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Calcareous nannoplankton and foraminiferal response to global Oligocene and Miocene climatic oscillations: a case study from the Western Carpathian segment of the Central Paratethys

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Abstract: The reactions of foraminiferal and calcareous nannoplankton assemblages to global warming and cooling events in the time intervals of ca. 27 to 19 Ma and 13.5 to 15 Ma (Oligocene and Miocene) were studied in subtropical epicontinental seas influenced by local tectonic and palaeogeographic events (the Central Paratethys). Regardless of these local events, global climatic processes significantly influenced the palaeoenvironment within the marine basin. Warm intervals are characterized by a stable, humid climate and a high-nutrient regime, due primarily to increased continental input of phytodetritus and also locally due to seasonal upwelling. Coarse clastics deposited in a hyposaline environment characterize the marginal part of the basin. Aridification events causing decreased riverine input and consequent nutrient decreases, characterized cold intervals. Apparent seasonality, as well as catastrophic climatic events, induced stress conditions and the expansion of opportunistic taxa. Carbonate production and hypersaline facies characterize the marginal part of the basins. Hypersaline surface water triggered downwelling circulation and mixing of water masses. Decreased abundance or extinction of K-specialists during each cold interval accelerated their speciation in the subsequent warm interval. Local tectonic events led to discordances between local and global sea-level changes (tectonically triggered uplift or subsidence) or to local salt formation (in the rain shadows of newly-created mountains).

Keywords: climate, foraminifera, calcareous nannoplankton, Oligocene, Miocene, Central Paratethys.

Introduction

The major Miocene cooling events in the Early and the late Middle Miocene can be correlated with two episodes of deciduous tree appearances in the Western Carpathian area (Planderová 1990):

(1) A brief event at the Oligocene/Miocene boundary, with increases of *Ulnus, Alnus* and *Betula,* which coincides with the global Mi-1 event, lasting approximately 250 ka around the Oligocene/Miocene boundary (23.03 Ma) (Zachos et al. 2001). The stomatal index data indicate a rapid increase in atmospheric carbon dioxide at 22.95 Ma, followed by a more gradual decrease (Kürschner et al. 2008). The cooling was connected with an increase in seasonality, as shown by palaeoclimate analysis based on plant macrofossils. In the study area (the Pannonian domain), cooling, especially of the coldest months, was documented by Erdei et al. (2007), who finds sub-zero winter temperatures. Aridity is indicated, based on leguminous elements (Erdei et al. 2007). The subsequent warming corresponds to the reappearance of palms from the genera *Arecipites, Myricipites,* etc. (Planderová 1990). Ozdínová & Soták (2014) documented this warming in the NP25 calcareous nannoplankton zone from foraminiferal and calcareous nannoplankton assemblages. Grunert et al. (2015) interpreted the following cooling to coincide with the NN1 and lower part of the NN2 Zones (to the FO of *H. ampliaperta*) based on oscillations in stable oxygen isotope values.

(2) The Middle Miocene event represents the beginning of the Middle and Late Miocene gradual environmental and climatic changes known as the MMCT (=Middle Miocene Climate Transition) (Holbourn et al. 2005). The cooling can be correlated with the Mi-3 global events (Mi-3a event 14.3 Ma, Mi-3b event 13.8 Ma; Gradstein et al. 2012). In terrestrial climates, the transition from the MMCO (=Middle Miocene Climate Optimum 15 Ma; Gradstein et al. 2012) to the MMCT is characterized by an increase in the mean annual range of temperatures, primarily due to decreasing cold month temperatures (Bruch et al. 2010), and increased seasonality is principally expressed in the seasonality of precipitation (Doláková et al. 2014). In the study area, climatic instability was connected with the appearance of small carbonate bodies (Holcová et al. 2015) as a consequence of the Langhian aridification events, which were described from the Mediterranean area at 15.074 Ma and 14.489 Ma (Hüsing et al. 2010). Findings of pollen grains of herbs and heliophilous plants, such as Poaceae, Asteraceae, Caryophyllaceae, Chenopodiaceae, *Olea*, *Buxus* and *Ephedra,* also indicate the existence of more open and drier areas at that time in the studied area.

Regardless of these climatic fluctuations, the studied area was located in the subtropical zone during the latest Oligocene to Middle Miocene (Planderová 1990; Böhme et al. 2010).

In epicontinental seas, the impact of global climatic changes may be influenced by local palaeogeographic events triggered by local tectonic and volcanic processes. The following local processes may have influenced global climatic oscillations in the study area: during the middle part of the Oligocene, the Paratethys returned to open marine conditions. Tropical water incursion from the Indian Ocean, which was described around the Oligocene/Miocene boundary (Rögl 1999), could locally minimize the impacts of global cooling.

The culmination of the MMCO was characterized by a large marine transgression affecting the entire circum-Mediterranean area, including the Central Paratethys (Rögl 1999; Popov et al. 2004; Kováč et al. 2007; Piller et al. 2007). The transgression enabled the incursion of warm Indo-Pacific water into the Paratethys. Moreover, the Central Paratethyan Basin was at that time strongly influenced by the so-called "Styrian phase" of tectonic and volcanic activity (Rögl 1998).

The aim of this work is to analyse the specific imprint of global climatic events on the subtropical epicontinental sea, as characterized by local oscillations in sea-water chemistry and/or nutrient content. In littoral to upper bathyal environments, sensitivity of ecosystems to sea-level oscillations can be expected; however, local sea-level cycles can differ from global ones due to tectonic influence. It is also expected that tectonic and volcanic activity can change geomorphology, seafloor topography and seaways connecting the Central Paratethys with surrounding areas, which could influence regional atmospheric circulation, the origin and circulation of water masses, and eventually local mesoclimate.

To determine climatic events based on oxygen and carbon isotopic data in the study area is problematic due to the small water body of the Paratethys and its restrictions in circulation to the world ocean causing local oscillations in water chemistry. In the Middle Miocene of the Carpathian Foredeep, the stable isotope record reflects more salinity than temperature oscillations (Scheiner 2015). Furthermore, the foraminiferal tests from the Oligo-Miocene "Schlier" are recrystallized and unsuitable for isotopic analysis. Therefore, two pronounced cooling events (the Oligo-Miocene and Middle Miocene cooling) were identified from the palaeobotanical interpretation (mainly palynological data; e.g., Planderová 1990; Doláková et al. 2014). Foraminiferal and calcareous nannoplankton events were used to increase resolution of the record based on the terrestrial plants around these cooling events by providing further subdivision of the time interval of the cooling event. Statistically significant differences in the composition of foraminiferal and calcareous nannoplankton assemblages were defined and used for palaeoenvironmental interpretation. Finally, points at which palaeoenvironmental changes and global climatic events coincide, are paid further attention in the discussion.

Regional setting

The area of the Central Paratethys examined in this study includes the Pannonian Basin system and the Carpathian Foreland basins (Seneš 1961; Fig. 1).

The Late Oligocene/Early Miocene climatic oscillations have been studied in the northern region of the Buda Basin (local geomorphological unit called the "South Slovak Basin"), which is a part of the Pannonian basin system. The stratigraphy, lithostratigraphy and sedimentology of this area were summarized in Vass (1995), Vass et al. (1979, 1993) and Vass

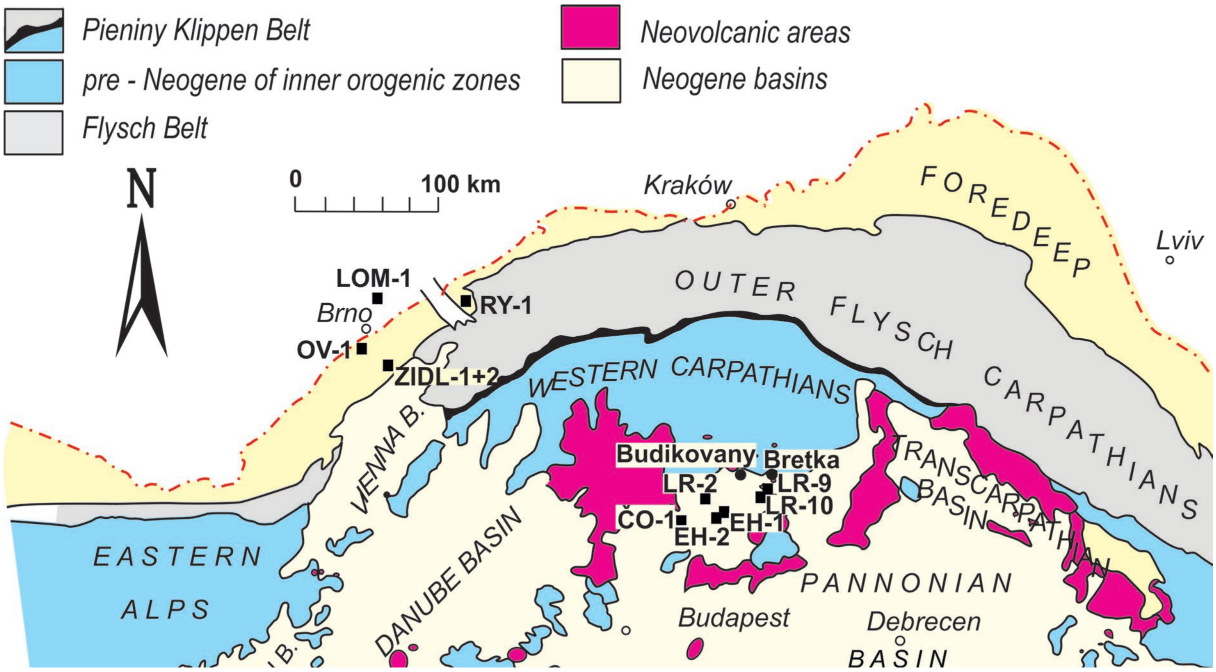

Fig. 1. Locations of studied sections.

& Elečko (1989). The succession starts with dark grey siltstones to claystones with evenly distributed $CaCO_3$ (14.2–18.3 %). They are overlain by monotonous calcareous siltstones to fine sandstones with mica and phytodetritus at dominant bedding surfaces ("Schlier") within the basin infill. Glauconite-rich intercalations and horizons with increased $CaCO_3$ were recorded in the transitional intervals between these lithotypes. In the marginal part of the basin, lagoonal evaporites (dolomite, anhydrite) were deposited (Vass et al. 1979). The overlying siltstones vary in silt and clay content, shell debris, intensity of bioturbation, and $CaCO_3$ content, which oscillates between 1.1 to 49.2 % (Vass et al. 1979, 1993; Vass & Elečko 1989). More variegated lithology was recorded in marginal facies, where organodetrital carbonate bodies are replaced by conglomerates and deltaic deposits (Vass et al. 1979, 1993; Vass & Elečko 1982, 1989; Šutovská-Holcová et al. 1993; Vass 1995).

The Middle Miocene samples have been collected from sections in the Carpathian Foredeep. The Early to Middle Miocene Carpathian Foredeep is a peripheral foreland basin that developed from the subsurface loading of the Alpine–Carpathian orogenic belt on the passive margin of the Bohemian Massif. The Carpathian Foredeep exhibits striking lateral variations in basin width, depth, and stratigraphy of deposits, along with variations in the pre-Neogene basement composition and tectonic subsidence. The basin continued to the south (the Alpine Foredeep/Alpine Molasse Zone) and to the NE (Polish part of the Carpathian Foredeep) (Oszczypko 1998; Nehyba & Šikula 2007; Nehyba et al. 2008). The pelitic sediments ("Tegel") with sandstone intercalations and biohermal bodies strongly dominate the basin volumetrically. These mudstones vary in silt and clay content, shell debris, intensity of bioturbation and sedimentary structure. The mudstones are interpreted as dominantly outer shelf deposits or hemipelagites (Papp et al. 1978; Nehyba et al. 2008).

Materials and methods

The studied material originates from six boreholes from the South Slovak Basin (Oligocene/Miocene interval): LR-9, LR-10 (Šutovská 1987), LR-2, EH-1, EH-2, ČO-1 (marginal deltaic facies; Šutovská-Holcová et al. 1993), two parastratotype sections (Budikovany and Bretka) of the local Egerian stage (Báldi & Seneš 1975), five boreholes from the Carpathian Foredeep (Middle Miocene): RY-1 (Kopecká 2012), ZIDL-1 and ZIDL-2 (Doláková et al. 2014), LOM-1 (Holcová et al. 2015), OV-1 (Nehyba et al. 2016) and one from the Danube Basin: ŠO-1 (Papp et al. 1978) (Fig. 1). Lithology, location and biostratigraphical correlation of the studied sections are given in Fig. 2. In total, 182 samples from the Lower Miocene and 246 samples from the Middle Miocene were analysed.

Foraminifera were studied in the 63 to 2000 μm fractions. Approximately 200 to 300 specimens of foraminifera from each sample were determined and their abundances were used for statistical analysis. The calcareous nannoplankton was studied in the same samples as the foraminifera. The abundance of nannoplankton was expressed semiquantitatively as the number of specimens in the visual field of the microscope (Zágoršek et al. 2007). Approximately 200 to 500 specimens of calcareous nannoplankton were determined from individual samples and used for further statistical analysis.

Foraminiferal, as well as calcareous nannoplankton assemblages were statistically analysed using the software PAST developed for palaeontologists (Hammer et al. 2001). For grouping samples non-metric multidimensional scaling (n-MMDS) was used; Kruskal-Wallis tests were applied for testing differences between biostratigraphically distinguished intervals, and relations among individual taxa were quantified by Spearman's correlation coefficient.

Results

Calcareous nannoplankton and planktonic foraminiferal biostratigraphical events

Biostratigraphical events around the Oligocene/Miocene boundary

The succession of bioevents from the broader Oligocene/Miocene boundary interval in the study area was synthesized by Holcová (2001, 2005), Ozdínová & Soták (2014) and Grunert et al. (2015).

(1) The interval between the last occurrence (LO) of *Globorotalia opima* (dated at 26.9 Ma in the global ocean; Gradstein et al. 2012) and the first occurrence (FO) of *Globigerinoides primordius* (dated at 26.1 Ma in the global ocean; Gradstein et al. 2012) can be correlated in the study area with lithological change from dark-grey claystones to light grey siltstone to sandstone ("Schlier").

In contrast to the biostratigraphic events, the change in lithology is very distinct and can be used as a correlation horizon if the position of the FO *Globigerinoides primordius* is unclear. Though dates of biostratigraphical events in the Central Paratethys may not exactly coincide with the record of the global ocean, this interval likely corresponds to the period of global warming between 26.5 and 25.2 Ma (Pekar et al. 2005; Villa & Persico 2006). This warming event from the same level was also described by Ozdínová & Soták (2014) in the studied area.

(2) The last common occurrence (LCO) of *Reticulofenestra bisecta*. The LO of this species is often used to approximate the Oligocene/Miocene boundary (Berggren et al. 1995; Young 1998; Ozdínova & Soták 2014). However, rare reworked specimens of *R. bisecta* occur commonly in the Lower Miocene of the Pannonian Basin (NN2 to NN4 Zones; Holcová 2005). Therefore, only the last continuous occurrence of *R. bisecta* was used as a biostratigraphical marker. The event is dated to 23.1 Ma in the global ocean agreeing with the global Mi-1 cooling event (23.2 Ma; Gradstein et al. 2012). Though the age of the LCO of *R. bisecta* in the Central Paratethys may differ

from the world ocean, the cooling around this event has been established by Planderová (1990) in the South Slovak Basin.

(3) The FO of *Helicosphaera scissura* and the FO of *Discoaster druggii* are isochronous events in the Central Paratethys (Holcová 2005). *Helicosphaera scissura* is, however, more abundant and its FO is more easily determined.

(4) The FO of *Helicosphaera ampliaperta* is a well defined event in the Central Paratethys (Holcová 2002, 2005). In the

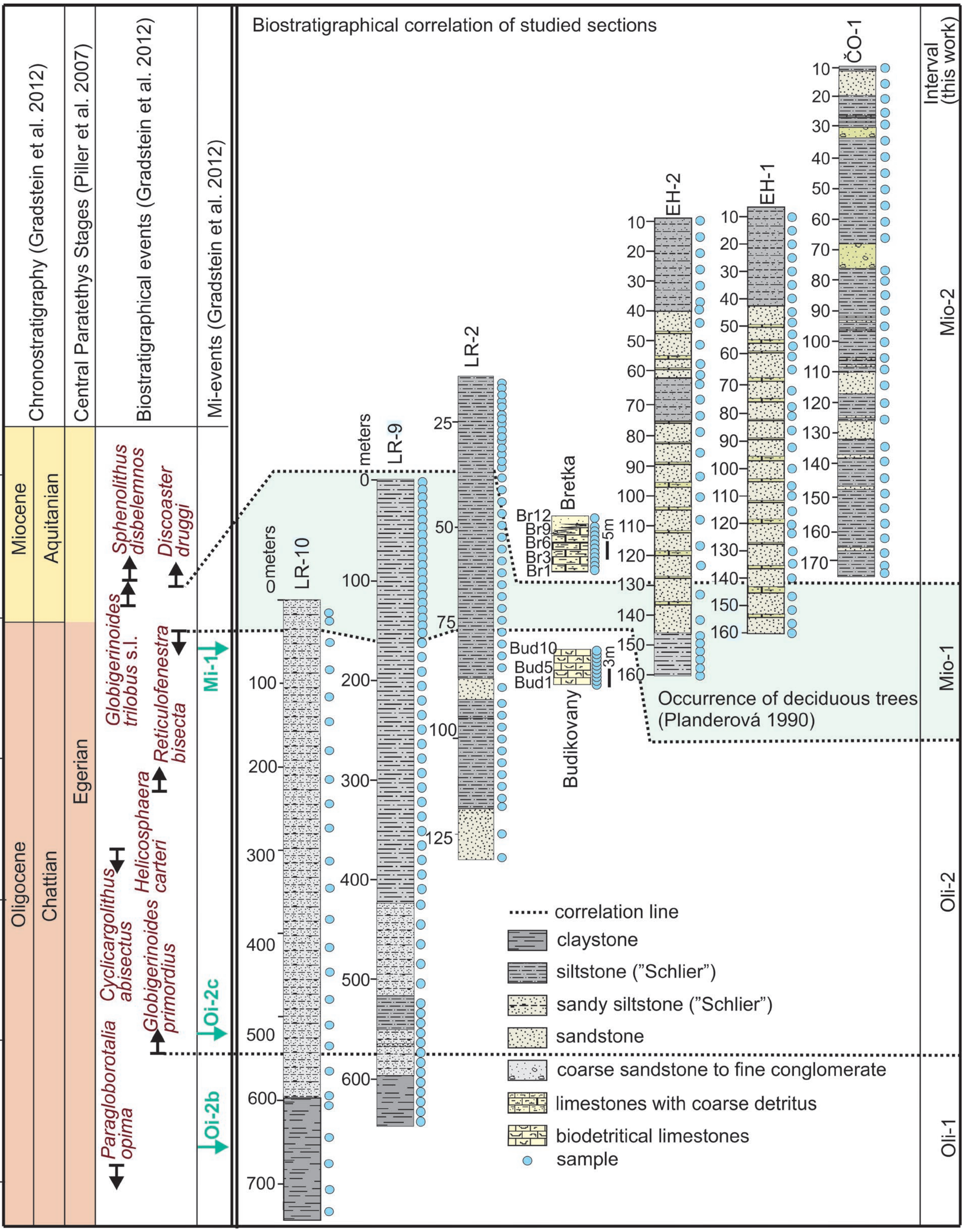

Fig. 2a. Biostratigraphic correlations, lithology and sampled intervals of studied sections — Oligocene–Miocene boundary interval.

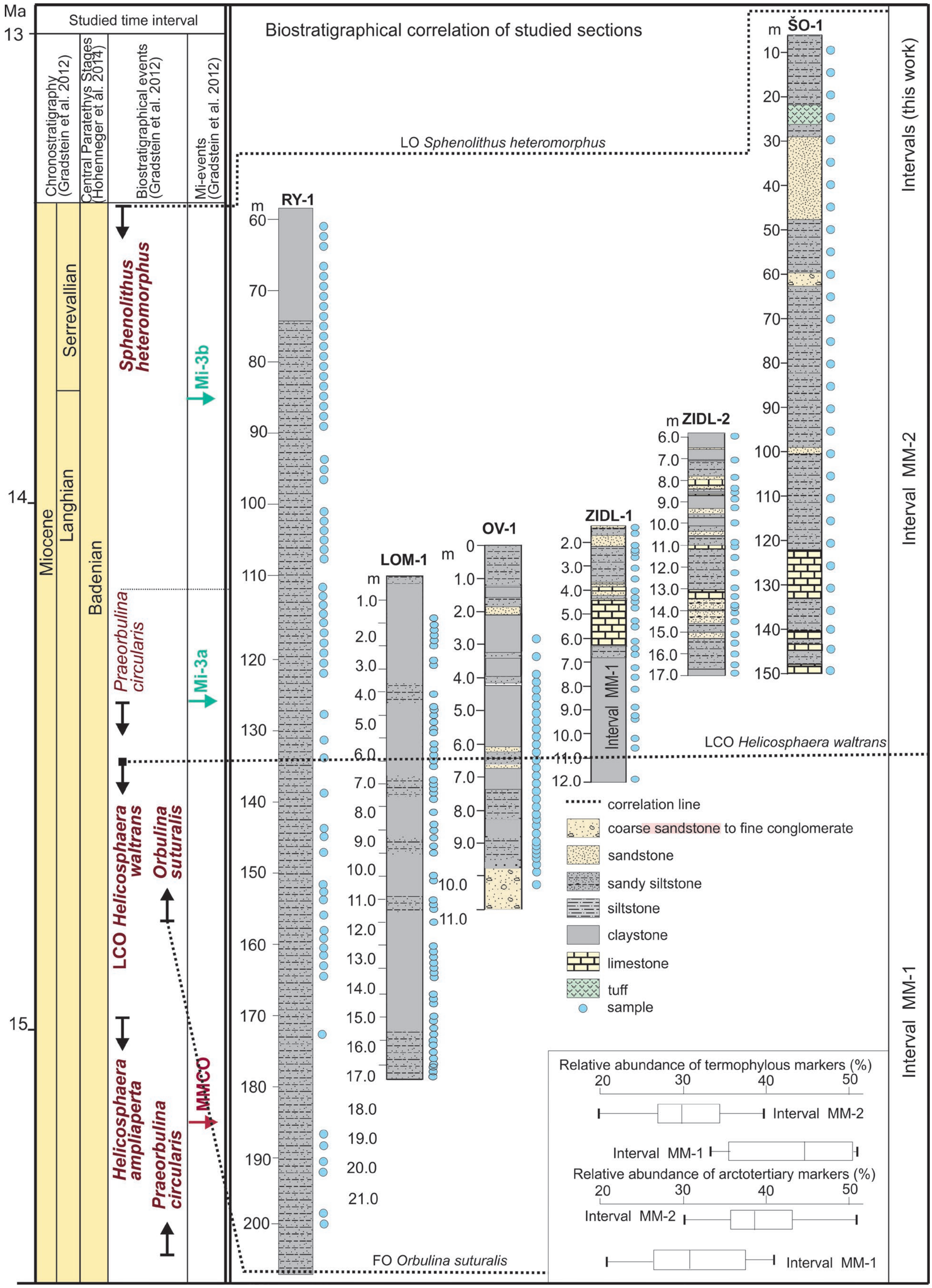

Fig. 2b. Biostratigraphic correlations, lithology and sampled intervals of studied sections — Middle Miocene.

Mediterranean region, the event was dated to approximately 20 Ma (Fornaciari & Rio 1996).

Events (3) and (4) approximately correlate with the disappearance of deciduous forests in the study area (Planderová 1990) which can be interpreted as warming. Elsewhere in the Central Paratethys area (the North Alpine Foreland Basin), a carbon isotope excursion indicating the cooling event was recorded between the FO of *Helicosphara carteri* and the FO of H. *scissura* (Grunert et al. 2015), supporting the use of the FO of *H. scissura* as a marker of the beginning of warming.

Based on these events, the studied sections were subdivided into the following intervals (Fig. 2a):

The Oligocene interval Oli-1 ranges from the base of the studied sections to the FO of *Globigerinoides primordius* whereas lithology changes from dark claystones to light siltstones marking the beginning of the interval Oli-2 that ends with the LCO of *Reticulofenestra bisecta.* The top of the Miocene interval Mio-1 is defined by the FO of *Helicosphaera scissura* and/or the FO of *Discoaster druggii* and is overlain by interval Mio-2 ending with the FO of *Helicosphara ampliaperta.* Intervals Oli-2 and Mio-1 are lithologically uniform. Around the Mio-1/Mio-2 boundary, the marginal limestone bodies ware replaced by marginal coarse clastics.

The early Middle Miocene biostratigraphical events

The dates of the Middle Miocene bioevents in the world ocean (Gradstein et al. 2012) differ from the astronomically calibrated dates from the Mediterranean area (Abdul Azis et al. 2008). Due to the communication of the Central Paratethyan Sea with the Mediterranean (Rögl 1998), correlation with the Mediterranean dates is more suitable.

(1) The FO of *Orbulina suturalis* is dated in the Mediterranean area to 14.5–14.6 Ma; (Iaccarino et al. 2011) and in the Central Paratethys to 15.03–14.2 Ma (Hohenegger et al. 2009a; Selmeczi et al. 2012; de Leeuw et al. 2013). Although some dating may not be fully accurate, all these ages correspond to a period slightly after the culmination of the MMCO.

(2) The use of the LCO of *Helicosphaera waltrans* was prioritized over using of its LO due to the common occurrence of reworked individuals. Dating of the event to 14.38 Ma can be approximated from the base of the Soos drill in which *H. waltrans* was not recorded (Hohenegger et al. 2009b). On the other hand, *H. waltrans* was recorded in a horizon radiometrically dated to 14.39 Ma (the Styrian Basin; Hohenegger et al. 2009a), which indicates that the event had to occur at approximately 14.38 Ma which agrees with the dating of this event in the Mediterranean (14.357 Ma; Abdul-Azis et al. 2008). The upper boundaries of all studied sections are erosive. However, *Sphenolithus heteromorphus* occurs in all samples, which indicates an age younger than 13.5 Ma for the upper boundary of the studied interval.

In the Middle Miocene, two intervals were studied (Fig. 2b): the MM-1 interval is defined by the FO of *Orbulina* (base) and LCO of *Helicosphaera waltrans* (top) and the MM-2 interval ended with the erosive boundary with *Sphenolithus heteromorphus* occurrence.

Distribution of foraminiferal and calcareous nannoplankton taxa in biostratigaphically defined intervals

The Late Oligocene/Early Miocene results of the n-MMDS showed differences between Oligocene and Miocene calcareous nannoplankton assemblages (Fig. 3a) which statistically significantly differ in the values of the first coordinate (Fig. 3b). The "core" samples from the Mio-2 interval indicate high similarity among the majority of assemblages from this interval (Fig. 3a).

Benthic foraminiferal assemblages from the Miocene are highly variable in comparison with Oligocene ones (Fig. 3c). The values of the first coordinate differentiate assemblages from the Mio-2 interval from older ones (Fig. 3d).

The box plots supported by Kruskal-Wallis tests (Fig. 3e) show that assemblages from the Oli-1 interval differ in having higher abundances of *Uvigerina* spp., the *Gyroidina–Gyroidoinoides*-group, and miliolids. In both Oligocene intervals, the highest relative abundances of *Helicosphaera euphratis* and *Cyclicargolithus floridanus* were recorded. The Oli-2 interval is characterized by abundant *Coccolithus pelagicus, Pullenia,* and *Melonis*, monoserial lagenids, and tubular agglutinated foraminifera. The Mio-1 interval differs from other intervals by an increase in *Bolivina* spp. without sculpture; markedly increased *Reticulofenestra minuta*, and the *Cassidulina–Globocassidulina* group also remained high in the Mio-2 interval. In this interval, the variability of cibicidoid abundances also increased, relative abundances of *Cyclicargolithus floridanus* decreased and large *Helicosphaera euphratis* nearly disappeared. The Mio-2 interval is characterized by increases in the abundances of large endemic *Reticulofenestra excavata*, *Discoaster* spp., *Helicosphaera scissura*, and the benthic foraminiferal genera *Ammonia*, *Elphidium,* and *Porosonion*. The Oli-1 and Mio-1 intervals are associated with increased abundances of *Lenticulina* spp., while abundances of *Nonion commune* and *Pontosphaera multipora* increased in the Mio-2 and Oli-2 intervals.

Relations between taxa characteristic for the Oligo-Miocene intervals were enumerated using statistically significant correlations among relative abundances of taxa (Fig. 4):

(1) *Hoeglundina, Uvigerina* and *Gyroidina* co-occur with *Reticulofenestra bisecta* and characterize the Oli-1 interval. *Lenticulina* spp. also correlates with this group, but the genus occurs in the Oli-1 and Mio-1 intervals.

(2) Miliolids, abundant in the Oli-1 interval, positively correlate with *Braarudosphaera bigelowi*.

(3) *Melonis, Pullenia,* monoserial lagenids, and tubular agglutinated foraminifera co-occur with *Coccolithus pelagicus, Helicosphaera euphratis* and *Pontosphaera multipora*; this group of taxa dominated in the Oli-2 interval. Relative abundances of *Nonion commune* also correlate with this group, though the species is abundant also in the Mio-2 interval.

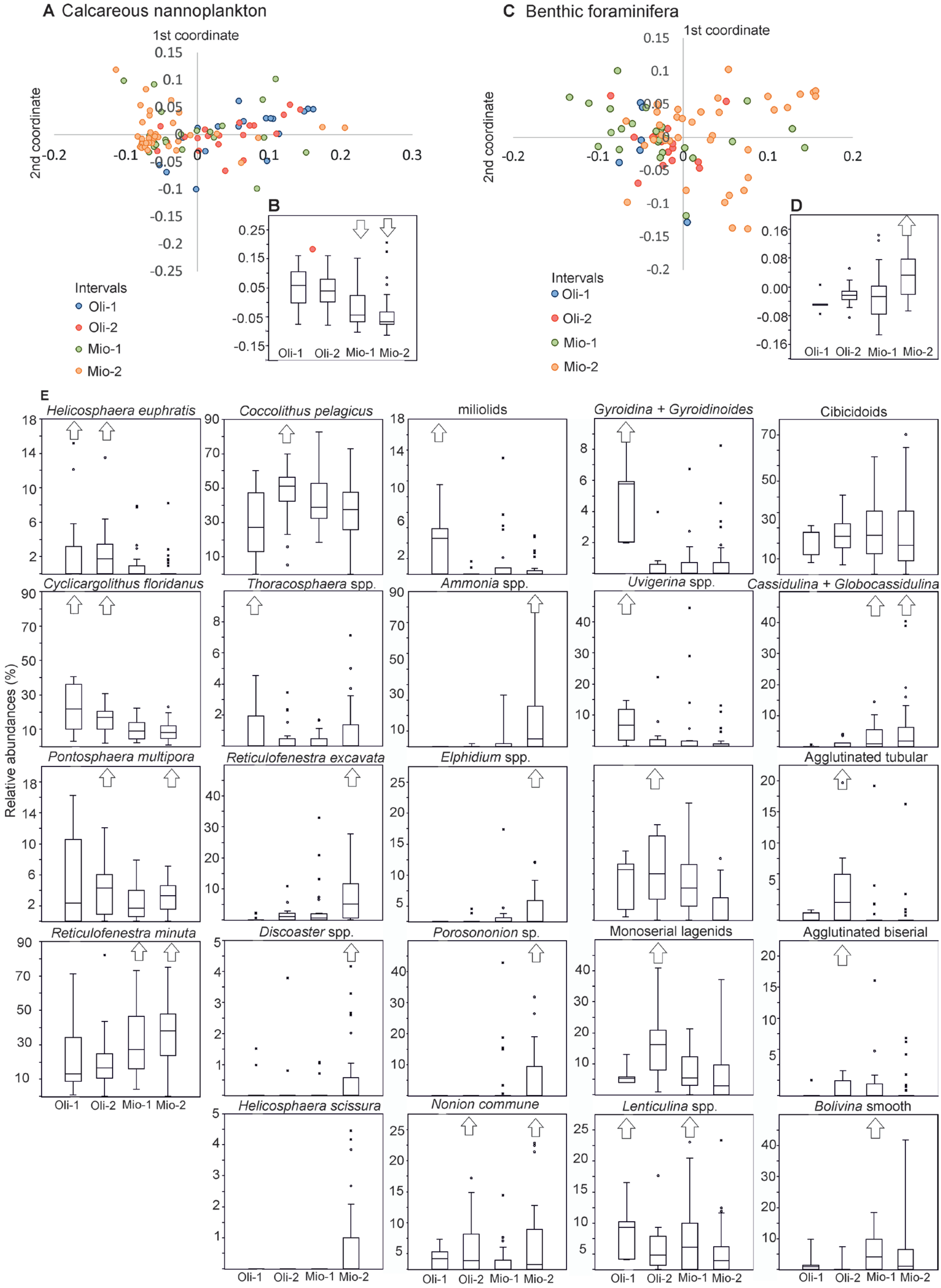

Fig. 3. Differences between late Oligocene to early Miocene benthic foraminiferal and calcareous nannoplankton assemblages from biostratigrafically defined Oli-1, Oli-2, Mio-1 and Mio-2 intervals: **a** — classification of calcareous nannoplankton assemblages using non-Metric Multidimensional Scaling (n-MMDS), **b** — statistically significant differences of values of the first coordinate from plot a; **c** — classification of benthic foraminifera assemblages using n-MMDS, **d** — statistically significant differences of values of the first coordinate from plot c; **e** — statistically significant differences in relative abundances of benthic foraminiferal and calcareous nannoplankton taxa from Oli-1, Oli-2, Mio-1 and Mio-2 intervals.

(4) *Bolivina* spp., characteristic of the Mio-1 interval, correlate with taxa abundant in both Miocene intervals: *Cassidulina*, *Reticulofenestra minuta* and *R. haqii*. *Bolivina* spp. are also contemporary with *Lenticulina* spp., which dominates in the Oli-1 and Mio-1 intervals.

(5) The group of genera *Elphidium, Ammonia, Porosononion* and *Thoracosphaera* spp. characterizes the Mio-2 interval. Moreover, *Cassidulina* co-occurs with these genera but is common in both Miocene intervals.

In the Oligocene-Early Miocene interval planktonic foraminifera are rare (up to 20 %) and poorly preserved; assemblages can therefore be characterized only qualitatively. *Globigerinoides primordius* appeared at the beginning of the Oli-2 interval, dominated by 4-chambered *Globigerina* spp. The Mio-1 interval is characterized by small 5-chambered globigerinids. In the Mio-2 interval, four-chambered globigerinids reappeared and the FO of *Globigerinoides trilobus* is observed.

The Middle Miocene climatic events

The n-MMDS showed a larger variability of benthic, as well as planktonic foraminiferal and calcareous nannoplankton assemblages during the MM-2 interval in comparison with the MM-1 interval (Fig. 5a–c). The MM-2 interval is characterized by a bimodal distribution of assemblages whereas assemblages from the MM-1 interval are less dispersed. The most pronounced similarity is found for planktonic foraminifera from the MM-1 interval, which are concentrated into a compact “core” group in the plot of the n-MMDS coordinates (Fig. 5b).

Box plots supported by Kruskal-Wallis tests (Fig. 5d) showed higher relative abundances of monoserial lagenids, *Melonis, Pullenia, Nonion commune, Bulimina* spp., 4-chambered *Globigerina bulloides*-*G. praebulloides* group, *Globigerinella regularis*, and large *Helicosphaera* spp. (>7 µm) in assemblages from the MM-1 interval. *Asterigerinata planorbis, Elphidium* spp., *Cibicidoides* spp., *Cassidulina, Globocassidulina*, miliolids, large foraminifera (mainly *Amphistegina* spp.), *Ammonia* spp., biserial agglutinated, *Paragloborotalia mayeri,* 5-chambered *Globigerina ottnangiensis* and *Turborotalita quinqueloba, Reticulofenestra haqii, Umbilicosphaera jafari*, and reworked Palaeogene taxa reached higher abundances in the MM-2 interval, while relative abundances of *Reticulofenestra minuta* were more varied (Fig. 5d).

The Spearman coefficient enables us to express the following relations among relative abundances of foraminifera and calcareous nannoplankton taxa (Fig. 6):

(1) Strong positive correlations among *Asterigerinata planorbis, Elphidium* spp., large foraminifera, *Cassidulina* spp., *Cibicidoides* spp., *Ammonia* sp., and miliolids from the MM-2 interval. *Reticulofenestra minuta*, 5-chambered *Turborotalita quinqueloba* and *Globigerina ottnangiensis*, plexus of very small *Globigerina* spp. (<100 µm), *Globorotalia mayeri*, and *Bolivina spp.* can also be added to this group.

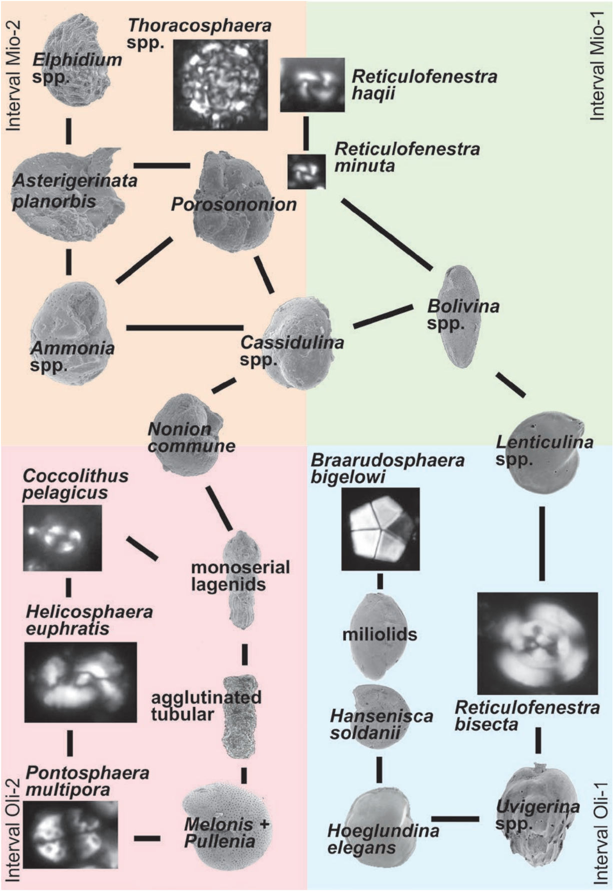

Fig. 4. Statistically significant ($p<0.05$) correlations among relative abundances of benthic foraminiferal and calcareous nannoplankton taxa, enumerated by Spearman correlation coefficient, from the late Oligocene to early Miocene. Groups of taxa with high correlation coefficients and their affinities to Oli-1, Oli-2, Mio-1 and Mio-2 intervals are indicated.

(2) The MM-1 interval is characterized by a group composed of *Nonion commune*, 4-chambered *Globigerina praebulloides–G. bulloides* group, *Globigerinella regularis*, and large *Helicosphaera* spp. (mainly *H. waltrans* and *H. carteri*).

(3) A group of taxa positively correlated with *Globigerinoides* spp. and *Orbulina suturalis–Praeorbulina circularis* was recorded in both intervals, and co-occurs with: (i) *Globorotalia bykovaye, Uvigerina* spp. and *Lenticulina* spp. in both intervals; (ii) monoserial lagenids, *Melonis, Pullenia,* and *Coccolithus pelagicus* in the MM-1 interval; and (iii) agglutinated foraminifera (biserial), *Hansenisca, Umbilicosphaera jafari* and *Reticulofenestra haqii* in the MM-2 interval.

Calcareous nannoplankton events in relation to climatic oscillations

The most prominent changes during the Mio-1 interval (Fig. 7) included a decrease in *Cyclicargolithus floridanus* and an increase of *Reticulofenestra minuta*. Extinctions of the largest reticulofenestrids (*Cyclicargolithus abisectus* and *Reticulofenestra bisecta*) can be correlated with the beginning of the Mio-1 interval, although the exact extinction level is hard to determine due to reworking. During the subsequent Mio-2 interval, the extinct large reticulofenestrids are substituted by large endemic *Reticulofenestra excavata,* and the abundance of *R. minuta* declined (Fig. 7b). The percentage of large *Helicosphaera euphratis* also decreased during the Mio-1 interval, whereas that of the new taxon *H. carteri* increased. In the following Mio-2 interval, new large helicosphaeras appeared: first *H. scissura*, then *H. ampliaperta* (Fig. 7b).

Changes in calcareous nannoplankton assemblages during the Middle Miocene are less prominent than in the Oligocene/Miocene interval. Similarly to the Mio-1 interval, abundances of large reticulofenestrids (*R. excavata, C. floridanus*) decreased during the MM-2 interval (Fig. 8a, b). Additionally, abundance of large helicosphaeras, characteristic for the MM-1 interval (alternating horizons with *H. waltrans* and *H. carteri*), gradually subsided and abundance of small *H. walbersdorfensis* increased in the MM-2 interval (Fig. 8c, d).

Interpretation and discussion

Transition between the Oli-1 and Oli-2 intervals (ca 26.5Ma; Fig. 9a)

As was discussed above, the Oli-1/Oli-2 boundary interval may be correlated with the global late Oligocene warming recognized by an increase in temperate-water taxa starting at 26.5 Ma (Vila & Persico 2006) or the appearance of a warm deep-water mass between 26.5 and 25.2 Ma (Pekar et al. 2005). Then the Oli-1 interval represents the end of the Oligocene cooling.

In the study area, nanno- and microfossils together with the dark claystones of the Oli-1 interval enable the interpretation of high nutrients and an O_2-depleted environment at the sea floor during the cold interval. The genera *Uvigerina* and *Gyroidina*, characteristic of this lithotype, typify regions of high organic productivity and a sustained flux of organic matter to the sea floor as the most important factor controlling their distribution (Caralp 1989; Hermelin 1992; Sjoerdsma & van der Zwaan 1992; Miao & Thunell 1993; Sen Gupta & Machain-Castillo 1993; Rathburn & Corliss 1994). Moreover, *Uvigerina* is a traditional indicator of oxygen-depleted water (Kaiho 1994; Murray 2006). *Gyroidina* is interpreted as an epifaunal detritivore occurring at the sediment-water interface (Murray 2006). Oxygen and carbon stable isotopic values (Scheiner 2015) showed a similarity between the life habitats of *Gyroidina* and that of *Melonis*, both preferring high organic productivity areas (Thomas et al. 1995). Large *Lenticulina* spp., another abundant benthic genus, are considered to be a high-oxygen-consuming epifaunal element (Kaiho 1994; van der Zwaan et al. 1999). However, the oxygen requirements of *Lenticulina* are classified inconsistently: after the morphotype analysis of Rosoff & Corliss (1992) and Kouwenhoven & Van der Zwaan (2006) *Lenticulina* species were considered oxyphilic, while Kaiho (1994) classified *Lenticulina* spp. as suboxic indicators. This discrepancy agrees with its opportunistic character, as interpreted since the Jurassic (Peryt & Lamolda 1996; Reolid & Martínez-Ruiz 2012), and *Lenticulina* may live in oxic, as well as dysoxic, environments. However, horizons with large *Lenticulina* wedged between sediments dominated by *Uvigerina* and *Gyroidina* may indicate perhaps an increase in oxygen content followed by its decrease. In any case, the oxygen content at the sea floor varied, though a hypoxic palaeoenvironment rich in nutrients prevailed with occasional episodes of oxygen increase.

In the surface water, *Cyclicargolithus floridanus* dominant during the Oli-1 interval (together with *Cyclicargolithus abisectus*), was previously considered to be an indication of temperate water (Wei & Wise 1990). However, its temperature affinity was questioned by Persico & Villa (2004). The species was more likely eurytopic, thriving under a large spectrum of environments (Shcherbinina 2010). It also confirms the observations of Sachsenhofer et al. (2010), who recorded blooms of *Cyclicargolithus floridanus* in both the organic-rich zone and the overlying organic-poor formation. The characteristic calcareous nannoplankton genus *Thoracosphaera* is a general proxy for oligotrophy or stratification (Höll et al. 1998; Vink 2004). Isotopic ratios for the common planktonic foraminifera group paragloborotaliids indicate that Oligocene representatives calcified in the upper-thermocline depth (Poore & Matthews 1984; Wade et al. 2009). All these data confirm stratification of the water column with oscillation of palaeoenvironmental parameters in the surface layer. A clear indicator of the quantity of nutrients in the upper part of the water column is absent.

Marginal facies are characterized by miliolids, mainly *Quinqueloculina* spp., representing epifaunal genera often living on plants and tolerating salinity increases (Murray 2006). Miliolids are accompanied by *Braarudosphaera bigelowi,* which also indicates fluctuating salinity conditions (Bartol et al. 2008). It agrees well with the occurrence of evaporites (Vass et al. 1979), all of which confirm salinity increase in the marginal part of the basin, probably as a consequence of low rainfall. Aridity is also expected from the high abundance of microfossils in the sediment, caused rather by low terrigenous input than by high primary productivity.

The lithological change from dark grey claystones to light grey siltstones with glauconite-rich and carbonate intercalations at the base (Vass et al. 1993) can be correlated with a change in the abundance and preservation of foraminiferal tests at the Oli-1/Oli-2 interval boundary. Abundant, large, well-preserved tests with pyrite infilling were substituted by less abundant, smaller foraminifera (Holcová 2001). The absence of pyrite infilling reflects an increase of oxygen content in the sediment caused by a regional palaeogeographic change from an isolated to an open marine basin (Báldi 1986; Rögl 1998; Popov et al. 2004). Glauconite and carbonate accumulation at the base of siltstones already indicates oxygenated to mildly reducing marine environments and continuing very low sedimentation rates (McRae 1972; Odin & Matter

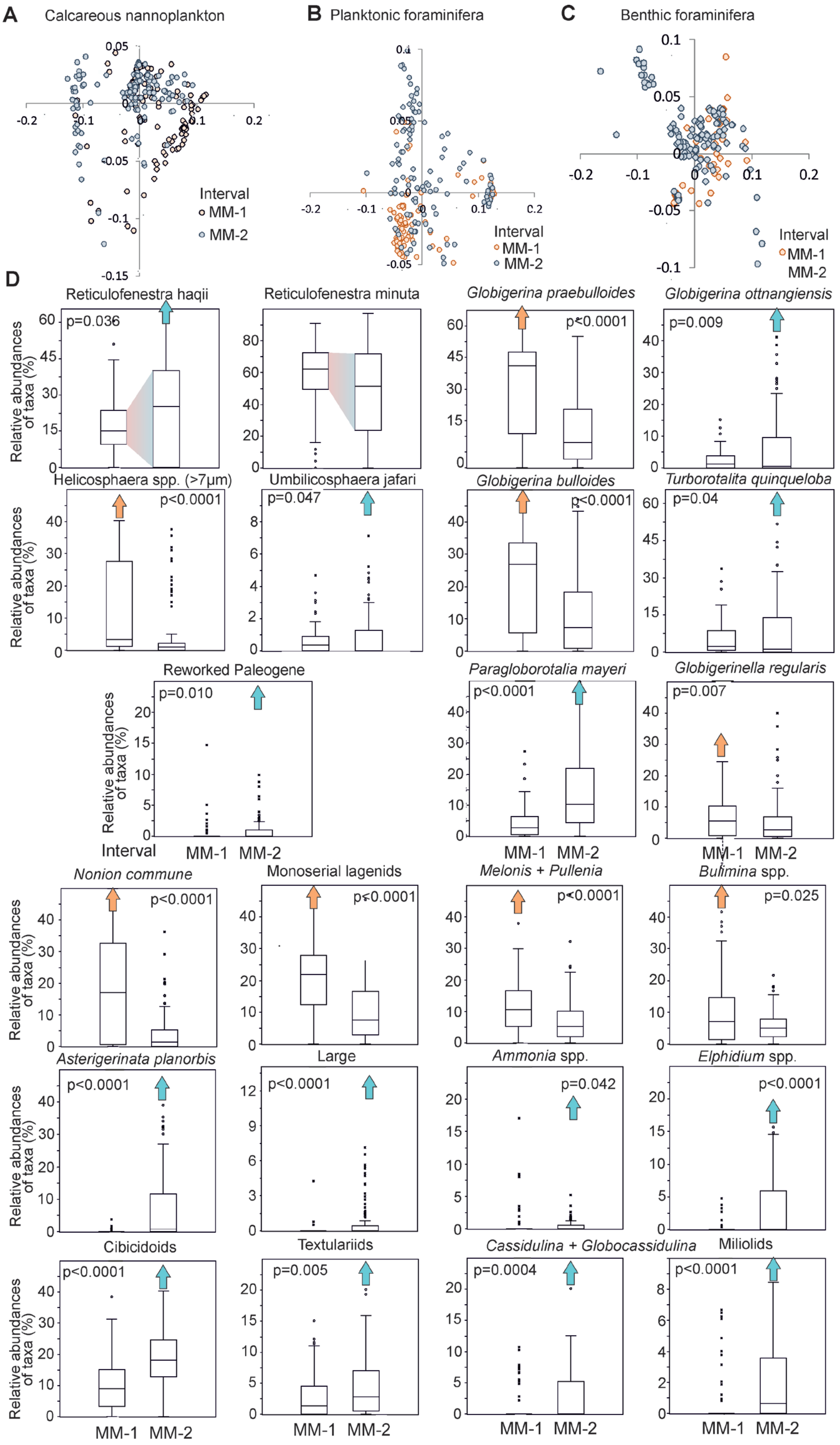

Fig. 5. Differences between the Middle Miocene foraminiferal and calcareous nannoplankton assemblages from biostratigraphicaly defined MM-1 and MM-2 intervals; **a–c**: classification of assemblages using non-metric multidimensional scaling (n-MMDS): **a** — calcareous nannoplankton, **b** — planktonic foraminifera; **c** — benthic foraminifera; **d** — statistically significant differences in relative abundances of foraminiferal and calcareous nannoplankton taxa from MM-1 and MM-2 intervals.

1981; Amorosi 1997). The subsequent decrease in foraminiferal abundance might reflect increased sediment input caused by climatic change from an arid to a humid climate.

Oli-2 interval (26.5 to 23.1 Ma; Fig. 9b)

Based on local palynological data, the Oli-2 interval represents a warm subtropical condition without arctotertiary elements (Planderová 1990). Though timing of biostratigraphic events marking the boundaries of this interval in the world ocean and the Central Paratethys can differ, correlation with the global late Oligocene warming is generally expected (26.5 to 23.1 Ma; Pekar et al. 2005; Gradstein et al. 2012).

Helicosphaera spp., with a peak at the base of the interval, has an affinity to warm mesotrophic to oligotrophic water and high light intensities (Knappertsbusch 1993; Ziveri et al. 1995, 2004; Haidar & Thierstein 2001). The horizon may indicate a palaeogeographic event — an influx of warm, oceanic water after the reopening of communication between the Paratethys and the Indo-Pacific realm (Rögl 1998) connected with the oxygenation of the bottom water. Rögl (1998, 1999) dated this incursion to the Oligocene/Miocene boundary; our data show a slightly older age for this event (upper Oligocene, NP25 Zone). Later, the abundance of the high-nutrient marker *Coccolithus pelagicus* (Okada & McInyre 1979; Winter et al. 1994; Cachao & Moita 2000) increased. This may correspond to an increase in terrigenous nutrients as a result of increased precipitation.

The quality of the surface water is also indicated by the planktonic foraminifera. The Upper Oligocene *Globigerina bulloides*-like tests, dominating the studied samples, have $\delta^{18}O$ values among the lightest of the assemblage, indicating a shallow mixed layer habitat for these foraminifera as well. However, the $\delta^{13}C$ signal suggests a symbiotic association with dinoflagellates (Poore & Matthews 1984); therefore the Upper Oligocene *Globigerina bulloides* group may not necessarily indicate strongly eutrophic areas as the modern planktonic foraminifera *Globigerina* ex gr. *bulloides* (Schiebel et al. 1997).The isotopic ratios of the new species *Globigerinoides primordius* are very similar to those of *Globigerina* cf. *bulloides* in the same size fraction, pointing to a similar mixed-layer and symbiotic life habit (Poore & Matthews 1984; Wade et al. 2009). Therefore, the coexistence of these species in the upper Oligocene cannot indicate seasonal alternation of mixed and stratified water, as in Recent assemblages, and only mixed water can be inferred. The appearance of new globigerinid forms with secondary apertures on the spiral side is considered to be a response to the Late Oligocene warming (Jenkins 1973).

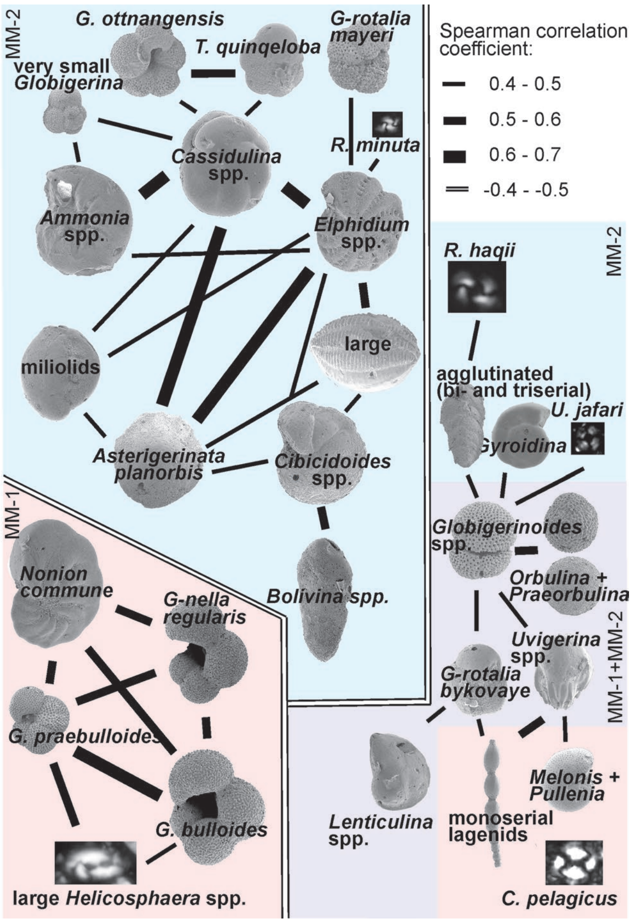

Fig. 6. Statistically significant (p<0.05) correlations among relative abundances of foraminiferal and calcareous nannoplankton taxa, enumerated by Spearman correlation coefficient, from the Middle Miocene. Groups of taxa with high correlation coefficients and their affinities to MM-1 and MM-2 intervals are indicated.

Melonis, Pullenia, and *Nonion commune*, characterizing sea-floor conditions during the Oli-2 interval, indicate a high supply of organic material to the sea floor (Caralp 1989; Hermelin 1992; Sjoerdsma & van der Zwaan 1992; Miao & Thunell 1993; Sen Gupta & Machain-Castillo 1993; Rathburn & Corliss 1994). Their classification as oxic vs. suboxic taxa varies (Kaiho 1994, 1999; Schönfeld 2001; Kouwenhoven & Van der Zwaan 2006), which might reveal that these genera can live under oxic conditions as well as tolerating dysoxic and suboxic pore-water. The co-occurrence of high-nutrient markers, planktonic *Coccolithus pelagicus* and benthic *Melonis, Pullenia,* and *Nonion commune*, might indicate an upwelling regime, but the absence of other upwelling indicators, as well as the symbiotic life habitat of the Upper Oligocene *Globigerina bulloides* group, strongly challenges this hypothesis; the mixing of water may have been caused, instead, by riverine input.

Horizons with agglutinated foraminifera gradually expanded in the upper part of the interval. In general, agglutinated foraminifera may reflect an oligotrophic character in the benthic ecosystem (Jorissen et al. 1998). This finding challenges the observations of Kaminski et al. (1988), Jones (1999), Kender et al. (2005), Jones (2006) and Kender et al. (2008) who recorded exceptionally high abundances of agglutinated foraminifers in delta fan environments with high sedimentation rates and strong terrestrial input. The recorded rounded planispiral (*Haplophragmoides, Cyclammina*) and tubular unilocular (*Bathysiphon*) morphotypes are considered epifaunal

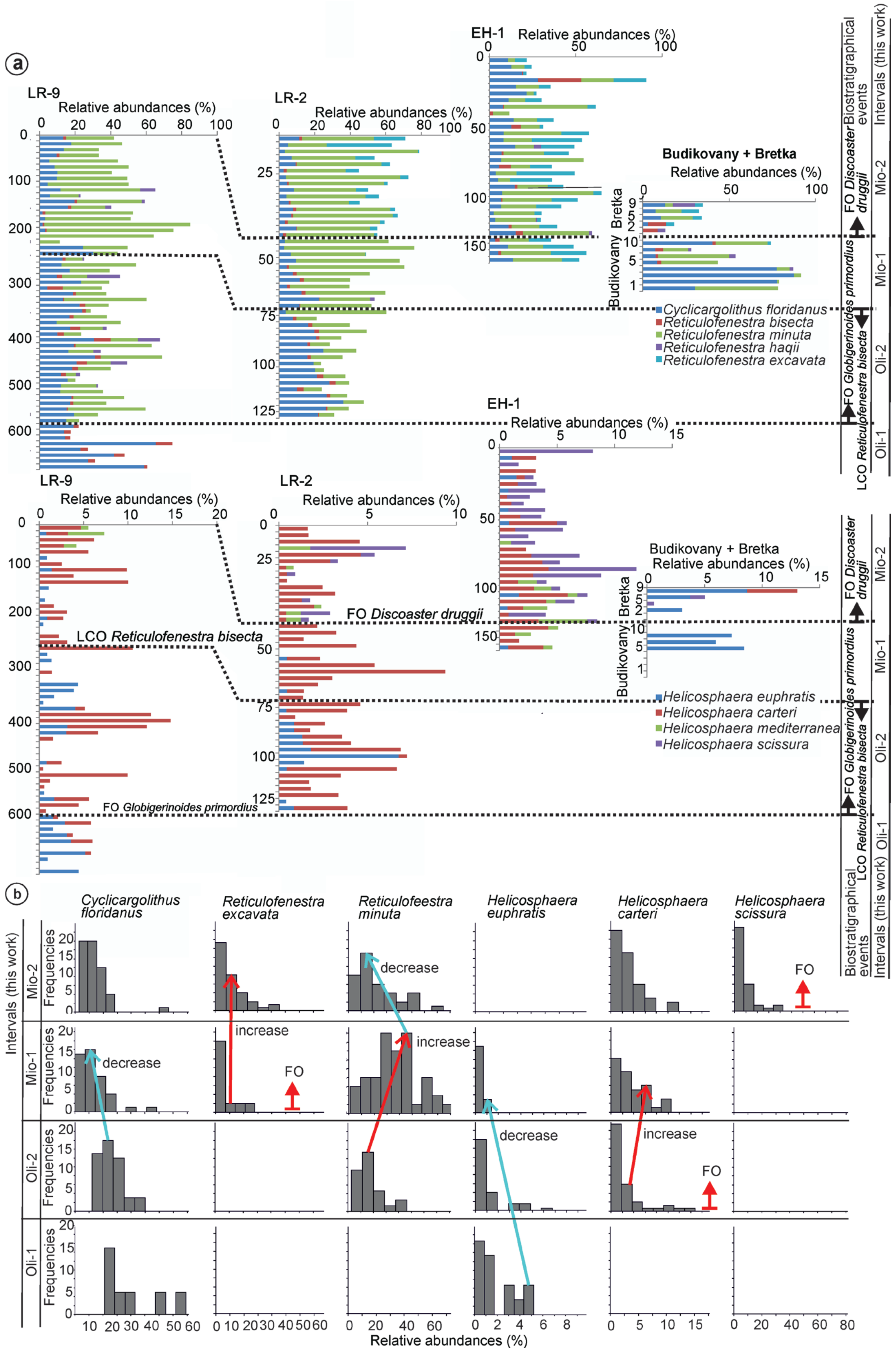

Fig. 7. Variability of calcareous nannoplankton assemblages in Oli-1, Oli-2, Mio-1 and Mio-2 intervals. **a** — Variability in relative abundances of reticulofenestrids and helicosphaeras in LR-9, LR-2, EH-1 boreholes and Budikovany and Bretka sections; **b** — Histograms summarizing abundances of reticulofenestrids and helicosphaeras in Oli-1, Oli-2, Mio-1 and Mio-2 intervals.

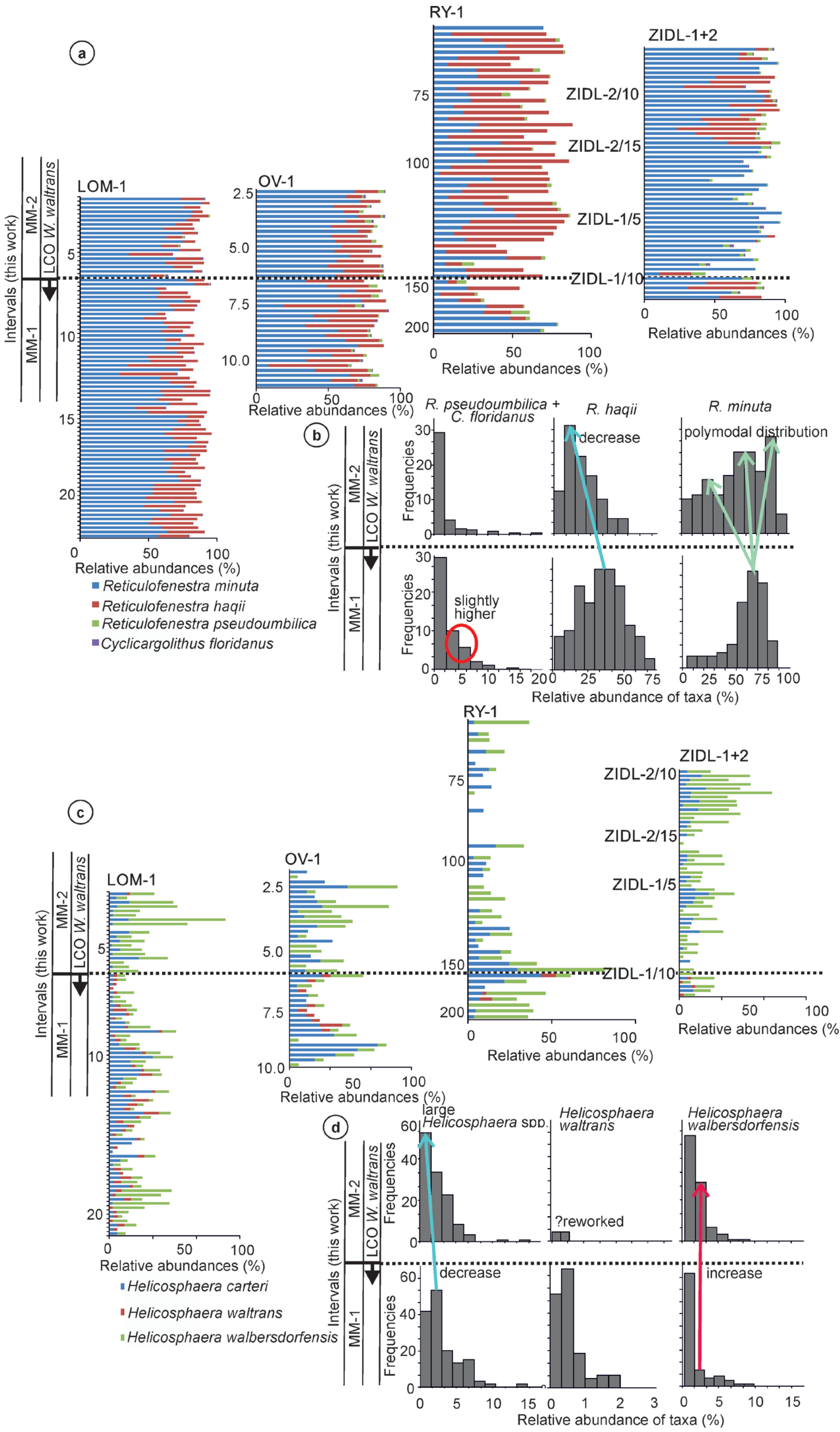

Fig. 8. Variability of calcareous nannoplankton assemblages in MM-1 and MM-2 intervals. **a** — Variability in relative abundances of reticulofenestrids in LOM-1, OV-1, RY-1 and ZIDL-1, 2 boreholes; **b** — Histograms summarizing abundances of reticulofenestrids in MM-1 and MM-2 intervals; **c** — Variability in relative abundances of helicosphaeras in LOM-1, OV-1, RY-1 and ZIDL-1, 2 boreholes; **d** — Histograms summarizing abundances of helicosphaeras in MM-1 and MM-2 intervals.

to shallow infaunal active deposit and suspension feeders (Tyszka 1994; Van den Akker et al. 2000; Kaminski et al. 2005; Reolid et al. 2008; Nagy et al. 2009). The frequent abundance of *Bathysiphon filiformis* indicates a high nutrient flux of shelf-derived organic matter to the seafloor (Gooday 1993, 1996; Kaminski et al. 2005; Murray 2006; Kender et al. 2008). For Early Miocene *Bathysiphon*-rich deposits, the TOC/S ratios suggest oxygen-depleted conditions with degraded organic material (Grunert et al. 2013). Similarly to oscillations of $CaCO_3$ content in siltstones (Vass et al. 2007), varying abundances of agglutinated foraminifera in these deposits indicate variance in the influx of terrigenous material, corresponding to variance in continental nutrient input. Hyposaline *Ammonia* spp. in the marginal part of the basin (Vass et al. 2007) also reveal a rather humid climate with salinity oscillations as a consequence of high riverine influx.

Generally, mixed water with high nutrients can be inferred for the probably warm Oli-2 period. Disturbances, including varying terrigenous input and varying quantity and quality of nutrients, can be expected in the upper part of the interval.

Mio-1 interval (ca 23 Ma; Fig. 9c)

In the uppermost Oligocene, organodetritic limestones appeared in the marginal part of the basin, for which strontium isotope dating provides an age of 23.39 Ma (Less et al. 2015). The production of limestones points to decreased terrigenous input before the Mi-1 cooling event. Besides large herbivorous oligotrophic foraminifera (*Miogypsina, Lepidocyclina, Heterostegina*; Murray 2006), the limestones contain the small opportunistic suspension feeder *Cibicidoides* sp. which may indicate episodic input of nutrients in suspension.

In the central part of the basin, no lithological change was observed. In biota, the LCO of *Reticulofenestra bisecta* is connected with occurrence of arctotertiary elements (Planderová 1990). Also protist assemblages changed: *Lenticulina* spp., also characteristic of the Oli-1 (cold) interval, reappeared. Low-oxygen and high-nutrient *Uvigerina* and *Melonis,* accompanying *Lenticulina* spp. during the Oli-1 interval, were substituted by smooth-walled *Bolivina* spp. In contrast to *Uvigerina* and *Melonis*, *Bolivina* is highly adaptable and tolerant of a wide range of different factors or combinations of environmental factors (e.g., Camacho et al. 2015) and the substitution of taxa points to an unstable environment. A new feeding strategy is represented by the *Cassidulina* group, which reveals an influence of seasonal phytodetritus pulses (Gooday 1993). Planktonic assemblages are characterized by substitution of large reticulofenestrids by small ones, indicating environmental stress with quick changes within that environment, including oscillations of salinity (Wade & Brown 2006) and nutrient content (Flores et al. 1997; Wells & Okada 1997; Kameo 2002). However, other authors recorded abundant small *Reticulofenestra* in high-nutrient conditions (Okada & Honjo 1973; Takahashi & Okada 2000; Bauman & Freitag 2004). Therefore, there are two explanations: unstable conditions or a high-nutrient environment. Due to the absence of other high-nutrient markers, instability is the preferred explanation. The common planktonic foraminiferal species *Turborotalita quinqueloba,* which substituted for four-chambered *Globigerina* spp., is a shallow-dwelling marker of cold, non-stratified waters (Rohling et al. 1993).

Generally, instability, decreased nutrients, phytodetritus pulses, and decreased terrigenous input due to aridity are expected for the cold interval. This interpretation is corroborated by palaeoclimate analysis based on plant macrofossils (Erdei et al. 2007), which inferred cooling, seasonality increase and aridity in the Pannonian domain.

Mio-2 event (19–22 Ma; Fig. 9d)

The reappearance of palms from the genera *Arecipites, Myricipites,* etc. (Planderová 1990) indicate warming during this interval.

Expansion of the shallow-water coarse clastic facies, including the deltaic one, reflects the local palaeogeographic and palaeotectonic event: tectonically triggered shallowing (Vass et al. 1993). High-tide markers indicate changes of basin configuration leading to high tides (Sztanó & de Boer 1995). The gradual substitution of marginal limestones by coarse clastics of the Bretka Formation is well documented and dated to 22.4–21.9 Ma by strontium isotopes (Less et al. 2015) and indicates an increase in humidity. Shallowing-influenced composition of the benthic foraminifera assemblage primarily consists of increase in the relative abundances of *Elphidium, Ammonia* and *Porosononion*. In addition, these genera indicate a salinity decrease, which can also be correlated to increased precipitation. In the central part of the basin, abundances of *Cassidulina* and *Nonion commune* rose, showing enrichment in nutrients mainly due to the strong influence of seasonal phytodetritus pulses (Gooday 1993; Murray 2006). In the upper part of the water column *Globigerinoides trilobus* appeared and four-chambered *Globigerina* ex gr. *praebulloides* reappeared. The co-occurrence of "real" *Globigerinoides* with *Globigerina praebulloides* may represent seasonal aspects: *Globigerina* in the colder season with mixed water, often connected with seasonal upwelling, and *Globigerinoides* in the warmer period with stratified water (Conan et al. 2002; Peeters et al. 2002; Keigwin et al. 2005). This is in agreement with the seasonality in phytodetritus pulses predicted from the increase of cassidulinids. Persistent small *Reticulofenestra minuta* records local and/or seasonal stress in the surface layer, alternating with stable marine conditions inferred from the appearance of large endemic *Reticulofenestra excavata* as well as *Helicosphaera scissura.*

MM-1 interval (14.9–14.4 Ma; Fig. 10a)

Mg/Ca data from foraminiferal tests from the marine environment as well as palynological analysis enable us to infer

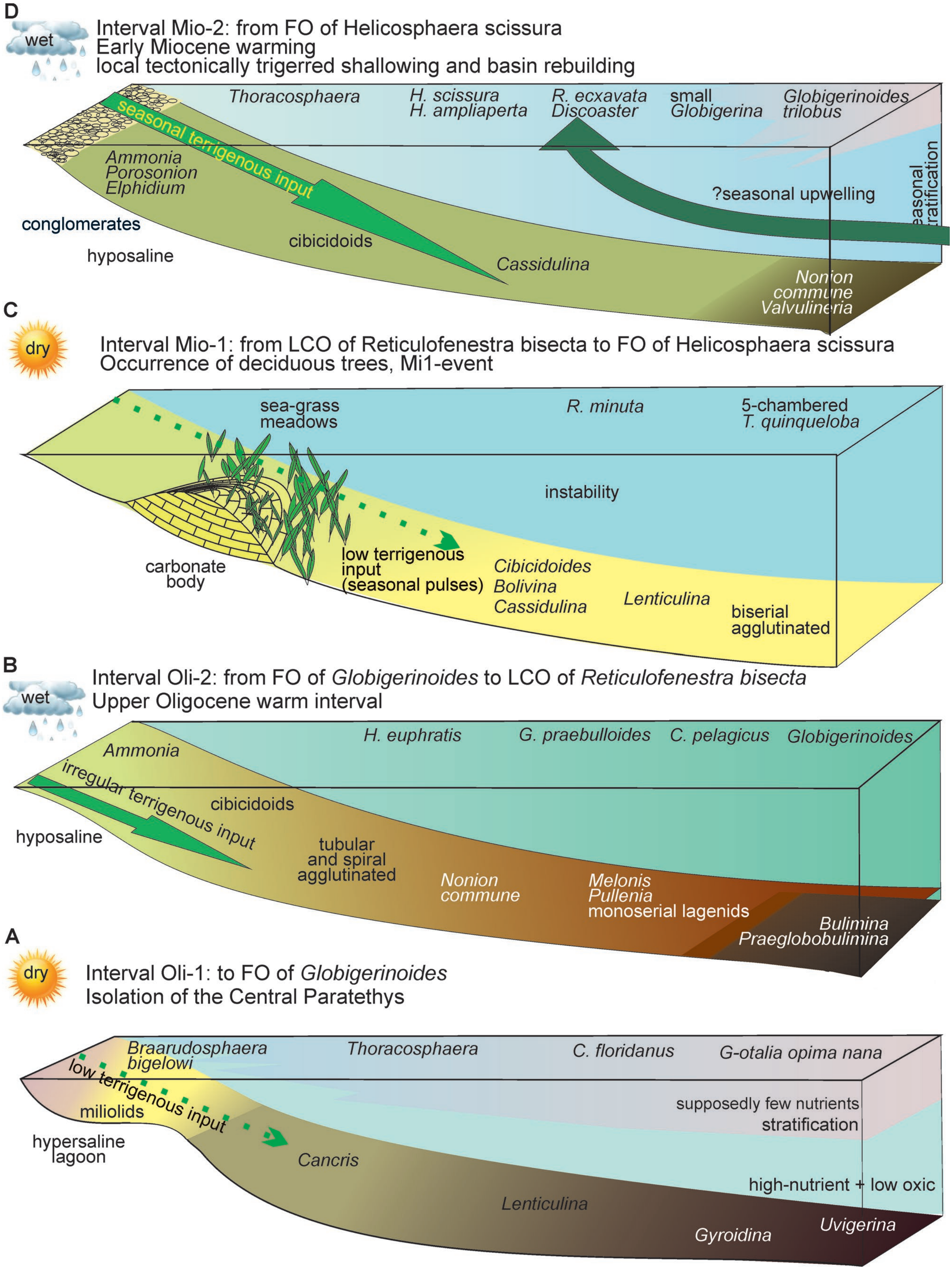

Fig. 9. Model of palaeobiotope distribution in the epicontinental Central Paratethys sea during the late Oligocene to early Miocene.

a stable subtropical climate for this interval (Holcová et al. 2015; Scheiner et al. 2016).

The co-occurrence of the planktonic species *Globigerina bulloides-praebulloides*, *Globigerinella regularis, Globigerinoides* spp., and *Orbulina* suggests a seasonal succession of assemblages characterized by the alternation of warm seasons with a stratified oligotrophic water and cool seasons with a mixed upper water column (e.g., Reynold & Thunell 1985; Rigual-Hernandez et al. 2012; Kuhnt et al. 2013; Salmon et al. 2014). Similarly, the co-occurrence of large *Helicosphaera* spp. indicating warm mesotrophic to oligotrophic water (Knappertsbusch 1993; Ziveri et al. 1995, 2004; Haidar & Thierstein 2001) with the high-nutrient marker *Coccolithus pelagicus* (e.g., Cachao & Moita 2000) suggests an alternation of warm oligotrophic and colder eutrophic surface waters. Seasons with cold, mixed water can be connected with local wind-driven coastal upwelling areas (Conan et al. 2002) as corroborated by oxygen isotopic data (Scheiner 2015) as well as blooms of diatoms (Holcová et al. 2015). Predominance of *Globigerinella* over *Globigerinoides* during this interval indicates stable conditions in the warm season, based on the observation of Schmuker (2000), who recorded *Globigerinoides* spp. in higher temperature and salinity variations, while *Globigerinella* spp. bloomed in narrower temperature and salinity ranges. Generally, this regime can be expected during the whole interval because the planktonic foraminiferal assemblages represent a compact group based on results of the nMMDS.

The sea floor was settled by *Bulimina* spp., monoserial lagenids, *Melonis, Pullenia, Nonion commune*, and *Uvigerina* spp., associated with high food availability, organic carbon content in the sediments, and traditionally low oxygen, although they can also live under oxic conditions (Miller & Lohman 1982; Caralp 1989; Hermelin 1992; Jorrisen et al. 1992; Sjoerdsma & van der Zwaan 1992; Miao & Thunell 1993; Sen Gupta & Machain-Castillo 1993; Rathburn & Corliss 1994; Murray 2003). Abundant *Uvigerina*, *Bolivina*, *Bulimina*, and *Melonis* typify regions of high organic productivity and a sustained flux of organic matter to the sea floor, for example, under areas of upwelling (Thomas et al. 1995), which support the interpretation of seasonal upwelling from the planktonic assemblages.

MM-2 interval (14.4–13.8 Ma; Fig. 10b)

The base of this interval can be dated to 14.3–14.4 Ma using the age calibration of the LCO of *Helicoshaera waltrans* in the Central Paratethys (see subchapter "The early Middle Miocene biostratigraphical events"). This age agrees well with the date of the Mi-3a event (14.3 Ma; Gradstein et al. 2012) and the beginning of the MMCT. This climatic change was characterized by an increase in the mean annual range of temperature, mainly due to decreasing cold-month temperatures in terrestrial climates (Bruch et al. 2010). Along the opposite coast of the Central Paratethys sea in Serbia, the Miocene cooling is also connected with increased seasonality most pronounced in winter temperatures (Utescher et al. 2007). Increased seasonality, mainly seasonality of precipitation, was corroborated by the Coexistence Approach in the study area (Doláková et al. 2014).

The n-MMDS showed a bimodal distribution of benthic and planktonic foraminiferal and calcareous nannoplankton assemblages in comparison with the previous stable MM-1 interval, which may be the consequence of higher seasonal and/or interannual variability. The surface water is characterized by *Paragloborotalia mayeri, Globigerinoides* spp., *Orbulina suturalis,* five-chambered *Globigerina ottnangiensis* and *Turborotalita quinqueloba.* The coexistence of these taxa also indicates a seasonal succession of assemblages (e.g., Reynold & Thunell 1985; Rigual-Hernandez et al. 2012; Kuhnt et al. 2013; Salmon et al. 2014), but substitution of *Globigerina bulloides*, dominating during the MM-1 interval, by *Turborotalita quinqueloba* means cooling during the cold and high-nutrient season. The lower abundance of *Globigerinella* and its replacement by *Globigerinoides* spp. during the warm oligotrophic season indicate more variable salinity during summer conditions leading to hypersaline surface water are also suggested by the occurrence of hypersaline dinoflagellates (Nehyba et al. 2016) as well as isotopic data (Scheiner 2015). An increase in the calcareous nannoplankton taxon *Umbilicosphaera* spp. also shows tolerance to saline water (Ziveri et al. 2004; Boeckel et al. 2006). Moroever, *Umbilicosphaera* prefers warm, rather oligotrophic water. The unstable conditions are corroborated by strongly dominating *Reticulofenestra minuta* as an environmental stress indicator. Size reduction in helicosphaeras (large *Helicosphaera waltras* is gradually substituted by small *Helicosphaera walbersdorfensis,* e.g., Holcová et al. 2015) is probably also a response to instability during the warm season. The lower abundance of *Coccolithus pelagicus* can be explained by fewer nutrients.

The sea floor protists are characterized by *Asterigerinata planorbis, Elphidium* spp., large foraminifera (mainly *Amphistegina* spp.), and *Ammonia* spp., which indicate the expansion of the shallow-water facies due to a sea-level drop. Regression is corroborated by the increase in reworked Palaeogene calcareous nannoplankton taxa. *Asterigerinata planorbis, Elphidium* spp. and large foraminifera indicate seagrass meadows (Murray 2006) and are independent of phytodetritus input as a nutrient source. On the contrary, *Cibicidoides* spp., *Cassidulina* and *Globocassidulina* need those nutrients. The riverine influxes may be either seasonal or catastrophic and repeated in decades-long cycles. This may correspond to the "extreme climate events" deduced from the strongly negative excursions in δ^{18}O and δ^{13}C in the *Ostrea* isotope archive (Harzhauser et al. 2011). The interpretation of horizons with biserial agglutinated foraminifera (*Spiroplectinella, Textularia* spp., *Semivulvulina*) is questionable because of poor knowledge of their ecological preferences in lower shelf-upper slope habitats. The biserial morphotypes are detritivorous bacterial scavengers adapted to a shallow to deep infaunal life strategy (Galeotti et al. 2005; Nagy et al. 2009). Shallow-water *Textularia agglutinans* is an opportunistic species and exhibits a preference for food-enriched conditions and a tolerance to oxygen deficiency (Barmawidjaja et al. 1995), while Jorissen et al. (1998) indicated that agglutinated foraminifera reflect oligotrophy on the sea-floor. In any case, agglutinated foraminifera may display an opportunistic behaviour which becomes evident after environmental disturbances when opportunists rapidly reproduce (Hess et al. 2013). These disturbances may be correlated with the "extreme climate events" of Harzhauser et al. (2011). The alternation of biserial agglutinated foraminifera with cassidulinids may reflect alternation in the quality of organic matter. Unlike *Cassidulina,* which needs fresh phytodetritus near the riverine influx, degraded organic matter far from its source is sufficient for agglutinated foraminifers. Miliolids accompanied by *Braarudoshaera bigelowi,* occurring in the marginal part of the basin, represent hypersaline environments (Murray 2006; Bartol et al. 2008). Together with carbonate production indicating a precipitation decrease, this agrees with the aridification events known from the Mediterranean (14.489 Ma; Hüsing et al. 2010) leading to the Wieliczkian salinity crisis (Gazdzicka 1994; Peryt 1997; Oszczypko 1998).

Common features of climatic events in the subtropical epicontinental sea (the Oligocene and Miocene Central Paratethys)

The studied warm intervals (Oli-2, Mio-2, MM-1) are characterized by enhanced humidity increasing riverine influx bringing terrigenous nutrients. Where marginal facies are preserved, coarse clastics, including deltaic deposits with hyposaline assemblages, prevail. Tectonically-triggered shallowing may also lead to broad distribution of hyposaline facies in warm intervals which are globally correlated with deepening. Typical taxa characterizing warm intervals include the high-nutrient markers *Coccolithus pelagicus*, four-chambered *Globigerina, Melonis, Pullenia*, and low-oxic *Bulimina.* In addition to an increase in nutrients due to increased terrigenous input, seasonal upwelling was also recorded. Its establishment probably depends on atmospheric circulation with seasonal winds, relating to, for example, the formation of mountain chains in coastal areas.

At the base of the warm interval, increased large *Helicosphaera* spp. (often new species replacing taxa driven extinct in the preceding cold interval) indicate the incursion of warm, oligotrophic surface water into the Central Paratethys. Beside new large *Helicosphaera*, new large *Reticulofenestra* also appeared.

These characteristics can also be recognized in another warm interval in the Central Paratethys. Eutrophication, indicated by the appearance of pyritized frustules of diatoms and tests of pteropods, precipitation increase, interpreted from the occurrence of deltaic deposits, and hyposaline facies were recorded in the warm period between the Oi2 and Oi2a-events (ca. 29–30 Ma; upper NP23–lower NP24). Monospecific associations of *Uvigerina hantkeni* (the "*Uvigerina* bloom") at the base of the NP24 Zone indicate a high-nutrient environment on the sea floor. The peak in *Helicosphaera* spp. is followed by an increase of the high-nutrient marker *Coccolithus pelagicus* (Horváth 1998; Ozdínova & Soták 2014).

Cold intervals (Oli-1, Mio-1 and MM-2) are characterized by decreased nutrient availability due to decreasing riverine input as a consequence of aridification. The synchronous cooling and drying approximately coincident with the Oi2b and/or Mi1 events is also recorded in Asia, where a causal linkage between late Oligocene global cooling and central Asian aridity was determined (Dong et al. 2013). Riverine input may be seasonal or episodic (decades-long cycles) based on occurrence of markers of phytodetritus pulses. The coincidence of aridification, pronounced seasonality and episodic extreme rainfalls caused increased stress and the appearance of r-specialists, such as small *Reticulofenestra* and small cibididoids.

Aridity-induced seasonal salinity increase in surface water may have triggered downwelling circulation, which agrees with the prevalence of mixed water in cold intervals. This regime is expected during the MMCT by Brzobohatý (1987) and Báldi (2006). The central part of the basin is dominated by opportunistic *Lenticulina* spp. and biserial agglutinated foraminifera. Deficiency in both terrigenous and upwelling-introduced nutrients caused the enlargement of sea-grass meadows in the photic zone with herbivorous foraminifera dependent only on nutrients from the sea-grass ecosystem.

Conclusions

1. The distribution of foraminiferal and calcareous nannoplankton assemblages in the Central Paratethys during time intervals ca. 27 to 19 Ma and 15 to 13.5 Ma refuted the working hypothesis, which predicted only a marginal impact of global climate changes on a subtropical epicontinental sea influenced by local tectonic and palaeogeographic events. Global climatic cycles influenced the palaeoenvironment in the studied subtropical epicontinental seas particularly in the intervals between the most significant tectonic events.
2. Warm intervals and associated global sea-level rises started with the opening of communication with the warmer Indo-Pacific and Mediterranean realms, which accelerated the influence of global warming.
3. Warm intervals can be characterized by a generally stable climate with weak seasonal signals, high evaporation increasing humidity, and then riverine inflow and input of terrigenous nutrients. Decreased salinity is expected in marginal facies and surface water, and may have caused stratification. Seasonal upwelling was locally established under favourable winds and mixed water masses. Suspension feeders and eutrophic markers prevailed in basinal assemblages.
4. Cold intervals are characterized by aridification due to decreased evaporation and marked seasonality, warm seasons having stratified water and hypersaline oligotrophic

water. This heavy, saline layer triggered downwelling mixing, persisting during the cold season. Moreover, episodic intensive rainfalls in decade-long cycles can be expected. Instability supported expansion of stress-tolerant, opportunistic taxa, often small-sized (*Lenticulina*, biserial agglutinated, small *Cibicidoides*, *Reticulofenestra minuta*). Oligotrophy triggered enlargement of sea-grass meadows with herbivorous foraminifera dependent on nutrient sources from their own ecosystem.

Local tectonic events led to certain discrepancies between global and local sea-level cycles, local salt formation (in the rain shadow of newly-created mountains), and establishment of an upwelling regime (geomorphological changes altering atmospheric circulation and creating stable winds with a direction driving surface water away from the coast causing upwelling).

5. Climatic change triggered nannofossil evolution. Large reticulofenestras and helicosphaeras were reduced in size during cool phases, which emptied habitats for new taxa appearing in the following warm interval (both endemics and colonists); for example, *Reticulofenestra bisecta* was substituted after the Mi-1 event by endemic *Reticulofenestra excavata*, while *Helicosphaera ampliaperta* and *H. scissura* replaced *Helicosphaera euphratis*.

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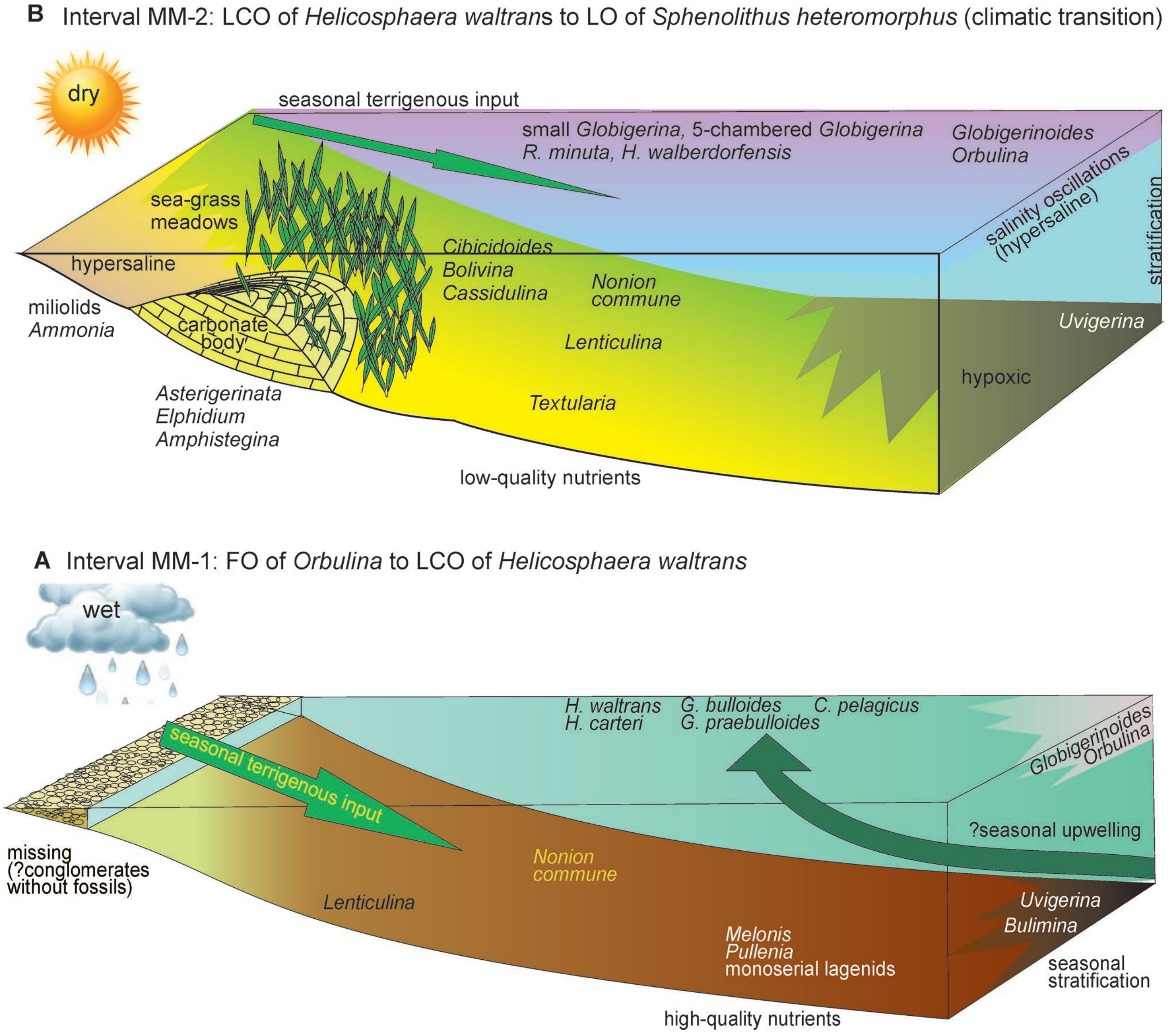

B Interval MM-2: LCO of *Helicosphaera waltrans* to LO of *Sphenolithus heteromorphus* (climatic transition)

A Interval MM-1: FO of *Orbulina* to LCO of *Helicosphaera waltrans*

Fig. 10. Model of palaeobiotope distribution in the epicontinental Central Paratethys sea during the Middle Miocene.

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