

Orobanche alba subsp. *alba* and subsp. *major* (Orobanchaceae) in Poland: current distribution, taxonomy, plant communities, hosts, and seed micromorphology

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Abstract: The paper presents the current distribution of *Orobanche alba* subsp. *major* and subsp. *alba* in Poland, based on a critical revision of herbarium and literature data as well as results of my field studies. Most of their localities are in south-eastern Poland: in the Małopolska Upland, Lublin Upland, Roztocze Hills, Polesie, Przemyśl Foothills (Pogórze Przemyskie), and Western Bieszczady Mts. These are the northernmost sites known for the species in Central Europe, so the new data extend its distribution range. Maps of distribution of both the subspecies in Poland and of subsp. *major* in Central Europe are included. Additionally, their seed micromorphology was compared using scanning electron microscopy (SEM). The taxonomy, biology, and ecology of both the subspecies of *O. alba* are also discussed.

Key words: *Orobanche alba* subsp. *alba*, *Orobanche alba* subsp. *major*, Orobanchaceae, taxonomy, distribution, phytocoenoses, micromorphology, seeds, Poland, Central Europe

1. Introduction

Orobanche alba Stephan ex Willd. (Orobanchaceae) has a European-West-Asiatic distribution (Pusch & Günther 2009). It is widely distributed but rare. It has been recorded in western, central, and southern Europe (from eastern Spain) and eastwards to Asia Minor and the Himalayas. Its northern limits are in Ireland, Scotland, Gotland, southern Belgium, central Germany, and south-eastern Poland (Kreutz 1995). The species belongs to subsection *Glandulosae* (Beck) Teryokhin, which in Poland includes also *O. pallidiflora* (Piwowarczyk *et al.* 2010). The analysed species is subdivided into many lower taxa, which differ in morphometric characteristics, colour, hosts, etc. (Beck 1890, 1922, 1930). In Central Europe, 2 subspecies are distinguished: subsp. *alba*, which parasitizes *Thymus*, and subsp. *major* (Čelakovský) Zázvorka, which parasitizes *Salvia* (Kirschner & Zázvorka 2000; Zázvorka 2000). Irrespective of the distinguished lower taxonomic units, the species infests mostly species of the genera *Thymus*

and *Salvia*, while rarely *Clinopodium*, *Acinos*, *Origanum*, *Satureja*, and *Stachys* (Beck 1930; Uhlich *et al.* 1995).

The range of preferred plant communities is poorly studied and described only in general terms. The species has been recorded most frequently from communities of the class *Festuco-Brometea* (orders *Festuco-Sedetalia*, *Seslerietalia varia*, alliances *Bromion erecti* and *Stipo-Poion xerophilae*, order *Festucetalia valesiacae*), class *Sedo-Scleranthetea* (order *Alysso-Sedetalia*), class *Querco-Fagetea* (order *Quercetalia pubescenti-petraeae*), class *Origanetalia vulgaris* (alliance *Geranion sanguinei*), class *Rhamno-Prunetea* (alliance *Prunion fruticosae*), class *Molinio-Arrhenatheretea* (alliance *Arrhenatherion*), and class *Artemisietea vulgaris* (order *Onopordetalia acanthii*) (Uhlich *et al.* 1995; Zázvorka 1997, 2000). *Orobanche alba* is usually found on dry sunny slopes, steppes, subalpine and alpine grasslands, dry or semi-dry-humid places, e.g. in loess valleys, forest clearings on Sarmatian limestone, rocky grasslands, abandoned vineyards, hills, steep field margins,

xerothermic grasslands, roadsides, forest edges, glades, shrubland, meadows, grassy fallow fields, pastures, and macchia (maquis); on calcareous, mostly alkaline, sandy or loamy soil; on calcareous sandstones, limestones, granite and serpentinite; in the lowlands and uplands, but also in mountains, to the alpine zone: in European mountains (440-)1300-2600 m, Caucasus (183)750-2000(-2700) m, and Central Asia 2740-4115 m (Novopokrovskij & Tzvelev 1958; Uhlich *et al.* 1995; Zázvorka 2000; Barina 2009).

The aim of this study was primarily to identify the distribution of *Orobanche alba* subsp. *alba* and subsp. *major* in Poland, based on my investigations and verified herbarium and literature data. The preferred habitats, plant communities, hosts, taxonomic problems, and seed micromorphology of both species (examined by scanning electron microscopy, SEM) are also discussed below. Additionally, a distribution map of subsp. *major* in Central Europe is presented.

2. Taxonomic problems

Orobanche alba Stephan ex Willdenow Sp. Pl. 3: 350, 1800. – Syn.: *Orobanche epithymum* De Candolle in Lamarck et De Candolle, Fl. Franc., ed. 3, 3: 490, 1805; *O. rubra* Sm. in Sm. et Sowerby Engl. Bot. 25, tab. 1786, 1807; *O. serpylli* Des Moulins, 1835; *O. chassia* Formánek 1897; *O. rubra* Hooker 1821, *O. rubiginosa* Dietrich 1836. Type: SE-Russia-in-Europe, “Habitat in Sibiria versus Mare Caspium.” Willdenow, 1800 (p. 350).

Orobanche alba is a polymorphic species, poorly studied, varying in morphometric traits, colour, phenological periods, and preferred hosts. Its taxonomy needs to be revised thoroughly. Majority of almost 30 infraspecific taxa listed has very little or no taxonomic value. They were often described on single and unimportant characters that manifest individual plasticity of the species: var. *typica* G. Beck; f. *capitata* G. Beck, f. *communis* G. Beck, f. *campanulata* G. Beck, f. *leptocalamus* G. Beck, f. *rubra* (Hook.) G. Beck, f. *hololeuca* (Borbás) G. Beck, f. *dasythrix* G. Beck, f. *ankylantha* G. Beck, f. *subalpina* G. Beck, f. *maxima* G. Beck, f. *rubiginosa* (Dietrich) G. Beck, f. *hellebori* (Miégevillie) G. Beck, f. *lutescens* (Boreau) G. Beck, f. *cuprea* G. Beck, f. *minutiflora* G. Beck, f. *viscidula* G. Beck, f. *ampla* G. Beck, f. *longebracteata* G. Beck, f. *stenophyllon* G. Beck, f. *microsepala* G. Beck; var. *raddeana* (G. Beck) G. Beck; var. *wiedemannii* (Boissier) G. Beck; var. *glabrata* (C. A. Meyer) G. Beck; var. *bidentata* G. Beck; f. *ingens* G. Beck, f. *areschensis* G. Beck, var. *nissana* G. Beck (Beck 1890, 1922, 1930). The variety *raddeana* was later classified as a species, *O. raddeana* G. Beck (Novopokrovskij & Tzvelev 1958). The taxon is reported from Asia Minor, Caucasus, Transcaucasus, and West

Iran. It infests mostly *Campanula collina* in alpine and subalpine grasslands (Tzvelev 1957; Novopokrovskij & Tzvelev 1958). Recently a new subspecies and form have been described from north-western Caucasus, as parasites on *Origanum vulgare*: *O. alba* subsp. *xanthostigma* Rätzel & Uhlich and f. *sineglandulosa* Rätzel & Uhlich (Rätzel & Uhlich 2004). The same subspecies is also found in Bulgaria (Stoyanov 2006). In Ukraine, in the Carpathians, on subalpine grasslands and in neighbouring habitats, *O. alba* subsp. *subalpina* is now regarded as a species, *O. subalpina* Herbich (Kotov 1999). The taxon is very similar to *O. alba* subsp. *alba*, so they are probably synonyms. *Orobanche subalpina* is supposed to be distinguished by intensive colour of the corolla, flowers up to 15 mm long, and occurrence mostly in the montane and subalpine zone. I have visited montane and subalpine grasslands and neighbouring habitats in the Chornohora mountain range (Outer Eastern Carpathians in Ukraine), but the individuals observed there look like *O. alba* subsp. *alba*, and the host is also the same (*Thymus*). In all probability, the most intensively coloured individuals were classified by Kotov (1999) as *O. subalpina* but in fact should be classified as a form or subspecies. This requires further research. *O. alba* subsp. *alba* is morphologically similar to *O. teucarii* Holandre (a parasite of *Teucrium*) and may be easily confused with it, especially in the case of herbarium specimens.

O. alba subsp. *major* was first described by Čelakovský (1871) as *O. epithymum* DC. var. *major* Čelak. Next, Beck (1890, 1930) listed it as *O. alba* f. *maxima*. Finally, Zázvorka (in Kirschner & Zázvorka 2000; Zázvorka 2000) classified it as a subspecies, *O. alba* subsp. *major* (Čelak.) Zázvorka. In Central Europe, Zázvorka (2000) distinguished 2 subspecies:

- *O. alba* subsp. *alba* – Syn.: *Orobanche epithymum* DC. [var.] α *minor* Čelak. Prodr. Fl. Böhm. 2: 341, 1871.
- *O. alba* subsp. *major* (Čelak.) Zázvorka in Kirschner et Zázvorka, Preslia 72: 88, 2000. – Syn.: *Orobanche epithymum* DC. [var.] β *major* Čelak. Prodr. Fl. Böhm. 2: 341, 1871; *O. alba* Stephan ex Willd. f. *maxima* Beck Bibl. Bot. 19: 210, 1890.

O. alba subsp. *alba* has smaller and less numerous flowers. It parasitizes mainly *Thymus*, while *O. alba* subsp. *major* parasitizes *Salvia*. The latter subspecies has larger, light-coloured, usually numerous flowers with widely open throats, longer bracts, sepals, and leaves (Table 1, Fig. 1).

O. alba subsp. *alba* is a widely distributed and much more frequent taxon with a European-West-Asiatic distribution. The distribution of *O. alba* subsp. *major* is poorly studied and limited by the distribution of *Salvia* to Central and (S)-SE Europe. Locus classicus of *O. alba*

Table 1. A comparison of the main characters distinguishing *Orobanche alba* subsp. *alba* and subsp. *major*, based on data from Zázvorka (2000)

Character	<i>O. alba</i> subsp. <i>alba</i>	<i>O. alba</i> subsp. <i>major</i>
Plant height (cm)	8-25(-30)	20-65
Distance between corolla base and free filament (mm)	(1.7-)1.8-2.3(-2.6)	(2.0-)2.3-2.7(2.9)
Sepal length (mm)	(5-)7-10(-14)	(5-)7-14
Inflorescence length (cm)	(4-)7-15(-30)	(10-)15-35(-40)
Number of flowers	5-15(-20)	15-35
Corolla length (mm)	(12-)15-20(-25)	12-25(-30)
Flowering period	May-June	June-July
Host (Central Europe)	<i>Thymus</i> spp., rarely <i>Clinopodium vulgare</i> , <i>Origanum vulgare</i>	<i>Salvia</i> spp. (<i>S. verticillata</i> , <i>S. pratensis</i> , <i>S. nemorosa</i>)

subsp. *major* is the hill Milá N of the town of Louny, České středohoří Mts., Northern Bohemia. In original wording it is: Milayer Berg bei Laun, leg. Čelakovský 1869 (Čelakovský 1871: 341). In the Czech Republic, subsp. *major* is distributed in N Bohemia and SE Moravia. It is frequent in the České (Lounské) středohoří Mts., rarely stretching east- and southeastwards to Roudnice nad Labem, single localities are in the north vicinity of Prague (Kováry, Veleň). In Moravia it occurs in Bílé Karpaty Mts. (SE Moravia), rarely up to the broader surroundings of Brno town (Zázvorka 2000). Distribution of subsp. *major* in Slovakia is still questionable;

Devinský hradný vrch near Bratislava-Devin, near Štúrovo and probably near Šahy (Zázvorka 1997). In Romania it is found near Feldru (Buia 1961), and at about a dozen localities in Hungary near Esztergom and Budapest (Barina 2009). Probably it also occurs in Ukraine (e.g. J. Mađalski, 1933, herbarium KRAM) (Fig. 2). It is listed also generally as a parasite on *Salvia* in Ukraine (Kotov 1999). From Bulgaria, only f. *maxima* has been reported, but as a parasite on *Acinos* and *Thymus* (Stoyanov 2006), and generally from Serbia (Kojić *et al.* 2001).

3. Materials and methods

Field research was conducted in 1999-2011, but mostly in 2006-2011. In parallel, I revised all the herbarium materials of *Orobanche alba* available in Poland. The materials are deposited in herbaria KRAM, KRA, KRAP, KTC, KTU, LOD, LBL, POZ. Herbarium acronyms are given after Mirek *et al.* (1997). The nomenclature of vascular plants follows Mirek *et al.* (2002). The nomenclature of syntaxa is based on Matuszkiewicz (2006) and Winnicki (1999). The localities are listed as Atlas of Distribution of Vascular Plants in Poland (ATPOL) cartogram units (10 km × 10 km, based on Zajac (1978); see <http://www.ib.uj.edu.pl/chronopol/>), in alphabetical order. Only localities recorded in my observations and identified or confirmed, as well as verified herbarium data are listed below. Published data not confirmed by me in the field and data not supported by herbarium material are not reliable, due to frequent determination errors, so wrong localities are listed separately. The localities are described as follows: ATPOL grid unit, geographic location, habitat description, abundance in brackets. The following information is also given for most localities: geographic coordinates and altitude (above sea level), and for revised exsiccata the collector and collection date, exsiccatum number and the herbarium acronym. Host plants were also observed by delicately exposing the soil with a gardening shovel.



Fig. 1. Plant habit of *Orobanche alba* subsp. *alba* in the Bieszczady Mts. (left) and subsp. *major* in Brzeźno near Chełm, Chełm Hills (right). Photos by R. Piwowarczyk, 14 Aug 2009; 12 Jul 2008

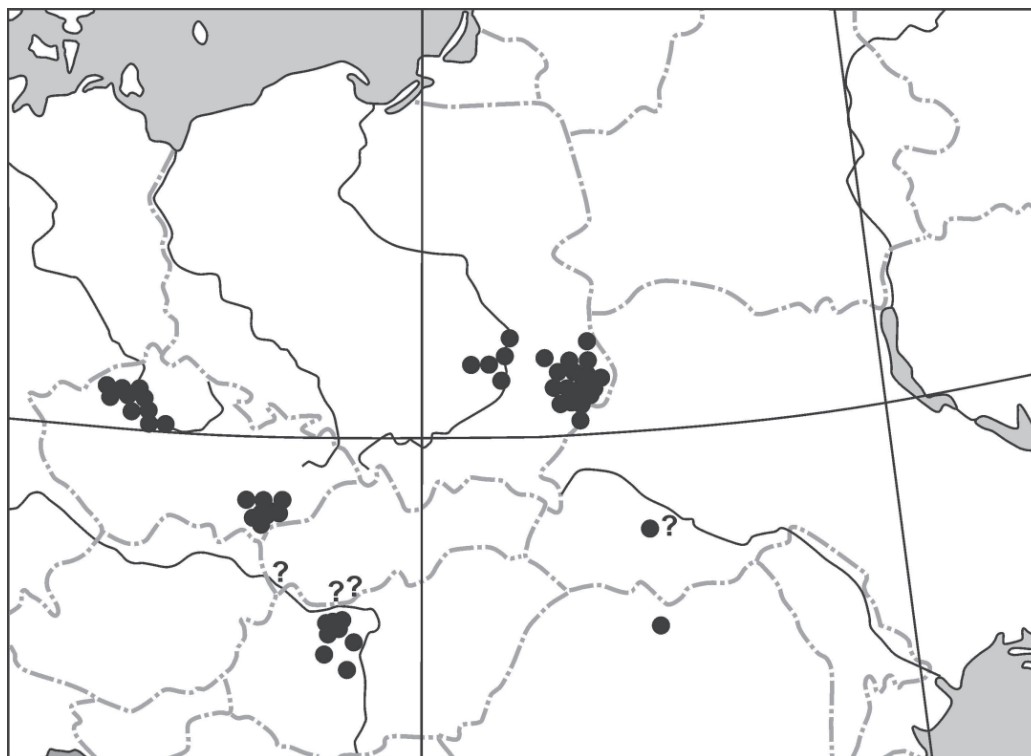


Fig. 2. Distribution of *Orobanche alba* subsp. *major* in Central Europe

In total, 60 seeds (30 of *O. alba* subsp. *alba* and 30 of subsp. *major*) were measured in respect of 10 characters listed in Table 4. The seeds were analysed and prepared in the laboratory of Seed Conservation Department, Millennium Seed Bank, Wakehurst Place, UK. Seed material was mounted onto stubs using double-sided tape, next coated with platinum by using an Emitech K550 sputter coater, and examined using a Hitachi cold field emission SEM S-4700-II (Hitachi High Technologies Corp., Tokyo, Japan) in the Royal Botanic Gardens, Kew, UK. Seeds were also examined in the Department of Botany, Jan Kochanowski University in Kielce. Microscopic observations were carried out with a stereo microscope NIKON SMZ800 and a biological microscope NIKON Eclipse 50i with COOLview programme. Data were examined using Statistica 7.1. The herbarium specimens from which the seeds were collected are listed in Appendix 1.

4. Results

4.1. Distribution in Poland

Orobanche alba subsp. *alba*

In the High Bieszczady Mts., the taxon is recorded from the foothills to the highest peaks (altitude 630-1300 m). As early as in the 19th century, it was observed in Berehy Górne (now Brzegi Górne), Przysłop, Bukowe Berdo, Wyżniański Wierch 950 m (Knapp 1869, 1872), Halicz, Krzemień 1180 m, Tarnica

1300 m, Beskid 1100 m, Czeremcha, Zwór near Bereżki 630 m, and Połonina Caryńska 840-900 m (Kotula 1883; Wołoszczak 1894). In the 1960s, it was confirmed on Wyżniański Wierch, Połonina Caryńska 840-900 m, and Zwór near Bereżki, 630 m (Jasiewicz 1965). The cited author reported that the material collected in the Bieszczady Mts. represented var. *alba*, and provided data on the occurrence of f. *lutescens* on Wyżniański Wierch, 950 m, and Połonina Caryńska. In the 1990s, the subspecies was found in Moczarne, on the southern slope of Szeroki Wierch, and confirmed on Połonina Caryńska over Brzegi Górne and in Zwór (Zemanek & Winnicki 1999). It was also recorded in the Low Bieszczady Mts. in Koziniec in the Polańczyk mountain range, 380 m, and in Dobra Rustykalna, in the Chwaniowa mountain range, 300 m (Zemanek 1989). In 2008-2010, the subspecies was confirmed in the Bieszczady National Park on Połonina Caryńska near Brzegi Górne, on eastern slopes of Połonina Wetlińska, and north-east of Wołosate in the Zwir stream valley (Gierczyk & Soboń 2008; Piwowarczyk 2009-2010 unpubl.) (Fig. 3, Appendix 2). In 2009-2010, my attempts to find the species in the Bieszczady Mts. on Wyżniański Wierch, Halicz, and Krzemień proved to be unsuccessful.

New localities have been found in the Bieszczady Mts. in the nature reserve Sine Wiry (leg. A. Kozłowska, 2010, KRA), in the Sanocko-Turczańskie Mts. (Gierczyk & Soboń 2008), and in Przemyśl Foothills (leg. M. Wolanin, KRA).

Orobanche alba* subsp. *major

Found mostly in south-eastern Poland, in the Lublin Upland (Wyżyna Lubelska): Grabowiec Divisions (Działy Grabowieckie), Małopolska Vistula Gorge (Małopolski Przełom Wisły), Zamość Depression (Padół Zamojski), Giełczew Elevation (Wyniosłość Giełczewska); Roztocze: Chełm Hills (Pagóry Chełmskie), Central Roztocze Hills; Polesie: Hrubieszów Basin (Kotlina Hrubieszowska), Sokal Ridge (Grzęda Sokalska), Belz Plain (Równina Belska) (Piwowarczyk *et al.* 2011). Only few localities are in the Małopolska Upland (Wyżyna Małopolska), in eastern Iłża Foreland (Przedgórze Iłżeckie) (Piwowarczyk 2010, 2012) (Fig. 3, Appendix 3). Most of its localities were discovered in 2006-2011 (Piwowarczyk 2010, 2012; Piwowarczyk *et al.* 2011). Only few records were made in the 1950s and 60s (based on herbarium specimens). Fijałkowski (1994, 1995) reported *Orobanche alba* only generally, from several unspecified localities in the Lublin Upland, as a rare species, found mostly in xerothermic grasslands and shrub communities of the classes *Festuco-Brometea*, *Trifolio-Geranietea sanguinei*, and of the association *Peucedano cervariae-Coryletum*, pri-

marily on rendzinas (humus-rich soils) on chalk. The species was also sporadically recorded by Kucharczyk (2001) in the Małopolska Vistula Gorge.

4.2. Preferred habitats, plant communities and flowering season

Orobanche alba* subsp. *alba in Poland is found in mountains and in the submontane zone, also in the Przemyśl Foothills (altitude 250-355 m). In the Western Bieszczady (part of Outer Eastern Carpathians), recorded at 630-1300 m, but now observed at (525)730-980 m, in upper parts of the lower montane zone and subalpine or alpine grasslands, usually on S and SW-facing slopes, with a slope angle of 20-30°, rarely also on railway embankments and steep roadside slopes. In the Low Bieszczady Mts., recorded at 300-380 m (Zemanek 1989), in rather specific topoclimatic conditions. Annual mean temperature is 2-4°C. The warmest month is July, while February is the coldest. Annual precipitation is about 1100-1200 mm, and snow cover lasts on average 120 days (Winnicki 1999). The Bieszczady are composed mostly of Carpathian flysch,

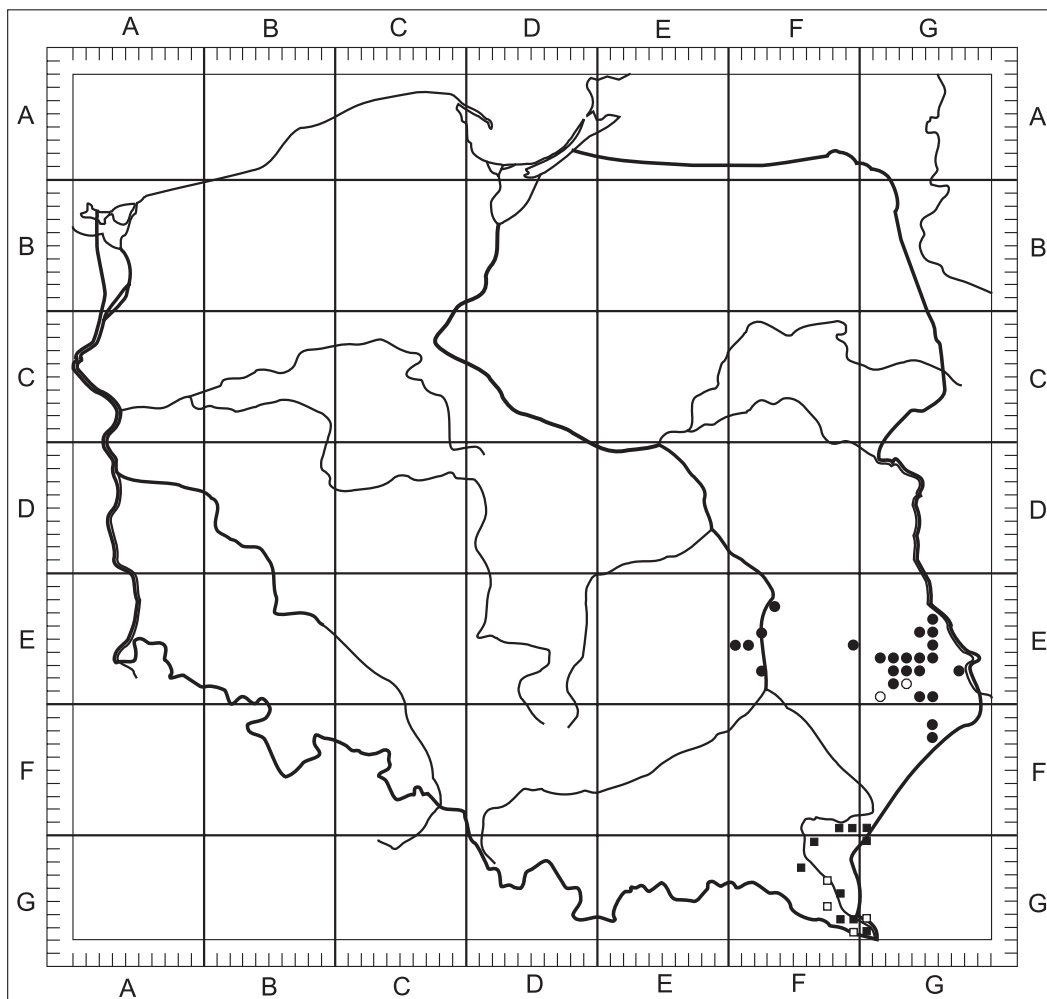


Fig. 3. Distribution of *Orobanche alba* in Poland
 Explanations: subsp. *major*, ○ – probably extinct, ● – present; subsp. *alba*, □ – probably extinct, ■ – present

Table 2. Plant communities with *Orobanche alba* subsp. *alba* in the Bieszczady Mts.

Number of relevé	1	2	3	4	5	6	7
Location	PC	PC	PC	PC	BG	BG	PW
Date	13.08.2009	13.08.2009	13.08.2009	14.08.2009	14.08.2009	14.08.2009	14.08.2009
Area of relevé (m ²)	50	50	50	25	25	25	25
Exposure	S	S	S	SSW	S	S	S
Inclination [°]	25	25	25	20	20	40	20
Latitude [N]	49°07'38.1"	49°07'41.1"	49°07'43.3"	49°08'19.2"	49°07'43.8"	49°08'28.1"	49°08'31.2"
Longitude [E]	22°35'35.9"	22°35'31.0"	22°35'31.2"	22°35'14.7"	22°35'04.5"	22°34'07.7"	22°34'03.2"
Altitude (a.s.l.) [m]	884	873	917	982	822	772	736
Density of tree layer A (%)	-	-	-	-	-	20	20
Density of shrub layer B (%)	15	25	15	-	5	15	15
Density of herb layer C (%)	100	100	100	100	90	95	95
Density of moss layer D (%)	5	5	10	5	15	5	15
Number of species	63	57	61	42	41	52	34
<i>Orobanche alba</i> subsp. <i>alba</i>	+	+	+	+	+	+	+
Trees and shrubs							
<i>Juniperus communis</i> subsp. <i>communis</i> B	1	2	1	.	+	1	1
<i>Juniperus communis</i> subsp. <i>communis</i> C	+	+	+	.	+	.	.
<i>Rosa canina</i> B	+	+	+	.	.	.	+
<i>Acer pseudoplatanus</i> C	+	+	+
<i>Fraxinus excelsior</i> C	+	+	+
<i>Salix caprea</i> B	+	.	.	.	+	.	+
Ch. Arrhenatherion, Arrhenatheretalia							
<i>Achillea millefolium</i>	1	1	2	1	+	+	1
<i>Trisetum flavescens</i>	+	1	1	+	+	+	+
<i>Galium mollugo</i>	+	2	1	+	+	+	+
<i>Knautia arvensis</i>	+	+	+	+	+	+	+
<i>Pimpinella major</i>	+	1	.	+	+	+	+
<i>Leucanthemum vulgare</i>	+	+	+	.	+	+	+
<i>Lotus corniculatus</i>	.	+	+	+	+	+	+
<i>Campanula patula</i> s.l.	+	+	+	.	.	+	+
<i>Dactylis glomerata</i>	+	.	+	.	.	+	+
<i>Trifolium repens</i>	+	.	.	.	+	+	+
Ch. Molinio-Arrhenatheretea							
<i>Deschampsia caespitosa</i>	1	1	+	2	+	+	2
<i>Centaurea jacea</i>	1	+	+	1	1	+	+
<i>Ranunculus acris</i>	.	+	+	+	+	+	+
<i>Euphrasia rostkoviana</i>	+	+	.	1	+	+	.
<i>Festuca rubra</i>	1	+	+	.	+	.	+
<i>Angelica sylvestris</i>	+	+	+	.	.	+	+
<i>Plantago lanceolata</i>	+	+	+	+	.	.	+
<i>Prunella vulgaris</i>	+	+	+	.	+	+	.
<i>Vicia cracca</i>	+	.	+	.	+	+	+
<i>Leontodon hispidus</i>	+	.	.	+	+	+	.
<i>Phleum pratense</i>	+	+	+
<i>Trifolium pratense</i>	.	.	+	+	.	1	.
Ch. Nardo-Callunetea							
<i>Nardus stricta</i>	+	1	4	1	+	.	.
<i>Potentilla erecta</i>	1	1	+	+	.	.	+
<i>Polygala vulgaris</i>	+	+	+	.	+	+	+
<i>Hieracium pilosella</i>	+	+	+	.	1	+	.
<i>Agrostis capillaris</i>	1	+	+	+	.	.	+
<i>Danthonia decumbens</i>	+	+	+	.	+	.	.
<i>Veronica officinalis</i>	+	+	.	.	.	+	.
Ch. Calamagrostion, Betulo-Adenostyletea							
<i>Hypericum maculatum</i>	+	1	+	1	.	+	+
<i>Poa chaixii</i>	1	1	+	+	.	.	.
<i>Luzula luzuloides</i>	+	+	+	.	.	.	+
<i>Calamagrostis arundinacea</i>	+	+	+
<i>Viola dacica</i>	.	.	+	+	.	+	.
Ch. Vaccinio-Piceetea							
<i>Vaccinium myrtillus</i>	1	2	3	+	+	.	+
<i>Vaccinium vitis-idaea</i>	+	+	+
<i>Luzula sylvatica</i>	+	+	+
Others							
<i>Thymus pulegioides</i>	3	2	3	2	2	1	3
<i>Briza media</i>	1	1	+	1	+	1	+
<i>Dianthus compactus</i>	1	+	+	+	.	+	.

	1	2	3	4	5	6	7
<i>Carlina acaulis</i>	+	+	+	+	+	.	.
<i>Gentiana asclepiadea</i>	+	+	+	+	.	+	.
<i>Gymnadenia conopsea</i>	+	.	+	+	.	+	.
<i>Veronica chamaedrys</i>	+	.	+	+	.	+	+
<i>Alchemilla</i> sp.	.	.	.	+	.	+	.
<i>Anthoxanthum odoratum</i>	+	+	+
<i>Astrantia major</i>	+	.	.	+	+	.	.
<i>Campanula glomerata</i>	+	+	+
<i>Carex</i> sp.	+	.	.	.	+	+	.
<i>Cruciata glabra</i>	.	+	+	.	.	+	.
<i>Equisetum arvense</i>	.	+	.	.	+	+	.
<i>Fragaria vesca</i>	+	.	.	+	.	+	.
<i>Linum catharticum</i>	+	.	.	.	+	+	.
<i>Ononis arvensis</i>	.	+	.	.	+	+	.
<i>Rubus idaeus</i>	+	.	.	+	.	+	.
<i>Silene vulgaris</i>	+	+	+
<i>Solidago virgaurea</i>	+	+	+

Explanations: PC – Polonina Caryńska, BG – Brzegi Górne, PW – Polonina Wetlińska E

Sporadic: **Ch. Molinio-Arrhenatheretea:** *Arrhenatherum elatius* 2, 5; *Cirsium oleraceum* 6; *Festuca pratensis* 1, 2; *Heracleum sphondylium* 6; *Mentha longifolia* 4, 6; *Myosotis palustris* 5, 6; *Trifolium hybridum* 5, 6; **Ch. Nardo-Callunetea:** *Hypochoeris uniflora* 3, 4; *Lycopodium clavatum* 3, 5; **Ch. Betulo-Adenostyletea:** *Crepis conyzifolia* 1, 2; *Rosa pendulina* C 3; **Ch. Vaccinio-Piceetea:** *Homogyne alpina* 3, 4; *Picea abies* A 6(2), 7(2), B 6, C 1; **Others:** *Agrostis canina* 3, 4; *Betula pendula* B 7, C 2, 5; *Carex lepidocarpa* 6; *C. pallescens* 1, 3; *Centaurea phrygia* 2; *Cirsium arvense* 7; *Clinopodium vulgare* 3, 6; *Galium verum* 1, 5; *Gnaphalium sylvaticum* 1; *Knautia dipsacifolia* 3; *Pimpinella saxifraga* 1, 4; *Pinus sylvestris* C 5; *Plantago media* 6(1); *Polytrichum commune* D 2, 3; *Rosa canina* C 3; *Salix silesiaca* B 1, C 2, 4; *Senecio jacobaea* 6; *Stellaria graminea* 2, 3; *Tanacetum corymbosum* subsp. *clusii* 3; *Thesium alpinum* 3; *Trifolium medium* 1, 2; *Tussilago farfara* 5, 6

sandstones resistant to denudation, and shales, which build parallel mountain ranges. Calcium-rich and poor rock layers may be close to each other. The taxon is recorded most frequently on mountain grasslands (so-called “poloninas”), interspersed with bilberry communities, and mat-grass pastures, juniper thickets, and tall-herb communities on S and SW-facing slopes. Poloninas are usually a mosaic of seral stages and transitional patches, very difficult to classify in phytosociological terms. They are transitional communities, some of them described relatively recently (Winnicki 1999), e.g. mesophilous meadows of the order *Arrhenatheretalia* (class *Molinio-Arrhenatheretea*), East Carpathian tall-herb communities *Diantho compacti-Hypericetum maculati*, grass-dominated communities of the alliance *Calamagrostion villosae* (e.g. *Tanaceto-Calamagrostietum arundinaceae*, *Poo chaixii-Deschampsietum caespitosae*) (class *Betulo-Adenostyletea*), East Carpathian mat-grass pasture *Hypochoeridi uniflorae-Nardetum strictae* (= *Nardetum carpaticum orientale*) of the alliance *Eu-Nardion* (class *Nardo-Callunetea*), high-mountain Carpathian bilberry communities *Vaccinietum myrtilli*, and e.g. *Vaccinietum myrtilli-Gentianetosum asclepideae* (class *Vaccinio-Piceetea*). Perhaps *O. alba* subsp. *alba* was recorded in the past also in communities of the class *Caricetea curvulae*. In the analysed communities with participation of *O. alba* subsp. *alba*, its host, *Thymus pulegioides* usually covers 25-50% of the area (Table 2). The communities develop on leached brown soils (Eutric Cambisols), acid brown soils (Dystric Cambisols), shallow or moderately deep, with a high contribution of gravel and rocks, on brown

rankers (Cambic Rankers), rarely on raw soils (Lithosols and Regosols). Soil pH varies widely: raw soils pH 3.5-5.0, highly acidic soils) pH (4.0)5.0-6.5(7.0); while saturation with alkalis in acid brown soils is 5-15% and 60-90% in brown soils proper (Skiba *et al.* 1998).

In Przemyśl Foothills, *O. alba* subsp. *alba* is recorded in distinct and much warmer and calciphilous communities of thermophilous forest edge communities of the class *Trifolio-Geranietea sanguinei*, and in xerothermic grasslands of the class *Festuco-Brometea*, as well as on dry and warm roadsides (M. Wolanin, oral communication).

Orobanche alba* subsp. *major prefers sunny sites, usually gentle S or SW-facing slopes; rarely found at flat sites; altitude about 130-300 m. These include xerothermic grasslands, thermophilous shrublands, frequently with a high contribution of *Juniperus communis*; located on slopes of hills, river valleys, gullies, edges of forests and fields, in former quarries, rarely on archaeological sites, e.g. remnants of medieval fortified settlements (e.g. Gródek in SE Poland), or on hills and calcareous islands (so-called *grądziki* in Polish) with xerothermic vegetation, located within wet meadows and marshes, e.g. *Cladietum marisci*, which is rare in Poland, and calcareous fens of the alliance *Caricetalia davallianae* (e.g. nature reserve Brzeźno near Chełm). *O. alba* subsp. *major* prefers alkaline soils, usually shallow rendzinas formed on chalk marl and limestone, loess, and chernozem (black-earth soil). It is recorded most frequently in communities of the alliance *Cirsio-Brachypodium pinnati* (class *Festuco-Brometea*), especially

Table 3. Plant communities with *Orobanche alba* subsp. *major* in Poland

Number of relevé	1	2	3	4	5	6	7
Location	Pełkowice	Bandocha hills	Kały	Mećmierz1	Mećmierz2	Mećmierz3	Brzeźno
Date	17.07.2007	15.07.2005	13.07.2008	26.07.2010	26.07.2010	26.07.2010	12.07.2008
Area of relevé (m ²)	25	40	30	25	40	40	50
Exposure	S	SW	SSE	SSE	SSE	S	S
Inclination [°]	20	10	15	10	20	15	5
Latitude [N]	51°01'03"	50°53'03"	50°40'37"	51°18'08,9"	51°18'05,3"	51°18'07,8"	51°09'19"
Longitude [E]	21°35'47"	21°45'14"	23°07'31"	21°53'56,4"	21°54'08,1"	21°54'02,1"	23°35'56"
Altitude a.s.l. (m)	170	160	270	136	135	130	170
Density of tree layer A (%)	-	15	-	-	-	-	-
Density of shrub layer B (%)	30	20	15	20	-	-	-
Density of herb layer C (%)	90	100	75	100	90	85	95
Density of moss layer D (%)	>5	>5	>5	>5	>5	>5	>10
Number of species	34	41	45	32	49	47	40
<i>O. alba</i> subsp. <i>major</i>	+	+	+	1	+	+	+
Ch. Cirsio-Brachypodium pinnati, Festucetalia valesiacae							
<i>Salvia verticillata</i>	1	3	1	2	1	1	2
<i>Melampyrum arvense</i>	.	.	.	+	+	+	1
<i>Aster amellus</i>	+	+	+
<i>Inula ensifolia</i>	.	.	+	.	.	.	2
<i>Potentilla arenaria</i>	1	.	.	.	+	.	.
<i>Campanula sibirica</i>	.	.	+	.	.	.	+
<i>Scabiosa ochroleuca</i>	.	.	.	+	.	+	.
Ch. Festuco-Brometea							
<i>Teucrium chamaedrys</i>	.	3	+	2	1	1	+
<i>Euphorbia cyparissias</i>	+	2	+	+	+	+	.
<i>Centaurea scabiosa</i>	+	.	+	.	+	3	+
<i>Brachypodium pinnatum</i>	+	+	.	.	+	.	+
<i>Plantago media</i>	.	.	+	+	1	.	.
<i>Acinos arvensis</i>	+	+	.
<i>Centaurea stoebe</i>	+	+	.
<i>Gentiana cruciata</i>	.	+	+
Ch. Trifolio-Geranietea sanguinei							
<i>Origanum vulgare</i>	1	2	+	3	1	1	+
<i>Galium verum</i>	1	3	.	+	+	+	+
<i>Medicago falcata</i>	1	2	+	+	1	+	.
<i>Fragaria viridis</i>	+	1	.	2	+	+	.
<i>Agrimonia eupatoria</i>	+	+	.	+	+	.	.
<i>Clinopodium vulgare</i>	.	1	.	+	+	.	.
<i>Peucedanum cervaria</i>	.	.	+	.	.	.	1
<i>Coronilla varia</i>	.	+	+
Ch. Molinio-Arrhenatheretea							
<i>Festuca rubra</i>	.	2	+	2	+	+	.
<i>Arrhenatherum elatius</i>	.	+	1	1	+	.	.
<i>Achillea millefolium</i>	.	1	.	+	+	+	.
<i>Anthyllis vulneraria</i>	.	.	2	.	.	+	+
<i>Knautia arvensis</i>	.	.	+	.	1	+	.
<i>Plantago lanceolata</i>	.	.	.	+	+	1	.
<i>Dactylis glomerata</i>	.	+	+	.	.	.	+
<i>Daucus carota</i>	.	+	+	.	+	+	.
<i>Galium mollugo</i>	.	+	+	.	.	+	.
<i>Leucanthemum vulgare</i>	.	.	1	.	.	.	+
<i>Carex tomentosa</i>	.	+	+
<i>Trifolium dubium</i>	+	+	.
Ch. Rhamno-Prunetea							
<i>Prunus spinosa</i> B	2	+	1	2	+	.	.
C	1	1	+	3	+	+	.
<i>Rhamnus cathartica</i> B	1	1	.	.	+	.	.
C	1	+	.	.	+	.	.
<i>Cornus sanguinea</i> B	+	+
C	+	+	.	.	.	+	.
<i>Rosa rubiginosa</i> B	1	+	+
C	.	+	.	.	+	+	.
<i>Crataegus monogyna</i> B	+	+
C	+	.	.	.	+	.	.
Ch. Artemisietea vulgaris							
<i>Cichorium intybus</i>	+	.	+	+	+	.	.
<i>Artemisia vulgaris</i>	.	.	.	+	+	+	.

	1	2	3	4	5	6	7
<i>Melilotus officinalis</i>	.	.	+	.	.	+	.
Others							
<i>Salvia pratensis</i>	1	.	1	+	+	+	.
<i>Pimpinella saxifraga</i>	+	+	.	+	+	+	.
<i>Brachythecium</i> sp. D	.	+	+	+	+	.	.
<i>Eryngium planum</i>	.	.	+	+	+	.	.
<i>Hypericum perforatum</i>	.	+	.	.	+	+	.
<i>Medicago lupulina</i>	.	+	+	.	.	+	.
<i>Briza media</i>	.	1	+
<i>Convolvulus arvensis</i>	.	+	.	.	+	.	.
<i>Equisetum arvense</i>	.	+	.	.	.	+	.
<i>Carex flacca</i>	.	.	+	.	.	.	+
<i>Carlina intermedia</i>	.	.	+	.	.	.	+
<i>Cerintho minor</i>	.	+	.	.	.	+	.
<i>Erigeron acer</i>	.	.	.	+	+	.	.
<i>Erigeron annuus</i>	.	.	.	+	.	+	.
<i>Hieracium pilosella</i>	+	+	.
<i>Linum catharticum</i>	.	.	+	.	.	.	+
<i>Ononis spinosa</i>	.	.	.	+	+	.	.
<i>Orobanche kochii</i>	+	+
<i>Rubus caesius</i>	+	.	.	.	+	.	.
<i>Sanguisorba minor</i>	.	+	.	.	.	+	.

Sporadic: **Ch. Cirsio-Brachypodion pinnati, Festucetalia valesiacae:** *Achillea pannonica* 1; *Adonis vernalis* 4; *Anthemis tinctoria* 5; *Asparagus officinalis* 4; *Cirsium pannonicum* 7(2); *Hieracium bauhini* 3; *Linum flavum* 3(1); *Senecio erucifolius* var. *tenuifolius* 5; *Seseli annuum* 2; *Thesium linophyllum* 7(1); **Ch. Festuco-Brometea:** *Artemisia campestris* 5(1); *Campanula glomerata* 3; *Festuca pallens* 1(1); *Filipendula vulgaris* 7; *Koeleria macrantha* 1(1); *Petrorhagia prolifera* 5; *Phleum phleoides* 1(1); *Veronica spicata* 1(2); **Ch. Trifolio-Geranietea sanguinei:** *Anemone sylvestris* 3(1); *Anthericum ramosum* 7; *Trifolium medium* 3; *T. montanum* 7; *Verbascum lychnitidis* 1; *Vicia tenuifolia* 6; *Viola hirta* 2; **Ch. Molinio-Arrhenatheretea:** *Galium boreale* 3; *Inula salicina* 7; *Molinia caerulea* 7; *Prunella vulgaris* 5; *Succisa pratensis* 7; *Tragopogon pratensis* 3; *Trifolium pratense* 2; **Ch. Artemisietea vulgaris:** *Anchusa officinalis* 6; *Cirsium vulgare* 6; **Ch. Rhamno-Prunetea:** *Berberis vulgaris* B 1(1), C 1; **Others:** *Abietinella abietina* D 2; *Arenaria serpyllifolia* 6; *Betula pendula* C 7; *Bryum* sp. D 2, 4; *Carex hirta* 2(1); *Cerasus vulgaris* C 4; *Chamaecytisus ratisbonensis* 3; *Cladium mariscus* 7(τ); *Cypripedium calceolus* 3; *Echium vulgare* 6; *Epipactis helleborine* 2; *E. palustris* 7(τ); *Erigeron ramosus* 6(1); *Falcaria vulgaris* 1(1); *Frangula alnus* B 1(1), C 1, 7; *Gymnadenia conopsea* 3; *Inula britannica* 5; *Juniperus communis* B 1(1), C 1; *Lappula squarrosa* 1; *Lathyrus tuberosus* 3; *Lavatera thuringiaca* 6; *Ligustrum vulgare* B 4; *Nonea pulla* 5; *Ononis arvensis* 7; *Potentilla anserina* 7; *Orobanche caryophyllacea* 3; *O. lutea* 5; *Peucedanum alsaticum* 3; *Pinus sylvestris* A 2(1), B 2(1), C 2, 3; *Potentilla anserina* 7; *Prunella grandiflora* 7; *Pyrus communis* B 3; C 1, 4; *P. pyraster* B 4; *Quercus robur* C 2, 5; *Sedum acre* 6; *Senecio jacobaea* 6; *S. macrophyllum* 7; *Silene inflata* 3; *Solidago gigantea* 6; *Tofieldia calyculata* 7; *Vicia hirsuta* 5

on flowery or initial dry grasslands, i.e. *Adonido-Brachypodietum pinnati*, *Inuletum ensifoliae*, *Thalictro-Salvietum pratensis*. As a result of natural plant succession in grasslands, the communities have a high contribution or mosaic of species of thermophilous herbaceous forest edge communities of the alliance *Geranion sanguinei* (class *Trifolio-Geranietea sanguinei*) and shrub communities, particularly of the alliance *Berberidion* (class *Rhamno-Prunetea*), as well as meadow species of the alliance *Arrhenatherion elatioris* (class *Molinio-Arrhenatheretea*). All the communities mentioned above include a high contribution of host

species of the genus *Salvia*, especially of *S. verticillata*, coverage about 25-50% (Table 3).

The height of the flowering season of *Orobanche alba* subsp. *alba* is usually about mid July in the Przemysl Foothills. In the Bieszczady Mts., flowering specimens were most often observed in late July, but sometimes the flowering season lasted till mid August. By contrast, *O. alba* subsp. *major* flowers slightly earlier. The height of its flowering season is usually in early June to early July. For comparison, in the Czech Republic and in Hungary, subsp. *alba* flowers from early May to mid June, while subsp. *major* from May (rare)

Table 4. A comparison of the main characters distinguishing seeds of *Orobanche alba* subsp. *alba* and subsp. *major*

Subsp.	<i>alba</i>	<i>major</i>
Seed length (µm)	(300)365(420)	(310)398(450)
Seed width (µm)	(190)243(370)	(200)255(320)
Cell length (µm)	(40)92(140)	(60)123(200)
Cell width (µm)	(30)59(100)	(30)67(100)
Perforation diameter (µm)	(1.5)2.4(4)	(1.8)3.4(6)
Wall width (µm)	(2)2.7(4)	(2.5)4.2(6)
Seed shape	Oblongoid to ellipsoid, ovoid, rarely pear-shaped	
Cell shape	Isodiametric to irregular, elongated	
Wall depth	Shallow or medium	
Narrow trough	Evident all around cell edges	

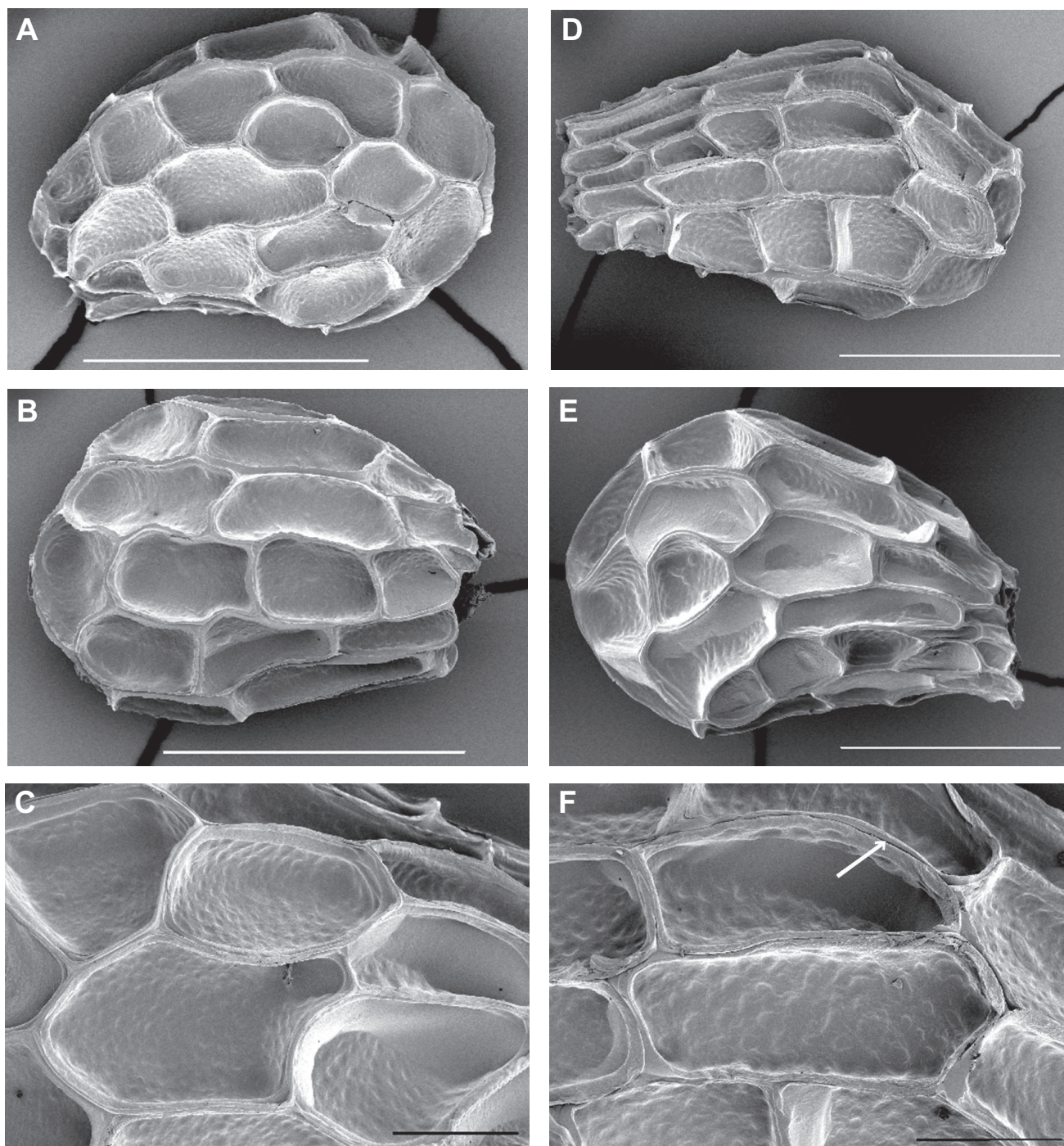


Fig. 4. Scanning electron micrographs of seeds of *Orobanche alba* subsp. *alba* (A, B, C) and subsp. *major* (D, E, F). Arrows point to a narrow trough all around the epidermal cell edges. Scale bars = 200 μm (A, B, D, E); 50 μm (C, F)

to mid June, sometimes to mid August (Barina 2009, Zázvorka 2000).

4.3. Seed micromorphology

Seeds of *Orobanche alba* are oblong to ellipsoid, ovoid, rarely pear-shaped, 300-450 \times 200-300 μm , dark brown. Epidermal seed coat reticulate, composed of isodiametric or tangentially elongated cells, 40-200 \times 30-100 μm . Anticlinal walls of shallow or medium depth, with a narrow trough evident all around the edges of the cells and at the vertices. Periclinal wall with perforations,

1.5-6 μm . Cell wall 2-6 μm thick. To analyse differences between subspecies of *O. alba*, 10 micromorphological characters of seeds were used (Table 4) by SEM. The results show that subsp. *alba* has slightly smaller seeds (on average 365 \times 243 μm) and epidermal cells (92 \times 59 μm). Their perforations are much smaller (2.4 μm) and more crowded. Mean wall width is 2.7 μm . By contrast, seeds of subsp. *major* have higher values of all the parameters: dimensions of seeds (on average 398 \times 255 μm), cells (123 \times 67 μm), perforation diameter (3.4 μm , shape often oval), wall width 4.2 μm (Table 4, Fig. 4).

5. Discussion

Orobanche alba in Poland is distributed only in the south-east, i.e. in the Lublin Upland, Roztocze Hills, Polesie, Przemyśl Foothills, and the Western Bieszczady Mts., rarely in the eastern part of Małopolska Upland. Both subspecies distinguished by Zázvorka (2000) in central Europe, because of differences in morphology and preferred hosts, are found also in Poland. Results of my research show that the 2 subspecies differ also in ranges of regional distribution, habitat types, plant communities, and phenological periods.

It is noteworthy that splitting of the species into the subspecies listed above is possible only in Central Europe and, in my opinion, it is rather simplistic, according to the current knowledge. Because of the large number of described forms, varieties and subspecies within the distribution range and the poor knowledge of hosts of this species, it is necessary to revise its classification and continue field research.

Orobanche alba subsp. *alba* in Poland is found in mountains and in the submontane zone, less frequent on foothills; recorded in the Polish part of Outer Eastern Carpathians: in the Bieszczady Mts., Sanocko-Turczańskie Mts., and in Przemyśl Foothills, at altitudes of (250)300-980(1300) m. In the Bieszczady Mts., climatic conditions are specific: long-lasting snow cover, low temperature, high precipitation, strong and drying winds, and short growing season. The taxon is reported most frequently from transitional communities, e.g. mesophilous meadows of the order *Arrhenatheretalia* (class *Molinio-Arrhenatheretea*), tall-herb communities and grass-dominated communities of the alliance *Calamagrostion villosae* (class *Betulo-Adenostyletea*), mat-grass pastures of the alliance *Eu-Nardion* (class *Nardo-Callunetea*), and high-mountain Carpathian bilberry communities *Vaccinietum myrtilli* (class *Vaccinio-Piceetea*). They are found chiefly on brown soils, rarely on rankers or raw soils with a relatively low pH. In Przemyśl Foothills, *O. alba* subsp. *alba* is recorded in much warmer and calciphilous communities of thermophilous forest edge communities of the class *Trifolio-Geranietea sanguinei*, and in xerothermic grasslands of the class *Festuco-Brometea*.

Most of the Polish localities of *Orobanche alba* subsp. *major* were discovered or confirmed in the last 6 years (Piwowarczyk 2010, 2012; Piwowarczyk *et al.* 2011). The taxon is recorded in Poland mostly in uplands, at altitudes of about 130-300 m. Its habitats are typically warm, sunny, with plant communities of the alliance *Cirsio-Brachypodium pinnati* (class *Festuco-Brometea*) interspersed with thermophilous herbaceous forest edge communities of the alliance *Geranion sanguinei* (class *Trifolio-Geranietea sanguinei*) and shrub communities, especially of the alliance *Berberidion*

(class *Rhamno-Prunetea*). It prefers alkaline soils, most frequently shallow rendzinas formed on chalk marls and limestones, loess, and czernozems. In the Czech Republic, *O. alba* subsp. *alba* was recorded at up to 868 m, while subsp. *major* at 200-350 m, up to 540 m (Zázvorka 2000).

My field research in 2006-2011 in Poland, including exposing the soil gently with a gardening shovel, showed that *O. alba* subsp. *alba* is a parasite on *Thymus pulegioides*, while *O. alba* subsp. *major* on *Salvia verticillata*, rarely on *S. pratensis*. It is also possible, although rarely, to observe *O. alba* subsp. *alba* as a parasite on *Clinopodium* or *Origanum* (?) in Poland and neighbouring countries. The above list does not include many host species reported in the literature and observed by me e.g. in the south of Europe. For example, subsp. *major* in the Czech Republic is a parasite on *Salvia pratensis*, *S. nemorosa*, and rarely on *S. verticillata* (Zázvorka 2000); in Hungary on *S. nemorosa* and rarely on *S. pratensis* (Barina 2009); while subsp. *alba* on *Thymus* and rarely on *Clinopodium vulgare* and *Origanum vulgare* (Zázvorka 2000).

Population size varies greatly between localities and between years. Local populations of *Orobanche alba* subsp. *alba* are usually small. In the Przemyśl Foothills, they are usually composed of 1-2 shoots, while in the Bieszczady Mts., usually of 5-10 shoots. The largest populations, of about 30-50 shoots, are located on Połonina Caryńska and the eastern part of Połonina Wetlińska. In total, more than 300 shoots have been observed there but they are scattered throughout nearly the whole range. Populations of *O. alba* subsp. *major* are much larger, composed of (5)10-20(30) shoots. The largest population was found near Lasocin and includes over 80 shoots. More than 50 shoots were recorded also in Brzeźno, Kolonia Leszczany, Huszczka Duża, Machnowska Mt., and Męcierz.

This study is first to compare seed micromorphology of both subspecies, by using SEM. The results show that subsp. *alba* has smaller seeds, epidermal cells, and thinner walls than subsp. *major*. Substantial differences were observed in ornamentation of periclinal walls. In subsp. *alba*, its perforations were much smaller and more rounded than in subsp. *major*, where they were often elongated or oval. Morphological characters of seeds may help in verification of herbarium specimens. Similar observations were made by Plaza *et al.* (2004), but they concerned *O. alba* s.l., without division into subspecies and without reference to preferred hosts. Seeds of *O. alba* were classified by the cited authors as Type II, subtype A: seed size 290-460 × 170-280 μm, cell shape isodiametric to tangentially elongated, narrow trough evident all around the cell edges.

Orobanche alba is classified as vulnerable in the Polish part of Carpathians (Kaźmierczakowa 2008), and

as critically endangered in the Małopolska Upland (Bróz & Przemyski 2009). It is also noteworthy that Poland lies at the northern limit of its distribution. The species is threatened mostly by secondary succession resulting from the abandonment of the traditional livestock farming system. The poloninas in the Bieszczady Mts. were created thanks to human activity (e.g. livestock grazing, hay harvesting), so when the human disturbance is stopped, they are gradually overgrown, mostly by *Vaccinium myrtillus* and *Deschampsia caespitosa*, or grass-dominated communities of the alliance *Calamagrostion villosae*. Thus active protection of the habitats is necessary (e.g. livestock grazing, hay harvesting). Moreover, the Bieszczady Mts. are visited by large numbers of tourists and this may have a negative effect on the natural environment, e.g. due to treading. Populations of this species are located within the Transboundary Biosphere Reserve „Eastern Carpathians” recognized under UNESCO’s Man and the Biosphere (MAB) Programme. The area is protected also as the Bieszczady National Park and Cisna-Wetlina Landscape Park, or the nature reserve Sine Wiry. Anyway, many of its local populations, first recorded in the 19th century, still exist. In the Przemyśl Foothills, most of the localities are within the Przemyśl Foothills Landscape Park (Park Krajobrazowy Pogórza Przemyskiego), while the one in Ulucz, within the East Beskid Landscape Protection Area (Wschodniobeskidzki Obszar Chronionego Krajo-

brazu). At present, those local populations do not seem to be threatened, but they need to be monitored.

Similarly, *O. alba* subsp. *major* is also exposed to secondary succession and colonization by woody vegetation. Many local populations are situated very close to arable fields, where they may be affected by agrochemicals. Most of such localities are not protected in any way, except for the nature reserves Żmudź, Brzeźno, Machnowska Mt., or some Natura 2000 sites. However, this does not ensure the survival of the species there, since active protection is necessary. At least some localities need to be monitored and actively protected as so-called “ecological grounds” (in Polish *użytki ekologiczne*), by means of hay harvesting or livestock grazing. This would prevent an excessive development of herbaceous vegetation and shrubs, and would preserve the specific mosaic of habitats and forest edge communities.

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Appendices

Appendix 1. List of herbarium specimens from which seeds were collected for SEM analysis

O. alba subsp. alba: Outer Eastern Carpathians, Ukraine, Chornohora: Dzembronia (Berestechko), behind mountain hut „U Kuby”, 48°06'24.2"N, 24°39'55.3"E, 1015 m, leg. R. Piwowarczyk, 08.08.2007; Kosaryszcze, meadow, 48°06'39.7"N, 24°41'24.8"E, 1118 m, leg. R. Piwowarczyk, 06.08.2007; Kostrzyca, forest edge, on a roadside, 1150, 1300 m, leg. R. Piwowarczyk, 02.08.2007; near Bystrec village, 48°07'28.2"N, 24°41'18.1"E, 825 m, leg. R. Piwowarczyk, 05.08.2007; Poland: Bieszczady Mts.: Połonina Caryńska, leg. R. Piwowarczyk, 13.08.2009; **subsp. major:** Lasocin, leg. R. Piwowarczyk, 15.07.2005; Żmudź, leg. R. Piwowarczyk, 13.07.2007; Białtów, leg. R. Piwowarczyk, 24.07.2007; Leszczany, leg. R. Piwowarczyk, 15.07.2006.

Appendix 2. List of localities of *Orbanche alba* subsp. *alba*

FF: 98: Bachów, dry field border 250 m, leg. M. Wolanin, 02.07.2008 (KRA); **99:** Śliwnica, dry bank at forest edge, 255 m, leg. M. Wolanin, 20.08.2009 (KRA); **FG: 06:** Ulucz, dry bank of river San 260 m, leg. M. Wolanin, 07.08.2009 (KRA); Dobra Rustykalna, 300 m (Zemanek 1989); **25:** Sanocko-Turczańskie Mts., between Zagórze and Lesko, near inn “U Kmity”, in shrubs at forest edge (>5) on *Thymus* sp., vid. J. Soboń, 11.07.2007 (Gierczyk & Soboń 2008); **37:** Koziniec 380 m, Zemanek 1989; **48:** bent of stream Wetlina, N of former village of Zawój, nature reserve Sine Wiry, xerothermic meadow, 525 m, 49°15'33.6"N, 22°26'22.2"E, leg. K. Kozłowska, 17.07.2010 (KRA); **57:** Przysłup (orig. Przysłóp), Knapp 1872; **68:** Moczarnie, train terminus, leg. M. Szewczyk, 1993 (KRA); **69:** Wyżniański Wierch, 950 m, Kotula 1883; leg. A. Jasiewicz, K. Zarzycki, 21.08.1956 (KRAM, 019560), Jasiewicz 1965, leg. K. Zarzycki, 14.07.1961 (KRAM, 297043, 423101); Połonina Caryńska, 840-900 m, (Kotula 1883; Wołoszczak 1894; Jasiewicz 1965); Połonina Caryńska, 1000 m, leg. K. Zarzycki, 15.07.1961 (KRAM 091800, KRA 70648, UAM, LOD 154407); Połonina Caryńska (>300), 873, 884, 917, 980 m, leg. R. Piwowarczyk, 13.08.2009 (KTC); Połonina Caryńska, rocks, near tree line, in direction of Brzegi Górne, leg. A. Jasiewicz, 26.07.1954, (KRAM, 413641); Połonina Caryńska, in direction of Brzegi Górne, dry fallow land, altitude 840 m, leg. A. Jasiewicz, 26.07.1954 (KRAM, 342601, 413631), leg. A. Jasiewicz, K. Zarzycki, 26.07.1954, (KRAM, 342329, 342470); Caryńskie, xerothermic meadow, on a roadside slope, leg. M. Szewczyk, 12.07.2009 (KRA); Zwór near Bereżki, 630 m, leg. A. Jasiewicz, 03.08.1960 (KRAM, 414007), Jasiewicz 1965; Brzegi Górne, Knapp 1872; 1.5 km NNE of Brzegi Górne, eastern slopes of Połonina Wetlińska near road to Nasiczne, on a steep roadside slope (4), on *Thymus pulegioides*, vid. B. Gierczyk, 10.08.2005 (Gierczyk & Soboń 2008); Berehy Górne, rocks, near road to Ustrzyki Górne, on *T. pulegioides* (>5), vid. B. Gierczyk, 10.08.2005, 10.07.2008 (Gierczyk & Soboń 2008); slope near road to Brzegi Górne (>10), 820 m, leg. R. Piwowarczyk, 13.08.2009 (KTC); Brzegi Górne, near a crossroads to Nasiczne, steep roadside slope (>10), 770 m, leg. R. Piwowarczyk, 14.08.2009 (KTC); Brzegi Górne, near start of tourist trail to Połonina Wetlińska, behind ticket office, dry grassland (>50), 735 m, leg. R. Piwowarczyk, 14.08.2009 (KTC); **79:** Czeremcha (Kotula 1883); **GF: 90:** Przemyśl, dry roadside, 355 m, leg. M. Wolanin, 30.07.2008 (KRA); Kruhel Mały (Krzemieniec), xerothermic grassland, 250 m, leg. M. Wolanin, 30.06.2009 (KRA); Jaksmanice, on a slope behind a pasture, leg. J. Maciurzyńska, 05.07.1986 (KRAM, 367415, 367696); **GG: 00:** between Dubnik and Sierakoście, xerothermic grassland, 260 m, leg. M. Wolanin, 03.07.2009 (KRA); dry grassland with *Salvia pratensis* on a slope of Wiar valley, between Przemyśl and Arłamowo, leg. M. Szewczyk, 12.07.2008 (KRA); **60:** Tarnica 1300 m (Kotula 1883), Halicz, (Kotula 1883); Bukowe Berdo, (Knapp 1872); Krzemień 1180 m, (Kotula 1883); Krzemień, grassland on S slopes, leg. K. Zarzycki, 28.08.1958 (KRAM, 065769); Krzemień, on a sunny grassland, leg. J. Twarogowa, 02.08.1953 (KRAP, 433); Szeroki Wierch, S slope, 960 m, vid. W. Paul, 1994 unpubl. (ATPOL database); **70:** Beskid 1100 m, Kotula 1883; 1.5 km NE of Wołosate, on a dry glade in Zwir stream valley (>10 shoots in 2 clumps), on *T. pulegioides*, vid. B. Gierczyk, 13.07.2008 (Gierczyk & Soboń 2008).

Appendix 3. List of localities of *Orbanche alba* subsp. *major*

GE: 35: nature reserve Brzeźno near Chełm (>50), 51°09'18"N, 23°35'31"E, leg. K. Zarzycki, 04.07.1972 (KRAM, 205709), leg. J. Wójciak, R. Piwowarczyk, 12.07.2008 (KTC); **44:** Kumów Majoracki, edge of Płachstocha forest complex (>10), 51°01'18"N, 23°33'03"E, vid. P. Chmielewski, 01.07.2007. **45:** between nature reserve Żmudź and Wólka Leszczańska village (>20), 51°00'36"N, 23°39'10"E, leg. P. Chmielewski, 2007, leg. R. Piwowarczyk, 08.06.2007 (KTC); Leszczany (<5), 51°01'28"N, 23°34'53"E, leg. P. Chmielewski, R. Piwowarczyk, 15.07.2006 (KTC); **55:** Żmudź (<5), GE5507, 51°00'16"N, 23°40'01"E, vid. P. Chmielewski, 2007; between Wólka Leszczańska and Kolonia Maziarnia villages (>5), 50°59'55"N, 23°38'16"E, leg. P. Chmielewski, 2007, leg. R. Piwowarczyk, 08.06.2007; Kolonia Leszczany, calcareous hill Kurawica (>40), 51°00'19"N, 23°35'41"E, vid. A. Cwener, P. Chmielewski, R. Piwowarczyk, 2007, leg. P. Chmielewski, R. Piwowarczyk, 2007 (KTC), **61:** Bryczówki (5), 50°52'55"N, 23°03'09"E, vid. P. Chmielewski, 01.08.2009; **62:** Dworzyska, slope of Wieprz

valley, (>10), 50°55'45"N, 23°09'53"E, leg. I. Iwaniak, 08.07.1957 (LBL), leg. A. Cwener, M. Wrzesień, 17.07.2006 (LBL), leg. A. Cwener, 24.06.2007 (LBL); Krynicy, Krasnystaw County, shrubland in a loess gully, leg. I. Iwaniak, 07.07.1958 (LBL); Izbica, Krasnystaw County, shrubland in a loess gully, leg. I. Iwaniak, 08.07.1957 (LBL); **63**: Drewniki near Skierbieszów, sunny chalk slopes, leg. D. Fijałkowski, 14.06.1965 (LBL); **63/73**: Huszczka Duża (>50), 50°50'40"N, 23°18'54"E, vid. A. Cwener, 2006 (LBL); **64**: Skomorochy Małe, slope of Wolica valley (>20), 50°50'21"N, 23°31'01"E, vid. P. Chmielewski, 01.07.2007; **65**: Białowody (>30), 50°52'34"N, 23°36'51"E, vid. P. Chmielewski, 27.06.2008; **72**: Grabowiec-Góra, on Wzgórze Zamkowe hill (<10), 50°49'01"N, 23°33'37"E, vid. P. Chmielewski, 01.07.2007; **74**: Świdniki near Grabowiec, Hrubieszów County, chalk slope, leg. D. Fijałkowski, 03.08.1958 (LBL); Rogów, Hrubieszów County, shrubland on a calcareous slope, leg. D. Fijałkowski, 07.07.1949 (LBL); **77**: Gródek (Czumów) (>15), 50°47'46"N, 23°57'11"E, leg. A. Cwener, 28.08.2007 (LBL), Czumów near Hrubieszów, loess slope, leg. D. Fijałkowski, 18.07.1956 (LBL); **82**: Kąty II, Wieprzecka Góra hill (>20), 50°40'37"N, 23°07'31"E, leg. R. Piwowarczyk, W. Michalczuk & P. Chmielewski, 13.07.2008 (KTC); **83**: near Zamość, clearings in beech forest, leg. D. Fijałkowski, 02.07.1951 (LBL); **91**: Kosobudy near Zamość, oak forest, leg. J. Motyka, 06.08.1949 (LBL); **94**: Komarów-Wieś, slope of Sieniocha river valley (>30), 50°37'03"N, 23°27'26"E, vid. P. Chmielewski, 2007; **95**: Kraczew, calcareous slope (>20), 50°35'51"N, 23°34'05"E, vid. W. Michalczuk, 2007, leg. R. Piwowarczyk, 2007 (KTC); **GF**: **15**: Kolonia Jarczów II (>20), 50°24'14"N, 23°34'24"E; 50°24'10"N, 23°33'06"E, vid. P. Chmielewski, R. Piwowarczyk, 13.07.2006; Korhynie, ecological site (<10), 50°24'19"N, 23°32'31"E, vid. A. Cwener, P. Chmielewski 28.07.2009; Przeorsk, Łysa Góra hill (>30), 50°25'22"N, 23°31'01"E, leg. P. Chmielewski, R. Piwowarczyk, 09.06.2007 (KTC); **25**: nature reserve Machnowska Mt. (>50), 50°22'10"N, 23°35'20"E, leg. P. Chmielewski, R. Piwowarczyk, 09.06.2007 (KTC); **FE**: **23**: Męcierz, xerothermic grasslands (<50), 51°18'25"N, 21°54'28"E, leg. P. Chmielewski, R. Piwowarczyk, 23.08.2008 (KTC), (Kucharczyk 2001); **42**: Kamień near Józefów, xerothermic grassland on a chalk slope, leg. M. Kucharczyk, 08.08.1980 (LBL); **50**: Bałtów, on left bank of Kamienna river (>15), 51°01'07.7"N, 21°32'55.8"E, leg. B. Maciejczak, 2007 (KTC), leg. R. Piwowarczyk, 24.06.2007 (KTC); [Bałtów, sunny slopes of steep edge of Kamienna valley, leg. T. Głazek (KRA, 0225393); clayey, dark ravine, Bałtów, leg. A. Pieńkowska, 05.06.1961 (KRAM); Bałtów, sunny slope, leg. A. Fotyga, 17.07.1974 (KTU, 10550)]; **51**: Skarbka Dolna, on slopes of Kamienna valley (<10), 51°00'58"N, 21°34'38"E, leg. R. Piwowarczyk, 04.07.2004 (KTC); Pętkowice, on a slope of Kamienna valley (>5), 51°01'07"N, 21°35'10"E, leg. R. Piwowarczyk, 26.06.2003, 04.07.2004 (KTC); **59**: Lipnik near Bychawa, on a chalk slope, leg. B. Małyszczek, 17.08.1963 (LBL); **72**: Mała Bandocha and Duża Bandocha hills near Lasocin (>80), 50°53'07.5"N, 21°45'12.2"E, leg. R. Piwowarczyk, 25.06.2002 (KRA, 0267162), leg. R. Piwowarczyk, 03.07.2004, 15.07.2005, 24.06.2007 (KTC).

Erroneous records:

Pieniny Mts.: reported only generally (as *O. alba*) by Filarszky 1898 (after Zarzycki 1981), from Homole Gully (Wąwóz Homole) in Small Pieniny Mts. (Małe Pieniny) by A. and J. Kornaś (after Zarzycki 1981), scree under Trzy Korony in Central Pieniny Mts., and glade Zaosice in Western Pieniny Mts. (Kaźmierczakowa 2008). My field research and verified herbarium specimens showed that they are localities of *O. caryophyllacea*.

Beskid Sądecki Mts.: open shrubland on S slopes of Poprad valley in Żegiestów, 430 m, parasite on *Veronica chamaedrys* (Nowiński 1962). Most probably it is a locality of *O. caryophyllacea*.

Ojców National Park: Near Ojców, Prądnik Korzkiewski, rocks on valley slopes, secondary xerothermic grassland (leg. S. Michalik, rocks on valley slopes, secondary xerothermic grassland, parasite on *Thymus*, 15.06.1959, KRAM, 456147, Michalik 1978). The specimen is very young, which makes its verification impossible, and my field research did not confirm this locality. Most probably it is a locality of *O. bartlingii*, which was recorded at several nearby sites in the Park.

Łódź Province: nature reserve Winnica, Burzenin Commune, xerothermic grassland, leg. M. Kurzac, 04.06.2010 (LOD, 155099) – misidentified *O. lutea*; Brzostek, Przedbórz Commune, hill near forest along road Brzostek-Policzko-Chojna, xerothermic grassland, leg. M. Kurzac, 07.07.2010 (LOD, 154948) – misidentified *O. kochii*; Włyn near Rossoszyca (Sowa R. *et al.*, unpubl. 1979, ATPOL database, Jakubowska-Gabara *et al.* 2011) – no herbarium specimens, so verification is impossible.

Małopolska Vistula Gorge: Kazimierz Dolny (Sławiński 1952) – needs to be confirmed, no herbarium specimens; Dorotka (Kucharczyk 2001) – field research detected only *O. lutea*, *O. picridis*, and *O. caryophyllacea* (Piwowarczyk *et al.* 2011); Dwikozy (Kucharczyk 2001) – field research detected only *O. lutea* (Piwowarczyk *et al.* 2011) and *O. caryophyllacea*.

Ambiguous localities, difficult to verify:

Podobień, leg. Prof. Polański, 28.07.1913 (KRAM, 037798).

Forester's lodge ("Leśniczówka"), leg. H. Zapałowicz, 16.07.1880 (KRAM, 251486).

Łysa Góra, leg. T. Wilczyński (KRAM, 295390).