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A PHENETIC STUDY ON *ACONITUM* ×*HEBEGYNUM* DC. (*RANUNCULACEAE*) IN THE EASTERN CARPATHIANS

Abstract: The aim of the study was to re-evaluate the taxon limits of the putative hybrid *A. ×hebegynum* (*A. degenii* × *A. variegatum*). The nothospecies was described on the specimen originated from a region of the Swiss Alps. Its occurrence in the Eastern Carpathians is controversial since one of the putative parents *A. variegatum* is extremely rare there. A phenetic analysis using quantitative and qualitative floral and leaf morphology characters in 159 herbarium specimens (OTUs) of *Aconitum* sect. *Aconitum* ser. *Variegata* (*A. variegatum*), ser. *Toxicum* (*A. degenii* and *A. lasiocarpum* and putative hybrid *A. ×gayeri*) and nser. *Toxigata* (*A. ×hebegynum*) from the Eastern Carpathians was carried out. The analyses included Detrended Correspondence Analysis (DCA), Canonical Correspondence Analysis (CCA), Monte Carlo permutation tests, and description statistics. This confirmed the intermediate position of the nothospecies in a morphospace delimited by the putative parents. One of the morphotypes showed introgression towards species of the ser. *Toxicum*. The other, relatively rare morphotype, was similar to that occurring in the Alps. The Helmet Index of the nothotaxon was exactly between the values found for the putative parents. The findings did not directly point to the existence of the genetic hybrid in the Eastern Carpathians; more molecular DNA and cytogenetic data are needed. They pointed to the existence of distinct morphotypes which, in the case of the rejection of the hypothesis of nothotaxon existence in the region, should be circumscribed in a low-rank taxon within *A. degenii*.

Key words: *Aconitum* sect. *Cammarum*, hybrids, Linnaean taxonomy, phenetics, species concept.

Introduction

The taxonomic classification of aconites is very difficult, since the group exhibits a wide range of geographic and ecological variation wherever it occurs (Kadota 1981). In the Carpathians the diploid species – circumscribed in the sect. *Cammarum* DC. subsect. *Cammarum* DC. Rapaics – are a typical example of

a group of closely related diploid species, easily interbreeding. One of the most controversial nothospecies is *A. ×hebegynum* DC., a putative hybrid between *A. degenii* Gayer and *A. variegatum* L.

Aconitum ×hebegynum was named by de Candolle'a in 1817 and based on a specimen "cultivé, provenant d'un pied vivant récolté à la Gemmi – G-DC" from the Swiss Alps. The history of the taxon and the typification of its name is given by Starmühler (1997). Recently, Mitka (2000, 2003) pointed to its existence in the Eastern Carpathians. The controversy arises from the fact that in the region of the Eastern Carpathians one of the putative parental species, *A. variegatum*, is very rare found only in the Rodna Mts (Mitka 2000). For this reason the nothospecies was claimed as an orphaned hybrid (Mitka 2003). However, it is also possible that the Carpathian morphotypes, circumscribed as *A. ×hebegynum*, form an extreme wing of the *A. degenii* variability.

Sectio *Cammarum* series *Toxicum* is a group of species of the same evolutionary lineage (Joachimiak et al. 1999), highly variable in morphology, not only due to ecological reasons, but also as an effect of their crossability (Oh & Park 1998). The aim of the present study is to show the morphological variability of the putative hybrid *A. ×hebegynum* against the group of allied taxa. The main question is whether the putative hybrid possesses its own morphological identity and to determine what its morphological limits are. In order to elucidate the problem a phenetic study based on the herbarium material was carried out. Specimens under study originated from the herbarium of the Institute of Botany of the Jagiellonian University (KRA) which carry rich collection of the Carpathian flora, and from materials collected by one of the author (JM) in the region between 1995–2007. A portion of the collected material has been previously published (Mitka 2000).

Materials and methods

The studies were carried out on 159 herbarium specimens, i.e. Operational Taxonomic Units (OTUs), belonging to three species and two nothospecies, from several localities in the Eastern Carpathians and the Alps (see Appendix). The samples encompassed 75 OTUs of *Aconitum degenii*, 13 of *A. ×gayeri*, 33 of *A. ×hebegynum*, 13 *A. lasiocarpum*, and 25 of *A. variegatum*. All of them but *A. variegatum* resembled, at first glance, *A. ×hebegynum*. They are circumscribed in the following series (Mitka 2003): ser. *Variiegata* Steinberg ex Starmühl. (*Aconitum variegatum* L.), ser. *Toxicum* (*A. degenii* Gayer, *A. lasiocarpum* (Rchb.) Gayer, *A. ×gayeri* Starmühl.), nothoser. *Toxigata* Starmühl. (*A. ×hebegynum* DC.).

Each OTU was described with the use of qualitative characters 1–12 (27 character states). Additionally, 5 dimensions of helmets and leaves under a Nikon SMZ800 binocular were measured to the nearest 1 mm (characters 13–20, Table

1). Measurements were taken on the second leaf borne at the node below the lowest axillary inflorescence. The measurements were made for the following characters: a – distance between proximal end of the middle lobe and the point of the primary incision of the lobe, mm; b – distance between the primary incision and the distal end of the middle lobe of the leaf, mm; c – terminal lacinia breadth of the middle lobe of the leaf; helmet height (h), mm; and helmet width (w), mm (Table 1). The shapes of the leaves and helmets of the exemplary OTUs of *A. xhebegynum* were drawn (Fig. 1).

Table 1. Characters coded for phenetic analysis. Binary characters 1–13 coded as 0 or 1. The values used for multistate characters are separated by the slash (/).

1. Hairiness of pedicels above bracteoles – (1) glabrous / (2) poor / (3) moderate / (4) strong
2. Hairiness of pedicels below bracteoles – (1) glabrous / (2) poor / (3) moderate / (4) strong
3. Shape of bracteoles – (1) linear / (2) lanceolate / (3) lanceolate-ovate
4. Hairiness of helmet – (1) glabrous / (2) poor / (3) moderate / (4) strong
5. Shape of helmet – (1) conical / (2) hemispherical
6. Hairiness of carpels – (1) glabrous / (2) on the suture / (3) poor / (4) entirely-moderate / (5) entirely-strong
7. Filaments ciliate – (0) no, (1) yes
8. Claws of nectarines erected – (0) no, (1) yes
9. Spurs of nectarines reaching the top helmet – (0) no, (1) yes
10. Spurs acephalous or capitate – no (0) backward bent or semispiral curved, (1) yes
11. Nectarines toothed – (0) no, (1) yes
12. Nectarines ciliate – (0) no, (1) yes
13. Height of the helmet h* – [mm]
14. Width of the helmet w* – [mm]
15. Length of the leaf segment a* – [mm]
16. Length of the leaf segment b* – [mm]
17. Length of the leaf segment c* – [mm]
18. Helmet index – character 13/character 14 [ratio]
19. Lobe index – character 16/character 15 [ratio]
20. Lobe Shape Leaf Index (character 15+character 16)/character 17 [ratio]

*see Fig. 1

By combining of these variables, the following parameters were also considered: Helmet Index (HI), indicating helmet shape, Lobe Index (LI), indicating depth of lobe incision, and Lobe Shape Index (LSI), indicating lobe shape (Table 1). A matrix of 32 qualitative and quantitative characters \times 159 OTUs was used in numerical analyses (Falniowski 2003). A phenogram was obtained using an UPGMA algorithm and Jaccard's similarity (NTSYS-pc ver. 2.11 – Rohlf 2002) and ordination of OTUs by a Detrended Correspondence Analysis (DCA). To display the effect of quantitative variables on the distribution of OTUs in the

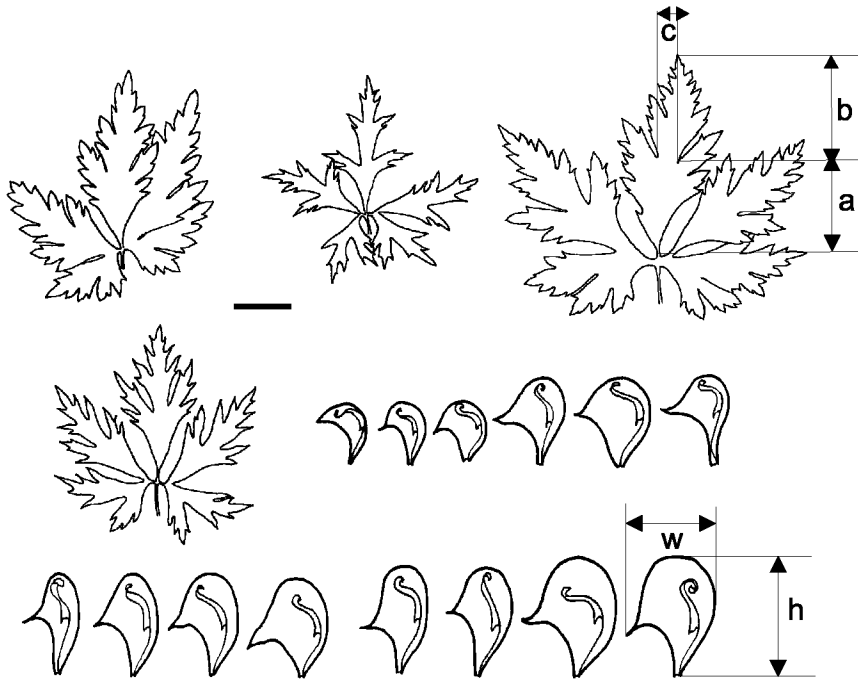


Fig. 1. Variation of leaves of *A. xhebegynum* in the Bieszczady Mts. and helmets in the Eastern Carpathians. Bar inside – 1 cm.

morphospace a Canonical Correspondence Analysis (CCA) was carried out. The ordinations procedures were done using CANOCO for WINDOWS (ter Braak & Šmilauer 2002).

Statistical significance of the quantitative data was analysed using Monte Carlo permutation tests which do not require normality of errors. The characters 13–20 (Table 1) were treated as predictor “environmental” variables, and species taxonomic groups of OTUs as dummy variables. Permutations (499 runs) under reduced model were conditioned by the dummy variables treated as covariables. Forward automatic selection was chosen. The relationships between the “environmental” and phenetic space for all OTUs were interrogated using General Linear Modelling (GLM) (McCullagh & Nelder 1983).

Basic statistics (mean, standard deviations and 95% confidence intervals) were calculated using STATISTICA ver. 8 (StatSoft, Inc. 1984–2007).

Results

In sum 9 taxa recognized in the group of OTUs generally resembled *A. xhebegynum* (Fig. 2, Appendix). The classification of data (results not shown) gave

two main clusters: the first composed of *Aconitum variegatum* and *Aconitum xhebegynum*, and the second of the remaining taxa. In the diagram the Alpine OTUs form a small cluster of six OTUs, with *xgayeri* and *A. degenii*, which have moderately pubescent pedicels. Two Carpathian *A. xhebegynum* specimens in the cluster have weakly pubescent helmets and glabrous carpels and pedicels below bracteoles, pointing to the introgression from other taxa of ser. *Toxicum*. The two OTUs of *A. xhebegynum* from the Alps (see Appendix) accompany the group of the Carpathian conspecific OTUs, however in their marginal position. The Alpine specimens had glabrous helmets and moderately pubescent carpels and pedicels below bracteoles. This morphotype is similar to that in the Carpathians. The ordination (Fig. 2a,b) along DCA Axis I and Axis II pointed to three groups. Two of them had extreme positions along the DCA Axis I. The first group formed

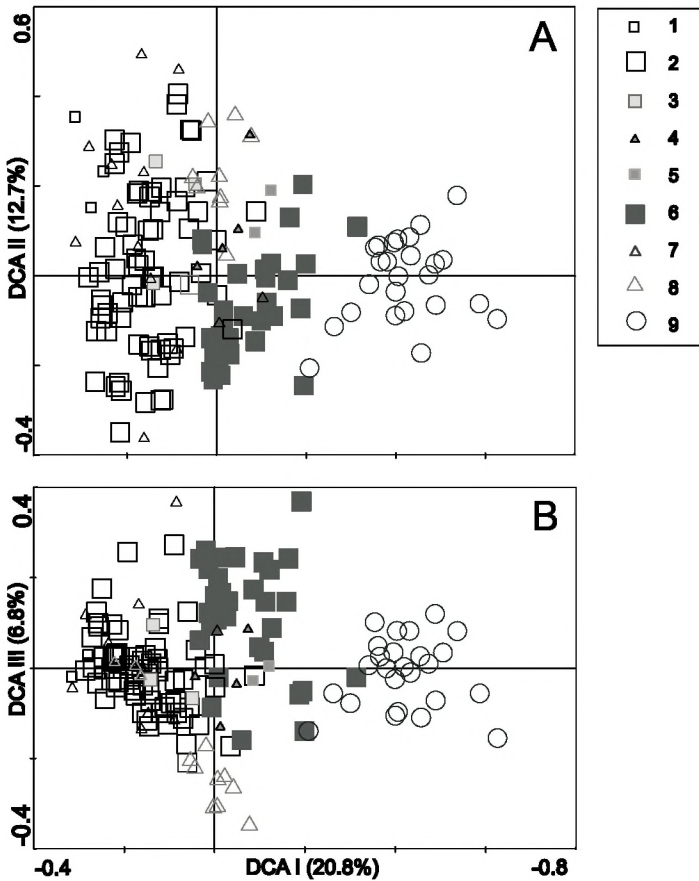


Fig. 2. Ordination of *Aconitum* OTUs using Detrended Correspondence Analysis alongside A: Axis I and II, and B: Axis I and III. 1 – *Aconitum degenii* subsp. *degenii* fo. *craciunelense*, 2 – *A. degenii* subsp. *degenii*, *A. d.* subsp. *paniculatum*, 3 – *A. degenii* subsp. *gandogerii*, 4 – *A. xgayeri*, 5 – *A. xhebegynum* – the Alps, 6 – *A. xhebegynum* – the Eastern Carpathians, 7 – *A. lasiocarpum* subsp. *kotulae*, 8 – *A. lasiocarpum* subsp. *lasiocarpum*, 9 – *A. variegatum* subsp. *variegatum*.

A. degenii, which is opposed by the *A. variegatum* in the right side of the diagram. Between them a transitional group of *A. ×hebegynum* is localised, partially overlapping with *A. lasiocarpum* and other taxa (Fig. 2a).

The ordination of OTUs along DCA Axis I and Axis III enable the discrimination of *A. lasiocarpum* in the lower part of the diagram (Fig. 2b).

The detailed analysis of the transitional group (Szajna 2008) showed three morphotypes. The first consists of OTUs with glabrous carpels and weakly pubescent helmets and pedicels. The second with weakly pubescent carpels, and glabrous helmets and pedicels. The third group had moderately pubescent carpels, helmets and pedicels. The first two morphotypes were designated as *A. ×hebegynum*, and the third as *A. lasiocarpum* with allied hybrids.

Monte Carlo permutation tests pointed to the statistical significance of three characters: no. 14, width of the helmet ($p = 0.019$), no. 15, length of leaf lobe "a" ($p = 0.002$) and no. 18, HI ($p = 0.038$). Only character no. 18 is related with the taxonomic structure. The OTUs can be arranged according to increasing values of HI along the CCA Axis I (Fig. 3). A clear trend exists in the General Linear Modelling with HI growing from 1.0 in *A. degenii* to 2.7 in *A. lasiocarpum* and *A. variegatum*. *A. ×hebegynum* covers middle range of the HI values. The exemplary helmets drawn from the herbarium specimens showed the pattern of their variability in the Eastern Carpathian population (Fig. 1). Basic statistics in Table 2 shows the non-overlapping 95% confidence intervals for HI values in *A. degenii* (1.3–1.4) and *A. variegatum* (1.8–2.1). *A. ×hebegynum* had 95% confidence interval of HI ranging between 1.5–1.7.

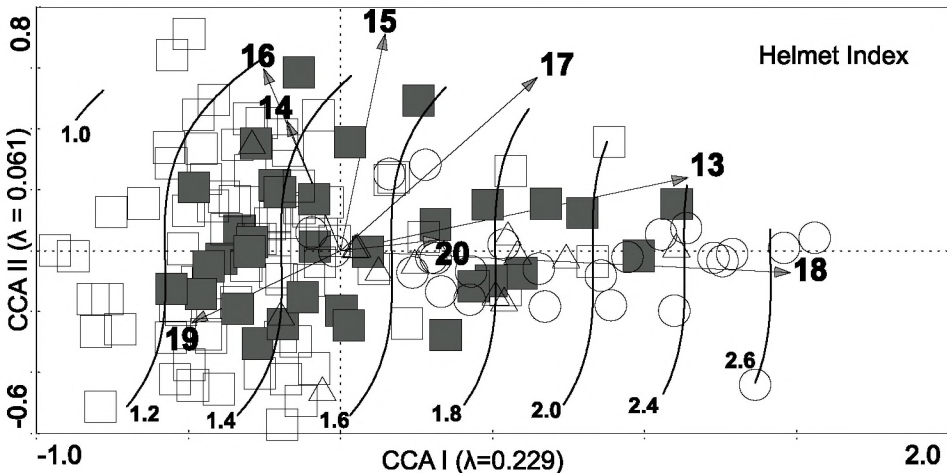


Fig. 3. Ordination of *Aconitum* OTUs using Canonical Corresponding Analysis with imposed the results of General Linear Modelling respective to the character no. 18, Helmet Index. The trend in the character's values and changing taxonomic structure is visible from the left to right side of the diagram: *A. degenii* → *A. hebegynum* and *A. lasiocarpum* → *A. variegatum*. Symbols as in Fig. 2.

Table 2. Mean \pm standard deviation and 95% confidence intervals for quantitative characters 13–20 (see Table 1). P – probability of Type I error for the quantitative characters under the null model (i.e. only for the first canonical axis) based on the Monte Carlo unrestricted permutation test conditioned on the blocks (taxonomic structure).

No. of character	<i>Aconitum degenii</i>	<i>Aconitum</i> \times <i>gayeri</i>	<i>Aconitum</i> \times <i>hebegynum</i>	<i>Aconitum lasiocarpum</i>	<i>Aconitum variegatum</i>	Total	p
	n=75	n=13	n=33	n=13	n=25	n=159	
13	18.7 \pm 3.9	18.5 \pm 6.0	20.5 \pm 5.6	23.2 \pm 2.8	25.3 \pm 5.5	20.4 \pm 5.2	0.574
	17.8–19.6	14.8–22.1	18.5–22.4	21.5–24.8	23.1–27.6	19.6–21.3	
14	14.1 \pm 2.9	13.3 \pm 4.0	13.2 \pm 3.0	14.2 \pm 2.7	13.2 \pm 2.4	13.7 \pm 2.9	0.018
	13.4–14.8	10.9–15.7	12.2–14.3	12.6–15.8	12.2–14.1	13.3–14.2	
15	25.5 \pm 10.2	23.5 \pm 10.2	26.4 \pm 7.3	25.2 \pm 8.3	25.4 \pm 6.9	25.5 \pm 9.0	0.002
	23.1–27.8	17.3–29.7	23.8–29.0	20.1–30.2	22.5–28.3	24.1–26.9	
16	40.2 \pm 14.1	39.5 \pm 15.8	43.2 \pm 12.8	32.1 \pm 7.5	33.8 \pm 10.4	39.1 \pm 13.4	0.880
	36.9–43.5	30.0–49.1	38.7–47.7	27.6–36.6	29.5–38.1	37.0–41.2	
17	6.1 \pm 2.9	5.7 \pm 4.2	6.8 \pm 2.1	6.8 \pm 2.4	7.8 \pm 2.0	6.5 \pm 2.8	0.188
	5.5–6.8	3.2–8.2	6.1–7.6	5.3–8.2	6.9–8.6	6.1–7.0	
18	1.3 \pm 0.2	1.4 \pm 0.3	1.6 \pm 0.3	1.7 \pm 0.3	1.9 \pm 0.3	1.5 \pm 0.3	0.038
	1.3–1.4	1.2–1.6	1.5–1.7	1.5–1.8	1.8–2.1	1.5–1.6	
19	1.7 \pm 0.5	1.7 \pm 0.3	1.7 \pm 0.5	1.4 \pm 0.6	1.4 \pm 0.5	1.6 \pm 0.5	0.194
	1.5–1.8	1.6–1.9	1.5–1.9	1.1–1.8	1.2–1.6	1.5–1.7	
20	1.7 \pm 0.4	1.6 \pm 0.1	1.6 \pm 0.2	1.8 \pm 0.4	1.8 \pm 0.3	1.7 \pm 0.3	0.136
	1.6–1.8	1.5–1.7	1.6–1.7	1.6–2.0	1.7–1.9	1.6–1.7	

Discussion

The results of DCA ordination clearly show morphotypes filling the gap in the morphospace between *A. degenii* and *A. variegatum* (Fig. 2). The morphotypes are well discriminated from *A. variegatum* (Axis I) and from *A. lasiocarpum* subsp. *lasiocarpum* (Axis III). However, the transitional OTUs marked as *A. ×hebegynum* are continuously, without any limit, distributed towards *A. degenii*. Helmet Index for *A. ×hebegynum* is exactly between values found for *A. degenii* and *A. variegatum*.

Among diagnostic characters for *A. ×hebegynum* in the Eastern Carpathians Mitka (2003) gives “carpels glabrous and pedicels below bracteoles glabrous or carpels pubescent and helmet and pedicels below bracteoles glabrous”. The expected morphotype of *A. ×hebegynum* should encompass glabrous carpels, helmets and pedicels. Such a combination was unique and found only in two specimens from the Chornogora region. In fact Zapałowicz’s (1908) specimens of *Aconitum intermedium* and *A. pratense*, found in the mountain range and forelands, seem conspecific to *A. ×hebegynum*. In the Eastern Carpathians a morphotype with glabrous carpels and helmets, and pubescent pedicels can be also found. The other morphotype, relatively rare, had slightly pubescent carpels, glabrous pedicels below bracteoles, and glabrous helmets. It was found in the Gorgans Mts. and on Mała Rawka Mt. in the Western Bieszczady mountain range. In the latter mountains, the region of Mała and Wielka Rawka Mts. was considered as a local center of occurrence of *A. degenii* and its hybrids (Mitka, Zemanek 1997). However, in the present study the most common encountered morphotype had glabrous carpels and pedicels below bracteoles, and slightly pubescent helmets. It looks like an introgressive form towards ser. *Toxicum*.

Two of the Alpine specimens had a combination of the characters not found in the Carpathian OTUs. The difference lies in the combination of glabrous helmets and pubescent carpels. In the Eastern-Carpathian population the glabrous helmets and pubescent carpels as a rule accompanied glabrous pedicels (at least below bracteoles). In the Alpine OTUs the pedicels were weakly pubescent. Thus, the key characters common for both the Carpathian and Alpine *A. ×hebegynum* were glabrous helmets and pubescent carpels.

Statistical analyses (Monte Carlo permutations and General Linear Modeling) showed that HI was linked with the taxonomic structure of the data set. This result is similar to the previous morphometric analysis of *A. degenii* and *A. lasiocarpum* (Mitka, Jodłowski 1977). In that study a significant difference was found between *A. lasiocarpum* and *A. degenii* in helmet height ($p = 0.02$) and Helmet Index ($p = 0.0001$).

All these results showed that in the Eastern Carpathians morphotypes of intermediate character between *A. degenii* and *A. variegatum* do exist, and can be

circumscribed as *A. xhebegynum*. However, the existence of the taxon in the Eastern Carpathians cannot be stated conclusively. The crucial point is the general lack in the Eastern Carpathians of *A. variegatum*. The species is very rare here, but its wider occurrence in the past cannot be ruled out (Mitka 2005). The nearest localities of the species are in the Beskid Niski and the Doły Jasielsko-Sanockie Basin (the Western Carpathians) to the west, and in the Rodna Mts (the Eastern Carpathians) to the east. On the other hand, *A. degenii* is also rare species in the Bieszczady Mts. (Mitka, Zemanek 1997, Mitka 2001). Recently, its locality in Wetlina village on the Wetlinka torrent as noted by Jasiewicz (1965), and confirmed in 2001 (Mitka 2008), was destroyed by the building of touristic infrastructure.

The cytogenetic studies on the series *Toxicum*, encompassing *A. degenii* and *A. lasiocarpum*, and on the series *Variegata* with *A. variegatum*, showed structural differences between the two series (Joachimciak et al. 1999). In ser. *Toxicum* the structural heterozygosity in two NOR-chromosome pairs (1 and 3) was found. In opposite, *A. variegatum* showed structural homozygosity in this respect. It is not clear whether the observed heterozygosity of two NOR-chromosome pairs in the karyotype of *A. degenii* and *A. lasiocarpum* arose through crossing between two different forms/taxa (with and without satellites on chromosomes 1 and 3). On the other hand, it can be argued that the observed polymorphism is caused by intraspecific structural variations in NOR-chromosomes (Joachimciak et al. 1999). *A. xhebegynum* was not studied in this respect, however it can be expected that in this hybrid species cytogenetic polymorphism, i.e. both homo- and heterozygosity, should be found (Ilnicki, pers. comm.).

In conclusion, the phenetic analyses presented here clearly pointed to the existence, in the Eastern Carpathians, of the morphotypes of intermediate character between *A. degenii* and *A. variegatum*. Future cytogenetic and molecular analyses of these morphotypes will enable a final conclusion to be reached. If the hypothesis on the existence of the hybrid taxon in the Eastern Carpathians will be refuted then the morphotypes should be circumscribed as low, intraspecific rank within *A. degenii*, presumably in the subspecies rank.

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Literature

- Falniowski A. 2003. Metody numeryczne w taksonomii. Wyd. Uniwersytetu Jagiellońskiego, Kraków.
- Jasiewicz A. 1965. Vascular plants of the Western Bieszczady Mts. (Eastern Carpathians). Monogr. Bot. 22: 1–340 [in Polish with English summary].
- Joachimiak A., Ilnicki T., Mitka J. 1999. Karyological studies on *Aconitum lasiocarpum* (Rchb.) Gayer (Ranunculaceae). Acta Biol. Cracoviensia, ser. Bot. 41: 205–211.
- Kadota Y. 1981. A taxonomic study of *Aconitum* (Ranunculaceae) of the Akaishi Mountain Range in Central Japan. Bull. Natn. Sci. Mus., Tokyo, Ser. B, 7(3): 91–112.
- McCullagh P. & Nelder J. A. 1983. Generalized linear models. Chapman & Hall, London.
- Mitka J. 2000. Systematics of *Aconitum* subgen. *Aconitum* in the Eastern Carpathians – preliminary results. Roczniki Bieszczadzkie 9: 79–116 [in Polish with English summary].
- Mitka J. 2001. *Aconitum degenii* Gayer, Tojad wiechowaty. In: R. Kaźmierczakowi & K. Zarzycki (eds.) Polska Czerwona Księga Roślin. Paprotniki i rośliny kwiatowe. Instytut Botaniki im. W. Szafera, PAN, Kraków, s.: 125–126.
- Mitka J. 2005. Historical-biogeographical backgrounds of the endemism in the genus *Aconitum* (monkshood – Ranunculaceae) in Central Europe. Roczniki Bieszczadzkie 13: 41–66 [in Polish with English summary].
- Mitka J. 2008. Tojad wiechowaty *Aconitum degenii* Gayer subsp. *degenii*. In: Mirek Z., Piękoś-Mirkowa H. (eds.) Czerwona Księga Karpat Polskich. Rośliny naczyniowe. Instytut Botaniki im. W. Szafera PAN, Kraków, s.: 64–65.
- Mitka J. & Jodłowski J. 1997. Phenetic variability of *Aconitum lasiocarpum* and *Aconitum degenii* in the Western Bieszczady Mts (Polish Eastern Carpathians). Rev. Valdôtaine Hist. Nat. 51, Suppl.: 135–145.
- Mitka J. & Zemanek B. 1997. The distribution of *Aconitum degenii* Gayer, *A. lasiocarpum* (Rchb.) Gayer and their hybrids in the Bieszczadzki National Park. Roczniki Bieszczadzkie 6: 97–111 [in Polish with English summary].
- Mitka J. 2003. The genus *Aconitum* L. (Ranunculaceae) In Poland and adjacent countries. Instytut Botaniki UJ, Kraków.
- Oh S.-H. & Park Ch.-W. 1998. Crossability of the *Aconitum jaluense* species complex (Ranunculaceae) in Korea. Korean J. Biol. Sci. 2: 435–438.
- Rohlf F. J. 2002. NTSYS-pc: numerical taxonomy and multivariate analysis system, version 2.11. Exeter Software, Setauket, NY.
- StatSoft, Inc. 1984–2007. STATISTICA for WINDOWS. StatSoft Inc., Tulsa, USA.
- Szajna B. 2008. *Aconitum xhebegynum* DC. (Ranunculaceae) na tle zmienności przypuszczalnych gatunków rodzicielskich w Karpatach. MSc. Thesis, Institute of Botany, Jagiellonian University.
- ter Braak C. J. F. and Šmilauer P. (2002). CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca NY, USA.

Streszczenie

Celem badań było określenie granic zmienności morfologicznej (Fig. 1) hipotetycznego mieszańca *A. ×hebegynum* (*A. degenii* × *A. variegatum*) na tle zmienności przypuszczalnych rodziców. Jego obecność w Karpatach Wschodnich jest kontrowersyjna z powodu bardzo rzadkiego występowania w tym obszarze

jednego z przypuszczalnych rodziców, tj. *A. variegatum*. Stąd postulowany status notogatunku to osierocony mieszańiec (Mitka 2003). Badania fenetyczne, z wykorzystaniem cech jakościowych i ilościowych, dotyczących zmienności kształtu kwiatów i liści (Tab. 1), zostały przeprowadzone na 159 okazach zielnikowych (OTU), pochodzących z zielnika Instytutu Botaniki UJ (KRA) oraz zbiorów własnych (JM) z lat 1995–2007. Należały one do *Aconitum* sect. *Aconitum* ser. *Aconitum* (*A. variegatum*), ser. *Toxicum* (*A. degenii* i *A. lasiocarpum*, *A. xgayeri*) oraz ser. *Toxigata* (*A. xhebegynum*) z Karpat Wschodnich i Alp. Macierz cech została poddana analizom numerycznym z wykorzystaniem nietendencyjnej analizy zgodności (DCA), kanonicznej analizy zgodności (CCA), permutacyjnych testów Monte Carlo i podstawowych statystyk opisowych. Przeprowadzone analizy potwierdziły pośrednie umiejscowienie notogatunku w przestrzeni morfologicznej, zdefiniowanej przez przypuszczalne gatunki rodzicielskie (Fig. 2). Najczęstszy morfotyp mieszańca wykazywał introgresję w kierunku gatunków ser. *Toxicum* (*A. degenii* i *A. lasiocarpum*). Najrzadszy był podobny do okazów pochodzących z Alp. Indeks hełmu przypuszczalnego mieszańca posiadał wartości pośrednie pomiędzy indeksem stwierdzonym dla gatunków rodzicielskich (Fig. 3, Tab. 2). Uzyskane wyniki nie wskazują bezpośrednio na istnienie genetycznego gatunku mieszańcowego. Potrzebne są w tym celu badania cytogenetyczne i molekularne DNA. Udowodniono istnienie odrębnych morfotypów, których pozycja taksonomiczna, w przypadku odrzucenia hipotezy o mieszańcowym pochodzeniu, powinna być ustalona przypuszczalnie w randze podgatunku *A. degenii*.

Appendix

Specimina visa

Aconitum degenii* Gayer subsp. *degenii: ROMANIA [Bihor] Skerišoara, Fagetum; 02.08.2007; *J. Mitka* (KRA).- Dobrin 1100 m, nad potokiem; 31.07.2003; *J. Mitka* (KRA). [Eastern Carpathians] Čeahlau, Fagetum; 08.08.2007; *J. Mitka* (KRA).- Rarau, Pietrele Doamnei 1500 m; 24.07.2003; *J. Mitka* (KRA). UKRAINE Eastern Carpathians [Chornogora] m. Pożyżewską a Dancerzem, ziołorośla; 22.07.2002; *B. Zemanek & al.* (KRA 0224812).- Bystrzec 1740 m, zarośla; 03.08.1997; *J. Mitka* (KRA).- Pożyżewska 1300 m, nad potokiem; 01.18.1997; *J. Mitka* (KRA).- Potok Homulski pod Homulem 1295 m, ziołorośla; 01.08.1997; *J. Mitka* (KRA).- Dolina Bystrzyca pod Czarną Horą, 20.08.1875; *A. Ślodziński* (KRA 003764).- między Howerłą a Pożyżewską nad wodospadem ok. 1500 m; 24.07.2002; *M. Graniszewska* (KRA 0224997).- Dancerz Mt., po drodze z Zaroślaka nad jezioro Niesamowite, stoki Dancerza ok. 1460 m; 27.07.2002; *M. Graniszewska* (KRA 0224488). [Svidovec] E Świdowiec, potok Rostinieckij 710 m, terasa

zalewowa; 29.07.1997; *J. Mitka* (KRA). [Bucovina] Hriebta Jarovicja; 05.08.1992; *Čornej* (KRA).- S. Vysšnia Jablonica; 19.08.1993; *Čornej* (KRA).- Sarata, Pastik; 13.08.1991; *Čornej*; (KRA).- S. Sarata; 18.07.1990; *Čornej* (KRA). [Maramureš Mts.] Javornik; 29.07.2002; *A. Prokopiv*; (KRA 0239284). [Gorgans] nad potokiem wpadającym do potoku Žeńca, ziołorośla; 15.08.1997; *K. Zarzycki* (KRA 0224813).- nad potokiem Bystra (dopływ Łomnicy), przy torze kolejki wąskotorowej ok. 950 m; 02.08.2002; *M. Graniszewska* (KRA 0224491).- nad Czarną (dopływ Młodej) ok. 960 m; 08.08.2002; *M. Graniszewska* (KRA 0223533).- Sywula 1790 m, stok płn.-wsch., murawa na grechocie; 12.08.1939; *A. Środoń* (KRAM 000704).- Sywula Wielka 1750 m, stok zachodni, ziołorośla na piargu; 12.08.1939; *A. Środoń* (KRAM 000699). [Chivchin] w potoku Albin ok. 1260 m; 15.07.2002; *M. Graniszewska* (KRA 0223526).- w dolinie Czarnego Czeremoszu, ok. 8 km przed potok Albin, ok. 960 m; 08.07.2002; *M. Graniszewska* (KRA 0223529).- ok. 1620 m, Hnitesa od pn. - skraj *Rumicetum alpini*; 24.07.1934; *B. Pawłowski* (KRA 003759).- Bałtaguł, Dolina Czeremosza; 25.07.1934; *T. Sulma* (KRA 003760).- Hnitesa od pn. – skraj *Rumicetum alpini*, ok. 1620 m; 28.04.1934; *B. Pawłowski* (KRA 116657).- Czywczyn NE, 1650 m, przy skałkach; 19.08.1997; *K. Zarzycki* (KRA 0224814).- Czywczyn N ; 14.09.1990; *Zalevska* (KRA).- Perkalab, Pereval' Szija; 11.18.1992; *Čornej, Budžak* (KRA).- na szifach góry Hnitesa; 20.07.1991; *Čornej* (KRA). ROMANIA [Rodna Mts] NW-Hang des Pietrosul (Nagy Pietrosz) 1500 m alt, Waldichtung; 04.08.1996; *C. Dragulescu & W. Starmühler* (KRA).- Mt. Cailor; 15.08.1997; *J. Mitka* (KRA). POLAND Eastern Carpathians [Western Bieszczady] Wetlina, nad potokiem k. mostu; 06.09.1995; *J. Mitka* (KRA 0224514).- Wetlina, nad potokiem k. mostu; 30.09.1999; *J. Mitka* (KRA 0224510). - Dwernik 490 m, na brzegu Sanu; 03.09.1996; *J. Jodłowski* (KRA).- dolina Terenowca, Alnetum ok. 700 m, FG 6968; 13.08.1996; *T. Winnicki* (KRA 0224517).

***Aconitum degenii* subsp. *degenii* forma *craciunelense* Gayér:** UKRAINE Eastern Carpathians [Bucovina] Pidvicznij, Hriebta Jarovicja; 05.08.1992; *Čornej* (KRA).- S. Sarata; 16.08.1991; *Čornej* (KRA). [Chornogora] Howerla, wilgotna młaka ziołoroślowa; 22.07.2002; *B. Zemanek & al.* (KRA 0224809).- Gutin Tomnatyk 1620 m, nad brzegiem jeziorka; 02.08.1997; *J. Mitka* (KRA).

***Aconitum degenii* subsp. *paniculatum* (Arcangeli) Mucher:** SWITZERLAND Schweiz, Kt. Waadt, N 46°14,47' E 07°06,58', 1450 m; 31.08.1998; *W. Starmühler* (KRA 0276795). CROATIA Kroatien, Istrien, Planik-Gipfen, Weiden – Buchen-Gebüsch, 1270m; 14.08.1991; *W. Mucher* (KRA 0277184). ITALY Italien, Wenetien, Dolomiten, an der Straße Auronzo nach Ginalba, Waldrand 1140 m; 16.08.1991; *W. Mucher* (KRA 0277183). AUSTRIA Kärnten, Steiner Alpen, Kotschnatal, Waldrand, 975 m; 20.08.1990; *W. Mucher* (KRA 0277192).- Höhe Tauren, Wörth Krumlal, brzeg rzeki; 11.09.1996; *D. Tumidajowicz* (KRA). SLOVENIA Alpes Juliae, Komna, in locis saxosis, inter frutices, solo calcareo 1520 m; 14.08.1957; *B. Pawłowski* (KRA 003769).- Triglavski PN, k. Slap Most-

nice, zarośla nad potokiem 730 m; 31.07.2003; *M. & A. Zajac* (KRA 0265661).- Alpy; 22.08.1991; *T. Ster & F. Steffan* (KRA 0277168).- Steiner Alpen (Kaminske Alpe) 1465m; 20.09.1991; *W. Mucher* (KRA 0277182).- Steiner Alpen (Kaminske Alpe), Straße von Kanker (Kokre), Waldrand 745 m; 20.08.1991; *W. Mucher* (KRA 0277181).- Steiner Alpen (Kaminske Alpe); Suhodolnik, Waldrand, 960 m; 20.08.1991; *W. Mucher* (KRA 0277180).- Kranjska (Krain), Steiner Alpen, am Weg von Bistrica (Feistitz) Tal zum Kaminiško sedlo; 18.08.2002; *U. & W. Starmühler* (KRA 0277279).- Steiner Alpen (Kaminske Alpe) 1440m; 20.08.1991; *W. Mucher* (KRA 0277185).

***Aconitum degenii* Gáyer nsubsp. *gandogeri* Mucher**

GERMANY Tyrol, In fruticesis subalpinis, Inter Trins et Gschnitz 4000–5000'; *A. Kerner* (KRA 003753).

***Aconitum* × *gayeri* Starmühl. (*A. degenii* × *A. lasiocarpum*)**

UKRAINE Eastern Carpathians [Bucovina] S. Sarata, Hrebto Čornyj Dil'; 18.07.1990; *Čornej* (KRA). [Gorgans], nad rzeką Kotelec 1150 m; 04.08.2002; *M. Graniszewska* (KRA 0224493).- Sywula Wielka, 1790 m, stok poł.-wsch., mura-wa na grechocie; 12.08.1939; *A. Środoń* (KRAM 000706). [Chivchin] Góry Czyw-czyńskie; 27.07.1999; *K. Zarzycki* (KRA).- S. Burkut, G. Chivchin; 31.07.2002; *Čornej* (KRA).- Perkalab, Gora Hnitesa; 14.07.1998; *Čornej* (KRA).- S. Burkut, Popodnica; 31.07.2002; *Čornej* (KRA).- między Czywczynem a Seligulem przy granicy ukraińsko-rumuńskiej na połoninie, ok. 1500 m; 09.07.2002; *M. Grani-szewska* (KRA 0223531). [Chornogora] między Pożyżewską a Dancerzem 1580 m, ziołorośla; 22.07.2002; *B. Zemanek & al.* (KRA 0224811). POLAND Eastern Car-pathians [Western Bieszczady] Chmiel, k. cerkwii nad stawem rybnym, Alnetum z *Matteucia struthiopteris*; 09.09.1996; *J. Jodłowski & J. Mitka* (KRA 0224509).- Procisne, potok Wołosaty, ok. 400 m za mostem w górę potoku, Alnetum ok. 515 m; 03.09.1996; *J. Jodłowski, J. Mitka* (KRA 0224508, 0224511).

***Aconitum* × *hebegnum* DC. (*A. degenii* × *A. varegatum*)**

FRANCE Alpy francuskie; ??; ?? (KRA 003613). GERMANY Bayern, Nationalpark Berchtesgaden, In der Röth, Weg von der Wasser – Alm zum Wildtörl, Hochstandenflur, 1455 m s.m.; 23.08.1994; *W. Starmühler* (KRA). UKRAINE Eastern Carpathians [Chornogora] Czarnohora; 09.08.1935; *B. Pawłowski* (KRA 003748).- Karpaty Pokuckie, Zawojela, Howerla, w paśmie Czarnej Hory; 07.1911; *M. Raciborski*; (KRA 003761).- Karpaty Pokuckie, nad brzegiem Prutu i koło drogi w Zawojeli pod Howerlą; 08.1911; *M. Raciborski* (KRA 003758).- Dolina Prutu, przy drodze w rowie w stronę Zaroślaka, 1150 m; 16.08.1996; *P. Bochenek* (KRA 0225148).- Worochta nad Prutem; 17.08.1888; *E. Wołoszczak* (KRAM 33630).- Pożyżewska; 24.07.1999; *K. Zarzycki* (KRA 0224515).- Foreszczenka; 16.09.1911; *K. Huppenthal* (KRA 003766).- Zaroślak, nad potokiem koło schroniska, ok. 700 m; 30.07.1997; *J. Mitka* (KRA 0224502).- Zaroślak; 06.08.2006; *J. Mitka* (KRA). [Gorgans] nad potok Negrowa pod Sywulą; 02.08.2002; *M. Graniszewska* (KRA

0224492).- Sywula 1790 m, stok płn.-wsch., murawa na grechocie; 12.08.1939; A. Środoń (KRAM 000698, 000705). POLAND Eastern Carpathians [Western Bieszczady] Mała Rawka, potok W od schroniska, ok. 1100 m; 12.09.1995; J. Mitka (KRA 0224504, 0225145).- Mała Rawka, nad potokiem, Fagetum ok. 1030 m; 09.09.1995; J. Mitka (KRA 0224512).- Górna Solinka FG6879, ok. 900 m; 02.08.1993; M. Szewczyk (KRA 0225140).- Dwernik, Potok Nasiczniański; 07/08.2003; T. Ilnicki (KRA).- Dolina Sanu, Rusinowa Polana; 02.09.2003; T. Ilnicki (KRA).- Nasiczne, potok Nasiczniański, Alnetum, ok. 750 m; 08.09.1995; J. Jodłowski & J. Mitka (KRA 0224506).- Procisne, potok Wołosaty ok. 400 m w górę za mostem, ok. 515 m; 03.09.1993; J. Jodłowski (KRA 0225166).- Dolina Terebowca, Alnetum; 20.09.1999; J. Mitka (KRA 0224505).- Dolina Terebowca, Alnetum; 13.08.1996; J. Jodłowski (KRA 0224518).- Dolina Terebowca; 1994; T. Winnicki (KRA 0225142).- potok Terebowiec, 400 m przed ujściem wody w górę potoku; 12.08.1996; J. Jodłowski (KRA 0224516).- Dolina Moczarnego, przy drodze; 06.09.1995; J. Mitka (KRA 0225143).- Fedkowskie, k. mostu, Alnetum ok. 705 m; 09.09.1995; J. Jodłowski & J. Mitka (KRA 0224507).- Ustrzyki Górne, potok Terebowiec, naprzeciw budynku dyrekcji BPN; 12.08.1996; J. Jodłowski (KRA 0225141).

***Aconitum lasiocarpum* (Rchb.) Gáyer subsp. *kotulae* (Pawl.) Starmühl. & Mitka**

POLAND Eastern Carpathians [Western Bieszczady] Górny Dział FG6849, młaka przy grani, ok. 1120 m; 11.08.1993; M. Szewczyk (KRA 0225146). UKRAINE [Chornogora] 7 km powyżej Zaroślaka nad Prutem; 30.07.1997; J. Mitka (KRA 0224501). [Gorgans] okol. Świcy 900 m; 11.08.2003; M. Graniszewska (KRA).

Aconitum lasiocarpum* (Rchb.) Gáyer subsp. *lasiocarpum

POLAND Eastern Carpathians [Western Bieszczady] Połonina Wetlińska; 22.08.2007; B. Szajna (KRA).- potok Wołosatka; 0,5 km powyżej stacji harcerskiej; 24.08.1996; J. Jodłowski (KRA).

***Aconitum variegatum* L.**

SLOVAKIA Western Carpathians [Stražovské vrchy] Súlov (pod skałami); 04.09.2001; J. Mitka (KRA). [Babia Góra] Rabczyce 830 m, ziołorośla; 25.08.2005; J. Parusel (KRA). [Slovenský raj] Podlesok; 16.08.2002; J. Mitka (KRA). [Nízke Tatry] Tale, Bistricanka torrent, 690–830 m; 18.08.2007; J. Mitka (KRA).- NW zbocze góry Skalka (1548 m), lewy dopływ potoku Lúznanka, świerczyna górnoreglowa; 19.08.2003; Z. Szeląg (KRA). POLAND Western Carpathians [Beskid Żywiecki] Pilsko, Korbielów; 30.08.2003; J. Mitka (KRA). [Doły Jasielsko-Sanockie Basin] Targowiska, Fraxinetum; 24.08.2001; J. Mitka (KRA). [Beskid Niski] Kornuty; 10.09.1998; J. Mitka (KRA). góra Kornuty 830 m, NE część, (Magurski PN), podmokły las jesionowy; 04.08.1998; K. Oklejewicz (KRA). [Pieniny] Wąwóz Homole, w zaroślach nad potokiem na dnie wąwozu; 01.09.2000; K. Oklejewicz (KRA).