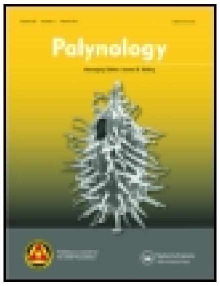


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# *Mendicodinium mataschenensis*: a new endemic dinoflagellate cyst from the Late Miocene (Tortonian) of Lake Pannon (Austria)

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The organic-walled dinoflagellate cyst *Mendicodinium mataschenensis* is introduced here as a new species. The taxon derives from lower Tortonian clays from the Mataschen clay pit in Styria, Austria. These deposits formed in Lake Pannon, which was characterized throughout the Late Miocene by its highly endemic and rapidly evolving biota. As most species of *Mendicodinium* are known from restricted marine and brackish paleoenvironments, its occurrence in Lake Pannon may be considered further evidence for the brackish water conditions prevailing in this lake.

**Keywords:** dinoflagellate cysts; *Mendicodinium*; Lake Pannon; Mataschen; Austria; Late Miocene



## 1. Introduction

*Mendicodinium* first appeared during the Early Jurassic and became established since then in shallow water environments, often associated with brackish conditions and freshwater influx. Due to its unspectacular and simple morphology it is frequently confused with other palynomorphs (e.g. *Inaperturopollenites*); its occurrence in Cenozoic assemblages therefore might be underestimated. One of these occurrences is documented in the early Tortonian of Lake Pannon which is characterized by brackish and alkaline water chemistry (Harzhauser et al. 2007). At that time, Lake Pannon was characterized by a highly endemic fauna and flora also including a very unusual dinoflagellate assemblage. Species had to adapt to the new environments that are atypical in marine settings. Among these, *Impagidinium* is most striking. This usually open marine taxon appears in high numbers even in very shallow lake settings during the early Tortonian.

## 2. Geologic setting and age of the Mataschen clay pit

The Mataschen clay pit (15°57′33″E/46°54′18″N) is located in the Eastern Styrian Basin, Austria (Gross 2004; figure 1). The *c*. 30 m thick section represents a lacustrine to fluvial lower Tortonian succession, which formed along the north-western margin of Lake Pannon. The lower part comprises *c*. 5 m of clays with abundant plant remains, molluscs and autochthonous *Glyptostrobus*-tree trunks. It is part of the Eisengraben Member of the Feldbach Formation. The sedimentary environment is interpreted as a shallow embayment that was surrounded by marshes. The material studied derives from two 0.5 m cores that were drilled in this unit. Up-section sandy clay and fine sand intercalations belong to the Sieglegg Member. This fluvially influenced unit is not studied here. A detailed description of the regional geology and the sedimentology of the section is given by Gross (2004) and Gross et al. (2008, 2011).

## 3. Materials and methods

Environmental shifts within paleo-lakes are detected through high-resolution analyses of cores, which allow changes to be described on decadal to millennial scales. In an ongoing project on the paleoenvironmental changes associated with the formation of Lake Pannon during the early Tortonian (early Pannonian), the Mataschen clay pit was selected (Kern et al. 2012). Within the current project, two subsequent 50 cm long cores (6 and 7) were sampled with a sample density of 10 mm (98 samples) and analyzed for dinoflagellate cysts and pollen assemblages. In addition, the ostracod assemblages were analyzed at 5 mm intervals (Gross et al. 2008).

The samples were crushed, 10 g dry weighed and one *Lycopodium* tablet was added before demineralization. Carbonates were removed using cold 35% HCl.

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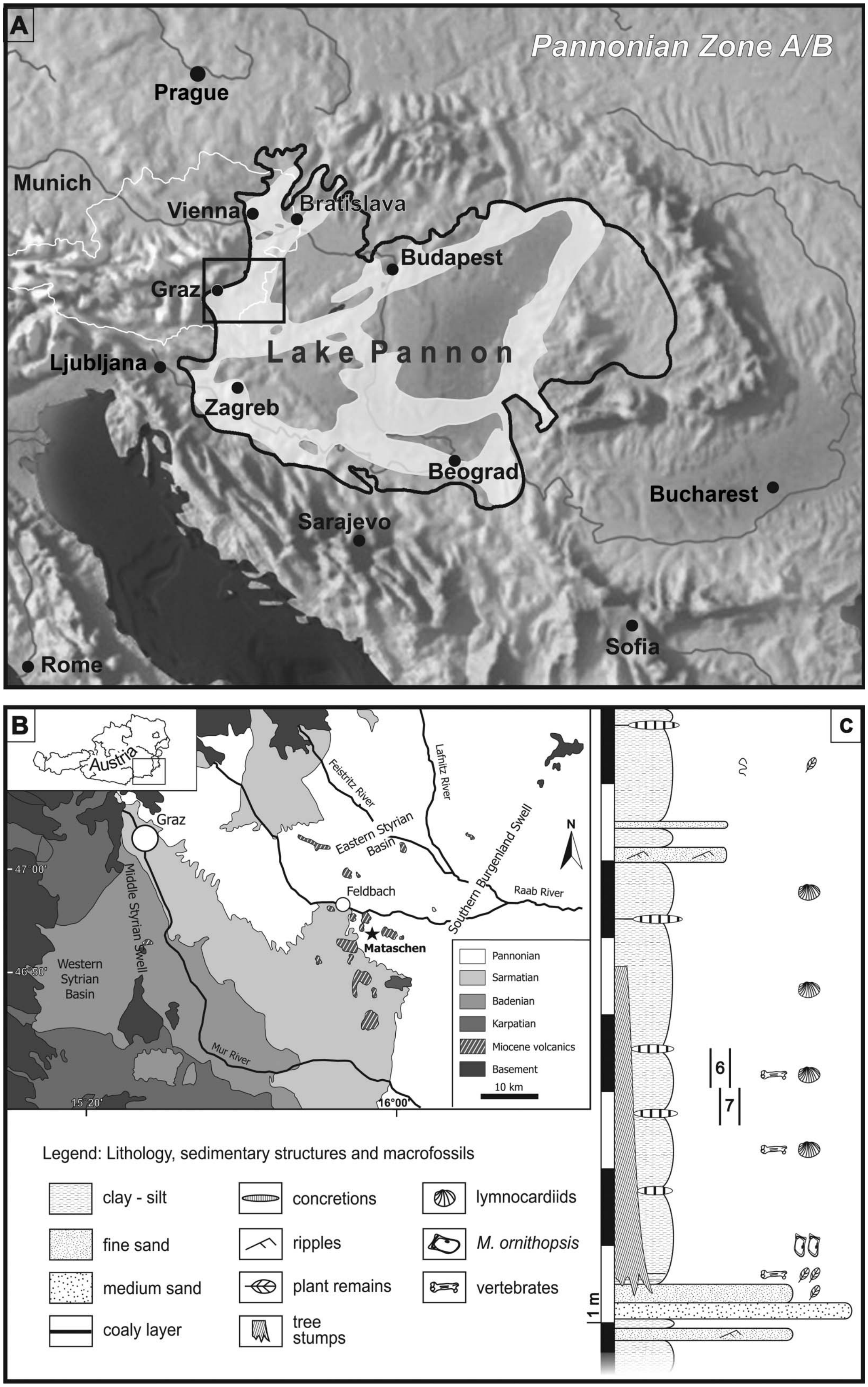


Figure 1. (A) Lake Pannon during the early Tortonian (light gray). The solid black line represents the extent of the Lake (for more details see Magyar et al. 1999). (B) Map illustrating the location of the Mataschen section and the distribution of Miocene sediments in the Styrian Basin. (C) The Mataschen section and the position of the two cores studied (based on Gross et al. 2008).

Silicates were removed by 48 hour treatment with 48% HF. Further treatment with dilute HCl was applied to some samples to remove any fluorides that may have formed during the HF treatment. No oxidation was applied. The residues from the 15–125 $\mu$m sieve fraction were used and stained with Safranin 'O' to facilitate the microscopic analysis. Two slides from each sample were prepared using glycerine jelly and sealed with nail varnish.

The slides were scanned using an Olympus BH2 microscope at 400 × magnification under normal transmitted light. Up to 200 dinoflagellate cysts were counted per sample, which is sufficient to cover the rather low diversity. Photomicrographs were taken of well-preserved representative specimens using a Leica DFC 320 digital camera fitted to a Carl-Zeiss (Axioplan 2) microscope. Mounts for SEM studies were made by air-drying water-suspended residues on a circular glass cover slip (12 mm) that were mounted on aluminium stubs. Stubs were coated with platinum. SEM observations and photomicrographs were made by using DSM 982 Gemini SEM, operating at a working voltage of 10 kV. All microscope slides, SEM stubs and residues are housed in the paleontological collection of the Institute of Earth Sciences, Graz University, Austria. Those systematic references that do not appear in the bibliography can be found in Fensome et al. (2008).

## 4. An overview of the recorded dinoflagellate cyst assemblage

*Mendicodinium mataschenensis* n. sp. is associated with a well-preserved dinoflagellate cyst assemblage of low diversity. Due to the endemic nature of the biota of Lake Pannon, none of the well-known Mediterranean or Atlantic Late Miocene dinoflagellates occured in this lake. Thirty-one taxa of dinocysts were identified including some unknown cyst morphotypes (Appendix 1). Gonyaulacoids, mainly represented by *Spiniferites*, *Achomosphaera* and *Impagidinium*, are the characteristic taxa of the assemblages. These taxa are known as characteristic components of the dinoflagellate cyst assemblages of Lake Pannon (Sütőné; Szentai 2002). *Protoperidinium* spp. and other protoperidinioid taxa such as *Selenopemphix* and small round brown cysts (cf. *Brigantedinium*) are also represented in low abundances. The remaining taxa comprise *Pyxidinopsis psilata*, cf. *Algidasphaeridium* sp., cysts of *Polykrikos* and dinoflagellate cyst type A of Matsuoka (1987). In addition to the dinoflagellate cysts, there is a considerable occurrence of freshwater algae, e.g. *Pediastrum* and *Botryococcus*, as well as fungal spores. Acritarchs are represented by *Nannobarbophora*, *Cyclopsiella* and *Cymatiosphaera*.

## 5. Systematic palynology

Division DINOFLAGELLATA (Bütschli 1885) Fensome et al. 1993
Subdivision DINOKARYOTA Fensome et al. 1993
Class DINOPHYCEAE Pascher 1914
Subclass PERIDINIPHYCIDAE Fensome et al. 1993
Order GONYAULACALES Taylor 1980

Genus *Mendicodinium* Morgenroth 1970 emend. Bucefalo Palliani, Riding & Torricelli 1997
Type: *Mendicodinium reticulatum* Morgenroth 1970

*Mendicodinium mataschenensis* Soliman & Feist-Burkhardt n. sp.
Plate 1, figures 1–9; Plate 2, figures 1–9; Plate 3, figures 1–12; Figure 2

**Holotype**. Plate 1, figures 1–3; England Finder H47/2; sample 20 of core 7, slide B, Mataschen clay pit, Styrian Basin, Austria.
**Paratypes**. Plate 1, figures 4–6; England Finder H48/3; sample 20 of core 7, slide B, Mataschen clay pit, Styria Basin, Austria.
**Repository**. The holotype and the type material (residue, rock sample and SEM stubs) are deposited in the Joanneum Museum, Graz, Austria under number UMJ G&P 210901 and UMJ G&P 210902, respectively.
**Type locality**. Mataschen clay pit near Kapfenstein (Styria, Austria), 15°57′33″E/46°54′18″N (2.3 km NW of Kapfenstein, 7.7 km SE of Feldbach, Styria, Austria).
**Type horizon**. Lower part of the Mataschen clay pit (Feldbach Formation, Sieglegg Member; Gross et al. 2008); samples of cores 6 and 7.
**Stratigraphic horizon**. Early Tortonian (early Pannonian).
**Derivation of name**. From the type locality near the village of Mataschen, Styria, Austria.
**Diagnosis**. A small species of *Mendicodinium* with an autophragm densely ornamented with rugulae of low relief.
**Description**. A subspherical, proximate and small species of *Mendicodinium*. The cyst is pale yellow or pale brown and sometimes colorless. The autophragm is thin (less than 0.3 $\mu$m) and densely ornamented with non-tabular rugulae of a maximum height of *c.* 0.5 $\mu$m. Three morphologies of the rugulae are observed: closely adjacent short, high and sinuous ridges (Plate 3, figures 1–4); wide ridges of moderate height (Plate 3, figures 5, 8), or partly fused ridges into granules (Plate 3, figure 6). The cyst is dorso-ventrally compressed and some specimens are partially folded or crumpled. The cyst broadens at the cingulum, and the hypocyst is slightly larger than the epicyst. The 'split' above the cingulum is spirally arranged, and causes an offset of the ends of the cingulum on the ventral side. The

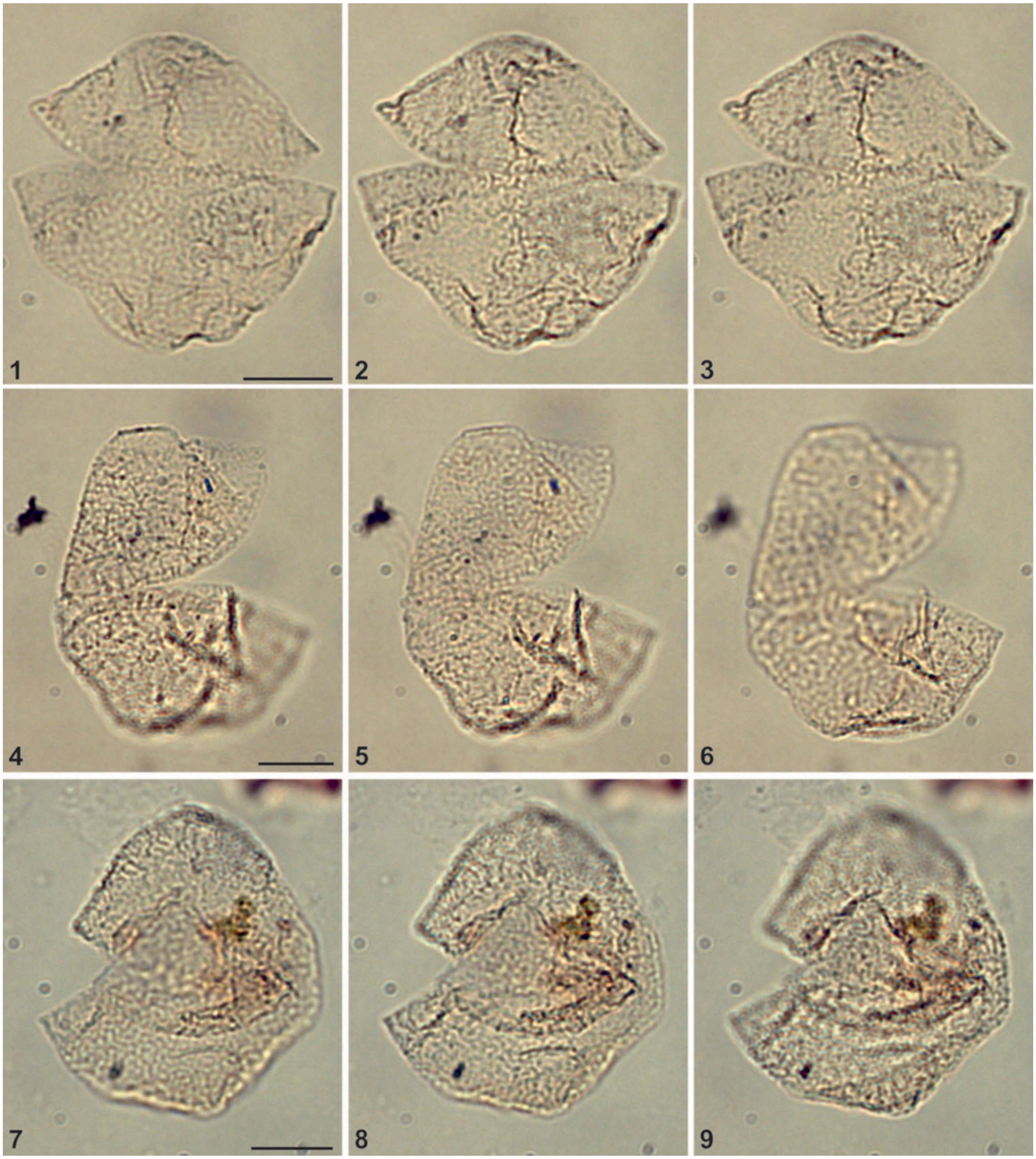


Plate 1. *Mendicodinium mataschenensis* n. sp., all photomicrographs were taken using plain transmitted light. Specimens are all from slide B of sample 20 of core no. 7, Mataschen, Styrian Basin, Austria. The England Finder reference (EF) is given. Scale bar = 10 $\mu$m. 1–3. Holotype, EF: H47/2; specimen in dorsal view, successive focal series from low to high focus. Figure 1. Ventral face in low focus. Figure 2. Mid-focus. Figure 3. Dorsal face in high focus. Figures 4–6. Paratype; EF; H48/3; specimen in left lateral view; successive foci. Note the detached epicyst (operculum). Figures 7–9. Paratype; EF: J46/0; specimen in lateral view, successive foci. Note the two cyst halves are partially separated (the archeopyle has not fully formed), and the roundly pointed apex of the epicyst.

epicyst is slightly pointed at the apex and the hypocyst is flattened at the antapex. There is no indication of horns or bosses. The cingulum may be indicated by a narrow strip of low ornamentation (Plate 3, figure 5) which is, however, rarely observed. The archeopyle is of epicystal type (tEa) with smooth sutures. The

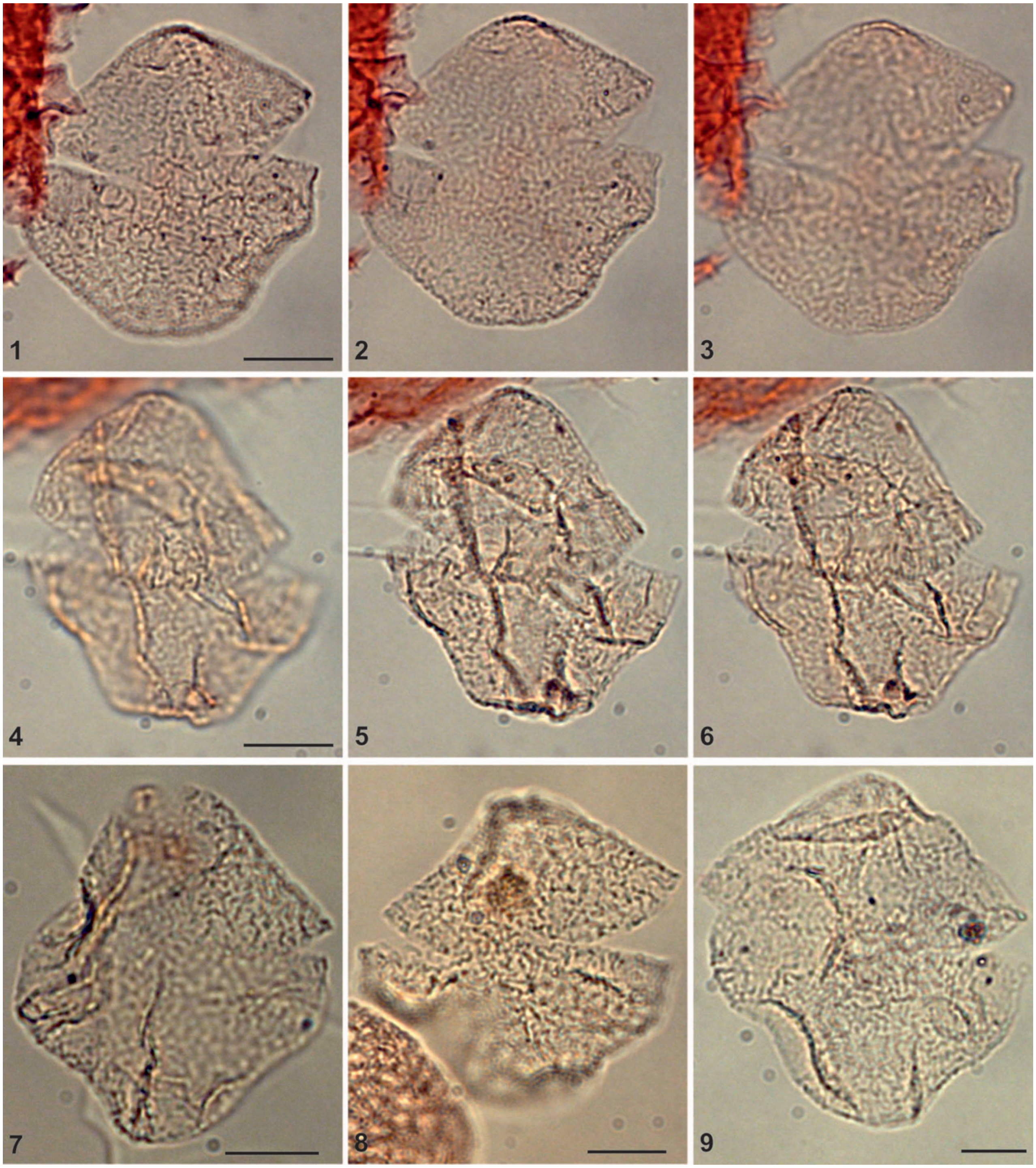


Plate 2. *Mendicodinium mataschenensis* n. sp., all images are in bright field illumination. All from slide B of sample 20 of core no. 7. The England Finder reference (EF) is given. Scale bar = 10 $\mu$m. Figures 1–3. Specimen in ventral view, successive focal series from high to low focus. Figure 1. Ventral face in high focus. Note the pointed apex and the flat antapical area. Figures 4–6. EF: U26/0; specimen in ventral view showing the longitudinal folds, successive foci. Figure 7. EF: U62/0; specimen in ventral view, dorsal face in low focus. Note the flattened antapical area. Figure 8. EF: F70/0; specimen in ventral view, ventral face in high focus, note the coarse rugulate ornamentation. Figure 9. EF: D63/0; partially deformed specimen in ventral view.

operculum is adnate ventrally. Tabulation is indicated only by the archeopyle and, sometimes, by a faintly indicated cingulum (Plate 3, figure 5).

**Dimensions**. Holotype length 35 $\mu$m; width 36 $\mu$m. Minimum cyst length: 26.0 $\mu$m; maximum cyst length 37.0 $\mu$m; mean: 30.5 $\mu$m. Minimum cyst width at

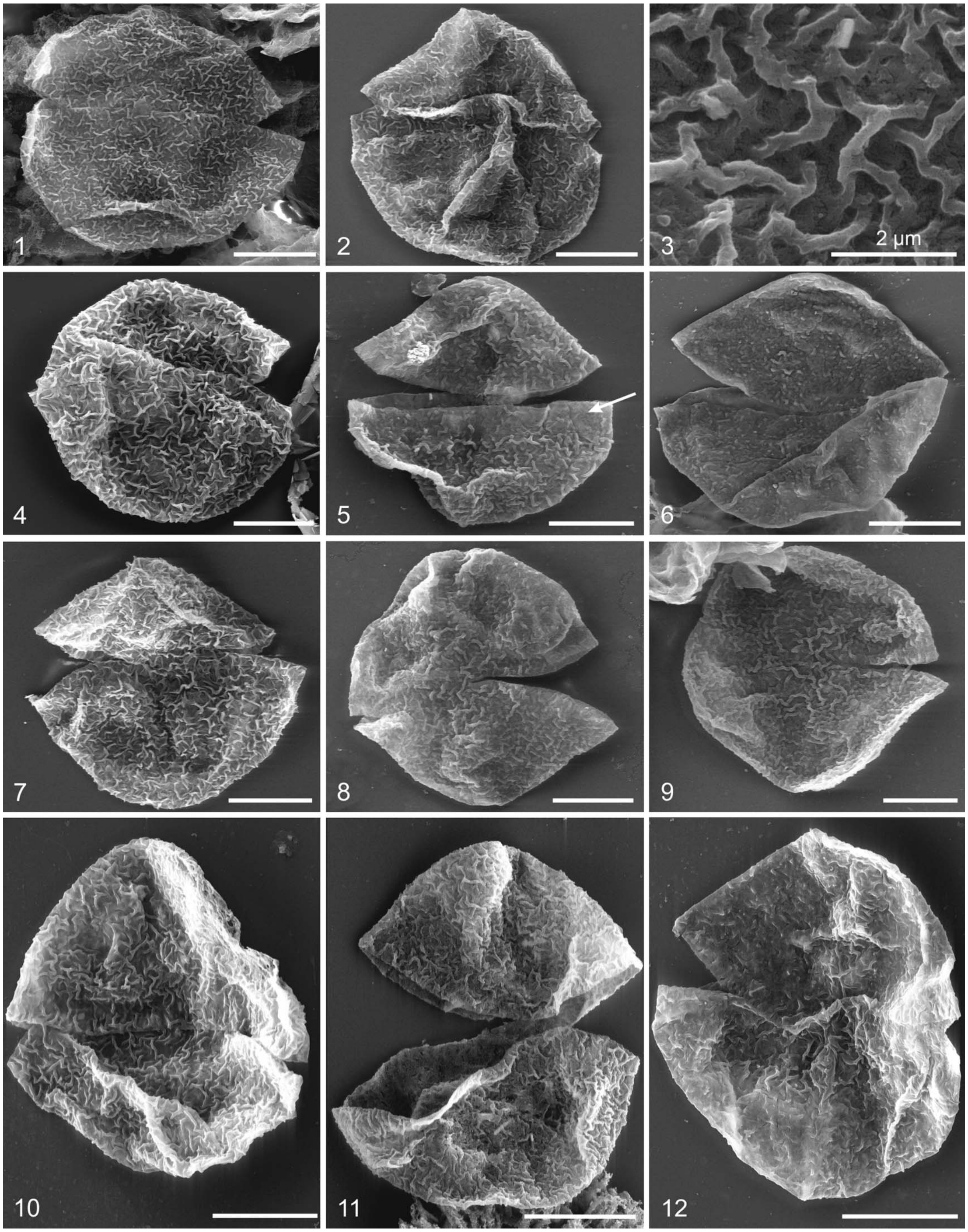


Plate 3. *Mendicodinium mataschenensis* n. sp. from the Mataschen section, Styrian Basin, Austria. All are scanning electron micrographs. The sample number is given for each specimen, where M6 = Core no. 6, M7 = Core 7. Scale bar = 10 $\mu$m. Figure 1. Sample M7–40; specimen in dorsal view. Note that the hypocyst is larger than the epicyst. Figure 2. Sample M6–25; partially folded specimen in ventral view. Figure 3. Samples M7–20; close up on the surface ornamentation showing the fine structure of the rugulae. Figure 4. Sample M7–30; specimen in lateral view. Note the coarse rugulate ornamentation. Figure 5. Sample M7–20; specimen in dorsal view. The cingulum is faintly indicated by subdued ornamentation (see arrow). Figure 6. Sample M7–20; specimen in dorsal view showing very low relief ornamentation. Figure 7. Sample M7–35; specimen in ventral view. Note the large hypocyst and the pointed apex of the epicyst. Figure 8. Sample M7–25; specimen in latero-ventral view with approximately equally sized epicyst and hypocyst. Figure 9. Sample M7–20; specimen in lateral view. Note the two cyst halves are partially separated and the cingulum is indicated by the furrow. Figure 10. Sample M7–20; partially deformed specimen in dorsal view. Figure 11. Sample M7–30; specimen in dorsal view. Note that the two cyst halves are still in contact on the ventral side. Figure 12. Sample M7–20; specimen in ventral view with low-relief ornamentation and pointed apex.

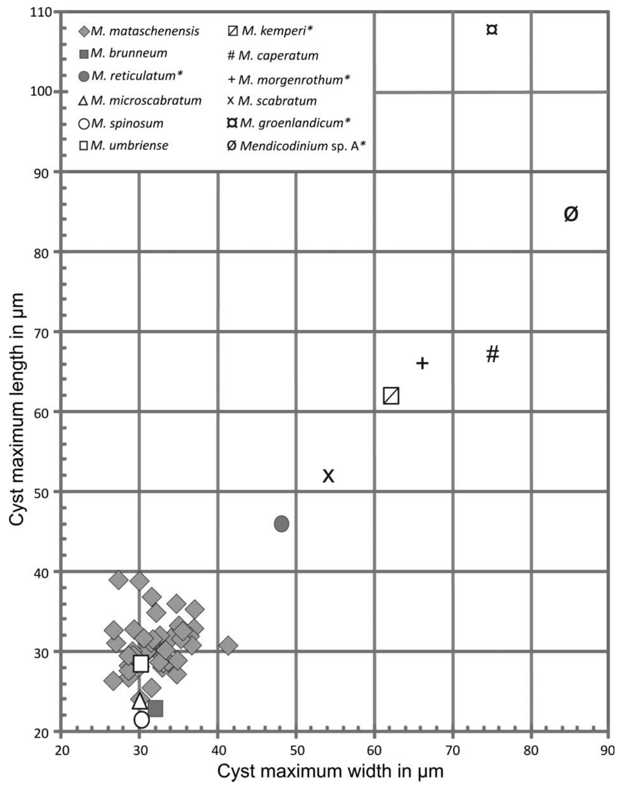


Figure 2. Measurements of *Mendicodinium mataschenensis* n. sp. (maximum cyst length versus maximum cyst width) in comparison with other *Mendicodinium* species. *Indicates one specimen measurement (mostly holotype) while others are averages.

cingulum: 27 $\mu$m; maximum cyst width at cingulum: 41.0 $\mu$m; mean: 32.0 $\mu$m (Figure 2). 52 specimens measured.

**Comparison**. *Mendicodinium reticulatum* Morgenroth 1970, described from the Lower Jurassic (Lias delta) of Germany, is morphologically very close to *Mendicodinium mataschenensis*. However, *Mendicodinium reticulatum* is slightly larger (length 45.0–46.0 $\mu$m, 3 specimens; width 41.0–48.0 $\mu$m, four specimens; Morgenroth 1970, p. 348) and has a reticulate surface ornamentation. In terms of surface ornamentation, it is similar to *Mendicodinium* sp. A of Wrenn and Kokinos (1986) from the Middle Miocene, De Soto Canyon, Gulf of Mexico; *Mendicodinium mataschenensis* is however smaller in size and characterized by an adnate operculum rather than by a free operculum (based on the specimens illustrated in Wrenn and Kokinos 1986; plate 4, figure 3 and plate 10, figure 4). '*Mendicodinium robustum*' Zevenboom and Santarelli 1995 ex Fensome et al. 2009 from the late Serravallian–early Tortonian, Giammoia-Falconara sections (Caltanissetta Basin), Italy, has a scabrate wall (Zevenboom 1995, p. 159). The wall of *Mendicodinium groenlandicum* (Pocock & Sarjeant 1972) Davey 1979 from the Middle Jurassic of Greenland is smooth or slightly punctate. *Mendicodinium mataschenensis* differs from *Mendicodinium kemperi* Heilmann-Clausen & Thomsen 1995, from the Barremian of Ahlum-1 borehole and Gott clay pit at Sarstedt, Lower Saxony Basin, Germany, by its small cyst width (32.0 $\mu$m versus 67.0 $\mu$m), in having a uniform type of surface ornamentation, a slightly pointed apex and the absence of sutures (Heilmann-Clausen and Thomsen 1995). With regard to cyst size, *Mendicodinium mataschenensis* is similar to the *Mendicodinium* species (*Mendicodinium umbriense*, *Mendicodinium spinosum*, *Mendicodinium microscabratum* and *Mendicodinium brunneum*) described form the Lower Jurassic of Italy by Bucefalo Palliani et al. (1997). However, it is characterized by its unique rugulate surface ornamentation, and accessory archeopyle sutures have never been observed. *Mendicodinium mataschenensis* is distinguished form the majority of *Mendicodinium* species by its small size and the rugulate surface ornamentation. Table 1 illustrates the characteristic morphologic features of *Mendicodinium* species.

**Remarks**. Like many dinoflagellate cysts with an epicystal archeopyle, *Mendicodinium* is also characterized by the separation of the epicyst and hypocyst caused by mechanical fragmentation or degradation. This is not the case for *Mendicodinium mataschenensis*, where both halves of the cysts are usually still connected ventrally. This may be the result of the more or less parautochthonous sedimentation without major transport and the high sedimentation rate of approximately one centimetre per decade (Gross et al. 2011).

**Discussion**. Doubts about the systematic affiliation of *Mendicodinium* species as dinoflagellate cysts have been raised several times. Due to their relatively simple morphology, in particular the proximate cyst shape, low-relief surface ornamentation and the absence of clear tabulation, identification of their dinoflagellate nature is not always certain. *Mendicodinium groenlandicum* (Pocock & Sarjeant 1972) Davey 1979 was originally described as an acritarch in the genus *Thuledinium*, before Davey (1979) recognized its dinoflagellate nature and transferred it to the genus *Mendicodinium*. The simple morphological features of *Mendicodinium* may have caused confusion, e.g. with some pollen grains such as *Inaperturopollenites*, especially in case of deformation and/or fragmentation. For example, Schrank (2004) studied specimens of the alleged dinoflagellate cyst *Mendicodinium*? *quadratum* Kumar 1987 from the Jurassic Tendaguru Beds in Tanzania. Based on SEM images, he demonstrated

Table 1. Morphological characters, age and paleoecology of *Mendicodinium* species.

| Taxon | Morphological characters (from the original description) | | | | | | Paleoecology | Age |
|---|---|---|---|---|---|---|---|---|
| | Shape | Cyst character | Wall | Ornamentation | Size | Specific characters | | |
| *M. brunneum* Bucefalo Palliani et al. 1997 | Ellipsoidal | Proximate | Thick | Nontabular granules, granules are variable in size and frequently fused into short, sinuous elements | Length: 17(22.8)29 μm; 22 μm*; Width: 28(32) 37 μm; 34* | – | Most frequent when TOC is greater than 0.5% (Bucefalo Palliani and Riding 1999) | Toarcian |
| *M. caperatum* Brideaux 1977 | Subspherical to spherical | Proximate | Thin | Scabrate, autophragm wrinkled with numerous fine folds | Length: 65–70 μm; Width: 64–85 μm | – | - | Aptian-Early Albian |
| *M. echinatum* Riding & Helby 2001 | Subcircular to ellipsoidal | Proximochorate | Thick | Scabrate to rugulate, bearing nontabular short, slender, solid, straight to recurved, distally pointed spines | Length: 47(60)75 μm; Width: 54(65)78 μm | The hypocyst is frequently subangular in the antapical area (1'''') | Deltaic, shallow marine, lacustrine (Riding & Helby 2001) | Early Jurassic |
| *M. granulatum* Kumar 1986 | Subspherical, elongate | Proximate | Thin | Scabrate to granulate | Diameter: 78–89 μm† | – | - | Kimmeridgian-Tithonian |
| *M. groenlandicum* (P. & S. 1972) Davey 1979 | Ellipsoidal | Proximate | Thin | Slight pitting or punctae | Length: 91.5–124 μm; 108 μm*; Width: 65–94 μm; 78.5 μm* | Large size | Lagoon with marine incursion (Riding 2005) | Mid Callovian |
| *M. kemperi* Heilmann-Clausen & Thomsen 1995 | Subspherical | Proximate | Thin | Fine discontinuous ridges, rugulae and granules | Diameter: 60 (67) 78 μm†; 62 μm* | The sculpture partially marks parasutures | - | Early Barremian |
| *M. mataschenensis* n. sp. | Subspherical | Proximate | Thin | Sinuous short rugulae | Length: 26(30.5)36.5 μm: 35 μm*; Width: 26.5(32)41 μm; 36 μm* | Hypocyst is antapically flattened, the epicyst is apically slightly pointed | Low salinity, high nutrients and warm (Gross et al. 2008, 2011; this study) | Late Miocene |
| *M. microreticulatum* Kumar 1986 | Biconical to subspherical | Proximate | Thin | Microreticulate, the lumina of the reticulation are very small and the muri are thin | Diameter: 80–90 μm** | – | – | Kimmeridgian-Tithonian |
| *M. microscabratum* Bucefalo Palliani et al. 1997 | Ellipsoidal | Proximate | Medium | Microscabrate | Length: 15(23.8)33 μm; 20 μm*; Width: 22(30)38 μm; 34 μm* | The hypocyst may be significantly larger than the epicyst | Most frequent when TOC is greater than 0.5% (Bucefalo Palliani and Riding 1999) | Early Toarcian |
| *M. morgenrothii* Butler 1995 | Subcircular | Proximate | Medium | Scabrate or micropunctate | Diameter: 51(62.5)89 μm†; 66 μm* | Reduced ornamentation in the cingular area | Brackish (Butler 1995) | Aalenian–Early Bajocian |
| *M. reticulatum* Morgenroth, 1970 | Biconical | Proximate | – | Coarsely reticulate, sometimes some hollow verrucae observed | Length: 46 μm*; Width: 48 μm* | – | Shallow to marginal marine (Lindström and Erlström 2007) | Late Pliensbachian |
| '*M. robustum*' Z. & S. in Zevenboom 1995 | Subspherical | Proximate | Thick | Scabrate | Length: 80–90 μm, Width: 80–90 μm | – | – | Late Miocene |
| *M. scabratum* Riding & Helby 2001 | Ellipsoidal | Proximate | Medium | Scabrate, microscabrate or granulate | Length: 41(52)67 μm Width: 45(54)62 μm | The paracingulum may be faintly indicated by low parasutural ridge or a lineation | Deltaic, shallow marine, lacustrine (Riding and Helby 2001) | Toarcian–Bajocian |
| *M. spinosum subsp. spinosum* Bucefalo Palliani et al. 1997 | Ellipsoidal | Proximochorate | Thick | Nontabular spines on a smooth autophragm | Length: 19(21.4)27 μm; 26 μm*; Width: 20(25.5)33 μm; 28 μm* | – | Most frequent when TOC is greater than 0.5% (Bucefalo Palliani and Riding 1999) | Early Toarcian |
| *M. umbriense* Bucefalo Palliani et al. 1997 | Ellipsoidal | Proximate | Medium | Nontabular granules on a scabrate to microgranulate autophragm | Length: 26(28.5)34 μm; 28 μm*; Width: 31(30.25)37 μm; 36 μm* | – | Most frequent when TOC is greater than 0.5% (Bucefalo Palliani and Riding 1999) | Early Toarcian |

*Holotype measurements. †Range provided by the author(s).

clearly that it is actually a monosulcate pollen grain. He emended and transferred the species to the gymnosperm pollen genus *Shanbeipollenites* Qian Lijun & Wu Jingyun in Qian et al. (1987), emend. Schrank 2004. *Mendicodinium* is also quite similar in its morphology to the zygospores of zygnematacean green algae, such as the extant species *Spirogyra* (Chlorophyta). Such zygospores with a fossil record in the Mesozoic and Cenozoic are e.g. *Schizophacus* (see Ensom et al. 2009).

In the case of *Mendicodinium mataschenensis* n. sp., the cingulum (although occasionally faintly indicated) and the helicoidal, equatorial suture causing an offset of the cingulum on the ventral face are evidence of an epicystal archeopyle with a ventrally adnate operculum, and dispel any doubts of its dinoflagellate affinity.

**Comments**. *Mendicodinium* is a widespread genus during the Jurassic and Early Cretaceous. Only few records are known from the Neogene: *Mendicodinium robustum* Zevenboom & Santarelli in Zevenboom 1995 ex Fensome et al. 2009 is documented from the Miocene of Italy (Zevenboom 1995) and the Scotian Margin (Fensome et al. 2009). *Mendicodinium* sp. A of Wrenn and Kokinos (1986) is abundant in the Middle Miocene of the Gulf of Mexico, but only rarely found in the Pliocene (Wrenn & Kokinos 1986). Further occurrences are known from the Burdigalian of France (Londeix & Jan du Chêne 1988), the Miocene of the Netherlands (Donders et al. 2009) and the Miocene of ODP Site 1168, off western Tasmania (Brinkhuis et al. 2003). *Mendicodinium* sp. A of Krijgsman et al. (1995) was described from the Late Miocene of the Gibliscemi Section in Sicily.

**Occurrence**. The occurrence of *Mendicodinium mataschenensis* is restricted to only *c.* 1 m (cores 6, 7) at the base of the Mataschen clay pit outcrop. Interestingly, its occurrence is contemporaneous with the occurrence of the ostracod species *Cyprides mataschensis* Gross 2008 (see Gross et al. 2008, figure 3). Investigation of samples above and below this horizon revealed the absence of this taxon.

**Paleoecology**. Most of the *Mendicodinium* species are described from restricted marine environments. Sarjeant (1972) reported *Mendicodinium groenlandicum* from a shelf environment of the Callovian in East Greenland, where it comprised 21% of the assemblage. Poulsen (1992) recorded an assemblage dominated by *Mendicodinium groenlandicum* from Horsens-I borehole (Jurassic, Denmark) and attributed its occurrence to ecological control. He proposed a calm and shallow bay environment with periodic anoxic conditions. High abundance of *Mendicodinium reticulatum* associated with frequent *Chasmatosporites* was found by Koppelhus and Nielsen (1994) in the Lower Jurassic of Denmark. As *Chasmatosporites* is a good indicator for warm to hot, sub-humid environments (Fu et al. 2009), a climatic link may be responsible for the *Mendicodinium*-dominated assemblages. Unusual dinoflagellate cyst assemblages including *Mendicodinium echinatum* and *Mendicodinium scabratum* are typical for the Lower Jurassic Plover Formation in the Timor Sea (north of Australia) which was deposited in a strongly fluvially influenced environment passing up-section into deltaic and shallow marine settings (Riding & Helby 2001).

Brackish and shallow water Barremian sediments of Siberia also proved to be rich in *Mendicodinium* (Pestchevitskaya 2008). More records of abundant *Mendicodinium* from very shallow, marginal marine environments have been reported (e.g. Feist-Burkhardt & Pittet 1996). Characteristic mass occurrences were even termed '*Mendicodinium* events' by Poulsen (1996) who considered these events to be indicative for restricted marine conditions. A somewhat comparable Jurassic counterpart to the Miocene section at Mataschen is represented by the Sorthat Beds, Bagå Formation from Bornholm, Denmark. These beds are characterized by bioturbated, laminated and cross-bedded sands topped by a thin coal seam with rootlets that formed in a brackish lagoon with tidal channels (Koppelhus and Nielsen 1994). Interestingly, both sections yield morphologically very similar specimens of *Mendicodinium*. In contrast to these findings, Bucefalo Palliani et al. (1997) described *Mendicodinium* taxa with ammonites and calcareous nannofossils: rich sediments, suggesting normal marine conditions.

## 6. The paleoecology of *Mendicodinium mataschenensis* n. sp.

The paleoenvironment at Mataschen was a shallow embayment of Lake Pannon (Gross et al. 2008) which is also indicated by the occurrence of *in situ* trunks of Taxodioideae. The mollusc fauna, with lymnocardiids and dreissenids, is typical for freshwater conditions or slightly brackish waters (Harzhauser 2004). The presence of *Pyxidinopsis psilata* confirms low salinities (Mudie et al. 2002, 2004). The abundance of heterotrophic taxa indicates surface waters rich in nutrients (e.g. Dale et al. 1999; Marret & Zonneveld 2003). Warm climatic conditions are assumed due to the presence of the acritarch genus *Nannobarbophora* (Head 2003).

Warm climatic conditions Mataschen were reconstructed previously from different paleobotanical records, which suggested a zonal subtropical evergreen broadleaf forest (Kovar-Eder & Hably 2006), prograding into a marsh vegetation around the lake

(Draxler et al. 1994; Meller & Hofmann 2004). For the Upper Miocene, an untypical high abundance of evergreen taxa at the top of the section, representing two-thirds of the whole macrobotanical assemblage, indicates a high relationship of the vegetation with Early–Middle Miocene plants or the Late Miocene–Pliocene flora of southern Europe (Romania, north Italy or Greece; Kovar-Eder & Hably 2006). Throughout Mataschen, the presence of Mastixiaceae in the pollen record along with other taxa such as *Reveesia*, *Platycaria* and *Engelhardia* point towards subtropical conditions (Draxler et al. 1994; Meller & Hofmann 2004). Based on this, climatic estimates resulted in a mean annual temperature of 17.2–20.5°C, where the coldest month temperature ranges from 9.6–13.3°C (Kern et al. 2012).

In summary, the success of *Mendicodinium* in the restricted environment of Lake Pannon is seen as part of the re-radiation of dinoflagellate cysts after the major extinction event in the Paratethys area at the boundary between the Mid and Late Miocene (Soliman et al. 2011).

## 7. Conclusions

*Mendicodinium* is characterized by its simple morphology which gave rise to confusion with other palynomorphs such as *Inaperturopollenites*. Hence, only a careful microscopic investigation allows a clear identification of this genus.

This genus favored restricted marine and brackish conditions. Its occurrence in Lake Pannon during the early Late Miocene indicates brackish lake waters even in coastal environments. Indeed, the associated palynoflora and mollusc fauna allow an independent estimation of the depositional environment and suggest very shallow and warm, brackish conditions in an embayment of Lake Pannon. Hence, the occurrence of *Mendicodinium* might be a valuable indicator for such conditions in other Neogene sections.


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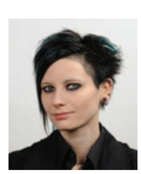

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## Appendix 1. A list of the dinoflagellate cysts identified from the two cores studied from the Mataschen section, Styria, Austria

*Achomosphaera argesensis* Demetresçu 1989
*Achomosphaera* cf. *A. fenestra* Kirsch 1991
*Achomosphaera* sp. A
Dinoflagellate cyst type A of Matsuoka 1987
cf. *Impagidinium eugubinum* Biffi & Manum 1988
*Impagidinium* sp. A
*Impagidinium* sp. B
*Impagidinium* sp. C
*Impagidinium sphaericum* (Wall) Lentin & Williams 1981
*Impagidinium spongianum* Sütőné Szentai 1985
*Islandinium cezare* de Vernal et al. (1989); Head et al. 2001
*Mendicodinium mataschenensis* n. sp.; Plate 1, figures 1–9; Plate 2, figures 1–9; Plate 3, figures 1–12
*Polykrikos kofoidii* Chatton 1914
*Polykrikos schwartzii* Bütschli 1873
*Protoperidinium* cyst type A
*Protoperidinium* cyst type B
*Protoperidinium* cyst type C
*Pyxidinopsis psilata* (Wall & Dale) Head 1994
Round brown cysts (cf. Brigantedinium)
*Selenopemphix brevispinosa* Head et al. 1989

*Selenopemphix nephroides* Benedek emend. Bujak in Bujak et al. 1980
*Selenopemphix*? sp. 2 of Head 1993
*Selenopemphix* sp. A
*Selenopemphix* sp. B
*Selenopemphix undulata* Verleye et al. 2011
*Spiniferites bentorii* subsp. *budajenoensis* Sütőné Szentai 1986
*Spiniferites bentorii* subsp. *oblongus* Sütőné Szentai 1986
*Spiniferites bentorii* subsp. *pannonicus* Sütőné Szentai, 1986
*Spiniferites bulloides* Deflandre & Cookson 1955
*Spiniferites delicatus* Reid 1974
*Spiniferites membranaceus* (Rossignol) Sarjeant 1970