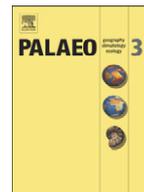




Contents lists available at SciVerse ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Precipitation driven decadal scale decline and recovery of wetlands of Lake Pannon during the Tortonian

Andrea K. Kern ^{a,*}, Mathias Harzhauser ^a, Ali Soliman ^{b,c}, Werner E. Piller ^b, Martin Gross ^d^a Natural History Museum Vienna, Geological–Paleontological Department, Burgring 7, 1010 Vienna, Austria^b Institute of Earth Sciences, Graz University, Heinrichstrasse 26, 8010 Graz, Austria^c Tanta University, Faculty of Sciences, Geology Department, Tanta 31527, Egypt^d Abteilung für Geologie & Paläontologie, Universalmuseum Joanneum, Weinzöttlstraße 16, 8045 Graz, Austria

ARTICLE INFO

Article history:

Received 31 October 2011

Accepted 25 November 2011

Available online 4 December 2011

Keywords:

High resolution analysis

Pollen

Tortonian

Paleoclimate

Paleoenvironment

Plant–climate–interaction

ABSTRACT

High resolution pollen and dinoflagellate analyses were performed on a continuous 98-cm-long core from Tortonian deposits of Lake Pannon in the Styrian Basin in Austria. The sample distance of 1-cm corresponds to a resolution of roughly one decade, allowing insights into environmental and climatic changes over a millennium of Late Miocene time. Shifts in lake level, surface water productivity on a decadal- to centennial-scale can be explained by variations of rainfall during the Tortonian climatic optimum. Related to negative fine scale shifts of mean annual precipitation, shoreline vegetation belts reacted in an immediate replacement of Poaceae by Cyperaceae as dominant grasses in the marshes fringing the lake. In contrast to such near-synchronous ecosystem-responses to precipitation, a delayed lake level rise of 4–6 decades is evident in the hydrological budget of Lake Pannon. This transgression, caused by a precipitation increase up to >1200 mm/yr, resulted in a complete dieback of marshes. Simultaneously, “open-water” dinoflagellates, such as *Impagidinium*, took over in the brackish lagoon and fresh water dinoflagellates disappeared. As soon as the rainfall switched back to moderate levels of ~1100–1200 mm/yr, the rise of the lake level slowed down, the marsh plants could keep up again and the former vegetation belts became re-established. Thus, mean annual precipitation, more than temperature, was the main driving force for high-frequency fluctuations in the Tortonian wetlands and surface water conditions of Lake Pannon. Such high resolution studies focusing on Tortonian decadal to centennial climate change will be crucial to test climate models which try to compare the Tortonian models with predictions for future climate change.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

The Early Tortonian is characterized by a short global warming phase with humid conditions in Europe (e.g. Bruch et al., 2006, 2007; Utescher et al., 2009; Pound et al., 2011; Utescher et al., 2011), also referred to as “washhouse climate” by Böhme et al. (2008). Simultaneously, Atlantic deep water temperatures did rise about 3 °C during the Early Tortonian (Lear et al., 2003). Therefore, the Tortonian is a major target for climate models calculating future climate change. Tortonian models (e.g.: François et al., 2006; Steppuhn, et al., 2006) are then sometimes compared with proxy data to test their fit (Micheels et al., 2007; Steppuhn et al., 2007). Nevertheless, there exists surprisingly little information on the variability of Tortonian climate on a decadal to centennial scale. An opportunity to study such a high resolution archive is the deposits of Lake Pannon, which covered the Pannonian basins complex during the Late Miocene (Magyar et al., 1999a; Harzhauser and Mandic,

2008; Lirer et al., 2009; Vasiliev et al., 2010). The Tortonian vegetation surrounding the lake is documented from numerous localities. Leaf floras, fruits, seeds and pollen have been extensively described (e.g. Draxler et al., 1994; Kovar-Eder et al., 1995; Hably and Kovar-Eder, 1996; Kovar-Eder et al., 2002; Meller and Hofmann, 2004; Kovar-Eder and Hably, 2006; Erdei et al., 2007; Harzhauser et al., 2008). Generally, most of these studies dealt with the alpha diversity of a locality without referring to short shifts in local and regional vegetation. Moreover, these data allow a rough estimate of climatic parameters and indicate large-scale temporal shifts in climate during the Late Miocene in this area (Bruch et al., 2006). Aside from a pioneer study on a 37-cm-long core, covering a major transgression of Lake Pannon (Harzhauser et al., 2008), no study tried to elucidate local changes in vegetation on a decadal or centennial scale so far. To enlarge our understanding of short-termed climate variability in the Late Miocene, we performed a high-resolution study on a 98-cm-long core from the Styrian Basin. The study focuses on dinoflagellates and pollen to reconstruct vegetation dynamics around the lake in context of surface water ecology. A suitable locality for such detailed analyses is Mataschen in the eastern Styrian Basin. First paleobotanical analysis on the c. 30-m-thick section showed a change in

* Corresponding author. Fax: +43 1 52177 459.

E-mail address: andrea.kern@nhm-wien.ac.at (A.K. Kern).

vegetation from a swampy environment with azonal leave-floras to a more diverse assemblage at the top indicating a zonal subtropical evergreen broad leaf forest (Meller and Hofmann, 2004; Kovar-Eder and Hably, 2006). These authors interpreted a warm climate for the Late Miocene with a mean annual temperature of 15–19°. Our aim is to detect vegetation dynamics and surface water productivity on a decadal scale over a very short time span of roughly one millennium. This will allow to describe and to quantify the bandwidth of rapid climate change of early Late Miocene time.

2. Geological setting

Several cores were taken from the Lias Austria GmbH clay pit at Mataschen (15°57'16"E/46°54'15"N), about 5 km SW of Fehring in the district of Feldbach (Styria, SE of Austria). Mataschen is located in the Eastern Styrian Basin, which is the westernmost part of the Pannonian Basin (Fig. 1). The basin comprises up to 4000 m of Neogene sediments ranging from the Lower Miocene to the Pliocene (Kollmann, 1965). The clay pit comprises c. 30 m of pelitic to psammitic deposits. The studied core was taken from the lower pelitic interval of the section belonging to the Feldbach Formation (Gross, 2004). This formation comprises lowermost Pannonian sediments, which were deposited when Lake Pannon was in its early phase and the lake level was still low. The water body was restricted to rather narrow basins with a large number of islands (Magyar et al., 1999a, b). The base is formed by a 1.5 m thick sandy unit. It is overlain by a 5-m-thick unit of clay and silt, with numerous fossils in the base. Vertebrate fossils, such as turtles, beavers and hamsters (Gross, 1994; 2004; Daxner-Höck, 2004), appear in this part, as well as leaves, seeds, pollen and in-situ tree trunks up to 4 m in height (Gross, 2004; Kovar-Eder, 2004; Meller and Hofmann, 2004). The tree trunks belong to the Taxodioidea, and might represent *Glyptostrobus* in respect to the frequent occurrence of seeds and leaves of this genus (Gross, 2004; Gross et al., in press). Above follows a coquina with shells of the bivalve *Mytilopsis neumayri* (Harzhauser, 2004) and scattered *Mytilopsis ornithopsis*, lymnocardiiids and fish remains. The analyzed cores comprise solely dark silty clay to clayey silt. No coquinas are intercalated, but debris of lymnocardiid bivalves is

frequent in the upper part. Only very little indication of bioturbation is observed.

2.1. Stratigraphy, dating and age model

The pelitic interval of the Mataschen section belongs to the Lower Pannonian Feldbach Formation (*Mytilopsis ornithopsis* zone; Gross, 2003, 2004a; Harzhauser, 2004; = Pannonian B sensu Papp, 1951). This indicates an Early Tortonian age (early Late Miocene), which correlates to the early Pannonian in regional stratigraphy.

Based on an integrated approach combining paleomagnetism, seismic data and mammal biostratigraphy, Gross et al. (in press) correlated the section to the short Chron C5r.2r-1n (11.308–11.263 Ma). This reduces the maximum time range of the section to about 45 kyr and suggests an average sedimentation rate of >0.7 mm/yr (maximal ~1.4 mm/yr) (Gross et al., in press). These values are also comparable to other estimations for Lake Pannon (Harzhauser et al., 2008; Lirer et al., 2009) and lacustrine-deltaic sequences in the Dacian Basin (Vasiliev et al., 2004). Thus, the studied cores of 98 cm represent between 700 and 1400 years (7–14 yr/sample). As a completely constant sedimentation rate is unlikely in such a marginal setting we consider the average resolution to range around one decade.

3. Material and methods

98 samples were selected from two successive cores with a diameter of 100 mm, which were taken by a percussion drill. These cores were cut with a sample distance of 5 mm, but only every second sample was investigated for this study, resulting in a 1-cm sample resolution. Preparation of the palynological samples followed the steps of Green (2001) and Wood et al. (1996). Each sample was dried, weighed and one *Lycopodium clavatum* tablet was added to calculate the absolute number of pollen and dinoflagellate cysts. Then they were treated with cold HCl (34%) to remove all carbonate. After washing with distilled water, the samples were treated with HF (48%) and cold HCl to fully remove all silicates and colloids. The residue was ultrasonicated (c. 15–30 s) and colored with Safranin O., before it was sieved at 15 µm with a nylon sieve. Two glass slides were

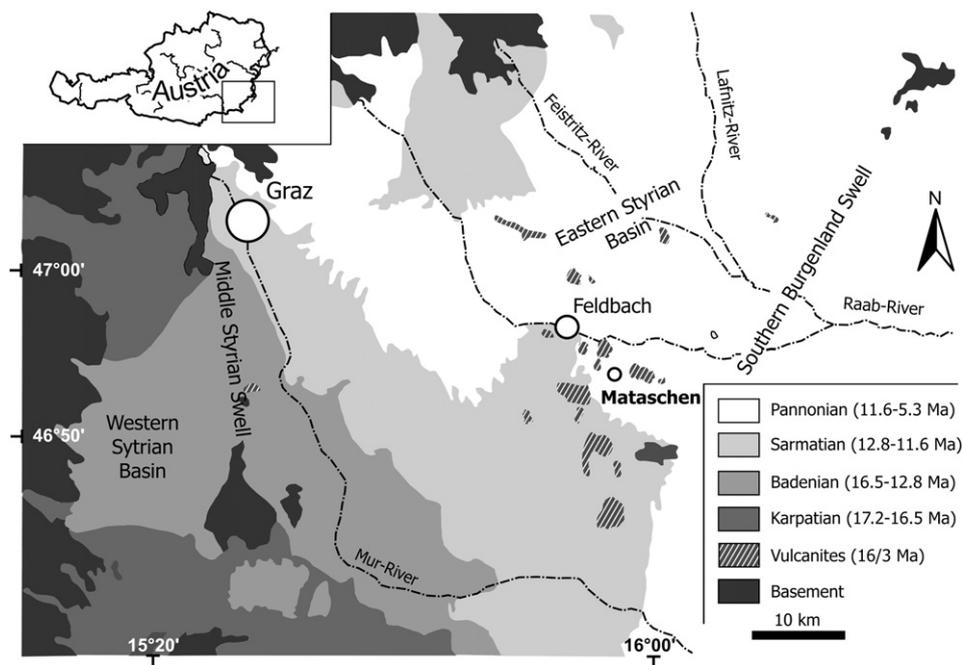


Fig. 1. Geological setting of the clay pit (Lias Austria GmbH) at Mataschen in the Styrian Basin (Austria). After Gross (2004) and Gross et al. (in press).

prepared from each sample using glycerin jelly and sealed with nail polish. In each sample, at least the first c. 250 dinoflagellate cysts and 200 pollen grains (excluding *Pinus*) were identified, respectively.

Although artificial staining was applied, some palynomorphs (less than 25 µm) still have a very pale yellow/brown color. Among the dinoflagellates, one palynomorph characterized by a surface covered by small spines could not be differentiated further in the light microscope. Therefore, during routine counting, these palynomorphs were grouped as “small spiny palynomorphs” (SSP). Scanning electron microscopy revealed that SSP comprise mostly *Protoperidinium* sp. sensu Londeix et al., 2009, *Algidasphaeridium minutum* var. *cezare* sensu de Vernal et al., 1989 and the acritarch genus *Nannobarbophora*.

The software PAST (Hammer et al., 2001) was used to calculate cluster analyses. The data used for these analyses were transformed using the arcsin-root method (Linder and Berchtold, 1976; Zúschin and Hohenecker, 1998). These clusters are only based on sample similarity and do not reflect pollen-zones as typical in Tilia graphs (Grimm, 2004). Statistical analyses were used to characterize clusters; abbreviations mentioned in the text are μ for mean value and σ for standard deviation, which are calculated based on the percentage data. The pollen diagram was created by Tilia and Tilia-Graph (Grimm, 2004). The climatic reconstructions were achieved with the Coexistence Approach (Mosbrugger and Utescher, 1997), which is based on the presence or absence of pollen taxa. For each plant taxon, the most appropriate nearest living relative is determined to get reliable climatic data. This information provides a climatic interval, in which the nearest living relative is able to survive and reproduce. Taxa, which are today only limited to retreat areas, such as *Cathaya* or *Sciadopitys*, were excluded from the climatic analysis, because their recent distribution might not reflect their Miocene habitat requirements. Additionally, taxa were not considered, if their living environment is probably far away and/or in different altitudes. They are only present in the studied assemblage because their pollen grains are suggested to be suitable for far-distance transport (e.g. *Picea*, *Tsuga*, *Ephedra* or *Keteleeria*) (Hopkins, 1950; Traverse and Ginsburg, 1966; Heusser and Balsam, 1977). All remaining taxa were analyzed to define an interval, in which all the nearest living relatives could “co-exist”. This is called the coexistence interval and is presented here as the climatic interval, in which the fossil taxa are most likely to have existed. This method helps to objectify the data, while the interpretation of the abundances (as given in the Tilia-Graph) depends more on the personal opinion and experience of the worker.

The studied material is stored at the Natural History Museum Vienna.

4. Results

4.1. Dinoflagellates – composition and patterns

4.1.1. Taphonomy

The dark gray-green clay to silt and the considerable amount of iron-sulfides document low oxygen conditions. Organic material was protected from oxidation by fast burial. Therefore, selective preservation due to aerobic degradation is unlikely (see Zonneveld et al., 2008 for discussion). The concentration of dinoflagellates and acritarchs per gram sediment fluctuates strongly between ~5000 and ~30,000. Values between 10,000 and 20,000 are typical on average in the lower part of the core while the upper part displays three phases of elevated values of 15,000–25,000 on average (samples 56–63, 71–80, 83–91) separated by shorter intervals of low dinoflagellate concentration. The statistical grouping of samples according to the composition as described below does not correlate at all with the pollen concentration values. This is taken as further proof that selective preservation does not obscure the overall patterns.

4.1.2. Composition

A rather low diversity of about 21 dinoflagellate taxa has been encountered (Table S1). Typical are Paratethyan endemic morphotypes of the *Spiniferites/Achomosphaera*-group spp. and *Impagidinium* spp. In addition, the assemblage is characterized by the occurrence of *Pyxidiniopsis psilata*, *Polykrikos kofoidii/schwartzii*, *Protoperidinium* sp., *Mendicodinium* sp., *Algidasphaeridium minutum* var. *cezare* and the acritarch genus *Nannobarbophora* (*N. gedlii*, *Nannobarbophora* sp. 1 and *Nannobarbophora* sp. 2). The heterotrophic taxa, *Selenopemphix nephroides* sp.1 and *Selenopemphix* sp.1 and “small round brown cysts” (RBC) are frequent in all samples as well. Other taxa as *Lejeunecysta* spp., *Nematosphaeropsis* sp., and *Batiacasphaera sphaerica* are rare.

The predominating *Spiniferites/Achomosphaera*-group and the small spiny palynomorphs (SSP) show a more or less opposing trend. Roughly parallel trends are documented for *Impagidinium* spp. and *Selenopemphix nephroides*. Similarly, *Spiniferites bentorii pannonicus* and *Spiniferites b. budajenoensis* display nearly parallel trends coinciding with *Selenopemphix* sp.1 with some offset. The core reveals 8 prominent peaks in the peridinioid–gonyaulacoid ratio (P/G ratio), which represents a rough estimate between heterotroph and autotroph dinoflagellates (samples 10, 15, 22, 34, 45, 60, 76 and 89). The ratio is mainly caused by the opposing trend between the SSP and the *Spiniferites/Achomosphaera*-group. These peaks seem to appear in more or less regular periodicities of 11–16 samples after sample 22. Aside from these marked fluctuations, the dinoflagellate record suggests several distinct phases.

The lower part of the core (samples 1–20) is characterized by moderate fluctuations in the RBC, SSP and *Spiniferites/Achomosphaera*-group records. Above follows a rather stable interval up to sample 48, in which none of the dominant groups shows major fluctuations. This interval coincides also with regular occurrences of *Polykrikos kofoidii/schwartzii* cysts and the main phase of *Pyxidiniopsis psilata*. The following interval to sample 55 displays a sudden drop in *Spiniferites b. pannonicus*, *S. b. budajenoensis* and the SSP record, followed by a drop in *Selenopemphix* sp.1 with a 3-sample-delay. This low is compensated by a peak of *Impagidinium* spp. and *Selenopemphix nephroides*. The pattern is reversed in the following interval up to sample 60. The *Impagidinium* peak decreases together with *S. nephroides*. Up to sample 76, the fluctuations of most groups, aside from the SSP, are moderate. Then, *Selenopemphix* sp.1 displays a slight peak, which is succeeded soon after by *S. b. pannonicus* and *S. b. budajenoensis* up to sample 80. The top of the core is characterized by the gradual increase of *Impagidinium* spp., RBC and *Selenopemphix nephroides* and a general decrease of the SSP.

4.1.3. Statistics

To achieve a more objective grouping of the data set, a cluster analysis (Ward's Method) was performed. This revealed a grouping of the samples according to their similarity into 4 clusters (D1–D4) and 2 sub-clusters (D4a and D4b). The four significant clusters have been transposed into a color code in Fig. 2 for a better visualization of the distribution within the core. Cluster D1 unites the most balanced samples ($n=28$). *Spiniferites/Achomosphaera* dominate ($\mu=39.1\%$, $\sigma=7.2$) followed by SSP ($\mu=25.8\%$, $\sigma=5.2$) and RBC ($\mu=17.1\%$, $\sigma=6.1$) while *Impagidinium* spp. are rare ($\mu=6.5\%$, $\sigma=2.2$). All other groups remain below 5%. Cluster D2 ($n=24$) is similar to D1 but differs in a slight decrease of *Spiniferites/Achomosphaera* ($\mu=34.0\%$, $\sigma=5.7$) and RBC ($\mu=12.1\%$, $\sigma=4.3$) and an increase of SSP ($\mu=32.9\%$, $\sigma=5.9$). *Impagidinium* remains low ($\mu=4.8\%$, $\sigma=1.5$). The samples which form clusters D1 and D2 are mainly found in the lower half of the core and in the interval 60–65. Scattered samples of these clusters in the upper part of the core coincide with peaks in the P/G ratio.

Samples of clusters D3–D4 dominate the upper half of the core and are generally characterized by lower SSP values and higher *Spiniferites/Achomosphaera* values when compared to D1 and D2.

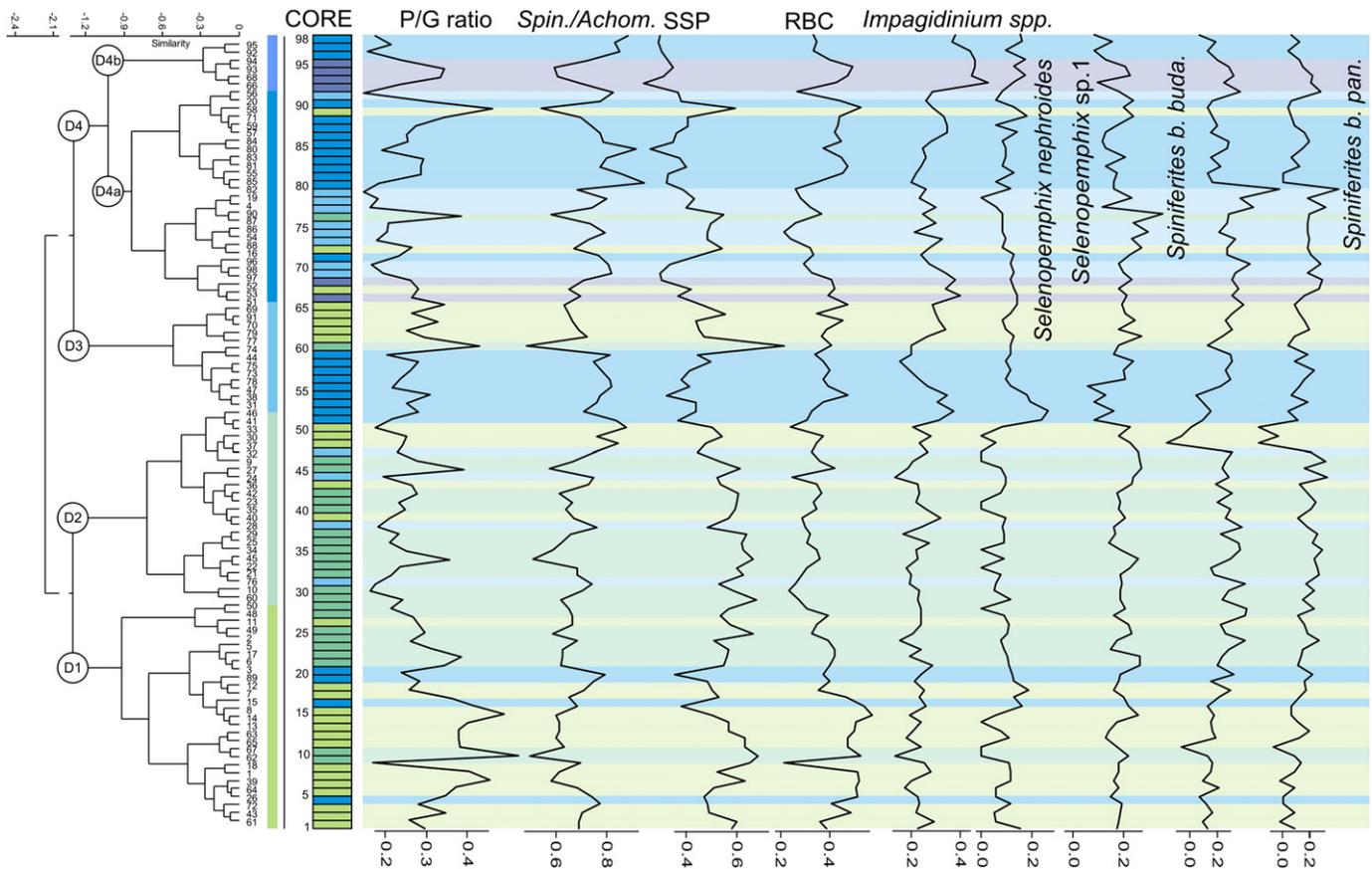


Fig. 2. Dinoflagellates: cluster analysis (Ward's Method) based on the arcsin-root method transformed percentages (see Table S1 for taxa included). The most significant clusters are labeled D1–D4 (a/b) and colors are assigned to the clusters. This color code was applied to the samples according to their cluster-affiliation along the core. Arcsin-root transformed percentage-based dinoflagellates diagrams for the most important constituents are presented on the right.

Cluster D3 ($n=13$) bears only a mean of 17.9% ($\delta=5.4$) of SSP and 7.6% ($\delta=1.8$) RBC but 48.1% ($\delta=4.2$) of *Spiniferites/Achomosphaera*. Simultaneously, *Spiniferites bentorii budajenoensis* increases to 8.7% ($\delta=3.6$) while *Impagidinium* remains at a low level of 6.8% ($\delta=2.6$). Samples of cluster D4a ($n=27$) dominate the intervals 51–59 and 80–90 and are marked by very low amounts of SSP ($\mu=14.1\%$, $\delta=4.3$) and higher contributions by RBC ($\mu=15.0\%$; $\delta=4.0$). *Spiniferites/Achomosphaera* attain the highest values ($\mu=51.2\%$, $\delta=6.2$) and *Impagidinium* remains at values of 7.9% ($\delta=3.4$). All other groups contribute less than 4% each to the assemblages. Cluster D4b comprises only few samples ($n=6$), encompassing interval 92–95 and samples 66 and 68, but is outstanding in its high amount of *Impagidinium* ($\mu=18.2\%$, $\delta=3.6$) and the lowest amounts of SSP ($\mu=9.6\%$, $\delta=2.7$). RBC values ($\mu=17.5\%$, $\delta=3.2$) and *Spiniferites/Achomosphaera* ($\mu=38.7\%$, $\delta=5.5$) are comparable to D1.

4.2. Pollen and spores

4.2.1. Taphonomy

The pollen preservation does not vary much within these 98 samples although the total number of pollen preserved per gram sediment differs between approximately 4500 and 22,000. The highest pollen density occurs in the upper part of the section. The number of pollen-taxa within one sample ranges from 22 to 40. The most diverse samples are situated between samples 39 and 48 (30 to 40 taxa) followed by a diversity-low between samples 49 and 62 containing only 23 to 28 different plants. This does not correlate with

the pollen-per-gram calculation indicating that the pattern is not based solely on taphonomic processes.

4.2.2. Composition

71 plant taxa have been detected in all samples (Table S1). The most abundant taxon is *Pinus*, which usually ranges between 20 and 30% except for 4 peaks with more than 40% (samples 42, 47, 48, 62). Therefore, *Pinus* was not excluded from the whole assemblage for further calculations and interpretations. The next most frequent taxa are *Cathaya* and Taxodiaceae, with a significantly high contribution between samples 16 and 44 (Fig. 3). Of the remaining gymnosperms, only *Picea* attains more than 10%, while *Abies* does hardly exceed 5%. Similar to *Abies*, *Sciadopitys* is present in almost all samples, while *Keteleeria*, *Ephedra*, *Ginkgo*, *Cedrus* and Cupressaceae (excluding Taxodiaceae) are only sporadically found in low numbers.

Among the angiosperms, Poaceae and *Sparganium/Typha* attain 4–14% and 2–13%, respectively (Fig. 3). These taxa along with Cyperaceae (up to 7.8%) show a clear increase up to sample 30, decrease thereafter, and increase again from sample 64 to the top. Only one angiosperm taxon, *Carya*, attains more than 15% while *Quercus*, *Ulmus*, *Fagus* and *Celtis* are less frequent. Gymnosperms dominate most samples compared with the angiosperms. Their amount reaches up to 76% at sample 42, but then decrease to the top, where many samples display a contribution by angiosperms of more than 40%.

The amount of spores is very low in all samples (<3%) and varies only on a small scale. Only a few taxa could be identified on genus level including *Osmunda*, *Lycopodium* and different taxa of Pteridaceae, Polypodiaceae and Schizaeaceae. These were excluded from statistical analysis.

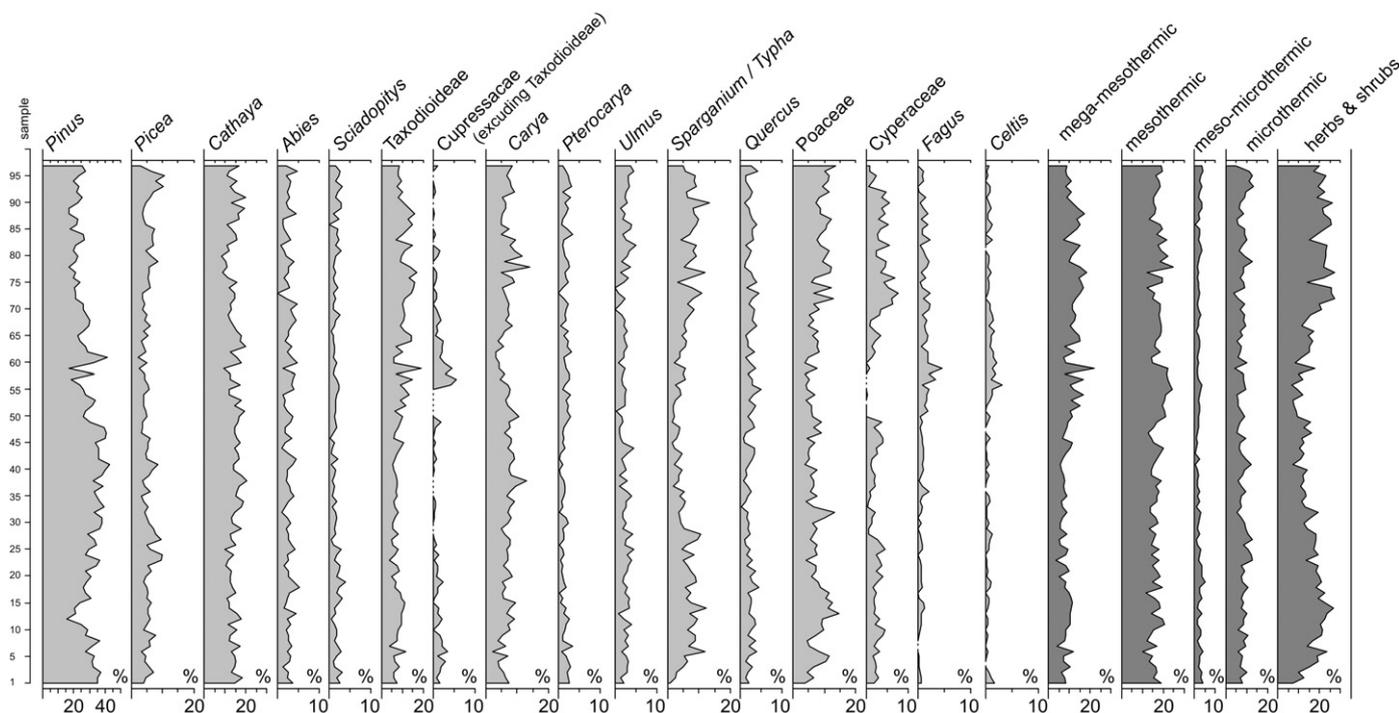


Fig. 3. Pollen-diagram, created after Grimm (2004), of the most important taxa and pollen groups according to their suggested ecological requirements after Jiménez-Moreno (2006) and Jiménez-Moreno and Suc (2007): 1. Megathermic–mesothermic elements (“thermophile” taxa): Araliaceae, Arecaceae, *Engelhardtia* Euphorbiaceae, Hamameliaceae, Mastixiaceae, *Myrica*, *Reevesia*, Rutaceae, *Platycarya*, *Symplocos*, Sapotaceae and Taxodioidae. 2. Mesothermic elements (warm temperate climate): *Acer*, *Alnus*, *Betula*, Buxaceae, *Carpinus*, *Carya*, *Castanea–Castanopsis*-type, *Celtis*, *Fagus*, Fagaceae, *Fraxinus*, *Ginkgo*, *Hedera*, *Ilex*, *Juglans*, *Liquidambar*, *Lonicera*, *Nyssa*, *Pterocarya*, *Quercus*, *Rhus*, *Salix*, *Tilia*, *Ulmus*, Vitaceae and *Zelkova*. 3. Meso-microthermic (cold temperate climate or elevated areas): *Cedrus*, *Sciadopitys* and *Tsuga*. 4. Microthermic (mountainous areas): *Abies* and *Picea*. 5. Herbs and shrubs: *Artemisia*, Asteraceae, Caryophyllaceae, Chenopodiaceae, Cyperaceae, *Ephedra*, Ericaceae, Malvaceae, *Myriophyllum*, Nymphaeaceae, Plumbaginaceae, Poaceae, Pontamogetaceae, *Sparganium/Typha* and Trapaceae.

The pollen-taxa were grouped according to their suggested climate and ecological requirements following Jiménez-Moreno (2006) and Jiménez-Moreno and Suc (2007) (Fig. 3) in megathermic–mesothermic elements (“thermophilous” taxa), mesothermic elements (warm temperate climate), meso-microthermic (cold temperate climate or elevated areas), microthermic (mountainous areas) and herbs and shrubs. Afterwards these groups were adjusted to include all significant plants present in this assemblage.

The whole assemblage is comparable with those described in previous studies of Draxler et al. (1994) and Meller and Hofmann (2004). The exact position of those samples, however, is not indicated and therefore we refrain from integrating additional information from their SEM investigations.

4.2.3. Statistics

A cluster analysis (Ward's Method) was performed based on all pollen taxa to define differences in the palyno-assemblages. This resulted in four main clusters (P1 to P4) with 2 subclusters (P3a and P3b) (Fig. 4).

Cluster P1 unifies samples from the middle part of the core (samples 51 to 62) characterized by a high contribution of Taxodioidae ($\mu = 10.4\%$, $\sigma = 4.0$), Cupressaceae ($\mu = 1.7\%$, $\sigma = 2.0$), *Nyssa* ($\mu = 0.9\%$, $\sigma = 0.5$) and mesothermic trees, such as *Celtis* ($\mu = 1.2\%$, $\sigma = 0.8$), *Liquidambar* ($\mu = 0.6\%$, $\sigma = 0.4$), *Quercus* ($\mu = 2.7\%$, $\sigma = 1.0$) and *Fagus* ($\mu = 2.0\%$, $\sigma = 1.1$).

The second cluster P2 comprises a large group of samples from samples 31 to 50, a smaller group in the base (samples 1–3, 6) and one single sample at the top (76). This group is characterized by the frequent occurrence of *Pinus* ($\mu = 36.0\%$, $\sigma = 3.8$) and *Cathaya* ($\mu = 15.8\%$, $\sigma = 1.8$), which is caused by the disappearance of many other taxa. Consequently, the main part of this cluster coincides with the lowest taxa concentration (Table S2). The decrease of

Sparganium/Typha and Poaceae as well as a breakdown of Cyperaceae shortly at sample 31 is most significant.

Cluster P3 is separated into subclusters P3a and P3b, which are dominating the lower third of the core. P3a comprises samples 4, 5, 7–10, 12, 17–21, 23 and 24, 27, 30, 64 and 85, while P3b-samples are represented by samples 11, 13–16, 25, 28–29, 73, 82, 84, 88 and 92–98. In both assemblages a high abundance of herbs and shrubs is typical. P3a's strongest element is *Sparganium/Typha* ($\mu = 7.1\%$, $\sigma = 1.9$), but also Poaceae ($\mu = 7.8\%$, $\sigma = 2.0$) and Cyperaceae ($\mu = 2.6\%$, $\sigma = 1.0$) are important constituents of the plant community. Nevertheless, *Pinus* is strongly present ($\mu = 30.6\%$, $\sigma = 4.0$). Cluster P3b is even more influenced by herbs and shrubs ($\mu = 21.3\%$, $\sigma = 2.6$), notably due to the presence of *Sparganium/Typha* ($\mu = 7.9\%$, $\sigma = 4.0$) and Poaceae ($\mu = 10.4\%$, $\sigma = 2.4$). Additionally, the appearance of Taxodioidae is important ($\mu = 9.0\%$, $\sigma = 1.9$).

Samples of cluster P4 are located mostly in the upper half of the section (samples 63, 65–72, 74–75, 77–81, 83, 86–87, 89–91) and two single occurrences in the lower part (samples 22 and 26). The assemblage is similar to cluster P3, due to the high amount of herb and shrub pollen ($\mu = 20.4\%$, $\sigma = 4.4$). Additionally to *Sparganium/Typha* ($\mu = 7.6\%$, $\sigma = 2.3$) and Poaceae ($\mu = 8.4\%$, $\sigma = 2.1$), Cyperaceae show their widest distribution ($\mu = 4.0\%$, $\sigma = 1.8$). Further, the high amount of Taxodioidae ($\mu = 12.2\%$, $\sigma = 2.6$), and the increasing number of *Nyssa* ($\mu = 0.4\%$, $\sigma = 0.3$) are present.

5. Discussion

5.1. Paleoclimate

The climatic reconstruction was performed by using the Coexistence Approach (CA) of Mosbrugger and Utescher (1997). In each sample, the ecological requirements of 11 to 25 pollen taxa were

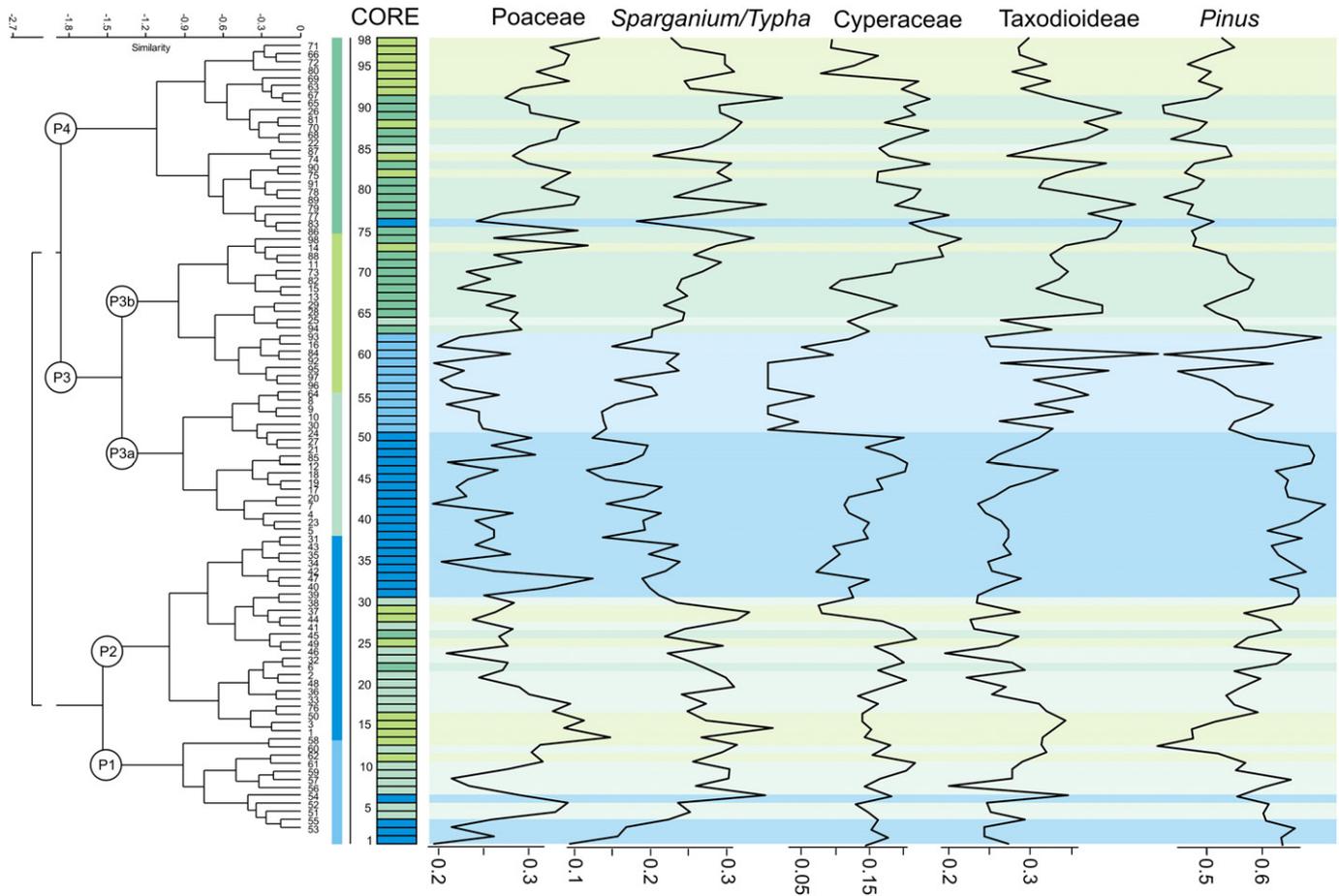


Fig. 4. Pollen data: cluster analysis (Ward's Method) based on the arcsin-root method transformed percentages (see Table S1 for taxa included). The most significant clusters are labeled P1–P4 and colors are assigned to the clusters. This color code was applied to the samples according to their cluster-affiliation along the core. Arcsin-root method transformed percentage-based pollen diagrams for the most important constituents of the pollen-assemblages are presented on the right.

compared with those of their supposed nearest living relatives to create a “coexistence interval” in which all modern relatives could co-exist. This method, applied on all 43 climatic relevant taxa, suggests a mean annual temperature (MAT) of 17.2–20.5 °C, a coldest month temperature (CMT) of 9.6–13.3 °C and a warmest month temperature (WMT) of 24.7–27.9 °C (Table S2). Mean annual precipitation (MAP) ranged within 1187–1520 mm, showing a seasonality with a dry month (MPdry) of 18–24 mm and a wet month (MPwet) of 178–236 mm. The rainy season was most likely in the warmer period of the year as the warmest month precipitation (MPwarm), ranges around 118–141 mm (Table S2). To reduce the white-noise-signal, we used a 5-point-average in the paleoclimate estimates in Fig. 5 illustrating rather stable climatic conditions during deposition of the core's sediment.

Within the short interval represented by the samples of the core, the only parameter significantly changing is the MAP. From a high in the first samples, it decreases to 1100 mm (around samples 8–23) before it step-wisely reaches the lowest values of less than 1000 mm during samples 38 to 44 (Fig. 5). This is caused by a sudden lack of mesothermic elements such as *Engelhardia*, *Rhus* and *Reevesia* (Table S1). Afterwards follows a significant increase of mean annual precipitation up to almost 1200 mm within the next 5 samples representing a maximum of 70 years. Several samples indicate even higher values than 1200 mm during the following interval until the MAP drops again above sample 66. For the rest of the core-section, rainfall is oscillating around 1150 mm/yr. Small scale, in-phase-shifts are also observed in the CMT and the MPdry estimates (Fig. 5).

Comparing these climatic data with the updated climatic classification of Koeppe and Geiger (Koeppe, 1936; Peel et al., 2007) a Cwa climate at the transition to a Cfa climate is indicated. Only if the most extreme CA precipitation estimates for the wettest and driest months are considered, the data range within the Cfa climate boundaries. This would point to no or only very weak seasonality comparable to modern regions in East Asia, southeast North America or east South America (Utescher et al., 2009). Cwa climates reflect a stronger influence of a dry summer period like today in northern India, south-eastern Asia (south Nepal, Myanmar, northern Thailand) to east China, and in central south Africa (east Angola, Zambia, north Zimbabwe, north Mozambique) (Peel et al., 2007). This interpretation suggests a slightly warmer climatic situation in comparison to other coeval Central European localities (Bruch et al., 2007). Especially the coldest month temperature of 10° or above (Fig. 5; Table S2), which is also well represented in the abundance of thermophilic and/or evergreen taxa (mega- and mesothermic up to 20%) (Fig. 3) and the occurrence of rare elements (Mastixiaceae, *Engelhardia*, *Platycarya*) during the Late Miocene, is surprising, which lead to discussion about a position of the embayment in a climatically favored refuge (Kovar-Eder and Hably, 2006).

5.2. Lake ecology and dynamics

The interpretation of the dinoflagellate assemblages in Lake Pannon is complex. Most taxa have roots in marine ancestors, which became adapted to brackish water conditions of Lake Pannon with

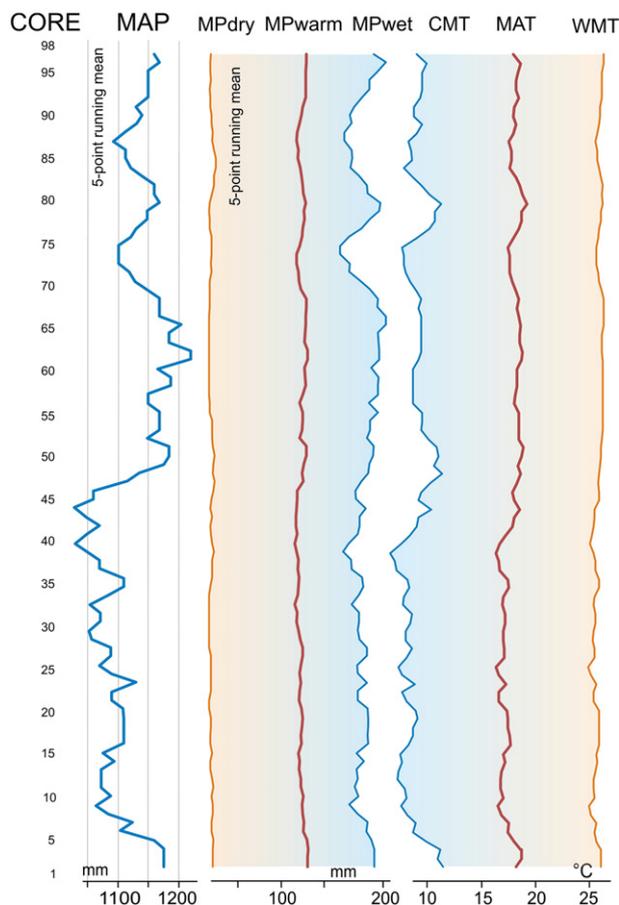


Fig. 5. Climate estimates based on the 5-point-running mean values calculated by the Coexistence Approach. Abbreviations refer to MAT (mean annual temperature), CMT (coldest month temperature), WMT (warmest month temperature), MAP (mean annual precipitation), MPwet (precipitation of the wettest month), MPdry (precipitation of the driest month) and MPwarm (precipitation of the warmest month).

the onset of the Late Miocene. Therefore, a straightforward comparison with congeneric open marine taxa is difficult. A more promising source for comparison is the marine-derived assemblages from the Black Sea, the Marmara Sea, the Caspian Sea, the Aral Sea and some adjacent lakes as described in numerous papers (e.g. Kouli et al., 2001; Mudie et al., 2001; 2002; 2007; Marret et al., 2004; 2007; 2009; Sorrel et al., 2006; Londeix et al., 2009; Leroy and Albay, 2010).

All samples are characterized by high terrestrial influx represented by phytoclasts and sporomorphs suggesting a near-shore depositional environment. This interpretation is also obvious based on the paleogeographic situation and sedimentological features (Gross et al., 2008). The data are thus documenting the development in an embayment of Lake Pannon during approximately one millennium. Color-code transposed cluster analysis suggests a division into a lower half of the core, rich in heterotrophs (clusters D1–D2) and an autotroph-dominated upper part (clusters D3–D4) (Fig. 2). The reason for the heterotroph peak is dubious. Increased diatom production is discussed by Bujak (1984) and Matsuoka (1999) as reason for the takeover by heterotrophs is unlikely as no diatoms are recorded from the Mataschen core. Matsuoka (1987) attributed the dominance of heterotrophic taxa to terrestrially originated nutrients which are transported by rivers to the area of deposition. Head et al. (2004) also concluded that the abundance of partially degraded woody tissues is an evidence for river input. Aside from high nutrient loads, this input might coincide with turbidity and reduced light penetration of surface waters due to a high fraction of suspended sediment and/or phytoplankton blooms. This in turn would impede growth of

light-depending autotrophic dinoflagellates (Dale, 2001). To test this hypothesis several samples have been selected to count the amount of phytoclasts (at 10 *Lycopodium clavatum* spores). Indeed, samples with high P/G ratio are characterized by a dominance of large wood fragments while samples of low P/G ratio contain fewer and relatively smaller phytoclasts. These samples are also marked by the most prominent contribution of *Polykrikos* spp., which is a good indicator for high nutrient loads in modern coastal environments (Matsuoka et al., 2009). In modern Adriatic Sea environments increased RBC levels (as in cluster D1) are linked to high winter primary production (Zonneveld et al., 2009). Elevated nutrient levels and low salinity fit also to the constant contribution of various morphotypes of *Spiniferites bentorii* (Pospelova et al., 2002). Thus, a very shallow, freshwater influenced lagoon or embayment of Lake Pannon is indicated by the samples in the lower half of the core and intervals 60–65.

Clusters D3–D4 bear the highest amounts of *Spiniferites/Achomosphaera* as well as the lowest values of heterotrophs (Fig. 2). A correlation of *Spiniferites*-domination and sea-level rise was documented by Morzadec-Kerfourn (2005) in estuaries of NW Europe. The decrease of heterotrophs in favor of autotrophs is also a hint to lowered nutrition loads (see above; Dale, 2009). Several species of *Spiniferites*, including *S. bentorii*, and *S. bulloides* have been documented to be indicative for stratified water bodies in marine settings (Marret and Scourse, 2003). The occurrence of *Polykrikos schwartzii/kofoidii* may suggest stratified water conditions as well (Marret and Scourse, 2003). Therefore, in the upper part of the Mataschen core, the rapid increase by *Spiniferites/Achomosphaera* and the reduction of heterotrophs is interpreted herein as transgressions of Lake Pannon waters coinciding with a reduction of fresh water influx. The occurrence of scattered samples of clusters D3–D4a in the lower half of the core indicates repeated phases of reduced nutrient/sediment loads, which allowed neritic taxa to dominate the embayment. Stratification of the water column might have been established as well.

Cluster D4b is characterized by the high contribution of *Impagidinium* spp. (Fig. 2). Extant *Impagidinium* species are usually found in open marine settings, indicate oligotrophic surface waters and prefer salinities above 32 psu (Rochon et al., 1999; Marret and Zonneveld, 2003). In Lake Pannon, however, the genus appeared in nearshore areas as well and had to cope with salinities far below 20 psu (Harzhauser et al., 2008). Similarly, the extant *Impagidinium caspiense* is recorded from low salinity waters of the Caspian Sea and the Aral Sea (Marret et al., 2004; Sorrel et al., 2006). In the Mataschen core, a first increase of *Impagidinium* spp. occurs between samples 51 and 55. Two further phases with high values of *Impagidinium* spp. occur at samples 66, 68 and 92–95, which are also grouping in cluster 5 (Fig. 2). This pattern is roughly paralleled by *Selenopemphix nephroides* and lowered amounts of heterotrophs. The increase in *Impagidinium* might thus reflect major transgressions of Lake Pannon and phases of increasing oligotrophy due to decreasing input of nutrients. A similar scenario from Lake Pannon was described by Harzhauser et al. (2008) when rapid transgressive pulses of the lake coincided with *Impagidinium* peaks. Sorrel et al. (2006), too, linked the sudden increase of *Impagidinium* in Holocene cores of the Aral Sea with a rising sea level. In the modern Adriatic Sea, however, water depth is not the main factor for the occurrence of *Impagidinium*-dominated assemblages (Zonneveld et al., 2009). Instead, these assemblages are rather linked to areas with well oxygenated bottom water and poor stratification. Samples of cluster 4b might thus indicate a reduced stratification of the lake in the embayment compared to samples of clusters 3 and 4.

5.2.1. Lake surface water salinity

The decrease of *Polykrikos* cysts in the upper half of the core fits to a scenario with lowered freshwater influx coinciding with the takeover by Lake Pannon waters as indicated by the *Impagidinium*

increase. Simultaneously, a decrease in nutrient input can be expected which fits to the decrease of *Polykrikos* occurrences (Matsuoka et al., 2009). This scenario is also supported by the rare occurrence of *Pyxidinospis psilata*. This is a brackish water species and can tolerate salinities between 3 and 7 psu in the modern Baltic Sea (Dale, 1996; Leroy et al., 2007). Its scarceness in the modern Caspian Sea is thus explained by Marret et al. (2004) with the comparatively higher salinity of 12–13 psu. An optimum zone for *P. psilata* between 7 and 12 psu was also proposed by Marret et al. (2007) for Holocene occurrences in the Black Sea. The occurrence pattern of this species in the Mataschen core would thus point to low salinities between 7 and 12 psu during the deposition of the lower half of the core and a take-over by saline Lake Pannon waters of > 13 psu thereafter. The absence of the acritarch *Cymatiosphaera* spp. in the upper part of the core supports this interpretation as it disappears at summer surface salinities above 18 psu in Black Sea environments (Mudie et al., 2002).

The generally lowered salinities are also indicated by the morphotypes of *Spiniferites*. Ellegaard (2000) shows, that cysts of *Spiniferites* spp. with apical boss and shortened and geminal processes are developed at low salinities in recent embayments of Denmark. In the current study, many *Spiniferites* and *Achomosphaera* morphotypes with shortened, geminal and membranaceous processes similar to those illustrated in Ellegaard (2000) have been recorded.

5.2.2. Peridinioid–gonyaulacoid ratio

The peaks in the P/G ratio are caused by a proportional increase of heterotrophs with a simultaneous decrease of autotrophs. The ratio of the heterotrophic protoperidinioid and autotrophic gonyaulacoid dinoflagellates is used to provide information about the productivity signal (Dale and Fjellsaf, 1994). However, the distribution of most gonyaulacoid dinoflagellates (e.g. *Spiniferites* and *Impagidinium*) is not directly related to nutrient availability (e.g. Dale, 1996; Devillers and de Vernal, 2000). Nevertheless, the takeover by heterotrophs – the heterotroph signal sensu Dale (2009) – is still interpreted as evidence for elevated nutrient availability or even eutrophication (Matsuoka, 1999; Dale, 2009). The decrease of autotrophs may be caused by shading due to high concentrations of blooming phytoplankton or turbidity by sediment load. The most likely scenario to achieve elevated nutrient levels in this embayment of Lake Pannon along the Eastern Alps is a pluvial phase. Precipitation-related eutrophication events, lasting few years or even only a single year, are thus suggested by the extraordinary peaks at samples 22, 34, 45, 60, 76 and 89.

5.2.3. Accessory taxa

Warm climatic conditions prevailed during the deposition of the studied samples based on the dominance of *Spiniferites* spp., *Selenopemphix nephroides*, and the warm-water acritarch genus *Nannobarbophora* (Head, 2003). In marine settings, *S. nephroides* is typical for river mouth areas and may be used as indicator for fluvial influx (Holzwarth et al., 2007). Although, *S. nephroides* is not exclusively neritic but may thrive in oceanic waters as well it has an affinity to eutrophic coastal settings and zones of high productivity (Marret and Zonneveld, 2003; Susek et al., 2005; Sorrel et al., 2006; Pospelova et al., 2008; Holzwarth et al., 2010). Freshwater influx is clearly documented by sporadic occurrences of coenobia of *Pediastrum boryanum* and *P. duplex* accompanied by *Botryococcus* (Batten, 1996; Matthiessen and Brenner, 1996). The heterotrophic species *Selenopemphix nephroides* and *Selenopemphix* sp.1 display a roughly opposing trend. Each is correlated in abundance with a certain gonyaulacoid: *Selenopemphix nephroides* is positively correlated with *Impagidinium* spp. and *Selenopemphix* sp.1 is positively correlated with *Spiniferites b. pannonicus* and *S. b. budajenoensis*. The decline of the *Spiniferites* taxa in samples 48–50 is clearly followed by a decline by *Selenopemphix* sp.1 in samples 51–54. The opposite pattern is evident for the *Selenopemphix* sp.1-peak in sample 76 which is paralleled

soon after by *Spiniferites* in samples 77–79. This relation of *Impagidinium* spp. with *Selenopemphix nephroides*, which is an open marine species characteristically present in coastal environments (Marret and Zonneveld, 2003) fits to the transgressive phase. The opposing trend in *Selenopemphix* sp.1, *Spiniferites b. pannonicus* and *S. b. budajenoensis* may thus indicate that these taxa have been adapted to low salinity environments in lagoons of Lake Pannon.

5.3. Vegetation dynamics

The Tortonian vegetation of Mataschen has already been described in several papers (e.g. Draxler et al., 1994; Kovar-Eder, 2004; Meller and Hofmann, 2004; Kovar-Eder and Hably, 2006). Herein, we try to detect changes of vegetation on a decadal to centennial scale, rather than describing a time-averaged assemblage as done in previous studies. Based on the sedimentation rate as calculated by Gross et al. (in press), the cores studied cover a time span of less than 1400 years. Thus, the documented trends and shifts happened within very short time in a geological context, but span a fairly long time in respect to ecological studies focusing on extant vegetation systems like swamps or marshes (e.g. Effler and Goyer, 2006; Kirwan and Temmerman, 2009).

The changing of the different vegetation types is visualized by the different plant clusters (Fig. 4). Cluster P1 represents samples which were deposited when swampy wetlands were fringing the lake. Taxodiaceae, especially the taxa *Taxodium* in the SE Asia (Visser and Sasser, 1995; Hoepfner et al., 2008) and *Glyptostrobus* in China (Averyanov et al., 2009), form vast swamp forests. There, the tree assemblages include representatives of *Nyssa*, *Liquidambar* and *Quercus*, followed by once-a-year-flooded vegetation and riparian wetlands mainly consisting of *Quercus*, *Liquidambar*, *Fagus*, *Carya*, and *Celtis* (Wilen and Tiner, 1993). The next plant association (cluster P3) suggests open grass vegetation close to the shore due to the lack of most tree genera (Fig. 4). Several genera of Poaceae, Cyperaceae and *Sparganium/Typha* are known to form marsh wetlands even in brackish environments. Therefore, a marsh comparable to modern marshes of coastal Louisiana (Webb et al., 1995) or Florida (Willard et al., 2001) is indicated by the composition of the samples in cluster P3a. Based on the high amount of Taxodiaceae pollen, a transition of these marshes into a Taxodiaceae swamp is suggested in samples of subcluster P3b, comparable to recent swamps in SE USA (Willard et al., 2001; Hoepfner et al., 2008). P4 cluster also describes a vegetation type with a high amount of marsh grasses, but further with a wide distribution of a forested wetland with Taxodiaceae and an increasing number of *Nyssa* (Fig. 4).

P2 describes an intermediate state of the vegetation. Due the lack of Poaceae, Cyperaceae and *Sparganium/Typha*, only *Pinus* and *Cathaya* dominate the cluster associated with other hinterland taxa. These are represented by species of the genera *Carya*, *Carpinus*, *Tilia*, *Alnus* and from the Oleaceae family.

Already the lower part of the core reveals considerable fluctuations and a marked change in pollen composition (Fig. 4). A high number of tree species (approximately 26 plant taxa) are present but decrease for the benefit of swamp and marsh plants (Taxodiaceae, Cyperaceae, Poaceae, *Sparganium/Typha*) within less than a century. Poaceae and Cyperaceae are one of the most common representatives in halophytic and brackish environments in subtropical climates (Adam, 1990; González and Dupont, 2009) and thus are the main components of many modern brackish marshes (Tzonev et al., 2008). Generally, Poaceae are more salt tolerant than Cyperaceae (González and Dupont, 2009). Therefore, the first vegetation belt around brackish Lake Pannon was presumably formed by Poaceae, followed by Cyperaceae, probably accompanied by *Typha*. Members of this genus may dominate marshes as well [e.g. New England (Mullan Crain et al., 2004), around North America's Great Lakes (Keddy and Reznicek, 1986), Florida and Louisiana (Doren et al.,

1997; Willard et al., 2001)], but are very sensitive to salt content of the water and soil. *Typha* can also be otherwise an important member of swamp vegetation (Bush, 2002).

This situation changes above sample 30, where samples of cluster P2 predominate (Fig. 4). Most characteristic is the breakdown of marsh grasses during several decades time. While Poaceae and *Sparganium/Typha* are subordinate, the number of Cyperaceae pollen is increasing. Taxodioidae and mesothermic elements become more and more important components of the assemblages. This coincides with the lowest plant diversity in the samples and with the lowest values for the mean annual precipitation (Fig. 6). Such a decrease in rainfall is a plausible scenario for the marsh dieback as a wetland ecosystem is highly vulnerable to changes in water supply (Lodge, 2010). For a marsh system, the hydroperiod, which means the time of total inundation of the soil, is an important factor for its proliferation. Especially the annual rainfall has been documented in ecological studies to be a crucial factor (Lodge, 2010). As a plausible scenario for the locality of Mataschen, a shorter hydroperiod causes non-ideal conditions for the Poaceae and *Sparganium/Typha* and plants adapted to the new conditions will soon take over (Keddy and Reznicek, 1986). Cyperaceae, with their lower tolerance to brackish water and their ability to cope with drier conditions, can now dominate the marsh area.

Marshes are rapidly regenerating and adapting vegetation systems. The surrounding forest, however, is more stable and is not

suspected to have changed considerably in such a multi-decadal period. Therefore, the relative increase in tree taxa within this part of the core (cluster P2; Fig. 4) may rather be caused by the disappearance of the marsh taxa in the samples.

Thereafter, the Cyperaceae are vanishing quickly within only a few samples, coinciding with a breakdown of other grasses at sample 50 (transition from clusters P2 to P1). This pattern seems again to be strongly linked to a short-termed climate event. Within these samples, the mean annual precipitation is rising roughly about 200–300 mm. This causes not only a change in the marsh vegetation, but more intense its dieback because due to the quick ingression of Lake Pannon. A high rate of relative sea level rise increases the depth and duration of inundation, often causing plant death (Mendelssohn and McKee, 1988; Webb et al., 1995). If the marsh's accretion cannot catch up with the acceleration of the lake level rise it will simply drown (Kirwan and Temmerman, 2009). The ingression resulted in forested swampy conditions, indicated by the gradual increase of Taxodioidae and *Nyssa* (Lodge, 2010) during this period.

Starting with sample 63, this transgressive pulse ends and assemblages of cluster P4 appear. Taxodioidae are the dominating plants forming forested swamps comparable to recent South Florida (Willard et al., 2001; Lodge, 2010). Accordingly, Poaceae, *Sparganium/Typha* and Cyperaceae become abundant again. Such a spread of non-forested wetland vegetation can be caused by the decline of

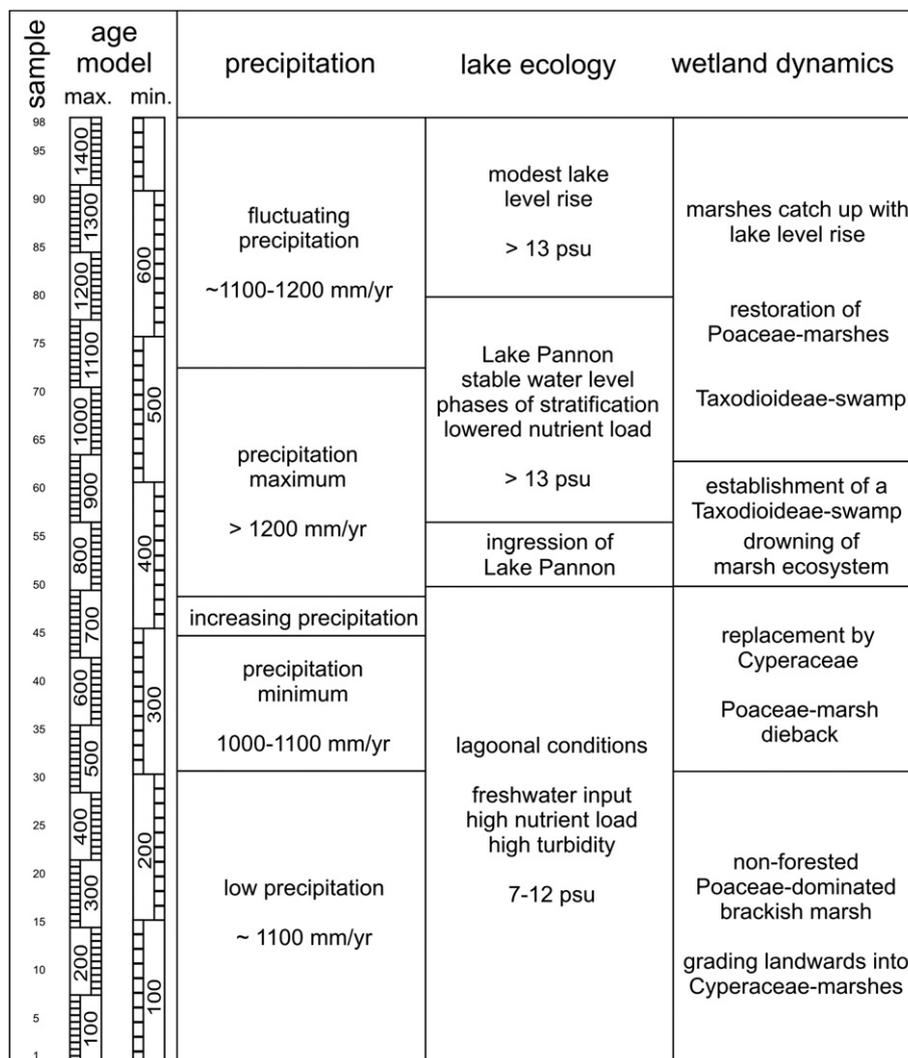


Fig. 6. Interpretation of the climatic parameters, lake ecology and vegetation dynamics in relation to the age model of Gross et al. (submitted). Major perturbations of the vegetation belts happened within few decades while the restoration phases take place on a centennial scale.

the transgressive pulse or an adaptation of the marsh plants to the lake level rise (Kirwan and Temmerman, 2009; Kolker et al., 2009). Model experiments by Kirwan and Temmerman (2009) demonstrated, that marshes can adapt to rapid rates of sea level rise within 100 years, which is supported by field observations of Clark and Patterson (1984). Further, a comparable “slow-down-scenario” might also explain the vegetation shift observed in the P4 samples of the Mataschen core.

As this trend follows on, Lake Pannon's shores become more and more dominated by widespread marshes again. Samples of subcluster P3b appear again, being characterized by pollen assemblages of forested and non-forested wetlands. Poaceae, Cyperaceae and *Sparganium/Typha* formed the first vegetation belt of Lake Pannon again, grading into Taxodioidae swamps behind. The hinterland is covered with forests, comprising tree taxa, typically for the Late Miocene, such as *Carya*, *Pterocarya*, *Fagus*, *Celtis*, *Ulmus* and *Carpinus*, but with a possible high amount of evergreen trees such as *Symplocos*, *Reevesia*, Sapotaceae, and Mastixiaceae.

6. Conclusions

The pollen and dinoflagellate records reveal a complex interplay between Tortonian climate, lake level and ecosystem response (Fig. 6). Within a presumed time span of only one millennium, a surprisingly rapid succession of environments is documented. Due to the high stratigraphic resolution of c. 7–14 years per sample (Gross et al., in press), the often asynchronous responses of lake-biota and its surrounding wetlands in relation to Late Miocene small scale climatic change can be described.

A brackish, but strongly freshwater influenced, lagoon with salinities between 7 and 12 psu developed at the margin of Lake Pannon under a moderate mean annual precipitation of c. 1100 mm. High nutrient input favored a high surface-water productivity of dinoflagellates, which have caused repeated algae bloom events of several years. During that time, the coasts were fringed by marshes of Poaceae grading into Cyperaceae landwards. Behind the brackish marsh vegetation, a forested wetland was developed, characterized by high abundances of Taxodioidae, which became replaced by mixed evergreen and deciduous forests in the hinterland. A decrease in MAP slightly below 1000 mm is expressed in the vegetation by the take-over by dry-adapted Cyperaceae grasses within c. 200–300 years. Soon after, a rapid transgression of Lake Pannon caused a total loss of the marsh ecosystem. This is reflected by the synchronous quick and strong increase of the “open-water” dinoflagellate *Impagidinium* suggesting that the marshes could not keep up with the rising lake level and drowned within some decades. Simultaneously, salinity increased above 13 psu and the nutrient load decreased. The rise of the lake level occurred with a five sample delay after a strong increase of precipitation of c. 300 mm/yr to more than 1200 mm/yr. This implies that the hydrological budget of Lake Pannon lagged with a delay of ca. 4–6 decades, probably caused by its very large size and depth. The strong transgressive pulse lasted ~100–130 years and then slowed down as the mean annual rainfall was decreasing. This slow-down-phase allowed the marshes to re-establish and to resist further small fluctuations of the lake level. After another ~100–200 years the vegetation system was adapted to the newly established environment and Poaceae and Cyperaceae formed the dominating shoreline vegetation again. Mean annual precipitation was thus the driving force for dieback or expansion of the marshes whereas temperature did not change significantly.

Although not completely in phase with the terrestrial ecosystem, the dinoflagellate spectra clearly reflect the beginning of the ingression of Lake Pannon and document an increase in salinity. A marked regularity of blooms of heterotroph dinoflagellates is observed throughout the core with a periodicity of 11–16 samples. This might suggest some influence of solar cycles such as the Gleissberg cycle or the de Vries/

Suess cycle (Braun et al., 2005). Unfortunately, the studied core is too short to apply a reliable time series analysis. In any case, dinoflagellate blooms have been quasi-periodic phenomena in coastal areas of Lake Pannon during the Early Tortonian.

These results from a Tortonian core are comparable to studies on Holocene lakes in sample density and time resolution (e.g. Hooghiemstra, 1989; Pellatt et al., 2001; Stebich et al., 2005; Tarasov et al., 2007; Jiménez-Moreno et al., 2008). Therefore, this method is capable to register climate-driven Miocene environmental dynamics on a similar high-frequency sub-Milankovitch scale. Understanding Tortonian climate as a pendant-scenario for the predicted global climate change will need much more such studies as our knowledge on pre-Quaternary high-resolution climate dynamics is still extremely poor.

Supplementary materials related to this article can be found online at [10.1016/j.palaeo.2011.11.021](http://dx.doi.org/10.1016/j.palaeo.2011.11.021)

Acknowledgments

The study was supported by the FWF-grants P21414-B16 (Millennial- to centennial-scale vegetation dynamics and surface water productivity during the Late Miocene in and around Lake Pannon) and P21748-N21 (Evolution and Phylogeny in Cyprideis, Ostracoda). The paper contributes to the NECLIME network.

References

- Adam, P., 1990. Saltmarsh Ecology. Cambridge University Press, Cambridge. (461 pp.).
- Averyanov, L.V., Phan, E.L., Nguyen, T.H., Nguyen, S.K., Nguyen, T.V., Pham, T.D., 2009. Preliminary observations of native *Glyptostrobus pensilis* (Taxodiaceae) stands in Vietnam. *Taiwania* 54, 191–212.
- Batten, D.J., 1996. Palynofacies and palaeoenvironmental interpretation. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation 1, Dallas, pp. 1011–1164.
- Böhme, M., Ilg, A., Winklhofer, M., 2008. Late Miocene “washhouse” climate in Europe. *Earth and Planetary Science Letters* 275, 393–401.
- Braun, H., Christl, M., Rahmstorf, S., Ganopolski, A., Mangini, A., Kubatzki, C., Roth, K., Kromer, B., 2005. Possible solar origin of the 1,470-year glacial climate cycle demonstrated in a coupled model. *Nature* 438, 208–211.
- Bruch, A.A., Utescher, T., Mosbrugger, V., Gabrielyan, I., Ivanov, D.A., 2006. Late Miocene climate in the circum-Alpine realm — a quantitative analysis of terrestrial palaeofloras. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 270–280.
- Bruch, A.A., Uhl, D., Mosbrugger, V., 2007. Miocene climate in Europe — patterns and evolution. A first synthesis of NECLIME. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253, 1–7.
- Bujak, J.P., 1984. Cenozoic dinoflagellate cysts and acritarchs from the Bering Sea and northern North Pacific. *D.S.D.P. Leg 19. Micropaleontology* 30, 180–212.
- Bush, M., 2002. On the interpretation of fossil Poaceae pollen in the lowland humid neotropics. *Palaeogeography, Palaeoclimatology, Palaeoecology* 177, 5–17.
- Clark, J.S., Patterson III, W.A., 1984. Pollen, ²¹⁰Pb and opaque spherules; an integrated approach to dating sedimentation in the intertidal environment. *Journal of Sedimentary Petrology* 54, 1251–1265.
- Dale, B., 1996. Dinoflagellate cyst ecology: modeling and geological applications. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation 3, Dallas, pp. 1249–1275.
- Dale, B., 2001. Marine dinoflagellate cysts as indicators of eutrophication and industrial pollution: a discussion. *The Science of the Total Environment* 264, 235–240.
- Dale, B., 2009. Eutrophication signals in the sedimentary record of dinoflagellate cysts in coastal waters. *Journal of Sea Research* 61, 103–113.
- Dale, B., Fjellsaf, A., 1994. Dinoflagellate cysts as paleoproductivity indicators: state of the art, potential and limits. In: Zahn, R., Pedersen, T.F., Kaminski, M.A., Labeyrie, L. (Eds.), *Carbon Cycling in the Glacial Ocean: Constraints on the Ocean's Role in Global Change*. NATO ASI Ser. I. 17. Springer-Verlag, Berlin, pp. 521–537.
- Daxner-Höck, G., 2004. Beavers and a Dwarf Hamster from Mataschen (Lower Pannonian, Styrian Basin). *Joannea Geologie und Paläontologie* 5, 19–33.
- Devillers, R., de Vernal, A., 2000. Distribution of dinoflagellate cysts in surface sediments of the northern North Atlantic in relation to nutrient content and productivity in surface waters. *Marine Geology* 166, 103–124.
- Doren, R.F., Armentano, T.V., Whiteaker, L.D., Jones, R.D., 1997. Marsh vegetation patterns and soil phosphorus gradients in the Everglades ecosystem. *Aquatic Botany* 56, 145–163.
- Draxler, I., Solti, G., Lobitzer, H., Cichocki, O., 1994. Erster Nachweis von “Alginin” (sensu Jámor Solti, 1975) im Süsteirischen Tertiärbecken (Österreich). *Jubiläumsschrift 20 Jahre Geologische Zusammenarbeit Österreich-Ungarn*, Wien, Bécs, pp. 19–54.
- Effler, R.S., Goyer, R.A., 2006. Baldcypress and water tupelo sapling response to multiple stress agents and reforestation implications for Louisiana swamps. *Forest Ecology and Management* 226, 330–340.

- Ellegaard, M., 2000. Variations in dinoflagellate cyst morphology under conditions of changing salinity during the last 2000 years. *Review of Palaeobotany and Palynology* 9, 65–81.
- Erdei, B., Hably, L., Kázmé, M., Utescher, T., 2007. Neogene flora and vegetation development of the Pannonian domain in relation to palaeoclimate and palaeogeography.
- François, L., Ghislain, M., Otto, D., Micheels, A., 2006. Late Miocene vegetation reconstruction with the CARAIB model. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 302–320.
- González, C., Dupont, L., 2009. Tropical salt marsh succession as sea-level indicator during Heinrich events. *Quaternary Science Reviews* 28, 939–946.
- Green, O.R., 2001. *A Manual of Practical Laboratory and Field Techniques in Palaeobiology*. Kluwer Academic Publishers, Dordrecht.
- Grimm, E.C., 2004. Tilia and TG View Version 2.0.2. Illinois State Museum, Research and Collector Center.
- Gross, M., 1994. Erster Nachweis der fossilen Schildkröte *Clemmydopsis turnauensis* aus dem Pannonium des Oststeirischen Tertiärbeckens (Testudines: Emydidae: Batagurinae). *Mitteilungen des Naturwissenschaftlichen Vereines für Steiermark* 124, 49–59.
- Gross, M., 2004. Contributions to the ostracode fauna (Crustacea), paleoecology and stratigraphy of the clay pit Mataschen (Lower Pannonian, Styrian Basin, Austria). *Joannea Geologie und Paläontologie* 5, 49–129.
- Gross, M., Minati, K., Danielopol, D.L., Piller, W.E., 2008. Environmental changes and diversification of *Cyprideis* in the Late Miocene of the Styrian Basin (Lake Pannon, Austria). *Senckenbergiana Lethaea* 88, 161–181.
- Gross, M., Piller, W.E., Scholger, R., Gitter, F., 2011. Biotic and abiotic response to palaeoenvironmental changes at Lake Pannons' western margin (Central Europe, Late Miocene). *Palaeogeography, Palaeoclimatology, Palaeoecology* 312, 181–193.
- Hably, L., Kovar-Eder, J., 1996. A representative leaf assemblage of the Pannonian Lake from Dozmat near Szombathely (Western Hungary), Upper Pannonian, Upper Miocene. *Advances in Austrian–Hungarian Joint Geological Research*. Budapest, pp. 69–81.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST; palaeontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4 (1) (9 pp.).
- Harzhauser, M., 2004. Mollusc based biostratigraphy of the clay pit Mataschen in the Styrian Basin (Pannonian). *Joannea Geologie und Paläontologie* 5, 149–161.
- Harzhauser, M., Mandic, O., 2008. Neogene lake systems of Central and South-Eastern Europe: faunal diversity, gradients and interrelations. *Palaeogeography, Palaeoclimatology, Palaeoecology* 260, 417–434.
- Harzhauser, M., Kern, A., Soliman, A., Minati, K., Piller, W.E., Danielopol, D.L., Zuschin, M., 2008. Centennial- to decadal scale environmental shifts in and around Lake Pannon (Vienna Basin) related to a major Late Miocene lake level rise. *Palaeogeography, Palaeoclimatology, Palaeoecology* 270, 102–115.
- Head, M.J., 2003. Neogene occurrences of the marine acritarch genus *Nannobarbophora* Habib and Knapp, 1982 emend., and the new species *N. gedlii*. *Journal of Paleontology* 77, 382–385.
- Head, M.J., Riding, J.B., Eidvin, T., Chadwick, R.A., 2004. Palynological and foraminiferal biostratigraphy of (Upper Pliocene) Nordland Group mudstones at Sleipner, northern North Sea. *Marine and Petroleum Geology* 21, 277–297.
- Heusser, L., Balsam, W.L., 1977. Pollen distribution in the Northeast Pacific Ocean. *Quaternary Research* 7, 45–62.
- Hoepfner, S.S., Shaffer, G.P., Perkins, T.E., 2008. Through droughts and hurricanes: tree mortality, forest structure, and biomass production on a coastal swamp targeted for restoration in the Mississippi River Deltaic Plain. *Forest Ecology and Management* 256, 937–948.
- Holzwarth, U., Esper, O., Zonneveld, K.A.F., 2007. Distribution of organic-walled dinoflagellate cysts in shelf surface sediments of the Benguela upwelling system in relationship to environmental conditions. *Marine Micropaleontology* 64, 91–119.
- Holzwarth, U., Esper, O., Zonneveld, K.A.F., 2010. Organic-walled dinoflagellate cysts as indicators of oceanographic conditions and terrigenous input in the NW African upwelling region. *Review of Palaeobotany and Palynology* 159, 35–55.
- Hooghiemstra, H., 1989. Quaternary and Upper-Pliocene glaciations and pollen development in the tropical Andes: evidence from a long high-resolution pollen record from the sedimentary basin of Bogotá, Colombia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 72, 11–26.
- Hopkins, J.S., 1950. Differential flotation and deposition of coniferous and deciduous tree pollen. *Ecology* 31, 633–641.
- Jiménez-Moreno, G., 2006. Progressive substitution of a subtropical forest for a temperate one during the middle Miocene climate cooling in Central Europe according to palynological data from cores Tengelic-2 and Hidas-53 (Pannonian Basin, Hungary). *Review of Palaeobotany and Palynology* 142, 1–14.
- Jiménez-Moreno, G., Suc, J.-P., 2007. Middle Miocene latitudinal climate gradient in Western Europe: evidence from pollen records. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253, 208–225.
- Jiménez-Moreno, G., Fawcett, P.J., Anderson, R.S., 2008. Millennial- and centennial-scale vegetation and climate change during the late Pleistocene and Holocene from northern New Mexico (USA). *Quaternary Science Reviews* 27, 1142–1452.
- Keddy, P.A., Reznicek, A.A., 1986. Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. *Journal of Great Lakes Research* 12, 25–36.
- Kirwan, M., Temmerman, S., 2009. Coastal marsh response to historical and future sea-level acceleration. *Quaternary Science Reviews* 28, 1801–1808.
- Koepfen, W., 1936. Das geographische System der Klimate. In: Koepfen, W., Geiger, R. (Eds.), *Handbuch der Klimatologie*. Bebrüder Bornträger, Berlin, pp. 1–44.
- Kolker, A.S., Goodbred, S.L., Hameed, S., Cochran, J.K., 2009. High-resolution records of the response of coastal wetland systems to long-term and short-term sea-level variability. *Estuarine, Coastal and Shelf Science* 84, 493–508.
- Kollmann, K., 1965. Jungtertiär im Steirischen Becken. *Mitteilungen der Geologischen Gesellschaft in Wien* 57, 479–632.
- Kouli, K., Brinkhuis, H., Dale, B., 2001. *Spiniferites cruciformis*. A fresh water dinoflagellate cyst? *Review of Palaeobotany and Palynology* 113, 273–286.
- Kovar-Eder, J., 2004. The Upper Miocene flora of Mataschen near Fehring, Styria – leaf assemblages. *Joannea Geologie und Paläontologie* 5, 163–176.
- Kovar-Eder, J., Hably, L., 2006. The flora of Mataschen – a unique plant assemblage from the late Miocene of eastern Styria (Austria). *Acta Palaeobotanica* 46, 157–233.
- Kovar-Eder, J., Hably, L., Derek, T., 1995. Neuhaus/Klausenbach – eine miozäne (pannone) Pflanzenfundstelle aus dem südlichen Burgenland. *Jahrbuch der Geologischen Bundesanstalt* 138, 321–347.
- Kovar-Eder, J., Schwarz, J., Wójcicki, J., 2002. The predominantly aquatic flora from Pellendorf, Lower Austria, Late Miocene, Pannonian – a systematic study. *Acta Palaeobotanica* 42, 125–151.
- Lear, C.H., Rosenthal, Y., Wright, J.D., 2003. The closing of a seaway: ocean water masses and global climate change. *Earth and Planetary Science Letters* 210, 425–436.
- Leroy, S.A.G., Albay, M., 2010. Palynomorphs of brackish and marine species in cores from the freshwater Lake Sapanca, NW Turkey. *Review of Palaeobotany and Palynology* 160, 181–188.
- Leroy, S.A.G., Marret, F., Gibert, E., Chalié, F., Reyss, J.-L., Arpe, K., 2007. River inflow and salinity changes in the Caspian Sea during the last 5500 years. *Quaternary Science Reviews* 26, 3359–3383.
- Linder, A., Berchtold, W., 1976. *Statistische Auswertung von Prozentzahlen*. 1–230. Birkhäuser, Basel.
- Lirer, F., Harzhauser, M., Pelosi, N., Piller, W.E., Schmid, H.P., Sprovieri, M., 2009. Astro-nomically forced teleconnection between Paratethyan and Mediterranean sediments during the Middle and Late Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 275, 1–13.
- Lodge, T.E., 2010. *The Everglades Handbook – Understanding the Ecosystem*. Taylor and Francis Group, Boca Raton.
- Londeix, L., Herreyre, Y., Turon, J.-L., Fletcher, W., 2009. Last Glacial to Holocene hydrology of the Marmara Sea inferred from a dinoflagellate cyst record. *Review of Palaeobotany and Palynology* 158, 52–71.
- Magyar, I., Geary, D.H., Müller, P., 1999a. Paleogeographic evolution of the Late Miocene Lake Pannon in Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 147, 151–167.
- Magyar, I., Geary, D.H., Sütö-Szentai, M., Lantos, M., Müller, P., 1999b. Integrated biostratigraphic, magnetostratigraphic and chronostratigraphic correlation of the Late Miocene Lake Pannon deposits. *Acta Geologica Hungarica* 45, 5–31.
- Marret, F., Scourse, J., 2003. Control of modern dinoflagellate cyst distribution in the Irish and Celtic seas by seasonal stratification dynamics. *Marine Micropaleontology* 47, 101–116.
- Marret, F., Zonneveld, K.A.F., 2003. Atlas of modern organic-walled dinoflagellate cyst distribution. *Review of Palaeobotany and Palynology* 125, 1–200.
- Marret, F., Leroy, S., Chalié, F., Gasse, F., 2004. New organic-walled dinoflagellate cysts from recent sediments of Central Asian seas. *Review of Palaeobotany and Palynology* 129, 1–20.
- Marret, F., Mudie, P.J., Aksu, A., Hiscott, R.N., 2007. Holocene dinocyst record of a two-step transformation of the Neoeuxinian brackish water lake into the Black Sea. *Quaternary International* 197, 72–86.
- Marret, F., Mudie, P.J., Aksu, A.E., Hiscott, R.N., 2009. A Holocene dinocyst record of a two-step transformation of the Neoeuxinian brackish water lake into the Black Sea. *Quaternary International* 197, 72–86.
- Matsuoka, K., 1987. Organic-walled dinoflagellate cysts from surface sediments of Akkeshi Bay and Lake Saroma, North Japan. *Bulletin of the Faculty of Liberal Arts, Nagasaki University, Natural Science* 28, 35–123.
- Matsuoka, K., 1999. Eutrophication process recorded in dinoflagellate cyst assemblages—a case of Yokohama Port, Tokyo Bay, Japan. *The Science of the Total Environment* 231, 17–35.
- Matsuoka, K., Kawami, H., Nagai, S., Mitsunori, I., Takayama, H., 2009. Re-examination of cyst–mottle relationships of *Polykrikos kofoidii* Chatton and *Polykrikos schwartzii* Bütschli (Gymnodinales, Dinophyceae). *Review of Palaeobotany and Palynology* 154, 79–90.
- Matthiessen, J., Brenner, W., 1996. Dinoflagellate cyst ecostratigraphy of Pliocene–Pleistocene sediments from the Yermak Plateau (Arctic Ocean, Hole 911A). *Proceedings of the ODP, Scientific Results* 151, 243–253.
- Meller, B., Hofmann, C.-C., 2004. Paleoecology of diaspore- and palynomorph assemblages from Late Miocene lake sediments (Mataschen near Fehring, East Styria, Austria). *Joannea Geologie und Paläontologie* 5, 177–217.
- Mendelssohn, I.A., McKee, K.L., 1988. *Spartina alterniflora* die back in Louisiana: time-course investigation of soil waterlogging effects. *Journal of Ecology* 76, 509–521.
- Micheels, A., Bruch, A.A., Uhl, D., Utescher, T., Mosbrugger, V., 2007. A Late Miocene climate model simulation with ECHAM4/ML and its quantitative validation with terrestrial proxy data. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253, 251–270.
- Morzadec-Kerfourou, M.T., 2005. Dinoflagellate cysts and the paleoenvironment of Late-Pliocene Early-Pleistocene deposits of Brittany, Northwest France. *Quaternary Science Reviews* 16, 883–898.
- Mosbrugger, V., Utescher, T., 1997. The coexistence approach – a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* 134, 61–86.
- Mudie, P.J., Aksu, A.E., Yasar, D., 2001. Late Quaternary dinoflagellate cysts from the Black, Marmara and Aegean seas: variations in assemblages, morphology and paleosalinity. *Marine Micropaleontology* 43, 155–178.
- Mudie, P.J., Rochon, A., Aksu, A.E., Gillespie, H., 2002. Dinoflagellate cysts, freshwater algae and fungal spores as salinity indicators in Late Quaternary cores from Marmara and Black seas. *Marine Geology* 190, 203–231.

- Mudie, P.J., Marret, F., Aksu, A.E., Hiscott, R.N., Gillespie, H., 2007. Palynological evidence for climatic change, anthropogenic activity and outflow of Black Sea water during the late Pleistocene and Holocene: centennial- to decadal-scale records from the Black and Marmara seas. *Quaternary International* 167–168, 73–90.
- Mullan Crain, C., Silliman, B.R., Bertness, S.L., Bertness, M.D., 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology* 85, 2539–2549.
- Papp, A., 1951. Das Pannon des Wiener Beckens. *Mitteilungen der Geologischen Gesellschaft in Wien* 39–41, 99–193.
- Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Köppen–Geiger climate classification. *Hydrology and Earth System Science Discussions* 4, 439–473.
- Pellatt, M.G., Hebda, R.J., Mathewes, R.W., 2001. High-resolution Holocene vegetation history and climate from Hole 1034B, ODP Leg 169S, Saanich Inlet, Canada. *Marine Geology* 147, 211–226.
- Pospelova, V., Chmura, G.L., Boothman, W.S., Latimer, J.S., 2002. Dinoflagellate cyst records and human disturbance in two neighboring estuaries, New Bedford Harbor and Apponagansett Bay, Massachusetts (USA). *The Science of the Total Environment* 298, 81–102.
- Pospelova, V., de Vernal, A., Pedersen, T.F., 2008. Distribution of dinoflagellate cysts in surface sediments from the northeastern Pacific Ocean (43–25°N) in relation to sea-surface temperature, salinity, productivity and coastal upwelling. *Marine Micropaleontology* 68, 21–48.
- Pound, M.J., Haywood, A.M., Salzmann, U., Riding, J.B., Lunt, D.J., Hunter, S.J., 2011. A Tortonian (Late Miocene, 11.6–7.25 Ma) global vegetation reconstruction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 300, 29–45.
- Rochon, A., de Vernal, A., Turon, J.-L., Matthiessen, J., Head, M.J., 1999. Distribution of recent dinoflagellate cysts in surface sediments from the North Atlantic Ocean and adjacent seas in relation to sea-surface parameters. *American Association of Stratigraphic Palynologists, Contributions Series* 35, 1–150.
- Sorrel, P., Popescu, S.-M., Head, M.J., Suc, J.P., Klotz, S., Oberhänsli, H., 2006. Hydrographic development of the Aral Sea during the last 2000 years based on a quantitative analysis of dinoflagellate cysts. *Palaeogeography, Palaeoclimatology, Palaeoecology* 234, 304–327.
- Stebich, M., Brüchmann, C., Kulbe, T., Negendank, J.F.W., 2005. Vegetation history, human impact and climate change during the last 700 years recorded in annually laminated sediments of Lac Pavin, France. *Review of Palaeobotany and Palynology* 133, 115–133.
- Steppuhn, A., Micheels, A., Geiger, G., Mosbrugger, V., 2006. Reconstructing the Late Miocene climate and oceanic heat flux using the AGCM ECHAM4 coupled to a mixed-layer ocean model with adjusted flux correction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 399–423.
- Steppuhn, A., Micheels, A., Bruch, A.A., Uhl, D., Utescher, T., Mosbrugger, V., 2007. The sensitivity of ECHAM4/ML to a double CO₂ scenario for the Late Miocene and the comparison to terrestrial proxy data. *Global and Planetary Change* 57, 189–212.
- Susek, E., Zonneveld, K.A.F., Fischer, G., Versteegh, G.J.M., Willems, H., 2005. Organic-walled dinoflagellate cyst production in relation to upwelling intensity and lithogenic influx in the Cape Blanc region (off north-west Africa). *Phycological Research* 53, 97–112.
- Tarasov, P., Bezrukova, E., Karabanov, E., Nakagawa, T., Wagner, M., Kulagina, N., Letunova, P., Abzaeva, A., Granoszewski, W., Riedel, F., 2007. Vegetation and climate dynamics during the Holocene and Eemian interglacials derived from Lake Baikal pollen records. *Palaeogeography, Palaeoclimatology, Palaeoecology* 252, 440–457.
- Traverse, A., Ginsburg, R.N., 1966. Palynology of the surface sedimentation of Great Bahamas Bank, as related to water movements and sedimentation. *Marine Geology* 4, 417–459.
- Tzonev, R., Lysenko, T., Gussev, C., Zhelev, P., 2008. The halophytic vegetation in south-east Bulgaria and along the Black Sea coast. *Hacquetia* 7, 95–121.
- Utescher, T., Mosbrugger, V., Ivanov, D., Dilcher, D.L., 2009. Present-day climate equivalents of European Cenozoic climates. *Earth and Planetary Science Letters* 284, 544–552.
- Utescher, T., Bruch, A.A., Micheels, A., Mosbrugger, V., Popova, S., 2011. Cenozoic climate gradients in Eurasia – a palaeo-perspective on future climate change? *Palaeogeography, Palaeoclimatology, Palaeoecology* 304, 351–358.
- Vasiliev, I., Krijgsman, W., Langereis, C.G., Panaiotu, C.E., Matenco, L., Bertotti, G., 2004. Towards an astrochronological framework for the eastern Paratethys Mio-Pliocene sedimentary sequences of the Focsani basin (Romania). *Earth and Planetary Science Letters* 227, 231–247.
- Vasiliev, I., de Leeuw, A., Filipescu, S., Krijgsman, W., Kuiper, K., Stoica, M., Briceag, A., 2010. The age of the Sarmatian–Pannonian transition in the Transylvanian Basin (Central Paratethys). *Palaeogeography, Palaeoclimatology, Palaeoecology* 297, 54–69.
- Visser, J.M., Sasser, C.E., 1995. Changes in tree species composition, structure and growth in a bald cypress-water tupelo swamp forest, 1980–1990. *Forest Ecology and Management* 72, 119–129.
- Webb, E.C., Mendelssohn, I.A., Wilsey, B.J., 1995. Causes for vegetation dieback in a Louisiana salt marsh: a bioassay approach. *Aquatic Botany* 51, 281–289.
- Wilén, B.O., Tiner, R.W., 1993. Wetlands of the United States. In: Whigham, D.F., Dykyjová, D., Hejný, S. (Eds.), *Handbook of Vegetation Science, Wetlands of the World I: Inventory, Ecology and Management*. Kluwer Academic Publishers, Dordrecht, Boston, London, pp. 129–194.
- Willard, D.A., Weimer, L.M., Riegel, W.L., 2001. Pollen assemblages as paleoenvironmental proxies in the Florida Everglades. *Review of Palaeobotany and Palynology* 113, 213–235.
- Wood, G.D., Gabriel, A.M., Lawson, J.C., 1996. Palynological techniques – processing and microscopy. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications, Vol. 1*. American Association of Stratigraphic Palynologists Foundation, Dallas, pp. 29–50.
- Zonneveld, K.A.F., Versteegh, G., Kodrans-Nsiah, M., 2008. Preservation and organic chemistry of Late Cenozoic organic-walled dinoflagellate cysts: a review. *Marine Micropaleontology* 68, 179–197.
- Zonneveld, K.A.F., Chen, L., Möbius, J., Mahmoud, M.S., 2009. Environmental significance of dinoflagellate cysts from the proximal part of the Po-river discharge plume (off southern Italy, Eastern Mediterranean). *Journal of Sea Research* 62, 189–213.
- Zuschin, M., Hohenegger, J., 1998. Subtropical coral-reef associated sedimentary facies characterized by mollusks (Northern Bay of Safaga, Red Sea, Egypt). *Facies* 38, 229–254.