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Sea-level dynamics and palaeoecological factors affecting trace fossil distribution in Eocene turbiditic deposits (Gorrondatxe section, N Spain)

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ABSTRACT

Ichnological analysis of the upper Ypresian–lower Lutetian interval at the Gorrondatxe section (W Pyrenees, N Spain), reveals a relationship between sea-level dynamics and the eco-sedimentary factors influencing trace fossil assemblages. The 600 m thick section of deep-sea turbiditic deposits contains 41 ichnospecies belonging to 28 ichnogenera, which are typical of the *Nereites* ichnofacies, and mostly of the *Paleodictyon* ichnosubfacies, suggesting deposition in a basin plain to fan-fringe setting. The trace fossil diversity and abundance fluctuate, irrespective of turbidite frequency. These ichnological features are strongly affected by trophic level changes related partly to sea-level dynamics according to the sequence stratigraphic interpretations for the studied section. Temperature, oxygenation and substrate changes are also considered as relevant factors. Increased ichnodiversity, particularly among graphoglyptids, coincides with moderate oligotrophy and stable ecological conditions. Eutrophisation, lowered oxygenation and drop of temperature, typical of low sea level, can reduce ichnodiversity.

1. Introduction

Eocene turbiditic sediments display the highest Phanerozoic trace fossil diversity. This is related to the general evolutionary trend of ichnofauna and to several palaeoecological factors, the most important of which is moderate oligotrophy (Uchman, 1999, 2004a) that is caused by a significant rise in deep water temperature (e.g., Brass et al., 1982; Shackleton, 1986). Such changes influence productivity, oxygenation, the development of microbes and turnover of organic matter (e.g., Thomas et al., 2000). Fluctuations in diversity and trace fossil composition are observed in the Eocene of the Western Pyrenees (Fig. 1), and are particularly pronounced in the 700 m thick study section at Gorrondatxe. Previous research on the section (Orue-Etxebarria and Lamolda, 1985; Payros et al., 2009a), leads to the interpretation of sea-level dynamics as well as the incidence of water temperature and trophic changes in the planktonic foraminifera assemblage. This provides for a rare opportunity to study deep-sea trace fossil distribution in relation to factors caused by sea-level dynamics. Such is the main aim of this paper.

2. Geological and palaeogeographical setting

Located just northwest of Bilbao (N43°23′, W003°01′), the Gorrondatxe beach section forms part of the northeastern limb of the Biscay Synclinorium (Fig. 1A). The succession is well exposed in 50 m high cliffs, where tilted beds dipping approximately 60º towards the southwest can be observed. This section is part of a 2300 m thick Lower–Middle Eocene succession that extends from the village of Sopela to the Galea Cape (Orue-Etxebarria et al., 1984), with the 700 m thick interval exposed in the Gorrondatxe beach corresponding to the middle part of the Eocene succession (Bernaola et al., 2006b; Payros et al., 2006, 2007).

During Eocene times the study area was part of a narrow marine gulf located at ~35°N latitude between the European and Iberian plates (Fig. 1B). The gulf, which opened northwest into the Atlantic Ocean, was about 1500 m deep and had shallow-water carbonate ramps on its northern and southern margins (Plaziat, 1981; Pujalte et al., 2002). It was originated by the oblique convergence of the Iberian and European plates during Late Cretaceous times. Further plate convergence in Eocene times caused the progressive tectonic uplift of the Pyrenees, which started in the east and then propagated westwards. The deposits exposed in the Gorrondatxe cliffs accumulated in the deep sea of the pre-Pyrenean gulf.

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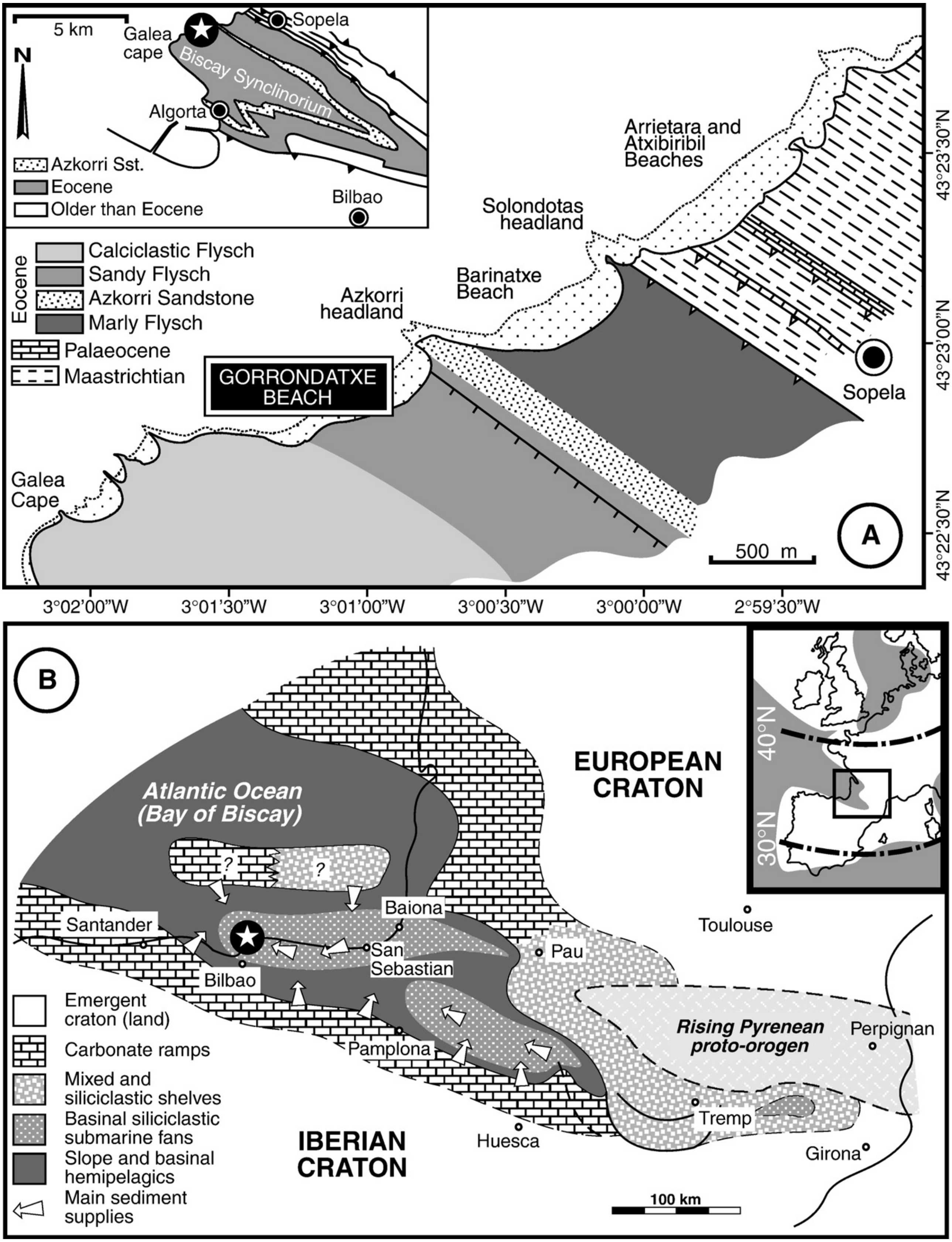

Fig. 1. (A) Simplified geological maps of the northwestern part of the Biscay Synclinorium in the Basque Coast, showing location of the Gorrondatxe section (encircled star) and the lithostratigraphic units that make up the Eocene succession. (B) European (inset) and Pyrenean Eocene palaeogeographic location of the Gorrondatxe section (encircled star).

3. Stratigraphy of the Gorrondatxe section

The succession is composed of background carbonate hemipelagic deposits interspersed with turbidites (Fig. 2). Despite the generally high turbiditic "noise", alternating marl-dominated and limestone-dominated hemipelagic intervals can be visually recognized in some intervals of the Gorrondatxe section. Their deposition was probably affected by astronomical cycles that operated at the Milankovitch band frequencies (Payros et al., 2007, 2009b). The hemipelagic deposits have been the subject of many bio- and magnetostratigraphic studies, which have demonstrated that the succession was accumulated at the late Ypresian–early Lutetian transition (Orue-Etxebarria, 1985; Orue-Etxebarria and Apellaniz, 1985). The E7–E8 planktonic foraminiferal zones of Berggren and Pearson (2005), the NP13–NP15 calcareous nannofossil zones of Martini (1971) and the magnetic chrons C22n to C20r are recognized here (see Bernaola et al., 2006b; Orue-Etxebarria et al., 2006; Payros et al., 2006). The integrated magnetobiostratigraphic studies carried out at the Agost (Ortiz et al., 2008) and Gorrondatxe sections provide conclusive evidence that both sections are almost continuous and contain diverse and well-preserved fossil groups.

The most common sediment gravity-flow deposits registered throughout the succession at Basque basin are plane-parallel, thin-bedded (<10 cm) siliciclastic turbidites, but tabular thick-bedded (up to 240 cm) mixed siliciclastic–carbonate turbidites occur at some levels of the succession (Payros et al., 2006). Some thick-bedded turbidites are relatively rich in shallow-water fossils and/or carbonized plant detritus, pointing to direct shelfal and/or terrestrial sources. Neither evidence of bed amalgamation, nor any particular vertical arrangement of beds, was observed in the Gorrondatxe section. Palaeocurrent indicators are generally directed towards the northwest, but some structures directed towards the north–northeast also occur. This shows that sediment gravity flows were generally axial to the basin, with minor supply being derived from the southern margin of the basin. Thus, a submarine fan fringe or basin plain, with occasional lateral sediment supply, is the most likely sedimentary setting (Fig. 1B).

Semiquantitative estimation of the vertical variations in turbidite abundance (Payros et al., 2006, 2007) made evident that the Lower/Middle Eocene succession consists of six distinct intervals with variable amounts of turbidites (Fig. 2). The turbidite content of three intervals (labelled "turbidite-poor") rarely exceeds 20%, with average values being lower than 10%, and some levels are almost completely devoid of turbidites. The other three intervals were labelled "turbidite-rich" (turbidite content 10%–80%, and averaging >20%). Payros et al. (2006) also noted an increase in the proportion of carbonized plant remains and reworked shallow-water benthic faunas in the three turbidite-rich intervals. Apart from sea-level dynamics, resedimentation processes can be, in part, tectonically induced; strong tectonic activity induced frequent turbiditic activity and occasional large-scale slope failures. The Gorrondatxe section studied herein includes the upper part of the second turbidite-poor interval (up to 1110 m), in which hemipelagic limestones progressively become more abundant upwards, the whole second turbidite-rich interval (up to 1400 m), and the lowermost part of the third turbidite-poor interval.

4. Sequence stratigraphic framework

Turbidite-poor and turbidite-rich intervals of the Gorrondatxe section have basinwide expressions; similar trends can be identified through the successions exposed along the 300-km long area that extends between the study area and the easternmost tip of the Pyrenean deep-marine gulf (Payros et al., 2006, 2009a). Based on sedimentological and stratigraphic correlations, it can be readily interpreted that the turbidite-rich intervals represent low sea-level periods, whereas the turbidite-poor intervals represent periods of high sea level (Fig. 2). Hence, a sequence stratigraphic framework was developed for the Early/Middle Eocene transition in the Pyrenean area. In the case study, the corresponding turbidite intervals (second turbidite-poor interval, second turbidite-rich interval, and third turbidite-poor interval), consist of one or two system tracts (Fig. 2).

The lowermost part of the Gorrondatxe section, which corresponds to the second turbidite-poor interval of the Sopela–Galea section, is interpreted as the transgressive systems tract of a third-order depositional sequence, recording the flooding of previously emerged platform areas, which resulted in greater accommodation space. Consequently, shelfal and terrestrially-derived sediments were sequestered in platform areas and this caused sediment starvation in the deep sea. The progressive increase in hemipelagic limestones close to the top of the second turbidite-poor interval is thought to represent a high sea-level stillstand (Fig. 2), determining the basinward progradation of shallow-water sedimentary systems. Unfortunately, there is no clear physical expression of the boundary between the transgressive and highstand systems tracts in the Gorrondatxe section and the gradual increase in hemipelagic limestones makes it difficult to reliably identify the maximum flooding surface. On the basis of correlation with other Pyrenean sections, however, Payros et al. (2009a) suggested that it may lie close to 965 m.

The conformable, but relatively sharp increase in turbidites at 1110 m corresponds to a sequence boundary (Fig. 2), and the overlying turbidite-rich deposits are interpreted as lowstand deposits accumulated when most of the platform areas were subaerially exposed. Thus, the large amount of carbonized plant remains in the upper part of the second turbidite-rich interval suggests direct terrestrial sediment supply.

The progressive lowering of the turbidite content from 1340 to 1400 m represents the onset of the third turbidite-poor interval, which extends up to the top of the Gorrondatxe section at 1500 m. Sedimentary characteristics of this interval resemble those of the preceding turbidite-poor interval, and hence it is interpreted as the result of a rising sea level (transgressive/highstand systems tracts). However, it is noteworthy that turbidite values of the third turbidite-poor interval are never as low as in the second turbidite-poor interval, implying a more sustained sediment supply and probably a closer location of the shelfal and terrestrial sediment sources, even in high sea-level conditions.

5. Palaeoecology of planktonic foraminiferal assemblage

The proportion of the planktonic versus total (planktonic plus benthic) foraminiferal content of the Gorrondatxe hemipelagic deposits is generally above 90% (Orue-Etxebarria, 1983, 1984). A water depth of approximately 1500 m can be inferred on the basis of the relationship between planktonic/benthic in present-day (Van der Zwaan et al., 1990; Nigam and Henriques, 1992) and in Eocene (Gibson, 1989) oceans. This is confirmed by ostracod assemblages, indicating depths greater than 600–800 m (Rodríguez-Lázaro and García-Zarraga, 1996).

Different and more variable palaeoenvironmental conditions seem to have dominated at the sea surface where planktonic foraminifers lived. Turbidite-poor intervals are characterized by symbiont-bearing K-strategist species, which thrived in oligotrophic warm waters, whereas turbidite-rich intervals are dominated by opportunistic and cosmopolitan species that characterize nutrient-enriched cool waters (Fig. 2). Either changes in trophic resources or in sea-water temperature, or a combination of both factors, could be responsible for the observed changes in planktonic foraminiferal. Payros et al. (2006) observed that the contrasting biotic assemblages apparently did not correlate with distinct climatic events. Thus, the cool-water cosmopolitan biotic assemblages might respond to increased rates of sediment resuspension and nutrient release during resedimentation

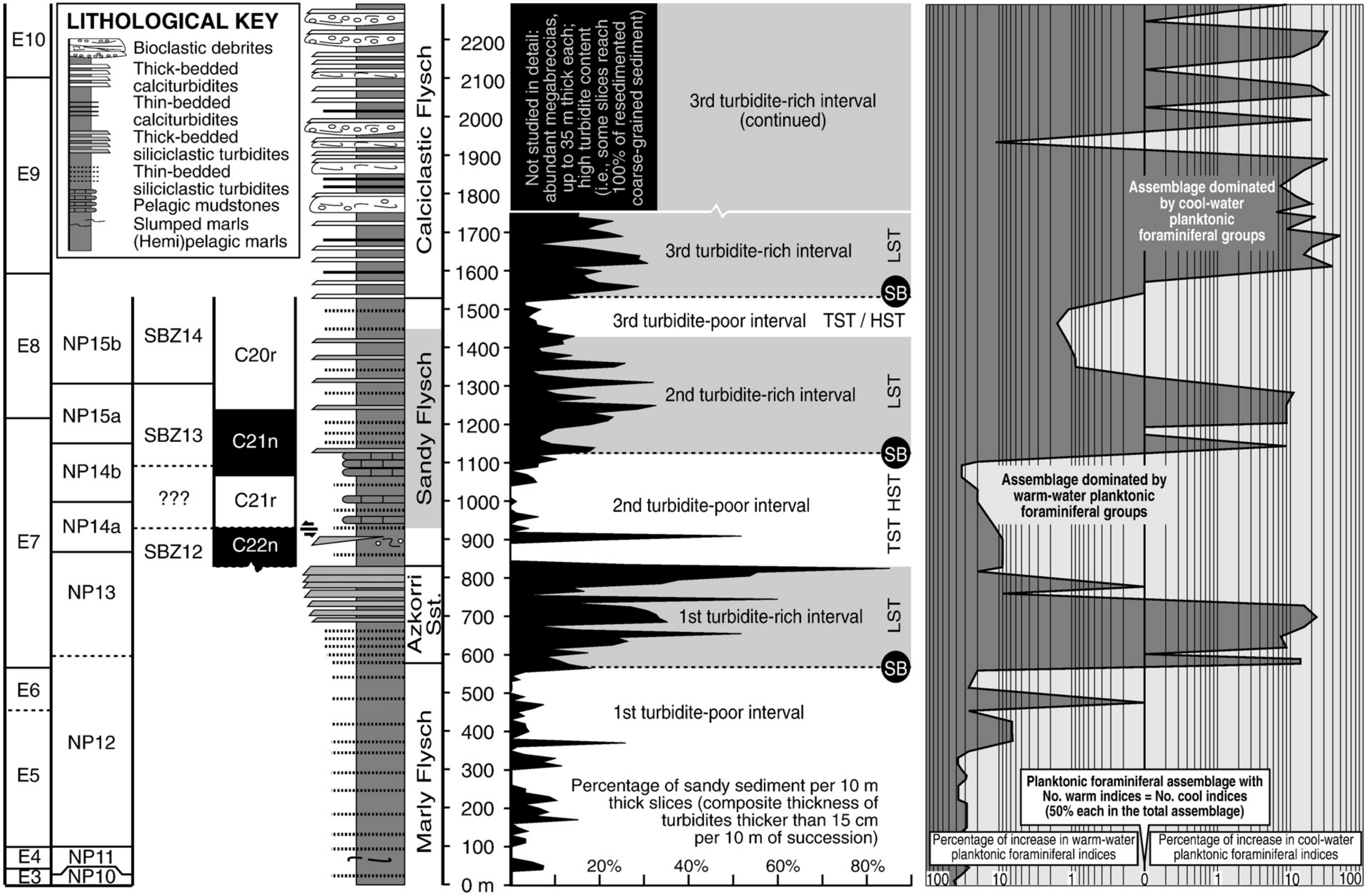

Fig. 2. Simplified lithology of the Eocene succession exposed in the sea cliffs between Sopela and Galea, which include those of the Gorrondatxe beach. The Gorrondatxe section studied herein (shaded) is part of the so-called Sandy Flysch. Planktonic foraminiferal biostratigraphy ("E" scale of Berggren and Pearson, 2005) is based on Bernaola et al. (2006b), Orue-Etxebarria et al. (2006) and Payros et al. (2006). Calcareous nannofossil biostratigraphy ("NP" scale of Martini (1971)) is from Bernaola et al. (2006a,b). Nummulitid biostratigraphy ("SBZ" scale of Serra-Kiel et al., 1998) and magnetostratigraphy ("C" scale) are based on Bernaola et al. (2006b). Vertical variations in abundance of pelagic and turbiditic deposits (Payros et al., 2006) allow definition of depositional sequences and systems tracts (SB: sequence boundary; LST: lowstand systems tract; TST: transgressive systems tract; HST: highstand systems tract). Stratigraphic distribution of planktonic foraminiferal assemblages and relationship with turbidite-poor and turbidite-rich intervals (right-hand graph from Payros et al. (2006).

processes. However, Payros et al. (2009a) updated the Gorrondatxe biostratigraphy and compared its sea-level record with that other European basins, reaching the conclusion that global climatic variations may be an alternative, or at least additional, inducing mechanism for the sea-level and biotic changes.

Thus during accumulation of the turbidite-poor intervals of the Gorrondatxe section, the waters at the sea surface were oligotrophic and warm, thereby making the second turbidite-poor interval records a more extreme case than the third turbidite-poor interval. The lower part of the second turbidite-rich interval (1110–1300 m) was characterized by nutrient-enriched cool surface waters, whereas its upper part (1300–1400 m) records the transition to oligotrophic warm-water conditions.

6. Ichnological analysis

6.1. Systematic ichnology

Trace fossils have been arranged in morphological groups according to Książkiewicz (1977), with further modifications by Uchman (1995). Because the grouping did not cover helical structures, the category of spiral structures is expanded to the spiral and helical structures. Ichnotaxa are only briefly described. They have been more extensively discussed in former publications (Uchman 1995, 1998, 1999). The trace fossil assemblage is characterized by a moderate diversity (Table 1), with 41 ichnospecies belonging to 28 ichnogenera observed.

All the numbered and figured specimens (labelled as GO) are housed in the University of Granada, while figured specimens only seen in the field and not collected have not been allocated numbers.

6.1.1. Simple and branched structures

Alcyonidiopsis isp. A (Fig. 3A): endichnial, simple, almost straight strongly flattened cylinder, 2.2 mm wide, filled with very small elongate pellets. It occurs in the upper part of sandstone beds and is filled with light marly sediment. For discussion of *Alcyonidiopsis* see Pickerill and Narbonne (1995) and Uchman (1998).

Alcyonidiopsis isp. B (Fig. 3B): endichnial, simple, almost straight subcylindrical structures filled with elongate pellets. The structure shows elliptical cross section and swellings with gentle passages to constrictions in the vertical plane. The swellings resulted from teichichnoid shifts. Its maximal width ranges from 5 to 15 mm. The pellets are 1.5–2 mm long and up to 0.5–0.8 mm wide.

Chondrites intricatus (Brongniart, 1823) (Fig. 3C, G): a system of tree-like branching, downward penetrating, markedly flattened tunnels with a width of 0.3–0.8 mm. Branches form sharp angles. The entire trace fossil is 10–40 mm wide. In cross section it is visible as a group of small spots (Fig. 3G). For discussion of *Chondrites* see Kotake (1991), Seilacher (1990) and Fu (1991).

Table 1
Ichnotaxa of the Gorrondatxe section, their ethology, relation to turbiditic beds, morphological affiliation with indication of graphoglyptids. BWM—branched winding and meandering; WM—winding and meandering; N—Network; SpH—spiral and helical.

Ichnotaxa	Ethological category	Pre-, post-depositional origin	Morphological group	Graphoglyptids
?*Acanthorhaphe* isp.	Agrichnia	Pre	BWM	x
Alcyonidiopsis isp. A	Pascichnia	Post	Simple	
Alcyonidiopsis isp. B	Pascichnia	Post	Simple	
Chondrites intricatus	Chemichnia	Post	Branched	
Chondrites targionii	Chemichnia	Post	Branched	
Cosmorhaphe sinuosa	Agrichnia	Pre	WM	x
?*Cosmorhaphe* isp.	Agrichnia	Pre	WM	x
Desmograpton dertonensis	Agrichnia	Pre	BWM	x
Glockerichnus alata	Agrichnia?	Pre	Radial	x
Helicodromites isp.	?chemichnia, ?fodinichnia	Post	SpH	
Helminthopsis abeli	Pascichnia	Pre	WM	
Helminthorhaphe japonica	Agrichnia	Pre	WM	x
Megagrapton submontanum	Agrichnia	Pre	Network	x
Multina minima	Pascichnia	Post	N-BWM	
Naviculichnium marginatum	?pascichnia	Post	WM	
Nereites irregularis	Pascichnia	Post	WM	
Nereites isp.	Pascichnia	Post	WM	
Ophiomorpha annulata	Domichnia	Post	Branched	
Ophiomorpha rudis	Domichnia	Post	Branched	
Palaeophycus tubularis	Fodinichnia/Domichnia	Post	Simple	
Paleodictyon minimum	Agrichnia	Pre	Network	x
Paleodictyon strozzii	Agrichnia	Pre	Network	x
Paleodictyon miocenicum	Agrichnia	Pre	Network	x
Paleodictyon majus	Agrichnia	Pre	Network	x
Paleodictyon arvense	Agrichnia	Pre	Network	x
Paleomeandron cf. *robustum*	Agrichnia	Pre	BWM	
Phycosiphon incertum	Fodinichnia	Post	Spreiten	
Planolites isp.	Pascichnia	Post	Simple	
Protopaleodictyon incompositum	Agrichnia	Pre	BWM	x
Scolicia prisca	Pascichnia	Post	WM	
Scolicia strozzii	Pascichnia	Pre	WM	
Scolicia vertebralis	Pascichnia	Post	WM	
Scolicia isp.	Pascichnia	Post	WM	
?*Spirocosmorhaphe labyrinthica*	Agrichnia	Pre	WM	x
Spirophycus bicornis	Pascichnia?	Pre	SpH	
Strobilorhaphe pusilla	Fodinichnia?	Post	Branched	
Thalassinoides isp.	Fodinichnia/Domichnia	Post	Branched	
Trichichnus linearis	Chemichnia	Post	Branched	
?*Urohelminthoida appendiculata*	Agrichnia	Pre	BWM	x
Zoophycos isp.	Fodinichnia	Post	Spreiten	
Meandering cylinder	?pascichnia	Post	WM	

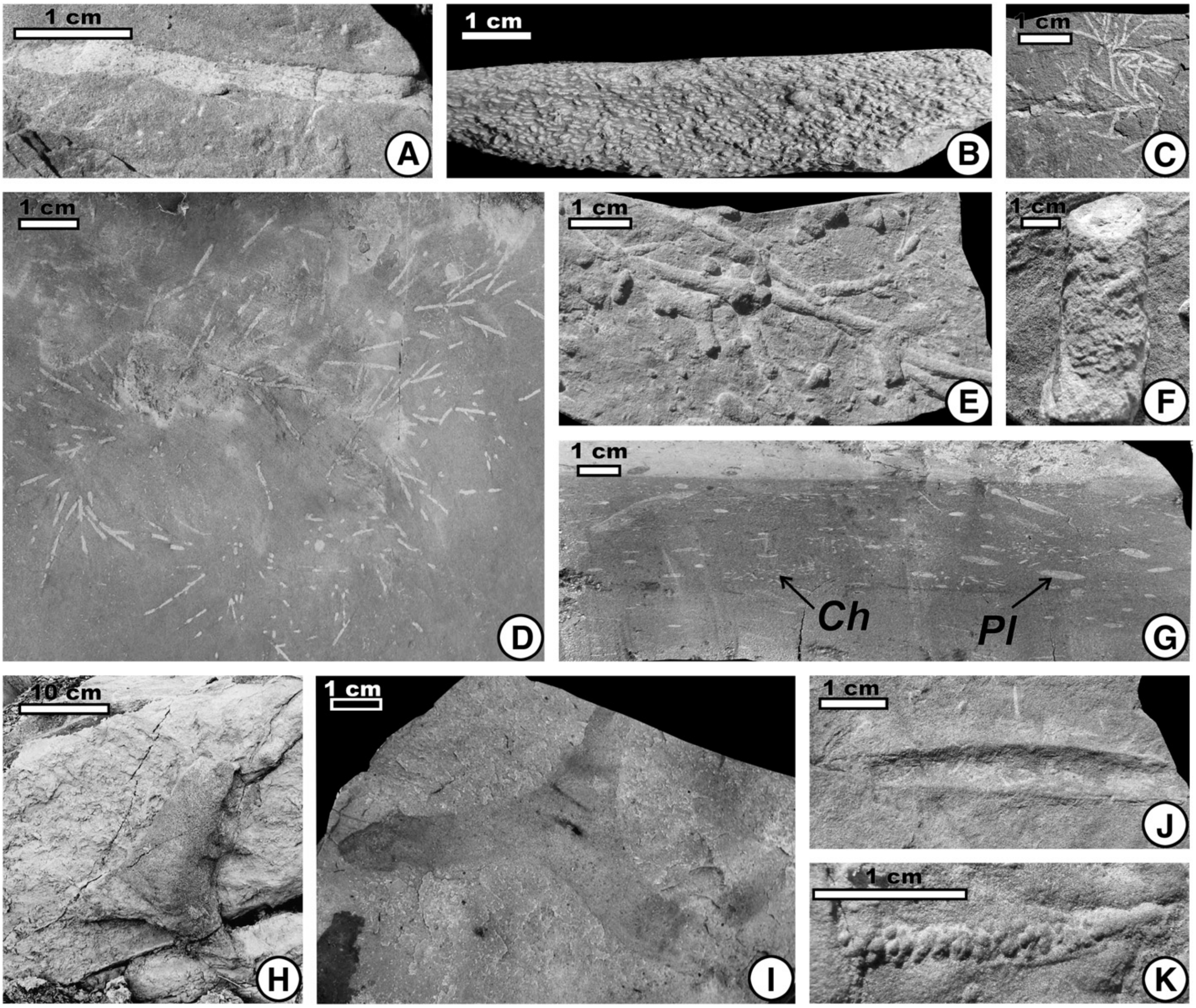

Fig. 3. Simple trace fossils: (A) *Alcyonidiopsis* isp. A. (B) *Alcyonidiopsis* isp. B. (C) *Chondrites intricatus.* (D) *Chondrites targionii*. (E) *Ophiomorpha annulata*. (F) *Ophiomorpha rudis*. (G) *Chondrites intricatus* (*Ch*) and *Planolites* isp. (*Pl*) in vertical cross section of a bed. The lower darker part shows turbiditic siltstone–mudstone and lighter upper part shows pelagic marly mudstone. (H) *Thalassinoides* isp. (I) *Thalassinoides* isp. (J) *Palaeophycus tubularis*. (K) *Strobilorhaphe pusilla*.

Chondrites targionii (Brongniart, 1828) (Fig. 3D): slightly winding or arcuate, branched, flattened, 2.5 mm wide tunnels. Branches are very long, some attaining at least 60 mm. The whole burrow system is at least 160 mm across. For discussion of this ichnospecies see Fu (1991) and Uchman (1999).

Ophiomorpha annulata (Książkiewicz, 1977) (Figs. 3E, 4H and 6C): mostly horizontal, hypichnial, or rarely vertical to oblique endichnial or exichnial, rarely branched cylinders, 2–4 mm, exceptionally 1.5 mm wide. The cylinders are straight to slightly winding, smooth or covered, commonly only partially, with delicate scratches or small, perpendicularly arranged granules. In some specimens, the branches form knots. This trace fossil is very common in Paleogene Alpine turbiditic successions (e.g., Uchman 1995, 2001).

Ophiomorpha rudis (Książkiewicz, 1977) (Fig. 3F): vertical, oblique to horizontal, endichnial or exichnial, straight, branched, sand-filled cylinders, 5–20 mm in diameter, smooth or covered locally with irregular granules or with short oblique ridges, which are casts of scratch marks. *O. rudis* is a typical species of sandy deep-sea sediments (Uchman, 2001).

Palaeophycus tubularis Hall, 1847 (Fig. 3J): a simple, straight, thinly lined furrow in epichnial position in thin-bedded sandstone, 5 mm wide. This is probably a weathered fragment of a tubular lined burrow; for discussion, see Pemberton and Frey (1982) and Keighley and Pickerill (1995).

Planolites isp. (Fig. 3G): horizontal, cylindrical trace fossils with sharp margins, but no distinct walls. Seen in cross section and filled with different material, 2 mm wide; for discussion, see Pemberton and Frey (1982) and Keighley and Pickerill (1995).

Strobilorhaphe pusilla Książkiewicz, 1968 (Fig. 3K): hypichnial ridges composed of an irregular row of small, densely packed, partially overlapping tubercules. The row is 12 mm long and about 2.5 mm wide. The tubercles represent short, blunt, clavate branches coming out from a central stem.

Thalassinoides isp. (Fig. 3H, I): endichnial or hypichnial, slightly winding, semicircular, straight or curved, branched ridges. They are 3–4 mm, 12 mm or 50 mm wide and mostly with Y-shaped branching, swelled up to 20 mm or up to 100 mm in width. For discussion of *Thalassinoides* see Frey et al. (1984).

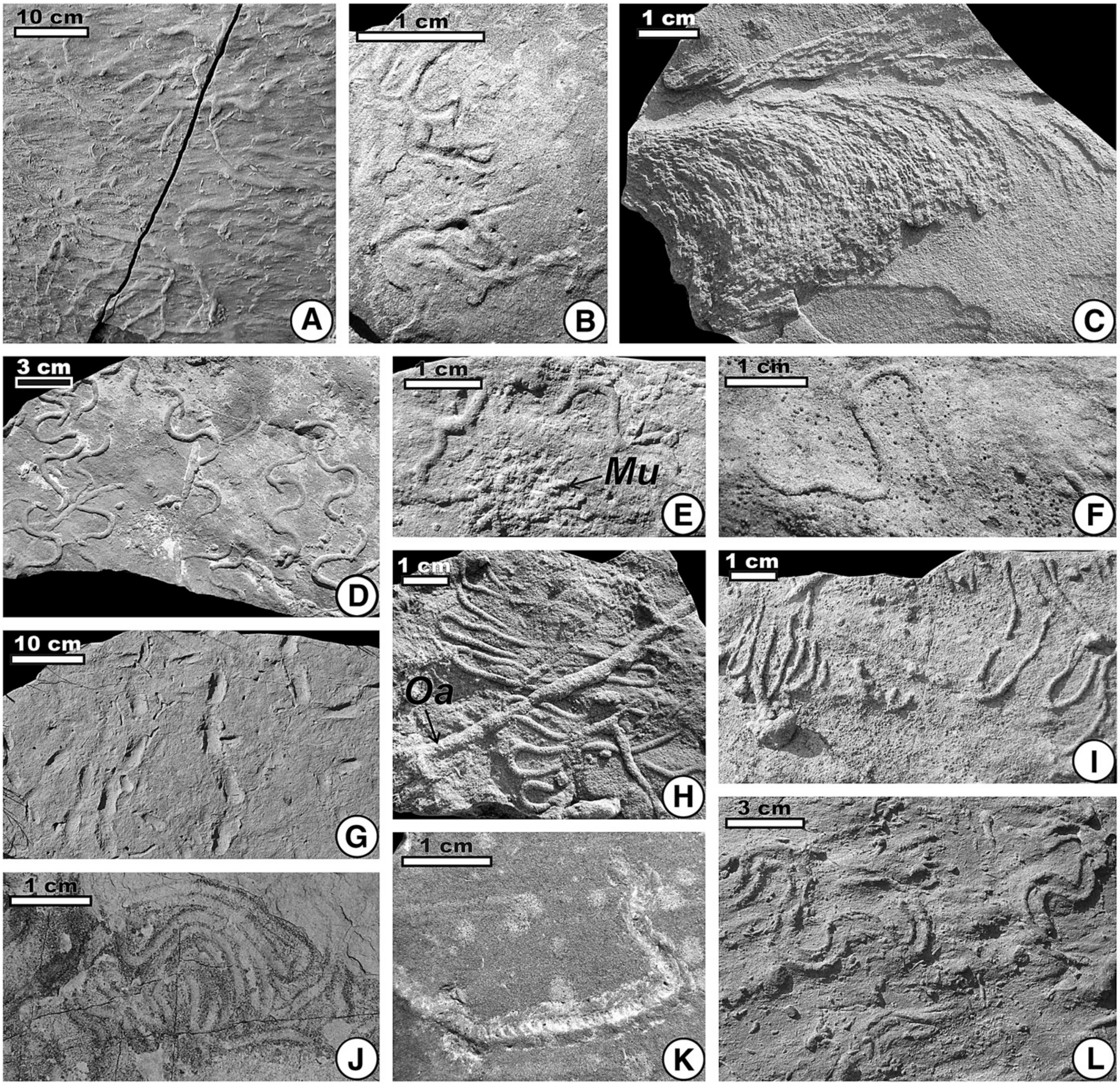

Fig. 4. Radial, spreite, winding and meandering trace fossils: (A) *Glockerichnus alata*. (B) *Phycosiphon incertum*. (C) *Zoophycos* isp. (D) *Cosmorhaphe sinuosa*. (E) ?*Cosmorhaphe* isp. and *Multina minima* (*Mu*). (F) *Helminthopsis abeli*. (G) *Naviculichnium marginatum*. (H) *Helminthorhaphe japonica* and *Ophiomorpha annulata* (*Oa*). (I) *Helminthorhaphe flexuosa*. (J) *Nereites irregularis*. (K) *Nereites* isp. (L) *Scolicia strozzii*.

Trichichnus linearis Frey, 1970: vertical to oblique, straight or slightly winding, rarely branched cylinders, up to 1 mm in diameter, filled with ferruginous material and commonly surrounded by a yellowish halo. For discussion of *Trichichnus* see McBride and Picard (1991) and Uchman (1999).

6.1.2. Radial structures

Glockerichnus alata (Seilacher, 1977) (Fig. 4A): hypichnial radiating anastomosing ridges with the characteristic U-shaped elements. The ridges are 8 mm wide. Only a fragment of the structure is preserved, which suggests that the whole structure is more than 200 mm in diameter. For discussion see Seilacher (1977).

6.1.3. Spreite structures

Phycosiphon incertum (Fischer-Ooster, 1858) (Fig. 4B): horizontal, curved, small repeated lobes, 1–3.5 mm wide, up to 6 mm long, surrounded at least partially by a 0.5–1 mm wide marginal tunnel. For discussion of *Phycosiphon* see Wetzel and Bromley (1994).

Zoophycos isp. (Fig. 4C): endichnial, horizontal to sub-horizontal planar spreite structures seen as fragmentarily preserved lobes, which are 30–52 mm wide or whorls with lobate margins. The lobes are encircled by a marginal tunnel, which is 3.3–4 mm wide. The whole structure is at least 400 mm wide and its fragments were observed on adjacent levels. Fine spreite laminae run arcuately according to the concavity of the lobe or as sub-circular, helical coiled structures, and contain poorly outlined, light pellets; higher whorls show a gradually smaller diameter, from 160 mm to 35 mm. Large spreite structures, at least 300 mm in diameter, belong to this type. Spreite laminae are slightly curved and run from the elevated centre towards a thin, indistinct marginal tunnel, where they tend to curve. The outer margin is slightly lobate. For discussion of *Zoophycos* see Bromley and Hanken (2003).

6.1.4. Winding and meandering structures

Cosmorhaphe sinuosa (Azpeitia Moros, 1933) (Fig. 4D): hypichnial semicircular ridges forming the first- and second-order meanders. The ridge is 3 mm wide. The second-order meanders are 12–14 mm wide and their amplitude attains 20–25 mm. Amplitude of the first-order meanders ranges between 100 and 120 mm. Turns of the second-order meanders in two limbs of the first-order meanders are locally even less than 1 mm apart. Short appendages running from the ridges suggest shortcuts between the limbs. For discussion of this trace fossil see Seilacher (1977).

?*Cosmorhaphe* isp. (Fig. 4E): Hypichnial meandering, semicircular ridges, 1.5–2.0 mm wide. The meanders are 7–12 mm wide with an amplitude of up to 3–7 mm. The first-order meander is limited to one incomplete turn.

Helminthopsis abeli (Książkiewicz, 1977) (Fig. 4F): hypichnial, smooth, semicircular ridges, 1 mm wide, preserved in semi-relief. It forms deep, irregular meanders.

Helminthorhaphe flexuosa (Uchman, 1995) (Fig. 4I): hypichnial, meandering 1 mm wide string. The meanders are at least 30 mm deep in different specimens, and 1.5–10 mm wide. Gentle, second-order undulations of the string are present. For discussion of *Helminthorhaphe* see Uchman (1995).

Helminthorhaphe japonica (Tanaka, 1970) (Fig. 4H): hypichnial, semi-cylindrical and slightly winding ridges, about 1–1.5 mm wide and forming meanders. The distance between meander limbs ranges from 1 to 5 mm. The meander amplitude ranges from 25 to 45 mm. There are distinct bulges at the meander bends.

Naviculichnium marginatum (Książkiewicz, 1977) (Fig. 4G): epichnial, elongate depressions with gently elevated rims. They are 13–17 mm wide and 30–50 mm long. Their axes are aligned along a winding line.

Nereites irregularis (Schafhäutl, 1851) (Fig. 4J): endichnial, tightly meandering horizontal ribbon composed of a central, wide part zone (the faecal string) and narrow, rarely observed side zones (the envelope zone). In most cases only the central part is visible on the rough surfaces as a light ribbon, which is 1–3 mm wide. The envelope, if visible, is very thin, less than 1 mm wide, with an uneven outer margin. Locally, the ribbon displays faint meniscate structure. For discussion of this ichnospecies see Uchman (1995).

Nereites isp. (Fig. 4K): epichnial, horizontal, irregularly winding trail, 3–4.5 mm wide, composed of central meniscate zone, which is 0.8–1.5 mm wide, and a slightly lobate envelope zone. The envelope zone is 1–1.5 mm wide from each side.

Scolicia prisca (de Quatrefages, 1849) (Fig. 5B): epichnial, winding trilobate furrow, 16–20 mm wide. The central ridge is semicircular and about 5 mm wide. The side lobes are coved with slightly oblique ribs.

Scolicia strozzii (Savi and Meneghini, 1850) (Figs. 4L and 6A): winding or meandering, smooth, bilobate hypichnial ridge, about 8–29 mm wide and up to 5 mm high, divided by a semicircular axial furrow that occupies up to two-thirds of the ridge width. The structure is preserved in semi-relief in fine-grained sandstone turbidites. Some of the ridges form coiling meanders. This ichnospecies was described in the earlier literature as *Taphrhelminthopsis* Sacco or *Taphrhelminthoida* Książkiewicz, but is considered to be a casted washed-out shallow *Scolicia* burrow (Uchman, 1995).

Scolicia vertebralis (Książkiewicz, 1977) (Fig. 5A): hypichnial, semicircular winding ridge with a single central, 1–2 mm wide string. The ridge is 17–22 mm wide. It is preserved in full relief; or epichnial, winding furrow, 20 mm wide, with a central string (1–2 mm wide) and the bottom and slopes covered with oblique ribs.

Scolicia isp. (Fig. 5C): endichnial, horizontal, winding, semi-cylindrical structure, 18–26 mm wide, which displays two parallel rows of menisci. This is the "laminites" preservation of *Scolicia*, which may belong to different ichnospecies (see Uchman, 1995).

?*Spirocosmorhaphe labyrinthica* (Heer, 1877) (Fig. 5D): Fragmentary preserved, hypichnial convex meandering semi-relief, 1 mm wide. One of the meanders displays characteristic omega-shaped geometry. The other meanders are 5 mm wide. Their amplitude attains 5 mm. For discussion see Seilacher (1989) and Wetzel and Uchman (1997).

Meandering cylinder (Fig. 5E): endichnial, horizontal, sand-filled meandering cylinder, about 8 mm in diameter, preserved in full relief in a turbiditic marly mudstone. General course of this trace fossil is straight. The meanders are 55–70 mm wide, with an amplitude of 2–25 mm.

6.1.5. Spiral and helical structures

Spirophycus bicornis (Heer, 1877) (Fig. 5F, K): hypichnial, winding semicircular ridges, 7–10 mm wide, with one clockwise or anticlockwise spiral whorl at the end, which is 18–35 mm wide. Its surface is smooth or covered with small tubercles. Incompletely preserved specimens are represented by hypichnial, winding, semicircular ridges, 7–12 mm wide. For discussion see Uchman (1998).

Helicodromites isp. (Fig. 5G, H): endichnial, horizontal, straight tightly spaced spiral, 2.5–3.5 mm wide, seen on parting surfaces in the top part of turbiditic marls as tightly spaced oval spots (1.5 mm in diameter) in an alternating position. At least a dozen helical turns are registered on a distance of 20 mm. In one specimen it is preserved as an almost straight double row of hypichnial very small knobs in alternating position. The knobs are about 1.2 mm apart, and the row is about 10 mm long. For *Helicodromites* see Bromley (1996).

6.1.6. Branched winding and meandering structures

?*Acanthorhaphe* isp. (Fig. 5I): five hypichnial short ridges pointing out from one side of an arcuate line. They are 3.5–6 mm long. Arrangement of the ridges is typical of *Acanthorhaphe*. For discussion of this ichnogenus see Uchman (1998).

Desmograpton dertonensis (Sacco, 1888) (Fig. 5J): hypichnial double rows of string-sized, U- or J-shaped semi-meanders. Their curved segments are inwardly oriented, in alternating position, with two opposing semi-meanders joined by short bars. The semi-meander string is 1–1.5 mm wide, and the axial elements are elevated. The connecting bars are 3–6 mm long, mostly perpendicular to the burrow axis and only locally preserved. The arms of semi-meanders are 3–5 mm apart. *Desmograpton* is a typical graphoglyptid; for discussion, see Uchman (1995).

Paleomeandron cf. *robustum* (Książkiewicz, 1968) (Fig. 5K): hypichnial meandering semicircular ridge, in which meanders are angular. The meanders display knobby swelling in kinks of the meanders. The ridge is 5 mm wide. The meanders are 25 mm wide and their amplitude ranges between 8 and 11 mm. The trace fossil displays general arcuate course. *P. robustum* displays tighter meanders (Książkiewicz, 1977).

Protopaleodictyon incompositum (Książkiewicz, 1970) (Fig. 5L): hypichnial, semi-cylindrical ridge, 1.5 mm wide, irregularly meandering and branched. The branches extend outwards from the meander bends, and some of the branches are long and winding. For discussion of *Protopaleodictyon*, see Uchman (1998).

?*Urohelminthoida appendiculata* (Heer, 1877) (Fig. 5M): hypichnial, semi-cylindrical meandering ridges, 2 mm wide. The meanders are 3–22 mm wide and more than 130 mm in amplitude, and their axis is curved. Tips of the meanders, where short appendages are expected, are not preserved. Nevertheless, geometry of the meanders

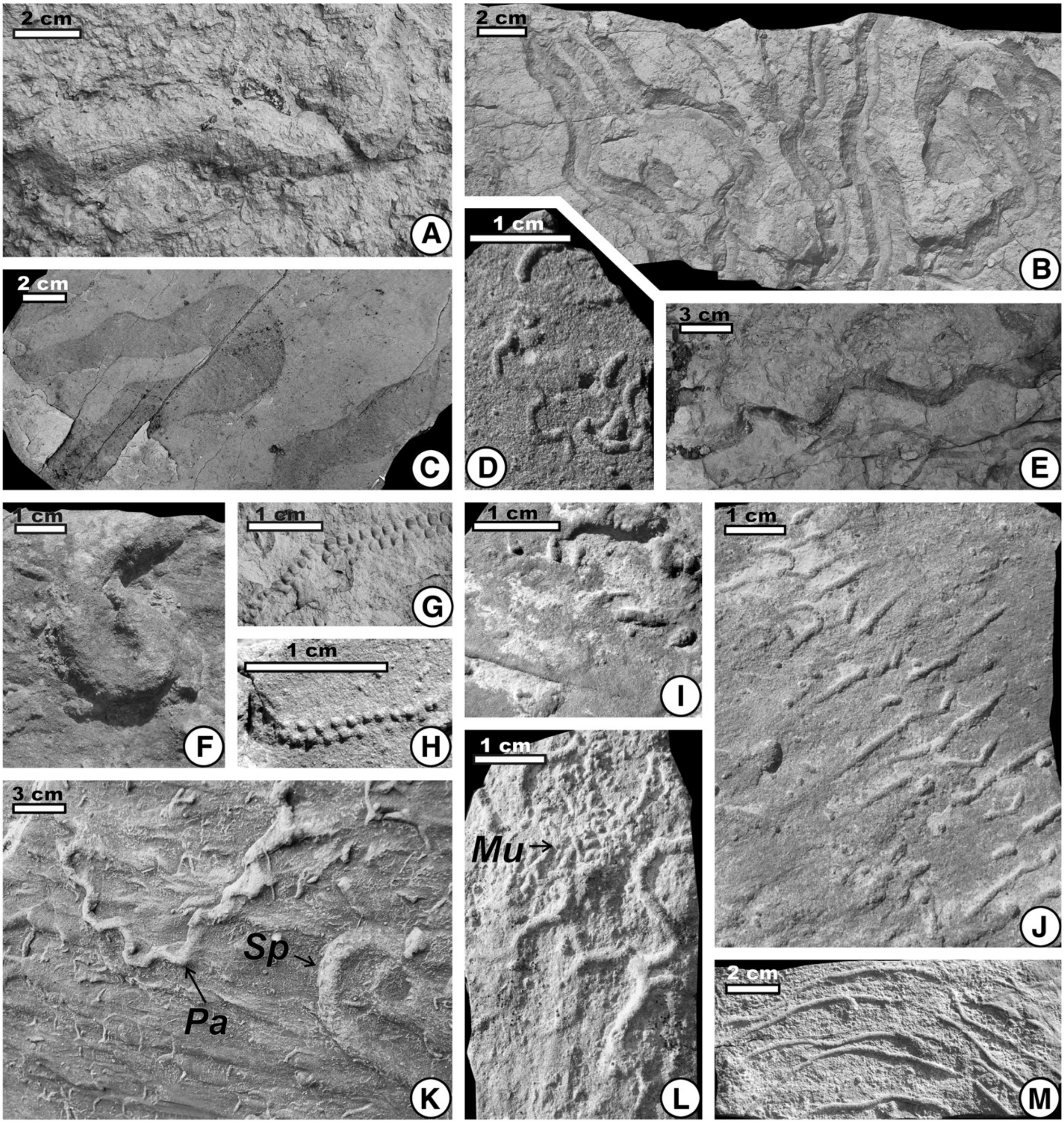

Fig. 5. Winding and meandering, spiral and helical, branched winding and meandering trace fossils: (A) *Scolicia vertebralis*. (B) *Scolicia prisca*. (C) *Scolicia* isp. (D) ?*Spirocosmorhaphe labyrinthica*. (E) Meandering cylinder. (F) *Spirophycus bicornis*. (G) *Helicodromites* isp., endichnion. (H) *Helicodromites* isp., hypichnion. (I) ?*Acanthorhaphe* isp. (J) *Desmograpton dertonensis*. (K) *Paleomeandron* cf. *robustum* (*Pa*) and *Spirophycus bicornis* (*Sp*). (L) *Protopaleodictyon incompositum* and *Multina minima* (Mu). (M) ?*Urohelminthoida appendiculata*.

is typical of this ichnospecies. For discussion of this graphoglyptid ichnospecies, see Uchman (1995).

6.1.7. Networks

Megagrapton submontanum (Azpeitia Moros, 1933) (Fig. 6A): hypichnial irregular net. Meshes are incomplete. They are bordered by distinctly winding strings, which are 2–2.5 mm wide. Branching at acute angles is common. Meshes of the net are 35–85 mm wide. For discussion see Uchman, 1998).

Multina minima (Uchman, 2001) (Figs. 4E, 5L and 6B, E): very irregular hypichnial net preserved in full relief, which may exhibit appendages and overlap of string within the same trace fossil. Meshes are less than 5 mm across. The string is 0.8–1.2 mm wide and displays several swellings, undulations, small meanders and overlaps. The overlaps can totally mask the meshes. Intensive sediment reworking in *M. minima* suggests deposit-feeding (pascichnial) activity of the tracemaker, a few centimetres below sea floor, along a sediment interface. For discussion see Uchman (2001).

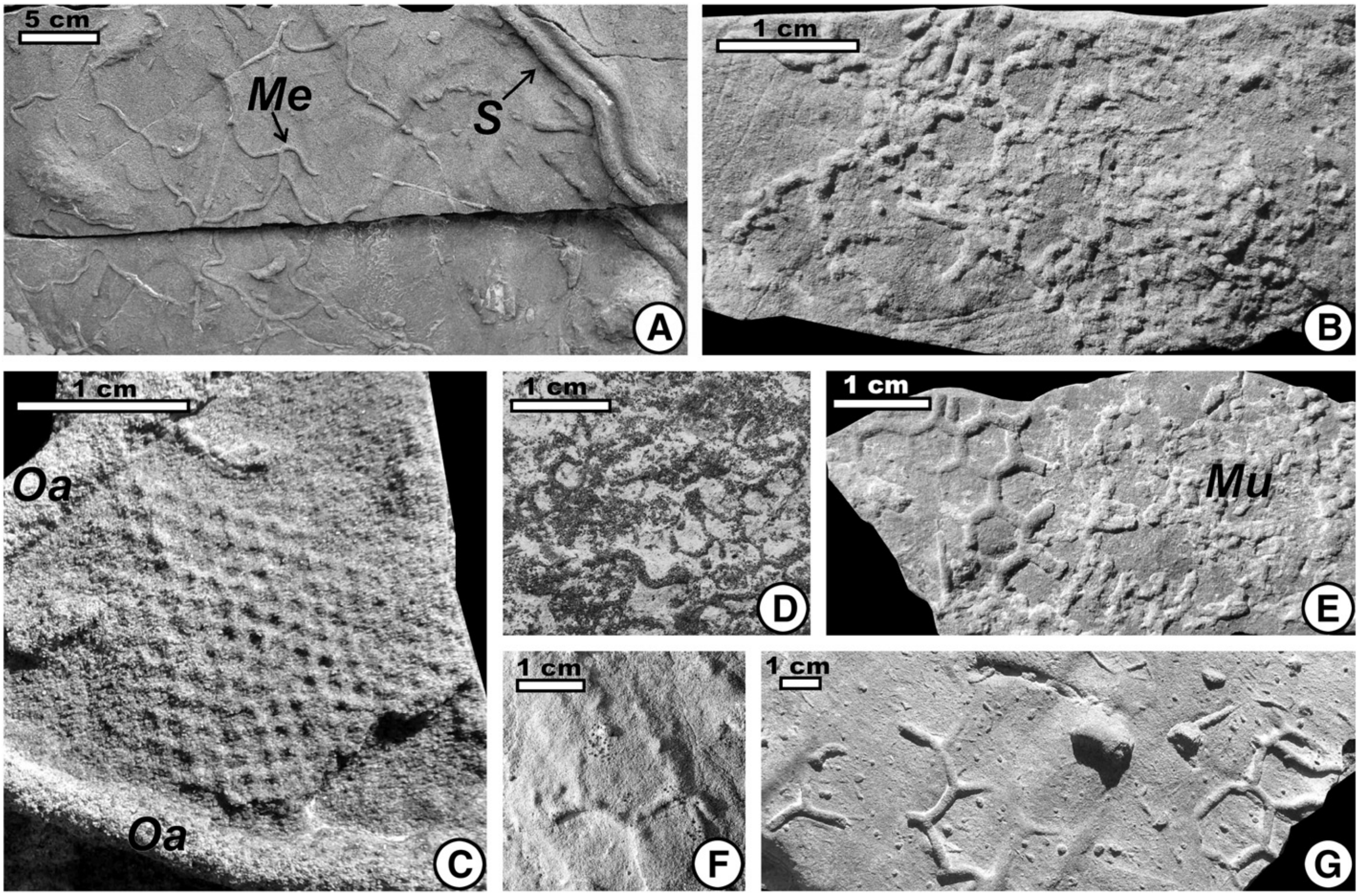

Fig. 6. Network trace fossils: (A) *Megagrapton submontanum* (*Me*) and *Scolicia strozzii* (*S*). (B) *Multina minima*. (C) *Paleodictyon minimum* and *Ophiomorpha annulata* (*Oa*). (D) *Paleodictyon strozzii*. (E) *Paleodictyon miocenicum* and *Multina minima* (Mu). (F) *Paleodictyon majus*. (G) *Paleodictyon arvense*.

Paleodictyon minimum (Sacco, 1888) (Fig. 6C): very small regular, hexagonal net; meshes are 1 mm and string is 0.5 mm. For discussion of *Paleodictyon* see Uchman (1995).

Paleodictyon strozzii Meneghini, 1850 in Savi and Meneghini (1850) (Fig. 6D): hypichnial, regular, hexagonal net; meshes are 3.5–4 mm and string is 0.8 mm.

Paleodictyon miocenicum (Sacco, 1886) (Fig. 6E): regular, hexagonal net; meshes are 5 mm and string is 1.3–1.5 mm.

Paleodictyon majus Meneghini in Peruzzi (1880) (Fig. 6F): fragmentary preserved, regular, hexagonal net; meshes are 12 mm and string is 1.5 mm.

Paleodictyon arvense (Barbier, 1956) (Fig. 6G): fragmentary preserved, regular, hexagonal net; meshes are 14–19 mm and string is 2–2.1 mm.

6.2. Trace fossil distribution

Trace fossil composition, diversity and abundance fluctuate significantly throughout the section (Fig. 7). Some trace fossils are continuously recorded. Amongst these, the most common and relatively abundant are *Chondrites intricatus*, *Ch. targionii*, *Ophiomorpha annulata* and *Scolicia strozzii*, which can be considered as the permanent background components of the trace fossil assemblage. *Planolites*, *Thalassinoides*, and *Zoophycos* also occur throughout the section, but less frequently and less continuously. *Spirophycus* also shows a discontinuous record in the entire section, except for the lowermost part, and the same is true for *Ophiomorpha rudis*. However, *O. rudis* is absent in the lowermost and uppermost parts of the section. Among these ichnotaxa, *C. intricatus*, *Ch. targionii*, *O. annulata*, *O. rudis, Planolites*, *Thalassinoides* and *Zoophycos* are post-depositional, representing trace makers that penetrated turbiditic sediment to different depths. *S. strozzii* and *Spirophycus bicornis* are pre-depositional forms, representing trace makers that penetrated the background sediment deposited between turbiditic events. Ethologically, the trace makers reflect a wide range of behaviours with chemichnia (*Chondrites*), domichnia (*Ophiomorpha*, *Thalassinoides*), pascichnia (*Planolites*, *Scolicia*, *Spirophycus*), and fodinichnia (*Thalassinoides*, *Zoophycos*).

Variations in the distribution and abundance of the remaining ichnotaxa enable five intervals to be established (Fig. 7):

Interval A in the lower part of the section corresponds to the second turbiditic-poor interval and is dominated by hemipelagic marlstones. This interval shows a moderate diversity and abundance of pre- and post-depositional trace fossils. Some of them occur exclusively within this interval, such as *Alcyonidiopsis* isp. A, ?*Urohelminthoida*, *Helminthorhaphe japonica*, *Multina*, *Protopaleodictyon*, and *Paleodictyon miocenicum*. Other ichnotaxa such as *Helminthopsis*, *Helicodromites* and *Trichichnus* also occur in the middle part of the section, and *Desmograpton* and *Phycosiphon*, which are rare in interval A, appear in the upper part of the section as well. Trace fossil morphologies are variable, including simple (*Alcyonidiopsis* isp. A), spreite (*Phycosiphon*), and helical (*Helicodromites*) forms, together with branched, winding and meandering forms, and occasional networks (*Multina*, *Paleodictyon*). Agrichnial behaviour dominates, with other behaviours such as pascichnia, fodinichnia and chemichnia being rare.

Interval B in the lower-middle part of the section corresponds to the uppermost part of the second turbidite-poor interval with an increase of hemipelagic limestones upwards and the beginning of the second turbidite-rich interval. Interval B is characterized by a highly significant decrease in trace fossil diversity and abundance. Apart

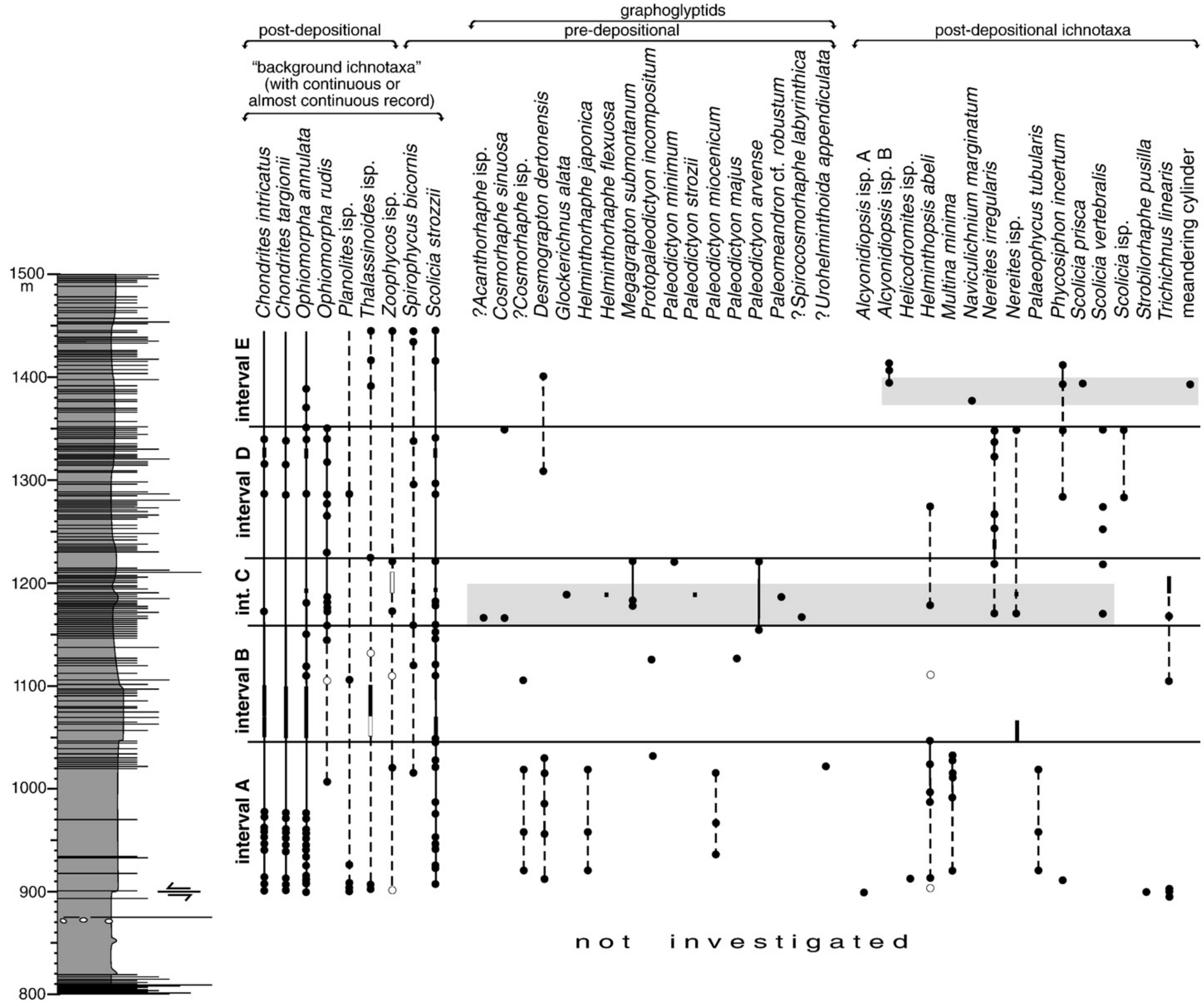

Fig. 7. Synthetic log of the Gorrondatxe section with the vertical distribution of trace fossils and subdivisions into ichnological intervals A–E. Continuous lines and rectangles for more or less continuous record, and filled points for punctual one. Dashed lines for discontinuous record. White rectangles and points for uncertain record (?) of a particular ichnotaxa. Grey bands for horizons with abundance of first appearances in the section.

from the background ichnotaxa, only patchy records of ?*Helminthopsis*, *Trichichnus*, *Nereites irregularis,* and *Protopaleodictyon* are noted. Most of the interval B ichnotaxa are post-depositional, winding and meandering structures, showing a dominant pascichnial behaviour.

Interval C in the middle part of the succession corresponds to the middle part of the second turbidite-rich interval. Interval C is characterized by an increase in trace fossil diversity and abundance, showing the highest values throughout the section. Together with the background ichnotaxa, 15 ichnospecies of 12 ichnogenera have been found. Some of them reappear from interval A (*Helminthopsis*, *Helicodromites*), or B (*Trichichnus*, *Nereites irregularis*, *Scolicia vertebralis*); others, mostly pre-depositional structures, are new, including *Paleodictyon majus, P. arvense*, *P. minimum*, *P. strozzii*, ?*Acanthorhaphe*, *Glockerichnus*, *Megagrapton*, *Paleomeandron*, *Nereites* isp, and *Cosmorhaphe sinuosa*. Especially significant is the reappearance of graphoglyptids from interval A, but with more common networks. Generally, agrichnial and pascichnial behaviours dominate.

Interval D in the upper part of the succession corresponds to the upper part of the second turbidite-rich interval. In this interval, trace fossil diversity and abundance significantly decrease, but less than in interval B. Apart from the background assemblage, the ichnotaxa known already from intervals A (*Desmograpton*, *Phycosiphon*) or C (*Nereites irregularis*, *Scolicia vertebralis*, *Cosmorhaphe sinuosa*) occur. The graphoglyptids include *Desmograpton* and *C. sinuosa*, but those from interval C are not present in interval D. The ichnotaxa belong to pre- and post-depositional, predominantly winding and meandering forms, and represent a variable ethology including agrichnia, pascichnia and fodinichnia.

Interval E in the uppermost part of the studied section covers the uppermost part of the second turbidite-rich-interval, characterized by a decrease of turbidite content and abundant plant detritus, and the lowermost part of the third turbidite-poor interval. The trace fossil abundance and diversity slightly decrease to interval D. Apart from *Desmograpton* and *Phycosiphon*, *Alcyonidiopsis* isp. B, *Naviculichnum marginatum* and *Scolicia prisca* occur for the first time in the section.

Most of the interval E ichnotaxa are post-depositional, branched, winding and meandering structures, representing a variable ethology with agrichnia, pascichnia and fodinichnia.

7. Discussion

7.1. Ichnofacies analysis and depositional-sedimentary environment

The trace fossil assemblage throughout the succession is typical of the deep-sea *Nereites* ichnofacies, with a significant contribution of shallow-tier, pre-depositional structures, mainly graphoglyptids, and shallow to deep-tier post-depositional forms. Some of the ichnotaxa display a distribution pattern similar to the turbiditic deposits of the generally coeval Hecho Group in the southern Pyrenees (Uchman, 2001; Heard and Pickering, 2008). *Ophiomorpha rudis* is very abundant in the channel and proximal lobe facies, *Ophiomorpha annulata* reaches its maximum in the fan-fringe and basin-plain facies, the planar fodinichnia *Nereites irregularis*, *Phycosiphon incertum*, and *Zoophycos* in fan-fringe and basin-plain facies, while the graphoglyptid reveals a more complex distribution (e.g., *Paleodictyon* tends to occur in more sandy facies than on the basin plain, *Desmograpton* and *Urohelminthoida dertonensis* in fan-fringe and basin-plain facies, and *Helminthorhaphe* and *Cosmorhaphe* show a more uniform distribution). In view of the three ichnosubfacies differentiated in the *Nereites* ichnofacies (*Nereites*, *Paleodictyon*, and *O. rudis* ichnosubfacies; Uchman, 2001; Uchman et al., 2004), the general presence of graphoglyptids throughout the section is typical of the *Paleodictyon* ichnosubfacies, which is common in distal turbiditic deposits (Seilacher, 1974; Uchman, 1999). The trace fossil association is typical of fan-fringe and basin-plain settings in the coeval Hecho Basin (Uchman, 2001; see above). This interpretation agrees with previous interpretations of the section (Payros et al., 2006). However, the common occurrence of *O. rudis* in intervals C and D, which is more typical of the *O. rudis* ichnosubfacies, is a signature of a more proximal setting (Uchman, 2007), even though *O. rudis* is also locally registered in distal fan environments (Heard and Pickering, 2008) . In particular, the local presence of *O. rudis* can be caused by an increase in availability of deeply buried plant detritus, used as an important nutrient for the *Ophiomorpha* trace maker (Uchman et al., 2004). The general ichnofacies interpretation corroborates previous interpretations for the sedimentary environment, a submarine fan fringe or basin plain, with occasional lateral sediment supply (Payros et al., 2006).

7.2. Bathymetry

The bathymetry is estimated to be around 1500 m on the basis of the planktonic/benthic foraminifera ratio (Van der Zwaan et al., 1990; Nigam and Henriques, 1992), and depths greater than 600–800 m according to ostracod assemblages (Rodríguez-Lázaro and García-Zarraga, 1996). In this range of bathymetry, in the studied section the vertical variation of trace fossils within the *Nereites* ichnofacies cannot be interpreted as an immediate, direct consequence of changes in water depth due to combined tectonism and eustasy. However, changes in palaeoenvironmental conditions related to productivity, bottom disturbances or substrate changes can be considered as indirect consequences.

7.3. Palaeoecology

The sediment was inhabited foremost by r-selected trace makers in shallow (*Planolites*), middle (*Thalassinoides*, *Ophiomorpha*), and deeper tiers (*Chondrites*, *Zoophycos, Ophiomorpha*). Bioturbation of all beds, at least partially, especially the interturbidite sediments, and the continuous record of trace fossils at different tiers indicate good oxygenation of the sea floor. This oxygenation was, probably, particularly good after deposition of turbidites, bringing oxygenated waters with the suspension, then decreasing later during the long interturbidite periods (Wetzel and Uchman, 2001). There is no evidence of anoxia on the sea floor.

The abundance of pre-depositional forms, especially relatively diverse graphoglyptids (Fig. 8), suggests moderate oligotrophy prevailing during interturbidite times. The graphoglyptids represent a K-selected equilibrium strategy of colonization (Ekdale, 1985; Uchman, 1995). In general, the presence of graphoglyptids in the studied section, especially in some intervals, could indicate relatively stable conditions on the sea floor between depositions of turbidites. Light-coloured interturbiditic sediments (Fig. 3G) confirm the oligotrophy.

As previously interpreted (Payros et al., 2006), variations in turbiditic activity determine changes in suspension of fine-grained sediment, organic matter and nutrients. Composition of the planktonic foraminifers assemblage shows changes throughout the section between symbiont-bearing K-strategist species and opportunistic and cosmopolitan species, which are interpreted as a consequence of mixing between warm oligotrophic and colder eutrophic upper waters. Differences in diversity and abundance of trace fossils among the intervals A–E can be related partly to fluctuations in the trophic level, related to productivity changes in the water column and to lateral flux of organic matter caused by bottom currents, mainly turbiditic currents.

7.4. Trace fossil distribution in relation to sea-level dynamics and planktonic foraminifera changes

Some of the alluded palaeoecological features, such as oxygenation and organic matter, are conditioned by the sea-level dynamics. Thus, the vertical distribution of trace fossils can be related to the sequence stratigraphic framework proposed for the studied section. According to this framework (Payros et al., 2009a), the turbidite-rich intervals were deposited during low sea-level periods, and the turbidite-poor intervals during high sea level. On this basis, the lowermost part of the Gorrondatxe section, corresponding to the second turbidite-poor interval, is interpreted as the transgressive systems tract of a third-order depositional sequence Cu2. The progressive increase in hemipelagic limestones towards the top of this turbidite-poor interval is related with the consequent high sea-level stillstand. The overlying second turbidite-rich interval is interpreted as lowstand deposits of the depositional sequence Cu–Lt, with the carbonized plant detritus from the upper part of these turbidite-rich sediments related to terrestrial input. The decrease to lower frequencies of turbidite beds (lowermost part of the third turbidite-poor interval) at the top of the studied section is interpreted as a sea-level rise (transgressive/highstand systems tract). The differentiated ichnological intervals can be analysed in relation to the sequence stratigraphy framework and changes in planktonic foraminifers (Fig. 8).

Interval A, in comparison to the remaining intervals, is characterized by a great diversity and abundance of pre-depositional trace fossils, which show high morphological variability, with the occasional record of networks. The abundance of agrichnia (all graphoglyptids) is significant. Interval A corresponds to a general sea-level rise during a TST and the lower-middle part of the subsequent HST, including the maximum flooding surface between both system tracts. Relatively abundant pre-depositional trace fossils, including several types of graphoglyptids, could be related to the generally well oxygenated, moderately oligotrophic environment, in which the feeding strategy (microbe gardening or trapping) is a successful adaptation to organic-poor, stable environments (Seilacher, 1977; Miller, 1991; Uchman, 1999, 2003). This correlates with the planktonic foraminiferal assemblage, which is dominated by low-latitude groups (Fig. 8), indicative of oligotrophic warm waters at the sea surface (Payros et al., 2006). Limited lateral flux of benthic food due to the scarcity of turbidites and limited flux of organic matter from the water column enhanced the

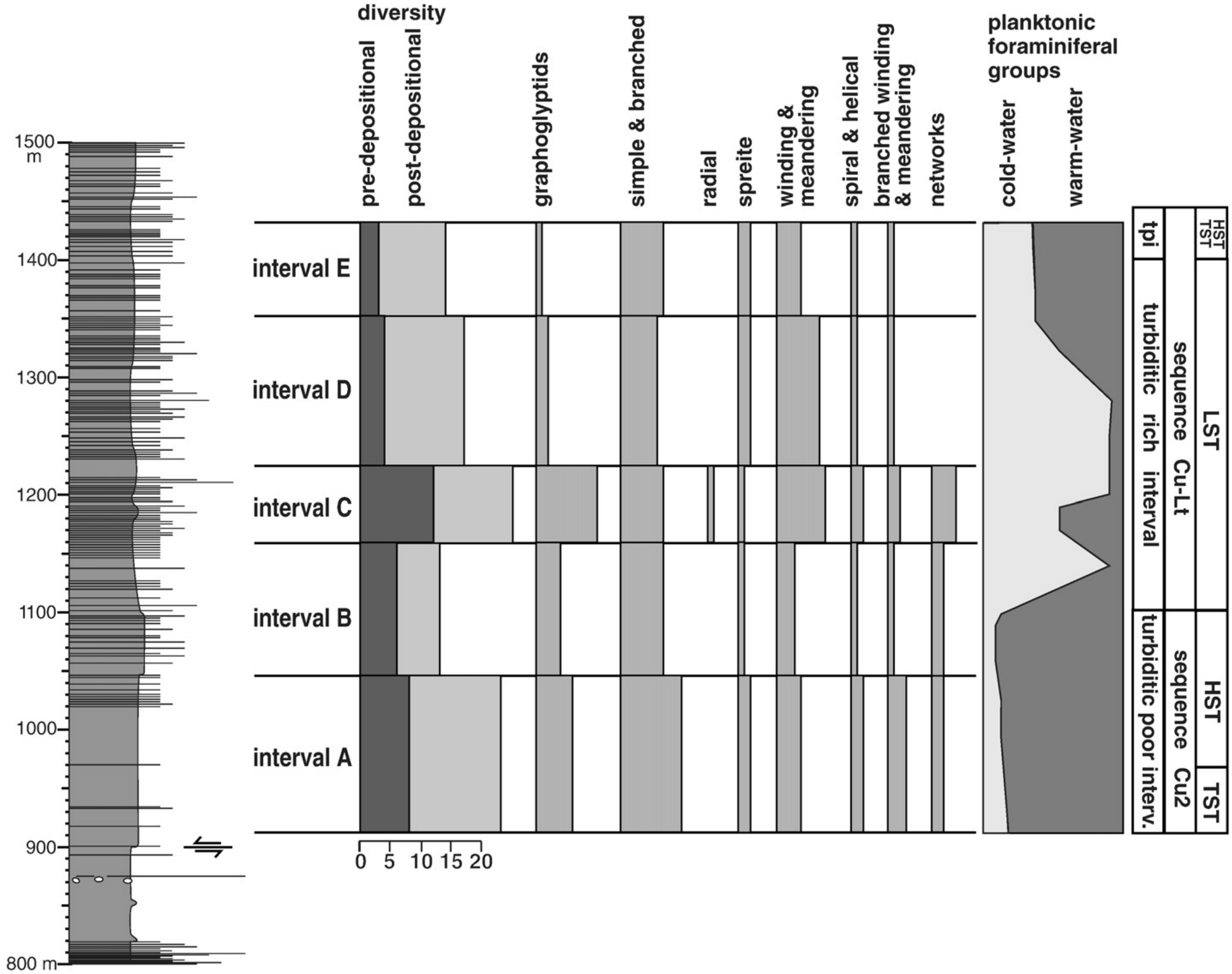

Fig. 8. Review of main ichnological features in intervals A–E). Main trends in planktonic foraminifers adapted from Payros et al. (2006) against the sequence stratigraphy proposal.

general Eocene oligotrophy and promoted variable trace maker behaviours in competition for food resulting in variable morphologies of trace fossils.

Interval B shows a significant change in the trace fossil assemblage. The diversity and abundance decreased, yielding the lowest values in the section. This interval is correlated with the progressive increase in hemipelagic limestones deposited during the high sea-level stillstand corresponding to the late sea-level highstand, and with the lowermost part of the turbidite-rich interval deposited during the beginning of the sea-level lowstand. The sharp near-disappearance of trace fossils, including some graphoglyptids, indicates a deterioration of ecological conditions, which can be attributed to several factors. The substrate of the background sediments changed from siliciclastic mud to marly or limy mud. This change would influence graphoglyptids, generally rare in marly turbiditic deposits (Uchman, 1999, 2007). The stillstand at the beginning of this interval could increase the oligotrophy. Strong oligotrophy negatively influences trace fossil diversity (Leszczyński and Uchman, 1993); and the beginning of the lowstand system tract in the upper part of the interval would also cause stressful conditions. Animals need some time to adapt to more frequent influx of land-derived organic matter. Moreover, higher organic matter content accompanying turbidite currents during sea-level drop can shift up the redox boundary. Furthermore, turbiditic currents can bring colder waters; temperature drops have been interpreted during lowering of sea level in the studied section (Payros et al., 2006). Finally, burrows produced in shallow tiers are less likely to be preserved as trace fossils (e.g., Werner and Wetzel, 1982; Bromley, 1996). It is envisaged that this possible set of changes disturbed the ecological stability and caused a general worsening of deep-sea floor life conditions. As a result, trace fossil diversity declined brusquely. This interpretation partly fits in with an important change in the foraminiferal assemblage registered from the middle part of this interval, characterized by the rapid fluctuation towards the dominance of opportunistic and cosmopolitan high-latitude planktonic taxa. Payros et al. (2006) related this dominance to global cooling episodes during lowstand resedimentation events combined with a resuspension of large volumes of mud and organic matter during turbiditic deposition, determining the eutrophication of seawater. It is not excluded that the cooling affected the deep sea prior to the surface waters, and the ichnofaunal crisis was ahead of the planktonic foraminiferal turnover.

Interval C is characterized by a significant increase in trace fossil diversity and abundance. It shows the highest values of the section on the whole, mainly corresponding to pre-depositional forms. Especially significant is the presence of numerous new and exclusive ichnotaxa, including several types of network graphoglyptids, and a predominant agrichnial behaviour. Interval C corresponds to the development of the lower-middle part of the lowstand system tract (LST). The ichnological features could indicate well oxygenated, moderately oligotrophic conditions. Explanation of this situation by sea-level dynamics is not obvious, and none of the invoked scenarios is fully convincing. It can be postulated that less mud is resuspended during development of lowstand systems tracts, and in consequence more oligotrophic conditions reappear. Tracemakers could adapt to the lateral influx of organic matter and to increasing siliciclastic inter-turbiditic mud. It is also possible that prolonging lithological diversification of sea floor due to deposition of turbidites promoted new behavioural adaptations, and consequently increased trace fossil diversity. However, it is striking that interval C is correlated with the punctual and significant increase of low-latitude planktonic foraminifers (Payros et al., 2006: fig. 10) (Fig. 8), most likely indicating an increase in surface-water temperature related with higher-order paleoenvironmental (ecological and/or depositional) changes during the development of the third-order lowstand system tract.

Interval D exhibits a low trace fossil diversity and abundance, while less important than in interval B. However, decrease of diversity of graphoglyptids is stronger. Interval D corresponds to the upper part of the lowstand system tract characterized by turbidite-rich sediments deposited during the relative sea-level fall, providing large volumes of fine-grained sediment, and probably, abundant organic matter, including abundant plant detritus (Payros et al., 2006). The land-derived non-refractable organic matter has low nutritional value for marine organisms. Common occurrence of *Ophiomorpha rudis* in this interval may be a response to the increased plant detritus content. It seems that its crustacean tracemaker penetrated deeply buried sediments rich in plant detritus, which became edible after conversion by microbes (Uchman, 2004b). In modern environments, *Scolicia* is interpreted as related to large amounts and high quality of benthic food (Wetzel, 2008). Habitats with high benthic food content and poorly oxygenated pore water containing *Nereites* have been described in the fossil record (Ekdale and Mason, 1988; Wetzel and Uchman, 1998). Eutrophisation of the environment is possible and compatible with the nutrient-enriched cool surface waters interpreted on the basis of abundant high-latitude planktonic foraminifers (Payros et al., 2006). However, a higher abundance and diversity of trace fossils, and the presence of graphoglyptids, in comparison with interval B, could be indicative of less extreme environmental conditions. We cannot discard that the scarcity of graphoglyptids might be directly related with the relative abundance of *Nereites* and *Scolicia*. As proposed for recent environments, the presence of *Nereites* trace makers probably prevents the production of graphoglyptids or may destroy these biogenic structures due to frequent vertical movements during feeding activity (Wetzel, 2002, 2008).

Interval E is characterized by a further decrease in trace fossil abundance and diversity, including graphoglyptids. Simple, branched, winding and meandering forms prevail. This interval corresponds to the progressive decrease in turbidite content during the development of the uppermost part of the lowstand system tract and the rising sea level during the subsequent transgressive/highstand systems tracts. Planktonic foraminifers suggest an incursion of dominant low-latitude groups, indicating less extreme oligotrophic warm waters than those interpreted for interval D (Payros et al., 2006). Trace fossils, however, do not show a high diversity as would be expected when compared to interval A, which is also related to TST–HST. Some ichnotaxa of interval E occur for the first time in the section. Interpretation of the changes registered in the trace fossils assemblage is difficult. It is not excluded that the decrease in diversity of this interval is related to the cooling of deep waters, as reflected by the later appearance of planktonic foraminiferal assemblages dominated by cold-water groups. Cooler-water planktonic foraminifers start to dominate again 50 m up the section (Payros et al., 2006). Too, the crisis of ichnofauna in interval B started about 50 m below incursion of cold-water foraminifers (Fig. 8). It is also possible that the decrease in diversity is related to the general decrease of deep-sea trace fossil diversity and graphoglyptids from the late Middle Eocene (Uchman, 2004a).

7.5. General remarks

The diversity and abundance of trace fossils in turbiditic sediments are largely independent of the frequency of turbidites. The most diverse intervals, A and C, are found in two different settings: in turbidite-poor and turbidite-rich intervals, respectively. The sea-level dynamics help to explain the distribution of trace fossils, but only to some extent. The differences in diversity of trace fossils between intervals A (correlating with TST and lower-middle part HST) and B (corresponding to upper HST and lower LST) could imply that the optimal conditions for diverse ichnofauna occur during high sea level. The low ichnodiversity from interval E (representing upper LST and TST–HST) contradicts this officious idea. However, the comparison is complicated in light of the anticipated different development of the TST and HST during two depositional sequences (Cu2 and Cu–Lt), and probably related with particular sea-level dynamics. Moreover, it is not excluded that the low ichnodiversity from interval E corresponds to the general declining of ichnodiversity since late Middle Eocene (Uchman, 2004a). The richest trace fossil interval C correlates with the lower-middle part of the LST, which is unexpected. It might reflect a lower order sea-level rise after the sequence boundary postulated for this part of the section. The trace fossil changes correlate partly with planktonic foraminifera fluctuations and both groups are related to trophic level changes. However, the crisis of ichnofauna (intervals A–B transition) precedes the incursion of cold-water groups. It is not excluded that incursion of cold water occurred in the deep sea before taking place in shallow zones. Unfortunately, changes of benthic foraminifera, which could clarify our interpretations, have not elaborated in the section to date.

It seems that the distribution of trace fossils in deep-sea turbiditic sediments is affected by several factors, none of them being exclusive. More turbiditic sections with well established sequence stratigraphic schemes, the distribution of microfossils and other parameters should be tested to arrive at a better understanding of the relationships between ichnofauna and palaeoenvironment.

8. Conclusions

1. The studied upper Ypresian–lower Lutetian interval at the 600 m thick Gorrondatxe section (W Pyrenees, N Spain) contains trace fossils typical of the *Nereites* ichnofacies, mostly of the *Paleodictyon* ichnosubfacies indicating basin plain to fan-fringe setting.
2. Bioturbation of all beds, at least partially, and the continuous record of trace fossils point to good oxygenation at the sea floor.
3. The trace fossil diversity and abundance show fluctuations throughout the section irrespective, at least in part, to frequency of turbidites.
4. The fluctuations are related foremost to changes of trophic level, and additionally to temperature, quality of substrate and ecological disturbances, which in turn are partly determined by the sea-level dynamics according to the sequence stratigraphic interpretation.
5. Increased diversity of trace fossils and particularly of graphoglyptids is interpreted as an occurrence of moderate oligotrophy and stabilization of ecological conditions.
6. The change of substrate from siliciclastic to marly or limy mud during stillstand, eutrophisation, lowered oxygenation and drop of temperature, typical of low sea level, can limit diversity of graphoglyptids and trace fossils in general.
7. The crisis of ichnofauna (intervals A–B transition) precedes incursion of cold-water groups, which could be related to temporal differences in the incursion of cold waters, earlier in the deep sea than in shallow zones.

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