Biodiv. Res. Conserv. 32: 29-44, 2013

BRC
www.brc.amu.edu.pl

DOI 10.2478/biorc-2013-0015

Submitted 28.02.2012, Accepted 29.10.2013

Melampyrum cristatum L. – a rare river corridor plant in Wielkopolska and Poland

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Abstract: *Melampyrum cristatum* is an extremely rare, native, hemi-parasitic, vascular plant, recently considered to be extinct in Poland. The article presents data concerning new localities of the species recorded in 2007-2012 in the valley of the River Warta (Wielkopolska, Poland). Local distribution of *M. cristatum* in the Natura 2000 sites: PLH300012 – Rogalińska Dolina Warty (ca. 147.5 sq. km) and PLH300053 – Lasy Żerkowsko-Czeszewskie (ca. 71.6 sq. km), as well as its updated regional (in Wielkopolska) and national (Poland) ranges are shown on maps and interpreted on the background of the geomorphic diversity of occupied habitats. The results suggest that in Poland the species is distributed mainly along valleys of large, lowland rivers, which corresponds with its 'River Corridor Plant' status in Central Europe. The species rarity is discussed considering its outline phytocoenological scale (comprising various plant communities within 6 syntaxonomical classes), the riverine distribution pattern and chosen biological features. Natural habitat heterogeneity along with changeable water regime in floodplains, as well as potential limitations of myrmecochoric seed dispersal, may constitute potential reasons for the species low frequency.

Key words: *Melampyrum cristatum*, distribution, large river valleys, rarity and threat of species, occurrence in plant communities, the River Warta, Natura 2000 sites (PLH300012, PLH300053)

1. Introduction

Any botanist experienced in long-term research on flora and vegetation in a particular area, sooner or later, realises that only a limited number of species are locally or even regionally common, whereas a majority of biodiversity components are actually rare (Kornaś & Medwecka-Kornaś 2002). In order to protect such species successfully, we should focus not only on potential negative genetic effects in small populations, but also on a conservation of appropriate habitats in possibly large areas. This view generally corresponds with the so-called 'habitat quality' paradigm, which does not actually contradict with the mentioned 'genetic' approach (Ouborg *et al.* 2006). Any successful implementation of this premise, however, would require a good recognition of habitats in which these rare plants are capable to exist.

An analysis of an extensive dataset (mostly stored in a computer database) on vascular plant flora (ca. 234450 records) and vegetation (4527 relevés) collected from the Wielkopolska region, has convinced me that even in large, relatively not transformed areas, there are many extremely rare, native species, though, without evidence whether or not they have been recently losing their localities. Moreover, our knowledge about their habitat requirements usually remains insufficient, just because they are so rare. The problem seems to be particularly important when considering the species threat status within certain areas.

This article focuses on a good example of the mentioned group, i.e. crested cow-wheat *Melampyrum cristatum* L. (Figs. 1-2) – a scarcely recorded, thus hardly known vascular plant, which was, incorrectly, considered to be extinct in Poland (Zarzycki & Szeląg 2006). In the light of accessible at that time (Zając & Zając 2001) and recently published (Brzeg 2005), as well as presented hereby data on distribution of crested cow-wheat in Poland, the species has several, though not numerous, currently existing localities in various parts of the country. *M. cristatum* has been considered (by Burkart 2001) as one of the 129 so-called River Corridor Plants (RCP) in Central Europe. This study was expected to demonstrate that in Poland this species

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Fig. 1. A flowering spike of crested cow-wheat *Melampyrum cristatum* growing in the purple-moor grass meadow *Molinietum caeruleae* in the Natura 2000 SCI Rogalińska Dolina Warty (photograph by W. Stachnowicz, June 2007)

Fig. 2. Upper inflorescence of crested cow-wheat *Melampyrum cristatum* growing in the riparian oak-elm-ash forest *Querco-Ulmetum minoris* in the Natura 2000 SCI Lasy Żerkowsko-Czeszewskie (photograph by W. Stachnowicz, June 2012)

is indeed linked to the valleys of large rivers and that its phytocoenological scale may be substantially wider than usually considered (e.g. Matuszkiewicz 2001). Nevertheless, as it will be shown below, even in relatively well explored, extensive sections of some river valleys, crested cow-wheat is still a rare species. In this light and also considering a lack of precise information on the species ecology and population biology, natural reasons for its rarity remain insufficiently recognised. Consequently, its threat status, particularly in the whole country, needs further assessment, similarly like in case of many other species reflecting more or less diversified geographical range in Poland (Załuski 2009).

The aims of this study are: (1) to document new and recently confirmed localities of *Melampyrum cristatum* observed in 2007-2012 in the middle part of the valley of the River Warta (Wielkopolska, Poland), (2) to update the species distribution map in Poland (using also other data available in pertinent literature); (3) to test the mentioned RCP status of *M. cristatum* in Poland, by making outline, quantitative analysis of potential links of the species range with riverine landscapes interpreted geomorphologically; (4) to check if the mentioned RCP pattern and rarity are noticeable at different scales of observation, i.e. from a local up to a supra-regional perspective.

2. Areas of research, material and methods

The article is based on chosen, so far unpublished observations made directly in-field in 2007-2012, and it also considers available phytogeographical data taken from Polish literature.

Results of original field investigations were used to describe the local or sub-regional distribution pattern of *Melampyrum cristatum*, its outline phytocoenological scale, and to assess the species current regional rarity. The author's geobotanical research comprised (mostly original) floristic and phytosociological data collected in more than 15120 sites (positioned with GPS) in the region of Wielkopolska (Fig. 3). This material contains detailed information on vegetation types analysed in a computer database linked to a multi-layer digital (GIS) map. Recently, i.e., in 2007-2013, the observations were concentrated on the chosen, middle sections of the valley of the River Warta and on adjacent non-riverine landscapes (Fig. 3). Altogether, out of 15124 investigated localities in the Wielkopolska Province, 8396 sites (55.5%) were precisely associated with the River Warta floodplains, whereas the remaining 6728 (44.5%) were situated definitely in non-riverine landscapes, though, sometimes in their proximity. None

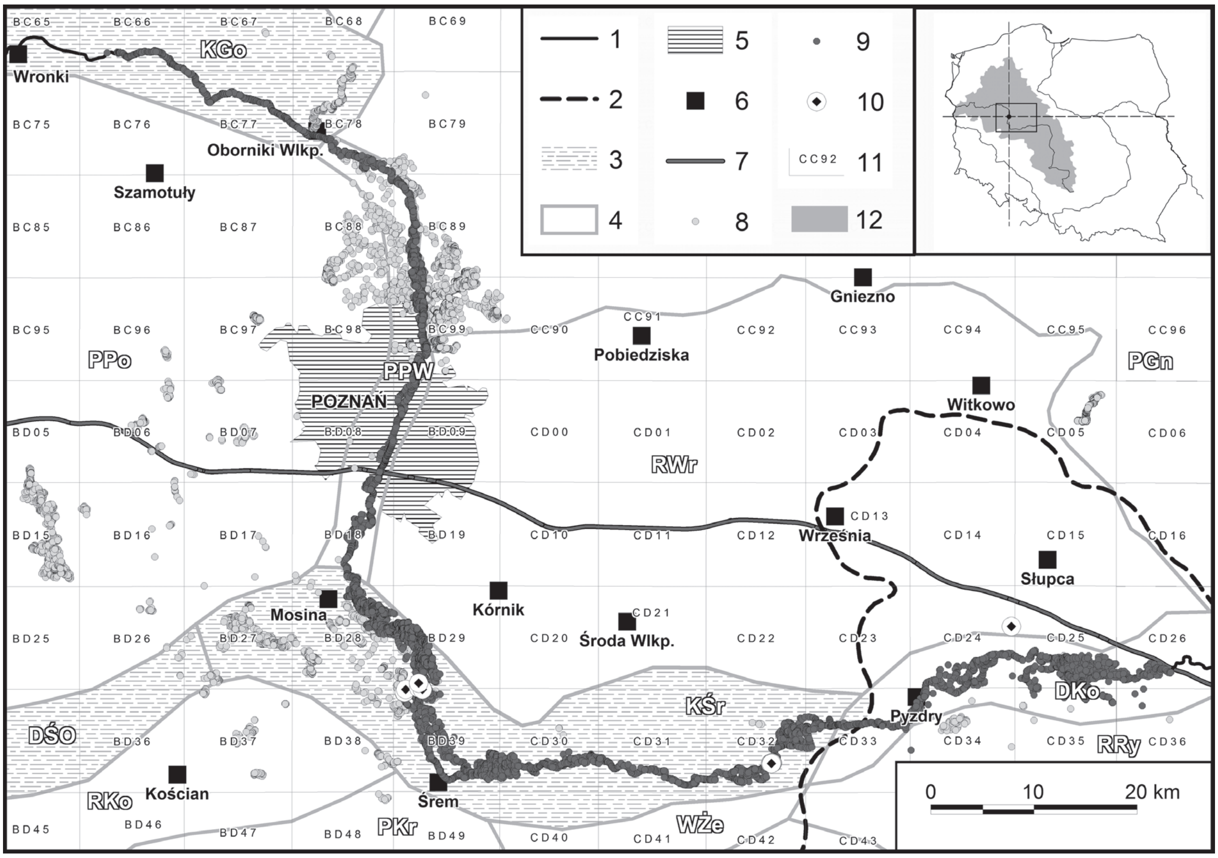

Fig. 3. Most intensively investigated areas in the Wielkopolska region with particular attention paid to chosen sections of the River Warta valley
Explanations: 1 – the river Warta; 2 – boundary of the last, Poznanian Phase of glaciation (according to Krygowski 2007); 3 – proglacial stream valleys (acc. to Kondracki 2002); 4 – physical-geographic meso-regions (Kondracki 2002), KGo – Kotlina Gorzowska (the Gorzów Basin), PPo – Pojezierze Poznańskie (the Poznanian Lakeland), PPW – Poznański Przełom Warty (the Poznanian Ravine of the River Warta), PGn – Pojezierze Gnieźnieńskie (the Gnieźnieńskie Lakeland), KŚr – Kotlina Śremska (the Śrem Basin), DŚO – Dolina Środkowej Obry (the Middle Obra Valley), RKo – Równina Kościańska (the Kościan Plateau), RWr – Równina Wrzesińska (the Września Plateau), RRy – Równina Rychwalska (the Rychwal Plateau), DKo – Dolina Konińska (the Konin Valley), PKr – Pojezierze Krajeńskie (the Krajeńskie Lakeland), WŻe – Wysoczyzna Żerkowska (the Żerków Upland); 5 – the city of Poznań (the capital of the Wielkopolska Province); 6 – other, more important towns; 7 – the A2 motorway; 8 – investigated sites (acc. to the GPS coordinates) outside the river valley; 9 – investigated sites positioned within riverine landscapes; 10 – localities of *Melampyrum cristatum* (a locality between Słupca and Pyzdry – acc. to description by Brzeg 2005); 11 – the ATPOL square grid (10x10 km) with codes of basic fields; 12 – the River Warta catchment area (on the background of the map of Poland)

of data was collected deliberately in order to find any particular species, including *M. cristatum*. Most of these observations were carried out in seven different physical-geographic meso-regions (according to Kondracki 2002) in the middle part of Wielkopolska (Fig. 3). The studied sites were situated both in and outside areas shaped under the Poznanian Phase of the Baltic (Vistulian, Weichselian) Glaciation, e.g., moraine plateaus, as well as large river valleys (Fig. 3). They referred to many different habitats, both non- and typically riparian ones, including at least 235 plant communities classified within 26 phytocoenological classes (out of 28 known from the widely considered Wielkopolska region – according to Brzeg & Wojterska 2001). Thus, the investigated sites sufficiently represented general geologic and geomorphic diversity of the central part of Wielkopolska. Considering also that most of them (i.e. ca. 199300 records from over 21380 localities) were collected in 2007-2013, these data could be used as an up-to-date reference for an outline assessment of crested cow-wheat's rarity in the middle part of Wielkopolska.

The current presence of *Melampyrum cristatum* was documented in 7 original phytocoenological relevés (Table 1) out of over 2700 made in 2007-2013 (according to the Braun-Blanquet's method). This documentation, along with pertinent literature, was used to discuss an outline phytocoenological scale of the species in Wielkopolska.

The new localities of *Melampyrum cristatum* were discovered in the Natura 2000 Site of Community Interest (SCI) Rogalińska Dolina Warty (PLH300012) established under the habitat directive (92/43/EEC), and extensively investigated by the author in 2007-2012. The site covers ca. 147.5 sq. km and comprises both the River Warta floodplains, as well as adjacent non-riverine landscapes (Fig. 4). Another, previously known (cf. Zając & Zając 2001) locality of *M. cristatum* in the valley of the River Warta near Dębno, ca. 2 km on the S of Orzechowo (Fig. 5), was confirmed by the author

Table 1. Occurrence of *Melampyrum cristatum* in plant communities in the investigated areas

Successive No.		1	2	3	4	5	6	7
Field No. of relevé		K-93	K-97	2234	K-94	9425	9422	3566
Author(s)		R&S	R&S	WSt	R&S	WSt	WSt	WSt
	day	20	20	10	20	16	16	20
Date:	month	6	6	10	6	6	6	10
	year	2007	2007	2007	2007	2012	2012	2008
Locality		RDW	RDW	RDW	RDW	LŻC	LŻC	RDW
Density of tree layer	a [%]	-	-	-	-		65	45
Density of shrub layer	b [%]	min	min	-	-	20	55	40
Cover of herb layer	c [%]	90	100	95	100	80	70	20
Cover of moss layer	d [%]	-	-	-	-	min	min	5
Area of relevé	[m^2]	15	15	6	8	16	250	300
Syntaxon		M-c	M-c	C-e	C-R	C-R	Q-U	Q-U
Syngenesis		SN	SN	NA	NA	NA	NP	NP
Number of species		25	15	12	15	21	44	41
I. Ch. *Trifolio-Geranietea*								
Melampyrum cristatum		1	+	+	+	+	2a	+
Agrimonia procera		.	+	.	.	.	.	+
Hypericum perforatum		.	.	1	+	.	.	+
Vincetoxicum hirundinaria		.	.	.	.	.	.	2a
II. Ch. *Molinietum coeruleae* and *Ch. *Molinion*								
* *Cnidium dubium*		1	1	+	.	.	.	1
* *Molinia caerulea*		2b	.	.	.	.	.	.
Galium boreale		2a	.	.	.	.	.	.
Carex tomentosa		+	.	.	.	.	.	.
* *Sanguisorba officinalis*		r	.	.	.	.	.	.
* *Inula salicina*		.	5	.	2b	.	.	.
Serratula tinctoria		.	1	.	.	.	.	+
Betonica officinalis		.	.	.	.	.	.	1
* *Selinum carvifolia*		.	.	.	.	.	.	+
III. Ch. *Molinietalia* and *Ch. *Molinio-Arrhenatheretea*								
* *Vicia cracca*		1	1	1	.	.	+	+
Veronica longifolia		+	.	.	1	.	+	.
* *Carex hirta*		2a	.	.	.	.	.	+
Lysimachia vulgaris		2a	.	.	+	.	.	.
* *Alopecurus pratensis*		1	+	.	.	.	.	.
* *Ranunculus acris*		+	+	.	.	.	.	.
* *Arrhenatherum elatius*		.	.	.	.	+	1	.
* *Lysimachia nummularia*		.	.	.	.	.	2a	+
* *Festuca rubra*		.	.	.	.	.	+	+
Scutellaria hastifolia		.	.	.	.	.	+	+
* *Veronica chamaedrys*		.	.	.	.	.	+	+
IV. Ch. (dom.) *Calamagrostietum epigeji* and *Ch. *Epilobietea*								
Calamagrostis epigejos		+	.	5	1	2b	2a	2a
* *Dactylis polygama*		.	.	.	.	.	+	1
V. Ch. (opt.) *Carduo crispi-Rubetum caesii* and *Ch. *Calystegion sepium*								
Rubus caesius		2b	2b	1	4	3	2a	+
* *Euphorbia palustris*		.	.	.	2b	.	.	.
* *Achillea salicifolia*		.	.	.	1	.	.	.

Carduus crispus		.	.	.	.	+	.	.
* *Humulus lupulus*		.	.	.	.	.	+	.
VI. Ch. *Convolvuletalia* and *Ch. *Artemisietea*								
* *Equisetum arvense*		1	.	.	+	1	+	.
* *Cirsium arvense*		1	+	.	.	.	.	.
Glechoma hederacea		.	.	.	.	2b	2b	+
Galium aparine		.	.	.	.	+	+	+
* *Tanacetum vulgare*		.	.	.	.	+	+	+
Torilis japonica		.	.	.	.	r	.	r
Chaerophyllum temulum		.	.	.	.	2a	2a	.
Elymus caninus		.	.	.	.	2a	2a	.
Geranium robertianum		.	.	.	.	2a	1	.
* *Urtica dioica*		.	.	.	.	+	1	.
* *Artemisia vulgaris*		.	.	.	.	+	+	.
Geum urbanum		.	.	.	.	.	1	1
Alliaria petiolata		.	.	.	.	.	1	+
VII. D. *Querco-Ulmetum minoris* and *Ch. *Querco-Fagetea*								
Acer campestre	b/c	.	.	.	.	./+	2a/1	.
Quercus robur	a	.	.	.	.	.	3	3
Fraxinus excelsior	a	.	.	.	.	.	2b	.
Tilia cordata	a	.	.	.	.	.	2b	.
Ulmus minor	c	.	.	.	.	.	+	.
* *Atrichum undulatum*	d	.	.	.	.	.	.	+
* *Brachypodium sylvaticum*		.	.	.	.	.	.	+
VIII. Ch. *Rhamno-Prunetea*								
Frangula alnus	b/c	r/.	+/.	./+	.	.	+/+	+/+
Cornus sanguinea	b/c	.	.	.	./+	2b/2b	.	3/2b
Rhamnus cathartica	b/c	.	.	.	.	r/.	3/2a	./r
IX. Others								
Agrostis capillaris		+	.	2a	.	.	.	1
Ulmus glabra	b	.	r	.	.	.	.	r
Viola canina		.	.	+	.	.	.	+
Brachythecium rutabulum	d	.	.	.	.	+.2	+.2	1
Poa palustris		.	.	.	.	1	2a	.
Convallaria majalis		.	.	.	.	.	1	+
Calamagrostis arundinacea		.	.	.	.	.	2a	.

Sporadic taxa: I. *Agrimonia eupatoria* 9422 (r); *Clinopodium vulgare* 3566 (+); *Trifolium medium* K-94 (+); **III.** **Briza media* 3566 (r); *Carex cespitosa* K-93 (+); *Filipendula ulmaria* K-93 (r); **Galium mollugo* 9422 (+); *Juncus conglomeratus* 2234 (+); **Lathyrus pratensis* K-97 (+); **V.** **Symphytum officinale* 3566 (r); **VI.** **Elymus repens* 9422 (1); **Linaria vulgaris* 3566 (+); **VIII.** *Crataegus monogyna* c 3566 (+); *Euonymus europaeus* c 3566 (+); *Prunus spinosa* c 9422 (+); *Pyrus communis* b 3566 (r); **IX.** *Anthoxanthum odoratum* K-93 (+); *Bidens frondosa* K-93 (r); *Cardaminopsis arenosa* 2234 (+); *Carex acutiformis* K-97 (1); *Carex gracilis* K-94 (+); *Carex pairae* 9422 (+); *Carex pallescens* K-93 (1); *Epipactis helleborine* 2234 (+); *Erysimum cheiranthoides* 9422 (+); *Euphorbia cyparissias* 3566 (+); *Galium palustre* K-93 (+); *Hieracium umbellatum* 3566 (+); *Moehringia trinervia* 9422 (+); *Padus avium* b/c 9422 (1/1); *Padus serotina* c 9422 (+); *Phragmites australis* K-94 (+); *Plagiomnium* sp. d 3566 (1); *Populus alba* c 9425 (+); *Potentilla erecta* K-93 (+); *Ribes nigrum* K-94 (+); *Saponaria officinalis* 9422 (+); *Scutellaria galericulata* K-97 (+)

Explanations: Author(s), R&S – W. Rakowski & W. Stachnowicz; WSt – W. Stachnowicz; Locality, RDW – the Natura 2000 SAC Rogalińska Dolina Warty (Fig. 4), LŻC – the Natura 2000 SAC Lasy Żerkowsko-Czeszewskie (Fig. 5); Syntaxon, M-c – *Molinietum coeruleae* Koch 1926, C-R – *Carduo crispi-Rubetum caesii* Brzeg in Brzeg et M. Wojterska 2001, C-e – *Calamagrostietum epigeji* Juraszek 1928, Q-U – *Querco-Ulmetum minoris* Issler 1924; Syngenesis (cf. Faliński 1969) of vegetation types – acc. to Brzeg & Wojterska (2001), SN – seminatural community, NA – natural auksochoric community, NP – natural perdochoric community

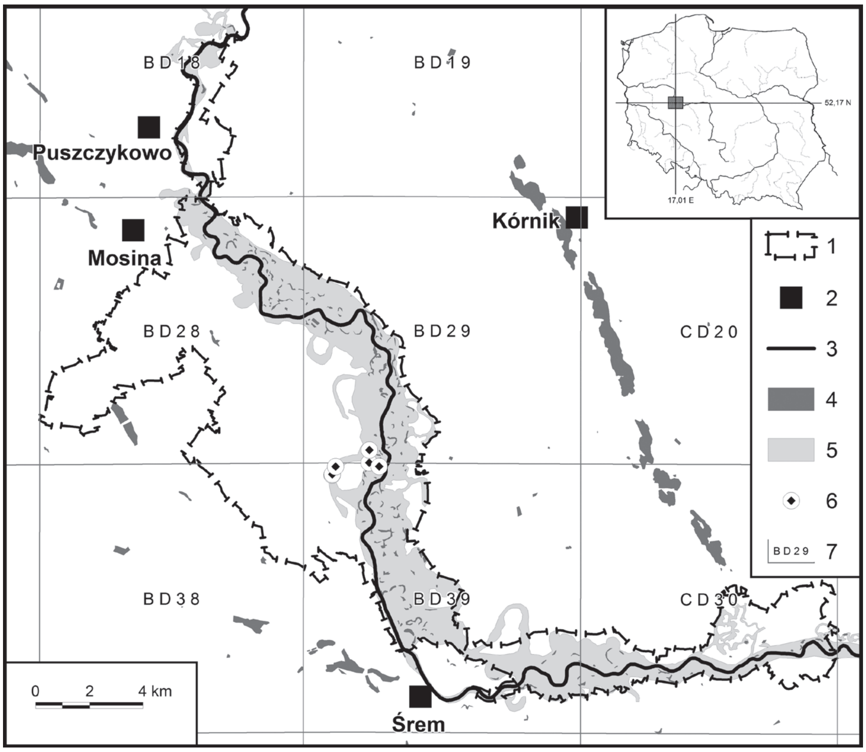

Fig. 4. Distribution of *Melampyrum cristatum* in the Natura 2000 site Rogalińska Dolina Warty (PLH300012)
Explanations: 1 – boundaries of the Natura 2000 Special Area of Conservation Rogalińska Dolina Warty (PLH300012), 2 – towns, 3 – the River Warta, 4 – lakes, ponds and oxbows, 5 – floodplain (today's river terrace drawn on the basis of hydrological maps, aerial photographs and field observations), 6 – localities of *Melampyrum cristatum* observed in 2007-2009, 7 – national cartogram square-grid (ATPOL) and codes of basic fields

in 2012. It is situated within the Natura 2000 SCI called Lasy Żerkowsko-Czeszewskie (PLH300053), which comprises ca. 71.6 sq. km.

The second, i.e., published sources of information, supplemented by new data, were used to chart a (supra-)regional range of the species in Wielkopolska and Poland. Eventually, chosen non-phytogeographic maps were treated as comparative backgrounds for interpretation of both regional, as well as national distribution patterns of *M. cristatum*. These comparisons were focused on large river valleys interpreted hydrogeomorphologically. The updated range of *M. cristatum*

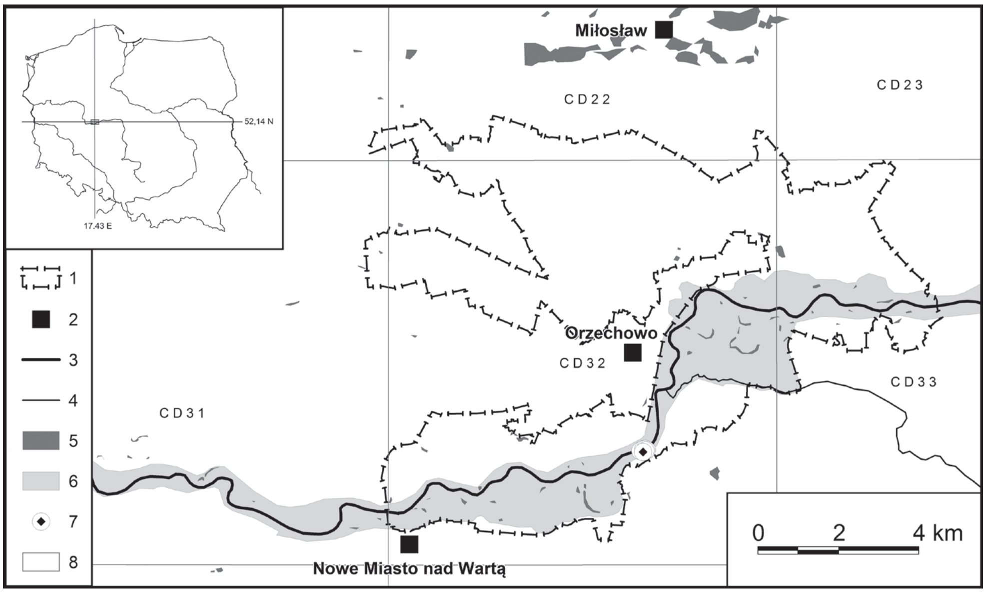

Fig. 5. Distribution of *Melampyrum cristatum* in the Natura 2000 site Lasy Żerkowsko-Czeszewskie (PLH300053)
Explanations: 1 – boundaries of the Natura 2000 Special Area of Conservation Lasy Żerkowsko-Czeszewskie (PLH300053), 2 – towns, 3 – the River Warta, 4 – the River Lutynia (a tributary of Warta), 5 – lakes, ponds and oxbows, 6 – floodplain (today's river terrace drawn on the basis of hydrological maps, aerial photographs and field observations), 7 – localities of *Melampyrum cristatum* observed in 2012, 8 – national cartogram square-grid (ATPOL) and codes of basic fields

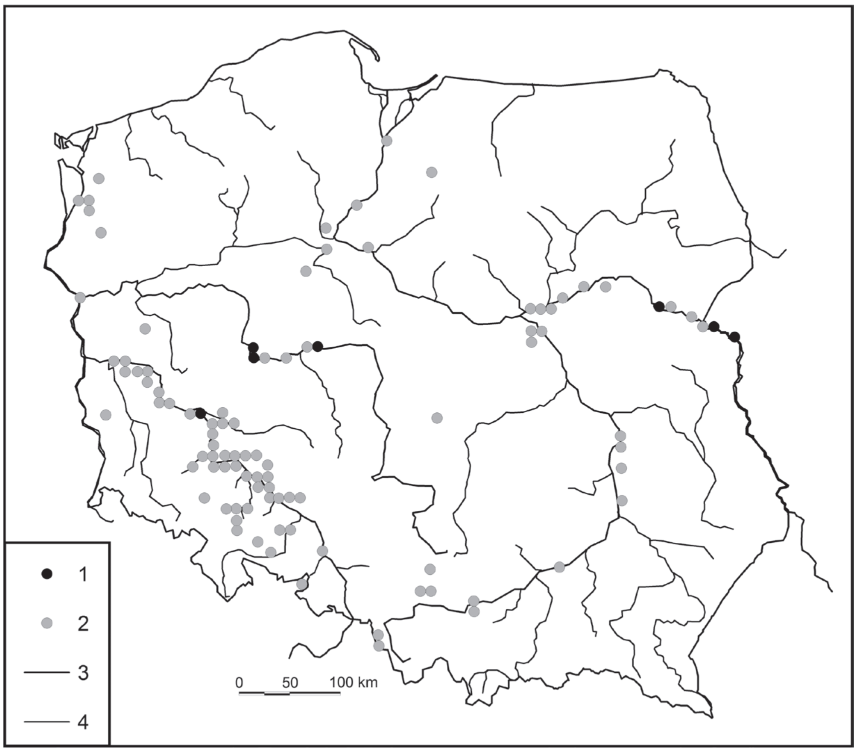

Fig. 6. Updated distribution of *Melampyrum cristatum* in Poland

Explanations: 1 – new localities of *Melampyrum cristatum* (including these presented in Fig. 3 and some localities specified by Brzeg 2005), 2 – localities previously published in the national vascular plants distribution atlas (Zając & Zając 2001), 3 – main rivers, 4 – others, more important rivers

in the whole country (Zając & Zając 2001; Fig. 6) was matched up to a generalised, geological map of Poland (Gilewska 1999; Fig. 7). To get the regional species distribution pattern, the updated part of the mentioned cartogram was displayed on the background of a GIS version of a geomorphic map of Wielkopolska

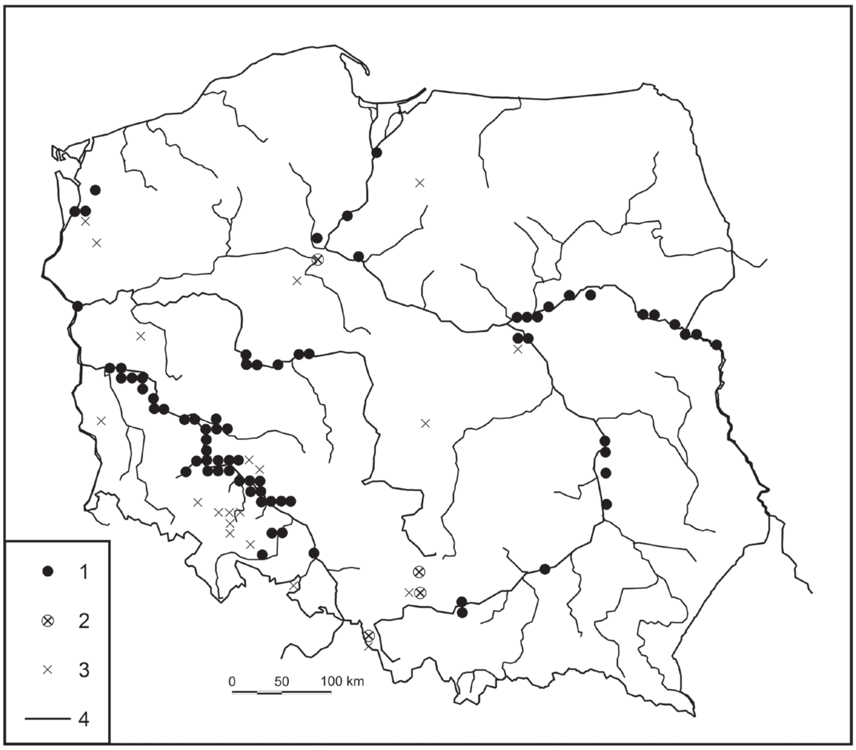

Fig. 7. Distribution of *Melampyrum cristatum* in Poland interpreted geomorphologically (on the background of a geo-registered copy of a geological map by Gilewska 1999)

Explanations: 1 – localities of *Melampyrum cristatum* connected with the main Holocene river terraces, 2 localities linked to the Pleistocene terraces, 3 – other localities (outside the Holocene or Pleistocene terraces), 4 – main, large rivers, 5 – other, more important rivers

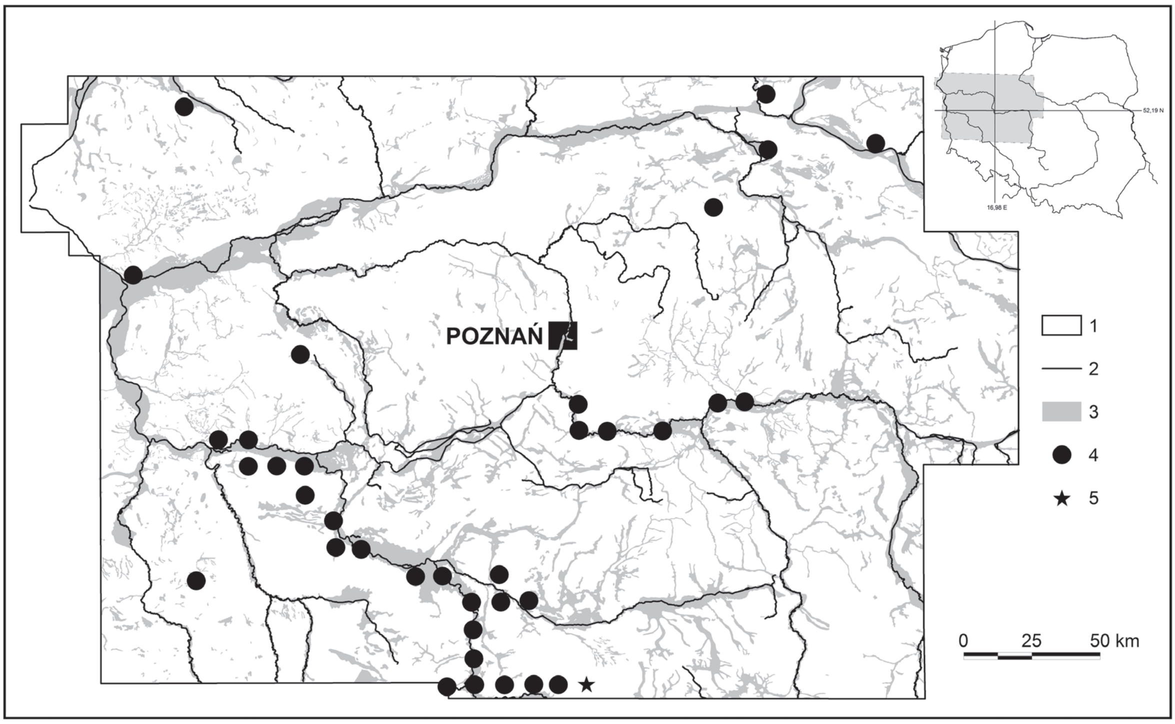

Fig. 8. Regional distribution of *Melampyrum cristatum* on the background of the river valleys according to a geomorphic map of Wielkopolska (Krygowski 2007)
Explanations: 1 – range of available layers of the digital geomorphic map of Wielkopolska (Krygowski 2007), 2 – main rivers, 3 – a GIS layer of the geomorphic map of Wielkopolska – floodplain terraces and bottoms of basins, 4 – localities (cartogram fields) of *Melampyrum cristatum*, which correspond to the mentioned GIS layer, 5 – other localities of *M. cristatum* in Wielkopolska

(Krygowski 2007), namely, on its layer called "floodplain terraces and bottoms of (river) basins" (Fig. 8). Finally, the results of general analysis (Figs. 6-8) were tested in local scale, based on the author's own in-field observations within the Natura 2000 sites: Rogalińska Dolina Warty (PLH300012) and Lasy Żerkowsko-Czeszewskie (PLH300053). This distribution maps (topograms) were presented with an originally drawn GIS-layer precisely reflecting the River Warta floodplain (Figs. 4-5), which was recognised using the results of in-field observations and available hydrological maps, as well as aerial photographs.

Names of vascular plants are used after Mirek *et al.* (2002). Names of syntaxa, their natural, semi-natural or synanthropic origin (according to the syngenesis concept by Faliński 1969, 1972) are listed after Brzeg & Wojterska (2001). The only exception of this principle is *Galietum borealis* Nowiński 1928, which is treated here as a synonym of a better known, nomenclatorically valid and in the author's opinion, more adequately defined association of *Molinietum caeruleae* W. Koch 1926. Legal protection status of plants in Poland was based on the Ministry of Environment Regulation of 5th January 2012 (Regulation 2012). The regional threat of vascular plants in Wielkopolska is discussed in reference to the most recent red list of vascular plants by Jackowiak *et al*. (2007), whereas in the whole Poland – according to Zarzycki & Szeląg (2006).

A few specimens documenting *M. cristatum* collected from the investigated sites were deposited in the Herbarium of the Department of Plant Taxonomy at Adam Mickiewicz University in Poznań (POZ).

3. Results

3.1. New localities of *Melampyrum cristatum*

In 2007-2008, altogether five separate localities of *Melampyrum cristatum* were found between Mosina and Śrem in the middle section of the valley of the River Warta in Central Wielkopolska (Fig. 4). All of them are situated on the left side of the river channel, in the vicinity of Tworzykowo, between the villages Jaszkowo and Krajkowo, within the Natura 2000 site Rogalińska Dolina Warty (PLH300012) and in the physical-geographical mesoregion Kotlina Śremska (the Śrem Basin; Fig. 3). Although the sites are separated from each other by a relatively short distance (less than 3 km), they can be attributed to two different 10x10 km squares of the national floristic ATPOL grid system: BD29 and BD39 (Fig. 4).

Another locality was recently confirmed from the Śrem Basin (the ATPOL square No. CD32) during the author's investigations in 2012 (Fig. 5). It is situated on the left bank of the River Warta in the vicinity of Dębno, within the Natura 2000 site Lasy Żerkowsko-Czeszewskie (PLH300053). *Melampyrum cristatum* grows there within and on the edge of the riparian oak-elm-ash forest *Querco-Ulmetum minoris*.

The mentioned two sites (Figs. 4-5) are separated by a distance of at least 35 km. Populations of *Melampyrum cristatum* were morphologically diversified between the sites and they probably represented different subspecies, which are, however, rarely cited and discussed in literature (cf. Jasiewicz 1958; Rutkowski 2004). Individuals observed in the Rogalińska Dolina Warty (Fig. 1) had singular, not branched stems with only few internodes, the lower of which were longer than leaves, which suggests that they belong to the *M. cristatum* subsp. *solstitiale* Ronn. (Jasiewicz 1958). Flowers on individuals found in the second locality were much less distinct in colour (Fig. 2). The following features (after Rutkowski 2004) seem to suggest that they should be attributed to *M. c.* ssp. *cristatum*: well-branched stems with relatively long, arched side-branches, often with flowers; numerous internodes [according to calculations made by Jasiewicz (1958): the lowest number of nodes was 7, though it usually exceeded 9]; leaves 2-5 mm in width. It should be mentioned, however, that whereas, the differences between the mentioned *M. c.* ssp. *solstitiale* and the other subspecies seem to be quite evident, the distinctiveness of *M. c.* ssp. *cristatum* and a very similar (at least in habit) *M. c.* ssp. *ronnigeri* (Poeverl.) Ronn. seems to be not convincingly defined. Moreover, rather high variability of such quantitative characters as the number of nodes, as well as the number of the so-called intercalary leaves (i.e., those situated between the inflorescence and the upper-most branches) makes them not particularly suitable for distinguishing between intra-species taxa. Such a view may be concluded from the results of measurements presented by Jasiewicz (1958), which also seem to suggest that the mentioned *M. c.* ssp. *ronnigeri* comprises a group of individuals which are more or less intermediate between *M. c.* ssp. *solstitiale* and ssp. *cristatum*.

Geomorphologically, both investigated localities (Figs. 4-5) are situated within an active floodplain of the River Warta, in a distance from ca. 5 to 50 m (in Dębno) up to ca. 250 m to 1.5 km from the river channel (in Tworzykowo). The most remote stations (from the river channel) were connected to a large palaeo-meander on the edge of the floodplain (Fig. 4). As far as general habitat conditions are concerned, the species was recorded in alluvial forests, semi-moist meadows, *Calamagrostis epigejos*-dominated grasslands and in mesophilous forest edge communities. These vegetation types will be described and discussed below.

3.2. Occurrence of *Melampyrum cristatum* in plant communities

In the Rogalińska Dolina Warty (Warta river valley near Rogalin) the species was recorded in four natural and semi-natural plant communities of four classes (Table 1) and in one (not documented phytosociologically) pine-oak plantation, situated in the potential habitat of the natural oak-elm-ash riparian forest. Two phytocoenoses (documented by relevés no. 1-2, Table 1) represented relatively rich-in-species, semi-moist purple-moor grass meadows, i.e. *Molinietum caeruleae* (rel. 1), sometimes dominated by *Inula salicina* (rel. 2). The species was also present in the forest edge community of *Carduo crispi-Rubetum caesii* (rel. 4, 5), neighbouring both mentioned meadows (rel. 4) and the riparian oak forests discussed later. Another non-forest locality was overgrown by a grassy aggregation of *Calamagrostietum epigeji* (rel. 3). Finally, *Melampyrum cristatum* was recorded on the edges of better insulated, and relatively rich-in species, parts of the riparian oak-elm forest *Querco-Ulmetum minoris* (rel. 6-7). Most of these communities, excepting *Querco-Ulmetum minoris*, represented relatively more or less stable, though in a longer period, temporary stages of the vegetation succession. Additionally, in the investigated area, the first three of the mentioned phytocoenoses occupied narrow, linear ecotone zones between floodplain forests and non-forest vegetation in regularly inundated palaeo-meanders (usually dominated by sedge communities, e.g. *Caricetum elatae*, often partially mown by farmers) or on the frequently eroded river bank. Considering that the localities of *Melampyrum cristatum* in the mentioned riparian oak-elm-ash forest (rel. 6-7, Table 1) were found on its very edge, thus noticeably less shaded than the inside, it may be concluded that the plant probably demands a relatively high sun exposure.

In the investigated communities, individuals of *Melampyrum cristatum* were never found in large quantities. Most abundantly they were recorded in the oak-elm-ash forest (in Dębno; rel. 6) and in a well-developed, though small patch of purple-moor grass meadow *Molinietum caeruleae* (in Tworzykowo; rel. 1). Such types of semi-moist meadows are not frequent in the valley of the river Warta, where they exhibit some floristic similarities to the more typical floodplain meadows of *Violo persicifoliae-Cnidietum dubii*. In most patches coeno-populations of *M. cristatum* were dominated by other herbaceous species, i.e. *Inula salicina* (rel. 2), *Calamagrostis epigejos* (rel. 3), *Rubus caesius* (rel. 4-5), or by trees (*Quercus robur*; rel. 6-7) and shrubs, such as *Rhamnus cathartica* (rel. 6) or *Cornus sanguinea* (rel. 7). Species richness in the investigated plant communities was diversified from a relatively low (12 species – in *Calamagrostietum* *epigeji* – rel. 3), through an average (15-21 species in *Carduo-Rubetum* – rel. 4-5; 15-25 species in *Molinietum coeruleae* – rel. 1-2), up to a relatively high number of 41-44 species in *Querco-Ulmetum minoris* (rel. 6-7).

3.3. Distribution of *M. cristatum* in Poland and its national, regional and local rarity

The above described local distribution of crested cow-wheat, considered in a (supra-) regional scale, represents only three ATPOL-grid (Zając & Zając 2001) squares (10x10 km): BD29, BD39 and CD32 (Figs. 3-5).

As far as the species regional rarity is concerned, the closest, recently confirmed locality of *M. cristatum* in Wielkopolska is situated in Działy near Ciążeń, in the valley of the small river Meszna, in the Lądek Community District (Brzeg 2005), situated in the vicinity of the N edge of the river Warta valley (ca. 2.5 km). The distance in a straight line between the mentioned locality and the above-presented site near Dębno (Fig. 5) is ca. 26.7 km, and along the river Warta course – 34 km (Fig. 3). The locality in Działy may be attributed approximately to 365th km of the river length, in Dębno – ca. 331st km, whereas those in the vicinity of Tworzykowo – ca. 282-283.5th km of Warta (counted from its mouth to the River Odra). Considering the most comprehensively investigated, in 2007-2013, section of the Warta valley, i.e. from Obrzycko (182 km) to Sługocinek – 385 km (altogether 135 km of the river length), there were only three (or four depending on the map scale) contemporary localities of *M. cristatum* (Fig. 3), which confirms that crested cow-weed is indeed a very rare species in Wielkopolska.

In a (sub-) regional or local scale, *M. cristatum* may also be treated as a very rare component of the relatively well-recognised areas of: the Rogalińska Dolina Warty SCI, where it was recorded only in five sites within two adjacent ATPOL-squares (Fig. 4), and in the Lasy Żerkowsko-Czeszewskie SCI (Fig. 5), where all observations may be treated as referring to a singular locality. Moreover, recently, the species has not been found in any other of the relatively well-explored areas in the middle part of Wielkopolska, including both the riverine landscapes (see darker marks in Fig. 3) and the adjacent uplands (ligther marks in Fig. 3).

An updated distribution map of *M. cristatum* in Poland (Fig. 6) was prepared using the mentioned new localities (BD29, BD39 and CD32), as well as five other sites cited by Brzeg (2005). From the national perspective, the species retains its status of a very rare taxon, as it has been reported from 97 (2.66%) of total 3646 cartogram basic fields (Fig. 6 and Zając & Zając 2001).

Taking into account the above-mentioned data (Zając & Zając 2001; Brzeg 2005 and new localities), *Melampyrum cristatum* has been reported, so far, from 37 basic ATPOL (10x10 km) squares in Wielkopolska, which is ca. 5.2% out of total 710 squares comprised (61 partially) by the analysed regional geomorphic map (Fig. 8). This seems to confirm the species regional rarity and its classification as an endangered (EN) taxon in Wielkopolska (Jackowiak *et al*. 2007).

To summarise, *M. cristatum* seems to be a very rare species, regardless of the scale of observation.

3.4. Distribution of *M. cristatum* along large lowland rivers

Considering that locally all of the investigated sites were situated in the river Warta valley, within its active floodplain (Figs. 3-5), it seems interesting to test if this riverine distribution pattern, in Central Europe attributed by Burkart (2001) as the 'River Corridor Plant' status (RCP), is confirmed regionally and in the whole Poland.

In Wielkopolska, a GIS layer "floodplain terraces and bottoms of basins" (from a digital version of a geomorphic map of the Wielkopolska Lowland – Krygowski 2007) was overlapped with a corresponding part of the updated cartogram (Fig. 8). It was found that almost all, except for one, localities of *M. cristatum* were potentially linked to the mentioned floodplain terraces.

A similar cartographic analysis was made for the whole Poland (Fig. 7), but because in this case there was no available digital version of a geomorphic map, it was based on a scanned and geographically co-ordinated copy of a generalised geological map by Gilewska (1999). The result (Fig. 7) is probably less accurate due to the generalisation and perhaps also not fully precise overlapping of cartographic data. Nevertheless, it seems quite convincing that 73 (i.e. 75.2%) of all 97 basic squares (10x10 km) occupied by *Melampyrum cristatum* were more or less connected with the Holocene river terraces (Figs. 7, 9). Considering both the Holocene, as well as Pleistocene terraces, this share increased even up to 79.4% (Fig. 9), which justifies the status of *M. cristatum* as a riverine species in Poland.

4. Discussion

Melampyrum cristatum is a good example of probably quite a large group of native species, which may be regarded as rare in different spatial scales, i.e. from a local (Figs. 4-5), through regional (Figs. 3, 8), up to national (Figs. 6-7) and perhaps also the Central-European perspective. Phytogeographically, *M. cristatum* is regarded as a Holarctic element, a western, Euro-Siberian sub-element (Zając & Zając 2009) or Euro-Siberian Temperate element (Preston & Hill 1997). It is present in all CE Europe and W Siberia, S Sweden, Finland, and in non-Mediterranean parts of W Europe (Jasiewicz 1958; Hultén & Fries 1986).

The species is rare not only in Poland (Fig. 6), where it was even considered to be extinct (Zarzycki & Szeląg 2006), but also in other European countries. In Germany it is considered to be endangered (the 3rd category of threat according to Korneck *et al*. 1996, after Haeupler & Muer 2000), similarly as in the Czech Republic (critically endangered – Holub & Procházka 2000; Procházka 2001; Štech *et al*. 2008). Crested cow-wheat is also rare outside Central Europe, e.g. in Great Britain it is regarded as a vulnerable (VU) species (Cheffings *et al.* 2005) or in Finland (endangered – after Leimu 2010). The rarity of *M. cristatum* is also detectable sub-regionally. Observations from Wielkopolska (Figs. 3-5, 8), where the species is endangered (Jackowiak *et al*. 2007), seem to be confirmed by data from other parts of its range, e.g. from Brandenburg in Germany, where crested cow-wheat is considered to be critically endangered (Ristow *et al*. 2006) or in Essex, England (the same status according to Adams 2009).

From the phytocoenological point of view, the species is considered to be characteristic of the *Geranion sanguinei* alliance (Matuszkiewicz 2001). According to Brzeg (2005), it is also a characteristic species of *Trifolio alpestris-Melampyretum cristati* Rameau 1974, a thermophilous forest edge community (*Geranion sanguinei*, *Trifolio-Geranietea*). Phytocoenoses classified to this association have been reported from ten ATPOL squares (Brzeg 2005), all of which may be linked to the valleys of four Polish rivers: Odra, Warta and Barycz (flowing in the western part of Poland) and the River Bug, stretching across the East of Poland. These observations corroborate a linkage between *M. cristatum* and large river valleys (Figs. 7-8). Additionally, crested cow-wheat was found in at least four other plant communities of four different phytocoenological classes: *Molinio-Arrhenatheretea*, *Epilobietea angustifolii*, *Artemisietea vulgaris* and *Querco-Fagetea* (tab. 1). In 2007-2008, the species was observed in phytocoenoses that were sporadically disturbed by flood regime, because they were situated in a transitional zone (an ecotone) between the relatively more stable (forests) and frequently inundated sedge communities. In the same (Fig. 4) and adjacent areas (Fig. 3), extensively investigated in 2007-2010, the species was never found in regularly flooded biotopes. It should be mentioned, however, that in spring-summer 2010, with exceptionally high and durable floods, all of the above-described localities were inundated for about a couple of weeks. Although there is no published data on flood-resistance of seeds, in this context it seems important that some of them can remain dormant for at least two years (Horrill 1972) or even longer, as suggested by Adams (2008). This could explain the species survival in disturbed habitats, such as floodplains, road verges and arable field margins (the last two typically occupied by crested cow-wheat in England – Adams 2008, 2009).

According to Kucharczyk (2003), *M. cristatum* grows in thermophilous grasslands (*Festucetalia valesiaceae*), in forest edge communities (*Geranion sanguinei*) and in thermophilous oak woods (*Quercetalia pubescenti-petraeae*). In this light, the phytocoenological scale of crested cow-wheat in the whole Poland seems to be considerably wider than in Wielkopolska. It comprises various forest and herbal communities representing at least the following six classes: *Trifolio-Geranietea*, *Querco-Fagetea*, *Molinio-Arrhenatheretea*, *Festuco-Brometea*, *Artemisietea vulgaris* and *Epilobietea angustifolii*. Considering the above-outlined phytocoenological scale, the species rarity, particularly in a large regional context, remains an intriguing issue which needs explanation. Some of the mentioned habitats (such as *Carduo crispi-Rubetum caesii*, *Calamagrostietum epigeji* or *Querco-Ulmetum minoris*) are not infrequent in Wielkopolska (Brzeg & Wojterska 2001), particularly in the investigated parts of the region (author's unpublished data). A distinct lack of any more observations of *M. cristatum* in such communities, particularly in the relatively well-investigated riverine landscapes of the middle section of the river Warta (cf. Borysiak 1994; Ratyńska 2001 and author's own data – Fig. 3), seems to suggest that some of the existing, rare populations of the species may represent relics of regionally decreasing successional stages of riparian vegetation (such as the *Molinion* meadows which are becoming rare). Perhaps, the species rarity may not only be determined by its attachment to sporadically disturbed habitats, but also by its small ability or almost incapability to cross adjacent, regularly flooded areas.

Distribution of *Melampyrum cristatum* is closely associated with the valleys of large rivers (Figs. 3-5, 7-8). This distinct phytogeographical pattern was recognised as early as 150 years ago in Germany (Ascherson 1859) and in Poland, where the German botanist Loew (1879) promoted the original 'Stromtalpflanzen' concept, which is now more widely known under its English name equivalent, i.e. the 'River Corridor Plants' (RCP). The Central-European list of RCP species was published by Burkart (2001) and it contains *M. cristatum* along with 128 other species. Another, preliminary list was prepared for Germany by Siedentopf (2005). It contains as many as 805 species, including *M. cristatum*. Although, there is still no published, more or less complete RCP list for Poland, Kucharczyk (2003) analysed 262 selected species reported from the middle Vistula valley. He mentioned *M. cristatum* as one of 38 species representing a "continuous compact range restricted only to (river) valleys". According to this author, crested cow-wheat was found mainly in the valleys of large rivers, which seems to correspond with the results presented above in this article (Figs. 7-9) and with the species

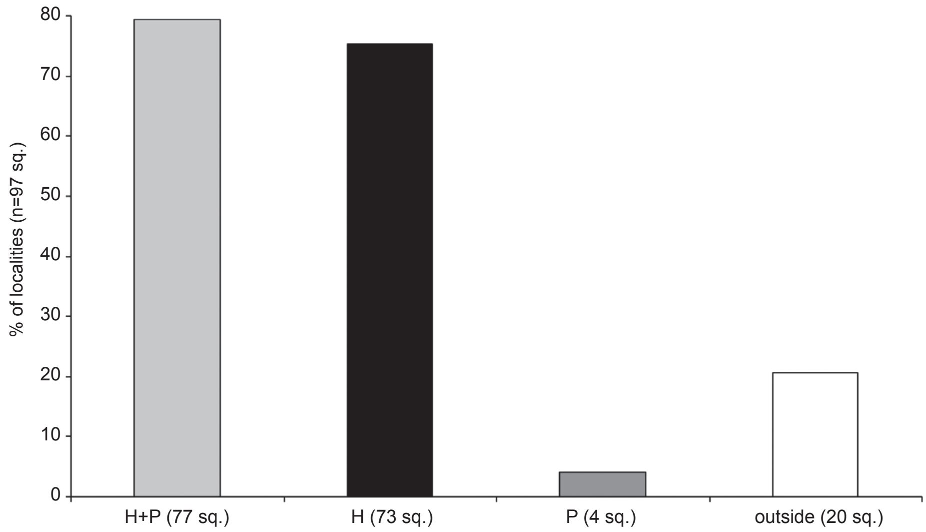

Fig. 9. Percentage share of the *Melampyrum cristatum* localities (national cartogram basic fields) linked to the main Holocene and the Pleistocene river terraces (cf. Fig. 7)
Explanations: H+P – all localities liked to the river terraces (both Holocene and Pleistocene terraces), H – localities linked to the Holocene terraces, P – localities linked to the Pleistocene terraces, outside – other localities situated apparently outside the main river terraces

distribution shown in the atlas of the River Bug valley (Faliński *et al*. 2000). All these observations confirm the species RCP status in Central Europe. Kucharczyk (2003) regarded *M. cristatum* as one of those species that are connected with some sections of large river valleys, where their edges are distinct. He named this type of distribution as the *Ononis spinosa* group. However, this consideration seems not to be confirmed in the middle Wielkopolska. *Melampyrum cristatum* is not present in the relatively incised Poznanian Ravine of the River Warta ("PPW" in Fig. 3), where the valley edges are more distinct than in the Śrem Basin ("KŚr"), from where the above-described localities of crested cow-wheat are reported hereby (Figs. 4-5). According to the author's unpublished data, *Silene tatarica*, another riverine species listed by Kucharczyk (2003) in the mentioned *Ononis spinosa* group, is more or less equally frequent (rare) in wide ("KŚr"), as well as in narrow and incised ("PPW") sections of the river Warta valley. Furthermore, some other species of this group, e.g. *Ononis spinosa,* are better known from various sites in non-riparian parts of the Poznanian Lakeland ("PPo" in Fig. 3).

At least three general explanatory hypotheses for the RCP distribution pattern, including the original 'Stromtalpflanzen' concept, should be considered (Burkart 2001): (1) RCP as remnants of prehistoric migration routes or previous climates, (2) the role of various habitats and (3) biological determinants of species distribution. Although, the first possible explanation type is particularly difficult to incorporate on a large scale due to a lack of most credible, palaeo-botanical data for extensive areas, there seems to be still lots of unused opportunities to test environmental (habitat diversity), as well as biological determinants of some RCP species.

Referring to the Ellenberg's indicator values (Ellenberg 1992), in case of *M. cristatum*, almost entirely confirmed by Hill *et al*. (1999) for use in the British Isles, it may be concluded that the species is generally attributed to: well lit places, but also occurring in partial shade (i.e 'L' – light = 7 or 6, respectively); relatively dry-sites ('F' – moisture = 3); soils of weakly acid to basic reaction ('R' – reaction = 8); infertile sites ('N' – nitrogen = 2); salt-free soils ('S' – salt = 0). There are some methodological differences in ecological indicator values elaborated for Poland (Zarzycki *et al*. 2002). Polish equivalents of the Ellenberg's 'R' and 'S' indices were not specified for *M. cristatum*, whereas in other cases the following values were attributed by Zarzycki *et al*. (2002): 'L' = 3 (half-shade); 'W' (an equivalent of 'F' – moisture) = 3 (fresh soils); 'Tr' (trophy value, similarly defined as 'N') = 3 (moderately poor, mesotrophic) and 'D' (soil granulometric value) = 4 (i.e. clay or dusty deposits). As far as the species riverine-distribution is considered, none of the above-mentioned values seems to constitute any considerable limitations of its range.

The last, large group of factors, i.e. biological determinants of the RCP-type of distribution, incorporates ecologically and evolutionary conditioned functional types of plants, such as e.g. life forms (Raunkiaer 1934) or life history traits (Grime 2002). *Melampyrum cristatum* is an annual, summer-flowering, hemi-parasitic species (Rutkowski 2004; Haeupler & Muer 2000). Although, more detailed data on which taxa it parasitizes are hardly accessible, it was suggested that individuals of *M. cristatum* are able to use various host species simultaneously (Horril 1972; Matthies 1996 after Leimu 2010). It is also known that crested cow-wheat can form haustoria not only with various grasses, but also with some shrubby species (Adams 2008). Germination of summer-dispersed seeds takes place in late winter, the seedlings are frost-resistant (Horrill 1972; Fitter & Peat 1994), but they need to establish haustorial connections to complete their growth (Adams 2008). So far, none of mycorrhiza types have been recorded in *M. cristatum* (Harley & Harley 1987). Considering the permanent presence of large elaiosome on relatively heavy seeds of *M. cristatum* (Adams 2008; Servigne 2008), it is likely to be almost exclusively dispersed by ants, similarly to most of other 35 myrmecochoric species of the *Melampyrum* genus (Lengyel *et al*. 2010). The seeds (maximum 4 per flower) are ca. 5 mm long and considerably heavy (7-10 mg); they are ant-dispersed in summer and require chilling for germination (Horrill 1972; Fitter & Peat 1994). Adams (2008) suggested that (ovoid in shape) seeds of crested cow-wheat coevolved to resemble the cocoons of ants. These insects take the seeds to their nests, where their larvae eat the elaiosomes and, eventually, the seeds are transported to the ants' disposal area. It was suggested (by Gibson 1993a, 1993b) that this seed-dispersal mutualism may have double advantages for plants, i.e.: (1) by providing favourable micro-sites for seed dormancy and germination, as well as (2) through avoidance of seed predation by small rodents. On the other hand, experimentally detected maximal seed fall distances (up to 25 cm from parental plant) for a similar species *Melampyrum pratense* (Heinken 2004) suggest that the species distribution may be considerably dispersal-limited, by means of myrmecochory. This could explain, indirectly, why crested cow-wheat is so rare even though suitable habitats, and probably also potential hosts are much more frequent within the river valley than the species localities. Perhaps for some ants a migration within the active floodplain, which is often divided by a complicated system of oxbows and frequently inundated palaeo-meanders, is so difficult that, in consequence, this may also limit certain plant species, the propagules of which are dispersal-dependent on these insects. Other studies in woodlands of NE Germany (Heinken *et al*. 2001) suggest that endozoochory of *Melampyrum* species by wild herbivores (roe deer, fallow deer and hare) is very unlikely. The postulated role of the mentioned ant-dispersal mechanism as a main limitation of local distribution of *M. cristatum* obviously remains a hypothesis, which needs to be tested by real evidences or through experiments.

As far as the RCP pattern is considered, although there is certainly no universal or widely applicable explanation for such a large and heterogenous group of species (cf. Burkart 2001; Siedentopf 2005), the author presumes that some important environmental determinants may still be discovered. This, however, particularly in case of very rare species, such as *Melampyrum cristatum*, would require intensification of modern geobotanical investigations on hydro-geomorphologically interpreted vegetation, within extensive sections of large river valleys. Further, autecological, long-term studies on selected local populations, optionally also accompanied by additional *ex-situ* experiments, may also help to explain this and other rare RCP species distribution. The impact (and period) of flooding, for instance, may be one of key factors favouring some non-aquatic, though relatively flood-resistant riparian species (e.g. *Cnidium dubium*, *Juncus atratus* or *Gratiola officinalis* – Geissler & Gzik 2008) against others. In case of *Melampyrum cristatum*, it seems also important to better recognise the ecological significance of its hemi-parasitic character, particularly: which hosts it parasitizes and how strongly this relation is exhibited in different habitats?

Considering three subspecies of *M. cristatum* reported from Poland, i.e.: *M. c.* subsp. *solstitiale* Ronn., *M. c.* subsp. *ronnigeri* Ronn. and *M. c.* subsp. *cristatum* Ronn. (Jasiewicz 1958; Rutkowski 2004), general topographic maps presented by Jasiewicz (1958) for distribution of these taxa suggest that all of them may be present along large rivers. However, as mentioned above, the definition and usefulness of some quantitative features defining these subspecies seem to be disputable (cf. results of measurements by Jasiewicz 1958). Additionally, currently available phytogeographical data and herbarium evidences might be still insufficient for further assessment of subspecies distribution.

A separate and important issue remains the species rarity versus its real threat considered in different spatial scales. In Wielkopolska, *Melampyrum cristatum* is regarded as a regionally endangered (EN) species (Jackowiak *et al*. 2007), whereas in Poland – it has recently been considered as an extinct (EX) taxon (Zarzycki & Szeląg 2006). The second example illustrates that, particularly for extremely rare species, the larger scale of observation is, the more cautious one should be as far as the species threat status and extinction is considered. In the light of recently reported data (Brzeg 2005 and Figs. 1-6 presented here), there is no doubt that status of *Melampyrum cristatum* in Poland should be reconsidered. Moreover, perhaps in case of this and other rare species, their overall 'threat' in a supra-regional scale requires further discussion taking into account limits of their natural range (Załuski 2009). Such re-consideration should be based not only on updated phytogeographical records but also on a better recognition and understanding of ecological determinants of their distribution, some of which may be detectable only locally. This evokes another general question: whether in certain areas some species are indeed rare in consequence of some not recognised yet, though possibly natural reasons or, perhaps, this is mainly an effect of recent intensification of certain human pressures? If the answer to the second part of the question is yes, then a more precise status of threat to these species should, indeed, be considered, whereas an opposite answer would rather suggest that the state of our knowledge remains often insufficient for such a consideration. National threat categories are sometimes not entirely adequate to regional differences in species distribution, population resources and dynamics (Załuski 2009). On the other hand, fluctuations in individuals of plants (often only assessed through observations of the above-ground parts) may be buffered by the seed bank (Cheffings *et al.* 2005). Thus, it seems that only a continuous, long-term monitoring of selected sites in different regions, may provide reliable and comparable data for application of the IUCN (2001, 2003) criteria of a supra-regional threat.

Nonetheless, the author assumes that many botanists would agree that in large areas relative rarity does not necessarily mean threat, as the majority of species in well-recognised floras are usually extremely rare (Kornaś & Medwecka-Kornaś 2002).

5. Final conclusions

Melampyrum cristatum is definitely a rare species, both in the Wielkopolska region, as well as in the whole Poland, where it has been recently (incorrectly) considered to be extinct (Zarzycki & Szeląg 2006). A preliminary analysis of the plant's phytocoenological scale (based on a few available relevés and literature) reveals that the species is capable of growing in different plant communities representing various successional stages of semi-natural and natural vegetation of six syntaxonomical classes.

From the comparative, cartographic analysis of geomorphic and floristic data it may be concluded that, in different (i.e. local to supra-regional) spatial scales, *M. cristatum* is a good example of the River Corridor Plant distribution type in Poland. This, however, still needs individual explanation of what caused such a distinct phytogeographical pattern for such a rare species, apparently capable of growing in some vegetation types that are also present outside the river corridors. Possible explanations of the species rarity may be sought within some natural reasons, e.g. its myrmecochory and habitat (hydro-geomorphic) limitations of seed dispersal or ecological mechanisms of hemi-parasitic interactions.

Acknowledgements: I would like to mention Dr Wojciech Rakowski, currently working at the Regional Directorate of Environmental Protection in Poznań, for his contribution to some field data, which we collected together during our joint investigations in 2007-2008 in the Rogalińska Dolina Warty. The locality of *Melampyrum cristatum* in Dębno was initially confirmed in 2011 by Ms. Natalia Olejnik. This encouraged me to update my field observations before publication of the article. I am grateful to Dr Alfred Stach, who provided me with the digitized geomorphological map of Wielkopolska edited by Krygowski (neatly elaborated by Karczewski A., Mazurek M., Stach A., Zwoliński Z., with assistance of their students specialised in geoinformation). I am also indebted to Prof. Dr Karol Latowski (Adam Mickiewicz University, Poznań, Poland) for encouraging me to continue long-term field investigations in riverine landscapes and for lots of interesting discussions on various aspects of the flora of Wielkopolska. Finally, I would like to thank Prof. Dr Maria Wojterska (Adam Mickiewicz University) for critical reading through and valuable comments on the raw version of the manuscript.

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