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Sequence biostratigraphy and paleoenvironmental reconstruction in the Early Eocene Figols Group of the Tremp–Graus Basin (south-central Pyrenees, Spain)

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Abstract

The dinoflagellate cyst, palynofacies and foraminiferal records from the Early Eocene Figols Group of the Spanish Pyrenees exhibit major changes associated with relative sea-level fluctuations and variations in efficiency of the fluvial systems. The mixed siliciclastic–carbonate marine succession exposed in the Merli–Esdolomada area was deposited on the shelf in a tectonically active basin, under oxic conditions, in shallow to moderately deep marine waters (close to the lower boundary of the photic zone) influenced by river discharge from adjacent emerged lands. Sedimentary cycles are mainly recorded by fine-grained deposits. The paleoenvironmental interpretation of palynological and calcareous microfaunal records allows the definition of depositional sequences and enables to trace basinward surfaces identified in more proximal settings by means of sedimentological facies analysis. At the same time, the solid regional stratigraphic framework already available for the Figols Group allows new insights on the paleoecology of extinct taxa.

The Merli–Esdolomada section (ME) spans two 3rd order sequences. The upper sequence reflects more marginal marine conditions than the lower one, thus pointing to an overall shallowing trend with time. In the lower sequence the maximum flooding interval is characterised by a rich and diverse microfauna, highest relative abundances of marine phytoplankton and typically neritic dinoflagellate cyst (dinocyst) assemblages dominated by *Spiniferites* and *Cordosphaeridium*. The final phase of the highstand systems tract, in proximity of the main sequence boundary, is characterised by a decrease in abundance and diversity of dinocysts, with the dominance of the lagoonal genus *Polysphaeridium*, and by decreased microfaunal diversity (discorbids, miliolids, larger foraminifers).

Palynological records permit the reconstruction of activation and deactivation phases of the fluvial systems, variations in runoff from the hinterland, nutrient delivery to the sea and productivity in surface waters of the Tremp–Graus Basin. The overall abundance of *Spiniferites* and the scarcity of peridinioid cysts, *Lingulodinium*, *Pediastrum* and *Botryococcus* algae are interpreted to indicate oligotrophic conditions during the deposition of the investigated succession. Recurrent intervals where the temporary disappearance of *Spiniferites* corresponds to highest relative abundances of *Operculodinium* and herbaceous debris are the main evidence for river plumes and denote periods of enhanced fluvial discharge reflecting a Milankovitch-type cyclicity. The *Rotalia* group, which shows abundance peaks of *Cuvillierina* spp. in the shallower intervals, is often associated with these episodes, thus suggesting for this taxon more tolerance to turbidity than larger foraminifera. Within the maximum flooding zone, a *Thalassiphora patula* acme corresponding to the local disappearance of *Homotryblium* is deemed to record the distal expression of a fluvial activation which triggered water salinity stratification. Despite broad morphological similarities, *Homotryblium* exhibits more cosmopolitan preferences than *Polysphaeridium*, which is instead confirmed as a lagoonal euryhaline taxon. The increase of

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Spinizonocolpites pollen toward the top of the Figols Group records the northwestward migration of *Nypa* mangrove-palms from southern Europe during the mid Early Eocene.

Keywords: Dinoflagellate cysts; Foraminifers; Paleoecology; Sequence stratigraphy; Early Eocene; Spanish Pyrenees

1. Introduction

The interplay between local tectonism and global sea level changes controls the geometry and distribution of the depositional systems. According to Luterbacher (1998), in marine Paleogene units of the central-southern Pyrenees biochronostratigraphical resolution is generally not sufficient to identify individual global eustatic 3rd order cycles without ambiguities. However, the possibility of reconstructing second- and third-order cyclicity in marginal marine sediments by interpreting the paleoecological significance of dinoflagellate cyst assemblages was already proven by Brinkhuis (1994) and Powell et al. (1996) in the Paleogene of Italy and southeastern England.

A multidisciplinary study performed in cooperation with the University of Parma (Italy) was focused on the Eocene successions of south-central Pyrenees in order to investigate relationships between biostratigraphic responses and depositional facies. Within this framework, the closely spaced sampled ME section gave us the opportunity to register the microfloral and microfaunal variations with a much higher detail than in previous studies in the area.

The aim of this paper is to show that the concepts originally developed by Brinkhuis (1994) and Powell et al. (1996), and recently updated by Sluijs et al. (2005), applied in conjunction with foraminiferal analyses to the Early Eocene shelf deposits of the Figols Group, allow a detailed reconstruction of relative sea-level fluctuations and the recognition of the constitutive elements of 3rd order depositional sequences.

Since during the Eocene the Tremp–Graus Basin was a tectonically active basin located on a convergent margin, global cyclicity is not unambiguously distinguishable from relative sea-level fluctuations induced by local tectonism; therefore it is not in the scope of the present study to try to recognize global eustatic cycles. Conversely, on the basis of the interpreted records, we develop ideas on variations in efficiency of the fluvial systems, runoff from adjacent areas, paleoclimate, nutrient delivery to the sea and productivity in surface waters during the deposition of the Figols Group.

2. Geological setting

In the eastern sector of the south-central Pyrenees, the Early Eocene Figols Group comprises a thick (up to 1000 m) unconformity-bounded stratigraphic unit made up of mixed siliciclastic–carbonate systems deposited in relatively shallow water. These are fluvio-deltaic to shelfal marine sediments deposited in the ESE–WNW oriented south Pyrenean foreland basin. The south Pyrenean foreland basin opened westward to the Atlantic Ocean and was subdivided into three main paleogeographical sectors (Mutti et al., 1972). The eastern sector, referred to as the Tremp–Graus Basin, comprises a

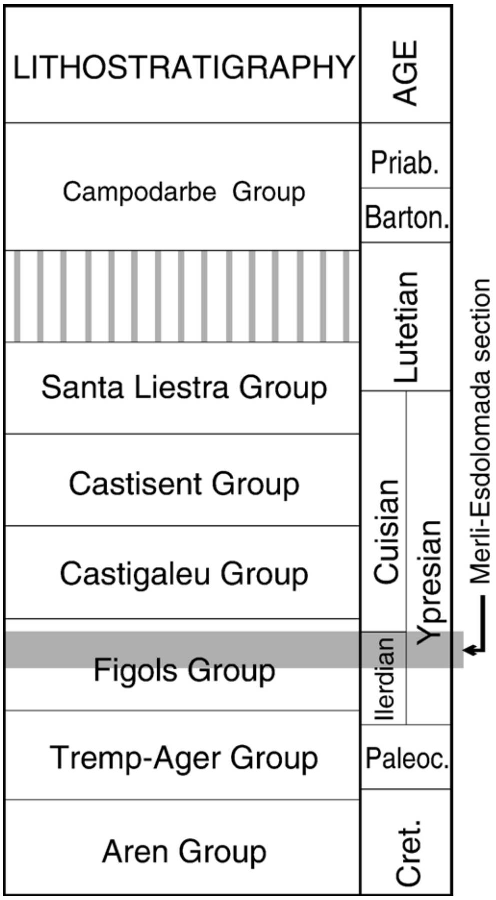

Fig. 1. General stratigraphic subdivisions of the Upper Cretaceous to Upper Eocene strata of the Tremp–Graus Basin, south-central Pyrenees, after Mutti et al. (1994). Vertical scale is not proportional to stratigraphic thicknesses.

Cretaceous to Eocene sedimentary succession subdivided into seven allogroups (Mutti et al., 1994; Remacha et al., 1998), i.e. sedimentary units separated by unconformities and correlative conformities recognisable at the basin scale. These allogroups are named, from base to top, Aren, Tremp–Ager, Figols, Castigaleu, Castisent, Santa Liestra, and Campodarbe (Fig. 1). The whole succession is detached at the base and displaced southwards by ESE–WNW oriented thrusts, giving the Tremp–Graus Basin a piggy-back geometry.

3. Materials and methods

The Merli–Esdolomada section (ME) crops out about 5 km west of the Isabena River and represents the middle part of the Figols Group (Figs. 1 and 2). It consists of mixed siliciclastic–carbonate sediments deposited in relatively shallow marine waters on the continental shelf, where the facies distribution was primarily controlled by terrigenous fluvial supply. Sedimentary facies analyses and basinwide correlations indicate that the succession is made up essentially by fluvial flood-related deposits in their proximal (mouth-bar) and distal (shelfal lobes) portions (Mutti et al., 1996, 2000).

The ME section has a stratigraphical thickness of 202 m. A total of 215 samples were collected from shale and silt for palynological and micropaleontological analyses. A schematic lithological log of the section is shown in Fig. 3A–D with precise sample positions.

3.1. Palynology

Twenty grams of shale were crushed into fragments smaller than 1.71 mm and processed in the ENI S.p.A.

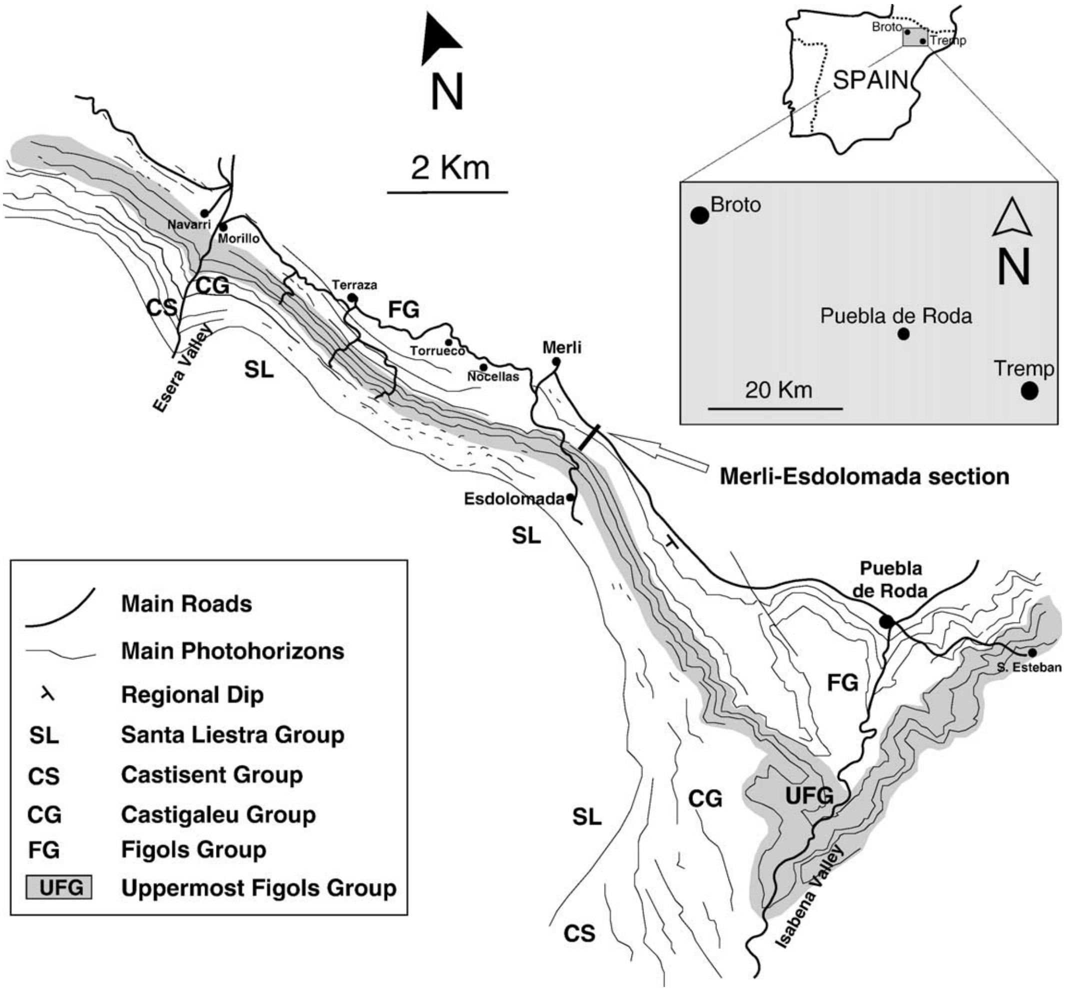

Fig. 2. Photogeologic sketch map of the Eocene strata cropping out in the study area (redrawn after Mutti et al., 1988) showing the location of the Merli–Esdolomada section.

laboratories with a standard palynological technique involving cold chemical treatment with 37% hydrochloric acid to remove the calcareous fraction and with 38% hydrofluoric acid to remove the silicates, sieving with 250 μm and 15 μm meshes, heavy liquid separation using $ZnCl_2$ and centrifuging (at 1250 rpm for 5 min) to concentrate the residue. After each step the residue was washed in distilled water. No oxidation was performed in order to retain the original kerogen composition. The residue greater than 15 μm was mounted on two palynological slides using Norland optical adhesive. Transmitted light microscopy analyses were undertaken with a Zeiss Axioplan microscope and interference-contrast illumination. One slide per sample was entirely scanned in order to obtain absolute counts of palynomorph taxa, whereas the second slide was examined to check for the presence of species not detected during the count. Approximately 200 particles of kerogen larger than 18 μm were counted in each sample by scanning the slide with a 20x objective. Analytical results were managed with the StrataBugs software package and tabulated as occurrence charts.

Following the methodology originally applied by Brinkhuis (1994) and Powell et al. (1996), successive shifts in the stratigraphic distribution of principal palynomorph morphogroups are used to reconstruct proximal–distal trends, interpreted as relative sea level fluctuations and activation/deactivation phases of the fluvial systems. The most crucial point in using fossils for paleoenvironmental reconstructions is judging their possible displacement correctly. In fact, apart from recycled forms which can be recognised on the basis of published stratigraphic records, the assessment of pre- and syn-depositional transport of dinoflagellate cysts far from their life settings, operated essentially by water and turbidity currents, is fundamental in order to prevent misleading interpretations (Dale, 1996). The occurrence of allochthonous dinocysts is primarily indicated by a mixing of species with incompatible ecological demands within the same assemblage. In the succession under investigation, deposited on the continental shelf in proximity to flood-dominated river-delta systems, major transportation is assumed to have occurred basinward. Therefore, when exclusively lagoonal-restricted marine forms are found in association with open marine indicators, we assume that the former are probably allochthonous, i.e. transported offshore by hydrodynamic systems related to the interplay between fluvial activation and relative sea level fall leading to increased runoff and sedimentary transportation across the shelf into more distal settings. Also water salinity ‘hyperstratification’ has been proven responsible for offshore dispersion of typically marginal marine dinoflagellates (Reichart et al., 2004).

3.2. Micropaleontology

Samples were disaggregated with Desogen, washed through a 63 μm sieve and dried. They were subdivided with a microsplitter in order to obtain statistically meaningful populations (at least 300 specimens, whenever possible). An approximate and indicative total abundance was obtained in the case of abundant washed residues, multiplying the counted micropaleontological constituents by the number of splitting times. Quantitative and semiquantitative analyses were performed on the fraction greater than 125 μm, and also the fraction smaller than 125 μm was qualitatively examined.

Foraminifer fragments were counted if unambiguously referable to a single taxon; generic larger foraminiferal fragments were evidenced apart if quantitatively relevant. Miliolids were not identified as separate genera and species but considered as a group, as they are mainly represented by internal casts (often broken), with only partially preserved parts of tests.

Data were computed and illustrated with Stratabugs. About 280 taxa were identified: most of them represent less than 1% of the total foraminiferal content and are reported as cumulative curves of main foraminiferal groups (Fig. 3), plotted as percentage of the total foraminiferal content, just as other fossil groups (e.g. echinoderms, molluscs, ostracods, bryozoans) as percen ages of micropaleontological content. In Figs. 4 and 5 quantitative distributions of selected taxa are given. Diversity is expressed as simple diversity (number of species/sample).

4. Significance of the kerogen components

4.1. Major kerogen groups

A number of papers investigate relationships between changes in the kerogen composition and changes in the relative sea level and distance from the coastline (Habib and Miller, 1989; Prauss, 1993; Blondel et al., 1993; Simmons et al., 1999; Schiøler et al., 2002). The kerogen groups considered in this study are described below with the corresponding environmental significance derived from the literature.

4.1.1. Black phytoclasts

Black phytoclasts (Plate III, fig. 12) are mainly charcoal fragments capable of prolonged floatation and their relative abundance tends to increase basinward (Tyson, 1995). The relative abundance of black debris may also reflect the frequency of wildfires in the hinterland (Batten, 1996a).

4.1.2. Brown phytoclasts

Brown phytoclasts (Plate III, figs. 10, 11) are essentially woody fragments. Their relative abundance generally decreases in an offshore direction exhibiting an inverse correlation to black phytoclasts.

4.1.3. Cuticles

Cuticles (Plate III, figs. 8, 9) are the outermost covering of the single layer of epidermal cells of leaves and stems of terrestrial plants. Their abundance in sediments rapidly decreases away from river mouths and they become finely broken and rare basinward (Batten, 1996a). An increased abundance of land plant cuticles indicate fresh water influx (Tyson, 1995). For the current purposes, both sporomorphs and freshwater algae, which represent a minor portion of the overall kerogen composition, are included in this category.

4.1.4. Amorphous organic matter (AOM)

Amorphous organic matter (Plate III, fig. 13) is the dominant kerogen component in low-energy, distal dysoxic to anoxic shelf environments (Tyson, 1995). Scarce oxygenation in the lower water column can be caused by stratification of the water masses.

4.1.5. Marine phytoplankton

Marine phytoplankton comprises essentially dinoflagellate cysts (Plates I–III). Indeed, all of the dinocysts encountered in this study are marine. The following section is wholly dedicated to discuss the paleoecological significance of dinocyst taxa.

4.2. Paleoecological significance of dinoflagellate cyst groups

A number of studies (Wall et al., 1977; Dale, 1996; Rochon et al., 1999; for a comprehensive summary see Marret and Zonneveld, 2003; Rochon and Marret, 2004) indicate that the distribution of dinoflagellate cysts in Recent sediments is controlled by the interplay among position relative to shore, water temperature, salinity, depth, light, nutrients and productivity. Most of these elements are a reflection of current patterns. Authors currently agree that nutrient supply and water stability are the main factors influencing cyst signals (Vink et al., 2000; Dale et al., 2002; Dale and Dale, 2002; Marret and Zonneveld, 2003). Since the beginning of the palaeoenvironmental studies applied to European marginal marine Paleogene successions (Köthe, 1990; Brinkhuis, 1994; Brinkhuis and Biffi, 1993; Powell et al., 1996), an actualistic approach has been followed for grouping dinoflagellate cysts according to their paleoecological affinities. The paleoecology of extinct taxa was interpreted from various sources, including information derived from associated fossils and morphological similarities with extant forms. The cyst groups established by Brinkhuis (1994) and Powell et al. (1996) were corroborated by a number of subsequent studies (Jaramillo and Oboh-Ikuenobe, 1999; Van Mourik et al., 2001; Iakovleva et al., 2001; Pross and Schmiedl, 2002; see Sluijs et al., 2005for a comprehensive summary). Most of them are used herein for the paleoenvironmental interpretation of the dinoflagellate cyst distribution (Fig. 3A–D). In addition, new insights on the paleoecological demands of extinct taxa are developed by integrating palynological, foraminiferal and sedimentary facies data.

The dinoflagellate cyst groups used in this study are generally coincident with the genera forming the bulk of the assemblages. They are summarized below with their corresponding paleoecological significance. For taxonomic citations reference is made to Williams et al. (1998).

4.2.1. *Cordosphaeridium* group

The *Cordosphaeridium* group consists mostly of *Cordosphaeridium gracilis*, *Cordosphaeridium inodes* and their intergrading forms (Plate II, fig. 2; Plate III, fig. 5). Sporadic specimens of *Cordosphaeridium fibrospinosum* are also included. This morphogroup is thought to represent open marine, outer neritic water masses (Köthe, 1990; Brinkhuis, 1994; Powell et al., 1996; Van Mourik et al., 2001). According to Islam (1984), *Cordosphaeridium* is most abundant during transgressions.

4.2.2. *Spiniferites* group

The *Spiniferites* group is here almost entirely represented by morphological varieties conspecific with *Spiniferites ramosus* (Plate II, fig. 3) but includes also rare specimens of *Spiniferites pseudofurcatus* and *Spiniferites mirabilis*. During our analyses, intergrading forms between *S. ramosus* and *Achomosphaera ramulifera* were assigned to this group as well. This group is unanimously regarded to represent oxygenated, open marine, neritic water masses (Wall et al., 1977; Brinkhuis, 1994; Dale, 1996; Powell et al., 1996; Rochon et al., 1999; Van Mourik et al., 2001). High percentages of *Spiniferites* are recorded when the influence of river plumes in the marine ecosystem is minimal (Zonneveld, 1989; Below and Kirsch, 1997) and in oligotrophic shelf areas characterised by well-mixed unstratified surface waters (Vink et al., 2000).

4.2.3. *Adnatosphaeridium* group

The *Adnatosphaeridium* group (Plate I, figs. 1–3) is here quantitatively dominated by *Adnatosphaeridium multispinosum*, but includes also *Adnatosphaeridium vittatum* and *Adnatosphaeridium robustum*.

Although *Adnatosphaeridium* exhibits morphological similarities with neritic to oceanic genera *Nematosphaeropsis* and *Cannosphaeropsis,* it is probably representative of inner to outer neritic rather than oceanic water masses (Brinkhuis and Biffi, 1993; Brinkhuis, 1994; Dale, 1996). This is confirmed in the material under investigation by the good match with *Spiniferites* and by the lack of other oceanic indicators.

4.2.4. *Areoligera* group

The *Areoligera* morphogroup includes species of *Areoligera* (Plate I, figs. 4, 6, 7) and *Glaphyrocysta* (Plate I, fig. 5; Plate II, fig. 11) and is retained by some workers as representative of open marine, inner to outer neritic settings (for a summary see Jaramillo and Oboh-Ikuenobe, 1999) and by others as indicative of high energy inner neritic water masses, especially as far as *Glaphyrocysta* species are concerned (Powell et al., 1996; Van Mourik et al., 2001; Crouch et al., 2003).

4.2.5. *Thalassiphora* group

The *Thalassiphora* group is here quantitatively characterized by the overwhelming dominance of *Thalassiphora patula* (Plate I, figs. 8, 9) and includes subordinately *Thalassiphora pelagica*. It is usually considered an outer neritic group (Van Mourik et al., 2001). High frequencies of *T. pelagica* have been reported from sediments deposited in shelf environments with low benthic oxygenation (Köthe, 1990; Pross, 2001) as well as from sediments deposited in pelagic settings in periods of enhanced water stratification and increased surface water productivity possibly triggered by climate cooling (Vonhof et al., 2000; Pross and Schmiedl, 2002). Salinity stratification is currently considered the main driving force behind *Thalassiphora* acmes (Sluijs et al., 2005).

4.2.6. *Operculodinium* group

The *Operculodinium* group includes forms referable to *Operculodinium centrocarpum* (Plate III, fig. 3) and subordinately to *Operculodinium microtriainum*. This is a typically cosmopolitan group as extant species of *Operculodinium* live in oceanic to restricted marine water masses. *O. centrocarpum* is proven to be tolerant of a wide range of temperature and salinity conditions (Rochon et al., 1999; Marret and Zonneveld, 2003). Increased frequencies of *Operculodinium* species and notably *O. centrocarpum* are the main signal for the river plume effect, interpreted as reflecting the environmental instability this creates (Zonneveld, 1989; Dale et al., 2002).

4.2.7. *Homotryblium* group

This group includes only *Homotryblium* species and *Homotryblium tenuispinosum* (Plate II, fig. 1) is overwhelmingly dominant. Several dinoflagellate workers used to lump *Homotryblium* and *Polysphaeridium* together, suggesting for both genera restricted inner neritic habitats with warm waters (Köthe, 1990; Brinkhuis, 1994; Powell et al., 1996; Van Mourik et al., 2001; Pross and Schmiedl, 2002). However, by considering separately trends in relative abundances of four distinct *Homotryblium* species along a proximal–distal depositional transect in the Danish Lower Miocene, Dybkjær (2004) pointed out that *H. tenuispinosum* was dominant in the more distal areas.

4.2.8. *Polysphaeridium* group

The *Polysphaeridium* group includes only dinoflagellate cysts referable to *Polysphaeridium subtile* (Plate II, fig. 4; Plate III, fig. 4). The extant species *Polysphaeridium zoharyi*, which is the cyst stage of *Pyrodinium bahamense*, was initially supposed to prefer lagoonal warm waters with increased salinity (Wall et al., 1977). Thereafter the *Polysphaeridium* group has been retained as indicative of restricted marine hypersaline water masses in several worldwide Paleogene studies (Brinkhuis, 1994; Powell et al., 1996; Van Mourik et al., 2001). However, *P. zoharyi* was also found to be abundant in the Musandam region, where salinity is lower than in the rest of the Persian Gulf (Bradford and Wall, 1984), thus suggesting that proximity to land is more important than salinity in influencing its distribution. This observation has been subsequently confirmed by investigations showing that *P. zoharyi* can also dominate associations in low-saline waters and must be considered a species characteristic for euryhaline tropical/subtropical coastal sites (Edwards and Andrle, 1992; de Verteuil and Norris, 1996; Marret and Zonneveld, 2003).

4.2.9. Other cysts

The rest of the dinoflagellate cyst assemblages was split into three further groups:

(a) other identified dinoflagellate cysts, including both taxa with uncertain paleoecological preferences (e.g. *Diphyes* spp., *Fibrocysta* spp., *Melitasphaeridium* spp., etc.) and very rare taxa (e.g. *Rhombodinium* spp., *Wetzeliella* spp.);

(b) badly preserved specimens, taxonomically undetermined;

(c) reworked dinoflagellate cysts: the status of 'reworked' was established for taxa which are reported to have become extinct before the Early Eocene (Hardenbol et al., 1998; Williams et al., 2004).

4.3. Paleoecological significance of selected sporomorphs

Pollen and spore assemblages are poorly diversified in the Merli–Esdolomada section. Owing to long stratigraphic ranges, it is sometimes impossible to judge if they are recycled or in situ. The following categories have been considered in the present study.

4.3.1. Bisaccate group

This is a morphogroup including undifferentiated bisaccate pollen referable to conifers. Owing to their high buoyancy, these grains can be transported in large numbers to open marine and even oceanic settings. Other pollen grains, and especially spores, are considered to be transported less far into the marine environment than bisaccates (Brinkhuis, 1994). It is difficult to state whether poorly preserved bisaccate pollen is in situ or reworked from older sediments. Either way it is worthwhile noting that frequency diagrams of bisaccate pollen show a marked increase during transgressions.

4.3.2. Leiotriletes group

The *Leiotriletes* group includes smooth, unornamented, mainly thin-walled trilete spores referable to pteridophytes (i.e. ferns and fern allies). These forms are common in Tertiary assemblages, as documented in the literature. River input is the main transport mechanism for these sporomorphs, which can be also generated by aquatic ferns growing in coastal marshes.

4.3.3. Spinizonocolpites group

This group is here represented by pollen referable to the fossil species *Spinizonocolpites echinatus* Muller, *Spinizonocolpites baculatus* Muller and their intergrading forms (Plate III, figs. 6, 7). These echinate zonosulcate grains are remarkably similar to pollen of *Nypa fructicans*, a mangrove palm that is the only modern representative of genus *Nypa*. Coastal areas with *Nypa* vegetation occur today from India through Malaysia where rivers carry high sediment loads into protected bays along gently shelving coastlines. *Nypa* favours intertidal zones of tropical areas, quiet estuaries or shallow lagoons into which freshwater may run. It does not grow on shores exposed to wave action and never in hypersaline conditions. Published information shows systematic relationships and ecological similarities between ancient and modern *Nypa* (Collinson, 1993). Therefore *Spinizonocolpites* can be considered a reliable palaeoecological indicator.

5. Paleoecological significance of foraminiferal groups

Ecological preferences of extinct microfossils can be assumed comparing fossil and recent assemblages (Romero et al., 2002). However Paleogene microfaunas differ considerably from living assemblages, hence the paleoenvironmental significance of the main foraminiferal groups is derived from records observed in well-known depositional settings (Luterbacher, 1984). Nonetheless fossil biofacies are also the result of taphonomic processes superimposing on the primary environmental conditions. In order to interpret our data, foraminiferal assemblages have been subdivided into six groups following Gaboardi (1994, 1996).

5.1. Planktonic foraminifera

The percentage of planktonic foraminifera is roughly related to water depth and distance from the coast, and highest values should correspond to transgressions. However, in the current context turbidity and fresh water probably have a strong effect even in relatively distal settings.

5.2. Larger foraminifera

A rich literature is available on larger foraminifera. Light and nutrient supply affect the distribution of symbiont-bearing larger foraminifera that are generally related to oligotrophic, warm, shallow waters. Water-depth range depends on the type of symbiont, as well as on light penetration; therefore turbidity greatly influences the lower limit of the photic zone (Murray, 1991; Hottinger, 1983, 1997; Hallock et al., 1991; Reiss and Hottinger, 1984).

According to Luterbacher (1998), beach deposits rich in *Alveolina* and *Orbitolites* are the shallowest facies, while *Nummulites* and *Operculina* are deposited in highly bioturbated mudstones in deeper water, and locally sediment-starved deeper intervals with *Assilina* and *Discocyclina* can be observed.

Nummulites, *Assilina* and *Operculina* smaller than 8 mm in diameter are found in almost all nearshore facies, but they are very frequent in prodelta silty shales (Luterbacher, 1984). Species larger than 8 mm are frequent in beach deposits and nearshore shoals. Matteucci and Pignatti (1988) provide a review of the taphonomy and paleoecological interpretations of *Nummulites*, considered mostly as non-epiphytic, bottom dweller.

Small lens and disk shaped *Discocyclina* are found in shaly intervals of the inner to middle neritic deposits, representing a small part of the association. Large flat specimens of *Discocyclina* are characteristic of very shallow water depths; they are frequent but rarely dominant in carbonate shoals intercalated with terrigenous levels (Luterbacher, 1998).

Gaboardi (1994) recorded and discussed a sudden increase in abundance of the genus *Assilina* in Figols units 6 and 7 (Carminatti, 1992) with respect to the underlying units dominated by *Nummulites* and ascribed this shift to substrate variations, as *Nummulites* preferred muddier sediments (Murray, 1991), while *Assilina*, associated with *Cibicides*, *Pararotalia* and *Neoeponides*, probably preferred sandier and harder substrates. However, Hohenegger (2000) reported extant *Nummulites* as living typically on sand.

Operculina is a herbivore genus living in muddy carbonate sediments (Murray, 1991), and lives on soft substrate as *Assilina* (Romero et al., 2002; Hohenegger et al., 1999).

5.3. Rotalia group

Gaboardi (1994) lumped within this group perforate smaller foraminifera restricted to shallow water such as *Rotalia*, *Pararotalia*, *Cuvillierina*, *Asterigerina*, *Neoeponides* gr. Depth distribution of large, probably symbiont bearing rotaliids, depends on light intensity and water transparency (Billman et al., 1980). Rotaliids are very frequent in inner neritic facies rich in terrigenous mud, but rarely found in clean carbonates (*Rotalia* s.l., in Luterbacher, 1984).

Extinct *Cuvillierina* is reported to be abundant in calcareous and terrigenous littoral deposits and rare in other facies in the Ager Formation (Ferrer et al., 1973; Gaboardi, 1996) and mainly in shaly littoral deposits (Luterbacher, 1984).

Gaboardi (1994) suggested for *Rotalia* a tolerance to salinity variations. Extinct *Rotalia trochidiformis* was considered to prefer water depths of 20–40 m (Levin, 1957) by analogy with similar modern asymmetrically biconvex shallow-water species; Ferrer et al. (1973) found it most abundant in littoral deposits of Eocene sediments in the Pyrenees. According to Gaboardi (1994), *Asterigerina* was a relatively deeper dweller with respect to *Rotalia*. Grüenig and Herb (1984) attributed it to outer neritic settings in Eocene sediments from SW France, while Murray (1991) reported recent *Asterigerina* as an epifaunal, herbivore, warm water, inner-shelf genus. *Asterigerina* was associated with rotaliids in shallow terrigenous facies of the upper photic zone in Middle to Late Eocene sediments (Romero and Caus, 2000). Fossil Asterigerinidae were possibly symbiont-bearing according to Le Calvez (1970), like living representatives of the family.

Extant *Pararotalia* is a herbivore taxon, indicator of warm, shallow and normal salinity water (Le Calvez, 1970; Murray, 1991).

5.4. Porcellanous foraminifera

Porcellanous foraminifers are most abundant in normal marine and hypersaline lagoons and marshes (Murray, 1991). Miliolids are most frequent in the lagoonal and beach deposits at the base of transgressive–regressive cycles and their frequencies are not affected by the amount of terrigenous mud in the sediment (Luterbacher, 1984); they are constituents of sea meadow assemblages (Le Calvez, 1970). *Quinqueloculina* and *Triloculina* are associated to hypersaline waters and they are epifaunal herbivores (Murray, 1991). The distribution of herbivores and epiphytes such as miliolids is influenced by turbidity because it prevents the colonization of the sea-floor by vegetation (Dominici, 1994) and consequently reflects the patchy distribution of seagrasses.

5.5. Agglutinated foraminifera

Agglutinated foraminifera are present in every environment, but organic-cemented taxa seem to be dominant in restricted, lowered salinity marginal marine settings or in deep settings.

5.6. Other calcareous perforate small benthic foraminifera

Within this group the subgroup ‘Deep water indicators’ was evidenced. It contains Nodosariacea, *Cibicidoides pseudoungerianus*, *Anomalinoides*, *Gyroidinoides*, *Trifarina*, and *Uvigerina* (Gaboardi, 1996). *Uvigerina*, *Bulimina* and *Brizalina* are part of the infauna and they are associated to fine, low-oxygen sediments such as in upwelling areas in outer shelf-

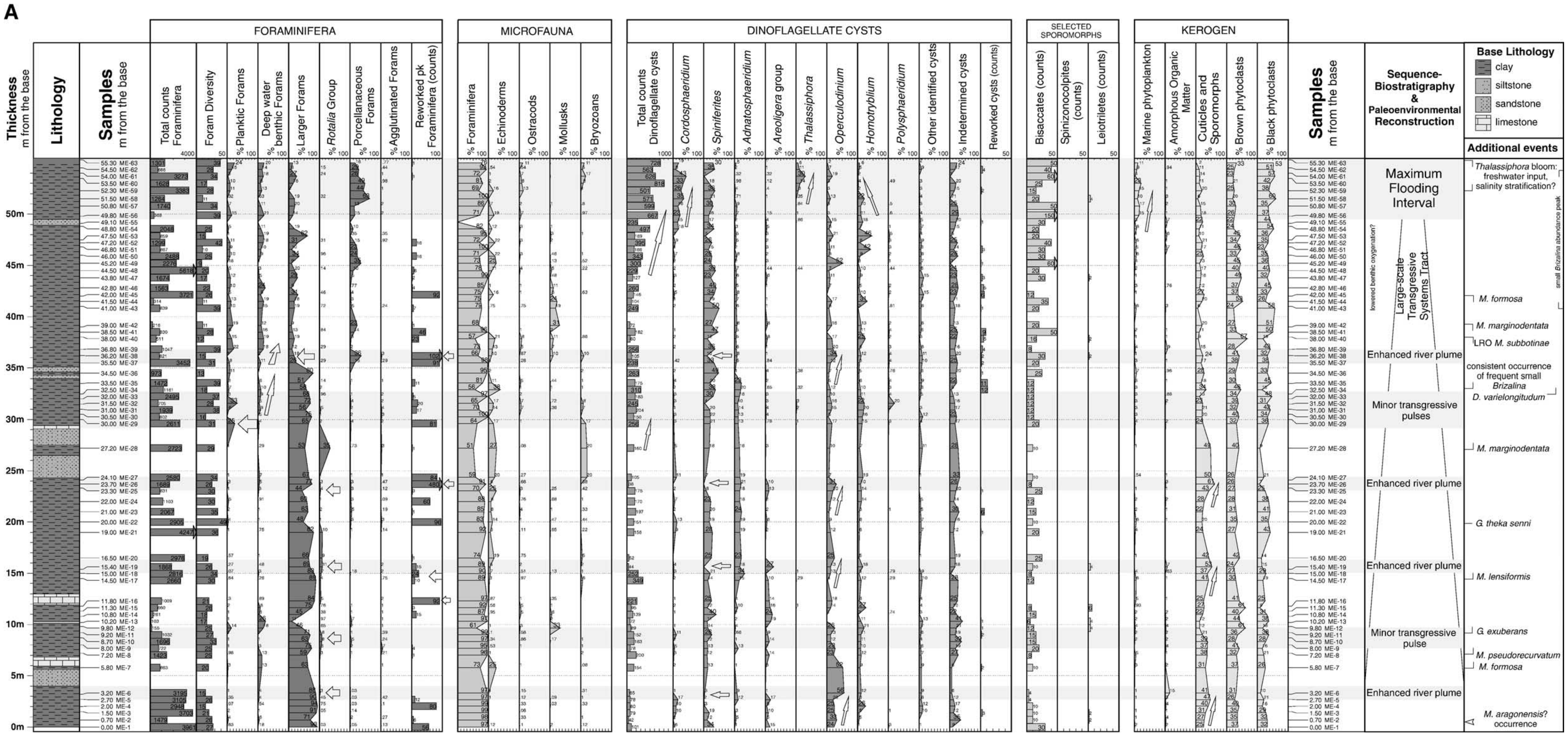

Fig. 3. (A–D) Composite range-chart showing quantitative distributions of foraminifera, dinoflagellate cysts, sporomorphs and kerogen groups in the Merli–Esdolomada section. Sequence biostratigraphy and paleoenvironmental reconstructions are interpreted from biosignals. Arrows and circles indicate the most prominent signals discussed in the text. Foraminifera diversity = species number.

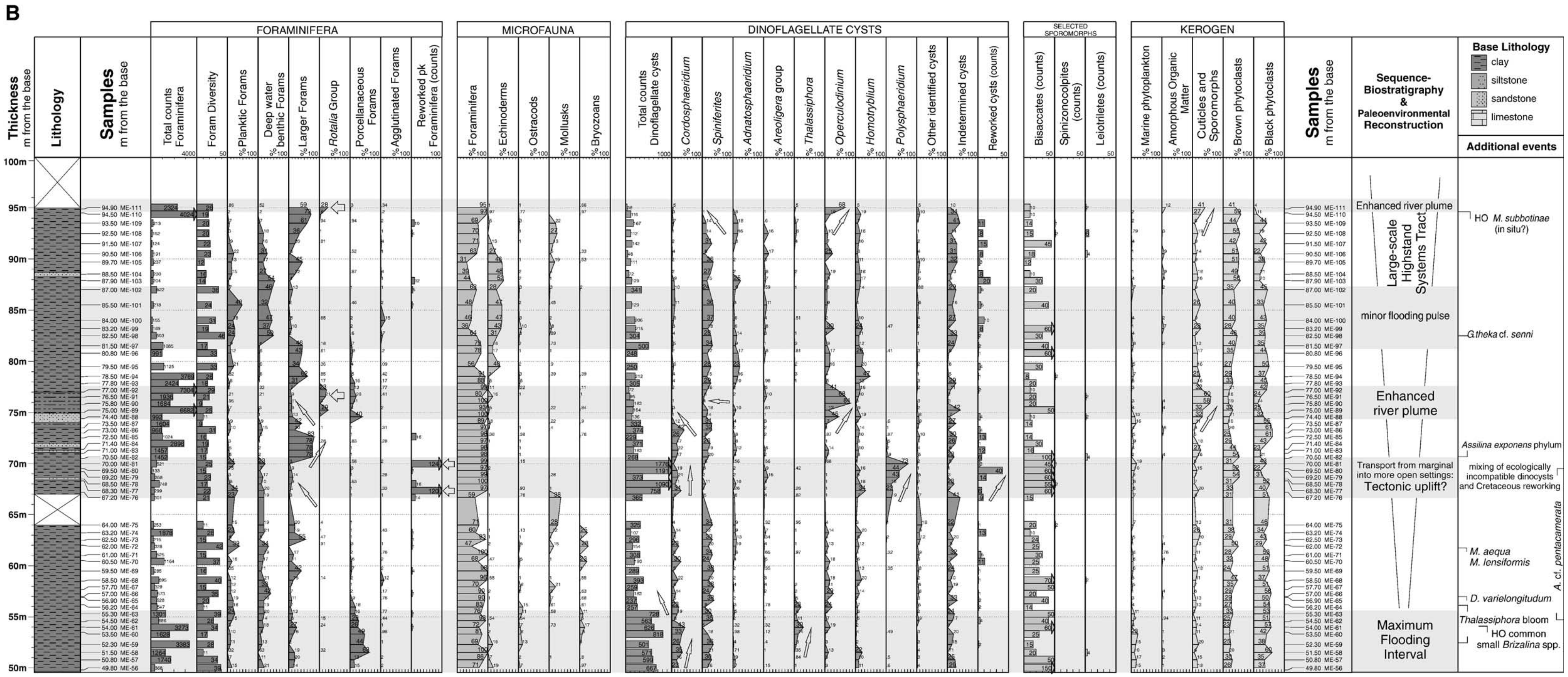

Fig. 3 (*continued*).

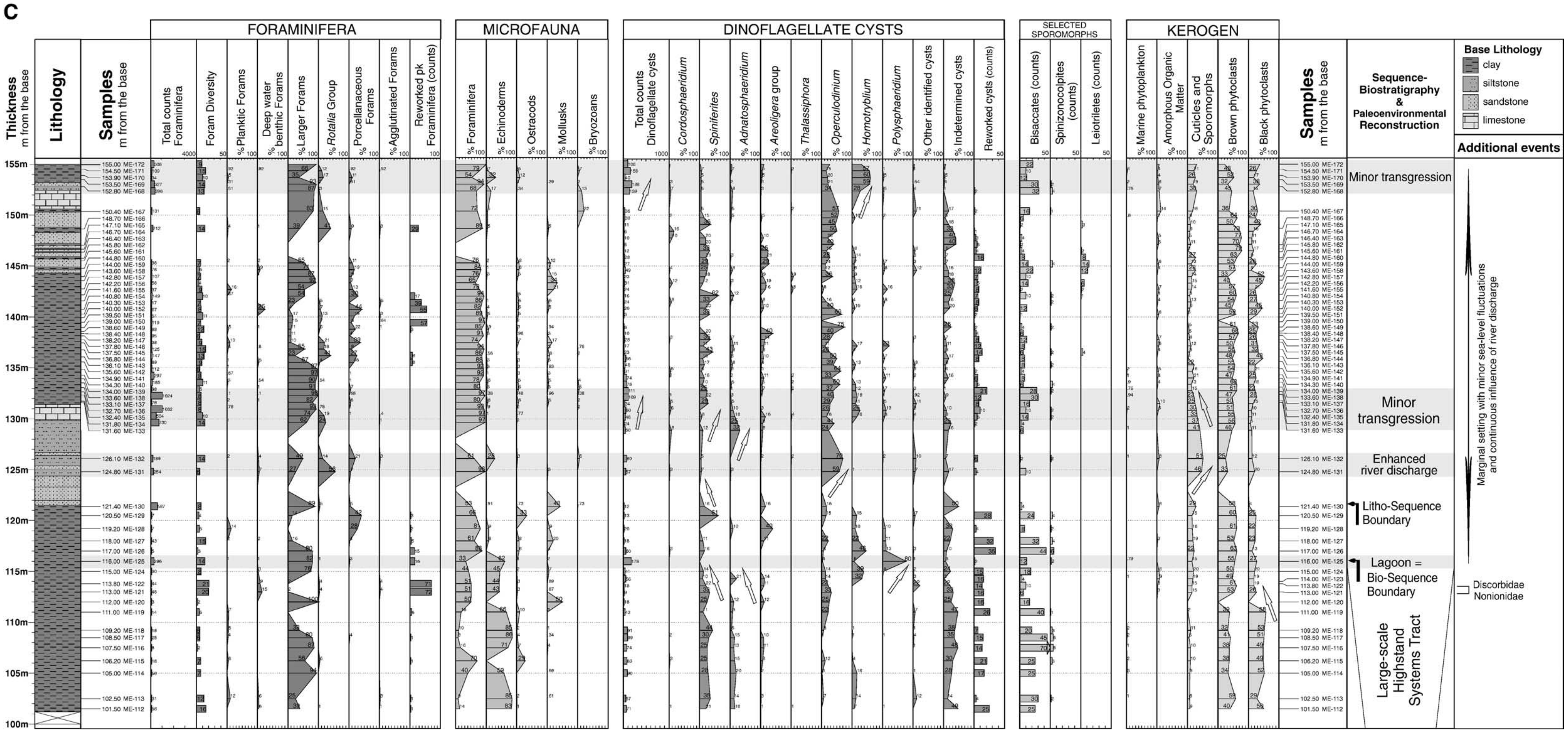

Fig. 3 (*continued*).

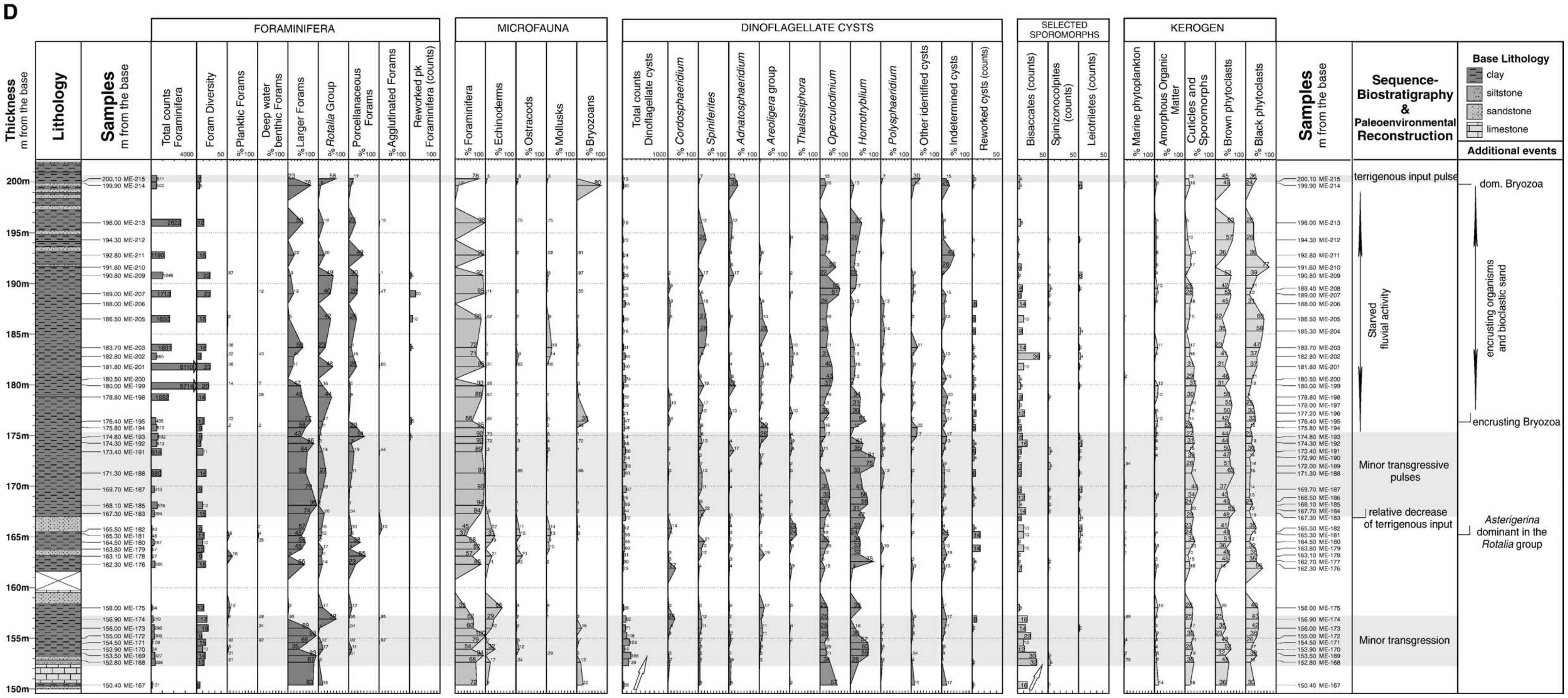

Fig. 3 (*continued*).

upper bathyal settings (Boersma, 1980, 1990). Lagenids are very rare in beach to shoal facies, absent in shallow-water carbonates and prominent in the shaly nearshore facies (Luterbacher, 1984).

Nodosariidae (Romero and Caus, 2000; Romero et al., 2002) are found in the lower part of the photic zone and increase in abundance in the aphotic zone and they are not compatible with lower than normal salinity (Le Calvez, 1970).

Among other taxa, living *Discorbis* is a temperate-warm epifaunal herbivore of inner shelf (Murray, 1991) and it was found restricted to littoral deposits and carbonate shoals in fossil assemblages (Luterbacher, 1984). *Nonionella* and *Elphidium* are well adapted to lagoonal conditions; *Nonion* and some Buliminacea are adapted to slightly lower salinities (Le Calvez, 1970).

6. Sequence biostratigraphy and paleoenvironmental interpretation of the Merli–Esdolomada section

6.1. Interval 0–55.3 m (Fig. 3A)

The consistent occurrence of *Spiniferites* and the absence of *Polysphaeridium* suggest for this part of the section relatively open marine conditions. However, the influence of cyclically enhanced fluvial discharge is evident throughout. From sample ME-1 to ME-6 (3.2 m) the progressive decrease of *Spiniferites* coincides with the increase of *Operculodinium* and herbaceous cuticles in the kerogen composition. Such inversely correlated signals are interpreted to reflect environmental instability created by incoming river plumes. In fact *O. centrocarpum* has a demonstrated capacity to thrive in unstable environments (Wall et al., 1977; Dale, 1996) and is dominant where the impact of river water on the marine environment is highest (Dale et al., 2002), whereas representatives of *Spiniferites* (notably *S. ramosus*) prefer shelf areas where the influence of the river plume is minimal (Zonneveld, 1989; Below and Kirsch, 1997).

Similar trends are observed from sample ME-13 (10.2 m) to ME-19 (15.4 m) and from ME-21 (19.0 m) to ME-27 (24.1 m), where the relative abundance of *Spiniferites* inversely correlates with abundances of *Operculodinium* and herbaceous debris. In particular, samples ME-6 and ME-26 lack *Spiniferites* and show highest abundances of *Operculodinium* and herbaceous cuticles, thus suggesting strong river plume effects. Both ME-6 and ME-26 were collected from shale a few decimetres beneath the base of sandstone beds, hence suggesting that palynological assemblages record the beginning of the fluvial activation still within fine grained sediments, i.e. expression of hypopycnal flows, where the litho-sedimentological evidence is poor. The palynological signal therefore anticipates the homo- and hyperpycnal flows (maximum fluvial discharge) recorded by immediately overlying sandstone.

From the base of the section up to sample ME-28 (27.2 m), planktonic foraminifera are subordinate (generally less than 5%) compared to benthic. Larger foraminifera dominate the assemblage and decrease slightly in relative abundance from the bottom upwards. They are mostly represented by *Nummulites* spp. and *Discocyclina* spp., which appear to be inversely correlated and reflect approximately 10 m thick cycles. From ME-1 to ME-27 three cycles can be detected. In this part of the section diversity peaks correspond to *Discocyclina* relative abundance peaks. *Operculina* is generally scarce, but apparently more frequent when associated with *Discocyclina* and therefore reasonably tied to water deepening as both taxa preferred muddier sediments (Caus and Serra-Kiel, 1984; Romero et al., 2002).

The *Rotalia* group is generally scarce, but presents some abundance shifts that sometimes correlate with the river–plume effects indicated by palynology. The *Rotalia* group was considered euryhaline by Gaboardi (1994) but could also have reflected less susceptibility to the turbidity generated by increased fluvial discharge with respect to larger foraminifera. From ME-17 to ME-21 the *Rotalia* group is about 10% and in ME-28 it reaches 25% of the foraminiferal assemblage. In ME-25 and -26, increased Cretaceous reworking plus reworked anhydrite and abundant mica are probably further expressions of the fluvial reactivation. Bryozoan fragments are more frequent constituents of the bioclastic fraction from ME-27 to ME-31, possibly marking transgressive pulses.

From sample ME-29 (30.0 m) upwards palynological and micropaleontological records consistently point to sea-level rise, except for the sporadic occurrences of likely allochthonous *Polysphaeridium* in *Spiniferites*-dominated dinocyst assemblages. The transgressive trend culminates within a maximum flooding interval from ME-56 (49.8 m) to ME-63 (55.3 m) characterised by highest relative frequencies of marine phytoplankton reaching 23% of the overall kerogen composition. Indeed, these samples are the richest in terms of concentration and diversification of in situ dinocysts. The highest abundances of the open marine groups *Spiniferites* and *Cordosphaeridium* are consistent with the absence of the lagoonal indicator *Polysphaeridium*. Black phytoclasts dominate the kerogen composition and this is consistent with the fact that their relative abundance is generally thought to increase in an offshore direction exhibiting an inverse correlation to brown phytoclasts (Tyson, 1995; Schiøler et al., 2002). Within this maximum flooding zone, an oceanographic change is documented by a dramatic turnover in the composition of the dinoflagellate cyst assemblages. From sample ME-59 to ME-64, the sharp increase of *T. patula* (Plate I, figs. 8, 9) corresponds with a drop of *Homotryblium*. The increase in abundance of *T. pelagica*, a species closely related to *T. patula*, was interpreted to reflect climate cooling and/or productivity increase in the Massignano section of central Italy (Vonhof et al., 2000). A marked inverse correlation between the abundances of *T. pelagica* and *H. tenuispinosum* was already documented in the Lower Oligocene of SW Germany and interpreted in terms of climatic changes triggering variations of nutrient supply, salinity and bottom water oxygenation. In particular, high proportions of *T. pelagica* were supposed to indicate enhanced stratification and eutrophication in the upper and/or oxygen-depletion in the lower water column (Pross and Schmiedl, 2002). On this basis, the *T. patula* acme recorded from ME-59 to ME-64 can be seen as the distal expression of the salinity stratification triggered by the cyclical activation of the fluvial systems already documented in the section beneath by river plume effects. No indications of eutrophication were detected.

These intervals denoting periods of enhanced fluvial discharge seem to reflect a Milankovitch-type cyclicity. In fact, considering the age assessments discussed in section 8 and a consequent average sedimentation rate of about 200 m/Ma, a 50–60 ky cyclicity (eccentricity) can be established for the five fluvial pulses documented in this part of the section (Fig. 3A).

Brizalina spp. (smaller than 125 μm, Fig. 5) are present from ME-34 (32.5 m) to ME-100 (84.0 m) and show an abundance peak from ME-43 to ME-62 in the sediments immediately underlying the maximum flooding zone, probably related to the water deepening. Therefore the increase of opportunistic infaunal small *Brizalina* spp., otherwise absent in the succession, could reflect a low-energy environment and perhaps a decrease in the sediment oxygen content.

From ME-37 (35.5 m) larger foraminifera exhibit a sharp drop in relative abundance (except for an isolated peak at ME-53) consistently with the transgressive trend. In ME-53 (47.5 m), at the base of the inferred maximum flooding interval, *Discocyclina* overwhelms *Nummulites*, and this could confirm a ‘deeper’ character for the former genus with respect to the latter. Also the *Rotalia* group markedly decreases in abundance (below 1%) from ME-35 to ME-73. These observations are consistent with water deepening toward the lower boundary of the photic zone, within the middle–outer shelf not deeper than 80 m. The larger foraminifera decrease could also be tied to diminished water energy related to deepening or reduced fluvial activity, if these elements were mostly transported.

Deep water indicators steadily increase from ME-29 to ME-66; *Cibicidoides alleni*, which has an upper depth limit from 25 m to 100 m (Van Morkhoven et al., 1986; Murray, 1991), increases from ME-37 and *Praeglobobulimina* gr. *ovata* from ME-56. Planktonic foraminiferal relative abundance increases above ME-29 and fluctuates between 10% and 20%; Cretaceous reworking drastically decreases above ME-52, thus supporting a steady deepening in this part of the section and lowered fluvial supply.

Within this framework, Miliolidae increase from ME-37 in correspondence with a drop in larger foraminiferal abundance, and show four relative abundance peaks (ME-38, -42, -49, -58); the highest is followed by a rapid decrease. It is not clear whether this is due to a preservation bias (they are generally broken and dissolved and only internal mold fragments are usually observed) or they reflect lower energy transportation pulses with respect to the larger foraminifera-dominated intervals. Indeed, as suggested in Dominici (1994), herbivore miliolid peaks could indicate a temporary expansion of sea-floor vegetation cover somewhat tied to nutrient content, turbidity and illumination variations induced by fluvial activity pulses.

6.2. Interval 55.3–100 m (Fig. 3B)

The drop in numbers of in situ dinocysts and foraminifera in sample ME-64 (56.2 m) is believed to represent the beginning of a regressive trend, which can be regularly followed upwards to the sequence boundary beneath the sandstone at 121.5 m. However, the gradual development of the highstand systems tract is affected between 67.2 m and 70.0 m by an event yielding a distinctive palynomorph record. From sample ME-76 to ME-81 dinoflagellate cyst assemblages are rich and diverse, and comprise taxa with incompatible paleoecological preferences. In fact, although *Polysphaeridium* is the dominant group, *Homotryblium*, *Glaphyrocysta*, *Cordosphaeridium*, *Spiniferites* and *Adnatosphaeridium* are still abundantly represented. We interpret this situation by postulating the displacement of *Polysphaeridium* from marginal into more open marine settings. The mass introduction of lagoonal indicators into more open marine environments can be the expression of a sudden relative sea level fall, leading to increased sediment transport across the shelf and a basinward shift of the optimum habitat of marginal marine species. Peaks of reworked dinoflagellate cysts, reworked foraminifera and bisaccate pollen recorded in this interval suggest enhanced erosion and terrestrial delivery to the sea. A tectonic uplift of the rising Pyrenean chain could reasonably be invoked to account for these records. An anomalous peak of the foraminifer *C. alleni*, bracketed between two pulses of Cretaceous reworking and correlating with the *Polysphaeridium* peak, could result from transport as well.

Larger foraminiferal percentages are comparable to the underlying interval. From ME-79 mainly lens-shaped pustulate *Assilina* spp. appear and dominate the assemblages from ME-82 to ME-87 where larger foraminifera increase again, even if more fluctuating than in the basal 35 m of the succession. *Assilina* spp. substitute *Nummulites* spp. as dominant elements of the larger foraminiferal group. This signal was tentatively explained by Gaboardi (1994) as a reflection of a change in sediment grain size.

Bryozoans increase in relative abundance from ME-60 to ME-63 and from ME-70 to ME-74, possibly marking small-scale transgressive pulses and/or temporary decrease of terrigenous input.

From sample ME-88 (74.4 m) to sample ME-92 (77.0 m) a significant oceanographic event can be inferred by the strong inverse correlation between abundances of *Operculodinium* and *Spiniferites*/*Cordosphaeridium*. The peak of *Operculodinium*, in agreement with the dominance of cuticles in the kerogen composition, reflects environmental instability created by incoming river plumes (Dale et al., 2002).

Samples ME-89, -91 and -92 are also characterized by rich foraminifera assemblages composed by representatives of the *Rotalia* group, Miliolidae, *C. alleni* and *Cibicides* spp., whereas the relative abundance of larger foraminifera drops sharply. *Stomatorbina* spp. are associated to the *Rotalia* increase as in ME-18–20 and ME-28. The enhanced influx of fine terrigenous sediments could reasonably have induced such biofacies change.

The microfauna gradually decreases in abundance from sample ME-95 to ME-109 with minor shifts, although it is still diverse. Larger foraminiferal abundance increases from ME-94 to -97, but drops again from ME-98 to ME-103. Consistently, planktonic foraminifera (with a relative abundance peak in ME-101) and *P.* gr. *ovata* constitute the bulk of the foraminiferal assemblage in a mostly shaly interval with diluted microfauna, often pyritized. *P.* gr. *ovata* is tentatively tied to disoxic conditions. These records suggest a temporarily enhanced marine signal which seems to be confirmed also by palynological data. In fact, the overall trend of progressive impoverishment of dinoflagellate cyst assemblages is interrupted by a minor transgressive pulse from ME-97 (81.5 m) to ME-102 (87.0 m), evidenced by high percentages of *Spiniferites*.

Successively, the relative increase of the *Areoligera* group witnesses an increasing influence of inner neritic water masses, in response to a relative sea-level highstand. At 94.9 m (sample ME-111), the dominance of *Operculodinium* (68% of the cyst assemblage) and cuticles plus wood (82% of the kerogen assemblage) again correlate with the temporary disappearance of *Spiniferites*, thus suggesting a river plume effect. Foraminifera also register a gradual shallowing as testified by the decrease of planktonic forms and *P.* gr. *ovata* from ME-102 up to ME-109. In this interval *Nonion* s.l. becomes an important component of an otherwise poor assemblage. Larger foraminifera become again dominant in samples ME-110 and -111, characterized by rich assemblages including lens-shaped *Assilina* spp., *Discocyclina* spp. and the *Rotalia* gr. This succession of events reflects the river plume effect just as in the interval ME-90–92: *Assilina* suddenly overcomes *Nummulites,* which is subsequently replaced by the *Rotalia* group, characterized by a peak of *Cuvillierina* spp. coinciding with the *Operculodinium* peak. *Operculina*, rare but constantly present from the base of the series, is virtually absent above ME-105.

6.3. Interval 100–152.8 m (Fig. 3C)

From ME-112 (101.5 m) upwards microfauna is less abundant and diverse than in the section beneath. The relative abundance of larger foraminifera fluctuates and *Nummulites* and *Assilina* are inversely correlated. Miliolidae and the *Rotalia* group are rare or absent from ME-112 to ME-125, while *Nonion* is scarce up to ME-120. Ostracods are common in ME-115 and ME-121 and 122 contain diversified very small Discorbidae/Nonionidae assemblages, thus suggesting a low energy/restricted environment. Pyrite is abundant and reworked Cretaceous planktonic foraminifera are particularly evident.

The general shallowing upward trend is strikingly confirmed by the palynological content of sample ME-125 (116.0 m) where *Polysphaeridium* is abundant and dominant in the dinoflagellate cyst assemblage. Such dominance is typical for taxa that can tolerate extreme environmental conditions where others fail. The establishment of a lagoonal setting is inferred for this part of the section also in agreement with the lack of open marine indicators. The scattered occurrence of *Spinizonocolpites* pollen is consistent with conditions favourable for the ecology of *Nypa* mangrove palms, i.e. protected lagoons with reduced wave action and salinity lowered by fluvial input. Accordingly, sample ME-125 documents the shallowing in the final portion of the highstand systems tract and provides palynological evidence for a sequence boundary.

Discorbidae, Miliolidae and gastropods together with common, but mostly broken and probably resedimented larger foraminifera, diluted in abundant terrigenous silty/sandy micaceous fraction, characterize the microfauna of this interval, becoming even poorer above ME-125, with abundant fine terrigenous input.

Increased delivery of terrigenous material to the Merli–Esdolomada region is documented from 121.5 m to 130.0 m both by coarser lithologies (silt and sand) and in samples ME-131 and ME-132 by the dominance of *Operculodinium* (up to 70% of the total dinocyst assemblages) and cuticles in the kerogen composition (more than 50%). The increased recovery of *Rotalia* from these samples is therefore consistent.

The palynological evidence of a minor transgression is observed from samples ME-133 to ME-139, immediately above the top a nodular limestone (131.5 m), where both absolute counts of dinoflagellate cysts and relative abundances of *Adnatosphaeridium*, *Spiniferites*, and *Homotryblium* increase. In this interval the sand component (>125 μm) of shales is mainly biogenic–bioclastic, with relatively richer foraminiferal assemblages dominated by *Assilina* spp. and rare *Discocyclina*.

From ME-143 the terrigenous fraction, with common micaceous sand, becomes dominant and the microfauna decreases. Assemblages are poor, being generally composed of small specimens of the *Rotalia* group (*Cuvillierina* spp., *Pararotalia* spp.), *Discorbis* spp., *Cibicides* spp., Miliolidae, Ostracoda, gastropods and common reworked Cretaceous planktonic foraminifera (from ME-149 to ME-155). The *Rotalia* group, together with Miliolidae, replace larger foraminifera that constitute again the bulk of the assemblage in ME-155, where the bioclastic sandy fraction reappears.

6.4. Interval 152.8–200.1 m (Fig. 3D)

Another minor transgressive–regressive cycle is recorded from sample ME-168 (152.8 m) to ME-174 (156.9 m), above a sandy interval capped at 150.5 m by limestone and characterised by scarce dinoflagellate assemblages dominated by *Operculodinium*. Indeed, a marked increase in abundance and diversity of dinoflagellate cysts is detected at 152.8 m and *Homotryblium* becomes temporarily dominant. This trend is confirmed by the foraminifer abundance curves. From ME-169 to ME-175 the bioclastic sandy fraction decreases, replaced by inorganic terrigenous sand. Assemblages are mainly represented by larger foraminifera with alternating peaks of *Assilina*, *Nummulites* and *Rotalia*; the latter dominates the association in ME-174 with prevalent *Cuvillierina* spp. (probably *C. vallensis*) and *Pararotalia* spp. Bryozoans are also present in this interval, thus apparently confirming a tie with transgressive phases.

Above the sand body at 167 m, a rather homogenous interval rich in bioclasts and fairly well preserved microfauna extends from ME-183 to ME-199. Larger foraminifera dominate the assemblage, with *Nummulites* spp. and *Discocyclina* spp. substituting *Assilina* spp. up to ME-191 (possible minor flooding interval), *Asterigerina* spp. prevalent in the *Rotalia* gr. (*Cuvillierina* spp. are still regularly present but in lower percentages) and Miliolidae following the trend of *Assilina* spp. These alternations are probably a reflection of variations in the substrate composition and/or micaceous sand input. Echinoids almost disappear, while bryozoans and gastropods are concentrated at some levels.

The uppermost part of the section, from ME-199 (180.0 m) upwards, is characterized by a fairly abundant microfauna represented by similar percentages of larger foraminifera (*Nummulites* spp. and *Assilina* spp.), *Rotalia* gr. (prevalent *Asterigerina* spp.), Miliolidae, subordinate Discorbidae. From ME-199 to ME-201 abundance peaks are dominated by larger foraminifera with Miliolidae, *Asterigerina* spp., and small *Cibicides* spp.In ME-207 and from ME-209 to ME-214 abundant *incertae sedis* encrusting microperforate organisms were observed together with encrusting bryozoans (marks on larger foraminifera), probably indicating temporarily lowered sedimentation rates. A mixing of nearly all the groups, with a prevalence of *Operculodinium* and *Homotryblium*, is the distinctive character of the dinocyst assemblages in the uppermost ME section. A certain degree of allochthony and constant fluvial influence in a marginal marine setting are likely to be responsible for these signals. However, it must be emphasised that dinocysts from the upper sequence (i.e. the section above the sequence boundary at 116 m) are less abundant than in the sequence beneath, as fewer than 100 specimens per slide were often counted. Hence percentages can be meaningless and paleoenvironmental reconstructions based on palynology are accordingly weaker than in the lower sequence. In conclusion both quantitative and qualitative data point to an overall shallowing trend with time throughout the Merli–Esdolomada section.

7. Discussion

7.1. Chorate versus proximate dinoflagellate cysts

The most striking feature of the dinoflagellate cyst assemblages recovered from the studied material is the overwhelming predominance of chorate over proximate forms. Indeed, all of the morphogroups reported in Fig. 3 comprise solely chorate taxa. This is a consequence of the lack of the proximate genus *Impagidinium* and of the scarcity of peridinioids, which are a very minor component within the group 'other identified cysts'. Such exclusions can be interpreted in terms of ecological preferences, although selective degradation of brown protoperidinioids could theoretically have played a role (Zonneveld et al., 1997; Zonneveld and Versteegh, 2003). However, recent studies question the influence of selective degradation on dinocyst assemblages (Reichart and Brinkhuis, 2003).

The lack of *Impagidinium*, which is a widely recognized oceanic taxon (Wall et al., 1977; Dale, 1996; Marret and Zonneveld, 2003), is consistent with the depositional setting of the Figols Group on the continental shelf. In contrast, the scarcity of peridinioids requires fuller discussion. Unlike gonyaulacoids, which are autotrophic, most extant peridinioids are heterotrophic and occur in high frequencies in areas with high primary production related to increased nutrient availability (Wall et al., 1977; Brinkhuis, 1994; Fensome et al., 1993; Dale, 1996; Vink et al., 2000; Marret and Zonneveld, 2003; Reichart and Brinkhuis, 2003; Sprangers et al., 2004; Rochon and Marret, 2004). Increased nutrient availability results from the introduction of deep waters or shelf-stored nutrients in the photic zone through turbulent mixing in upwelling areas and/or increased runoff from the continent. Therefore we can infer that, although we could expect a considerable nutrient supply by rivers, no nutrient-enriched waters were present in the photic zone during the deposition of the Figols Group, despite phases of intensive runoff. This situation can be tentatively explained by considering the paleogeographical reconstruction of the study area in Eocene times. Dercourt et al. (1985) placed the southeastern margin of the Pyrenean basin at about 35°N at the northern fringe of the global desert belt, where continental runoff was probably low. Accordingly, input of nutrients to the shallow marine ecosystems was probably limited in spite of the considerable amount of terrigenous material transported by rivers. Instead, the outer portion of the continental shelf in the Tremp–Graus Basin extended far to the West and was isolated from upwelling currents expected to mark the ecosystems on the western passive margin of the European continent (Romero et al., 2002).

7.2. Other elements supporting surface water oligotrophy

The reconstruction delineated above, suggesting low primary production in response to reduced nutrient availability, besides matching the scarcity of peridinioid dinoflagellate cysts is consistent with:

(a) the overall abundance of cysts referable to *S. ramosus*, a morphological complex which was found to thrive in oligotrophic waters in the shelfward area of the northeast Brazilian margin (Vink et al., 2000) and exhibited an inverse correlation with the nutrient concentration in the whole North Atlantic dataset (Marret and Zonneveld, 2003);
(b) the lack of brown protoperidinioid cysts, which are known to be a eutrophic and/or upwelling signal (Vink et al., 2000; Dale et al., 2002; Marret and Zonneveld, 2003; Reichart and Brinkhuis, 2003);
(c) the scarcity of *Lingulodinium machaerophorum*, which occurs only in sample ME-75 (5.5% of the overall dinoflagellate cyst assemblage). Indeed, this taxon has often been reported as an indicator of nutrient enrichment accompanying eutrophication, particularly in coastal areas (Dale, 1996; Lewis and Hallet, 1997; Dale and Dale, 2002; Dale et al., 2002; Taragona et al., 1999; Marret and Zonneveld, 2003; Sprangers et al., 2004);
(d) the lack of the freshwater alga *Pediastrum*, which is believed to thrive especially in slow-moving rivers enriched with nutrients (Batten, 1996b);
(e) the scarcity of the brackish water alga *Botryococcus*, which is known from lacustrine, fluvial,

lagoonal and deltaic facies, but favours quiet waters free from sediments and rich of humic degradation products (Batten and Grenfell, 1996).

In conclusion, palynological data consistently suggest that during the deposition of the investigated portion of the Figols Group, in the Early Eocene, oligotrophic conditions prevailed in surface waters of the Tremp–Graus Basin.

7.3. The distribution of Spinizonocolpites/Nypa pollen

Published sources prove systematic relationships and ecological similarities between ancient *Spinizonocolpites* and pollen of modern mangrove-palm *Nypa* (Collinson, 1993). *Spinizonocolpites* pollen is almost absent in the lower part of the ME section and increases from 92.5 m upwards. Within the uppermost part of the Figols Group (not represented in the ME section) and in the overlying lower Castigaleu Group, *Spinizonocolpites* pollen is common and locally abundant (pers. obs.). *Spinizonocolpites* has been extensively reported in the literature from early to middle Eocene sediments of central and northwestern Europe (Collinson, 1993): most of the European *Spinizonocolpites* occurrences are in Ypresian deposits (Gruas-Cavagnetto, 1977) except those in Spanish sediments that have a Cuisian–early Lutetian distribution (Haseldonckx, 1972). In spite of still problematic correlations of the local chronostratigraphic units (Molina et al., 2003), we believe that the inception of *Spinizonocolpites* pollen in the Merli–Esdolomada section and its increase towards the top of the Figols Group record the northwestward migration from southern Europe of *Nypa* mangrove-palms during the middle Early Eocene.

7.4. The distribution of Polysphaeridium cysts

In the final phase of the main highstand systems tract documented from 116 m to 121.4 m, *Spinizonocolpites* pollen occurs together with *Polysphaeridium* cysts. Still in samples collected from the uppermost portion of the Figols Group and from the overlying Castigaleu Group within intervals interpreted to record the final phases of marine regressions, *Spinizonocolpites* is sometimes common within *Polysphaeridium*-dominated dinoflagellate cyst assemblages (pers. obs.). As previously discussed, *Spinizonocolpites* is quite similar to pollen of modern *Nypa* mangrove-palms which favour brackish waters in quiet estuaries or shallow lagoons into which freshwater may run and never grow in hypersaline conditions (Collinson, 1993). The occurrence of *Spinizonocolpites* pollen in *Polysphaeridium*-dominated cyst assemblages is most probably a reflection of the capacity of *Polysphaeridium* to tolerate reduced salinities (Edwards and Andrle, 1992; Marret and Zonneveld, 2003), but it could alternatively reflect the coexistence of brackish and hypersaline waters in the lagoon. Two different water masses (inner lagoon and lower lagoon water) are present in modern lagoons and these can be vertically and laterally differentiated by the salinity gradient depending on seasonal freshwater runoff and position within the lagoon (Phleger, 1969). *Polysphaeridium* may have thrived in hypersaline waters in the lower lagoon, whereas *Nypa* vegetation grew in brackish waters in the inner lagoon and these two species may have subsequently become associated by hydrodynamic motions within the lagoon. Either way, present data confirm the opportunistic lifestyle of *Polysphaeridium* which dominated in Eocene tropical lagoons where other cyst-forming dinoflagellates failed owing to extreme conditions involving salinity variations.

7.5. Planktonic foraminifera

Foraminifera abundance and diversity fluctuations provide a rough indication of sea-level and fluvial activity trends. Planktonic foraminifera are generally rare, not only because of the relatively shallow marine settings (the maximum water depth is estimated close to the lower boundary of the photic zone), but they were influenced by fresh-water input and turbidity. Nonetheless they reach the highest (though fluctuating) abundances in the central part of the lower sequence (from ME-29 to ME-106) hence reflecting a combination of sea level rise and/or starving of the fluvial systems.

Reworked Cretaceous planktonic foraminifera are mostly found in the <125 μm fraction and only rarely in the >125 μm fraction. They are common to abundant in several samples up to ME-27 and in the regressive facies of ME-78 and ME-80; they are still more evident in the poor samples of the topmost highstand systems tract of the lower sequence (ME-112 to ME-125), where they are common also in the >125 μm fraction. Heterohelicidae dominate the reworked fraction with subordinate hedbergellids, *Globigerinelloides* and rare Globotruncanidae. Le Calvez (1970) interpreted this evidence as a higher preservation potential (i.e. lower dissolution susceptibility) of Heterohelicidae.

7.6. Larger foraminifera (Fig. 4)

The occurrence of heterodimensional larger foraminiferal assemblages suggests mostly in-situ taphocoenosis. However, a certain amount of allochthony is inferred on the basis of variable test preservation.

The abundance of larger foraminifera drops dramatically in the interval containing the maximum flooding surface, where the associated increments of deep-marine indicators and planktonic foraminifera suggest deepening toward the lower boundary of the photic zone. Also in correspondence with the river plume effects the abundance of larger foraminifera decreases as a reflection of water turbidity, whereas the *Rotalia* group and/or the Cretaceous reworking increase.

Larger foraminifera identified in this section are generally smaller than 8 mm which is a distinctive character of fine sediments in a prodelta setting (Luterbacher, 1984).

Alveolina is absent due to the relatively deep character of the lower sequence and to the fluvial influx (fresh water and terrigenous sediment input) in the upper sequence. It was observed only in the uppermost part of the section in sample ME-198, but this occasional occurrence is probably resedimented.

Discocyclina and *Nummulites* abundances appear to be inversely correlated, with *Discocyclina* increments possibly suggesting deepening, whereas *Assilina*/*Nummulites* alternances seem associated to fine terrigenous sediment variations.

Flat *Operculina* was found only in the lower section and in the deepest settings. Lens-shaped and subordinate disc-shaped *Assilina* (pustulate forms, probably of the *A. exponens* plexus) is present from ME-78 and apparently exhibits major abundance peaks in sediments anticipating river plumes, where instead its abundance decreases.

7.7. The Rotalia group (Fig. 4)

The overall abundance of the *Rotalia* group is lower in the deeper, lower sequence with respect to the shallower, upper sequence. Minimum values are recorded in the interval comprising the maximum flooding zone. Nonetheless several abundance shifts, of increasing importance in the regressive tract, were also found in the lower sequence, often associated to *Operculodinium* and cuticle peaks interpreted as river plume signals. *Cuvillierina* generally is the dominant element of the *Rotalia* group in these levels, suggesting a possible parallelism with *Laffitteina* that Hottinger (1997) compared to *Pseudorotalia* and inferred to be r-strategists adapted to estuaries of tropical rivers (Billman et al., 1980).

Asterigerina spp. are prevalent in the *Rotalia* group only in the uppermost part of the section, from ME-181 upwards, associated with *Nummulites* and *Assilina*. *Cuvillierina* co-occurs with *Asterigerina* but its relative abundance decreases above ME-200, which could be interpreted as a relative deepening (Gaboardi, 1994). *R. trochidiformis* is present in low numbers in the upper sequence above limestone levels and within the shales of the uppermost 45 m where bioclastic sand fraction is higher than the terrigenous component; based on the preferential depth range of *R. trochidiformis* of 20 to 40 m (Levin, 1957), and on the scarcity of *C. alleni* that is associated with an upper depth limit of 25 m (Murray, 1991), a water depth not deeper than 20–30 m can be estimated for most of the upper sequence.

Small *Pararotalia* spp. are present in the rich and diversified assemblages in the lower part of the lower sequence, whereas they characterize impoverished, probably lagoonal levels with Discorbidae, *Nonion* spp. and Ostracoda in the upper sequence.

7.8. Agglutinated foraminifera

Agglutinated foraminifera are generally rare, mostly represented by Textulariidae and Ataxophragmiidae. Abundance is mostly below 1% and only a few peaks exceed 5%. A more continuous distribution is observed in the lower sequence, without any apparent trend.

7.9. Porcellaneous foraminifera

Miliolids are generally scarce in the transgressive section of the lower sequence where there is evidence for repeated river plumes, with reduced shifts often positively correlated with *Discocyclina* abundance peaks. They suddenly become important constituents of the rich foraminiferal assemblages within the maximum flooding zone. This behaviour could reflect more open marine conditions, less influenced by fluvial activity, and/or expansion of sea-floor vegetation, as miliolids are herbivore epiphytes. In fact they show very low values in the regressive interval where the enhanced terrigenous input diluted microfaunal content and probably reduced bottom vegetation cover as an effect of increased water turbidity. In the upper part of the upper sequence, where starved fluvial activity is suggested, miliolids are important constituents of the foraminiferal assemblage together with *Asterigerina* spp., *Nummulites* and *Assilina*.

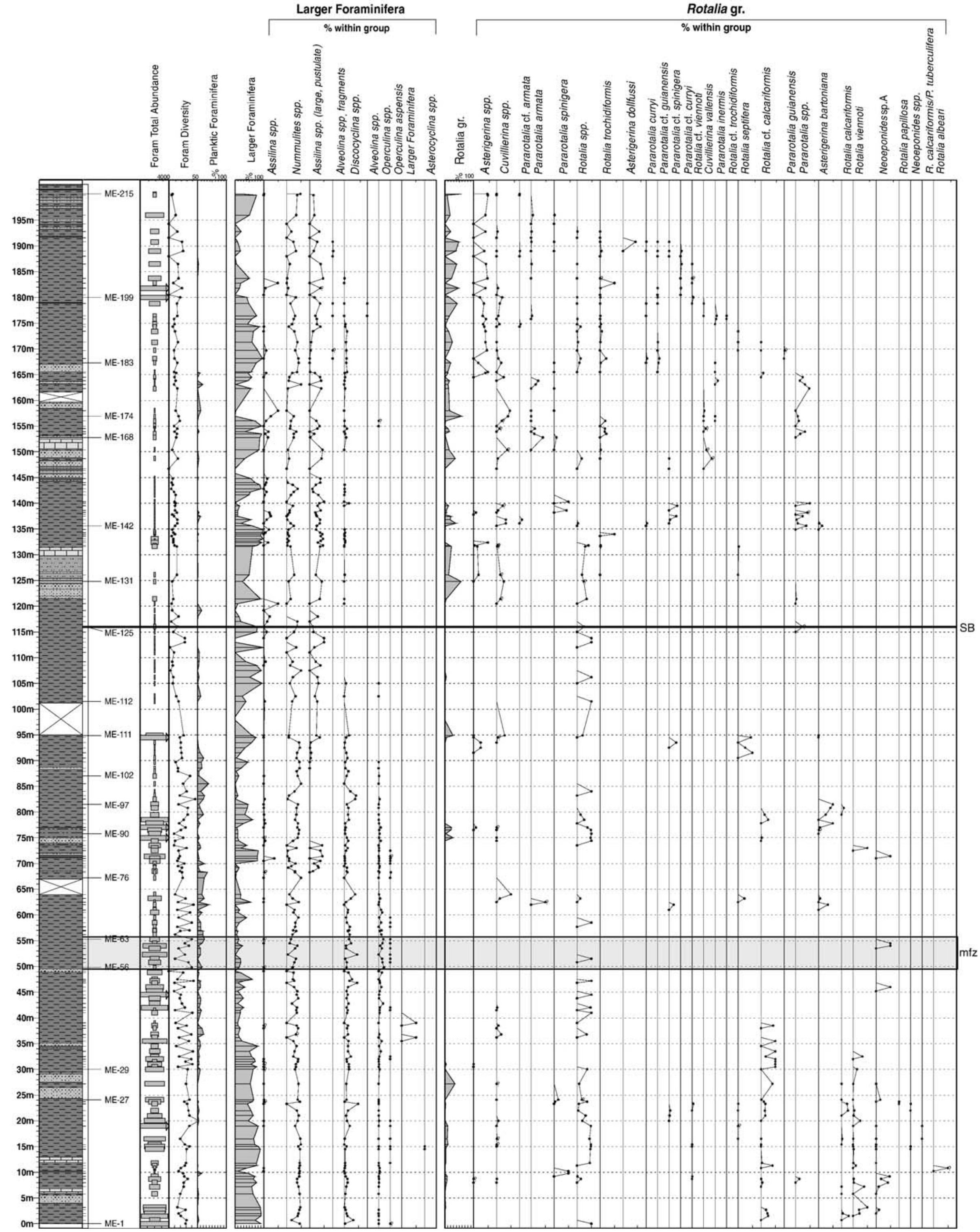

Fig. 4. Range-chart showing quantitative distribution of selected groups relative to the entire foraminifera population and of identified taxa within each group. SB: sequence boundary; mfz: maximum flooding zone.

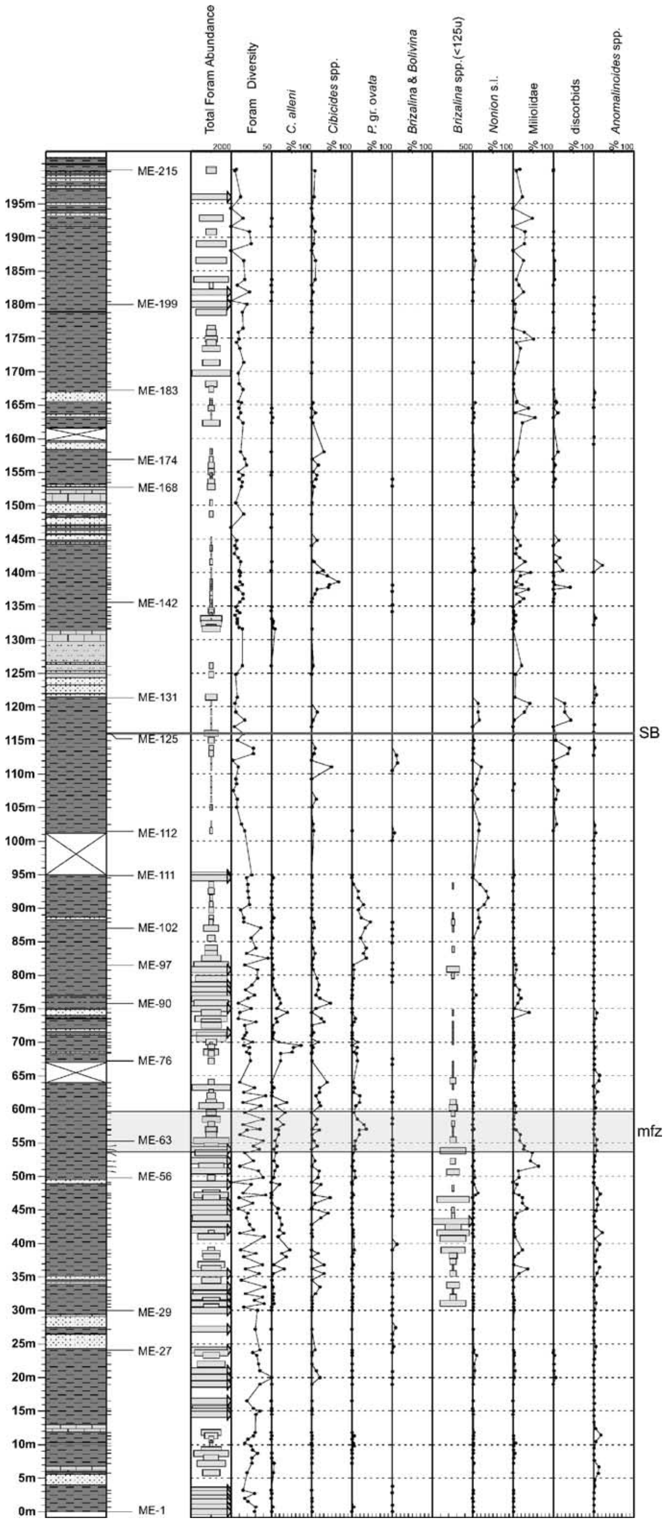

Fig. 5. Range-chart showing quantitative distribution of selected taxa relative to the entire foraminifera population. SB: sequence boundary; mfz: maximum flooding zone.

7.10. Other calcareous benthic foraminifera (Fig. 5)

Deep-water indicators are significantly present in the lower sequence, consistently associated with planktonic foraminiferal fluctuations, while in the upper sequence they are rare and scattered. *P.* gr. *ovata* is the dominant element of this group, the secondary elements being represented by Nodosariacea, *Anomalinoides* spp., *Cibicidoides* spp., *Uvigerina* spp., *Trifarina muralis*, *Spiroplectammina* spp. *Vaginulinopsis fragaria*, *Gyroidinoides octocameratus*, *Anomalinoides affinis* and *Anomalinoides acutus* regularly occur within the maximum flooding zone and persist a little above.

C. alleni was considered by Gaboardi (1994) an intermediate depth indicator; this preference can be confirmed from its relative abundance curve in the present study, showing an abundance increase that anticipates the *P.* gr. *ovata* positive shift in the maximum flooding zone. *Uvigerina*, *Bulimina*, and *Brizalina* are very rare and generally small (<125 μm). Since these taxa are typical of upwelling areas, their scarcity is in agreement with the scarcity of Peridiniaceae in the dinocyst record. Nonetheless *Brizalina* spp. (mainly <125 μm) are present in the lower sequence from ME-34 up to ME-100 and display an abundance peak in the sediments immediately underlying the maximum flooding zone, probably related to the deep-

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Plate I. Dinoflagellate cysts from the Merli–Esdolomada section, Figols Group (Early Eocene). For all magnifications reference is made to the scale bar=40 μm. (see page 27)

1 *Adnatosphaeridium vittatum* Williams and Downie, 1966, sample ME-16.
2, 3 *Adnatosphaeridium multispinosum* Williams and Downie, 1966, sample ME-17.
4, 7 *Areoligera coronata* (Wetzel, 1933) Lejeune-Carpentier, 1938, sample ME-76, high and low focus respectively.
5 *Glaphyrocysta exuberans* (Deflandre and Cookson, 1955) Stover and Evitt, 1978, sample ME-75.
6 *Glaphyrocysta ordinata* (Williams and Downie, 1966) Stover and Evitt, 1978, sample ME-17.
8, 9 *Thalassiphora patula* (Williams and Downie, 1966) Stover and Evitt, 1978, sample ME-60.
10 *Fibrocysta bipolaris* (Cookson and Eisenack, 1965) Stover and Evitt, 1978, sample ME-7.

Plate II. Dinoflagellate cysts from the Merli–Esdolomada section, Figols Group (Early Eocene). For all magnifications reference is made to the scale bar=40 μm. (see page 28)

1 *Homotryblium tenuispinosum* Davey and Williams, 1966, sample ME -7.
2 *Cordosphaeridium gracilis* (Eisenack, 1954) Davey and Williams, 1966/*Cordosphaeridium inodes* (Klumpp, 1953) Eisenack, 1963, sample ME-16.
3 *Spiniferites* gr. *ramosus* (Ehrenberg, 1938) Mantell, 1954, sample ME-18.
4 *Polysphaeridium subtile* Davey and Williams, 1966, sample ME-33.
5 *Turbiosphaera galatea* Eaton, 1976, sample ME-43.
6 *Rhombodinium* cf. *perforatum* (Jan du Chêne and Châteauneuf, 1975) Lentin and Williams, 1977, sample ME-84. Very rare.
7 *Melitasphaeridium pseudorecurvatum* (Morgenroth, 1966) Bujak, 1980, sample ME-10.
8 *Diphyes colligerum* (Deflandre and Cookson, 1955) Cookson, 1965, sample ME-35.
9 *Rhombodinium longimanum* Vozzhennikova, 1967/*Rhombodinium pentagonum* Vozzhennikova, 1967, sample ME-87. Very rare.
10 *Rhombodinium longimanum* Vozzhennikova, 1967/*Rhombodinium pentagonum* Vozzhennikova, 1967, sample ME-84. Very rare.
11 *Glaphyrocysta* spp., sample ME-30.
12 *Apectodinium homomorphum* (Deflandre and Cookson, 1955) Lentin and Williams, 1977, sample ME-37.

Plate III. Dinoflagellate cysts, pollen and other kerogen components from the Merli–Esdolomada section, Figols Group (Early Eocene). For all magnifications reference is made to the scale bar=40 μm. (see page 29)

1 *Fibrocysta vectensis* (Eaton, 1976) Stover and Evitt, 1978, sample ME-62.
2 *Diphyes colligerum* (Deflandre and Cookson, 1955) Cookson, 1965, sample ME-36
3 *Operculodinium* gr. *centrocarpum* (Deflandre and Cookson, 1955) Wall, 1967, sample ME-10.
4 *Polysphaeridium subtile* Davey and Williams, 1966, sample ME-29.
5 *Cordosphaeridium gracilis* (Eisenack, 1954) Davey and Williams, 1966, sample ME-7.
6, 7 *Spinizonocolpites echinatus/baculatus* Muller, 1968, sample ME-208.
8, 9 Herbaceous cuticles.
10, 11 Brown phytoclasts.
12 Black phytoclast.
13 Amorphous organic matter.

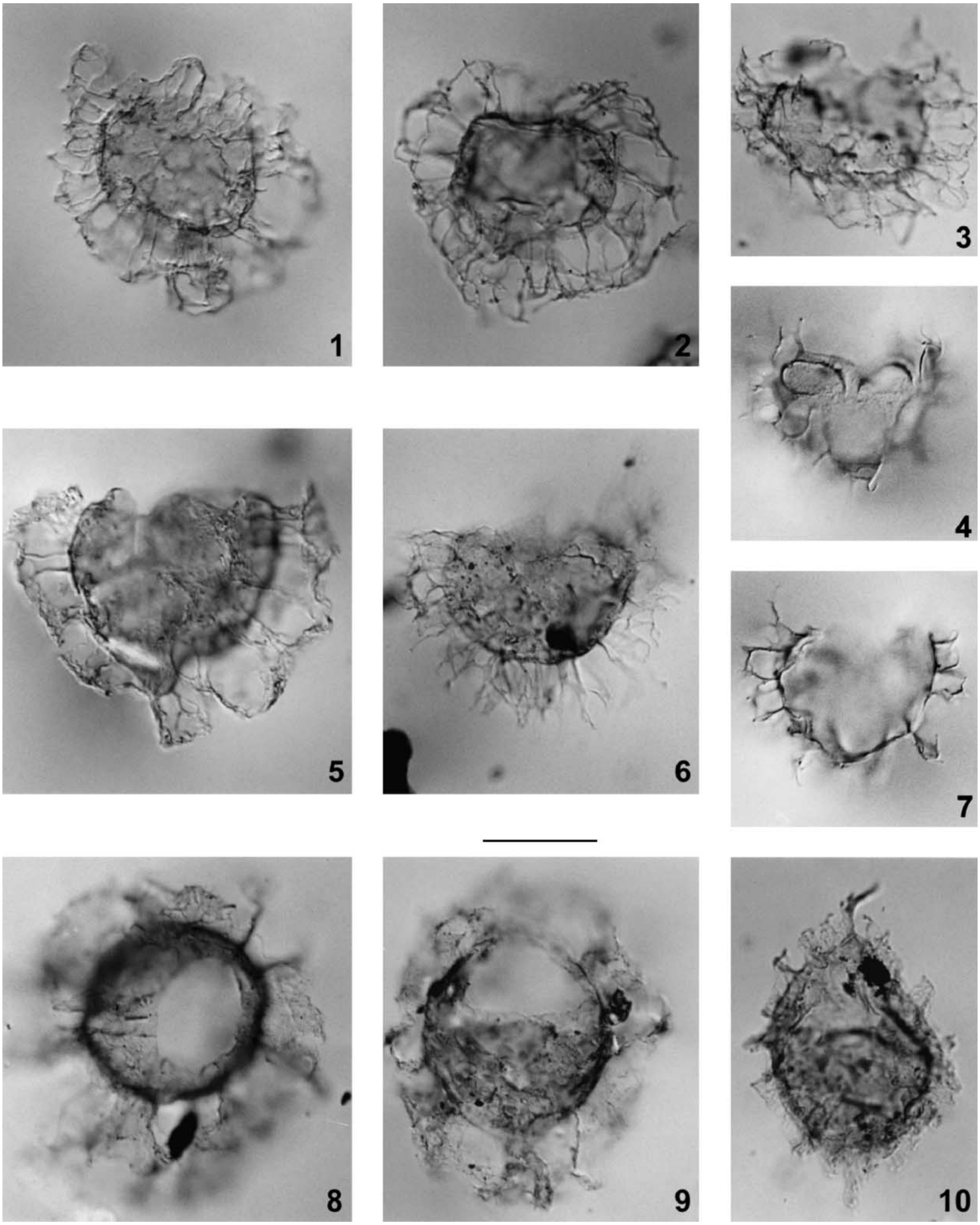

Plate I (*caption on page 26*).

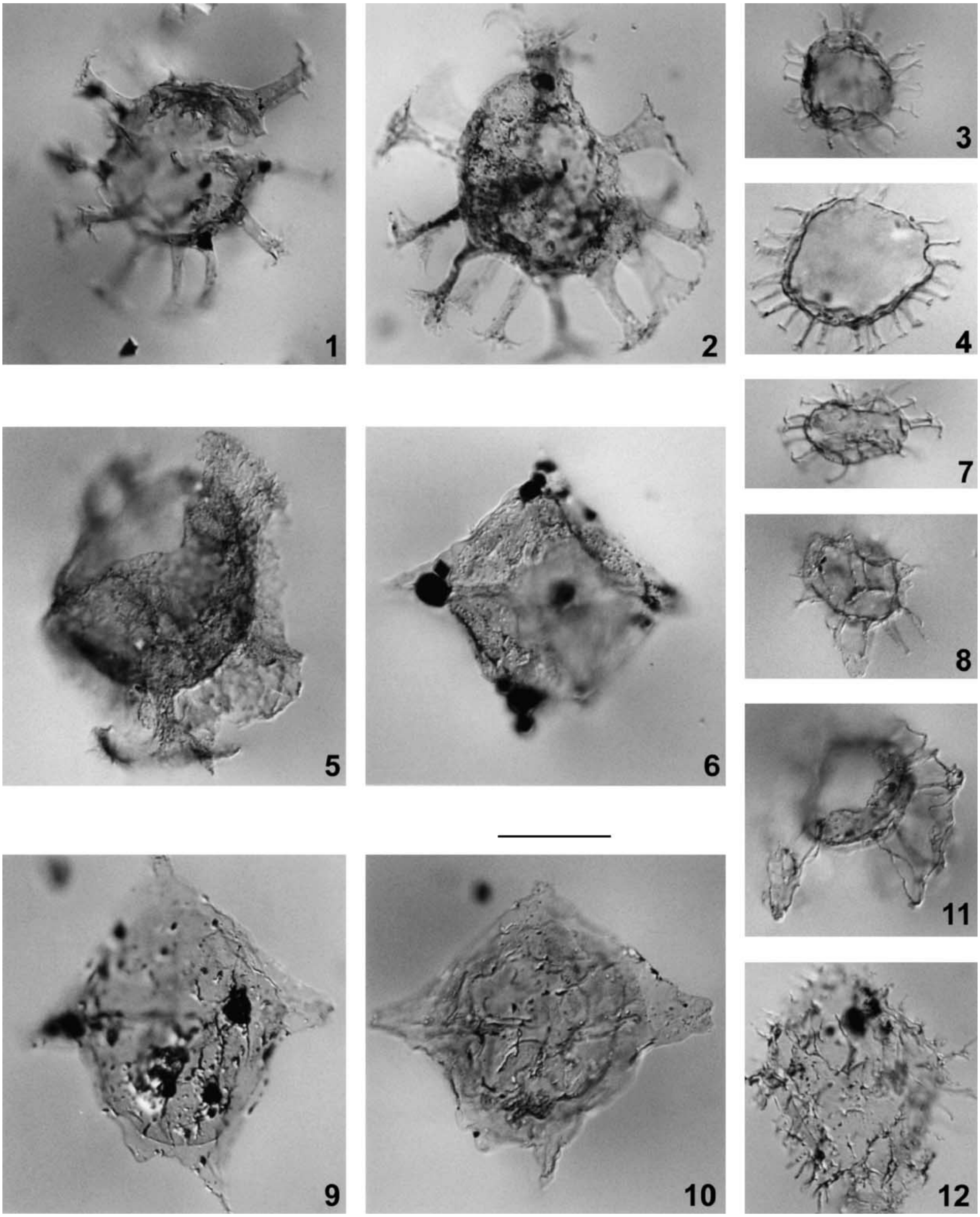

Plate II (*caption on page 26*).

ening and consequent lowered bottom energy that allowed temporary organic matter preservation. Somehow the acme of *Thalassiphora* could be tied to evolving conditions anticipated by the presence of *Brizalina* spp.

Discorbis is relatively frequent in the shallowing upwards, regressive facies at the top of the lower sequence, probably associated with lagoonal, restricted conditions. *Nonion* s.l. is occasionally present in low percentages in the rich and diversified assemblages of

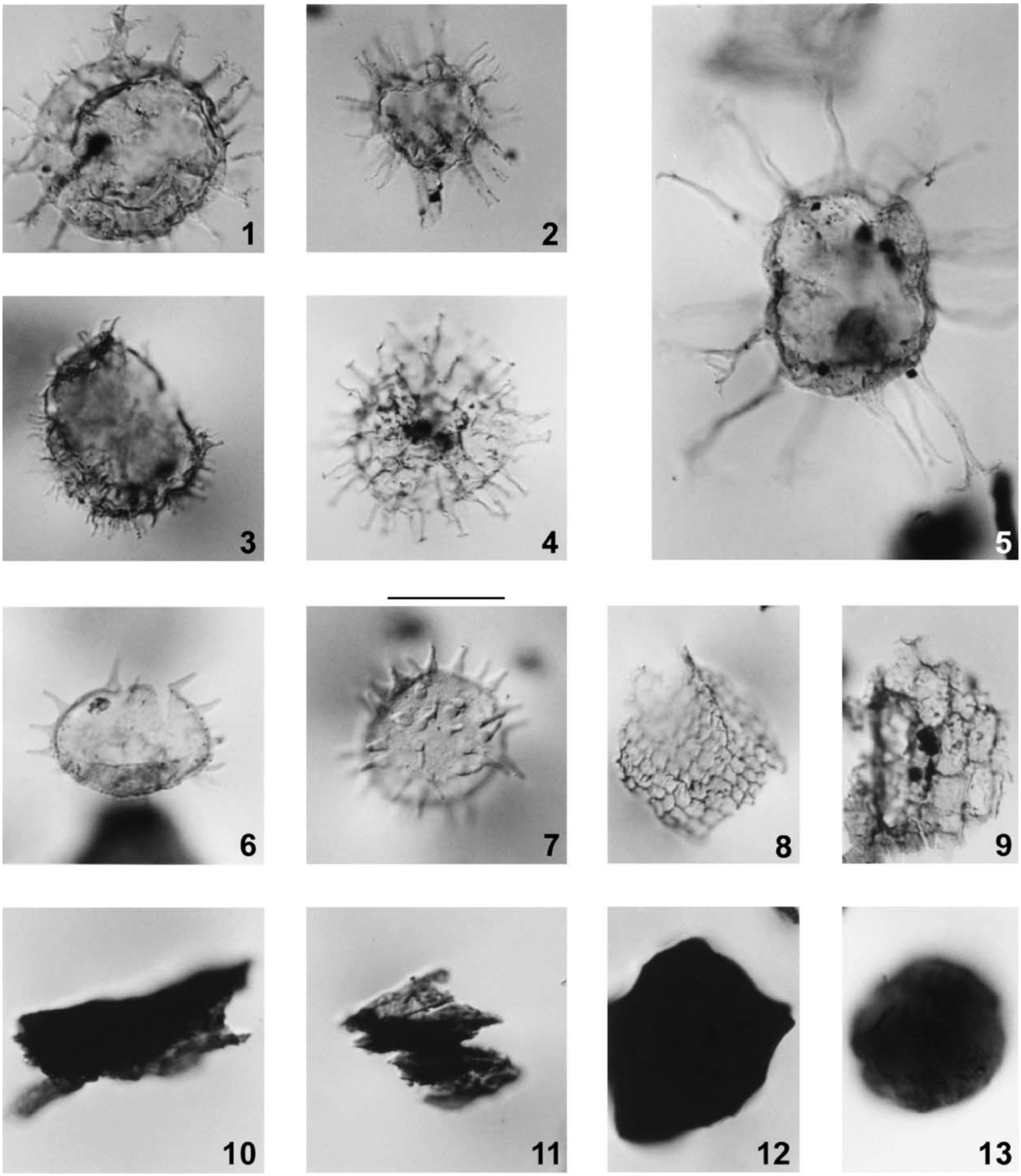

Plate III (*caption on page 26*).

the lower sequence but becomes dominant in the regressive, poor, probably restricted levels recorded from ME-102 to ME-130.

8. Biostratigraphy

The Figols Group is entirely Ypresian and spans the Ilerdian and lowermost Cuisian stages (Molina et al., 1992, 2003; Gaboardi et al., 1994; Waehry, 1999). The present biochronostratigraphic observations are essentially limited to the lower part of the Merli–Esdolomada section (up to 116 m) where the marine signal is stronger (Fig. 6).

The Early Eocene dinoflagellate cyst biostratigraphy in northwestern Europe relies mainly on representatives of the Order Peridiniales (Powell, 1992; Bujak and Mudge, 1994). Indeed species of Wetzeliellaceae and Deflandreaceae provide most of the well calibrated bio-

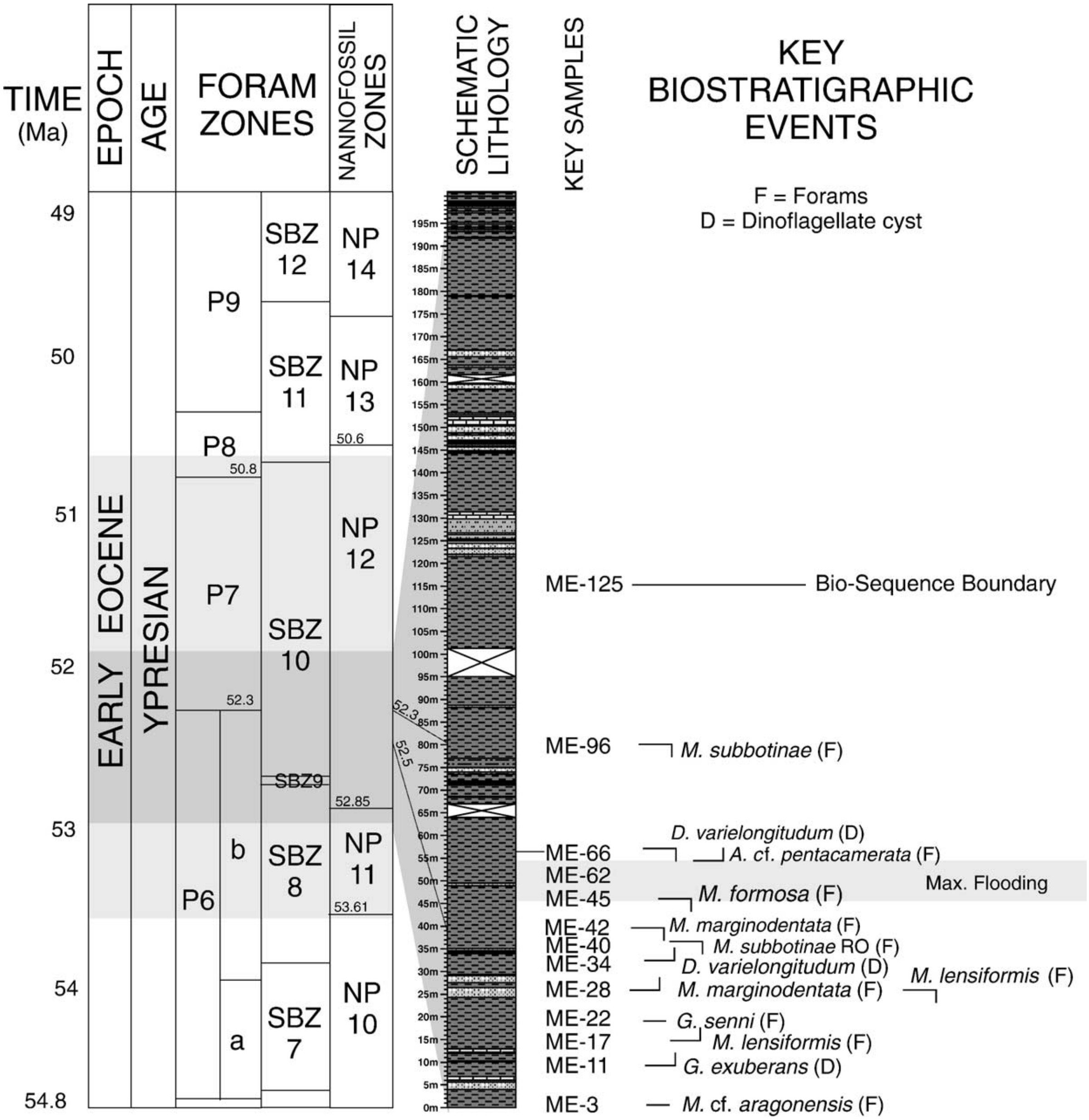

Fig. 6. Bio-chronostratigraphic log of the Merli–Esdolomada section showing key biostratigraphic events and corresponding zonal attributions. Light and heavy shadowing indicates respectively the chronostratigraphic attributions for the Figols Group (according to the literature) and for the studied section. Timescale is after Berggren et al. (1995). Shallow benthic foram zonation (SBZ) after Serra-Kiel et al. (1998).

horizons (Williams et al., 2004). A dinoflagellate cyst zonation based on peridinioids was also presented for the type-Ilerdian section that outcrops near Campo, in the Esera Valley (Caro, 1973). Unfortunately, peridinioid cysts are rare in the Merli–Esdolomada section due to environmental exclusion. Nevertheless the events listed below can help in the age assessment (LO: lowest occurrence; HO: highest occurrence; FAD: first appearance datum; LAD: last appearance datum).

A. multispinosum occurs throughout the section. Its FAD is calibrated at 53.19 Ma in northwestern Europe (Hardenbol et al., 1998). However, most recent calibrations date this event at 56 Ma (Williams et al., 2004). This biohorizon is underneath the base of the ME section.

H. tenuispinosum occurs throughout the section. Its FAD is calibrated at 53.57 Ma in northwestern Europe (Hardenbol et al., 1998). This biohorizon is therefore underneath the base of the MR section.

LO of *Melitasphaeridium pseudorecurvatum* at 7.2 m (sample ME-8). Its FAD is calibrated at 54.2 Ma at middle latitudes in the Northern Hemisphere (Williams et al., 2004). However, recent findings from the North-Western Atlantic point to a calibration at 55 Ma (A. Sluijs, pers. comm.).

LO of *Glaphyrocysta exuberans* at 9.2 m (sample ME-11). Its FAD is tentatively calibrated at 53.0 Ma (Williams et al., 2004).

LO of *Dracodinium varielongitudum* at 32.5 m (sample ME-34). Its FAD is calibrated at 52.93 Ma in northwestern Europe (Williams et al., 2004).

HO of *D. varielongitudum* at 57.0 m (sample ME-66). Its LAD is calibrated at 51.5 Ma in northwestern Europe (Williams et al., 2004).

Planktonic foraminifer data present some ambiguities both in the present and previous studies concerning the Figols Group, probably due to the unfavourable facies, poor preservation, discontinuous distribution and problematic taxonomic determinations. Nevertheless the investigated assemblages are referable to P6b-lower P7 Zones (Berggren et al., 1995). The lower sequence can be attributed either to the uppermost P6b Zone based on the regular occurrences of *Morozovella subbotinae*, *M. marginodentata*, and *M. formosa* or to the P7 Zone based on single occurrences of *M. aragonensis* and *G. senni*, with consistent P6 reworking. We consider more realistic a P6b zonal attribution and the P6 Zone top can be approximately identified in sample ME-96 (80.8 m). In the interval above *M. aragonensis* is absent and was probably ecologically excluded. Planktonic foraminifers are almost absent in the upper, more proximal sequence (i.e. from 116 m upwards). However, taxa referable to P7 and P8 Zones, including *M. aragonensis*, *A. pentacamerata* and occasional *M. formosa*, have been observed in the uppermost Figols strata outcropping in the Esera Valley, that are stratigraphically overlying the Merli–Esdolomada succession (pers. obs.). In these strata the dinoflagellate cyst species *Samlandia chlamydophora* and *Charlesdowniea coleothrypta* (FAD at 52 Ma according to Williams et al., 2004) also occur, whereas they are absent in the ME section. In conclusion the top of the ME section is remarkably older than 50.8 Ma (P7/P8 boundary) and its age is probably close to 52 Ma.

Some calcareous nannofossil analyses were also carried out on selected samples. The occurrences of *Tribrachiatus orthostylus*, *Sphenolithus radians* and rabdolites in the lowermost part of the ME section indicate the upper NP11 Zone. Upwards, the lower boundary of the NP12 Zone cannot be defined due to the overall scarcity of discoasterids; only very rare recrystallized *D. binodosus* and *D. kuepperi* were observed, but no specimens of *D. lodoensis*.

Finally, an average sedimentation rate of about 200 m/Ma is tentatively estimated relying on the highest occurrence of *M. marginodentata* recorded in sample ME-42 (LAD calibrated at 52.5 Ma) and on the highest occurrence of *M. subbotinae* in sample ME-96 (LAD at the top of P6b according to Berggren and Norris, 1997, dated at 52.3 Ma in Berggren et al., 1995; Hardenbol et al., 1998).

9. Conclusions

Two 3rd order sequences have been identified and analysed by interpreting dinoflagellate cyst, palynofacies and calcareous microfaunal records in the Merli–Esdolomada section. Sediment starved intervals and enhanced fluvial discharges yielding river plumes and salinity water stratification have been better recognised in the lower sequence, where both dinoflagellate cyst and foraminiferal assemblages are rich and diverse. They reflect a prodelta to open shelf setting not deeper than 80 m, subjected to a Milankovitch-type cyclical influence of the fluvial activity. A 3rd order sequence boundary has been identified by means of dinoflagellate cyst signals within the shale immediately beneath sandstone lobes representing the sedimentary evidence of the regression and/or fluvial reactivation.

The upper sequence was deposited in an inner shelf setting, probably not deeper than 30 m. The renewed terrigenous input, physically expressed in its lower part by sandstone lobes, was responsible for the dilution of the biogenic content and reduced microfossil recovery. Toward the upper part of the section, in the shale overlying the forestepping–backstepping cycles of the fluvial system, lowered terrigenous input is substantiated by a strong increase of the biogenic and bioclastic calcareous sand component, constituted by forams and encrusting bryozoans.

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