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PUTATIVE FOREST GLACIAL REFUGIA IN THE WESTERN AND EASTERN CARPATHIANS

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Abstract. An examination of thermophilous species pollen deposits found in the Plenivistulian river alluvial terraces in the Polish Western Carpathians was conducted. Of the 16 palaeobotanical sites evaluated, most often noted were *Alnus* and *Betula* t. *alba*; *Abies*, *Carpinus* and *Corylus* occurred less frequently, and *Quercus, Tilia* and *Ulmus* were rare. *Fagus* and *Fraxinus* pollen were absent. *Abies* and *Carpinus* were relatively overrepresented, because their frequency of occurrence was similar to *Corylus avellana*, i.e. one of the most cold-resistant species. Based on a literature survey of phylogeographic studies and data regarding the forest species *Aconitum moldavicum, A. variegatum, Bromus benekenii, Carpinus betulus, Lathyrus vernus, Lonicera nigra*, and the moderately thermophilous *Rosa pendulina*, 47 cryptic refugial areas of temperate plant species are postulated. The combined analysis indicates that they could have survived the last glaciation in the W & E Carpathian microrefugia close to 650 m a.s.l., and in Podolia (north of the Eastern Carpathians) along a contour of 300 m a.s.l.

Key words: Carpathian Mountains, forest cryptic refugia, LGM, phylogeography, Plenivistulian, pollen analysis

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Introduction

The Plenivistulian in West Europe was characterized by the development of treeless landscape and prevalence of the tundra type plant vegetation. In Central and East Europe, climate had becoming more continental and in consequence tundra gradually turned into forest-tundra with patches of the boreal trees as *Larix, Betula nana, Picea abies, Pinus cembra* (Mamakowa 2003). Their existence in the Plenivistulian, including full-glacial, is evidenced not only by pollen records, but also by macrofossil wood charcoal assemblages indicative at least 17 different taxa (Willis & van Andel 2004). Most of them belong to the boreal group represented by e.g. *Pinus, Picea* and *Larix*, however thermophilous species, for example *Alnus, Betula, Salix*, and even *Carpinus*, were also found. The Lower Plenivistulian (75-58 ky BP) was cold and the Carpathian forelands were devoid of a continuous plant cover and covered by the periglacial tundra. The Middle Plenivistulian (Interpleniglacial 58-28/25 ky BP) was characterized by several cold and warm climate oscillations, with the most pronounced the Denekamp interstadial. The most severe climatic conditions were during the Upper Plenivistulian (full glacial, LGM), dated to 23-17 ky BP (Gębica 2004).

The occurrence of diversified flora and vegetation in the Polish Western Carpathians and their forelands in the Late Glacial and Early Holocene were related to the areal variety of geomorphological processes and sediments (Starkel 1988). In the periglacial zone an open tundra, forest tundra and steppe-tundra developed. The crucial for the thriving of the thermophilous elements was Younger Dryas (10.7-10.0 ky BP). At that time dense *Pine-Betula* forest developed in the Bølling phase (13.7-13.5 ky BP) turned into an opened-forested vegetation. Probably, at that time the thermophilous elements found shelter sites in the intermountain valleys and southern-facing slopes in the lower Carpathian zone. Accordingly, a mosaic of vegetation, similar to that observed up to the present-day in the central-Mongolian mountains at southern limits of the forest and permafrost (Kowalkowski & Starkel 1984), as well on the hills in Scania during the late Vistulian

Table 1. Pollen profiles dated to Plenivistulian with broadled trees + coniferous *Abies* and some herbaceous species noted in the Polish Western Carpathians. Sources of information: **1** – Niedziałkowska & Szczepanek (1993-1994); **2** – Niedziałkowska *et al.* (1985); **3** – Gilot *et al.* (1982); **4** – Koperowa & Środoń (1965); **5** – Mamakowa & Rutkowski (1989); **6** – Środoń (1987); **7** – Mamakowa & Środoń (1977); **8** – Gębica *et al.* (1998); **9** – Środoń (1968); **10** – Mamakowa & Starkel (1974); **11** – Mamakowa *et al.* (1997).

no.	Locality	C-dating/ Phase*	Alt. [m]	N	E	*Abies*	*Alnus*	*Betula 'alba'*	*Carpinus*	*Corylus*	*Quercus*	*Tilia*	*Ulmus*	*Armeria*	*Filipendula*	*Frangula*	*Geranium*	*Sanguisorba*	*Melandrium*	*Valeriana*	*Veratrum*	Type of vegetation	Source
1	Pierściec 1	36-29 ka BP D/uP	265	49 51	18 48		+	+	+	+	+											Steppe-tundra/tundra/ forest-tundra	1
2	Chybie 2	25-17 ka BP uP	255	49 54	18 48	+	+	+	+	+			+									tundra	1
3	Chybie 1	>41 ka BP lmP	260	49 53	18 52	+	+	+	+													tundra	2
4	Kaniów	<39-27 ka BP lmP-uP	245	49 57	19 03	+	+	+	+	+	+	+	+		+							tundra/forest-tundra	3
5	Zator	<40 ka BP lmP	235	49 59	19 26		+							f	+	+	+		+	+	+	wet tundra	4
6	Orawka	n.d D	637	49 30	19 43	+?	+	+?	+?	+?	+?	+?	+?	+								tundra/forest tundra	9
7	Ściejowice	38-23 ka BP D-uP	203	50 00	19 47	+	+	+	+	+				+								tundra	5
8	Myślenice	n.d. D	300	49 50	19 56		+	+		+	+											forest-tundra	6
9	Kryspinów	32 ka BP D	230	50 02	19 47			+						+								steppe-tundra/ tundra	5
10	Sadowie	30 ka BP D	280	50 10	20 03		+			+					+					+		wet tundra	6
11	Nowa Huta	28-18 ka BP D/uP	222	50 04	20 07	+?	+	+	+?	+?			+?	+				+				sedge-grass swamps/wet tundra	7
12	Dobra k. Limanowej	33 ka BP D	470	49 43	20 16	+	f	f				+		+	+	+	+		+			tundra/forest-tundra	9

13	Brzesko Nowe	33-28 ka BP D	185	50 07	20 23	+	+	+	+	+										tundra/forest-tundra/wet meadows	8
14	Sowliny	30 ka BP D	410	49 43	20 24	+	+						f							tundra/forest-tundra/ steppe tundra	6
15	Wola Żyrakowska	35-21 ka BP D-uP	185	50 06	21 24	+	+						+	+			+		+	moss-sedge-grass swamps/ wet meadows/steppe like grasslands	11
16	Brzeźnica B	48-36 ka BP lmP	202	50 05	21 27	+								+			+		+	moss-sedge-grass swamps/ wet meadows/steppe-tundra	10

* **D** – Denekamp; **lmP** – Lower-Middle Plenivistulian; **uP** – Upper Plenivistulian; **ka** – calendar dates in millennia based on calibrated ^{14}C data; **f** – macrofossil; **n.d.** – not determined; **?** – probably rebedded.

(Berglund & Rapp 1988), could have existed in the lower situations of the Polish W Carpathians and foreland.

The aim of the present paper is to characterize the Plenivistulian localities in the Western Carpathians based on the palinological records. At that time in the river alluvial deposits pollen grains of thermophilous tress: *Abies, Alnus, Betula, Carpinus, Fagus, Quercus* and *Ulmus*, were noted. As a rule, their appearance was interpreted as a result of the long-distance pollen transport. However, nobody knows where those localities were, but surely they existed in further or nearer distances from the palaeobotanical locations. On the other hand, charcoals, as direct evidences, and phylogeographical investigations, indirectly, could point to their geographic distribution in the area under interest. Recently, the phylogeographical studies, based mostly on DNA fingerprinting, deliver growing body of information that enabled some synthetic conclusions to be drawn (Ronikier 2011). Thus, the second aim of the paper was to find localities that fulfill the criteria of northerly (Bhagwat & Willis 2008) or cryptic (Stewart & Lister 2001) forest refugia. We concentrated on the Western Carpathians and adjoining areas and on records referred to thermophilous forest taxa. We do not attempt to make some conclusive statements on the full-glacial forest refugia in the West Carpathians; instead we expect that in the effect some areas with high concentration of the putative cryptic forest refugia will be uncover. It could give an additional clue to the solving this exciting problem of modern phytogeography.

Material and methods

A list of the palaeobotanical Plenivistulian localities in the Polish Western Carpathians (Mamakowa 2003) was examined. A checklist comprised putative forest cryptic refugia in the northern Carpathians (W and E Carpathians, including Transcarpathia) and Podolia (north of the Ukrainian E Carpathians) was compiled based on the published and unpublished (Mitka *et al.* in revision) data. The maps were prepared with the use of the GRASS GIS and

QGIS software based on the srtm 90 m digital elevation data (www.srtm.csi.cgiar.org).

Results and discussion

The list of localities with thermophilous, broadleafed trees and one hardwood *Abies alba*, including some mesophilous herbaceous species found in the Plenivistulian in the Polish Western Carpathians are presented in Tab. 1. They are located mostly in valley-bottom terraces of the rivers flowing from the Carpathian's northern slopes to the Sandomierz Basin. Generally, they are built of deposits with a gradual transition from gravels through Dryas silts dated back to the Lower and Middle Plenivistulian. Most of the pollen deposits come from the Denekamp interstadial (c. 32-28 ka BP) and continue to the Upper Plenivistulian (28-14 ka BP). Only a few profiles were dated to the Lower-Middle Plenivistulian (< 36 ka BP). The most common were *Alnus* (15 occurrences) and *Betula* t. *alba* (13), otherwise the most abundant in pollen profiles. *Corylus* (7), *Carpinus* (6) and *Abies* (5) belonged to a moderately occurring species, and *Quercus* (4), *Tilia* (2) and *Ulmus* (2) to the rarest noted. Among the herbaceous species the most common were *Armeria* (8) and *Filipendula* (6). The pollen-based model of the vegetation includes treeless plant communities of the open sites, forest-tundra and sometimes forest-steppe with a mosaic of the moss-sedge-grass swamps and wet meadows. Thermophilous species could have thrived the cold periods in small microenvironmentally favourable locations (microrefugia). They encompass both presumably the long-term and "secondary" refugia (Brewer *et al.* 2002).

Fagus and *Fraxinus* in the Plenivistulian deposits were absent (in Orawka – locality no. 6 in Tab. 1, pollen grains were probably rebedded).

The presented data show that in the whole Plenivistulian patches of termophilous trees in the vicinity of the palaeobotanical sites existed. What interesting, their frequency of occurrence is only partially related to the present day tolerances of minimum growing temperatures (Willis & van Andel 2004). The most resistant are *Betula pendula* and *B. pubescens* (–40°C), *Tilia cordata* (–18°C), *Quercus robur* and *Fraxinus excelsior* (–16°C), *Alnus glutinosa, Corylus avellana* and *Ulmus glabra* (–15°C). The moderately resisistant is *Carpinus betulus* (–8°C), and weakly resistant are *Fagus sylvatica* (–5°C) and *Abies alba* (–3°C). The frequent occurrence of *Betula* and *Alnus* agrees with the thermal resistance of the species. It seems that *Abies* and *Carpinus* are relatively overrepresented, because their frequency is similar to cold resistant species, i.e. *Corylus avellana*. On the other hand, the absence of *Fagus* could be explained by its cold sensitivity, but not in a case of *Fraxinus*, also absent, however being resistant to low temperatures. Also, the frequency of *Quercus, Tilia* and *Ulmus* should be higher, taking into consideration their cold resistance.

The distribution of putative full-glacial refugia of thermophilous forest species and *Rosa pendulina* is displayed on Fig. 1. It is seen that they could have existed on the western and eastern edges of the Western Carpathians and on the western wing of the Eastern Carpathians. Most of them were placed in close proximity to a contour of 650 m. An isolated forest island could have also thrived in Podolia, north of the Eastern Carpathians. The putative Podolian refugium was probably restricted to close proximity of a 300 m a.s.l. contour.

Conclusions

Concluding, the Plenivistulian refugia of some thermophilous species could have existed in the in the Western and Eastern Carpathians, including Podolia. Their distribution was inferred from the phylogeographical studies with the use of various genetic (cpDNA, AFLP, ISSR) and cytogenetic (chromosome Giemsa C-band staining) markers, and also pollen and macrofossil charcoal records. This hypothesis is partially validated by the Plenivistulian pollen records. Phylogeographic studies also support an European full-glacial refugial model in the northern-Carpathian context;

Table 2. Putative glacial refugia of thermophilous vegetation in the Northern Carpathians and adjoining areas based on various sources. Sources of information: **1** – Sutkowska *et al.* (2014); **2** – Mitka *et al.* (in revision); **3** – Hajnalová & Hajnalová (2005); **4** – Schiemann *et al.* (2000); **5** – Jasiewiczowa (1980); **6** – Daneck *et al.* (2011); **7** – Fér *et al.* (2007); **8** – Willis & van Andel (2004); **9** – Ilnicki *et al.* (2011); **10** – Mitka *et al.* (2013). **MAU** – Małopolska Upland; **PB** – Pannonian Basin; **PEC** – Polish E Carpathians; **PO** – Podolia; **PWC** – Polish W Carpathians; **SEC** – Slovak E Carpathians; **SWC** – Slovak W Carpathians; **TP** – Transcarpathia; **UEC** – Ukrainian E Carpathian.

no.	Locality	Region	Altitude [m a.s.l]	N	E	Species*	Marker	Source
1	Ojców	MAU	430	50 00	19.00	*A. variegatum*	C-bands	9
2	Barc	PB	120	45 57	17 31	*B. benekenii*	ISSR	1
3	Hidas	PB	200	46 14	18 18	*B. benekenii*	ISSR	1
4	Santovka	PB	210	48 09	18 45	*C. betulus*	AFLP	2
5	Keštolc	PB	350	47 34	18 48	*B. benekenii*	ISSR	1
6	Hajnačka	PB	375	48 12	19 55	*C. betulus*	AFLP	2
7	Gortva	PB	270	48 15	19 57	*C. betulus*	AFLP	2
8	Teply Vrch	SWC	210	48 28	20 05	*C. betulus*	AFLP	2
9	Szabolcs	PB	100	48 10	21 30	*C. betulus*	charcoals	8
10	Różanka	PEC	325	49 55	21 40	*C. betulus*	AFLP	2
11	Strachocina	PEC	365	49 37	22 04	*C. betulus*	AFLP	2
12	Sine Wiry	PEC	710	49 15	22 25	*C. betulus*	AFLP	2
13	Wołosate	PEC	705	49 04	22 40	*B. benekenii*	ISSR	1
14	Tarnawa Wyżna	PEC	670	49 06	22 50	*L. nigra*	pollen	5
15	Monasterzyska	PO	230	48 56	25 01	*C. betulus*	AFLP	2
16	Zarwanica	PO	315	49 14	25 21	*C. betulus*	AFLP	2
17	Jazłowiec	PO	250	48 57	25 26	*C. betulus*	AFLP	2
18	Yabluniv	PO	335	49 07	25 52	*C. betulus*	AFLP	2
19	Tresna	PWC	430	49 43	19 12	*C. betulus*	AFLP	2
20	Sobotnia	PWC	870	49 32	19 15	*B. benekenii*	ISSR	1
21	Obrożyska	PWC	570	49 21	20 52	*C. betulus*	AFLP	2
22	Mt Wysoka	PWC	1050	49.00	20.00	*A. variegatum*	C-bands	9
22a	Mt Wysoka	PWC	1050	49.00	20.00	*A. moldavicum*	ISSR	10
23	Siedliska	PWC	335	49 43	21 00	*C. betulus*	AFLP	2
24	Gilowa Góra	PWC	450	49 50	21 07	*C. betulus*	AFLP	2
25	Vihorlat Mts	SEC	770	48 53	22 06	*L. nigra*	AFLP	6
26	Zboj	SEC	425	49 00	22 06	*C. betulus*	AFLP	2
27	Jalove	SEC	340	49 02	22 14	*C. betulus*	AFLP	2
28	Ruske	SEC	400	49 00	22 24	*C. betulus*	AFLP	2
29	Mokra valley	SWC	450	48 30	17 19	*Acer, Corylus, Fagus, Quercus, Ulmus*	charcoals	3
30	Radošina	SWC	325	48 33	17 55	*Fagus, Fraxinus, Quercus*	charcoals	3
31	Bojnice	SWC	380	48 47	18 34	*Carpinus, Fagus, Fraxinus, Quercus*	charcoals	3
32	Kl'ak	SWC	900	48 59	18 36	*B. benekenii*	ISSR	1

Table 2. Continued.

no.	Locality	Region	Altitude [m a.s.l]	N	E	Species*	Marker	Source
33	Skalka	SWC	1115	48 44	18 59	*L. vernus*	allozymes	4
34	Horne diery	SWC	1060	49 24	19 09	*R. pendulina*	cpDNA	7
35	Kralovany	SWC	450	49 11	19 11	*C. betulus*	AFLP	2
36	Luborec	SWC	350	48 19	19 11	*C. betulus*	AFLP	2
37	Horka-Ondrej	SWC	670	49 01	20 23	*Carpinus*	charcoals	3
38	Monkova dolina	SWC	800	49 26	20 23	*R. pendulina*	cpDNA	7
39	Sucha Bela	SWC	850	48 94	20.39	*R. pendulina*	cpDNA	3
40	Horbok	TP	120	48 18	22 53	*C. betulus*	AFLP	2
41	Mala Uholka	TP	500	48 15	23 37	*C. betulus*	AFLP	2
42	Kuzij	TP	690	47 56	24 07	*C. betulus*	AFLP	2
43	Uzhok Pass	UEC	435	48 57	22 36	*C. betulus*	AFLP	2
44	Kasova Hora	UEC	250	49 13	24 41	*C. betulus*	AFLP	2
45	Mt Petrosul	UEC	1850	48 17	24 47	*R. pendulina*	cpDNA	7
46	Podhorce	UEC	395	49 56	24 59	*C. betulus*	AFLP	2
47	Yaremcha	UEC	644	48 41	24 60	*R. pendulina*	cpDNA	7

however a conclusive statement in this exciting matter has not to be posed yet.

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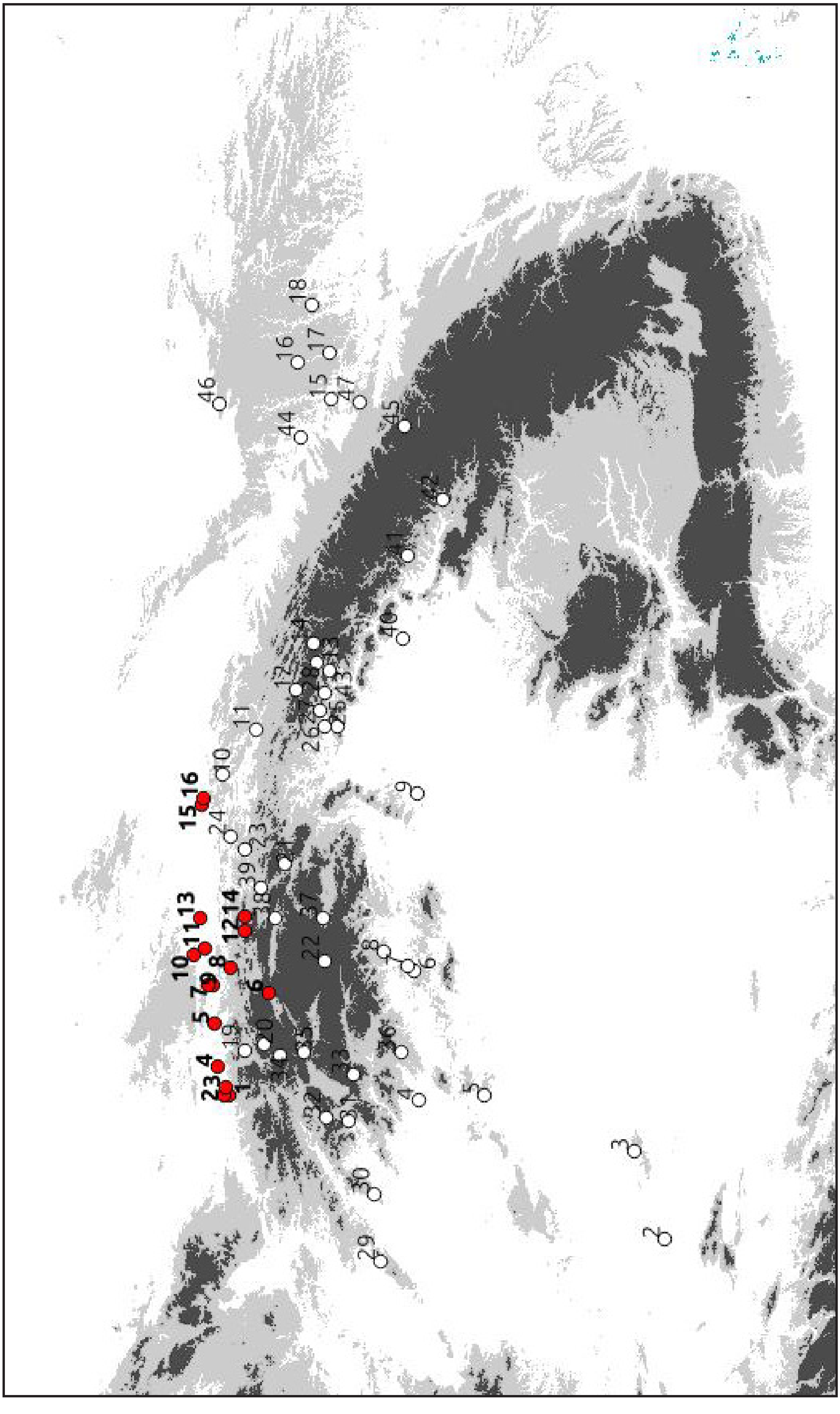

Fig. 1. Localities of the Plenivistulian pollen, micro- and macrofossil deposits in the Polish Western Carpathians and foreland (**dark dots**) and distribution of the putative refugia of the forest species: *Aconitum moldavicum*, *A. variegatum*, *Bromus benekenii*, *Carpinus betulus*, *Lathyrus vernus*, *Lonicera nigra* and moderately thermophilous *Rosa pendulina* in the Western Carpathians, Eastern Carpathians, Transcarpathia and Podolia, based mostly on the phylogeographis studies (**light dots**). The numbers of localities according to those in Tabs. 1 and 2. Two altitudinal belts are marked: in the mountains above 650 m a.s.l., and in the lowlands above 300 m a.s.l.

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