Research paper

Distribution patterns of benthic foraminifera across the Ypresian–Lutetian Gorrondatxe section, Northern Spain: Response to sedimentary disturbance

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ABSTRACT

We present a study of benthic foraminiferal assemblages from an Ypresian–Lutetian distal submarine fan system in the lower bathyal Gorrondatxe section (Basque-Cantabrian Basin, northern Spain). The objective of our study is to analyze the benthic foraminiferal distribution patterns and their response to sedimentary disturbance and related factors.

Assemblages contain a high percentage of allochthonous taxa, such as asterigerinids and other shallow water taxa, which were transported downslope by turbidity currents.

Detailed quantitative analyses, supported by R-mode cluster and Detrended Correspondence Analyses (after removing allochthonous taxa from the foraminiferal counts) allowed us to identify 6 assemblages that are divided into two groups related to the turbidite content in the Gorrondatxe section. Assemblages 1, characteristic of the turbidite-poor intervals with low sedimentary disturbance, include assemblage 1a (with highly diverse common middle–lower bathyal calcareous taxa) assemblage 1b (with common agglutinated taxa, mainly trochamminids), and assemblage 1c (characterized by calcareous taxa that are also common in the turbidite-rich interval).

Assemblages 2, characterized by a high dominance, prevail in the turbidite-rich interval, and include assemblage 2a (characterized by the dominance of infaunal bolivinids and epifaunal cibicids), assemblage 2b (typified by moderate to low diversity and dominated by deep-infaunal *Globobulimina* species), and assemblage 2c (typified by very abundant suspension-feeding astrorhizids). The high abundance of bolivinids and *Globobulimina* species may be related to an enhanced input of low-quality organic matter transported by turbidity currents to the seafloor, representing different stages of recolonisation after disturbance and different energy regimes. High current activity was probably responsible for the abundance of cibicids, while moderate to low diverse and high dominance assemblages characterize the recolonisation of the substrate after disturbance.

We conclude that sedimentary disturbance and other related factors such as current activity, resuspension of sediments at the seafloor, and supply of organic matter (and its quality) played an important role in the distribution of benthic foraminifera in the Gorrondatxe section. The identification of allochthonous taxa emerges as an essential aspect of the study of environments with sedimentary disturbance.

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1. Introduction

Submarine fan systems are characterized by downslope sediment transport processes such as turbidity currents, which imply transfer of sediment and organic material from continental shelf and upper slope to the deep sea. These processes often disturb the seafloor by erosion or input of new sediment and consequently they have a strong impact on deep-sea benthic communities. Intensified bottom water currents are responsible for the resuspension of fine-grained sediments, including organic matter (e.g., Tengberg et al., 2003), and they have been shown to influence the microhabitats and composition of the benthic foraminiferal fauna (Lutze and Thiel, 1989; Linke and Lutze, 1993; Schönfeld, 2002; Jorissen et al., 2007). Deep-sea benthic foraminiferal faunas are thought to be affected by the complex interaction of interdependent parameters, mainly the organic flux to the seafloor and bottom water oxygenation, while water currents are believed to be a minor controlling parameter or at least, difficult to estimate (e.g., Miller and Lohmann, 1982; Lutze and Coulbourn, 1984;

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Mackensen et al., 1990, 1995; Schmiedl et al., 1997; Jorissen et al., 1995, 2007; Koho, 2008).

The interpretation of deep-sea benthic foraminiferal assemblages affected by turbidity currents is hampered by the fact that these currents can lead to winnowing or addition of new components (e.g., Jorissen et al., 2007). Downslope transport of shallower material usually includes foraminiferal tests and, therefore, it is essential to know the water depth preferences of species. Investigation of the distribution of benthic foraminifera in modern submarine canyon systems and deep-sea fans has significantly increased in recent years (e.g., Jorissen et al., 1994; Schmiedl et al., 2000; Anschutz et al., 2002; Smith and Gallagher, 2003; Fontanier et al., 2005; Hess et al., 2005; Koho et al., 2007; Hess and Jorissen, 2009). However, studies of benthic foraminiferal distribution in fossil canyon and fan systems are scarce (e.g., Brouwer, 1965; Jones, 1999; Gallagher et al., 2001, 2003; Jones et al., 2005; Rogerson et al., 2006; Kender et al., 2009).

Here, we contribute to fill this gap by the quantitative analysis of benthic foraminifera of the early-middle Eocene (Ypresian-Lutetian; hereafter Y-L) Gorrondatxe section in the western Pyrenees. The Gorrondatxe section represents a deep-marine basinal setting that was frequently disturbed by sediment gravity flows. This paper assesses the environmental controlling parameters on benthic foraminiferal assemblage composition and the response of benthic foraminifera to sedimentary disturbance in a distal basinal siliciclastic submarine fan.

2. The Gorrondatxe section: geological setting and stratigraphy

The Gorrondatxe section is a 700-m-thick succession that is well exposed on the coastal cliffs northwest of Bilbao (Basque-Cantabrian Basin, northern Spain). This section is accessible by a beach named Gorrondatxe but also known as Azkorri owing to the so-called headland on the NE side of the beach (Fig. 1). During the Eocene, deformation of the Pyrenees reached its maximum intensity (e.g., Pujalte et al., 2002; Payros et al., 2009a) and two foreland basins developed to the south and north of the rising orogen. The study area was located in the north Pyrenean foreland basin, at approximately 35ºN latitude, and received sediments from several sources, notably pelagic carbonates, calciclastic turbidites and debrites derived from northern sources, and siliciclastic turbidites coming from northern and eastern sources (Payros et al., 2006). The Gorrondatxe section is composed of hemipelagic limestones and marls with abundant intercalations of plane-parallel thin-bedded (<15 cm) siliciclastic turbidites and thick-bedded (up to 240 cm) mixed calciclastic–siliciclastic turbidites (Figs. 1 and 2; Bernaola et al., 2006; Payros et al., 2006). The succession is characterized by the recurrent occurrence of tripartite sequences, generally 10–40 cm thick, each of which consists of a basal sandy turbidite, its capping grey marl (division E of the Bouma sequence) and a whitish pelagic mudstone bed (Payros et al., 2007). Relatively soft marly and harder limy varieties can be distinguished between the whitish pelagic mud-stones, which show the changing character of the pelagic sedimentation as a response to astronomically driven precession cycles (Payros et al., 2009b). No evidence for bed amalgamation or any large-scale vertical arrangement of beds was observed in the Gorrondatxe section. Paleocurrent indicators are generally directed towards the northwest, but some structures directed towards the north–northeast also occur, suggesting that sediment gravity flows were generally axial to the basin, with minor supply being derived
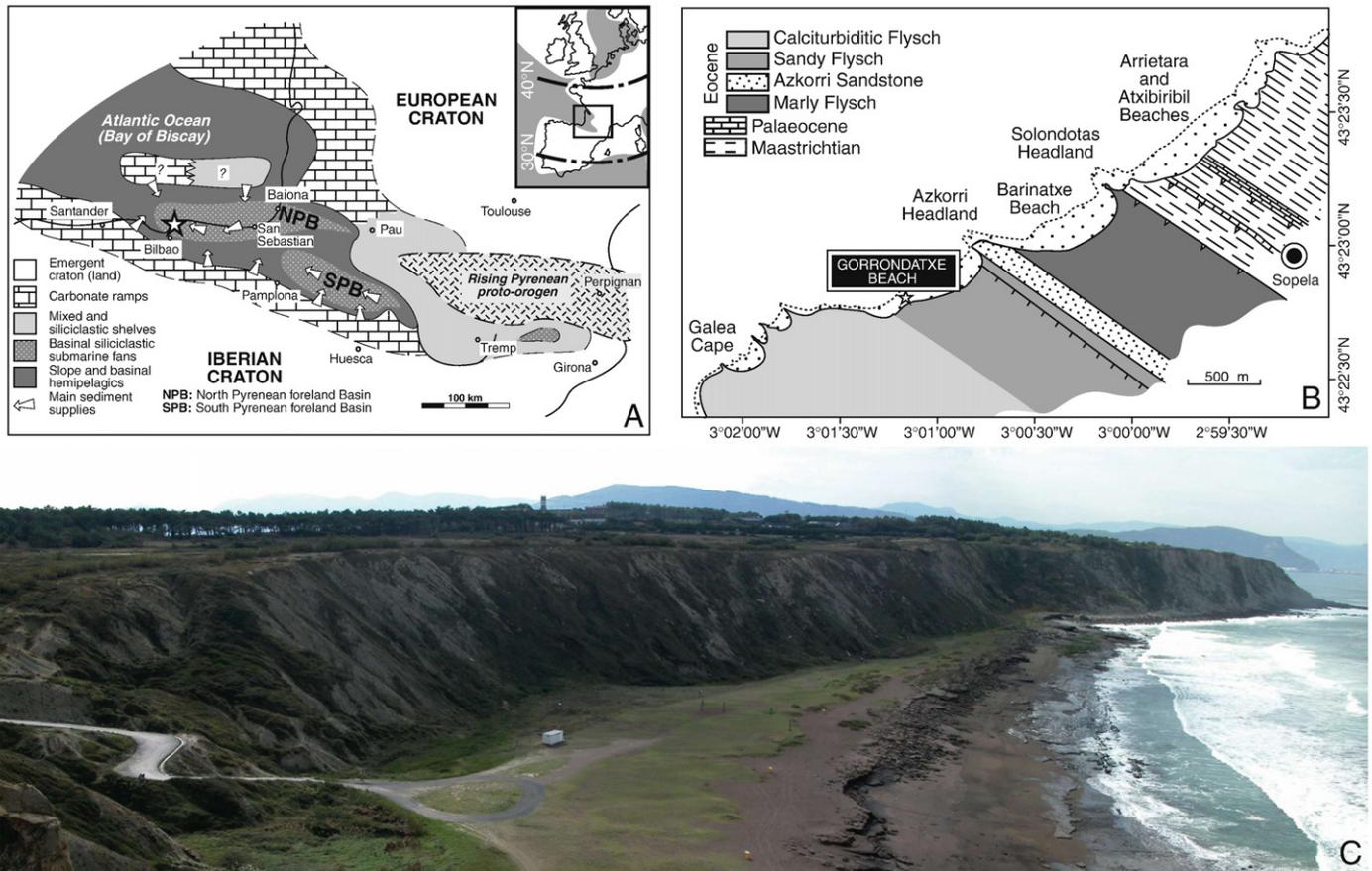

Fig. 1. Location of the Gorrondatxe section. A, paleogeographical reconstruction of the Pyrenean area in early Paleogene times (Payros et al., 2006). B, simplified geological map of the study area, showing lithostratigraphic units as used by Bernaola et al. (2006). The Gorrondatxe section is located at 43ºN23′N, 3º91′W. C, panoramic exposure of the Ypresian–Lutetian transition at Gorrondatxe beach.
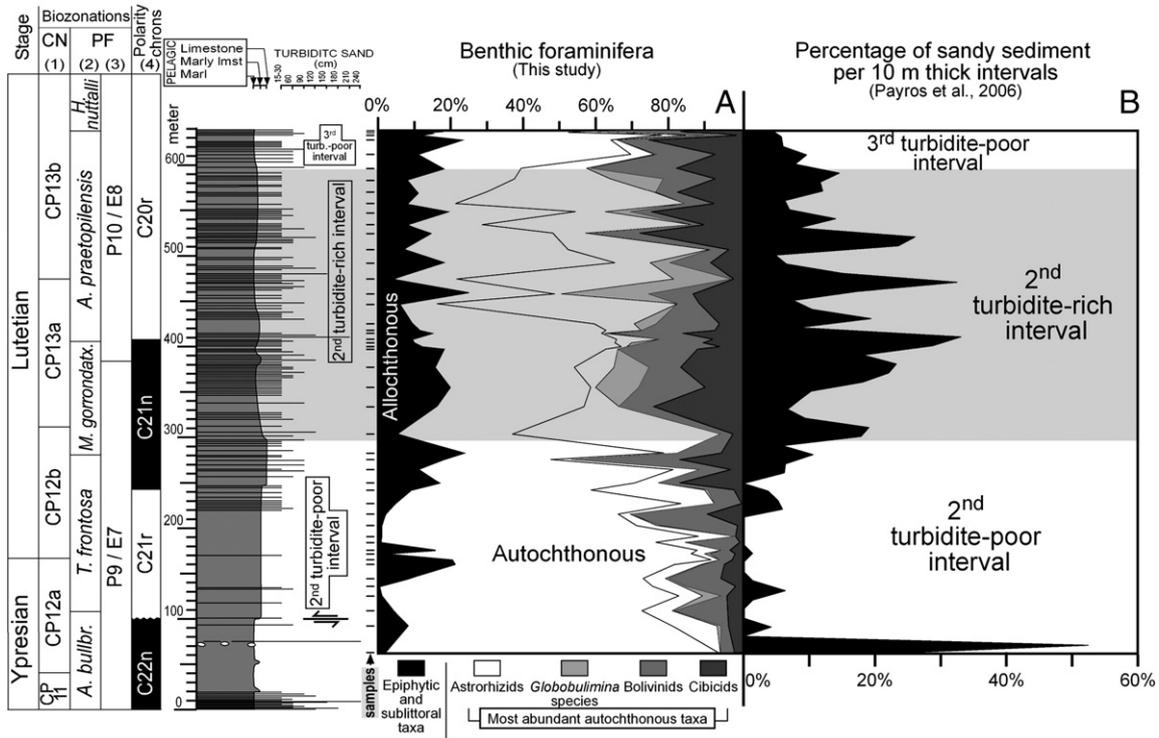
Fig. 2. A, stratigraphic distribution and relative abundance of autochthonous and allochthonous benthic foraminiferal taxa in the Gorrondatxe section. B, vertical variations in turbidite content (modified from Payros et al., 2006). Biostratigraphic data from Bernaola et al. (2006) and Payros et al. (2007): (1), calcareous nannofossil biostratigraphic zonation (Okada and Bukry, 1980). (2) and (3), planktic foraminiferal biostratigraphic zonation (Orue-Etxebarria et al., 1984, and Berggren et al., 1995 and Berggren and Pearson, 2005). (4), polarity chrons by Bernaola et al. (2006). A. bullbr. = Acarinina bullbrooki; H. nut. = Hantkenina nuttalli; M. gorrondatx. = Morozovella gorrondatxensis; T. frontosa = Turborotalia frontosa.

from the southern margin of the basin (Payros et al., 2006). A submarine fan fringe or basin plain, with occasional lateral sediment supply, has been suggested as the most likely sedimentary setting (Rodríguez-Tovar et al., 2010).

The Gorrondatxe section corresponds to the middle part of a 2300-m-thick Eocene (Y–L transition) succession (meter 800 to 1500 in Payros et al. (2006), meter 0 to 700 in this study) that extends from Solondotas Headland to the Galea Cape (Fig. 1). Payros et al. (2006, 2007) assessed volumetric variations in turbidites through this succesion, obtaining a semiquantitative estimation of the vertical variations in turbidite abundance and differentiating several intervals with variable amounts of turbidites (Fig. 2). In the studied Gorrondatxe section, three main intervals can be differentiated according to turbidite frequencies. The lower part of the section (20 to 294 m above base) corresponds to a "turbidite-poor" interval defined by a turbidite content that seldom exceeds 20% (2nd turbidite-poor interval of Payros et al., 2006, 2007). Higher up in the section, this interval becomes progressively richer in hemipelagic limestones. It is followed by a "turbidite-rich" interval (295 to 595 m above base), which is defined by a turbidite content that ranges between 10% and 80%, and averages higher than 20% (2nd turbidite-rich interval). Another turbidite-poor interval occurs towards the top of the studied section (596 to 638 m above base) (3rd turbidite-poor interval).

Reworked larger foraminifera and ostracods, fragments of other shallow water organisms (e.g., red algae) and carbonized plant remains are abundant in the basal part of many thick-bedded, mixed carbonate–siliciclastic turbidites at Gorrondatxe (Bernaola et al., 2006; Payros et al., 2006). The hemipelagic limestones and marls are rich in calcareous planktic microfossils, which have led to a complete biostratigraphic characterization of the Gorrondatxe section (Fig. 2; Orue-Etxebarria, 1985; Orue-Etxebarria and Apellaniz, 1985; Bernaola et al., 2006; Orue-Etxebarria et al., 2006; Payros et al., 2009b). Due to its high sedimentation rate and abundance of diverse

and well-preserved fossil groups, this section has been designated as the Global Stratotype Section and Point (GSSP) for the Ypresian/Lutetian boundary (Orue-Etxebarria et al., 2009; Molina et al., 2010).

3. Materials and methods

For the analysis of planktic and benthic foraminifera, we collected 124 samples from marly intervals throughout the Gorrondatxe section (this study, Bernaola et al., 2006 and Payros et al., 2006, 2007, 2009b). All samples were collected from sedimentologically similar deposits in order to compare results from different samples and to avoid artefacts produced by heterogeneous sampling. In order to elucidate the environmental conditions that prevailed in the Eocene deep sea it would be desirable to study the presumably autochthonous foraminiferal assemblages from the pelagic mudstones of the tripartite sequences, as the assemblages of the underlying turbiditic grey marls might contain allochthonous specimens transported by turbidity currents. Unfortunately, the limy variety of the pelagic mudstones was too hard to extract microfossils. Therefore, all samples were systematically collected at the transition from the turbiditic grey marl to the overlying whitish pelagic mudstone, where primary mixing is probably small. Artificial mixing caused by large bulk sampling over sedimentary intervals that include several thin-bedded layers can be readily ruled out.

The distribution of the 124 samples is quite homogeneous throughout the section and encompasses the two turbidite-poor intervals and the intervening turbidite-rich interval exposed in the Gorrondatxe section. The intervals of two distinct planktic foraminiferal biostratigraphic events, namely the first occurrence of *Morozovella gorrondatxensis* (398 to 418 m above base) and the first occurrence of *Hantkenina nuttalli* (627 to 638 m above base), were more closely sampled as this sampling also aimed at biostratigraphic studies. The turbidite-rich interval was thoroughly analysed in order to identify
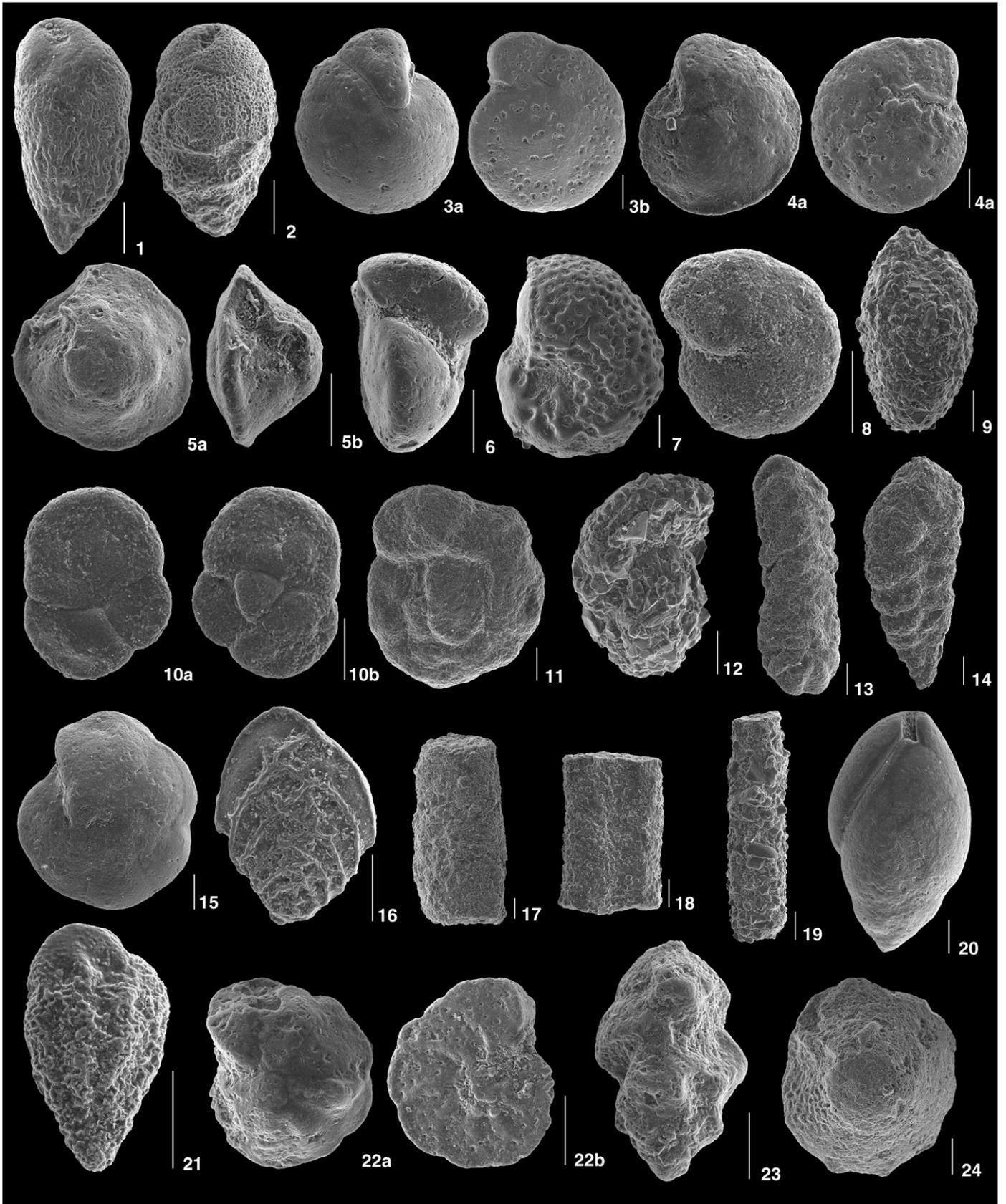
Plate 1. Scanning electron-micrographs of the most significant benthic foraminiferal taxa across the Ypresian–Lutetian transition in the Gorrondatxe section. All scale-bars represent 100 μm. 1, *Bulimina jarvisi* (meter 216). 2, *Bulimina trinitatensis* (meter 135.5). 3, *Cibicidoides eocaenus* (meter 65). 4, *Cibicidoides praemundulus* (meter 65). 5, *Nuttallides truempyi* (meter 216). 6, *Gyroidinoides girardanus* (meter 203). 7, *Anomalinoides capitatus* (meter 216). 8, *Nonion havanense* (meter 65). 9, *Karrerulina coniformis* (meter 190.8). 10, *Ammosphaeroidina pseudopauciloculata* (meter 611). 11, *Paratrochamminoides* sp. (meter 203). 12, *Recurvoides* sp. (meter 216). 13, *Spiroplectammina spectabilis* (meter 225). 14, *Spiroplectammina navarroana* (meter 611). 15, *Oridorsalis umbonatus* (meter 203). 16, *Aragonia aragonensis* (meter 216). 17, *Bathysiphon* sp. (meter 635.8). 18, *Nothia* sp. (meter 216). 19, *Rhabdammina* sp. (meter 265). 20, *Globobulimina ovata* (meter 354). 21, *Bolivinoides crenulata* (meter 203). 22, *Cibicides* sp. (meter 277). 23, *Angulogerina muralis* (meter 398). 24, *Asterigerina* sp. (meter 277).

vertical sedimentary variations that might indicate different environments within the submarine fan fringe. Although the turbidite content varies within this interval (Fig. 2), paleoenvironmental differences were not deduced (Payros et al., 2006). It was consequently concluded that the fossil assemblages would probably not vary along the turbidite-rich interval due to this reason and, therefore, that the sampling resolution would not affect the correct characterization of this interval.

All the samples were soaked in distilled water and washed under running water through 630 and 100 μm mesh sieves after ruling out the >63 to 100 μm fraction as the main component were juvenile planktic foraminifera. The residue was studied under a binocular microscope, showing that the abundance and preservation of benthic foraminifera are highly variable, especially in the 2nd turbidite-rich interval, where some of the samples are almost barren of benthic foraminifera. All the samples that proved unsuitable for quantitative studies were excluded from this study. This resulted in 50 samples being analysed; the turbidite-poor and turbidite-rich intervals are well represented by the selected samples, including the slices with higher and lower turbidite content within the turbidite-rich interval. Quantitative analyses of benthic foraminifera were based on representative splits (using a modified Otto micro-splitter) of approximately 300 specimens.

All identified taxa are listed in Appendix A, and the most significant ones are illustrated in Plate 1 and listed with their original references in Appendix B. The abundance of allochthonous taxa (epiphytic and reworked, sublittoral taxa) is noticeably high in the Gorrondatxe section (Fig. 2; Appendix A). In order to obtain information on local environments, the allochthonous taxa were excluded from the benthic foraminiferal data set. For foraminiferal assemblage characterization, we used relative abundances of autochthonous taxa and the ratio between calcareous and agglutinated taxa (C/A ratio) and infaunal and epifaunal morphogroups (I/E ratio). The diversity of the assemblages is expressed by the Fisher-α diversity index and the Shannon–Weaver heterogeneity index, H(S) (Fig. 3). They were obtained using PAST of Hammer et al. (2005). Rarefaction analysis was used to calculate species richness for 90 specimens (Sanders, 1968). The relative abundances of the main autochthonous benthic foraminiferal groups and species from the Gorrondatxe section are shown in Figs. 4 and 5. Elongate cylindrical calcareous and agglutinated taxa are usually broken into fragments and, therefore, we counted one specimen per every 3 fragments.

The most probable microhabitat preferences and environmental parameters (organic flux and bottom water oxygen levels) were inferred from the benthic foraminiferal morphotype analysis (Corliss, 1985, 1991; Corliss and Chen, 1988; Jones and Charnock, 1985; Jorissen et al., 1995; Kaminski and Gradstein, 2005). Interpretations based on morphotype analysis must be considered with caution as they rely on the shape of the tests as the only foraminiferal response to environmental change (e.g., Smart, 2002). Moreover, as most of the Eocene species are extinct, we assigned them to groups based on their morphological similarities (Appendix A; for more details see table 2 in Alegret et al., 2003).

We based the paleo-water depth estimates on the occurrence and abundance of depth-related species, their upper depth limits, and on the comparison between fossil and recent assemblages (e.g., Van Morkhoven et al., 1986; Murray, 1991, 2006; Alegret et al., 2001, 2003).

A hierarchical cluster analysis was carried out using PAST (Hammer et al., 2005). The similarity coefficient employed was the Pearson coefficient. The data matrix was standardized by converting real count data to relative abundances of autochthonous specimens in each sample. An R-mode analysis was performed on selected taxa
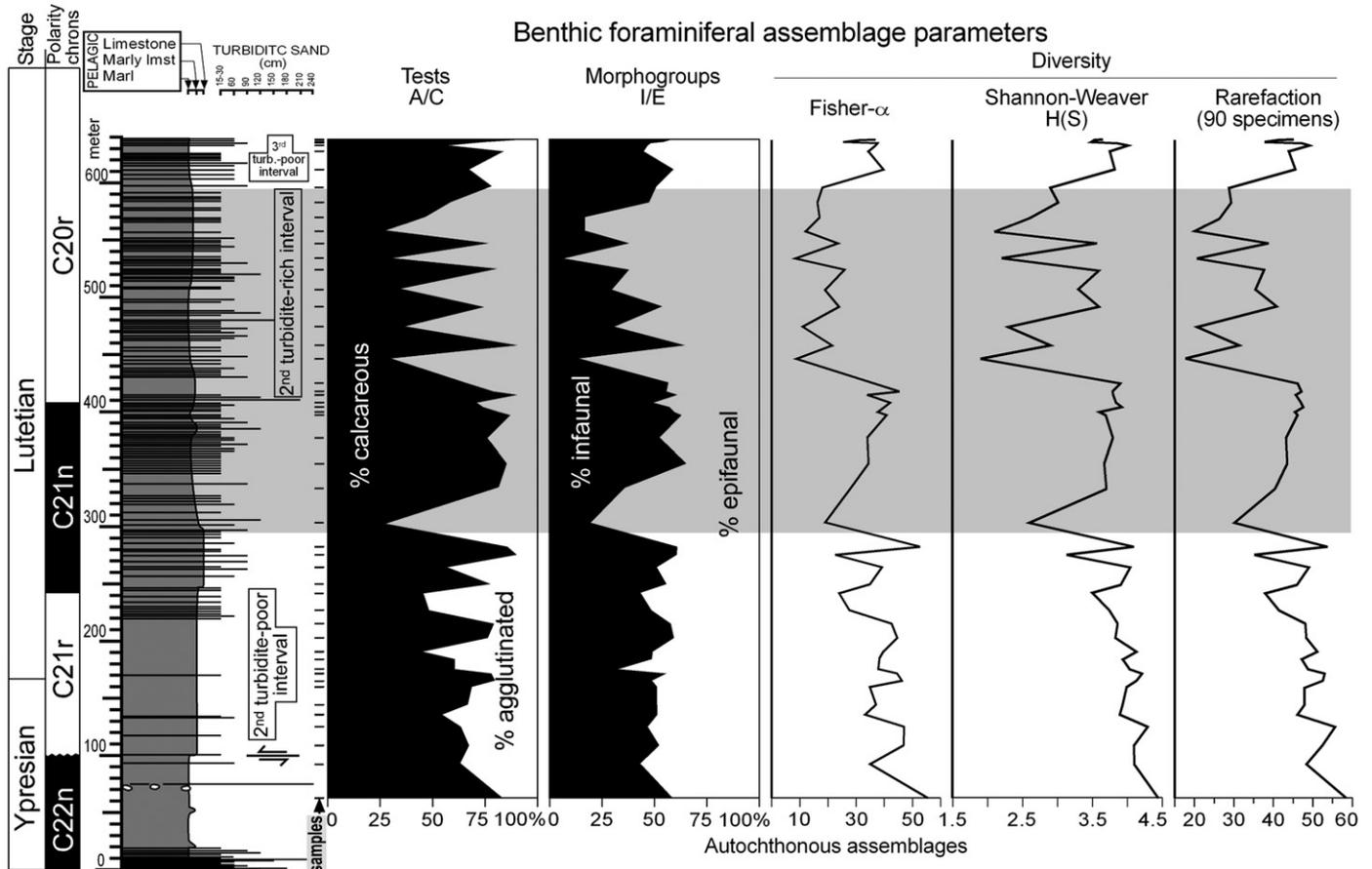

Fig. 3. Benthic foraminiferal assemblage parameters for the autochthonous taxa, including agglutinated/calcareous taxa ratio (A/C), infaunal/epifaunal taxa ratio (I/E), and Fisher -α, Shannon–Weaver H(S) and rarefaction diversity indices across the Ypresian–Lutetian transition in the Gorrondatxe section.
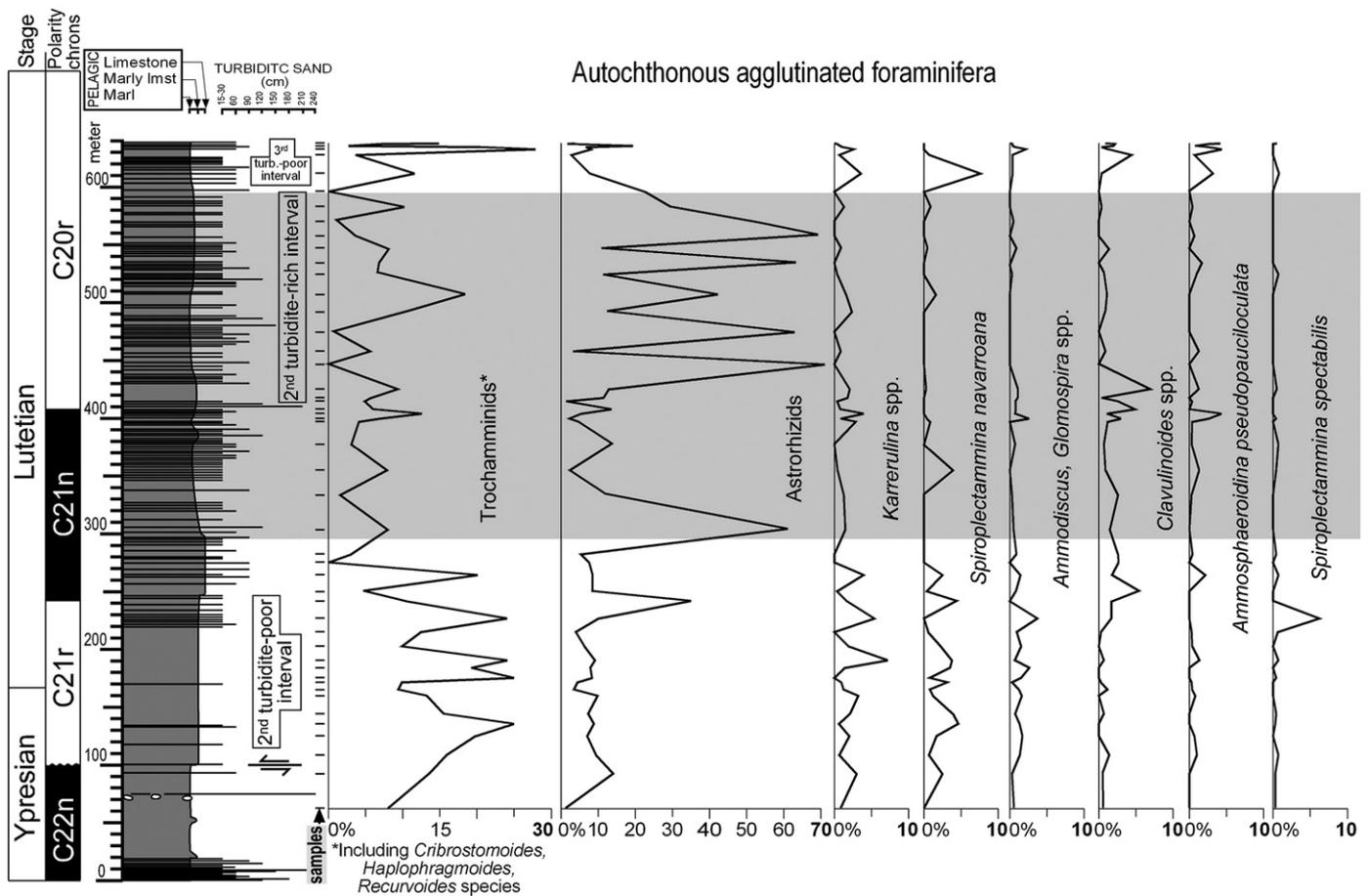
Fig. 4. Relative abundance of selected autochthonous agglutinated benthic foraminiferal taxa across the Ypresian–Lutetian transition in the Gorrondatxe section. Note the different scale for astrorhizids.

which showed a relative abundance >5% in at least one sample following Rogerson et al. (2006). Due to the high number of species at Gorrondatxe, we sorted species into genera or groups (e.g., trochamminids) that include several genera, taxonomically, morphologically or ecologically related (Table 1; Fig. 6). Species such as *Nuttallides truempyi*, *Spiroplectammina navarroana*, *Spiroplectammina spectabilis* and *Aragonia aragonensis* showed a distinct distribution, enough to consider them as independent components in our analyses. A total number of twenty-two taxa (16 calcareous and 6 agglutinated) from 50 samples were finally used for the analysis.

Detrended Correspondence Analysis (DCA) results were obtained using PAST (Hammer et al., 2005). DCA places both species and samples in the same space, samples and species that are clustered together sharing similar assemblages or distributions. The analysis was based on the same data set used for cluster analysis, in order to check the veracity of the assemblages derived from clustering (Table 1; Fig. 7). Ordinations of the samples and species were plotted on the first two DCA axes. DCA is also useful to investigate the relationship between benthic foraminifera and environmental variables. The first axis has been found to represent primary ecological gradients (Hammer and Harper, 2006).

4. Results

4.1. Autochthonous versus allochthonous taxa

Turbidity currents imply reworking and transport of material from the continental shelf and shallow upper slope towards deeper parts of the basin, where the allochthonous material is redeposited together with the authochtonous sediment. Therefore, in order to elucidate the environmental conditions that prevailed in the deep sea during the

deposition of the Gorrondatxe section, here we first deal with the distinction between allochthonous from autochthonous taxa. Total assemblage refers to autochthonous plus allochthonous assemblages.

Calcareous benthic foraminiferal assemblages in the Gorrondatxe section are characterized by a high dominance of asterigerinids, cibicids, bolivinids and *Globobulimina* species, whose relative abundance is very variable throughout the section (Fig. 2).

Asterigerinids and other taxa such as *Pararotalia audouini*, *Discorbis*, *Reusella* or *Quinqueloculina* species display moderate to poorly preserved tests. These taxa are more abundant in the 2nd turbidite-rich and 3rd turbidite-poor intervals than in the 2nd turbidite-poor interval, showing a positive correlation with the turbidite content (Fig. 2). All these taxa have been reported as shallow water taxa for Recent sediments, while asterigerinids have also been reported as free epiphytic taxa (e.g., Murray, 1991, 2006). Bolivinid species, mainly *Bolivinoides crenulata*, and cibicid species such as *Cibicides lobatulus*, show a similar distribution and occurrence, being more abundant up in the section, in the 2nd turbidite-rich and 3rd turbidite-poor intervals. Bolivinids and cibicids also occur in the 2nd turbidite-poor interval, bolivinids being fairly more abundant than cibicids. *Globobulimina* species, mainly *Globobulimina ovata*, show high fluctuations in abundance, being common to dominant (up to 24% of the total assemblages) in nine samples from the 2nd turbidite-rich interval. *Globobulimina* species are rare in the turbidite-poor intervals. Recent cibicids have an epifaunal mode of life, and are usually attached to and inhabiting elevated microhabitats, fixed to animals, plants or hard substrates like pebbles (e.g., Murray, 1991, 2006; Schweizer, 2006). The presence of cibicids in fossil bathyal assemblages has been related to sediment transportation (e.g., Phleger et al., 1953), or to plant material (to which cibicids lived attached) that floats into pelagic environments

Autochthonous calcareous foraminifera

Bolivinids

Cibicids

Globobulimina spp.

Angulogerina spp.

Uniserial calcareous

Anomalinoides spp.

Osangularia spp.

Unilocular calcareous

Cibicidoides spp.

Buliminids

Nuttallides truempyi

Gyroidinoides spp.

Nonion + Nonionella spp.

Oridorsalis umbonatus

Aragonia aragonensis

- - *Bolivinoides crenulata*

Fig. 5. Relative abundance of selected autochthonous calcareous benthic foraminiferal taxa across the Ypresian–Lutetian transition in the Gorrondatxe section. *Bolivinoides crenulata* is included in bolivinds.

Table 1

Relative abundance of groups of taxa selected for cluster analysis and Detrended Correspondence Analysis.

Taxa	Samples (m above section base)																							
	65	92	109	125	135	143.9	160.8	166.6	171.8	176.4	183.9	190.8	203	216	225	242	250	265	277	283	303	333	354	378
Angulogerina spp.	0.6	0.8	0.7	0.3	1.6		0.4	0.4		0.4		0.3	1.5	0.6	0.4	0.6	5.8	2.2	2.7	1.3		0.9	2.6	1.7
Anomalinoides spp.	1.7	3.0	2.4	3.8	2.0	1.1	2.0	5.7	5.4	7.7	3.5	2.4	2.7	1.2	4.1		4.7	3.2	3.9	4.0	4.0	5.8	3.5	2.4
Aragonia aragonensis	0.3	2.5	2.0	0.7		0.7							2.3	3.7					6.5					0.7
Astrorhizids	0.6	13.5	8.8	6.5	8.2	6.7	9.3	2.9	3.8	7.7	7.3	8.6	5.7	3.4	9.5	34.4	7.8	7.9	7.0	4.8	60.5	11.4	1.7	13.1
Bolivinids	4.0	2.2	15.3	1.7	13.8	15.5	7.3	4.5	7.0	3.1	14.9	0.3	21.4	21.7	7.9	7.8	7.0	9.7	36.4	15.9	3.5	11.4	22.7	10.3
Buliminids	7.5	1.1	2.0	5.1	5.9	6.4	5.2	4.5	6.4	2.7	5.0	2.7	5.0	5.2	5.0		0.8	1.8		6.2		1.6	2.6	1.4
Cibicids	2.3	4.4	4.4	4.4	2.0	6.7	6.5	3.7	2.2	4.2	0.9	2.1	1.5	10.1	0.4	2.8	21.0	4.0	21.3	7.9	3.0	29.5	13.1	20.3
Cibicidoides spp.	8.9	9.6	2.7	6.5	3.0	9.2	10.0	6.1	5.7	5.0	6.7	3.8	9.5	2.4	3.3	1.7	0.8	0.4	4.3	3.5	0.5	5.2	2.6	2.4
Clavulinoides spp.	0.6	0.5	1.4			0.7		1.2	0.3				0.7		0.3	1.7	1.7	5.4	1.8	2.7	2.6	1.5	0.9	0.7
Globobulimina spp.		1.1	0.7	5.1	1.0	1.1	0.8		1.6		0.3		1.1				1.1						14.8	11.4
Gyroidinoides spp.	3.4	1.1	3.1	3.4	2.0	2.1	2.8	9.4	5.1	7.3	3.5	1.7	1.9	1.5	2.1		0.8	2.5	1.2	3.1	0.5	1.0	2.2	0.7
Karrerulina spp.	0.9	3.0	0.7	2.0	0.7	2.1	3.2	1.2	1.0		1.5	7.2	1.9		5.4	1.7	0.4	4.0				1.5	1.3	0.4
Nonion and *Nonionella* spp.	7.2	0.8	3.4	2.0	2.3	1.1	2.8	2.9	4.1	1.5	4.1	2.4	2.7	3.4	1.7		2.3	1.4	3.5	5.7	0.5	0.3	1.7	2.4
Nuttallides truempyi	4.0	4.1	4.4	4.4	2.3	5.3	4.0	8.2	5.1	6.5	5.2	3.4	4.2	1.8	3.7	1.1	0.4	4.3	0.4	5.3		1.3	0.4	2.1
Oridorsalis spp.	5.2	2.5	3.4	2.7	3.3	3.2	2.8	3.3	2.9	5.8	2.0	5.5	3.1	5.5	8.7	1.1	2.7	4.3	0.8	1.8		1.6	0.9	0.7
Osangularia spp.	7.2	3.6	2.0	2.7	2.3	0.7		4.5	4.5	1.2	3.2	2.4	3.8	2.8	2.5	4.4	3.5	4.7	0.8	3.5	2.5	5.5	0.4	2.4
Spiroplectammina navarroana		2.5	0.7	1.7	4.6	3.9	1.2	0.8	3.2	0.8	3.5	3.8	2.3	0.6			4.4	0.4	2.5				3.9	
Spiroplectammina spectabilis	0.3	0.3	0.7		0.3	0.4		0.4					0.7		0.6	6.2		0.7		0.4			0.4	0.7
Trifarina spp.		0.3	1.0	0.3		1.1		0.4	0.6		0.3					0.4		2.7	0.7	1.6	0.9	1.0	1.7	0.7
Trochamminids	8.1	13.7	15.9	19.8	25.0	15.5	13.3	9.4	9.9	25.0	19.2	24.1	9.9	12.5	24.1	10.6	4.7	20.1		3.1	8.0	1.6	7.9	3.1
Unilocular calcareous	6.0	0.8	3.1	0.7	1.3	1.1	3.2	7.8	4.1	1.9	2.6	1.7	3.4	3.7	0.4	0.6	0.4	2.2	3.1	4.8			2.2	1.4
Uniserial calcareous	8.6	16.6	7.1	8.9	4.6	5.3	11.7	6.6	12.4	6.5	3.2	11.0	4.6	2.1	2.5	13.3	14.4	5.8	3.9	5.7	5.5	4.9	2.2	6.9

Table 1 (*continued*)

| Taxa	Samples (m above section base)																									
	398	400	405	409	415	418	425	446	459	474	492	508	524	535	547	557	570	583	596	611	627	633.5	635.4	635.8	636.2	638
Angulogerina spp.	5.0		2.5	2.0	5.3	0.7	0.6		2.6				3.8		2.3	0.7	1.1	0.4	4.0	2.4	3.7	3.1	1.4	2.4	4.5	2.3
Anomalinoides spp.	2.9	5.2	2.5	6.1	3.4	4.3	6.4		1.7		3.8		3.5	6.8	5.9	0.7	3.1	1.8	3.3	4.8	1.9	3.9	3.6	1.6	2.6	3.7
Aragonia aragonensis			0.4			0.4	0.3						0.7		0.5	0.7			0.4							1.4
Astrorhizids	4.1	1.7	5.0	13.0	0.8	10.8	12.3	70.5	2.6	62.33	11.8	41.6	10.8	62.7	10.4	68.6	52.4	28.8	22.1	7.2	2.2	7.4	6.1	18.8	1.1	3.3
Bolivinids	26.9	29.0	18.0	16.2	23.3	22.7	19.2	6.41	16.3	0.7	13.7	5.4	16.8	3.4	7.2	8.8	6.8	15.5	28.7	17.9	11.5	10.0	20.1	18.8	30.0	26.5
Buliminids	3.7	1.3	2.2	3.6	1.9	5.1	1.9		2.6	0.7	3.8	0.5	0.7		0.5	0.9	0.4			2.4	4.3	2.6	4.3	3.5		1.9
Cibicids	15.3	7.4	12.2	9.3	19.5	8.7	7.2	12.8	18.5	2.7	10.9	4.3	33.2	11.9	32.2	8.76	20.4	8.4	22.4	8.8	33.7	2.2	7.9	18.0	21.0	17.2
Cibicidoides spp.	2.5	3.9	2.5	3.2	2.6	4.7	2.4	1.3	1.3	1.4	2.4	2.2	1.4		1.4	0.7		0.9	0.4	2.0	5.2	3.9	2.2	0.4	0.7	1.4
Clavulinoides spp.	1.2	3.0	1.1	4.9	2.6	0.4	6.9		0.9		0.9	1.1	0.7		1.4			0.4		0.4	4.4	1.3	0.4	2.0	2.2	0.9
Globobulimina spp.			4.0		1.9	0.4	6.7		32.2	16.4	6.6	0.4	0.7		8.6			0.5	15.9	1.5	0.8		5.7	1.1	0.4	1.1
Gyroidinoides spp.	4.1	1.3	1.4	2.4	3.4	1.1	0.3	1.3	3.9		1.4	1.1	0.7		1.8		1.1	0.9		1.2	1.1	1.7	3.2		1.9	2.8
Karrerulina spp.	2.9	0.9	4.0	0.8	0.4	1.8	2.1		0.9		2.4	1.6	0.4		0.9			1.3		3.6	0.7	2.6	1.1	0.8	0.4	
Nonion and *Nonionella* spp.	2.5	1.7	2.9	3.6	5.3	4.0	0.8		2.1			1.9	0.5	1.1	1.8		0.5		1.5	0.8		3.9	2.9	3.5	3.0	2.8
Nuttallides truempyi	1.2	2.6	1.8	1.6	1.5	4.7	1.1		0.4	0.7	1.0		1.4		1.8					0.8	0.7	0.9	4.7	0.4	3.0	0.9
Oridorsalis spp.		1.3	1.1	1.6	0.4	0.7	0.8		0.4	0.7	1.4	0.5	0.4		0.9	0.7		0.4		2.8	1.5	0.4	1.4		0.7	2.3
Osangularia spp.	2.5	7.8	3.6	4.9	2.3	2.9	1.9			0.7	3.3	1.1	2.5	5.1			1.6	1.8	0.7	0.8	3.0	3.1		0.4	3.0	3.3
Spiroplectammina navarroana	0.8	0.4					0.3					1.6			0.5			0.9		7.6	0.7					
Spiroplectammina spectabilis		0.4					0.5						0.7							0.8						0.5
Trifarina spp.	0.4		1.4	2.3	0.8					0.7				1.7		2.2	1.1	0.4	1.5	0.8	2.6	0.9	0.7	7.5	2.2	1.4
Trochamminids	4.1	6.9	12.6	6.1	4.9	5.8	9.3		5.6	0.7	10.9	18.4	6.6	6.8	8.1	3.7	1.1	10.2		11.6	3.7	27.9	20.5	2.7	7.1	14.9
Unilocular calcareous	2.1	3.5	3.2	3.6	5.3	4.7		2.6	0.4		1.9	2.2	1.4		1.4		2.6	1.8	2.9	1.2	0.7	1.7	1.4	7.5	2.6	2.8
Uniserial calcareous	6.2	6.9	9.4	3.6	4.1	4.3	9.6	3.9	2.6	8.9	13.7	10.3	5.2	1.7	4.1	2.2	1.6	4.0	1.1	5.2	5.2	5.2	5.0	2.7	4.9	1.9
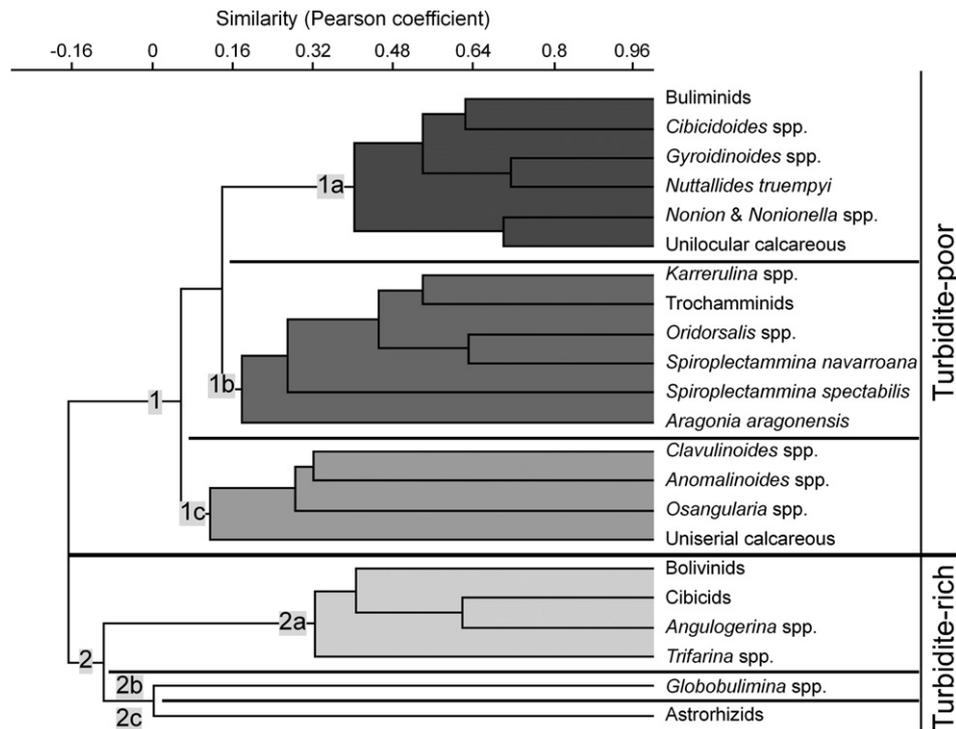
Fig. 6. Dendogram resulting from the cluster analysis of the taxa that comprise >5% of the autochthonous assemblages in any sample in the Gorrondatxe section. Distinguished assemblages are named with 1a, 1b, 1c, 2a, 2b and 2c, and shown on the right.

after storms (Sprovieri and Hasegawa, 1990). However, living specimens are found down to 1000 m depth, and attached to hard substrates in high-energy settings with strong currents, and are thought to be suspension feeders (Murray, 1991, 2006; Lutze and Thiel, 1989; Schönfeld, 2002). *C. lobatulus* seems to be closely linked to near-bottom currents for its nutritional needs (Altenbach et al., 1999). Bolivinids and *Globobulimina* species have infaunal microhabitat preferences, i.e., they live in the uppermost 10 cm of the sediments, and are dominant in marine areas with high organic matter fluxes (e.g., Jorissen et al., 2007).

Agglutinated benthic foraminiferal assemblages are dominated by astrorhizids and trochamminids, which show a striking negative correlation (Fig. 2). Astrorhizids are strongly dominant in the 2nd turbidite-rich interval (up to 66% of the total assemblage), while trochamminids are the most abundant taxa of the total assemblage in the 2nd turbidite-poor interval (up to 25% of the total assemblage). Both astrorhizids and trochamminids are typical components of deep water agglutinated foraminifera (DWAF) biofacies (e.g., Kaminski and Gradstein, 2005).

Although the aforementioned taxa seem to be controlled by different parameters, they (with the exception of trochamminids) show a common distribution in our dataset (high abundance in the 2nd turbidite-rich interval), suggesting that turbidite accumulation played an important role in their abundance and distribution.

We consider asterigerinids and other shallow water or sublittoral taxa as reworked taxa that were transported downslope by turbidity currents. Conversely, cibicids, bolivinids, *Globobulimina* species and astrorhizids seem to be autochthonous taxa.

4.2. Benthic foraminiferal assemblage parameters

Autochthonous assemblages are dominated by calcareous tests throughout the studied section, except for the samples where astrorhizids dominate (all of them in the 2nd turbidite-rich interval, and three samples in the 2nd turbidite-poor interval where trochamminids are abundant although with figures close to 50%; Fig. 3). The ratio of infaunal and epifaunal morphotypes shows values encompassed between 40–60% throughout the Gorrondatxe section, except for the samples characterized by a high abundance of epifaunal astrorhizids in the 2nd turbidite-rich interval, and one sample (meter 176.4) in the 2nd turbidite-poor interval (Fig. 3).

Diversity (Fisher-α and Shannon–Weaver H(S)) indices values show a decreasing trend from the 2nd turbidite-poor interval into the 2nd turbidite-rich interval, and a distinct recovery in the 3rd turbidite-poor interval (Fig. 3).

Species richness is highly variable at Gorrondatxe, with values between 28 and 110 species for the autochthonous assemblages (Appendix A). In order to avoid artifacts after substracting allochthonous specimens, we recalculated the species-richness values by using rarefaction (Fig. 3). Rarefaction shows the highest number of species in the 2nd turbidite-poor interval, decreasing numbers in the 2nd turbidite-rich interval, and a clear recovery in the 3rd turbidite-poor interval. The lowest values are recorded in the samples with a high abundance of astrorhizids.

4.3. Assemblage composition

Trochamminids (e.g., *Trochamminoides* and *Paratrochamminoides* species), *Recurvoides*, *Haplophragmoides* and *Cribrostomoides* species are the most abundant agglutinated taxa in the turbidite-poor intervals in the studied section (all together up to 28% of the autochthonous assemblages; Fig. 4). Astrorhizids (e.g., *Bathysiphon*, *Nothia* and *Rhabdammina* species) strongly dominate among agglutinated taxa in the 2nd turbidite-rich interval (up to 70.5% of the autochthonous assemblages; Fig. 4). Astrorhizids from the turbidite-rich interval mostly include taxa with a rough finish. *Karrerulina* species and *S. navarroana* are also abundant, while *Ammodiscus* and *Glomospira* species, and *Ammosphaeroidina pseudopauciloculata* are common (Fig. 4). *Clavulinoides*, *Vulvulina* and *Gaudryina* species dominate among the less common calcareous-cemented agglutinated taxa at Gorrondatxe (Fig. 4; Appendix A).

Among calcareous taxa, cibicids and bolivinids clearly dominate the autochthonous assemblages (Fig. 5). *B. crenulata* is the most
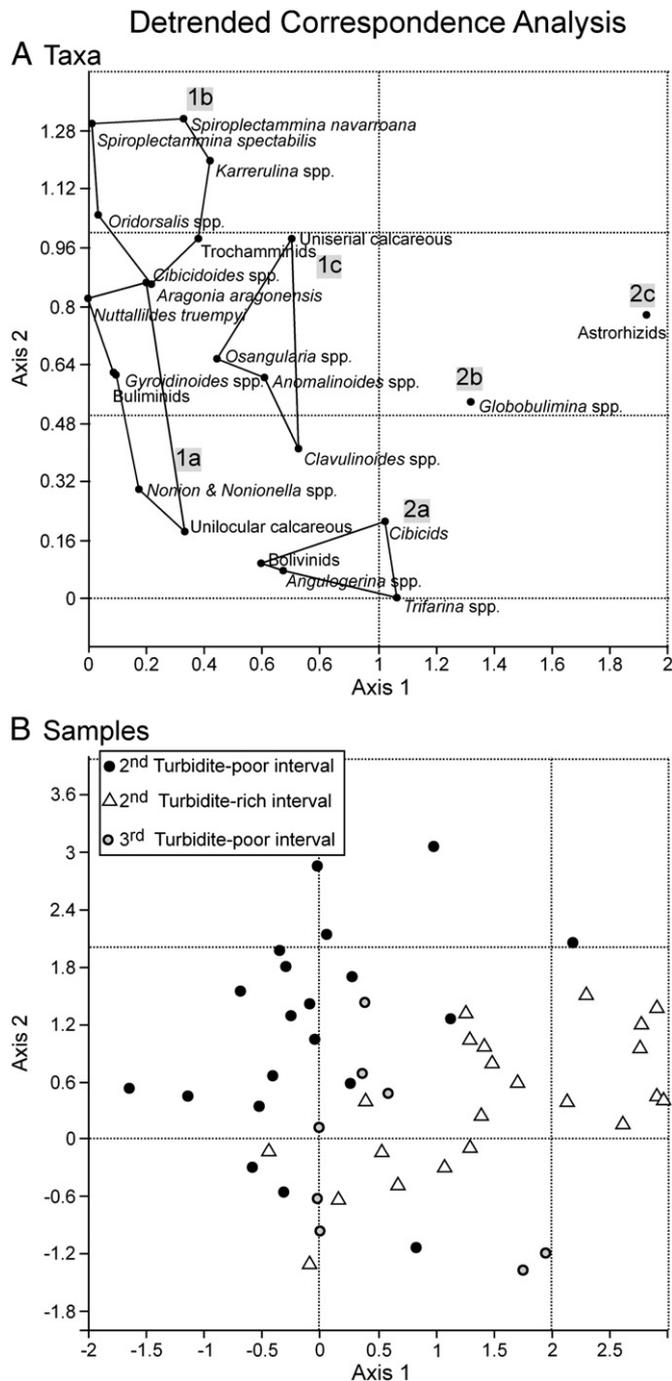
Detrended Correspondence Analysis

A Taxa

B Samples

Fig. 7. Results of Detrended Correspondence Analysis for those taxa that comprise five percent or more of the autochthonous assemblages in any sample (A), and for samples (B) in the Gorrondatxe section. The samples are shown by symbol, relating to the interval they belong to.

abundant bolivinid (up to 32% of the autochthonous assemblages at meter 277; Fig. 5). *Globobulimina* species are common to dominant in 9 samples from the 2nd turbidite-rich interval. Buliminids, *Cibicidoides*, *Oridorsalis*, *Osangularia*, *Anomalinoides*, *Gyroidinoides*, *Nonion* and *Pullenia* species, as well as uniserial (e.g., siphonodosariids, nodosariids) and unilocular calcareous taxa (e.g., *Fissurina* and *Palliolatella* species) are common at Gorrondatxe (Fig. 5). Uniserial calcareous, *Anomalinoides* and *Osangularia* species are distributed fairly evenly throughout the section, while the other taxa are more abundant in the turbidite-poor intervals. The aforementioned groups usually include a high number of species (e.g., *Bulimina kugleri*, *Bulimina mexicana*, *Bulimina glomarchallangeri* or *Bulimina trinitatensis*

among buliminids), without any species in particular being distinctively more abundant (Appendix A).

4.4. Definition of foraminiferal assemblage types

Based on the results from cluster analysis together with quantitative analyses of benthic foraminifera, we can distinguish 6 types of assemblages in the studied section (Fig. 6). Assemblages type 1 show preference for the turbidite-poor intervals, while assemblages type 2 do so for the turbidite-rich interval:

- Assemblage 1a: defined by common buliminids, *N. truempyi*, *Cibicidoides*, *Nonion*, *Nonionella* and *Gyroidinoides* species, and unilocular calcareous taxa; high diversity.
- Assemblage 1b: defined by high abundance of agglutinated taxa (trochamminids, *Karrerulina* species, *S. navarroana* and *S. spectabilis*), and the occurrence of *Oridorsalis* species and *A. aragonensis*.
- Assemblage 1c: defined by common uniseral calcareous taxa, *Clavulinoides*, *Anomalinoides* and *Osangularia* species. These taxa are less abundant but also common in the turbidite-rich interval.
- Assemblage 2a: defined by high dominance of bolivinids or cibicids, and occurrence of *Angulogerina* and *Trifarina* species; moderate diversity.
- Assemblage 2b: defined by high dominance of *Globobulimina* species; moderate to low diversity.
- Assemblage 2c: defined by strong dominance of astrorhizids; very low diversity.

The results from DCA added statistical evidence for the assemblages designated in this study (Fig. 7A). Assemblages 1a and 1b (turbidite-poor intervals) have low axis 1 values, while assemblages 2a, 2b and 2c (turbidite-rich interval) have high axis 1 values. Assemblage 1c (turbidite-poor intervals) has intermediate axis 1 values.

It is possible to observe a trend in the DCA ordination for samples (Fig. 7B): samples from the 2nd turbidite-poor interval have low axis 1 values; samples from the 3rd turbidite-poor interval have intermediate axis 1 values; and samples from the 2nd turbidite-rich interval have highest axis 1 values. Axis 1 represents primary ecological gradients (Hammer and Harper, 2006), and it seems to be related to disturbance and other closely related parameters such as supply of organic matter to the seafloor in the Gorrondatxe section.

5. Discussion

5.1. Influence of water depth

Benthic foraminiferal assemblages have traditionally been used as paleobathymetric proxies (e.g., Van Morkhoven et al., 1986; Murray, 2006). Representatives of the bathyal and abyssal Velasco-type fauna (Berggren and Aubert, 1975), such as *N. truempyi* and *B. trinitatensis* are common at Gorrondatxe. Other common taxa at Gorrondatxe include bathyal species such as *Buliminella grata* and *Gyroidinoides* species, as well as other species that were common at lower bathyal and abyssal depths during the Paleogene, such as *B. jarvisi*, *B. semicostata* and *B. glomarchallangeri* (e.g., Tjalsma and Lohmann, 1983; Van Morkhoven et al., 1986). Representatives of the sublittoral Midway-type fauna (Berggren and Aubert, 1975), including *Anomalinoides acutus*, *Osangularia plummerae* and *Pullenia quinqueloba*, are slightly common at Gorrondatxe. *Abyssamina quadrata* and *Quadrimorphina profunda*, which are most common at abyssal water-depths during the Paleogene (Tjalsma and Lohmann, 1983), are very scarce at Gorrondatxe.

Species of *Cibicidoides* are common at Gorrondatxe and are excellent paleobathymetric markers: *Cibicidoides eocaenus* was primarily a bathyal species in the Eocene, while *Cibicidoides mexicanus* was common at middle and lower bathyal depths during the Oligocene (Van Morkhoven et al., 1986; Katz et al., 2003). There are some

discrepancies in the literature about *Cibicidoides praemundulus*. Katz et al. (2003) considered that it was common in upper to middle bathyal zones during the Oligocene, whereas Van Morkhoven et al. (1986) considered it was mostly a lower bathyal and abyssal form. Therefore, *Cibicidoides* species suggest a middle to lower bathyal paleo-water depth during the deposition of the Gorrondatxe section.

The mixture of flysch-type and calcareous-cemented agglutinated taxa observed at Gorrondatxe is typical of the "low to mid-latitude slope" DWAF biofacies of Kuhnt et al. (1989). This biofacies was also found in upper Paleocene and lower Eocene sediments in the nearby Zumaia section (e.g., Alegret et al., 2009) and in the submarine fan/channel complex of the Eocene Ainsa System (Southern Pyrenees; Jones et al., 2005).

Benthic foraminiferal data indicate a lower bathyal depth of deposition during the Y–L transition at Gorrondatxe. This is in agreement with the estimated paleodepth of about 1500 m based on paleogeographic studies for the area (Orue-Etxebarria and Lamolda, 1985; Payros et al., 2006).

5.2. Influence of sedimentary disturbance

Turbidites have a strong influence on the benthic foraminiferal occurrence and distribution at Gorrondatxe. Turbidites and other downslope sediment transport processes often disturb the seafloor by erosion and/or rapid sedimentation of new, usually azoic material. Studies of living assemblages from active canyons indicate that opportunistic, simple agglutinated species (e.g., *Technitella melo*, *Reophax*) are able to colonize habitats rapidly after sediment disturbance (e.g., Hess et al., 2005; Koho et al., 2007). The absence of this typical ruderal (i.e., initial recolonisation) assemblage at Gorrondatxe may be due to taphonomic processes as agglutinated foraminifera have a lower preservation potential than calcareous foraminifera (Rogerson et al., 2006; Koho, 2008).

Flysch-type foraminiferal assemblages characterize clastic substrates that are commonly found within the hemipelagic intercalations of the turbidite flysch-sequences, and therefore are considered to represent early colonization assemblages (Kaminski et al., 1996). Deep-sea fan environments are commonly composed of autochthonous agglutinated "*Rhabdammina* faunas" and transported allochthonous shelfal faunas, related to hemipelagic-dominated and turbidite-dominated sedimentation respectively (Jones, 2006). At Gorrondatxe, assemblage 2c is characterized by strong abundance of astrorhizids, arborescent and tubular agglutinated foraminifera, which are the main component of flysch-type assemblages. This assemblage shows a strong preference for the turbidite-rich interval. Astrorhizids are epifaunal suspension feeders that are usually associated with oligotrophic conditions (e.g., Kaminski and Gradstein, 2005; de Mello e Sousa et al., 2006), but also with higher food supply or increased bottom water activity (e.g., Murray, 2006; Szarek et al., 2009). At Gorrondatxe, specimens with a roughly finished agglutinated test, included in *Bathysiphon* genera, are noticeably more abundant in the turbidite-rich interval (Fig. 4), being probably related to increased sedimentary disturbance or increased supply of organic matter. Instead, other astrorhizids are less abundant. A similar distribution has been recorded at the Nazarén Canyon, Portuguese continental margin, where *Bathysiphon* species occur in sediments with higher bio-available carbon flux, while arborescent and tubular foraminifera are common on the canyon terraces and in the lower canyon, being nearly absent from the canyon axis (Koho et al., 2007). The fact that different genera of astrorhizids have different ecological preferences suggests that their distribution is probably related to controlling parameters such as sedimentary disturbance and food availability.

The clear preference of agglutinated foraminifera (excluding astrorhizids) for the turbidite-poor intervals, combined with the high diversity of calcareous assemblages (assemblage 1b) at Gorrondatxe

compares well with climax assemblages from oligotrophic low-energy extra-canyon environments (Rogerson et al., 2006).

As discussed above, taphonomical processes may have played an important role at Gorrondatxe. Active currents may also constitute a main taphonomical factor leading to either winnowing or addition of components (e.g., Jorissen et al., 2007). At Gorrondatxe, we have regarded epifaunal cibicids, a main component of the turbidite-rich interval, as autochthonous taxa whose abundance was probably controlled by current activity, as in recent assemblages (e.g., Schönfeld, 2002). Samples with low benthic foraminiferal standing stocks in the turbidite-poor interval also support high-energy environments with common sedimentary disturbance.

5.3. Organic matter supply

Sediment transport processes like turbidity currents imply the remobilization of shallower material, disturbance of seafloor and resedimentation in deeper parts of the basin. The remobilized material may include substantial amounts of organic matter, such as algal remains, which could be further distributed by lateral advection. Consequently, most of the organic matter would be of fairly low quality, i.e., refractory organic matter, a condition that especially favors opportunistic, shallow-infaunal taxa (e.g., Koho et al., 2008).

Bolivinids and *Globobulimina* species have infaunal microhabitat preferences, i.e., they live in the uppermost 10 cm of the sediments, and are dominant in marine areas with high organic matter fluxes, such as canyons and continental margins (e.g., Jorissen et al., 1994, 2007; Schmiedl et al., 2000; Thomas, 2007). A strong dominance of these taxa has also been correlated with oxygen depletion, resulting from the oxidation of organic carbon (e.g., Lutze and Coulbourn, 1984; Corliss and Emerson, 1990; Corliss, 1991; Gooday, 1994; Schmiedl et al., 1997; Bernhard and Sen Gupta, 1999; Thomas et al., 2000). However, no sedimentary evidence for low oxygen conditions has been observed at Gorrondatxe, and trace fossils point to good oxygenation at the seafloor (Rodríguez-Tovar et al., 2010).

The dissimilarity between the occurrence and abundance of bolivinids and *Globobulimina* species at Gorrondatxe may represent different environmental conditions. Bolivinids quickly take advantage of the organic-rich turbidite deposits and are able to reproduce rapidly, dominating the assemblages between the recurrent turbidite events (Hess and Jorissen, 2009). Assemblages dominated by bolivinids and buliminids have been interpreted as typifying an early stage of ecosystem recolonisation in environments with frequent sediment resuspension (e.g., Rogerson et al., 2006; Hess and Jorissen, 2009). The high abundance of bolivinids and the moderate diversity of assemblage 2a from the Gorrondatxe section compares well with the former assemblages, with common low-quality organic matter in the turbidite-rich interval. We consider bolivinids (mainly *B. crenulata*) as opportunistic taxa that proliferate in high-energy environments, with sedimentary disturbance and increased supply of refractory organic matter.

Assemblages dominated by *Globobulimina* species have been reported from stable distal canyon and fan environments, and are thought to indicate relatively stable ecosystem conditions, no longer influenced by repeated resedimentation events (e.g., Rogerson et al., 2006; Koho et al., 2007; Hess and Jorissen, 2009). Axis 1 on DCA, which represents primary ecological gradients, seems to be related to disturbance and other closely related parameters such as supply of organic matter to the seafloor. If we assume that *Globobulimina* species (assemblage 2b) reflect relatively stable ecosystem conditions, their distribution on DCA (showing high values of axis 1) is difficult to explain (Fig. 7). However, this lack of strong correlation between axis 1 and one single controlling parameter supports the idea that benthic foraminifera are controlled by interdependent parameters. The distribution pattern of *Globobulimina* species reflects distinct conditions probably related to abundant refractory organic matter and, as compared to fossil and Recent assemblages, a low-energy regime. However, there is no

evidence for stable conditions since taxa indicative of current activity, such as cibicids, are also common in samples with abundant *Globobulimina* species. Cibicids show a stronger positive correlation with bolivinids, though.

6. Conclusions

Quantitative studies of benthic foraminifera from the lower bathyal Gorrondatxe section (Basque-Cantabrian Basin), together with R-mode cluster and Detrended Correspondence Analyses, allowed us to define 6 deep-sea autochthonous assemblages after removing allochthonous taxa from the foraminiferal counts. These assemblages have been related to the turbidite content, revealing the importance of different environmental controlling parameters, such as sedimentary disturbance, organic matter supply and quality, and current activity in a lower–middle Eocene submarine fan system.

High diversity assemblages (type 1) with common middle–lower bathyal calcareous and agglutinated (mainly trochamminids) benthic foraminifera show preference for the turbidite-poor intervals (turbidite content <20%). It may be inferred that these assemblages reflect climax conditions from low-energy environments.

Moderate to low diverse and high dominance assemblages (type 2) prevail in the turbidite-rich interval (turbidite content >20%), and they characterize different environments. Assemblage 2a is dominated by cibicids and bolivinids. Cibicids seem to be related to high current activity while bolivinids (mainly *B. crenulata*) emerge as opportunistic taxa that proliferate in high-energy environments, with sedimentary disturbance and a high input of low-quality organic matter. Assemblage 2b is restricted to the turbidite-rich interval and is dominated by deep-infaunal *Globobulimina* species, probably related to an enhanced input of low-quality organic matter in a low-energy regime. Assemblage 2c is characterized by a very strong dominance of roughly finished astrorhizids and very low diversity, and it has been related to a high bottom water activity and sedimentary disturbance.

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