

Oligocene plant assemblage from Rębiszów, Lower Silesia: First “volcanic flora” from Poland

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Fossil plant macroremains preserved in laminated diatomites from Łysa Góra near Rębiszów, Lower Silesia, have been documented for the first time. The fossil assemblage consists mostly of leaves, but fruits, seeds and sporadic flowers also occur. Forty-three identified taxa represent nineteen plant families: Aceraceae, Berberidaceae, Betulaceae, Cornaceae, Cupressaceae, Elaeocarpaceae, Ericaceae, Fagaceae, Lauraceae, ?Leguminosae, ?Meliaceae, Magnoliaceae, Pinaceae, Rhamnaceae, Rosaceae, Salicaceae, Tilioidae, Ulmaceae, Vitaceae, and one incertae sedis. The prevalence of entire margined leaves, mostly represented by *Majanthemophyllum basinerve* and *Daphnogene cinnamomifolia*, and a significant presence of *Calocedrus suleticensis* and *Liriodendron haueri*, are characteristic features of the Rębiszów flora. The composition of the plant assemblage points to a mesophytic forest with some riparian elements and suggests favourable, warm climatic conditions. Radiometrically dated basalts overlying fossiliferous layers and composition of palynoflora suggest at least Chattian (late Oligocene) age. The lithology and floristic composition link the Rębiszów flora with the so-called volcanic floras of the Nerchau-Flörsheim or Kleinsaubernitz floristic complex (Oligocene) from Germany and Czech Republic with Suletice-Berand flora being especially close.

Key words: Acrogymnospermae, Angiospermae, sporomorphs, volcanic floras, diatomites, Paleogene, Poland.

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Introduction

Localities where the late Paleogene plant remains occur are quite common in Central Europe, but fossil plant assemblages which were formed in connection with volcanic activity, so-called volcanic floras (Kvaček and Walther 1998), are rare. These floras, however, have particular relevance for our knowledge of Central European Paleogene vegetation. The importance of these type of floras is due to the fact that they represent zonal, upland vegetation and, often, they can be radiometrically dated. They also frequently provide exceptionally well preserved macro- and microfossils, both of plants and animals. The Oligocene volcanic floras are connected with distribution of the Central European Tertiary intraplate volcanic province (Birkenmajer et al. 2011) and have been documented so far from Germany and Czech Republic. Lower Silesia (SW Poland) belongs to the north-eastern part of this volcanic province as a part of

the Bohemo-Silesian volcanic belt though Paleogene fossil macrofloras have not yet been reported from this area.

The fossil plant remains documented here were discovered at Łysa Góra (Urwista), located in the western part of Lower Silesia, ca. 2 km south of Rębiszów village (Fig. 1) by Stanisław Dyjor in 1979. The first attempts to investigate this fossil flora were undertaken much later, in the early 2000s by Katarzyna Krajewska. Krajewska and Dyjor planned a comprehensive collaborative paper about fossil flora from Rębiszów. Unfortunately, their untimely death thwarted this plan.

Considering the uniqueness of the Rębiszów flora among other Cenozoic floras from Poland, and its significance to knowledge of the Oligocene volcanic floras of Central Europe, we decided to continue the investigations of Krajewska and Dyjor. This paper also commemorates Katarzyna Krajewska as a paleobotanist as well as the efforts she made in studying this flora.

Some data on the site location and local geology presented in the Geological settings originate from a draft by Stanisław Dyjor given in a letter to Katarzyna Krajewska dated March 14, 2006. However, we also present an alternative view on the general geology of this locality based on more recent studies on the geology of the Rębiszów locality. The taxonomic composition within the assemblage was preliminarily recognised by Krajewska and prepared in the form of a list of indicated specimens. She investigated some of the remains in consultation with Zlatko Kvaček in 2004.

In preparation of the present treatment, we carefully re-examined (RK and GW) the whole collection to evaluate the taxonomic determinations made by Krajewska. Most of the carpological remains in the collection that remained unrecognised or unnoticed by Krajewska were studied during the preparation of this paper. Preliminary palynological analysis of the deposits containing the macroremains was conducted by Aleksandra Kohlman-Adamska and Maria Ziemińska-Tworzydło (unpublished material), but while preparing this report new and detailed palynological investigations were made (EW) to supplement the preliminary results.

This paper briefly documents current knowledge on the Łysa Góra fossil assemblage, including palynological analysis, interpretation of the vegetation and paleoclimate, and comparison with other European assemblages of the same age and age determination. In recognition of the work already done on this collection we decided to include Katarzyna Krajewska posthumously as a co-author of this paper.

Institutional abbreviation.—KRAM-P: Palaeobotanical collections of W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland.

Geological settings

Volcanic vents in the Rębiszów area are connected with the Rębiszów fault zone, where a tectonic contact with the gneisses and granitic gneisses of the Izera complex and the Neoproterozoic Stara Kamienica mica schist can be observed (Birkenmajer et al. 2011).

According to Birkenmajer et al. (2011), volcanic activity in Lower Silesia began in the Rupelian (early Oligocene) and continued with variable intensity to Zanclean (early Pliocene). One of the latest radiometric datings suggests that volcanic activity in the Rębiszów area took place in the late Oligocene. Dates obtained from ankaratrites exposed in the Łysa Góra quarry are of ca. 25.3 ± 1.0 Ma, and those exposed in Grudza quarry, ca. 4 km East of the Rębiszów village, are of ca. 26.0 ± 1.0 Ma (Birkenmajer et al. 2011).

According to Stanisław Dyjor (unpublished material, a letter to Katarzyna Krajewska, 14.03.2006), the layers with plant remains which he found were exposed somewhere in or near the “lower quarry”. Despite the imprecise localisation, we are almost certain that the “lower quarry” could equate to an abandoned quarry that is located within a hill called

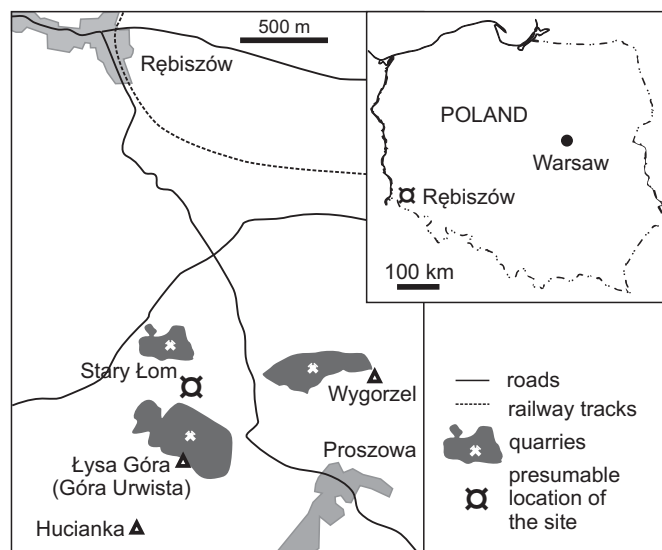


Fig. 1. Location of the Łysa Góra near Rębiszów, Lower Silesia, Poland.

“Łysa Góra” (Fig. 1). Unfortunately, despite two excursions to search this area, we were unable to find the exact position of the site where the fossils were collected. Below, we summarise the interpretation of the local geological settings left by Stanisław Dyjor. According to him, some of the basaltic vents or lava flows in the Rębiszów area are covered with small patches of various Cenozoic sedimentary rocks, which were deposited in a small lake. The lake probably formed after the stream was restricted by lava flow. Layers with plant remains are a part of a sedimentary series that originally filled the paleovalley, although much of their northern part was eroded in the Pleistocene. Sedimentary series were deposited between the lava flow on the southern margin and gneisses on the northern erosional margin of the valley, and consisted mostly of loamy sand and gravel with tuff and tuffite intercalations in the lower part, and diatomite with fossil flora in the upper part of the profile. Mass development of diatoms was probably induced by silica-rich water. The high-silica content probably resulted from percolation of waters through silica-rich volcanic rocks.

We have, however, considerable doubts about the above presented interpretation. The chronological order proposed by Stanisław Dyjor (unpublished material) is in contradiction with the technical report on the geological setting of the basalt resources in Rębiszów, which we had the opportunity to see during our visit to the main office of Pri Bazalt S.A. mining company and information provided by Adameczyk (2008). Both of the mentioned sources clearly state that sedimentary rocks with fossiliferous layers found in the study area are overlain by basalt. According to Adameczyk (2008), Cenozoic sedimentary series in the Rębiszów area were preserved only due to the protective basalt layer. This alternative interpretation suggests that sedimentary rocks are older than the basalts, in this case providing the upper age limit of the Rębiszów fossil flora.

During an excursion (31.07.2019) to an abandoned quarry located on the Urwista and Odarte Skały hills, RK and Olaf

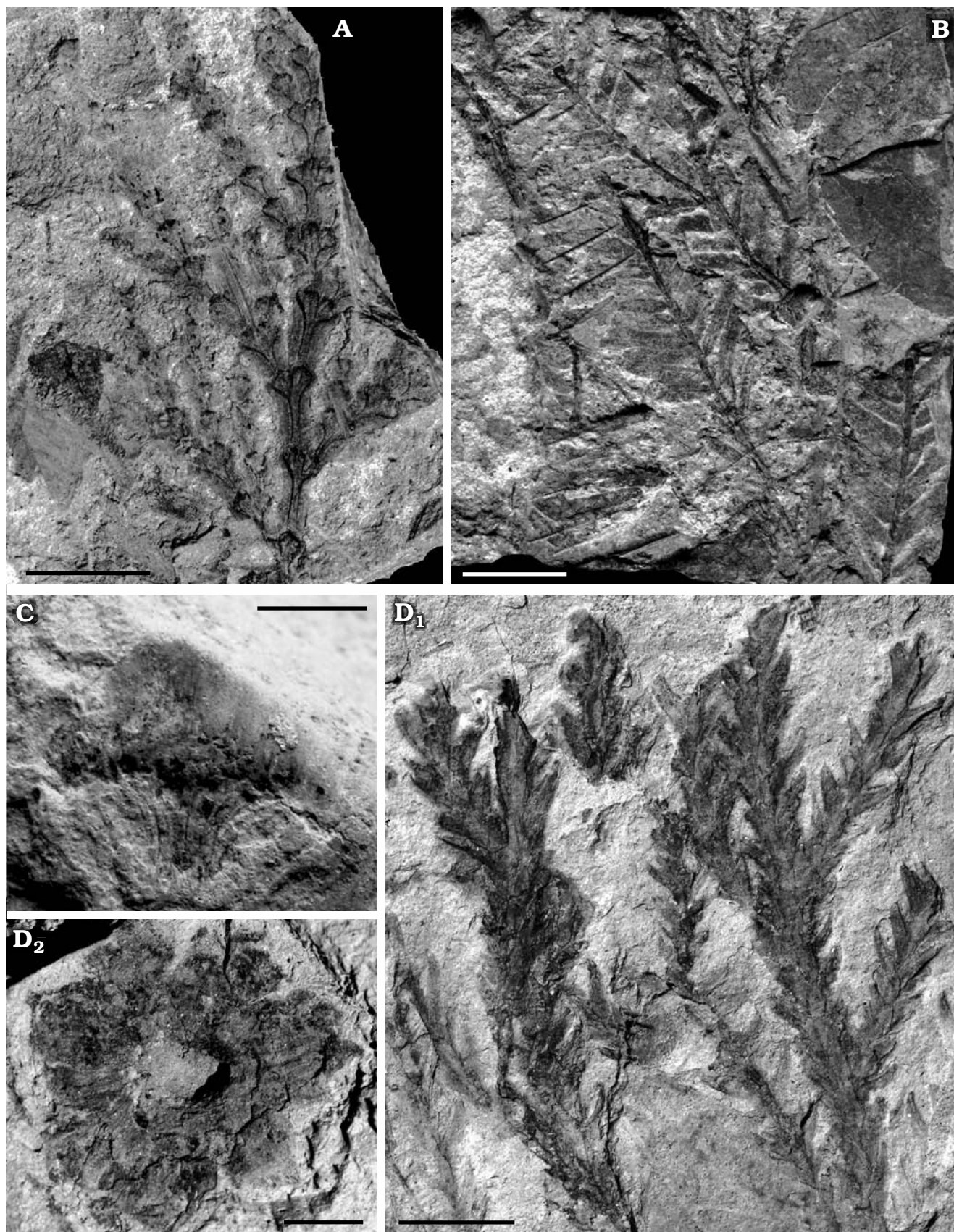


Fig. 2. Conifers impressions from Łysa Góra near Rębiszów, Poland, late Oligocene. A. *Calocedrus suleticensis* (Brabenc, 1909) Kvaček, 1999, KRAM-P 128/38, twig. B. cf. *Tsuga* sp., KRAM-P 128/50, twigs. C. *Cunninghamia* cf. *miocenica* Ettingshausen, 1872, KRAM-P 128/251, cone scale. D. *Cryptomeria* cf. *rhenana* Kilpper, 1968, KRAM-P 128/1; twigs (D₁), cone (D₂). Scale bars: A, B, D₁, 10 mm; C, D₂, 5 mm.

Tietz and Joerg Büchner (both Senckenberg Museum of Natural History, Görlitz, Germany) discovered three new sites where sedimentary sequences are exposed. According to Olaf Tietz and Joerg Büchner (personal communication 2019), the lithological characteristics and position of the sedimentary sequences in relation to the overlying basalts suggest that these deposits may represent maar lake infill rather than the infill of a lake formed by the damming of a river by a lava flow.

Thus, the fossil plant assemblage from Rębiszów represents a so-called volcanic flora *sensu* Walther (2005), which is similar to the Oligocene floras from Northern Bohemia, Czechia and Upper Lusatia, Germany (Akhmetiev et al. 2009). These assemblages were usually preserved in diatomaceous deposits of maar crater lakes, such as late Oligocene fossil flora from Kleinsaubernitz (Walther 1999, 2005).

The genesis and lithology of the deposits with a plant assemblage from Rębiszów (diatomaceous sediments in a volcanogenic lake) are also similar to the late Eocene Florissant fossil beds from Colorado, USA, yielding the renowned plant and animal fossil Lagerstätte (Meyer et al. 2004).

Material and methods

Fossil leaves from Rębiszów are mostly impressions, although sometimes traces of coalified tissues are preserved, especially in the case of fruits or cones. Considering the state of preservation, leaf remains usually lacking cuticles were identified based only on their macromorphology. The studied fossil material (almost 600 rock samples) are housed in the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków (KRAM-P 128/1–595). The studied fossil material from Rębiszów is probably the only such material obtained from the Łysa Góra (Urwista) locality. To our knowledge, no more material can be collected from the locality discovered by Stanisław Dyjor because the fossiliferous layer is no longer accessible.

Two samples from the sediments containing plant macroremains were used for the palynological study. They were prepared in the laboratory of the W. Szafer Institute of Botany PAS, using HCl, KOH, and HF (Moore et al. 1991). Ten slides were studied and in each sample more than 1000 sporomorphs (pollen grains and spores), as well as all co-occurring non-pollen palynomorphs, were counted.

Results

Plant macroremains assemblage.—We recognised 43 taxa among the plant macroremains from Rębiszów, but 36 are illustrated in this paper (Figs. 2–8, Table 1). Most numerous are angiosperm remains, but gymnosperms also represent a significant group. In respect of the systematic diversity the flowering plants also prevail and are represented by 19

families, including Aceraceae (Figs. 3D, 4F), Berberidaceae (Fig. 4G, K), Betulaceae (Figs. 3A, F, 4I, 5A, 7B), Cornaceae, Elaeocarpaceae (Fig. 6E), Ericaceae, Fagaceae (Fig. 6A–C, F–H), Lauraceae (Fig. 4A–E), ?Leguminosae (Fig. 4J), ?Meliaceae (Fig. 7A, E), Magnoliaceae (Fig. 3C), Rhamnaceae (Fig. 5B), Rosaceae (Figs. 7D, 8B), Salicaceae (Fig. 6D), Tilioideae (Fig. 3E), Ulmaceae (Fig. 3B), and Vitaceae (Fig. 5E, G). Conifers are represented by Cupressaceae: *Calocedrus suleticensis* (Brabenec, 1909) Kvaček, 1999 (Fig. 2A), *Cunninghamia cf. miocenica* Ettingshausen, 1872 (Fig. 2C), *Cryptomeria cf. rhenana* Kilpper, 1968 (Fig. 2D₁, D₂) and Pinaceae: *Tsuga cf. moenana* Kirchheimer, 1935 (Fig. 4H) and *Tsuga* sp. (Fig. 2B).

The plant assemblage is dominated by entire-margined leaves, which significantly overweigh toothed leaves, representing ca. 80% of the whole leaf assemblage. Among those, the most common species is *Majanthemophyllum basinerve* (Rossmässler, 1840) Knobloch and Kvaček, 1996 (ca. 46% of all leaves), which is a taxon of uncertain affinity. Representatives of Lauraceae (ca. 22% of all leaves) and Fagaceae (ca. 11% of all leaves) are less abundant in the Rębiszów flora. Among Lauraceae, the most common is *Daphnogene cinnamomifolia* (Brongniart, 1822) Unger, 1851 (ca. 96%), but the form *D. lanceolata* *sensu* Kvaček and Walther (1995) prevails over the form *D. cinnamomifolia*. Fagaceae are represented by *Eotrigonobalanus furcinervis* (Rossmässler, 1840) Walther and Kvaček, 1989, *Trigonobalanopsis exacantha* (Mai, 1970) Kvaček and Walther, 1988, cf. *Trigonobalanopsis rhamnoides* (Rossmässler, 1840) Walther and Kvaček, 1988, cf. “*Quercus*” *bavarica* Knobloch and Kvaček, 2004, and *Quercus* sp. or *Castanopsis* sp.

The most common among toothed leaves are *Alnus* cf. *gaudinii* (Heer, 1856) Knobloch and Kvaček, 1976 and *Alnus* sp. (ca. 65%). Aside from leaf remains, *Alnus* Miller, 1754 is also represented by infructescence of *A. kefersteinii* (Goeppert, 1838) Unger, 1845. A very common element of the Rębiszów assemblage are fruits of *Liriodendron haueri* Ettingshausen, 1869 (more than 53 specimens). Characteristic but less common is *Craigia bronniei* (Unger, 1845) Kvaček, Bůžek, and Manchester, 1991 (ca. 11 specimens). Elements such as *Ulmus* sp., *Ostrya atlantidis* Unger, 1850, *Mahonia* sp., *Dombeyopsis lobata* Unger, 1850, *Acer* sp., *Carpinus* sp. vel *Ostrya* sp., *Sloanea artocarpites* (Ettingshausen, 1869) Kvaček and Hably, 2001, *Populus* cf. *zaddachii* Heer, 1859, cf. *Rosa lignitum* Heer, 1869, cf. *Leguminosites* sp. (or cf. *Rhodomyrtophyllum* sp.), and *Vitis* sp. or *Ampelopsis* sp. (arranged according to the number of specimens, see also Table 1) are sparse.

Palynoflora.—Palynological analysis revealed rich and well-preserved palynoflora. A total of 88 fossil-species were identified, including 19 species of spores, 15 species of pollen grains of gymnosperms, and 54 species of angiosperms. Palaeotropical and palaeotropical/warm-temperate elements dominate the spore-pollen spectra (Table 2).

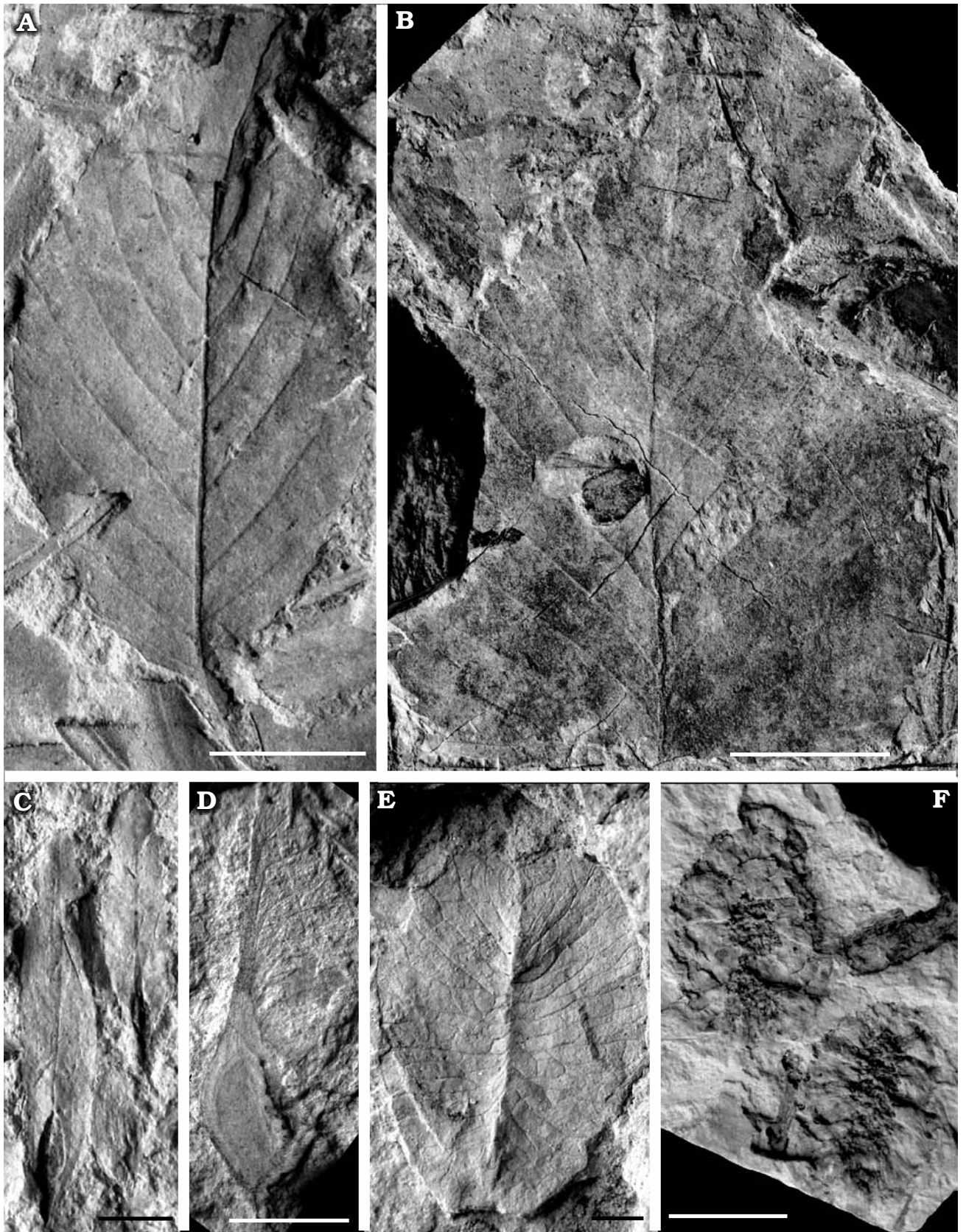


Fig. 3. Angiosperms impressions from Lysa Góra near Rębiszów, Poland, late Oligocene. **A.** *Alnus julianiformis* (Sternberg, 1823) Kvaček and Holy, 1974, KRAM-P 128/347, leaf. **B.** *Ulmus fischeri* Heer, 1856, KRAM-P 128/149, leaf. **C.** *Liriodendron haueri* Ettingshausen, 1869, KRAM-P 128/318, fruit. **D.** *Acer* cf. *hercynicum* Mai, 1978, KRAM-P 128/118, fruit. **E.** *Craigia bronni* (Unger, 1845) Kvaček, Bůžek, and Manchester, 1991, KRAM-P 128/203, fruit. **F.** *Alnus kefersteinii* (Goeppert, 1838) Unger, 1845, KRAM-P 128/44, infructescence. Scale bars: A, B, F, 10 mm; C, D, 5 mm; E, 2 mm.

Table 1. Taxa recorded among leaf and fruit/seeds remains from Rębiszów. N, number of specimens.

	Type of remain	N	Specimens (KRAM-P 128)
Cupressaceae			
<i>Calocedrus suleticensis</i> (Brabenec, 1909) Kvaček, 1999	leaf	71	1, 3, 11, 14, 32, 38, 43–45, 48, 52, 78, 79, 99, 101, 109, 119, 121, 122, 124, 139, 141, 143, 161, 209, 213, 214, 237, 238, 240, 258, 261, 263, 277, 291, 293, 298, 305, 307, 308, 318, 329, 335, 337, 343, 350, 361, 363, 366, 378, 397, 411, 417, 426, 437, 470, 472, 508, 519, 526–529, 531, 558, 562, 564, 567, 570, 571, 578
<i>Cryptomeria cf. rhenana</i> Kilpper, 1968	leaf, cone	16	1, 40, 95, 142, 159, 200, 202, 239, 311, 321, 331, 354, 377, 386, 391, 442
<i>Cunninghamia cf. miocenica</i> Ettingshausen, 1872	scale	1	251
Pinaceae			
<i>Tsuga cf. moenana</i> Kirchheimer, 1935	cone	5	33, 75, 245, 311, 351
<i>cf. Tsuga sp.</i>	leaf	1	50
Aceraceae			
<i>cf. Acer tricuspidatum</i> Bronn, 1838	leaf	1	388
<i>Acer cf. hercynicum</i> Mai, 1978	fruit	1	118
<i>Acer cf. polymorphoides</i> Mai, 1987	fruit	1	415
<i>Acer sp.</i>	leaf	1	501,
	fruit	2	27, 558
Betulaceae			
<i>Alnus cf. gaudinii</i> (Heer, 1856) Knobloch and Kvaček, 1976	leaf	1	390
<i>Alnus julianiformis</i> (Sternberg, 1823) Kvaček and Holy, 1974	leaf	1	347
? <i>Alus rostaniana</i> Saporta emend. Mai and Walther	leaf	1	290
<i>Alnus kefersteinii</i> (Goepfert, 1838) Unger, 1845	infructescence	7	42, 44, 275–277, 298, 570
<i>Alnus sp.</i>	leaf	37	45, 49, 83, 112, 187, 196, 197, 198, 233, 262, 264, 290, 293, 297, 317, 338, 341, 343, 347, 355, 375, 386, 390, 391, 395, 429, 440, 444, 457, 461, 467, 507, 508, 509, 512, 527, 585
<i>Ostrya atlantidis</i> Unger, 1850	fruit	3	120, 318, 526
<i>Carpinus sp.</i> or <i>Ostrya sp.</i>	leaf	1	546
Berberidaceae			
<i>Mahonia sp.</i>	leaf	3	34, 35, 291
Cornaceae			
<i>Cornus cf. gorbunovii</i> (Dorofeev, 1963) Negru, 1972	fruit	1	51
Elaeocarpaceae			
<i>Sloanea artocarpites</i> (Ettingshausen, 1869) Kvaček and Hably, 2001	leaf	1	433
Ericaceae			
Ericaceae gen. et sp. indet.	fruit	2	408, 417
Fagaceae			
<i>Eotrigonobalanus furcinervis</i> (Rossmässler, 1840) Walther and Kvaček, 1989	leaf	2	234, 241
<i>Trigonobalanopsis exacantha</i> (Mai, 1970) Kvaček and Walther, 1988	fruit	5	49, 52, 185, 332, 346
<i>cf. Trigonobalanopsis rhamnoides</i> (Rossmässler, 1840) Walther and Kvaček, 1988	leaf	16	12, 78, 80, 92, 105, 118, 134, 138, 150, 151, 180, 305, 307, 397, 547, 570
<i>cf. "Quercus" bavarica</i> Knobloch and Kvaček, 2004	leaf	20	64, 79, 89, 93, 99, 195, 202, 216, 235, 259, 303, 349, 379, 437, 440, 519, 528, 542, 547, 563
<i>Quercus sp.</i> or <i>Castanopsis sp.</i>	fruit	1	313 (part and counterpart)
Lauraceae			
<i>Daphnogene cinnamomifolia</i> (Brongniart, 1822) Unger, 1850 forma <i>cinnamomifolia</i> sensu Kvaček and Walther (1995)	leaf	3	256, 280, 285

	Type of remain	N	Specimens (KRAM-P 128)
<i>Daphnogene cinnamomifolia</i> (Brongniart, 1822) Unger, 1850 forma <i>lanceolata</i> sensu Kvaček and Walther (1995)	leaf	72	1, 4, 10, 11, 15, 28, 32, 50, 52, 66, 78, 79, 80, 82, 94, 101, 108, 113, 127, 131, 151, 160, 178, 181–183, 201, 202, 215, 237, 238, 257, 263–265, 268, 273, 280, 285, 293, 296, 298, 305, 316, 322, 325, 327, 338, 349, 356, 359, 361, 365, 376, 391, 397, 418, 433, 436, 440, 456, 459, 470, 471–475, 496, 502, 524, 525, 537, 547, 565, 576, 588, 592
cf. <i>Laurophyllum acutimontanum</i> Mai, 1963	leaf	3	129, 190, 436
?Leguminosae			
cf. <i>Leguminosites</i> sp or cf. <i>Rhodomyrtophyllum</i> sp.	leaf/ leaflet	1	88
Magnoliaceae			
<i>Liriodendron haueri</i> Ettingshausen, 1869	fruit or seed	53	10, 13, 14, 22, 26, 78, 98, 99, 101, 156, 162, 169, 188, 207, 209, 211, 212, 218, 265, 293, 318, 321, 360, 376, 378, 387, 400, 402, 403, 407, 413, 414, 423, 428, 439, 444, 462, 465, 470, 487, 500, 519, 522, 525, 527, 528, 529, 542, 543, 563, 568, 571, 576
?Meliaceae			
cf. <i>Cedrela macrophylla</i> Andreánszky, 1955	leaf	3	516, 569, 570
Rhamnaceae			
<i>Paliurus favonii</i> Unger, 1847	fruit	1	165, 170 (part and counterpart)
Rosaceae			
<i>Prunus</i> cf. <i>scharfii</i> Gregor, 1978	fruit	2	39, 352
cf. <i>Rosa lignitum</i> Heer, 1869	leaf/ leaflet	1	401
Salicaceae			
<i>Populus</i> cf. <i>zaddachii</i> Heer, 1859	leaf	1	511, 513 (part and counterpart)
Tilioidae			
<i>Craigia brononii</i> (Unger, 1845) Kvaček, Bůžek and Manchester, 1991	fruit	11	83, 158, 203, 264, 319, 378, 413, 440, 543, 574, 582
<i>Dombeyopsis lobata</i> Unger, 1850	leaf	3	490, 584, 585
Ulmaceae			
<i>Ulmus fischeri</i> Heer, 1856	leaf	1	149
<i>Ulmus</i> sp.	leaf	5	94, 118, 264, 443, 529
Vitaceae			
<i>Ampelopsis</i> cf. <i>rotundata</i> Chandler, 1925	seed	1	109
<i>Vitis</i> sp. or <i>Ampelopsis</i> sp.	leaf	1	205, 207 (part and counterpart)
Incertae sedis			
<i>Majanthemophyllum basinerve</i> (Rossmässler, 1840) Knobloch and Kvaček, 1996	leaf/ leaflet	162	1, 6, 10–12, 18, 23, 25, 29–32, 43, 58, 63, 65, 74, 76, 77, 79, 80, 84–87, 95, 98, 100, 102, 109, 114, 115, 132, 133, 135, 136, 139, 141, 144, 150, 158, 165, 171–173, 181, 188, 197, 202, 203, 209–212, 215, 220, 221, 223, 224, 232, 235, 240, 244, 247, 248, 251, 255, 260, 265, 270, 285, 288, 289, 292, 293, 295, 298, 300, 301, 302, 304, 307, 313, 315, 316, 318–322, 324, 333, 337, 340, 342, 345, 348–350, 357, 359, 367, 372, 375, 376, 377, 379, 384, 391, 392, 397, 413, 421, 429, 433, 436, 442, 444, 450, 452, 453, 456, 464, 468, 476, 480, 483, 485, 490, 498, 502, 503, 510, 513, 515, 518, 522, 526, 528, 531, 533–535, 541–543, 547, 549, 551, 553–555, 562, 563, 569–571, 576, 582, 589, 591, 595

Among gymnosperms, the most common are pollen grains of Cupressaceae (fossil-genera *Inaperturopollenites* Pflug and Thomson, 1953 and *Sequoiapollenites* Thiergart, 1958), *Tsuga* (Endlicher) Carrière, 1855 (mainly fossil-species *Zonalapollenites verrucatus* Krutzsch, 1971) and bisaccate Pinaceae. Angiosperms are dominated by pollen grains of Fagaceae, including small tricolporate grains: *Cupuliferoipollenites oviformis* (Potonié, 1934) Potonié, 1951, *C. pusillus* (Potonié, 1934) Potonié, 1951, *Fususpollenites fusus* (Potonié, 1931) Kedves, 1978), *Tricolporopollenites villensis* (Thomson, 1950) Thomson and Pflug, 1953, *T. dolium*

(Potonié, 1931) Thomson and Pflug, 1953, *Quercoidites microhenricii* (Potonié, 1931) Potonié, Thomson, and Thiergart, 1950, *Q. henricii* (Potonié, 1931) Potonié, Thomson, and Thiergart, 1950, and a few specimens of *Faguspollenites* Raatz, 1937. The pollen of Betulaceae: mainly *Alnipollenites verus* (Potonié, 1931) Potonié, 1931 and *Carpinipites carpinoides* (Pflug, 1953) Nagy, 1985); Cyrillaceae/Clethraceae: mainly *Cyrillaceapollenites exactus* (Potonié, 1931) Potonié, 1960); Fabaceae: *Tricolporopollenites fallax* (Potonié, 1934) Krutzsch, 1960, *T. liblarensis* (Thomson, 1950) Hochuli, 1978, and *T. quisqualis* (Potonié, 1934) Krutzsch, 1954);

Table 2. Spores, pollen grains, non-pollen palynomorphs, and palynoclasts recorded in palynological samples from the Rębiszów. Taxonomy and botanical affinity according to Stuchlik et al. (2001, 2002, 2009, 2014). The following paleofloristical elements have been distinguished: palaeotropical (P), including: tropical (P1) and subtropical (P2), "arctotertiary" (A), including: warm-temperate (A1) and temperate (A2), and cosmopolitan (P/A). ×, unassigned.

Fossil taxa	Botanical affinity	Element	Sample 1	Sample 2
Spores				
<i>Baculatisporites</i> sp.	Osmundaceae: <i>Osmunda</i> Linnaeus, 1753	P/A	2	1
<i>Cicatricosisporites chattensis</i> Krutzsch, 1961	Schizaeaceae: <i>Anemia</i> Swartz, 1806	P1	1	
<i>Concavisporites pseudopartitus</i> Krutzsch, 1959	Gleicheniaceae?	P	2	
<i>Cryptogrammasporis</i> sp.	Pteridaceae: <i>Cryptogramma</i> Brown in Franklin, 1823	A1	1	
<i>Distancoraesporis</i> sp.	Sphagnaceae: <i>Sphagnum</i> Linnaeus, 1753	P/A	1	
<i>Echinatisporis</i> sp.	Selaginellaceae: <i>Selaginella</i> P. de Beauvois, 1804	P/A	1	1
<i>Foveotriletes semifovearis</i> Krutzsch, 1967	unknown	unknown	1	
<i>Laevigatosporites haardtii</i> (Potonié and Venitz, 1934) Thomson and Pflug, 1953 + <i>Laevigatosporites</i> sp.	Polypodiaceae, Davalliaceae, and other ferns	P/A	9	1
<i>Leiotriletes maxoides</i> Krutzsch, 1962 + <i>L. wolffii</i> Krutzsch, 1962 + <i>Leiotriletes</i> sp.	Lygodiaceae and other ferns	P	12	1
<i>Polypodiaceosporites</i> sp.	Pteridaceae: <i>Pteris</i> Linnaeus, 1753	P/A1	1	
<i>Retitriletes</i> sp.	Lycopodiaceae: <i>Lycopodium</i> Linnaeus, 1753	P/A	2	2
<i>Selagosporis</i> sp.	Lycopodiaceae: <i>Huperzia</i> Bernhardt, 1801	P/A	2	
<i>Triplanosporites</i> sp.	unknown	P	3	1
<i>Verrucatosporites alienus</i> (Potonié, 1931) Thomson and Pflug, 1953 + <i>V. favus</i> (Potonié, 1931) Thomson and Pflug, 1953 + <i>Verrucatosporites</i> sp.	Davalliaceae, Dennstaedtiaceae, and other ferns	P/A	3	3
Pollen grains of gymnosperms				
<i>Cathayapollis wilsonii</i> (Sivak, 1976) Ziemińska-Tworzydło in Stuchlik et al., 2002 + <i>Cathayapollis</i> sp.	Pinaceae: <i>Cathaya</i> Chun and Kuang, 1962	A1	1	6
<i>Cunninghamiapollenites</i> sp.	Cupressaceae: <i>Cunninghamia</i> Brown in Richard, 1826	A1	4	
<i>Cupressacites</i> sp.	Cupressaceae	A1	7	5
<i>Inaperturopollenites concedipites</i> (Wodehouse, 1933) Krutzsch, 1971 + <i>I. dubius</i> (Potonié and Venitz, 1934) Thomson and Pflug, 1953	Cupressaceae: <i>Taxodium</i> Richard, 1810, <i>Glyptostrobus</i> Endlicher, 1847	P2/A1	590	317
<i>Piceapollis</i> sp.	Pinaceae: <i>Picea</i> Dietrich, 1824	A	2	11
<i>Pinuspollenites labdacus</i> (Potonié, 1931) Raatz, 1937 ex Potonié, 1958 + <i>Pinuspollenites</i> sp.	Pinaceae: <i>Pinus</i> Linnaeus, 1753	A	7	51
<i>Sciadopityspollenites crassus</i> Krutzsch, 1971 ex Kohlman-Adamska, 1993 + <i>Sciadopityspollenites</i> sp.	Sciadopityaceae: <i>Sciadopitys</i> Siebold and Zuccarini, 1842	A1	3	1
<i>Sequoiapollenites gracilis</i> Krutzsch, 1971 + <i>Sequoiapollenites</i> sp.	Cupressaceae: <i>Sequoia</i> Endlicher, 1847, <i>Sequoiadendron</i> Buchholz, 1939, <i>Metasequoia</i> Hu and Cheng, 1948, <i>Cryptomeria</i> Don, 1838	A1	59	32
<i>Zonalapollenites verrucatus</i> Krutzsch, 1971 ex Ziemińska-Tworzydło, 1974 + <i>Zonalapollenites</i> sp.	Pinaceae: <i>Tsuga</i> (Endlicher, 1847) Carrière, 1855	A1	29	76
Pollen grains of angiosperms				
<i>Aceripollenites</i> sp.	Sapindaceae: <i>Acer</i> Linnaeus, 1753	A1	4	2
<i>Alnipollenites verus</i> (Potonié, 1931) Potonié, 1931	Betulaceae: <i>Alnus</i> Miller, 1754	P2/A	6	20
<i>Araliaceoipollenites</i> sp.	Araliaceae	P/A1	1	
<i>Arecipites</i> sp.	Arecaceae, Butomaceae, Ammarylidaceae, Araceae	P/A	1	
<i>Boehlensipollis hohli</i> Krutzsch, 1962	Elaeagnaceae, Lythraceae	P2/A1	3	
<i>Carpinipites carpinooides</i> (Pflug in Thomson and Pflug, 1953) Nagy, 1985	Betulaceae: <i>Carpinus</i> Linnaeus, 1753	P2/A1	10	25
<i>Caryapollenites simplex</i> (Potonié, 1931) Raatz, 1937 ex Potonié, 1960	Juglandaceae: <i>Carya</i> Nuttall, 1818	A1	4	3
<i>Cornaceapollis satzveyensis</i> (Pflug in Thomson and Pflug, 1953) Ziemińska-Tworzydło in Ziemińska-Tworzydło et al., 1994 ex Jansonius, Hills, and Hartkopf-Fröder, 1998	Mastixiaceae	P1	14	4

Fossil taxa	Botanical affinity	Element	Sample 1	Sample 2
<i>Cupuliferoipollenites oviformis</i> (Potonié, 1934) Potonié, 1951 ex Potonié, 1960 + <i>C. pusillus</i> (Potonié, 1934) Potonié, 1951 ex Potonié, 1960	Fagaceae: <i>Castanea</i> Miller, 1754, <i>Castanopsis</i> (Don, 1825) Spach, 1841, <i>Lithocarpus</i> Blume, 1826	P2/A1	45	134
<i>Cyrrillaceapollenites exactus</i> (Potonié, 1931) Potonié, 1960 + <i>C. brühlensis</i> (Thomson in Potonié et al., 1950) Durska in Stuchlik et al., 2014	Cyrrillaceae, Clethraceae	P	5	16
<i>Dicolpopollis middendorffii</i> (Potonié, 1931) Krutzsch, 1961	Arecaceae	P		1
<i>Edmundipollis edmundii</i> (Potonié, 1931) Konzalová, Słodkowska and Ziemińska-Tworzydło in Stuchlik et al., 2014	Mastixiaceae	P1	2	1
<i>Ericipites roboreus</i> (Potonié, 1931) Krutzsch, 1970 + <i>Ericipites</i> sp.	Ericaceae	P/A	3	3
<i>Faguspollenites</i> sp.	Fagaceae: <i>Fagus</i> Linnaeus, 1753	A	2	3
<i>Fraxinipollis</i> sp.	Oleaceae: <i>Fraxinus</i> Linnaeus, 1753	P/A	5	5
<i>Fususpollenites fusus</i> (Potonié, 1931) Kedves, 1978	Fagaceae: <i>Trigonobalanus</i> Forman, 1962 s.l. (incl. <i>Colombobalanus</i> Nixon and Crepet, 1989)	P1	36	119
<i>Ilexpollenites margaritatus</i> (Potonié, 1931) Thiergart, 1938	Aquifoliaceae: <i>Ilex</i> Linnaeus, 1753	P2	4	
<i>Intratrirporopollenites insculptus</i> Mai, 1961 + <i>Intratrirporopollenites</i> sp.	Malvaceae: Tilioideae (incl. <i>Craigia</i> Smith and Evans, 1921)	P/A1	5	1
<i>Juglanspollenites verus</i> Raatz, 1937	Juglandaceae: <i>Juglans</i> Linnaeus, 1753	A1	5	8
<i>Magnoliaepollenites neogenicus</i> (Krutzsch, 1970) Mohr, 1984	Magnoliaceae: <i>Magnolia</i> Linnaeus, 1753	P/A1		1
<i>Meliaceoidites</i> sp.	Meliaceae	P	2	
<i>Momipites quietus</i> (Potonié, 1931) Nichols, 1973	Juglandaceae: <i>Engelhardia</i> Leschenault and Blume, 1826, <i>Alfaroa</i> Standley, 1927, <i>Oreomunnea</i> Oersted, 1856	P	2	2
<i>Myricipites</i> sp.	Myricaceae	P2/A	1	4
<i>Nyssapollenites contortus</i> (Pflug and Thomson, 1953) Nagy, 1985	Nyssaceae: <i>Nyssa</i> Linnaeus, 1753	P2/A1	3	
<i>Oligopollis bilateralis</i> Krutzsch, 1959	unknown	unknown	1	
<i>Quercoidites microhenricii</i> (Potonié, 1931) Potonié, Thomson and Thiergart, 1950 ex Potonié, 1960 + <i>Q. henricii</i> (Potonié, 1931) Potonié, Thomson and Thiergart, 1950 ex Potonié, 1960	Fagaceae: Quercoideae	P2/A1	11	12
<i>Quercopollenites</i> sp.	Fagaceae: <i>Quercus</i> Linnaeus, 1753	P2/A1	1	
<i>Parthenopollenites formosus</i> (Mamczar, 1960) Worobiec in Stuchlik et al., 2014	Vitaceae	P/A1	4	4
<i>Platanipollis ipelensis</i> (Pacltová, 1966) Grabowska in Ziemińska-Tworzydło et al., 1994	Platanaceae: <i>Platanus</i> Linnaeus, 1753	P/A1	1	
<i>Platycaryapollenites</i> sp.	Juglandaceae: <i>Platycarya</i> Siebold and Zuccarini, 1843	P2/A1		1
<i>Polyatriopollenites</i> sp.	Juglandaceae: <i>Pterocarya</i> Kunth, 1824	A1	7	7
<i>Reevesiapollis triangulus</i> (Mamczar, 1960) Krutzsch, 1970	Malvaceae: <i>Reevesia</i> Lindley, 1827	P	1	
<i>Salixipollenites</i> sp.	Salicaceae: <i>Salix</i> Linnaeus, 1753	A	2	3
<i>Sapotaceoidaepollenites</i> sp.	Sapotaceae	P	4	4
<i>Styraxipollis</i> sp.	Styracaceae: <i>Styrax</i> Linnaeus, 1753	P/A1	4	
<i>Symplocoipollenites</i> sp.	Symplocaceae: <i>Symplocos</i> Jacquin, 1760	P	1	
<i>Tricolporopollenites fallax</i> (Potonié, 1934) Krutzsch in Krutzsch et al., 1960 + <i>T. liblarensis</i> (Thomson in Potonié et al., 1950) Hochuli, 1978 + <i>T. quisqualis</i> (Potonié, 1934) Krutzsch, 1954	Fabaceae	P/A	13	85
<i>Tricolporopollenites pseudocingulum</i> (Potonié, 1931) Thomson and Pflug, 1953	?Fagaceae, ?Styracaceae	P/A1	3	1
<i>Tricolporopollenites spinus</i> Krutzsch, 1962	unknown	P	2	
<i>Tricolporopollenites staresedloensis</i> Krutzsch and Pacltová in Krutzsch, 1969	Hamamelidaceae: <i>Parrotia</i> Meyer, 1831, <i>Distylium</i> Siebold and Zuccarini, 1841	P2	11	7
<i>Tricolporopollenites theacoides</i> (Roche and Schuler, 1976) Kohlman-Adamska and Ziemińska-Tworzydło, 2000	Theaceae	P	1	

Fossil taxa	Botanical affinity	Element	Sample 1	Sample 2
<i>Tricolporopollenites villensis</i> (Thomson in Potonié et al., 1950) Thomson and Pflug, 1953 + <i>T. dolium</i> (Potonié, 1931) Thomson and Pflug, 1953	?Fagaceae	unknown	34	13
<i>Tricolporopollenites</i> sp.	?Fagaceae	P/A	3	1
<i>Trivestibulopollenites betuloides</i> Pflug in Thomson and Pflug, 1953	Betulaceae: <i>Betula</i> Linnaeus, 1753	A	1	7
<i>Ulmipollenites undulosus</i> Wolff, 1934	Ulmaceae: <i>Ulmus</i> Linnaeus, 1753	A	2	1
<i>Vitispollenites tener</i> Thiele-Pfeiffer, 1980	Vitaceae: <i>Vitis</i> Linnaeus, 1753	P2/A1	5	4
Other pollen grains	unknown	unknown	9	8
Sum of spores and pollen grains			1027	1019
Selected non-pollen palynomorphs and palynoclads				
<i>Botryococcus braunii</i> Kützing, 1849	Dictyosphaeriaceae: <i>Botryococcus braunii</i> Kützing, 1849	×	5	3
<i>Diagonalites diagonalis</i> Krutzsch and Pacltová, 1990	Zygnemataceae: <i>Mougeotia laetevirens</i> (Braun 1855) Wittrock, 1877 type	×		1
<i>Ovoidites elongatus</i> (Hunger, 1952) Krutzsch, 1959 + <i>O. grandis</i> (Pocock, 1962) Zippi, 1998	Zygnemataceae: <i>Spirogyra</i> Link in Nees, 1820	×	1	1
?fragment of microsporangium	?Salviniaceae: <i>Salvinia</i> Séguier, 1754	×		1
Leaf-spines	Ceratophyllaceae: <i>Ceratophyllum</i> Linnaeus, 1754	×		3
Spores of fungi	fungi	×	2	1
Total			1035	1029

Hamamelidaceae: *Tricolporopollenites staresedloensis* Krutzsch and Pacltová, 1969); Juglandaceae; Mastixiaceae: *Cornaceapollis satzveyensis* (Pflug, 1953) Ziemińska-Tworzydło, 1994; Sapotaceae and Vitaceae are also common. In addition, pollen grains of the families Aquifoliaceae: *Ilexpollenites margaritatus* (Potonié, 1931) Thiergart, 1938; Ericaceae; Meliaceae; Nyssaceae: *Nyssapollenites contortus* (Pflug and Thomson, 1953) Nagy, 1985; Oleaceae; Salicaceae; Tilioidae: mainly *Intratrisporopollenites insculptus* Mai, 1961; Sapindaceae: *Aceripollenites* Nagy, 1969; Ulmaceae, and others are present.

Cryptogams are represented mainly by ferns from the families Lygodiaceae, Osmundaceae, Pteridaceae, Schizaeaceae, and others, plus a few spores of Lycopodiaceae and Selaginellaceae. Among non-pollen palynomorphs, freshwater algae (*Botryococcus* Kützing, 1849 and zygospores of Zygnemataceae) are present. Spores of fungi are almost absent. In addition, some leaf-spines of plants with submerged leaves (Alismataceae, Hydrocharitaceae vel *Ceratophyllum* Linnaeus, 1754) and probably a fragment of a microsporangium of *Salvinia* Séguier, 1754, were encountered.

Discussion

Taphonomy and vegetation reconstruction.—In view of the lithology of the fossiliferous layer and preservation of the plant remains, as well as composition of the plant assemblage, we can interpret the sedimentary environment as calm, and most probably related to a small water body (maar lake?). This is confirmed by the presence of *Botryococcus* algae and zygospores of Zygnemataceae (*Spirogyra* Link, 1820, and *Mougeotia* Agardh, 1824). Extant representatives

of Zygnemataceae occur in shallow, stagnant waters, which warm up easily, and these algae produce resting cells (e.g., zygospores) that enable them to survive through unfavourable growth conditions, e.g., desiccation (Worobiec 2014 and literature cited therein). The presence of leaf-spines of plants with submerged leaves also points to the occurrence of submerged (entirely under water) aquatic plants, such as Hydrocharitaceae or *Ceratophyllum* commonly found in ponds, marshes, and quiet streams. Remains of the water fern *Salvinia* are another example of floating aquatics growing in standing waters.

Well-preserved leaves and sparse flowers suggest that the plant remains were carried by wind and water only over a short distance and originated from vegetation surrounding the basin (see e.g., Ferguson 1985).

Based on the floristic composition of the Rębiszów fossil assemblage we can distinguish three types of vegetation. The vast majority of the fossil remains represents plants of the mesophytic forest around the sedimentary basin. The angiosperm elements of this vegetation are as follows (arranged according to frequency): *Majanthemophyllum basinerve* (Rossmässler, 1840) Knobloch and Kvaček, 1996, *Daphnogene cinnamomifolia* (Brongniart, 1822) Unger, 1851, *Liriodendron haueri* Ettingshausen, 1869; Fagaceae (*Trigonobalanopsis* cf. “*Quercus*” *bavarica*), *Craigia brononii* (Unger, 1845) Kvaček, Bůžek, and Manchester, 1991, *Sloanea artocarpites* (Ettingshausen, 1869) Kvaček and Hably, 2001, *Ostrya* sp., *Acer* sp. div, *Mahonia* sp., cf. *Laurophyllum acutimontanum* Mai, 1963, cf. *Leguminosites* sp. or cf. *Rhodomyrtophyllum* sp., and cf. *Rosa lignitum* Heer, 1869. Conifers, especially *Calocedrus* Kurz, 1873, but also *Cunninghamia* Brown, 1826, *Cryptomeria* Don, 1838, and *Tsuga* (Endlicher, 1847) Carrière, 1855, were also import-

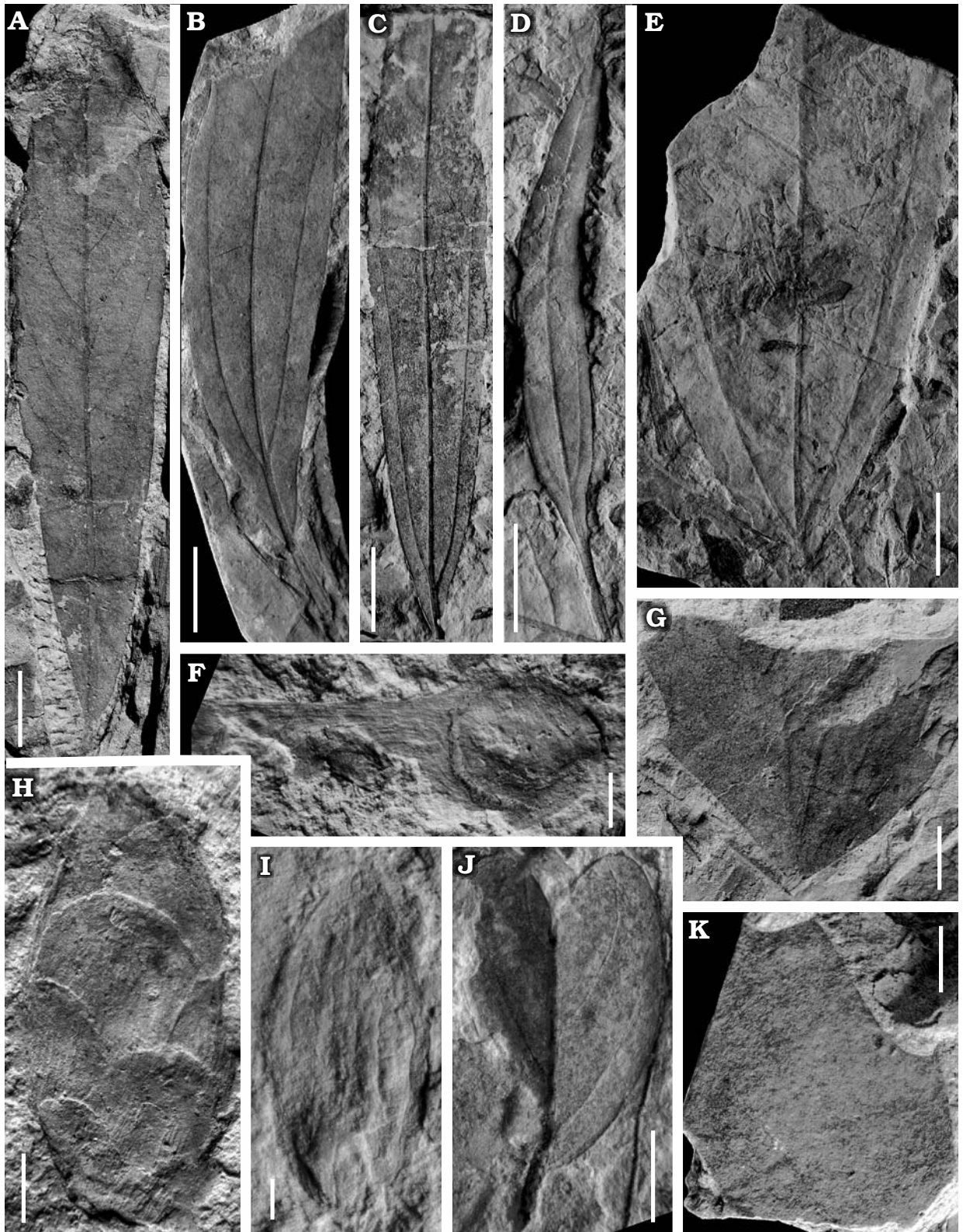


Fig. 4. Angiosperms impressions from Lysa Góra near Rębiszów, Poland, late Oligocene. **A.** cf. *Laurophyllum acutimontanum* Mai, 1963, leaf, KRAM-P 128/436. **B–D.** *Daphnogene cinnamomifolia* (Brongniart, 1822) Unger, 1850 forma *lanceolata* sensu Kvaček and Walther (1995), leaves. **B.** KRAM-P 128/131. **C.** KRAM-P 128/397. **D.** KRAM-P 128/298. **E.** *Daphnogene cinnamomifolia* (Brongniart, 1822) Unger, 1850 forma *cinnamomifolia* sensu Kvaček and Walther (1995), KRAM-P 128/256, leaf. **F.** *Acer* cf. *polymorphoides* Mai, 1987, KRAM-P 128/415, fruit. **G.** *Mahonia* sp., KRAM-P 128/35, leaf. **H.** *Tsuga* cf. *moenana* Kirchner, 1935, KRAM-P 128/75, cone. **I.** *Ostrya atlantidis* Unger, 1850, KRAM-P 128/318, fruit. **J.** cf. *Leguminosites* sp. or cf. *Rhodomyrtophyllum* sp., KRAM-P 128/88, leaf. **K.** *Mahonia* sp., KRAM-P 128/291, leaf. Scale bars: A–E, 10 mm; H, G, 5 mm; K, 3 mm; F, H, J, 2.5 mm; I, 1 mm.

ant components of the Oligocene vegetation of Rębiszów. The tree layer of that mesophytic forest can probably be subdivided into the upper (canopy) and lower tree layer (understory). Based on their modern habits, we can infer that the upper canopy was composed of *Cunninghamia*, *Cryptomeria*, *Liriodendron* Linnaeus, 1753, Fagaceae, and *Sloanea* Linnaeus, 1753, whereas in the understory, trees and shrubs such as *Calocedrus*, *Daphnogene* Unger, 1850, *Craigia* Smith and Evans, 1921, *Ostrya* Scopoli, 1760, *Acer* Linnaeus, 1753, *Laurophyllum* Goeppert, 1853, *Mahonia* Nuttall, 1818, and probably *Rosa* Linnaeus, 1753 may have occurred. Lianas are modestly represented by a single leaf of *Vitis* Linnaeus, 1753 or *Ampelopsis* Michaux, 1803 and one seed impression of *Ampelopsis* cf. *rotundata* Chandler, 1925. Some authors suggest that *Majanthemophyllum* Weber, 1852, which is a dominant element in the Rębiszów fossil assemblage, could be a climber (Walther 1999), but this assumption lacks conclusive evidence. Palynological analysis supports the results obtained from the investigations of plant macroremains. Many fossil taxa from the spore-pollen assemblage have their counterparts in macroremains. In addition, based on the palynoflora, several elements could be added or some details could be provided. For example, we could add to the list of taxa: *Fagus* Linnaeus, 1753, Mastixiaceae, and Sapotaceae. Fossil macroremains of the herbaceous layer have not been found. Similarly, palynological analysis shows almost exclusively pollen of trees and shrubs. On the other hand, various spores of cryptogams, including ferns and lycopods, have been recorded. These cryptogams could be elements of the forests' herbaceous layer, or it is probable that they grew on the lake margin.

Riparian taxa were probably confined on the shore of the water body and were not so abundant. The main component among the riparian taxa was probably *Alnus* Miller, 1754, presumably accompanied by *Craigia*, *Ulmus* Linnaeus, 1753, *Acer*, *Populus* Linnaeus, 1753, and *Vitis* vel *Ampelopsis*. Palynological analysis also revealed the presence of *Carya* Nuttall, 1818, *Fraxinus* Linnaeus, 1753, *Pterocarya* Kunth, 1824, and *Salix* Linnaeus, 1753. Presumably, also *Daphnogene cinnamomifolia* may have played a part, as it was suggested that it might tolerate riparian conditions (Kvaček and Walther 1998). On the other hand, according to Mai and Walther (1991) *Populus zaddachii* Heer, 1859 might be a component of a mesophytic forest as well. Species typical for swamp communities were not found among the macroremains from Rębiszów. However, as in both palynological samples taken from Rębiszów, pollen grains of *Taxodium*/*Glyptostrobus* type prevail, and we could not exclude the presence of swamp communities in the vicinity. The absence of swamp plant macroremains in this fossil assemblage reflect the absence or scarcity of temporarily inundated areas around the basin. Besides, this could also be related with the fact that volcanic floras typically represent the mesophytic climax vegetation (Walther 2005; Akhmetiev et al. 2009). Thus, the results of palynological analysis increased our

knowledge on the diversity of plant communities occurring in the Rębiszów area during the Oligocene.

Moreover, the experience derived from the autecology of modern relatives of fossil plants shows that many extant species thrive in a relatively wide range of habitats (Reed 1988). Therefore, we believe that the majority of those species found in Rębiszów were not confined to one particular vegetation type (compare Worobiec and Szykiewicz 2016), but we could contend that, generally, it was of mixed mesophytic forest type.

Palaeoclimate.—The composition of the assemblage of plant macroremains from Rębiszów, especially the presence of representatives of genera *Calocedrus* Kurz, 1873, *Craigia* Smith and Evans, 1921, *Cunninghamia* R. Brown, 1826, *Daphnogene* Unger, 1850, *Laurophyllum* Goeppert, 1853, *Sloanea* Linnaeus, 1753, and *Trigonobalanopsis* Kvaček and Walther, 1988 points to subtropical (sensu Belda et al. 2014) climatic conditions in this part of the Oligocene in Lower Silesia. Recent counterparts of Rębiszów vegetation could be found in the Mixed Mesophytic Forests of China (Wang 1961).

Composition of spore-pollen spectra (domination of palaeotropical and palaeotropical/warm-temperate elements) also points to warm, subtropical climatic conditions.

Comparison between the Rębiszów flora and Central European Oligocene floras and age evaluation.—Taxonomic composition clearly links the Rębiszów flora with the late Paleogene, so-called volcanic floras from the neighboring regions of the Czech Republic and SE Germany (Kvaček and Walther 2001, 2004; Walther 2005; Akhmetiev et al. 2009). With only 43 taxa, it is relatively poorly diversified in relation to other coeval fossil floras. Comparing the composition of the Rębiszów flora and some Oligocene floras from Kundratice, Seifhennersdorf, Markvartice, Suletice-Berand, and Kleinsaubernitz, several common elements can be indicated: *Daphnogene cinnamomifolia* forma *lanceolata* Kvaček and Walther, 1995, *D. cinnamomifolia* forma *cinnamomifolia* Kvaček and Walther, 1995, *Laurophyllum acutimontanum* Mai, 1963, *Craigia bronni* (Unger, 1845) Kvaček, Bůžek, and Manchester, 1991, *Sloanea artocarpites* (Ettingshausen, 1869) Kvaček and Hably, 2001 (Kvaček and Walther 2001). Also, *Rosa lignitum* Heer, 1869, *Populus zaddachii* Heer, 1859, and *Liriodendron haueri* Ettingshausen, 1869 quite often occur in those floras. However, *Mahonia* Nuttall, 1818 is relatively sparse and has been documented only in some sites, including early Oligocene of Bechlejovice (Kvaček and Walther 2004) and late Oligocene of Suletice-Berand (Kvaček and Walther 1995). One of the characteristic features of the Rębiszów flora is an abundance of *Calocedrus suleticensis* (Brabenec, 1909) Kvaček, 1999, which has been reported so far only from the late Oligocene of Matřý, near Sebužín (Kvaček et al. 2018) and the early Oligocene of Holý Kluk (Radoń et al. 2006) both Czechia, the early Miocene of Kymi, Greece (Kvaček 1999), the early Oligocene of Eger-Kiseged, Hungary (Kvaček

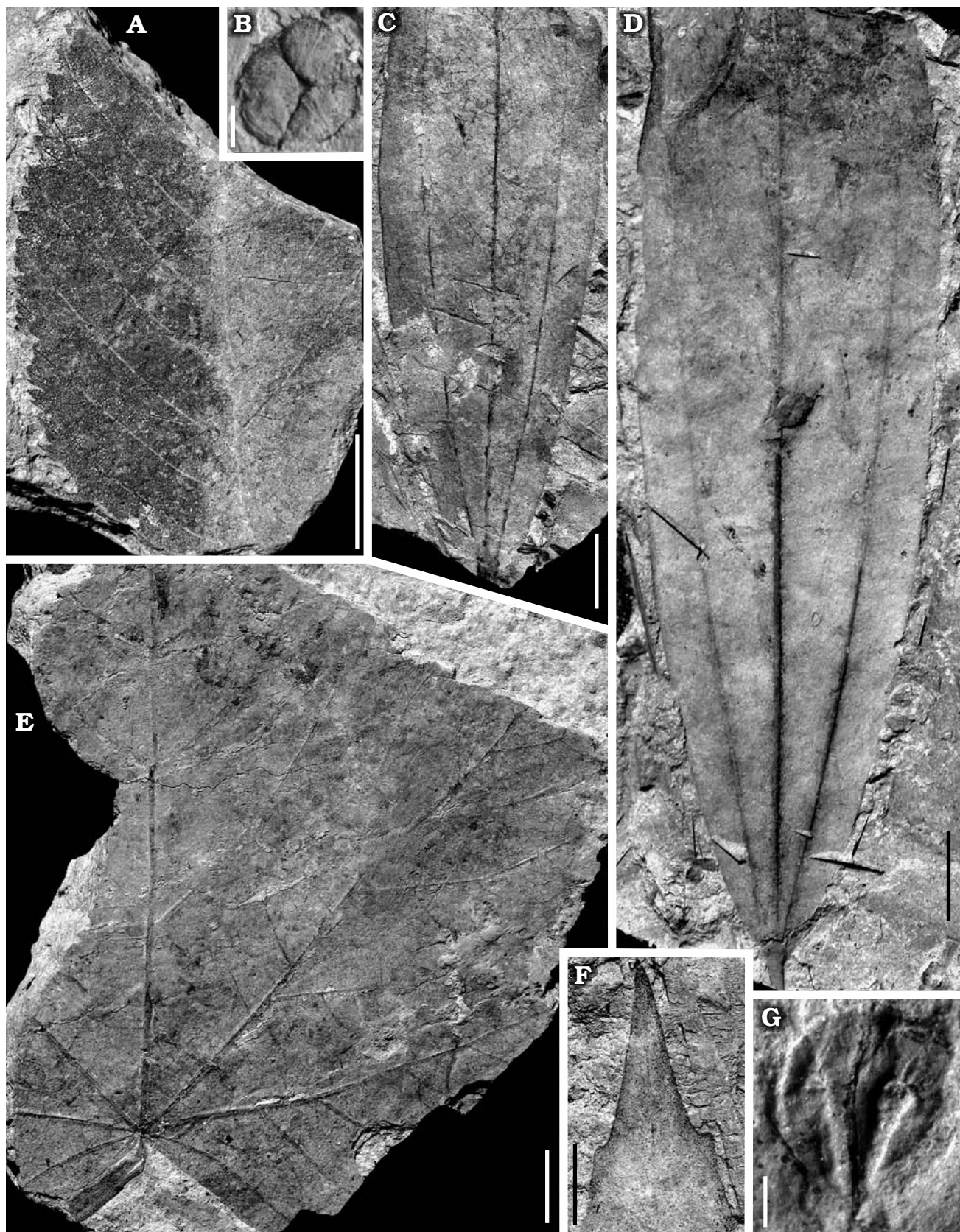


Fig. 5. Angiosperms impressions from Lysa Góra near Rębiszów, Poland, late Oligocene. **A.** *Carpinus* sp. vel *Ostrya* sp., KRAM-P 128/546, leaf. **B.** *Paliurus favonii* Unger, 1847, KRAM-P 128/165, fruit. **C, D, F.** *Majanthemophyllum basinerve* (Rossmässler, 1840) Knobloch and Kvaček, 1996, leaves. **C.** KRAM-P 128/571. **D.** KRAM-P 128/289. **F.** KRAM-P 128/212. **E.** *Vitis* sp. or *Ampelopsis* sp., KRAM-P 128/205, leaf. **G.** *Ampelopsis* cf. *rotundata* Chandler, 1925, KRAM-P 128/109, seed. Scale bars: A, C–F, 10 mm; B, G, 1 mm.

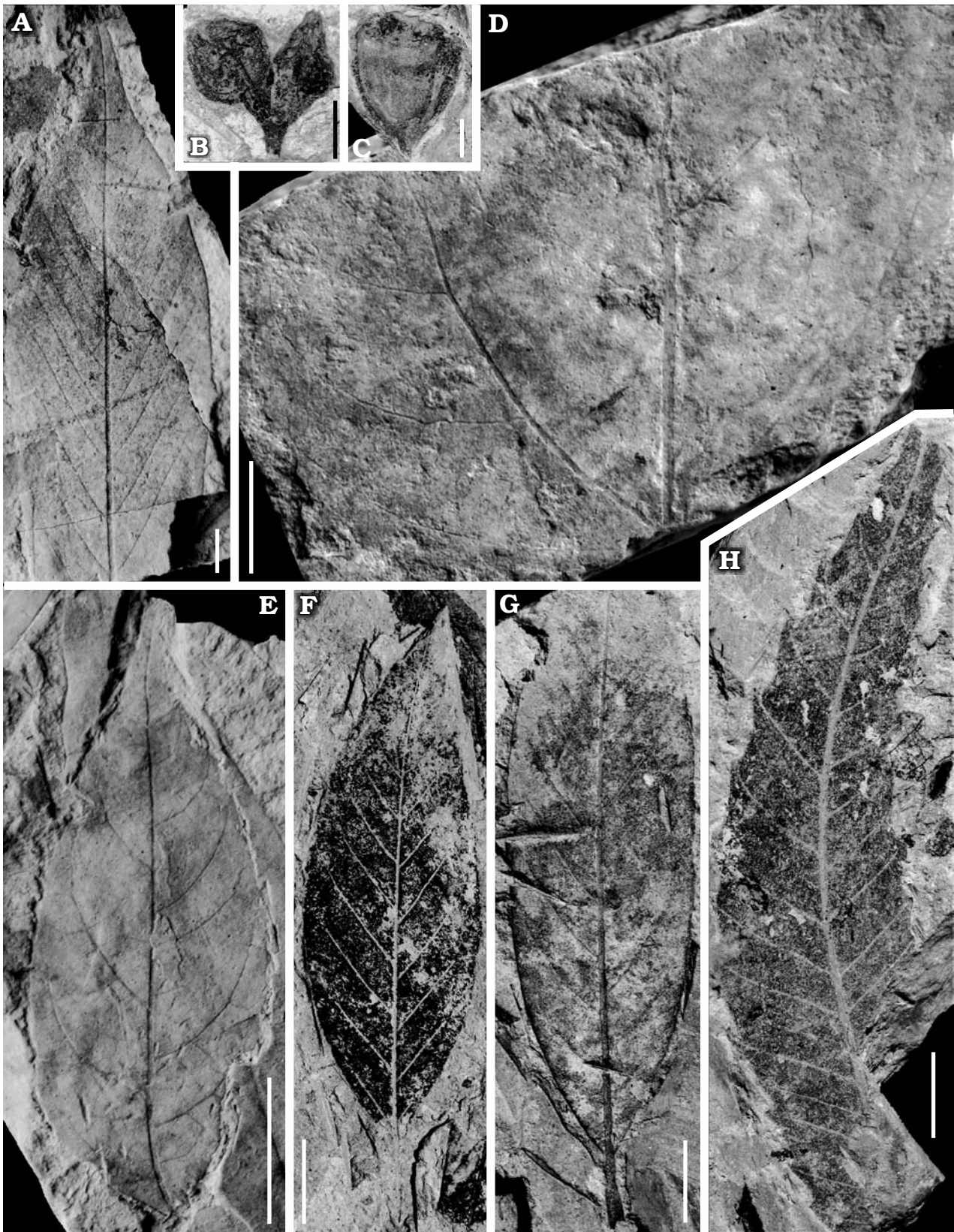


Fig. 6. Angiosperms impressions from Lysa Góra near Rebiszów, Poland, late Oligocene. **A.** cf. *Trigonobalanopsis rhamnoides* (Rossmässler, 1849) Walther and Kvaček, 1988, KRAM-P 128/305, leaf. **B.** *Trigonobalanopsis exacantha* (Mai, 1970) Kvaček and Walther, 1988, KRAM-P 128/185, cupules. **C.** *Quercus* sp. or *Castanopsis* sp., KRAM-P 128/313, fruit. **D.** *Populus* cf. *zaddachii* Heer, 1959, KRAM-P 128/511, leaf. **E.** *Sloanea artocarpites* (Ettingshausen, 1869) Kvaček and Hably, 2001, KRAM-P 128/433, leaf. **F., G.** cf. "*Quercus*" *bavarica* Knobloch and Kvaček, 2004, leaves. **F.** KRAM-P 128/79. **G.** KRAM-P 128/212. **H.** *Eotrigonobalanus furcinervis* (Rossmässler, 1840) Walther and Kvaček, 1989, KRAM-P 128/234, leaf. Scale bars: A–C, 5 mm; D–H, 10 mm.

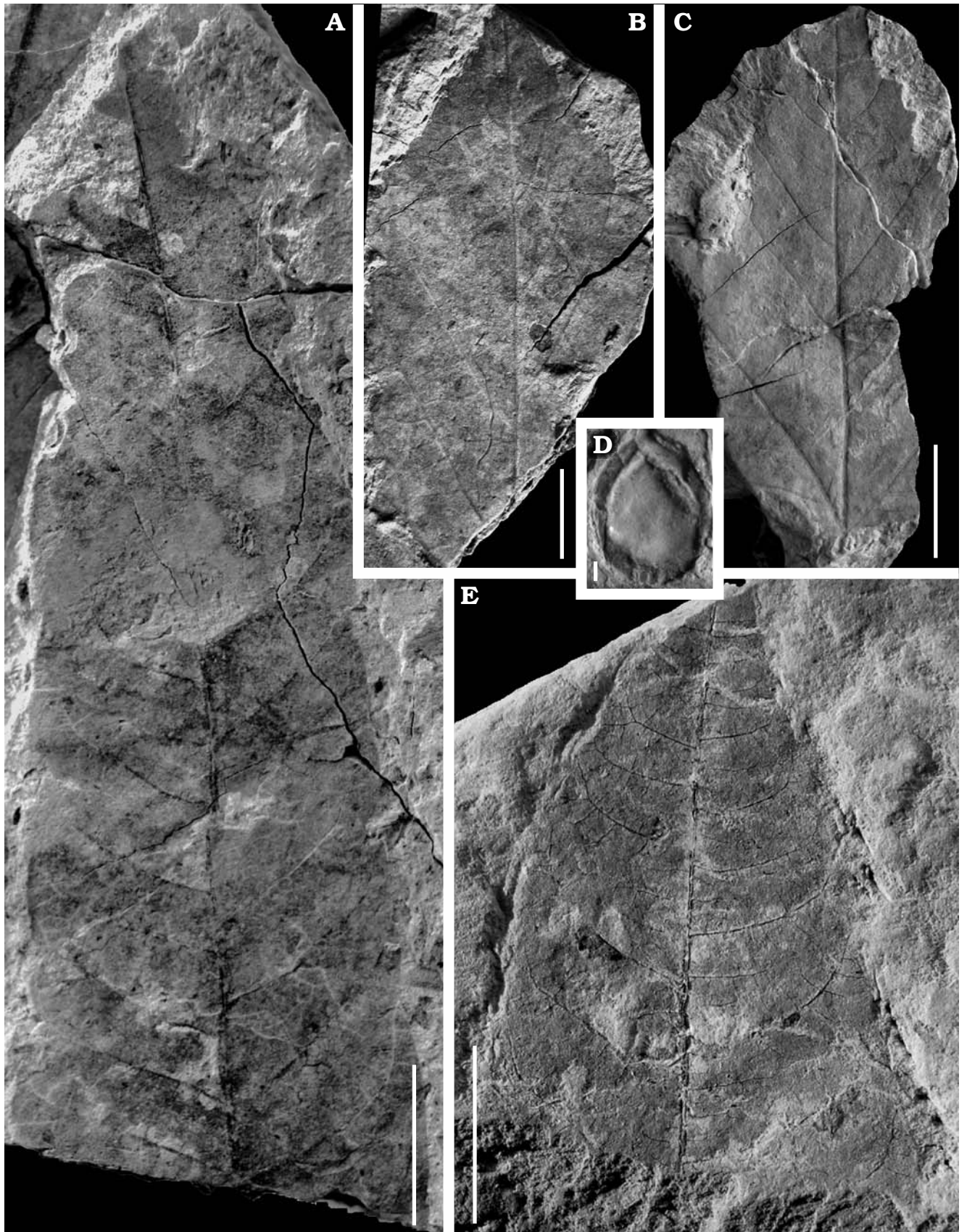


Fig. 7. Angiosperms impressions from Łysa Góra near Rębiszów, Poland, late Oligocene. **A**, **E**. cf. *Cedrela macrophylla* Andreánszky, 1955, leaves. **A**. KRAM-P 128/570. **E**. KRAM-P 128/516. **B**. *Alnus* cf. *gaudinii* (Heer, 1856) Knobloch and Kvaček, 1976, KRAM-P 128/390, leaf. **C**. cf. *Acer tricuspidatum* Bronn, 1838, KRAM-P 128/388, leaf. **D**. *Prunus* cf. *scharfii* Gregor, 1978, KRAM-P 128/352, endocarp. Scale bars: A–C, E, 10 mm; D, 1 mm.

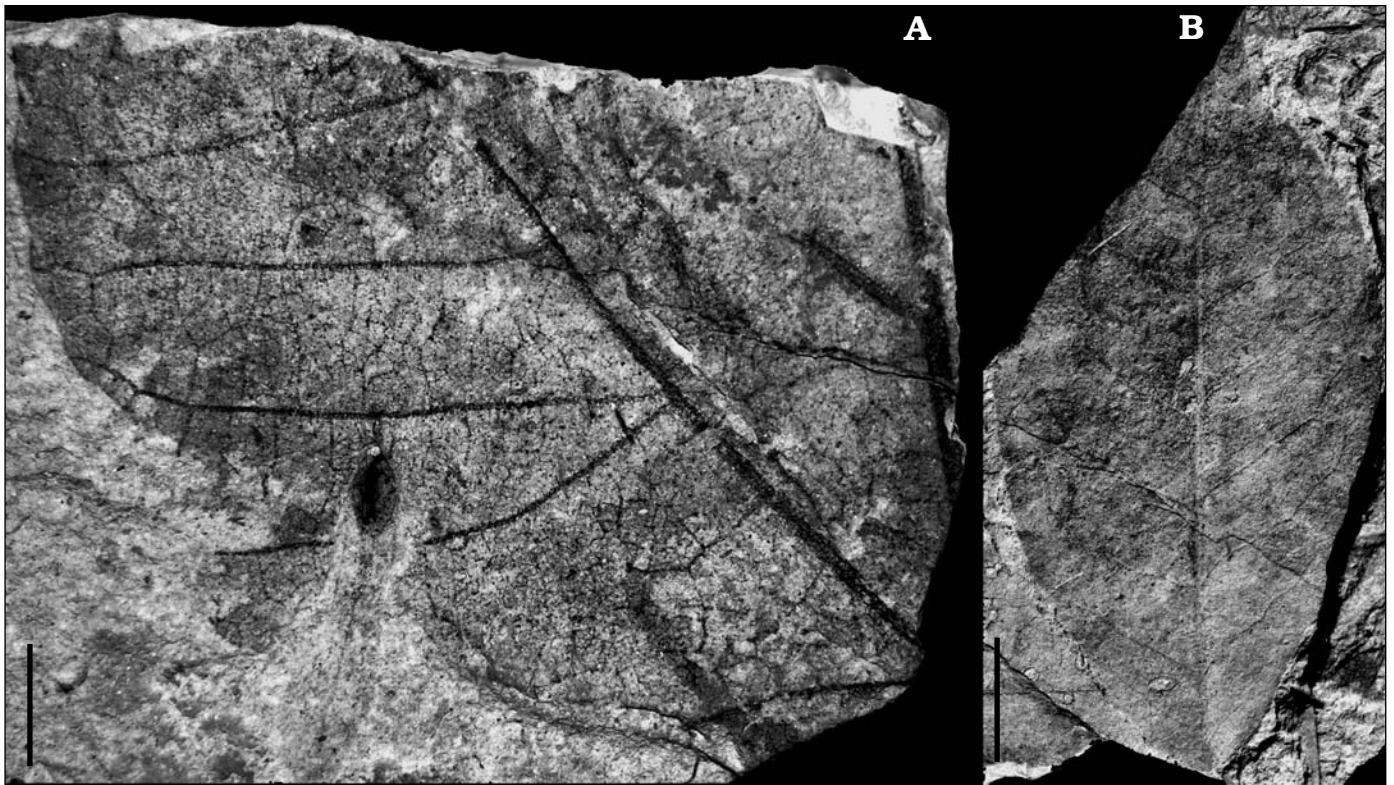


Fig. 8. Angiosperms impressions from Łysa Góra near Rębiszów, Poland, late Oligocene. A. *Dombeyopsis lobata* Unger, 1850, KRAM-P 128/462, leaf. B. cf. *Rosa lignitum* Heer, 1869, KRAM-P 128/401, leaf. Scale bars 5 mm.

and Hably 1998), and the late Oligocene of Suletice-Berand (Kvaček and Walther 1995). The occurrence of *C. suleticensis* is rather important. According to Kvaček and Walther (1998, 2001), it starts to appear in early/late Oligocene floras of the Nerchau-Flörsheim floristic complex. The domination of *Majanthemophyllum basinerve* (Rossmässler, 1840) Knobloch and Kvaček, 1996 in Rębiszów is unique in comparison to other Oligocene volcanic floras. *Majanthemophyllum basinerve* is only sparsely reported from Europe, it is known from the late Eocene (Staré Sedlo; Knobloch et al. 1996), and can provide only a little help in determining the age of the Rębiszów flora.

Considering the comparison mentioned above, the Rębiszów flora shows the closest relations only with some Oligocene floras. The high proportion of the laurophyllous element, and especially the presence of *Calocedrus suleticensis*, links the Rębiszów flora with early/late Oligocene floras of the Nerchau-Flörsheim floristic complex (especially Suletice) (Bůžek et al. 1976; Kvaček and Walther 1995, 1998, 2001). On the other hand, *Majanthemophyllum basinerve* has not been reported in floras of the Nerchau-Flörsheim floristic complex.

The composition of the Rębiszów palynoflora also clearly points to its Oligocene age. Crucial for the stratigraphic position of the studied flora is the presence of indicative taxa, such as *Boehlensipollis hohli* Krutzsch, 1962 (recorded in our samples and in the previous unpublished results by Kohlman-Adamska and Ziemińska-Tworzydło) and *Cupa-*

neidites eucalyptoides Krutzsch, 1962 (unpublished results reported by Kohlman-Adamska and Ziemińska-Tworzydło, announced here with permission of the authors). The ranges of these taxa are confined to the Rupelian–Eochattian (Krutzsch et al. 1992) or the Rupelian–early Chattian (Grabowska and Słodkowska 2003). The Rupelian has relatively rich palynological documentation due to the presence of lignites of the 5th Czempień group of seams in the Polish Lowlands (Słodkowska 2004; Kasiński and Słodkowska 2016). In contrast, the Chattian palynofloras are very rare (Grabowska and Piwocki 1975). The Rębiszów spore-pollen assemblage is generally similar to the palynofloras from the 5th Czempień seam (Kasiński and Słodkowska 2016). Nevertheless, the lack of some “older” taxa (for example *Aglaoreidia cyclops* Erdtman, 1960, and *Cicatricosisporites dorogensis* Potonié and Gelletich, 1933), and the presence of some “new” elements (for example *Faguspollenites* Raatz, 1937) rather point to the early Chattian age of the Rębiszów assemblage.

The Rębiszów flora is the first volcanic flora found in Poland and second Oligocene macroflora known from Poland. The Oligocene macroremain assemblage found in the marine Jasło limestone at Sobniów, southern Poland, consists of only 36 specimens of plant macroremains, including a few leaves (or leaflets) of dicotyledons (*?Palaeocarya* sp., *Laurophyllum princeps* (Heer, 1856) Krausel and Weyland, 1951, Theaceae, and Leguminosae (“*Leguminosentypus*”) type sensu Berger (1955), monocotyledons, and predomi-

nat marine algae remains (Zastawniak and Worobiec 1997). The assemblage from Sobniów (marine deep water limestone deposits), however, represents a sedimentary environment completely different to the Rębiszów flora (shallow, freshwater lake). The Rębiszów flora is definitely richer, better preserved and accompanied by rich palynoflora. The fact that the fossil assemblage from Rębiszów represents the easternmost locality among the known Oligocene volcanic floras of Central Europe makes this site unique and of great value, and complements our knowledge of the Oligocene floras of this part of Europe.

Conclusions

The fossil plant assemblage from Rębiszów is the second Oligocene macroflora known from Poland. The Oligocene age of the deposits from this site is confirmed by the radiometrically dated basalts covering fossiliferous layers (ca. 25 Ma) and the presence of pollen *Boehlensipollis hohli* that constrains the possible age to the Rupelian–Chattian. The lithology, preservation of the plant remains, and the composition of the plant assemblage suggest that the sedimentary environment was calm, and most probably took place in a small and shallow, arguably maar lake. Based on the floristic composition three types of vegetation could be deduced from the Rębiszów flora. Most of the fossil remains represent plants of the mesophytic forest surrounding the sedimentary basin. Riparian vegetation was probably confined to the lake shore. Species typical for swamp communities were not found among macroremains. However, in palynological samples pollen grains of *Taxodium/Glyptostrobus* were found, suggesting the presence of swamp communities probably in a distant neighborhood. The composition of the assemblage of plant macroremains and spore-pollen spectra point to subtropical climatic conditions. Recent counterparts of Rębiszów vegetation could be found in Mixed Mesophytic Forests of China.

In light of the sedimentary environment and floristic composition, it is clear that the Rębiszów flora corresponds to so-called volcanic floras of the early/late Oligocene. Among them, it is closest to floras of the Nerchau-Flörsheim or Kleinsaubernitz floristic complex. When considering the lithology, preservation and floristic composition, Rębiszów shows a close similarity to the early/late Oligocene fossil plant locality, Suletice-Berand (Kvaček and Walther 1995). The Rębiszów flora is the first volcanic flora found in Poland. A conclusive explanation of the position of the basalts in relation to the fossiliferous layers, sedimentary environment of deposits and detailed analysis of the palaeoclimate requires further studies of the Rębiszów floras. Considering the state of preservation of the plant remains and sedimentary environment of the newly found sites described and noted here, they may be productive for additional discoveries of well-preserved plant and animal fossils.

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