Taxonomy, ecology and biogeographical trends of dominant benthic foraminifera species from an Atlantic-Mediterranean estuary (the Guadiana, southeast Portugal)

Sarita Graça Camacho, Delminda Maria de Jesus Moura, Simon Connor, David B Scott, and Tomasz Boski

ABSTRACT

This study analyses the taxonomy, ecology and biogeography of the species of benthic foraminifera living on the intertidal margins of the Guadiana Estuary (SE Portugal, SW Spain). Of the 54 taxa identified during sampling campaigns in winter and summer, 49 are systematically listed and illustrated by scanning electron microscope (SEM) photographs. *Ammonia* spp. were the most ubiquitous calcareous taxa in both seasons. Morphological analysis and SEM images suggested three distinct morphotypes of the genus *Ammonia*, two of which proved to be *Ammonia aberdoveyensis* on the basis of partial rRNA analyses. *Jadammina macrescens* and *Miliammina fusca* were the most ubiquitous agglutinated taxa in the estuary. *Jadammina macrescens* dominates the upper-marsh zones almost exclusively, occurring at very high densities. *Ammonia* spp. are the most abundant in the low-marsh and tidal-flats of the lower reaches of the Guadiana Estuary, but are widespread throughout the estuary, especially during summer when environmental conditions favor their proliferation. *Miliammina fusca* dominates the sparsely vegetated low-marsh and tidal-flat zones of the upper reaches, where it is associated with calcareous species. Due to its geographical position, the Guadiana system shares characteristics of both Atlantic and Mediterranean estuaries. This is reflected in the foraminiferal assemblages, with a dominance of thermophilous species and an ecological zonation typical of the Mediterranean climatic zone.

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INTRODUCTION

Foraminifera are single-celled organisms that possess a hard test, which often remains in the sediment where it may fossilize. Foraminifera were first described and illustrated in the sixteenth century but only studied systematically in the nineteenth century following the remarkable voyage of HMS Challenger (Lowe and Walker, 1997). Their usefulness in stratigraphy was gradually realized, and they attained a fundamental role in applied science as stratigraphical index fossils (Albani et al., 2001). Widely used in petroleum assessment, foraminifera are also important in paleoclimatic, paleo-sea-level, paleo-depth and paleoceanographic studies and in age determinations using oxygen isotopes (Albani et al., 2001). Stratigraphically, foraminifera appear in the Early Cambrian at about the same time as the metazoans with skeletons (Pawlowski et al., 2003), diversifying into thousands of species adapted to all marine and coastal environments, from the most superficial to the greatest oceanic depths (Scott et al., 2001). Currently, around 6800 species of foraminifera are estimated to exist (Hayward et al., 2014).

Accurate taxonomy is essential for classifying the fossil species and to create reliable environmental analogies. The test is the most commonly studied element of foraminifera, as classification relies essentially on morphological characteristics (Debenay et al., 1996). However, the taxonomic value of those characteristics is questionable due to the influence of environmental factors on the morphology of foraminiferal tests, which makes the distinction between ecophenotypes and species difficult (Holzmann and Pawlowski, 1997). These difficulties are particularly problematic in the case of species of cosmopolitan distribution and with high morphological variability, such as the genera *Ammonia* (Hayward et al., 2004) and *Elphidium* (Feyling-Hanssen, 1972; Miller et al., 1982). The high morphological variability of *Ammonia,* for instance, rendered its status uncertain and controversial (Pawlowski et al., 1995; Holzmann and Pawlowski, 1997; Debenay et al., 1998a; Holzmann et al., 1998; Langer and Leppig, 2000) until molecular studies were used to better under-

stand its taxonomy (Hayward et al., 2004). More than 40 species and subspecies (or varieties) of *Ammonia* have been described worldwide, and at least 30 species were expected to be recognizable by molecular techniques (Hayward et al., 2004). The application of molecular techniques has brought new insights into foraminiferal taxonomy. Pawlowski et al. (1994) demonstrated that the analysis of RNA ribosomal sequences can be applied in the identification of foraminiferal species, providing a new taxonomic criterion, independent of the morphological characteristics of the test. Molecular analysis also enables an evaluation of the ecological significance of various morphological characteristics and the determination of intraspecific morphological variability (Pawlowski et al., 1994). Since 1994, molecular techniques improved and became more accessible. Thus, is expected that taxonomic descriptions of new and/or modern species of foraminifera with controversial classifications include genetic data in addition to morphologic information.

Along with taxonomy, it is essential to study the living assemblages, their main features, life cycles and ecological tolerances in order to perform consistent and reliable paleo-interpretations (Calonge et al., 2001). In Portugal, most ecological studies based on estuarine foraminifera have been performed in order to establish modern databases through which fossil foraminiferal assemblages can be compared and interpreted (e.g., Fatela and Silva, 1990; Cearreta et al., 2002, 2007; Andrade et al., 2004; Moreno et al., 2005; Fatela et al., 2009; Leorri et al., 2010). Nevertheless, the resulting taxonomic data are very limited, with little systematic study and no molecular analysis. Recently, the seasonal and spatial patterns of live benthic foraminifera in intertidal margins of the Guadiana Estuary were studied (Camacho et al., 2015). That analysis lacked detailed taxonomical information and genetic data. In order to address these knowledge gaps, this study presents a photographic and systematic compendium of almost all species found in the estuary and provides preliminary genetic information on two of the most important taxa. These data, along with the ecology and bio-

geography of the main species, are expected to complement the previous study by Camacho et al. (2015) and contribute to a more robust taxonomic basis for foraminiferal identification.

Study area

From its headwaters located in Lagoas de Ruidera (1700 m altitude) in Spain, the Guadiana River runs 810 km until it reaches the Atlantic Ocean between the Portuguese town of Vila Real de Santo António and Spanish town of Ayamonte (Figure 1). The terminal 200-km stretch of the river follows a north-south course and sets the national border between the two countries (M.A., 1999). The estuarine system is characterized by semi-diurnal mesotidal regime (Morales et al., 2006), with tidal influence, in a physical sense, extending 44 km upstream to Pomarão (Barros and Candeias, 1998). The mean tidal range at the river mouth is approximately 2 m, reaching 3.4 m during spring tides (I.H., 2011). Its basin has Mediterranean climatic characteristics, with hot, dry summers, strong insolation and high evapotranspiration. The winters are relatively cold and continental in the upper reaches of the river and become milder downstream (M.A., 1999).

The Estuary includes a series of habitats of high ecological value, such as a rich wetland zone (saltmarshes, salt pans, tidal creeks and ponds), intertidal flats, barrier islands and sandy spits. The wetland is noteworthy for its halophytic saltmarsh communities (Ramsar, 2013), which carry out an essential role in the functioning and maintenance of a healthy ecosystem (Simonson, 2007) and have earned the estuary its status as a Natural Reserve in the Portuguese conservation network (ICNB, 2007).

METHODOLOGY

Sampling and Processing

During the two most contrasting seasons, i.e., winter (February and March) and summer (August), of the year 2010, 49 samples of the top 1 cm of surface sediment of the river's intertidal margins were collected in order to cover the environmental range of living benthic foraminiferal assemblages in the Guadiana Estuary. The sampling extended over 27 km, from the most upstream site located at Laranjeiras (LAR site) to the mouth of the river at Lagoa (LG site), covering the entire salinity gradient of the estuary (see Table 1, Appendix). In total, 11 sites were sampled, with the majority located on the right bank of the river

(Figure 1). In the middle and upper estuary, only one sample was collected per site due to the absence of saltmarsh zonation. In the lower estuary, where the environmental zonation is well-marked due to a more pronounced tidal range, three to four samples were collected along topographic profiles at each site, usually running perpendicular to the river course. These transects were placed according to the vertical zonation of halophytic vegetation, with the aim of sampling the distinct pedomorphic units, from unvegetated mudflats (permanently wet) to the higher levels of the marsh. Topographic profiles were surveyed in detail using a differential Global Positioning System (d-GPS) and a Trimble 5800 mobile unit (a Nikon DTM 310 Total Station was employed in places without a radio signal). Elevation was measured in relation to mean sea level (MSL) (datum 73). Samples were divided into upper marsh (collected at 1–2 meters above MSL), lower marsh (0–1 meters above MSL) and mud zone (-1–0 meters in relation to MSL). The salinity gradient was divided in three sectors: lower, middle and upper estuary (Figure 1) according to Boski et al. (2006).

At each sampling point, two pseudoreplicates were collected (replicates of the same sample) (Hurlbert, 1984) with the aim of avoiding the effect of patchiness (Debenay et al., 2006), which is the non-uniform distribution trend of benthic foraminiferal assemblages in shallow, marginal environments usually caused by asynchronous reproduction pulses (Buzas et al., 2002). Each pseudoreplicate was collected using small PVC cores of 15-cm length and 5-cm diameter, keeping the first cm of sediment (19.6 cc) for foraminiferal analysis. Samples for foraminifera, sediment texture and elemental composition analysis were collected during ebb time. Physico-chemical parameters of river water (salinity, temperature and dissolved oxygen) and the sediment (pH) were also measured (Camacho et al., 2014).

In the laboratory, 20 cc aliquots of the samples were separated and kept in a mixture of Rose Bengal and ethanol (2 g/l) for two days. After this period, samples were wet-sieved in a column of two sieves: 63 µm to retain the fraction for analysis and 500 µm to remove large organic debris. Samples with high organic content and with high number of foraminifera, both calcareous and agglutinated, were split into smaller aliquots using a wet splitter (Scott and Hermelin, 1993). Samples with few individuals, or with calcareous tests only, were dried and sprinkled into carbon tetrachloride to float off the tests. Whenever possible, 100 to 300
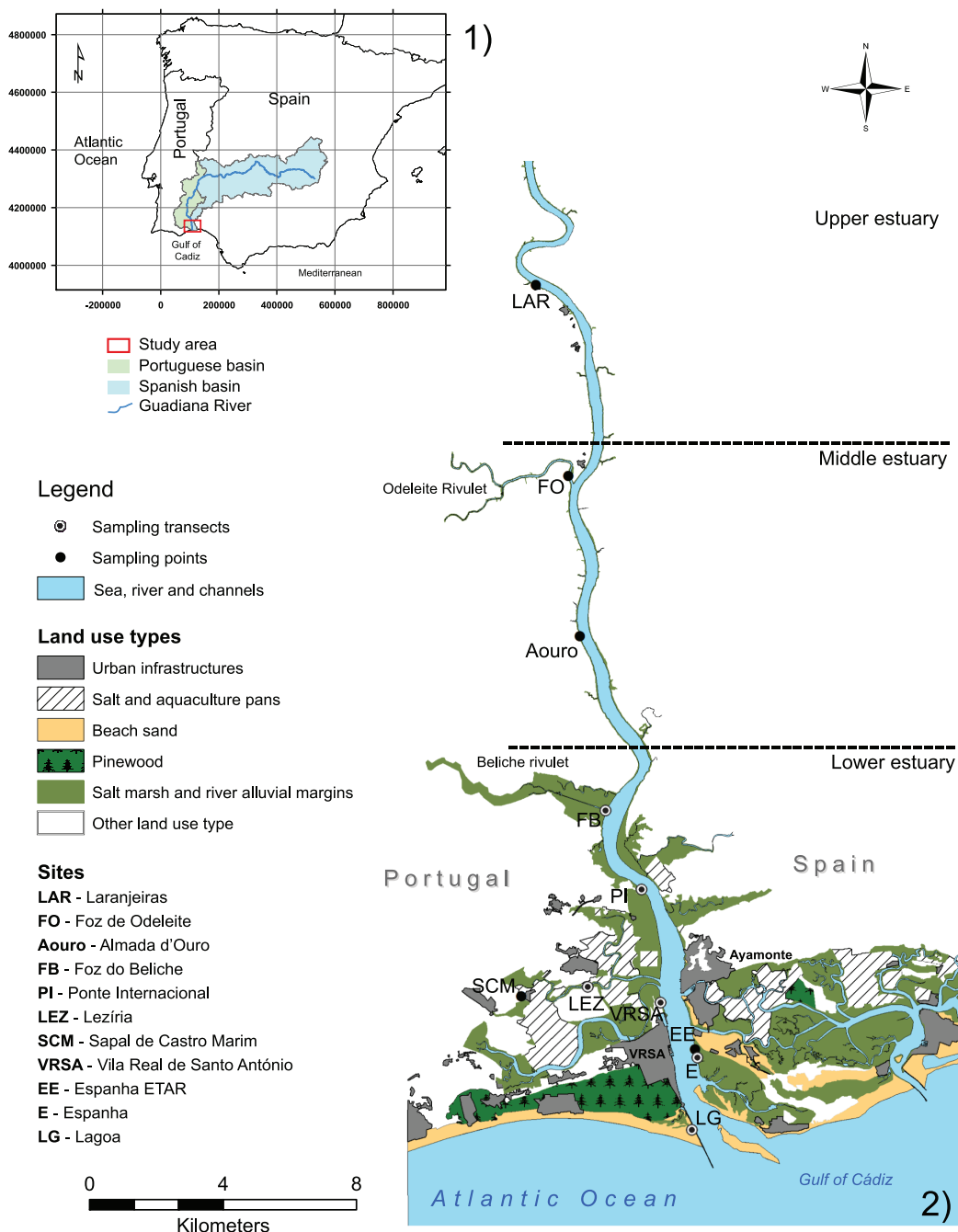
FIGURE 1. Location of the study area; 1) Geographical context of the Guadiana River basin in the Iberian Peninsula (Europe). Adapted from chguadiana.es (2012). Coordinate system: Datum ETRS89 UTM Zone 30N; 2) Study area: Map of the Guadiana Estuary with site locations.

living individuals were counted. Due to low numbers of stained individuals in some samples, an exceptional threshold of 48 living individuals was adopted for the purpose of statistical significance (see details in Camacho et al., 2015). Samples with fewer than 48 living individuals were not analyzed statistically (in grey in Tables 2 and 3, Appendix).

Identification and Classification

Forty-nine species were photographed using a scanning electron microscope (SEM), model JEOL JSM–5410, based at Huelva University and are presented in plates (Figures 2, 3, 4, 5).

Several guides were used for identification, especially Colom (1974), Loeblich and Tappan
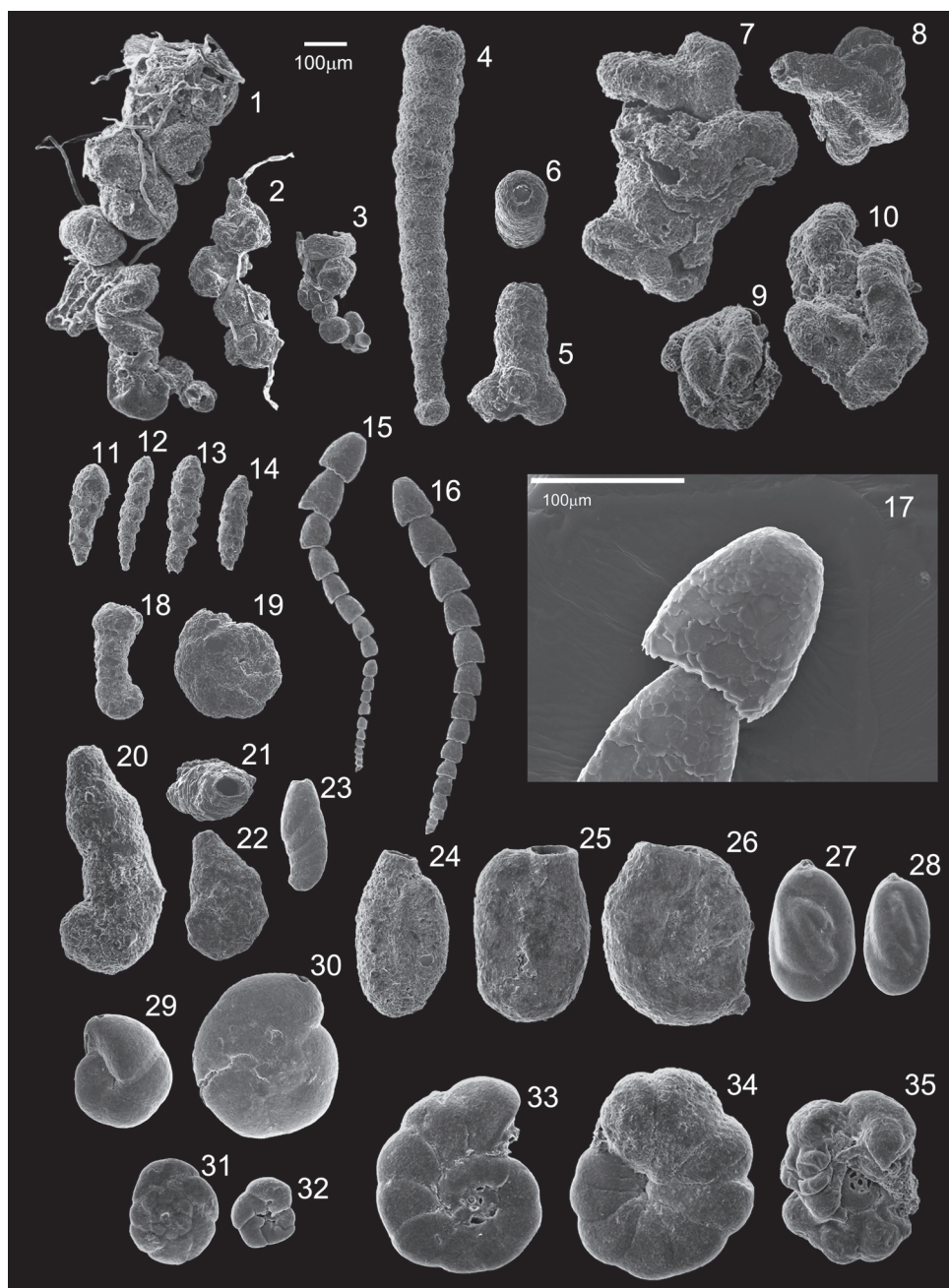
FIGURE 2. Scanning electron micrographs of the foraminifera specimens. Scale bar equals 100 μm. **1-3-** Three different specimens of *Polysaccammina ipohalina* Scott, 1976b, illustrating the differences in size and form. In all specimens it is possible to see attached organic matter; **4-5-** *Polysaccammina hyperhalina* Medioli, Scott, and Petrucci, 1983. **4-** complete specimen of *P. hyperhalina*; **5-** aperture view; **6-** specimen with several side branches; **7-10-** different sized specimens of *Ammovertellina* sp.; **11-14-** various specimens of *Reophax nana* Rhumbler, 1913; **15-17-** *Leptohalysis scottii* (Chaster, 1892); **15** and **16-** side view of two complete specimens; **17-** detail on the agglutination of the last chamber; **18-** complete specimen of *Ammobaculites exiguus* Cushman and Brönnimann, 1948b; **19-** *Ammobaculites* sp. with the uncoiled portion broken; **20-22-** *Ammotium salsum* (Cushman and Brönnimann, 1948a); **20-** best specimen; **21-** smaller specimen; **22-** aperture detail; **23-** *Ammotium* sp.; **24-26-** different specimens of *Miliammina fusca* (Brady, 1870); **27-28-** *Miliammina obliqua* Heron-Allen and Earland, 1930; **27-** view of the interio-marginal arch of the aperture; **29-30-** *Arenoparrella mexicana* (Kornfeld, 1931); **29-** ventral side with view to main aperture and supplementary apertures; **30-** dorsal side with view to supplementary apertures; **31-32-** *Deuterammina eddystonensis* Brönnimann and Whittaker, 1990; **31-** dorsal view; **32-** ventral view; **33-35-** *Jadammina macrescens* (Brady, 1870); **33-** dorsal view; **34-** ventral view; **35-** dorsal view of a deformed test.
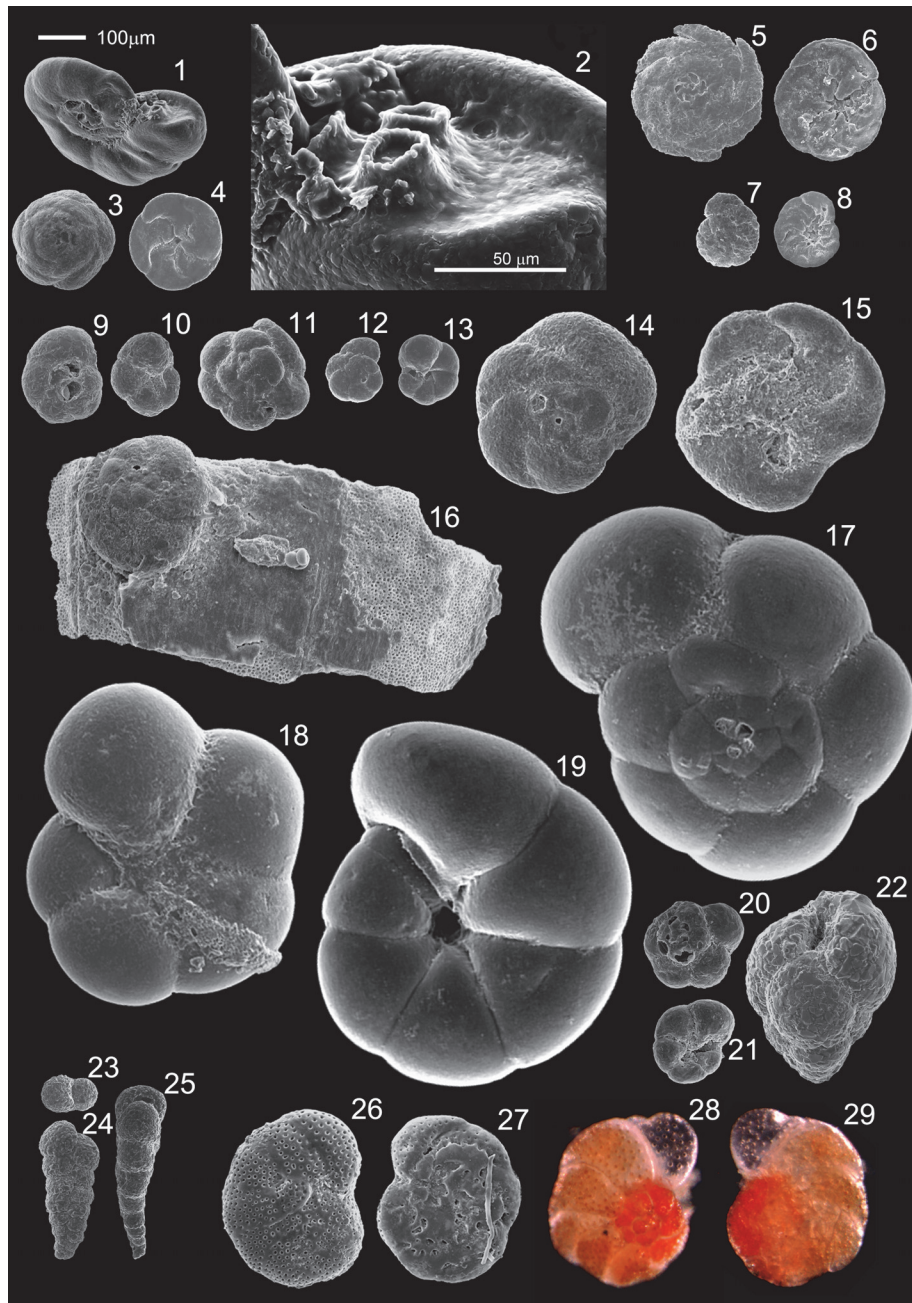
FIGURE 3. Scanning electron and light microscope micrographs of the foraminifera specimens. Scale bar equals 100 µm except where noted otherwhise; **1-2-** *Jadammina macrescens* (Brady, 1870); **1-** supplementary apertures view; **2-** detail of supplementary apertures (scale bar = 50 µm); **3-4-** *Lepidodeuterammina plymouthensis* Brönnimann and Whittaker, 1990; **3-** dorsal view; **4-** ventral view; **5-8-** *Lepidodeuterammina ochracea* (Williamson, 1858); **5-** dorsal view; **6-** ventral view; **7-** dorsal view of a smaller specimen; **8-** ventral view of a smaller specimen; **9-10-** *Portatrochammina* sp.; **9-** dorsal view; **10-** ventral view; **11-13-** *Siphotrochammina* sp.; **11-** dorsal side with inter-cameral foramen view; **12-** dorsal view of a smaller specimen, also with inter-cameral foramen; **13-** ventral view of a smaller specimen; **14-16-** *Tiphotrocha comprimata* Saunders, 1957; **14-** dorsal view; **15-** ventral view; **16-** individual strongly attached to a sea-grass leaf; detail of a *Pinus* pollen grain at the center of the leaf; **17-21-** *Trochammina inflata* (Montagu, 1808); **17-** dorsal view; **18-** ventral view; **19-** ventral view with umbilical tube detail; **20-** microspheric form dorsal view; **21-** microspheric form ventral view; **22-** *Eggerelloides scaber* (Williamson, 1858); **23-25-** *Textularia earlandi* Parker, 1952; **23-** apertural view; **24-** lateral view; **25-** profile view with aperture in detail; **26-29-** *Discorinopsis aguayoi* (Bermúdez, 1935); **26-** scanning electron dorsal view; **27-** scanning electron ventral view; **28-** light microscope dorsal view; **29-** light microscope ventral view.
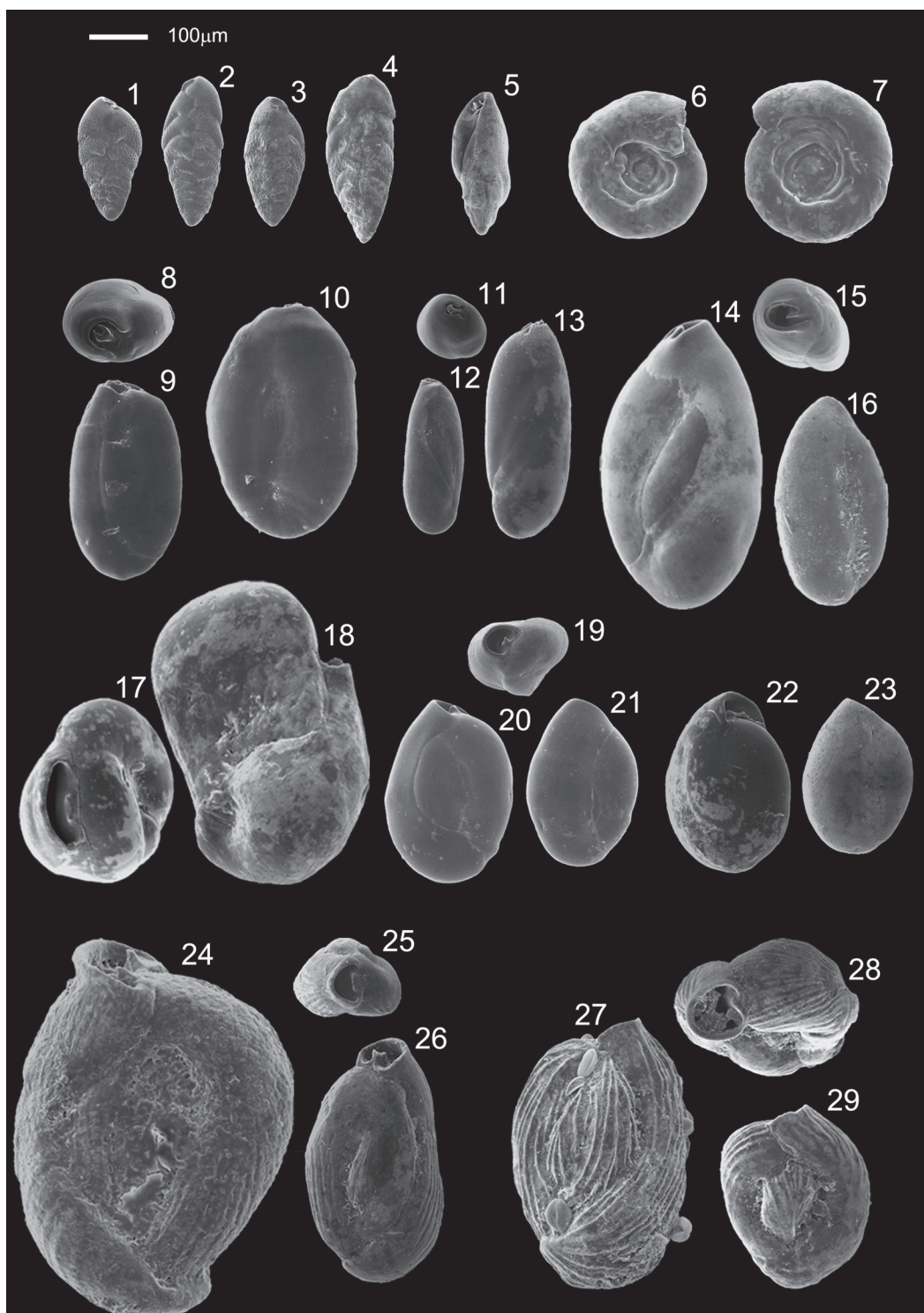
FIGURE 4. Scanning electron micrographs of the foraminifera specimens. Scale bar equals 100 µm. **1-4-** different sized specimens of *Bolivina ordinaria* Phleger and Parker, 1952, new name; **5-** *Buliminella elegantissima* (d'Orbigny, 1839b); **6-7-** *Cornuspira involvens* (Reuss 1850); **8-10-** Miliolid sp1; **8-** apertural view; **9-** front view; **10-** back view; **11-13-** Miliolid sp2; **11-** apertural view; **12-** front view; **13-** back view; **14-16-** Miliolid sp3; **14-** front view; **15-** apertural view; **16-** back view; **17-18-** Miliolid sp4; **17-** apertural view; **18-** front view; **19-21-** Miliolid sp5; **19-** apertural view; **20-** front view; **21-** back view; **22-23-** Miliolid sp6; **22-** front and apertural view; **23-** back view; **24-26-** Miliolid sp7; **24-** front view; **25-** apertural view; **26-** front and apertural view; **27-29-** Miliolid sp8; **27-** front view; **28-** apertural view; **29-** front view of a smaller specimen.
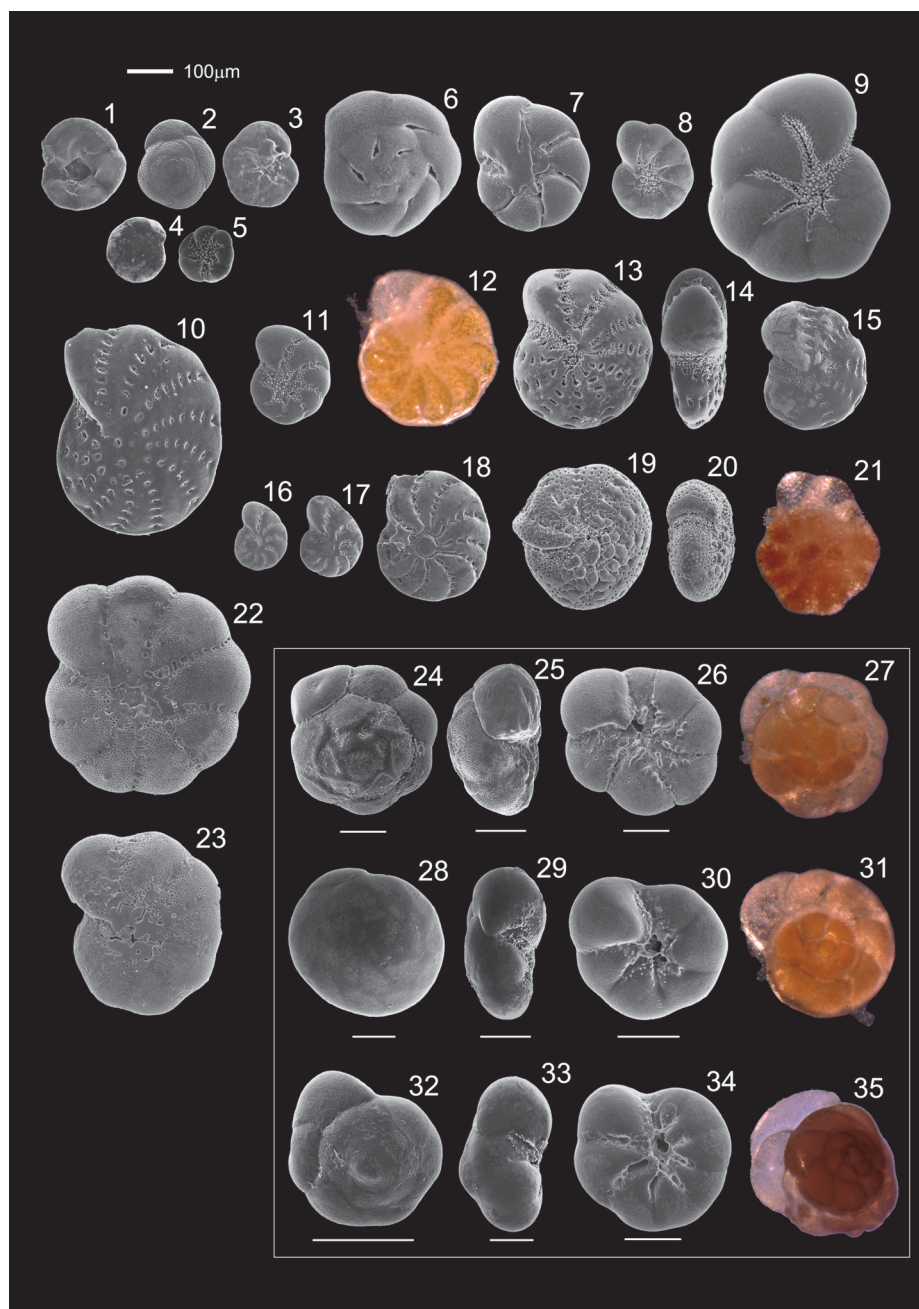
FIGURE 5. Scanning electron and light microscope micrographs of the foraminifera specimens. Scale bar equals 100 µm. **1-** *Lamarckina haliotidea* (Heron-Allen and Earland, 1911) ventral view; **2-3-** *Asterigerinata mamilla* (Williamson, 1858); **2-** dorsal view; **3-** ventral view; **4-5-** *Discorbis* sp.; **4-** dorsal view; **5-** ventral view; **6-7-** *Helenina anderseni* (Warren, 1957); **6-** dorsal view; **7-** ventral view; **8-** *Haynesina depressula* (Walker and Jacob, 1798) side view; **9-** *Haynesina germanica* (Ehrenberg, 1840) side view; **10-** *Elphidium advenum* (Cushman, 1922) side view; **11-** *Elphidium excavatum* (Terquem, 1875) side view; **12-15-** *Elphidium wiliamsoni* Haynes, 1973; **12-** side view in light microscope image; **13-** side view in scanning electron image; **14-** profile view in scanning electron image; **15-** side view of a smaller specimen in scanning electron image; **16-18-** side view of different size *Elphidium gerthi* Van Voorthuysen, 1957; **19-21-** *Elphidium oceanensis* (d'Orbigny, 1826); **19-** side view in scanning electron image; **20-** profile view in scanning electron image; **21-** side view in light microscope image; **22-** *Elphidium poeyanum* (d'Orbigny, 1826) side view; **24-27-** *Ammonia* sp1; **24-** dorsal view; **25-** profile view; **26-** ventral view; **27-** dorsal view in light microscope image; **28-31-** *Ammonia* sp2 (*Ammonia aberdoveyensis* Haynes, 1973); **28-** dorsal view; **29-** profile view; **30-** ventral view; **31-** dorsal view in light microscope image; **32-35-** *Ammonia* sp3 (*Ammonia aberdoveyensis* Haynes, 1973); **32-** dorsal view; **33-** profile view; **34-** ventral view; **35-** dorsal view in light microscope image.

(1987), Jones (1994) and the Ellis and Messina (1942-2012) online catalogue. The foraminiferal collection gathered during the study of Guadiana River paleoenvironments (Boski et al., 2002, 2008) was the main reference for taxonomic identification.

Most of the foraminifera were classified according to the generic classification proposed by Loeblich and Tappan (1987). For the higher levels of taxonomy, other than genus and species, the WoRMS classification was followed (Hayward et al., 2014), including the recent modifications proposed by Cavalier-Smith (2010).

In collaboration with the project foram BAR-CODING, a molecular database of foraminifera based at Geneva University and coordinated by Pawlowski and Holzmann (2014), several species were analysed at genetic level. To accomplish this, two extra field campaigns were made with the aim of collecting live specimens, the first in November 2010 and the second in March 2011. During both campaigns, the most fruitful sites identified during the previous sampling campaigns in terms of foraminiferal densities were revisited and resampled. Samples of the top centimeter of sediment were collected by hand with a scraper. In the laboratory, two subsamples were taken and washed. One was stained with Rose Bengal to evaluate the quantity and quality of live specimens; the other was left to settle for 2 hours in sea water. Living foraminifera (indicated by bright, colorful protoplasms, movement and sediment aggregation) were isolated using a stereomicroscope, and selected specimens were put into tubes, each containing 50 µl guanidine extraction buffer. Up to 10 live specimens of each species were separated and sent to the Geneva laboratory for genetic analysis and stereomicroscope photography.

The DNA extraction methodology was adapted from the general procedure in Pawlowski and Holzmann (2014), detailed in Pawlowski (2000). The analyzed barcoding region is situated at the 3' end of the SSU rRNA gene and is amplified using the primer pairs s14F3 (acgcamgtgtgaaacttg)-sB (tgatccttctgcaggttcacctac). It is usually necessary to perform a nested PCR, replacing primer 14F3 with primer 14F1 (aagggcaccacaagaacgc). The barcoding region spans six foraminifera-specific hypervariable expansion segments, 37f, 41f, 43f, 45e, 47f and 49e, which were shown to be sufficiently variable to differentiate between closely related species. The length of the barcoding region varies between 1000-1200 nucleotides depending on the species. Most amplifica-

tions are done on single-cell DNA extractions. Because of intra-individual polymorphism, the amplification products are cloned and two to three clones are sequenced. After sequencing the results were aligned to confirm the presence of the species.

Data Analysis

Statistical analyses were performed based on the relative abundance of the living foraminiferal species with representations higher than 10% (Boltovskoy and Totah, 1985) in at least one sample.

Redundancy Analysis (RDA) (a constrained form of the linear ordination method of PCA) was chosen to analyse the relationships between the dominant species and elevation and distance-to-sea, which were the two most important environmental variables in living foraminiferal distribution in Guadiana River Estuary (Camacho et al., 2015). In the present work, RDA was performed with a focus on inter-species correlations, where abundances of individual dominant species are transformed to a comparable scale. The relationship between species and environmental variables is represented by an attribute plot, where arrows represent the environmental variables, and species are represented by symbols of variable size according to its abundance in the sample scores fitted by the model (Leps and Smilauer, 2003).

RESULTS AND DISCUSSION

Classification and Genetic Analysis

There is a tendency among foraminiferal taxonomists to raise varieties and subspecies to species rank and to distinguish new species on the basis of subtle morphologic differences. Likewise, differences between genera are becoming smaller. Collectively these trends reduce the chances of consistent identification because the system depends on the judgment of each observer, rather than on unambiguously defined criteria (Murray, 2007). In order to avoid contributing to this general trend towards taxonomic entropy, several taxa were left in open nomenclature or in *incertae sedis.* This was the case of the miliolids, which, in the absence of type material and similarities with other miliolids in the same geographical area (e.g., Colom, 1974; Villanueva et al., 1999), were assigned code names.

Analysis of partial rRNA genes only yielded results for a limited number of species, among which only two were sucessfuly identified and reg-

istered in the European Nucleotide Archive (http://www.ebi.ac.uk/ena/data/view/LN551930-LN551935): *Ammonia aberdoveyensis* Haynes (1973) (accession numbers: LN551930-LN551933) and *Elphidium williamsoni* Haynes (1973) (accession numbers: LN551934-LN551935).

The *Ammonia* genus includes species that are among the most common benthic foraminifera in the shallow waters of marginal marine environments globally (Langer and Leppig, 2000). With 35 taxa so far described, the genus *Ammonia* exhibits a significant range of morphological variants, making species-level identification particularly difficult morphologically (Holzmann et al., 1998; Langer and Leppig, 2000; Hayward et al., 2004). A variety of specific epithets for *Ammonia* morphotypes are in current use along the Guadiana Estuary and adjacent shelf (see Ruiz et al., 1996, 2005; Boski et al., 2002, 2008; Mendes et al., 2004, 2012; Delgado et al., 2012). Aiming to better understand *Ammonia* genetic affinities and clarify some of these taxonomic problems, we subjected three morphological variants to genetic analysis. Of these, only two produced successful results (*Ammonia* sp2 and sp3), being both aligned with *Ammonia* T2 (Hayward et al., 2004), thus corresponding to the species *Ammonia aberdoveyensis* Haynes (1973). Further field collections were performed, but genetic analysis of *Ammonia* sp1 proved fruitless. While some morphological dissimilarity was observed between the three variants (Figure 5.24-35), these characteristics were not significantly correlated with specific environmental conditions. Thus, further analysis is required to determine whether *Ammonia* sp1 is a different taxon or belongs to the species *A. aberdoveyensis,* with morphological differences resulting only from intergradational morphology.

Seasonal Species Distribution

Seasonal species distribution within the estuary was studied in detail in Camacho et al. (2015). Here we synthesize the main findings in that work with new observations on species distribution patterns and major environmental forcing parameters. Of the 54 living foraminifera taxa identified in the Guadiana Estuary, only 15 presented abundances ≥ 10%. *Jadammina macrescens* (Brady, 1870)*, Trochammina inflata* (Montagu, 1808)*, Miliammina fusca* (Brady, 1870)*, Ammonia* spp. and *Haynesina germanica* (Ehrenberg, 1840) were dominant in both seasons. *Bolivina ordinaria* Phleger and Parker (1952)*, Miliolid sp3 and the miliolids group

(dominant) and *Asterigerinata mamilla* (Williamson, 1858), *Discorinopsis aguayoi* (Bermúdez, 1935) and *Miliammina obliqua* Heron-Allen and Earland (1930) (common) were only found in winter. *Polysaccammina hyperhalina, Polysaccammina ipohalina* and *Elphidium oceanensis* (dominant) and *Siphotrochammina* sp. were only found in summer. Seasonal distribution profiles for each dominant species, according to the environmental variables of elevation and distance-to-sea, are shown in Figure 6.

Winter distribution of the main species. The distribution of common and dominant species during winter is represented in Figure 7. According to the division of the marsh into different elevation zones, it is clear that the upper marsh was almost exclusively colonized by the agglutinated species *J. macrescens*. In two of these samples, LEZ2 and VRSA2, there was a marked abundance of porcelaneous species, especially in LEZ2, where this group represents 82.3% of the total individuals (Appendix, Tables 2 and 3).

The lower marsh zone had more diverse foraminiferal composition than in the upper marsh. At the most confined sites (E1, located in the margin of a small tidal pond, and LG2 and LG3, located at the margin of a shallow, small lagoon), *J. macrescens* was dominant alongside *T. inflata*. *Ammonia* spp. and *H. germanica* had their highest representation in the samples collected in the lower marsh and mud zones of the lower estuary (Figure 7). *Ammonia* spp. exhibited a more euryhaline behavior than *H. germanica*, being abundant in the upper reach sample (FO), as well as in the lagoonal environment (LG3), which occupies the most downstream position. The agglutinated species *M. fusca* had its optimum spanning from the upper reaches of the lower estuary to the middle estuary, in samples from lower marsh-mud zone. *Bolivina ordinaria* is common in the lower marsh but had its optimum in mud zone areas, occurring together with *Ammonia* spp. and *H. germanica*. *Polysaccammina hyperhalina* Medioli et al. (1983) (Petrucci et al., 1983) occurred mainly in the mud zone.

It is worth pointing out that the porcelaneous forms, represented here by the miliolids group and Miliolid sp3, only occurred in environments subject to some degree of confinement, such as the samples located in the upper marsh and the small lagoon site (LG).

Summer distribution of the main species. The distribution of the common and dominant taxa during summer is represented in Figure 8. It is pos-
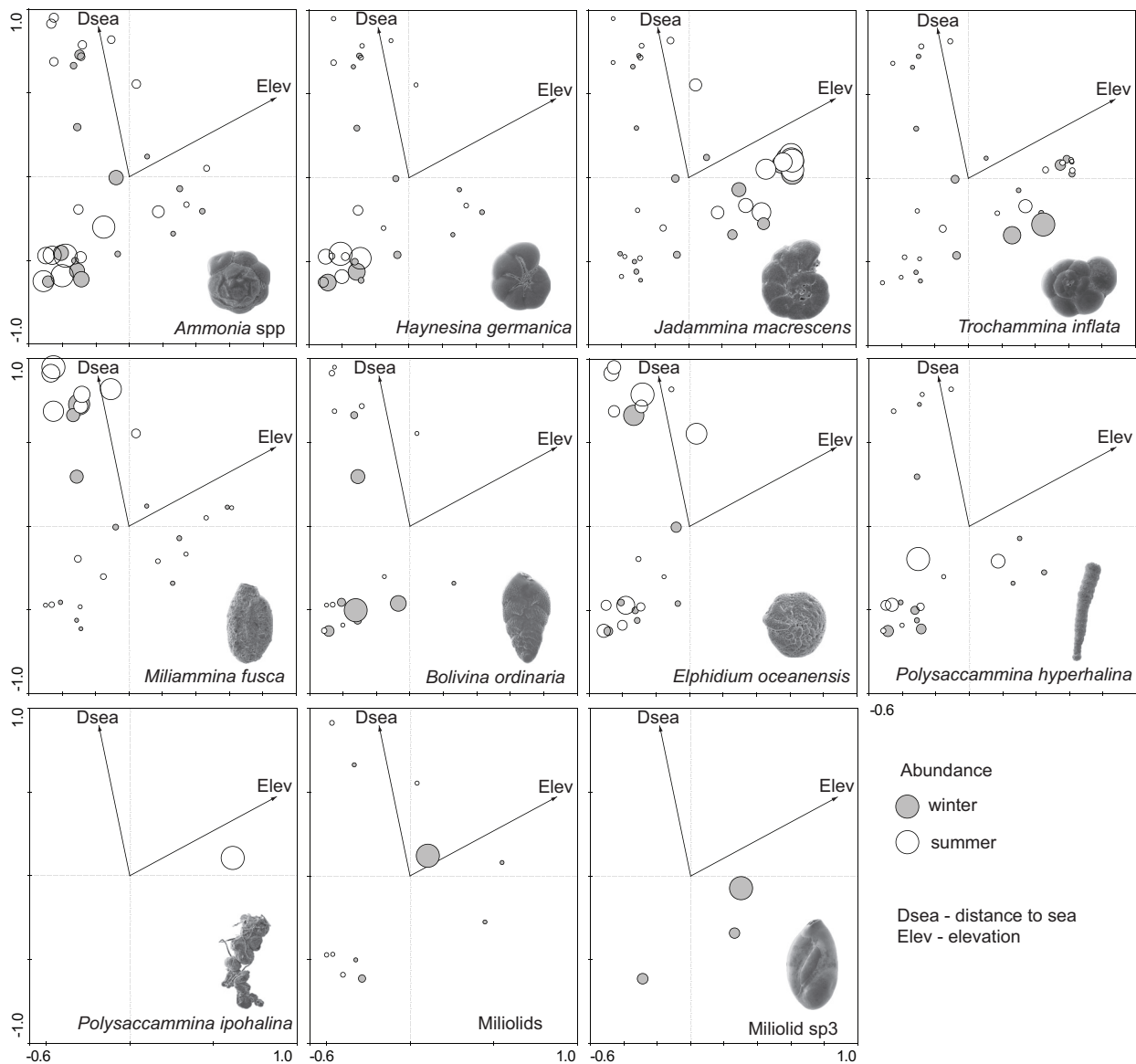
FIGURE 6. RDA attribute plot representing the distribution and abundance of the dominant species in Guadiana Estuary according to elevation and distance-to-sea variables.

sible to see that the upper marsh was almost exclusively colonized by the agglutinated species *J. macrescens*, similarly to the situation during winter. The exceptions were samples SCM, LEZ2 and VRSA2, where other species had significant abundances. At SCM, the site farthest inland from the estuary channel, *J. macrescens* shares dominance with *P. ipohalina* Scott (1976b), the latter representing more than 20% of the individuals and exclusive to that sample, suggesting specific environmental conditions. At LEZ2 and VRSA2, both samples located in the lowermost position within the upper marsh (1.06 and 1.03 meters above MSL), *J. macrescens* lost prominence to other spe-

cies, such as *P. hyperhalina*, *M. fusca*, *Ammonia* spp. and *E. oceanensis*, suggesting that the elevation thresholds for the latter species were above the 1 m level.

In the lower marsh the assemblages are more diversified, especially in samples located on the channel margin, where *J. macrescens* loses dominance. At more confined locations (FB2, E1, LG2 and LG3) *J. macrescens* is still prominent but shares dominance with *T. inflata, Ammonia* spp. and *M. fusca*. When considering foraminifera distribution in the lower marsh, the dominance of *M. fusca* stands out. This species had its optimum in the middle elevations (0 – 1 m) of the upper
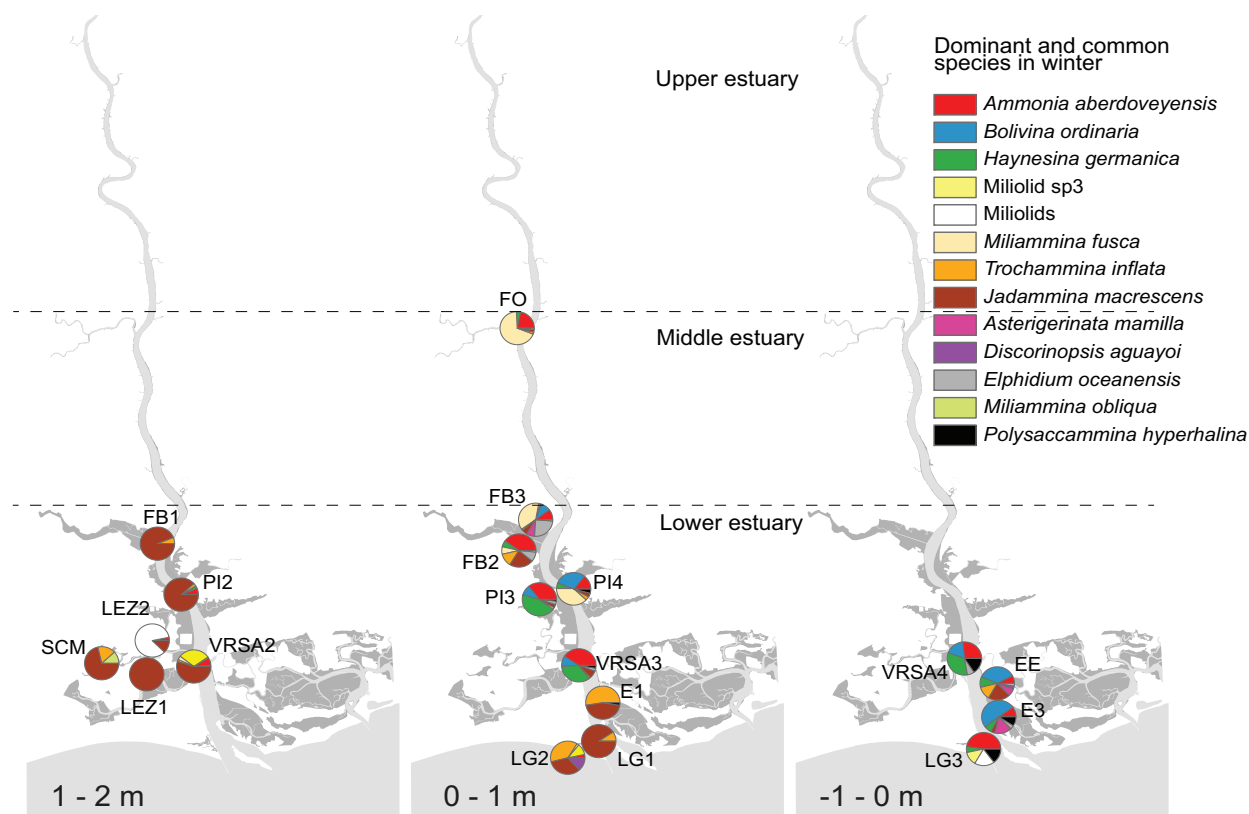
FIGURE 7. Distribution patterns of the common to dominant species in the samples collected in winter along a distance-to-sea and elevation gradients (in relation to MSL).

reaches of the lower estuary to middle estuary and is associated with *Ammonia* spp. and *E. oceanensis*. In the lower marsh, it is important to point out that the species *Siphotrochammina* sp. was only found alive at the Aouro site, located approximately 16 km upstream from the inlet, showing significant abundance. *Ammonia* spp. had its optimum in the samples collected in the mud zone, where it was dominant. Of all studied species, it was the most euryhaline, being recorded at considerable percentages along the distance-to-sea gradient and in the most confined environments of the lower marsh, as well as in some samples of the upper marsh. It was closely associated with *H. germanica*, especially in the mud zone, and with *E. oceanensis* in both lower marsh and mud zone. *Polysaccammina hyperhalina*, which was restricted to the mud zone in winter, had a patchy distribution in summer, more dependent on site location than on the elevation of the sample.

Species Ecology and Biogeography

Almost all the common and dominant species described in the present work are cosmopolitan,

occurring in other estuaries all over the world (Sen Gupta, 1999) and several of them were previously recorded by Ruiz et al. (1996, 2005) and González et al. (2000) in Guadiana Estuary. A new finding is that both *M. fusca* and *P. hyperhalina*, which are presently very abundant and constant along the estuary, were not reported by previous authors who studied the same area. Moreover, *P. hyperhalina*, *P. ipohalina*, *M. obliqua* and *D. aguayoi* are reported for the first time in the Guadiana Estuary, and, to our knowledge, in Portugal.

Jadammina macrescens is one of the species with the greatest scientific consensus in terms of life position and ecological indicator value. The first applications of marsh foraminifera in reconstruction of episodes of mean sea-level change were based in monospecific assemblages of *J. macrescens* (syn. *Trochammina macrescens*) collected near the continental limit (high marsh) in Nova Scotia marshes (Scott and Medioli, 1978, 1980). Being the most tolerant species to subaerial exposure, its relative abundance is very useful in sea-level change studies because it reflects the elevation of the depositional environment in relation to the high-
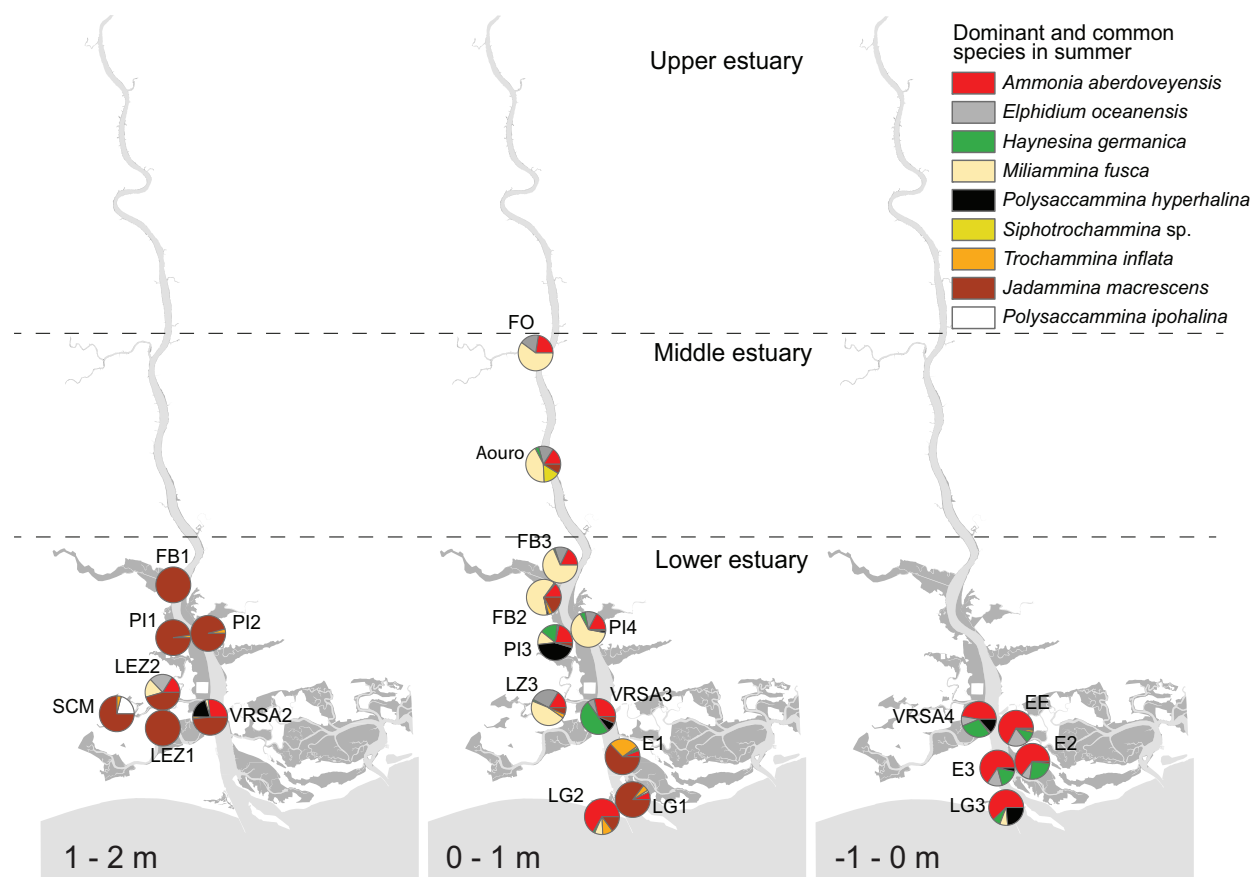
FIGURE 8. Distribution patterns of the common to dominant species in the samples collected in summer along a distance-to-sea and elevation gradients (in relation to MSL).

est high-water level, where it may represent 100% of foraminiferal assemblages, decreasing towards the low marsh, where it is almost absent (Scott and Medioli, 1978, 1980). Therefore, its relative abundance is inversely related to tide-flood frequency and other species' relative abundance (diversity) and has thus been used as an indicator of flood frequency (Thomas and Varekamp, 1991; Varekamp et al., 1992). In the present work, *J. macrescens* is the most widespread species, occurring in almost all samples from winter (94.7%) and summer (82.6%) (Figure 6). In the most elevated positions, the assemblages are almost exclusively (and in some cases, exclusively) composed of *J. macrescens*, exhibiting uncommonly high densities in some places (e.g., 68266 individuals/ 20 cc, in sample LG1 during winter) (Figures 7, 8). In a time-series study performed in the Tees Estuary, UK, Horton and Murray (2007) monitored *J. macrescens* standing crops fortnightly over 12 months and recorded peaks in abundance during the year. The maximum standing crop was 864/10 cc in October, being far less than the 34133 individ-

uals/10 cc in Guadiana sample LG1. Furthermore, Horton and Murray (2007) observed a progressive decline of this species from May/June, where it represents more than 80%, to March (5th day), when it temporarily disappeared. Our winter sampling, with high densities of *J. macrescens*, coincided exactly with the absence period verified by Horton and Murray (2007). These samples have a strong component of juveniles (generally more than 50% of the total, pers. obs.), extremely small and fully stained, which were 'hidden' in small mucous sediment aggregates, and were only visible when these were disaggregated with a probe. The counting of these hidden specimens may explain the large differences between the densities found in this work and others in which *J. macrescens* was also dominant. In summer, the juvenile component is always present and, although generally less than 50%, there are some samples in which it is higher. These observations lead us to conclude that, in the Guadiana, this species has the capacity of reproducing in both seasons, although winter seems more favorable. While juve-

niles are always present in samples containing adult *J. macrescens*, there are considerable differences between the adult/juvenile proportions from sample to sample, especially in summer. This seems to suggest that, within the same geographical area, the species does not reproduce at the same time, or at least at the same scale, which points to the influence of other abiotic and/or biotic factors acting locally and in parallel with seasonality in triggering reproduction.

Trochammina inflata is closely related to *J. macrescens,* occurring together in almost all the samples and being more abundant during winter, although it has higher abundances in the lower marsh (0.2 to 0.8 m above MSL at samples E1, LG2 and FB2) where *J. macrescens* abundance starts to decrease and species diversity starts to increase (Figures 7, 8). This relationship was reported previously for the Guadiana (González et al., 2000; Ruiz et al., 2005), and in other areas (some of the Nova Scotia marshes–Scott and Medioli, 1980; Fraser River Delta–Patterson, 1990). In other estuarine systems all over the Iberian Peninsula (Morbihan, Basque, Minho-Lima and Sado–Leorri et al., 2010), both *J. macrescens* and *T. inflata* are dominant components at the most elevated zones, but species association/succession is not exactly the same as that found in the Guadiana, probably due to local environmental differences. No other species is intrinsically related to *J. macrescens* and *T. inflata,* but several species with ephemeral occurrences seem to share similar habitat preferences. In the lower estuary in winter, the Miliolids group and Miliolid sp3 have peaky occurrences, each in a distinct sample of the upper marsh: LEZ2 (82.3%) and VRSA2 (28.8%), respectively (Figure 7). In summer it is worth noting the ephemeral occurrence of *P. ipohalina* at SCM, where it is subdominant to *J. macrescens* (20.8 and 75%, respectively). *Polysaccammina ipohalina* is a high marsh species (or upper mangrove, Barbosa et al., 2005), usually representing a minor component in estuarine systems (Scott, 1976b; Scott and Medioli, 1980; Scott et al., 1990). It was firstly described by Scott (1976b) in San Dieguito Marsh, California, associated with a few other species, especially *J. macrescens polystoma* and *T. inflata.* Although the latter species are common to almost every marsh, from brackish to hypersaline, when the association includes *P. ipohalina* it indicates a brackish marsh environment (Scott, 1976b). In the present study, salinity was measured in both seasons at site SCM, a sample located at the margin of a salt-works pond (Cama-

cho et al., 2014). Here, salinity is relatively high in both seasons (winter – 14.3 and summer – 26.1) when compared with those measured by Scott (1976b) (2–10‰). A common characteristic of SCM and San Dieguito marsh is the lack of tidal activity, which raises the possibility that this species is conditioned primarily by confinement and temperature.

In winter, at the SCM site, *P. ipohalina* is replaced by *T. inflata* and *M. obliqua*. Hayward et al. (1999b) have characterized *M. obliqua* as largely restricted to Southern Hemisphere shores (New Zealand marsh environments) where it occurs with *J. macrescens* and *T. inflata*. Based on the present experience, we believe that the strong morphological similarities between *M. obliqua* and *M. fusca* may be a hindrance to accurate identification, not only in Portuguese estuarine systems, but also worldwide, since the former taxon is rarely mentioned in the literature. In the Guadiana, *M. obliqua* exhibits higher incidence in winter in the lower marsh of the upper estuary and in two samples of the upper marsh with a more confined position.

Discorinopsis aguayoi, like *M. obliqua*, is a species of narrow distribution, occurring with *J. macrescens* and *T. inflata* in significant abundances (11.9%) during winter. In the living assemblage, its occurrence seems limited to the lower marsh zone, at the sheltered marine lagoon in the inlet (LG). *Discorinopsis aguayoi* is regarded as an indicator of landlocked marine/brackish ponds, mangrove marshes (Javaux and Scott, 2003) and high marsh in warm temperate environments (Scott, 1976a; Scott et al., 1990). Despite being very well documented by the latter authors, *D. aguayoi* was never mentioned as an epiphytic species. In the Guadiana it is found strongly attached to vegetal structures, each specimen having to be carefully detached using a needle probe.

The *Ammonia* genus includes species that are among the most common benthic foraminifera in shallow waters of marginal marine environments (Langer and Leppig, 2000; Debenay and Guilou, 2002). In the Guadiana Estuary, *Ammonia* spp. (*A. aberdoveyensis* and *Ammonia* sp1) is the most ubiquitous calcareous taxon, being absent only from the most elevated samples (> 1.3 m in relation to MSL - PI1, FB1, SCM, LEZ1). Its optimum occurrence is in the mud zone to lower marsh (-1 – 1 m) of the lower and middle estuary (Figures 7, 8). Its peak of occurrence is observed in summer, especially in the mud zone where it is always the dominant taxon (Figure 8). It is noteworthy that, in

summer, *Ammonia* spp. are able to migrate farther up the marsh, occupying higher elevation stands, probably due to decreased inter-species competition. *Ammonia* spp. are dominant in two of the main assemblages found for Guadiana: the lower marsh (0 – 1 m) upper reaches assemblage, where they are subdominant to *M. fusca*, and the mud zone (-1 – 0 m) of the lower estuary, where they are co-dominant with *B. ordinaria* in winter.

Haynesina germanica is closely associated with *Ammonia* spp., occurring as subsidiary species in almost all samples where *Ammonia* spp. are present (Figures 7, 8). The dominance of these two hyaline forms (*Ammonia tepida* (Cushman, 1926) or *Ammoni beccarii* (Linné, 1758) instead of our *Ammonia* spp.) has been documented for the estuarine systems of the whole of Europe (see Redois and Debenay, 1996). Both species are resistant to strong physico-chemical changes such as anoxia crises (common in the Mediterranean Sea and stratified lagoons), which require rapid recolonization (Debenay et al., 1998c; Frontalini and Coccioni, 2011). In the temperate paralic environments of the Atlantic coast of France, *H. germanica* is the most euryhaline and opportunistic hyaline species, marking the transition between agglutinated forms from upper paralic environments (where it is dominant) to calcareous forms from environments of higher marine influence, being progressively replaced by *A. tepida* (Redois and Debenay, 1996; Debenay et al., 2000; Debenay and Guilou, 2002). Horton and Murray (2007) found *H. germanica* among the dominant calcareous species from the tidal flats to middle marsh environments, and *Ammonia* spp. as sub-dominant, ephemeral-occurrence taxa. Martins et al. (2010, 2013) found *H. germanica* to be the most abundant species, followed by *A. tepida*, in the Ria de Aveiro, NW Portugal. In the Guadiana Estuary, *H. germanica* is not as prominent as *Ammonia* spp. but is very constant and is even dominant in a few samples of the lower marsh-mud zone. However, our data do not reveal the zonation pattern observed by Redois and Debenay (1996), Debenay et al. (2000) and Debenay and Guilou (2002). Instead, it seems that *Ammonia* spp. is the best-established calcareous taxon in the estuary, and, together with *E. oceanensis,* the most able to migrate farther up the marsh and upstream. A similar distribution was found in Venice Lagoon (Serandrei-Barbero et al., 1999) and at Acheloos and Evinos Estuaries (Greece) (Scott et al., 1979), where in both areas the lower stands are dominated by *Ammonia* with significant components of *Elphidium* and *Hayne-sina*. These and the Guadiana Estuary distributions seem to indicate that *Ammonia* is the dominant component in the low stands of the estuarine wetlands in southern Europe's warmer Mediterranean environments; whilst in north Europe's colder oceanic environments, *H. germanica* has higher prominence as a lower stands species.

According to Hayward et al. (1997), *E. gunteri* (here *E. oceanensis*) has a middle to low latitude distribution, with preference for warmer waters. It is also associated with brackish waters (Fatela and Silva, 1990; Debenay et al., 2003). In the Guadiana, *E. oceanensis* has its optimum during summer, being a dominant species in the lower marsh-mud zones (-0.7 to 1.1 m in relation to MSL) (Figure 6). In terms of distribution range, it is almost as eurytopic as *Ammonia* spp., occupying the entire study range of elevation and latitude.

Bolivina ordinaria has a controversial taxonomic history in the literature, as various names have been used by different authors to describe similar specimens worldwide (see Mendes, 2010, for review). The direct comparison of our specimens with the specimens of Mendes (2010) led us to conclude that both belong to the same species and thus Mendes' (2010) identification criteria were adopted. *Bolivina ordinaria* distribution within the Guadiana Estuary was surprising, as it is primarily described as an abundant species at great depths on the Portuguese continental shelf (Mendes et al., 2004; Martins et al., 2006, 2007; Mendes, 2010). Mendes (2010) considered *B. ordinaria* as a ubiquitous, very abundant species, highly adaptable and tolerant to a wide range of different factors or combination of factors, living at two different continental-shelf depth ranges (25-100 m in the southeast and 20-60 m in the northwest Gulf of Cadiz), and strongly associated with the direct influence of river discharges. She also found a peak abundance of *B. ordinaria* at 50 m depth and related it to a high rate of productivity at that depth. Mendes et al. (2004) previously described *B. ordinaria* as an important component of the shelf deep-water assemblage, relating it to low hydrodynamic levels, low-oxygen fine-grained sediments and to cold-water incursion derived from upwelling events. This species was also found in significant numbers in benthic foraminiferal assemblages from areas of greater marine influence offshore from the Ria de Aveiro, associated with fine-grained sediments enriched in TOC (Martins et al., 2014). Debenay and Redois (1997a,1997b), in a survey regarding foraminiferal distribution on the continental shelf in North Senegal, related the presence of *Bolivina*

spp. to the fertility of upwelling waters and Senegal River discharges. Likewise, Lévy et al. (1993) related two species of *Bolivina* with upwelling events along the southern coast of Portugal. In the Guadiana Estuary, *B. ordinaria* occurs as a dominant species in winter. In summer it is less frequent and less abundant (Figure 7). Depth and low hydrodynamics are not regarded as conditioning factors, as the species occurs in environments above MSL (< 0.61 m) and during winter, when the estuary experiences higher hydrodynamics. Passive upriver transportation by tides could explain its distribution, but then it would be expected to occur mainly in summer when the residence times are higher due to low river flows (Oliveira et al., 2006). From the overall environmental drivers discussed here, productivity and low temperatures seem to be the common factors in controlling the occurrence of *B. ordinaria* in both the estuary and deep shelf environments. In the Guadiana Estuary, during the rainy seasons (winter and spring), river inputs of freshwater are higher, enhancing the bioavailability of nutrients, especially Si, promoting the bloom of diatoms, which are the preferred food source for healthy foodwebs (Dias et al., 2001; Rocha et al., 2002). The low temperatures (indirectly) and productivity (directly) could be triggering *B. ordinaria* reproduction and proliferation inside the estuary.

Miliammina fusca is a very common species in worldwide paralic environments, dominating the continental end-member, and associated with direct freshwater influence (see Debenay and Guilou, 2002 for review). It is considered as an indicator species of the low-mid marsh zone (Varekamp et al., 1992) and the most ubiquitous agglutinated shallow-water species (Murray and Alve, 1999). In the Guadiana estuary, *M. fusca* is the most ubiquitous agglutinated shallow-water species, dominating assemblages either in the upper reaches of the lower estuary and upstream, at middle elevation zones (0 – 1 m) (Figure 6). Along with the indigenous calcareous species (*Ammonia* spp. and *Elphium oceanensis*), *M. fusca* is most abundant during summer, when it often represents more than 50% of the total assemblage (Figure 8). The species also seems able to migrate farther up the marsh in summer (e.g., LEZ and FB transects), reaching 16.3% at 1.06 m above MSL (LEZ2 sample).

Polysaccammina hyperhalina is a common and nearly constant agglutinated species in the Guadiana Estuary. In winter, its distribution seems to be restricted to the mud zones, whilst in summer it reaches higher abundances in the lower marsh as well (Figure 6). *Polysaccammina hyperhalina* is a species of hypersaline environments and was first reported and described from Venice Lagoon (Petrucci et al., 1983). In the Guadiana Estuary, the species has its optimum at the lower elevations of the lower estuary (Figures 7, 8), where marine processes are more pronounced. In northwest Portugal's paralic systems, *P. hyperhalina* was not recorded as a prominent species by Martins et al. (2010) in the Canals of Ria de Aveiro, nor found by Moreno et al. (2005) and Fatela et al. (2009) in the Minho and Coura estuaries. The presence/absence of this species may be related not only to salinity but also to temperature, as *P. hyperhalina* seems to prefer warmer climates, as noted by Petrucci et al. (1983) when they compared faunas from Venice Lagoon, Greece and Southern California.

Debenay et al. (2000) and Debenay and Guilou (2002) reviewed ca. 1500 samples collected worldwide by several authors in various types of transitional environments and synthesized the main foraminiferal distribution trends for each geographical and climatic zone. Despite several similarities between the general distribution model they proposed for temperate North Atlantic transitional environments and those studied by Horton and Murray (2007) (UK), Moreno et al. (2005), Fatela et al. (2009) and Martins et al. (2010) (north of Portugal), the benthic foraminifera distribution trends found in Guadiana Estuary present greater similarities with the distribution trends observed in Mediterranean transitional environments (Scott et al., 1979; Petrucci et al., 1983; Serandrei-Barbero et al., 1999; Debenay et al., 2000). In Mediterranean transitional environments, *J. macrescens* and *T. inflata* are prominent species in the upper marsh zone, occasionally associated with *D. aguayoi*. The middle marsh is characterized by the presence of *M. fusca*, occasionally associated with *Ammonia*, *P. hyperhalina*, *T. inflata* and *Quinqueloculina seminula*. Mudflats and low marshes are characterized by the presence of *Ammonia*, sometimes alongside *Haynesina germanica*.

The high diversities observed in Guadiana (Camacho et al., 2015) and the dominance of thermophilous taxa (*Ammonia* spp., *D. aguayoi*, *E. oceanensis* and *P. hyperhalina*) reflect the estuary's geographical position, which is subject to both Mediterranean and Atlantic influences.

SYSTEMATIC PALAEONTOLOGY

Order ASTRORHIZIDA Lankester, 1885
Family POLYSACCAMMINIDAE Loeblich and Tappan, 1984
Genus *POLYSACCAMMINA* Scott, 1976b
Polysaccammina ipohalina Scott, 1976b
Figure 2.1-3

1976b   *Polysaccammina ipohalina* Scott: p. 316, pl. 2, figs. 1-4, text fig. 4a-c.

1980   *Polysaccammina ipohalina* Scott; Scott and Medioli, p. 43, pl. 2, figs. 8-11.

1991   *Polysaccammina ipohalina* Scott; Scott, Suter and Kosters, p. 386, pl. 2, fig. 3.

2005   *Polysaccammina ipohalina* Scott; Barbosa, Scott, Seoane, and Turcq, p. 40, pl. 1, fig. 12.

Morphological description. Test free, finely arenaceous with pseudochitinous base; globular chambers, irregularly shaped, in uniserial arrangement but sometimes irregularly developed; with terminal aperture; test is flexible at sutures; earlier chambers appear to collapse; sutures distinct and depressed; arenaceous outer layer is not continuous between chambers.

Occurrence. Dominant species along with *Jadammina macrescens* and *Trochammina inflata*. Narrow occurrence, recorded only in one site in the Guadiana, in the vegetated margin of a saltworks pond which feeds salt-pans reservoirs, during summer, at 1.96 m above MSL.

Remarks. Its amorphous aspect and similarities with organic matter debris could hinder identification of this taxon as it is rarely mentioned in other works concerning marsh and estuarine foraminiferal analysis. The species was originally described as non-attached; however, many of the species observed in Nova Scotia (Scott and Medioli, 1980) and in the present work were attached to organic debris (Figure 2.1-3).

Polysaccammina hyperhalina (Medioli, Scott and Petrucci, 1983 *in* Petrucci et al., 1983)
Figure 2.4-2.6

1870   *Lituola findens* Parker, 1870; Dawson, p. 8, fig. 1.

1913   *Reophax findens* (Parker, 1870); Rhumbler, p. 466, fig. CLXXV.

1983   *Polysaccammina hyperhalina* Medioli, Scott and Petrucci; Petrucci, Medioli, Scott, Pianetti and Cavazzini, p. 73, 74, pl. 1, 2.

1996   *Reophax moniliformis* Siddall, 1886; Redois and Debenay, p. 258, pl. 1, fig. 3.

2005   *Polysaccammina hyperhalina* Medioli, Scott and Petrucci; Barbosa, Scott, Seoane and Turcq, p. 40, pl. 1, figs. 10, 11.

Morphological description. Test coarsely to fine agglutinated, usually uniserial but often irregular and sometimes branching (Figure 2.5); chambers of irregular shape, either regularly increasing in size or remaining of the same size throughout; test flexible due to an inner pseudochitinous lining which can be observed at broken chamber connections; aperture terminal, round and ivaginated to form a inner, backward pointing funnel (Figure 2.6).

Occurrence. Common and nearly constant agglutinated species; more common at the lower reaches of the estuary; in winter, its distribution seems restricted to the lower elevation zones, whilst in summer it reaches higher abundances at both the middle and lower elevations of the marshes.

Remarks. This species has a fragile test, easily broken during washing.

Order LITUOLIDA Lankester, 1885
Family AMMODISCIDAE Reuss, 1862
Genus AMMOVERTELLINA Suleymanov, 1959
Ammovertellina sp.
Figure 2.7-2.10

Morphological description. Proloculus followed by streptospirally wound tubular second chamber, later becoming planispiral; final stage uncoiling and with zig-zag or irregular growth; wall agglutinated, of angular quartz grains in insoluble cement; aperture at the open end of the tube.

Occurrence. Occurred only in the lower estuary, as a rare species.

Family REOPHACIDAE Cushman, 1927
Genus REOPHAX de Montfort, 1808
Reophax nana Rhumbler, 1913
Figure 2.11-2.14

1913   *Reophax nana* Rhumbler: p. 471, pl. 8, figs. 6-12.

1957   *Reophax nana* Rhumbler; Todd and Brönnimann, p. 22, pl. 1, fig. 17.

1980   *Reophax nana* Rhumbler; Scott and Medioli, p. 43, pl. 2, fig. 6.

2005   *Reophax nana* Rhumbler; Barbosa, Scott, Seoane and Turcq, p. 40, pl. 1, figs. 15-17.

Morphological description. Test agglutinated, uniserial, elongated; aperture simple on the top of the last chamber.

Occurrence. Accessory species, occurring mainly at the lower stands of the marsh.

Genus LEPTOHALYSIS Loeblich and Tappan, 1984
Leptohalysis scottii (Chaster, 1892)
Figure 2.15-2.17

1892 *Reophax scottii* Chaster: p. 27, pl. 1, fig. 1.

1971 *Reophax scottii* Chaster; Murray, p. 17, pl. 1, figs. 6-9.

1995 *Reophax scottii* Chaster; Lévy, Mathieu, Poignant, Rosset-Moulinier, Ubaldo and Lebreiro, p. 18, pl. 1, fig. 15.

2011 *Leptohalysis scottii* (Chaster); Murray and Alve, p. 30, fig. 18.5.

Morphological description. Test agglutinated uniserial and elongated; usually very thin and with somewhat angular chambers; an inner organic lining makes the test particularly flexible.

Occurrence. Species with rare occurrence along the estuary, at middle to low elevations of the marsh, revealing an exotic behavior.

Family LITUOLIDAE de Blainville, 1827
Genus AMMOBACULITES Cushman, 1910
Ammobaculites exiguus Cushman and Brönnimann, 1948b
Figure 2.18

1948b *Ammobaculites exiguus* Cushman and Brönnimann: p. 38, pl. 7, figs. 7, 8.

1953 *Ammobaculites exiguus* Cushman and Brönnimann; Parker, Phleger and Pierson, p. 5, pl. 1, fig. 16.

1986 *Ammobaculites exiguus* Cushman and Brönnimann; Brönnimann and Keij, pl. 3, fig. 7.

1995 *Ammobaculites exiguus* Cushman and Brönnimann; Scott, Hasegawa, Saito, Ito and Collins, p. 292, fig. 6.1.

2005 *Ammobaculites exiguus* Cushman and Brönnimann; Barbosa, Scott, Seoane and Turcq, p. 39, pl. 1, fig. 9.

Morphological description. Test agglutinated, elongate, initially planispirally coiled and latter with several uniserial chambers; aperture terminal and rounded.

Occurrence. Very rare, occurring only in one sample, near the Ayamonte Sewage Treatment Plant.

Ammobaculites sp.
Figure 2.19

Morphological description. Similar to *A. exiguus* although larger and usually with the uncoiled por-

tion broken; chambers better differentiated than *A. exiguus*.

Occurrence. Occurred only at the lower estuary, as a rare species, between the middle and low marsh stands.

Genus AMMOTIUM Loeblich and Tappan, 1953
Ammotium salsum (Cushman and Brönnimann, 1948a)
Figure 2.20-2.22

1948a *Ammobaculites salsus* Cushman and Brönnimann: p. 16, pl. 3, figs. 7-9 (holotype figs. 7a, 7b).

1962 *Ammotium salsum* (Cushman and Brönnimann); Closs and Madeira, p. 15, Est. 3, fig. 8; p. 43, Est. 7, fig. 2.

1980 *Ammotium salsum* (Cushman and Brönnimann); Scott and Medioli, p. 35, pl. 1, figs. 11-13.

1991 *Ammotium salsum* (Cushman and Brönnimann); Scott, Suter and Kosters, p. 384, pl. 1, figs. 11-13.

1993 *Ammotium morenoi* (Acosta, 1940); Brönnimann and Whittaker, p. 121, fig. 54.

2003 *Ammotium salsum* (Cushman and Brönnimann); Duleba and Debenay, p. 77, pl. 1, fig. 10.

2011 *Ammoscalaria pseudospiralis* (Williamson, 1858); Murray and Alve, p. 28, fig. 16.12.

Morphological description. Test agglutinated, initially planispirally coiled and latter chambers tend to uncoil, forming a wide uniserial pattern with poorly defined, slightly slanting suture lines; aperture is terminal and oval (Figure 2.21).

Occurrence. Accessory species (<10%) along the estuary, preferring the middle-low stands of the marsh; higher proliferation and densities during summer.

Ammotium sp.
Figure 2.23

Morphological description. Test finely agglutinated, initially planispirally coiled and latter chambers tend to uncoil, forming a wide uniserial pattern with slanting, well defined suture lines; much smaller than *A. salsum*.

Occurrence. Very rare species.

Family RZEHAKINIDAE Cushman, 1933
Genus MILIAMMINA Heron-Allen and Earland, 1930

Miliammina fusca (Brady, 1870)
Figure 2.24-2.26

1870   *Quinqueloculina fusca* Brady: p. 286, pl. 11, figs. 2, 3.

1953   *Miliammina fusca* (Brady, 1870); Parker, Phleger and Pierson, p. 10, pl. 1, figs. 40, 41.

1980   *Miliammina fusca* (Brady, 1870); Scott and Medioli, p. 40, pl. 2, figs. 1-3.

1990   *Miliammina fusca* (Brady, 1870); Scott, Schnack, Ferrero, Espinosa and Barbosa, p. 731, pl. 1, fig. 4.

2003   *Miliammina fusca* (Brady, 1870); Javaux and Scott, p. 16, fig. 6.7.

2013   *Miliammina fusca* (Brady, 1870); GenBank, ID: 302103, www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi?id=302103&lvl=0

Morphological description. Test agglutinated, elongated, ovate, of half coil in a quinqueloculine pattern; wall relatively thick, medium to coarse agglutinated; aperture at the end of the chamber, rounded to semilunate, depending on the degree of compression against the previous whorl and may be produced on a short neck.

Occurrence. One of the most ubiquitous agglutinated species in the Guadiana Estuary, dominating mid-low environments in the upper reaches of the estuary.

Miliammina obliqua Heron-Allen and Earland, 1930
Figure 2.27-2.28

1930   *Miliammina obliqua* Heron-Allen and Earland: p. 42, pl. 1, figs. 7, 12.

1999a *Miliammina obliqua* Heron-Allen and Earland; Hayward, Grenfell, Reid and Hayward, p. 82, pl. 1, figs. 7, 8.

2005   *Miliammina obliqua* Heron-Allen and Earland; Horton, Whittaker, Thomson, Hardbattle, Kemp, Woodroffe and Wright, p. 3, pl. 1, fig. 2.

2006   *Glomospira* sp. Debenay and Luan: pl. 1, fig. 9.

Morphological description. Broadly ovate, quinqueloculine test with early chambers oblique to main axis; thin wall composed of well-cemented fine silt grains, with a smoothly finished, light brown shinning surface; aperture is an interio-marginal arch (Figure 2.27); smaller than *M. fusca.*

Occurrence. Reported for the first time in Guadiana, where it is common, with higher incidence in winter, at middle elevations of the northernmost

positions and at upper elevations with a more confined position.

Remarks. Strong morphological similarities with *M. fusca* may prevent accurate identification, not only in Portuguese estuarine systems, but also worldwide; rarely mentioned in the literature.

Family TROCHAMMINIDAE Schwager, 1877
Genus ARENOPARRELLA Andersen, 1951
Arenoparrella mexicana (Kornfeld, 1931)
Figure 2.29-2.30

1931   *Trochammina inflata* (Montagu) var. *mexicana* Kornfeld: p. 86, pl. 13, fig. 5.

1957   *Arenoparrella mexicana* (Kornfeld); Todd and Bronnimann, p. 30, pl. 4, figs. 23, 24.

1981   *Arenoparrella mexicana* (Kornfeld); Haynes, p. 104, pl. 6.10, fig. 12.

1991   *Arenoparrella mexicana* (Kornfeld); Scott, Suter and Kosters, p. 384, pl. 1, figs. 16, 17.

2003   *Arenoparrella mexicana* (Kornfeld); Duleba and Debenay, p. 77, pl. 1, figs. 11, 12.

2013   *Arenoparrella mexicana* (Kornfeld); GenBank ID: 164132, www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi?id=164132andlvl=0

Morphological description. Test agglutinated, trochospiral, with supplementary apertures in the apertural face which differentiate the genus from other trochospiral forms.

Occurrence. Rare species in the live fraction, appearing mainly in the mid-low stands of the mid-upper estuary.

Genus DEUTERAMMINA Brönnimann, 1976
Deuterammina eddystonensis Brönnimann and Whittaker, 1990
Figure 2.31-2.32

1990   *Deuterammina eddystonensis* Brönnimann and Whittaker: pl. 4, figs. 1-8; pl. 8, fig. 2.

2001   *Deuterammina eddystonensis* Brönnimann and Whittaker; Debenay, Tsakiridis, Soulard and Grossel, p. 86, pl. 1, figs. 17, 18.

2004   *Deuterammina eddystonensis* Brönnimann and Whittaker; Diz, Francés, Costas, Souto and Alejo, p. 270, pl. 1, fig. 7.

Morphological description. Wall is thin and agglutinated; the test is low trochospirally enrolled and slightly concavo-convex; chambers increasing in size as added; sutures are radial and the periphery is rounded.

Occurrence. Very rare species in the live fraction (common in dead fraction).

Genus JADAMMINA Bartenstein and Brand, 1938
Jadammina macrescens (Brady, 1870)
Figures 2.33-2.35 and 3.1-3.2

1870   *Trochammina inflata* (Montagu) var. *macrescens* Brady: p. 290, pl. 11, fig. 5.

1938   *Jadammina polystoma* Bartenstein and Brand: p. 381, fig. 1, 2.

1953   *Jadammina polystoma* (Brady); Parker, Phleger and Pierson, p. 9, pl. 2, figs. 35-37.

1976b   *Trochammina inflata* (Montagu) var. *macrescens* Brady; Scott, p. 320, pl. 1, figs. 4-7.

1980   *Trochammina macrescens* (Brady); Scott and Medioli, p. 44, pl. 3, figs. 1-11.

1990   *Trochammina macrescens* (Brady); Scott, Schnack, Ferrero, Espinosa and Barbosa, p. 733, pl. 1, figs. 1, 2.

2003   *Trochammina macrescens* (Brady); Javaux and Scott, p. 23, figs. 6.14-6.19.

2014   *Jadammina macrescens* (Brady); GenBank ID: 164128, www.ncbi.nlm.nih.gov/Taxonomy/Browser/ wwwtax.cgi?id=164128andlvl=0

Morphological description. Test a flattened trochospiral, that tends to be nearly planispiral in the adult; chambers increasing gradually in size as they are added, sutures radial to slightly curved, periphery rounded; wall finely and sparsely agglutinated on a proteinaceous base; imperforate; the primary aperture is a low interiomarginal equatorial slit, with one or more supplementary areal openings in the lower portion of the apertural face, each bordered by a projecting lip (Figure 3.1-2).

Occurrence. Indigenous species in the modern estuary; the most ubiquitous agglutinated species, occurring along the entire estuary, but with an optimum of occurrence at the marine estuary, in the most elevated positions of the marsh, where the assemblages are almost exclusively (and in some cases, exclusively) composed of *J. macrescens.* This species exhibits uncommonly high densities in some places, surpassing 65,000 individuals/20 cc in sample LG1 (confined environment) in winter; dominant in both winter and summer, seems to be better adapted to winter conditions.

Genus LEPIDODEUTERAMMINA Brönnimann and Whittaker, 1983
Lepidodeuterammina plymouthensis Brönnimann and Whittaker, 1990
Figure 3.3-3.4

1974   *Trochammina rotaliformis* (Wright); Lévy, Mathieu, Poignant, Rosset-Molinier and Rouvillois, p. 128, pl. 1, figs. 4, 5.

1981   *Trochammina rotaliformis* (Wright); Todd and Low, p. 18.

1990   *Lepidodeuterammina plymouthensis* Brönnimann and Whittaker: p. 117-118, pl. 3, figs. 1-14.

2004   *Lepidodeuterammina plymouthensis* Brönnimann and Whittaker; Martins and Gomes, p. 31, fig. 2.13.

Morphological description. The wall is thin and agglutinated; test is low trochospirally enrolled and concavo-convex; sutures are radial and the periphery is rounded.

Occurrence. Very rare in the living assemblages.

Lepidodeuterammina ochracea (Williamson, 1858)
Figure 3.5-3.8

1858   *Rotalina ochracea* Williamson: p. 55, pl. 4, fig. 112; pl. 5, fig. 113.

1865   *Trochammina squamata* Parker and Jones: p. 407, pl. 15, figs. 30, 31.

1920   *Trochammina ochracea* (Williamson); Cushman, p. 75, pl. 15, fig. 3.

1952   *Trochammina squamata* Parker and Jones; Parker, p. 460, pl. 3, fig. 4.

1954   *Trochammina ochracea* (Williamson); Boltovskoy, p. 265, pl. 22, fig. 5.

1962   *Trochammina ochracea* (Williamson); Closs and Madeira, pl. 2B, fig. 8.

1971   *Trochammina ochracea* (Williamson); Murray, p. 37, pl. 11, figs. 1-5.

1980   *Trochammina ochracea* (Williamson); Scott and Medioli, p. 45, pl. 4, figs. 4, 5.

1987   *Lepidodeuterammina ochracea* (Williamson); Loeblich and Tappan, p. 127, pl. 135, figs. 10-14.

2004   *Lepidodeuterammina ochracea* (Williamson); Martins and Gomes, p. 29, fig. 2.12.

2005   *Trochammina ochracea* (Williamson); Barbosa, Scott, Seoane and Turcq, p. 40, pl. 2, figs. 16-20.

Morphological description. The wall is thin, agglutinated and single layered; trochospirally enrolled, very flat and concave ventrally; sutures are radial and the periphery is rounded.

Occurrence. Very rare in the living assemblages.

Genus PORTATROCHAMMINA Echols, 1971
Portatrochammina sp.
Figure 3.9-3.10

Morphological description. Agglutinated test, trochospirally enrolled, with few, gradually enlarging chambers per whorl; periphery is rounded; wall thin, agglutinated light mineralogical material (transparent).

Occurrence. Very rare in the living assemblages.

Genus SIPHOTROCHAMMINA Saunders, 1957
Siphotrochammina sp.
Figure 3.11-3.13

1995 *Trochammnina inflata* Montagu 1808; 'Sipho' type, Scott, Hasegawa, Saito, Ito and Collins, p. 294, figs. 6.11, 6.13-6.17.

Morphological description. Test a low trochospiral, chambers ovate, increasing gradually in size as added, sutures gently curved, periphery rounded; wall light brown in color, finely and sparsely agglutinated on a proteinaceous base, the early whorl darker brown and with very little agglutinated material; aperture interiomarginal, at the end of a siphon-like lobe projecting from the umbilical margin of the chamber and directed forward (Loeblich and Tappan, 1987). Although not recognizable through binocular microscope observation, the SEM images of the two photographed specimens (Figure 3.11-12) exhibit a well defined, dorsal, inter-cameral foramen. As far as we know, this characteristic is not documented elsewhere and more photographs should be taken to confirm this morphological characteristic.

Occurrence. Common species in the modern estuary, with a well-defined position along the north-south gradient, appearing (live and dead) only in the northernmost samples (from Aouro upstream).

Genus TIPHOTROCHA Saunders, 1957
Tiphotrocha comprimata (Cushman and Brönnimann, 1948b)
Figure 3.14-3.16

1948b *Trochammina comprimata* Cushman and Brönnimann: p. 41, pl. 8, figs. 1-3.

1957 *Tiphotrocha comprimata* (Cushman and Brönnimann); Saunders, p. 20, pl. 4, figs. 1-4.

1980 *Tiphotrocha comprimata* (Cushman and Brönnimann); Scott and Medioli, p. 44, pl. 5, figs. 1-3.

1991 *Tiphotrocha comprimata* (Cushman and Brönnimann); Scott, Suter and Kosters, p. 388, pl. 2, figs. 5, 6.

2004 *Tiphotrocha comprimata* (Cushman and Brönnimann); Edwards, Wright and van de Plassche, p. 15, pl. 1, figs. 12, 13.

Morphological description. Agglutinated test, trochospirally enrolled, flattened, with ventral side slightly concave; with few gradually enlarging chambers per whorl; periphery is rounded; wall thin; siphon-like extension to the aperture in the umbilical area.

Occurrence. Rare in the living assemblages.

Genus TROCHAMMINA Parker and Jones, 1859
Trochammina inflata (Montagu, 1808)
Figure 3.17-3.21

1808 *Nautilus inflatus* Montagu: p. 81, pl. 18, fig. 3.

1858 *Rotalina inflata* (Montagu); Williamson, p. 50, pl. 4, figs. 93, 94.

1952 *Trochammina inflata* (Montagu); Parker, p. 459, pl. 3, fig. 1.

1957 *Siphotrochammina lobata* Saunders: p. 9, pl. 3, figs. 1, 2.

1977 *Siphotrochammina elegans* Zaninetti, Brönnimann, Beurlen and Moura: pl. 2, figs. 8, 10, 11.

1990 *Trochammina inflata* (Montagu); Scott, Schnack, Ferrero, Espinosa and Barbosa, p. 733, pl. 1, fig. 3.

2005 *Trochammina inflata* (Montagu); Horton, Whittaker, Thomson, Hardbattle, Kemp, Woodroffe and Wright, p. 3, pl. 1, fig 4.

Morphological description. Agglutinated test, trochospirally enrolled, chambers rather inflated, increasing in size gradually; aperture a low arch with a bordering lip; smoothly agglutinated.

Occurrence. Dominant in the living assemblages of the modern estuary; closely related to *J. macrescens*, occurring together in almost all the samples, although it has higher abundances in middle elevations (0.2 to 0.8 m above MSL at samples E1, LG2 and FB2) where *J. macrescens* abundance starts to decrease and species diversity starts to increase; like *J. macrescens*, it is more common in winter.

Remarks. This taxon is the type species of the genus *Trochammina*; perhaps the best known and most distinctive of all the endemic marsh species, as well as being one of the earliest species ever described (Scott et al., 2001); the specimens found in Guadiana often present a proteinaceous umbilical tube (Figure 3.18), covered with fine sediment, the purpose of which is unknown.

Order TEXTULARIIDA Mikhalevich, 1980
Family EGGERELLIDAE Cushman, 1937
Genus EGGERELLOIDES Haynes, 1973
Eggerelloides scaber (Williamson, 1858)
Figure 3.22

1858   *Bulimina scabra* Williamson: p. 65, pl. 5, figs. 136, 137.

1960   *Eggerella scabra* (Williamson); Hofker, p. 236, pl. A, figs. 11, 12.

1971   *Eggerella scabra* (Williamson); Murray, p. 45, pl. 15, figs. 1-6.

1987   *Eggerelloides scabrus* (Williamson); Loeblich and Tappan, p. 48, pl. 189, figs. 5-7.

1994   *Eggerelloides scaber* (Williamson); Jones, p. 52, pl. 47, figs. 15-17.

1995   *Eggerella scabra* (Williamson); Lévy, Mathieu, Poignant, Rosset-Moulinier, Ubaldo and Lebreiro, p. 19, pl. 2, fig. 9.

2004   *Eggerelloides scaber* (Williamson); Mendes, Gonzalez, Dias, Lobo and Martins, p. 178, pl. 1, fig. 3.

2012   *Eggerelloides scabrus* (Williamson); Milker and Schmiedl, p. 37, fig. 10.9.

2014   *Eggerelloides scaber* (Williamson); GenBank ID: 160331, www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi?id=160331andlvl=0

Morphological description. Agglutinated, oblong test; initial part is trochospirally arranged but is reduced to triserial in the adult; chambers gradually increasing in size as added, so the last whorl commonly forms half the length of the test; the aperture is an interiomarginal arch in the center of the apertural face; coarsely agglutinated wall.

Occurrence. Rare species in the living assemblage but abundant in the dead assemblage; occurs mainly at the lower reaches of the estuary, at the lower stands of the marsh; more abundant in winter.

Remarks. The juvenile specimens can be easily confused with other *Eggerella* species.

Family TEXTULARIIDAE Ehrenberg, 1838
Genus TEXTULARIA Defrance, 1824
Textularia earlandi Parker, 1952
Figure 3.23-3.25

1933   *Textularia tenuissima* Earland: p. 95, pl. 3, figs. 21-30.

1952   *Textularia earlandi* Parker: p. 458, pl. 2, figs. 4-5.

1962   *Textularia earlandi* Parker; Closs and Madeira, p. 15, est. 3, figs. 6-7; 43, est. 7, fig. 5.

1995   *Textularia earlandi* Parker; Lévy, Mathieu, Poignant, Rosset-Moulinier, Ubaldo and Lebreiro, p. 20, pl. 3, fig. 4.

2004   *Spiroplectinella earlandi* (Parker); Martins and Gomes, p. 21, fig. 2.7.

2007   *Textularia porrecta* (Brady, 1884); Duchemin, Fontanier, Jorissen, Barras and Griveaud, p. 28, pl. 1, fig. 8.

Morphological description. Test agglutinated, chambers biserially arranged, laterally compressed; aperture is a simple arch at the base of the last chamber (Figure 3.25).

Occurrence. Rare species, preferring the lower stands of the marsh.

Family VALVULAMMINIDAE Loeblich and Tappan, 1986
Genus DISCORINOPSIS (Cole, 1941)
Discorinopsis aguayoi (Bermúdez, 1935)
Figure 3.26-3.29

1935   *Discorbis aguayoi* Bermúdez: p. 204, pl. 15, figs. 10-14.

1948b   *Discorinopsis vadescens* Cushman and Brönnimann: p. 20, pl. 4, figs. 9, 10.

1953   *Discorinopsis aguayoi* (Bermúdez); Parker, Phleger and Pierson, p. 7, pl. 4, figs. 23, 24.

1957   *Discorbis*? *aguayoi* Bermúdez; Todd and Brönnimann: pl. 9, fig. 24.

1963   *Trichohyalus aguayoi* (Bermúdez); Bermúdez and Seiglie, p. 176, pl. 26, fig. 4.

1971   *Discorinopsis aguayoi* (Bermúdez); Bock, p. 50, pl. 18, fig. 42.

1979   *Discorinopsis aguayoi* (Bermúdez); Scott, Piper and Panagos, p. 257, pl. 16, figs. 1, 2.

1998b   *Discorinopsis aguayoi* (Bermúdez); Debenay, Eichler, Duleba, Bonetti and Eichler-Coelho, p. 80, pl. IV, figs. 24, 25.

2003   *Discorinopsis aguayoi* (Bermúdez); Javaux and Scott, p. 14, figs. 6.1, 6.2.

Morphological description. Test with low trochospiral coil, with about five chambers in the first whorl; the increased height of the spire results in an auriculate test, spiral side strongly convex, umbilical side flattened to concave with broad umbilicus; sutures strongly curved in spiral side, nearly radial on the umbilical side; wall agglutinated of calcareous particles.

Occurrence. Species of narrow distribution, occurring with *J. macrescens* and *T. inflata* in significant abundances (11.9%) during winter. In the living assemblage, its occurrence seems limited to confined sites of the lower estuary (LG and E1), at low to middle elevations where vegetation occurs.

Remarks. In Guadiana environments *D. aguayoi* is epiphytic, found strongly attached to vegetal structures.

Order BULIMINIDA Fursenko, 1958
Family BOLIVINIDAE Glaessner, 1937
Genus BOLIVINA d'Orbigny, 1839b
Bolivina ordinaria Phleger and Parker, 1952, new name
Figure 4.1-4.4

1952   *Bolivina ordinaria* Phleger and Parker: p. 14, pl. 7, figs. 4-6.

1980   *Bolivina ordinaria* Phleger and Parker; Boltovskoy, Giussaani, Watanabe and Wright, p. 18, pl. 3, figs. 1-3.

2001   *Bolivina variabilis* (Williamson, 1858); Debenay, Tsakiridis, Soulard and Grossel, pl. 4, figs. 3, 4.

2004   *Bolivina dilatata* (Reuss, 1850); Duijnstee, de Lugt, Noordegraaf and van der Zwaan, p. 145, pl. I.

2004   *Brizalina britannica* (Macfadyen*,* 1942); Leorri and Cearreta, p. 93, pl. 1, fig. 9.

2004   *Bolivina pseudoplicata* Heron-Allen and Earland, 1930; Diz, Francés, Costas, Souto and Alejo, p. 273, pl. 2, fig. 4.

2004   *Bolivina ordinaria* Phleger and Parker; Martins and Gomes, p. 90, fig. 2.53.

2008   *Brizalina spathulata* (Williamson, 1858); Diz and Francés, p. 184, pl. 1, figs. 8-10.

2012   *Bolivina ordinaria* Phleger and Parker; Mendes, Dias, Schönfeld and Ferreira, p. 22, fig. 2.8.

Morphological description. Calcareous wall; test small, compressed, tapering regularly throughout to subacute initial end, slightly ovate at apertural end; chambers increasing gradually as added, narrow, seven to ten pairs in adult; sutures depressed, broad and curved; wall smooth, distinctly perforate; aperture a narrow loop at the base of the apertural face, bordered on one margin by a thickened and imperforated rim.

Occurrence. Dominant species in winter, associated with *A. aberdoveyensis* and *H. germanica*, at low-middle stands of the marsh. In summer it is less frequent and less abundant.

Bolivina cf. *variabilis* (Williamson, 1858)

1858   cf. *Textularia variabilis* Williamson: p. 76, pl. 6, figs. 162, 163.

1971   cf. *Brizalina variabilis* (Williamson); Murray, p. 113, pl. 46, figs. 1-3.

2005   cf. *Bolivina variabilis* (Williamson); Debenay, Millet and Angelidis, p. 336, pl. 3, fig. 4.

2012   cf. *Bolivina variabilis* (Williamson); Milker and Schmiedl, p. 81, figs. 19.25, 19.26.

2014   cf. *Bolivina variabilis* (Williamson); GenBank ID: 212447, www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi?id=212447andlvl=0

Morphological description. The wall is calcareous; test elongate, compressed, tapering regularly throughout to subacute initial end; numerous chambers increasing gradually as added; sutures depressed, straight and oblique; wall rough, strongly perforate over full width of chambers; aperture a narrow loop at the base of the apertural face, bordered on one margin by a thickened and imperforated rim.

Occurrence. Accessory species, occurring only at LG site, a tidal lagoon at the estuary mouth.

Family BULIMINELLIDAE Hofker, 1951
Genus BULIMINELLA Cushman, 1911
Buliminella elegantissima (d'Orbigny, 1839b)
Figure 4.5

1839b   *Bulimina elegantissima* d'Orbigny: p. 51, pl. 7, figs. 13, 14.

1953   *Buliminella elegatissima* (d' Orbigny); Parker, Phleger and Pierson, p. 6, pl. 4, figs. 8, 9.

1971   *Buliminella elegatissima* (d' Orbigny); Murray, p. 105, pl. 42, figs. 1-4.

1980   *Buliminella elegatissima* (d' Orbigny); Scott, Schafer and Medioli, p. 226, pl. 3, figs. 1, 2.

1994   *Buliminella elegatissima* (d' Orbigny); Jones, p. 55, pl. 50, figs. 20-22.

2003   *Buliminella elegatissima* (d' Orbigny); Duleba and Debenay, p. 77, pl. 2, fig. 3.

2014   *Buliminella elegatissima* (d' Orbigny); GenBank ID: 379345, www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi?id=379345andlvl=0

Morphological description. The test is coiled in a high trochospire of many chambers; only two to three whorls oblongs are developed, well separated by depressed sutures; chambers are numer-

ous, very narrow and very oblique; the radial calcite wall is perforate except around the aperture.
Occurrence. Very rare species, occurring mainly in lower reaches of the estuary.

Order MILIOLIDA Delage and Herouard, 1896
Family CORNUSPIRIDAE Schultze, 1854
Genus CORNUSPIRA Schultze, 1854
Cornuspira involvens (Reuss, 1850)
Figure 4.6-4.7

1850   *Operculina involvens* Reuss: p. 370, pl. 46, fig. 20.

1884   *Cornuspira involvens* (Reuss); Brady, p. 200, pl. 11, figs. 1-3.

1917   *Cornuspira involvens* (Reuss); Cushman, p. 25, pl. 1, fig. 2; pl. 2, fig. 2; text figs. 2, 3.

1929   *Cornuspira involvens* (Reuss); Cushman, p. 80, pl. 20, figs. 6, 8.

1994   *Cornuspira involvens* (Reuss); Jones, p. 26, pl. 11, figs. 1-3.

2003   *Cornuspira involvens* (Reuss); Murray, p. 15, fig. 4.5.

2012   *Cornuspira involvens* (Reuss); Milker and Schmiedl, p. 44, fig. 12.1.

Morphological description. Wall is calcareous, porcelaneous and imperforate, with smooth surface; test free, discoidal, circular in outline and flattened; the proloculus is followed by a second enrolled and undivided tube that gradually increases in size; aperture is at the end of the tube.
Occurrence. Very rare species.

Miliolid sp.1
Figure 4.8-4.10

Occurrence. Accessory species, predominant at the lower reaches of the estuary.

Miliolid sp.2
Figure 4.11-4.13

Occurrence. Accessory species, with narrow occurrence; recorded only in winter.

Miliolid sp.3
Figure 4.14-4.16

Occurrence. Dominant species; predominant in winter, mainly at the lower reaches of the estuary.

Miliolid sp.4
Figure 4.17-4.18

Occurrence. Accessory species, predominant mainly at the lower reaches of the estuary.

Miliolid sp.5
Figure 4.19-4.21

Occurrence. Accessory species, predominant mainly at the lower reaches of the estuary; recorded only in summer.

Miliolid sp.6
Figure 4.22-4.23

Occurrence. Rare species, with narrow distribution (LG site); recorded only in winter.

Miliolid sp.9
Figure 4.24-4.26

Occurrence. Rare species, with narrow distribution (LG site); recorded only in winter.

Miliolid sp.10
Figure 4.27-4.29

Occurrence. Rare species, with narrow distribution (LG site); recorded only in winter.

Order ROBERTINIDA Loeblich and Tappan, 1984
Family CERATOBULIMINIDAE Cushman, 1927
Genus LAMARCKINA Berthelin, 1881
Lamarckina haliotidea (Heron-Allen and Earland, 1911)
Figure 5.1

1911   *Pulvinulina haliotidea* Heron-Allen and Earland: p. 338, pl. 11, figs. 6-11.

1971   *Lamarckina haliotidea* (Heron-Allen and Earland); Murray, p. 205, pl. 86, figs. 1-6.

2004   *Lamarckina haliotidea* (Heron-Allen and Earland); Martins and Gomes, p. 80, fig. 2.47.

Morphological description. Calcareous wall, test planoconvex or inequally biconvex, trochospiral, coiling dextral, chambers enlarging rapidly and becoming progressively broader and lower; final chamber strongly overlapping; periphery subacute to carinate; wall calcareous, aragonitic, finely perforate; surface smooth and polished on the umbilical side.
Occurrence. Very rare species.

Order ROTALIIDA Delage and Herouard, 1896
Family ASTERIGERINATIDAE Reiss, 1963
Genus ASTERIGERINATA Bermúdez, 1949
Asterigerinata mamilla (Williamson, 1858)
Figure 5.2-5.3

1858   *Rotalia mamilla* Williamson: p. 54, pl. 4, figs. 109-111.

1971   *Asterigerinata mamilla* (Williamson); Murray, p. 141, pl. 59, figs. 1-6.

1974   *Discorbis mamilla* (Williamson); Colom, p. 124, fig. 21, *f-i* and *o-s*.

1995 *Asterigerinata mamilla* (Williamson); Lévy, Mathieu, Poignant, Rosset-Moulinier, Ubaldo and Lebreiro, p. 46, pl. 10, fig. 10.

2004 *Eoeponidella pulchella* (Parker, 1952); Diz, Francés, Costas, Souto and Alejo, p. 273, pl. 2, fig. 14.

2012 *Asterigerinata mamilla* (Williamson); Milker and Schmiedl, p. 111, figs. 24.21-24.24.

Morphological description. Calcareous wall, test planoconvex, trochospiral and conical in peripheral view; spiral side is convex and evolute; umbilical side is involute; chambers increasing rapidly in breadth and becoming broad; sutures are curved and oblique; on the umbilical side only the five chambers of the final whorl are visible; sutures are slightly depressed; both sides are perforate with larger pores on the spiral; aperture is a low interiomarginal, umbilical arch at the base of the final chamber.

Occurrence. Common species (10-20%) in the biocenosis; more abundant at the lower estuary; higher densities during winter.

Family DISCORBIDAE Ehrenberg, 1838
Genus DISCORBIS Lamarck, 1804
Discorbis sp.
Figure 5.4-5.5

1994 *Bucella frigida* (Cushman, 1921); Hayward and Hollis, p. 212, pl. 3, figs. 11-13.

1999a *Ammonia pustulosa* (Albani and Barbero, 1982); Hayward, Grenfell, Reid and Hayward, p. 163, pl. 16, figs. 4-6.

Occurrence. Rare species, occurring only in summer, at the lower reaches of the estuary.

Family HELENINIDAE
Genus HELENINA Saunders, 1961
Helenina anderseni (Warren, 1957)
Figure 5.6-5.7

1957 *Pseudoeponides anderseni* Warren: p. 39, pl. 4, figs. 12-15.

1961 *Helenina anderseni* (Warren); Saunders, p. 148;

1980 *Helenina anderseni* (Warren); Scott and Medioli, p. 40, pl. 5, figs. 10, 11.

1991 *Helenina anderseni* (Warren); Scott, Suter and Kosters, p. 385, pl. 2, figs. 19, 20.

1999a *Helenina anderseni* (Warren); Hayward Grenfell, Reid and Hayward, p. 138, pl. 10, figs. 1-3.

2003 *Helenina anderseni* (Warren); Javaux and Scott, p. 16, figs. 6.3, 6.4.

Morphological description. Test calcareous, finely perforate; surface smooth; low trochospiral, both sides flattened; chambers enlarging gradually; sutures curved, oblique, depressed, on the opposite side the somewhat produced umbilical flaps of successive chambers overlap to close the umbilicus; aperture an extraumbilical interiomarginal slit, bordered by a lip; supplementary sutural apertural slits present on both sides.

Occurrence. Rare species, with a narrow distribution restricted to the estuary's lower reaches.

Family NONIONIDAE
Genus HAYNESINA Banner and Culver, 1978
Haynesina depressula (Walker and Jacob, 1798)
Figure 5.8

1798 *Nautilus depressulus* Walker and Jacob: p. 641, pl. 14, fig. 33.

1994 *Haynesina depressula* (Walker and Jacob); Hayward and Hollis, p. 217, pl. 5, figs. 13-16.

2012 *Haynesina depressula* (Walker and Jacob); Milker and Schmiedl, p. 109, figs. 25.17, 25.18.

Morphological description. The wall is calcareous, planispiral, circular in outline and biumbilicate with narrow and depressed umbilici in peripheral view; the sutures are radial, backward curved; about eight to ten chambers per whorl, enlarging gradually as added; the umbilical region is filled with large pustules; test surface is smooth.

Occurrence. Rare species.

Haynesina germanica (Ehrenberg, 1840)
Figure 5.9

1840 *Nonionina germanica* Ehrenberg: p. 23, pl. 2, fig. 1a-g.

1930 *Nonion germanicum* (Ehrenberg); Cushman, p. 8, 9, pl. 3, fig. 5.

1959 *Protelphidium tisburyense* (Butcher, 1948); Parker and Athearn, p. 342, pl. 50, figs. 26, 32.

1980 *Protelphidium orbiculare* (Brady, 1881); Scott and Medioli, p. 43, pl. 5 fig. 7.

1990 *Haynesina germanica* (Ehrenberg); Lee, pl. 5, fig. 20.

2000 *Haynesina germanica* (Ehrenberg); Langer, p. 643, figs. 1A, B, C.

2007 *Haynesina germanica* (Ehrenberg); Cearreta, Alday, Freitas and Andrade, p. 134, pl. 1, fig. 2.

2014 *Haynesina germanica* (Ehrenberg); GenBank, ID: 45993,

www.ncbi.nlm.nih.gov/Taxonomy/Browser/
wwwtax.cgi?id=45993andlvl=0

Morphological description. The wall is calcareous, planispiral, circular in outline, and biumbilicate with narrow and depressed umbilici in peripheral view; the sutures are radial, backward curved; about eight to ten chambers per whorl, enlarging gradually as added; the umbilical region is filled with pustules; the periphery is subrounded and the test surface is smooth.

Occurrence. Dominant and constant species in Guadiana Estuary, predominant at the middle and lower elevations of the marsh; strongly associated with *A. aberdoveyensis.*

Family ELPHIDIIDAE Galloway, 1933
Genus ELPHIDIUM de Montfort, 1808
Elphidium advenum (Cushman, 1922)
Figure 5.10

1922   *Polystomella advena* Cushman: p. 56, pl. 9, figs. 11, 12.

1930   *Elphidium advenum* (Cushman); Cushman, p. 25, pl. 10, figs. 1, 2.

1994   *Elphidium advenum* (Cushman); Jones, p. 108, pl. 110, fig. 1.

2006   *Elphidium advenum* (Cushman); Debenay and Luan, pl. 2, fig. 46.

Morphological description. The wall is calcareous, planispiral enrolled; peripheral outline slightly lobate, slightly compressed, biconvex profile; periphery acute, with a strong rounded keel; 12 to 15 chambers in final whorl; sides flattened to slightly concave; sutures flush to slightly depressed, moderately curved backwards; flattened boss in the umbilicus; wall opaque white.

Occurrence. rare species in Guadiana Estuary; only recorded in summer, at the estuary lower reaches*.*

Elphidium excavatum (Terquem, 1875)
Figure 5.11

1858   *Polystomella umbilicatula* Williamsom: p. 42, pl. 3, fig. 81.

1875   *Polystomella excavata* Terquem: p. 25, pl. 2, fig. 2a-f.

1952   *Elphidium excavatum* (Terquem); Parker, p. 448, pl. 3, fig. 13.

1994   *Elphidium excavatum* (Terquem) f. *excavatum* (Terquem); Hayward and Hollis, p. 214, pl. 5, figs. 1-5.

1998b   *Elphidium excavatum* (Terquem); Debenay, Eichler, Duleba, Bonetti and Eichler-Coelho, p. 80, pl. IV, figs. 9, 10.

2003   *Cribroelphidium excavatum* (Terquem) f. *selseyensis* (Heron-Allen and Earland, 1911); Duleba and Debenay, p. 77, pl. 2, fig. 7.

2014 *Elphidium excavatum* (Terquem); GenBank, ID: 212501, www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi

Morphological description. The wall is calcareous, planispiral enrolled; peripheral outline slightly lobate, rounded in edge view; eight to ten chambers in outer whorl; sutures straight to moderately curved backwards, narrow, extending into umbilical area; umbilicus depressed, covered by numerous papillae.

Occurrence. Rare species in Guadiana Estuary; only recorded at the estuary lower reaches*.*

Elphidium williamsoni Haynes, 1973
Figure 5.12-5.15

1973   *Elphidium williamsoni* Haynes: p. 207, pl. 24, fig. 7; pl. 25, figs. 6, 9; pl. 27, figs. 1-3.

1997   *Elphidium excavatum* (Terquem, 1875) f. *williamsoni* Haynes; Hayward, Hollis and Grenfell, p. 79, pl. 10, figs. 11-18.

2004   *Elphidium williamnsoni* Haynes; Leorri and Cearreta, p. 93, pl. 1, fig. 4.

2014   *Elphidium williamnsoni* Haynes; Pawlowski and Holzmann, forambarcoding.unige.ch/specs/105-elphidium-williamsoni

2014   *Elphidium williamnsoni* Haynes; GenBank, ID: 139273, www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi?id=139273andlvl=0

2014   *Elphidium williamnsoni* Haynes; this study; European Nucleotide Archive (ENA) http://www.ebi.ac.uk/ena/data/view/LN551930-LN551935

Morphological description. The wall is calcareous, planispiral enrolled; test with evenly rounded outline, becoming lobulate in later part; periphery broadly rounded to sub-acute; septal bridges long, evenly spaced and numerous.

Occurrence. Relatively abundant species (<10%) in Guadiana lower estuary, mainly during winter.

Elphidium gerthi Van Voorthuysen, 1957
Figure 5.16-5.18

1957   *Elphidium gerthi* Van Voorthuysen: p. 32, pl. 23, fig. 12.

1995 *Cribrononion gerthi* (Van Voorthuysen); Lévy, Mathieu, Poignant, Rosset-Moulinier, Ubaldo and Lebreiro, p. 51, pl. 12, fig. 2.

2004 *Cribrononion gerthi* (Van Voorthuysen); Martins and Gomes, p. 257-258, fig. 2.152.

2008 *Elphidium* sp. Diz and Francés: pl. 2, fig. 3.

2012 *Elphidium gerthi* Van Voorthuysen; Mendes, Dias, Schönfeld and Ferreira, p. 24, fig. 4.8.

Morphological description. The wall is calcareous; test is planispiral, compressed and slightly evolute; the umbilical area is large and slightly depressed; nine to eleven chambers in the final whorl; sutures depressed, curved close to the periphery, crossed by sutural bridges or retral processes, with several fossettes; the aperture is multiple with several interomarginal arches.

Occurrence. Relatively abundant species (< 10%) in Guadiana estuary, along middle to lower estuary.

Elphidium oceanensis (d'Orbigny, 1826)
Figure 5.19-5.21

1826 *Polystomella oceanensis* d'Orbigny: p. 285.

1948a *Cribroelphidium vadescens* Cushman and Bronnimann: p. 18, pl. 4, fig. 5.

1951 *Elphidium littorale* Le Calvez and Le Calvez: p. 251, figs. 5a, 5b.

1971 *Elphidium oceanensis* (d'Orbigny); Murray, p. 165, pl. 69, figs. 1-7.

1982 *Elphidium gunteri* Cole, 1931; Buzas and Severin, p. 37, pl. 8, fig. 4.

1988 *Elphidium oceanensis* (d'Orbigny); Cearreta, p. 36, pl. I, fig. 8.

1994 *Elphidium gunteri* Cole, 1931; Hayward and Hollis, p. 209, pl. 4, figs. 10-12.

2004 *Elphidium oceanensis* (d'Orbigny); Leorri and Cearreta, p. 78, pl. 1, fig. 5.

2006 *Cribroelphidium mirum* n. sp. Langer and Schmidt-Sinns: p. 669, figs. 1.1-1.23.

2007 *Elphidium oceanensis* (d'Orbigny); Cearreta, Alday, Freitas and Andrade, p. 134, pl. I, fig. 3.

Morphological description. The wall is calcareous; test planispiral, involute and inflated with eight to fifteen chambers in outer whorl; periphery broadly rounded, slightly to irregularly lobate; sutures depressed, straight to gently curved; septal bridges irregular in number and degree of development; umbilicus may be slightly depressed or raised due to growth of irregular bosses; tubercular development in sutural pits, umbilical depression and base of apertural face; aperture is an interiomarginal row of arches; wall is coarsely perforate and usually golden brown.

Ocurrence. Has its optimum during summer, being a dominant species at middle and lower elevations (-0.7 to 1.1 m in relation to MSL); in terms of distribution range it is almost as eurytopic as *Ammonia* spp., occupying the entire study range of elevation and latitude.

Elphidium poeyanum (d'Orbigny, 1839a)
Figure 5.22-5.23

1839a *Polystomella poyana* d'Orbigny: p. 55, pl. 6, figs. 25, 26.

1930 *Elphidium poeyanum* (d'Orbigny); Cushman, p. 25, pl. 10, figs. 4, 5.

1953 *Elphidium poeyanum* (d'Orbigny); Parker, Phleger and Pierson, p. 9, pl. 3, fig. 26.

1998b *Elphidium poeyanum* (d'Orbigny); Debenay, Eichler, Duleba, Bonetti and Eichler-Coelho, p. 80, pl. IV, fig. 11.

2001 *Cribroelphidium cuvillieri* (Lévy, 1966); Debenay, Tsakiridis, Soulard and Grossel, p. 96, pl. 6, fig. 18.

2003 *Cribroelphidium poeyanum* (d'Orbigny); Duleba and Debenay, p. 77, pl. 2, fig. 8.

2007 *Cribroelphidium excavatum* (Terquem, 1875); Cearreta, Alday, Freitas and Andrade, p. 134, pl. 1, fig. 7.

2008 *Elphidium translucens* Natland, 1938; Diz and Francés, p. 185, pl. 2, fig. 2.

Morphological description. The wall is calcareous, planispiral enrolled; test outline circular to slightly lobulate; periphery broadly rounded with no keel; eight to nine slightly inflated chambers per adult whorl, broadly finely to medium perforated; umbilical area small, without tubercles.

Occurrence. Rare species in Guadiana Estuary only found in winter.

Family ROTALIIDAE Ehrenberg, 1839
Genus AMMONIA Brünnich, 1772
Ammonia sp1
Figure 5.24-5.27

Ammonia aberdoveyensis Haynes, 1973
Figure 5.28-5.35

1973 *Ammonia aberdoveyensis* Haynes: p. 184, fig. 38, nos. 1-7.

1990 *Ammonia beccarii* (Linné) f. *tepida* (Cushman, 1926); Walton and Sloan, pl. 1, figs. 1-4; pl. 2, fig. 2.

1995 *Ammonia beccarii* (Linné, 1758); Yassini and Jones, p. 175, figs. 994-999.

2004   *Ammonia aberdoveyensis* Haynes; Hayward, Holzmann, Grenfell, Pawlowski and Triggs, p. 253, pl. II, fig. T2; p. 256, pl. III, fig. T2; p. 258, pl. IV, fig. T2.

2007   *Ammonia aberdoveyensis* Haynes; Wennrich, Meng and Schmiedl, p. 321, pl. 1, fig. 3.

2014   *Ammonia aberdoveyensis* Haynes; Pawlowski and Holzmann: forambarcoding.unige.ch/specs/72-ammonia-aberdoveyensis-t2

2014   *Ammonia aberdoveyensis* Haynes; this study; European Nucleotide Archive (ENA) http://www.ebi.ac.uk/ena/data/view/LN551930-LN551935

Morphological description. Small proloculus, test medium-size (0.3 – 0.5 mm); whorls medium width on spiral side; moderate inflation, a broadly rounded periphery, six to nine chambers per whorl; small pores and longer radial sutural furrows on the umbilical side than the other 'Ammonias'; little to no secondary calcite, usually with no umbilical boss.

Occurrence. Together with Ammonia sp1, this is the most ubiquitous calcareous species in the modern estuary, being absent only from the most elevated stands of the marsh; its optimum occurrence is in the lower to middle elevations of the lower and middle estuary; its peak of occurrence is observed in summer, especially in the lower elevations where it is always the dominant species; in summer, it is able to migrate farther up the marsh, occupying higher elevation stands; is a dominant element in two of the main assemblages found for Guadiana: in the middle elevations of upstream assemblage, where it is subdominant to *M. fusca*, and in the lower elevations of the lower estuary assemblage, where it is co-dominant with *B. ordinaria* in winter.

Remarks. Found on Mediterranean coasts, France and Italy (Hayward et al., 2004).

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APPENDIX

TABLE 1. Table 1 – Spatial data of study sites.

Place	Sample	Datum 73			WGS 84	
		Eastings	Northings	Elev MSL	Latitude	Longitude
Laranjeiras	LAR	59841.474	-251196.821	0.311	37°24'12.28"N	7°27'26.09"W
Foz de Odeleite	FO	60808.447	-256955.96	0.334	37°21'5.26"N	7°26'48.47"W
Almada d'Ouro	Aouro	61149.393	-261793.396	0.532	37°18'28.28"N	7°26'36.06"W
Foz do Beliche	FB1	61922.506	-267062	1.432	37°15'37.21"N	7°26'6.24"W
	FB2	61924.614	-267057	0.752	37°15'37.38"N	7°26'6.15"W
	FB3	61927.302	-267051	0.471	37°15'37.57"N	7°26'6.04"W
Ponte Internacional	PI1	62974.271	-269471.977	1.188	37°14'18.79"N	7°25'24.29"W
	PI2	62997.536	-269452.581	1.198	37°14'19.42"N	7°25'23.34"W
	PI3	63006.818	-269442.632	0.614	37°14'19.74"N	7°25'22.97"W
	PI4	63012.253	-269438.821	0.011	37°14'19.86"N	7°25'22.74"W
Sapal de Castro Marim	SCM	59401.402	-272673.316	1.960	37°12'35.80"N	7°27'50.15"W
Lezíria	LEZ1	61394.114	-272397.855	1.317	37°12'44.28"N	7°26'29.26"W
	LEZ2	61390.198	-272388.367	1.062	37°12'44.58"N	7°26'29.41"W
	LEZ3	61391.183	-272387.306	0.202	37°12'44.62"N	7°26'29.37"W
Vila Real da Santo António	VRSA1	63557.17	-272825.6	1.210	37°12'29.88"N	7°25'1.68"W
	VRSA2	63560.61	-272836.35	1.030	37°12'29.95"N	7°25'1.23"W
	VRSA3	63571.94	-272863.74	0.290	37°12'30.22"N	7°25'0.07"W
	VRSA4	63589.81	-272904.11	-0.470	37°12'30.65"N	7°24'58.37"W
Espanha ETAR	EE	64604.906	-274266.784	-0.743	37°11'42.88"N	7°24'19.63"W
Espanha	E1	64684.93	-274521.467	0.574	37°11'34.60"N	7°24'16.47"W
	E2	64677.255	-274521.922	-0.066	37°11'34.58"N	7°24'16.78"W
	E3	64637.258	-274532.308	-0.743	37°11'34.26"N	7°24'18.41"W
Lagoa	LG1	64513.526	-276692.511	0.397	37°10'24.26"N	7°24'24.06"W
	LG2	64509.007	-276696.394	0.167	37°10'24.14"N	7°24'24.24"W
	LG3	64506.052	-276699.545	-0.090	37°10'24.03"N	7°24'24.36"W

TABLE 2. Absolute and relative frequencies of living for-aminifera in winter samples. In gray – samples with less than 48 living individuals (presented in PDF format online at palaeo-electronica.org/content/2015/269-512/1130-estuarine-forams-from-iberia).

TABLE 3. Absolute and relative frequencies of living for-aminifera in summer samples. In gray – samples with less than 48 living individuals. (presented in PDF format online at palaeo-electronica.org/content/2015/269-512/1130-estuarine-forams-from-iberia)