Studia Quaternaria, vol. 37, no. 2 (2020): 59–67 DOI: 10.24425/sq.2020.133751

UNIQUE FINDS IN PALYNOLOGICAL SPECTRA: ACETOLYZE RESISTANT VEGETATIVE FORMS OF FRESHWATER DINOFLAGELLATE BASED ON THE LAKE MŁYNEK RECORD FROM NORTHEASTERN POLAND

Krzysztof Bińka[1*], Fabian Welc[2], Jerzy Nitychoruk[3], Dominika Sieradz[4], Antoni Lewczuk[5]

[1] *University of Warsaw, Department of Palaeontology, Faculty of Geology, Żwirki i Wigury 93, 02-089 Warszawa, Poland; e-mail: k.binka@uw.edu.pl*
[2] *Cardinal Stefan Wyszyński University, Institute of Archaeology, Dewajtis 5, 01-815 Warszawa, Poland; e-mail: f.welc@uksw.edu.pl*
[3] *Państwowa Szkoła Wyższa, im. Jana Pawła II w Białej Podlaskiej, Wydział Nauk Technicznych i Ekonomicznych, ul. Sidorska 95/97, 21-500, Biała Podlaska, Poland; e-mail: jerzy.nitychoruk@pswbp.pl*
[4] *Polish Geological Institute, National Research Institute, 4 Rakowiecka Street, 00 975, Warsaw, Poland; e-mail: dominika.fsieradz@pgi.gov.pl*
[5] *University of Warsaw, Department of Palaeontology, Faculty of Geology, Żwirki i Wigury 93, 02-089 Warszawa, Poland; e-mail: antex73@wp.pl*

** corresponding author*

Abstract:
The freshwater dinoflagellate represent microfossils which are very rarely noted in lake deposits. In Late Holocene sediments of the Lake Młynek, the Iława Lakeland, northern Poland, we identified intense blooms of algae of the genus Palatinus. They occurred primarily in the period of strong human impact during expansion of the Monastic State of the Teutonic Order. The most amazing thing is that samples in which conventional palynological maceration has been used dinoflagellate are represented by armored vegetative forms instead of cysts. During this laboratory processes, especially acetolysis, cellulosic thecae of armored forms should be destructed. This is the second known example of acetolysis resistant thecae of modern dinoflagellate, built by substance other than cellulose. Palatinus blooms were associated probably with the hydrotechnical works made by Teutonic Knights in the catchment, which caused supply and discharge of micronutrients e.g. selenium in the basin.

Key words: freshwater dinoflagellate, microfossil, human impact, Holocene

Manuscript received 16 November 2019, accepted 3 January 2020

INTRODUCTION

Function of some early medieval Prussian strongholds in the Mazurian Lake District, northern Poland, is not fully clear. One of them is located at Janiki Wielkie near the Młynek Lake in the Iława Lakeland (Fig. 1). The collected core of lacustrine deposits, examined by pollen analysis, reveals two settlement phases – the Roman Period and the second one since the early medieval time. In reality, however, abundantly blooming dinoflagellate are quite unusual find in the spectra. Dinocysts or exceptionally not destructed thecae of vegetative freshwater species are very rarely noted in the Holocene sediments (Evitt *et al.*, 1985; Burden *et al.*, 1986; Tardio *et al.*, 2006; McCarthy *et al.*, 2011; Danesh *et al.*, 2013; McCarthy and Krueger, 2013; Drjlepan *et al.*, 2014). Cysts of freshwater forms may be a good indicator of trophic status of the lake. Advanced trophy, induced by natural factors or human impact fruits in the expansion of more eutrophic species, eliminating those preferring oligotrophic or mesotrophic waters (Krueger 2012, McCarthy and Krueger, 2013, Drjlepan *et al.*, 2014). However, identification of cyst morphology of modern freshwater species is still limited and has not been described yet for most of the freshwater vegetative forms resting cysts (Mertens *et al.*, 2012). Blooms of the specimens of the *Palatinus* Craveiro, Calado, Daugbjerg et Moestrup

Fig. 1. Location of the study area.

gen. nov. (Craveiro *et al*., 2009), a recently described genus found in the Młynek Lake are still interesting for another reason. They represent most probably not a cyst but acetolysis resistant thecae of vegetative forms! The aim of this work is identification and description of their morphology and first of all, the examination of reasons for abundant blooms in a historical context.

MATERIAL AND METHODS

The 3.5 m long core was collected for pollen analysis from the small and shallow Lake Młynek (Fig. 2), on a northern bank of which an early medieval stronghold has been located

(borehole coordinates: 53.82486`N, 019.72419`E). The core is composed almost entirely of gray-brown gyttja with slightly higher content of organic matter at 1.45–1.70 m depth. 64 samples from 0.15–3.40 m depth were collected to further analysis. The samples were treated using standard palynological procedures including hot 10% KOH, cold HF (2 days) and finally, the Erdtman's acetolysis.

AMS dating was conducted in the Poznań Radiocarbon Laboratory in Poland. Conventional ^{14}C ages were calculated using corrections for isotopic fractionation according to Stuiver and Polach (1977). Calibration of ^{14}C age was performed using OXCAL v. 4.2 software and the Northern Hemisphere terrestrial calibration curve IntCal13 (Reimer *et al*., 2013). An age-depth model was produced using the Bayesian software Bacon (Blaauw and Christen, 2011), which assumed a piece-wise linear accumulation of the lake sediment constrained by prior information on the lake's accumulation rate and its variability between neighboring depths (Fig. 3).

RESULTS

In the pollen diagram we distinguished 5 local pollen zones: M1 (5 samples at 3.20–3.40 m), M2 (10, 2.70–3.15 m), M3 (13, 2.05–2.65 m), M4 (11, 1.45–2.00 m), M5 (25, 0.15–1.40 m) (Fig. 4). Pollen zones M1 and M3 represent natural communities, not affected by settlements and they are dominated by *Carpinus*, *Quercus*, *Alnus* and in the upper level by *Fagus*. They are separated by M2 pollen zone with clear signs of human activity recorded by decline of *Carpinus* (logging of trees), increase in *Corylus* and *Betula*, expanding into forest clearings and *Quercus* (caused probably by its higher pollen production in better light conditions) and by higher percentages of human impact indicators noted in NAP – Gramineae, *Artemisia*, *Cannabis*/*Humulus*, *Plantago lanceolata*, *Rumex acetosella*, *Secale* and other pollen types. ^{14}C ages indicate that the settlement phase corresponds with the Roman Period, which is represented in this area by the so-called Wielbark culture. It is followed by the Migration Period (pollen zone M3). The next pollen zones (M4 and M5) differ from each other by intensity of human impact. The zone M4 does not differ basically in human transformation of the vegetation from the one recorded in the Roman Period (small-scale pastures and arable fields). ^{14}C dates support correlation of this activity with the Prussian tribe called Pomesanians. They built the stronghold at Janiki near the northeast border with the neighboring Prussian territory of Pogesania. The key phase, in which dinoflagellates were found, is associated with expansion of the Monastic State of the Teutonic Order in the first half of the 13th century (a beginning of the M5 zone). The nearest Teutonic fortress established in 1236–1242 is located at Dzierzgoń

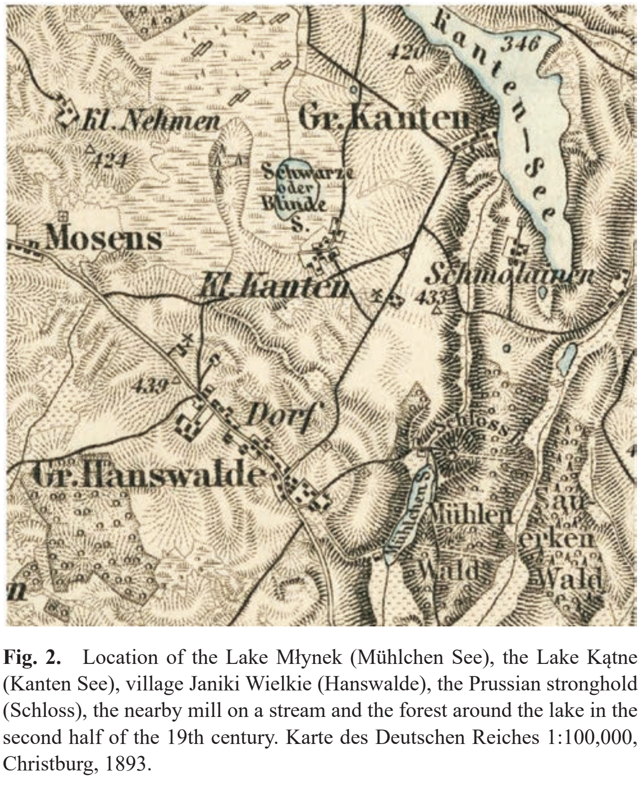

Fig. 2. Location of the Lake Młynek (Mühlchen See), the Lake Kątne (Kanten See), village Janiki Wielkie (Hanswalde), the Prussian stronghold (Schloss), the nearby mill on a stream and the forest around the lake in the second half of the 19th century. Karte des Deutschen Reiches 1:100,000, Christburg, 1893.

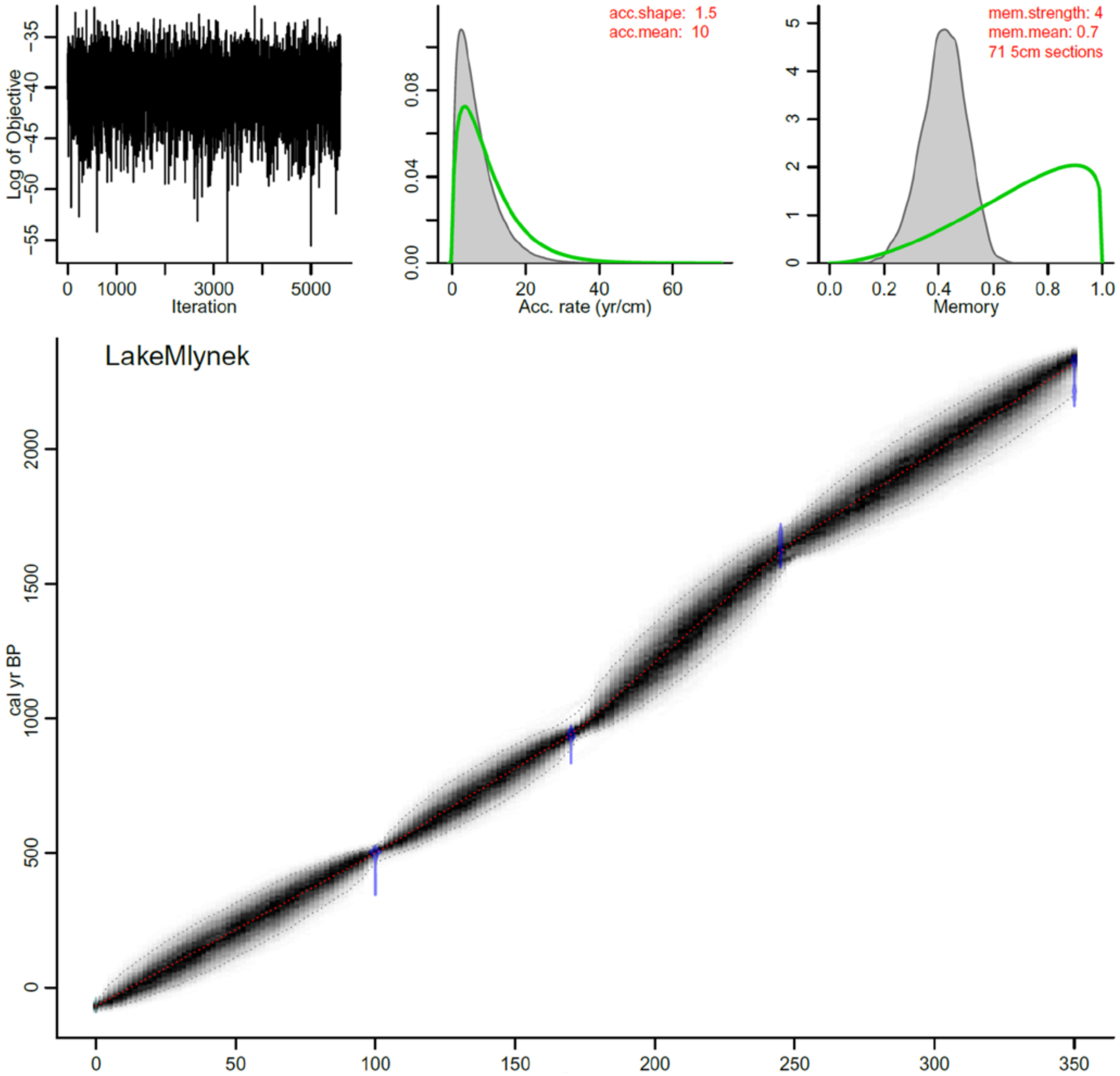

Fig. 3. Age-depth model of the analyzed sequence.

Stary (Christburg) whereas the village Janiki (Hanswalde) close to the Lake Młynek was founded by Sieghard von Schwarzburg, komtur of Dzierzgoń in 1308 (Semrau, 1935). In the vicinity of the stronghold farming and deforestation were intensive: *Cannabis* (hemp, especially in the early phase), *Secale* (rye) and later other cereals as *Fagopyrum* (buckwheat) and *Linum* (flax) were grown. A rather wider area was occupied by pastures as indicated by high percentages of NAP. Cultivated fields were located fairly close to the lake, however they were surely separated by a narrow forest strip in the east and west as suggested by marginal presence of *Riccia* spores in deposits (Fig. 5/H). Such mosaic of fields and forest is still visible on the 19th century maps (Fig. 2).

The lake remained eutrophic throughout the examined period and it is marked by temporary maxima of green algae (sometimes concurrent): *Pediastrum* (5 maxima in various periods – mainly *P. boryanum*), *Coelastrum* (3 peaks in human impact intervals, Fig. 4, 5/I), *Scendesmus* (1 peak at the beginning of the Roman Period), *Tetraedron* (culmination mainly at the beginning of the Roman Period, the Monastic State of the Teutonic Order and in modern times).

Fossil dinoflagellates are noted with high concentration (from 31% to 45%) basically in 2 samples at 0.90 and 0.95 cm depth; they rare above. Preservation of cells is good. Thickness of their walls in the acetolyzed material seems to be similar, but specimens with thinner walls and weaker

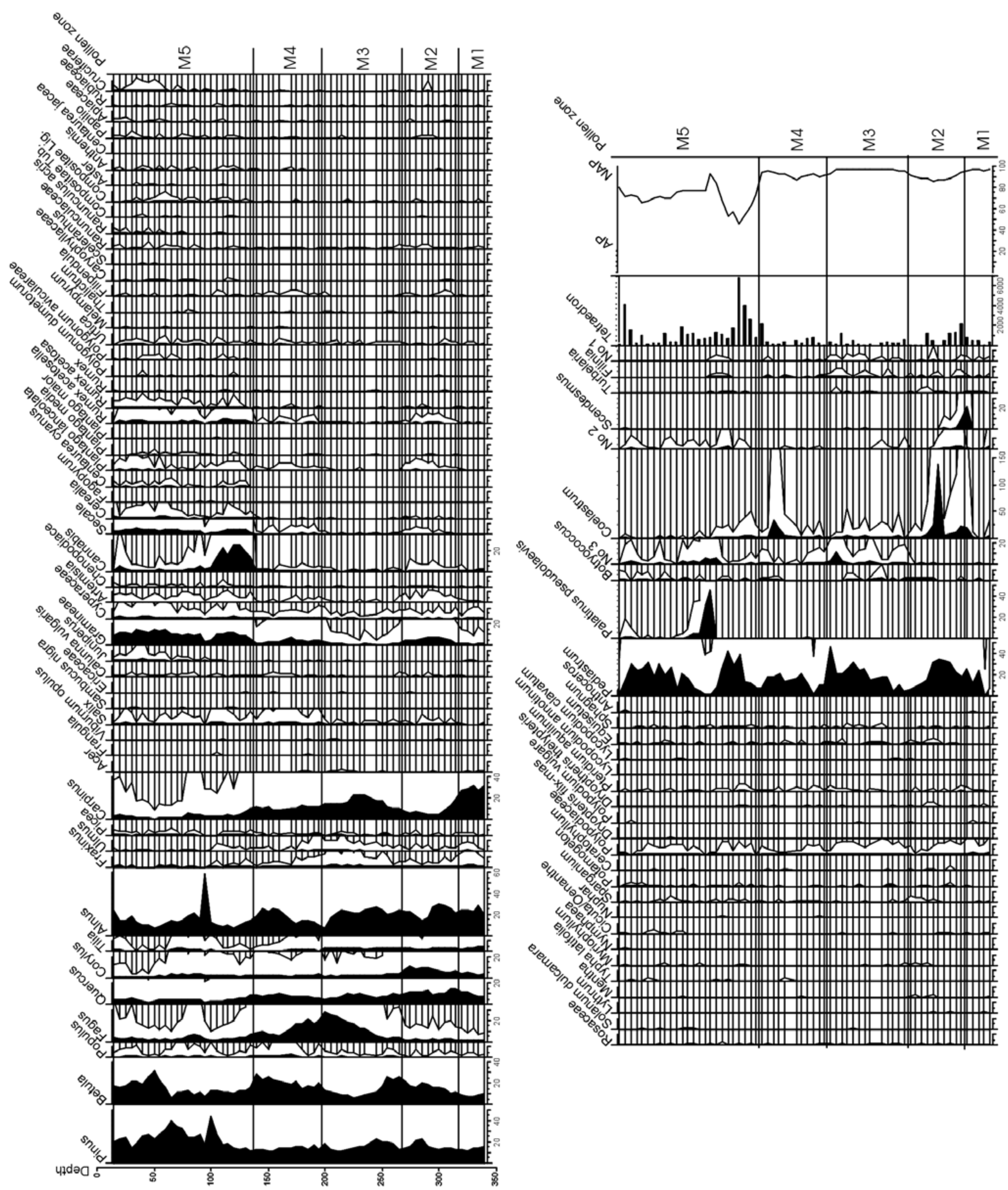

Fig. 4. Pollen diagram of bottom deposits of the Lake Młynek.

Fig. 5. LM of Palatinus specimens from the lake deposits. A, B – ventral view, general outline of the cyst. Plates covered by projections. Plates of cingulum (1c, 2c, 6c), sulcus (as, ras and ps), precingular p. (1'', 6'', 7''), apical p. (1', 2', 4'), postcingular p. (1''', 5'''). Posterior p. (1''', 2''', 3'''), antapical p. (1'''', 2'''') ad, ps. C – dorsal view. Intercalary apical p. (1a, 2a), postcingular p. (3'', 4'', 5''), cingular p. (3c, 4c, 5c) and postcingular p. (2''', 3''', 4'''). D – antapical view. E–F. SEM photograph – specimens with a good expressed sutures. Various shapes of projections – sharp spines or bulbiform ones. G – Branch of Bulbochaete. H. Riccia sorocarpa, distal face. I. Coelastrum. J. Microfossils of unknown origin (pollen diagram – no. 1), K, (no. 2), L. (no. 3). →

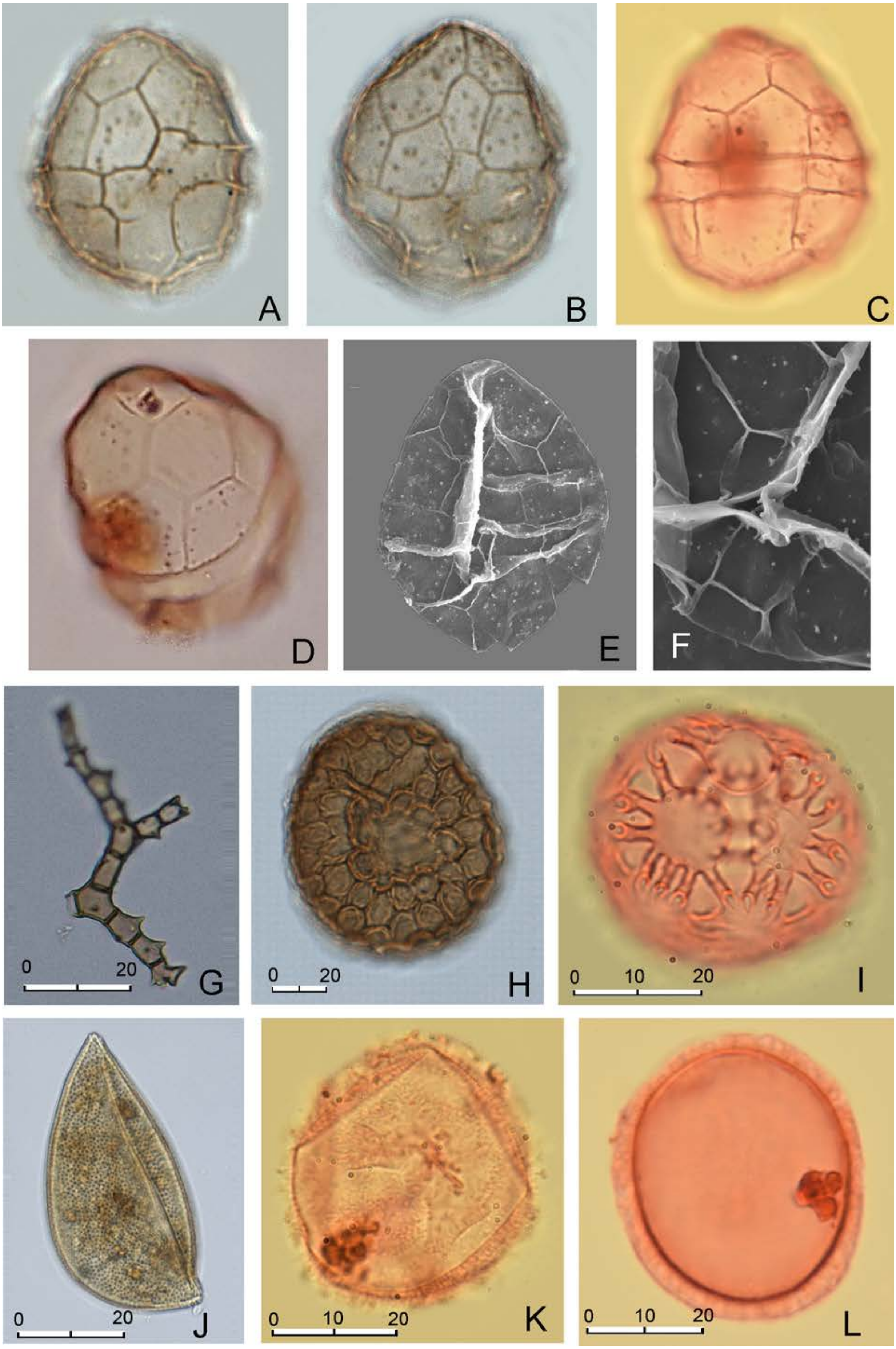
A
B
C
D
E
F
0
20
G
0
20
H
0
10
20
I
0
20
J
0
10
20
K
0
10
20
L

Fig. 6. Agglutinated shell of testate amoebae – A, B Cucurbitella tricuspis, C,D Difflugia (1.10 cm depth).

expressed sutures are also present (Fig. 5/F). The shape of dinoflagellate cells is mainly ovoid with a more elongated epitheca (rarely spherical) about 40–50 µm long and 40 µm wide. They look like armor of vegetative forms rather than resting cysts with a strong representation of thecamorphic features. Individual plates of specimens are clearly visible and separated by narrow and raised sutures. Plates are covered by randomly distributed sharp or blunt and rounded (sometimes capitate), minute punctae (Fig. 5D–F). The cells are characterized by a number of plates – epitheca (4', 2a, 7''), cingulum (6), hypotheca (5''' 2'''''). Arrangement of plates in the apical part is almost symmetrical and the 3' plate is less or more quadrangular (Fig. 5A–C). Specimens are often destructed in the antapical part, suggesting existence of archeopyle. This description fits well with the characteristics of thecae and the way of its shading of the newly created *Palatinus* Craveiro, Calado, Daugbjerg et Moestrup gen. nov (Craveiro *et al*., 2009). Clear tabulation as well as texture suggests that specimens represent rather armor of thecae of motile cells.

In the opinion of Professor Calado (personal communication) a lack of intercalary bands makes precise identification to the species level less possible. However, the shape of the plates of epitheca resembles rather these observed in *Palatinus apiculatus* var. *laevis* (Huitfeldt-Kaas) Craveiro, Calado, Daugbjerg et Moestrup comb. nov. than these in Palatinus pseudolaevis (M. Lefèvre) Craveiro, Calado, Daugbjerg et Moestrup comb. nov. First of the species is also characterized by spiny projections, especially expressed on the hypotheca (Craveiro *et al*., 2009). In the examined material spines are rather small over the whole surface. Starmach (1974) observed inconspicuous projections in *Palatinus apiculatus*, however in young specimens only.

DISCUSSION

In the case of examined fossil specimens with strong representation of the camorphic features we cannot be completely sure if they represent dinoflagellate cysts or what is exceptional, acetolysis resistant thecae of vegetative forms. Cellulosic armor of motile form is able to preserve in sediments only under specific taphonomic condition. It is degraded finally under acetolysis.

Dinocyst display a more complex case. They can be represented by temporary pellicle stage, cyst of which is temporal and thin-walled in contrast to long-term and most often multilayered and thick-walled and composed of acetolyze resistant dinosporin-resting cyst. Both can be formed in haploid and diploid stages (Bravo and Figueroa, 2014). A wall structure and composition of temporary cysts are very variable as to their resistance and half of the examined modern taxa are represented by pellicle cyst resistant to acetolysis (Morrill and Loeblich, 1981; Höhfeld and Melkonian, 1992). However, in meromictic or seasonally anoxic lakes even the preserved thecae (as well as resting cysts) were sometimes noted in several century old deposits and this exceptional preservation was attributed to favorable taphonomic factors (McCarthy and Krueger, 2013; McCarthy *et al.,* 2011). In the Holocene, Drljepan *et al*., (2014) noted also a presence of thecae in a partially meromictic lake of abundant *Peridinium* cysts. In both these cases acetolysis was omitted in laboratory procedures, in order not to destroy wall of cysts. So, it is not excluded, that also laboratory procedures can be responsible for destruction of cysts of freshwater species and their absence in the palynological slides and/or their preservation in deposits is associated with favorable taphonomic processes. In Europe, fossil freshwater dinocysts are rarely found. They are noted by Evitt *et al.* (1985) in a subsurface material from the Lake Zürich and in Greece, Kouli *et al.* (2001) reported freshwater and brackish taxa from the late glacial deposits. In turn, in the non-acetolysed samples from a low-alkaline high mountain lake, Tardio *et al.* (2006) found cysts of peridiniods.

Dinoflagellate-rich samples from the Lake Młynek underwent full palynological preparation, including acetolysis. To confirm the results, maceration of the same sample was repeated. The cells of dinoflagellate have not been destroyed, which means that they are acetolysis resistant. Such unusual modern species with a non-cellulosic glucan wall in vegetative stadia, resistant to palynological procedure has been reported only by Nevo and Sharon (1969) in *Peridinium westii*. In our specimens a clear tabulation pattern rather indicates to thecate motile cells, because freshwater cysts are most often characterized by weak thecamorphic features (Mertens *et al*., 2012), and it may protect from definite identification of nondescript cysts to genera or to species levels. Within *Peridinium* group *Palatinum*, cysts are noted only in *P. apiculatus* by West (1909) and Dangeard (1939) as spherical bodies inside a vegetative cell, however without providing further details. Besides, in samples with *Palatinus*, no rounded, undetermined cyst like specimens were found. And, for that reason we treat these finds as thecae of the vegetative forms.

A lack of intercalary bands in the examined specimens appears to be anomalous. This suggests that younger and smaller individuals were preserved only after the post-depositional processes. It is not excluded that an armor of mature specimens split into fragments along secondary growth zones, formed from different weaker substances. Frequent occurrence of larger or smaller forms only within particular species or genera in a lake can be also explained by the size-efficiency hypothesis (Brooks and Dodson, 1965). Then defragmentation into particular plates or complete degradation of thecae could be achieved in the counterfactual scenario – the passage through guts of predators in food chains and a lack of larger forms with intercalary bands may suggest their consumption. Literature data on scale of feeding on dinoflagellates (especially lacustrine ones) are limited and some data are inconsistent. They are consumed, among others by Copepoda and Cladocera (Harvey *et al*., 1987; Craig, 1991; Carty, 2002; Bucka and Żurek, 1992). Additionally, indirect evidence of possible consumption of dinoflagellates could be a presence of adaptation, protected from predators such as – spines and more resistant wall (like in *Palatinus)* (van Donk *et al*., 2011).

The question arises about the reasons of blooms of freshwater dinoflagellates in the Lake Młynek and whether it is indicated by their higher frequency in deposits. According to Carty (2002) a few species of freshwater dinoflagellates only are capable to benign blooms, mostly in response to rise of nutrients.

Generally, resting cysts are formed when conditions become sub-optimal and unfavorable temperature and nutrient conditions are the most common reasons. In fact, examination of *Peridinium cinctum* Stein shows that encystment, among others environmental factors is triggered by lack of available source of nitrogen and temperature (Grigorszky *et al*., 2006). Similarly, the encystment in blooming species (*Peridiniopsis cunningtonii and P. penardii*) was induced by inoculation into N- and P-free medium (Sako *et al*., 1984, 1987*).* In turn, Alster *et al.,* (2006) in the Lake Kinneret did not find clear environmental factors and nitrogen limitations that influenced production of *Peridinium gatunense* cyst. Examination of subsurface sediments from this lake shows however evident coincidence of *Peridinium* blooms and peak cyst formation. Thus we may presume that abundance of dinoflagellate cells (armors of motile forms or cysts) in the Lake Młynek deposits must have been finally accompanied by high frequency of vegetative forms. In the case of *Palatinus* the frequency of specimens in the sediments is probably lower than the real abundance of vegetative forms was in the water, because, as mentioned above, some specimens might disintegrate along the intercalary bands.

In the Lake Młynek as ^{14}C dates indicate, dinoflagellates were deposited around 1400 A.D. that is about 160 years after expansion of the Teutonic Order State in this region and it falls within the period of intensive human impact in the examined area (Fig. 3). This event is preceded probably by reinforcement works on the Prussian stronghold since 1180 A.D. (from 1.40/1.45 m depth) and they are positively correlated with invasive expansion of *Tetraedron*, occurring at 1.40–1.15 m depth (to about 1500 A.D.) and it was replaced by *Pediastrum*. Signs of these works could be also expressed by agglutinate shell of testate amoebae (Fig. 6). In the pollen sequences, *Tetraedron* is very often, but with various frequencies. It is noted in periods and areas, climate of which is not favorable for plants, marking somewhat warmer intervals e.g. in the Holocene (Rangkul Lake at 3700 m a.s.l. in Pamir Mts: Mętrak *et al*., 2019), in the late glacial interstadials in Austria (Huber *et al*., 2010), in the late glacial and beginning of the Holocene (Ralska-Jasiewiczowa *et al*., 2003). In the Holocene sequences, maxima of *Tetraedron* can indicate of warmer climate periods **(**Pędziszewska *et al*., 2015). However very abundant concentration of coenobia in deposits (incalculable residuum after laboratory procedures) is rarely noted during strong environmental disturbances, either natural or human induced. In the Holsteinian Interglacial section at Ossówka (Nitychoruk *et al*,, 2018), abrupt and complete destruction of fir forest caused exceptionally strong blooming of *Tetraedron*, result from supply of micronutrients to the lake. Similarly invasive content of *Tetraedron*, forming even its own spring-summer layers, were identified also in the annually laminated Eocene oil shales (Lenz *et al.,* 2010) owing to supply with nutrients and rare elements from volcanic soils as result of the cyclic El Niño-Southern Oscillation. Also in historical times, impressive blooms of *Tetraedron* are correlated with human induced environmental disturbances (Goslar *et al.,* 1990). Thus, it is almost sure, that supply of micronutrients during reinforcement of the Prussian stronghold at Janiki is the key factor of strong *Tetraedron* blooms. Similar higher frequency of coenobia is noted in the Lake Młynek not only about 1180–1500 A.D. but also at the beginning of the Roman Period. At Janiki, just before the culmination of *Palatinus*, percentage of *Tetraedron* decreased.

Detailed ecological preferences are not given for Palatinus *apiculatus* var. *laevis*. Specimens are noted in various water bodies without closer ecological characteristic (Popovsky and Pfiester, 1990; Craveiro *et al*., 2009). It was noted in the artificial lake (flooded sand quarry) in Kyiv (Ukraine) under strong human impact (Krahmalny, 2018). A light on reasons of dinoflagellate blooms in the Lake Młynek, because of the similarity of the scenario, shed modern, long term observation of the algal blooms in the Lake Kinneret in Israel. Zohary *et al.* (Zohary, 2004; Zohary *et al.,* 2012) found that regular, annual blooms of *Peridinium gatunense* occurred until the mid-1990s. Hydrotechnical works made in that time in the catchment decreased inflow of the Jordan River water enriched with microelements and organics. This, in turn, caused irregular, but exceptionally intense blooms of *Peridinium* only in the high-rainfall years. Zohary *et al*., (2012) connects supply of phosphorous during winters as the triggering factor of this higher presence. However Lindström and Rhode (1978) proved during laboratory simulations that selenium is an important factor in blooms of *P. gatunense*. Similar examinations prove that blooms of Peridiniopsis borgei are stimulated also by higher content of selenium as well as micronutrients (copper, vanadium, iodine and bromine) (Lindström, 1985).

Examination of Zohary (2004) in the Lake Kinneret suggested that disturbances in the catchment, resulted not only in invasive presence of *Peridinium*, but also of *Tetraedron*. This last taxon in the laboratory simulations reacts also positively on additional supplementation of selenium (Lindström, 1983). However, it only doubles the percentage. Precipitation and runoff are a sources of Se in lakes (Lindström, 1983).

It seems that a mill on a small watercourse, which enters the Lake Młynek had the major impact on disturbance in water environment and blooms of dinoflagellate. This mill is firstly mentioned in written sources in 1423 and Caspar Luppold was its owner (Semrau, 1935). The mill was build near the stronghold on a small stream, which links the lakes Młynek and Kęty (Kanten See) (Fig. 2). It is hard to say of whether this stream located in a wide glacial channel was active earlier or it was newly formed or/and dug out. The mill located near the stronghold is present on the map from 1893 A.D. (Karte des Deutschen Reiches 1:100,000, Christburg). It is possible, that its construction was essential for blooms and the elevated dinoflagellate populations can be linked, similarly as in the Lake Kinneret, with hydrological changes in a wet and peaty area on which water canal (stream?) between the Lake Młynek and the Lake Kęty was located. In periods with increased precipitation and/or water release from the mill pond, micronutrients deposited in the Holocene in the stream catchment were transported to the lake. Additional proof of such processes may be the maxima of *Pinus* (1.0 m depth) and *Alnus* (0.95 m), pollen of which were transported to the lake with a flowing water. Sporadic appearance of dinoflagellate in younger layers may be linked with depletion of these resources. In turn, it is likely that the reason of the major blooms of *Tetraedron* (preceding blooms of dinoflagellate) was mainly caused by a supply with microelements during the stronghold construction and economic activity of the Prussian. This factor lost significance with disappearance of the Prussian settlement near the lake.

CONCLUSIONS

Abundant specimens of dinoflagellate of the genus *Palatinus*, identified in the late medieval deposits represent thecae of motile forms. Cysts of freshwater genera express completely different morphology. It is very interesting that thecae of analyzed specimens were acetolysis resistant. This is the second known example of armor composed of such substance.

The cause of strong dinoflagellate bloom was a supply of micronutriens concentrated in a peaty valley as result of hydrotechnical works within the catchment.

Acknowledgement

We would like to thank Professor António J. Calado from Universidade de Aveiro for suggestions concerning identification of Palatinus. We thank also the anonymous reviewers for careful reading of manuscript and identification of Cucurbitella. The work was performed thanks to the research project funded by the Polish National Science Centre (NCN): Correlation of prehistoric and early medieval settlement phases in northeast Poland with changes of the natural environment in the light of lacustrine sediments study (ID: UMO-2016/21/B/ST10/03059/ID:335021/ no.2016/21/BST10/03059) and partly also by internal grant of the Faculty of Geology of the University of Warsaw.

REFERENCES

Alster, A., Dubinsky, Z., Zohary, T., 2006. Encystment of *Peridinium gatunense*: occurrence, favourable environmental conditions and its role in the dinoflagellate life cycle in a subtropical lake. Freshwater Biology 51, 1219–1228.

Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Analysis 6 (3), 457–474.

Bravo, I., Figueroa, R.I., 2014. Towards an Ecological Understanding of Dinoflagellate Cyst. Functions Microorganisms 2, 11–32.

Brooks, J.L., Dodson, S.I., 1965. Predation, Body Size, and Composition of Plankton. Science 150, 28–35.

Bucka, H., Żurek, R., 1992. Trophic relations between phyto- and zooplankton in a field experiment in the aspect of the formation and decline of water blooms. Acta Hydrobiologica 34 (1–2), 139–155.

Burden, E.T., McAndrews, J.H., Norris, G., 1986. Palynology of Indian and European forest clearance and farming in lake sediment cores from Awenda Provincial Park, Ontario. Canadian Journal of Earth Sciences 23, 43–54.

Carty, S., 2002. Dinoflagellates. In: Wehr, J.,D. and Sheath R.G. (Eds) Freshwater Algae of North America: Ecology and Classification. San Diego, CA: Academic Press, pp. 685–709.

Craveiro, S.C., Calado, A.J., Daugbjerg, N., Moestrup, Ø., 2009. Ultrastructure and LSU rDNA – based revision of Peridinium group Palatinum (Dinophyceae) with the description of Palatinus gen. nov. Journal of Phycology 45, 1175–1194.

Dangeard, P.A., 1939. Second Mémoire sur la famille des Péridiniens. Le Botaniste 29, 267–309.

Danesh, D.C., McCarthy, F.M.G., Volik, O., Drjlepan, M., 2013. Non-pollen palynomorphs as indicators of water quality in Lake Simcoe, Ontario, Canada. Palynology 37 (2), 231–245.

van Donk, E., Ianora, A., Vos, M., 2011. Induced defences in marine and freshwater phytoplankton: a review. Hydrobiologia 668 (1), 3–19.

Drljepan, M., McCarthy, F.M.G., Hubeny, J.B., 2014. Natural and cultural eutrophication of Sluice Pond, Massachusetts, USA, recorded by algal and protozoan microfossils. Holocene 24 (12), 1731–1742.

Evitt, W.R., Gocht, H., Netzel, H., 1985. Gonyaulax cysts from Lake Zürich sediments. Review of Palaeobotany and Palynology 45 (1–2), 35–46.

Goslar, T., Ralska-Jasiewiczowa, M., van Geel, B., Łącka, B., Szeroczynska, K., Chrost, L., Walanus, A., 1990. Anthropogenic changes in the sediment composition of Lake Gościaż (central Poland), during the last 330 yrs. Journal of Paleolimnology 22 (2), 171–185.

Grigorszky, I., Kiss, K.T., Beres, V., Bacsi, I., M-Hamvas, M., Mathe, C., Vasas, G., Padisak, J., Borics, G., Gligora, M., Borbely, G., 2006. The effects of temperature, nitrogen, and phosphorus on the encystment of *Peridinium cinctum*, Stein (Dinophyta). Hydrobiologia 563, 527–535.

Harvey, H.R., Eglinton, G., O'Hara, S.C.M., Corner, E.D.S., 1987. Biotransformation and assimilation of dietary lipids by *Calanus* feeding on a dinoflagellate. Geochimica et Cosmochimica Acta 51 (11), 3031–3040.

Höhfeld, I., Melkonian, M., 1992. Amphiesmal ultrastructure of dinoflagellates: A reevaluation of pellicle formation. Journal of Phycology 28, 82–89.

Huber, K., Weckström, K., Drescher-Schneider, R., Knoll, J., Schmidt, J., Schmidt, R., 2010. Climate changes during the last glacial termination inferred from diatom-based temperatures and pollen in a sediment core from Längsee (Austria). Journal of Paleolimnology 43, 131–147.

Kouli, K., Brinkhuis, H., Dale, B., 2001. Spiniferites cruciformis: a fresh water dinoflagellate cyst? Review of Palaeobotany and Palynology 113, 273–286.

Krahmalny, A.F., 2018. Mass Development of *Palatinus apiculatus* (Dinoflagellata) in the Verbne Lake (Kyiv, Ukraine). Hydrobiological Journal 54 (2), 47–54.

Krueger, A.M., 2012. Freshwater dinoflagellates as proxies of cultural eutrophication: a case study from Crawford Lake, Ontario. MSc Thesis, Brock University.

Lenz, O.K., Wilde, V., Riegel, W., Harms, F.-J., 2010. A 600 k.y. record of El Niño-Southern Oscillation (ENSO): Evidence for persisting teleconnections during the Middle Eocene greenhouse climate of Central Europe. Geology 38 (7), 827–630.

Lindström, K., 1983. Selenium as a growth factor for plankton algae in laboratory experiments and in some Swedish lakes. Hydrobiologia 101, 35–48.

Lindström, K., 1985. Selenium requirement of the Dinoflagellate *Peridiniopsis borgei* (LEMM). International Revue of Hydrobiology 70, 77–85, Berlin.

Lindström, K., Rhode, W., 1978. Selenium as a micronutrient for the dinoflagellate *Peridinium cinctum* fa. *westii*. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 21, 168–173.

McCarthy, F.M.G., Mertens, K.N., Ellegaard, M., Sherman, K., Pospelova, V., Ribeiro, S., Blasco, S., Vercauteren, D., 2011. Resting cysts of freshwater dinoflagellates in southeastern Georgian Bay (Lake Huron) as proxies of cultural eutrophication. Review of Palaeobotany and Palynology 166, 46–62.

McCarthy, F.M.G., Krueger, A.M., 2013. Freshwater dinoflagellates in paleolimnological studies: Peridinium cysts as proxies of cultural eutrophication in the southeastern Great Lakes region of Ontario, Canada. In: Lewis, J.M., Marret, F., Bradley, L. (Eds), Biological and Geological Perspectives of Dinoflagellates. London: The Micropalaeontological Society, The Geological Society (Special Publications), 133–139.

Mertens, K.N., Rengefors, K., Moestrup, Ø., Ellegaard, M., 2012. A review of recent freshwater dinoflagellate cysts: Taxonomy, phylogeny, ecology and palaeocology. Phycologia 51 (6), 612–619.

Mętrak, M., Szwarczewski, P., Bińka, K., Rojan, E., Karasiński, J., Górecki, G., Suska-Malawska, M., 2019. Late Holocene development of Lake Rangkul (Eastern Pamir, Tajikistan) and its response to regional climatic changes. Palaeogeography, Palaeoclimatology, Palaeoecology 521, 99–113.

Morrill, L.C., Loeblich, A.R., 1981. The dinoflagellate pellicular wall layer and its occurrence in the Division Pyrrhophyta. Journal of Phycology 17, 315–323.

Nevo, Z., Sharon, N., 1969. The cell wall of *Peridinium westii*, a non-cellulosic glucan. Biochimica et Biophysica Acta 173, 161–175.

Nitychoruk, J., Bińka, K., Sienkiewicz, E., Szymanek, M., Chodyka, M., Makos, M., Ruppert, H., Tudryn, A., 2018. A multiproxy record of the Younger Holsteinian Oscillation (YHO) in the Ossówka profile, eastern Poland. Boreas 47 (3), 855–868.

Pędziszewska, A., Tylmann, W., Witak, M., Piotrowska, N., Maciejewska, E., Latałowa, M., 2015. Holocene environmental changes reflected by pollen, diatoms, and geochemistry of annually laminated sediments of Lake Suminko in the Kashubian Lake District (N Poland). Review of Palaeobotany and Palynology 216, 55–75.

Popovsky, J., Pfiester, L.A., 1990. Süßwasserflora von Mitteleuropa. Vol. 6. Dinophyceae (Dinoflagellida). 1–272. Jena & Stuttgart: Gustav Fischer.

Ralska-Jasiewiczowa, M., Goslar, T., Różański, K., Wacnik, A., Czernik, J., Chróst, L., 2003. Very fast environmental changes at the Pleistocene/Holocene boundary, recorded in laminated sediments of Lake Gościąż, Poland. Palaeogeography, Palaeoclimatology, Palaeoecology 19, 225–247.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 Years cal BP. Radiocarbon 55 (4), 1869–1887.

Sako, Y., Ishida, T., Kadota, H., Hata, Y., 1984. Sexual reproduction and cyst formation in the freshwater dinoflagellate *Peridinium cunningtonii*. Bulletin of the Japanese Society of Scientific Fisheries 50, 743–750.

Sako, Y., Ishida, T., Nishijama, T., Hata, Y., 1987. Sexual reproduction and cyst formation in the freshwater dinoflagellate *Peridinium penardii*. Nippon Suisan Gakkaishi 53, 473–478.

Semrau, A., 1935. Mitteilungen des Coppernicus-Vereins für Wissenschaft und Kunst zu Thorn. Heft 42. Elbing.

Starmach, K., 1974. Cryptophyceae-Kryptofity. Dinophyceae-Dinofity. Raphidophyceae-Rafidofity. In: Starmach, K., Siemińska, J. (Eds), Flora słodkowodna Polski, 4, 520 pp. PWN, Warszawa-Kraków.

Stuiver, M., Polach, H.A., 1977. Discussion: reporting of 14C data. Radiocarbon19 (3), 355–363.

Tardio, M., Sangiorgi, F., Brinkhuis, H., Filippi, M.L., Cantonati, M., Lotter, A.F., 2006. Peridinioid dinoflagellate cysts in a Holocene high-mountain lake deposits in Italy. Journal of Paleolimnology 36, 315–318.

West, G.S., 1909. A biological investigation of the Peridinieae of Sutton Park, Warwickshire. The New Phytologist 8, 181–196.

Zohary, T., 2004. Changes to the phytoplankton assemblage of Lake Kinneret after decades of a predictable, repetitive pattern. Freshwater Biology 49, 1355–1371.

Zohary, T., Nishri, A., Sukenik, A., 2012. Present-absent: A chronicle of the dinoflagellate *Peridinium gatunense* from Lake Kinneret. Hydrobiologia 698 (1), 161–174.