# THE BADENIAN SALINITY CRISIS IN THE PALYNOLOGICAL RECORD: VEGETATION DURING THE EVAPORATIVE EVENT (CARPATHIAN FOREDEEP, SOUTHERN POLAND)

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**Abstract**: The Badenian Salinity Crisis took place at the early/late Badenian boundary and resulted in massive chemical sedimentation in the central Paratethys. The evaporating basin of the northern Carpathian Foredeep left behind gypsum and halite deposits tens of meters thick. As a very good medium for preservation, these evaporites are a fine source of diversified terrestrial palynomorphs. Plant communities reconstructed on the basis of both palynological analysis of sediments from the Bochnia and Wieliczka salt mines, as well as previously published studies from different localities within the evaporite basin, reveal the presence of wetland and mesic environments along the coasts of the northern part of the central Paratethys during the evaporative event. Among the most important taxa are *Engelhardia*, Ericaceae, *Fagus*, *Liquidambar*, *Quercus*, *Taxodium/Glyptostrobus*, *Tricolporopollenites pseudocingulum*, and *Ulmus*. The most characteristic feature of the palynofloras studied is the large amount (up to even 50%) of Ericaceae pollen in the spectra. Taxa representing a warm-temperate climate predominate in the palynofloras examined; however, representatives of a tropical/subtropical climate (i.a. Mastixiaceae) are also present. The presence of plant communities associated with wetland areas shows that the climate remained humid.

Key words: Miocene, Paratethys, pollen, plant communities, evaporation, fossilized cytoplasm.

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#### **INTRODUCTION**

At the lower/upper Badenian boundary (chronostratigraphy by Kovač *et al.*, 2017 with references), the northern, eastern and south-eastern parts of the central Paratethys lost its open connection with the Mediterranean Sea and this caused extensive evaporation (Peryt, 2006). The event is called the Badenian Salinity Crisis (BSC) and is marked in sediments by the presence of evaporites developed in sulphate and chloride facies. These deposits have proved to be a very good source of palynological material; Kita (1963); Oszast (1967); Sadowska (1997), and Durska (2016, 2018) have presented data collected from anhydrites and halite, sulphuriferous limestone that arose as a result of gypsum transformation, and clays, anhydrites and gypsum, and halite and gypsum, respectively. In this paper, the reconstruction of plant communities surrounding the northern part of the central Paratethys during the BSC is presented on the basis of both the aforementioned palynological data and new data obtained through the studies of pollen from the salt series in the Bochnia and Wieliczka salt mines (Figs 1, 2).

Palynological investigations of evaporites were conducted mainly in the 1950s and 1960s and concerned Permian and Triassic salts in Europe (Reissinger, 1938; Klaus, 1953 a, b, 1955 a, b, 1963, 1964, 1970, 1972; Potonié and Klaus 1954; Leschik 1956; Grebe, 1957; Deák, 1959; Stuhl, 1962; Freudenthal, 1964; Kłosowska and Dowgiałło, 1964; Vissher, 1966; and Dybová-Jachowicz, 1974). Other Palaeozoic salts

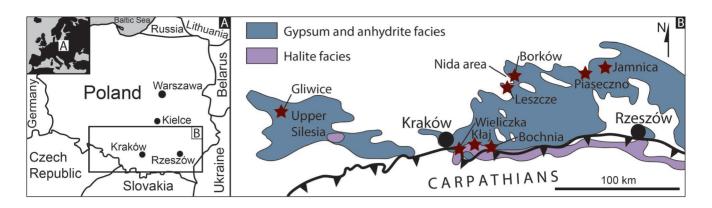


Fig. 1. Location of palynological profiles. A. Location of the study region. B. Location of the study area (after Bąbel, 2004, changed).

were examined in Asia (Varencov *et al.*, 1964) and North America (Shaffer, 1964 *vide* Rueger, 1996; Kosanke, 1995; Rueger, 1996). The palynomorphs in Mesozoic evaporites were studied by Jux (1961 *vide* Rueger, 1996) and Kirkland (1969 *vide* Rueger, 1996). Cenozoic (Miocene) salts in and around the Carpathians have been studied palynologically by Kirchheimer (1950), Kita (1963), Oszast (1967), Balteş (1967), Sadowska (1997), Petrescu *et al.* (1999), Petrescu and Bican-Brişan (2005) and Durska (2016, 2018). Garofalo *et al.* (2010) analyzed 35 ka selenites from the Naica Mine (Mexico).

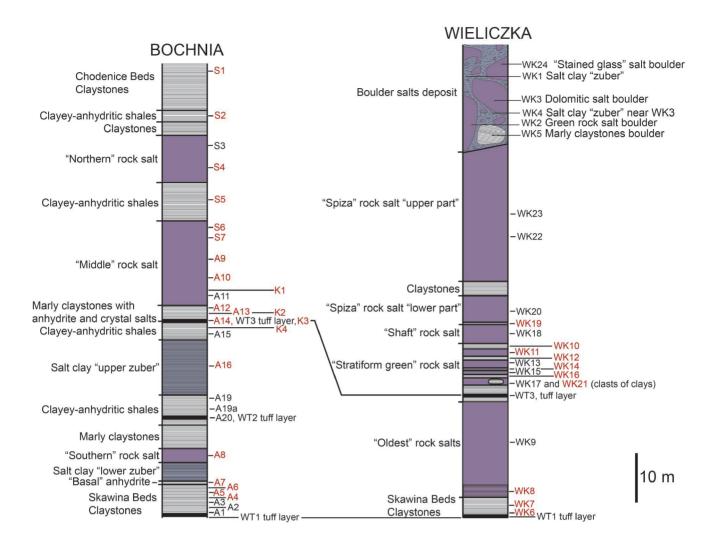
Plant macro-remains were frequently found during the exploitation of salt in the Wieliczka Mine. They were collected and described by Unger (1850), Stur (1873), Zabłocki (1928, 1930a, b), Łańcucka-Środoniowa (1984) and Zastawniak (1996). The entire collection also was restudied by Łańcucka-Środoniowa and Zastawniak (1997).

## **GEOLOGICAL SETTING**

The average thickness of the evaporites deposited in the northern part of the Carpathian Foredeep during the BSC is measured in the tens of metres. Studies of facies distribution have shown that the chloride facies occupied the axial, deepest part of the Carpathian Foredeep, whereas its margins were dominated by sulphate and carbonate facies (Garlicki, 1968a, b, 1970, 1973, 1979). The chloride series, called the Wieliczka Beds, are approx. 40 to 200 m thick and comprise five cyclothems in their normal profile. Each cyclothem comprises claystones, anhydritic claystones, clayey-anhydritic shales, and rock salt which is replaced with anhydrite in the youngest cyclothem (Garlicki, 2008). The evaporitic depositional cycles resulted from tectonically caused changes in sea level (Czapowski, 1994). The formation of salt deposits was affected by bottom mass movement, as a result of which both clastics and evaporites were relocated into the deeper parts of the basin (Ślączka and Kolasa, 1997) and underwent partial dissolution and recrystallization (Bukowski, 1999). The salt deposits in Bochnia and Wieliczka owe their origins to their close proximity to the Carpathian margin. The allochthonous strata were folded in front of the Carpathian nappes and thrust over the autochthonous beds, which resulted in the presence of folds and the strong deformation of salt layers and breccias with blocks of rock salt (Garlicki, 2008). The Bochnia and Wieliczka profiles studied here are exposed in the deep salt mines located near Kraków (Fig. 1). The evaporite series, called the Wieliczka Beds, belong to the Wieliczka Formation and the underlying marine deposits are called Skawina Beds and belong to the Skawina Formation, while the overlying ones, called the Chodenice Beds, belong to the Machów Formation (Jasionowski et al., 2004).

Gypsum deposits were formed in the northern, marginal part of the Carpathian Foredeep. These evaporites are called the Nida Gypsum deposits and belong to the Krzyżanowice Formation. They are represented by spectacular primary deposits, which include selenite facies, similar to those known from the Messinian deposits in the Mediterranean (Bąbel, 199a, b; Bąbel *et al.*, 2015). The gypsum deposits are accessible in the outcrops, e.g., at Borków and Leszcze (Fig. 1). The underlying Baranów Beds belong to the Pińczów Formation and the overlying Krakoviec Clay belong to the Machów Formation (Jasionowski *et al.*, 2004).

The BSC took place at the early/late Badenian boundary – the earliest part of the Neogene Nannoplankton Zone NN6 (Peryt, 1999; Garecka and Olszewska, 2011). According to radiometric data, the evaporites appeared after  $13.81 \pm 0.08$  Ma and the crisis ended before  $13.60\pm0.11$  Ma. The event might have been relatively short, only 20–40 ka (Peryt,



**Fig. 2.** Geological profiles of Bochnia and Wieliczka salt deposits after Garlicki and Wiewiórka (1981, changed). The terms given in quotation marks are the traditional names given by the miners. Palynologically positive samples are marked in red.

2006 with references), or perhaps considerably longer, i.e., 200–600 ka, according to other studies (de Leeuw *et al.*, 2010; Bukowski, 2011; Śliwiński *et al.*, 2012).

# **MATERIAL AND METHODS**

The samples studied were taken at the Bochnia and Wieliczka saltmines (Fig. 1) from salt and clastic beds (Fig. 2). Thirty-one samples were taken in Bochnia, and twenty-five in Wieliczka. For each palynologically positive sample at least 150 palynomorphs (including bisaccate grains) were counted (e.g. 150 in palynomorph-poor WK14, and 572 in palynomorph-rich A14). Palynomorphs are present in all but the tuff samples from Bochnia and Wieliczka. However,

in some samples they are scarce and are represented mainly by saccate pollen. Twenty-one samples from Bochnia and only ten from Wieliczka proved to be sufficiently rich in palynomorphs to conduct a palynological analysis and are marked in red on Figure 2. In the samples from Wieliczka, the palynomorphs are less abundant and less taxonomically diversified than in those from Bochnia. The state of preservation of the palynomorphs is generally good, although corroded grains also are frequently found. Sometimes pollen grains with the cellular content preserved can be found (see the detailed studies in Durska, 2016, 2018). However, this feature was observed only occasionally and is not useful for further analysis.

Although samples differ in lithology (Fig. 2), no distinct differences in the state of preservation of the palynomorphs

Percentages of pollen and spore taxa in samples from Bochnia

were noted between samples. It is probable that the palynological composition of the samples was affected by redeposition.

Maceration was conducted after washing the samples. In the case of salts, hot water was applied first to dissolve NaCl. The remained residuum as well as all clastic samples were treated with 30% HF to dissolve silica. Then the residuum was filtered through a 10- $\mu$ m sieve. A heavy liquid (ZnCl<sub>2</sub> solution) was used to separate any remaining mineral particles. Acetolysis was not provided. The slides were prepared using glycerin jelly as the mounting medium.

The macerates and slides are housed at the Department of Palaeontology, Faculty of Geology, University of Warsaw.

## RESULTS

Fifty-two pollen and spore taxa were determined at Bochnia and thirty-one at Wieliczka (Tables 1, 2). In both profiles the pollen spectra are similar, with the pollen of gymnosperms dominant. In Bochnia (Table 1), Pinuspollenites reaches a maximum of 82.3% in A5, Cathayapollis 15.6% in A13, Inaperturopollenites 15.8% in S7, Sciadopityspollenites 3.7% in S7, Zonalapollenites 2.9% in S1, and Sequoiapollis 1.4% in K1. Among the angiosperms, Ericipites reaches 28.2% in S5, Cupuliferoipollenites pusillus 5.5% in S5, Cyrillaceaepollenites exactus - C. megaexactus 2.0% in K4, Intratriporopollenites 2.2% in A5, Juglanspollenites 1.9% in A6, Momipites 5.7% in S7, Periporopollenites 1.4% in S2, Polyatriopollenites 2.8% in K3, Quercoidites + Quercopollenites 5.3% in S1, Sparganiaceaepollenites 2.4% in K4, Tricolporopollenites pseudocingulum + + T. dolium + T. villensis 10.0% in S5, and Ulmipollenites 3.0% in A6; the other taxa do not exceed 1%. Among the pteridophytes, Laevigatosporites reaches 1.4% in K3, Leiotriletes 1.3% in S2, and Stereisporites 1.4% in K3. At Wieliczka (Table 2), Pinuspollenites reaches a maximum of 87.5% in WK11, Cathayapollis 17.5% in WK21, Inaperturopollenites 8.0% in WK19, Sciadopityspollenites 3.2% in WK7, and Zonalapollenites 2.7% in WK6. Among the angiosperms, Ericipites reaches 9.2% in WK14, Intratriporopollenites 1.5% in WK14, Momipites 3.4% in WK8, Polyatriopollenites 1.1% in WK8, Quercoidites + + Quercopollenites 1.1% in WK8, and Tricolporopollenites pseudocingulum + T. dolium + T. villensis 1.5% in S5. Other taxa do not exceed 1%. Among the pteridophytes, Leiotriletes reaches 1.9% in WK21, and Verrucatosporites 1.1% in WK7.

The list of taxa found at both localities is given in Table 3, along with their nearest living relatives.

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Taxon\Sample number	A5	A6	A16	K4	A14	L4	Q	A13	A12	KI	A10	S7	S6	S5	S4	S2	Sl
PTERIDOPHYTES																	
Baculatisporites sp.	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Camarozonosporites sp.	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Corrugatisporites sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cryptogammasporis sp.	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Distancoraesporis sp.	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Intrapunctisporis sp.	0.0	0.0	0.0	0.3	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Laevigatosporites sp.	0.5	0.0	0.0	0.0	0.4	0.0	1.4	0.0	0.0	0.3	0.0	0.7	0.0	0.0	0.0	0.0	0.0
Leiotriletes sp.	1.1	0.0	0.0	0.3	0.0	0.0	0.0	0.5	0.0	0.3	0.0	0.3	0.0	0.0	0.0	1.3	0.0
Neogenisporis sp.	0.0	0.0	0.0	0.3	0.2	0.0	0.5	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.9	0.3	0.5
Stereisporites sp.	0.0	0.0	0.0	0.0	0.0	0.2	1.4	0.0	0.5	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Toroisporis sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Undulozonosporites sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5
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Table	

Taxon\Sample number	A5	A6	A16	K4	A14	L4	K3	A13	A12	K1	A10	S7	S6	S5	S4	S2	S1
GYMNOSPERMS																	
Cathayapollis sp.	10.8	8.3	9.9	8.8	6.8	7.4	5.0	15.6	6.4	9.1	9.5	0.7	3.5	1.4	7.1	8.0	0.0
Inaperturopollenites sp.	0.0	3.6	0.2	2.0	2.5	2.5	0.0	5.5	0.3	3.5	1.1	15.8	6.7	12.7	11.8	4.1	1.4
<i>Pinuspollenites</i> sp. + <i>Piceapollis</i> sp.	82.3	75.8	81.9	58.8	76.2	63.9	78.9	66.3	82.5	68.2	83.6	54.7	70.2	25.5	62.1	73.6	63.6
Sciadopityspollenites sp.	1.1	1.1	0.0	0.9	0.2	2.7	0.5	2.0	0.0	2.1	0.5	3.7	0.7	1.4	0.9	0.3	2.4
Sequoiapollis sp.	0.0	0.6	0.7	0.0	0.5	0.0	0.0	0.5	0.3	1.4	0.0	0.0	0.0	0.9	0.0	0.3	0.0
Zonalapollenites sp.	1.6	1.1	0.0	0.6	0.3	0.4	0.5	0.2	0.0	0.7	0.0	0.7	0.0	0.9	0.3	1.0	2.9
ANGIOSPERMS																	
Alnipollenites sp.	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Carpinipites sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Caryapollenites sp.	0.0	0.0	0.2	0.0	0.2	0.4	0.0	0.5	0.0	0.3	0.0	0.7	0.4	0.9	0.3	0.0	0.0
Cornaceaepollis microscabratus + C. satzveyensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Cupuliferoipollenites pusillus + C. oviformis	0.0	0.8	0.0	0.3	0.2	0.2	0.9	0.0	1.1	0.3	0.5	0.3	2.1	5.5	0.0	0.0	1.0
<i>Cyrillaceaepollenites exactus</i> + <i>C. megaexactus</i>	0.0	0.3	0.2	2.0	0.3	0.2	0.5	0.5	0.3	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0
Ericipites sp.	0.0	1.1	1.9	12.6	5.2	7.6	1.8	2.2	4.5	4.9	0.5	7.7	8.5	28.2	3.2	1.0	11.5
Eucommiapollis sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Faguspollenites sp.	0.0	0.0	0.0	0.9	0.2	1.9	0.5	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ilexpollenites sp.	0.0	0.0	0.0	0.3	0.2	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Intratriporopollenites sp.	2.2	0.0	0.5	0.9	0.3	1.3	0.0	0.7	0.0	0.0	0.5	0.7	0.4	0.5	0.6	1.0	1.9
Juglanspollenites sp.	0.0	1.9	0.2	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.4	0.0	0.3	0.0	0.0
Magnoliaepollenites sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.2	0.0	0.3	0.0	0.0	0.4	0.0	0.0	0.3	0.0
Momipites sp.	0.0	0.0	2.6	2.0	1.7	5.3	1.8	1.2	2.4	1.7	1.6	5.7	0.7	3.2	3.2	5.7	4.3
Myricipites sp.	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Oleidearumpollenites sp.	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ostryoipollenites sp.	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Periporopollenites sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.6	0.0	0.0
Platycaryapollenites sp.	0.0	0.0	0.2	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.5
Polyatriopollenites sp.	0.5	0.3	0.5	1.5	0.6	2.1	2.8	0.5	0.3	0.0	0.0	1.0	0.7	1.4	1.8	0.6	2.4
Potamogetonacidites sp.	0.0	0.0	0.0	0.3	0.3	0.2	0.0	0.2	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Quercoidites sp. + Quercopollenites sp.	0.0	0.0	0.7	0.6	2.6	0.8	0.5	1.0	0.8	0.3	0.0	1.0	0.7	1.8	1.5	1.9	5.3
Slovakipollis sp.	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sparganiaceaepollenites sp.	0.0	0.0	0.0	1.8	0.3	0.2	0.0	0.2	0.0	0.0	0.0	1.3	0.7	0.5	2.4	0.0	0.0
Tricolporopollenites liblarensis	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.3	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Tricpolporopollenites pseudocingulum + T. dolium + T. villensis	0.0	2.2	0.0	4.1	0.9	1.1	0.0	1.2	0.3	2.4	1.1	4.4	3.2	10.0	2.6	0.0	1.9
Ulmipollenites sp.	0.0	3.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.3	0.0	0.3	0.4	0.5	0.6	0.6	0.0

### Table 2.

Taxon\Sample number	WK6	WK7	WK8	WK21	WK16	WK14	WK12	WK11	WK10	WK19
PTERIDOPHYTES										
Baculatisporites sp.	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0
Corrugatisporites sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5
Leiotriletes sp.	0.0	0.5	0.0	1.9	0.0	0.0	0.9	0.0	0.9	1.5
Neogenisporis sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0
Radialisporis sp.	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0
Segmentizonosporites sp.	0.0	0.5	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0
Stereisporites sp.	0.0	0.5	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0
Verrucatosporites sp.	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0
GYMNOSPERMS										
Cathayapollis sp.	2.7	2.7	1.1	17.3	5.6	1.5	5.9	4.3	4.7	7.5
Inaperturopollenites sp.	1.8	0.5	1.1	0.6	2.5	0.0	7.6	1.7	0.9	8
Pinuspollenites sp. + Piceapollis sp.	83.1	83.9	81.8	75.0	82.8	83.1	77.9	87.5	85.8	72.5
Sciadopityspollenites sp.	2.7	3.2	1.1	1.3	0.8	3.1	0.2	0.9	0.9	1
Zonalapollenites sp.	2.7	1.1	0.0	1.3	0.0	0.0	0.2	0.0	0.0	1
ANGIOSPERMS			-							
Caryapollenites sp.	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0
Cupuliferoipollenites pusillus + C. oviformis	0.0	0.5	0.0	0.0	0.6	0.0	0.4	0.2	0.0	0
Ericipites sp.	3.1	3.8	6.8	0.0	4.0	9.2	5.0	3.4	4.7	1.5
Intratriporopollenites sp.	0.4	0.5	0.0	0.0	0.3	1.5	0.2	0.0	0.0	1
Juglanspollenites sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0
Momipites sp.	1.8	1.1	3.4	0.6	1.4	0.0	1.1	0.6	0.0	3
Periporopollenites sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0
Platycarya sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.9	0
Polyatriopollenites sp.	0.9	0.0	1.1	0.6	0.0	0.0	0.0	0.2	0.0	1
Quercoidites sp. + Quercopollenites sp.	0.0	0.5	1.1	0.0	0.8	0.0	0.2	0.4	0.0	0.5
Sparganiaceaepollenites sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0
Tricolporopollenites liblarensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0
Tricolporopollenites pseudocingulum + T. dolium + T. villensis	0.9	0.5	0.0	0.0	0.6	1.5	0.0	0.2	0.0	1

#### Percentages of pollen and spore taxa in samples from Wieliczka

## DISCUSSION

The Carpathian Foredeep during the Badenian Salinity Crisis is interpreted to have been a drawdown salina basin that occurred as a result of severed connections with the ocean, as in the Mediterranean during the Messinian Salinity Crisis (Bąbel, 2004). The salina model proposed by Bąbel (2004) is opposed to the traditional evaporite lagoon model and assumes that the basin was in fact a salina lake.

An interesting and unique feature of the pollen preserved in evaporites is the presence of fossilized pollen content (Durska, 2016, 2018). The frequencies of such grains in particular taxa are a valuable indicator of the proximity of the pollen-producing plants to the depositional basin. This is based on the assumption that the pollen content degrades quickly — the viability is a few hours to a few days (Dafni and Firmage, 2000) - and therefore it could not have been fossilized in situations of prolonged transportation. In the samples from Wieliczka, fossilized cytoplasms occur rarely and this is also the case for samples from Bochnia, except for one that previously was examined in detail (Durska, 2016). Fossilized pollen content also frequently occurs in some gypsum samples (Durska, 2018). These frequencies have allowed the author to indicate the plants growing nearest to the Paratethys coastline: Carpinus, Engelhardia, Ericaceae, Fagus, unknown Fagoideae?/Styracaceae? (Tricolporopollenites pseudocingulum group), Liquidambar, Quercus, Taxodium/ Glyptostrobus, and Ulmus. The results are consistent with both of the studies mentioned and thus are considered reliable and applicable to the reconstruction of plant communities during the BSC.

## Table 3.

# List of identified fossil pollen and spore taxa, their nearest living relatives (based mainly on Stuchlik *et al.* 2001, 2002, 2009, 2014) and probable climatic and environmental requirements. Wetland- saturated with water, either permanently or seasonally; mesic- containing a moderate, balanced amount of moisture; xeric- deficient in moisture

FOSSIL TAXON	NEAREST LIVING RELATIVE	PROBABLE CLIMATIC AND ENVIRONMENTAL REQUIREMENTS
PTERIDOPHYTES		
Baculatisporites sp.	Osmundaceae	subtropical/temperate; wetland, mesic
Camarozonosporites sp.	Lycopodiella	tropical/subtropical; wetland, mesic
Corrugatisporites sp.	Lygodiaceae	subtropical; wetland, mesic
Cryptogammasporis sp.	Pteridaceae	warm-temperate; wetland, mesic
Distancoraesporis sp.	?	tropical/subtropical/temperate; wetland, mesic
Echinatisporis sp.	Selaginella	tropical/subtropical/temperate; wetland, mesic
Intrapunctisporis sp.	?	tropical/subtropical/temperate; wetland, mesic
Laevigatosporites	Polypodiaceae	tropical/subtropical/temperate; wetland, mesic
Leiotriletes sp.	Lygodiaceae	tropical/subtropical; wetland, mesic
Neogenisporis sp.	Gleicheniaceae	tropical; wetland, mesic
Radialisporis sp.	Lygodiaceae/Parkeriaceae	tropical/subtropical; wetland, mesic
Retitriletes sp.	Lycopodium	temperate; wetland, mesic
Segmentizonosporites sp.	Pteridaceae	tropical/subtropical/warm-temperate; wetland, mesic
Stereisporites sp.	Sphagnaceae	temperate
Toroisporis sp.	Cyatheaeceae?/Lygodiaceae?	tropical/subtropical/warm-temperate; wetland, mesic
Undulozonosporites sp.	Pteridaceae	warm-temperate/temperate; wetland, mesic
Verrucatosporites pseudoalienus	Polypodium vulgare	temperate; wetland, mesic
GYMNOSPERMS		
Cathayapollis sp.	Cathaya	warm-temperate; mesic
Inaperturopollenites sp.	Taxodium/Glyptostrobus	subtropical/warm-temperate; swamp
Pinuspollenites sp.	Pinus	warm-temperate/temperate; wetland, mesic, xeric
Piceapollis sp.	Picea	warm-temperate, temperate; mesic, xeric
Sciadopityspollenites sp.	Sciadopitys	warm-temperate; mesic
Sequoiapollenites sp.	Sequoia	warm-temperate mesic, xeric
Zonalapollenites sp.	Tsuga	temperate; mesic
ANGIOSPERMS		
Aceripollenites sp.	Acer	warm-temperate; wetland, mesic
Alnipollenites sp.	Alnus	temperate; wetland
Arecipites sp.	Araceae/Arecaceae/ Butomaceae/ Amaryllidaceae	tropical/subtropical/warm-temperate; wetland, mesic, xeric
Carpinipites sp.	Carpinus	warm-temperate/temperate; swamp, mesic
Caryapollenites sp.	Carya	warm-temperate; wetland, mesic
Caryophyllidites sp.	Caryophyllaceae	temperate; mesic, riparian in some cases
Celtipollenites sp.	Celtis	warm-temperate; wetland
Cornaceaepollis microscabratus	Cornaceae, Cornus sp.	warm temperate/temperate; mesic
Cornaceaepollis satzveyensis	Mastixiaceae	tropical/subtropical; mesic
Cupuliferoipollenites pusillus, C. oviformis	Castanea/Castanopsis/Lithocarpus	subtropical/warm-temperate; wetland
Cyrillaceaepollenites exactus group (C. exactus, C. megaexactus, C. brühlensis)	Cyrillaceae/Clethraceae	tropical/subtropical; wetland, mesic

#### Table 3. continued

FOSSIL TAXON	NEAREST LIVING RELATIVE	PROBABLE CLIMATIC AND ENVIRONMENTAL REQUIREMENTS
Ericipites sp.	Ericaceae	tropical/subtropical/temperate; wetland, mesic, xeric
Eucommiapollis sp.	Eucommia	warm-temperate; wetland, mesic
Faguspollenites sp.	Fagus	temperate; mesic, riparian in some cases
Fraxinipollis sp.	Fraxinus	warm-temperate/temperate; wetland, mesic
Graminidites sp.	Poaceae	tropical/subtropical/temperate; wetland, mesic, xeric
Ilexpollenites sp.	Ilex	tropical/subtropical/warm-temperate; wetland, mesic
Intratriporopollenites sp.	Craigia/Tilia	tropical/subtropical/temperate mesic
Juglanspollenites sp.	Juglans	warm-temperate; wetland, mesic
Lythraceaepollenites sp.	Lythraceae	warm-temperate; wetland
Magnoliaepollenites sp.	Magnolia	tropical; wetland, mesic
Momipites sp.	Engelhardia	tropical/subtropical; wetland, mesic
Myricipites sp.	Myrica	subtropical/warm-temperate; wetland
Nyssapollenites sp.	Nyssa	warm-temperate; wetland
Oleidearumpollenites sp.	Oleaceae	subtropical/warm-temperate; wetland, mesic, xeric
Ostryoipollenites sp.	Ostrya	warm-temperate; wetland, mesic
Periporopollenites sp.	Liquidambar	subtropical/warm-temperate; wetland
Platycaryapollenites sp.	Platycarya	subtropical; mesic
Polyatriopollenites sp.	Pterocarya	warm-temperate; wetland, mesic
Potamogetonacidites sp.	Potamogeton	tropical/subtropical/temperate; wetland
Quercoidites sp.	Quercus	subtropical/warm-temperate; wetland, mesic, xeric
Quercopollenites sp.	Quercus	warm-temperate/temperate; wetland, mesic, xeric
Slovakipollis sp.	Eleagnaceae	subtropical/warm-temperate; mesic
Sparganiaceaepollenites sp.	Sparganium/Typha	tropical/subtropical/temperate; wetland
Symplocoipollenites sp.	Symplocos	tropical/subtropical; mesic
Tricolporopollenites pseudocingulum group (T. pseudocingulum, T. dolium, T. leonensis)	Fagoideae?/Styracaceae?	subtropical/warm-temperate; wetland?, mesic?
Tricolporopollenites liblarensis	Fabaceae	tropical/subtropical/temperate; wetland?, mesic?
Tricolporopollenites villensis	Fagaceae?	?; wetland? mesic?
<i>Ulmipollenites</i> sp.	Ulmus	temperate; wetland, mesic

The palynological results obtained for the samples from Bochnia and Wieliczka are similar to those of previous studies of deposits of the same age from Piaseczno, Kłaj, Gliwice, Borków, and Leszcze (Fig. 1; Table 4). The pollen profiles from the western (Durska, 2018), southern (Bochnia, Wieliczka referred here; Kita, 1963) and south-western (Sadowska, 1997) parts of the Carpathian Foredeep are dominated by saccate pollen, which is a typical feature for open water bodies. According to the frequencies of preserved pollen content (see discussion above) it can be stated that most of the plants, producing saccate pollen (*Pinus, Picea*, and *Cathaya*), and also *Tsuga* with grains that are equipped with a collar, grew at greater distances from the depositional basin. In spite of the large amounts of pollen grains of these taxa in spectra (up to ca. 87% in the WK11 sample from Wieliczka), the fossilized pollen content occurs very rarely (up to 2% of *Pinus + Picea*, and 3% of *Cathaya* pollen grains, Durska, 2018). The coniferous forest possibly grew on the slopes of the emerging Carpathians to the south, the Bohemian Massif to the south-west, and the Holy Cross Mountains to the north-west. Samples with the prevalence of angiosperms were present only in the material studied by Oszast (1967) in the Piaseczno profile (Fig. 1). Among the angiosperms in all of the palynofloras studied, Ericaceae are a significant element reaching a frequency of even as much as 50% (Oszast, 1967). This seems to be a very characteristic feature for plant communities during the BSC. All of the Ericaceae are entomophylous so that

Bochnia	Wieliczka	Borków/Leszcze Durska, 2018	Piaseczno Oszast, 1967	Kłaj Kita, 1963	Gliwice Sadowska, 1997
Cathaya, Pinus + Picea, Sciadopitys, Taxodium/ Glyptostrobus, Tsuga Castanea/ Castanopsis/ Lithocarpus, Cyrillaceae/ Clethraceae, Engelhardia, Ericaceae, Juglans Tricolporopollenites pseudocingulum, Pterocarya, Quercus, Tilia, Ulmus pteridophytes	Cathaya, Pinus + Picea, Sciadopitys, Taxodium/ Gyptostrobus, Tsuga Engelhardia, Ericaceae, Tricolporopollenites pseudocingulum group, Pterocarya, Quercus pteridophytes	Cathaya, Pinus + Picea, Sciadopitys, Taxodium/ Glyptostrobus, Tsuga Celtis, Engelhardia, Ericaceae, Fagus, Liquidambar, Quercus, Tricolporopollenites pseudocingulum, Ulmus	Glyptostrobus, Pinus diploxylon + P. haploxylon, Picea, Sciadopitys, Taxodium, Tsuga Alnus, Araliaceae, Carya, Castanea- Castanopsis, Celtis, Cercidiphyllum, Cotinus, Engelhardia, Ericaceae, Leguminosae, Liquidambar, Myrica, Nerium, Oleander, Ostrya-Ostryopsis, Pistacia, Platycarya, Pterocarya, Rutaceae, Tamarix, Ulmus	Abies, Cerdus, Laricoidites, Picea, Pinus silvestris, Pinus haploxylon, Podocarpus, Pollenites magnus dubius, Taxodium, Tsuga Alnus, Betula, Castanea, Carya, Corylus, Engelhardia, Ericaceae, Nyssa, Pterocarya, Quercus, Tillia	Abies, Cedrus, Picea, Pinus sylvestris, Pinus haploxylon, Taxodiaceae- Cupressaceae, Tsuga Carpinus + Ostrya, Engelhardia + Platycarya, Ericaceae, Juglans + Carya + Pterocarya, Liquidambar, Myrica, Quercus, Rhus + Anacardiaceae, Ulmus pteridophytes

Main taxa of pollen assemblages from evaporites, present and previous studies. Some taxa given in the literature (marked in blue) are difficult to compare to known fossil pollen species because the authors did not include pictures or a list of fossil and corresponding Recent taxa

the high percentages in the spectra – with up to 59% of the grains with preserved cytoplasm (Durska, 2018) clearly show that they grew in areas closest to the coastline. The shores were at least temporarily inundated and could not be well drained or arid, because pollen or even whole flowers must have fallen directly into the water and then were transported to the depositional basin. Otherwise, such amounts of pollen could not have been preserved in the sediments, as they were not transported by the wind. Ericaceae in Recent times live in very different habitats and are found in mesic, but also frequently in swampy areas. The open Ericaceae scrubs in swale areas with Leuocothoe revoluta are known from Brazil (Araujo, 1992). Vaccinium (V. formosum, V. fuscatum) and Leucothoe (L. racemosa) are an important part of the Coastal Plain Depression Swamp of Quercus phellos-Acer rubrum-Liquidambar styraciflua type on the Mid-Atlantic Coastal Plain (USA; Sneddon et al., 2007). Bogs dominated by Erica tetralix occur in temperate climates in Europe. Ericaceae pollen, usually remaining in tetrads, looks similar for most of the taxa. The variety of forms (differing in size or details of fine sculpture) even in one genus (Sarwar and Takahashi, 2013) does not allow assignment of the fossil to Recent taxa with certainty. The whole Ericaceae family is known

to be salt-sensitive (Waisel, 1972). A very frequent pollen in the evaporites studied is Inaperturopollenites. Taxodium, considered to be a Recent relative of the plant producing this pollen, is also intolerant of increased salinity (Conner and Inabinette, 2005). The aforementioned facts indicate that fresh-water wetlands occupied the shores of the northern part of the central Paratethys during the BSC. Some other taxa, presumed to have grown near the depositional basin (see the discussion on pollen content, above), also can be related to swamp or riparian habitats (Table 3). These are Carpinus, Engelhardia (considered to have been a riparian taxon in Neogene time, see Hofmann and Zetter, 2005; Kunzmann, 2012), Liquidambar, Quercus (recently occurring above all in mesic habitats; however, Q. laurifolia, for instance, is commonly associated in North American with bald cypress swamps; Sneddon et al., 2007), Tricolporopollenites pseudocingulum (usually occurring in peat-producing communities in the Neogene deposits of the Polish Lowlands, Kasiński et al., 2010), Ulmus, but also Fagus, usually connected to well-drained areas, has been discovered in riparian habitats in Japan (Masaki et al., 2005; Sashimura et al., 2008) and mentioned as a facultative wetland plant in the Miocene (Worobiec and Szynkiewicz, 2016; Worobiec and Worobiec, 2016). However, mesic habitats near the Paratethys coastline cannot be excluded. Two modern plant communities can reflect to some extent the fossil varieties closest to the coastline. Probably a kind of floodplain swamp occurred, similar to the ones recently present in Florida. These communities are located within the floodplain of permanently moving streams and can form narrow strips, expansive stands along rivers or freshwater swamps near river mouths. The dominant plants here are Acer, Carya, Fraxinus, Nyssa, Quercus, Taxodium, and Ulmus. The understory and groundcover are formed by flood-tolerant shrubs, ferns, and herbs [Florida Natural Areas Inventory (FNAI), 2010]. Extensive wetland areas colonized by shrubby plants, mainly Ericaceae, were also present. This community could have been similar to a recent shrub bog, known from Florida. It is found on the border of swamps in stream head drainages, in flat, poorly drained areas between rivers, and it may cover large portions of low-lying areas of the coastal plain. The typical plants here are *Cliftonia*, *Clethra*, *Cyrilla*, *Ilex*, Itea, Leucothoe, Myrica, and Photinia [Florida Natural Areas Inventory (FNAI), 2010]. From habitats similar to these, pollen was undoubtedly transported by water to the depositional basin filled with brine.

The other taxa (less frequent pollen and with rarely occurring fossilized cytoplasm) represent either rare plants or communities that were more remote from the depositional basin. They could have occurred in wetland but also mesic habitats. The plants of poorly-drained soils could have been Acer, Alnus, Carya, Castanea/Castanopsis/Lithocarpus, Celtis, Eucommia, Fraxinus, Juglans, Lythraceae, Myrica, Nyssa, Oleaceae, Ostrya, Platycarya, Pterocarya, and Sciadoopitys. Well-drained soils might have been inhabited by Araceae/Arecaceae/Amaryllidaceae/Butomaceae, Caryophyllaceae, Cornaceae, Craigia/Tilia, Mastixiaceae, Poaceae, Ilex, Magnolia, Eleagnaceae, Symplocos, Fabaceae, Cyrillaceae/Clethraceae, Fagaceae (Tricolporopollenites liblarensis, T. villensis), Sequoia but possibly also Cathaya, Pinus, and Tsuga. In the undergrowth, pteridophytes were present. Many of the previously mentioned taxa might well have grown in both wetland and mesic habitats (see Table 3), so this division is not strict.

The list of taxa and taxa frequencies, as established on the basis of plant macro-remains found in the salt from Wieliczka (Zastawniak, 1996; Łańcucka-Środoniowa and Zastawniak, 1997 with references), differs from those based on pollen and spores. The discrepancy in the composition of fossil assemblages made up of micro- *versus* macro-remains could be due to various factors: biota-dependent, such as the structure of the vegetation, and the properties of the species (pollen, fruits, seeds production, type of pollination), or taphonomy-dependent (West, 2000). For instance, Ericaceae macro-remains are not exceptionally frequent, while Ericaceae pollen is one of the most important components in pollen spectra. For example, this could be due to flooding of the area occupied by this taxon that occurred only within the flowering period and thus enabled the preservation of large quantities of pollen. On the other hand, many of the Ericaceae are evergreen and lose leaves infrequently, so the probability of fossilization of leaves is smaller than in the case of abundantly produced pollen. Such a situation can be observed in the material presented by Worobiec and Worobiec (2016). However, the causes of such differences could be manifold and complex and are usually difficult to define. Łańcucka-Środoniowa and Zastawniak (1997) consider the macroflora from Wieliczka to be of an allochthonous nature and the plant remains to have been transported by air or water (rivers, streams). The important role of water transport is especially stressed because of the presence of heavily worn and rounded plant remains that often resemble large fruits (Łańcucka-Środoniowa, 1984). The pollen flora seems to be more autochthonous. Pollen of plants more distant from the depositional basin usually is represented by single grains. It is possible that the pollen of many such taxa did not access the sedimentary basin.

Worthy of discussion is the presence of numerous macro-remains of Ruppia and Eulimnocarpus, considered by Łańcucka-Środoniowa and Zastawniak (1997) to be halophytes, although no pollen of these taxa was found. Pollen of Ruppia has a very thin exine (indeed, it is absent over most of the pollen grain) and this is one reason why it is usually not preserved as a fossil (Couper, 1953). Machin (1971 vide Gandolfo et. al., 2009) considered the possibility that Limnocarpus produced pollen of the Aglaoreidia type. The similar monoporate pollen type probably could have been produced by Eulimocarpus, also related to the Potamogetonaceae (Collinson, 1982 vide Gandolfo et al., 2009). The Aglaoreidia pollen is similar in general aspects to the Sparganium/Typha/Potamogeton type. However, the characteristic features - a thick annulus, surrounding a pore and heterobrochate reticulum - make it easy to distinguish. Recently, Ruppia can grow in fresh water to 132 ppt (Zhao et al., 2004, with references). The fossil taxon Eulimnocarpus is considered a part of brackish-water plant communities (Mai, 1995). Water plants, the pollen of which is present in evaporites, are Potamogeton (only one genus living in brackish water is known; Reimold and Queen, 1972), Sparganium that grows rather in fresh water, and Typha, which is euryhaline, being common both in fresh and brackish waters. The data on macro- and micro-remains show that both fresh and brackish water

bodies were present at the littoral of the central Paratethys during the BSC.

On the basis of plant macro-remains, Mai (1995) characterized the flora from Wieliczka as a taxonomically diversified mesophytic forest with a prevalence of ca. 70%, of deciduous and ca. 30% of evergreen trees and shrubs with East-Asiatic and Northern American elements dominant.

The proportion of plants considered to represent a tropical and subtropical climate, as compared to those of a temperate climate, is also different for the assemblages of macro- and micro-remains. Łańcucka-Środoniowa and Zastawniak (1997) specified one-third (ca. 30 taxa, their table 8, p. 37, and fig. 10, p. 38) as tropical and subtropical, while this value is about one quarter (ca. 15 taxa) for pollen taxa (Table 3). Among the important taxa is Mastixiaceae, the very characteristic family for the Neogene of western and central Europe. The presence of various Mastixia seeds became a basis for distinguishing floral zones (Mai, 1995). The appearance of Mastixia in fossil floras gives an indication of warm periods. Zastawniak (1996) noted three genera: Mastixia amygdalaeformis (nearest living relative Mastixia subcaudata), Mastixicarpum limnophilum (nearest living relative Diplopanax), and Eomastixia persicoides. In the pollen material, grains of Mastixia type (Cornaceaepollis satzveyensis fossil species - see the discussion on Neogene Mastixiaceae pollen in Słodkowska and Ziembińska-Tworzydło, 2017) appear rarely and never possess fossilized cytoplasm. This proves that plants, belonging to the Mastixiaceae, colonized areas remote from the sedimentary basin. Nowadays, Mastixiaceae occur in a tropical climate. On the other hand, in both the macro- and micro-remains assemblages, fossils of plants of temperate climates predominate. The coexistence of both these elements indicates that the climate probably was temperate, but warm enough for some plants of tropical and subtropical climatic requirements to thrive. Furthermore, the presence of Taxodium/Glyptostrobus and other plants of wetland habitats indicates humidity. This could have been an important factor that shaped regional climatic conditions.

The palynofloras in the Romanian evaporites, described by Petrescu *et al.* (1999) and Petrescu and Bican-Brisan (2005), also originated during the BSC. In the Turda-Cheia region (Petrescu *et al.*, 1999), angiosperms predominate in the spectra, while in Praid (Petrescu and Bican-Brisan, 2005) conifers are dominant. The percentages of taxa are not given, but rather only three classes of frequencies: frequent, rare, and very rare. Among angiosperms the most important are *Alnus*, *Araliaceoipollenites*, *Betula*, *Carya*, *Caprifoliipites*, *Ericipites*, *Eucommia*, *Liquidambar*, *Myrica*, *Nyssa*, *Pterocarya*, *Tilia*, *Tricolporopollenites*  *liblarensis, T. cingulum* (probably *Cupuliferoipollenites oviformis*), *T. exactus*, and *Quercoidites microhenricii*. The authors did not mark the particularly high frequencies of Ericaceae pollen; however, three *Ericipites* species were tagged, 1 species as "frequent" and 2 species as "rare". *Inaperturopollenites* pollen is noted as "very rare". These two issues are the most significant differences with respect to the Polish palynofloras. On the other hand, the presence of "local wet conditions" in close proximity to the sedimentary basin is highlighted.

The Carpathian Foredeep basin, sealed off from marine water inflow during the BSC, experienced a substantial sea-level fall (Babel, 2004 with references). Sedimentological data show that the evaporite drawdown reached a few tens of metres (Bąbel, 2004; Oszczypko, 1998). The other characteristic feature is a substantial input of continental water during the precipitation of chemical deposits, as was indicated in various geochemical studies (e.g. chlorine stable isotope values, Eastoe and Peryt, 1999; solutes in fluid inclusions, Cendón et al., 2004; and bromine content, Garlicki and Wiewiórka, 1981). The presence of wetland and mesic habitats and the postulated climate are compatible with these observations. On the one hand, palynological data show that the climate, which remained humid, could not have been the main cause of the salinity crisis; however, on the other, the data indicate that it was warm enough (e.g. in a seasonal manner), to provide evaporation. The latter condition also was postulated by Bąbel (2004), who mentioned that the deposition of aggradational shallow-water evaporites was related to water-level fluctuations within the basin, caused mainly by the regional climate. Interesting and to some extent similar observations are presented by Faquette et al. (2006), who studied pollen records in the Mediterranean region, dating back to the Messinian Salinity Crisis. These authors proved that the climate did not cause evaporation, nor did the salinity crisis change the climate of the region. On the basis of the pollen spectra obtained from the deposits overlying the Badenian evaporites in Bochnia (sample S1, Chodenice Beds; Fig. 1, Table 1) and presented by Kita (1963), Oszast (1967) and Sadowska (1997, 1999), it also can be stated that the climate did not noticeably change immediately after the BSC. The S1 sample is poorly diversified taxonomically – however, plants characteristic for the evaporative event, Ericaceae, *Engelhardia*, *Cupuliferoipollenites pusillus* + *C. oviformis*, Fagus, Taxodium/Glyptostrobus, Pterocarya, Quercus, and Sparganium/Potamogeton, are still the main components of the plant communities. In the Jamnica S-119 borehole, located in Krakoviec Clay, overlying the evaporitic complex, Sadowska (1999) characterized a flora with abundant Taxodium/Glyptostrobus, Alnus, Ericaceae, Quercus, Ulmus, Fagus, Carya, Pterocarya, and Engelhardia. The environmental conditions seem to have changed gradually, which can be observed in the decreasing frequencies of Ericaceae, Engelhardia, Carya, Pterocarya, T. pseudocingulum, and Ulmus in Gliwice (Sadowska, 1997), Ericaceae in the upper part of Piaseczno profile (Oszast, 1967), and Ericaceae, Carya, and Engelhardia at Kłaj (Kita, 1963). There was no distinct change in the composition of the pollen spectra that could be correlated with the end of evaporite deposition.

## CONCLUSIONS

The evaporites and clastic deposits formed in the northern part of the central Paratethys during the Badenian Salinity Crisis contain well-preserved and abundant palynomorphs. Pollen analysis of samples from Bochnia and Wieliczka salt mines (southern Poland) shows that the littoral of the evaporating sea was overgrown by plants of wetland, mesic, and upland communities. These results are similar to those of previous studies of deposits of the same age. The fossilized pollen content commonly occurring in some samples (studies presented in previous articles) together with pollen frequencies, allows specification of the plants that inhabited the areas closest to the depositional basin. This deduction is based on the assumption that pollen cytoplasm remains alive for up to several days and thus its fossilization in the condensed brine was likely to have occurred after only very brief transportation. In taking account of this factor, it can be assumed that the areas closest to the sedimentary basin were occupied by Carpinus, Engelhardia, Ericaceae, Fagus, Liquidambar, Quercus, Potamogeton, Taxodium/Glyptostrobus, plants producing the Tricolporopollenites pseudocingulum pollen type, and Ulmus. These taxa represent aquatic, wetland, and mesic habitats. The most characteristic feature of the floras during the BSC is high percentages of Ericaceae pollen. The plants of the Ericaceae family, along with other taxa, probably developed thickets in poorly-drained or temporarily inundated areas, from which the pollen was transported by surface water into the sea. The other important plant community was a swamp forest (recent bald-cypress type). The presence of such habitats along the coastline of the evaporating Paratethys indicates that the climate remained humid. Most of the pollen taxa found are considered to represent a warm-temperate climate. However, taxa associated with a tropical and subtropical climate (with representatives of the Mastixiaceae family, important in the Neogene) are also present. No sharp change in taxonomic composition can be

observed at the end of the evaporative event. All this shows that the climate may be of lower importance among the factors that caused the salinity crisis.

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