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Foraminiferal assemblages as palaeoenvironmental bioindicators in Late Jurassic epicontinental platforms: Relation with trophic conditions

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Foraminiferal assemblages from the neritic environment reveal the palaeoecological impact of nutrient types in relation to shore distance and sedimentary setting. Comparatively proximal siliciclastic settings from the Boreal Domain (Brora section, Eastern Scotland) were dominated by inner-shelf primary production in the water column or in sea bottom, while in relatively seawards mixed carbonate-siliciclastic settings from the Western Tethys (Prebetic, Southern Spain), nutrients mainly derived from the inner-shelf source. In both settings, benthic foraminiferal assemblages increased in diversity and proportion of epifauna from eutrophic to oligotrophic conditions. The proximal setting example (Brora Brick Clay Mb.) corresponds to Callovian offshore shelf deposits with a high primary productivity, bottom accumulation of organic matter, and a reduced sedimentation rate for siliciclastics. Eutrophic conditions favoured some infaunal foraminifera. Lately, inner shelf to shoreface transition areas (Fascally Siltstone Mb.), show higher sedimentation rates and turbidity, reducing euphotic-zone range depths and primary production, and then deposits with a lower organic matter content (high-mesotrophic conditions). This determined less agglutinated infaunal foraminifera content and increasing calcitic and aragonitic epifauna, and calcitic opportunists (i.e., *Lenticulina*). The comparatively distal setting of the Oxfordian example (Prebetic) corresponds to: (i) outer-shelf areas with lower nutrient input (relative oligotrophy) and organic matter accumulation on comparatively firmer substrates (lumpy lithofacies group) showing dominance of calcitic epifaunal foraminifera, and (ii) mid-shelf areas with a higher sedimentation rate and nutrient influx (low-mesotrophic conditions) favouring potentially deep infaunal foraminifers in comparatively unconsolidated and nutrient-rich substrates controlled by instable redox boundary (marl-limestone rhythmite lithofacies).

Key words: Foraminifera, neritic shelf, trophic conditions, Jurassic, Boreal Realm, Tethys.

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Introduction

Recent papers on foraminiferal assemblages reveal the usefulness of these organisms for interpreting the palaeo-environmental parameters that characterise the sea environment, both in the water column and substrate (Van der Zwaan et al. 1990, 1999; Loubere 1994, 1997; Bernhard et al. 1997; Lüning et al. 1998; Loubere and Fariduddin 1999; Gooday and Hughes 2002; Hanagata 2004; Mello e Sousa et al. 2006; Mojtahid et al. 2006). Especially interesting is the application of foraminifera to determine the productivity in the photic zone, which affects organic matter content and oxygenation of the sea-bottom (e.g., Sjoerdsma and Van der Zwaan 1992; Tyszka 1994a, b; Jorissen et al. 1995; Nagy et al. 1995; Kaminski et al. 1995; Van der Zwaan et al. 1999; Kuhnt et al. 1999; Gooday et al. 2000; Bouhamdi et al. 2000, 2001). The importance of these organisms also stems from the trophic position that they occupy in the food web, constituting the nexus in the lower trophic levels (Lipps and Valentin 1970; Gooday et al. 1992; Van Oevelen et al. 2006). Although bacteria and fungi are probably the most important agents in the decomposition of labile phytodetritus, both through the water column (Turley et al. 1995) and sea-bottom (Turley and Lochte 1990), the foraminifera play an important role in the cycle of benthic organic matter.

Among the foraminifera, the benthic taxa are particularly important as direct bioindicators of physico-chemical parameters at the sea-bottom, and indirectly of the water column features (Loubere 1996). Changes in superficial oceanic productivity may be reflected in the concentration of organic matter and oxygen in the bottom, exercising a direct influence on the features of the foraminiferal assemblage (e.g., diversity, shell composition, and morphotypes). Several papers show the relationship between shell morphology and different life styles

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(Jones and Charnock 1985; Corliss and Chen 1988; Corliss and Fois 1990; Corliss 1991; Nagy 1992; Tyszka 1994a; Nagy et al. 1995; Szydło 2004, 2005; Lemańska 2005, Reolid et al. 2008). The depth in the sediment where the foraminifera live is predominantly determined by oxygen and nutrient availability (Tyszka 1994a; Jorissen et al. 1995; Van der Zwaan et al. 1999; Ernst and Van der Zwaan 2004). The epifaunal microhabitat is advantageous in environments with nutrient and/or oxygen limitations, whereas environments with high organic content in the sediment are dominated by infaunal taxa. On the other hand, the opportunistic behaviour of some foraminifera as well as the diversity of the foraminiferal assemblages are related to nutrient input; a nutrient increase favours proliferation of opportunist taxa (r-type strategy) and produces the diminution of foraminiferal diversity (Sjoerdsma and Van der Zwaan 1992).

The aim of this research is to analyse and compare the foraminiferal assemblages (e.g., composition, shell type, and life habit) from different eco-sedimentary settings belonging to the shelf environment, in order to approach the incidence of such control parameters as sedimentation rate, organic matter content and oxygenation degree. With this purpose in mind, four examples were selected from Mid–Upper Jurassic sediments belonging to two different contexts in the continental platform environment, characterised by siliciclastic (Boreal domain in east Scotland) and mixed carbonate-siliciclastic (Tethyan domain in south Spain) systems. The interpretations related to foraminiferal assemblages of the south Spain are specially interesting due the scarcity of researches in Upper Jurassic foraminifera in this region.

Institutional abbreviations.—JNF-UIO, Jenö Nagy Foraminiferal Collection, University of Oslo, Norway; MRfC-UJA, Matías Reolid Foraminiferal Collection, Universidad de Jaén, Spain.

Review of foraminiferal palaeoecology

Nutrients and oxygenation degree in marine shelf environments

Origin of nutrients.—The organic matter that foraminifers exploit directly or indirectly as nutrients in a shelf environment can have different origins: (i) authochtonous or parauthochtonous, mainly proceeding from primary photosynthetic production; or (ii) exported from other sectors (shallower or emerged areas), in relation to detritic influx.

The primary production is directly dependent on light availability. A photic zonation in the water column, according to light intensity, and based on characteristic microboring assemblages in Jurassic samples, has recently been proposed (Glaub 1994; Vogel et al. 1999). Within the euphotic zone, the shallow euphotic zone is the well-illuminated part of the subtidal zone, where the light is more than 10% of the water surface light; while in the deep euphotic zone the light ranges between 10 and 1% of superficial light. The limit between these zones would be situated in water with good translucency, at around 50 m (Glaub 1994), while the limit between the lower euphotic zone (deep euphotic zone) and the aphotic zone would be located around 100 m (Vogel et al. 1999). However, there is no direct association between light intensity and bathymetry, as turbidity is an additional factor—higher in the sea bed and related to type of sediment and productivity. Moreover, the lower limit of the photic zone is influenced by latitude, being shallower in high-latitude shelves (Akpan and Farrow 1985; Farrow and Fyfe 1988). Primary photosynthetic production can take place in the sea-bottom by phytobenthos, and/or in the water column by phytoplankton. Production in the bottom depends on light intensity (related to depth and turbidity degree), while the primary production in the water column is principally dependent on shallow euphotic zone depth (limited by local sea depth and turbidity degree). The primary production is scarce under the lower limit of the shallow euphotic zone. Accordingly, the primary production and therefore the nutrient availability for foraminifera, is higher in shallow environments of the shelf where planktic and benthic primary production exist. In carbonate platforms these areas usually coincide with the maximum carbonate production area (carbonate factory sensu James and Kendall 1992; Schlager 1993; Pomar and Ward 1995; Homewood 1996) located in the inner shelf. In distal areas of the shelf, where the sea-bottom is beneath the lower limit of the shallow euphotic zone and the phytobenthos is scarce or absent, there is lower primary production.

In the distal areas of the platform, corresponding to mid- and outer shelf (in a ramp model), with lower primary production, the organic matter input is related to influx from emerged and more proximal areas (inner shelf), diminishing along with the distance to shore. The phytodetritus inputs represent one means of distribution of organic matter from a euphotic zone toward more distal areas (Gooday 1996). The phytodetritus may arrive at sea-bottom as aggregate partially damaged by microbes during transport through the water column (Turley et al. 1995). The relation between inputs of siliciclastics and nutrients, decreasing offshore, has been shown recently on Upper Jurassic epicontinental platforms (Pittet and Gorin 1997; Pittet and Mattioli 2002; Bartolini et al. 2003; Olóriz et al. 2003a; Olivier et al. 2004).

Organic matter content.—The sediment organic matter would be fundamental in the control of benthic foraminiferal assemblages as both a direct and an indirect food resource; organic matter could be consumed directly by foraminifera and microbes (bacteria and fungi), and the latter are also a food resource for foraminifera. According to Turley (2000) both bacteria and foraminifera respond to organic matter input by increasing biomass and activity, when foraminifera possibly related to the consumption of dense bacterial populations are involved. The increase of phytodetritus in the sed-

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iment produces increasing "phytodetritus-exploiters" and other foraminifera that use labile components or bacterial population proliferating in relation to phytodetritic deposits (Thiel et al. 1990; Lochte 1992; Gooday 1996; Nomaki et al. 2005). Present examples show the relation between phytodetritus input and microbiota (bacteria, protists, smaller metazoan meiofauna) in bathyal zone, with increasing metabolic activity, enzymatic production and growth of populations (Gooday and Hughes 2002).

The sediment organic matter content—and consequently the content of available nutrients—depends on sedimentation rate and organic matter accumulation. In turn, the sedimentation rate depends on several factors including type of sedimentary environment and accomodation. The sediment has two possible origins: allochthonous (detritic siliciclastic and carbonate sediment) and autochthonous (mainly carbonate related to biogenic productivity). In siliclastic shelves, sediment influx and changes in accomodation are generally independent. The sediment influx is controlled by drainage area, climatology and tectonics, while accomodation is related to eustatic changes and subsidence of the sea-bottom (Swift and Thorne 1991; Pomar 2001). The situation is more complex in carbonate shelfs, being the sediment produced inside the shelf, and directly related to accomodation, an interdependent factor (Pomar 2001; Pomar et al. 2005). Accomodation also controls the primary production through shallow euphotic zone depth. The area occupied by the different types of carbonate-producing biota (or carbonate factory) and its efficiency is controlled by sea-level changes, seafloor morphology and changes in intrabasinal (ecological and hydrodynamic) conditions (James and Kendall 1992; Schlager 1993; Pomar 2001). Carbonate production mainly derives from biological systems, being related to water depth and dependent on intrabasinal conditions in terms of nutrients, salinity, temperature, water energy or transparency; hence several variables are involved in the sediment organic matter content in carbonate platforms.

Oxygenation degree.—The oxygenation degree and therefore the position of the redox boundary in the sediment (under this limit the pore water is anoxic) controls the ecological structure of the benthic foraminiferal assemblages. An increase in sediment organic matter content produces an increase in the metabolic activity of the microbiota, consuming the oxygen of the pore water. Gooday (1996) indicates the close association between organic matter input and penetration of oxygen in the sediment. According to Kuhnt et al. (1996), the position of the redox boundary under oligotrophic conditions may be some meters deep below the sediment-water interface and thus below the zone of benthic activity; whereas under conditions of very high organic influx, the redox boundary layer may be close to the sediment-water interface (unfavourable to infaunal forms). However, some agglutinated foraminiferal infauna from the Jurassic were probably able to tolerate a very low level of oxygenation (Bernhard 1986; Nagy 1992; Tyszka 1994a).

The grain-size and the sedimentation rate have a direct impact on oxygenation of the infaunal microhabitats. A high sedimentation rate and fine grain-size (clay and silt) limit substrate oxygenation. In contrast, oxygenation is usually better in sand and pebbles. The development of bacterial communities in the sediment is also favoured by a higher content in the fine siliciclastics such as silt and clays (Lipps and Valentine 1970; Copper 1992), entailing greater oxygen consumption related to the sedimentary recycling of organic matter. The presence of burrowers may bear an influence on the oxygenation degree in infaunal microhabitats. Moreover, the relation between organic matter content and oxygenation degree of the sediment may be affected by such external factors as sea-water mass stratifications with low oxygenation in the sea-bottom.

Foraminiferal life style and feeding strategies

Studies of modern and ancient foraminiferal assemblages have shown that the morphology of the shell, mode of coiling, type of aperture or existence of pores, all reflect different life styles and feeding strategies (e.g., Corliss 1985, 1991; Jones and Charnock 1985; Bernhard 1986; Nagy 1992; Tyszka 1994a). In palaeoenvironmental studies, the use of morphological categories instead of species can be advantageous for two reasons (Nagy 1992): (i) the morphological approach allows reliable comparisons of assemblages of different ages because it reduces the effect of taxonomic divergences caused by biological evolution and, (ii) because taxonomical determinations at the species level are not required. The influence of variations in oxygen and organic carbon content on benthic foraminiferal morphogroups has been described (e.g., Bernhard 1986; Corliss and Chen 1988; Corliss 1991; Nagy 1992; Tyszka 1994a; Bąk 2004; Reolid et al. 2008), as well as the assignment of the morphogroups to life styles (epifaunal, shallow infaunal and deep infaunal) and secondarily to feeding strategies (e.g., suspension-feeder, deposit feeder, herbivores). Assignment of Jurassic genera of foraminifera to morphogroups is especially useful for interpreting the benthic microhabitat of different foraminifera (Nagy 1992; Tyszka 1994a; Nagy et al. 1995).

Geological setting

The Brora section.—This section is located close to the Brora River estuary, on the northeastern margin of the Inner Moray Firth Basin (Fig. 1). The Brora Argillaceous Formation comprises two members, Brora Brick Clay (11.4 m thick) and Fascally Siltstone (15.7 m thick), showing a coarsening upward succession from shales to siltstones from Middle to Upper Callovian (upper *Erymnoceras coronatum* and *Peltoceras athleta* zones). The Brora Brick Clay was interpreted as offshore shelf deposits, and the Fascally Siltstone as belonging to an offshore shelf to shoreface setting (Nagy et al. 2001).

The basal contact of the Brick Clay is located at a sharp lithological change from lower shoreface sandstones (Glau-

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conitic Sandstone Member) to offshore mudstones, representing a regional flooding surface marking the basis of a 4th order transgressive-regressive sequence with the onset of a major transgression (Nagy et al. 2001). The lower part of the Brick Clay, consisting of dark silty mudstones usually with around 3% (locally 8%) of organic carbon, is interpreted as the transgressive phase of the sequence. Specially interesting is a concretionary level interpreted as the maximum flooding surface. It appears as a row of large limestone doggers exposed in the Brora foreshore section and in a clay pit 1.3 km inland. It extends into offshore areas of the Moray Firth Basin, at least to the Beatrice Oil Field ca. 60 km northeast from Brora (Stephen et al. 1993). The age of the horizon is Late Callovian (*Peltoceras athleta* Zone *Kosmoceras phaeinum* Subzone). The lithology of the horizon is characterised by high organic carbon content. The upper part of the Brick Clay shows increased silt content and a reduced amount of organic carbon.

The Fascally Siltstone Member is composed of numerous upward coarsening parasequences, from mudstone to siltstone or very fine sandstone. The member shows a decreasing organic carbon content and overall coarsening upward development culminating in the overlying Fascally Sandstone. The interval corresponding to the upper Brick clay, the Fascally siltstone and the Fascally Sandstone is interpreted to represent the regressive phase of the sequence (Nagy et al. 2001).

Riogazas-Chorro and Navalperal sections.—The Riogazas-Chorro-SP (RGCH) and Navalperal (NV) sections are located respectively in the External and Internal Prebetic (Betic Cordillera, SE Spain; Fig. 1). During the Oxfordian the External and Internal Prebetic correspond to mid and outer shelf environments, respectively. The RGCH succession is 18.5 m thick and consists of a marl-limestone rhythmite with dominant limestone beds disposed in three upward-thickening calcareous sequences that include a microbial-sponge buildup (Olóriz et al. 2003a). The NV section is about 10.4 m thick, and mainly consists of limestones with a nodular appearance.

The stratigraphic interval studied belongs to *Dichotomoceras bifurcatus* and *Epipeltoceras bimammatum* zones (Upper Oxfordian). The base is defined by a discontinuity visible at the top of Middle Jurassic oolitic limestones and dolomites. The upper boundary corresponds to the last appearance of the genus *Epipeltoceras* (*Epipeltoceras bimammatum*/*Subnebrodites planula* zones boundary), and cannot be related to any significant change in lithofacies, but only to an increasing terrigenous content (Olóriz et al. 1999; Reolid 2005).

Within the RGCH section, the marl-limestone rhythmite lithofacies group is registered, consisting of well-bedded limestones alternating with marls. In the microfacies, packstones-wackestones predominate, with abundant peloids, unclassifiable bioclasts, and glaucony. Two lithofacies belonging to the lumpy lithofacies group can be distinguished within the NV section: lumpy-oncolitic limestone and condensed lumpy-oncolitic limestone. The lumpy-oncolitic limestone has a nodular appearance, although locally near the top of bed, both nodularity and clay content diminish. Packstone-wackestones of peloids and bioclasts with abundant lumps and microbial oncoids with nubeculariids are dominant (Reolid et al. 2005). The condensed lumpy-oncolitic limestone shows a marked nodular appearance (due to the large amounts of ammonite remains, the microbial encrustations and the condensation degree) and poorly-defined, irregular stratification surfaces. The texture is packstone with lumps and microbial oncoids with nubeculariids, and abundant bioclasts.

Recent palaeontological studies—taphonomic analysis of the macroinvertebrate assemblages and composition of foraminiferal assemblages (Olóriz et al. 2002; 2003b, 2004)—allow us to interpret for the studied interval a transgressive-regressive cycle with a maximum flooding zone related to the microbial-sponge buildup (RGCH) and the upper part of the condensed lumpy-oncolitic limestone lithofacies (NV).

Material and methods

Previous lithological and palaeontological analyses on the studied area revealed a close relationship between the registered lithofacies and the eco-sedimentary conditions (Nagy et al. 2001; Reolid 2005). We selected for this research four types of lithofacies, from Callovian (Middle Jurassic) to Oxfordian (Upper Jurassic), representing very different settings and trophic conditions in the shelf environment from Boreal and Tethyan domains (Fig. 1).

Two examples, Brora Brick Clay and Fascally Siltstone, were selected at the Brora section (BR, Inner Moray Firth Basin, Scotland), representing two different eco-sedimentary settings in the comparatively proximal siliciclastic shelf environment from the Boreal Domain during the Callovian. The Brora Brick Clay represents an offshore shelf environment with eutrophic conditions, while the Fascally Siltstone corresponds to an offshore shelf to shoreface environment with high-mesotrophic conditions (Nagy et al. 2001).

A comparatively distal mixed carbonate-siliciclastic shelf is developed in the Tethyan Domain during the Oxfordian. From this environment we have selected two representative groups of lithofacies; marl-limestone rhythmite and lumpy lithofacies groups (Reolid 2005), from sections Riogazas-Chorro (RGCH, External Prebetic, SE Spain) and Navalperal (NV, Internal Prebetic, SE Spain). The marl-limestone rhythmite is interpreted as deposited in a mid-shelf environment with low-mesotrophic conditions, while the lumpy lithofacies group (NV, Internal Prebetic) represents the outer shelf environment with oligotrophic conditions (Reolid 2005).

Part of the material studied in these two domains was analysed previously in the sequence stratigraphy framework (Nagy et al. 2001; Olóriz et al. 2003b; Reolid 2005). Mainly what is new in this study we analyse the foraminiferal assemblages from the palaeoecological standpoint comparing very different shelf environments, taking into account their inferred life-habits and trophic conditions. In the case of Prebetic samples, the new perspective of foraminiferal analysis is improved with some revision and the inclusion of new

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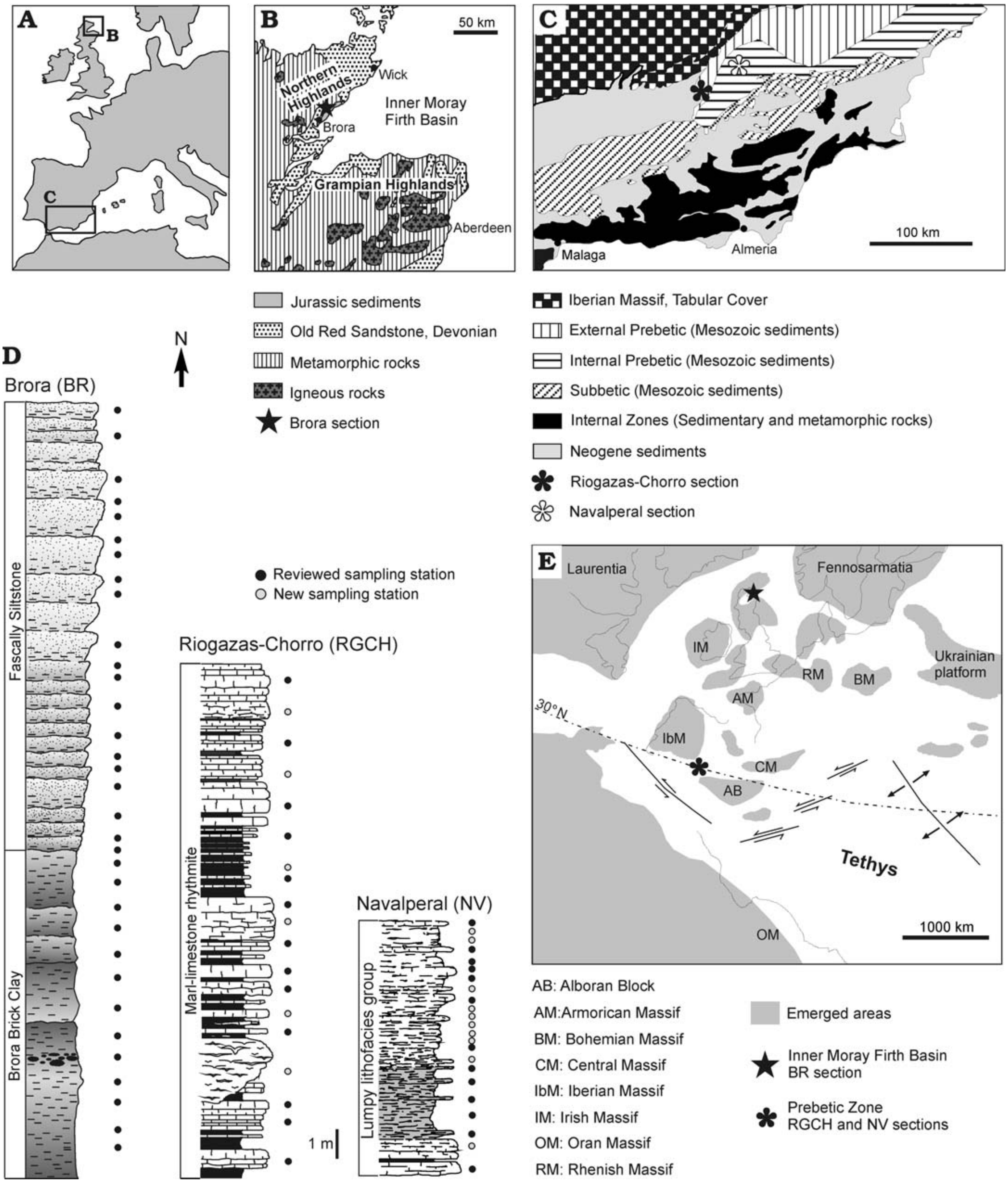

Fig. 1. Location of the sections studied Brora, Riogazas-Chorro, and Navalperal (**A**) with geological sketch of northeastern Scotland (**B**) and southeastern Spain (**C**), lithological columns (**D**) with detailed sample locations (reviewed in black circle and new in white circle), and palaeogeographic reconstruction of the western Tethys during the Callovian–Oxfordian transition (**E**).

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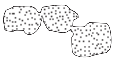
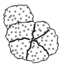
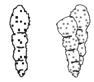
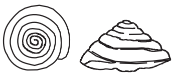
sampling horizons. Supplementary online material of the Brora, Navalperal and Riogazas-Chorro section is available at http://app.pan.pl/SOM/app53-Reolid_SOM.pdf with the proportions of the genera of foraminifera.

Distinct analytic methods were applied on foraminiferal assemblages in the Riogazas-Chorro-SP, Navalperal, and Brora samples, in light of significant lithological differences between lithified carbonates from the Prebetic materials and semiconsolidated mudstones and siltstones from the Inner Moray Firth Basin sediments. Problems related to the retrieval of foraminifera from indurated limestones have recently been addressed in Reolid and Herrero (2004). The different analytic methods applied make it impossible for us to directly compare the diversity and composition of foraminiferal assemblages between Prebetic and Inner Moray Firth Basin samples; but using interpretations based on morphogroups, we can analyse changes in the life style and shell type for each example (Spain and Scotland) according to different gradients in trophic conditions.

In the Brora section, 37 horizons were sampled. In the laboratory, these samples were disintegrated by the kerosene method (Nagy and Johansen 1991), which principally involves boiling the sediment with sodium hydroxide. Then the samples were sieved, and the fraction with size > 125 µm was used for the foraminiferal analyses. In the Brora section 12600 specimens have been studied.

Table 1. Microhabitat and feeding strategy according to shell morphology based on interpretations of Jurassic foraminifera (Nagy 1992; Tyszka 1994a) and modern studies (e.g., Corliss 1985, 1991; Jones and Charnock 1985; Bernhard 1986; Corliss and Chen 1988). Modified from Reolid et al. (2008).

	Test form	Life style	Feeding strategy	Examples
Agglutinated	plano-convex irregular	sessile epifaunal	passive herbivores (suspension-feeders?)	*Subdelloidina* *Thurammina* *Tolypammina* 
	discoidal coiled (unilocular)	epifaunal (phytal)	active herbivores, detritivores	*Ammodiscus* *Glomospira* 
	planispiral to high trochospiral	epifaunal to shallow infaunal	detritivores bacterial scavengers	*Ammoglobigerina* *Recurvoides* *Trochammina* 
	very high trochospiral	shallow infaunal	detritivores bacterial scavengers	*Valvulina* *Redmondoides* 
	elongated uniserial, initial coiled phase	shallow infaunal	detritivores bacterial scavengers	*Ammobaculites* *Haplophragmoides* *Ammomarginulina* 
	elongated uniserial and biserial	shallow to deep infaunal	detritivores bacterial scavengers	*Reophax* *Textularia* *Gaudryina* 
Calcareous	plano-convex and meandering initial phase coiled	sessile epifaunal	passive herbivores (suspension-feeders?)	*Vinelloidea* *Nubecularia* *Bullopora* 
	plano-convex trochospiral	epifaunal	primary weed fauna grazing herbivores	*Epistomina* *Reinholdella* *Pseudolamarckina* 
	discoidal flattened (planispiral) and plano-convex (trochospiral)	epifaunal	primary weed fauna grazing herbivores/ phytodetritivores	*Spirillina* *Trocholina* 
	discoidal flattened spiral, elongated	epifaunal	active deposit-feeders herbivores, detritivores	*Ophthalmidium* *Quinqueloculina* *Triloculina* 
	elongated uniserial	shallow infaunal	active deposit-feeders, herbivores, bacterial scavengers	*Nodosaria* *Dentalina* *Pyramidulina* 
	elongated flattened	shallow infaunal	active deposit-feeders grazing omnivores	*Planularia* *Astacolus* 
	elongated with straight periphery	shallow to deep infaunal	active deposit-feeders grazing omnivores	*Eoguttulina* *Laevidentalina* 
	biconvex (lenticular) planispiral	epifaunal to deep infaunal	active deposit-feeders, grazing omnivores	*Lenticulina* 

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Foraminiferal assemblage data from the marl-limestone rhythmite and the lumpy lithofacies groups in the RGCH and NV sections were obtained by analysing thin sections from 42 sampling horizons. This approach is advantageous for analysing sessile foraminifera except for encrustations by nubeculariids which form aggregates (Reolid et al. 2005). The nubeculariids are studied qualitatively. In the Prebetic sections 8500 specimens have been studied.

Several parameters were used in order to reflect the main features of foraminiferal assemblages: (i) proportions of foraminifera according to shell type composition (agglutinated, calcitic, and aragonitic); (ii) proportions of foraminifera according to microhabitat depth in the sediment (epifaunal, shallow infaunal and potentially deep infaunal); and (iii) foraminiferal diversity expressed as both number of genera and a-index (Fisher et al. 1943).

Based on the nature of our sample material and on considerations of the results of several palaeoecological studies using foraminiferal test morphology (Bernhard 1986; Corliss 1991; Nagy 1992; Tyszka 1994a; Nagy et al. 1995), we applied three life styles related with the microhabitat depth in the sediment, similar to those interpreted for morphogroups in the Jurassic sediments by Nagy (1992) and Tyszka (1994a):

(i) Epifaunal foraminifera: living on the sediment surface and above weeds or in the topmost centimetre (Corliss 1991). In our material the group includes all sessile taxa, as well as ophthalmidiids, miliolids, spiral agglutinated taxa and spiral calcareous taxa except *Lenticulina*.

(ii) Shallow infaunal foraminifera: living in the sediment at a depth of less than 5 cm (Kuhnt et al. 1996). This group comprises elongated agglutinated and calcareous genera, in some cases with partially coiled initial stage.

(iii) Potentially deep infaunal foraminifera (ubiquitous): represented mainly by *Lenticulina*, which seems to have tolerated a wide range of microhabitats from epifaunal to deep infaunal in the Jurassic (Tyszka 1994a), as well as elongated uniserial and biserial agglutinated taxa (mostly *Reophax*) varying in vertical distribution between shallow to deep infaunal positions.

In this study we directly use groups according to microhabitat depth within the sediment that indirectly reflect the morphological groups used by Nagy (1992) and Tyszka (1994a) for Jurassic foraminiferal assemblages. Table 1 shows the feeding strategies and life style of the main registered foraminifera of this study. Here we present a detailed analysis of the foraminiferal assemblages according to the microhabitat and the shell type. Bearing in mind the advantage of the morphological approach, we can standardise and compare foraminiferal assemblages of Callovian and Oxfordian according to life-habit, reducing the effect of taxonomic and methodological divergences. However, a direct comparison is not attempted between Boreal and Tethyan assemblages for diversity and composition of the assemblages at genus level, but rather between samples from the same domain with different trophic conditions and settings in the shelf.

Results

Inner Moray Firth Basin

The microfaunal content of the Brora section is dominated by foraminifera, but radiolaria and ostracods are also abundant in the Fascally Siltstone. All foraminifera are benthic, with a general dominance of agglutinated taxa in the Brick Clay and calcareous perforated taxa in the Fascally Siltstone. Planktic foraminifera and porcelaneous benthic taxa are absent. A total of 39 genera, representing the suborders Textulariina, Lagenina, Robertinina, and Spirillinina were differentiated in the foraminiferal assemblage. The suborder Textulariina is represented essentially by four families: Verneuilinidae (*Gaudryina*, *Verneuilinoides*), Trochamminidae (*Trochammina*, *Ammoglobigerina*, *Trochamminoides*), Hormosinidae (*Reophax*), and Lituolidae (*Ammobaculites*, *Haplophragmoides*). The calcareous group consists mainly of calcitic taxa but also includes subordinate aragonitic forms; the calcitic taxa belong to Lagenina (mostly *Lenticulina* and *Astacolus*) and scarce Spirillinina (*Spirillina*), while the aragonitic forms are represented by Robertinina (*Pseudolamarckina* and *Epistomina*).

Foraminiferal assemblages from Brora Brick Clay Member.—The mean composition of the foraminiferal assemblage from the Brora Brick Clay shows the occurrence exclusively of vagile benthic forms, constituted by Textulariina (73%), Lagenina (23%), and scarcer Robertinina (<5%) (Table 2). Spirillinina occurs in negligible amounts. By shell

Table 2. Mean values (%) of the main foraminiferal orders in the facies studied.

Domain and environment		Lithology	Textulariina	Lagenina	Spirillinina	Miliolina	Robertinina	Others
Boreal	proximal	Fascally Siltstone	10.7	63.5	0.2	–	25.4	–
	distal	Brora Brick Clay	72.7	22.8	0.1	–	4.1	–
Tethyan	proximal	marl-limestone rhythmite lithofacies	37.4	12.1	35.0	7.9	0.1	7.5
	distal	lumpy lithofacies group	42.3	14.9	12.9	15.6	7.9	6.4

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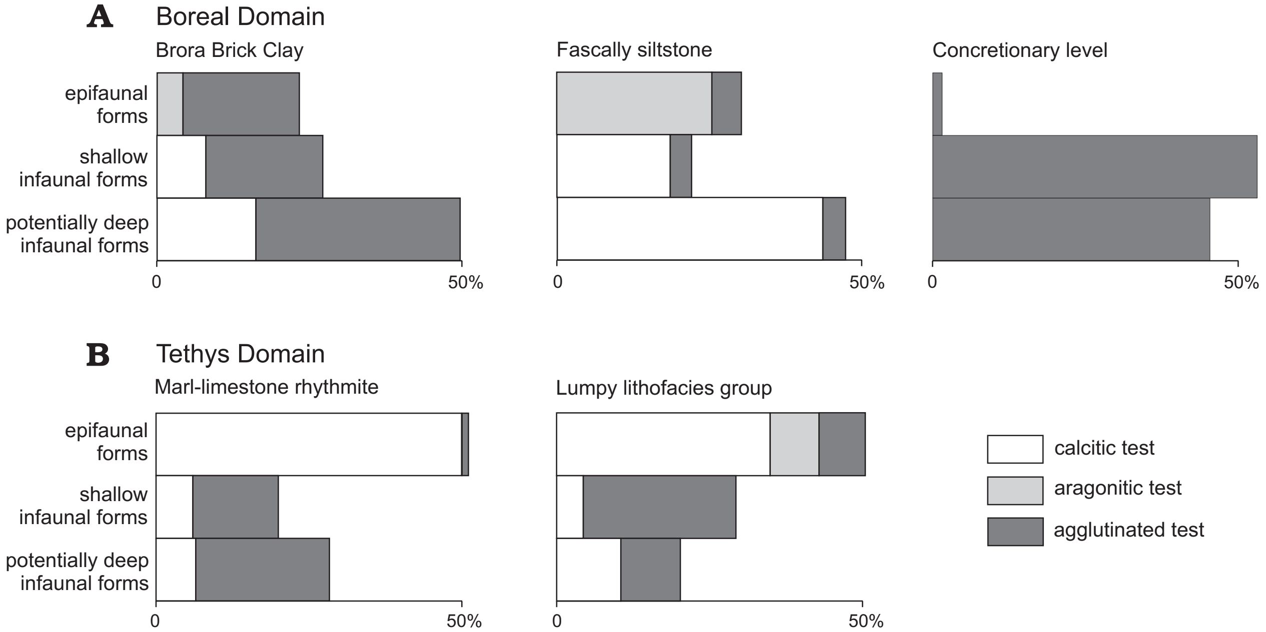

Fig. 2. Mean values of the proportions of test type and life habit of the foraminiferal assemblages in the examples studied from Boreal (Inner Moray Firth Basin) (**A**) and Tethyan (Prebetic) domains (**B**).

type, the agglutinated forms are dominant (72%), followed by calcitic (24%) and scarce aragonitic forms (4%). With respect to the life style, the infaunal forms represent the most important group (Fig. 2), made up of potentially deep infaunal foraminifera (50%) and shallow infaunal (27%). The epifauna presents lower values (23%). The abundance of specimens shows a mean value of 45.2 tests per gram. The mean a-index for the assemblage registered in Brora Brick Clay is 4.4. However, in the concretionary level in which there is the highest value of total organic carbon, decrease in the diversity (1.5) and the abundance (24.8 tests per gram) is observed. The most abundant foraminifera in the Brora Brick Clay Member are *Gaudryina* (16%), *Trochammina* (14%), *Lenticulina* (13%), and *Reophax* (12%) congruent with the most common agglutinated infaunal forms.These proportions change stratigraphically throughout the Brora Brick Clay Member (Nagy et al. 2001). The concretionary level is of special interest due the abundance of *Ammobaculites* and *Trochammina*. Two species of *Ammobaculites* are identified: *A. agglutinans* and *A. fontinensis*.

Foraminiferal assemblages from Fascally Siltstone Member.—The Fascally Siltstone features mean foraminiferal assemblages (Table 2) of Lagenina (64%), Robertinina (25%) and Textulariina (11%). As result of these suborder proportions calcitic forms are dominant, whereas aragonitic and agglutinated ones are less abundant. The life style of the foraminifera (Fig. 2) is dominated by infaunal forms, mainly potentially deep infaunal (47%), and epifaunal foraminifera (31%). The mean value of the abundance of specimens is 62.3 tests per gram, but the Fascally Siltstone Member shows a decreasing trend (from 183.6 to 24.1 tests per gram). The mean value of diversity for the foraminiferal assemblage is 5.6. The most frequent genera are *Lenticulina* (31%), *Epistomina* (20%), and *Astacolus* (7.5%) although there is considerable fluctuation through the Brora section (Nagy et al. 2001).

Prebetic

The quantitatively dominant and environmentally most significant group of microbiota composing the microfacies of the Oxfordian Prebetic sections are the foraminifera (planktic and benthic components), although radiolaria are abundant in some intervals of the Navalperal section (Internal Prebetic). Agglutinated, calcareous-perforated and porcelaneous forms are registered, giving a total of identified 33 genera. In this material seven suborders are recognized: Textulariina, Lagenina, Spirillinina, Involutinina, Globigerinina, Miliolina, and Robertinina. The genus *Tubiphytes* is interpreted as an incrusting genus, in accordance with Leinfelder et al. (1993) and Schmid (1995, 1996).

The planktic component consists exclusively of *Globuligerina*. The suborder Textulariina is mainly represented by *Reophax* (Hormosinidae) and *Ammobaculites* (Lituolidae), and by minor amounts of *Tolypammina*, *Thurammina*, *Verneuilinoides*, *Textularia*, *Subdelloidina*, *Redmondoides*, *Ammodiscus,* and *Trochammina*. The calcareous group comprises forms with calcitic perforated [Lagenina, Spirillinina, and Globigerinina (but see Boudagher-Fadel et al. 1997, for *Globuligerina*)], porcelaneous (Miliolina) and aragonitic walls (Involutinina and Robertinina). Dominant calcareous genera include *Vinelloidea*, *Globuligerina*, *Spirillina*, *Lenticulina*, *Dentalina*, *Nodosaria*, *Ophthalmidium*, and *Bullopora*.

Foraminiferal assemblages from marl-limestone rhythmite lithofacies.—The foraminiferal assemblage from this

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lithofacies corresponds to the proximal assemblage type described by Olóriz et al. (2003b). Vagile benthic forms (80%) are dominant as opposed to planktic (13%) and sessile benthic (7%) foraminifera. The benthic foraminiferal assemblage is mainly composed (Table 2) by Textulariina (37%) and Spirillinina (35%). The benthic forms present calcitic (63%) and agglutinated (37%) tests, while the aragonitic taxa are almost absent (<1%). There is a similar proportion between epifauna (52%) and infauna (48%), in turn with higher proportions of potentially deep infaunal forms (28%) versus shallow infaunal forms (20%) (Fig. 2). The mean value of the abundance is 10 tests/cm^2 (excluding planktic forms). The mean a-index value is 2.8, yet it is necessary to bear in mind the difficulty of the taxonomic identification of foraminiferal genera from thin section analysis. The most common genera are *Spirillina* (37%), *Reophax* (20%), *Ammobaculites* (13%), and *Ophthalmidium* (10%).

Foraminiferal assemblages from lumpy lithofacies group.—The general composition of the foraminiferal assemblages in this lithofacies group corresponds to the distal assemblage type described by Olóriz et al. (2003b). The dominant component of the assemblages consists of vagile benthic foraminifera (54%), followed by planktic taxa (31%) and sessile benthic forms (15%). The benthic taxa (Table 2) are mainly Textulariina (42%) and secondly Miliolina (16%), Lagenina (15%) and Spirillinina (13%). The sessile benthic forms are principally nubeculariids. The non-aggregate sessile group is dominated by siliceous agglutinated forms (54%), followed by *Bullopora*, *Tubiphytes*, and some undetermined forms. Among the benthic taxa, calcitic (50%) and agglutinated foraminifera (42%) are the most common, with low values of aragonitic forms (8%). The epifaunal and infaunal forms present the same proportion (~50%), with predominance in the latter of shallow infauna (29%) over potentially deep infaunal foraminifera (20%) (Fig. 2). The mean value of the abundance is 13 tests/cm^2 (excluding planktic forms). The mean a-index value is 3.9, higher than in the marl-limestone rhythmite. The most abundant genera are *Ammobaculites* (24%), *Ophthalmidium* (16%), *Spirillina* (13%), and *Reophax* (9%).

Discussion

Siliciclastic shelf example (Boreal Domain)

In the context of a comparatively proximal siliciclastic shelf environment represented by the Brora section (Inner Moray Firth Basin, Scotland), we compare two different eco-sedimentary settings (Table 3), corresponding to the Brora Brick Clay (an offshore shelf environment with eutrophic conditions), and the Fascally Siltstone (an offshore/inner shelf to shoreface environment with high-mesotrophic conditions) (Nagy et al. 2001). In these environments, the nutrient resources were probably directly related to primary photosyntethic production in the water column and sea-bottom.

Brora Brick Clay Member.—The organic matter content in the sediment of the Brora Brick Clay was high. The foraminiferal assemblages, dominated by agglutinated and calcitic potentially deep infaunal forms and agglutinated epifauna, are congruent with high nutrient contents in the sediment as well as low oxygen availability. Under such conditions, the oxygen concentration in the sediment pore water is the main limiting factor—the foraminiferal assemblages are made up principally of taxa that tolerate low oxygenation (Sen-Gupta and Machain-Castillo 1993). Moreover, some agglutinated infaunal foraminifera from the Jurassic were probably able to tolerate a low level of oxygenation (Bernhard 1986; Tyszka 1994a). Schumacher and Lazarus (2004) indicate that the infaunal species are more common in high organic-productivity environments, which explains the greater values in the Brora Brick Clay with respect to the Fascally Siltstone.

In the epifaunal microhabitat (Fig. 2), foraminifera are represented by coiled (trochospiral) agglutinated forms (*Trocha-*

Table 3. Summarizing of the results from palaeoenvironmental conditions to foraminiferal assemblages.

Domain	Lithofacies	Paleoenvironment		Trophic conditions	Bottom oxygenation	Sedimentation rate	Test type	Life style
Boreal	fascally siltstone	inner shelf	offshore to shoreface	high mesotrophic	oxic	higher	agglutinated 11% aragonitic 25% calcitic 64%	epifauna 31% shallow infauna 22% ubiquitous 47%
	Brora Brick Clay		offshore to shoreface	eutrophic	dysoxic/anoxic	lower	agglutinated 72% aragonitic 4% calcitic 24%	epifauna 23% shallow infauna 27% ubiquitous 50%
Tethyan	marl-limestone rhythmite	middle shelf		low mesotrophic	dysoxic	higher	agglutinated 37% aragonitic 0% calcitic 63%	epifauna 52% shallow infauna 20% ubiquitous 28%
	lumpy lithofacies group	outer shelf		oligotrophic	oxic	lower	agglutinated 42% aragonitic 8% calcitic 50%	epifauna 51% shallow infauna 29% ubiquitous 20%

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mmina and *Ammoglobigerina*) and, secondly, by aragonitic forms (Robertinina). In shallow infaunal microhabitats, agglutinated forms dominate (represented mainly by *Ammobaculites* and *Haplophragmoides*), and calcitic Lagenina (mainly *Astacolus*) is a minor component. In deep infaunal microhabitats, agglutinated foraminifera (mainly represented by *Gaudryina* and *Reophax*) are dominant over calcitic ones (almost exclusively *Lenticulina*, Fig. 2). The latter is congruent with the opportunistic behaviour inferred for *Lenticulina* during the Jurassic (Tyszka 1994a), which probably tolerated fluctuations in the redox boundary and possessed the ability to migrate vertically in soft substrate. Yet both *Reophax* and *Lenticulina* are potentially deep infaunal forms with a broader range of microhabitats inside the sediment; and thus, according to Jorissen et al. (1992), these genera could tend to occupy higher and higher levels within the sediment column following redox boundary fluctuations, sometimes even taking over microhabitats occupied by shallower forms (see Fig. 4 and legend in Fig. 3).

The above interpretation is coherent with previous studies (Nagy et al. 2001) revealing an increase in the organic productivity and stagnation in accordance with the development of a maximum flooding surface located in relation to a concretionary level. Nagy et al. (2001) proposed a period of accentuated oxygen reduction in the sea-bottom explained by increasing depth and organic matter. This situation is reflected by a progressively higher proportion in agglutinated forms with epifaunal and shallow infaunal microhabitats. Such interpretation accomodates a redox boundary layer close to the sediment-water interface, and thus unfavourable to infaunal forms, under conditions of very high organic influx (Kuhnt et al. 1996).

Fascally Siltstone Member.—This member is characterised by a coarsening upward trend, reflecting a decrease in distance to shore and an increase in sedimentation rate, as compared to the Brora Brick Clay (Table 3). The foraminiferal assemblages show a higher proportions of calcitic shells and potentially deep infaunal and epifaunal forms, the latter showing strong cyclic fluctuations.

The greater sedimentation rate and coarser grain-size determine the deterioration in sea-bottom conditions for benthic forms. Moreover, the increase in sedimentation rate could produce higher turbidity and the reduction of primary photosyntethic production, which finally conditioned decreasing organic matter content in the sediment. These conditions would explain the comparatively favourable environmental features of epifaunal forms and the scarcer record of agglutinated taxa (mainly infauna) with respect to the Brora Brick Clay assemblages.

The epifaunal microhabitat is characterised by forms with aragonitic tests while shallow and deep infaunal environments are dominated by forms with calcitic tests (Fig. 2). The increased oxygenation degree (with respect to Brora Brick Clay) produced a deeper redox boundary and allowed more diversity of calcareous forms and an increase in infaunal microhabitats (Figs 2 and 4).

Mixed carbonate-siliciclastic shelf example (Tethyan Domain)

In the comparatively distal mixed carbonate-siliciclastic shelf developed in the Tethys during the Oxfordian, we can compare foraminiferal assemblages belonging to environments which represent a proximal-distal gradient, from mid shelf (marl-limestone rhythmite in the RGCH section) to outer shelf (lumpy lithofacies group in the NV section), and low-mesotrophic to oligotrophic conditions, respectively (Table 3).

Foraminiferal assemblages from both the marl-limestone rhythmite and the lumpy lithofacies groups are dominated by epifaunal forms—mainly calcitic tests—while shallow infaunal and potentially deep infaunal forms present lower proportions. These relationships between components are indicative of higher nutrient availability in the epifaunal microhabitat and the progressively downward impoverishment inside the sediment. This strong vertical gradient in nutrients was probably controlled by efficient organic matter decomposition at the water-sediment interface (see Walker and Bambach 1974; Van der Zwaan et al. 1999). Nevertheless, nutrient availability would also be subjected to influx variations from more proximal areas (Olóriz et al. 2003a; Reolid 2005). The epifauna could exploit either organic matter or bacteria by means of grazing (Turley 2000; Gradziński et al. 2004) as is shown in modern foraminiferal populations (Bernhard and Bowser 1992).

Nutrient input during the Late Jurassic of the Prebetic has been related to currents from emerged and shallower areas in the shelf, characterised by high primary photosyntethic pro-

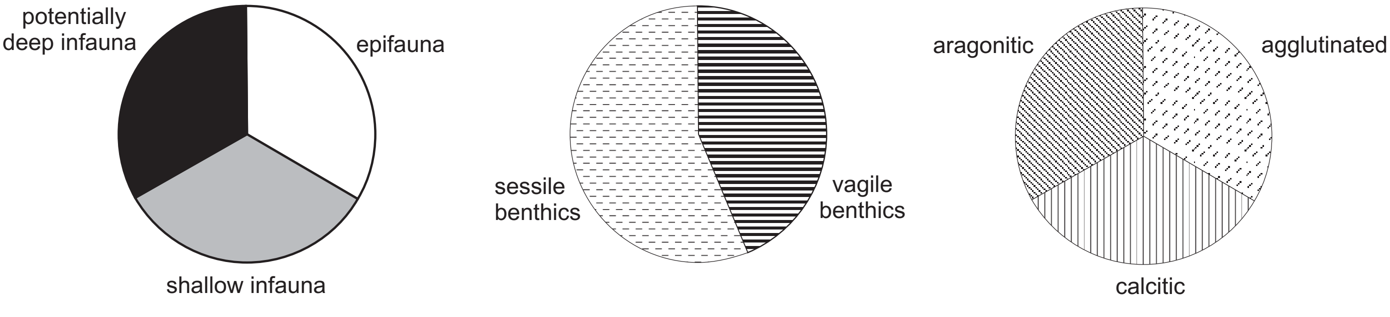

Fig. 3. Explanatory legend of foraminiferal pie-diagram represented in Figs. 4 and 5.

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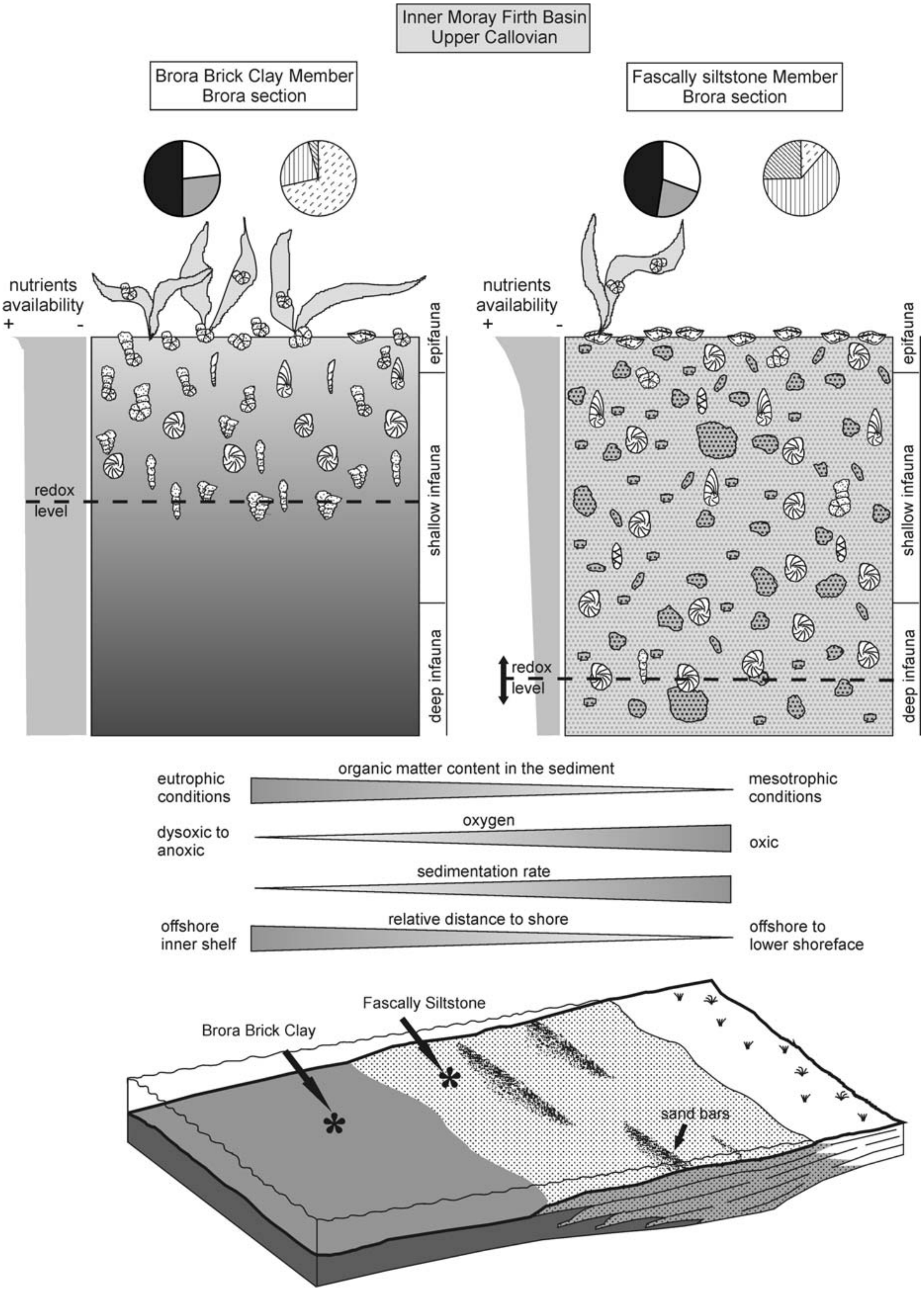

Fig. 4. Palaeoecological model of foraminiferal assemblages from Brora Brick Clay and Fascally Siltstone members, and changes in selected palaeoenvironmental features (organic matter content, oxygenation, sedimentation rate and relative distance to shore). The model tries to give a rough idea about what was deeper and shallower, but the Brora Brick Clay and Fascally Siltstone are not contemporaneous. Legends of foraminifera and pie-diagrams are in Table 2 and Fig. 3.

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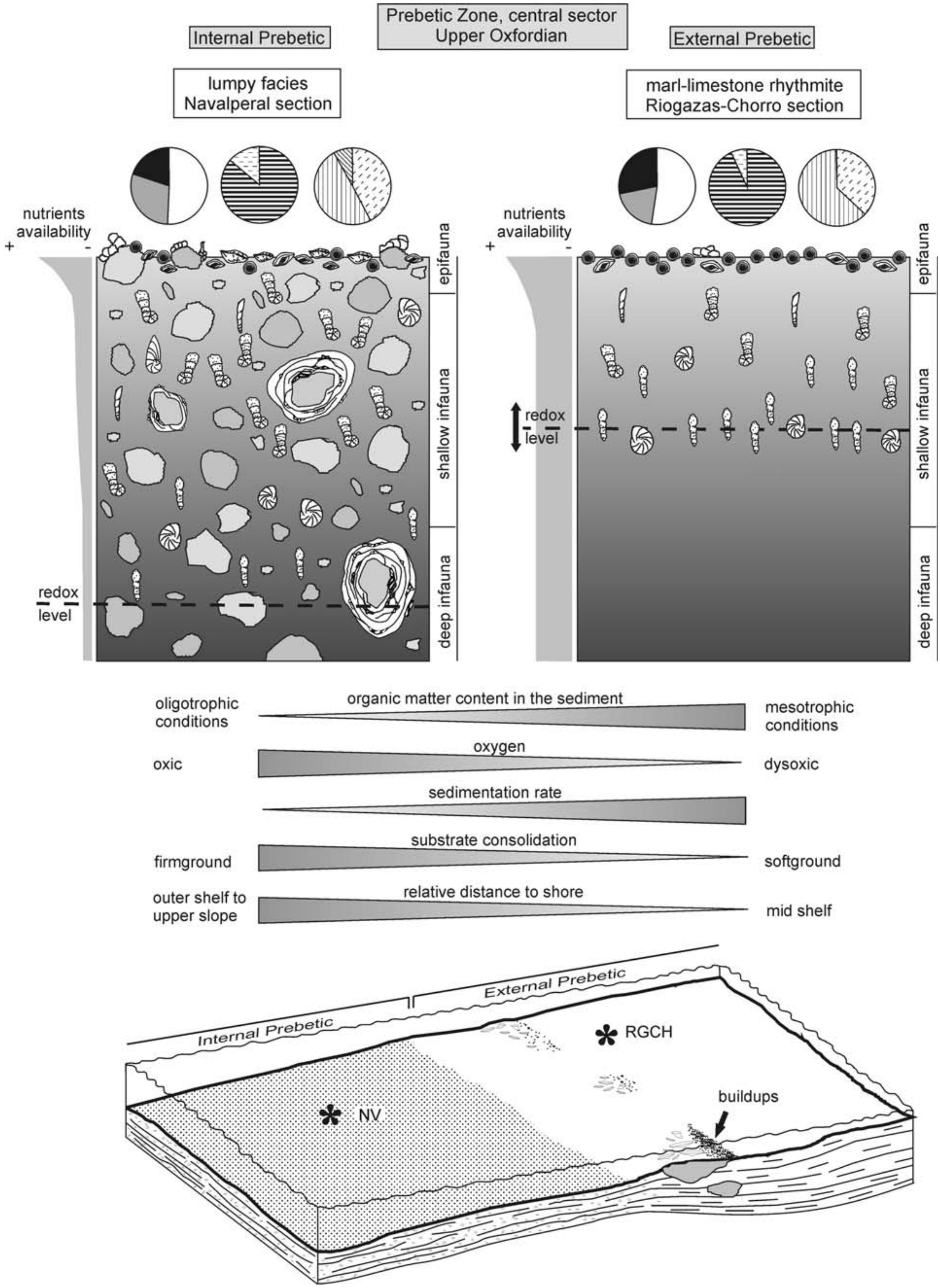

Fig. 5. Palaeoecological reconstruction of foraminiferal assemblages from lumpy lithofacies group and marl-limestone rhythmite, and changes in selected palaeoenvironmental features (organic matter content, oxygenation, sedimentation rate, consolidation of substrate and relative distance to shore). Legends of foraminifera and pie-diagrams are in Table 2 and Fig. 3.

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duction related to phytobentos and phytoplankton (Olóriz et al. 2003a, 2006; Reolid 2005), which could correspond to the shallow euphotic zone I in Vogel et al. (1999). There is no outcrop record of this shallower area in the Prebetic.

Marl-limestone rhythmite lithofacies (External Prebetic).—The comparatively proximal area of the epicontinental platform developed in the South-Iberian palaeomargin during the Late Jurassic, and represented by the External Prebetic, registered a higher input of fine siliciclastics, and therefore of nutrients, probably in relation to a reduced distance from shore and from the main area of primary production of nutrients (Olóriz et al. 2003b, 2006). The increasing organic matter accumulation in the sediment (greyish coloration), associated with terrigenous input favoured the bacterial activity in the sediment-water interface. This bacterial activity influenced oxygen consumption (e.g., Turley 2000), playing an important role in the decomposition and remineralization of organic matter as well as in the solubilization of organic carbon. The growth of bacterial communities may have been favoured by a high fine terrigenous content (silts and clays) and the abundance of organic matter (Copper 1992), producing fluctuations in the redox boundary position. The fine grain-size, which obstructed pore water circulation and oxygenation, favoured a redox boundary close to the sediment-water interface (Fig. 5). The high sedimentation rate implies a lower degree of the substrate firmness and a quick burial of organic matter, reflected by the high amount of potentially deep infaunal foraminifera (Fig. 2). Shallow infaunal foraminifera (mainly agglutinated, e.g., *Ammobaculites*) were less developed with respect to others such as *Reophax*, whose microhabitat shows variable depth related to fluctuation in the Mn reduction front (e.g., Van der Zwaan et al. 1999). The high proportions of opportunist forms—potentially deep infaunal forms with high vertical mobility, as *Reophax* and *Lenticulina* (r-type strategies)—lead us to interpret fluctuations in the redox boundary regulated by organic flux. This agrees with previous interpretations (Reolid 2005), on mesotrophic conditions during the marl-limestone rhythmite sedimentation, with oscillations in nutrient level depending upon terrigenous input from proximal areas. In examples similar to the Prebetic setting (Late Oxfordian sponge-microbialite reefs and calcareous nannoplankton from south Germany; Olivier et al. 2004) mesotrophic conditions are registered for marls-dominated intervals, while oligotrophic conditions were favoured for carbonate dominated intervals featuring reef growth.

Among the epifauna, calcitic forms dominate due to the high proportion of spirillinids (Table 2, Fig. 2), revealing good nutrient availability, taking into account the relation between *Spirillina* in the shelf and trophic resource availability proposed by Bouhamdi (2000) and Bouhamdi et al. (2001). The spirillinids are epifaunal grazers indicative of the presence of dense bacterial populations related to organic carbon particles in the flocculent layer, probably phytodetritus, and to macroscopic algae (e.g., Morris 1982; Kitazato 1988; Nagy 1992; Tyszka 2001). The scarce record of sessile epifaunal forms (mainly allochthonous fragments of *Tubiphytes*; Reolid 2005) is coherent with the high sedimentation rate proposed for this lithofacies.

Lumpy lithofacies group (Internal Prebetic).—The comparatively more distal areas of the epicontinental platform developed in the South-Iberian palaeomargin during the Upper Jurassic, and represented by the Internal Prebetic, correspond to outer shelf and possibly upper slope settings. The sediment exported from proximal areas decreases, with sedimentation mainly corresponding to the accumulation of shells of planktic and nectonic faunas (ammonoids, radiolaria and *Globuligerina*), and calcareous benthic microbial communities (Reolid et al. 2005). Previous research evidences the relationship between the higher proportion of *Globuligerina* and *Epistomina* and the higher distality degree and ecospace (Henderson and Hart 2000; Oxford et al. 2000, 2002; Olóriz et al. 2003b), confirmed by increasing radiolaria and ammonoids (Reolid 2005). The reduced terrigenous input from proximal and shallower areas determined a lower nutrient level as well as a higher stability of the redox boundary (Fig. 5). The lower sedimentation rate produced a higher degree of consistency and a longer exposition of nutrients on the sea-bottom, where they would be preferentially consumed. This situation is accentuated in the more condensed interval (condensed lumpy-oncolitic limestone). The proportion of spirillinids (Table 2) indicates reduced nutrient availability (oligotrophic conditions) in this lithofacies group. The low nutrient content in infaunal microhabitats would explain the lower proportions of potentially deep infaunal foraminifera (*Reophax*) with respect to shallower infaunal forms (*Ammobaculites*, Fig. 5). Availability of oxygen in the substrate was favoured by the heterometry of the grains and the low oxygen consumption related to organic matter decomposition. Abundant miliolids confirm normal oxygenation conditions, in view of the absence of miliolids in oxygen-reduced environments (Gooday et al. 2000).

A low sedimentation rate allowed the development of sessile foraminifera and benthic microbial communities. The abundance of microbial oncoids with nubeculariids (Reolid et al. 2005) could be interpreted, according to Gradziński et al. (2004), as a consortium of microbes and foraminifers, well adapted to oligotrophic conditions, prevailing on the sea floor. Nubeculariids and microbes (cyanobacteria) were related by comensalism, where biofilms were a source of nutrients and substrate for the attachment of encrusting foraminifers.

A comparison of foraminiferal assemblages from the marl-limestone rhythmite and lumpy lithofacies groups proves particularly interesting insofar as the diminution of spirillinids with respect to marl-limestone rhythmite, indicating less nutrient availability (oligotrophic conditions) in distal sectors of the shelf. In these areas, the lower nutrient content in infaunal microhabitats would explain the reduction of potentially deep infaunal foraminifera (*Reophax*) as opposed to shallower infaunal forms (*Ammobaculites*) related to

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marl-limestone rhythmite (Fig. 5). A higher oxygen concentration in the substrate was favoured by the heterometry of the grains and lower oxygen consumption related to organic matter decomposition, whereas in marl-limestone rhythmite just the opposite situation prevailed. The diversity of foraminiferal assemblages of the lumpy lithofacies group is higher than foraminiferal assemblages of marl-limestone rhythmite lithofacies, probably due to better oxygenation. Higher diversity values and large number of sessile epifaunal and suspension-feeder genera are indicatives of the oligotrophic conditions and relatively high dissolved oxygen levels in the bottom waters (Mello e Sousa et al. 2006). Regarding the planktic/benthic foraminiferal relation, Van der Zwaan et al. (1999) indicate that the decrease in organic matter flux in the sea-bottom along with greater depth determines an increasing planktic/benthic foraminiferal relation. This relationship is seen comparing foraminiferal assemblages from the External and Internal Prebetics, and is also reflected by macroinvertebrate assemblages (Olóriz et al. 2002, 2006; Reolid 2005). However, the increase in planktic forms might also be related to increasing ecospace.

Ecological fidelity of foraminiferal genera and trophic conditions

The diversity at genus level and the number of genera showing high ecological fidelity present significant differences that could be related to variations in lithofacies and trophic conditions. The number of genera showing high ecological fidelity has been considered as the numerically more important elements, constituting 80% of the assemblage, (the trophic nucleo sensu Walker 1972 and Aberhan 1994). In the examples of the Brora section (Fig. 6), the number of genera making up 80% belonging to eutrophic conditions (Brora Brick Clay) is composed by eight genera and the mean α-index value is 4.4, whereas nine genera making up 80% for mesotrophic conditions (Fascally Siltstone) and the mean diversity index value is 5.6. In the concretionary level, characterised by the highest contents in organic matter, only two agglutinated genera (*Ammobaculites* and *Trochammina*) show high ecological fidelity and the diversity index shows the lowest value (1.5). Of special significance is the fact that the more important elements, in quantitative terms, are not exclusive of a particular life style, but are distributed over the three microhabitats differentiated (epifaunal, shallow and deep infaunal). Within the infaunal microhabitat, the dominant genus is *Gaudryina* in eutrophic conditions and *Lenticulina* in mesotrophic conditions. In the epifaunal microhabitat the dominant genus is *Trochammina* for eutrophic conditions, while *Epistomina* increases in mesotrophic conditions (Fig. 6).

The differences in the number of benthic genera making up the trophic nucleus, along with the diversity index between the lithofacies studied in the Prebetic (Fig. 7), allow us to compare mesotrophic (marl-limestone rhythmite) and oligotrophic (lumpy lithofacies group) conditions, corresponding to different settings in the shelf. Mesotrophic conditions are characterised by five genera making up 80% of the foraminiferal assemblage with a mean diversity index of 2.8, whereas in the oligotrophic conditions there are six genera making up 80% of the assemblage and the mean value of the diversity index is 3.9. As occurs in foraminiferal assemblages from Brora, the numerically more important elements are distributed over different microhabitats. In epifaunal

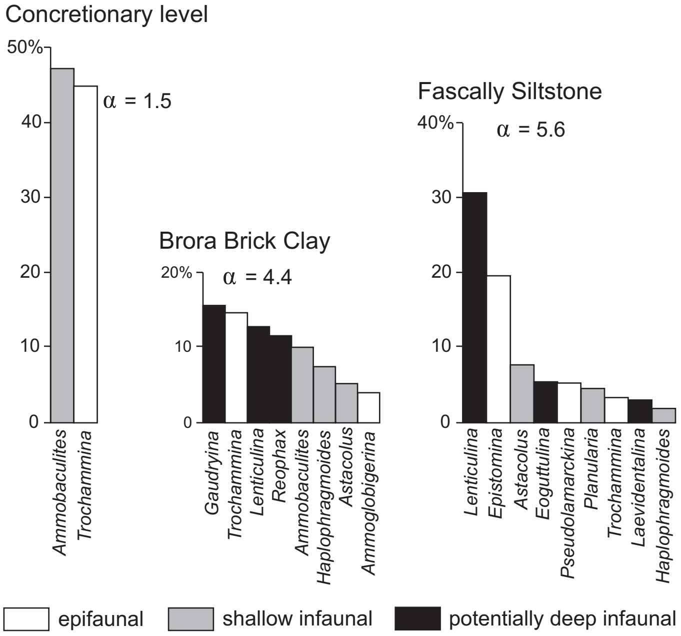

Fig. 6. Genera making up 80% of the foraminiferal assemblage from Brora Brick Clay (with concretionary level differentiated) and Fascally Siltstone with indication of microhabitat and α-index.

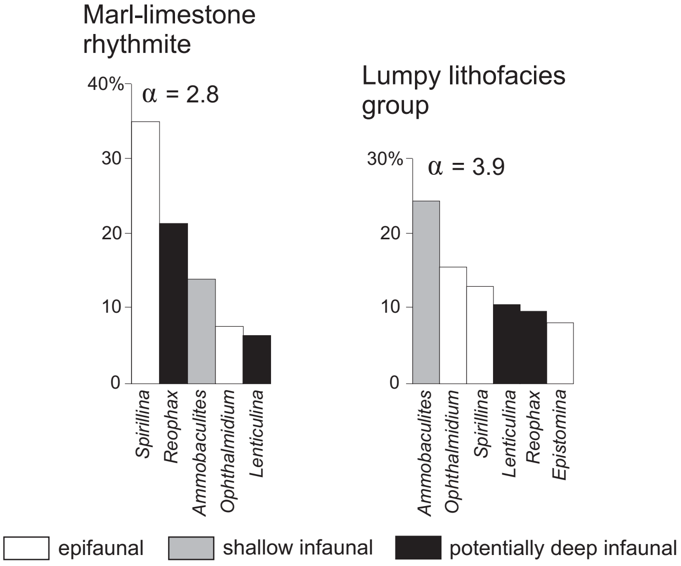

Fig. 7. Genera making up 80% of the foraminiferal assemblage from marl-limestone rhythmite lithofacies and lumpy lithofacies group with indication of microhabitat and α-index.

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microhabitats the dominant genus is *Spirillina* for mesotrophic conditions and *Ophthalmidium* for oligotrophic conditions. In infaunal microhabitats the dominant genus is *Reophax* for mesotrophic conditions, while *Ammobaculites* increase in oligotrophic conditions.

There is an apparently contradictory behaviour of *Ammobaculites* as a response to organic matter content from the concretionary level in Brora section and the Prebetic. These differences are related to species and domain considered. On the Prebetic shelf *Ammobaculites* is ubiquitous, it usually agglutinates coarse grains, and might be assigned to *A. coprolitiformis* with mean sizes of 680 μm. The *Ammobaculites* registered in the Prebetic usually have a well developed uncoiled portion. In the case of the Brora section, the *Ammobaculites* registered belong to the species *A. agglutinans* and *A. fontinensis*. These species are smaller (mean size 380 μm) than the forms from the Prebetic and the coiled portion is well developed whereas the uncoiled phase is short or absent. Probably these two different types of *Ammobaculites* from different realms and sedimentary contexts showed different answer respect to the trophic conditions and organic carbon content. A long controversy is related to the life style of *Ammobaculites* and the environmental significance of the coarseness of the agglutinated test in the Jurassic. Barnard et al. (1981) suggest that small *Ammobaculites* of the Oxford Clay represent shallow water environments with reduced salinity or oxygen, while coarser forms (e.g., *A. coprolitiformis*) represent comparatively deeper shelf settings. In Kimmeridgian sediments of southern England, Jenkins (2000) found a negative correlation between infaunal *Ammobaculites* and the total organic carbon (TOC) and correlates increased values of TOC with specimens of *Ammobaculites* lacking an uncoiled portion and having a shallow infaunal habitat.

In both examples (Inner Moray Firth Basin and Prebetic) we observe higher values for the diversity index and number of benthic genera forming the trophic nucleus in the lowest trophic conditions. This supports previous studies revealing decreased foraminiferal diversity when nutrient content increases (e.g., Sjoerdsma and Van der Zwaan 1992). Such records may also be related to higher oxygenation, though additional factors including greater grain heterometry and grain size must be considered. The distribution of the quantitatively more representative genera in each microhabitat could be related to different mechanisms of competition.

Concluding remarks

Foraminiferal assemblage analysis (e.g., composition, shell type, life habit) from different eco-sedimentary settings pertaining to the shelf environment can reveal the distinctive influence of parameters such as sedimentation rate, organic matter content, and oxygenation degree according to the particular environment. The response of foraminiferal assemblages registered varies depending on the distance from the shore in relation to the sedimentary context, whose location governs the origin and type of nutrients. Comparatively proximal siliciclastic settings from the Boreal Domain (Brora section, east Scotland) were dominated by primary production in the water column and sea-bottom, while relatively distal mixed carbonate-siliciclastic settings from the Tethyan Domain (Prebetic sections, south Spain) were characterised by allochthonous production arriving from proximal and shallower areas. Thus:

(i) The proximal example (Boreal Domain, Brora Brick Clay Member) corresponds to Callovian inner shelf deposits with a high organic photosyntethic productivity and reduced sedimentation rate, where sediment organic matter content was high (eutrophic conditions), favourable to infaunal foraminifera. Local reduction in the degree of oxygenation was produced in relation to maximum transgression, where a higher organic matter accumulation determined the punctual dominance of agglutinated epifaunal and shallow infaunal foraminifera and the disappearance of calcitic and aragonitic forms. In the Fascally Siltstone Member, which represents the transition from inner shelf to shoreface environments, the organic matter content in sediment was lower (high-mesotrophic conditions) than in the Brora Brick Clay, due to a higher sedimentation rate and the possible reduction of primary photosyntethic production in the water column (lesser depth of shallow euphotic zone and higher turbidity). Therefore, sedimentary conditions were comparatively less favourable for agglutinated infaunal foraminifera, benefitting calcitic and aragonitic epifaunal forms, and calcitic opportunists like *Lenticulina*.

(ii) The Oxfordian example from the Tethyan Domain reveals significant differences according to lithofacies. The lumpy lithofacies group represents deposits from the outer shelf, with reduced nutrient input and sedimentation rate (oligotrophic conditions), and consequently a scarce organic matter content in comparatively more consistent substrate. This determined the dominance of calcitic epifaunal foraminifera, frequently with sessile behaviour. The marl-limestone rhythmite lithofacies represents Oxfordian deposits from mid-shelf, with a comparatively higher sedimentation rate and nutrient influx (low-mesotrophic conditions), producing a more favourable environment for potentially deep infaunal forms in an unconsolidated substrate with greater nutrient availability and with a fluctuating redox boundary. These results are new in Jurassic shelf deposits represented by the Prebetic where the foraminiferal studies are almost absent.

(iii) The two examples, from the Boreal and Tethyan domains, show an increase in diversity of benthic foraminiferal assemblages as well as in the number of genera showing high ecological fidelity (making up 80% of the assemblage), according to higher oxygenation degree and lower trophic conditions. There is a clear pattern in the foraminiferal microhabitat depth revealing a relative increase in proportions of epifaunal forms from eutrophic to oligotrophic conditions.

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