 2014) opened several crevasses in the northern bank three kilometres upstream from the former active mouth, offering a shorter distance to the sea (see Fig. 1; Maldonado and Riba, 1971). Then, the flow through the breach created a new shallower embayment (nowadays known as Garxal lagoon) that since 1950 has gradually become isolated from the Mediterranean Sea due to formation of sandy barriers (Maldonado and Riba, 1971). The slight increase in Garxal D11 of *C. selseyensis*, *C. poeyanum* and *C. excavatum*, which are characteristic of living assemblages in marine habitats adjacent to the Delta (Scrutton, 1969), suggests a certain marine influence in this site.

Besides the Ebro Delta, a number of other Mediterranean coastal wetlands are fresher nowadays than they originally were, mainly due to the effects of hydrologic alterations caused by rice cultivation. This is the case, for instance, in the Albufera de Valencia (Soria, 2006; Marco-Barba et al., 2013) and Mar Menor lagoon (Pérez-Ruzafa et al., 1991) in Spain, and the Rhône Delta wetlands in France (Pont et al., 2002). Not surprisingly, therefore, studies dealing with benthic foraminifera as palaeoenvironmental proxies have focused on human-induced salinity variations as the sole predictor of coastal wetland impacts (Brewster-Wingard and Ishman, 1999; Cheng et al., 2012; Sousa et al., 2014). However, we observed that not only salinity but also water depth and sand content play a significant role in explaining the variation of the buried species composition. This suggests that foraminiferal assemblages did not change only as a result of salinity modifications, but were due instead to a combination of factors that represent a change in habitat-type. In natural systems such as deltas where most environmental factors show high spatial and temporal variability, identification of the single main factor determining foraminiferal distribution is a difficult or impossible task (Murray, 2001). This is because the foraminifera living there have a wide ecological tolerance for a high number of factors (i.e. they are eurytopic species). Thus, explanations of changes observed in the foraminiferal assemblages of the Ebro Delta and similar systems should take into account not only salinity modifications but also water depth and its fluctuations (e.g. subtidal/supratidal conditions), substrate characteristics, eutrophication, hydrological isolation (impoundment), etc.

The pattern of changes in organic matter content in our cores is consistent with the idea of habitat alteration accompanying the extensive development of rice cultivation. Seasonal inputs of rice drainage water (in April–September, i.e. during the rice growing season), with high levels of organic matter and nutrients, promote the accumulation of organic-rich sediments due to low salinities (Ibáñez et al., 2010). The general upcore increase of organic matter at Olles, Tancada, Alfacs and Clot is statistically related to changes in species composition, with a clear shift from calcareous to agglutinated foraminifera. A very similar pattern (i.e. increase of agglutinated and decrease of calcareous taxa) has been recorded in cores from Mobile Bay, Gulf of Mexico (USA), and Bedford Bay, Nova Scotia (USA) as a response to high organic loading (Osterman and Smith, 2012; Scott et al., 2005). Therefore, this core gradient may be tentatively associated to an indirect measure of habitat modification.

Human-induced changes also provoked reduction of species richness towards the top of the cores, likely reflecting deteriorating of ecological status through time (Alve et al., 2009). The very low diversity assemblages of agglutinated species observed in D11 (of Olles, Tancada and Alfacs, and to a lesser extent in Clot), might be related to increasing abundance of a few opportunistic species, at the expense of species more sensitive to unfavourable conditions, e.g. low oxygen, more acidic

conditions (Alve, 1995; Osterman and Smith, 2012). However, many naturally stressed habitats can also possess low diversity assemblages dominated by agglutinated forms (e.g. Murray, 2006).

The long-term results obtained give insights into the ecological conditions present in the Ebro Delta before intensive rice cultivation began at the end of 1800s and early 1900s. By characterizing present-day conditions via living foraminiferal assemblages (Benito et al., under review), the degree of deviation from natural conditions can therefore be assessed. Studies in northern Europe (Bouchet et al., 2013; Schönfeld et al., 2012) have also shown the potential of benthic foraminifera for monitoring coastal ecosystems and in fact, the Ecological Quality Status of Norwegian fjords is classified as “unacceptable” or “acceptable” using benthic foraminifera (Dolven et al., 2013). Our study indicates that this approach could usefully be extended to Mediterranean coastal wetlands to better define restoration goals and support environmental policies (e.g. Water Framework Directive).

## 5. Conclusions

The Ebro Delta wetland habitats have undergone clear shifts since the beginning of intensive human colonization started approximately 150 years ago. Foraminiferal assemblages track both natural- (Garxal) and anthropogenic (Olles, Tancada, Alfacs and Clot) environmental changes. At the beginning of 1900s, a significant decrease occurred in both calcareous and allochthonous foraminifera, which can be related to the transformation of most of the Delta wetlands to extensive rice agriculture. A further upcore trend is a significant loss of diversity and dominance of agglutinated foraminifera, which seems to have been a response to the increased organic matter in the sediment due to inputs of agricultural runoff.

The paleoenvironmental data obtained in this study provide a historical perspective on the Ebro Delta wetlands, which are in many ways representative of other anthropogenically impacted Mediterranean coastal wetlands. Long-term studies that combine indicators of land alterations (e.g. organic matter) and downcore changes linked to foraminifera ecology, will help to provide baselines for future monitoring and restoration strategies in Mediterranean deltas. This should be especially relevant for the Ebro Delta, which is at risk due to global change consequences such as sea-level rise and sediment deficit (Ibáñez et al., 2014).

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## Appendix A

Taxonomic reference list. Each species is classified as autochthonous (AU) or allochthonous (AL) according to their components (living vs dead) in the modern assemblages of the Ebro Delta samples (see **Material and methods** for our definition of autochthonous and allochthonous foraminifera).

### Agglutinated forms

*Ammobaculites balkwilli* Haynes, 1973: AL  
*Ammobaculites* sp.1: AL  
*Eggerella advena* (Cushman) = *Verneuilina advena* Cushman, 1921: AL  
*Eggerelloides scaber* (Williamson) = *Bulimina scabra* Williamson, 1858: AL  
*Haplophragmoides wilberti* Anderson, 1953: AU  
*Haplophragmoides* sp.1: AL  
*Jadammina macrescens* (Brady) = *Trochammina inflata* (Montagu) var. *macrescens* Brady, 1870: AU  
*Miliammina fusca* (Brady) = *Quinqueloculina fusca* Brady, 1870: AU  
*Scherochorella moniliformis* (Siddall) = *Reophax moniliformis* Siddall, 1886: AL  
*Textularia bocki* Höglund, 1947: AL  
*Textularia* cf. *calva* Lalicker, 1935: AL  
*Trochammina inflata* (Montagu) = *Nautilus inflatus* Montagu, 1808: AU  
*Trochammina* sp.1: AL  
Texturalid undetermined: AL

### Porcellaneous forms

*Adelosina laevigata* (d'Orbigny) = *Quinqueloculina laevigata* d'Orbigny, 1939: AL  
*Cornuspira involvens* (Reuss) = *Operculina involvens* Reus, 1850: AL  
*Massilina secans* (d'Orbigny) = *Quinqueloculina secans* d'Orbigny, 1826: AL  
*Milonella subrotunda* (Montagu) = *Vermiculum subrotundum* Montagu, 1803: AL  
*Quinqueloculina jugosa* (Cushman) = *Quinqueloculina seminula* var. *jugosa* Cushman, 1944: AU  
*Quinqueloculina longirostra* d'Orbigny, 1826: AL  
*Quinqueloculina oblonga* (Montagu) = *Vermiculum oblongum* Montagu, 1893: AL  
*Quinqueloculina quadrata* Nörvang 1945: AL  
*Quinqueloculina seminula* (Linné) = *Serpula seminulum* Linné, 1758: AU  
*Quinqueloculina stelligera* Schlumberger, 1893: AL  
*Quinqueloculina vulgaris* d'Orbigny, 1826: AL  
*Triloculina dubia* d'Orbigny, 1826: AL  
*Triloculina marioni* Schlumberger, 1893: AL  
*Triloculina rotunda* d'Orbigny, 1939: AL  
*Triloculina trigonula* (Lamarck) = *Miliolites trigonula* Lamarck, 1804: AL  
*Triloculina* sp.1: AL  
Miliolid undetermined: AL

### Hyaline forms

*Ammonia beccarii* (Linné) = *Nautilus beccarii* Linné, 1758: AU  
*Asterigerinata mamilla* (Williamson) = *Rotalia mamilla* Williamson, 1858: AL  
*Aubygnina* cf. *perlucida* (Heron-Allen and Earland) = *Rotalia perlucida* Heron-Allen and Earland, 1913: AL  
*Bolivina pseudoplicata* Heron-Allen and Earland, 1930: AL  
*Bolivina striatula* (Cushman) = *Brizalina striatula* Cushman, 1922: AL  
*Bolivinnella pseudopunctata* (Höglund) = *Bolivina pseudopunctata* Höglund, 1947: AL  
*Brizalina spathulata* (Williamson) = *Textularia variabilis* Williamson var. *spathulata* Williamson, 1858: AL  
*Brizalina variabilis* (Williamson) = *Textularia variabilis* Williamson, 1859: AL  
*Buccella granulata* (di Napoli Alliata) = *Eponides frigidus* var. *granulatus* di Napoli Alliata, 1952: AL  
*Buliminella elegantissima* (d'Orbigny) = *Bulimina elegantissima* d'Orbigny, 1939: AL  
*Bulimina elongata* d'Orbigny, 1926: AL  
*Bulimina gibba* Fornasini, 1902: AL  
*Bulimina marginata* d'Orbigny, 1826: AL  
*Cassidulina laevigata* d'Orbigny, 1826: AL

*Cibicides lobatulus* (Walker and Jacob) = *Nautilus lobatulus* Walker and Jacob, 1798: AL  
*Criboelphidium excavatum* (Terquem) = *Polystomella excavatum* Terquem, 1875: AU  
*Criboelphidium magellanicum* (Heron-Allen and Earland) = *Elphidium magellanicum* Heron-Allen and Earland, 1932: AL  
*Criboelphidium oceanensis* (d'Orbigny) = *Polystomella oceanensis* d'Orbigny, 1826: AU  
*Criboelphidium selseyensis* (Heron-Allen and Earland) = *Elphidium selseyensis* Heron-Allen and Earland, 1911: AU  
*Criboelphidium williamsoni* (Haynes) = *Elphidium williamsoni* Haynes, 1973: AL  
*Criboelphidium* sp.1: AL  
*Elphidium* cf. *earlandi* Cushman, 1936: AL  
*Elphidium advenum* (Cushman) = *Polystomella advenum* Cushman, 1922: AL  
*Elphidium crispum* (Linné) = *Nautilus crispum* Linné, 1758: AL  
*Elphidium gerthi* Van Voorthuysen, 1957: AL  
*Elphidium incertum* (Williamson) = *Polystomella umbilicatula* var. *incerta* Williamson, 1858: AL  
*Elphidium margaritaceum* (Cushman) = *Elphidium advenum* var. *margaritaceum* Cushman, 1930: AL  
*Elphidium* undetermined: AL  
*Fissurina marginata* (Montagu) = *Vermiculum marginatum* Montagu, 1803: AL  
*Fissurina lucida* (Williamson) = *Entosolenia marginata* (Montagu) var. *lucida* Williamson, 1848: AL  
*Gavelinopsis praegeri* (Heron-Allen and Earland) = *Discorbina praegeri* Heron-Allen and Earland, 1913: AL  
*Gyroidina* sp.1: AL  
*Haynesina depressula* (Water and Jacob) = *Nautilus depressulus* Walker and Jacob, 1798: AL  
*Haynesina germanica* (Ehrenberg) = *Nonionina germanica* Ehrenberg, 1840: AU  
*Melonis pompilioides* (Fitchel and Moll) = *Nautilus pompilioides* Fitchel and Moll, 1798: AL  
*Nonionella atlantica* Cushman, 1947: AL  
*Nonionella opima* Cushman, 1947: AL  
*Planorbulina mediterraneensis* d'Orbigny, 1826: AL  
*Pyrgo inornata* (d'Orbigny) = *Biloculina inornata* d'Orbigny, 1846: AL  
*Reussella aculeata* Cushman, 1945: AL  
*Riminopsis* cf. *asterizans* (Fichtel and Moll) = *Nonion* cf. *asterizans* Fichtel and Moll, 1798: AL  
*Rosalina anomala* Terquem, 1875: AL  
*Rosalina globularis* d'Orbigny, 1826: AL  
*Rosalina irregularis* (Rhumbler) = *Discorbina irregularis* Rhumbler, 1906: AL  
*Trichohyalus aguayoi* (Bermudez) = *Discorinopsis aguayoi* Bermudez, 1935: AU  
*Tretomphalus* cf. *concinus* (Brady) = *Discorbina concinna* Brady, 1884: AL  
*Valvulineria bradyana* (Fornasini) = *Discorbina bradyana* Fornasini, 1899: AL  
Unidentified forms: AL

### Appendix B. Supplementary data

Supplementary data associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.marpolbul.2015.11.003>. These data include the Google map of the most important areas described in this article.

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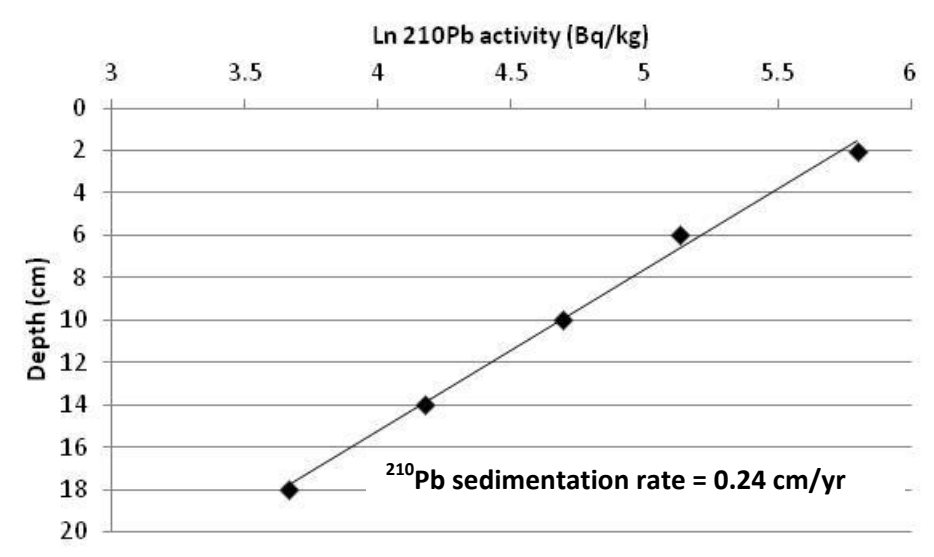
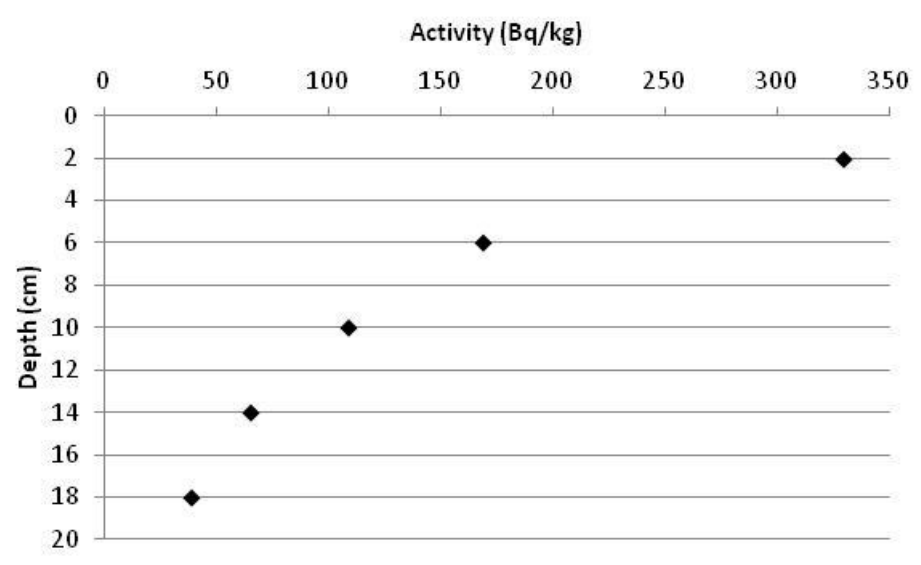


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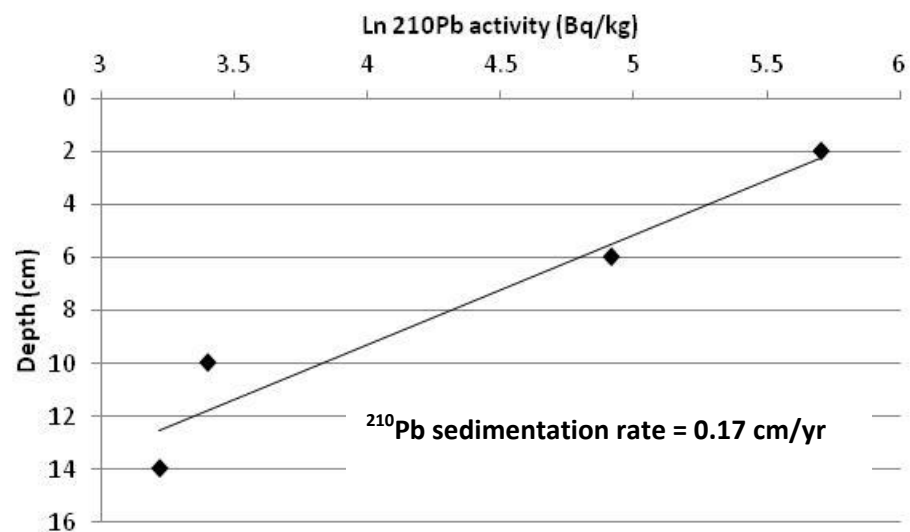
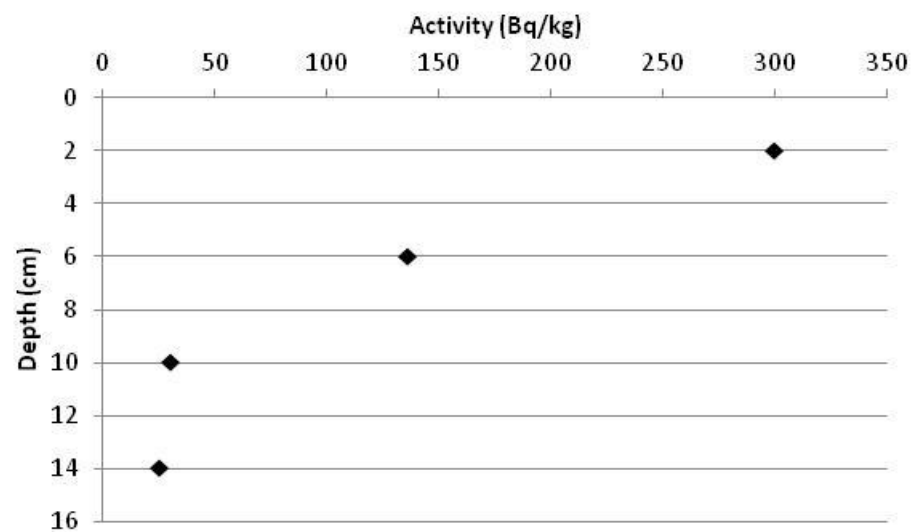
### Supplementary material

**Figure S1** Down-core profile of excess  $^{210}\text{Pb}$  in the Ebro Delta cores. Left figures: excess  $^{210}\text{Pb}$  activity (Bq/kg). Right figures: natural logarithm of  $^{210}\text{Pb}$  activity. The solid regression line provides the average sedimentation rate.

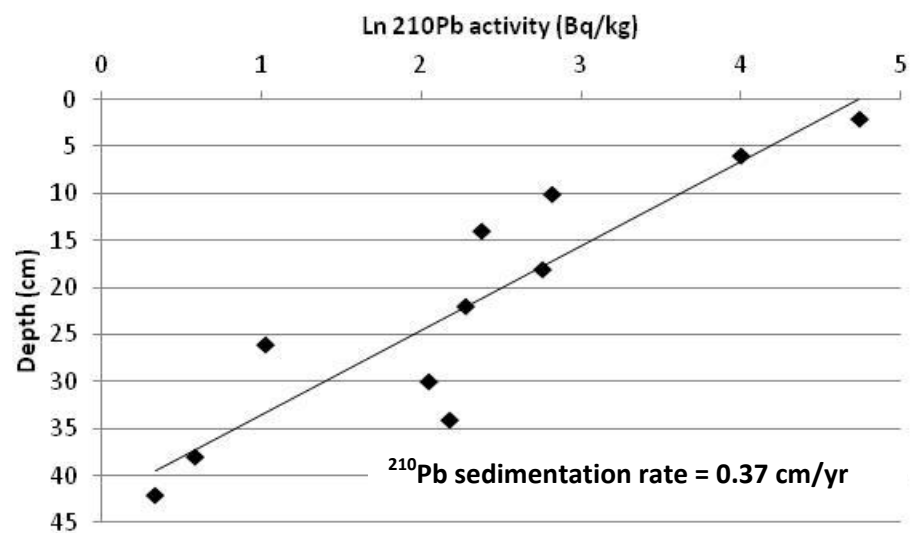
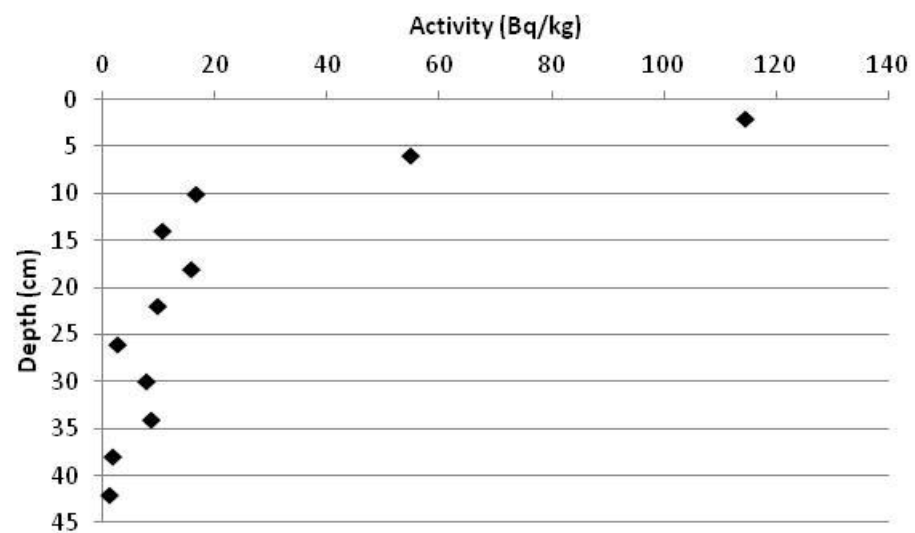
### Olles



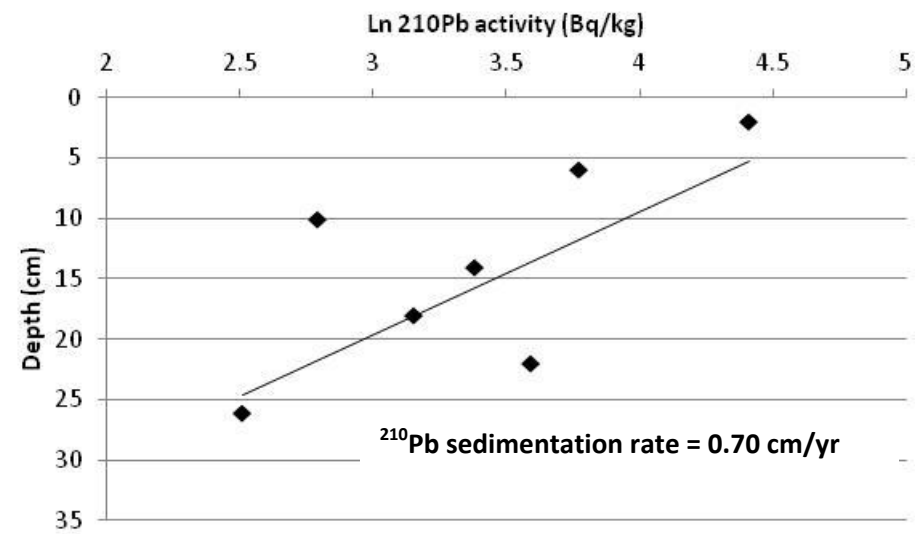
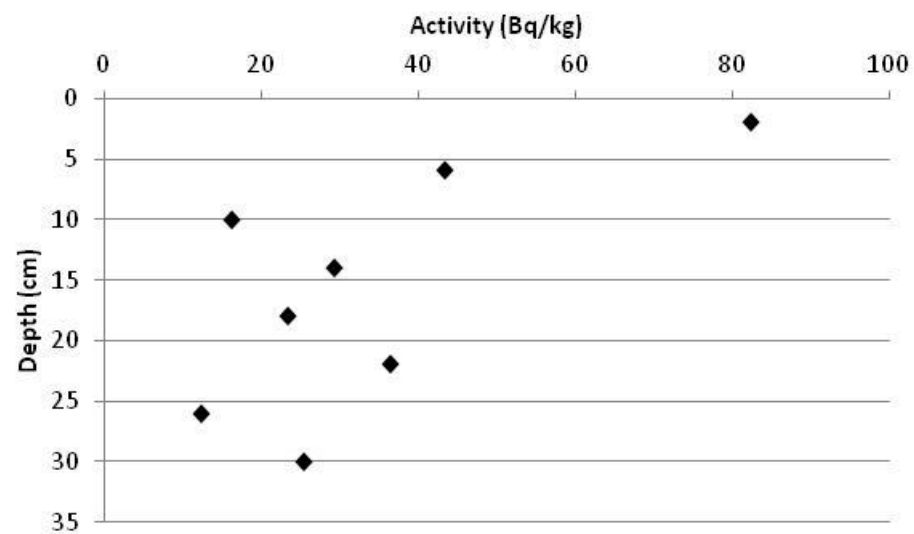
## Tancada



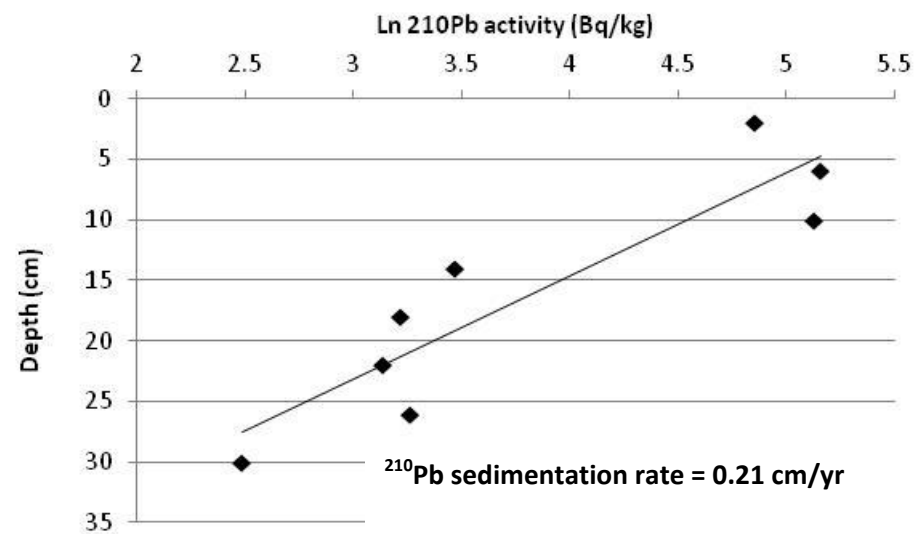
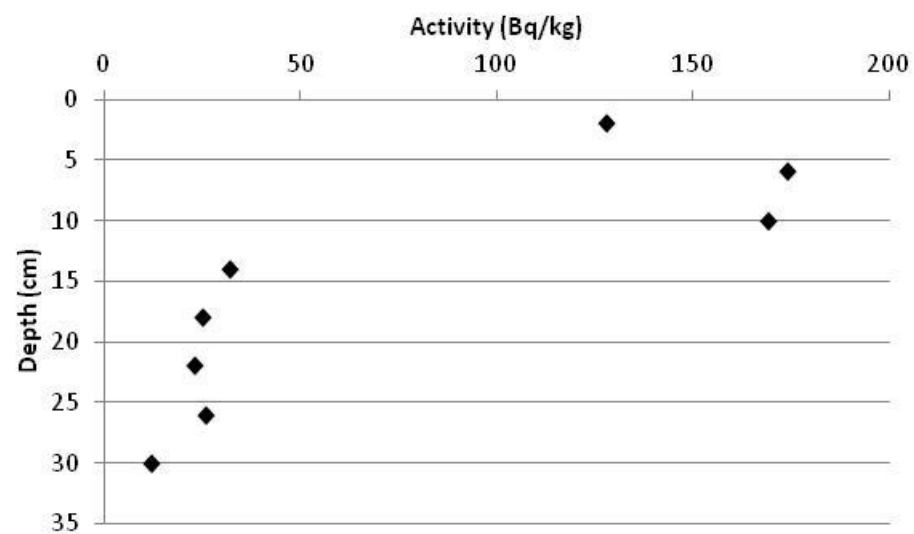
## Alfacs



## Clot



## Garxal



*Chapter 4: Recent human impacts*

**Table S1** Summary of foraminifera and core data. Excel sheet 1: Foraminiferal abundances (relative abundance [RA] expressed as percentage). In green: dominant species (RA  $\geq$  10%). In yellow: secondary species (RA = 1–10%); Excel sheet 2: Microfaunal parameters; Excel sheet 3:  $^{210}\text{Pb}$ -based chronology. Uncoloured: estimated chronology directly from  $^{210}\text{Pb}$  excess. In grey: extrapolated chronology (depths below the level of  $^{210}\text{Pb}$  detection).

The table can be found in the online version at the *Marine Pollution Bulletin* website <http://dx.doi.org/10.1016/j.marpolbul.2015.11.003>.

UNIVERSITAT ROVIRA I VIRGILI

BENTHIC DIATOMS AND FORAMINIFERA AS INDICATORS OF COASTAL WETLAND HABITATS: APPLICATION TO PALAEOENVIRONMENTAL RECONSTRUCTION

Xavier Benito Granel



## ***Chapter 5***

### **Modelling habitat distribution of Mediterranean coastal wetlands: the Ebro Delta as case study**

Benito, X., Trobajo, R. and Ibáñez, C. 2014

*Wetlands* 34: 775-785

*Chapter 5: Potential habitat distribution*



# Modelling Habitat Distribution of Mediterranean Coastal Wetlands: The Ebro Delta as Case Study

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**Abstract** Present-day altered distribution of the natural habitats in the Ebro Delta is consequence of intensive human settlement in the last two centuries. We developed spatial predictive models of potential natural wetland habitats of the Ebro Delta based on ecogeographical predictors and presence/pseudo-absence data for each habitat. The independent variables (i.e. elevation, distance from the coast, distance from the river and distance from the inner border) were analysed using Generalized Additive Models (GAMs). Elevation and the distance from the coast appeared as key predictors in most of the coastal habitats (coastal lagoons, sandy environments, *Salicornia*-type marshes and reed beds), whereas distances from the river and from the inner border were relevant in the most terrestrial or inland habitats (salt meadows, *Cladium*-type marshes and riparian vegetation). Our findings suggest that the most inland habitats (i.e. *Cladium*-type marshes, salt meadows and riparian vegetation) would have undergone a severe reduction (higher than 90 %), whereas in the most coastal habitats (coastal lagoons, sandy environments, *Salicornia*-type marshes) the reduction in relation to their potential distribution would be around 70 %. This modelling approach can be applied to other deltaic areas, since all them share a similar topography.

**Keywords** Predictive modelling · Mediterranean wetlands · Deltas · Generalized additive models · Geographic information system

## Introduction

Deltas play an important ecological and economic role, and host different kinds of coastal habitats. The Ebro Delta (NE Iberian Peninsula) contains some of the most important wetland areas in the western Mediterranean and is a good example of coastal wetland with a wide variation of habitats influenced by many environmental factors (topography, hydrology and climate) (Ibáñez et al. 2000). Consequently, many ecological studies have been carried out in the Ebro Delta and its estuary (Rodrigues-Capítulo et al. 1994; Mañosa et al. 2001; Martínez-Alonso et al. 2004; Ibáñez et al. 2011; Nebra et al. 2011; Prado et al. 2012; Rovira et al. 2012a, b) but the original distribution of wetland habitats is not well known (Curcó et al. 1995). Unfortunately, the natural habitats of the Delta have been drastically reduced from their original distribution in the delta plain during the last century up to 70 % due to human settlement for rice farming (Cardoch et al. 2002). Significant changes in habitat distribution have been also observed in Mediterranean and other world deltas (Coleman et al. 2008). To assess changes in wetland habitat, research on habitat-environment relationship has become increasingly important since the understanding of such relations might be a useful conservation tool in the context of future restoration projects.

Habitat distribution models and species distribution models are among those tools that statistically relate species distributions to environmental conditions; however, these statistical models are able to project the distribution of species into the geographical space but are not able to provide a description of species niches (Jiménez-Valverde et al. 2008). Such predictive models have been used in a wide range of studies within

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terrestrial and aquatic ecosystems (Guisan and Zimmermann 2000). Commonly used methods include regression techniques such as Generalized Linear Models (GLMs, Shoutis et al. 2010) and Generalized Additive Models (GAMs, Joye et al. 2006; Peters et al. 2008). Some of these studies, however, lack of spatial predictions which could be solved combining them with Geographic Information Systems (GIS) (Franklin 1995).

Field research into vegetation-environment relationships has been carried out in some Mediterranean coastal marshes and has taken into account abiotic factors such as soil elevation (Curcó et al. 2002; Silvestri et al. 2005), groundwater (Pont et al. 2002) or mineral inputs (Ibáñez et al. 2010). These data are required as the basis for predictive habitat modelling, since they relate species occurrence to specific measured variables. However, direct measurement is often impractical, because of cost and time constraints (Austin 2002). Instead, GIS methods can be used to extrapolate from the available field data, by using ecogeographical variables (i.e. predictors) derived from a Digital Elevation Model (DEM) and aerial photographs. In this way, models can be developed to predict the actual or potential distribution of habitats across large areas that have not been surveyed in detail (Heinänen et al. 2012). To our knowledge, no study has previously been made using such techniques to predict the distribution of natural habitats in Mediterranean wetlands.

The main objective of this study was to predict the distribution of natural habitats of the Ebro Delta assuming a scenario of no human disturbance; the focus is on the exploration of habitat occurrences in relation with ecogeographical variables that are typically related to topographic and ecologic gradients of wetland areas. We used Generalized Additive Models (GAMs) to predict and map the potential distribution of habitats across the whole of the Delta, including the areas presently occupied by farmland or devoted to other uses (e.g. urban settlements). The models were evaluated on their goodness-of-fit. An additional goal was to assess the percentage of change accounted for each type of habitat in order to provide information that could aid land managers in managing or restoring natural habitats.

## Methods

### Study Area

The study was performed in the Ebro Delta (330 km<sup>2</sup>), which is one of the largest deltas in the northwestern Mediterranean. Rice fields occupy most of the delta plain (65 % of the total surface), while natural habitats cover only about 25 % (80 km<sup>2</sup>) (Fig. 1). These remaining natural habitats are of great environmental value and represent excellent examples of Mediterranean wetland habitats such as riparian vegetation, salt, brackish and fresh water marshes, coastal lagoons, bays,

sand dunes and mudflats. The present spatial distribution of Ebro Delta habitats is also shown in Supplementary Fig S1.

There were various reasons for choosing this study area. Firstly, there is good available information, both biological (habitat maps) and physical data (surface elevation). Secondly, there is a substantial spatial heterogeneity in this area, favouring the existence of diverse environments, and allowing a wide range of ecological gradients to be assessed with the actual deltaic plain configuration. And thirdly, there is a wide set of aerial and topographic maps for carrying the GIS analysis.

### Habitat Occurrence Data

The natural habitats in the Ebro Delta (Table 1) were classified following the Catalanian Habitats Map (CHM) at 1:50,000 scale (Vigo and Carreras 2003) which is an adaptation of the Corine Land Cover Mapping (CLC, a map of the European environmental landscape based on interpretation of satellite images, Bossard et al. 2000). For each of the natural habitats, present-day surface cover was determined according to their polygon area mapped in the CHM. Because binary models require presence/absence data, circa 300 presence points for each habitat were randomly obtained with the “Random point generator” extension of ArcGis 9.3. Due to the fact that the Ebro Delta salt meadows are the habitats that have been reduced the most (Curcó et al. 1995) 40 extra points were used for this habitat, obtained from field work in March 2012.

### Ecogeographical Variables

Variables derived from topography and landscape position were used as potential predictors. The following variables were considered in this study: surface elevation, distance from the coast, distance from the river and distance from the inner border of the deltaic plain. This set of distances and land elevation are strongly correlated with deltaic soil salinity and they indirectly reflect hydrological conditions (Ibáñez et al. 2000; Casanova et al. 2002). The variables “distance from the coast”, “distance from the river” and “distance from the inner border” were obtained from GIS using the “Euclidean distance” tool of the Spatial Analyst extension at 1 m of pixel resolution. For the deltaic plain topography, a Digital Elevation Model (DEM) with a spatial resolution of 1 m and a height accuracy of 15 cm built with LIDAR data by the Cartographic Institute of Catalonia was used. Topographic data are referred to mean sea level in Alicante datum (MSLA).

### Habitat Model

Generalized Additive Models (GAMs, Hastie and Tibshirani 1990) were used to model the relationship between natural habitat distribution and the ecogeographical predictors.

**Fig. 1** Location of the study area, the Ebro Delta



GAMs are a non-parametric extension of the Generalized Linear Models and are often used when there is a no priori reason for choosing a particular response function (i.e. linear, quadratic, etc.).

Because the impossibility of working with true absence data due to human-induced reduction and alteration of the habitats (i.e. impossibility to know whether the habitat absence is a result of environmental factors or of human activities), only pseudo-absence data were considered for building the models, as other authors have already recommended and applied (Chefaoui and Lobo 2008; Jiménez-Valverde et al. 2008).

Pseudo-absences for each habitat were generated randomly over the total area of concern (i.e. the Ebro Delta) but excluding the two spits (i.e. sandy barriers placed on both northern and southern hemideltas, see Fig. 1 and Supplementary Fig. S1). The morphology of these structures contributed to a large distortion of the variable “distance from the coast”. These pseudo-absence points were created at least 400 m apart from the presence points and were weighted according to the number of presence points in order to perform an equal number of presences and pseudo-absences (Ferrier et al. 2002; Phillips et al. 2009).

Because the response variable of habitat distribution to independent variables is a binary value (presence or pseudo-absence of the habitat), a binomial distribution of error was assumed and the probability of habitats occurrence was related to the ecogeographical variables via a logit link function.

The models were built including all the predictors, and step.gam function of GAM 1.06.2 package (Hastie 2012) of R software was used to select both relevant explanatory variables and the level of complexity of the response shapes to each variable. Then a series of models was fitted based on a bidirectional step by step process. The lowest Akaike Information Criterion (AIC) was used to select the subset of variables among the AIC resulting from those fitted variables with up 3 degrees of freedom for the smoothing cubic spline function (i.e. linear, non-linear or non-existent terms) (Wood and Augustin 2002).

Furthermore visual inspection of fitted response shapes was used in order to evaluate the ecological meaning of the final selected models. Such response shapes, based on GAM’s partial residuals, show the relative effect of the ecogeographical predictors on the probability of occurrence.

#### Model Validation

The predictive capability of the models was validated using a k-fold cross-validation test (See for instance Bekkby and Moy 2011 and Martínez et al. 2012). For each habitat, we performed 5 iterations of a 80–20 % splitting procedure. The training set (80 %) was used in the modelling phase referred above, whereas test set (20 %) was used to validate the models. The validation measures were averaged from the 5-generated datasets and two different parameters were

**Table 1** Brief description of Ebro Delta habitats considered in this work (urban areas, crops and spits are excluded) with actual area (obtained after the Catalonian Habitats Map), predicted area (obtained in this work after model spatial predictions) and % of change of the habitat area in relation

to the original distribution. Total surface area of the Delta=330 km<sup>2</sup> (Ibáñez et al. 2010). Habitats are arranged according to their mean surface elevation (from lower to higher elevations)

Habitat	Description	Actual area (km <sup>2</sup> )	Predicted area (km <sup>2</sup> )	% change
Coastal lagoons	Shallow coastal water bodies. Salinity may vary from brackish to marine. Usually with submerged macrophytes	14.08	60.97	-76.9
Reed beds	Marshes dominated by <i>Phragmites australis</i> growing in fresh or brackish water rich in nutrients	8.62	7.59	+13.5
<i>Salicornia</i> -type marshes	Marshes composed of succulent shrubby species of <i>Chenopodiaceae</i> which occur in areas with high soil salinity and periodic flooding events	7.89	14.18	-44.4
<i>Cladium</i> -type marshes	Marshes composed of dense helophytic communities dominated by <i>Cladium mariscus</i> affected by significant inputs of underground freshwater	3.35	32.65	-89.7
Sandy environments	Sandy beaches and dunes of the Delta front with or without vegetation. Wave action and winds are continually modelling this habitat	3.85	17.37	-77.8
Salt meadows	Meadows dominated by rushes (e.g. <i>J.maritimus</i> and <i>J.acutus</i> ) in salty soils. Adapted to occasional flooding	0.52	125.41	-99.6
Riparian vegetation	Habitat growing along river levees composed by trees	0.02	32.29	-99.1

calculated. First the Cohen's Kappa index was calculated, which estimates the rate of correct classification after removing the probability of chance agreement. Kappa index ranges from 0 (indicating poor model performance) to 1 (almost perfect) (Seoane et al. 2003). Second, the area under the receiver operating characteristic (ROC) curve, known as AUC, was calculated, where  $AUC \leq 0.5$  indicates prediction no better than random and  $AUC = 1.0$  indicates perfect discrimination (Fielding and Bell 1997). For the analysis, we used dismo 0.8 library (Hijmans et al. 2011) for R software and own scripts.

### Mapping Model Habitat Predictions

Based on fitted models, we calculated spatial predictions at 10 m grid-cell resolution using predict.gam function from GAM 1.06.2 package, and results were transferred to maps using ArcGIS 9.3. Because the response variable of habitat occurrences is a continuous variable (i.e. probability of occurrence), a threshold value was set to convert model predictions of probability of occurrence in presence/absence classifications. Since the reliability of the predictive models is affected by the frequency of presences (i.e. prevalence, Manel et al. 2001; Jiménez-Valverde and Lobo 2007) datasets with equal number of presences and pseudo-absences were created for each habitat in order to obtain datasets with prevalence of almost 50 % to build models. The prevalence of each habitat model was taken as threshold to classify predictions in terms of presence and absence following Liu et al. (2005) and Zucchetto et al. (2010). In case of spatial overlap between habitats, the models were ranked on the basis of explained deviance (0–100 %; the higher the better) (Planque et al. 2007).

### Results

A summary of the ecogeographic predictors for each of the studied Ebro Delta habitats is shown in Table 2. The actual distribution of these environments mostly varies according to the elevation and the distance from the inner border. The habitats can be classified into 2 main groups: i) habitats located at higher elevation and closer to inner border (comprising *Cladium*-type marshes, salt meadows and riparian vegetation habitats) and thus representing the most terrestrial or inland habitats, and ii) those located at lower elevations, closer to the sea, which include coastal lagoons, sandy environments, *Salicornia*-type marshes and reed beds.

The accuracy of the fitted models in predicting habitat distributions (probability of occurrence) was rather high (Table 3). The models explained 97.9 %, 84.9 % and 81.5 % of the deviance in predicting distribution for sandy environments, riparian vegetation and *Cladium*-type marshes; and 76.4 %, 67.6 % and 63.1 % for predicting the distribution of salt meadows, *Salicornia*-type marshes and coastal lagoons respectively. The lowest deviance explained, 59.5 %, was found in the reed bed habitat.

Though the combination of significant predictors in the fitted models differed, distance from the inner border of the Delta was selected for all models except for sandy environments. Furthermore, models of all inland habitats (i.e. *Cladium*-type marshes, salt meadows and riparian vegetation) also selected distance from the river, whereas elevation and distance from the coast were selected for the coastal habitats except for the reed beds.

The shapes of the effect of each ecogeographical predictor on the models' response are shown in Fig. 2 and 3. In particular, the models' responses (y-axes) indicate the relative



**Table 2** Mean value and range (minimum–maximum) of the ecogeographic predictors for each of the Ebro Delta habitats studied. Habitats are arranged according to their mean surface elevation (from lower to higher elevations)

	Elevation (m)	Distances (m)		
		from the coast	from the river	from the inner border
Coastal lagoons	0.02 (−0.59–0.11)	1567.3 (168.5–3107.1)	4540. (0–7935.3)	11140.1 (1467.1–18018.2)
Reed beds	0.39 (0.00–1.71)	1727. (85.47–3385.1)	4425. (1–8279.0)	11015.6 (1005.1–18285.0)
<i>Salicornia</i> -type marshes	0.59 (0.00–2.39)	582.0 (9.2–2522.2)	3289.0 (19.4–8890.7)	14392.3 (569.0–1811.6)
<i>Cladium</i> -type marshes	0.62 (0.00–1.42)	2116. (878.2–6240.6)	7013.0 (3035.3–8292.4)	2572.1 (856.1–5587.0)
Sandy environments	0.83 (0.00–3.90)	141.1 (1.2–1247.3)	3437.74 (63.5–7803.6)	15361.1 (841.7–18423.8)
Salt meadows	1.23 (0.45–2.26)	1556.1 (57.6–8285.2)	3926.1 (4.3–7550.9)	7792.2 (531.6–16989.3)
Riparian vegetation	2.45 (0.31–4.56)	6818.1 (2454.0–10654.2)	145.5 (0.0–1169.2)	5746.0 (141.3–15974.6)

influence of the ecogeographical predictors (x-axes) on the prediction and therefore these responses supply a direct comparison with the probability of occurrence under binomial models (Zuur 2012). For the coastal habitat models, a very similar pattern of response was found for elevation and distance from the coast, except for the sandy environments, where elevation showed a distinct response (Fig. 2). The probability of the occurrence of any of the coastal habitats increased towards the coastline (Fig. 2b and c). The probability of occurrence of coastal lagoons was higher near sea level whereas the probability of occurrence of *Salicornia*-type marshes is high at around 0.5 m of elevation (Fig. 2a). Regarding the sandy environments their probability of occurrence increased linearly with elevation (Fig. 2a).

In the most terrestrial habitats, the partial effects of both distances from the river and the inner border varied among the

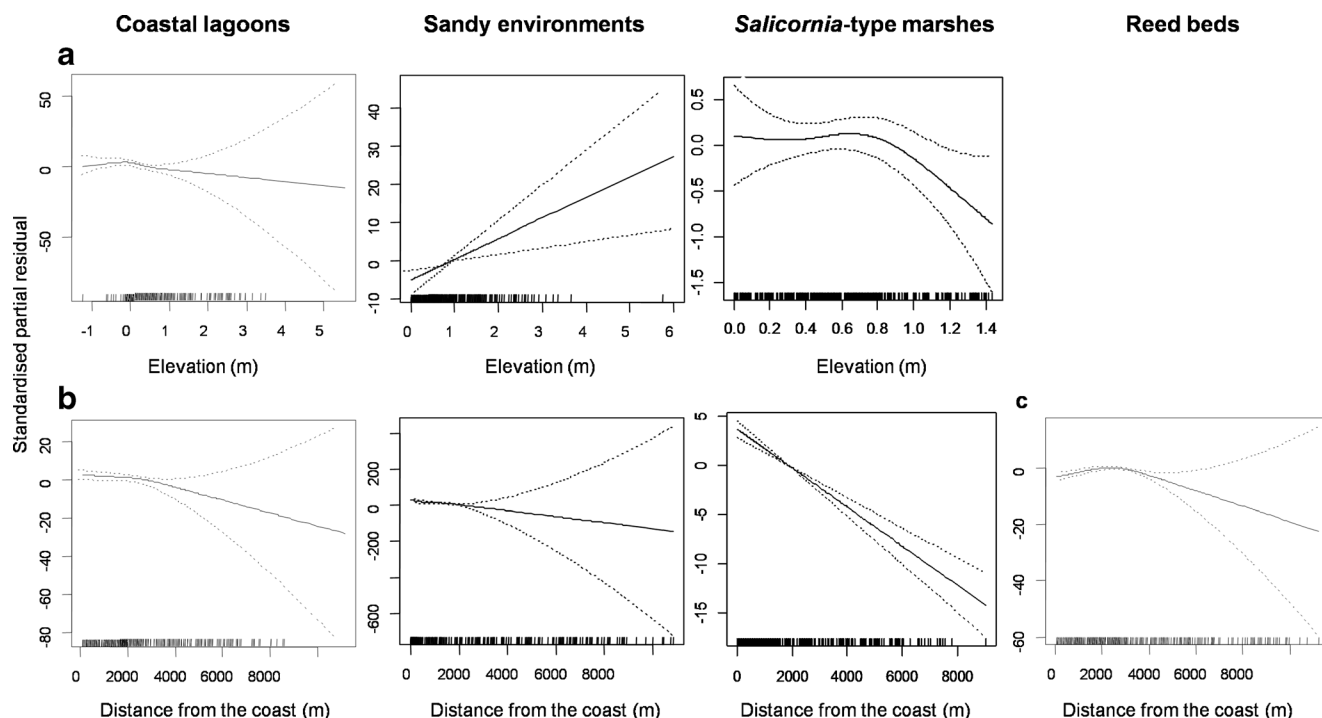
habitats. Thus, the probability of *Cladium*-type marshes occurrence was high near the inner border of the Delta (Fig. 3b) and at ca. 7 km of distance from the river Fig. 3a. The probability of salt meadow occurrence was high up to ca 5 km from the river and underwent a strong decrease after this distance (Fig. 3a), but it increased again towards the inner border and the coast (Fig. 3b). Finally, the probability of presence of riparian vegetation was high in areas close to the river and close to the inner border (Fig. 3c).

Altogether, mean AUC values from k-fold cross-validation showed good agreement for the natural habitats distribution (AUC>0.94), except for the reed beds model, which had lower performance (AUC=0.83). Results of the kappa index showed that most of the models (i.e. coastal lagoons, sandy environments, *Salicornia*-type marshes, *Cladium*-type marshes and riparian vegetation) had moderate agreement

**Table 3** Generalized Additive Models (GAMs) built for each of the Ebro Delta habitats, showing the degrees of freedom for the smoothing parameters (s) and the proportion of the explained deviance. Abbreviations: z =

elevation, sea = distance from the coast, river = distance from the river, border = distance from the inner border. Habitats are arranged according to their mean surface elevation (from lower to higher elevations)

Habitat	Model	Deviance explained (%)
Coastal lagoons	s (z, 3) + s (sea, 3) + s (border, 3)	63.03
Reed beds	s (sea, 3) + s (river, 3) + s (border, 3)	59.49
<i>Salicornia</i> -type marshes	s (z, 2) + sea + border	67.64
<i>Cladium</i> -type marshes	s (river, 3), s (border, 3)	81.53
Sandy environments	z + s (sea, 3) + s (river, 3)	97.90
Salt meadows	s (z, 3) + s (sea, 3) + s (river, 3) + s (border, 3)	76.64
Riparian vegetation	s (z, 3) + s (river, 3) + s (border, 3)	84.93



**Fig. 2** Partial effects of the variables **a.** "elevation" and **b.** "distance from the coast" on coastal lagoons, sandy environments, *Salicornia*-type marshes and reed beds **c** in those GAMs where these variables were retained. Dotted lines indicate 2 times the standard error. X-axes show the

location of observations along the variable. Y-axes represent the partial residuals of the predictors in the response variable and indicate the relative influence of the ecogeographical predictors (x-axes) on the prediction

between predictions and observations ( $\kappa > 0.43$ ). Salt meadows and reed beds showed  $\kappa$  values lower than 0.4 and thus would be considered poor according to Fielding and Bell (1997).

Maps of the probability of occurrence of the habitats studied (Fig. 4) showed some overlaps between the distributions of the different coastal habitat types (Fig. 4a, c), whereas there was much less overlap between the predicted distributions of the most terrestrial habitats (Fig. 4d, g).

After ranking habitat models based on their explained deviance and using the prevalence of each habitat as threshold to translate the probability of occurrence to a presence/absence map, results revealed that the potential natural habitats are unequally distributed across the Ebro Delta (Fig. 5 and Supplementary Fig. S2). Results show that, with the present topographic and morphologic structure of the Delta, salt meadows should potentially occupy the highest surface in the Delta (125.4 km<sup>2</sup>, 43 % of the study area, prevalence=0.51) followed by coastal lagoons (60.7 km<sup>2</sup>, 20.9 %, prevalence=0.47), *Cladium*-type marshes (32.6 km<sup>2</sup>, 11.3 %, prevalence=0.48), riparian vegetation (32.3 km<sup>2</sup>, 11.1 %, prevalence=0.47), sandy environments (17.37 km<sup>2</sup>, 5.9 %, prevalence=0.49), *Salicornia*-type marshes (14.18 km<sup>2</sup>, 4.9 %, prevalence=0.53) and reed beds (7.6 km<sup>2</sup>, 2.6 %, prevalence=0.52).

Results suggest that the most inland habitats (i.e. *Cladium*-type marshes, salt meadows and riparian vegetation) would have undergone a severe reduction (higher than 90 %),

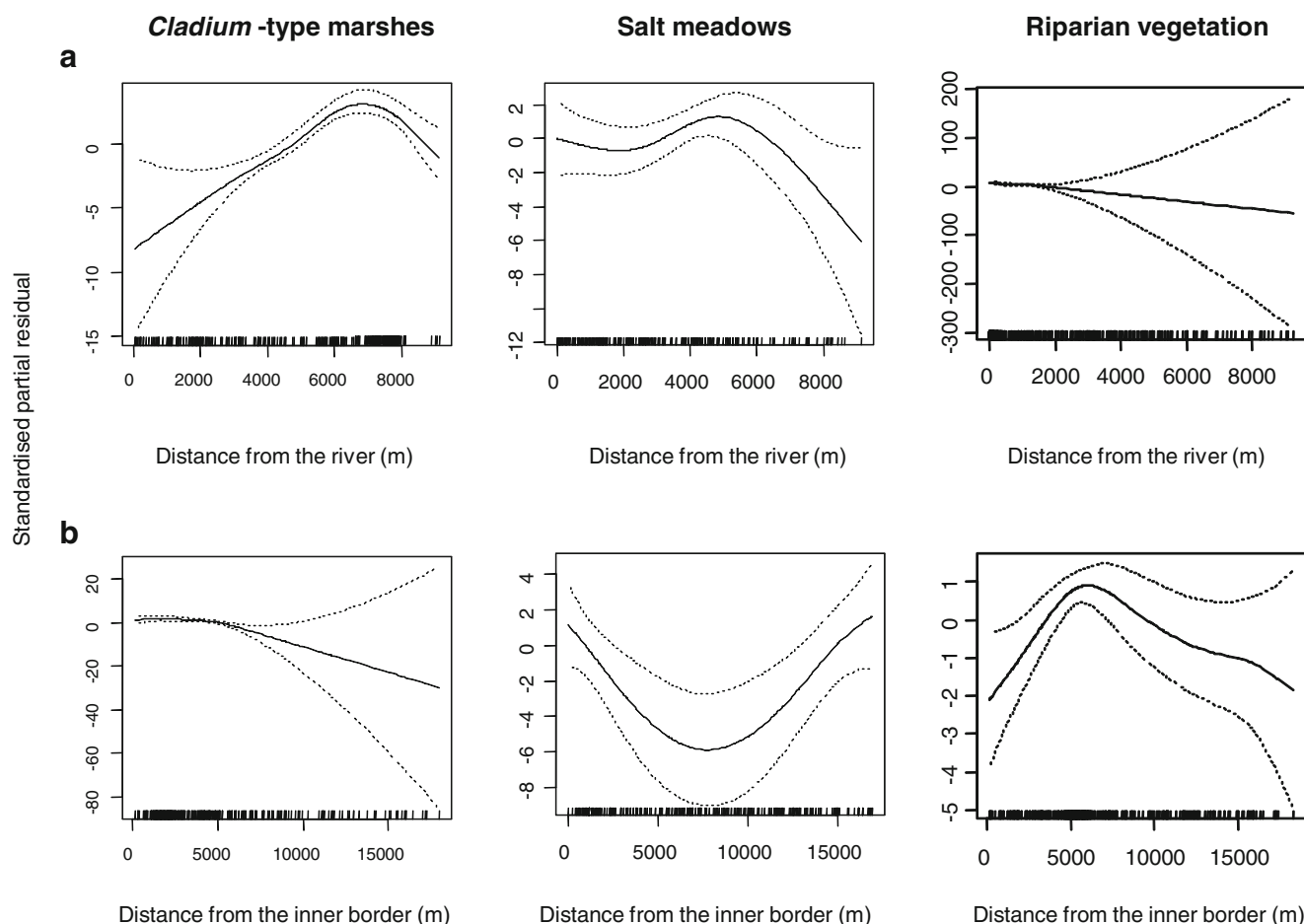
whereas in the most coastal habitats (coastal lagoons, sandy environments, *Salicornia*-type marshes) the reduction in relation to their potential distribution would be around 70 % (Table 1).

## Discussion

### The Potential Distribution of Ebro Delta Habitats Under Natural Conditions

By using predictive habitat models, we were able to draw maps of potential distribution for the Ebro Delta wetland habitats. Our models, including elevation and distances from the coast, from the river and from the inner border of the Delta as ecogeographical predictors, were capable to discriminate between areas where coastal habitats (i.e. coastal lagoons, sandy environments, *Salicornia*-type marshes) and inland habitats (i.e. *Cladium*-type marshes, salt meadows and riparian vegetation) should potentially exist under natural conditions across the whole of the Delta plain. Among all the habitat models the one for reed beds showed the lowest discrimination power, but statistically it can still be considered a good model. This low discrimination power suggests that the potential distribution of reed beds under natural conditions would be quite different than under altered conditions. This is because, at present, the widespread distribution of reed beds





**Fig. 3** Partial effects of the variables **a.** “distance from the river” and **b.** “distance from the inner border” on *Cladium*-type marshes, salt meadows and riparian vegetation in those GAMs where these predictors were retained. Dotted lines indicate 2 times the standard error. X-axes show

the location of observations along the variable. Y-axes represent the partial residuals of the predictors in the response variable and indicate the relative influence of the ecogeographical predictors (x-axes) on the prediction

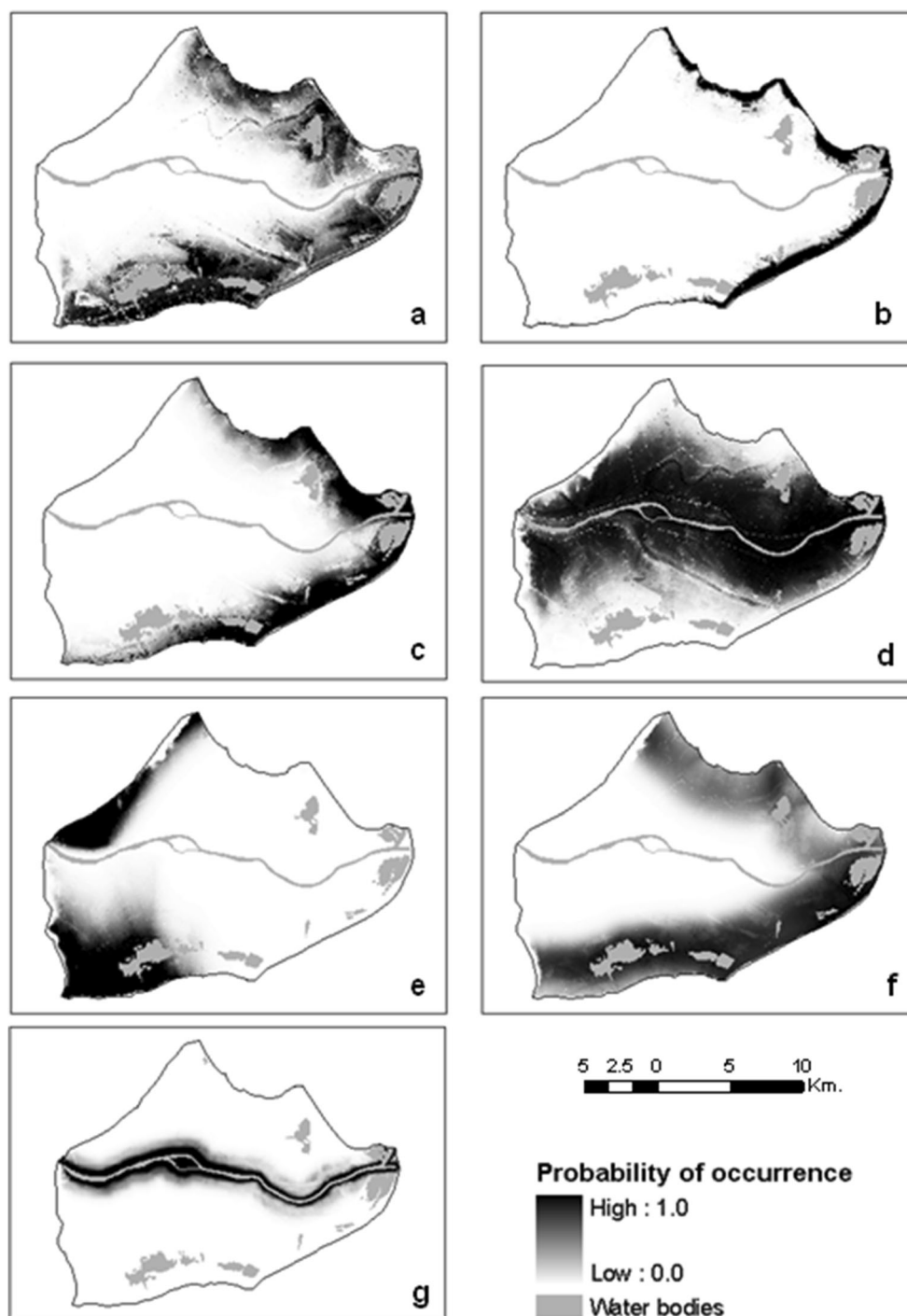
in the Ebro Delta is mainly linked to the littoral zones around brackish lagoons, which are fresher than originally due to the fresh water inputs from the rice drainage channels (Sanmartí and Menéndez 2007). Thus the predicted distribution by the reed bed model might partially be attributed to a suboptimal selection of the predictors used in this study. For the reasons discussed before, predictors linked to hydrological alteration should be considered in order to better estimate the potential distribution of the reed bed habitat.

Model predictions showed more spatial overlap among coastal habitats than in inland habitats, and this can be due to the fact that Mediterranean coastal marshes are known to display a patchy distribution (Ibáñez et al. 2000). The most terrestrial or inland habitats are mainly predicted in higher elevation areas and far from the coast, and are the ones that accounted for most of the natural habitat reduction in relation to their potential distribution. This is not surprising since in the Ebro Delta these areas are the most altered by human activities (e.g. farmland, urban settlement etc.), while areas occupied by

coastal habitats are more difficult to be transformed for human purposes due to the strong marine influence.

Results on the potential distribution of Ebro Delta habitats under natural conditions is in concordance with the work of Curcó et al. (1995) who also found that the most terrestrial habitats had been drastically reduced (>95 %) while coastal lagoons, sandy environments and *Salicornia*-type marshes had had less dramatic reduction (ca. 70 %). However, results obtained by Curcó et al. (1995) predict a higher surface for the *Salicornia*-type habitat, and this can be partially explained by the fact that in our study part of the potential area of this habitat corresponds to areas where the model does not predict any of the considered habitats; this is the area of transition between the salt meadows and the coastal lagoons and bays (see white spots in Fig. 5 and in Supplementary Fig S2). An additional reason could be that the present elevation of the delta plain is higher than would be in natural conditions due to the inputs of fluvial sediments deposited in the rice fields through the irrigation system before the construction of dams (Ibáñez et al. 1997).

**Fig. 4** Probability of occurrence for: **a.** costal lagoons, **b.** sandy environments, **c.** *Salicornia*-type marshes, **d.** salt meadows, **e.** *Cladium*-type marshes, **f.** reed beds, and **g.** riparian vegetation



#### Habitat Responses to Ecogeographical Variables

Habitat response functions should be evaluated not only by their fit, but also by their ecological meaning. Although the variables chosen to study habitat distribution were relatively simple, they might be ecologically relevant (i.e. they accounted for more than 50 % of explained deviance for the seven habitat models). While surface elevation in general and micro-topography in particular has been already used as

indicator of wetland habitat distributions (Zedler et al. 1999; Álvarez-Rogel et al. 2007), the relevance of ‘distance’ variables had not been shown before. We found that distances from the river and from the inner border appear to be significant for the most inland habitats (*Cladium*-type marshes, salt meadows and riparian vegetation), since the models selected both variables. Despite this, the responses of the habitat types to distance (from the river and from the inner border) were complex functions (i.e. requiring smoothing with 3 degrees of

**Fig. 5** Map showing the potential distribution (presence/absence) of natural habitats in the Ebro Delta predicted by the models. The overlap of the habitats have been made on the basis of the explained deviance by the GAM models



freedom; (Fig. 3), which may reflect other ecological processes not modelled but influencing the shape of the responses (Bio et al. 1998). Therefore, these variables may be used as good proxies of a complex set of factors within the Delta, such as freshwater influence around the edge of the deltaic inner border and near the river; that influence is in part related to the upwelling of freatic waters and river flood events respectively (Rodrigues-Capítulo et al. 1994; Day et al. 1995). The results pointing out the high probability to found *Cladium*-type marshes in areas close to the inner border is in some measure a result of the mentioned complex factors. Interestingly, the probability of occurrence of the salt meadows was high in areas both near and far from the inner border. The partial effects of these predictors may reveal differences within vegetal communities of Mediterranean salt meadows adopted from Corine Land Cover map, which are known for having difficulties in separating overlapping classes (i.e. due to high heterogeneity of Mediterranean coastal marshes) (Felcisimo and Sánchez-Gago 2002). In this study this habitat type actually represents a combination of exclusive halophytic vegetation near the coast (i.e. salt marshes with presence of *Juncus maritimus*) and areas of higher elevation usually more distant from the coast (i.e. rushes-marshes and meadows with *Juncus acutus*).

In deltas the variability of topographic variables (elevation, distance to the coast, etc.) is mostly related to two spatial axis: the longitudinal one (along the river) and the

transversal one (across the river); both axis are related to environmental variables such as salinity, flooding frequency, soil moisture, type of soil, etc., but this relation is often different in each axis (i.e. flooding from the river or from the sea) and creates complex environmental gradients.

#### Restoration and Management Implications

Our results may be particularly useful for management strategies because we showed that: i) the potential distribution of the natural habitats under a scenario of complete abandonment of the human activity in the Delta can be predicted with good accuracy, ii) information on the main ecogeographical variables influencing wetland habitat distribution is easy to obtain, iii) there is a straightforward way to investigate the habitat distribution by using GIS methods in combination with statistical models and iv) predictive maps could be a useful tool for identifying areas to be restored or to know the type of habitat to be restored in a particular area. The methodology employed can also be used to predict habitat distribution with past and future deltaic configurations, as well as to other deltaic areas since they share a similar topographic structure. For instance, it can be used to predict the future habitat distribution as a function of scenarios of relative sea-level rise and coastal retreat due to climate change and sediment deficit, since the model shows that habitats are highly sensitive to elevation and distance to the coast. Existing bibliography shows that this is

one of the main threats to the future sustainability of deltaic systems (Ibáñez et al. 2013).

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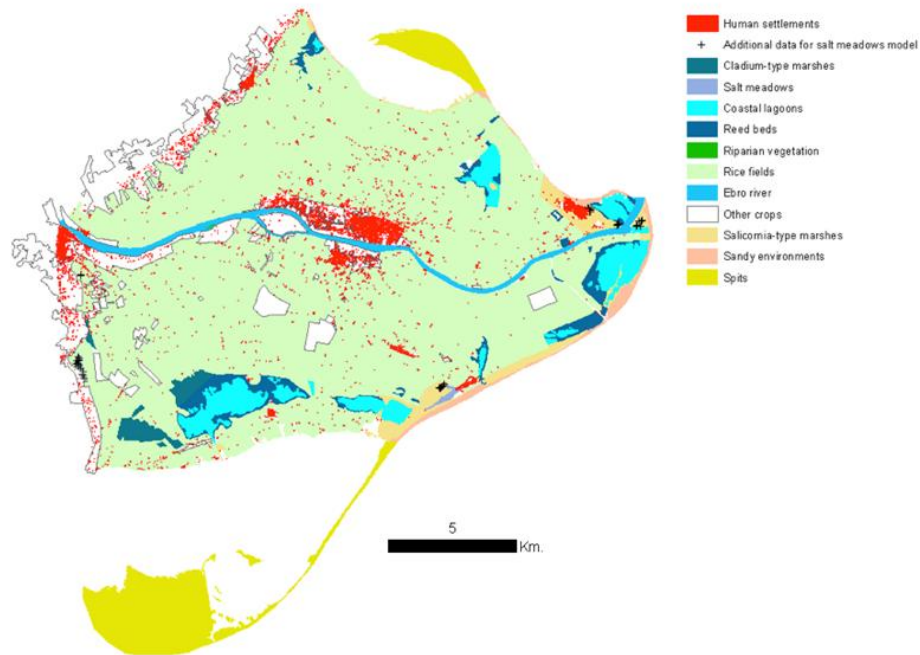


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## Supplementary material

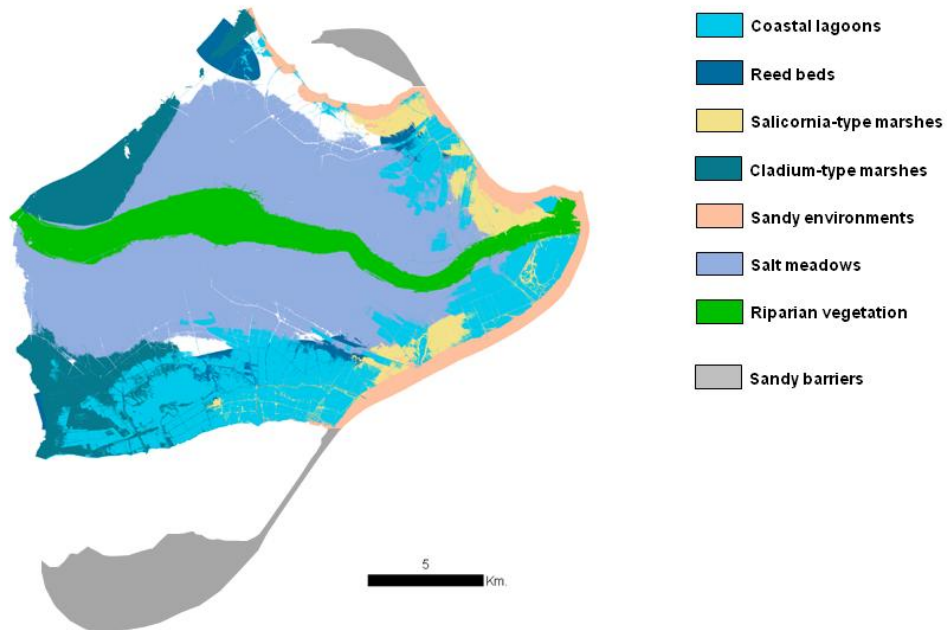
### Supplementary Fig. S1. Location of the study area, the Ebro Delta, and its present-day main habitats

Title: Modelling habitat distribution of Mediterranean wetlands: the Ebro Delta as case study  
Journal: Wetlands  
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**Supplementary Fig. S2.** Map showing the potential distribution (presence/absence) of natural habitats in the Ebro Delta predicted by the models. The overlap of the habitats have been made on the basis of the explained deviance by the GAM models.

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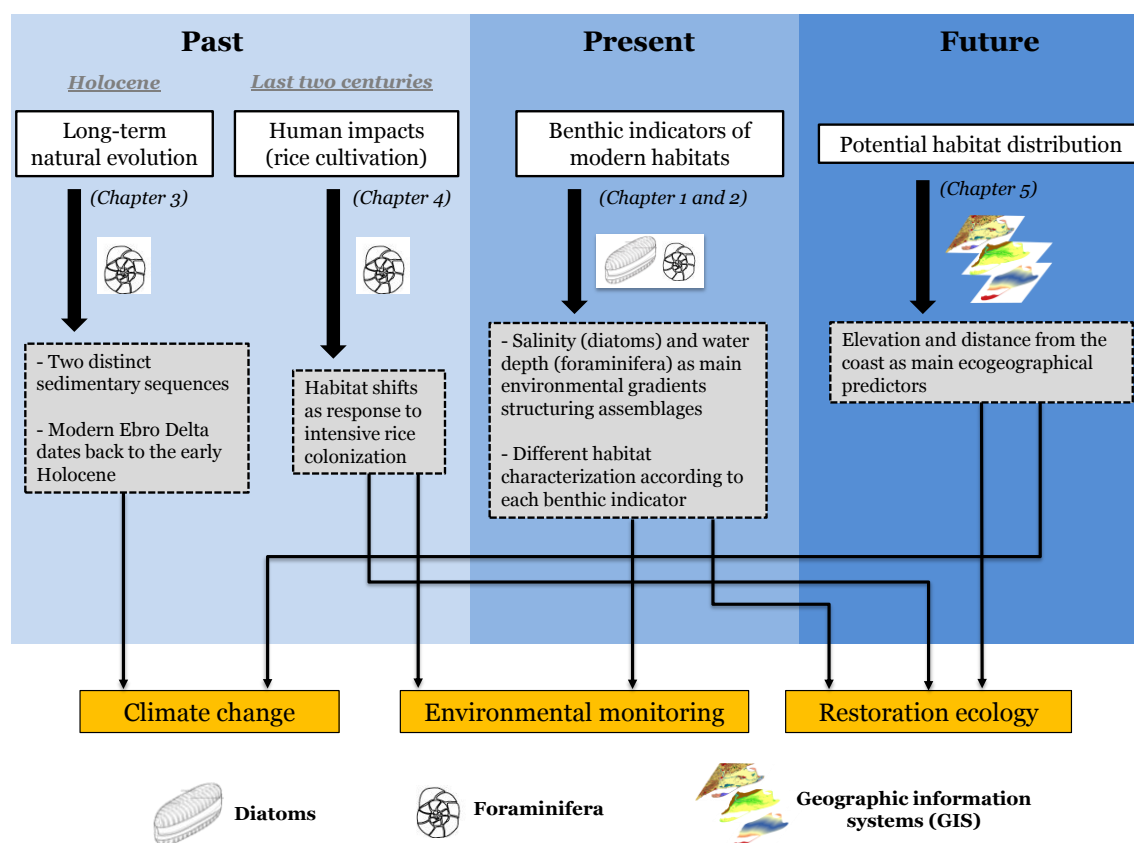
BENTHIC DIATOMS AND FORAMINIFERA AS INDICATORS OF COASTAL WETLAND HABITATS: APPLICATION TO PALAEOENVIRONMENTAL RECONSTRUCTION

Xavier Benito Granel



## General discussion

The general discussion aims to provide an overview of the main results and to context them in the temporal framework: present, past and future (Figure 1). The present thesis showed that benthic diatoms and foraminifera can be useful indicators of the Ebro Delta habitats in different ways. According to a modern perspective, each group of indicators is sensitive to diverse environmental factors and typifies distinctively a wide range of Ebro Delta habitats (excluding the non-flooded ones). However, according to a palaeoecological perspective, only foraminiferal assemblages have proven to be useful to reconstruct past deltaic habitats, since no well-preserved diatoms were recorded in the Delta sediments. Moreover, the potential habitat distributions, and the use of the benthic assemblages as indicators of habitat change can be used to inform environmental restoration and monitoring schemes, as well as to assess future impacts of climate change in this highly sensitive area.



**Figure 1** Diagram of the main results derived from the present thesis (grey boxes) with their corresponding elements of analysis (diatoms, foraminifera and GIS). Blue colours indicate the temporal framework that comprise the thesis (past, present and future), and orange boxes indicate the main implications of the results.

**Present: benthic indicators of modern habitats**

Benthic biota usually responds to a wide array of biological, chemical and physical factors (Adams 2005). However, in shallow fluctuating coastal wetlands, which exhibit high spatial and temporal variability, benthic assemblages seems to be more influenced by physical factors (Reizopoulou and Nicolaidou 2004, Gascón et al. 2007). According to this, the environmental gradients structuring benthic diatom and foraminiferal assemblages in the Ebro Delta habitats can be considered basically physical: shallowness (water depth), salinity and sediment characteristics (**Chapters 1 and 2**). Furthermore, both group of indicators (unicellular protists) are mostly influenced by the same environmental factors, despite being different organisms, i.e. algae (diatoms) and microfauna (foraminifera). In this context, salinity, shallowness and sediment characteristics have been already considered important gradients in explaining the distribution of these and other benthic communities in similar transitional environments (salt marshes: Trobajo et al. 2004, Roe et al. 2009, Leorri et al. 2010; estuaries: Cearreta 1988, Juggins 1992, Hassan et al. 2009, Nebra et al. 2011, Rovira et al. 2012a, Ribeiro et al. 2013; coastal lagoons: Gascón et al. 2007, Ferreira 2013, Prado et al. 2014).

Environmental variability (natural and/or human-induced) of salinity, water depth, sediment type and nutrients are inherently intense and dynamic at the land-sea transitions in coastal wetlands (Debenay and Guillou 2002). Within this transition, the physicochemical co-variation and the influence of other unquantified processes that are difficult to identify in the field (e.g. light availability, physical instability, competence, etc.) make it difficult to determine the effect of single environmental variables upon benthic biota (Van der Zwaan et al. 1999, Thronton et al. 2002, Juggins 2013). In this sense, it would be more meaningful to examine environmental gradients, which integrate combinations of ecological processes. In the Ebro Delta, salinity and shallowness can be considered surrogates of freshwater-to-marine and water-to-land transitions – integrative factors including conductivity and water depth but also other underlying gradients of habitat features like subaerial exposure, wave action, light, food availability, etc., – all of which influence diatoms and foraminiferal assemblages. This is consistent with the qualitative ecological zonation of benthic biota along a confinement gradient, which has been previously studied in the Mediterranean coastal ecosystems (Guélorget and Perthuisot 1983, Albani et al. 1991, Debenay and Guillou 2002, Trobajo et al. 2004, Gascón et al. 2007, Pérez-Ruzafa et al. 2008, Carboni et al. 2009, Sigala et al. 2012). Therefore, salinity and shallowness can be considered integrative factors to explain ecosystem processes in deltas.

The importance of water depth as integrative factor is also shown at the adjacent marine area of the Ebro Delta. The increased physical stability from nearshore to offshore environments is reflected by small changes in benthic foraminiferal species composition and abundance. As a

result, open sea foraminiferal assemblages had wider depth ranges than those inhabiting the delta plain. Moreover, water depth may be also relevant due to its relationship with the availability of sandy substrates for both porcellaneous (foraminifera) and epipsammic (diatom) species in nearshore coastal areas (e.g. Vilbaste et al. 2000, Goineau et al. 2011). In deltas, water depth is normally strongly correlated with wave energy and bottom currents, therefore very likely having an indirect effect upon benthic assemblages by sorting sand fractions near the shallower delta front, and mud fractions in deeper, prodelta environments (Scrutton 1969, Maldonado 1972). Hence, local bathymetric zonations have proved to be meaningful for developing foraminifera-based water depth transfer function (e.g. Hayward 2004, Horton et al. 2007, Rossi and Horton 2009, **Chapter 2** of this thesis). Nevertheless, more research is needed to overcome the paucity of information on the autoecology of benthic foraminifera inhabiting near microtidal Mediterranean river deltas that intrinsically have high environmental variability due to riverine inputs (e.g. organic matter, oxygen layers) (Mojtahid et al. 2010).

In the Ebro Delta habitats, diatoms form high-diversity assemblages and vary significantly among sites, whereas foraminifera had low-diversity assemblages with lesser compositional changes among sites. In this sense, the dominance of few ubiquitous foraminifera such as *Ammonia tepida* and *Haynesina germanica* in the Ebro Delta coastal lagoons may explain their failure to distinguish lagoons with different salinity regimes (salt/brackish vs. freshwater). Instead, these two habitats were clearly identified using diatoms, thus providing a finer-grained habitat characterization. Although the degree of accuracy of habitat characterization is higher using diatoms, it must be stressed that the higher number of species inhabiting the Ebro Delta together with their confusing and scattered taxonomy (e.g., Rovira, 2013 and references therein), required time-consuming analyses and added an extra level of difficulty to assign taxa to a known species. Indeed, a total of 424 diatoms were identified in the Ebro Delta of which 96 remained as unknown or ascribed as “*cf.*” or “*aff.*”, therefore hampering the study of the ecology of the species. On the other hand, foraminifera taxonomy is relatively better resolved than diatoms (but by no means complete, e.g. Hayward et al. 2004), with coastal assemblages frequently composed by the same species distributed globally (Murray, 2006, Kemp et al. 2009). Therefore, the most cost-effective analysis of benthic foraminifera (i.e. easier taxonomy, less number of species) can be suitable when a coarse grained habitat characterization is sufficient.

The identification of groups of diatom and foraminifera indicator species in the Ebro Delta habitats has provided a complementary approach to the individual species’ response to single variables. That is, even if quantitative predictions of conductivity and water depth could be inferred using diatoms and foraminifera, respectively, the habitat type would not be necessarily the same. For instance, for the same range of conductivity (e.g. 30–40 mS/cm), both salt

## *General discussion*

marshes and coastal lagoons could be possible. Instead, groups of diatom indicator species were able to discriminate between them. Likewise, for the same range of water depth (e.g. 2–3 m), foraminifera indicator species can discriminate between two distinct subtidal habitats (i.e. coastal lagoon, and nearshore/ outer bay habitats). To our knowledge, only Goineau et al. (2011) used groups of indicator foraminiferal species in a Mediterranean delta (i.e. the Rhône prodelta although the analysis was not applied within the delta plain). Another exception is Wachnicka (2010, 2011) who used diatom indicator species as complement of transfer functions for water quality (nutrients and salinity) in Tropical bays of the Everglades (USA). The indicator species analysis using benthic diatoms and foraminifera has proven to be a potential new tool to distinguish different habitat types in Mediterranean deltas, in which heterogeneity, both spatial and temporally, is a fundamental feature (Ibáñez et al. 2000).

Any palaeoenvironmental reconstruction, either quantitative or qualitative, must rely on the similarity between modern and fossil assemblages (Birks and Birks, 1980). For the Ebro Delta case, the combination of qualitative (through indicator species analysis) and quantitative (through transfer functions) approaches have provided an integrated view of modern habitats. Unfortunately, diatom-based palaeoenvironmental reconstructions were not possible in the Delta, since no well-preserved diatoms were recovered below *ca* 10 cm depth in any of the analysed sediment cores. Existing literature showed that diatom dissolution is often an important issue in brackish-saline sediments (Reed 1998, Flower et al. 2001, Ryves et al. 2004, Zalat and Vildary 2007, Lewis et al. 2013). In all of these cases, however, diatom dissolution was never strong enough to prevent palaeoenvironmental reconstructions by means of fossil diatom analyses. To date, no previous published work has reported the lack of well-preserved diatoms in all studied core samples, being Logan et al. (2010) the only exception in Australian marine bays. However, that seems to be an issue in coastal systems elsewhere (Atlantic Iberian coast: Manel Leira personal communication; Baltic Sea coast: Slawomir Dobosz personal communication). Therefore, careful selection of proxies is needed in deltaic systems, and future research should span different Mediterranean deltas and associated wetlands in order to compare diatom dissolution under different site-specific conditions.

### **Past: long-term natural evolution and human impacts**

The long-term paleoenvironmental reconstruction of deltaic habitats along the Holocene period has been carried out through the study of benthic foraminifera from two boreholes (**Chapter 3**). Holocene sea level rise periods have been recorded as transgressive marine deposits in deltaic and lagoon-barrier systems along the Spanish Mediterranean coast (Goy et al. 2003, Zazo et al. 2008, Marco-Barba et al. 2013). For the case of the Ebro Delta, maximum Holocene transgression was interpreted as marine deposits (clays) radiocarbon dated at 7860–6900 yr BP near Amposta city (in the inner border of the Delta) (Somoza et al. 1998). Moreover, the study of Maldonado (1972) also interpreted that transgressive marine sequences reached the inner border of the Delta around 7600 yr BP. Unfortunately, these seminal works lack of micropaleontological evidences to unveil whether the Delta was transgressed at the inner border via open sea or deltaic plain habitats. The foraminiferal record obtained from the Carlet borehole shown that there were no evidences of marine flooding through the entire sequence (last 7500 yr). The interpretation of these results would have been different if foraminifera from the deltaic plain environments would have not been included in the analyses, especially for the Carlet borehole in which only modern analogues of coastal lagoon habitats have been identified. Consequently, the modern Ebro Delta dates back to the early Holocene as other large Mediterranean deltas (Stanley and Warne 1994), and therefore the hypothesis that the Delta was an estuary prior to the Roman period is not tenable anymore (Guillén and Palanques 1997, Serra 1997, Palanques and Guillén 1998, Maselli and Trincardi 2013, Somoza and Rodríguez-Santalla 2014). An equally important implication is that the present thesis gave the possibility of a finer habitat reconstruction of deltas, since it is the first study based on the quantitative and qualitative analyses of modern (living and dead) foraminiferal assemblages from both the deltaic plain and the adjacent marine habitats, providing therefore adequate and sounder analogues for interpreting deltaic sedimentary sequences.

Deltaic plain habitats recorded in the lower half of the Carlet borehole (*ca.* 7500–2000 yr BP) indicated distinct degree of marine influence (lagoon/ inner bay). Within deltaic sedimentary sequences, the existence of habitats with marine influence should be expected as a function of distance to the coast due to delta lobe evolution and/or periods of relative sea level rise (RSLR). These conditions, however, can be compatible with the maintenance of the deltas (Ibáñez et al. 2014). For instance, modern deltas such as the Mississippi show active lobes growing while the abandoned ones are eroding, and both processes occur at the same time under RSLR rates of >1 cm/yr (Roberts 1997). Despite the impossibility to reconstruct the extent of specific habitats from one single point (i.e. Carlet borehole), sufficient information has been obtained to distinguish deltaic plain and open marine environments based on their foraminiferal content. In addition, other non-faunal characteristics based on diversity and wall-structure has been used in

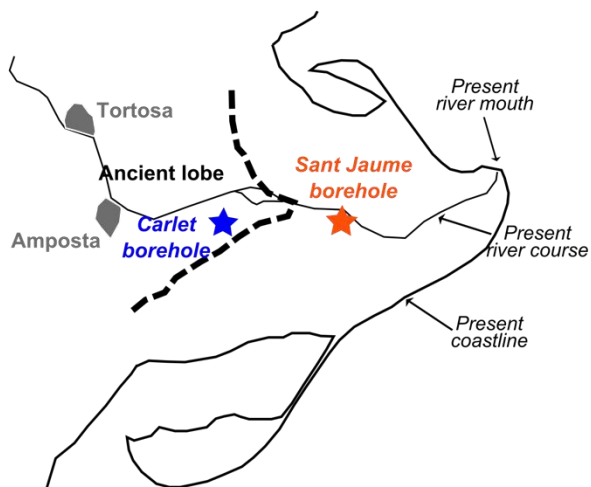
this thesis to further distinguish deltaic and adjacent marine habitats, thus providing a more integrated habitat description; foraminiferal assemblages from the deltaic plain habitats were invariably less diverse and marine habitats (nearshore and outer bays) contained more porcellaneous species (Scrutton 1969, **Chapter 2** of this thesis).

The Sant Jaume borehole showed a stronger marine influence and a more recent chronology than the Carlet borehole (**Chapter 3**). Distinct marine and deltaic plain habitat successions, caused by differential delta lobe progradation, characterized the evolution of the Ebro Delta during the last 2000 yr and these were associated to particular foraminiferal palaeoassemblages (Fig. 2). For instance, around 1700–1100 yr BP, and 1100–560 yr BP, shoreline progradations in the area of Sant Jaume borehole implied the development of progressively shallower habitats (coastal lagoons) through the advance of the Riet Vell and Riet de Zaida lobes, respectively. Very similar habitat successions have been recorded in the progradation of the Rotta di Ficarolo lobe in the Po Delta (Rossi and Vaiani 2008, Rossi and Horton 2009). Then, it can be proposed that the progradation of the Riet Vell and Riet de Zaida lobes at the location of Sant Jaume borehole occurred approximately 1700 and 1100 yr ago, respectively. These results have offered the opportunity to extend and improve the chronology regarding Ebro Delta evolution beyond the most recent few centuries (Table 1).

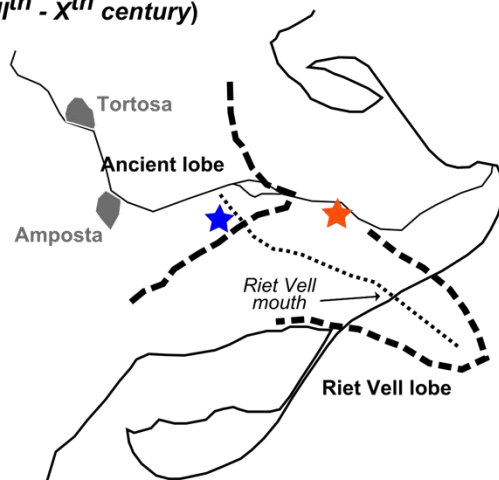
**Table 1** Approximate chronology (centuries) of the last three lobes of the Ebro Delta according to the existing bibliography and as reconstructed by benthic foraminiferal palaeoassemblages together with radiocarbon age estimation (this study).

Reference	Lobes		
	Riet Vell	Riet de Zaida	Migjorn
Maldonado & Murray 1975	?–XVI <sup>th</sup>	XVII <sup>th</sup> –XVIII <sup>th</sup>	XVIII <sup>th</sup> –present
Ibáñez et al. 1997	VI <sup>th</sup> –X <sup>th</sup>	X <sup>th</sup> –XVI <sup>th</sup>	XVII <sup>th</sup> –present
Somoza et al. 1998	XII <sup>th</sup> –XIV <sup>th</sup>	XIV <sup>th</sup> –XVIII <sup>th</sup>	XVIII <sup>th</sup> –present
Maselli & Trincardi 2013	IX <sup>th</sup> –XV <sup>th</sup>	XV <sup>th</sup> –XVII <sup>th</sup>	XVII <sup>th</sup> –present
<i>This study</i>	III <sup>th</sup> –X <sup>th</sup> (1700–1100 yr BP)	X <sup>th</sup> –XVI <sup>th</sup> (1100–560 yr BP)	XVI <sup>th</sup> –present (~500 yr BP –present)

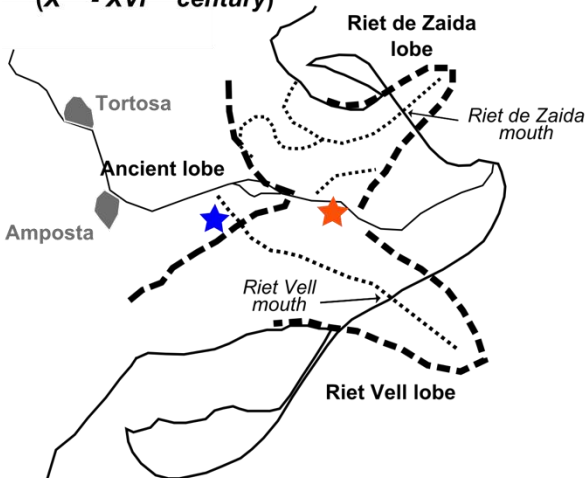
**A) 7500 - 2000 yr BP**



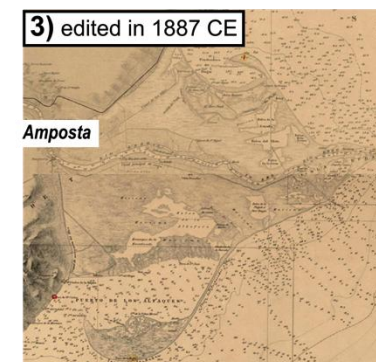
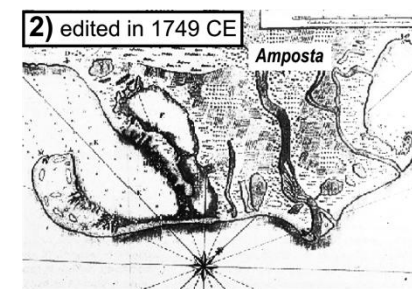
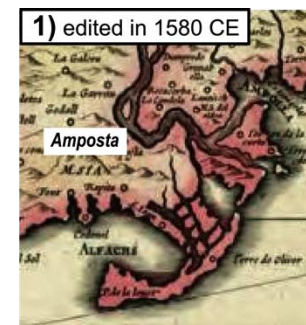
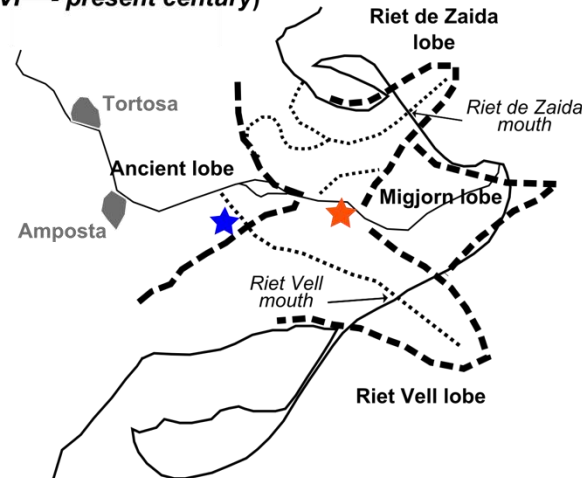
**B) 1760 - 1120 yr BP  
(III<sup>th</sup> - X<sup>th</sup> century)**



**C) 1120 - 560 yr BP  
(X<sup>th</sup> - XVI<sup>th</sup> century)**



**D) 560 yr BP - present  
(XVI<sup>th</sup> - present century)**



**Figure 2** Schematic reconstruction of the four main evolutive phases (A–D) of the Ebro Delta as reconstructed by benthic foraminifera from radiocarbon dated boreholes (Carlet and Sant Jaume). Approximate position of the last three deltaic lobes (B–D) is adapted from Maldonado (1972). The three most recent reliable maps with their corresponding dates are also shown: 1) the Mercator-Hondius Map, 2) the Miguel Marin Map and 3) “*las Golas del Ebro*” Map.

## General discussion

Natural processes that mostly moulded the Ebro Delta environments during the Holocene have been progressively altered (or replaced) by direct anthropogenic effects, especially in the last two centuries. At scale of 10s and 100s of years, benthic foraminiferal palaeoassemblages have revealed habitat shifts as response to land use changes, mostly due to the onset and expansion of rice farming after 1860's (**Chapter 4**). Regardless of site location and dominant habitat type within the Delta, the foraminiferal record share a very similar pattern: shift from coastal lagoon habitats with varying degree of marine influence (highly diverse, calcareous-dominated foraminiferal assemblages) to very restricted marshes (lowly diverse, agglutinated-dominated foraminiferal assemblages). These results indicate that recent past habitats were mainly characterized by coastal lagoons with high marine influence, somewhat similar to coastal habitats that would potentially exist under a scenario of no human disturbance according to results obtained from GIS-based habitat models (**Chapter 5**).

### Future: potential habitat distribution

Habitat distribution models applied to the Ebro Delta were highly sensitive to elevation and distance to the coast (**Chapter 5**). This methodology can be used together with the response of diatom communities to salinity gradients (**Chapter 1**) in order to assess the evolution of salt water intrusion and future habitat changes as a function of scenarios of relative sea level rise (RLSR) and coastal retreat due to climate change and subsidence. For instance, the conversion of *Salicornia* marshes into open water will likely come through gradual submergence in low-lying areas of the Ebro Delta (e.g. at the two semi-enclosed bays in Alfacs and Fangar). Likewise, the conversion of rice fields and adjacent fresh-brackish marshes to higher salinity marshes could be result of enhanced subsurface salt intrusion (Genua-Olmedo et al. 2015). Both scenarios are rather inevitable in Mediterranean deltas, where progressive RSLR could already be implicated in the loss of coastal wetlands (Nicholls 2004) and where freshwater supply can be expected to decline due to water resource scarcity (Thompson and Flower 2009).

Benthic diatoms and foraminifera are not currently recommended as biological quality elements for assessing the ecological status of transitional and coastal waters under the Water Framework Directive (WFD, Annex V). **Chapters 1** and **2** of the thesis suggested that benthic foraminifera and diatoms could provide an additional and in fact a very useful tool to biomonitor the present and future status of Mediterranean coastal habitats. For instance, the foraminifera *Haplophragmoides wilberti* emerged as indicator species of *Phragmites* marshes in the Ebro Delta (high specificity, > 99%). This is considered a strongly altered habitat in the Delta (Curcó 2006), characterized by fresh-brackish conditions and organic-rich sediments due to inputs of drainage waters coming from rice fields. Likewise, several small *Fragilaria* species (including



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revised genera) were indicative of coastal lagoons with moderate eutrophication and freshwater conditions (e.g. Olles and Clot lagoons). Therefore, the appearance of these two groups of foraminifera and diatoms that apparently thrive well in fresher and nutrient enriched conditions, in brackish and marine influenced habitats, can be used in regular monitoring as early impacts of human-mediated freshwater inflows (i.e. rice field runoff).

The assessment of environmental quality is based upon the extent of deviation from pre-disturbance conditions. This degree of deviation can be determined by comparing pre-impacted conditions in sediment cores to the modern ones at the same location (Alve et al. 2009, Dolven et al. 2013). However, this comparison might be obscured by the natural background variability of coastal environments, which often share similar features with anthropogenically stressed areas in terms of low diversity assemblages of opportunistic species (Elliot and Quintino, 2007, Dijkstra et al. 2013, Barras et al. 2014). Therefore, long term data on natural variability is required to distinguish if present-day low diversity conditions are result of natural or anthropogenic stressed conditions (Alve et al. 2009). For the Ebro Delta habitats, down-core foraminiferal changes included, among others, a strong decrease of species diversity (at the expense of more stress-tolerant species such as agglutinated *T. inflata*) since the early 1900s. Most of the benthic foraminifera-based environmental assessments were based upon assemblage diversity, reflecting poorer ecological conditions as diversity decreases (Alve 1995, Bouchet et al. 2012, Dolven et al. 2013, Barras et al. 2014). On the basis of these results, realistic pre-impacted conditions for monitoring and management purposes could be set at the late 1800s.

The joint interpretation of all short cores in **Chapter 4** allowed some inferences to be made regarding human impacts at both lower Ebro River and Delta in the context of future restoration projects. With the exception of the Garxal wetland which is directly connected to the river, the other analysed cores (Olles, Tancada, Alfacs and Clot), showed a strong reduction of allochthonous (marine) tests and sand content since the early 1900s. These results suggest a hydrologically-isolated nature of the modern wetlands due to the construction of extensive system of infrastructures accompanying the rice cultivation (e.g., canals, roads). This means that they will capture less re-suspended inorganic sediment from local sediment sources (river, lagoons, bays) than naturally. This situation together with the present and ongoing Ebro's regulation due to land use changes (irrigated agriculture) will exacerbate the sediment deficit in the Ebro Delta. Existing literature shows that this is one of the main threats to the future sustainability of deltaic wetlands (Day et al. 1995, Pont et al. 2002, Calvo-Cubero et al. 2013, Ibáñez et al. 2014). The long-term perspective defined here can serve to support environmental management seeking to restore habitats supported by natural fluxes of water, sediments and nutrients with the aim to mitigate wetland loss due to the effects of RSLR.

## **Research prospects**

The research carried out in the present PhD thesis has been crucial for acquiring a present-day and long term vision of the Ebro Delta. Perhaps, the analysis of additional boreholes is the most necessary research task towards a more accurate reconstruction of the Ebro Delta in early Holocene times. In this sense, new sedimentary sequences are particularly encouraged at landward Delta locations with the aim to confirm the results obtained in Carlet borehole. Moreover, by combining with independent and complementary proxies such as shell geochemistry (isotopes), past environmental inferences could be more precise. The study of oxygen and carbon isotopes from biogenic carbonates and silicates can provide high-resolution salinity changes (e.g. Marco-Barba et al. 2013). Several studies proved the utility of benthic foraminifera and diatoms as palaeosalinity and palaeoclimatic proxies in marginal marine environments (Reinhardt et al. 2003, Leng and Barker 2006, Abu-Zied et al. 2011). For instance, high-resolution studies could be applied on foraminiferal species commonly found in both surface and core sediment samples of the Ebro Delta such as *Ammonia beccarii* (and *A. tepida*) and *Cribrorhynchium excavatum* (and its morphotypes such as *C. selseyensis*) which have demonstrated its ability to record sensitively salinity changes (Peros et al. 2007, Lewis et al. 2013), but also temperature (Kristensen and Knudsen 2006).

Another essential point is to improve the identification of some taxonomically difficult diatom taxa that are abundant in the Ebro Delta habitats. For instance, several small naviculoid and fragilarioid taxa (i.e. *Fragilaria* and its recently revised genera) are among indicator diatoms of the deltaic habitats, but many remained unidentified at species level due to few (or lack of) differential characters when using just light microscope. Because only when species taxonomy can be reliably determined that a sound ecology is possible and thus also a proper comparison with works of similar environments (Kocielek and Stoermer 2001). Improvement of this kind should be a very useful help to refine the use of these diatoms as ecological indicators of coastal wetlands and lagoons in the Mediterranean region, becoming as well an important source of information for other diatomists dealing in similar systems or in similar taxa.

Palaeoenvironmental inferences in systems that exhibit high spatial variability like the Ebro Delta can benefit from enlarged modern data sets to fully capture relationships between benthic assemblages and key environmental variables (e.g., Lapointe, 2000). For the case of foraminifera-based water depth reconstructions, future research should span a wider range of Mediterranean coastal wetlands (e.g. Usera et al. 2002, Guillem 2007) and adjacent marine deltaic areas (Mojtahid et al. 2010, Goineau et al. 2011, López-Belzunce et al. 2014). If modern datasets could be improved, quantitative inferred conditions could be more precise, specially regarding the accuracy of water depth reconstructions (species optima and tolerances) in marine

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environments, since foraminifera living there did not show clear lower and upper depth limits unlike species inhabiting the Delta plain habitats (coastal lagoons and marshes).

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## Conclusions

1. In the Ebro Delta habitats, benthic diatom assemblages showed high diversity. A total of 424 species were identified, representing 85 genera. The most abundant and widespread species were *Cocconeis placentula*, *Achnanthes submarina*, *Navicula salinicola* and *Pseudostaurosiropsis geocollegarum*.
2. Five habitat types were identified according to the similarity in diatom species composition and abundance, namely salt marshes (i.e. *Salicornia* and *Juncus* marshes and microbial mats), brackish marshes (i.e. *Phragmites* marshes), brackish coastal lagoons and bays, coastal lagoons with fresher conditions, and nearshore open sea. Although several environmental variables determined the distribution and composition of the assemblages (i.e. water depth, sand proportion, organic matter), conductivity (as proxy of salinity) was found to be the major control on benthic diatoms.
3. Diatom indicator species of each habitat type were recognised (species are arranged according to their Indicator Value (IV), from higher to lower values):
  - a. *Navicymbula pusilla*, *Amphora* sp. 1, *Mastogloia braunii*, *Mastogloia aquilegiae* and *Amphora* cf. *roettgeri* were indicative of salt marshes (i.e. *Salicornia* and *Juncus* marshes and microbial mats).
  - b. *Achnanthes brevipes* var. *intermedia*, *Navicula perminuta*, *Diploneis smithii*, *Navicula microcari*, *Nitzschia inconspicua* and *Fragilaria* cf. *neoelliptica* were indicative of brackish marshes (i.e. *Phragmites* marshes).
  - c. *Cocconeis scutellum*, *Achnanthes* sp.1, *Seminavis strigosa*, *Cocconeis* cf. *neothumensis* var. *marina*, *Nitzschia pararostrata*, *Achnanthes amoena*, *Amphora* sp.5, *Nitzschia constricta*, *Seminavis robusta*, *Nitzschia liebethuthii*, *Planothidium deperditum*, *Cocconeis peltoides*, *Navicula vimineoides*, *Navicula* cf. *hansenii*, *Ardissonea crystallina* and *Navicula* sp. 7 were indicative of brackish coastal lagoons and bays.
  - d. cf. *Fragilaria* sp. 1, *Fragilaria atomus*, *Pseudostaurosiropsis geocollegarum*, *Pseudostaurosiropsis* cf. *geocollegarum*, *Fragilaria* cf. *sopotensis*, *Navicula gregaria*, *Fragilaria gedanensis*, cf. *Fragilaria* sp. 2, cf. *Opephora* sp. 1 were indicative of coastal lagoons with fresher conditions.
  - e. *Delphineis surirella* and *Nitzschia coarctata* were indicative of nearshore open sea.

## Conclusions

4. Unfortunately, no well preserved diatom valves were found in sediments below *ca.* 10 cm depth, and therefore the past environmental conditions of the Ebro Delta could not be inferred using diatoms.
5. Benthic foraminiferal assemblages of the Ebro Delta showed lower diversity than diatom assemblages. A total of 138 living (rose Bengal stained) and 150 dead species were identified, with the calcareous *Ammonia beccarii* group (including varieties and species such as *A. tepida* and *A. beccarii* var. *batavus*), *Haynesina germanica* and *Quinqueloculina stelligera*, and the agglutinated *Jadammina macrescens*, *Trochammina inflata* and *Haplophragmoides wilberti* as often very abundant and widespread species. In the sediment record, a total of 140 foraminiferal species were found and they were well represented by modern assemblages.
6. Both the living and dead foraminiferal assemblages were used to characterise the whole range of deltaic environments (from deltaic plain to adjacent marine area), resulting in the identification of four distinct habitat types: salt and brackish marshes, coastal lagoons and inner bays, nearshore and outer bays, and offshore. Water depth proved to be the most important factor determining the distribution of foraminifera, although it probably integrates the effects of other abiotic (e.g., food availability, oxygen) and biotic (density, competition) variables.
7. Foraminiferal indicator species of each habitat type were also recognised (species are arranged according to their Indicator Value (IV), from higher to lower values):
  - a. *Bulimina aculeata*, *Nonionoides scaphus*, *Ammosphaeroidina sphaeroidiniforme*, *Bulimina gibba*, *Textularia calva*, *Elphidium matagordanum*, *Elphidium incertum*, *Valvulineria bradyana*, *Bolivinellina pseudopunctata*, *Haplophragmoides canariensis*, *Uvigerina* sp. 1, *Reussella aculeata*, *Criboelphidium selseyensis*, *Gavelinopsis praegeri*, *Elphidium* cf. *flexuosum*, *Eggerelloides scaber*, *Cassidulina laevigata*, *Elphidium advenum*, *Reophax subfusiformis*, *Elphidium* sp. 2, *Planorbulina mediterraneanensis* and *Elphidium crispum* were indicative of offshore habitats.
  - b. *Quinqueloculina stelligera*, *Triloculina* sp. 1, Miliolid undetermined, *Nonionella atlantica*, *Epistominella vitrea*, *Asterigerinata* sp. 1, *Buliminella elegantissima*, *Nonion laevigatum* and *Brizalina striatula* were indicative of nearshore and outer bays habitats.
  - c. *Trochammina inflata*, *Jadammina macrescens*, *Trichohyalus aguayoi* and *Haplophragmoides wilberti* were indicative of salt and brackish marshes.

## Conclusions

- d. *Haynesina germanica*, *Ammonia beccarii* agg, *Quinqueloculina jugosa*, *Cribrorhynchium oceanensis* and *Quinqueloculina seminula* were indicative of coastal lagoons and inner bays.
8. The recognition of indicator species of both diatoms and foraminifers proved to be a powerful tool to identify and characterise the Ebro Delta habitats. This tool was complementary to the quantitative transfer functions, since conductivity (in the case of diatoms) and water depth (for foraminifera), though very important, are not the only factors structuring the Ebro Delta habitats.
  9. Benthic diatom and foraminiferal assemblages can be used as early indicators of habitat change conditions, since altered habitats of the Ebro Delta were recognised through the presence of several indicator species of freshwater and organic-rich conditions (i.e. *Phragmites* marshes and coastal lagoons with fresher conditions).
  10. The multiproxy approach (foraminifera plus diatoms) reinforced the environmental characterisation of habitats (i.e. salt marshes, brackish marshes, brackish coastal lagoons and bays, coastal lagoons with fresher conditions and nearshore open sea) and salinity prediction (i.e. transfer function) obtained using benthic diatoms solely. Furthermore, each benthic indicator individually had strengths and weaknesses: diatoms gave a finer-grained habitat characterization (i.e. five different habitat types) but they do not preserve well in Ebro Delta sediments, while foraminifera provided a coarser-grained habitat characterization (i.e. three or four different habitat types) but preserve well in sediment and are therefore available for palaeoenvironmental reconstruction.
  11. The high similarity found between living and dead foraminiferal assemblages indicated that dead foraminifera, which integrate seasonal and post-depositional variations on the modern assemblages, can be reliably used on a comparative basis for the interpretation of the well preserved buried assemblages of the Ebro Delta.
  12. The detailed environmental characterization of delta habitats using benthic foraminifera from both the deltaic plain and the adjacent marine area provided adequate modern analogues for palaeoenvironmental reconstruction. This is demonstrated particularly well by the more landward Carlet borehole, which only recorded shallow deltaic plain habitats (i.e. coastal lagoons), and the more seaward Sant Jaume borehole, which registered deeper habitats typical of the delta front (i.e. nearshore and outer bays habitats).
  13. The fossil foraminiferal assemblages from the two studied boreholes (Carlet and Sant Jaume) assisted in the validation and rejection of hypotheses advanced previously concerning the origin and evolution of the Ebro Delta during the Holocene:

## Conclusions

- a. the presence of coastal lagoon/ inner bay habitats throughout the entire Carlet borehole (last 7500 yr) refuted the assumption that the present Delta plain formed mostly during the last 2000 yr (in the post-Roman period), and hence it can be stated that the central plain of the Delta was never an estuary, as suggested before by some authors.
  - b. the differential progradation of the two ancient lobes Riet Vell and Riet de Zaida lobes, around 1700 and 1000 yr BP respectively, at the location of Sant Jaume borehole, provided a more accurate chronological frame for these lobes in comparison with existing literature, which had indicated a younger development.
14. Recent environmental changes (during the last *ca* 150 years) registered in short sediment cores of the Ebro Delta indicated a clear replacement of high-diversity calcareous by low-diversity agglutinated foraminiferal assemblages, together with significant correlation with organic matter increases. This shift can be explained by the effect of factors associated with rice cultivation (salinity, water depth, organic matter content, eutrophication).
  15. Down-core foraminiferal changes in the Ebro Delta habitats gave insights about their pre-impact conditions which could be set at the late 1800s. This knowledge contributes to the use of benthic foraminifera as bio-monitoring tool for Mediterranean coastal wetlands to better define restoration goals and support environmental policies (e.g. the Water Framework Directive).
  16. In the Ebro Delta, the potential distribution of coastal habitats (sandy environments, coastal lagoons, *Salicornia* marshes and *Phragmites* marshes) and inland habitats (salt meadows, *Cladium* marshes and riparian vegetation) would be different as a function of variables such as elevation and ‘distance to the coast’ under a scenario of no human disturbances. Inland habitats would naturally occupy the largest surface within the Delta (~56%), which is nowadays occupied by rice fields. The highest habitat loss corresponds to those habitats.
  17. Since habitat predictive models showed high sensitivity to elevation and distance to the coast, these habitat models can be used to predict future habitat distributions in the context of climate change and sediment deficit, and inform restoration and adaptation programs. It is suggested that the habitat models developed here can be used in other Mediterranean deltaic areas since they share similar eco-geographic features.

# **Appendix I: Benthic diatom assemblages of the Ebro Delta**

## **Appendix I: Benthic diatom assemblages of the Ebro Delta**

### **List of diatom taxa and relative abundances**

List of the 424 diatom taxa found in the Ebro Delta (arranged alphabetically) with their corresponding codes and their relative abundances (% RA) considering all samples. Plates are also indicated for those taxa illustrated here. Indicator species are highlighted in bold; for these taxa the habitat they characterize is also given.



*Appendix I: Benthic diatom assemblages of the Ebro Delta*

Code	Diatom taxa	RA (%)	Habitat	Plates
AHAMO	<i>Achnanthes amoena</i> Hustedt	0.798	Brackish coastal lagoons and bays	1 (LM)
AHBRE	<i>Achnanthes brevipes</i> var. <i>intermedia</i> (Kützing) Cleve	1.906	Brackish marshes	1 (LM)
AHBRO	<i>Achnanthes brockmannii</i> Simonsen	0.008		
AHDEL	<i>Achnanthes delicatissima</i> Simonsen	0.044		
AHFOG	<i>Achnanthes fogedii</i> Hakansson	0.760	Coastal lagoons with fresher conditions	
AHLON	<i>Achnanthes longipes</i> C. Agardh	0.005		
AHSP1	<i>Achnanthes</i> sp.1	0.969	Brackish coastal lagoons and bays	1 (LM), 1 (EM)
AHSUB	<i>Achnanthes submarina</i> Hustedt	6.684		1 (LM), 1 (EM)
AHMIN	<i>Achnantheidium minutissimum</i> (Kützing) Czarnecki	0.031		
AHMIG	<i>Achnantheidium minutissimum</i> var. <i>gracillima</i> (Meister) Lange-Bertalot	0.019		
ACSPL	<i>Actinoptychus splendens</i> (Shadbolt) Ralfs	0.004		
AULSP1	<i>Aulacoseira</i> sp.1	0.014		
APANT	<i>Amphitetras antediluviana</i> Ehrenberg	0.004		
AMACU	<i>Amphora acutiuscula</i> Kützing	1.232		1 (LM)
aAMATA	<i>Amphora</i> aff. <i>atacamana</i> Patrick	0.010		
aAMHYA	<i>Amphora</i> aff. <i>hyalina</i> Kützing	0.145		
AMANG	<i>Amphora angustissima</i> Heiden	0.482		
AMARS	<i>Amphora arcus</i> var. <i>sulcata</i> (A. Schmidt) Cleve	0.890		1 (LM)
AMARE	<i>Amphora arenicola</i> (Grunow) Cleve	0.033		
AMBOR	<i>Amphora borealis</i> Kützing	0.029		
cAMANG	<i>Amphora</i> cf. <i>angusta</i> Gregory	0.022		
cAMLUC	<i>Amphora</i> cf. <i>luciae</i> Cholnoky sensu Archibald	0.574		1 (LM)
cAMROE	<i>Amphora</i> cf. <i>roettgeri</i> Lee & Reimer	0.370	Salt marshes	2 (LM)
cAMSUB	<i>Amphora</i> cf. <i>subacutiuscula</i> Schoeman	0.360		
cAMTEN	<i>Amphora</i> cf. <i>tenerrima</i> Aleem & Hustedt	0.061		
AMCOF	<i>Amphora coffeaeformis</i> (C. Agardh) Kützing	0.697		2 (LM)
AMCOM	<i>Amphora commutata</i> Grunow	0.090		
AMCOP	<i>Amphora copulata</i> (Kützing) Schoeman & Archibald	0.139		
cAMCYM	<i>Amphora</i> cf. <i>cymbamphora</i> Cholnoky	0.034		
AMEXI	<i>Amphora exilissima</i> Giffen	0.025		

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Code	Diatom taxa	RA (%)	Habitat	Plates
AMHEL	<i>Amphora helenensis</i> Giffen	0.021		
AMHOL	<i>Amphora holsatica</i> Hustedt	0.260		
AMINA	<i>Amphora inariensis</i> Krammer	0.014		
AMIND	<i>Amphora indistincta</i> Levkov	0.053		
AMLAE	<i>Amphora laevissima</i> Gregory	0.004		
AMLIN	<i>Amphora lineolata</i> Ehrenberg	0.052		
AMLYB	<i>Amphora lybica</i> Ehrenberg	0.011		
AMMAL	<i>Amphora margalefii</i> X. Tomàs	0.061		
AMMAR	<i>Amphora marina</i> W. Smith	0.004		
AMMER	<i>Amphora meridionalis</i> Levkov	0.035		
AMMEX	<i>Amphora mexicana</i> A.Schmidt	0.019		
AMMIC	<i>Amphora micrometra</i> Giffen	0.136		
AMNOR	<i>Amphora normanii</i> Rabenhorst	0.029		
AMOVA	<i>Amphora ovalis</i> (Kützing) Kützing	0.042		
AMPED	<i>Amphora pediculus</i> (Kützing) Grunow	0.172		
AMPRC	<i>Amphora proteus</i> var. <i>contigua</i> (Gregory) Cleve	0.040		
AMPSE	<i>Amphora pseudoaequalis</i> Levkov	0.012		
AMPSU	<i>Amphora pseudoholsatica</i> Nagumo & Kobayasi	0.024		
AMPUS	<i>Amphora pusio</i> Cleve	0.802		2 (LM)
<b>AMPS1</b>	<b><i>Amphora</i> sp.1</b>	<b>0.660</b>	<b>Salt marshes</b>	2 (LM)
AMSP3	<i>Amphora</i> sp.3	0.021		
<b>AMSP5</b>	<b><i>Amphora</i> sp.5</b>	<b>0.806</b>	<b>Brackish coastal lagoons and bays</b>	2 (LM)
AMSP6	<i>Amphora</i> sp.6	0.011		
AMSTA	<i>Amphora staurophora</i> Juhlin-Dannfelt	0.305		
AMSUB	<i>Amphora subacutiuscula</i> Schoeman	0.975		2 (LM)
AMSUH	<i>Amphora subholsatica</i> Krammer	0.051		
AMSYD	<i>Amphora sydowii</i> Cholnoky	0.029		
AMTUM	<i>Amphora tumida</i> Hustedt	0.029		
AMTUR	<i>Amphora turgida</i> Gregory	0.023		
AMVET	<i>Amphora vetula</i> Levkov	0.008		

## Appendix I: Benthic diatom assemblages of the Ebro Delta

Code	Diatom taxa	RA (%)	Habitat	Plates
cANTEN	<i>Anorthoneis</i> cf. <i>tenuis</i> Hustedt	0.005		
<b>ARCRY</b>	<b><i>Ardissonea crystallina</i> (C. Agardh) Grunow</b>	<b>0.429</b>	<b>Brackish coastal lagoons and bays</b>	
ARFUL	<i>Ardissonea fulgens</i> (Greville) Grunow	0.008		
ASBAH	<i>Astartiella bahusiensis</i> (Grunow) Witkowski, Lange-Bertalot & Metzeltin	0.023		
cASBRE	<i>Astartiella</i> cf. <i>bremeyeri</i> (Lange-Bertalot) Witkowski & Lange-Bertalot	0.004		
cASPUNC	<i>Astartiella</i> cf. <i>punctifera</i> (Hustedt) Witkowski & Lange-Bertalot	0.095		
BAPAX	<i>Bacillaria paxillifera</i> (O.F. Müller) Hendey	0.143		
BEFEN	<i>Berkeleya fennica</i> Juhlin-Dannfelt	0.239		2 (LM)
BERUT	<i>Berkeleya rutilans</i> (Trentepohl ex Roth) Grunow	0.027		
BESCO	<i>Berkeleya scopulorum</i> (Brébisson) E.J. Cox	0.022		
BESPI	<i>Berkeleya</i> sp.1	0.011		
BESP2	<i>Berkeleya</i> sp.2	0.021		
BILUC	<i>Biremis lucens</i> Sabbe, Witkowski & Vyverman	0.264		2 (LM)
BRAPO	<i>Brachysira aponina</i> Kützing	0.041		
BREST	<i>Brachysira estoniarum</i> Witkowski, Lange-Bertalot & Metzeltin	0.183		
aCABAC	<i>Caloneis</i> aff. <i>bacillum</i> (Grunow) Cleve	0.009		
CAMOL	<i>Caloneis molaris</i> (Grunow) Krammer	0.004		
CAORE	<i>Caloneis oregonica</i> (Ehrenberg) Patrick	0.028		
CASP1	<i>Caloneis</i> sp.1	0.011		
CASUB	<i>Caloneis subsalina</i> (Donkin) Hendey	0.019		
CMCLY	<i>Campylodiscus clypeus</i> Ehrenberg	0.140		
CTADH	<i>Catenula adhaerens</i> Mereschkowsky	0.047		
CESMI	<i>Cerataulus smithii</i> Ralfs	0.004		
CHALE	<i>Chamaepinnularia alexandrowiczii</i> Witkowski, Lange-Bertalot & Metzeltin	0.125		2 (LM)
cCHMAR	<i>Chamaepinnularia</i> cf. <i>margaritiana</i> (Witkowski) Witkowski	0.034		
CHSP1	<i>Chamaepinnularia</i> sp.1	0.057		
cCOBAR	<i>Cocconeis</i> cf. <i>bardawilensis</i> Ehrlich nomen nudum	0.090		
<b>cCONEM</b>	<b><i>Cocconeis</i> cf. <i>neothumensis</i> var. <i>marina</i> De Stefano, Marino &amp; Mazzella</b>	<b>0.328</b>	<b>Brackish coastal lagoons and bays</b>	2 (LM)
cCOPEL	<i>Cocconeis</i> cf. <i>pelta</i> A. Schmidt	0.011		
COHAU	<i>Cocconeis hauniensis</i> Witkowski emend Witkowski	0.088		

## Appendix I: Benthic diatom assemblages of the Ebro Delta

Code	Diatom taxa	RA (%)	Habitat	Plates
CONEO	<i>Cocconeis neodiminuta</i> Krammer	0.041		
COPEP	<i>Cocconeis pediculus</i> Ehrenberg	0.287		2 (LM)
<b>COPEL</b>	<b><i>Cocconeis peltoides</i> Hustedt</b>	<b>0.654</b>	<b>Brackish coastal lagoons and bays</b>	2 (LM)
COPEU	<i>Cocconeis placentula</i> var. <i>euglypta</i> (Ehrenberg) Grunow	1.203		3 (LM)
COPEY	<i>Cocconeis placentula</i> var. <i>euglyptoides</i> (Ehrenberg) Geitler	0.281		
COPPL	<i>Cocconeis placentula</i> var. <i>placentula</i> Ehrenberg	1.236		3 (LM), 1 (EM)
COPTR	<i>Cocconeis placentula</i> var. <i>trilineata</i> (M. Peragallo & J. Héribaud) Cleve	0.303		3 (LM)
<b>COSCU</b>	<b><i>Cocconeis scutellum</i> Ehrenberg</b>	<b>0.590</b>	<b>Brackish coastal lagoons and bays</b>	3 (LM)
COSP1	<i>Cocconeis</i> sp.1	0.076		
CRHA1	<i>Craticula halophila</i> (Grunow ex Van Heurck) D.G. Mann	0.012		
CRHA2	<i>Craticula halophila</i> m2 (Grunow ex Van Heurck) D.G. Mann	0.047		
CYATO	<i>Cyclotella atomus</i> Hustedt	0.012		
CYHAK	<i>Cyclotella hakanssoniae</i> Wendker	0.247		3 (LM)
CYMEN	<i>Cyclotella meneghiniana</i> Kützing	0.217		
CMSOL	<i>Cymatopleura solea</i> (Brébisson) W. Smith	0.004		
CMSP1	<i>Cymatosira</i> sp.1	0.004		
<b>DESUR</b>	<b><i>Delphineis surirella</i> (Ehrenberg) Andrews</b>	<b>1.772</b>	<b>Nearshore habitat</b>	3 (LM)
DNSUB	<i>Denticula subtilis</i> Grunow	0.549		3 (LM)
DITEN	<i>Diatoma tenue</i> C. Agardh	0.004		
DILEG	<i>Dickieia legleri</i> (Hustedt) Clavero & Hernández-Mariné	0.113		
DISP1	<i>Dickieia</i> sp.1	0.290		3 (LM), 1 (EM)
DMMIN	<i>Dimeregramma minor</i> (Gregory) Ralfs	0.028		
DPCAF	<i>Diploneis caffra</i> (Giffen) Witkowski, Lange-Bertalot & Metzeltin	0.031		
DPCAM	<i>Diploneis campylodiscus</i> (Grunow) Cleve	0.038		
cDPBOL	<i>Diploneis</i> cf. <i>boldtiana</i> Cleve	0.089		
DPDID	<i>Diploneis didyma</i> (Ehrenberg) Cleve	0.368		4 (LM)
DPELL	<i>Diploneis elliptica</i> (Kützing) Cleve	0.051		
DPLIT	<i>Diploneis litoralis</i> (Donkin) Cleve	0.035		
DPOBL	<i>Diploneis oblongella</i> (Naegeli) Cleve	0.009		
<b>DPSMI</b>	<b><i>Diploneis smithii</i> (Brébisson) Cleve</b>	<b>0.288</b>	<b>Brackish marshes</b>	4 (LM)

## Appendix I: Benthic diatom assemblages of the Ebro Delta

Code	Diatom taxa	RA (%)	Habitat	Plates
DPSMD	<i>Diploneis smithii</i> var. <i>dilatata</i> (M.Peragallo) Terry	0.004		
DPWEI	<i>Diploneis weissflogii</i> (Schmidt) Cleve	0.018		
cENPSE	<i>Entomoneis</i> cf. <i>pseudoduplex</i> Osada & Kobayasi	0.236		4 (LM), 1 (EM)
ENPAL	<i>Entomoneis paludosa</i> var. <i>subsalina</i> (Cleve) Krammer	0.090		
EOMIN	<i>Eolimna minima</i> (Grunow) Lange-Bertalot	0.003		
EPADN	<i>Ephitemia adnata</i> (Kützing) Brébisson	0.007		
EUDUB	<i>Eunotogramma dubius</i> Hustedt	0.004		
FAAEQ	<i>Fallacia aequora</i> (Hustedt) D.G. Mann	0.008		
cFAINS	<i>Fallacia</i> cf. <i>insociabilis</i> (Krasske) D.G. Mann	0.013		
cFAPLA	<i>Fallacia</i> cf. <i>plathii</i> (Brockmann) Snoeijs	0.005		
cFATEN	<i>Fallacia</i> cf. <i>teneroides</i> (Hustedt) D.G. Mann	0.007		
FACLE	<i>Fallacia clepsidroides</i> Witkowski	0.020		
FACRY	<i>Fallacia cryptolyra</i> (Brockmann) Stickle & D.G. Mann	0.083		
FAFOR	<i>Fallacia forcipata</i> (Greville) Stickle & D.G. Mann	0.031		
FALIT	<i>Fallacia litoricola</i> (Hustedt) D.G. Mann	0.004		
FAOCU	<i>Fallacia oculiformis</i> (Hustedt) D.G. Mann	0.008		
FAPYG	<i>Fallacia pygmaea</i> (Kützing) Stickle & D.G. Mann	0.258		5 (LM)
FASCH	<i>Fallacia schaeferae</i> (Hustedt) D.G. Mann	0.023		
FATEN	<i>Fallacia tenera</i> (Hustedt) D.G. Mann	0.081		
FAWUE	<i>Fallacia wuestii</i> (Simonsen) Sabbe & Muylaert	0.029		
FRAMI	<i>Fragilaria amicorum</i> Witkowski & Lange-Bertalot	0.176		5 (LM), 2 (EM)
<b>FRATO</b>	<b><i>Fragilaria atomus</i> Hustedt</b>	<b>0.866</b>	<b>Coastal lagoons with fresher conditions</b>	<b>5 (LM), 2 (EM)</b>
FRCAP	<i>Fragilaria capensis</i> Grunow	0.013		
FRCAU	<i>Fragilaria capucina</i> Desmazières	0.004		
FRCAS	<i>Fragilaria cassubica</i> Witkowski & Lange-Bertalot	0.034		
cFRELL	<i>Fragilaria</i> cf. <i>elliptica</i> Schumann	0.231		5 (LM)
cFRHYA	<i>Fragilaria</i> cf. <i>hyalina</i> (Kützing) Grunow	0.022		
<b>cFRNEO</b>	<b><i>Fragilaria</i> cf. <i>neoe elliptica</i> Witkowski</b>	<b>0.395</b>	<b>Brackish marshes</b>	<b>5 (LM)</b>
<b>cFRSOP</b>	<b><i>Fragilaria</i> cf. <i>sopotensis</i> Witkowski &amp; Lange-Bertalot</b>	<b>0.734</b>	<b>Coastal lagoons with fresher conditions</b>	<b>5 (LM)</b>
<b>FRGED</b>	<b><i>Fragilaria gedanensis</i> Witkowski</b>	<b>1.009</b>	<b>Coastal lagoons with fresher conditions</b>	<b>5 (LM)</b>

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Code	Diatom taxa	RA (%)	Habitat	Plates
FRMAR	<i>Fragilaria martyi</i> (Héribaud) Lange-Bertalot	0.980		
FRPUL	<i>Fragilaria pulchella</i> (Ralfs ex Kützing) Lange-Bertalot	0.025		
<b>FRSP1</b>	<b>cf. <i>Fragilaria</i> sp.1</b>	<b>2.793</b>	<b>Coastal lagoons with fresher conditions</b>	5 (LM), 2 (EM)
<b>FRSP2</b>	<b>cf. <i>Fragilaria</i> sp.2</b>	<b>1.024</b>	<b>Coastal lagoons with fresher conditions</b>	5 (LM)
FRSP3	cf. <i>Fragilaria</i> sp.3	0.129		
FRCRE	<i>Frustulia creuzburgensis</i> (Krasske) Hustedt	0.041		
GOACI	<i>Gomphonema acidoclinatum</i> Lange-Bertalot & Reichardt	0.014		
cGOGRO	<i>Gomphonema</i> cf. <i>groveri</i> var. <i>lingulatum</i> (Hustedt) Lange-Bertalot	0.007		
GOCLA	<i>Gomphonema clavatum</i> Reichardt	0.010		
GOLAT	<i>Gomphonema lateripunctatum</i> Reichardt & Lange-Bertalot	0.007		
GOMIN	<i>Gomphonema minutum</i> (C. Agardh) C. Agardh	0.004		
GOOLI	<i>Gomphonema olivaceum</i> (Hornemann) Brébisson	0.004		
GOPAR	<i>Gomphonema parvulum</i> (Kützing) Kützing	0.014		
GORHO	<i>Gomphonema rhombicum</i> Fricke	0.004		
GOOBS	<i>Gomphonemopsis obscurum</i> (Krasske) Lange-Bertalot	0.449		5 (LM)
GRMAR	<i>Grammatophora marina</i> (Lyngbye) Kützing	0.111		
GYBAL	<i>Gyrosigma balticum</i> (Ehrenberg) Rabenhorst	0.004		
GYFAS	<i>Gyrosigma fasciola</i> (Ehrenberg) Griffith & Henfrey	0.291		
GYPEI	<i>Gyrosigma peisonis</i> (Grunow) Hustedt	0.004		
GYWAN	<i>Gyrosigma wansbeckii</i> (Donkin) Cleve	0.125		
GYWPE	<i>Gyrosigma wansbeckii</i> var. <i>peisonis</i> (Grunow) Cleve	0.166		5 (LM)
HADOM	<i>Halamphora dominici</i> Acs & Levkov	0.004		
HAVIR	<i>Hantzschia virgata</i> (Roper) Grunow	0.004		
HASP1	<i>Haslea</i> sp.1	0.009		
HASPI	<i>Haslea spicula</i> (Hickie) Bukhtiyarova	0.025		
HICAO	<i>Hippodonta caotica</i> Witkowski, Lange-Bertalot & Metzeltin	0.061		
HIHUN	<i>Hippodonta hungarica</i> (Grunow) Lange-Bertalot, Metzeltin & Witkowski	0.029		
HYSKO	<i>Hyalodiscus scoticus</i> (Kützing) Grunow	0.018		
HYSP1	<i>Hyalosira</i> sp.1	0.004		
cLUGOE	<i>Luticola</i> cf. <i>goeppertiana</i> (Bleisch in Rabenhorst) D.G. Mann	0.030		

## Appendix I: Benthic diatom assemblages of the Ebro Delta

Code	Diatom taxa	RA (%)	Habitat	Plates
LUMUT	<i>Luticola mutica</i> (Kützing) D.G. Mann	0.080		
LUVEN	<i>Luticola ventricosa</i> (Kützing) D.G. Mann	0.007		
LYSPE	<i>Lyrella spectabilis</i> (Gregory) D.G. Mann	0.021		
MAAFI	<i>Mastogloia affirmata</i> (Leuduger-Fortmorel) Cleve	0.022		
MAAQU	<b><i>Mastogloia aquilegiae</i> Grunow</b>	<b>1.009</b>	<b>Salt marshes</b>	6 (LM)
MABEL	<i>Mastogloia belaensis</i> Voigt	0.033		
MABRA	<b><i>Mastogloia braunii</i> Grunow</b>	<b>0.852</b>	<b>Salt marshes</b>	6 (LM)
MADES	<i>Mastogloia desertorum</i> Voigt	0.022		
MAELL	<i>Mastogloia elliptica</i> (C. Agardh) Cleve	0.008		
MAEXI	<i>Mastogloia exigua</i> Lewis	0.007		
MAIGN	<i>Mastogloia ignorata</i> Hustedt	0.004		
MAPUM	<i>Mastogloia pumila</i> (Grunow) Cleve	0.427		6 (LM)
MAPUS	<i>Mastogloia pusilla</i> (Grunow) Cleve	0.030		
MAPUL	<i>Mastogloia pusilla</i> var. <i>linearis</i> Østrup	0.008		
MASMI	<i>Mastogloia smithii</i> Thwaites	0.076		
MASMA	<i>Mastogloia smithii</i> var. <i>amphicephala</i> Grunow	0.007		
MYFOS	<i>Mayamaea fossalis</i> (Krasske) Lange-Bertalot	0.004		
cMEMON	<i>Melosira</i> cf. <i>moniliformis</i> (O.F.Muller) C. Agardh	0.009		
NOSHI	<i>Nanofrustulum shiloi</i> (Lee, Reimer & McEnery) Round, Hallsteinsen & Paasche	0.197		
aNALUS	<i>Navicula</i> aff. <i>lusoria</i> Giffen	0.030		
aNAMOL	<i>Navicula</i> aff. <i>mollis</i> (W. Smith) Cleve	0.874		7 (LM)
aNAPEM	<i>Navicula</i> aff. <i>perminuta</i> Grunow	0.181		
aNARAM	<i>Navicula</i> aff. <i>ramosissima</i> (C.Agardh) Cleve	0.061		
NAANT	<i>Navicula antonii</i> Lange-Bertalot	1.597		7 (LM)
NAARE	<i>Navicula arenaria</i> Donkin	0.210		
NABIP	<i>Navicula bipustulata</i> A. Mann	0.019		
NACAP	<i>Navicula capitoradiata</i> Germain	0.015		
NACAR	<i>Navicula cari</i> Ehrenberg	0.447		
NACRI	<i>Navicula cariocincta</i> Lange-Bertalot	0.304		7 (LM)
cNAALE	<i>Navicula</i> cf. <i>aleksandrae</i> Lange-Bertalot, Bogaczewicz-Adamczak & Witkowski	0.073		

## Appendix I: Benthic diatom assemblages of the Ebro Delta

Code	Diatom taxa	RA (%)	Habitat	Plates
cNAAPI	<i>Navicula</i> cf. <i>apiculata</i> Brébisson	0.031		
cNAARE	<i>Navicula</i> cf. <i>arenaria</i> Donkin	0.067		
cNACAR	<i>Navicula</i> cf. <i>cari</i> Ehrenberg	0.100		
cNACRY	<i>Navicula</i> cf. <i>cryptocephaloides</i> Hustedt	0.008		
cNACRP	<i>Navicula</i> cf. <i>cryptotenelloides</i> Lange-Bertalot	0.034		
cNADIG	<i>Navicula</i> cf. <i>digitoradiata</i> (Gregory) Ralfs	0.016		
cNAMIC	<i>Navicula</i> cf. <i>microcari</i> Lange-Bertalot	0.104		7 (LM)
<b>cNAHAN</b>	<b><i>Navicula</i> cf. <i>hansenii</i> Möller</b>	<b>0.105</b>	<b>Brackish coastal lagoons and bays</b>	7 (LM)
cNANOR	<i>Navicula</i> cf. <i>normaloides</i> Cholnoky	0.098		
cNAPHY	<i>Navicula</i> cf. <i>phylleptosoma</i> Lange-Bertalot	0.239		
cNAPSE	<i>Navicula</i> cf. <i>pseudosalinarum</i> Giffen	0.964		
cNAREC	<i>Navicula</i> cf. <i>recens</i> (Lange-Bertalot) Lange-Bertalot	1.196		7 (LM)
cNASAL	<i>Navicula</i> cf. <i>salinicola</i> Hustedt	0.210		
cNAVEN	<i>Navicula</i> cf. <i>veneta</i> Kützing	0.019		
NACIN	<i>Navicula</i> <i>cincta</i> (Ehrenberg) Ralfs	0.014		
NACON	<i>Navicula</i> <i>consentanea</i> Hustedt	0.103		
NACRP	<i>Navicula</i> <i>cryptocephala</i> Kützing	0.030		
NACRT	<i>Navicula</i> <i>cryptotenella</i> Lange-Bertalot	0.067		
NADIG	<i>Navicula</i> <i>digitoradiata</i> (Gregory) Ralfs	0.148		
NADIL	<i>Navicula</i> <i>dilucida</i> Hustedt	0.030		
NADIR	<i>Navicula</i> <i>directa</i> (W. Smith) Ralfs	0.019		
NADIS	<i>Navicula</i> cf. <i>diserta</i> Hustedt	0.178		7 (LM)
NADUE	<i>Navicula</i> <i>duerrenbergiana</i> Hustedt	0.036		
NAERI	<i>Navicula</i> <i>erifuga</i> Lange-Bertalot	0.130		
NAFLA	<i>Navicula</i> <i>flagellifera</i> Hustedt	0.038		
NAGER	<i>Navicula</i> <i>germanopolonica</i> Witkowski & Lange-Bertalot	0.012		
<b>NAGRE</b>	<b><i>Navicula</i> <i>gregaria</i> Donkin</b>	<b>0.375</b>	<b>Coastal lagoons with fresher conditions</b>	7 (LM)
NAGRO	<i>Navicula</i> <i>groschopfii</i> Hustedt	0.041		
NAMEN	<i>Navicula</i> <i>menisculus</i> Schumann	0.004		
<b>NAMIC</b>	<b><i>Navicula</i> <i>microcari</i> Lange-Bertalot</b>	<b>0.232</b>	<b>Brackish marshes</b>	7 (LM)



## Appendix I: Benthic diatom assemblages of the Ebro Delta

Code	Diatom taxa	RA (%)	Habitat	Plates
NAMCR	<i>Navicula microdigitoradiata</i> Lange-Bertalot	0.043		
NANOR	<i>Navicula normaloides</i> Cholnoky	0.266		
NAOES	<i>Navicula oestrupii</i> Héribaud-Joseph	0.022		
NAPAR	<i>Navicula pargemina</i> Underwood & Yallop	0.039		
NAPAV	<i>Navicula pavillardii</i> Hustedt	0.406		
NAPER	<i>Navicula peregrina</i> (Ehrenberg) Kützing	0.811		7 (LM)
<b>NAPEM</b>	<b><i>Navicula perminuta</i> Grunow</b>	<b>1.782</b>	<b>Brackish marshes</b>	7 (LM), 2 (EM)
NAPHL	<i>Navicula phyllepta</i> Kützing	0.625		7 (LM)
NAPSE	<i>Navicula pseudocrassirostris</i> Hustedt	0.050		
NAPSU	<i>Navicula pseudosalinarum</i> Giffen	0.055		
NAREC	<i>Navicula recens</i> (Lange-Bertalot) Lange-Bertalot	0.050		
NAROS	<i>Navicula rostellata</i> Kützing	0.003		
NASAL	<i>Navicula salinarum</i> Grunow	0.316		
NASAI	<i>Navicula salinicola</i> Hustedt	2.531		7 (LM)
NASLE	<i>Navicula sleviscensis</i> Grunow	0.008		
NASP1	<i>Navicula</i> sp.1	0.543		8 (LM)
NASP2	<i>Navicula</i> sp.2	0.355		8 (LM)
NASP3	<i>Navicula</i> sp.3	0.032		
NASP4	<i>Navicula</i> sp.4	0.186		
NASP5	<i>Navicula</i> sp.5	0.121		8 (LM)
NASP6	<i>Navicula</i> sp.6	0.194		8 (LM)
<b>NASP7</b>	<b><i>Navicula</i> sp.7</b>	<b>0.298</b>	<b>Brackish coastal lagoons and bays</b>	8 (LM)
NASP8	<i>Navicula</i> sp.8	0.715		8 (LM)
NASTA	<i>Navicula stachurae</i> Witkowski	0.093		
NASTR	<i>Navicula starmachioides</i> (Witkowski & Lange-Bertalot)Witkowski & Lange-Bertalot	0.210		
NASTE	<i>Navicula streckeriae</i> Lange-Bertalot & Witkowski	0.084		
NASTU	<i>Navicula stundlii</i> Hustedt	0.510		8 (LM)
NASUB	<i>Navicula subrhynchocephala</i> Hustedt	0.004		
NATEN	<i>Navicula tenelloides</i> Hustedt	0.019		
NATRD	<i>Navicula transitans</i> var. <i>derasa</i> fo.delicatula Heimdal	0.051		

## Appendix I: Benthic diatom assemblages of the Ebro Delta

Code	Diatom taxa	RA (%)	Habitat	Plates
NATRI	<i>Navicula tripunctata</i> (O.F. Müller) Bory	0.101		
NATRV	<i>Navicula trivialis</i> Lange-Bertalot	0.004		
NAVAN	<i>Navicula vandamii</i> Schoeman & Archibald	0.025		
NAVAE	<i>Navicula vaneei</i> Lange-Bertalot	0.085		
NAVIM	<b><i>Navicula vimineoides</i> Giffen</b>	<b>0.219</b>	<b>Brackish coastal lagoons and bays</b>	8 (LM)
NAVUL	<i>Navicula vulpina</i> Kützing	0.004		
NVPU1	<b><i>Navicymbula pusilla</i> m1 (Grunow) Krammer</b>	<b>3.816</b>	<b>Salt marshes</b>	9 (LM), 2 (EM)
NVPU2	<i>Navicymbula pusilla</i> m2 (Grunow) Krammer	0.397		9 (LM)
NIAEQ	<i>Nitzschia aequorea</i> Hustedt	0.301		9 (LM)
aNIPAL	<i>Nitzschia</i> aff. <i>paleaeformis</i> Hustedt	0.008		
aNIROS	<i>Nitzschia</i> aff. <i>rosenstockii</i> Lange-Bertalot	0.132		
NIAMP	<i>Nitzschia amphibia</i> Grunow	0.007		
NIANG	<i>Nitzschia angularis</i> W. Smith	0.022		
NIARE	<i>Nitzschia aremonica</i> Archibald	0.004		
NIBAC	<i>Nitzschia bacillum</i> Hustedt	0.219		
NICAL	<i>Nitzschia calida</i> Grunow	0.004		
NICAP	<i>Nitzschia capitellata</i> Hustedt	0.103		
cNIAGN	<i>Nitzschia</i> cf. <i>agnita</i> Hustedt	0.008		
cNIARD	<i>Nitzschia</i> cf. <i>ardua</i> Cholnoky	0.129		
cNICLAU	<i>Nitzschia</i> cf. <i>clausii</i> Hantzsch	0.005		
cNIDIS	<i>Nitzschia</i> cf. <i>distans</i> Gregory	0.085		
cNIFON	<i>Nitzschia</i> cf. <i>fonticola</i> (Grunow) Grunow	0.003		
cNIHUN	<i>Nitzschia</i> cf. <i>hungarica</i> Grunow	0.162		
cNIGRO	<i>Nitzschia</i> cf. <i>grossestriata</i> Hustedt	0.007		
cNIINV	<i>Nitzschia</i> cf. <i>invisitata</i> Hustedt	0.005		
cNILES	<i>Nitzschia</i> cf. <i>lesbia</i> Cholnoky	0.212		9 (LM)
cNILIE	<i>Nitzschia</i> cf. <i>liebetruthii</i> Rabenhorst	0.128		
cNIPAL	<i>Nitzschia</i> cf. <i>palea</i> (Kützing) W.Smith	0.019		
cNIPER	<i>Nitzschia</i> cf. <i>perindistincta</i> Cholnoky	1.410		9 (LM), 2 (EM)
cNIPES	<i>Nitzschia</i> cf. <i>perspicua</i> Cholnoky	0.036		

*Appendix I: Benthic diatom assemblages of the Ebro Delta*

Code	Diatom taxa	RA (%)	Habitat	Plates
cNIQUA	<i>Nitzschia</i> cf. <i>quadrangula</i> (Kützing) Lange-Bertalot	0.103		
cNITUB	<i>Nitzschia</i> cf. <i>tubicola</i> Grunow	0.353		
<b>NICOA</b>	<b><i>Nitzschia coarctata</i> Grunow</b>	<b>0.670</b>	<b>Nearshore habitat</b>	9 (LM)
NICMN	<i>Nitzschia communis</i> Rabenhorst	0.071		
NICOM	<i>Nitzschia commutata</i> Grunow	0.004		
NICOP	<i>Nitzschia compressa</i> (J.W.Bailey) Boyer	0.175		
<b>NICON</b>	<b><i>Nitzschia constricta</i> (Kützing) Ralfs</b>	<b>1.448</b>	<b>Brackish coastal lagoons and bays</b>	10 (LM)
NIDES	<i>Nitzschia desertorum</i> Hustedt	0.016		
NIDID	<i>Nitzschia didyma</i> Hustedt	0.004		
NIDIP	<i>Nitzschia dippelii</i> Grunow	0.009		
NIDIS	<i>Nitzschia dissipata</i> (Kützing) Grunow	0.004		
NIELE	<i>Nitzschia elegantula</i> Grunow	0.431		10 (LM)
NIEPI	<i>Nitzschia epithemioides</i> Lange-Bertalot	0.059		
NIFIL	<i>Nitzschia filiformis</i> (W. Smith) Van Heurck	0.072		
NIFRU	<i>Nitzschia frustulum</i> (Kützing) Grunow	0.008		
NIFU1	<i>Nitzschia fusiformis</i> m1 Grunow	0.020		
NIFU2	<i>Nitzschia fusiformis</i> m2 Grunow	1.244		10 (LM)
NIGRA	<i>Nitzschia granulata</i> Grunow	0.248		
NIHEU	<i>Nitzschia heufleriana</i> Grunow	0.015		
<b>NIINC</b>	<b><i>Nitzschia inconspicua</i> Grunow</b>	<b>2.493</b>	<b>Brackish marshes</b>	10 (LM)
NILAN	<i>Nitzschia lanceola</i> Grunow	0.009		
NILEV	<i>Nitzschia levidensis</i> (W.Smith) Grunow	0.025		
NILSA	<i>Nitzschia levidensis</i> var. <i>salinarum</i> Grunow	0.021		
<b>NILIE</b>	<b><i>Nitzschia liebetruthii</i> Rabenhorst</b>	<b>0.423</b>	<b>Brackish coastal lagoons and bays</b>	10 (LM)
NILIT	<i>Nitzschia littoralis</i> Grunow	0.007		
NILOR	<i>Nitzschia lorenziana</i> Grunow	0.008		
NIMIC	<i>Nitzschia microcephala</i> Grunow	0.204		
<b>NIPAR</b>	<b><i>Nitzschia pararostrata</i> (Lange-Bertalot) Lange-Bertalot</b>	<b>0.312</b>	<b>Brackish coastal lagoons and bays</b>	10 (LM)
NIPEL	<i>Nitzschia pellucida</i> Grunow	0.150		
NIPEM	<i>Nitzschia perminuta</i> (Grunow) M.Peragallo	0.013		

*Appendix I: Benthic diatom assemblages of the Ebro Delta*

Code	Diatom taxa	RA (%)	Habitat	Plates
NIPUS	<i>Nitzschia pusilla</i> (Kützing) Grunow	0.066		
NIREC	<i>Nitzschia recta</i> Hantzsch	0.007		
NISCA	<i>Nitzschia scalaris</i> (Ehrenberg) W. Smith	0.087		
NISCL	<i>Nitzschia scalpelliformis</i> (Grunow) Grunow	1.291		11 (LM), 2 (EM)
NISER	<i>Nitzschia serpenticola</i> Cholnoky	0.049		
NISIG	<i>Nitzschia sigma</i> (Kützing) W. Smith	0.379		11 (LM)
NISPI	<i>Nitzschia</i> sp.1	0.021		
NISP2	<i>Nitzschia</i> sp.2	0.009		
NISUP	<i>Nitzschia supralitorea</i> Lange-Bertalot	0.111		
NITHE	<i>Nitzschia thermaloides</i> Hustedt	0.469		11 (LM)
NITRY	<i>Nitzschia tryblionella</i> Hantzsch	0.032		
NITUB	<i>Nitzschia tubicola</i> Grunow	0.030		
NIVAL	<i>Nitzschia valdecostata</i> Lange-Bertalot & Simonsen	0.004		
NIVID	<i>Nitzschia vidovichii</i> (Grunow) Grunow	0.361		
NIVIT	<i>Nitzschia vitrea</i> G. Norman	0.164		11 (LM)
ODAUR	<i>Odontella aurita</i> (Lyngbye) C. Agardh	0.037		
cOPBUR	<i>Opephora</i> cf. <i>burchardtia</i> Witkowski, Metzeltin & Lange-Bertalot	0.022		11 (LM)
cOPKRU	<i>Opephora</i> cf. <i>krumbeinii</i> Witkowski, Witak & Stachura	0.007		
OPGUE	<i>Opephora guenter-grassii</i> (Witkowski & Lange-Bertalot) Sabbe & Vyverman	1.095		12 (LM)
OPMIN	<i>Opephora minuta</i> (Cleve) Witkowski, Lange-Bertalot & Metzeltin	0.004		
OPMUT	<i>Opephora mutabilis</i> (Grunow) Sabbe & Vyverman	0.184		12 (LM)
<b>OPSP1</b>	<b>cf. <i>Opephora</i> sp.1</b>	<b>0.384</b>	<b>Coastal lagoons with fresher conditions</b>	12 (LM)
PASUL	<i>Paralia sulcata</i> (Ehrenberg) Cleve	0.015		
PRCRU	<i>Parlibellus cruciculoides</i> (Brockmann) Witkowski, Lange-Bertalot & Metzeltin	0.008		
PRHAG	<i>Parlibellus hagelsteinii</i> E.J. Cox	0.288		12 (LM)
PRSP1	<i>Parlibellus</i> sp.1	0.110		12 (LM)
PRSP2	<i>Parlibellus</i> sp.2	0.004		
PEGEM	<i>Petrodictyon gemma</i> (Ehrenberg) D.G. Mann	0.004		
PTMAR	<i>Petroneis marina</i> (Ralfs) D.G. Mann	0.007		
PIELE	<i>Pinnuavis elegans</i> (W. Smith) Okuno	0.003		

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Code	Diatom taxa	RA (%)	Habitat	Plates
PIBOR	<i>Pinnularia borealis</i> var. <i>rectangularis</i> Carlson	0.004		
PIBRE	<i>Pinnularia brebissonii</i> (Kützing) Rabenhorst	0.004		
PLPLA	<i>Placoneis placentula</i> (Ehrenberg) Heinzerling	0.008		
PGMED	<i>Plagiogrammopsis mediaequatus</i> Gardner & Crawford	0.013		
PGMIN	<i>Plagiogrammopsis minima</i> Sabbe, Vaneslander, Witkowski, Ribeiro & Vyverman	0.004		
PILEP	<i>Plagiotropis</i> cf. <i>lepidoptera</i> (Gregory) Kuntze	0.030		
cPNLEM	<i>Planothidium</i> cf. <i>lemmermannii</i> (Hustedt) Morales	0.032		
PNDE1	<i>Planothidium delicatulum</i> m1 (Kützing) Round & Bukhtiyarova	0.921		12 (LM), 3 (EM)
PNDE2	<i>Planothidium delicatulum</i> m2 (Kützing) Round & Bukhtiyarova	0.490		12 (LM)
PNDE3	<i>Planothidium delicatulum</i> m3 (Kützing) Round & Bukhtiyarova	0.015		
<b>PNDEP</b>	<b><i>Planothidium deperditum</i> (Giffen) Witkowski &amp; Lange-Bertalot</b>	<b>0.166</b>	<b>Brackish coastal lagoons and bays</b>	12 (LM)
PNENG	<i>Planothidium engelbrechtii</i> (Cholnoky) Round & Bukhtiyarova	0.070		
PNIBE	<i>Planothidium iberense</i> Rovira & Witkowski	0.004		
PNLAN	<i>Planothidium lanceolatum</i> (Brébisson ex Kützing) Lange-Bertalot	0.004		
PNLEM	<i>Planothidium lemmermannii</i> (Hustedt) Morales	0.037		
PNSEP	<i>Planothidium septentrionalis</i> (Østrup) Round & Bukhtiyarova	0.015		
PNSP1	<i>Planothidium</i> sp.1	0.066		
PEANG	<i>Pleurosigma angulatum</i> (Queckett) W.Smith	0.041		
PEDEL	<i>Pleurosigma delicatulum</i> W.Smith	0.022		
PEFOR	<i>Pleurosigma formosum</i> W.Smith	0.024		
PULAE	<i>Pleurosira laevis</i> (Ehrenberg) Compere	0.035		
PRCOM	<i>Proshkinia complanata</i> (Grunow) D.G. Mann	0.003		
aPSAME	<i>Pseudostaurosira</i> aff. <i>americana</i> E.A. Morales	0.018		
PSALV	<i>Pseudostaurosira alvareziae</i> Cejudo-Figueiras, E.A. Morales & Ector	0.017		13 (LM)
PSBRE	<i>Pseudostaurosira brevistriata</i> (Grunow) Williams & Round	0.645		13 (LM)
cPSBREV	<i>Pseudostaurosira</i> cf. <i>brevistriata</i> (Grunow) Williams & Round	0.172		13 (LM)
cPSPER	<i>Pseudostaurosira</i> cf. <i>perminuta</i> (Grunow) Sabbe & Vyverman	0.032		
cPSSUB	<i>Pseudostaurosira</i> cf. <i>subsalina</i> (Hustedt) E.A.Morales	0.264		13 (LM)
PSSUB	<i>Pseudostaurosira subsalina</i> (Hustedt) E.A.Morales	0.220		13 (LM)
<b>FRGEO</b>	<b><i>Pseudostaurosira</i> cf. <i>geocollegarum</i> (Witkowski &amp; Lange-Bertalot) E.A.Morales</b>	<b>3.383</b>	<b>Coastal lagoons with fresher conditions</b>	13 (LM), 3 (EM)

## Appendix I: Benthic diatom assemblages of the Ebro Delta

Code	Diatom taxa	RA (%)	Habitat	Plates
<b>cFRGEO</b>	<b><i>Pseudostaurosiropsis geocollegarum</i> (Witkowski &amp; Lange-Bertalot) E.A.Morales</b>	<b>1.223</b>	<b>Coastal lagoons with fresher conditions</b>	13 (LM)
RHABR	<i>Rhoicosphenia abbreviata</i> (C.Agardh) Lange-Bertalot	0.024		
RHLIN	<i>Rhoicosphenia linearis</i> Østrup	0.026		
RHMAR	<i>Rhoicosphenia marina</i> (Kützing) M.Schmidt	0.012		
ROACU	<i>Rhopalodia acuminata</i> Krammer	0.028		
ROBRE	<i>Rhopalodia brebissonii</i> Krammer	0.192		
ROCON	<i>Rhopalodia constricta</i> (W.Smith) Krammer	0.885		13 (LM), 3 (EM)
ROMUS	<i>Rhopalodia musculus</i> (Kützing) O.Muller	0.161		13 (LM)
cSADEL	<i>Sarcophagodes cf. delicatula</i> E.A. Morales	0.014		13 (LM)
cSCTUM	<i>Scolioneis cf. tumida</i> (Brebisson ex Kützing) D.G.Mann	0.094		
SEOST	<i>Seminavis ostenfeldii</i> (Hustedt) Clavero & Hernández-Mariné	0.049		
<b>SEROB</b>	<b><i>Seminavis robusta</i> Danielidis &amp; Mann</b>	<b>0.534</b>	<b>Brackish coastal lagoons and bays</b>	14 (LM)
<b>SESTR</b>	<b><i>Seminavis strigosa</i> (Hustedt) Danielidis &amp; Economou-Amilli</b>	<b>2.414</b>	<b>Brackish coastal lagoons and bays</b>	14 (LM)
STAMP	<i>Stauroneis amphioxys</i> Gregory	0.040		
SACOB	<i>Staurosira construens</i> var. <i>binodis</i> (Ehrenberg) Hamilton	0.004		
SACOV	<i>Staurosira construens</i> var. <i>venter</i> (Ehrenberg) Bukhtiyarova	0.177		14 (LM)
SAPUN	<i>Staurosira punctiformis</i> Witkowski, Metzeltin & Lange-Bertalot	0.037		
cSRPIN	<i>Staurosirella cf. pinnata</i> (Ehrenberg) Williams & Round	0.024		
SRSP1	<i>Staurosirella</i> sp.1	0.058		
STUNI	<i>Striatella unipunctata</i> (Lyngbye) C. Agardh	0.077		15 (LM)
aSUSAL	<i>Surirella</i> aff. <i>salina</i> W.Smith	0.004		15 (LM)
SUBRE	<i>Surirella brebissonii</i> Krammer & Lange-Bertalot	0.015		15 (LM)
SUFAS	<i>Surirella fastuosa</i> Ehrenberg	0.027		15 (LM)
SUSTR	<i>Surirella striatula</i> Turpin	0.011		
SUTNE	<i>Surirella tenera</i> var. <i>nervosa</i> A.Schmidt	0.005		
TAFAS	<i>Tabularia fasciculata</i> (C. Agardh) Williams & Round	0.025		
TAGAI	<i>Tabularia gaillonii</i> (Bory) Ehrenberg	0.005		
TATAB	<i>Tabularia tabulata</i> (C. Agardh) Snoeijis	0.328		14 (LM)
THNIT	<i>Thalassionema nitzschioides</i> (Grunow) Mereschkowsky	0.013		
TLANG	<i>Thalassiosira angulata</i> (Gregory) Hasle	0.049		14 (LM)

*Appendix I: Benthic diatom assemblages of the Ebro Delta*

<b>Code</b>	<b>Diatom taxa</b>	<b>RA (%)</b>	<b>Habitat</b>	<b>Plates</b>
TLHYP	<i>Thalassiosira hyperborea</i> (Grunow) Hasle	0.010		
TLSP1	<i>Thalassiosira</i> sp.1	0.015		
TOUND	<i>Toxarium undulatum</i> J.W.Bailey	0.079		
TRDUB	<i>Triceratium dubium</i> Brightwell	0.004		

*Appendix I: Benthic diatom assemblages of the Ebro Delta***Light Microscope (LM) and Electron Microscope (EM) plates of diatom taxa**

LM pictures were taken under differential interference contrast (DIC), all at the same magnification (1000x). Scale bar represents 10  $\mu\text{m}$  for LM and 1  $\mu\text{m}$  for EM, except when specified.

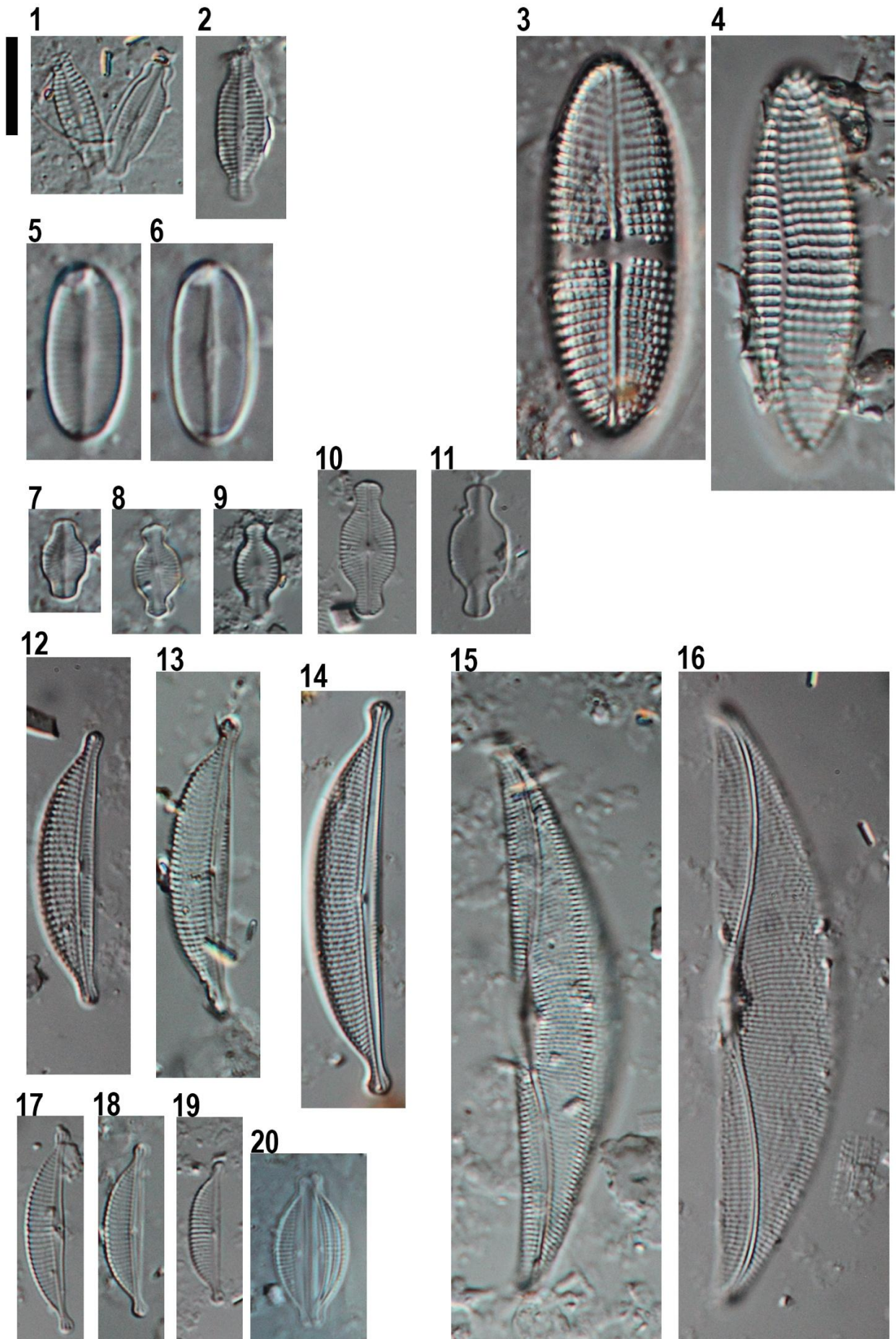


*Appendix I: Benthic diatom assemblages of the Ebro Delta*

*Appendix I: Benthic diatom assemblages of the Ebro Delta***Plate 1 LM**

- Figs 1–2      *Achnanthes amoena* Hustedt  
Fig. 1: Rapheless (SV) and raphe valves (RV)  
Fig. 2: SV
- Figs. 3–4      *Achnanthes brevipes* var. *intermedia* (Kützing) Cleve  
Fig. 3: RV  
Fig. 4: SV
- Figs. 5–6      *Achnanthes* sp.1  
Fig. 5: SV  
Fig. 6: RV
- Figs. 7–11      *Achnanthes submarina* Hustedt  
Figs. 7–8: RV  
Fig. 9: SV  
Fig. 10: RV  
Fig. 11: SV
- Figs. 12–14      *Amphora acutiuscula* Kützing
- Figs. 15–16      *Amphora arcus* var. *sulcata* (A. Schmidt) Cleve
- Figs. 17–20      *Amphora* cf. *luciae* Cholnoky sensu Archibald  
Figs. 17–19: valves  
Fig. 20: frustule

*Appendix I: Benthic diatom assemblages of the Ebro Delta*

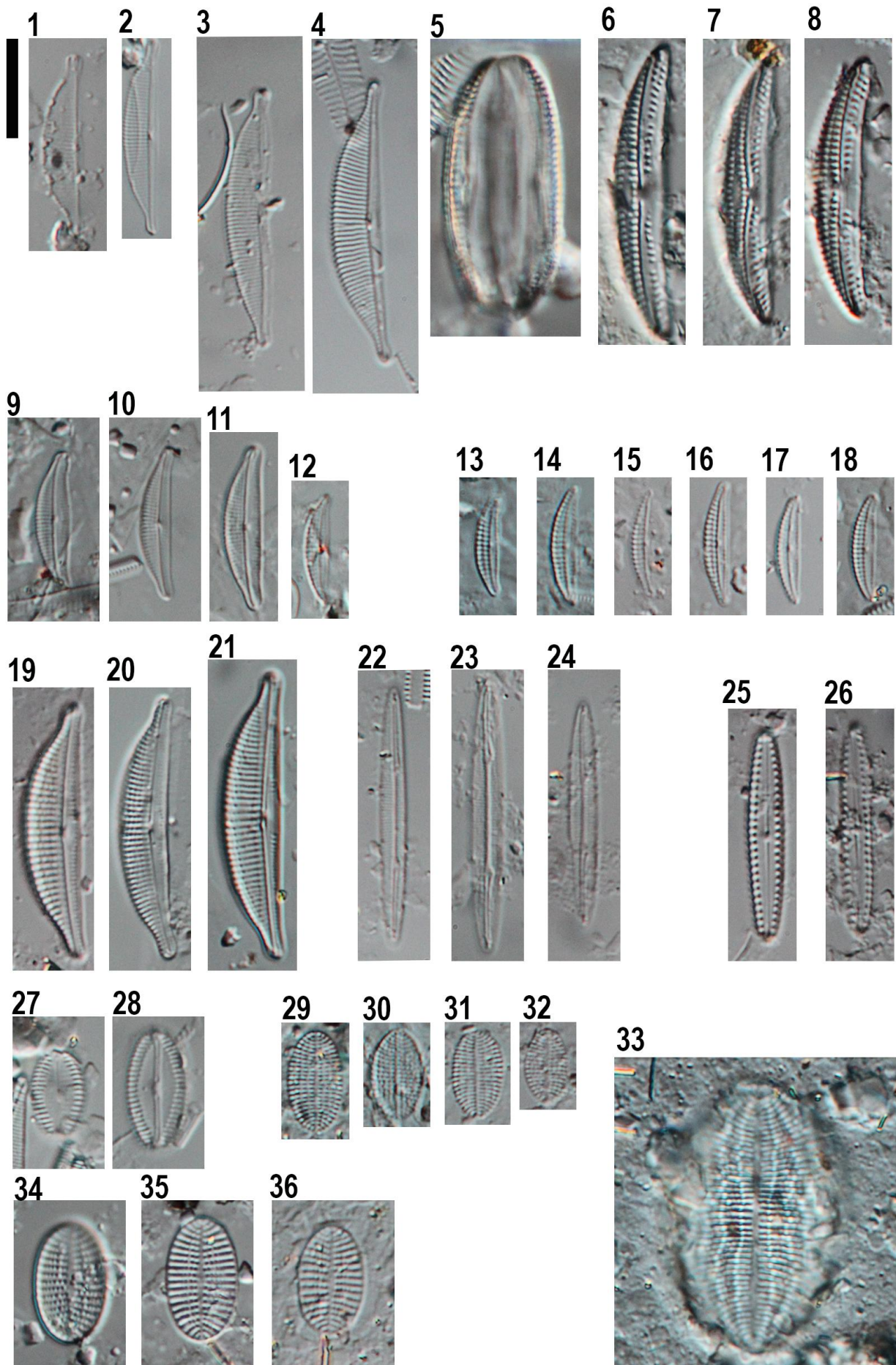


*Appendix I: Benthic diatom assemblages of the Ebro Delta***Plate 2 LM**

- Figs. 1–2      *Amphora* cf. *roettgeri* Lee & Reimer
- Figs. 3–4      *Amphora coffeaeformis* C. Agardh (Kützing)
- Figs. 5–8      *Amphora pusio* Cleve  
Fig. 5: frustule  
Figs. 6–8: valves
- Figs. 9–12     *Amphora* sp.1
- Figs. 13–18    *Amphora* sp.5
- Figs. 19–21    *Amphora subacutiuscula* Schoeman
- Figs. 22–24    *Berkeleya fennica* Juhlin-Dannfelt
- Figs. 25–26    *Biremis lucens* K.Sabbe, A.Witkowski & W.Vyverman
- Figs. 27–28    *Chamaepinnularia alexandrowiczii* Witkowski, Lange-Bertalot & Metzeltin
- Figs. 29–32    *Cocconeis* cf. *neothumensis* var. *marina* De Stefano, Marino & Mazzella, SV
- Fig. 33        *Cocconeis pediculus* Ehrenberg, SV
- Figs. 34–36    *Cocconeis peltoides* Hustedt, SV



*Appendix I: Benthic diatom assemblages of the Ebro Delta*

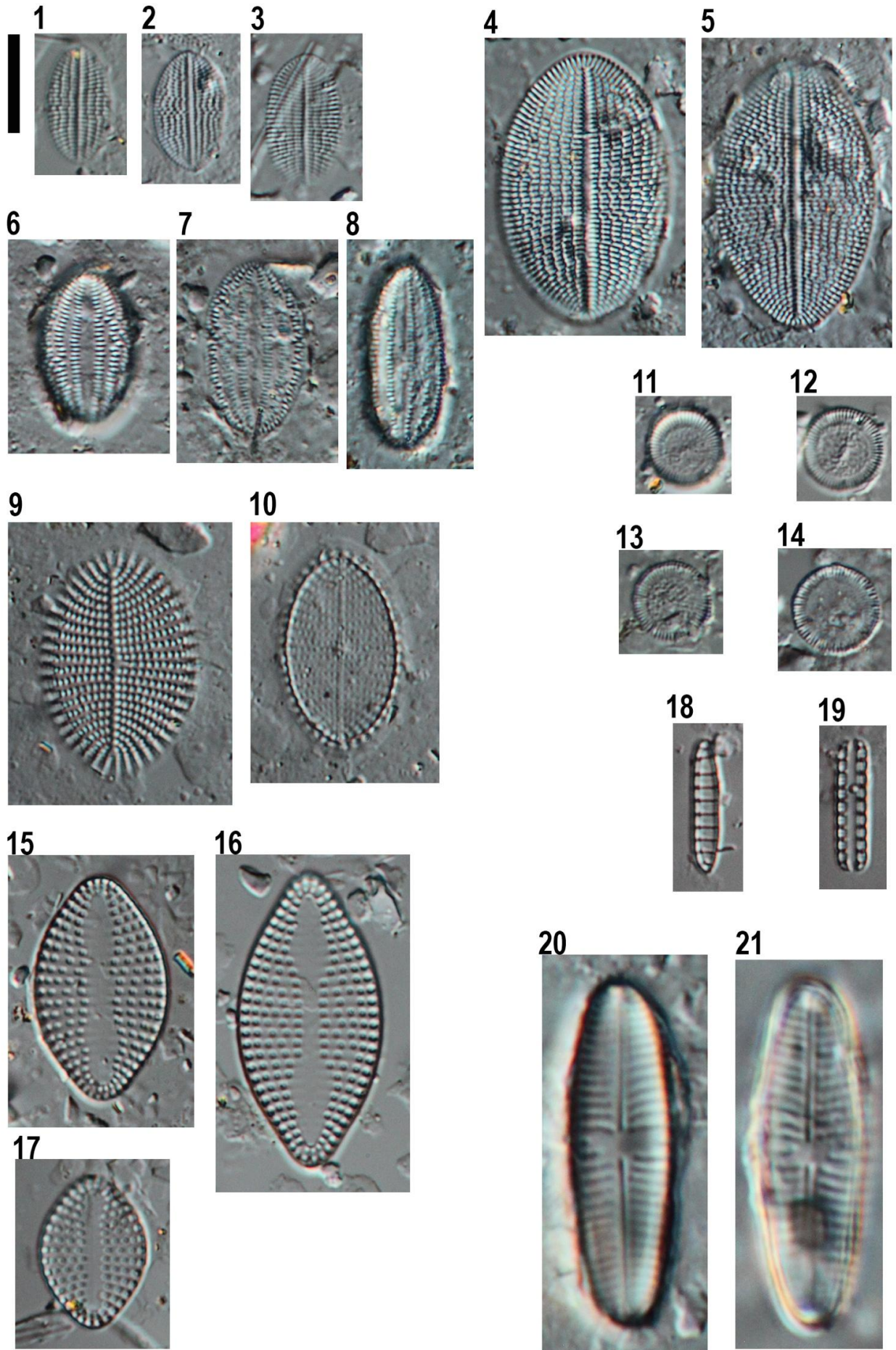


*Appendix I: Benthic diatom assemblages of the Ebro Delta***Plate 3 LM**

- Figs. 1–3      *Cocconeis placentula* var. *euglypta* (Ehrenberg) Grunow, SV  
Figs. 4–5      *Cocconeis placentula* var. *placentula* Ehrenberg, SV  
Figs. 6–8      *Cocconeis placentula* var. *trilineata* (M. Peragallo & J. Héribaud) Cleve, SV  
Figs. 9–10     *Cocconeis scutellum* Ehrenberg  
                  Fig. 9: SV  
                  Fig. 10: RV  
Figs. 11–14    *Cyclotella hakanssoniae* Wendker  
Figs. 15–17    *Delphineis surirella* (Ehrenberg) Andrews  
Figs. 18–19    *Denticula subtilis* Grunow  
Figs. 20–21    *Dickieia* sp.1, RV



*Appendix I: Benthic diatom assemblages of the Ebro Delta*



*Appendix I: Benthic diatom assemblages of the Ebro Delta*

**Plate 4 LM**

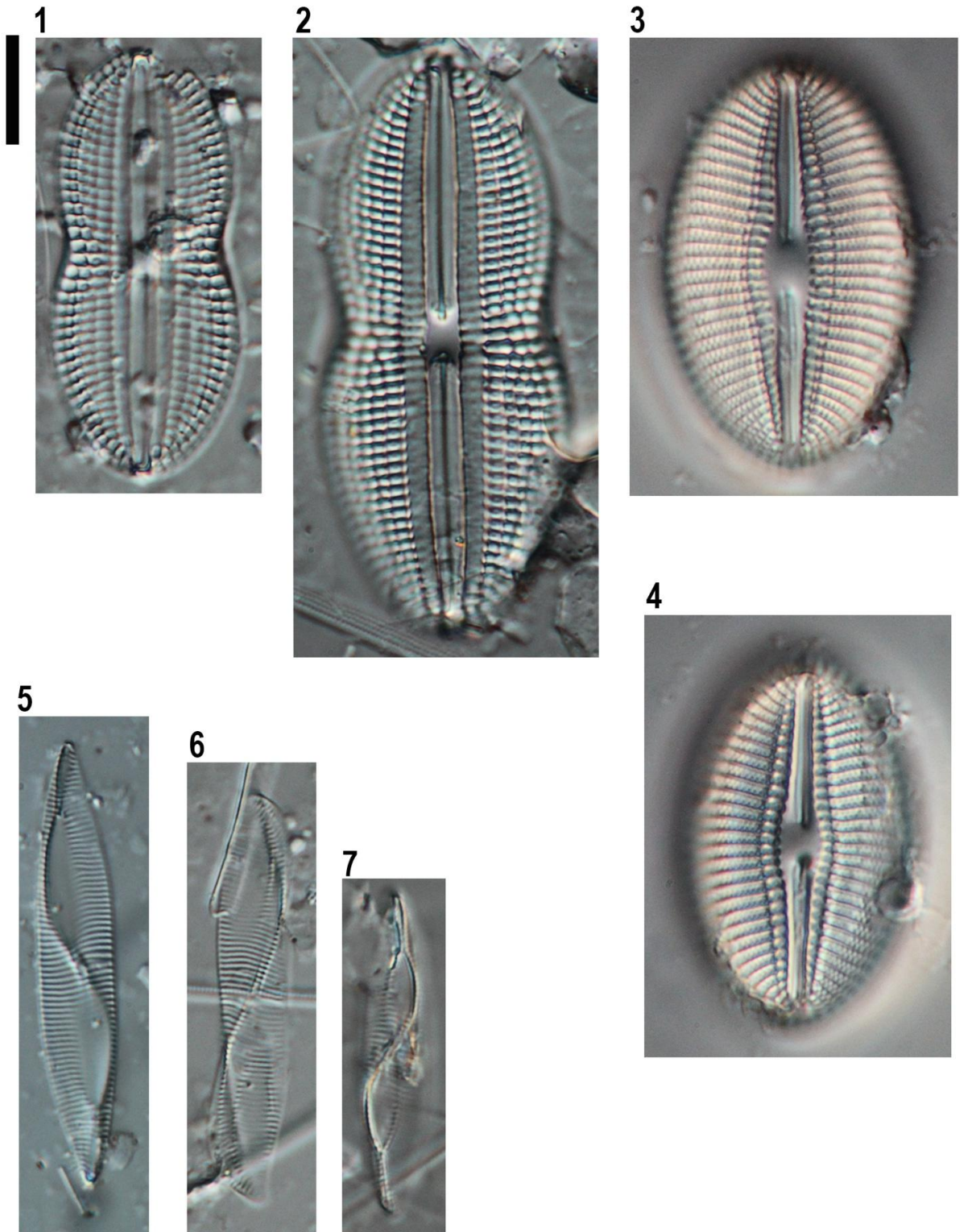
Figs. 1–2 *Diploneis didyma* (Ehrenberg) Cleve

Figs. 3–4 *Diploneis smithii* (Brébisson) Cleve

Figs. 5–7 *Entomoneis* cf. *pseudoduplex* Osada & Kobayasi



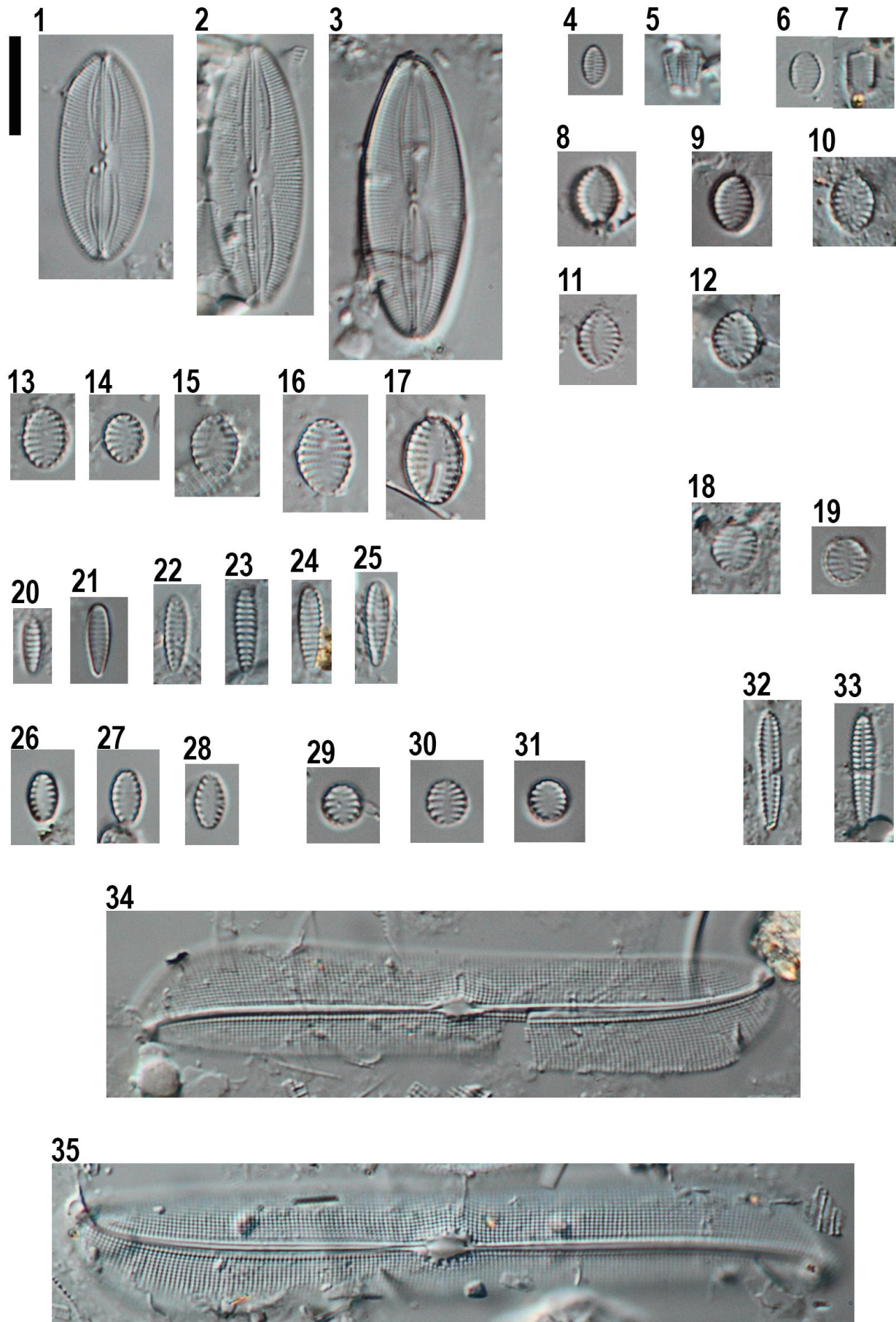
*Appendix I: Benthic diatom assemblages of the Ebro Delta*



*Appendix I: Benthic diatom assemblages of the Ebro Delta***Plate 5 LM**

- Figs. 1–3      *Fallacia pygmaea* (Kützing) Stickle & D.G.Mann
- Figs. 4–5      *Fragilaria amicornum* Witkowski & Lange-Bertalot  
Fig. 4: valve  
Fig. 5: frustule
- Figs. 6–7      *Fragilaria atomus* Hustedt  
Fig. 6: valve  
Fig. 7: frustule
- Figs. 8–12     *Fragilaria cf. elliptica* Schumann
- Figs. 13–17    *Fragilaria cf. neoelliptica* Witkowski
- Figs. 18–19    *Fragilaria cf. sopotensis* Witkowski & Lange-Bertalot
- Figs. 20–25    *Fragilaria gedanensis* Witkowski
- Figs. 26–28    cf. *Fragilaria* sp.1
- Figs. 29–31    cf. *Fragilaria* sp.2
- Figs. 32–33    *Gomphonemopsis obscurum* (Krasske) Lange-Bertalot
- Figs. 34–35    *Gyrosigma wansbeckii* var. *peisonis* (Grunow) Cleve

*Appendix I: Benthic diatom assemblages of the Ebro Delta*



*Appendix I: Benthic diatom assemblages of the Ebro Delta*

**Plate 6 LM**

Figs. 1–2      *Mastogloia aquilegiae* Grunow

Figs. 3–6      *Mastogloia braunii* Grunow

Fig. 3: valve

Fig. 4: partecta

Fig. 5: valve

Fig. 6: partecta

Figs. 7–10     *Mastogloia pumila* (Grunow) Cleve

Fig. 7: valve

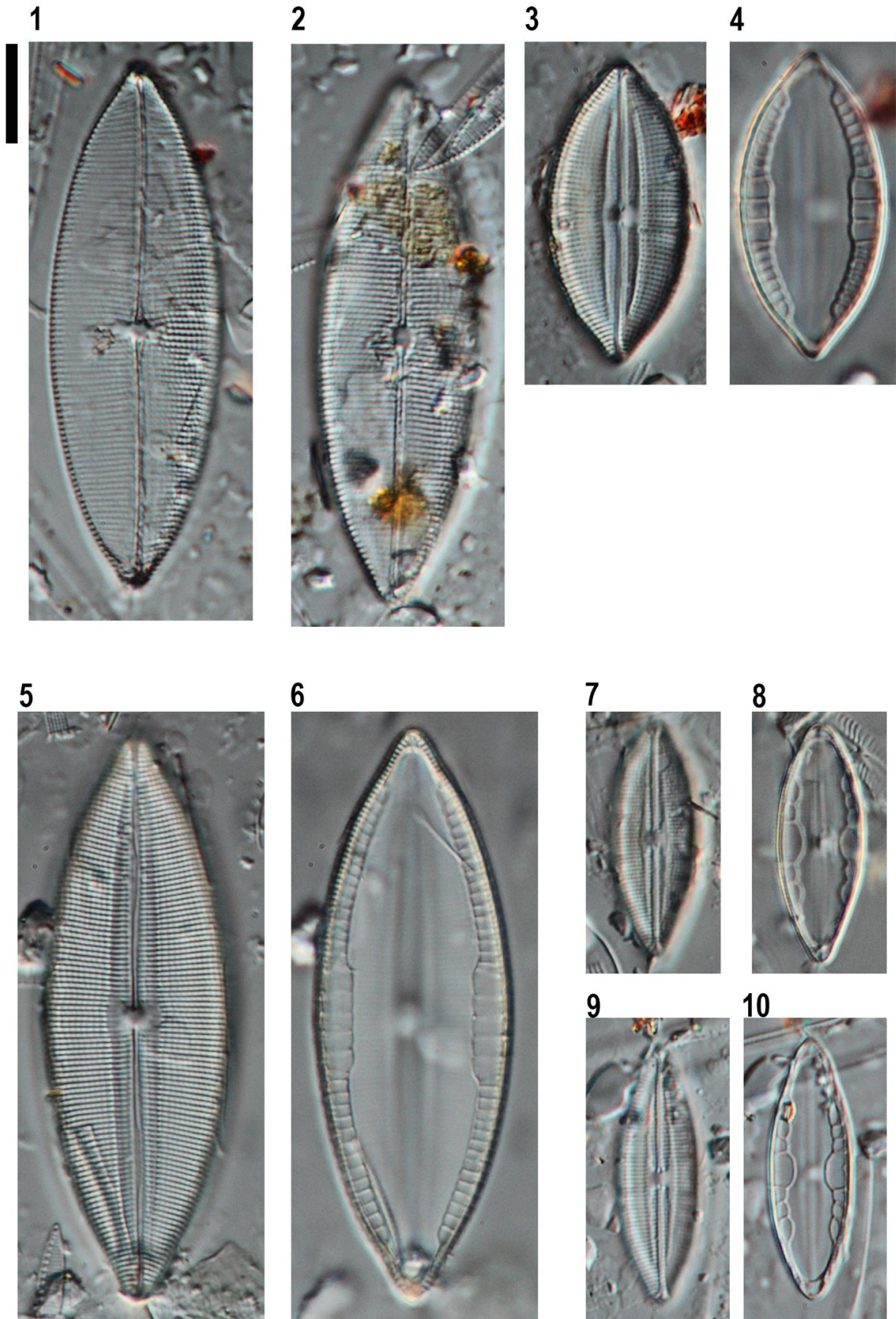
Fig. 8: partecta

Fig. 9: valve

Fig. 10: partecta



*Appendix I: Benthic diatom assemblages of the Ebro Delta*

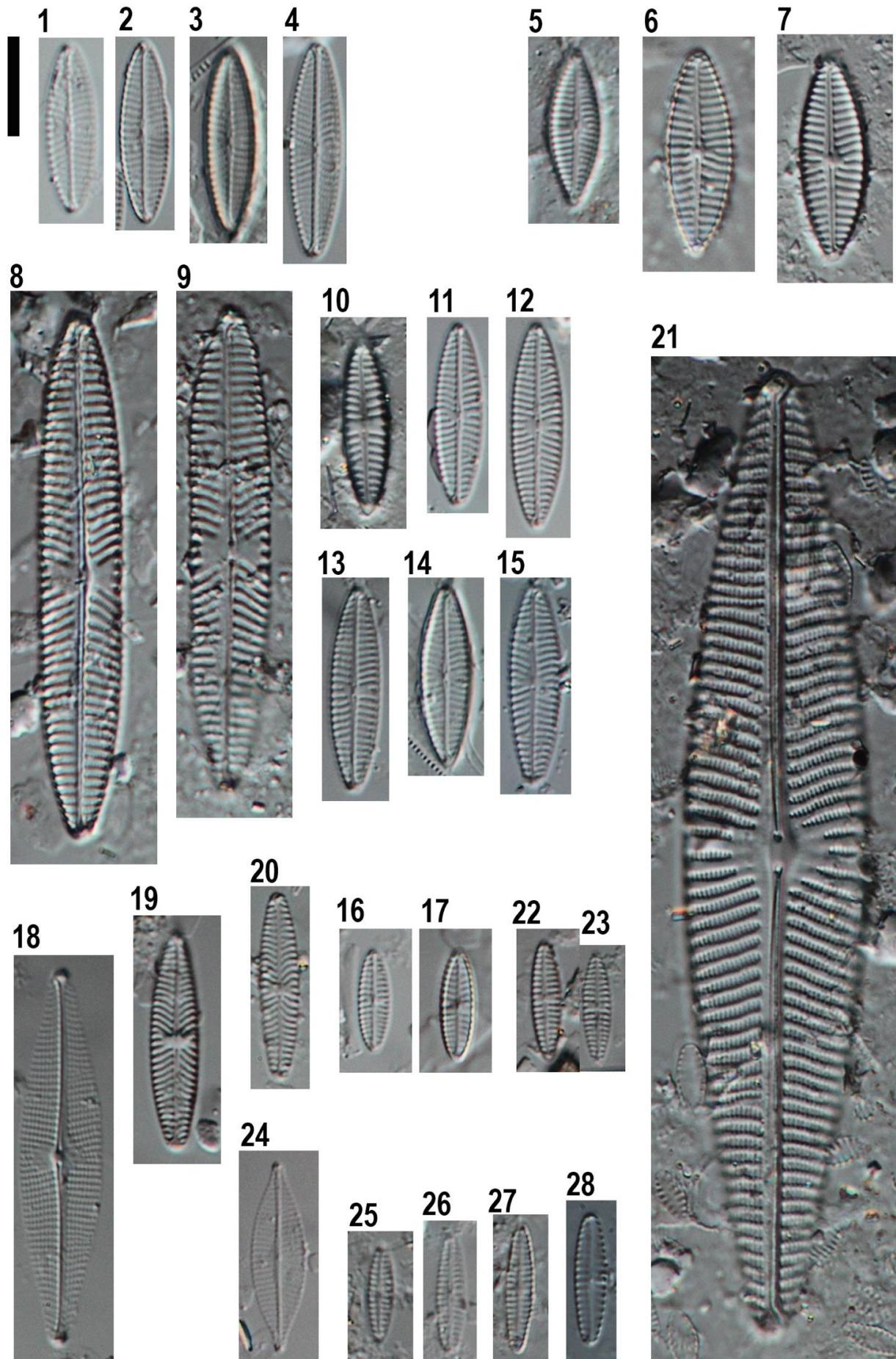


*Appendix I: Benthic diatom assemblages of the Ebro Delta***Plate 7 LM**

- Figs. 1–4      *Navicula* aff. *mollis* (W. Smith) Cleve  
Figs. 5–7      *Navicula antonii* Lange-Bertalot  
Figs. 8–9      *Navicula cariocincta* Lange-Bertalot  
Fig. 10        *Navicula* cf. *hanseni* Möller  
Figs. 11–15    *Navicula* cf. *recens* (Lange-Bertalot) Lange-Bertalot  
Figs. 16–17    *Navicula* cf. *diserta* Hustedt  
Fig. 18        *Navicula gregaria* Donkin  
Figs. 19–20    *Navicula microcari* Lange-Bertalot  
Fig. 21        *Navicula peregrina* (Ehrenberg) Kützing  
Figs. 22–23    *Navicula perminuta* Grunow  
Fig. 24        *Navicula phyllepta* Kützing  
Figs. 26–29    *Navicula salinicola* Hustedt



*Appendix I: Benthic diatom assemblages of the Ebro Delta*

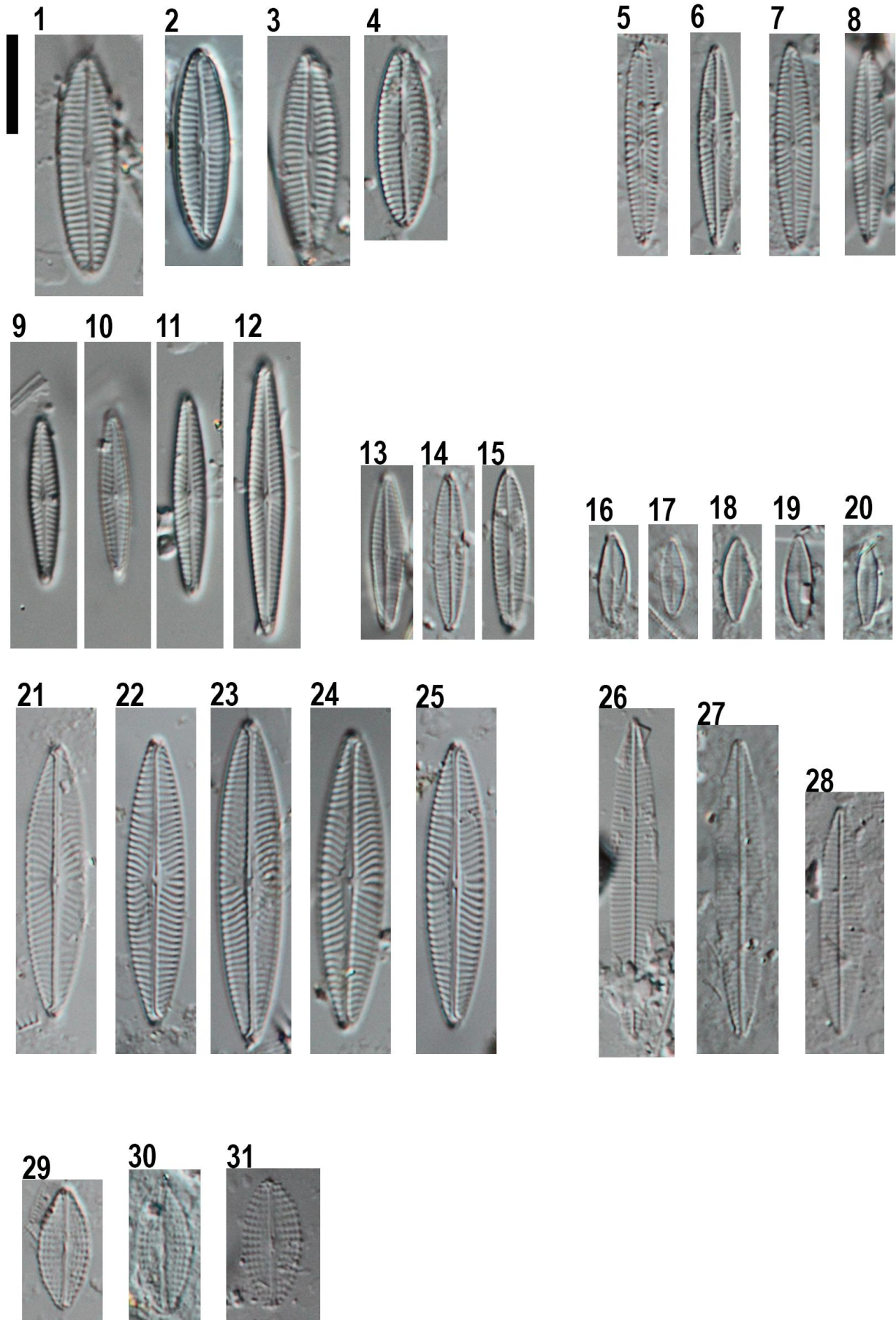


*Appendix I: Benthic diatom assemblages of the Ebro Delta***Plate 8 LM**

- Figs. 1–4      *Navicula* sp.1  
Figs. 5–8      *Navicula* sp.2  
Figs. 9–12     *Navicula* sp.5  
Figs. 13–15    *Navicula* sp.6  
Figs. 16–20    *Navicula* sp.7  
Figs. 21–25    *Navicula* sp.8  
Figs. 26–28    *Navicula stundlii* Hustedt  
Figs. 29–31    *Navicula vimineoides* Giffen



*Appendix I: Benthic diatom assemblages of the Ebro Delta*



*Appendix I: Benthic diatom assemblages of the Ebro Delta***Plate 9 LM**

Figs. 1–5      *Navicymbula pusilla* m1 (Grunow) Krammer

Figs. 6–8      *Navicymbula pusilla* m2 (Grunow) Krammer

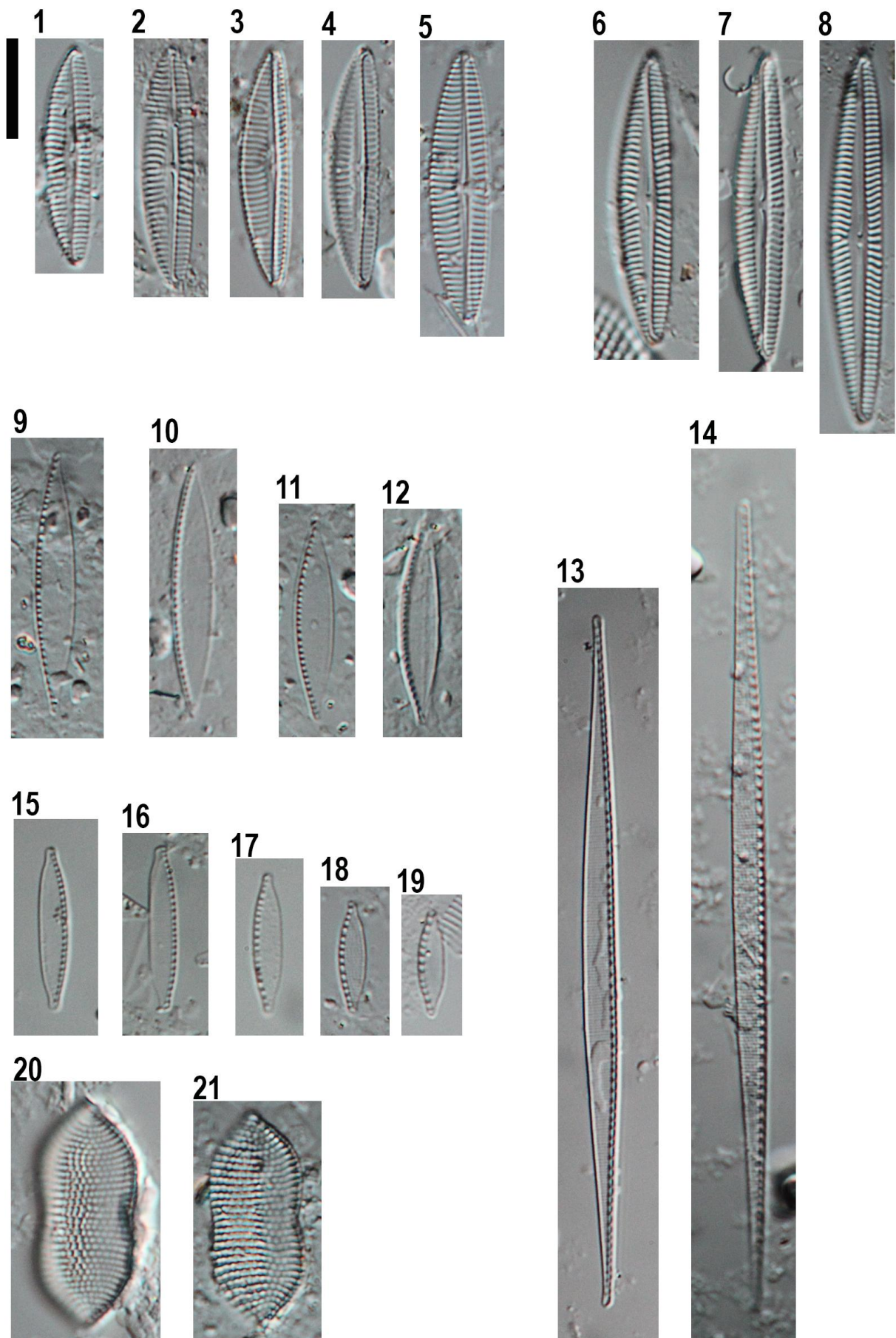
Figs. 9–12     *Nitzschia aequorea* Hustedt

Figs. 13–14    *Nitzschia* cf. *lesbia* Cholnoky

Figs. 15–19    *Nitzschia* cf. *perindistincta* Cholnoky

Figs. 20–21    *Nitzschia coarctata* Grunow

*Appendix I: Benthic diatom assemblages of the Ebro Delta*

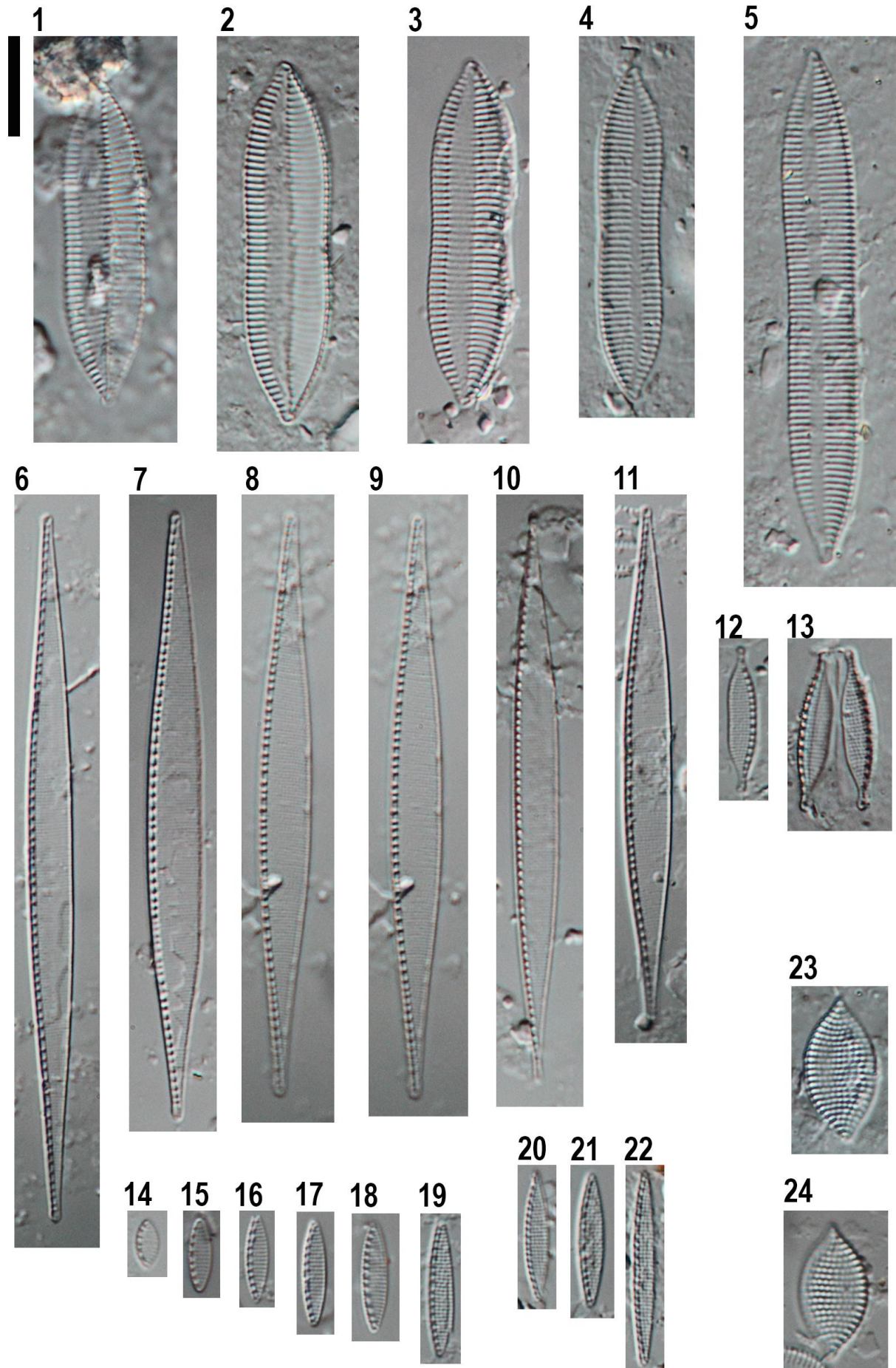


*Appendix I: Benthic diatom assemblages of the Ebro Delta***Plate 10 LM**

- Figs. 1–5      *Nitzschia constricta* (Kützing) Ralfs  
Figs. 12–13    *Nitzschia elegantula* Grunow  
Figs. 6–11     *Nitzschia fusiformis* m2 Grunow  
Figs. 14–19    *Nitzschia inconspicua* Grunow  
Figs. 20–22    *Nitzschia liebetruithii* Rabenhorst  
Figs. 23–24    *Nitzschia pararostrata* (Lange-Bertalot) Lange-Bertalot



*Appendix I: Benthic diatom assemblages of the Ebro Delta*



*Appendix I: Benthic diatom assemblages of the Ebro Delta*

**Plate 11 LM**

Figs. 1–3 *Nitzschia scalpelliformis* (Grunow) Grunow

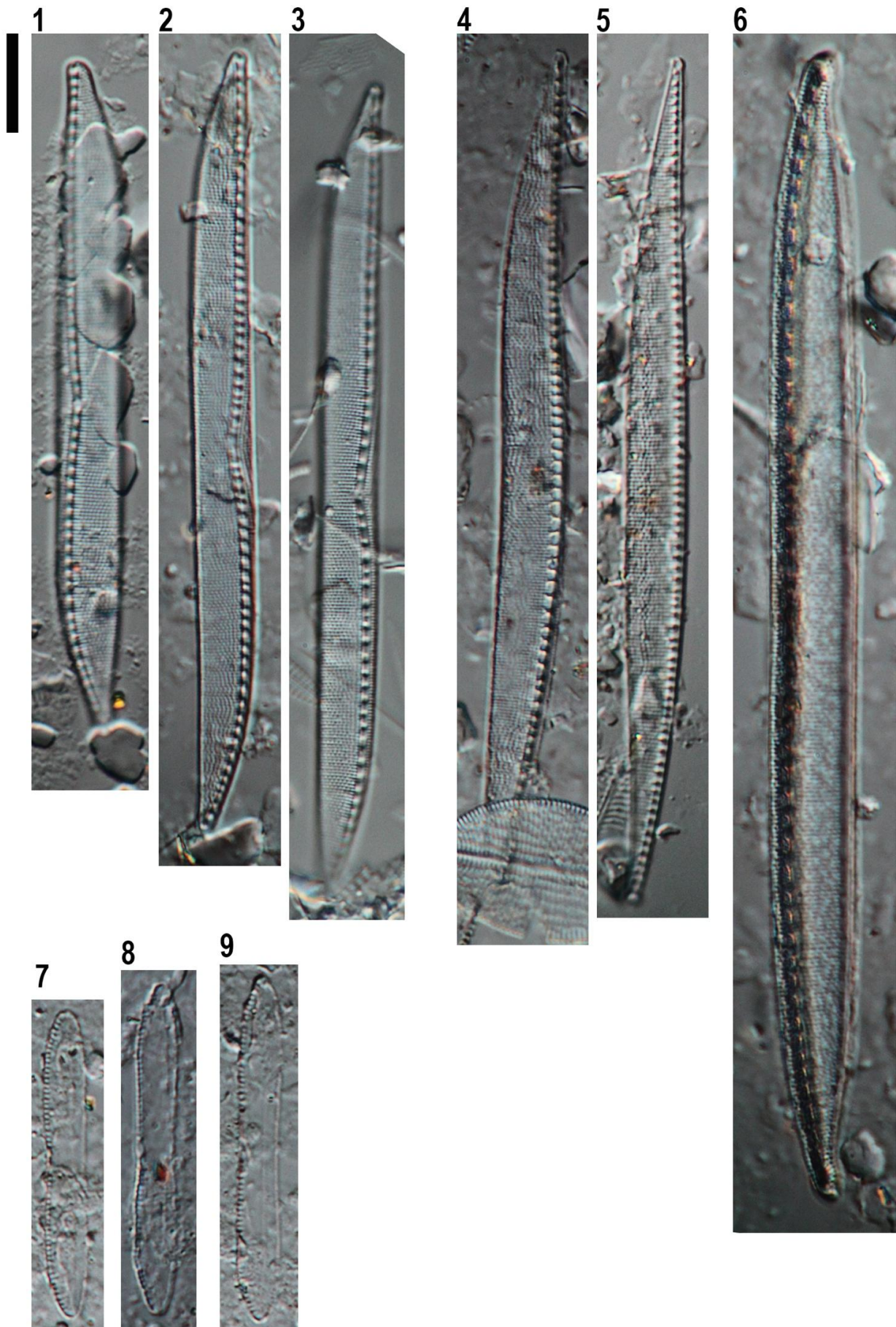
Figs. 4–5 *Nitzschia sigma* (Kützing) W. Smith

Figs. 7–9 *Nitzschia thermaloides* Hustedt

Fig. 6 *Nitzschia vitrea* G. Norman



*Appendix I: Benthic diatom assemblages of the Ebro Delta*

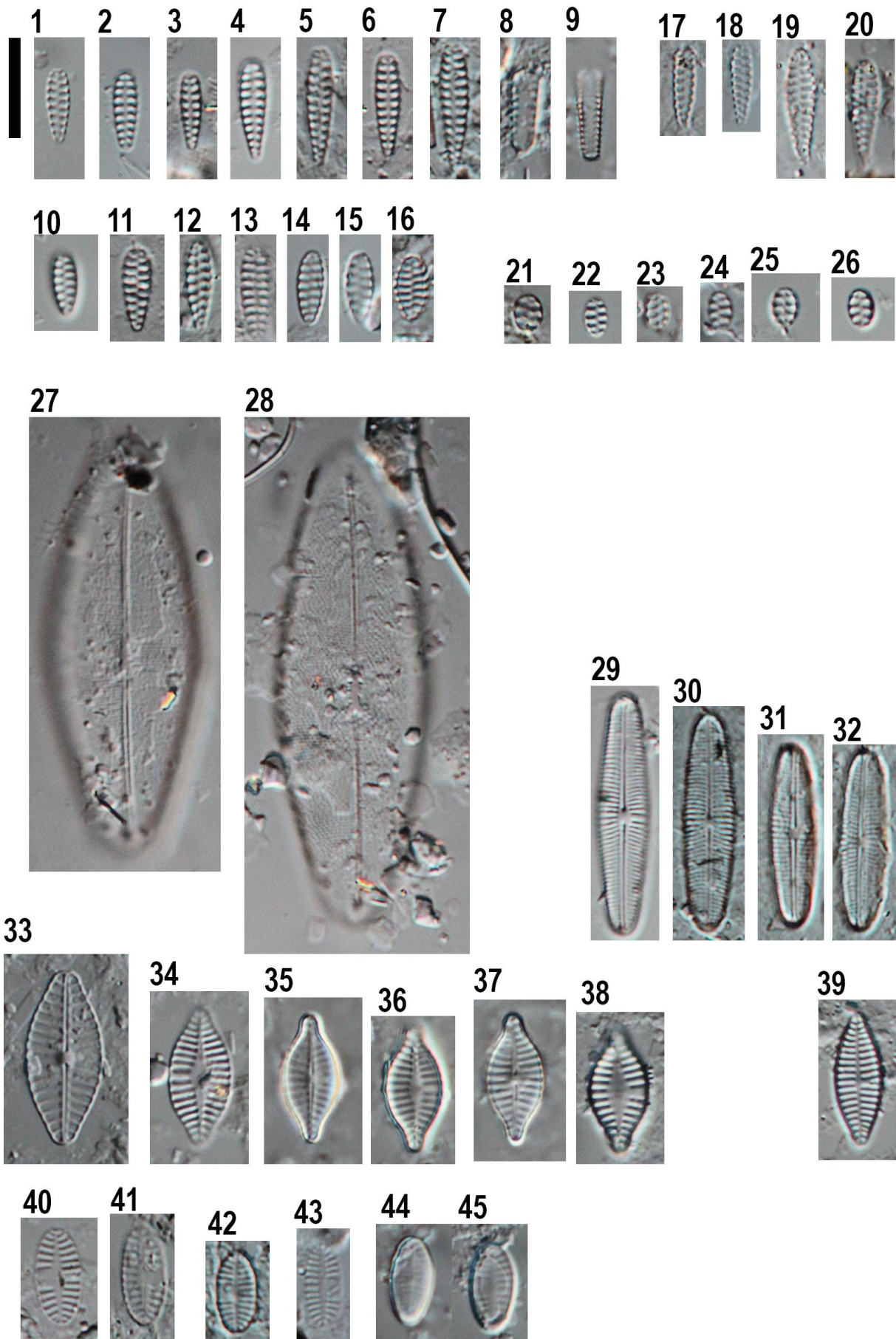


*Appendix I: Benthic diatom assemblages of the Ebro Delta***Plate 12 LM**

- Figs. 1–9        *Opephora guenter-grassii* (Witkowski & Lange-Bertalot) Sabbe & Vyverman  
Figs. 1–7: valves  
Figs. 8–9: frustules
- Figs. 10–16    *Opephora mutabilis* (Grunow) Sabbe & Vyverman
- Figs. 17–20    *Opephora* cf. *burchardiae* Witkowski, Metzeltin & Lange-Bertalot
- Figs. 21–26    cf. *Opephora* sp.1
- Figs. 27–28    *Parlibellus hagelsteinii* Cox
- Figs. 29–32    *Parlibellus* sp.1
- Figs. 33–38    *Planothidium delicatulum* m1 (Kützing) Round & Bukhtiyarova  
Fig. 34–36: SV  
Fig. 37–38: RV
- Fig. 39        *Planothidium delicatulum* m2 (Kützing) Round & Bukhtiyarova, SV
- Figs. 40–45    *Planothidium deperditum* (Giffen) Witkowski & Lange-Bertalot  
Figs. 40–43: SV  
Fig. 44: RV  
Fig. 45: SV



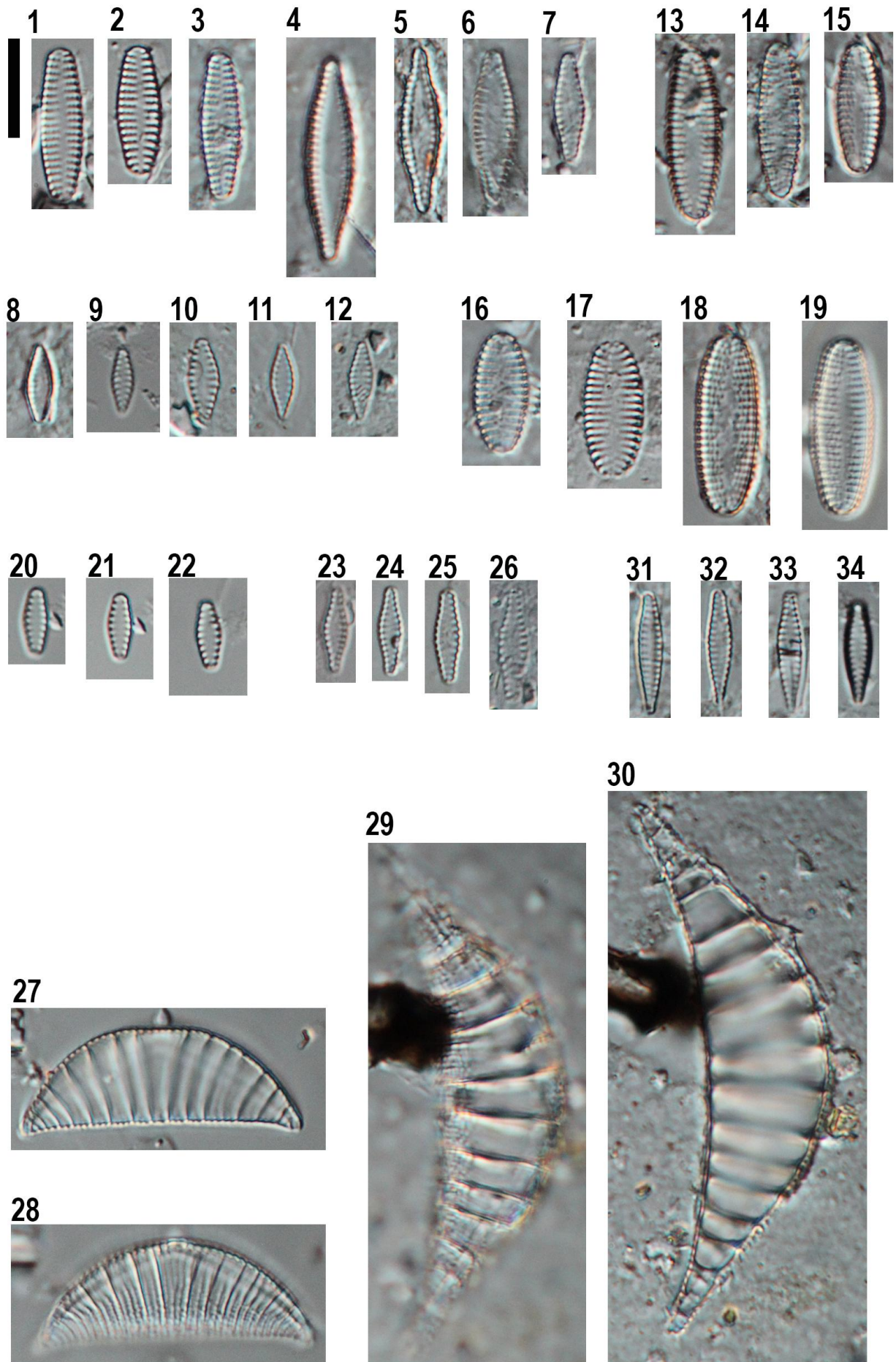
*Appendix I: Benthic diatom assemblages of the Ebro Delta*



*Appendix I: Benthic diatom assemblages of the Ebro Delta***Plate 13 LM**

- Figs. 1–3      *Pseudostaurosira alvareziae* Cejudo-Figueiras, E.A. Morales & Ector
- Figs. 4–7      *Pseudostaurosira brevistriata* (Grunow) Williams & Round
- Figs. 8–12     *Pseudostaurosira* cf. *brevistriata* (Grunow) Williams & Round
- Figs. 13–15    *Pseudostaurosira* cf. *subsalina* (Hustedt) E.A.Morales
- Figs. 16–19    *Pseudostaurosira subsalina* (Hustedt) E.A.Morales
- Figs. 20–22    *Pseudostaurosiropsis* cf. *geocollegarum* (Witkowski & Lange-Bertalot)  
E.A.Morales
- Figs. 23–26    *Pseudostaurosiropsis geocollegarum* (Witkowski & Lange-Bertalot)  
E.A.Morales
- Figs. 27–28    *Rhopalodia constricta* (W.Smith) Krammer
- Figs. 29–30    *Rhopalodia musculus* (Kützing) O.Muller
- Figs. 31–34    *Sarcophagodes* cf. *delicatula* E.A. Morales

*Appendix I: Benthic diatom assemblages of the Ebro Delta*

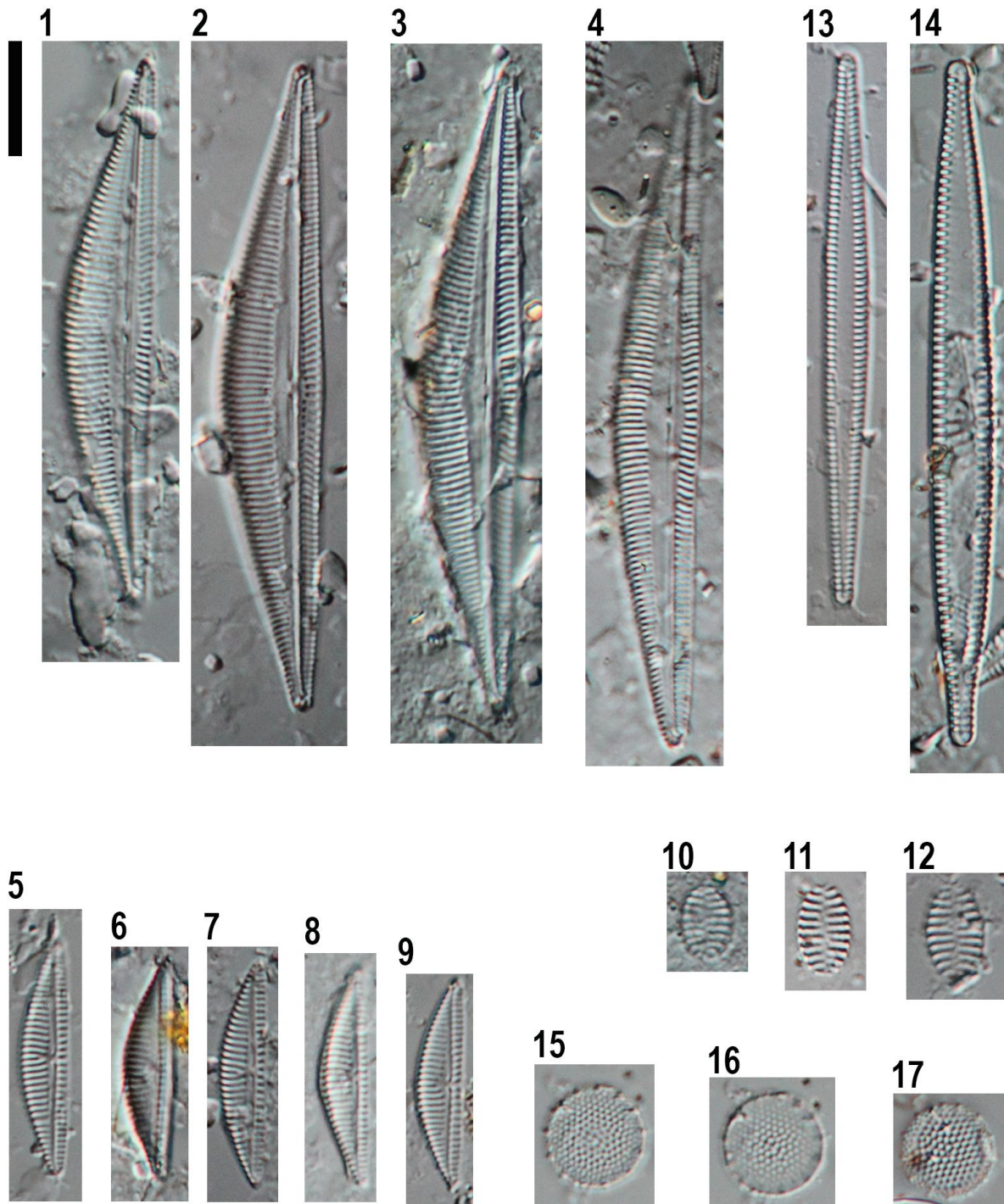


*Appendix I: Benthic diatom assemblages of the Ebro Delta***Plate 14 LM**

- Figs. 1–4        *Seminavis robusta* Danielidis & Mann  
Figs. 5–9        *Seminavis strigosa* (Hustedt) Danielidis & Economou-Amilli  
Figs. 10–12     *Staurosira construens* var. *venter* (Ehrenberg) Bukhtiyarova  
Figs. 13–14     *Tabularia tabulata* (C. Agardh) Snoeijs  
Figs. 15–17     *Thalassiosira angulata* (Gregory) Hasle



*Appendix I: Benthic diatom assemblages of the Ebro Delta*

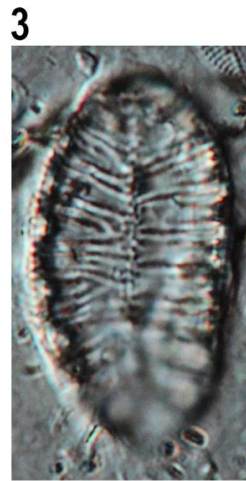
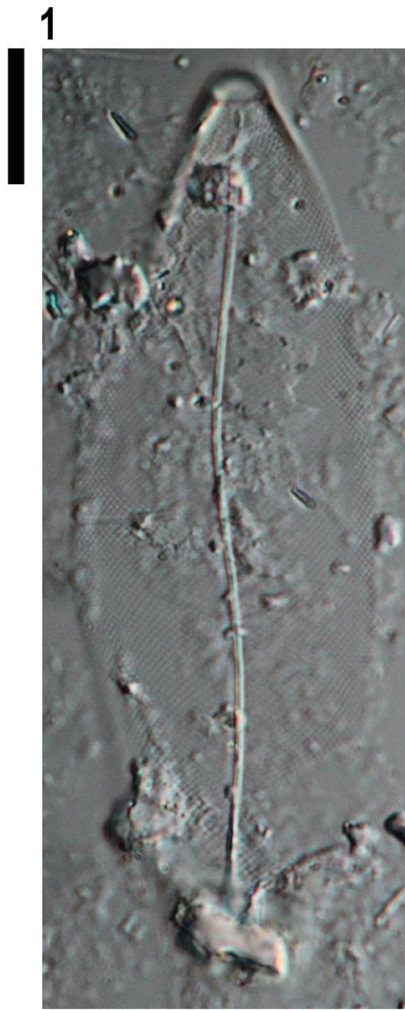


*Appendix I: Benthic diatom assemblages of the Ebro Delta*

**Plate 15 LM**

- Fig. 1        *Striatella unipunctata* (Lyngbye) C. Agardh  
Fig. 2        *Surirella* aff. *salina* W. Smith  
Figs. 3–4    *Surirella brebissonii* Krammer & Lange-Bertalot  
Fig. 5        *Surirella fastuosa* Ehrenberg

*Appendix I: Benthic diatom assemblages of the Ebro Delta*



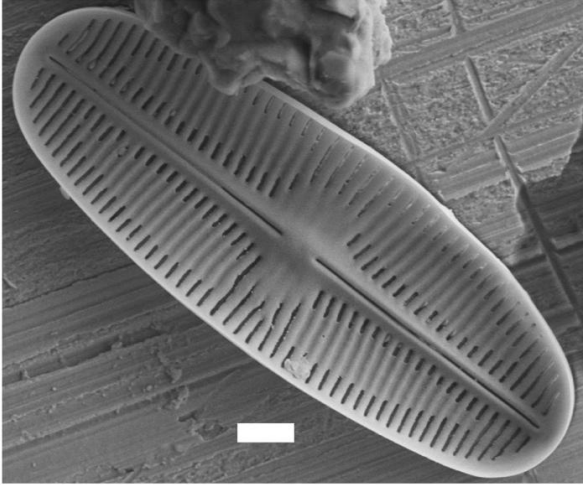
*Appendix I: Benthic diatom assemblages of the Ebro Delta***Plate 1 EM**

- Figs. 1–2      *Achnanthes* sp.1  
Fig. 1: internal SV valve  
Fig. 2: external SV valve
- Fig. 3      *Achnanthes submarina* Hustedt  
Fig. 3: frustule
- Fig. 4      *Cocconeis placentula* Ehrenberg (sensu lato), scale bar = 5 µm
- Figs. 5–6      *Dickieia* sp.1, scale bar = 2 µm  
Fig. 5: internal SV valve  
Fig. 6: external SV valve
- Fig. 7      *Entomoneis* cf. *pseudoduplex* Osada & Kobayasi, scale bar = 5 µm

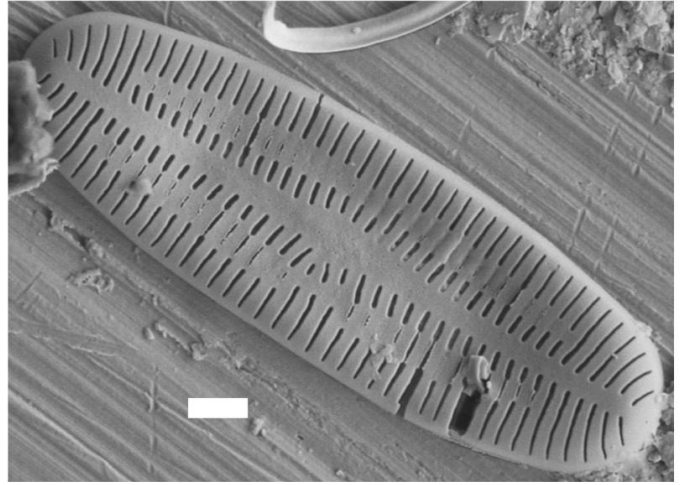


*Appendix I: Benthic diatom assemblages of the Ebro Delta*

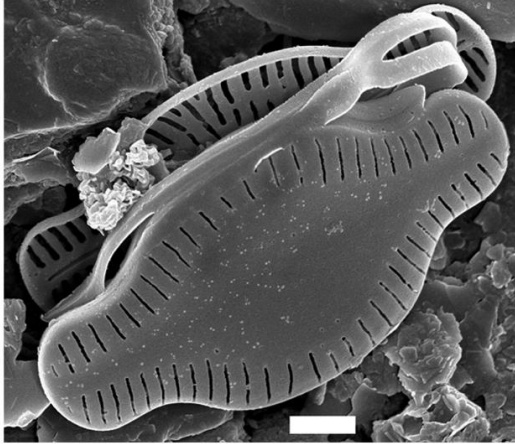
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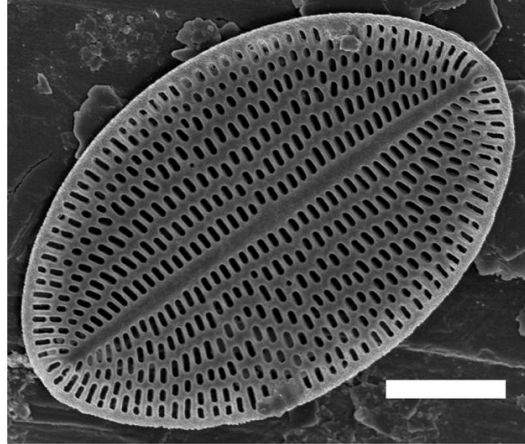
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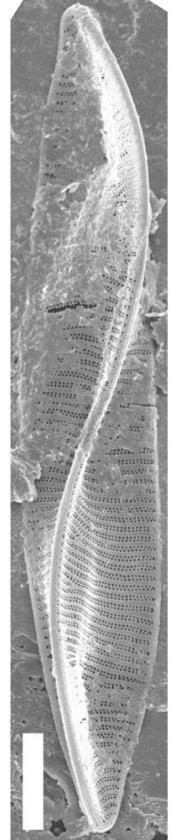
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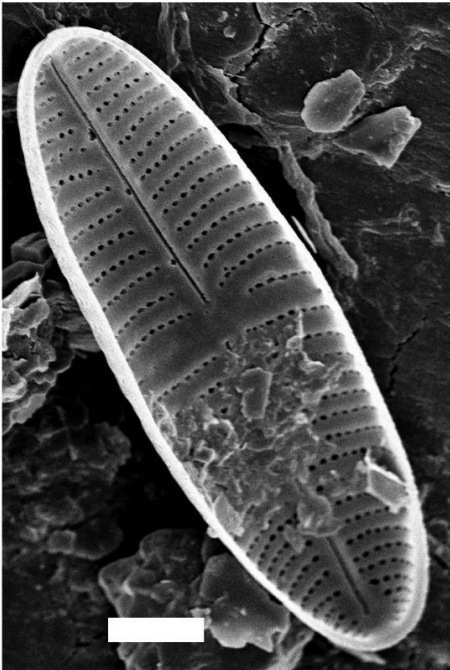
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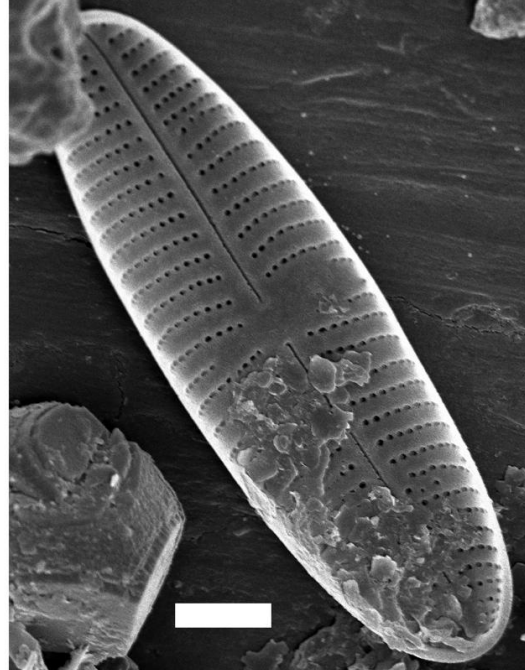
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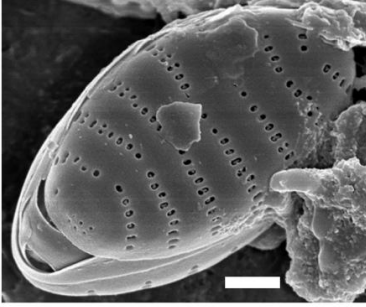


*Appendix I: Benthic diatom assemblages of the Ebro Delta***Plate 2 EM**

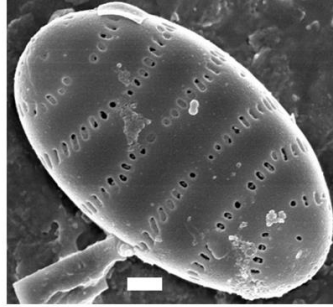
- Figs. 1–2      *Fragilaria amicornum* Witkowski & Lange-Bertalot  
Fig. 1: frustule ventral view  
Fig. 2: external valve view
- Fig. 3      *Fragilaria atomus* Hustedt  
Fig. 3: external valve view
- Fig. 4      cf. *Fragilaria* sp.1, external valve view
- Fig. 5      *Navicula perminuta* Grunow  
Fig. 5: internal SV valve  
Fig. 6: external SV valve
- Figs. 6–7      *Navicymbula pusilla* m1 (Grunow) Krammer, scale bar = 2  $\mu$ m  
Fig. 6: external valve view  
Fig. 7: internal valve view
- Fig. 8      *Nitzschia scalpelliformis* (Grunow) Grunow, scale bar = 10  $\mu$ m
- Fig. 9      *Nitzschia* cf. *perindistincta* Cholnoky, scale bar = 2  $\mu$ m

*Appendix I: Benthic diatom assemblages of the Ebro Delta*

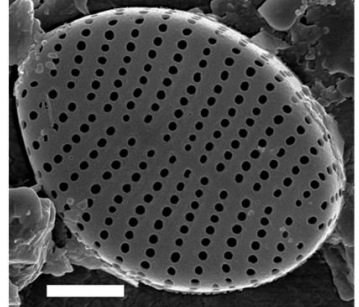
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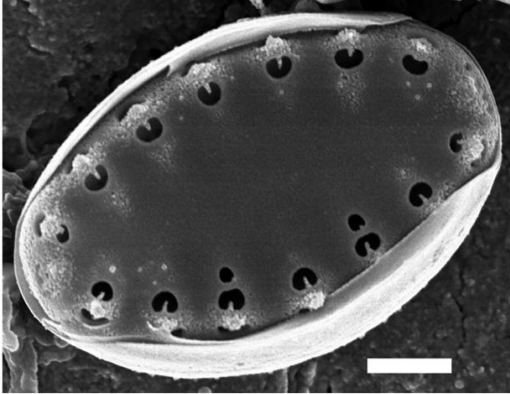
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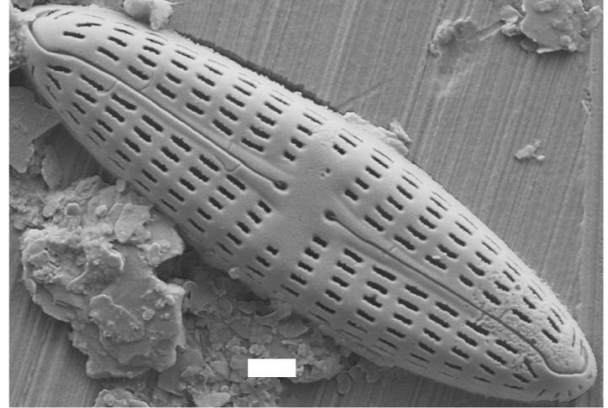
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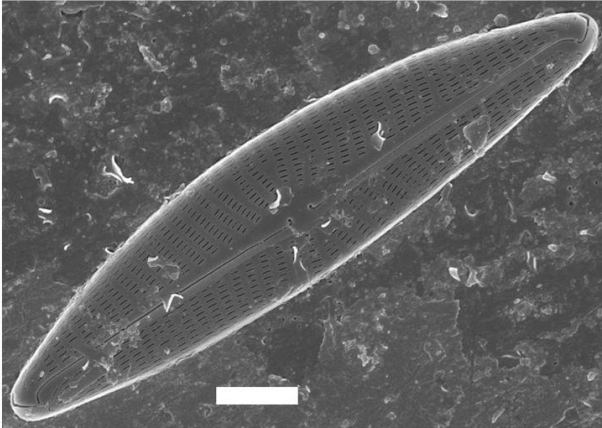
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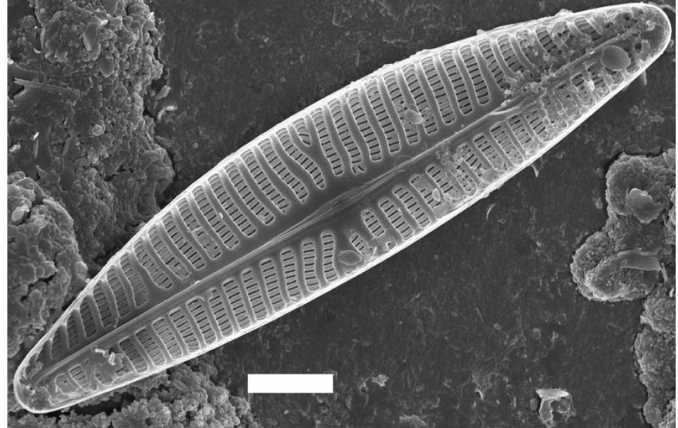
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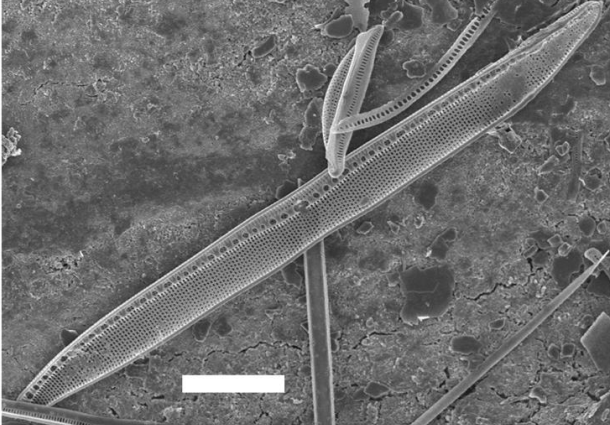
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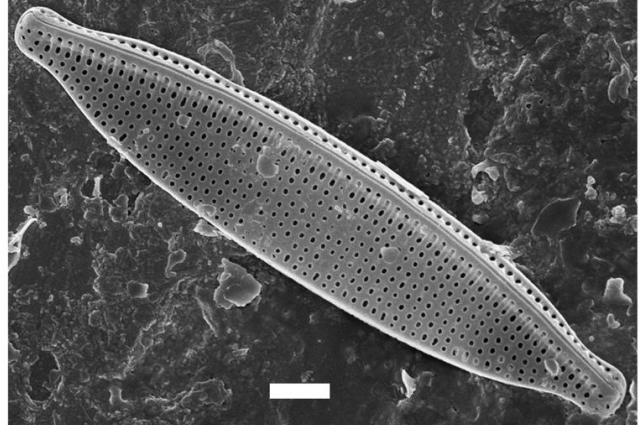
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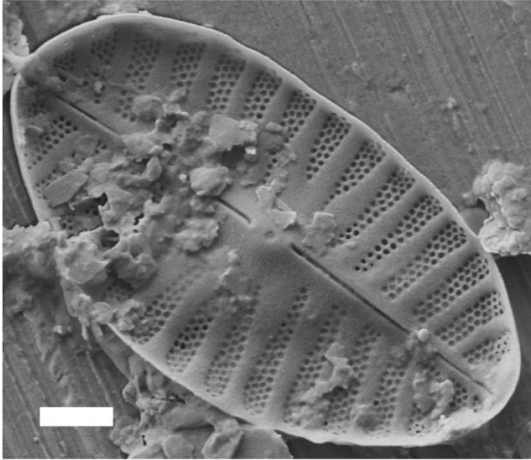
*Appendix I: Benthic diatom assemblages of the Ebro Delta***Plate 3 EM**

- Fig. 1 *Planothidium delicatulum* m1 (Kützing) Round & Bukhtiyarova, internal valve view
- Figs. 2–4 *Pseudostaurosira* cf. *geocollegarum* (Witkowski & Lange-Bertalot)  
E.A.Morales  
Fig. 2: frustule ventral view  
Figs. 3-4: external valve view
- Figs. 5–6 *Rhopalodia constricta* (W.Smith) Krammer, scale bar = 5  $\mu$ m

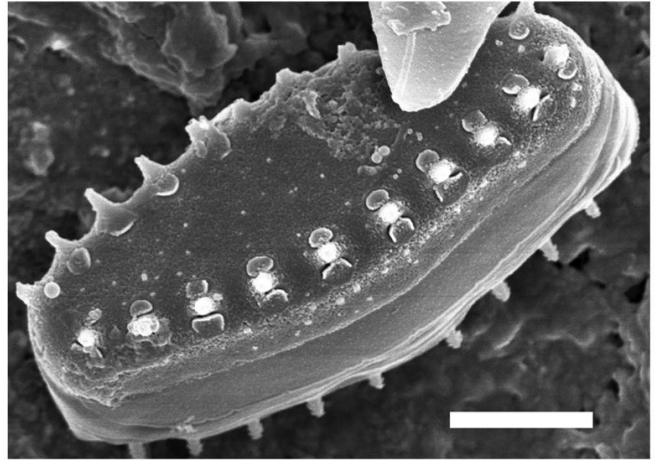


*Appendix I: Benthic diatom assemblages of the Ebro Delta*

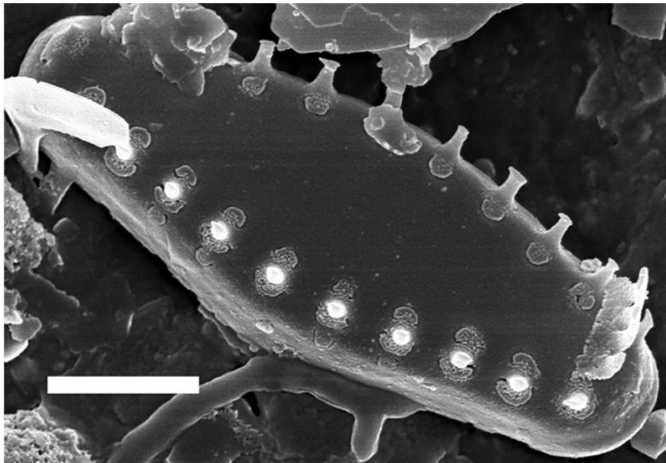
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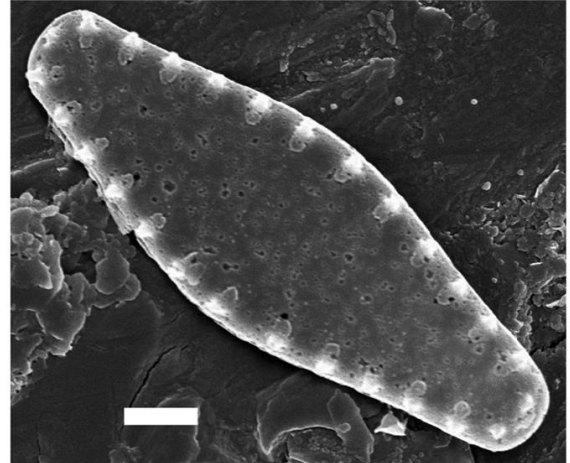
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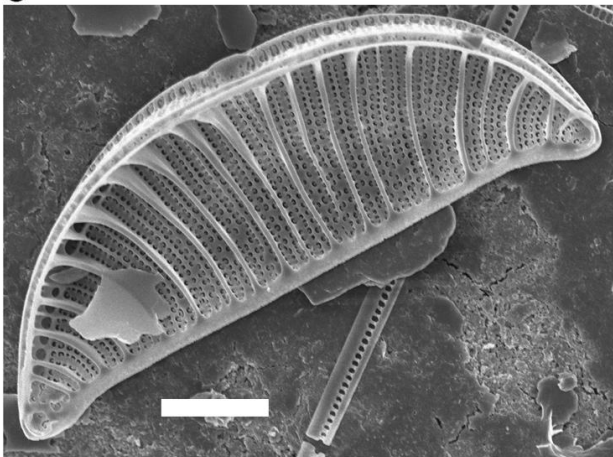
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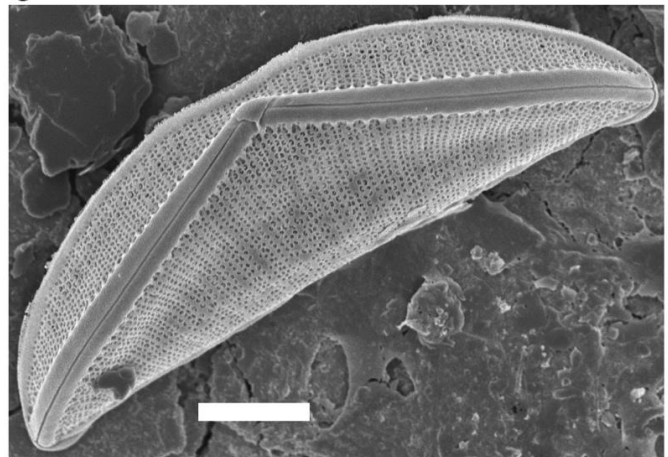
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## **Appendix II: Benthic foraminiferal assemblages of the Ebro Delta**

*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta***Appendix II: Benthic foraminiferal assemblages of the Ebro Delta****List of living foraminifera taxa and relative abundances**

List of the 138 living foraminiferal species found in the Ebro Delta (arranged by wall structure and alphabetically) with their corresponding codes and their relative abundances (% RA) considering all the samples. Plates are also indicated for those taxa illustrated here. Indicator species are highlighted in bold; for these taxa the habitat they characterize is also given. The synonyms of all taxa are also given following Murray (1991).



## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Code	Foraminifera taxa	RA(%)	Habitat	Plate
	<b>Agglutinated forms</b>			
AMBAL	<i>Ammobaculites balkwilli</i> Haynes, 1973	0.086		
cAMARE	<i>Ammobaculites</i> cf. <i>arenaria</i> Natland, 1938	0.013		
AMMSP1	<i>Ammosphaeroidina</i> sp.1	0.002		
<b>AMMSPH</b>	<b><i>Ammosphaeroidina sphaeroidiniforme</i> (Brady) = <i>Haplophragmium sphaeroidiniforme</i> Brady, 1884</b>	<b>0.508</b>	<b>Offshore habitat</b>	
cATSAL	<i>Ammotium</i> cf. <i>salsum</i> (Cushman and Brönniman) = <i>Ammobaculites salsum</i> Cushman and Brönniman, 1948	0.037		1
ARMEX	<i>Arenoparella mexicana</i> (Kornfeld) = <i>Trochammina inflata</i> var. <i>mexicana</i> Kornfeld, 1931	0.029		1
CLOBS	<i>Clavulina obscura</i> Chaster, 1982	0.245		
EGADV	<i>Eggerella advena</i> (Cushman) = <i>Verneuilina advena</i> Cushman, 1921	0.052		
<b>EGSCA</b>	<b><i>Eggerelloides scaber</i> (Williamson) = <i>Bulimina scabra</i> Williamson, 1858</b>	<b>0.411</b>	<b>Offshore habitat</b>	1
<b>HACAN</b>	<b><i>Haplophragmoides canariensis</i> (d'Orbigny) = <i>Nonionina canariensis</i> d'Orbigny, 1839</b>	<b>0.279</b>	<b>Offshore habitat</b>	
HASP1	<i>Haplophragmoides</i> sp.1	0.097		
<b>HAWIL</b>	<b><i>Haplophragmoides wilberti</i> Anderson, 1953</b>	<b>1.396</b>	<b>Salt and brackish marshes</b>	1
<b>JAMAC</b>	<b><i>Jadammina macrescens</i> (Brady) = <i>Trochammina inflata</i> (Montagu) var. <i>macrescens</i> Brady, 1870</b>	<b>3.514</b>	<b>Salt and brackish marshes</b>	1
LADIF	<i>Lagenammina difflugiformis</i> (Brady) = <i>Reophax difflugiformis</i> Brady, 1879	0.075		
LALAG	<i>Lagenammina laguncula</i> Rhumbler, 1911	0.388		
LESCO	<i>Leptohalysis scottii</i> (Chaster) = <i>Reophax scotti</i> Chaster, 1892	0.015		
MIFUS	<i>Miliammina fusca</i> (Brady) = <i>Quinqueloculina fusca</i> Brady, 1870	0.913		1
NODEN	<i>Nodulina dentaliniformis</i> (Brady) = <i>Reophax dentaliniformis</i> Brady, 1844	0.055		1
NOPOL	<i>Nouria polymorphides</i> Heron-Allen and Earland, 1914	0.036		
PSBOW	<i>Psammosphaera bowmani</i> Heron-Allen and Earland, 1912	0.011		
RECYL	<i>Reophax cylindrica</i> Brady, 1884	0.024		
cREFUS	<i>Reophax</i> cf. <i>fusiformis</i> (Williamson) = <i>Proteonina fusiformis</i> Williamson, 1858	0.123		
REMON	<i>Reophax moniliformis</i> Siddall, 1886	0.046		1
RENAN	<i>Reophax nana</i> Rhumbler, 1913	0.123		
RESCO	<i>Reophax scorpiurus</i> Montfort, 1808	0.054		
<b>RESUB</b>	<b><i>Reophax subfusiformis</i> Earland, 1933</b>	<b>0.212</b>	<b>Offshore habitat</b>	
RESP1	<i>Reophax</i> sp.1	0.002		

## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Code	Foraminifera taxa	RA(%)	Habitat	Plate
SAATL	<i>Saccammina atlantica</i> (Cushman) = <i>Proteonina atlantica</i> Cushman, 1944	0.055		
TEBOC	<i>Textularia bocki</i> Höglund, 1947	0.002		
<b>TECAL</b>	<b><i>Textularia calva</i> Lalicker, 1935</b>	<b>0.272</b>	<b>Offshore habitat</b>	
TESP1	<i>Textularia</i> sp.1	0.003		
TETEN	<i>Textularia tenuissima</i> Earland, 1933	0.183		
cTRADV	<i>Trochammina</i> cf. <i>advena</i> Cushman, 1922	0.047		
<b>TRINF</b>	<b><i>Trochammina inflata</i> (Montagu) = <i>Nautilus inflatus</i> Montagu, 1808</b>	<b>5.222</b>	<b>Salt and brackish marshes</b>	<b>1</b>
TRLOB	<i>Trochammina lobata</i> Cushman, 1944	0.188		
TEXUN	Texturalid undetermined	0.002		1
<b>Porcellaneous forms</b>				
ADLAE	<i>Adelosina laevigata</i> (d'Orbigny) = <i>Quinqueloculina laevigata</i> d'Orbigny, 1939	0.093		2
COINC	<i>Cornuspira incerta</i> (d'Orbigny) = <i>Cyclogyra incerta</i> d'Orbigny, 1939	0.458		2
MASEC	<i>Massilina secans</i> (d'Orbigny) = <i>Quinqueloculina secans</i> d'Orbigny, 1826	0.006		
QUDEP	<i>Quinqueloculina depressa</i> d'Orbigny, 1852	0.031		
<b>QUJUG</b>	<b><i>Quinqueloculina jugosa</i> (Cushman) = <i>Quinqueloculina seminula</i> var. <i>jugosa</i> Cushman, 1944</b>	<b>0.283</b>	<b>Coastal lagoons and inner bays</b>	<b>2</b>
QULAT	<i>Quinqueloculina lata</i> Terquem, 1876	0.059		
QULON	<i>Quinqueloculina longirostra</i> d'Orbigny, 1826	0.056		
QUOBL	<i>Quinqueloculina oblonga</i> (Montagu) = <i>Vermiculum oblongum</i> Montagu, 1893	0.136		
QURUG	<i>Quinqueloculina rugosa</i> d'Orbigny, 1839	0.066		
<b>QUSEM</b>	<b><i>Quinqueloculina seminula</i> (Linné) = <i>Serpula seminulum</i> Linné, 1758</b>	<b>0.987</b>	<b>Coastal lagoons and inner bays</b>	<b>2</b>
QUSP1	<i>Quinqueloculina</i> sp.1	0.064		
<b>QUSTE</b>	<b><i>Quinqueloculina stelligera</i> Schlumberger, 1893</b>	<b>4.745</b>	<b>Nearshore and outer bays</b>	
TRDUB	<i>Triloculina dubia</i> d'Orbigny, 1826	0.081		
TRMAR	<i>Triloculina marioni</i> Schlumberger, 1893	0.047		
TRROT	<i>Triloculina rotunda</i> d'Orbigny, 1939	0.111		
TRSP1	<i>Triloculina</i> sp.1	1.259	<b>Nearshore and outer bays</b>	
<b>MIUND</b>	<b>Miliolid undetermined</b>	<b>2.265</b>	<b>Nearshore and outer bays</b>	<b>2</b>

## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Code	Foraminifera taxa	RA(%)	Habitat	Plate
	<b>Hyaline forms</b>			
AMBEagg	<i>Ammonia beccarii</i> agg (Linné) = <i>Nautilus beccarii</i> Linné, 1758 (Variants included in this taxon)	21.991	Coastal lagoons and inner bays	3
AMSCA	<i>Amphicoryna scalaris</i> (Batsch) = <i>Nautilus scalaris</i> Batsch, 1791	0.004		
ASMAM	<i>Asterigerinata mamilla</i> (Williamson) = <i>Rotalia mamilla</i> Williamson, 1858	0.387		
ASSP1	<i>Asterigerinata</i> sp.1	2.950	Nearshore and outer bays	
AUPER	<i>Aubignyna perlucida</i> (Heron-Allen and Earland) = <i>Rotalia perlucida</i> Heron-Allen and Earland, 1913	0.501		
BLPSE	<i>Bolivina pseudopunctata</i> (Höglund) = <i>Bolivina pseudopunctata</i> Höglund, 1947	5.340	Offshore habitat	3
BODIL	<i>Bolivina dilatata</i> Reuss, 1850	0.013		
BOPSE	<i>Bolivina pseudoplicata</i> Heron-Allen and Earland, 1930	0.180		
BOSUB	<i>Bolivina subaenariensis</i> (Cushman) = <i>Brizalina subaenariensis</i> Cushman, 1922	0.002		3
cBRAEN	<i>Brizalina</i> cf. <i>aenariensis</i> (Costa) = <i>Bolivina</i> cf. <i>aenariensis</i> Costa, 1856	0.036		
BRSPA	<i>Brizalina spathulata</i> (Williamson) = <i>Textularia variabilis</i> Williamson var. <i>spathulata</i> Williamson, 1858	0.230		3
BRSTR	<i>Bolivina striatula</i> (Cushman) = <i>Brizalina striatula</i> Cushman, 1922	1.385	Nearshore and outer bays	3
BRVAR	<i>Brizalina variabilis</i> (Williamson) = <i>Textularia variabilis</i> Williamson, 1859	0.104		
BUACU	<i>Bulimina aculeata</i> d'Orbigny, 1926	2.752	Offshore habitat	
BUELE	<i>Buliminella elegantissima</i> (d'Orbigny) = <i>Bulimina elegantissima</i> d'Orbigny, 1939	0.430	Nearshore and outer bays	
BUELO	<i>Bulimina elongata</i> d'Orbigny, 1926	0.143		
BUGIB	<i>Bulimina gibba</i> Fornasini, 1902	0.588	Offshore habitat	
BCGRA	<i>Buccella granulata</i> (di Napoli Alliata) = <i>Eponides frigidus</i> var. <i>granulatus</i> di Napoli Alliata, 1952	0.008		
BUMAR	<i>Bulimina marginata</i> d'Orbigny, 1826	0.061		
BUSP1	<i>Bulimina</i> sp. 1	0.034		
CALAE	<i>Cassidulina laevigata</i> d'Orbigny, 1826	0.215	Offshore habitat	
cCACRA	<i>Cassidulina</i> cf. <i>crassa</i> d'Orbigny, 1939	0.015		
CIBRA	<i>Cibicides bradyi</i> (Trauth) = <i>Truncatulina bradyi</i> Trauth, 1918	0.031		
CREXC	<i>Cribrulphidium excavatum</i> (Terquem) = <i>Polystomella excavatum</i> Terquem, 1875	0.816		3
CROCE	<i>Cribrulphidium oceanensis</i> (d'Orbigny) = <i>Polystomella oceanensis</i> d'Orbigny, 1826	0.915	Coastal lagoons and inner bays	3
CRSEL	<i>Cribrulphidium selseyensis</i> (Heron-Allen and Earland) = <i>Elphidium selseyensis</i> Heron-Allen and Earland, 1911	1.188	Offshore habitat	3
CRSP1	<i>Cribrulphidium</i> sp.1	0.071		4
CRWIL	<i>Cribrulphidium williamsoni</i> (Haynes) = <i>Elphidium williamsoni</i> Haynes, 1973	0.044		4

## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Code	Foraminifera taxa	RA(%)	Habitat	Plate
DECOM	<i>Delosina complexa</i> (Sidebottom) = <i>Polymorphina complexa</i> Sidebottom, 1907	0.052		
ELADV	<b><i>Elphidium advenum</i> (Cushman) = <i>Polystomella advenum</i> Cushman, 1922</b>	<b>0.872</b>	<b>Offshore habitat</b>	4
cELERL	<i>Elphidium</i> cf. <i>earlandi</i> Cushman, 1936	0.076		
ELCRI	<b><i>Elphidium crispum</i> (Linné) = <i>Nautilus crispus</i> Linné, 1758</b>	<b>0.319</b>	<b>Offshore habitat</b>	
cELFLE	<b><i>Elphidium</i> cf. <i>flexuosum</i> (d'Orbigny) = <i>Polystomella flexuosa</i> d'Orbigny, 1936</b>	<b>0.501</b>	<b>Offshore habitat</b>	
ELINC	<b><i>Elphidium incertum</i> (Williamson) = <i>Polystomella umbilicatula</i> var. <i>incerta</i> Williamson, 1858</b>	<b>1.039</b>	<b>Offshore habitat</b>	
ELLID	<i>Elphidium lidoense</i> Cushman, 1936	0.026		
ELMAT	<b><i>Elphidium matagordanum</i> (Kornfeld) = <i>Nonion depressula</i> (Walker and Jacob) var. <i>matagordana</i> Kornfeld, 1931</b>	<b>0.802</b>	<b>Offshore habitat</b>	
cELSMI	<i>Elphidium</i> cf. <i>schmitti</i> Cushman and Wickenden, 1929	0.199		
ELSP1	<i>Elphidium</i> sp.1	0.086		
ELSP2	<b><i>Elphidium</i> sp.2</b>	<b>0.439</b>	<b>Offshore habitat</b>	
EPVIT	<b><i>Epistominella vitrea</i> Parker, 1953</b>	<b>0.597</b>	<b>Nearshore and outer bays</b>	
FILUC	<i>Fissurina lucida</i> (Williamson) = <i>Entosolenia marginata</i> (Montagu) var. <i>lucida</i> Williamson, 1848	0.022		
FISP1	<i>Fissurina</i> sp.1	0.016		
FUSCH	<i>Fursenkoina schreibersiana</i> (Czjzek) = <i>Virgulina schreibersiana</i> Czjzek, 1848	0.423		
FUSP1	<i>Fursenkoina</i> sp.1	0.132		
cFUCOM	<i>Fursenkoina</i> cf. <i>complanata</i> (Egger) = <i>Virgulina schreibersiana</i> Czjzek var. <i>complanata</i> Egger, 1893	0.102		
cFUFUS	<i>Fursenkoina</i> cf. <i>fusiformis</i> (Williamson) = <i>Bulimina pupoides</i> d'Orbigny var. <i>fusiformis</i> Williamson, 1858	0.006		4
GAPRA	<b><i>Gavelinopsis praegeri</i> (Heron-Allen and Earland) = <i>Discorbina praegeri</i> Heron-Allen and Earland, 1913</b>	<b>0.238</b>	<b>Offshore habitat</b>	
HAGER	<b><i>Haynesina germanica</i> (Ehrenberg) = <i>Nonionina germanica</i> Ehrenberg, 1840</b>	<b>6.823</b>	<b>Coastal lagoons and inner bays</b>	4
cHAGER	<i>Haynesina</i> cf. <i>germanica</i> (Ehrenberg) = <i>Nonionina</i> cf. <i>germanica</i> Ehrenberg, 1840	0.489		
HADEP	<i>Haynesina depressula</i> (Walker and Jacob) = <i>Nautilus depressulus</i> Walker and Jacob, 1798	0.686		
HOPAC	<i>Hopkinsina pacifica</i> Cushman, 1933	0.653		4
cLASEM	<i>Lagena</i> cf. <i>semistriata</i> (Williamson) = <i>Lagena striata</i> Walker var. <i>semistriata</i> Williamson, 1848	0.039		
LASUB	<i>Lagena substriata</i> Williamson, 1848	0.033		
LASUL	<i>Lagena sulcata</i> (Walker and Jacob) = <i>Serpula sulcata</i> Walker and Jacob, 1798	0.014		
LATEN	<i>Lagena tenuis</i> (Börneman) = <i>Ovulina tenuis</i> Börneman, 1855	0.018		
LAVUL	<i>Lagena vulgaris</i> Williamson, 1858	0.002		

## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Code	Foraminifera taxa	RA(%)	Habitat	Plate
MEPOM	<i>Melonis pompilioides</i> (Fichtel and Moll) = <i>Nautilus pompilioides</i> Fichtel and Moll, 1798	0.031		
NOAST	<i>Nonion asterizans</i> (Fichtel and Moll) = <i>Riminopsis asterizans</i> Fichtel and Moll, 1798	0.024		
NOATL	<b><i>Nonionella atlantica</i> Cushman, 1947</b>	<b>1.045</b>	<b>Nearshore and outer bays</b>	4
NOLAE	<b><i>Nonion laevigatum</i> (d'Orbigny) = <i>Nonionina laevigata</i> d'Orbigny, 1826</b>	<b>3.211</b>	<b>Nearshore and outer bays</b>	
NOOPI	<i>Nonionella opima</i> Cushman, 1947	0.498		4
cNOJAP	<i>Nonionoides</i> cf. <i>japonicum</i> (Asano) = <i>Florilus</i> cf. <i>japonicum</i> Asano, 1938	0.043		
NOSCA	<b><i>Nonionoides scaphus</i> (Fichtel and Moll) = <i>Florilus scaphus</i> Fichtel and Moll, 1798</b>	<b>7.258</b>	<b>Offshore habitat</b>	
PACOR	<i>Patellina corrugata</i> Williamson, 1858	0.072		
PLARI	<i>Planulina ariminensis</i> d'Orbigny, 1826	0.108		
PLMED	<b><i>Planorbulina mediterraneensis</i> d'Orbigny, 1826</b>	<b>0.187</b>	<b>Offshore habitat</b>	
POLAT	<i>Poroeponides lateralis</i> (Terquem) = <i>Rosalina lateralis</i> Terquem, 1878	0.067		
PRCLA	<i>Procerolagena clavata</i> (d'Orbigny) = <i>Lagena clavata</i> d'Orbigny, 1826	0.002		
REACU	<b><i>Reussella aculeata</i> Cushman, 1945</b>	<b>0.477</b>	<b>Offshore habitat</b>	
cRECOM	<i>Rectuvigerina</i> cf. <i>compressa</i> (Cushman) = <i>Uvigerina compressa</i> Cushman, 1925	0.015		
ROANO	<i>Rosalina anomala</i> Terquem, 1875	0.012		
ROARC	<i>Robertina arctica</i> d'Orbigny, 1846	0.210		
ROBUL	<i>Rosalina bulbosa</i> (Parker) = <i>Discorbis bulbosa</i> Parker, 1954	0.033		
ROGLO	<i>Rosalina globularis</i> d'Orbigny, 1826	0.048		4
ROIRR	<i>Rosalina irregularis</i> (Rhumbler) = <i>Discorbina irregularis</i> Rhumbler, 1906	0.019		
cROMED	<i>Rosalina</i> cf. <i>mediterraneensis</i> Brady, 1826	0.050		
cROVAL	<i>Rosalina</i> cf. <i>valvulata</i> d'Orbigny, 1826	0.010		
TRAGU	<b><i>Trichohyalus aguayoi</i> (Bermudez) = <i>Discorinopsis aguayoi</i> Bermudez, 1935</b>	<b>2.998</b>	<b>Salt and brackish marshes</b>	4
TRANG	<i>Trifarina angulosa</i> (Williamson) = <i>Uvigerina angulosa</i> Williamson, 1858	0.008		
TRCON	<i>Tretomphaloides concinnus</i> (Brady) = <i>Discorbina concinna</i> Brady, 1884	0.135		
UVSP1	<b><i>Uvigerina</i> sp.1</b>	<b>0.482</b>	<b>Offshore habitat</b>	
VABRA	<b><i>Valvulineria bradyana</i> (Fornasini) = <i>Discorbina bradyana</i> Fornasini, 1899</b>	<b>1.611</b>	<b>Offshore habitat</b>	
INDET	Unidentified hyaline forms	0.449		

*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta***List of dead foraminifera taxa and relative abundances**

List of the 150 dead foraminiferal species found in the Ebro Delta (arranged by wall structure and alphabetically) with their corresponding codes and their relative abundances (% RA) considering all the samples. Plates are also indicated for those taxa illustrated here. The synonyms of all taxa are also given following Murray (1991).

## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Code	Foraminifera taxa	RA(%)	Plate
	<b>Agglutinated forms</b>		
AMBAL	<i>Ammobaculites balkwilli</i> Haynes, 1973	0.025	
AMSP1	<i>Ammobaculites</i> sp.1	0.009	
AMMSP1	<i>Ammosphaeroidina</i> sp.1	0.328	5
AMMSPH	<i>Ammosphaeroidina sphaeroidiniforme</i> (Brady) = <i>Haplophragmium sphaeroidiniforme</i> Brady, 1884	0.348	
cAMARE	<i>Ammobaculites</i> cf. <i>arenaria</i> Natland, 1938	0.012	
ARMEX	<i>Arenoparella mexicana</i> (Kornfeld) = <i>Trochammina inflata</i> var. <i>mexicana</i> Kornfeld, 1931	0.025	
cATSAL	<i>Ammotium</i> cf. <i>salsum</i> (Cushman and Brönniman) = <i>Ammobaculites salsum</i> Cushman and Brönniman, 1948	0.087	5
CLOBS	<i>Clavulina obscura</i> Chaster, 1982	0.219	
EGSCA	<i>Eggerelloides scaber</i> (Williamson) = <i>Bulimina scabra</i> Williamson, 1858	1.705	5
ELADV	<i>Eggerella advena</i> (Cushman) = <i>Verneuilina advena</i> Cushman, 1921	1.083	
HACAN	<i>Haplophragmoides canariensis</i> (d'Orbigny) = <i>Nonionina canariensis</i> d'Orbigny, 1839	0.228	
HASP1	<i>Haplophragmoides</i> sp.1	0.065	
HAWIL	<i>Haplophragmoides wilberti</i> Anderson, 1953	3.041	5
JAMAC	<i>Jadammina macrescens</i> (Brady) = <i>Trochammina inflata</i> (Montagu) var. <i>macrescens</i> Brady, 1870	4.011	5
LADIF	<i>Lagenammina difflugiformis</i> (Brady) = <i>Reophax difflugiformis</i> Brady, 1879	0.316	
LALAG	<i>Lagenammina laguncula</i> Rhumbler, 1911	0.080	
LESCO	<i>Leptohalysis scottii</i> (Chaster) = <i>Reophax scotti</i> Chaster, 1892	0.029	
MIFUS	<i>Miliammina fusca</i> (Brady) = <i>Quinqueloculina fusca</i> Brady, 1870	1.006	5
NODEN	<i>Nodulina dentaliniformis</i> (Brady) = <i>Reophax dentaliniformis</i> Brady, 1844	0.017	
cPOSP1	<i>Polysacamina</i> sp. 1	0.004	
RECYL	<i>Reophax cylindrica</i> Brady, 1884	0.006	
cREFUS	<i>Reophax</i> cf. <i>fusiformis</i> (Williamson) = <i>Proteonina fusiformis</i> Williamsoni, 1858	0.018	
REMON	<i>Reophax moniliformis</i> Siddall, 1886	0.010	
RENAN	<i>Reophax nana</i> Rhumbler, 1913	0.012	
RESCO	<i>Reophax scorpiurus</i> Montfort, 1808	0.038	
RESP1	<i>Reophax</i> sp.1	0.012	
RESUB	<i>Reophax subfusiformis</i> Earland, 1933	0.003	
SAATL	<i>Saccamina atlantica</i> (Cushman) = <i>Proteonina atlantica</i> Cushman, 1944	0.014	

## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Code	Foraminifera taxa	RA(%)	Plate
SASPI	<i>Saccamina</i> sp.1	0.017	
TEBOC	<i>Textularia bocki</i> Höglund, 1947	0.003	
TECAL	<i>Textularia calva</i> Lalicker, 1935	0.672	
cTECAL	<i>Textularia</i> cf. <i>calva</i> Lalicker, 1935	0.007	
TESP1	<i>Textularia</i> sp.1	0.040	
TETEN	<i>Textularia tenuissima</i> Earland, 1933	0.338	
cTRADV	<i>Trochammina</i> cf. <i>advena</i> Cushman, 1922	0.058	
TRINF	<i>Trochammina inflata</i> (Montagu) = <i>Nautilus inflatus</i> Montagu, 1808	4.909	5
TRLOB	<i>Trochammina lobata</i> Cushman, 1944	0.003	
TEXUN	Texturalid undetermined	0.011	
<b>Porcellaneous forms</b>			
ADLAE	<i>Adelosina laevigata</i> (d'Orbigny) = <i>Quinqueloculina laevigata</i> d'Orbigny, 1939	0.063	
COINC	<i>Cornuspira incerta</i> (d'Orbigny) = <i>Cyclogyra incerta</i> d'Orbigny, 1939	0.048	6
MASEC	<i>Massilina secans</i> (d'Orbigny) = <i>Quinqueloculina secans</i> d'Orbigny, 1826	0.019	
MISUB	<i>Miliolinella subrotunda</i> (Montagu) = <i>Vermiculum subrotundum</i> Montagu, 1803	0.006	
PYINO	<i>Pyrgo inornata</i> (d'Orbigny) = <i>Biloculina inornata</i> d'Orbigny, 1846	0.003	
QUDEP	<i>Quinqueloculina depressa</i> d'Orbigny, 1852	0.011	
QUJUG	<i>Quinqueloculina jugosa</i> (Cushman) = <i>Quinqueloculina seminula</i> var. <i>jugosa</i> Cushman, 1944	0.430	
QULAE	<i>Quinqueloculina lata</i> Terquem, 1876	0.097	
QULAT	<i>Quinqueloculina longirostra</i> d'Orbigny, 1826	0.112	
QUOBL	<i>Quinqueloculina oblonga</i> (Montagu) = <i>Vermiculum oblongum</i> Montagu, 1893	0.167	
QURUG	<i>Quinqueloculina rugosa</i> d'Orbigny, 1839	0.464	
QUSEM	<i>Quinqueloculina seminula</i> (Linné) = <i>Serpula seminulum</i> Linné, 1758	1.830	6
QUSP1	<i>Quinqueloculina</i> sp.1	0.006	
QUSTE	<i>Quinqueloculina stelligera</i> Schlumberger, 1893	4.424	6
TRDUB	<i>Triloculina dubia</i> d'Orbigny, 1826	0.015	6
TRMAR	<i>Triloculina marioni</i> Schlumberger, 1893	0.007	
TRROT	<i>Triloculina rotunda</i> d'Orbigny, 1939	0.255	
TRSP1	<i>Triloculina</i> sp.1	0.565	6



## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Code	Foraminifera taxa	RA(%)	Plate
MIUND	Miliolid undetermined	6.427	6
	<b>Hyaline forms</b>		
AMBEagg	<i>Ammonia beccarii</i> agg (Linné) = <i>Nautilus beccarii</i> Linné, 1758 (Variants included in this taxon)	31.574	7
AMSCA	<i>Amphicoryna scalaris</i> (Batsch) = <i>Nautilus scalaris</i> Batsch, 1791	0.041	
ASMAM	<i>Asterigerinata mamilla</i> (Williamson) = <i>Rotalia mamilla</i> Williamson, 1858	0.363	
ASSP1	<i>Asterigerinata</i> sp.1	1.640	
AUPER	<i>Aubignyna perlucida</i> (Heron-Allen and Earland) = <i>Rotalia perlucida</i> Heron-Allen and Earland, 1913	0.449	7
BCGRA	<i>Buccella granulata</i> (di Napoli Alliata) = <i>Eponides frigidus</i> var. <i>granulatus</i> di Napoli Alliata, 1952	0.305	
BCHAN	<i>Buccella hannai</i> (Phleger and Parker) = <i>Eponides hannai</i> Phleger and Parker, 1951	0.003	
BMELE	<i>Buliminella elegantissima</i> (d'Orbigny) = <i>Bulimina elegantissima</i> d'Orbigny, 1939	0.048	
BODIL	<i>Bolivina dilatata</i> Reuss, 1850	0.004	7
BOPSE	<i>Bolivina pseudoplicata</i> Heron-Allen and Earland, 1930	0.109	
BOSTR	<i>Bolivina striatula</i> (Cushman) = <i>Brizalina striatula</i> Cushman, 1922	0.158	
cBRAEN	<i>Brizalina</i> cf. <i>aenariensis</i> (Costa) = <i>Bolivina</i> cf. <i>aenariensis</i> Costa, 1856	0.025	
BRSPA	<i>Brizalina spathulata</i> (Williamson) = <i>Textularia variabilis</i> Williamson var. <i>spathulata</i> Williamson, 1858	0.175	
BRVAR	<i>Brizalina variabilis</i> (Williamson) = <i>Textularia variabilis</i> Williamson, 1859	0.025	7
BUACU	<i>Bulimina aculeata</i> d'Orbigny, 1926	0.784	
BUELO	<i>Bulimina elongata</i> d'Orbigny, 1926	0.051	
BUGIB	<i>Bulimina gibba</i> Fornasini, 1902	0.923	7
BUMAR	<i>Bulimina marginata</i> d'Orbigny, 1826	0.041	
BUSP1	<i>Bulimina</i> sp. 1	0.041	
CAAUR	<i>Cancris auricula</i> (Fichtel and Moll) = <i>Nautilus auricula</i> Fichtel and Moll, 1798	0.002	7
CALAE	<i>Cassidulina laevigata</i> d'Orbigny, 1826	0.340	
CAOBT	<i>Cassulina obtusa</i> Williamson, 1858	0.002	
cCACRA	<i>Cassidulina</i> cf. <i>crassa</i> d'Orbigny, 1939	0.024	
CIBRA	<i>Cibicoides bradyi</i> (Trauth) = <i>Truncatulina bradyi</i> Trauth, 1918	0.004	
CILOB	<i>Cibicides lobatulus</i> (Walker and Jacob) = <i>Nautilus lobatulus</i> Walker and Jacob, 1798	0.048	
CREXC	<i>Cribrolophidium excavatum</i> (Terquem) = <i>Polystomella excavatum</i> Terquem, 1875	1.343	7
CRMAG	<i>Criboelphidium magellanicum</i> (Heron-Allen and Earland) = <i>Elphidium magellanicum</i> Heron-Allen and Earland, 1932	0.003	

## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Code	Foraminifera taxa	RA(%)	Plate
CROCE	<i>Criboelphidium oceanensis</i> (d'Orbigny) = <i>Polystomella oceanensis</i> d'Orbigny, 1826	2.100	7
cCRPOE	<i>Criboelphidium</i> cf. <i>poeyanum</i> (d'Orbigny) = <i>Polystomella poeyana</i> d'Orbigny, 1839	0.017	7
CRSEL	<i>Criboelphidium selseyensis</i> (Heron-Allen and Earland) = <i>Elphidium selseyensis</i> Heron-Allen and Earland, 1911	0.698	7
CRSP1	<i>Criboelphidium</i> sp.1	0.125	8
CRWIL	<i>Criboelphidium williamsoni</i> (Haynes) = <i>Elphidium williamsoni</i> Haynes, 1973	0.182	8
EGADV	<i>Elphidium advenum</i> (Cushman) = <i>Polystomella advenum</i> Cushman, 1922	0.098	8
cELERL	<i>Elphidium</i> cf. <i>earlandi</i> Cushman, 1936	0.230	
ELCRI	<i>Elphidium crispum</i> (Linné) = <i>Nautilus crispus</i> Linné, 1758	0.308	8
ELGER	<i>Elphidium gerthi</i> Van Voorthuysen, 1957	0.020	
ELINC	<i>Elphidium incertum</i> (Williamson) = <i>Polystomella umbilicatulula</i> var. <i>incerta</i> Williamson, 1858	0.118	
ELLID	<i>Elphidium lidoense</i> Cushman, 1936	1.329	
ELMAR	<i>Elphidium margaritaceum</i> (Cushman) = <i>Elphidium advenum</i> var. <i>margaritaceum</i> Cushman, 1930	0.016	
ELMAT	<i>Elphidium matagordanum</i> (Kornfeld) = <i>Nonion depressula</i> (Walker and Jacob) var. <i>matagordana</i> Kornfeld, 1931	0.009	
ELSP1	<i>Elphidium</i> sp.1	1.281	
ELSP2	<i>Elphidium</i> sp.2	0.165	
EPVIT	<i>Epistominella vitrea</i> Parker, 1953	0.166	
cELFLE	<i>Elphidium</i> cf. <i>flexuosum</i> (d'Orbigny) = <i>Polystomella flexuosa</i> d'Orbigny, 1936	0.194	
cELSMI	<i>Elphidium</i> cf. <i>schmitti</i> Cushman and Wickenden, 1929	0.003	
DECOM	<i>Delosina complexa</i> (Sidebottom) = <i>Polymorphina complexa</i> Sidebottom, 1907	0.003	
FILUC	<i>Fissurina lucida</i> (Williamson) = <i>Entosolenia marginata</i> (Montagu) var. <i>lucida</i> Williamson, 1848	0.096	8
FIMAR	<i>Fissurina marginata</i> (Montagu) = <i>Vermiculum marginatum</i> Montagu, 1803	0.002	
FISP1	<i>Fissurina</i> sp.1	0.209	
cFUCOM	<i>Fursenkoina</i> cf. <i>complanata</i> (Egger) = <i>Virgulina schreibersiana</i> Czjzek var. <i>complanata</i> Egger, 1893	0.221	
cFUFUS	<i>Fursenkoina</i> cf. <i>fusififormis</i> (Williamson) = <i>Bulimina pupoides</i> d'Orbigny var. <i>fusififormis</i> Williamson, 1858	0.002	
FUSP1	<i>Fursenkoina</i> sp.1	0.009	
FUSCH	<i>Fursenkoina schreibersiana</i> (Czjzek) = <i>Virgulina schreibersiana</i> Czjzek, 1848	0.047	
GAPRA	<i>Gavelinopsis praegeri</i> (Heron-Allen and Earland) = <i>Discorbina praegeri</i> Heron-Allen and Earland, 1913	0.180	8
cGYUMB	<i>Gyroidina</i> cf. <i>umbonata</i> (Silvestri, 1898)	0.025	
HADEP	<i>Haynesina depressula</i> (Water and Jacob) = <i>Nautilus depressulus</i> Walker and Jacob, 1798	1.738	8
cHAGER	<i>Haynesina</i> cf. <i>germanica</i> (Ehrenberg) = <i>Nonionina</i> cf. <i>germanica</i> Ehrenberg, 1840	0.029	

## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Code	Foraminifera taxa	RA(%)	Plate
HAGER	<i>Haynesina germanica</i> (Ehrenberg) = <i>Nonionina germanica</i> Ehrenberg, 1840	8.778	8
HOPAC	<i>Hopkinsina pacifica</i> Cushman, 1933	0.103	8
cLASEM	<i>Lagena</i> cf. <i>semistriata</i> (Williamson) = <i>Lagena striata</i> Walker var. <i>semistriata</i> Williamson, 1848	0.011	
LASUB	<i>Lagena substriata</i> Williamson, 1848	0.027	
LASUL	<i>Lagena sulcata</i> (Walter and Jacob) = <i>Serpula sulcata</i> Walter and Jacob, 1798	0.181	8
LATEN	<i>Lagena tenuis</i> (Börneman) = <i>Ovulina tenuis</i> Börneman, 1855	0.039	
MEPOM	<i>Melonis pompilioides</i> (Fitchel and Moll) = <i>Nautilus pompilioides</i> Fitchel and Moll, 1798	0.018	
NOAST	<i>Nonion asterizans</i> (Fichtel and Moll) = <i>Riminopsis asterizans</i> Fichtel and Moll, 1798	0.134	
NOATL	<i>Nonionella atlantica</i> Cushman, 1947	0.062	
NOLAE	<i>Nonion laevigatum</i> (d'Orbigny) = <i>Nonionina laevigata</i> d'Orbigny, 1826	0.283	
cNOJAP	<i>Nonionoides</i> cf. <i>japonicum</i> (Asano) = <i>Florilus</i> cf. <i>japonicum</i> Asano, 1938	0.009	
NOOPI	<i>Nonionella opima</i> Cushman, 1947	1.262	
NOPOL	<i>Nouria polymorphides</i> Heron-Allen and Earland, 1914	0.006	
NOSCA	<i>Nonionoides scaphus</i> (Fitchel and Moll) = <i>Florilus scaphus</i> Fitchel and Moll, 1798	0.012	
PACOR	<i>Patellina corrugata</i> Williamson, 1858	0.015	
PLARI	<i>Planulina ariminensis</i> d'Orbigny, 1826	0.013	
PLMED	<i>Planorbulina mediterraneensis</i> d'Orbigny, 1826	0.027	
POLAT	<i>Poroepionides lateralis</i> (Terquem) = <i>Rosalina lateralis</i> Terquem, 1878	0.006	
PRCLA	<i>Procerolagena clavata</i> (d'Orbigny) = <i>Lagena clavata</i> d'Orbigny, 1826	0.045	
REACU	<i>Reussella aculeata</i> Cushman, 1945	0.188	
ROANO	<i>Rosalina anomala</i> Terquem, 1875	0.040	
ROARC	<i>Robertina arctica</i> d'Orbigny, 1846	0.020	
ROBUL	<i>Rosalina bulbosa</i> (Parker) = <i>Discorbis bulbosa</i> Parker, 1954	0.022	
cRECOM	<i>Rectuvigerina</i> cf. <i>compressa</i> (Cushman) = <i>Uvigerina compressa</i> Cushman, 1925	0.166	
ROGLO	<i>Rosalina globularis</i> d'Orbigny, 1826	0.003	9
cROMED	<i>Rosalina</i> cf. <i>mediterraneensis</i> Brady, 1826	0.003	
ROIRR	<i>Rosalina irregularis</i> (Rhumbler) = <i>Discorbina irregularis</i> Rhumbler, 1906	0.111	9
cROVAL	<i>Rosalina</i> cf. <i>valvulata</i> d'Orbigny, 1826	0.012	
SVSP1	<i>Svratkina</i> sp.1	0.041	
TRAGU	<i>Trichohyalus aguayoi</i> (Bermudez) = <i>Discorinopsis aguayoi</i> Bermudez, 1935	3.416	9

*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*

<b>Code</b>	<b>Foraminifera taxa</b>	<b>RA(%)</b>	<b>Plate</b>
TRANG	<i>Trifarina angulosa</i> (Williamson) = <i>Uvigerina angulosa</i> Williamson, 1858	0.003	
TRCON	<i>Tretomphaloides concinnus</i> (Brady) = <i>Discorbina concinna</i> Brady, 1884	0.037	
UVSPI	<i>Uvigerina</i> sp.1	0.064	
VABRA	<i>Valvulineria bradyana</i> (Fornasini) = <i>Discorbina bradyana</i> Fornasini, 1899	0.708	9
PLANK	Planktonic forms	0.884	9
INDET	Unidentified hyaline forms	0.189	

*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta***List of fossil foraminifera taxa and relative abundances**

List of the 140 foraminifera taxa found in the Ebro Delta boreholes (Carlet and Sant Jaume) and short cores (Olles, Tancada, Alfacs, Clot and Garxal) with their corresponding codes and their relative abundances (% RA) considering all the samples. Taxa are arranged by wall structure and alphabetically. Plates are also indicated for those taxa illustrated here. The synonyms of all taxa are also given following Murray (1991). + indicates presence of the taxa in the assemblages with few tests.

Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Foraminifera taxa	Cores (% RA)						Plate	
	Carlet	Sant Jaume	Olles	Tancada	Alfacs	Clot		Garxal
<b>Agglutinated forms</b>								
<i>Ammobaculites balkwilli</i> Haynes, 1973			0.000	0.013	0.000	0.000	0.000	
<i>Ammobaculites</i> sp.1			0.000	0.000	0.000	0.000	0.218	
<i>Eggerelloides scaber</i> (Williamson) = <i>Bulimina scabra</i> Williamson, 1858		0.026	0.000	0.000	0.000	0.000	0.020	
<i>Eggerella advena</i> (Cushman) = <i>Verneuilina advena</i> Cushman, 1921			0.021	0.000	0.000	0.000	0.000	
<i>Haplophragmoides</i> sp.1			0.000	0.000	0.000	0.015	0.000	
<i>Haplophragmoides wilberti</i> Anderson, 1953		0.011	35.772	0.016	0.000	0.325	0.120	10
<i>Jadammina macrescens</i> (Brady) = <i>Trochammina inflata</i> (Montagu) var. <i>macrescens</i> Brady, 1870		0.032	0.476	9.175	14.882	4.498	0.165	
<i>Miliammina fusca</i> (Brady) = <i>Quinqueloculina fusca</i> Brady, 1870			0.945	0.000	0.000	0.101	0.120	
<i>Reophax moniliformis</i> Siddall, 1886			0.062	0.000	0.000	0.000	0.000	
<i>Textularia agglutinans</i> d'Orbigny, 1839		0.237						
<i>Textularia bocki</i> Höglund, 1947	0.160	0.053	0.000	0.000	0.000	0.000	0.025	
<i>Textularia calva</i> Lalicker, 1935		0.038						
<i>Textularia</i> cf. <i>calva</i> Lalicker, 1935			0.000	0.000	0.000	0.000	0.071	10
<i>Textularia</i> sp.1		0.088						
<i>Trochammina inflata</i> (Montagu) = <i>Nautilus inflatus</i> Montagu, 1808	+	0.007	5.318	0.701	4.109	0.212	0.321	
Texturalid undetermined			0.000	0.000	0.026	0.000	0.050	
<b>Porcellaneous forms</b>								
<i>Adelosina bicornis</i> (Walker and Jacob) = <i>Serpula bicornis</i> Walker and Jacob, 1798	0.071	0.020						
<i>Adelosina laevigata</i> (d'Orbigny) = <i>Quinqueloculina laevigata</i> d'Orbigny, 1939	0.705	1.430	0.000	0.015	0.390	0.029	0.418	10
<i>Adelosina mediterraneensis</i> (Le Calvez and Le Calvez) = <i>Quinqueloculina mediterraneensis</i> Le Calvez and Le Calvez, 1958		0.006						
<i>Adelosina striata</i> d'Orbigny, 1826	0.212							
<i>Adelosina</i> sp. 1		0.050						
<i>Cornuloculina</i> sp.1		0.006						
<i>Cornuspira incerta</i> (d'Orbigny) = <i>Cyclogyra incerta</i> d'Orbigny, 1939		0.221						10

## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Foraminifera taxa	Cores (% RA)							Plate
	Carlet	Sant Jaume	Olles	Tancada	Alfacs	Clot	Garxal	
<i>Cornuspira involvens</i> (Reuss) = <i>Operculina involvens</i> Reus, 1850	0.221	0.192	0.000	0.000	0.896	0.015	0.000	
<i>Lachlanella undulata</i> (d'Orbigny) = <i>Quinqueloculina undulata</i> d'Orbigny, 1852		0.059						
<i>Massilina secans</i> (d'Orbigny) = <i>Quinqueloculina secans</i> d'Orbigny, 1826	0.257	0.040	0.000	0.157	0.000	0.000	0.089	
<i>Miliolinella subrotunda</i> (Montagu) = <i>Vermiculum subrotundum</i> Montagu, 1803	0.212	0.383	0.000	0.061	0.122	0.000	0.000	
<i>Miliolinella webbiana</i> (d'Orbigny) = <i>Triloculina webbiana</i> d'Orbigny, 1839	0.048							
<i>Pyrgo inornata</i> (d'Orbigny) = <i>Biloculina inornata</i> d'Orbigny, 1846		0.056	0.000	0.000	0.536	0.000	0.000	
<i>Pyrgo</i> sp.		0.020						
<i>Quinqueloculina berthelotiana</i> d'Orbigny, 1839	0.029							
<i>Quinqueloculina depressa</i> d'Orbigny, 1852		0.136						10
<i>Quinqueloculina jugosa</i> (Cushman) = <i>Quinqueloculina seminula</i> var. <i>jugosa</i> Cushman, 1944			0.020	0.087	0.285	0.000	0.074	
<i>Quinqueloculina lata</i> Terquem, 1876	0.269	0.317						
<i>Quinqueloculina longirostra</i> d'Orbigny, 1826		0.187	0.000	0.000	0.052	0.000	0.000	10
<i>Quinqueloculina oblonga</i> (Montagu) = <i>Vermiculum oblongum</i> Montagu, 1893	0.305	0.592	0.000	0.182	0.926	0.189	0.000	
<i>Quinqueloculina seminula</i> (Linné) = <i>Serpula seminulum</i> Linné, 1758	5.307	4.217	0.000	2.204	5.853	2.047	2.060	10
<i>Quinqueloculina</i> sp.1		1.029						
<i>Quinqueloculina</i> sp.2		0.020						
<i>Quinqueloculina stelligera</i> Schlumberger, 1893		0.655	0.000	0.504	4.025	0.000	0.025	10
<i>Quinqueloculina vulgaris</i> d'Orbigny, 1826		+	0.000	0.000	0.000	0.000	0.143	
<i>Siphonaperta quadrata</i> (Nørvang) = <i>Quinqueloculina quadrata</i> Nørvang, 1945	0.045							
<i>Triloculina dubia</i> d'Orbigny, 1826		0.075	0.000	0.012	0.128	0.000	0.268	10
<i>Triloculina marioni</i> Schlumberger, 1893	0.952	0.159	0.000	0.000	0.000	0.000	0.062	
<i>Triloculina rotunda</i> d'Orbigny, 1939		0.364	0.020	0.000	0.041	0.000	0.000	
<i>Triloculina trigonula</i> (Lamarck) = <i>Miliolites trigonula</i> Lamarck, 1804	1.122		0.000	0.014	0.000	0.000	1.096	
<i>Triloculina</i> sp.1			0.000	0.013	0.292	0.000	0.000	
Miliolid undetermined		0.087	0.020	4.419	21.497	2.767	1.897	10
<b>Hyaline forms</b>								
<i>Acervulina inhaerens</i> Schulze, 1854		0.143						

## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Foraminifera taxa	Cores (% RA)							Plate
	Carlet	Sant Jaume	Olles	Tancada	Alfacs	Clot	Garxal	
<i>Ammonia beccarii</i> agg (Linné) = <i>Nautilus beccarii</i> Linné, 1758 (Variants included in this taxon)	72.339	47.044	31.376	40.790	20.765	69.623	43.555	
<i>Asterigerinata mamilla</i> (Williamson) = <i>Rotalia mamilla</i> Williamson, 1858	0.090	1.922	0.604	0.043	0.528	0.091	0.308	11
<i>Astacolus crepidulus</i> (Fichtel and Moll) = <i>Nautilus crepidula</i> Fichtel and Moll, 1798		0.005						
<i>Aubignyna perlucida</i> (Heron-Allen and Earland) = <i>Rotalia perlucida</i> Heron-Allen and Earland, 1913	0.494	1.049	0.143	0.089	0.296	0.030	0.317	11
<i>Buccella granulata</i> (di Napoli Alliata) = <i>Eponides frigidus</i> var. <i>granulatus</i> di Napoli Alliata, 1952		0.065	0.000	0.256	0.502	0.049	2.152	11
<i>Buliminella elegantissima</i> (d'Orbigny) = <i>Bulimina elegantissima</i> d'Orbigny, 1939		0.055	0.043	0.000	0.000	0.000	0.000	
<i>Bolivina difformis</i> (Williamson) = <i>Textularia variabilis</i> var. <i>difformis</i> Williamson, 1858		0.169						
<i>Bolivina dilatata</i> Reuss, 1850 (SD;L)		0.268						
<i>Bolivina pseudoplicata</i> Heron-Allen and Earland, 1930	0.061	0.363	0.000	0.000	0.017	0.015	0.000	11
<i>Bolivinellina pseudopunctata</i> (Höglund) = <i>Bolivina pseudopunctata</i> Höglund, 1947		1.124	0.084	0.091	0.020	0.014	0.000	
<i>Bolivina striatula</i> (Cushman) = <i>Brizalina striatula</i> Cushman, 1922		0.033	0.169	0.087	0.020	0.000	0.000	
<i>Brizalina spathulata</i> (Williamson) = <i>Textularia variabilis</i> Williamson var. <i>spathulata</i> Williamson, 1858		0.296	0.020	0.000	0.000	0.000	0.000	
<i>Brizalina variabilis</i> (Williamson) = <i>Textularia variabilis</i> Williamson, 1859	0.208	3.222	0.292	0.245	0.026	0.031	0.000	11
<i>Bulimina aculeata</i> d'Orbigny, 1926		0.065						
<i>Bulimina elongata</i> d'Orbigny, 1926	0.462	0.218	0.000	0.012	0.026	0.000	0.021	
<i>Bulimina gibba</i> Fornasini, 1902	0.192	1.361	0.021	0.000	0.016	0.000	0.087	11
<i>Bulimina marginata</i> d'Orbigny, 1826		0.004	0.000	0.000	0.000	0.000	0.101	
<i>Cassidulina carinata</i> Silvestri, 1896	0.019	0.004						
<i>Cassidulina laevigata</i> d'Orbigny, 1826			0.000	0.000	0.000	0.000	0.025	
<i>Cassulina obtusa</i> Williamson, 1858		0.032						11
<i>Cibicides lobatulus</i> (Walker and Jacob) = <i>Nautilus lobatulus</i> Walker and Jacob, 1798	0.629	0.152	0.021	0.015	0.100	0.000	0.928	11
<i>Cribrorhaphidium excavatum</i> (Terquem) = <i>Polystomella excavatum</i> Terquem, 1875	1.161		0.042	0.605	0.026	0.795	12.284	11
<i>Cribrorhaphidium magellanicum</i> (Heron-Allen and Earland) = <i>Elphidium magellanicum</i> Heron-	0.051		0.041	0.000	0.000	0.000	0.017	



## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Foraminifera taxa	Cores (% RA)							Plate
	Carlet	Sant Jaume	Olles	Tancada	Alfacs	Clot	Garxal	
Allen and Earland, 1932								
<i>Criboelphidium oceanensis</i> (d'Orbigny) = <i>Polystomella oceanensis</i> d'Orbigny, 1826	0.042	3.634	0.124	1.588	0.020	1.261	7.777	
<i>Criboelphidium</i> cf. <i>poeyanum</i> (d'Orbigny) = <i>Polystomella poeyana</i> d'Orbigny, 1839		2.523	0.000	0.014	0.000	0.000	2.657	12
<i>Criboelphidium selseyensis</i> (Heron-Allen and Earland) = <i>Elphidium selseyensis</i> Heron-Allen and Earland, 1911	10.649	15.088	0.389	0.336	0.153	0.132	1.516	12
<i>Criboelphidium</i> sp.1			0.041	0.744	6.913	4.109	0.000	12
<i>Criboelphidium williamsoni</i> (Haynes) = <i>Elphidium williamsoni</i> Haynes, 1973		0.069	0.061	0.012	0.000	0.016	3.339	
<i>Discorbis</i> sp. 1	0.048							
<i>Elphidium advenum</i> (Cushman) = <i>Polystomella advenum</i> Cushman, 1922		0.013	0.073	0.026	0.000	0.000	0.130	
<i>Elphidium</i> cf. <i>earlandi</i> Cushman, 1936			0.000	0.000	0.000	0.016	0.000	
<i>Elphidium crispum</i> (Linné) = <i>Nautilus crispus</i> Linné, 1758	0.459	0.115	0.044	0.000	0.026	0.000	0.179	12
<i>Elphidium gerthi</i> Van Voorthuysen, 1957		0.454	0.000	0.000	0.000	0.000	0.166	
<i>Elphidium incertum</i> (Williamson) = <i>Polystomella umbilicatula</i> var. <i>incerta</i> Williamson, 1858		0.283	0.000	0.000	0.167	0.000	0.071	
<i>Elphidium margaritaceum</i> (Cushman) = <i>Elphidium advenum</i> var. <i>margaritaceum</i> Cushman, 1930	0.167	0.052	0.145	0.000	0.000	0.017	0.020	
<i>Elphidium</i> sp.1		0.165	0.000	0.056	0.000	0.190	0.020	
<i>Epistominella vitrea</i> Parker, 1953		+						
<i>Elphidium</i> cf. <i>flexuosum</i> (d'Orbigny) = <i>Polystomella flexuosa</i> d'Orbigny, 1936		0.051						
<i>Favulina melo</i> (d'Orbigny) = <i>Oolina melo</i> d'Orbigny, 1839		+						
<i>Fissurina lucida</i> (Williamson) = <i>Entosolenia marginata</i> (Montagu) var. <i>lucida</i> Williamson, 1848	0.022	0.243	0.017	0.014	0.534	0.000	0.065	
<i>Fissurina marginata</i> (Montagu) = <i>Vermiculum marginatum</i> Montagu, 1803	0.013	0.171	0.017	0.000	0.000	0.000	0.025	12
<i>Fissurina</i> sp.1		0.101						
<i>Fursenkoina</i> cf. <i>fusiformis</i> (Williamson) = <i>Bulimina pupoides</i> d'Orbigny var. <i>fusiformis</i> Williamson, 1858			0.000	0.000	0.000	0.000	0.166	
<i>Fursenkoina schreibersiana</i> (Czjzek) = <i>Virgulina schreibersiana</i> Czjzek, 1848		0.046						12
<i>Gavelinopsis praegeri</i> (Heron-Allen and Earland) = <i>Discorbina praegeri</i> Heron-Allen and Earland, 1913	0.055	0.060	0.000	0.000	0.208	0.397	0.021	12

## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

Foraminifera taxa	Cores (% RA)							Plate
	Carlet	Sant Jaume	Olles	Tancada	Alfacs	Clot	Garxal	
<i>Gyroidina</i> sp.1	0.026		0.000	0.000	0.000	0.014	0.000	
<i>Globobulimina</i> sp.1		0.023						
<i>Haynesina depressula</i> (Water and Jacob) = <i>Nautilus depressulus</i> Walker and Jacob, 1798	0.151	0.229	0.103	0.000	8.979	0.000	0.514	12
<i>Haynesina germanica</i> (Ehrenberg) = <i>Nonionina germanica</i> Ehrenberg, 1840	0.244	4.974	23.390	37.270	5.177	12.429	14.315	12
<i>Lagena</i> cf. <i>semistriata</i> (Williamson) = <i>Lagena striata</i> var. <i>semistriata</i> Williamson, 1848		0.016						13
<i>Lagena sulcata</i> (Walter and Jacob) = <i>Serpula sulcata</i> Walter and Jacob, 1798		0.038						13
<i>Lagena vulgaris</i> Williamson, 1858		0.052						
<i>Melonis pompilioides</i> (Fichtel and Moll) = <i>Nautilus pompilioides</i> Fichtel and Moll, 1798			0.000	0.000	0.086	0.000	0.000	
<i>Nonion asterizans</i> (Fichtel and Moll) = <i>Riminopsis asterizans</i> Fichtel and Moll, 1798			0.000	0.000	0.000	0.000	0.071	
<i>Nonionella atlantica</i> Cushman, 1947	0.071		0.000	0.000	0.021	0.000	0.522	
<i>Nonionoides boueanum</i> (d'Orbigny) = <i>Nonionina boueana</i> d'Orbigny, 1846	0.038							13
<i>Nonionella opima</i> Cushman, 1947		0.320	0.000	0.000	0.061	0.016	0.020	13
<i>Nonionoides turgida</i> (Williamson) = <i>Nonionina turgida</i> Williamson, 1858		0.100						
<i>Patellina corrugata</i> Williamson, 1858		+						13
<i>Planorbulina mediterraneensis</i> d'Orbigny, 1826	0.170		0.000	0.000	0.000	0.000	0.021	
<i>Rectuvigerina compressa</i> (Cushman) = <i>Uvigerina compressa</i> Cushman, 1925		0.086						13
<i>Reussella aculeata</i> Cushman, 1945		0.152	0.021	0.000	0.000	0.000	0.000	
<i>Reusoolina laevis</i> (Montagu) = <i>Vermiculum laeve</i> Montagu, 1803		0.057						
<i>Rosalina anomala</i> Terquem, 1875	0.827	0.074	0.063	0.000	0.000	0.000	0.423	13
<i>Rosalina globularis</i> d'Orbigny, 1826			0.000	0.000	0.000	0.000	0.215	
<i>Rosalina irregularis</i> (Rhumbler) = <i>Discorbina irregularis</i> Rhumbler, 1906	1.100	0.620	0.000	0.000	0.084	0.000	0.280	13
<i>Rosalina</i> cf. <i>valvulata</i> d'Orbigny, 1826		0.183						
<i>Rosalina</i> sp. 1		0.103						
<i>Rosalina</i> sp. 2		+						
<i>Rosalina williamsoni</i> (Chapman and Parr) = <i>Discorbis williamsoni</i> Chapman and Parr, 1932		0.011						

*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*

Foraminifera taxa	Cores (% RA)							Plate
	Carlet	Sant Jaume	Olles	Tancada	Alfacs	Clot	Garxal	
<i>Spirillina vivipara</i> Ehrenberg, 1843	0.141	0.093						13
<i>Svratkina</i> sp.1		0.200						
<i>Trichohyalus aguayoi</i> (Bermudez) = <i>Discorinopsis aguayoi</i> Bermudez, 1935	0.208		0.000	0.099	0.111	0.259	0.000	
<i>Trifarina angulosa</i> (Williamson) = <i>Uvigerina angulosa</i> Williamson, 1858		0.021						
<i>Tretomphaloides concinnus</i> (Brady) = <i>Discorbina concinna</i> Brady, 1884		0.206	0.000	0.000	0.453	0.027	0.104	
<i>Uvigerina</i> sp.1								
<i>Valvulineria bradyana</i> (Fornasini) = <i>Discorbina bradyana</i> Fornasini, 1899		0.957	0.000	0.000	0.000	0.000	0.025	13
Unidentified hyaline forms			0.000	0.000	0.286	0.272	0.302	

*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*

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**Binocular stereomicroscope plates of foraminifera taxa**

Scale bar represents 100  $\mu\text{m}$ .

*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta***Plate 1 Living foraminifera**

Figs. 1–2      *Ammotium cf. salsum* (Cushman and Brönniman) Cushman and Brönniman, 1948

Figs. 3–4      *Arenoparella mexicana* (Kornfeld) Kornfeld, 1931

Fig. 3: spiral view

Fig. 4: umbilical view

Fig. 5      *Eggerelloides scaber* (Williamson) Williamson, 1858

Fig. 6      *Haplophragmoides wilberti* Anderson, 1953

Figs. 7–8      *Jadammina macrescens* (Brady) Brady, 1980

Fig. 7: spiral view

Fig. 8: umbilical view

Figs. 9–10      *Miliammina fusca* (Brady) Brady, 1980

Fig. 11      *Nodulina dentaliniformis* (Brady) Brady 1844

Fig. 12      *Reophax moniliformis* Siddall, 1886

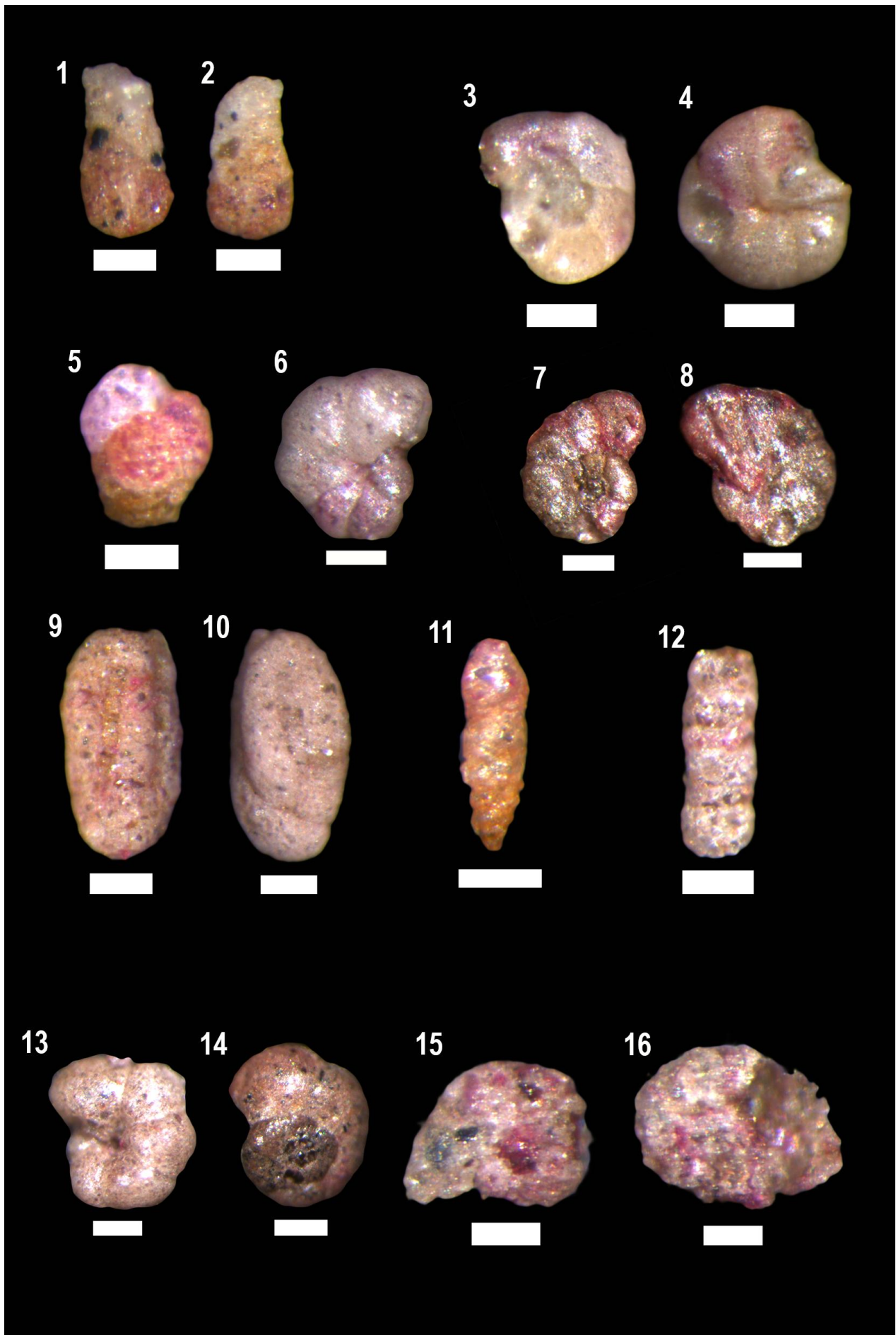
Figs. 13–14      *Trochammina inflata* (Montagu) Montagu, 1808

Fig. 13: umbilical view

Fig. 14: spiral view

Figs. 15–16      Texturalid undetermined

*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta***Plate 2 Living foraminifera**

Fig. 1 *Adelosina laevigata* (d'Orbigny) d'Orbigny, 1939

Fig. 2 *Cornuspira incerta* (d'Orbigny) d'Orbigny, 1939

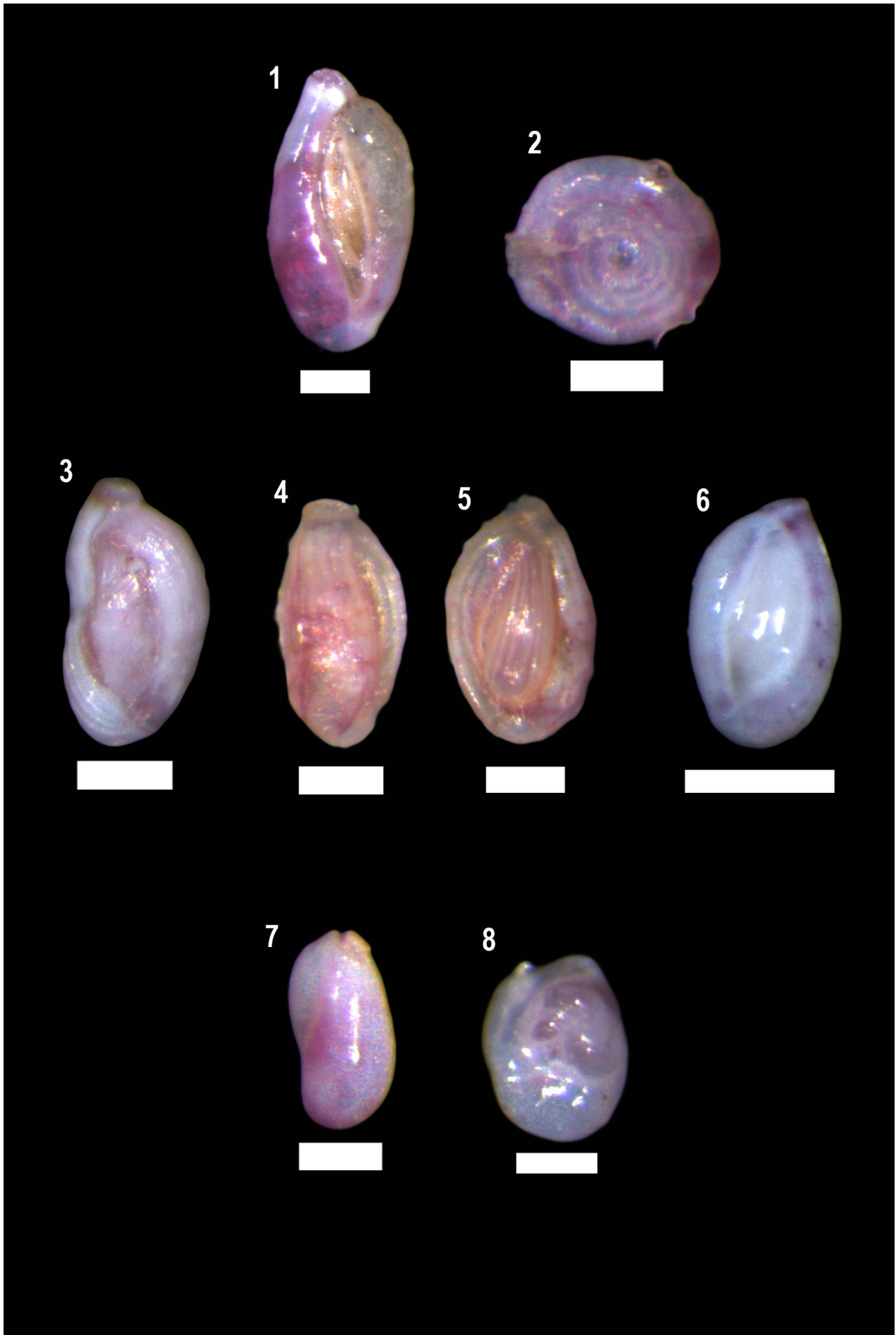
Figs. 3–5 *Quinqueloculina jugosa* (Cushman) Cushman 1944

Fig. 6 *Quinqueloculina seminula* (Linné) Linné, 1758

Figs. 7–8 Miliolid undetermined



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*

**Plate 3 Living foraminifera**

Figs. 1–4      *Ammonia beccarii* agg (Linné) Linné, 1758 (Variants included in this taxon)

Fig. 1: *Ammonia tepida* spiral view

Fig. 2: *Ammonia tepida* umbilical view

Fig. 3: *Ammonia tepida* spiral view

Fig. 4: *Ammonia tepida* umbilical view

Fig. 5      *Bolivinelina pseudopunctata* (Höglund) Höglund, 1947

Figs. 6–7      *Bolivina subaenariensis* (Cushman) Cushman, 1922

Fig. 6: general view

Fig. 7: general view

Fig. 8      *Brizalina spathulata* (Williamson) Williamson, 1858

Fig. 9      *Bolivina striatula* (Cushman)

Figs. 10–11      *Criboelphidium excavatum* (Terquem) Terquem, 1875

Fig. 10: general view

Fig. 11: general view

Fig. 12      *Criboelphidium oceanensis* (d'Orbigny) d'Orbigny, 1826

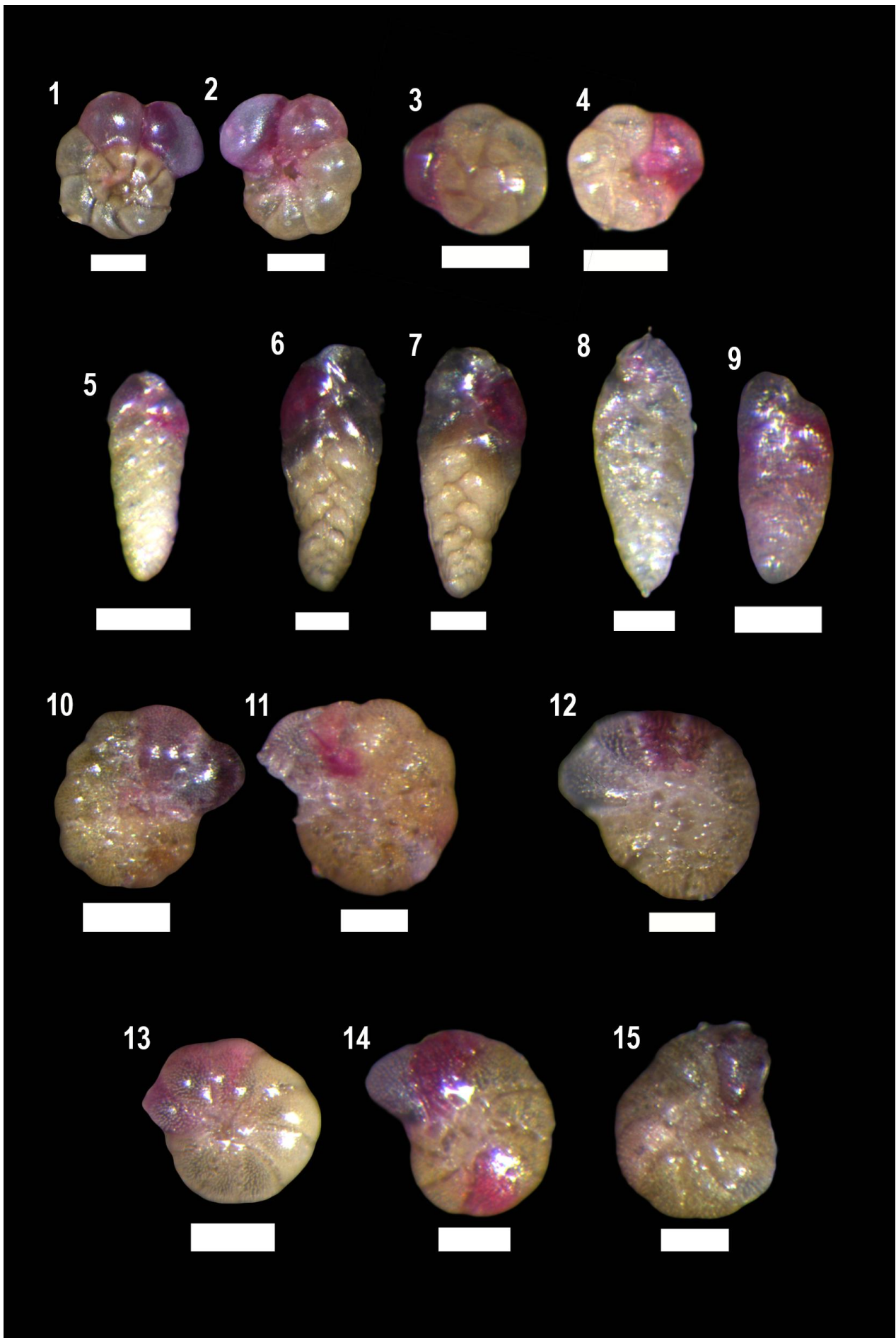
Figs. 13–15      *Criboelphidium selseyensis* (Heron-Allen and Earland) Heron-Allen and Earland,  
1911

Fig. 13: general view (*C. cf. selseyensis*)

Fig. 14: general view

Fig. 15: general view

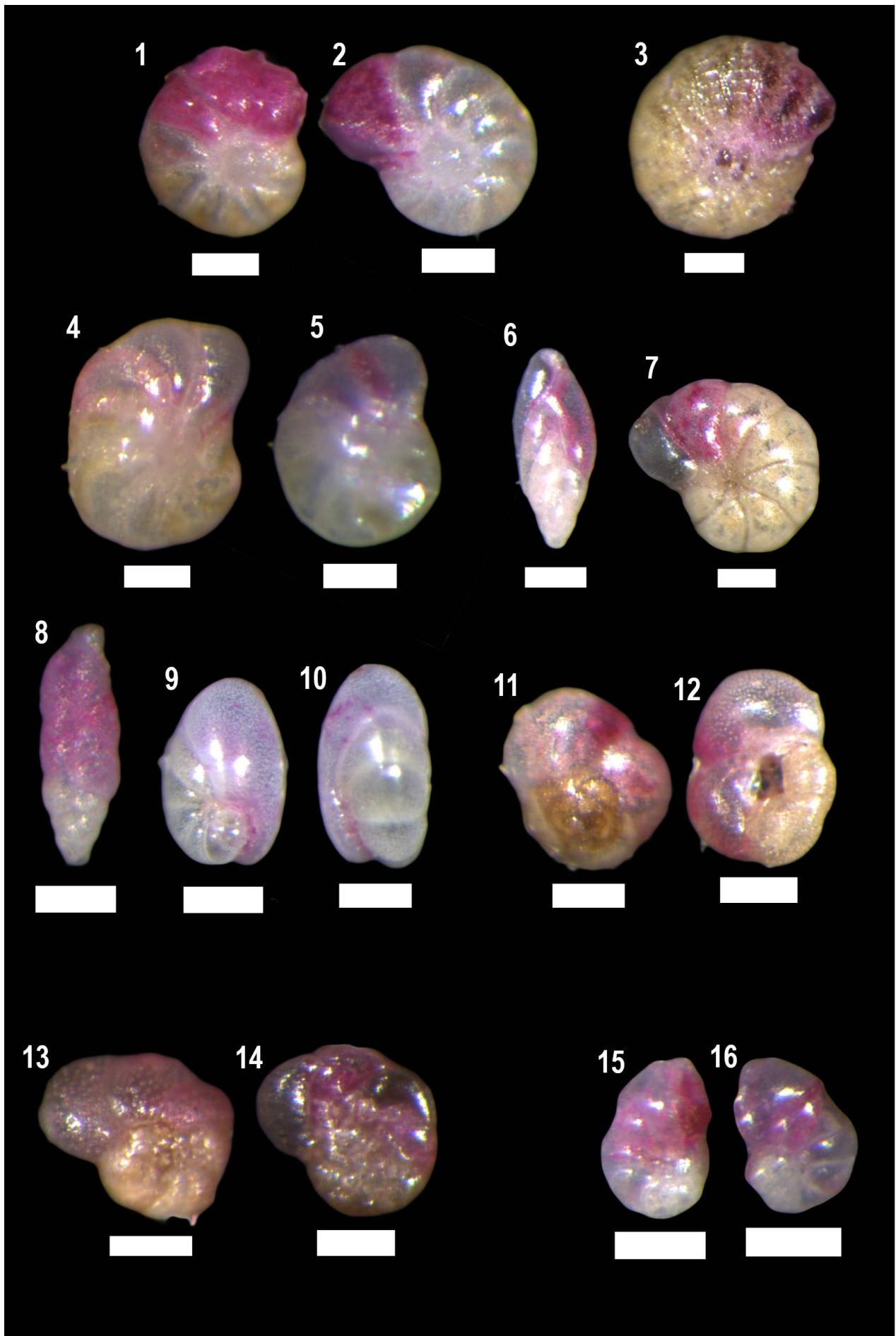
*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta***Plate 4 Living foraminifera**

- Figs. 1–2      *Criboelphidium* sp.1  
Fig. 1: general view  
Fig. 2: general view
- Fig. 3      *Criboelphidium williamsoni* (Haynes) Haynes, 1973
- Figs. 4–5      *Elphidium advenum* (Cushman) Cushman, 1922  
Fig. 4: general view  
Fig. 5: general view
- Fig. 6      *Fursenkoina* cf. *fusiformis* (Williamson) Williamson, 1858
- Fig. 7      *Haynesina germanica* (Ehrenberg) Ehrenberg, 1840
- Fig. 8      *Hopkinsina pacifica* Cushman, 1933
- Figs. 9–10      *Nonionella opima* Cushman, 1947  
Fig. 9: general view  
Fig. 10: general view
- Figs. 11–12      *Rosalina globularis* d'Orbigny, 1826  
Fig. 11: dorsal view  
Fig. 12: ventral view
- Figs. 13–14      *Trichohyalus aguayoi* (Bermudez) Bermudez, 1935  
Fig. 13: spiral view  
Fig. 14: umbilical view
- Figs. 15–16      *Nonionella atlantica* Cushman, 1947  
Fig. 15: general view  
Fig. 16: general view

*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta***Plate 5 Dead foraminifera**

Figs. 1–2      *Ammosphaeroidina* sp.1

Fig. 1: general view

Fig. 2: general view

Fig. 3      *Ammotium* cf. *salsum* (Cushman and Brönniman) Cushman and Brönniman, 1948

Fig. 4      *Eggerelloides scaber* (Williamson) Williamson, 1858

Figs. 5–7      *Haplophragmoides wilberti* Anderson, 1953

Fig. 5: general view

Fig. 6: general view

Fig. 7: edge view

Figs. 8–9      *Jadammina macrescens* (Brady) Brady, 1870

Fig. 8: umbilical view

Fig. 9: spiral view

Fig. 10      *Miliammina fusca* (Brady) Brady, 1870

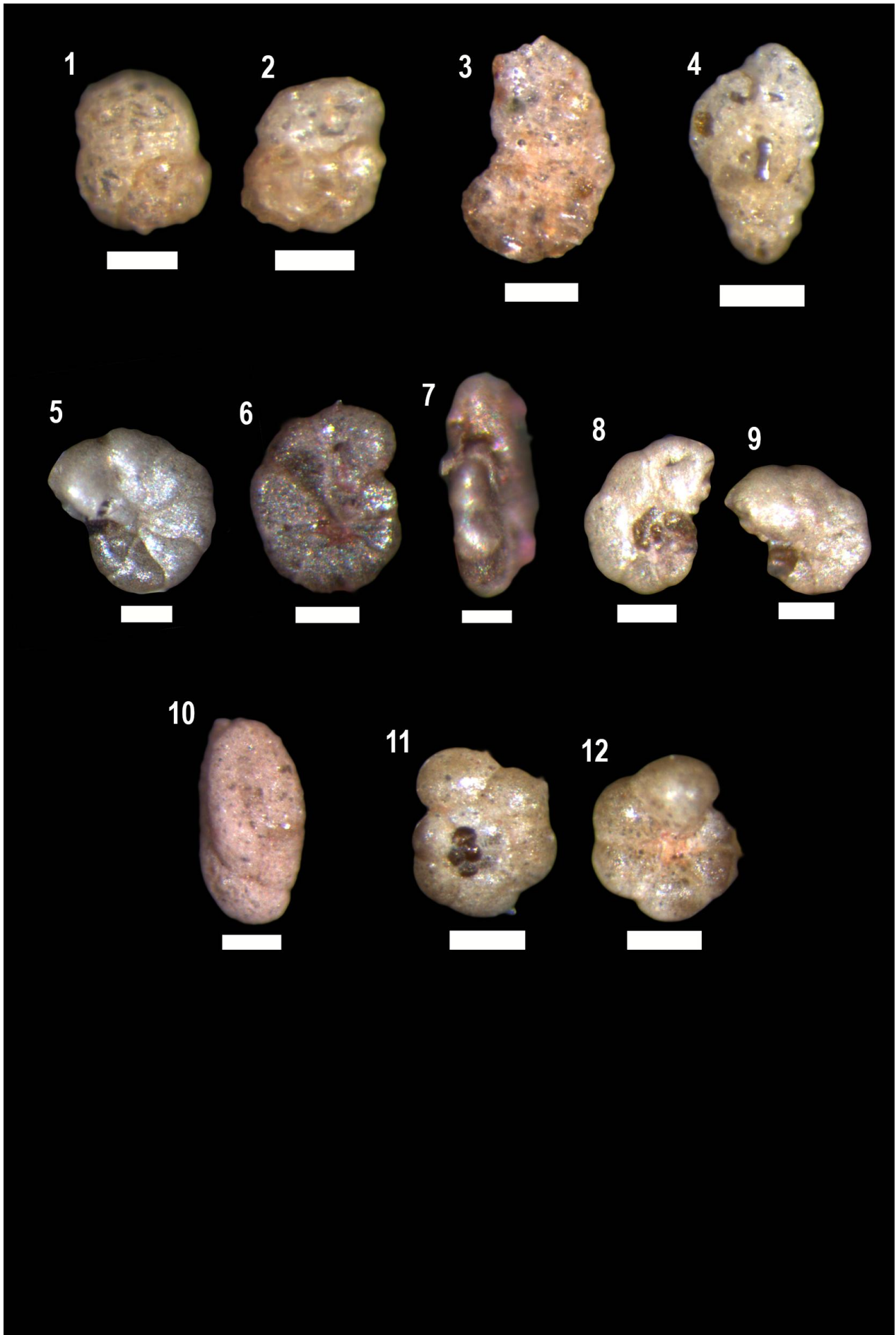
Figs. 11–12      *Trochammina inflata* (Montagu) Montagu, 1808

Fig. 11: spiral view

Fig. 12: umbilical view



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta***Plate 6 Dead foraminifera**

Fig. 1            *Cornuspira incerta* (d'Orbigny) d'Orbigny, 1939

Figs. 3–4        *Quinqueloculina seminula* (Linné) Linné, 1758

Fig. 3:

Fig. 4:

Figs. 4–5        Miliolid undetermined

Figs. 6–7        *Quinqueloculina seminula* (Linné) Linné, 1758

Fig. 6: general view, pyritized test

Fig. 7: general view, pyritized test

Figs. 8–9        *Quinqueloculina stelligera* Schlumberger, 1893

Fig. 8: general view

Fig. 9: oblique view

Figs. 10–11     *Triloculina dubia* d'Orbigny, 1826

Fig. 10: general view

Fig. 11: general view

Figs. 12–13     *Triloculina* sp. 1

Fig. 12: general view

Fig. 13: aperture



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*

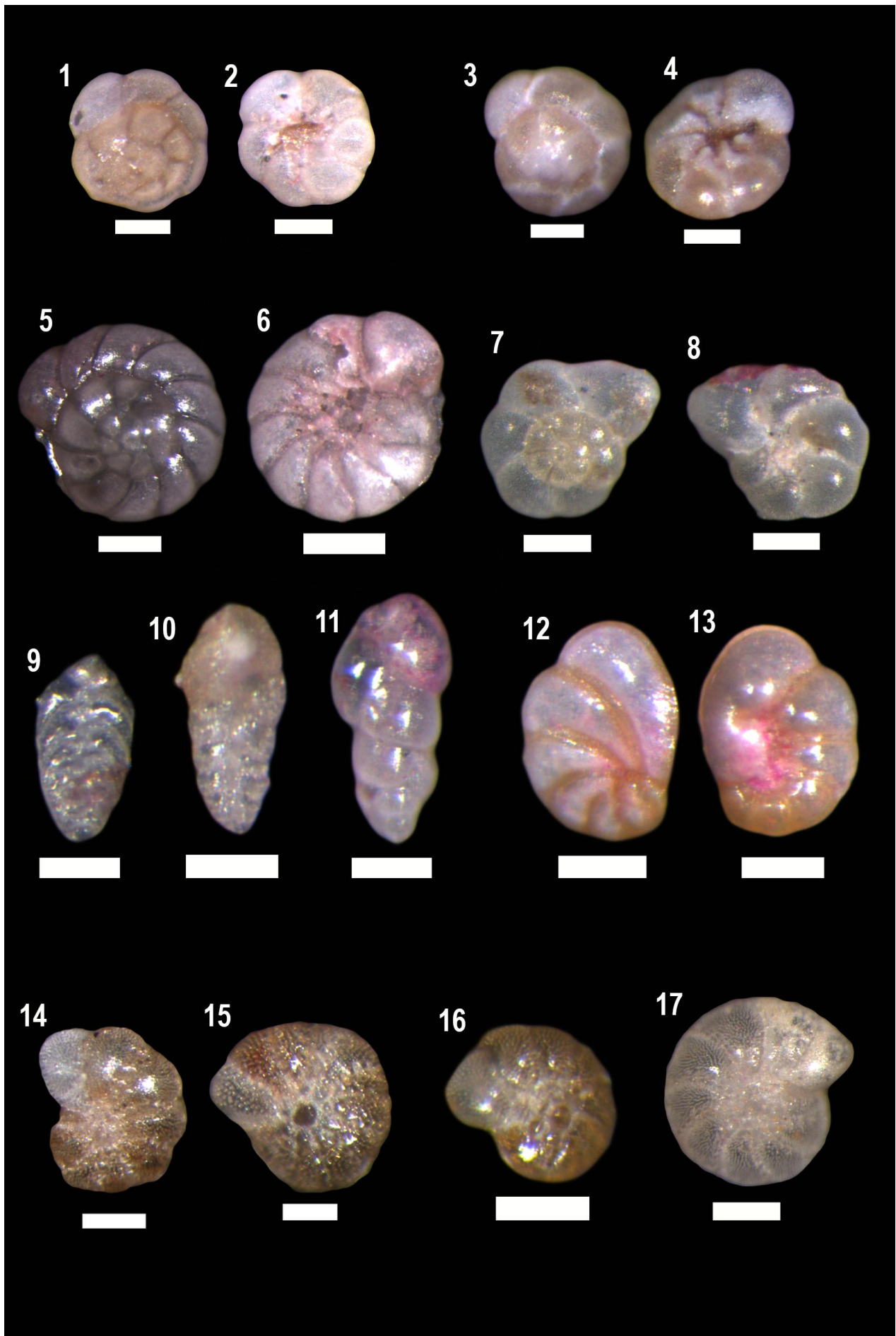


*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*

**Plate 7 Dead foraminifera**

- Figs. 1–6      *Ammonia beccarii* agg Linné, 1978 (Variants included in this taxon)
- Fig. 1: *Ammonia tepida*, spiral view
- Fig. 2: *Ammonia tepida*, umbilical view
- Fig. 3: *Ammonia tepida*, spiral view
- Fig. 4: *Ammonia tepida*, umbilical view
- Fig. 5: *Ammonia beccarii*, spiral view
- Fig. 6: *Ammonia beccarii*, umbilical view
- Figs. 7–8      *Aubignyna perlucida* (Heron-Allen and Earland) Heron-Allen and Earland, 1913
- Fig. 7: spiral view
- Fig. 8: umbilical view
- Fig. 9          *Bolivina dilatata* Reuss, 1850
- Fig. 10        *Brizalina variabilis* (Williamson) Williamson, 1859
- Fig. 11        *Bulimina gibba* Fornasini, 1902
- Figs. 12–13    *Cancris auricula* (Fichtel and Moll) Fichtel and Moll, 1798
- Fig. 14        *Criboelphidium excavatum* (Terquem) Terquem, 1875
- Fig. 15        *Criboelphidium oceanensis* (d'Orbigny) d'Orbigny, 1826
- Fig. 16        *Criboelphidium* cf. *poeyanum* (d'Orbigny) d'Orbigny, 1839
- Fig. 17        *Criboelphidium selseyensis* (Heron-Allen and Earland) Heron-Allen and Earland, 1911

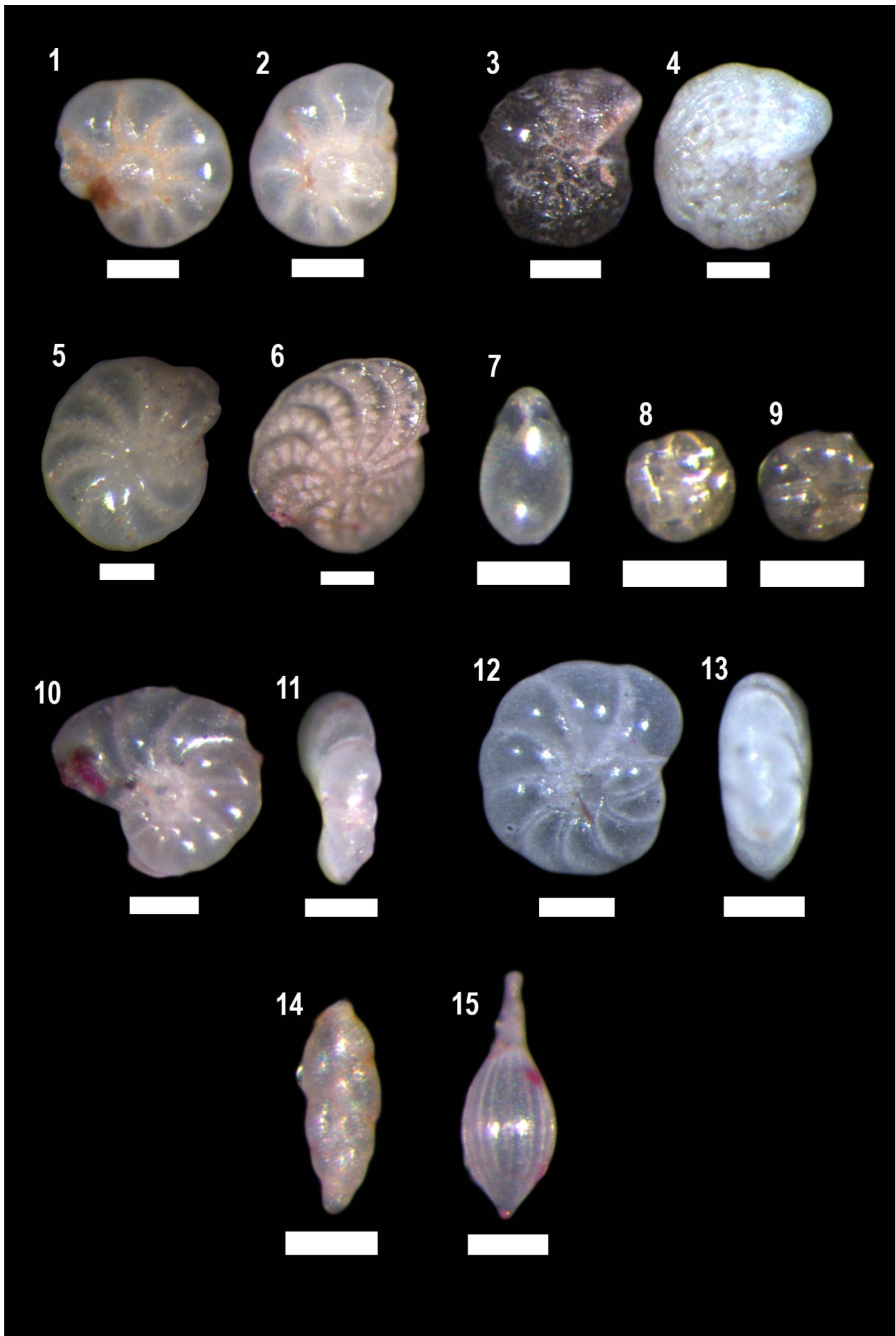
*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta***Plate 8 Dead foraminifera**

- Figs. 1–2      *Criboelphidium* sp.1
- Figs. 3–4      *Criboelphidium williamsoni* (Haynes) Haynes, 1973
- Fig. 3: general view, pyritized test
- Fig. 4: general view
- Fig. 5      *Elphidium advenum* (Cushman) Cushman, 1922
- Fig. 6      *Elphidium crispum* (Linné) Linné, 1758
- Fig. 7      *Fissurina lucida* (Williamson) Williamson, 1858
- Figs. 8–9      *Gavelinopsis praegeri* (Heron-Allen and Earland) Heron-Allen and Earland, 1913
- Figs. 10–11      *Haynesina depressula* (Water and Jacob) Walker and Jacob, 1798
- Fig. 10: dorsal view
- Fig. 11: edge view
- Figs. 12–13      *Haynesina germanica* (Ehrenberg) Ehrenberg, 1840
- Fig. 12: dorsal view
- Fig. 13: edge view
- Fig. 14      *Hopkinsina pacifica* Cushman, 1933
- Fig. 15      *Lagena sulcata* (Walter and Jacob) Walter and Jacob, 1798

*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta***Plate 9 Dead foraminifera**

Figs. 1–2     *Rosalina globularis* d'Orbigny, 1826

Fig. 1: spiral view

Fig. 2: umbilical view

Figs. 3–5     *Rosalina irregularis* (Rhumbler) Rhumbler, 1906

Fig. 3: spiral view

Fig. 4: edge view

Fig. 5: umbilical view

Figs. 6–7     *Trichohyalus aguayoi* (Bermudez) Bermudez, 1935

Fig. 6: spiral view

Fig. 7: umbilical view

Figs. 8–9     *Valvulineria bradyana* (Fornasini) Fornasini, 1899

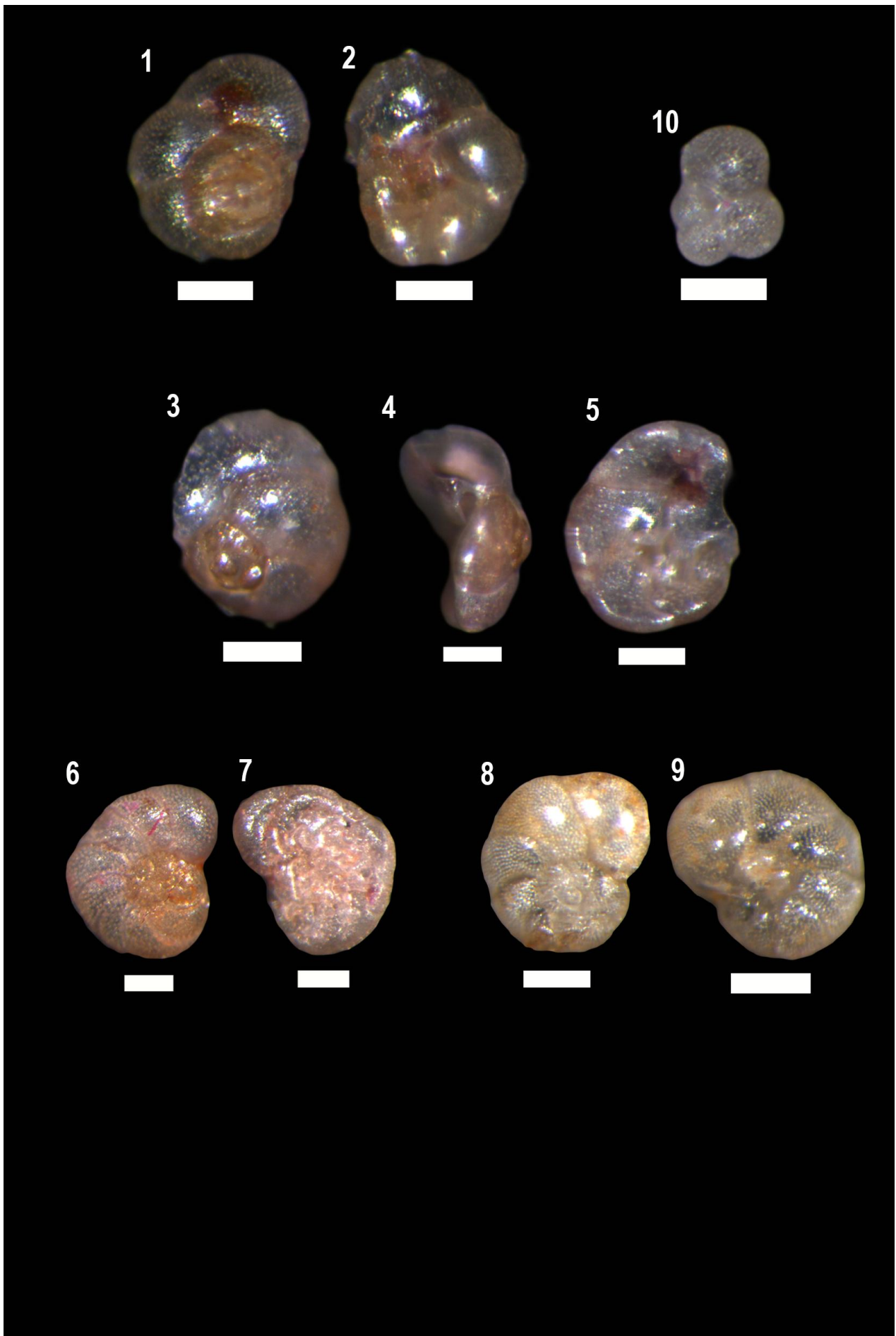
Fig. 8: spiral view

Fig. 9: umbilical view

Fig. 10     Planktonic test (cf. *Globigerina* sp.)



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*



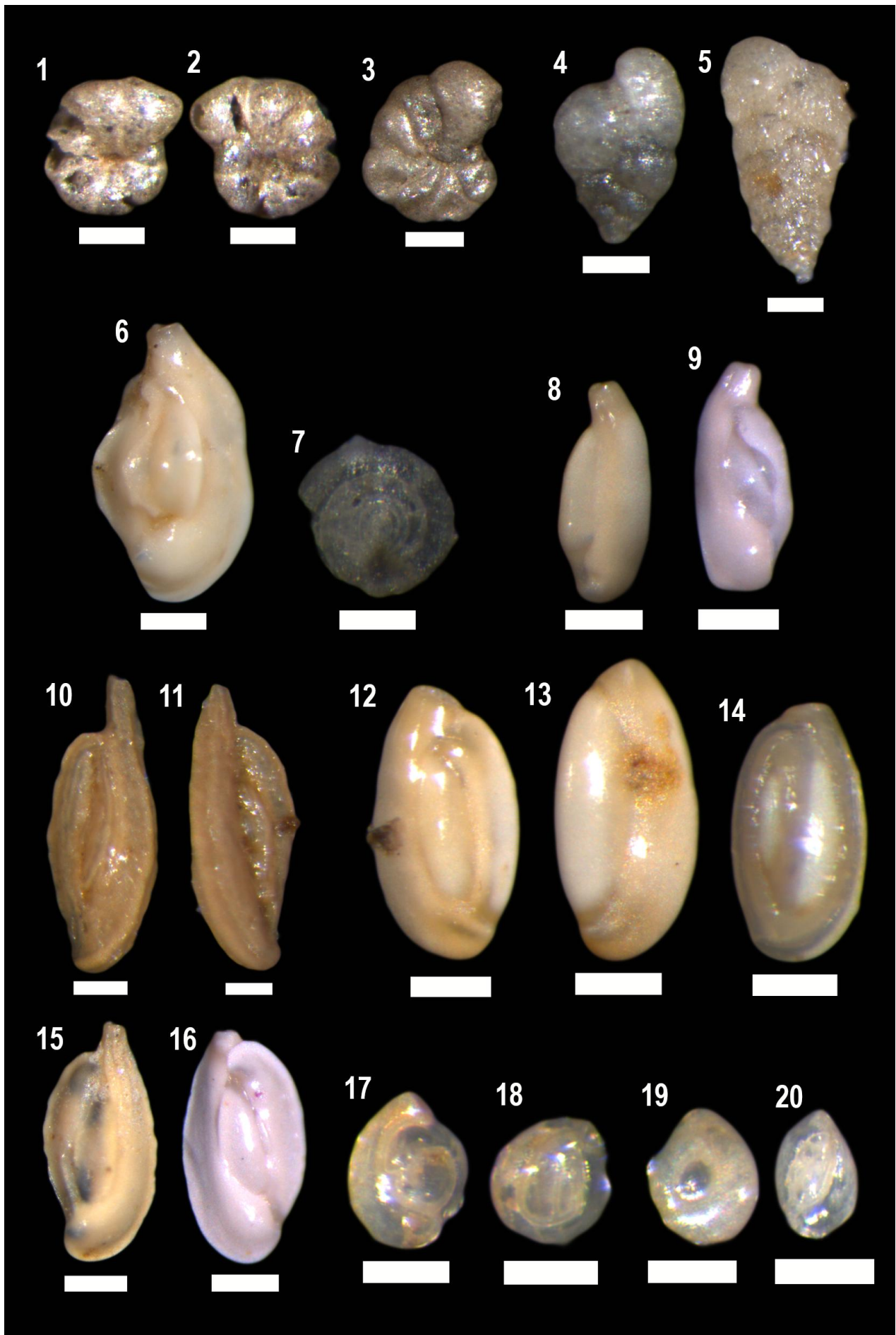
## Appendix II: Benthic foraminiferal assemblages of the Ebro Delta

### Plate 10 Fossil foraminifera

- Figs. 1–3      *Haplophragmoides wilberti* Anderson, 1953  
Fig. 1: dorsal view, Olles core (15–20 cm depth)  
Fig. 2: dorsal view, Olles core (15–20 cm depth)  
Fig. 3: dorsal view, Olles core (15–20 cm depth)
- Figs. 4–5      *Textularia cf. calva* Lalicker, 1935  
Fig. 4: general view, Sant Jaume borehole (20.71 m depth)  
Fig. 5: general view, Garxal core (50–55 cm depth)
- Fig. 6      *Adelosina laevigata* (d'Orbigny) Walker and Jacob, 1798  
Sant Jaume borehole (18.33 m depth)
- Fig. 7      *Cornuspira incerta* (d'Orbigny) d'Orbigny, 1939  
Sant Jaume borehole (10.72 m depth)
- Figs. 8–9      *Quinqueloculina depressa* d'Orbigny, 1852  
Fig. 8: general view, Sant Jaume borehole (20.81 m depth)  
Fig. 9: general view, Sant Jaume borehole (20.81 m depth)
- Figs. 10–11      *Quinqueloculina longirostra* d'Orbigny, 1826  
Fig. 10: general view, Sant Jaume borehole (15.10 m depth)  
Fig. 11: general view, Sant Jaume borehole (20.91 m depth)
- Figs. 12–13      *Quinqueloculina seminula* (Linné) Linné, 1758  
Fig. 12: general view, Sant Jaume borehole (19.60 m depth)  
Fig. 13: general view, Sant Jaume borehole (19.60 m depth)
- Fig. 14      *Quinqueloculina stelligera* Schlumberger, 1893  
Sant Jaume borehole (18.53 m depth)
- Figs. 15–16      *Triloculina dubia* d'Orbigny, 1826  
Fig. 15: general view, Alfacs core (35–40 cm depth)  
Fig. 16: general view, Sant Jaume borehole (29.91 m depth)
- Figs. 17–20      Miliolid undetermined  
Fig. 17: general view, Sant Jaume borehole (13.80 m depth)  
Fig. 18: general view, Sant Jaume borehole (13.80 m depth)  
Fig. 19: general view, Sant Jaume borehole (20.42 m depth)  
Fig. 20: general view, Sant Jaume borehole (20.42 m depth)



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*

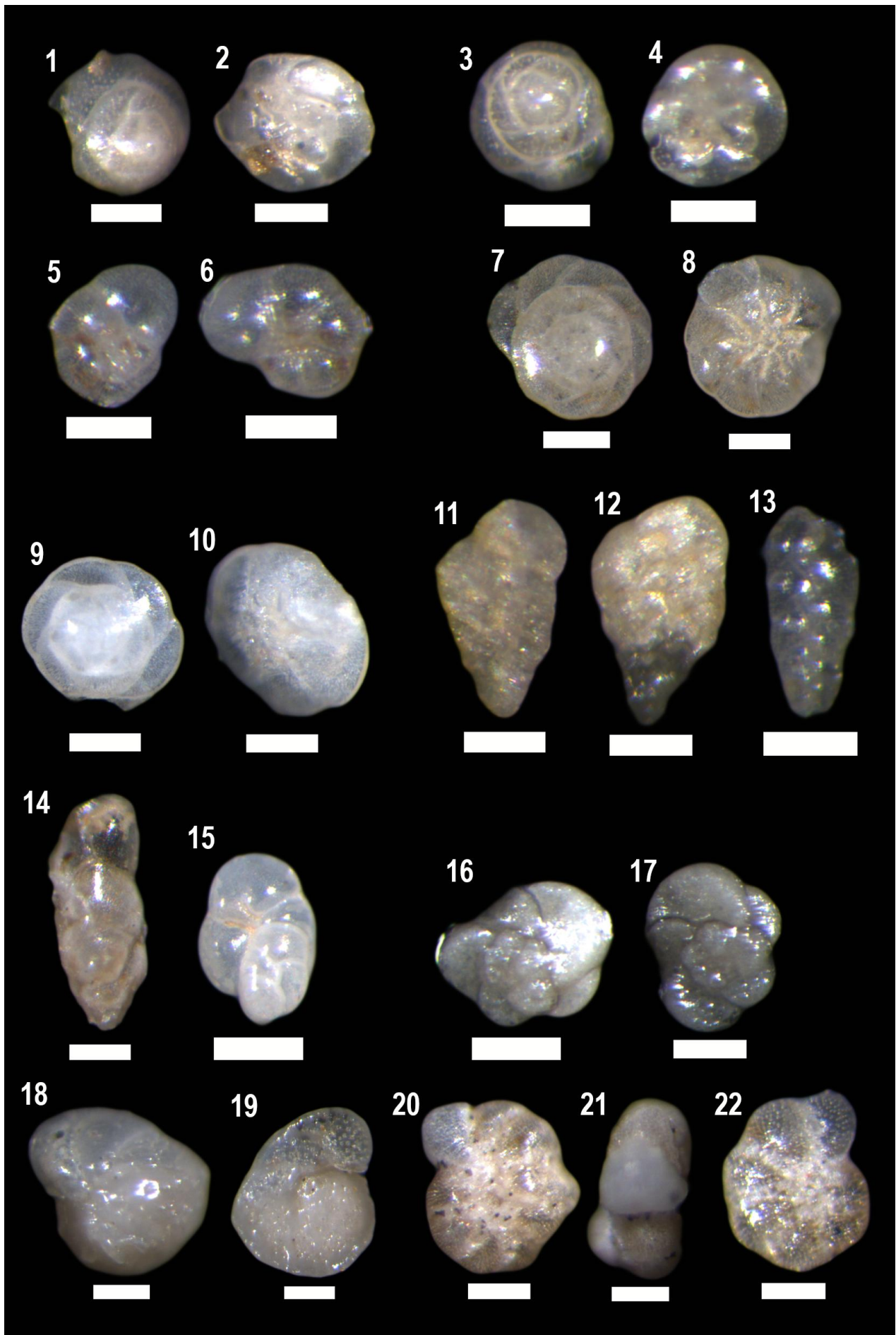


*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*

**Plate 11 Fossil foraminifera**

- Figs. 1–4      *Asterigerinata mamilla* (Williamson) Williamson, 1858  
Fig. 1: dorsal view, Olles core (40–45 cm depth)  
Fig. 2: ventral view, Olles core (40–45 cm depth)  
Fig. 3: dorsal view, Sant Jaume borehole (12.45 m depth)  
Fig. 4: ventral view, Sant Jaume borehole (12.45 m depth)
- Figs. 5–6      *Aubignyna perlucida* (Heron-Allen and Earland) Heron-Allen and Earland, 1913  
Fig. 5: spiral view, Sant Jaume borehole (20.71 m depth)  
Fig. 6: umbilical view, Sant Jaume borehole (20.71 m depth)
- Figs. 7–10      *Buccella granulata* (di Napoli Alliata) di Napoli Alliata, 1952  
Fig. 7: spiral view, Sant Jaume borehole (12.45 m depth)  
Fig. 8: umbilical view, Sant Jaume borehole (12.45 m depth)  
Fig. 9: spiral view, Alfacs core (35–40 cm depth)  
Fig. 10: umbilical view, Alfacs core (35–40 cm depth)
- Figs. 11–12      *Bolivina pseudoplicata* Heron-Allen and Earland, 1930  
Fig. 11: general view, Sant Jaume borehole (10.32 m depth)  
Fig. 12: general view, Sant Jaume borehole (14.70 m depth)
- Fig. 13      *Brizalina variabilis* (Williamson) Williamson, 1859  
Sant Jaume borehole (14.40 m depth)
- Fig. 14      *Bulimina gibba* Fornasini, 1902  
Sant Jaume borehole (18.33 m depth)
- Fig. 15      *Cassulina obtusa* Williamson, 1858  
Sant Jaume borehole (19.40 m depth)
- Figs. 16–19      *Cibicides lobatulus* (Walker and Jacob) Walker and Jacob, 1798  
Fig. 16: ventral view, Garxal core (20–25 m depth)  
Fig. 17: ventral view, Garxal core (20–25 m depth)  
Fig. 18: dorsal view, Garxal core (60–65 cm depth)  
Fig. 19: ventral view, Garxal core (60–65 cm depth)
- Figs. 20–22      *Criboelphidium excavatum* (Terquem) Terquem, 1875  
Fig. 20: general view, Garxal core (25–30 cm depth)  
Fig. 21: edge view, Garxal core (25–30 cm depth)  
Fig. 22: general view, Garxal core (25–30 cm depth)

*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*

**Plate 12 Fossil foraminifera**

- Figs. 1–2      *Criboelphidium cf. poeyanum* (d'Orbigny) d'Orbigny, 1839  
Fig. 1: general view, Sant Jaume borehole (15.10 m depth)  
Fig. 2: general view, Garxal core (60–65 cm depth)
- Figs. 3–10     *Criboelphidium selseyensis* (Heron-Allen and Earland) Heron-Allen and Earland, 1911  
Fig. 3: general view, Sant Jaume borehole (15.10 m depth)  
Fig. 4: edge view, Sant Jaume borehole (15.10 m depth)  
Fig. 5: general view, Alfacs core (35–40 cm depth)  
Fig. 6: general view, Alfacs core (35–40 cm depth)  
Fig. 7: general view, Alfacs core (35–40 cm depth)  
Fig. 8: general view, Alfacs core (35–40 cm depth)  
Fig. 9: general view, Garxal core (55–60 cm depth)  
Fig. 10: general view, Garxal core (55–60 cm depth)
- Figs. 11–12    *Criboelphidium* sp.1  
Fig. 11: general view, Alfacs core (32–35 cm depth)  
Fig. 12: edge view, Alfacs core (32–35 cm depth)
- Fig. 13        *Elphidium crispum* (Linné) Linné, 1758  
Fig. 13: oblique view, Sant Jaume borehole (18.53 m depth)
- Figs. 14–15    *Fissurina marginata* (Montagu) Montagu, 1803  
Fig. 14: general view, Sant Jaume borehole (20.20 m depth)  
Fig. 15: general view, Olles core (40–45 cm depth)
- Fig. 16        *Fursenkoina schreibersiana* (Czjzek) Czjzek, 1848  
Fig. 16: general view, Sant Jaume borehole (9.88 m depth)
- Figs. 17–18    *Gavelinopsis praegeri* (Heron-Allen and Earland) Heron-Allen and Earland, 1913  
Fig. 17: spiral view, Sant Jaume borehole (20.71 m depth)  
Fig. 18: umbilical view, Sant Jaume borehole (20.71 m depth)
- Figs. 19–21    *Haynesina depressula* (Water and Jacob) Walker and Jacob, 1798  
Fig. 19: general view, Alfacs core (32–35 cm depth)  
Fig. 20: general view, Alfacs core (32–35 cm depth)  
Fig. 21: edge view, Alfacs core (32–35 cm depth)
- Figs. 22–23    *Haynesina germanica* (Ehrenberg) Ehrenberg, 1840  
Fig. 22: general view, Olles core (30–35 cm depth)  
Fig. 23: edge view, Olles core (30–35 cm depth)



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta*



*Appendix II: Benthic foraminiferal assemblages of the Ebro Delta***Plate 13 Fossil foraminifera**

- Fig. 1 *Lagena cf. semistriata* (Williamson) Williamson, 1848  
Sant Jaume borehole (20.40 m depth)
- Fig. 2 *Lagena sulcata* (Walter and Jacob) Walter and Jacob, 1798  
Sant Jaume borehole (9.48 m depth)
- Figs. 3–5 *Nonionoides boueanum* (d'Orbigny) d'Orbigny, 1846  
Fig. 3: general view, Carlet borehole (12.47 m depth)  
Fig. 4: edge view, Carlet borehole (12.47 m depth)  
Fig. 5: general view, Carlet borehole (12.47 m depth)
- Figs. 6–7 *Nonionella opima* Cushman, 1947  
Fig. 6: general view, Sant Jaume borehole (17.11 m depth)  
Fig. 7: general view, Sant Jaume borehole (19.40 m depth)
- Figs. 8–9 *Patellina corrugata* Williamson, 1858  
Fig. 8: general view, Sant Jaume borehole (20.20 m depth)  
Fig. 9: general view, Sant Jaume borehole (20.20 m depth)
- Figs. 10–11 *Rectuvigerina compressa* (Cushman) Cushman, 1925  
Fig. 10: general view, Sant Jaume borehole (19.40 m depth)  
Fig. 11: general view, Sant Jaume borehole (20.71 m depth)
- Figs. 12–15 *Rosalina anomala* Terquem, 1875  
Fig. 12: ventral view, Sant Jaume borehole (19.80 m depth)  
Fig. 13: dorsal view, Sant Jaume borehole (19.80 m depth)  
Fig. 14: dorsal view, Sant Jaume borehole (20.40 m depth)  
Fig. 15: ventral view, Sant Jaume borehole (20.40 m depth)
- Figs. 16–19 *Rosalina irregularis* (Rhumbler) Rhumbler, 1906  
Fig. 16: dorsal view, Sant Jaume borehole (21.71 m depth)  
Fig. 17: ventral view, Sant Jaume borehole (21.71 m depth)  
Fig. 18: ventral view, Sant Jaume borehole (10.72 m depth)  
Fig. 19: dorsal view, Sant Jaume borehole (21.91 m depth)
- Figs. 20–21 *Svratkina* sp.1  
Fig. 20: dorsal view, Sant Jaume borehole (16.51 m depth)  
Fig. 21: ventral view, Sant Jaume borehole (16.51 m depth)
- Figs. 22–25 *Valvulineria bradyana* (Fornasini) Fornasini, 1899  
Fig. 22: dorsal view, Sant Jaume borehole (20.71 m depth)  
Fig. 23: ventral view, Sant Jaume borehole (20.71 m depth)  
Fig. 24: dorsal view, Sant Jaume borehole (20.91 m depth)  
Fig. 25: ventral view, Sant Jaume borehole (20.91 m depth)

