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Author: Holcová, Katarína

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Morphological variability of the Paratethyan Oligocene–Miocene small reticulofenestrid coccolites and its paleoecological and paleogeographical implications

KATARÍNA HOLCOVÁ



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The analysis of size changes (length of placoliths, their width, length of central opening and its width) in elliptical reticulofenestrids from the NP25–NN5 zonal interval of the Central Paratethys allowed to dicriminate two size categories of placoliths: (i) small *Reticulofenestra minuta* (< 3.5 μm); (ii) *Reticulofenestra haqii–pseudoumbilicus* group (4–10.0 μm). The latter group appeared for the first time (FO, first occurrence) in the upper Egerian (size 4–7 μm) with the size of placoliths in this plexus increasing gradually. The FO of *R. pseudoumbilicus* > 8.0 μm has been established in the Zone NN2 while its FCO (first common occurrence) in the Zone NN5. This study shows that the FOs of size-defined morphotypes of the *R. haqii–pseudoumbilicus* group differ in the Central Paratethys and oceanic realm. Blooms of *R. minuta* at the Oligocene–Miocene boundary and in the Early Middle Miocene may be correlated with the incoming of warm water into the higher latitude Central Paratethys basins during connection with the Mediterranean Sea. Transgression favored the expansion of near-shore areas associated probably by some short-time oscillations of salinity. The FO of *R. haqii–pseudoumbilicus* group and the FO of *R. pseudoumbilicus* > 8.0 μm can be correlated with the opening of new pathways between the Mediterranean and the Central Paratethys. Gradual size changes in the *R. haqii–pseudoumbilicus* group probably reflect climatic changes: the decrease of coccolith size in the late Egerian may reflect cooling (Mi1 event) while the increase in coccolith size in the interval from the FO of *Helicosphaera ampliaperta* to the FO of *Sphenolithus heteromorphus* occurred due to warming. Two size categories of placoliths in the *R. haqii– pseudoumbilicus* group (3.5–6 μm and 6–8 μm) recorded in the interval from Zone NN1 to the lower part of the Zone NN2 may represent seasonal populations.

Key words: Calcareous nannofossils, size changes, paleoecology, Oligocene, Miocene, Central Paratethys.

Katarína Holcová [holcova@natur.cuni.cz], Department of Geology and Paleontology, Charles University in Prague, Albertov 6, 128 43 Praha 2, Czech Republic.

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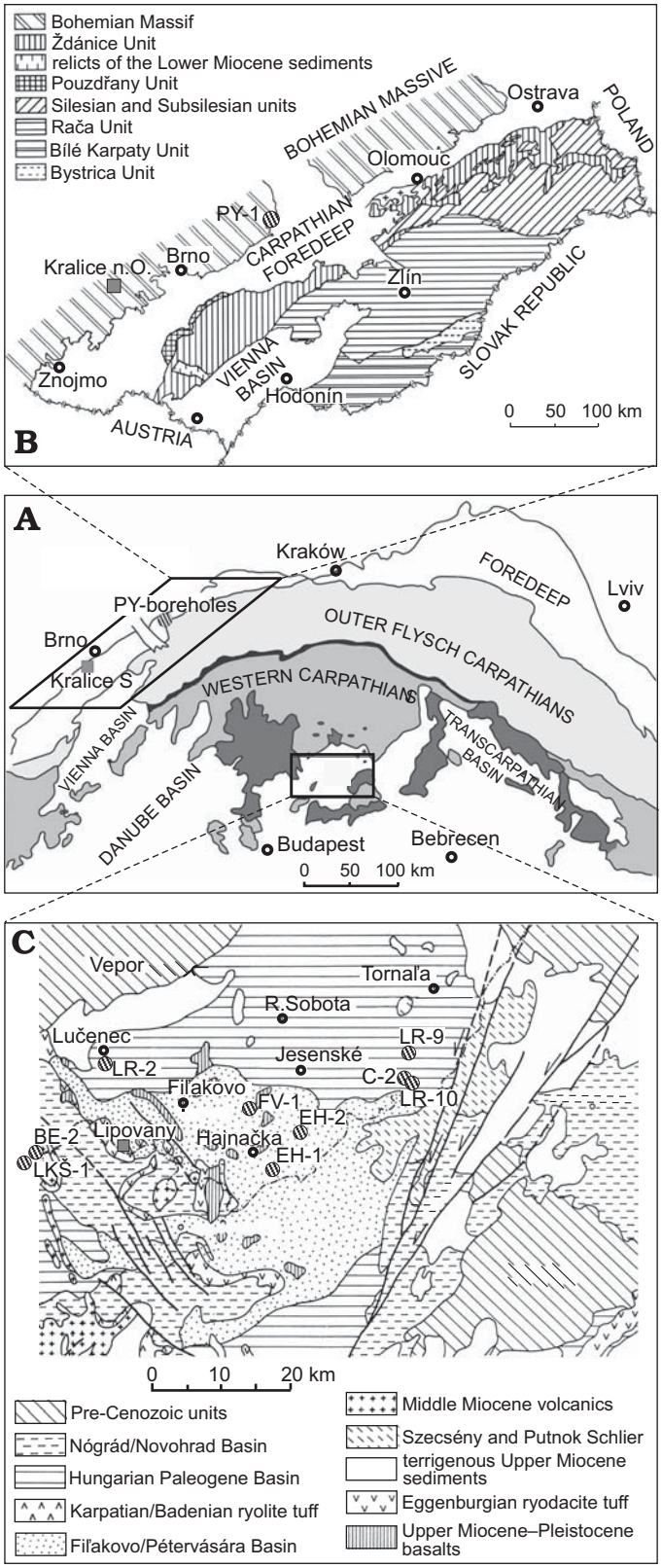
Introduction

The collision of the African/Apulian/Arabian plates and Eurasian continent began during the Eocene, and resulted in the uplift and emergence of the Alpine chains and the break-up of the Tethyan Realm into the Mediterranean and Paratethyan domains (Popov et al. 2004). This resulted in the differentiation of the Paratethys as a biogeographic entity. The first endemic Paratethyan assemblages of mollusks, calcareous nannoplankton and foraminifera appeared in the Oligocene (Báldi 1986). The subsequent history of the Paratethys involved periods of isolation from the adjacent Mediterranean Sea and Indian Ocean during which endemic biota evolved, and periods of oceanic communication during exchanges occurred with the faunas of the Mediterranean and the Indo-Pacific provinces. Additionally episodical paleogeographic changes, global climatic variations, local oscillations of salinity, oxygen content and globally and locally affected sea-level changes also influenced the evolution of Paratethyan ecosystems (Rögl 1998; Kováč 2000; Popov et al. 2004; Piller et al. 2007; etc.). Interactions of the local geodynamic and the global climatic factors lead to major problems in their biostratigraphical, paleoecological and paleogeographical interpretation. As a consequence of periodical paleogeographic changes affecting them, the morphological changes (size) of Central Paratethys populations may be local, differing those from contemporaneous oceanic populations.

Coccolithophorids were widespread autotrophs in marine Paratethyan ecosystems and are of great biostratigraphical importance. Besides *Coccolithus pelagicus*, reticulofenestrids are the most common components of the assemblages and their detailed study can provide important data for reconstruct-

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ing the factors that have induced morphologic changes in calcareous nannoplankton. *Reticulofenestra bisecta*, *R. abisecta* and *Cyclicargolithus floridanus* are common in the late Oligocene while in the lower and early Middle Miocene, reticulofenestrids are represented by *Reticulofenestr minuta*, *R. haqii*, and *R. pseudoumbilicus* together with endemic *R. excavata* (Lehotayová 1975, 1984; Marunteanu 1992; Andreyeva-Grigorovich et al. 1997; Holcová 2005). The aim of this study is to show the relationship between size changes in reticulofenestrids and paleogeographic and paleoecologic evolution in an intracontinental basin.

Abbreviations.—FCO, first common occurrence; FO, first occurrence; LCO, last common occurrence; LO, last occurrence.

Geological setting

The area of the Central Paratethys studied here includes the Pannonian Basin system and the Carpathian Foreland basins (Seneš 1961).

The majority of samples were taken from the South Slovak Basin (Fig. 1). Sediments filling of this geomorphological unit were deposited in the northern part of the Buda Basin during the Late Oligocene (Kiscellian Stage) to the Chattian and lower Aquitanian (Egerian Stage), in the Fiľakovo/Pétervására Basin during the upper Aquitanian and lower Burdigalian (Eggenburgian Stage) and in the Novohrad/Nógrád basin in the upper Burdigalian and Langhian (Ottnangian, Karpatian, and early Badenian; Vass 1996). These three basins form the northern part of the Pannonian Basin system. Biostratigraphy, lithostratigraphy and sedimentology of this areawere summarized in Vass et al. (1979, 1989, 2007). Lithostratigraphic units have been defined by Vass and Elečko (1982) and correlation with standard nannoplankton zones (Martini 1971) has been established by Lehotayová (1982). The paleogeographical maps for every Central Paratethys stage have been produced by Vass et al. (1979, 1989, 2007). Vass et al. (1993), Márton et al. (1995), and Vass (1996) delineated the most important tectonic events and local sea-level changes; the latter by have been correlated with the global sea level curve of Haq et al. (1988) by Vass (1995).

The Middle Miocene samples have been collected from sections in the Carpathian Foredeep. These sections are described in detail by Zágoršek et al. (2008, 2009) and Zágoršek and Holcová (2009; Fig. 1).

The study interval from the Oligocene/Miocene boundary interval to the lower Middle Miocene (zones NP25–NN5) corresponds to the Egerian, Eggenburgian, Ottnangian, Karpatian, and Lower Badenian stages of the Central Paratethys (Popov et al. 2004; Harzhauser and Piller 2007; Hohenegger et al. 2009).

Fig. 1. **A**. Sketch of the main Middle European geological units (after Kováč 2000). **B**. Moravian part of the Carpathian Foredeep with location of borehole PY-1 near village Přemyslovice; and section Kralice (KRA), geological situation according Chlupáč et al. (2002). **C**. Eastern part of the South Slovak Basin with location of boreholes LKŠ-1, BE-2, FV-1, EH-1, and EH-2 drilled by State Geological Institute of Dionýz Štúr; boreholes LR-9 and LR-10 drilled by "Geologický prieskum n.p." regional centrum Rožňava and section Lipovany (LIP). Geological situation after Halásová et al. (1996).

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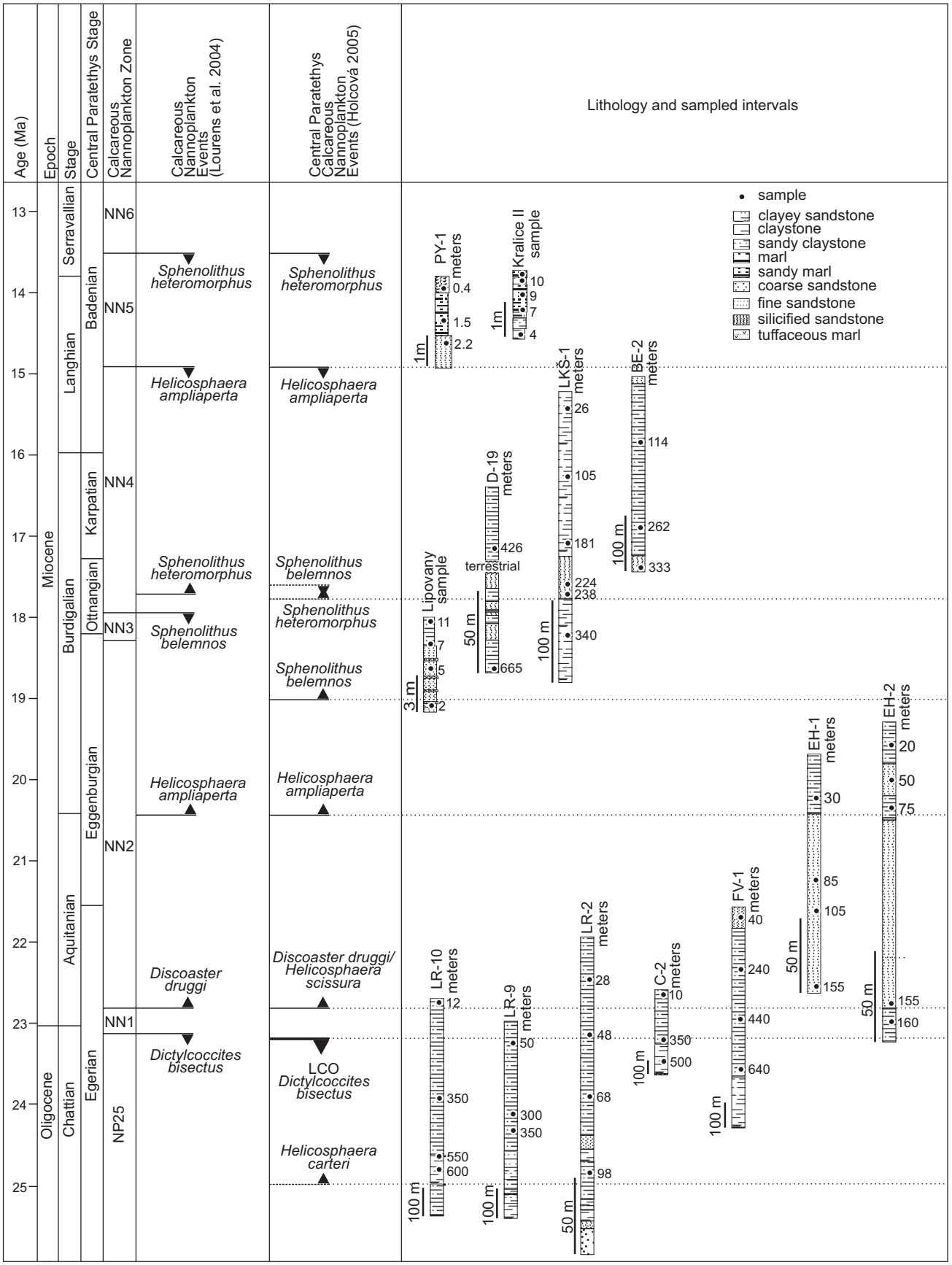


Fig. 2. Lithology, stratigraphical ranges, and sampled interval of studied sections. Location of boreholes LR-10, LR-9, LR-2, C-2, FV-1, EH-1, EH-2, D-19, LKŠ-1, BE-2,PY-1, and sections Lipovany and Kralice II is illustrated on Fig. 1.

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Material and methods

A total of 49 samples taken from 13 sections have been studied. The set of samples were chosen from about 500 of samples analysed in the study area in previous years (e.g., Holcová 2001, 2005). Nannofossils in selected samples were common to abundant (10–30 specimens in visual field of microscope) and well preserved without apparent diagenetic changes (dissolution, recrystallization). Relative abundances of reticulofenestrids in studied samples varied from 10 to 30% with exception of samples from the zones NN1 and NN5 with more than 50% of reticulofenestrids. Besides Langhian samples (Zone NN5) were dominated by *Coccolithus pelagicus* in the studied assemblages. The location of the sections, their lithology and stratigraphical ranges are summarized in Figs. 1 and 2.

Calcareous nannofossils were examined and photographed using a light microscope and 1000× magnification with both bright field and crossed polarized light. Smear slides were prepared from about 1 cc of rock sample (claystone, siltstone, and fine sandstone) using the method of Švábenická (2002). The first 50 specimens of reticulofenestrids were measured in every sample. Placoliths of *Reticulofenestra* spp. were measured from the digital microphotographs. In total, 2447 specimens were analyzed. The following characters were measured for each placolith: length (the largest diameter of placoliths), width (diameter of placolith perpendicular to the length of the placolith), length of central opening (along the length of the placolith) and its width (across the width of the placolith) (Fig. 3).

The measurements were analyzed by simple statistical methods using STATISTICA software. Frequency histograms were used for the first graphical evaluation of the distribution type of a simple biometric parameter. XY-plots and the Pearson correlation coefficient were used for evaluation of correlations between two parameters.

The size-dependent classification of *Reticulofenestra minuta–haqii–pseudoumbilicus* group (Young 1999) has been used as an initial taxonomic concept (*Reticulofenestra minuta*: < 3 μm, *R. haqii*: 3–5 μm, and *R. pseudoumbilicus* > 5 μm). This classification is broadly accepted also in the Central Paratethys (Ćorić and Švábenická 2004; Tomanová Petrová and Švábenická 2007; Ćorić and Hohenegger 2008). However, the small-sized placoliths identified like *Reticulofenestra minuta* may represent two or more species which cannot be distinguished under the light microscope (Haq 1980).

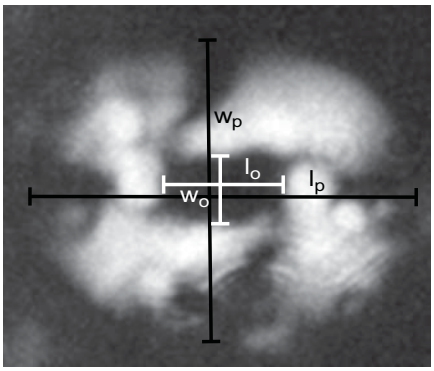


Fig. 3. Dimensions measured in placoliths. Abbreviations: lo, length of central opening; lp, length of placoliths; wo, width of central opening; wp, width of placoliths.

To analyze size changes in reticulofenestrids over time, the studied interval was divided into seven intervals on the basis of six calcareous nannoplankton events. The age of these bioevents in the Central Paratethys may differ from their age in the world ocean (Berggren et al. 1995; Lourens et al. 2004) because new taxa were only able to migrate into the Central Paratethys when communication existed between them.

(i) The FO of *Helicospheara carteri* was recorded within Zone NP 25 in the study area (Holcová 2005).

(ii) The LCO of *Reticulofenestra bisecta*. The extinction of this species is often used to approximate the Oligocene/Miocene boundary (Berggren et al. 1995; Young 1999). However, in the Buda Basin, rare specimens of *R. bisecta* occur in zones NN1 and NN2 (Holcová 2005). These are probably reworked specimens and therefore only the LCO of *R. bisecta* was used to characterize the NP25/NN1 zonal boundary.

(iii) 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.

(iv) The FO of *H. ampliaperta* was recorded in Zone NN2 in the Central Paratethys (Marunteanu 1992; Holcová 2002, 2005).

(v) The FO of *S. belemnos* was established to lie at the NN2/NN3 boundary in the Central Paratethys (Marunteanu 1992, Andreyeva-Grigorovich et al. 1997).

(vi) The FO of *S. heteromorphus*/LO of *S. belemnos*: In the Central Paratethys both species briefly co-occur.

(vii) For comparison reticulofenestrids from Zone NN5 were studied. This zone is characterized by the absence of *H. ampliaperta* and the presence of *S. heteromorphus* (Martini 1971).

Seven samples were intended to analyze from every interval. However, from the LO of *Helicosphaera ampliaperta* to the FO of *Sphenolithus heteromorhus* (upper part of the Zone NN2 and Zone NN3), terrigenous sedimentation dominated in the study area. Therefore only limited number of samples with well preserved and abundant nannofossils was found in this interval. On the other hand, longer intervals with variegated marine facies (zones NP25 and NN4) were sampled to more detail.

Results

Morphologic variability of placoliths

Size and length/width-ratio of placoliths and size of central opening.—The length of the placoliths varies from 1.6 to 10 μm, their width from 1 to 9 μm. The length-width scatter plot and the correlation coefficient (0.95) between the length

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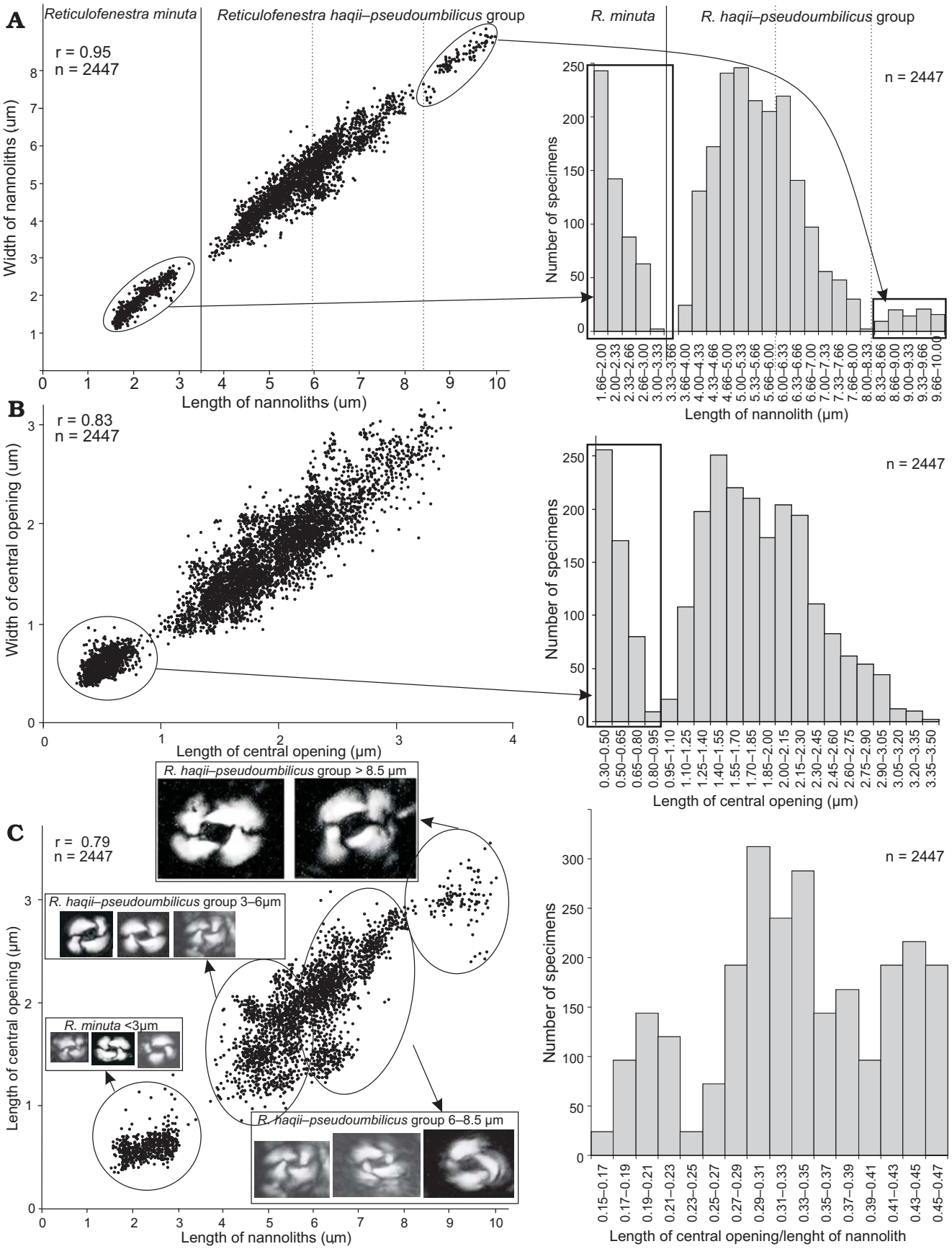


Fig. 4. Scatter plots and frequency histograms visualizing correlations between biometric characteristics of the placoliths. **A**. Length/width-ratio of placoliths. **B**. Length/width-ratio of central opening. **C**. Length of placolith/length of central opening.

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and width of the placoliths indicate a very high correlation between these two parameters (Fig. 4A). The distribution of these characters is polymodal and shows three groups that are also distinct on the width-length plot (Fig. 4A): (i) small placoliths (1.6–3 μm); (ii) medium-size placoliths (3.5–8 μm), and (iii) large placoliths (8–10 μm). The small placoliths constitute a distinct size group, but transitional size categories occur between the medium-size and large placoliths.

Relative size and length/width-ratio of central opening.—The size of the central opening varied from 0.35 to 3.5 μm. The correlation between the length and width of the central opening is high (0.83) with two groups in which the length are (i) 0.35–1 μm and (ii) 1–3.5 μm (Fig. 4B).

The relative size of the central opening was expressed as a ratio between the size of the placolith and the size of the central opening (Fig. 4C). The ratio varies from 0.15 to 0.48, and shows a polymodal distribution with three groups: (i) placoliths with narrow central opening (size of placolith/size of central opening varies from 0.15 to 0.24), the placoliths with narrow central opening are small and reach maximum diameter 7.5 μm; (ii) placoliths with medium central opening (size of placolith/size of central opening from 0.25 to 0.40) were recorded in all size categories of placoliths; (iii) placoliths with wide central opening (size of placolith/size of central opening from 0.40 to 0.48) were not recorded among the smallest placoliths (1.6–3 μm).

Size changes over time

Correlations between the parameters analyzed here for placoliths and the age of samples were investigated on the basis of correlation coefficient. A negative correlation was recorded between the length of the placoliths ($p = 0.01$) and their age. The shift in the total size of placoliths and that of their central opening over time is illustrated in Figs. 5–8 for individual samples. A summary of the data is showed in Fig. 9. From these data we may conclude the following:

(i) Small placoliths (1.6–3 μm) constitute a well separated group in all assemblages, independent of age. However, they are abundant in two intervals: (1) in the lowest Miocene (Zone NN1 and lower part of Zone NN2 below the FO of *H. ampliaperta*), in these intervals they account for 30–70% of the nannoplankton assemblages; (2) in the lower Middle Miocene (Zone NN5), where they account for 50–95% of the assemblages.

(ii) The size of the oldest placoliths in the *R. haqii–pseudoumbilicus* group (upper Zone NP25) varies from 4.0–7.0 μm. Than the size of placoliths in the group slightly increased though this trend may differ in some individual samples (Figs. 5, 6). In the Zone NN3, the size varies from 4.0–8.0 μm.

(iii) Bimodal size distribution was recorded firstly during Zone NN1; it dominates in the lower part of the NN2 Zone (Figs. 9, 10).

(iv) Wide variations in the relative size of the central opening characterize interval from zones NP25 to lower part of NN2; generally, the relative size of the central opening increases (Fig. 9). At the level of the FO of *H. ampliaperta*, larger *R. haqii* (6–7 μm) with small central opening (1.7–2.0 μm) appeared, and relative size of central opening at this level decreased (Fig. 9).

(v) Broad variability of size of placolith as well as of the central opening characterizes the assemblages in Zone NN4 (Fig. 9).

(vi) Large placoliths (> 8 μm) occur first at the Zone NN5 (Fig. 9).

Discussion

Taxonomic implications

The size of placoliths is commonly used for classification of *Reticulofenestra* species. Using principal component analysis, Backman (1980) showed that the majority of morphological variation in *Reticulofenestra* can be explained by variation in the size of placoliths. However, the degree of closure of the central area can also be used for classification of *Reticulofenestra* (Backman 1978, 1980; Pujos 1985). Young (1990) suggested that this latter character is an unstable ecophenotypic character, and based his classification of the Late Miocene–Pliocene *Reticulofenestra* mainly on the length of the placoliths.

Young (1999) also differentiated the Early Miocene *R. minuta–haqii–pseudoumbilicus* group on the basis of overall size of the placoliths. The taxonomic difference between *R. minuta* and *R. haqii* was based on a superior limit size of 3 μm for the former. This criterion is well applicable to the reticulofenestrids of the Central Paratethys among which 3.1 to 3.7 μm long placoliths have not been observed (Fig. 4A).

Two different size limits have been used to separate *R. haqii* from *R. pseudoumbilicus*: Backman (1980) proposed an upper size limit of 5 μm for *R. haqii*, whereas Rio et al. (1990) and Raffi et al. (1995) proposed 7 μm. In any case, *R. haqii* and *R. pseudoumbilicus* represent a continuous plexus in world ocean and therefore Young (1990) classified them as one species, *R. pseudoumbilicus*, with two varieties: *R. p. pseudoumbilicus* and *R. p. haqii*. Nevertheless, separation of two species at 5 μm has prevailed.

As in the oceanic realm, the length of the placoliths in the *R. haqii–pseudoumbilicus* group changes continuously in the Central Paratethys. Limit of 5 μm has also been used for separation of *R. pseudoumbilicus* and *R. haqii* (Ćorić and Švábenická 2004; Tomanová Petrová and Švábenická 2007; Ćorić and Hohenegger 2008). In addition, Ćorić and Hohenegger (2008) have distinguished two size groups among *R. pseudoumbilicus,* one between 5–7 μm, the other > 7 μm. In studied material, boundary 8 μm seems to be pronounced. It appears that separation of group > 8 μm is specific only for studied set of samples because qualitative examination of placoliths from the other Central Paratethys sections of Zone NN5 and NN6 showed gradual changes in size of *R. pseudoumbilicus* from 5 to 10 μm (Jamrich and Halásová 2010).

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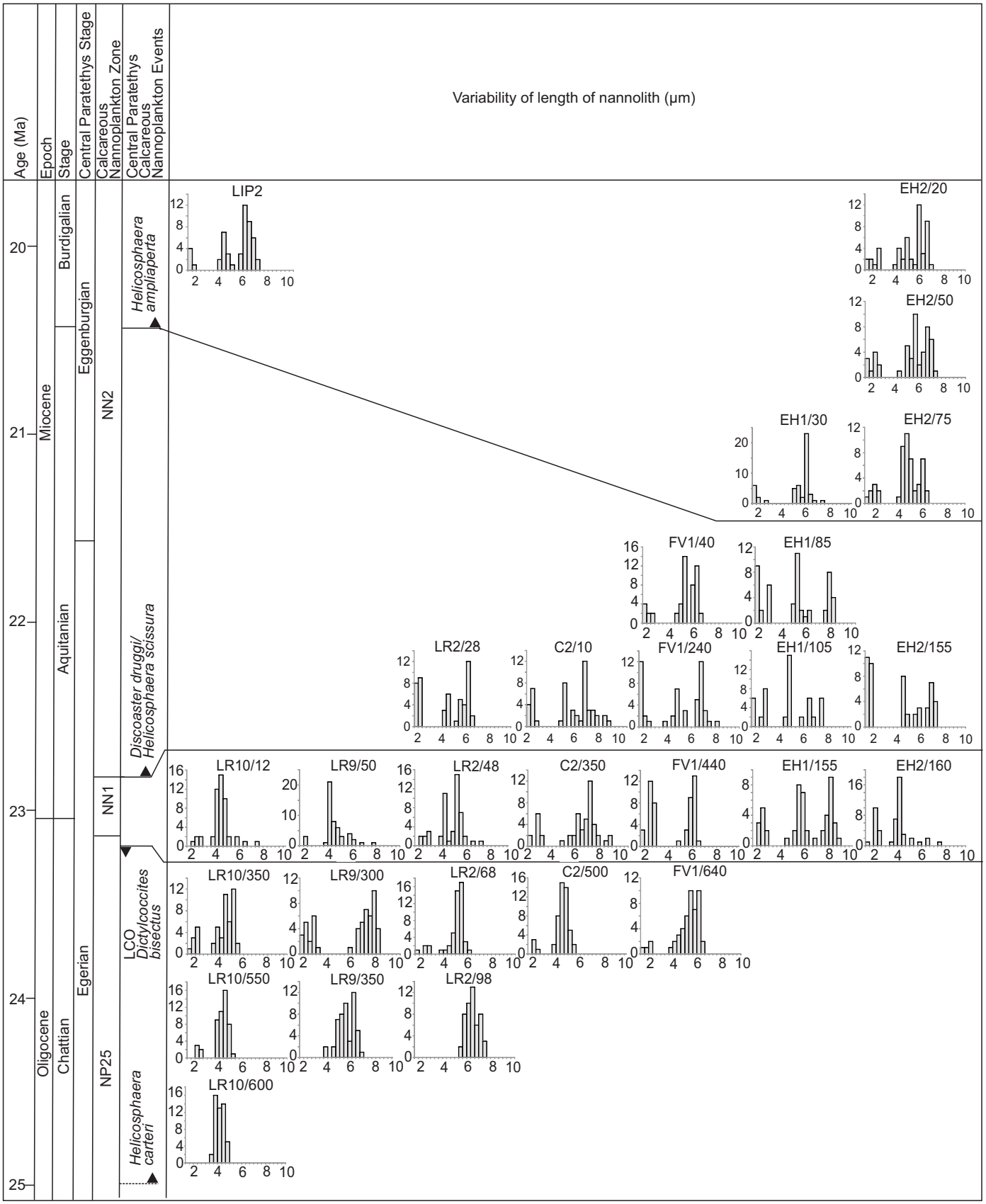


Fig. 5. Variability of the placolith size for the individual assemblages, Egerian to Eggenburgian. Vertical axis, number of specimens; horizontal axis, placolith size (in μm). Location of the boreholes LR10, LR9, LR2, C2, FV1, EH1, EH2, and section Lipovany (LIP) is illustrated on Fig. 1, their lithology and sampled intervals on Fig. 2. Abbreviation: LO, last occurrence.

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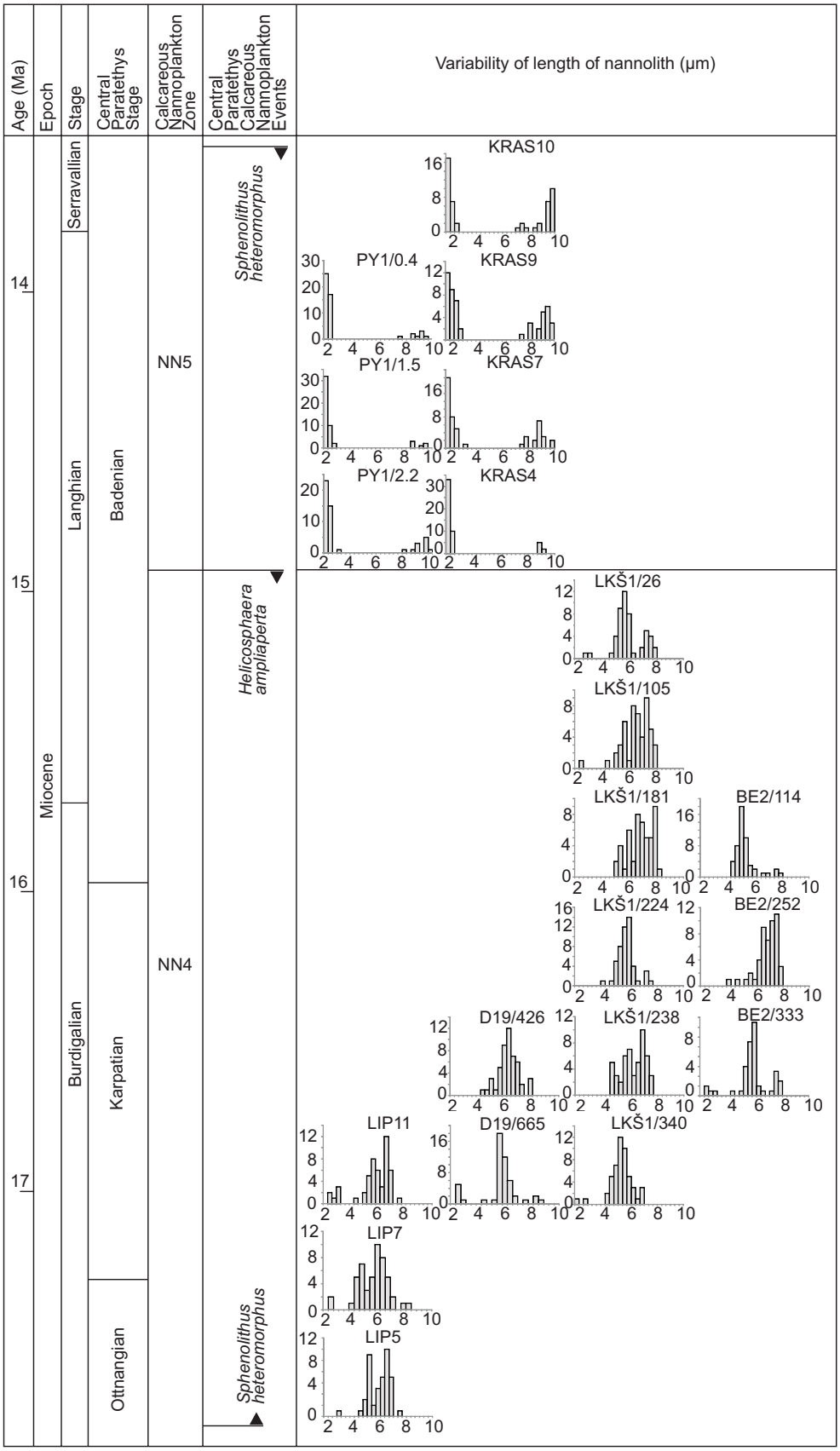


Fig. 6. Variability of the placolith size for the individual assemblages, Ottnangian to Early Badenian. Vertical axis, number of specimens; horizontal axis, placolith size (in μm). Location of the boreholes D19, LKŠ1, BE2, PY1, and sections Lipovany (LIP) and Kralice (KRAS) is illustrated on Fig. 1, their lithology and sampled intervals on Fig. 2.

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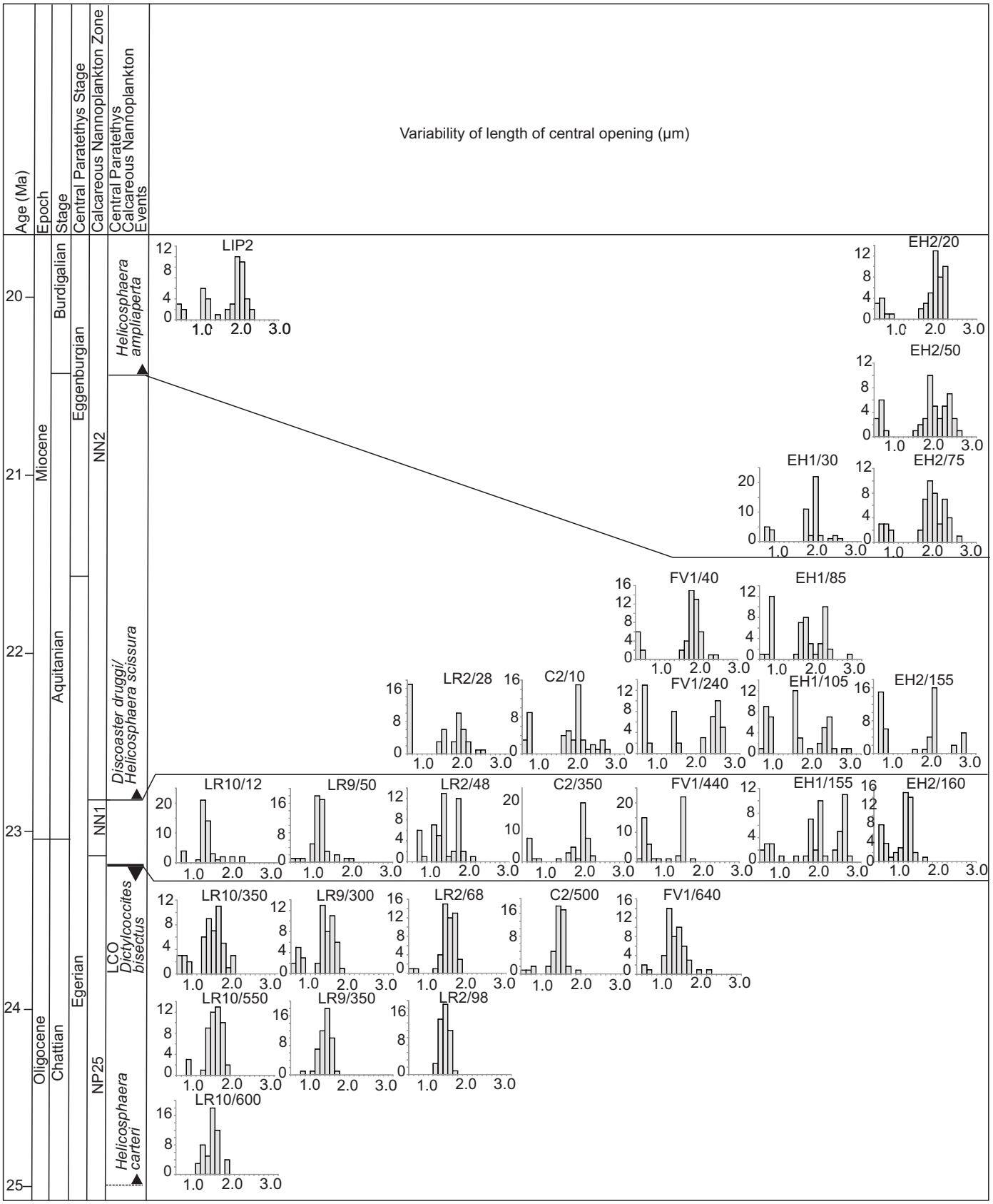


Fig. 7. Variability of the central opening size for the individual assemblages, Egerian to Eggenburgian. Vertical axis, number of specimens; horizontal axis, central opening size (in µm). Location of the boreholes LR10, LR9, LR2, C2, FV1, EH1, EH2, and section Lipovany (LIP) is illustrated on Fig. 1, their lithology and sampled intervals on Fig. 2. Abbreviation: LO, last occurrence.

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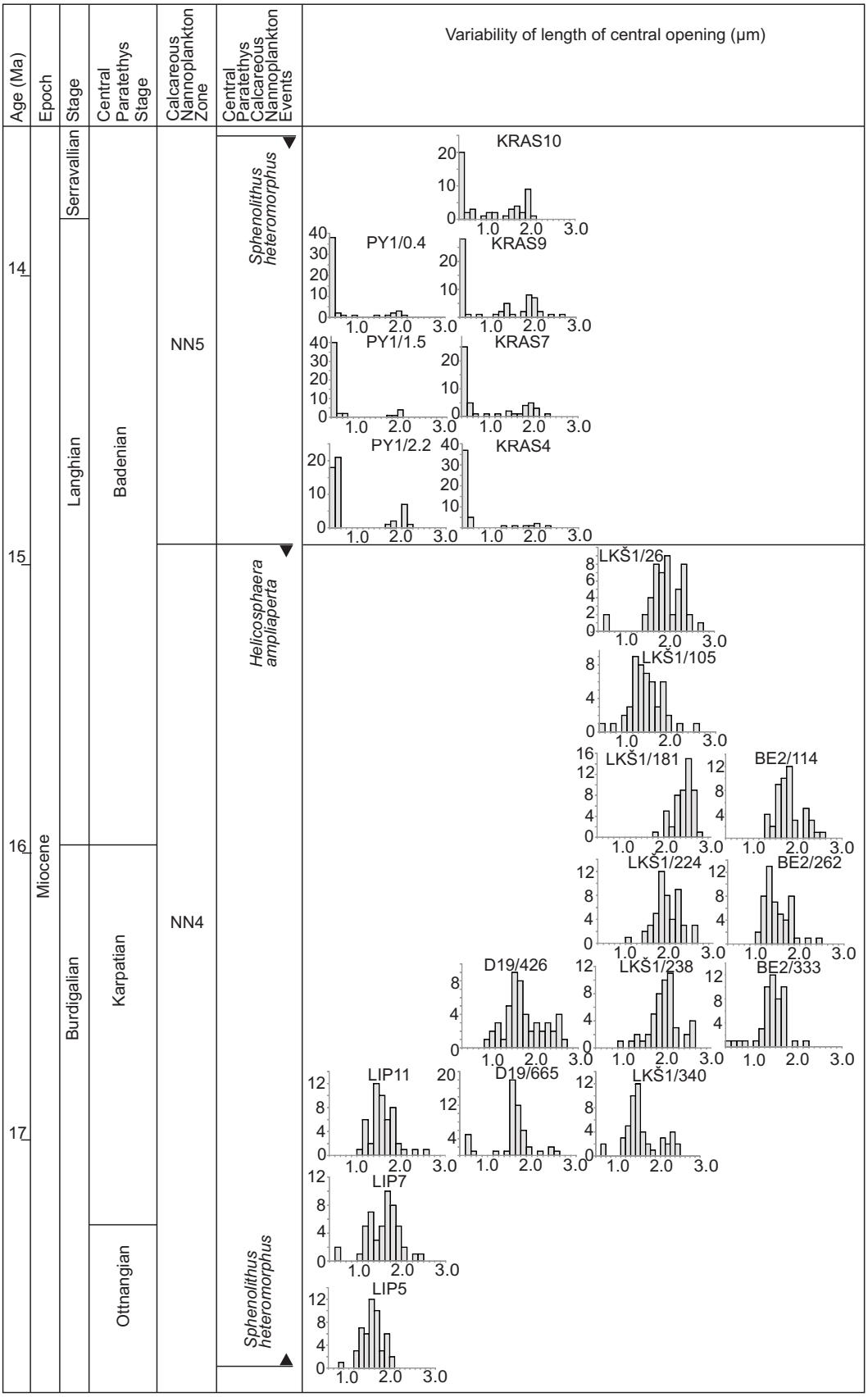


Fig. 8. Variability of the central opening size for the individual assemblages, Ottnangian to Early Badenian. Vertical axis, number of specimens; horizontal axis, central opening size (in µm). Location of the boreholes D19, LKŠ1, BE2, PY1, and sections Lipovany (LIP) and Kralice (KRAS) is illustrated on Fig. 1, their lithology and sampled intervals on Fig. 2.

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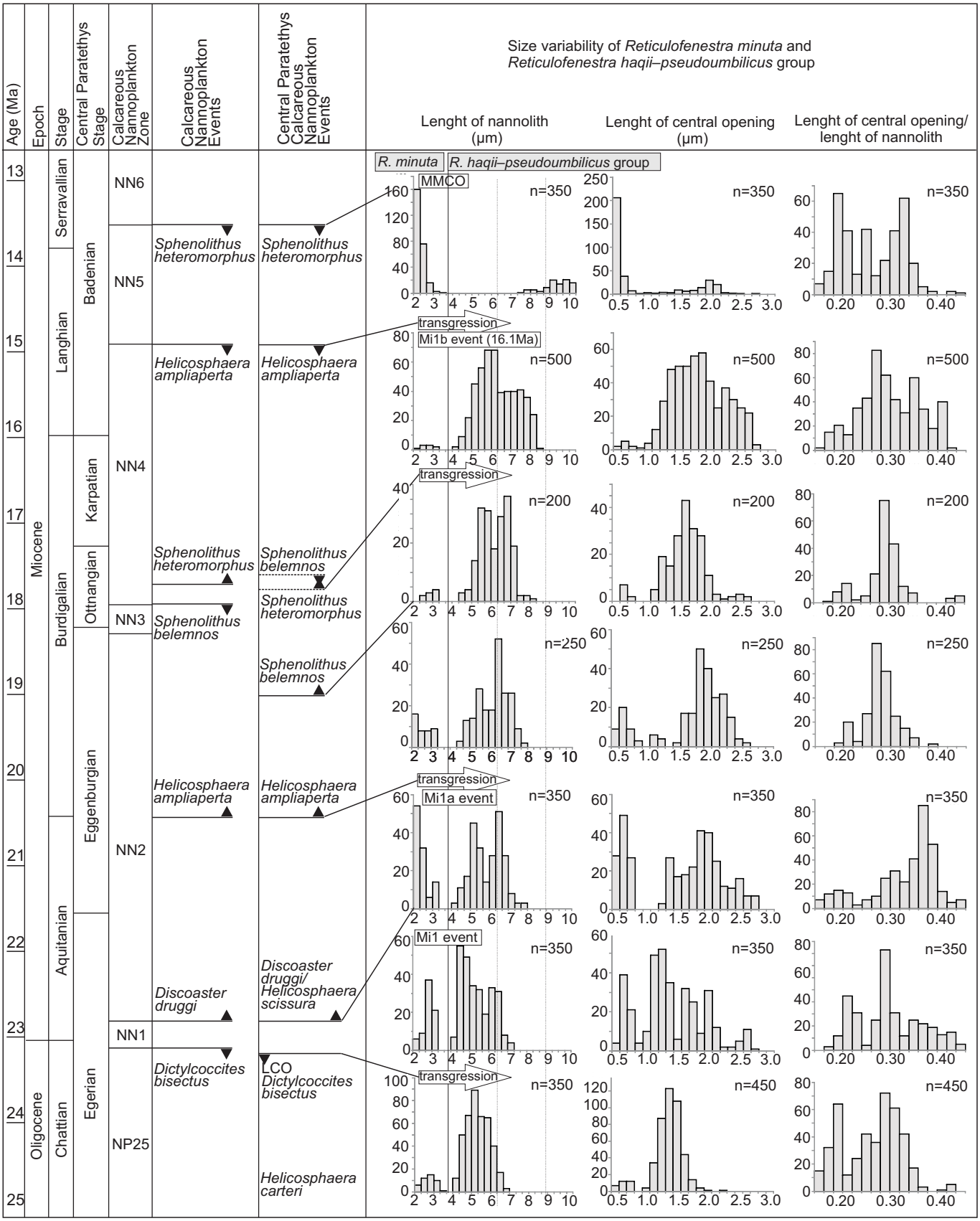


Fig. 9. Morphometric changes of placoliths of *Reticulofenestra minuta* and *Reticulofenestra haqii–pseudoumbilicus* group from the Egerian to the Early Badenian (Burdigalian–Langhian) in the Central Paratethys. Cooling Mi events according Zachos et al. 2001. MMCO = the Middle Miocene Climatic Optimum (Zachos et al. 2001). Abbreviation: LO, last occurrence.

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In conclusion, a satisfactory size has not been found upon which to distinguish species in the *R. haqii–pseudoumbilicus* group and its taxonomy is simply a matter of convention.

Size changes in the Late Oligocene–Early Miocene *Reticulofenestra* and paleoecologic and paleogeographic events in the Central Paratethys

Blooms of *Reticulofenestra minuta*.—Two blooms of the small *R. minuta* were observed in the studied material (Figs. 9, 11): (i) the oldest one in the earliest Miocene (Biochron NN1 and early part of Biochron NN2), is described for the first time. It is probably a local event in the northern part of the Pannonian Basin; (ii) the early Middle Miocene (NN5) event was already documented; it occurred throughout the Central Paratethys (Ćorić and Švábenická 2004; Ćorić and Hohenegger 2008, Spezzaferi et al. 2009). In addition to these two widespread blooms, sporadical blooms of *R. minuta* have also been described in the Central Paratethys, having occurred during the Eggenburgian (Holcová 2002, 2005) and the Karpatian (Spezzaferi and Ćorić 2001; Švábenická et al. 2003).

Besides the Central Paratethys, blooms of *R. minuta* have been described from several stratigraphical levels in the Miocene from the middle to high latitudes (e.g., Cita et al. 1978; Backman 1980). These blooms are heterochronous with the Central Paratethys ones and reflect local paleoenvironmental events (e.g., Messinian salinity crisis; Cita et al. 1978; Wade and Bown 2006).

Interpretation of the causes of the blooms is ambiguous due to inconsistent data about the ecological requirements of small *Reticulofenestra*. Generally, the species is opportunistic and characterizes assemblages from near-shore environment (Haq 1980). Their blooms are connected with environmental stress characterized by rapid environmental changes (Wade and Bown 2006).

Gartner et al. (1983) suggested that variations in the relative abundance of *R. minuta* correlate with changes in nutrient dynamics. Wells and Okada (1997), Flores et al. (1997), Bollmann et al. (1998) and Kameo (2002) regard small *Reticulofenestra* spp. as eutrophic species while Hallock (1987), Beaufort and Aubry (1992), Ćorić and Rögl (2004) suggested that blooms of small *Reticulofenestra* indicate oligotrophic warm water. Wade and Bown (2006) showed that *R. minuta* may have tolerated the brackish to hypersaline, high productivity environments, which prevailed immediately before and after the evaporite deposition during the Messinian salinity crisis.

The two conspicuous blooms of small *R. minuta* in the Central Paratethys occurred during transgression events when the Slovenian corridor permitted incursions of warm water into the Paratethys (Rögl 1998, 1999; Popov et al. 2004). These events are marked by horizons with larger Foraminifera—*Miogypsina* and *Lepidocyclina* in the lowermost Miocene (Váňová 1975), *Amphistegina* and *Planostegina* in the Lower Badenian—and replacement of small *Globigerina* fauna by diversified assemblages with large-sized warm-water species—*Globigerinoides* in the Lower Miocene and *Globigerinoides*, *Praeorbulina*, and *Orbulina* in the Middle Miocene). At the beginning of the blooms, *R. minuta* replaces *Coccolithus pelagicus*, which is an indicator of cold and nutrient-rich waters (McIntyre and Be 1967; Rahman and Roth 1990). Among the benthic foraminifera, the abundance of agglutinated foraminifera decreases (Vass et al. 1983; Holcová 2001; Spezzaferi et al. 2009). The paleoenvironmental turnover correlatable with the Middle Miocene bloom of *R. minuta* has been well explained: Upwelling regime with cooler surface waters and partly dysoxic bottom conditions of the latest Early Miocene were gradually changed to the warm-water condition in the early Middle Miocene and antiestuarine circulation with evaporation prevailing over fresh-water input (Brzobohatý 1987; Ćorić and Rögl 2004; Báldi 2006; Spezzaferri et al. 2009). Comparable circulation turnover due to mixing of in situ cold and incoming warm water masses and paleogeographical changes may be expected also in the earliest Miocene in the South Slovak Basin (Halásová et al. 1996).

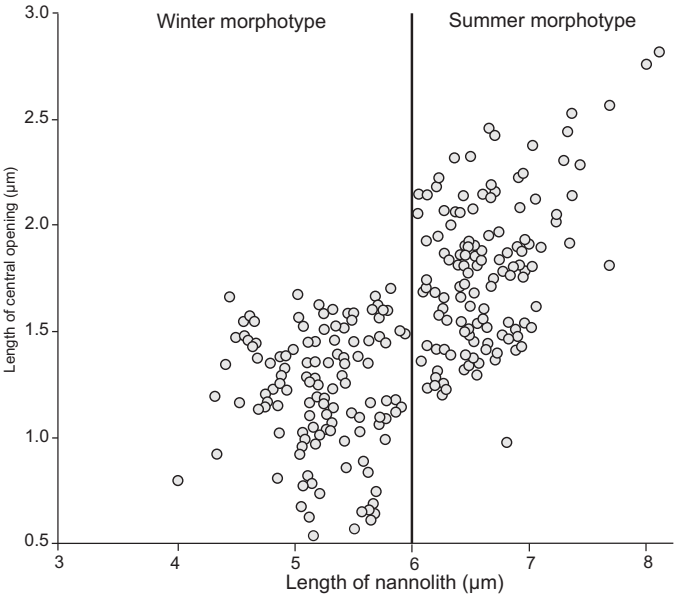


Fig. 10. Two morphotypes of *Reticulofenestra haqii–pseudoumbilicus* group in the lower part of the Zone NN2. Interval FO *Helicosphaera scissura*/FO *Discoaster druggii*–FO *Helicosphaera ampliaperta* lower Zone NN2 (22.8–20.0 Ma); n = 243 (samples LR2/28, C2/10, FV1/240, FV1/40, EH2/155, EH1/85, EH1/105).

Although the incoming of warm-water elements in the marine realm is specific of the two transgressive events, the Early and Middle Miocene conditions in the Central Paratethys substantially differed from the global paleoclimatic situation. The Early Miocene event was marked with the appeareance of arctotertiary elements among palynomorphs (Vass et al. 1988; Planderová 1990) indicative of a global cooling correlated with the Mi1 and Mi1a events. In contrast, the Middle Miocene event can be correlated with the Middle Miocene Climatic Optimum (Gonera et al. 2000; Bicchi et al. 2003; Böhme 2003). Short-term oscillations in the abundance of *R. minuta* during the two blooms were observed (Ćorić and Hohenegger 2008; own unpublished data). These may indicate unstable

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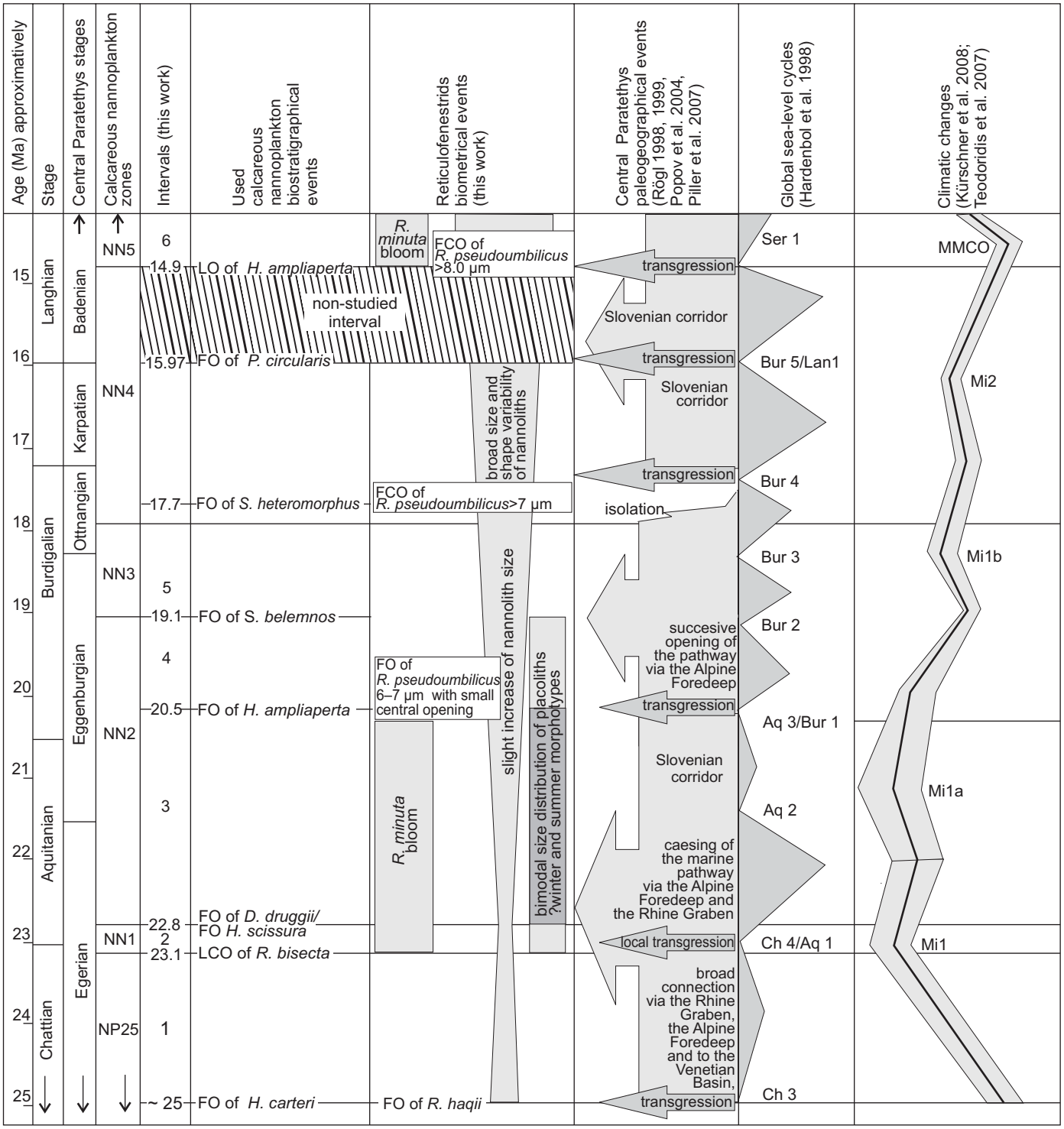


Fig. 11. Correlations between reticulofenestrid biometric events, local and global sea-level changes and paleogeographical events in the Egerian–Early Badenian (Burdigalian–Langhian) of the Central Paratethys. Abbreviations: FCO, first common occurrence; FO, first occurrence; LCO, last common occurrence; LO, last occurrenceFCO; MMCO, the Middle Miocene Climatic Optimum; *D.*, *Discoaster*; *H.*, *Helicosphaera*; *P.*, *Praeorbulina*; *R.*, *Reticulofenestra*; *S.*, *Sphenolithus*.

conditions with short-term oscillations of paleoenvironmental parameters mainly salinity and nutrients. These oscillations have been interpreted in the Biochron NN5 by Hohenegger et al. (2008): warm intervals characterized by high terrigenous input and higher seasonality were alternated with cold periods with lower terrigenous input and lower seasonality. *Reticulofenestram minuta* strongly dominated in the near-shore facies during warm intervals (more than 80%) where high terrigenous input during wet seasons may cause seasonal oscillations of salinity in the upper layer of water column (own unpublished data).

The expansion of near-shore facies as a result of transgres-

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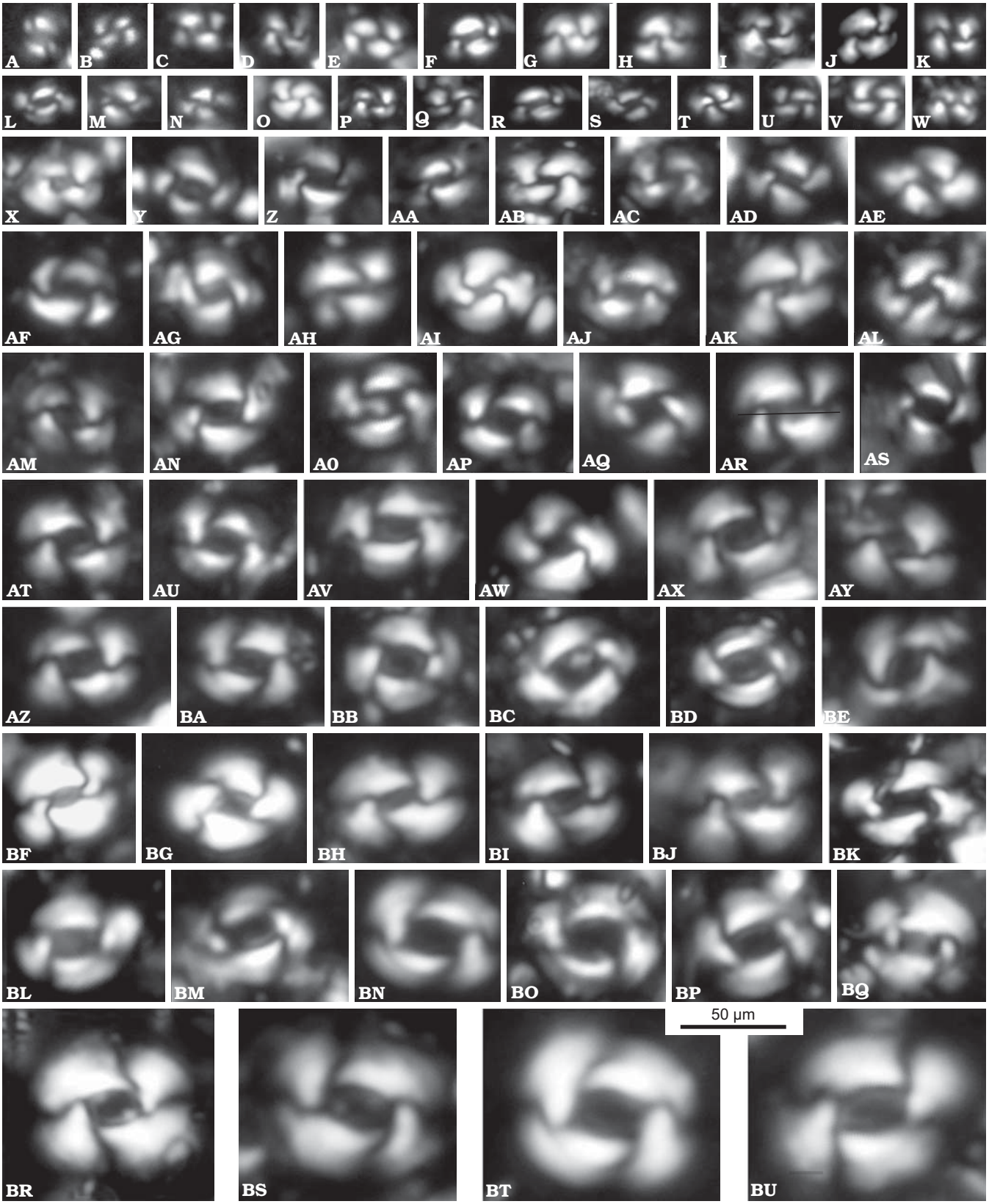


Fig. 12. Elliptical reticulofenestrids from the Central Paratethys Oligocene and Early Miocene. **A**–**K**. *Reticulofenestra minuta* Roth, 1970, < 3.5 µm, zones NN1 and NN2. **A**. Borehole LR-10/12 m, Zone NN2. **B**–**D**. Borehole LR-2/48 m, Zone NN1. **E**, **F**. Borehole LR-2/28 m, Zone NN2. **G**. Borehole FV-1/440 m, Zone NN1. **H**. Borehole EH-1/155 m, Zone NN2. **I**, **J**. Borehole EH-1/85 m, Zone NN2. **K**. Borehole EH-2/155 m, Zone NN2. **L**–**W**. *Reticulofenestra minuta* Roth, 1970, < 3.5 µm, Zone NN5. **L**–**N**. Section Kralice, sample 4. **O**, **P** Section Kralice, sample 7. **Q**, **R**. Section Kralice, sample 10. **S**–**U**. Borehole PY-1/2.2 m. **V**, **W**. Borehole PY-1/1.5 m. **X**–**AY**. *Reticulofenestra haqii–pseudoumbilicus* group (4–5 µm), zones NP25–NN4. **X**, **Y**. Borehole LR-10/350 m, Zone NP25. →

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sion, the changes in water circulation due to the mixing of incoming warmer and in situ colder water masses and, probably, unstable conditions as a result of short term (?seasonal) oscillations of ecological parameters (such as salinity in the upper layers of water column) may have produced conditions favourable to the blooms of small-sized *Reticulofenestra*.

Size changes of the *Reticulofenestra haqii–pseudoumbilicus* group.— Discrepancies between the FOs of individual size categories in the *R. haqii–pseudoumbilicus* group (see chapter: Size changes over time) in the Central Paratethys and in the oceanic realm is notable for interpretation of local vs. global character of size changes in the group. The following discrepancies have been recorded:

(i) The FO of *R. haqii* (> 4 μm) was observed in the studied area in Zone NP25 (Holcová 2005) whereas in the world ocean it lies at the NN1/NN2 boundary (Young 1999).

(ii) The FO of *R. pseudoumbilicus* (> 5 μm) is given in Zone NN4 in the world ocean (Young 1999). In the Central Paratethys, Marunteanu (1999) and Chira (2004) reported this species from near the NN1/NN2 boundary, Andreyeva-Grigorovich et al. (2008) from Zone NN2 and Molčíková and Straník (1987) from Zone NN1. Holcová (2005, this paper) describe the FO of specimens > 5 μm together with FO of *R. haqii* > 4 μm in the uppermost part of the NP25 Zone (Figs. 5, 6, 9).

(iii) The FO of *R. pseudoumbilicus* > 7 μm is given most often being a Middle Miocene event. In the Mediterranean, the FO has been described from Zone NN6 (Fornaciari and Rio 1996), and the FCO of *R. pseudoumbilicus* > 7.0 μm to define the z ones MNN6a and MNN6b (Fornaciari et al. 1996); in the Eastern equatorial Pacific the event was recorded near the NN5/NN6 boundary (Raffi and Flores 1995). However, Howe and Sblendorio-Levy (1998) described the FO of *R. pseudoumbilicus* > 7 μm from the upper part of Zone NN 2 in the Atlantic Ocean near Madeira. This correlates with its FO in the Central Paratethys in Zone NN2 (Molčíková and Straník 1987; this paper). The FCO of *R. pseudoumbilicus* > 7 μm in the Central Paratethys has been recorded from the NN4 Zone. (Molčíková 1983; Švábenická et al. 2003; Eva Halásová, personal communication 2009; this paper).

The Central Paratehys FOs of all three size categories in *R. haqii–pseudoumbilicus* group occurred earlier in the global ocean (including the Mediterranean realm) and cannot be used for interregional biostratigraphic correlations.

The evolution of size in the *R. haqii–pseudoumbilicus* group in the Central Paratethys would suggest an earlier appearance of larger specimens owing to specific conditions in an intracontinental basin. However, the most important morphological changes in the *R haqii–pseudoumbilicus* group can be correlated with the opening of new pathways between the Central Paratethys and the Mediterranean and the immigration of incoming species in the Central Paratethys (Fig. 11). First, the FO of *R. haqii* is associated with the reopening of sea-ways after the Kiscellian anoxia, which is marked by the immigration of foraminifera (Holcová 2008). Second at the upper part of Zone NN2 marked by the FO of *H. ampliaperta,* larger specimens of *R. haqii* (6–7 μm) with small central opening (1.5–1.7 μm) were recorded. The FO of *H. ampliaperta* can be correlated with transgression from the Mediterranean via the Pre-Alpine passage (Rögl 1998; Popov et al. 2004). The transgression is characterized by substantial faunal turnover marked by numerous first occurrences of species of western Mediterranean origin (Kroh and Harzhauser 1999; Vávra 1979; Mandic and Steininger 2003; Piller et al. 2007). Third, the FCO of *R. pseudoumbilicus* > 7 μm at the base of Zone NN4 correlates with the transgression and paleogeographic reorganization and the establishment of a new broad connection via the "Trans-Tethyan trench corridor". The connection enabled faunal exchange between the Mediterranean and Paratethys (Rögl 1998; Rögl et al. 2003; Popov et al. 2004). Fourth, the FO of *R. pseudoumbilicus* > 8 μm is associated with the reopening of the Mediterranean–Indo-Pacific seaway (Rögl and Steininger 1983; Rögl 1998, 1999; Popov et al. 2004). This large transgression caused rapid immigration of the marine fauna (e.g., Harzhauser and Piller 2007; Holcová 2008) termed the EBBE, or Early Badenian-Build-up-Event (Harzhauser and Piller 2007).

Slight gradual size changes in the *R. haqii–pseudoumbilicus* group were recorded during periods without paleogeographical changes (Fig. 11). The decrease in the placoliths size in the late Egerian (upper NP25 to NN1 zonal interval) may correspond with cooling interpreted from occurrence of arctotertiary elements among palynomorphs (Planderová 1990). Also Kürschner et al. (2008) hypothesized a cooling during this interval correlatable with the Mi1/1a event.

The size of placoliths slightly increased in the Eggenburgian, although this increase is not general (Figs. 5, 6, 9). This size increase can be correlated with warming (Kürschner et al. 2008).

Bimodal size distribution in the *R. haqii–pseudoumbilicus* group was recorded firstly during the Zone NN1 and in the lower part of the Zone NN2 (Fig. 9, 10). The smaller

Z, **AA**. Borehole LR-9/350 m, Zone NP25. **AB**. Borehole LR-2/98 m, Zone NP25. **AC**–**AE**. Borehole C-2/500 m, Zone NP25. **AF**, **AG**. Borehole EH2/160 m, Zone NN1. **AH**, **AI**. Borehole EH-1/105 m, Zone NN2. **AJ**, **AK**. Borehole EH-1/85 m, Zone NN2. **AL**. Borehole EH-2/75 m, Zone NN2. **AM**, **AN**. Borehole LKŠ-1/340 m, Zone NN3. **AO**–**Q**. Borehole LKŠ-1/181 m, Zone NN4. **AR**, **AS**. Borehole LKŠ-1/105 m, Zone NN4. **AT**–**BE** *Reticulofenestra haqii–pseudoumbilicus* group (5–7 μm), zones NP25–NN4. **AT**, **AU**. Borehole LR-10/350 m, Zone NP25. **AV**. Borehole LR-9/350 m, Zone NP25. **AW**, **AX**. Borehole C-2/500 m, Zone NP25. **AY**. Borehole EH2/160 m, Zone NN1. **AZ**, **BA**. Borehole EH-1/105 m, Zone NN2. **BB**, **BC**. Borehole EH-1/85 m, Zone NN2. **BD**, **BE**. Borehole EH-2/155 m, Zone NN2. **BF**–**BK**. *Reticulofenestra haqii–pseudoumbilicus* group (6–7 m) narrow central opening, Zone NN2. **BF**, **BG**. Borehole EH-1/155 m, Zone NN2. **BH**, **BI**. Borehole EH-1/105 m, Zone NN2. **BJ**, **BK**. Borehole EH-2/85m, Zone NN2. **BL**–**BQ**. *Reticulofenestra haqii–pseudoumbilicus* group (6–8 μm), Zone NN4. **BL**, **BM**. Borehole LKŠ-1/105 m, Zone NN4. **BN**, **BO**. Borehole LKŠ-1/26 m, Zone NN4. **BP**, **BQ** Borehole BE-2/114 m, Zone NN4. **BR**, **BU**. *Reticulofenestra haqii–pseudoumbilicus* group (> 8 μm), Zone NN5. **BR**. Borehole PY-1/2.2 m. **BS**. Borehole PY-1/1.5 m. **BT**, **BU**. Section Kralice, sample 4.

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morphotype (< 6 μm) is characterized by a small central opening 0.5–1.5 μm. Larger morphotype (> 6 μm) have larger central openings (Fig. 10).

Backman (1980) and Beaufort and Aubry (1992) described a dependence of the morphometric variability of *R. pseudoumbilicus* on seasonal or latitudinal temperature differences during the Miocene and Pliocene. According to Backman (1980) low latitude individuals are characterized by a larger central opening and can be slightly larger. High latitude individuals are distinguished by a smaller central opening. Beaufort and Aubry (1992) have proposed alternations of winter and summer morphotypes in the Lower Miocene of high-latitude populations. The occurrence of two size categories (3.5–6 μm and 6–8 μm) in the late Egerian–early Eggenburgian of analysed samples may also represent seasonal morphotypes: the smaller morphotype could represent the winter morphotype while the larger morphotype with a larger central opening could represent the summer morphotype (Fig. 10) This assumed seasonality has been corroborated by palaeoclimate estimates based on plant macrofossils preserved in the Břešťany Clay from the Most Basin (Teodoridis and Kvaček 2006; Kvaček and Teodoridis 2007). These studies have shown a significant difference between a Coldest Month Mean Temperature (CMMT) and Warmest Month Mean Temperature (WMMT), which is 15–20°C (Teodoridis 2007; Teodoridis et al. 2011).

Conclusions

Based on biometric analysis, two size groups of elliptical reticulofenestrids from the NP25–NN5 zonal interval were distinguished. One group corresponds to the small *R. minuta* (< 3 μm); the other is the *R. haqiii–pseudoumbilicus* group (3.5–10 μm). A clear criterion upon which to define species in this group has not been found, and species taxonomy (*R. haqii* vs. *R. pseudoumbilicus*) can only be conventional (Fig. 12).

Two blooms of small *R minuta* were observed. The earliest Miocene bloom (NN1 and lower part of Zone NN2) is probably a local event for the northern part of the Pannonian Basin. The early Middle Miocene bloom (Zone NN5) was already known and has a global occurrence in the Central Paratethys basins. These blooms can be correlated with the expansion of near-shore facies associated with transgression, the incursions of warm water into the Paratethys, which may cause changes in water circulation due to the mixing of warmer and colder water masses. Unstable conditions with short-term oscillations of ecological parameters (probable salinity in the upper layers of water column) can be also expected.

The FOs of all three size categories in *R. haqii–pseudoumbilicus* group (3–5 μm, 5–7 μm, > 7 μm) occurred earlier in the Central Paratehys than in the global ocean and the Mediterranean region. They cannot be used for interregional biostratigraphical correlations.

The slight gradual changes in size in the *R. haqii–pseudoumbilicus* group can be correlated with paleoclimatic trends. The decrease in size of the placoliths in the late Egerian (upper Zone NP25 and Zone NN1) may result from cooling during the Mi1/1a event.

The size of placoliths slightly increased from the Eggenburgian to the Badenian; the interval can be generally characterized by warming.

The two morphotypes occurring in the late Egerian–Early Eggenburgian may represent seasonal morphotypes. The smaller morphotype could represent the winter morphotype while the larger morphotype with a slightly larger central opening could represent the summer morphotype.

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