

PHENETIC AND GEOGRAPHIC PATTERN
OF *ACONITUM* SECT. *NAPELLUS* (RANUNCULACEAE)
IN THE EASTERN CARPATHIANS – A NUMERICAL APPROACH

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(Received: February 26, 2001. Accepted: June 16, 2001)

ABSTRACT

Aconitum sect. *Napellus* in the Eastern Carpathians was explored with the use of methods of numerical taxonomy*. The taxon consists of *A. bucovinense* Zapał. pro hybr., *A. firmum* Rchb. subsp. *firmum*, *A. firmum* subsp. *fissuræ* Nyárády, *A. firmum* n. subsp. *fussianum* Starmühl. (*A. firmum* subsp. *firmum* × subsp. *fissuræ*), *A. ×nanum* (Baumg.) Simonk. (*A. bucovinense* × *A. firmum*) and a hybrid *A. firmum* × *A. ×nanum*. The taxa form phenetic continuum in a character hyperspace and their delimitation bases on a few traits, hitherto neglected, e.g. type of hairiness and flower morphology. A key is provided to identify taxa at all ranks within the supplemented of sect. *Napellus*. There is a regional pattern of particular OTUs distribution, which show local morphological uniqueness within a taxon. The phenomenon was inquired using the concept of „centers of phenetic coherence” (CPC) based on overall morphological similarity. The CPC may be interpreted as regions of neoendemism and/or may reflect a post-glacial migratory route. High-mountain flora of the Western Bieszczady Mts. (sect. *Napellus* as its example) has features of neoendemism (schizoendemism), being most probably a result of geographical vicarism.

KEY WORDS: *Aconitum* center of phenetic coherence, endemism, geographical distribution, nothotaxon, migratory route, numerical taxonomy.

INTRODUCTION

The rich, and in a great extent endemic, flora of the Eastern Carpathians has attracted attention of botanists from the beginning of modern botany (Hacquet 1790, Baumgarten 1816). Systematics of *Aconitum* in this area was investigated by, among others, Reichenbach (1923-1927), Zapałowicz (1908), Gáyer (1930), Grințescu (1953), Götz (1967), Seitz (1969) and Skalický (1988).

In spite of such much effort, the systematics and species concepts in the genus have remained still unclear. The main drawback is too much enlarged system consisting of several minor taxa, attempting to cover extraordinary morphological variation of the genus, often restricted to local areas. It is a result of either biological features, e.g. possible between-species crosses, human activity, breaking natural barriers between hitherto isolated populations (Mitka, Jodłowski 1997), or fixed morphological differences among local populations due to inbreeding (Utelli et al. 2000). As an effect, on one side, the species borders are broken yield-

ing morphologically intermediate (F_1 or introgressive) diploidal and allopolyploidal hybridogenous forms (Zieliński 1982a, b), and, on the other hand, local biotypes are genetically fixed, contributing to a taxon variation.

In a series of papers on the genus *Aconitum* in the Alps and Carpathians (Mucher 1993, Starmühler 1996, 2000, Starmühler, Mitka 2001, Mitka, Zemanek 1997, Mitka, Starmühler 2000a, b) some new systematic solutions are to be posed. They are based on rich comparative herbarium material and were supplemented by methods of cytotaxonomy and numerical taxonomy (Joachimiak et al., 1999, Mitka, Starmühler 2000a, b).

The area under this study encompasses a large part of the Eastern Carpathians between rivers Samoș-Bistrica (Romania) and the Łupków Pass (Poland) and includes the following mountain chains: the Bieszczady, Negrovec, Svidovec, Čornogora, Maramureș (Chyvchyn and Gryniawa Mts.), Rodna, and Bistrica and Čeahlău (Fig. 1). These ranges of the Carpathians were floristically and geobotanically elaborated by, among others, Zapałowicz (1889), Wołoszczak (1893), Pax (1898-1908), Borza (1931) Pawłowski (1946) and Jasiewicz (1965). In fact, these mountain systems do not cover the whole area of the Eastern Carpathians, however they seem to be representative of this physico-geographical unit (Kondracki 1989).

* **Abbreviations:**

CA – Correspondence Analysis, DFA – Discriminant Function Analysis, CPC – Center of Phenetic Coherence; nomenclature follows Starmühler 2000

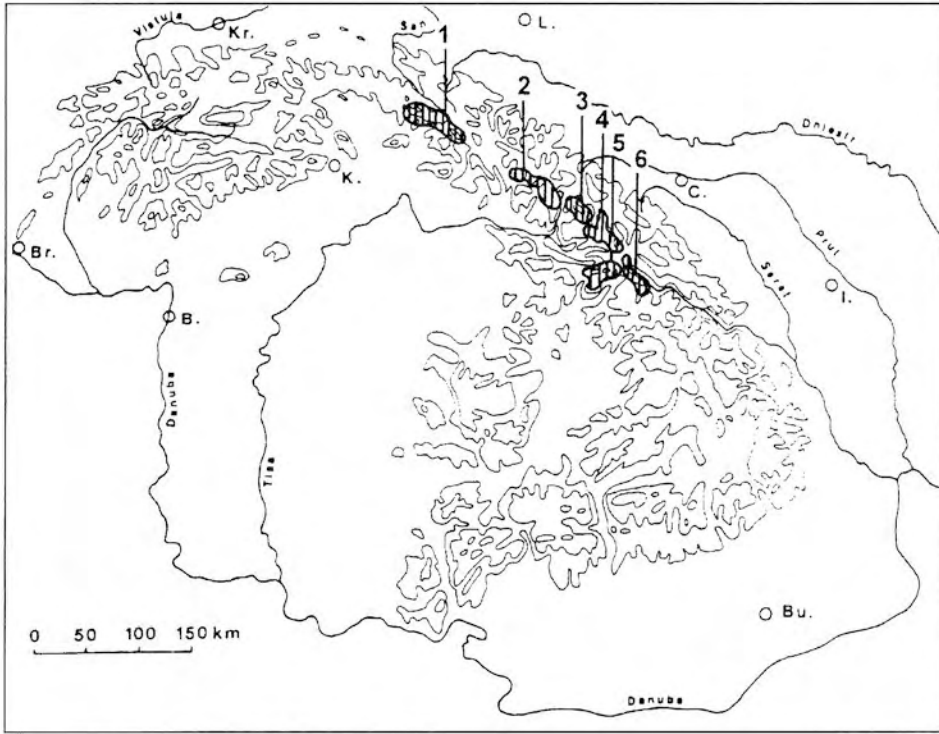


Fig. 1. The investigated regional centers of *Aconitum* sect. *Napellus* occurrence in the Eastern Carpathians; 1 – Bieszczady Mts.; 2 – Svidovec-Negrovec Mts.; 3 – Čornogora Mts.; 4 – Maramureș; 5 – Rodna Mts.; 6 – Bistirica and Čeahlău Mts.; Kr. – Kraków, L. – Lviv, K. – Košice, C. – Černivce, Br. – Bratislava, B. – Budapest, I – Iassy, Bu. – București.

The preliminary aim of the present paper was to give some new systematic solutions in *Aconitum* subgen. *Aconitum* sect. *Napellus* in the Eastern Carpathians, a neglected area in the study by Seitz (1969). In the work I use some concepts expressed previously in the papers by Starmühler (2000) and Starmühler and Mitka (2001). Here the novum is, in comparison to above mentioned, somewhat different area of investigations and numerical approach to classification and ordination of Operational Taxonomic Units (OTUs). However, during the data analysis I found some regularities in geographic distribution of OTUs across *Aconitum* sect. *Napellus*, irrespective of species status. So, the second aim of the paper is to link the phenetic variation with geographical pattern in concept of "centres of phenetic coherence – CPC".

Phylogenetic and vicariance models of historical biogeography are concerned with „recognizing of centers of origin and pathway of dispersal” (Cracraft 1975) using the information stored in the monophyletic groups (e.g. Morrone, Crisci 1995). Here I propose the similar in aim, but different in assumptions and methodology the way of delimiting the "centres of phenetic coherence" (see Materials and Methods). The method is based on the concept of overall phenetic similarity (Sneath, Sokal, 1973).

In the paper the following systematics of the genus *Aconitum* was adopted:

- Aconitum* L. subgenus *Aconitum*
 sectio *Aconitum* ser. *Toxicum* (Rchb.) Mueh. (1993)
A. degenii subsp. *degenii*
 (= *A. paniculatum* Lam., *nom. illeg.*)
 (see also Mitka, Starmühler 2000a)

sectio *Napellus* (Wolf) DC. subsectio *Napellus* (Wolf) Rapaics in the Eastern Carpathians (see Starmühler 2000, Starmühler, Mitka 2001)

- A. bucovinense* Zapal. pro hybr.
A. firmum Rchb. subsp. *firmum*
A. firmum Rchb. subsp. *fissurae* Nyárády
A. firmum Rchb. nsubsp. *fussianum* Starmühler
 (*A. f.* subsp. *firmum* × *A. f.* subsp. *fissurae*)
A. ×nanum (Baumg.) Simonk.
 (*A. bucovinense* × *A. firmum*)
A. firmum × *A. ×nanum*

MATERIALS AND METHODS

Numerical taxonomy

The herbarium material used in the work have originated from the herbaria in Poland, Slovakia, Czech Republic, Hungary and Romania (BP, CL, KO, KRA, KRAM, LW, LWA, PR, PRC) and my collection gathered during field trips to the Western Bieszczady, Čornogora and Rodna Mts. in 1995-1998 and maintained in the Botanical Garden of the Jagiellonian University. The selected material from the Database of *Aconitum* in the Carpathians (ACARP) consists of 150 OTUs numerically analysed, in this 108 with traits of sect. *Napellus* (Table 1), supplemented by 42 OTUs of *Aconitum degenii* subsp. *degenii* (sect. *Aconitum* ser. *Toxicum*) to test a hypothesis on hybridogenous origin of some taxa.

Each herbarium specimen (OTU) was described with the use of simple, carefully chosen qualitative characters, concerning mainly the morphology of generative elements of flowers. The 16 characters used in the analysis consisted of

TABLE 1. Morphological characters and states used in the phenetic analysis.

| | |
|---|--|
| 1. Inflorescence branched | (0) no, (1) yes |
| 2. Terminal inflorescence* | (0) lax with few flowers, (1) dense with many flowers |
| 3. Intensity of hairiness of pedicels above bracteoles* | (0) glabrous, (1) moderate, (2) strong |
| 4. Intensity of hairiness of pedicels below bracteoles* | (0) glabrous, (1) moderate, (2) strong |
| 5. Localisation of bracteoles | (0) in middle of pedicel, (2) in 2/3, (3) in 4/5 or just below flower |
| 6. Shape of bracteoles | (0) minute, acicular, (1) linear, (2) lanceolate, (3) spatulate, (4) obovate, (5) lobate |
| 7. Hairiness of helmets* | (0) glabrous, (1) moderate, (2) strong |
| 6. Shape of helmets | (0) conical, (1) hemisphaerical, (2) obtuse |
| 7. Hairiness of lateral petals | (0) glabrous, (1) ciliate |
| 8. Number of carpels | (0) 3, (1) 4, (2) 5 |
| 9. Hairiness of carpels | (0) glabrous, (1) on the suture, (2) overall |
| 10. Hairiness of filaments | (0) no, (1) yes |
| 11. Shape of nectaries | (0) erected, (1) curved |
| 12. Localisation of spurs | (0) not reached the top helmet, (1) reached |
| 13. Shape of spurs* | (0) capitate, (1) curved |
| 14. Leaf shape ¹ | (0) "variegatum" type (1) "stoerkianum" type, (2) "cernuum" type (3) "tauricum" type |
| 15. Type of inflorescence hairiness* | (0) glandular, (1) eglandular |

* – polymorphic or intermediate

¹ – according to Reichenbach (1823-1827)

8 binary and 8 unordered multistate characters (Sneath, Sokal 1973; Stace 1993), including, e.g. shape of bracteoles, intensity and type of hairiness of inflorescence, morphology of nectaries, etc. (Table 1, Mitka, Starmühler 2000a, b). There were distinguished three types of hairs (Fig. 2). One typical of *Aconitum* sect. *Toxicum* series (Mucher 1993), i.e. relatively long, erected, bright opalescent glandular ("pilose") hair, the second one typical of *Napellus* sect., i.e. short, curved or crisped, non-opalescent ("pubescent") hair. The third type is of intermediate character, consists of curved and crisped eglandular hair and glandular pubescent and glandular pilose hair. Also, three types of spurs of the nectaries were distinguished. The first globose (capitate – sect. *Napellus*) and the second – backward bent or semispiral coiled (sect. *Aconitum*). The intermediate type has spurs half backward bent or elongated at right angle.

Classification of OTUs was performed using Ward's minimum variance cluster method (Ward 1963), based on City-block (Manhattan) distance (Fig. 3), and their ordination with the use of a CA (correspondence analysis – Jongman et al. 1987). The latter method enables the ordination of OTUs in a multidimensional space (hyperspace according to Stace 1993), described with the use of CA scores along particular axes. They form a measure of general similarity between particular OTUs. Then, to evaluate the specificity of the taxa distinguished, a DFA (Jeffers 1978) was applied, based on the OTU's scores along first three axes of CA and a priori imposed taxa. So, in DFA

used the CA scores as a "supercharacters", the "best" reflecting internal relationships among OTUs (Fig. 4). The procedure enabled also the observed (a priori imposed) and expected (from DFA) classifications to be compared in the form of a classification matrix (Table 2).

Geographical analysis

The area of the Eastern Carpathians was divided into 6 regions of *Aconitum* sect. *Napellus* occurrence; from the north-west: 1 – Bieszczady Mts.; 2 – Svidovec-Negrovec Mts. (a part of the Transcarpathia); 3 – Čornogora Mts.; 4 – Maramureş (Chyvhyn and Gryniava Mts.); 5 – Rodna Mts.; 6 – Bistrica (with the Bucovina region and Čeahlău Mts.) (Fig. 1).

A numerical analysis was also performed to distinguish the regional pattern of *Aconitum* sect. *Napellus* morphological diversity. The reasoning of the approach is as follows. Morphologically similar OTUs (using any coefficient of similarity or distance measure; here on the first three axes' scores of CA) are expected to be found in the same region. It means that they share the same gene pool or, in other words, come from the same "source". The among-regional delimitation of the taxon is analogous to seeking for the among-population distances (e.g. Bobowicz, Korczyk 1994) in the phenetic studies or for among-site component of diversity in the population-genetic studies (e.g. Prentice, White 1988).

The geographical analysis consists of two steps: 1) the measurement of the among-region phenetic distance and 2)

TABLE 2. Discriminant function analysis – classification matrix of OTUs; observed – based on a priori imposed classification, predicted – from DFA.

| Discriminant Analysis Taxon | Discriminant Analysis Percentage of correctly classified | Classification matrix – observed vs. predicted classification | | | | | Total (observed) |
|--|--|---|----|----|----|---|---------------------|
| | | 1 | 2 | 3 | 4 | 5 | |
| 1. <i>A. degenii</i> subsp. <i>degenii</i> | 92.86 | 39 | 3 | 0 | 0 | 0 | 42 |
| 2. <i>A. bucovinense</i> | 88.14 | 6 | 52 | 0 | 0 | 1 | 59 |
| 3. <i>A. firmum</i> | 100.00 | 0 | 0 | 16 | 0 | 0 | 16 |
| 4. <i>A. xnanum</i> | 95.45 | 0 | 1 | 0 | 21 | 0 | 22 |
| 5. <i>A. firmum</i> × <i>A. xnanum</i> | 54.54 | 0 | 0 | 0 | 5 | 6 | 11 |
| Total (predicted) | 89.33 | 45 | 56 | 16 | 26 | 7 | 150 |

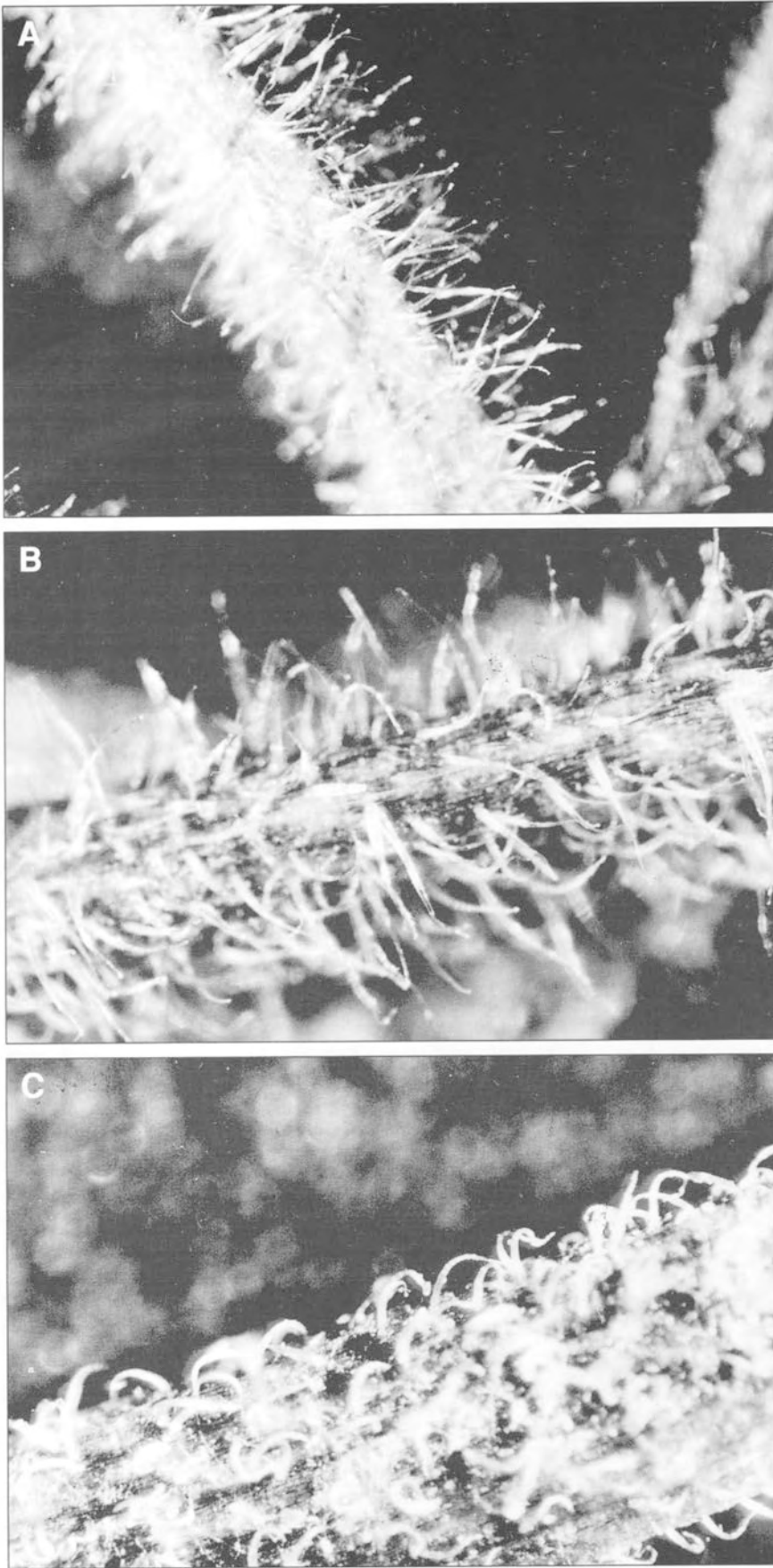


Fig. 2. Type of hairiness of *Aconitum* sect. *Napellus* in the Carpathians: A – glandular hair (also typical of *Aconitum* sect. *Aconitum* ser. *Toxicum*), *A. firmum* Rchb. subsp. *maninense* (Skalický) Starmühl., the Tatras, $\times 60$; B – mixed glandular and eglandular hair (typical of *A. bucovinense*), *A. firmum* nsubsp. *paxii* Starmühl., the Tatras, $\times 65$; C – eglandular hair, *A. bucovinense*, the Bieszczady Mts., $\times 70$ (also typical of *A. f.* subsp. *moravicum* Skalický from the Western Carpathians). See Mitka and Starmühler (2000b), Starmühler and Mitka (2001).

the construction of a dendrogram based on a matrix of distances between OTUs and regions' centroids. Then, it serves for the delimitation of the centers of phenetic coherence.

Based on a taxonomical DFA analysis the phenetic centroids of OTUs in each a priori imposed region, represent-

ing means of all variables (CA scores) in a three-dimensional space of DF, were calculated. Then, the distances among centroids of regions were calculated (Table 3). Additionally, a distance between each phenotype (OTU) to each region's centroid was calculated with the use of

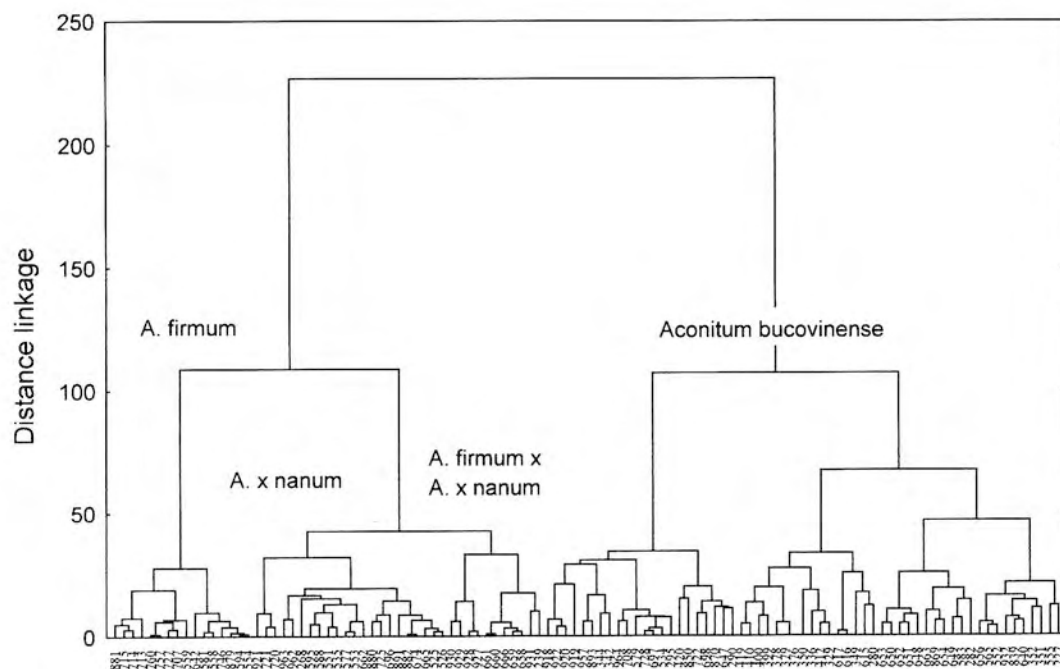


Fig. 3. Phenogram of 108 *Aconitum* sect. *Napellus* OTUs originating from the Eastern Carpathians. Ward's method of classification and City-block distance based on characters listed in Table 1.

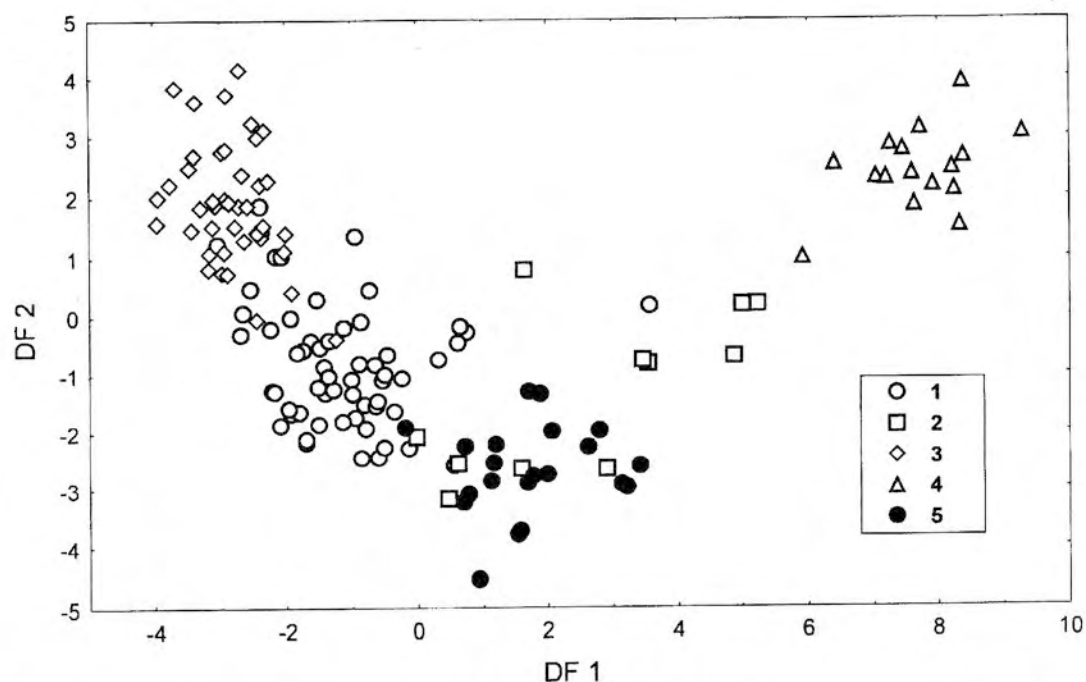


Fig. 4. Ordination of 150 OTUs of *Aconitum* sect. *Napellus* and *A. degenii* subsp. *degenii* (sect. *Aconitum* ser. *Toxicum*) from the Eastern Carpathians along the first two discriminant functions (DF) of discriminant function analysis (DFA). As variables the OTUs scores in a three dimensional space of correspondence analysis (CA) were used; 1 – *A. bucovinense*, 2 – *A. firmum* × *A. x nanum*, 3 – *A. degenii* subsp. *degenii*, 4 – *A. firmum*, 5 – *A. x nanum*.

Mahalanobis distance (D^2) measure (an option of DFA). In this way a derived (phenetic) distance data matrix (OTUs × Regions) was created. Then, the regions were hierarchically classified (UPGMA and Euclidean distance) in terms of their "phenetic" coherence, using the matrix of Regions × OTUs, and interpreted as the centers of phenetic coherence (CPC) or regions of coherent phenetic similarity (see Fig. 5).

Also, the phenetic distances (distances among regions' centroids) may be superimposed on a map (Fig. 5) and then interpreted in term of first and second-order regions of phenetic coherence. The method is especially suitable for geographic analysis of phenetically overlapping taxa.

All numerical calculations were made with the statistical package STATISTICA (StatSoft, Inc., 1984-1995).

TABLE 3. Mahalanobis distances of phenetic centroids of *Aconitum* sect. *Napellus* among regions of the Eastern Carpathians.

| Region | Bieszczady | Svidovec-Negrovec | Čornogora | Rodna | Maramureş | Bistrica |
|-------------------|------------|-------------------|-----------|-------|-----------|----------|
| Bieszczady | – | | | | | |
| Svidovec-Negrovec | 2.61 | – | | | | |
| Čornogora | 2.14 | 0.44 | – | | | |
| Rodna | 5.73 | 0.90 | 1.16 | – | | |
| Maramureş | 4.55 | 3.78 | 3.20 | 3.31 | – | |
| Bistrica | 4.65 | 4.19 | 3.30 | 3.64 | 0.05 | – |

RESULTS

Numerical taxonomy

Classification of 150 OTUs with the use of Ward's method (the result not shown) gives two main clusters: one with *A. degenii* subsp. *degenii* (sectio *Aconitum* ser. *Toxicum*) and the second one with *Aconitum* subsp. *fissurae*, *A. xnanum*, *A. bucovinense* and *A. firmum* × *A. xnanum* (sectio *Napellus*).

The sub-cluster of sect. *Napellus* (108 OTUs), analysed separately, consists of OTUs with glabrous (left main cluster) and pilose helmets (right main cluster) (Fig. 3). The left cluster is differentiated according to the type of pedicels hairiness. So, *A. firmum* has glabrous pedicels, *A. firmum* × *A. xnanum* has solely glandular hairs and *A. xnanum* has intermediate type of hairiness (often with curved pubescence prevailing), as well *A. bucovinense*. The latter taxon, forming the right cluster has pubescent helmets, the trait differentiating it from *A. firmum* and *A. xnanum*, both having glabrous ones.

There is a differentiation within *A. bucovinense* reflected in different position of its clusters on the phenogram (Fig. 3). The right sub-cluster consists of typical forms of the taxon with mixed glandular and eglandular hairiness (Fig. 2B) and the left sub-cluster, mostly from the Bieszczady Mts., i.e. at the border of geographic range, has prevailing eglandular hair (Fig. 2C) and other unique traits as e.g. half backward bent spurs of the nectaries.

The ordination of OTUs along Discriminant Function 1 (DF 1) and DF 2, based on OTUs score along axes I-III of Correspondence Analysis (which explain 24.4% of a total variance) show some morphological relationships between *A. degenii* subsp. *degenii* and *A. bucovinense* (Fig. 4). The diversification of *A. xnanum* and its hybrid with *A. firmum* is not so clear than on the classification phenogram, and shows that the hybrid may close to both presumed parents likely in the result of backcrosses.

All the taxa considered, excluding the hybrid *A. firmum* × *A. xnanum*, have a high degree of phenetic coherence, what is visible in the classification matrix (76-100% of properly classified OTUs – Table 2). The misclassified OTUs point to morphological affinities between taxa, e.g.

A. bucovinense shares morphological characters with *A. degenii* subsp. *degenii* and hybrid *A. firmum* × *A. xnanum* with *A. firmum* (Table 2, Fig. 4).

Geographical analysis

Mahalanobis distances among regions' centroids (Table 3) show close phenetic similarities between OTUs from the Maramureş and Bistrica Mts., and their strong delimitation from the other regions. The weakest relationships are between the Rodna and Bieszczady Mts. The dendrogram based on the whole distance data (i.e. on a matrix: Regions × OTUs) shows three CPC (Fig. 5). The first consists of the Bistrica and Maramureş, the second of the Bieszczady Mts., and the third of the remaining regions, in which the Rodna Mts. region has the dominant position. The Čornogora Mts. and the Negrovec-Svidovec regions have the subordinate position on the dendrogram, however they have the highest degree of similarity (Fig. 5).

The superimposing of information on the centroid's distances on the map (Fig. 5) show two the most similar phenetic centres of *Aconitum* sect. *Napellus*: one in the the Maramureş-Bistrica Mts., and the second in the Čornogora – Svidovec-Negrovec Mts. There is a moderate phenetic connection between the Rodna and Čornogora Mts., and the Rodna and Negrovec-Svidovec Mts. The Bieszczady Mts. are relatively isolated in terms of phenetic distance both to the Čornogora and Svidovec-Negrovec Mts. (Table 3), however they form the center of the high phenetic coherence. The Svidovec-Negrovec and the Čornogora Mts. are closely related, nevertheless their phenetic coherence is of secondary provenience in comparison to the Rodna Mts. (Fig. 5).

The mean values of Mahalanobis distances between the taxa and region's centroids (Table 4) reveal that *A. bucovinense* in three regions has high phenetic coherence: in the Bistrica Mts. (Bukovina is the *locus classicus* -1.36), Bieszczady Mts. (1.53) and in Maramureş (2.21). The region of high phenetic coherence for *A. xnanum* is the Čornogora Mts. and Negrovec-Svidovec, for *A. firmum* × *A. xnanum* is the Čornogora Mts., and for *A. firmum* – the Rodna Mts. and Negrovec-Svidovec region.

TABLE 4. Means of Mahalanobis distances between taxa's and regions' centroids. In parentheses no. of OTUs.

| Taxon | Region | Bieszczady | Svidovec-Negrovec | Čornogora | Rodna | Maramureş | Bistrica | no. of OTU |
|-------------------------------------|--------|------------|-------------------|-----------|----------|-----------|-----------|------------|
| <i>A. bucovinense</i> | | 1.53 (15) | 4.63 (5) | 3.82 (11) | 6.38 (5) | 2.21 (13) | 1.36 (10) | 59 |
| <i>A. firmum</i> | | – | 3.93 (5) | 7.50 (1) | 3.21 (8) | 10.19 (1) | 11.25 (1) | 16 |
| <i>A. xnanum</i> | | – | 1.90 (7) | 1.67 (12) | 3.00 (3) | – | – | 22 |
| <i>A. firmum</i> × <i>A. xnanum</i> | | – | – | 1.47 (6) | 3.20 (5) | – | – | 11 |
| Total | | 15 | 17 | 30 | 21 | 14 | 11 | 108 |

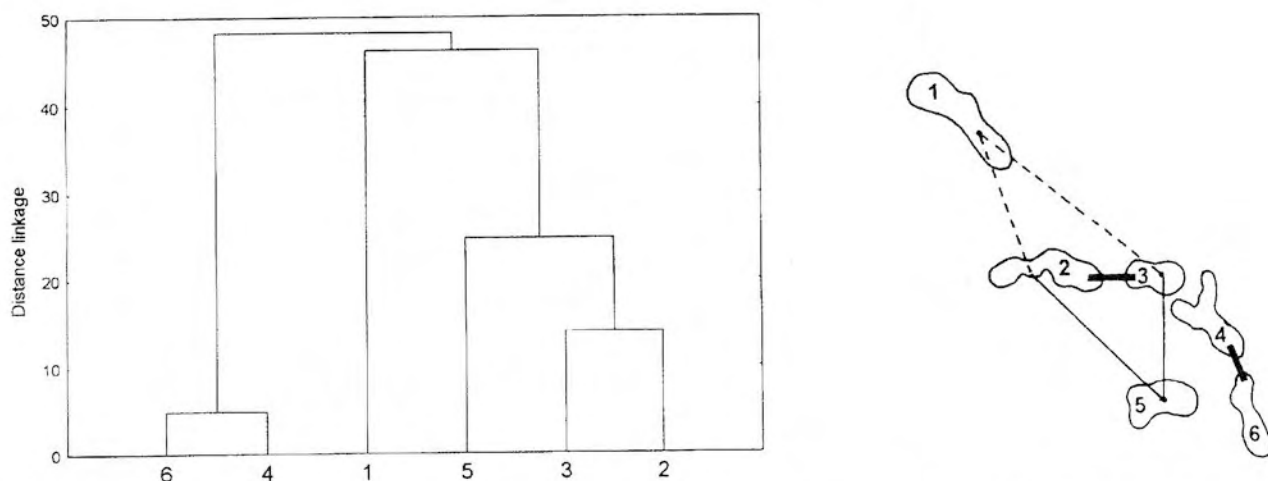


Fig. 5. Classification of Eastern-Carpathian regions (UPGMA and Euclidean distance) according to their phenetic coherence (based on a matrix OTUs \times regions' centroids) and Mahalanobis distances among regions; thick line – ≤ 0.50 ; thin line – $> 0.50 \leq 2$; broken line – $> 2 \leq 3$ (based on data in Table 3); 1 – Bieszczady Mts.; 2 – Svidovec-Negrovec Mts.; 3 – Čornogora Mts.; 4 – Maramureş Mts.; 5 – Rodna Mts.; 6 – Bistrica and Čeahlău Mts. (see Fig. 1).

DISCUSSION

Taxonomic remarks

Starmühler and Mitka (2001) proposed a revised systematics of *Aconitum* sect. *Napellus* and its hybrids in the Forest Carpathians, which cover western part of the Eastern Carpathians and the whole Western Carpathians in Poland territory. In present work some OTUs from the Čornogora and the Bieszczady Mts. are included, which were poorly represented in the previous paper. It enabled a new nothotaxon to be described (see Systematic Note), which known geographical range is within the Eastern Carpathians, however it may probably extend southwards of the region covered in the present investigations.

The hybrid *A. firmum* \times *A. xnanum* forms a phenetic continuum between both presumed parents. Its key characters are glandular pubescent pedicels and glabrous helmets. It was found in the Čornogora and Rodna Mts., however it is expected to be found also in the whole range of parental taxa. It is probably identical with Zapałowicz's (1908) *A. napellus* var. *czarnohorensis*, with an adnotation "*A. nanum* Baumg. pro parte?". It well illustrates the problems with the *Aconitum* genus systematics, where hybridogenous and backcrossed forms abundantly occur.

Very similar to this hybrid is *A. degenii* subsp. *degenii* fo. *craciulense* (Starmühler 2000) belonging to *Aconitum* sect. *Aconitum* ser. *Toxicum* (Mucher 1993). It has glandular pilose helmets and from the typical fo. *degenii* differs with capitatus spur of nectaries, which closes it to sect. *Napellus*. Maybe it is an introgressive form possessing some admixture of genes from this group.

A. firmum subsp. *fissuriae* is the taxon very similar to *A. firmum* subsp. *firmum*, having its abundance (and maybe genetic) center in the Western Carpathians. The second hypothesis points that the primary genetic center of *A. firmum* subsp. *firmum* would be in the Eastern Carpathians and the taxon might vanish from the area in the effect of mainly genetic phenomena (genetic meltdown?).

A. f. subsp. *fissuriae* seems to be also closely related to *A. tauricum* subsp. *tauricum*, which is distributed in the

Alps. The differences between them are, for example, in the shape of helmets and leaves and their nervature (W. Starmühler, pers. comm.).

In addition to the above taxa also *A. firmum* nsubsp. *fussianum* Starmühl., a hybrid between *A. firmum* subsp. *firmum* \times subsp. *fissuriae*, and *A. firmum* subsp. *firmum* occur in the Eastern Carpathians (Starmühler 2000). They are included to the list of localities in the Appendix. The above mentioned relations among sect. *Napellus* taxa, both in the Carpathians as well as in the Alps, proves an old history of the genus in European mountain ranges (Starmühler 1996).

A. bucovinense is very distinct taxon. In the Bieszczady Mts. it should be synonymised with *A. tauricum* subsp. *nanum*. It was originally described by Zapałowicz (1908) from the Bucovina region as a hybrid between *A. napellus* (= *A. xnanum*) and *A. paniculatum* (= *A. degenii*). At its western border of the geographical range in the Western Bieszczady Mts. it has morphological traits different from the other, more easternward populations. There is a phenetic continuum of taxa (Fig. 4), shared each with other starting from *A. degenii* subsp. *degenii*, *A. bucovinense*, *A. xnanum*, *A. firmum* \times *A. xnanum*, and *A. firmum*.

The last taxon, additionally considered here, is *A. xcammarum*, occurring as a decorative plant in house-gardens throughout all Europe and sometimes naturalized.

These are the first attempts (Starmühler 2000; Starmühler, Mitka 2001) to the solution of the Eastern Carpathian *Napellus*-group systematics. It will be complemented and refined when the material from this part of the Carpathians becomes more available than now. Also, it should be also compared with those originated from the Southern Carpathians. Certainly it is not the last statement about the systematics of the *Napellus*-group in these parts of the Carpathians.

Geographical remarks

One of the most conspicuous results of the geographical analysis of *Aconitum* sect. *Napellus* phenetic variability in the Eastern Carpathians was the strong delimitation of the

Bieszczady Mts. as a center of phenetic coherence. This result becomes quite clear when we look on the map and the dendrogram of the phenetic coherence (Fig. 5). Undoubtedly the Maramureş-Bistrica regions may be considered as a first-order centers of the taxon phenetic coherence. In term of phenetic relationships they are both isolated and form separate cluster. In these regions *A. bucovinense* has also high phenetic coherence (Table 4).

The second first-order center are the Rodna Mts. They are moderately affiliated to both the Čornogora Mts. and the Svidovec-Negrovec region. It seems obvious that the latter one should be considered as a secondary in phenetic relation to the Čornogora Mts., owing to their high similarity (Fig. 5). The peripheral Bieszczady Mts. are weakly connected to neighbouring area of Svidovec-Negrovec Mts. and it is a result of their phenetic distinctness, seemingly also of a secondary origin. This result comes mainly from the morphological distinctness (and also coherence), of *A. bucovinense* populations in the Western Bieszczady Mts. in comparison to those in the Maramureş and Bistrica Mts. (Bukovina) (see Fig. 3, Table 4 and Appendix).

It is worthy to mention that the phenetic relationships in *Aconitum* sect. *Napellus* among regions considered fits well to the geobotanical relationships by Pawłowski (1948). In this division the Maramureş (especially the Chyvchyn Mts.) plays a special role as a local center of endemism and the region of high affinity to both the Bucovina and more south-eastern mountain ranges, and the Rodna Mts. have a status of the most peculiar geobotanic sub-district. The weak phenetic affiliation between the Čornogora and Chyvchyn Mts. is also reflected in Pawłowski's geobotanical analysis.

The knowledge on centers of phenetic coherence may contribute some new prospects to the problem of polytopic (vicariant) origin or to migratory history of a taxon (Szafer 1964; Kornaś, Medwecka-Kornaś 1986).

The concept of a moderate polytopism, which advocates were, among others, De Candolle, Hackel and Engler, accepts the possibility of a multiple origin of the parallel low systematic units (e.g. geographic race or biotype) in various regions independently. In fact it is a vicariant hypothesis. In this scenario we may expect that in every region an own biotype evolves and it displays here uniform morphology (low polymorphism). In terms of population genetics it is often expressed as the hypothesis that among-population genetic diversity exceeds the within-population diversity (e.g. Samuel et al. 1995; Tarayre et al. 1997).

On the other hand, the problem may be deeper inquired within the concept of neoendemism. In this attitude a center of high phenetic coherence may be regarded as a narrow range of low taxonomic unit, including non-polymorphic biotypes (Szafer 1964). In the Carpathian context inner morphological diversification of *A. bucovinense* (Table 4), contributing to the regional hierarchy of CPC (Fig. 5) may be regarded as centers of neoendemism. It seems that it may be an example of schizoendemism (endemovariant), i.e. a continuous diversification of an ancestral taxon into derived taxa of identical chromosome numbers in various parts of the range (Kornaś, Medwecka-Kornaś 1986).

Other than cytological criteria may also call a hypothesis relies on the historical context. In this attitude the Bieszczady population may be regarded as neoendemic or even

holoendemic taking the following criteria (Richardson 1978): the polymorphic rather than distinct taxonomical isolation, geographical isolation and weak potential to expand area. It is hardly to say about the age of this population. However, it may be regarded as an old (at least pre-glacial) and relict assuming its persisting throughout the Ice-Ages and holocene climatic optimum (Mitka, Zemanek 1996). Both events might reduce the population size (ecological bottleneck) with subsequent genetic consequences (e.g. genetic meltdown) leading to its morphological differentiation. The present-day occurrence in the Bieszczady Mts. the alpine zone with such light-demanding species as *Carex rupestris*, *Saxifraga paniculata* and *Anemone narcissiflora* proves their persisting here at least from the Pleistocene (Jasiewicz, Zarzycki 1956).

The pattern of centers of phenetic coherence may also reflect a post-glacial migratory route of the Carpathian flora from the Southern-Carpathian – Balkan refugia during the Holocene (e.g. Konner, Bergmann 1995; Utelli et al. 1999). In this sense it is a dispersalistic hypothesis. According to it the Carpathian flora after withdrawing of the last glacier migrated during Holocene (most probably in the Atlantic phase) from southern refugia northwards as so called Dacian migroelement (Hendrych, Hendrychová 1979). So, the arrangement of the first- and secondary centres of phenetic coherence reflects the migration routes. The prediction coming from this hypothesis is that together with the acquisition of new areas the genetic fixation of some alleles in newly-established populations has occurred, resulting in morphological distinctness of particular populations.

It seems that this dispersalistic hypothesis has weaker foundations in relation to the *Napellus*-group in the Eastern Carpathian than the vicariant one. The alpine and subalpine zones of the Bieszczady Mts. are often seen as an old, relictual areas of both phanerogamic (Jasiewicz, Zarzycki 1956; Mitka, Zemanek 1997) and hepatic flora (Szwejkowski, Buczkowska 1996). On the other hand, the Holocene-Atlantic migration (dispersalistic) hypothesis sounds more convincingly in relation to the more thermophilous, montane forest flora.

However, the nature of the presumed genetic processes involved in the among-region differentiation in *A. bucovinense* may be various, from typical events in small or marginal populations as founder effect, genetic drift, etc. (Shaal, Leverich 1996; Mitka 1997) to recently claimed (Utelli et al. 1999, 2000) hypothesis on strong inbreeding in local populations of *Aconitum* due to geitonogamy (i.e. visiting of flowers by bumble-bees on the same plant and subsequent selfing). The same process was found in an apoendemic *Delphinium bolosii*, a plant known from only two populations in Spain, derived from a widespread *D. fissum* (Bosch et al. 1998). It could be owing to "of extreme area border effect" in which adaptive selection on self-compatibility occurred in face of nectar robbery and less functional architecture of flowers, e.g spur length higher than the available insect proboscis.

The counteracting process of genetic changes in populations is phenotypic plasticity which should be first distinguished prior the conclusion about the role of natural selection to be drawn (Krauss 1996).

It is interesting that high morphological differentiation within particular taxa in *Aconitum* genus is often not

accompanying by the genetic diversity. For instance Kita et al. (1995) found within so called Japanese tetraploid complex, i.e. a set of well morphologically differentiated species occurring from Hokkaido to Kyushu, no genetic markers (based on RFLP and cpDNA *trnL-trnF*). They hypothesized that a single original tetraploid species has become adapted to various environments, with subsequent variation in the external morphology of each more or less isolated populations. This adaptive diversification has resulted in the production of many biormorphs, but they have not yet become genetically diversified.

Similarly, Utelli et al. (1999, 2000) found in *Aconitum lycoctonum* the lack of genetic differences (rDNA ITS region and cpDNA *psbA-trnH*) between e.g. such well morphologically differentiated species as *A. moldavicum* and *A. lycoctonum* or even the lack any differentiation in the subgen. *Lycoctonum* between European mountain ranges and the Caucasus Mts. These findings persuaded authors to hypothesis on quantum speciation of *A. moldavicum* which could happen during the Ice Ages. *A. lycoctonum* might at that time be split into small isolated populations and then rapid and radical genetic processes affecting genotypes or phenotypes or both occurred giving in turn a new species (*A. moldavicum*). Moreover, on that basis authors also questioned any division in *A. lycoctonum* complex based on morphology and claimed, for instance, that in this group the value of flower colour as a systematic character is valueless. Maybe a study on less conservative regions of DNA enable to another conclusions to be drawn.

These examples points to the problem that any taxonomic revision in *Aconitum* taxa based on solely molecular-genetic data can hardly be drawn. The first-order and information redundant have still stayed morphological data considered in a geographic range. In this context the proposed method of geographical-phenetic pattern analysis bound in the concept of CPC seems to be a useful tool for preliminary (pilot) hypotheses generation. As Bachmann (1995) noted "once the molecular are more routine, the preliminary morphological sorting can possibly be simplified, but it never be abandoned".

SYSTEMATIC NOTE

Aconitum firmum × *Aconitum* × *nanum* form. noth. et stat. nova

Diagnosis: cassis glabris, pedunculis supra bracteolae glanduloso erecto-pilosis vel glabris, infra bracteolae glanduloso pilosis et/vel curvatae puberulis.

Description: Planta perennis, radix napiformis, caule erecto, dense folioso, inflorescentia simplex vel subsimplex, cassis hemisphaerica vel convexo-hemisphaerica, 12-17 mm longa, 7.5-10 alta, glabris; bracteolae lineare ut lanceolatae vel partitae, 3.5-6.5(12) mm longae; folia 5-10 cm lata, venae laminae superiore crispule pubescentes, digitato tri-, quinque partitis; ovaria tria glabra vel pauce pilosa, cuculli calcarum capitatum, semina triangle, alatis, rugulosis; filamentis pilosis.

Distribution and habitat: In the Eastern Carpathians, expected to be found in the whole range of *A. xnanum* and *A. firmum* subsp. *fissurae*, in communities of *Adenostylyon* all. in subalpine and alpine zones.

KEY TO *ACONITUM* SECT. *NAPELLUS* IN THE EASTERN CARPATHIANS

- 1 Helmet 0.5-2.5 times as high as long, conical to cylindrical or obtuse, nectary spurs capitate to semispiral curved, leaves with narrow or broad segments (then divided to the base)
 - 2 Leaves with narrow segments divided to the base 1-2 mm wide, carpels 5, densely pubescent, tepals persistent, yellow or purple-violet – *Aconitum* subgen. *Anthora* (DC.) Petermann
 - 2* Leaves with segments >2 mm wide divided to the base, carpels 3(-5), glabrous or pilose, tepals bright to dark blue
 - 3 Helmet pilose and/or pubescent
 - 1 Helmet and pedicels exclusively with ± erected, glandular hair (Fig. 2a), filaments glabrous/scarsely pilose
 - 2 Spur of nectaries capitate, carpels glabrous – *A. degenii* subsp. *degenii* f. *craciulenense* (Starmühler 2000)
 - 2* Spur of nectaries half backward bent or semispirally coiled, carpels glabrous or pubescent – subgen. *Aconitum* ser. *Toxicum* (Rchb.) Mucher and not-hoser. *Acotoxicum* Mucher
 - 1* Helmet and pedicels curved and crisped glandular and/or eglandular pubescent and pilose (Fig. 2b, c), filaments pilose – *A. bucovinense*
 - 3* Helmet glabrous
 - 1 Pedicels pilose and/or pubescent
 - 2 Spur of nectaries half backward bent or semispirally coiled, filaments glabrous, seeds with laminae – subgen. *Aconitum* ser. *Toxicum* (Rchb.) Mucher (1993)
 - 2 Spur of nectaries capitate, filaments pilose, carpels sterile or seeds smooth
 - 3 Pedicels above bracteoles eglandular pubescent (on indumentum), below glabrous – *A. xcammarum*
 - 3* Pedicels at least above bracteoles glandular pilose (Fig. 2a) or ± glabrous – *A. firmum* × *A. xnanum*
 - 3** Pedicels with mixed eglandular and glandular hairs or exclusively eglandular pubescent below and under bracteoles (Fig. 2b, c) – *A. xnanum*
 - 1* Pedicels glabrous
 - 2 Bracteoles at least of lower flowers in the terminal inflorescence divided, filaments glabrous or pilose
 - 3 Filaments glabrous – *A. firmum* subsp. *firmum*
 - 3* Filaments pilose – *A. firmum* nsubsp. *fussianum* (*A. firmum* subsp. *firmum* × subsp. *fissurae*)
 - 2* Bracteoles undivided, filaments pilose – *A. firmum* Rchb. subsp. *fissurae* Nyárády
- 1* Helmet cylindrical, c. 2.5-3 times as high as long, nectary spurs spirally coiled, leaves with broad segments not divided to the base – subgen. *Lycoctonum* (DC.) Petermann

ACKNOWLEDGEMENTS

I am grateful to Dr. W. Starmühler and the anonymous Referee for their valuable comments on the manuscript. The study was performed within the framework of the State Committee for Scientific Research (KBN) grant no. PB 0295/P04/97/13.

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FENETYCZNY I GEOGRAFICZNY WZORZEC ROZMIESZCZENIA
ACONITUM SECT. *NAPELLUS* (RANUNCULACEAE)
 W KARPATACH WSCHODNICH – PODEJŚCIE NUMERYCZNE

STRESZCZENIE

Aconitum sect. *Napellus* w Karpatach Wschodnich został krytycznie opracowany metodami taksonomii numerycznej. Taxon ten składa się z *A. bucovinense* Zapał. pro hybr. (w Bieszczadach do tej pory ujmowany jako *A. tauricum* subsp. *nanum*), *A. firmum* Rechb. subsp. *fissurae* Nyárády, *A. firmum* nsubsp. *fussianum* Starmühl. (*A. firmum* subsp. *firmum* × subsp. *fissurae*), *A. ×nanum* (Baumg.) Simonk. and *A. firmum* × *A. ×nanum*. Taksony te tworzą fenetyczne kontinuum w przestrzeni cech, a ich wyróżnienie opiera się na niewielu cechach, dotychczas pomijanych, np. na typie owłosienia i morfologii kwiatu. Dla ich wyróżnienia został opracowany klucz. Stwierdzono prawidłowości w geograficznym rozmieszczeniu poszczególnych roboczych jednostek taksonomicznych (OTU), które pod względem morfologicznym wykazują wewnątrzgatunkową regionalną zmienność. Zjawisko to zostało zbadane przy pomocy koncepcji „centrów fenetycznej spójności” (CFS) opierającej się na ogólnym morfologicznym podobieństwie (Sneath, Sokal 1973). CFS mogą być interpretowane jako obszary neoendemizmu, bądź też wskazujące szlaki migracyjne. Pierwsza możliwość nawiązuje do hipotezy geograficznych gatunków zastępczych (wikariantów), które mogą powstawać politopicznie i przybierać postać drobnych taksonów (ras geograficznych lub biotypów). Druga zakłada, iż populacje w nowo zdobytych terenach, w wyniku zjawisk ekologiczno-deograficznych, typowych dla małych, izolowanych populacji, zyskują unikatowy zestaw cech w porównaniu do populacji w centrum zasięgu. Wysokogórska flora Bieszczadów Zachodnich, zbadana na przykładzie sect. *Napellus* (*A. bucovinense*), posiada cechy unikatowe, wskazujące prawdopodobnie na jej neoendemizm (schizoendemizm). Mniej prawdopodobna w tym przypadku jest hipoteza migracji (dispersalizmu), która w zamian lepiej może tłumaczyć pochodzenie flory leśnej badanego obszaru.

SŁOWA KLUCZOWE: centrum fenetycznej spójności *Aconitum*, endemizm, rozmieszczenie geograficzne, nototakson, droga migracji, taksonomia numeryczna.

APPENDIX

A. bucovinense Zapał. pro hybr.
 (in the Bieszczady Mts. = *A. tauricum* Wulf. subsp. *nanum* (Baumg.) Gáyer)
 Bieszczady Mts.: [290] Połonina Caryńska, 1045 m, stok N, w lesie bukowym nad potokiem; 7.9.1995; J. Mitka (KRA).- [295] Halicz, na półce skalnej, ok. 1260 m; 23.7.1997; J. Mitka (KRA).- [552] In alp. Pikuj, 1400 m; 5.7.1934; A. Margittai (CL).- [565] Karpatukrajna; 20.7.1959; F. Istvan (BP).- [583, 697] In subalp. Pikuj (pertinent ad montes "Beszkidek") supra pagum Sebestyen-falva, Com. Bereg.; 23.8.1907; L. de Thaisz (PR).- Na

Zełeminie koło Pikuja; 8. 1891; H. Wołoszczak (KRAM).- [656] Połonina Wetlińska, Hnatowe Berdo, ok. 1150 m; 15.8.1996; B. Zemanek, T. Winnicki, J. Mitka (KRA).- [850] Halicz; 4.9.1999; J. Mitka (KRA).- [918] Połonina Caryńska; 1996; J. Mitka (KRA).- [919-922, 957] Halicz; 2.8. 2000; J. Mitka (KRA).- [870, 964] Połonina Caryńska, ziołorośla przy ścieżce; 20.7.1971; R. Ochrya (KRAM).- Północne stoki Połoniny Caryńskiej poniżej szczytu 1212 m, młaka na wys. ok. 1050 m; A. Jasiewicz, K. Zarzycki (KRAM). Čornogora Mts.: [280] pod Homulem nad p. Homulskim, ok. 1295 m; 1.8.1997; J. Mitka (KRA).- [342,

344] Czeremosz wyżej ujścia Dzembronii; 11.8.1880; H. Zapałowicz (KRAM).- [349] ziołorośla pod Howerlą; ?8.1911; M. Raciborski (KRAM).- [412] W dolinie Bystrzyca, łąka; 20.8.1875; A. Śleńdziński (KRAM).- [400, 420] Szpyci, ziołorośla z *Cirsium pauciflora* na zach. zboczu Rebry, ok. 1800 m; 9.8.1935; B. Pawłowski (KRAM).- [534] Tiszobogdany in monte Čornogora; 5.8.1908; A. Richter (CL).- [555] In alp. Pietros, c. 1800 m, ad Jasina, Maramureș; 15.7.1931; A. Margittai (CL).- [579] In alp. Hoverla, c. 1800 m; 21.7.1928; A. Margittai (BP).- [663] Gutin Tomnatyk, nad jeziorem, ok. 1620 m; 2.8.1997; J. Mitka (KRA). Bucovina: [653] Bucovina, Jacobeni, distr. Dorna Watra, na otwartych miejscach; 30.8.1903; E. Wołoszczak (KRAM).- [650] Czokanestie (Kurus).- 22.8.1911; H. Zapałowicz (KRAM).- [652] Złota Bystrzyca powyżej Jakobeny; 9.8.1909; H. Zapałowicz (KRAM).- [648] Jakobeny [sp. orig. cultum Leopoli]; 7.8.1904; H. Zapałowicz (KRAM).- [649] Jakobeny; 27.8.1900; E. Wołoszczak (KRAM).- [651] Pojana Negry; 16.8.1908; H. Zapałowicz (KRAM).- [654] Jakobeni; L. Rehmman (KRAM – Lektotyp).- [869, 932] Flora Polonica Exsiccata. 904. *Aconitum multifidum* Koch in Reichb. III Acon. t. 70 (1827). Bucovina, Jacobeni, distr. Dorna Vatra. Na otwartych miejscach; 30.8.1903; E. Wołoszczak (KRAM). Maramaroș Mts.: [329] Burkut, nad Czeremoszem Czarnym, w lesie; 9.8.1875; A. Śleńdziński (KRAM).- [336] Albin nad Czarnym Czeremoszem; 5.8.1875; A. Śleńdziński (KRAM).- [350] Pot. Stewiora, Riu Vaser; 27.7.1905; H. Zapałowicz (KRAM).- [351] Czeremosz Czarny, ujście Popadii; 19.8.1906; H. Zapałowicz (KRAM).- [352] Trojaga; 14.8.1907; H. Zapałowicz (KRAM).- [376] Gryniava nad Białym Czeremoszem; 7.8.1887; E. Wołoszczak (KRAM).- [378] Na Górnym Dziale przy Białym Czeremoszu na Bukowinie, na wapieniach 1480 m; 2.8.1887; E. Wołoszczak (KRAM).- [379] Nad Perkalabem za Saratą; 3.8.1887; E. Wołoszczak (KRAM).- [399, 410, 419] Hnitesa od pn., skraj Rumicetum alpini, ok. 1620 m; 24.7.1934; B. Pawłowski (KRAM).- [893] W jednym ze stoków pod Luzdonem, stok pn.; 21.7.1935; J. Mądalski (KRAM-Mądalski). Svidovec-Negrovec Mts.: [227] Negrovec Mt., Vołowieckij raj., Zakarpatskaja obl.; 18.8.1946; M.H. Popov (LWS).- [282] Svidovec, Kwasy, pot. Kostinieckij, ok. 710 m; 29.7.1997; J. Mitka (KRA).- [698] In monte Zadna prope Sinovir, alt. c. 1200 m; 7.1936; A. Láska (PR).- [708] Monte Negrovec prope op. Sinovir, 1400 m; 21.7.1931; A. Láska (PRC).- [722] In vallis glaciali montis Negrovec [Piskonia] prope vicum Koločava, alt. c. 1650 m, solo calcareo; 13.8.1936; M. Deyl, A. Láska (PR).- [728] In jugo Sikla prope opp. Sinovir; 7. 1932; A. Láska (PRC). Rodna Mts.: [615] Pietrosul, przy drodze do schroniska, las świerkowy, ok. 1640 m; 12.8.1998; J. Mitka (KRA).- [616] Pietrosul, jez. Iezerul, ziołorośla, ok. 1400 m; 19.8.1998; P. Bochenek (KRA).- [617] p. Negoiescu, ziołorośla, ok. 890 m; 16.8.1998; J. Mitka (KRA). Southern Carpathians: [640] Munții Cindrelului, SW Sibiu (Hermannstadt), am Weg von der Paltiniș (Hohe Rinne) zur Bătrâna, 1580 m alt., am Bauchfer im Picea abies-Wald; 11.8.1992; C. Drăgulescu, W. Mucher, U. Starmühler (KRA) [A. bucovinense, det. W. Mucher].- [839] Fogarascher Alpen, Mahlbaugebirgen, am Besineu, 1900 m; 19.8.1897; F. Pax (BP). Specimina selecta: Muntenia, Fogarascher Gebirge, S-Hang unterhalb vom Lacul Capra (Gemsens-See), 2200 m alt.; Hochstaudenflur; 8.8.1992; C.

Drăgulescu, M. Magnes, W. Mucher, U. Starmühler (KRA).- Comit. Fogaras, vallis Bullea, 1700 m; 20.7.1920; Z. Zsabo (BP).- Piatra Craiului, canyon Zamești, c. 850 m; 11.8.1998; P. Bochenek (KRA).- Distr. Ciuc, in abruptis fissuris Bicz pr. opp. Gheorgheni, alt. 950-800 m; 13.9.1928; E. Nyárady (CL).- Mtibus Făgărensis, circa lacum Bălea, 2030 m; E. Nyárady (CL).- Bucegi; 1905; M. Futo (CL).- Comit. Csik, in rupestribus calcar. vallis Kis-Békás-szoros inter pag. Gyergyó-Békás et Gyilkostó, alt. c. 800 m; 25.7.1941; A. Boros (BP).- Comit. Fogaras, in partibus subalpinis vallis Búlea, supra pag. Skercesora, 1800 m; 22.7.1914; I. Andreászky (BP).-

A. firmum Rchb. subsp. *fissurae* Nyárady

Svidovec-Negrovec Mts.: [720] In vallis glaciali montis Negrovec [Piskonia] prope vicum Koločava, alt. c. 1650 m, solo calcareo; 13.8.1936; M. Deyl, A. Láska (PR). Čornogora Mts.: [707] Pietros; 19.8.1929; M. Deyl (PRC). Specimina selecta: Turkuł, ± 1650 m; 27.8.1935; G. Kozij (KRAM-Mądalski).- Plantae Poloniae Exsiccate. Kozioł Wielki; 19.8.1935; G. Kozij (KRAM).- Gutin Tomnatyk Mt., on the lake side, 1620 m; 2.8.1997; J. Mitka (KRA).- cott. Maramureș, mt. Czarnohóra in saxosis alpinis summi mt. Hoverla; 19.8.1939; R. Soó (BP).- Howerla w dziedzinie alpejskiej; 8.1911; M. Raciborski (KRAM-Mądalski).- Na skałach grani pn. zach. ramienia Smotrycza; 7.8.1935; J. Mądalski (KRAM-Mądalski).- Szpyci w Czarnej Horze, 21.8.1875; A. Śleńdziński (KRAM).- Kocioł Dzembronii, w Juniperus nana, ok. 1800 m; ?; B. Pawłowski (KRAM-Pawłowski).- Zbocza nad Zaroślakiem; 1.9.1921; T. Wilczyński (KRAM). Gorgans Mts.: Grofa, potok Kotelec przy rz. Łomnica; 20.7.1889; E. Wołoszczak (KRAM).- Nad potokiem Kodełów pod Grofą przy rz. Łomnica; 20.7.1889; H. Zapałowicz (KRAM).- Pod szczytem Wysokiej (Ihrowiszcze) w okol. rzeki Łomnicy; 27.07.1889; E. Wołoszczak (KRAM). Maramaroș Mts.: [581] Pop-Ivan, Trebușany, c. 1800 m; 19.7.1938; A. Margittai (BP, CL). Specimina visa: Na dużej wapiennej skale Lozduna na pd. wsch. od koty 1600, ok. 1480 m; 28.7.1935; J. Mądalski (KRAM-Mądalski).- Farcău, 1711 m; 31.7.1938; A. Coman (CL).- In valle glacialis muntis Nieněska prope Bogdan, ca. 1800 m; 3.7.1935; M. Deyl (PR). Rodna Mts.: [642] NW unterhalb vom Gipfel der Piatra Rea, 1660 m alt., Juniperus-Gebüsch; 6.8.1986; C. Dragulescu, G. Panzariu, A. Podobnik, W. Starmühler (KRA).- [757, 760] Mt. Nagy-Pietrosz, in dumetis infra lacum Mosolygó-tó supra pag. Borsa, 1500 m; 26.8.1942; Z. Karpati (BP).- [879] Petrile Doarnei; ?; H. Zapałowicz (KRAM).- In der Marmaros zu Borsa auf de Alpe Petrosa; 8.1857; L. Vagner (BP). Svidovec-Negrovec Mts.: [554, 713] In vallis glaciali montis Negrovec [Piskonia] prope vicum Koločava, alt. c. 1650 m, solo calcareo; 13.8.1936; M. Deyl, A. Láska (PR).- [714] Svidovec, Dragobrad; 17.8.1929; M. Deyl (PRC).- [715] Bliźnica prope Jasina, 1700 m; 6.8.1928; V. Krajina (PRC).- [716] Monte Negrovec prope op. Sinovir, 1400 m; 21.7.1931; A. Láska (PRC).- [727] In jugo Sikla prope opp. Sinovir; ?7.1932; A. Láska (PRC).- Specimina selecta: uroczysko Kedren, Tiacivskij raj., p. Łopuszanka; 7.8.1957; J.V. Vajnagij (LWS).- In valle Heršovec prope opp. Koločava; 7.1932; A. Láska (PRC).- In alp. Szvidovec, 1700 m; 4.7.1936; A. Margittai (CL).- Mt. Dragobat, 1700 m; 25.7.1940; Andreászky (BP). Bucovina, Bi-

strica and Čeahlău Mts.: [594] In montibus Ceahlău, in pratis alpinis in monte Ocolasul Mare prope pagum Neagra, 1900 m; 26.8.1955; G. Vida (BP).- [746] Bukowina, Kräuterreiche Schluchtes am Gipfel Rareú, Kalk, 1650 m; 24.8.1895; F. Pax (BP).- [881] Nad górna Dorna; 24.8.1911; H. Zapałowicz (KRAM).- Ceahlău, in rupibus subalpinis Ocolaşul Mare supra pagum Neagra, ca. 1860 m; 25.8.1955; T. Pócs (BP).- Farko; 10.8.1912; H. Zapałowicz (KRAM).- Exsiccata Florae Galiciensis, Watra Dorna na Bukowinie; ?; A. Rehmann (KRAM).- Flora Poloniae Exsiccata, A. romanicum, in monte Adam prope Pojorítam [Pożorita], distr. Campulung, 650-1500 m; 25.8.1903; E. Wołoszczak (KRAM). Southern Carpathians: [559] Trans., distr. Hunedoara, Mt. Retezat; 29.7.1961; St. Csürös (CL).- Specimina selecta: Piatra Craiului; 23.8.1906; Z. Zsáky (CL).- Mtii Páring, inter vrf. Páring et vrf. Cirja, 2000-2300 m; 5.9.1961; E. Vicol (CL).- In Carp. Merid., in montibus Paring, in juniperetis naeae sub cacum montis Paring, alt. 1750 m; 25.7.1956; T. Pócs (BP).- Distr. Hunedoara, in valle superiore Lapusnicul mare in Mtbus Rătezat, 1600-1700 m; 27.8.1930; E.I. Nyárády (CL).- Transsilvania, distr. Hunedoara, Mtibus Rătezatenses, in decl. te "Fata Rătezatului", 2000 m, solo gran.; 12.8.1928; E.I. Nyárády (CL).- Transsilvania, distr. Hunedoara, Mtibus Rătezat, in declivibus mtis M. Papuşa adversus Lacul Bacura supra vallem Lăpusnicul mare, 1600-1800 m; 27.8.1930; E.I. Nyárády (CL).- Comit. Hunyad., Mt. Retezat, in valle Pietrile supra pagum Nuksora: in graminosis; 25.7.1941; A. Boros (BP).- Comit. Hunyad., Retezat, in reg. superiore 2000-2400; 1.8.1907; A. Degen (BP).- Transsylv., distr. Cluj, vallis prope Sebieşului prope pag. Floroiu; 28.7.1975; I. Gergely (CL).- Comit. Hunyad., in monte Dealu Plesiu pr. pag. Kimpulunyag; 20.8.1906; A. Degen (BP).

A. firmum Rchb. subsp. *firmum*

Svidovec-Negrovec Mts.: Bliźnica; 11.8.1920; M. Deyl (PR).- In alp. Bliźnica, Marmaros, c. 1700 m, 8.7.1930; A. Margittai (CL).- In rupestribus aranaceis alpinis culminis montis Dragobrat prope Kőrösmező, 1500-1700 m; 18.7.1934; A. Boros (PR). Čornogora Mts.: Plantae Poloniae Exsiccatae, Carpati Orient., Montes Czarnohora, Turkuł, ± 1650 m; 27.8.1935; G. Kozij (KRAM, CL).- Plantae Poloniae Exsiccatae, Montes Czarnohora, Kozioł Wielki, stok zach., in latere occid., ± 1680 m; 19.8.1935; G. Kozij (KRAM, CL, SAV).- Pod Szpyciami; 16.8.1930; G. Kozij (KRAM). Rodna Mts.: Nagy-Pietrosz, in dumetoris infra locum Mosalygó-tó supra pag. Borsa; 26.8.1942; Z. Karpati (BP).- In der Marmaros zu Borsa auf der Alpe Perosa; 8.1857; L. Vagner (BP).- In locis petrosis alpium circa oppidum Rodna, Transsilvaniae boreali-orientalis; - ; Porcius (CL).- Romunia, Transsilvania, Muntii Rodnei, in pratis glareosis vallis fluvii Cimpoasa sub monte Piatra Rea, supra complexul turistic Borso, 1220-1270 m s.m.; 6.8.1996; A. Podobnik and W. Starmühler (Herb. Podobnik, Ljubljana).- Rodnaer Gebirge (Muntii Rodnei, Radnai-havasok), SE Borşa (Borsa), W-Hang des Schlechtstein (Piatra Rea) zum Cimpoiasa-Tal, 1220-1270 m alt.; Hochstaudenflur über einem Schuttkegel; 6.8.1996; A. Podobnik and W. Starmühler (Herb. Starmühler, Graz).- Rodnaer Gebirge, NE Rodnen (Rodna, Óradna), etwa 400 m NW der Kuhhorn-Spitze (Ineu, Ünökő), E-Hang, 1980 m alt.; *Juniperus*-Gebüsch;

7.8.1996; W. Starmühler (JACA, OSC, Herb. Starmühler, Graz).- Bucovina, Bistrica and Čeahlău Mts.: [558] Moldova, distr. Neamtu, in monte Čeahlău, alt. 1300-1800 m.s.m., solo calc., 21.7.1931; E.I. Nyárády (CL).- Góry Kelemeńskie, Stina Gruiu; 24.8.1911; H. Zapałowicz (KRAM). Southern Carpathians: Mt. Retezat, in graminosis montis Boreszko supra Gura Api; 31.7.1931; Z. Karpati (BP).- In rupestribus ad cacumen alpis Cisia ad pagum Rodna-Borberek; 24.8.1904; B. Kümmerle (BP).- Pareng; 5.8.1871; J. Csato (BP).

A. firmum Rchb. nsubsp. *fussianum* Starmühler (A. f. subsp. *firmum* × A. f. subsp. *fissurae*)

Čornogora Mts.: Kozioł Wielki; 19.8.1935; G. Kozij (KRAM). Svidovec-Negrovec Mts.: Góry Świdowskie, Dragobrat, Bliźnica; 10.8.1882; H. Zapałowicz (KRAM). Rodna Mts.: In locis alpinum oppidem Rodna; ?; Porcius (CL).- Piatra rei [fo. amoenum Zapał.]; 15.8.1907; H. Zapałowicz (KRAM). Maramaroş Mts.: Góry Czywczyńskie 1650 m; 7.8.1935; J. Walas (KRA.). Southern Carpathians: Montes Retezat, Vallea Bulei nad Câmpul-lui-Neagu, nad potokiem, 1200-1300 m, podł. kryst.; 8.8.1935; B. Pawłowski (KRAM).- Montes Fagarenses, pn. ramię Vrf. Şerbostii ku dolinie Valea Şerbostii, granit 1700-1800 m; 22.8.1937; Pawłowski (KRAM).- Mts. Pařing, in humidis alpinis in decl. merid. montis Păpuşa, alt.c. 1850 m; 15.8.1960; T. Pócs (BP).

A. xnanum (Baumg.) Simonk.

Svidovec-Negrovec Mts.: [268] Bliźnica; 23.7.1934; Zlatnik (SAV).- [553] Hab. in alp. Bliźniacz, Marmarureş, 1700 m.; 8.7.1930; A. Margittai (CL).- [577] In alp. Bliźnica, Marmarureş; 8.7.1930; A. Margittai (BP).- [588] Comit. Maramaroreş, in alpe Dragobrat supra page Kőrösmező, in declivibus graminosis, c. 1700 m.; 24.7.1939; Z. Karpati (BP).- [880] G. Świdowskie: Apszyńiecka pod Todiaską; 28.7.1910; H. Zapałowicz (KRAM). Specimina selecta: In valle glacili sub cota 1735 prope montis Tatulska, solo calcareo; 7.1935; M. Deyl (PR).[921] In alp. Strimba pr. Kaloesa [Koloczawa], c. 1200 m; 7.1924; A. Margittai (CL).- [720] In vallis glaciali montis Negrovec [Piskonia] prope vicum Koločava, alt. c. 1650 m, solo calcareo; 13.8.1936; M. Deyl, A. Láska (PR). Čornogora Mts.: [420] [535] Tiszobogdany, in monte Čornogora; 5.8.1908; A. Richter (CL).- [595] In cacuminum montis Pietrosz, prope Tisza-burkut, com. Marmaros; 7.1939; L. Vajda (BP).- [662, 665] Gutin Tomnatyk Mt, on the lake side, 1620 m; 2.8.1997; J. Mitka (KRA).- [696, 725] Mt. Černa Hora, in alpinis mtes Tomnatek, alt. c. 1900 m; 7.1938; M. Deyl (PR).- [579] In alp. Hoverla, c. 1800 m; 21.7.1928; A. Margittai (BP).- [721] Čorna Hora, in saxosis et graminosis montis Pietroş prope vicum Jasina, 1600-2020 m; 1936; M. Deyl, A. Láska (PR).- [882] Pop Ivan; 22.7.1880; H. Zapałowicz (KRAM).- [891] Na skałach Kozła Dużego; 16.8.1930; J. Mądalski (KRAM-Mądalski).- [962] Pietrosu, kr.[aina] kos[ówki]; 25.7.1905; H. Zapałowicz (KRAM).- [963] Kocioł Dzembroni, w kosówce ok. 1650 m; 7.8.1935; B. Pawłowski (KRAM). Maramaroreş Mts.: [696] In montis Pop Ivan, prope vicum Trebuşany; 8.1936; M. Deyl (PR).- [551] In alp. Pop Ivan, Marmarureş; 4.7.1936; A. Margittai (CL). Rodna Mts.: [674] Comit. Besztercze-Naszod. In rupestribus ad cacumen alpis Cisia ad pagum Rodna-Borberek; 24.8.1904; B. Kümmerle

(BP).- [525] Maramureş, Mt. Rodnei, in graminosis subalpinis; 27.7.1986; Gh. Groza (BP).- [526] Corongişul la Rodna la inceptulang; 1860; G. Czetz (CL). Specimina selecta: Pietrosul, in herbicidis Adenostylion subalpinis, c. 2950 m; 13.8.1998; J. Mitka (KRA).- Distr. Bistriţa-Nasaud, in sax. calc. Corongis, 1994 m; 7.8.1925; Al. Borza (CL). Southern Carpathians: Specimina selecta: Piatra Craiului; 23.8.1906; Z. Zsáky (CL).- [640] Romania, Transilvania (Siebenbürgen, Erdely), Sud-Karpaten, Munti Cindrelului (Zibiüs-Gebirge, Szebeni-havasok), SW Sibiu (Hermanstadt, Nagyszeben) am weg von der Palnitis (Hohe Rinne) zur Batrina, 1580 m alt., am Bachufer im Picea abies-Wald; 11.8.1992; C. Dragulescu, W. Mucher, U. Starmühler [A. bucovinense, det. W. Mucher] (KRA).- Montes Retiezat, in declivibus montis Vrf. Zanoga in scaturiginosis, alt. 2000 m, substr. silic.; 25.8.1934; I. Scheffer (BP).- Fogarascher Alpen, Alpen matten am Szüsül, 2000 m; 14.8.1897; F. Pax (BP).- Comit. Besztercze-Naszód, in declivibus humid et fertilit. montis Ünökö; 25.7.1937; Andreászky (BP).

A. firmum × *A. xnanum*

Čornogora Mts.: [239] Brebeneskuł, wśród bloków (grechotów), ok. 1198 m; 23.8.1997; K. Zarzycki (KRA).-

[658] Pietros, alpine zone, among rocks, c. 2000 m; 28.7.1997; J. Mitka (KRA).- [659] Turkuł Mt., in subalpine Juniperus nana, 1775 m; 1.8.1997; J. Mitka (KRA).- [660] Pod Brebenieskullem, wśród złomów skalnych; 2.8.1997; J. Mitka (KRA).- [661] Howerla, alpine zone, among rocks, c. 1990 m; 31.7.1997; J. Mitka (KRA).- [666] Čornogora Mts., Gutin Tomnatyk Mt, on the lake side, 1620 m; 2.8.1997; J. Mitka (KRA).- [866] Czarna Hora, Szpyci, in Calamagrostidetis, 1700-1800 m; 3.9.1925; B. Pawłowski (KRAM-Pawłowski).- [931] Czarna Hora [Aconitum napellus L. var. czarnohorensis Zapałowicz, 12.2.1908]; ?; 18.7.1881 (KRAM – 132277, Holotypus). Svidovec-Negrovec Mts.: Góry Świdowskie, Apuszyńska pod Todiaską; 28.7.1910 [A. napellus L. var. svidovense fo. subvestitum Zapał.; H. Zapałowicz (KRAM). Rodna Mts.: [927, 928] Rodna Mts., Cailor Mt., springs of Cimpaiacul torrent, 1750 m; 15.8.1998; J. Mitka, P. Bochenek (KRA).- [929, 930] Pietrosul, ziołorośla ok. 350 m pod szczytem; 13.8.1998; J. Mitka (KRA). Southern Carpathians: Mts. Rătezatyenses, in decl. „Fața Rătezatului”, alt. c. 2000 m, solo gran.; 12.8.1928; E.I. Nyárády (KRAM).