

Taxonomy and ecology of the genus *Aconitum* L. in the Ukrainian Carpathians

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Summary: In the Ukrainian Carpathians 12 species of the genus *Aconitum* occur, circumscribed by three subgenera. General descriptions, ecological characteristics, chorology and threat of 20 *Aconitum* taxa are given based on herbarium materials and field investigations. It was found out that all studied taxa belong to three ecological groups, which are distributed in different altitudinal belts, to four biomorphological groups and to two main life forms.

Keywords: *Aconitum*, Eastern Carpathians, Linnaean taxonomy, chorology

In spite of the long history of investigation, taxonomy of the genus *Aconitum* is still much discussed and perhaps will remain unresolved. Many taxonomical problems arise from the notorious hybridity within the genus and subsequent origin of putative genetic hybrids, which form a morphological continuum between the parental species (KADOTA 1987; STARMÜHLER 2001). In the Ukrainian keys for the species identification often labile and indistinct features as shape of leaves, size of flowers and height of plants are used. For example, in one of the most popular Ukrainian keys, the 'Plants identification guide for Ukrainian Carpathians' (CHOPIK 1977), ten species of the genus *Aconitum* are cited. In another work 'Identification guide for higher plants of Ukraine' (PROKUDIN 1987) eleven monkshood species are recognized. In both cases, some species were not taxonomically clearly sound. They were clarified in recent taxonomical revisions of the genus *Aconitum* by MITKA (2000, 2003, 2008) and STARMÜHLER & MITKA (2001). Here, the morpho-geographical species concept (DAVIS & HEYWOOD 1963) was used.

MITKA (2003, 2008) points to 13 taxa in the genus *Aconitum* in the Eastern Carpathians. All species belong to the three subgenera *Aconitum*, *Lycocotnum* and *Anthora*. They are described on the basis of root and flower morphology. Among them the subgenus *Aconitum* is the richest in the Ukrainian Carpathians and consists of two sections (*Aconitum*, *Cammarum* DC.), one nothosection *Acomarum* Starm. (sect. *Aconitum* × sect. *Cammarum*) and ten species. The second subgenus *Lycocotnum* (DC.) Peterm. is represented by only one species, *A. moldavicum* Hacq. Although *A. lycocotnum* is considered possible for this territory (MITKA 2003), no native localities have been found up to now. The third, controversial subgenus *Anthora* (DC.) Peterm. is represented by just one species, *A. anthora* L. From the total number, six species are endemics to the South-Eastern Carpathians, one is endemic to the Carpathians and three are Carpathian subendemics. In the Ukrainian part of the Eastern Carpathians theoretically should occur altogether 13 species, but a complete revision of the genus *Aconitum* in this territory has not yet been carried out. The high level of endemism and a lack of relevant information on the genus make the territory a very interesting object of the taxonomic studies. We propose here the revised chorology of the genus *Aconitum* in the Ukrainian part of the Eastern Carpathians alongside with a new determination key.

Materials and methods

In 2008–2010 the first author made several field studies in all regions of the Ukrainian Carpathians and collected herbarium material, which is kept in LW, LWS and LWKS. For the morphological study he investigated 576 specimens, excluding *A. variegatum*, *A. lycoctonum* and *A. ×cammarum*. The first two species are possible for the Ukrainian Carpathian's native flora and the last one is ornamental. Raw data were processed in StatSoft Statistica 8.0 program.

For the chorological and morphological investigations we also used the herbarium collections from CHER, KRA, KRAM, KW, LW, LWS, LWKS, W, WU and YALT (for abbreviations see HOLMGREN et al. 1990). For the chorology we also used published data on *Aconitum* species.

Localities found in the field are marked on a map (CARPATHIANS 2007) by rings, localities based on herbarium data are marked by squares, localities taken from the literature, but not confirmed in the field or by herbarium investigations, are marked by triangles. We also used the asterisk for marking suspicious localities cited in literature. The synonyms follow MITKA (2003) and others (PACZOSKI 1927; DOMIN 1929; STEINBERG 1937; KMEŤOVÁ 1982; SKALICKÝ 1990; VOROSHILOV 1990; TASENKEVICH 1998; MOSYAKIN & FEDORONCHUK 1999; TZVELEV 2001). Some of them should be checked in future because their names are not typified. Taxonomic names were also checked by IPNI (2010), GRIN (2010) and ESFEDS (2010) databases. Threat categories to the species follow the IUCN (2001) criteria.

Determination key

1. Hood of the flower cylindrical, up to 2.5–3 times higher than wide; nectaries not reaching the top of hood, nectary spurs coiled; seeds often without longitudinal wings; leaf lobes broad, incised less than $\frac{1}{2}$; semirosette plants with clinopogonotropic shoots; rhizomes: subgen. *Lycoctonum* (DC.) Peterm. sect. *Lycoctonum* DC. 2
- 1*. Hood elongated conical or hemispherical, less than in 2.5 times higher than wide; nectaries reaching or not the top of hood, nectary spurs semicoiled or bent; seeds with only one longitudinal wing; leaf lobes incised near $\frac{1}{2}$ – $\frac{2}{3}$; erosulate plants with elongated apogeotropic shoots; spherical tubers with short stolons: subgen. *Aconitum* sect. *Cammarum* DC. & sect. *Acomarum* Starm. 5
- 1**. Hood hemispherical or crescent-shape, as high as wide; nectaries always reaching the top of hood, nectary spurs capitate; seeds with three longitudinal wings, one of which is distinctly more developed; leaf lobes incised near to $\frac{2}{3}$; high mountain non-rosellate plants with short apogeotropic shoots; elongated napiform tubers: subgen. *Aconitum* sect. *Aconitum* 12
- 1***. Hood hemispherical or rarely elongated, most often as high as wide; yellow or yellowish perianth not falling after blossom; nectaries always reaching the top of hood, nectary spurs coiled; seeds with three wings of comparable size on the edges; leaf lobes narrow, greatly incised up to $\frac{3}{4}$; xerophytic non-rosellate plants with short or long apogeotropic shoots; tubers in early ontogenesis spherical and later elongated napiform, sometimes divided: subgen. *Anthora* (DC.) Peterm. sect. *Anthora* DC. *A. anthora*
- 2 (1). Carpels glabrous 3
- 2*. Carpels entirely pubescent 4

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3 (2). Perianth yellow or yellowish	<i>A. lycoctonum</i> subsp. <i>lycoctonum</i>	
3*. Perianth from blue to dirty-violet	<i>A. moldavicum</i> subsp. <i>moldavicum</i>	
4 (2*). Carpels with short hooked hairs	<i>A. moldavicum</i> subsp. <i>hosteanum</i>	
4*. Carpels with long straight hairs	<i>A. moldavicum</i> subsp. <i>simonkaianum</i>	
4**. Carpels with mixed hairiness, with long protruding hairs at the base and short hooked hairs above	<i>A. moldavicum</i> subsp. <i>porcii</i>	
5 (1*). Hood elongated conical with pronounced rostrum		6
5*. Hood conical or hemispherical		8
6 (1*). Hood glabrous or rarely pubescent with solitary protruding hairs, carpels pubescent rarely along ventral sutures	<i>A. variegatum</i> subsp. <i>variegatum</i>	
6*. Hood and carpels densely pubescent with long glandular hairs		7
7 (6*). Pedicels with dense glandular protruding hairs	<i>A. lasiocarpum</i> subsp. <i>lasiocarpum</i>	
7*. Pedicels entirely glabrous or with solitary glandular hairs above bracteoles and with hooked hairs below bracteoles	<i>A. lasiocarpum</i> subsp. <i>kotulae</i>	
8 (5*). Hood glabrous or rarely pubescent with short protruding hairs		9
8*. Hood entirely pubescent with short protruding hairs, pedicel more or less densely and entirely pubescent with protruding hairs		10
9 (8). Hood glabrous, pedicel pubescent just below receptacle, carpels glabrous and sterile, thread of the nectaries pilose, tubers napiform elongated	<i>A. ×cammarum</i>	
9*. Hood glabrous or rarely pubescent, pedicels above the bracteoles rarely pubescent and glabrous below the bracteoles, carpels glabrous or rarely pubescent and fertile, thread of the nectaries glabrous, tubers spherical	<i>A. degenii</i> subsp. <i>degenii</i> var. <i>intermedium</i>	
10 (8*). Carpels densely pubescent	<i>A. ×gayeri</i>	
10*. Carpels glabrous or with solitary hairs		11
11 (10*). Spur of the nectaries coiled or bent	<i>A. degenii</i> subsp. <i>degenii</i> fo. <i>degenii</i>	
11*. Spur of the nectaries capitate	<i>A. degenii</i> subsp. <i>degenii</i> fo. <i>craciunelense</i>	
12 (1**). Pedicels glabrous		13
12*. Pedicels pubescent		14
13 (12). Bracteoles divided, filaments glabrous	<i>A. firmum</i> subsp. <i>firmum</i>	
13*. Bracteoles lanceolate, filaments pubescent	<i>A. firmum</i> subsp. <i>fissurae</i>	
14 (12*). Hood glabrous or with glandular hairs		15
14*. Hood densely pubescent with short hooked hairs		16
15 (14). Pedicels above the bracteoles glabrous or with protuberant hairs and below the bracteoles with protuberant, hooked or mixed hairiness	<i>A. ×czarnohorensis</i>	

- 15*. Pedicels above the bracteoles with hooked or mixed hairiness and below the bracteoles – with similar hairiness or glabrous *A. xnanum*
- 16 (14*). Carpels glabrous or with rarely hairs *A. bucovinense* fo. *bucovinense*
- 16*. Carpels entirely pubescent *A. bucovinense* fo. *orthotricha*

Descriptions of the taxa

Aconitum anthora L., Sp. Pl. 1: 532. 1753 (Fig. 1)

Synonyms: *A. anthoroideum* DC., *A. anthorum* St.-Lag., *A. coeruleum* Błocki, *A. confertiflorum* (DC.) Gáyér, *A. De Candollii* Rchb., *A. eulophum* Rchb., *A. jacquini* Rchb., *A. jacquinianum* Rchb., *A. jacquinii* Rchb., *A. nemorosum* Bieb., *A. pallasii* Rchb., *A. pseudanthora* Błocki. ex Pacz.

Description: Xerophyte, erosulate, upright standing plants, 20–80(100) cm of height; tubers globose or napiform; stem and pedicels pubescent; leaves greatly divided, lacinias linear or lancetiform; inflorescence rigid or dense ramified, densely pubescent with hooked or protruded hairs; perianth yellow or yellowish, not falling after blooming; hood pubescent, spherical or elongated, often fabiform; 5 carpels densely pubescent; filaments dentate or not, sometimes pubescent; nectary spurs coiled, always reaching the top of the hood; pedicels pubescent with hooked, protuberant or mixed hairs; seeds with three wings of comparable size on the edges.

Distribution: In the Ukrainian Carpathians *A. anthora* is a rare species. It occurs in Chornohora, Nyzki Polonyny, Marmarosh, Chyvchyny and Hrynyava (Fig. 6). It mainly grows in the mountane and subalpine belts on calcareous outcrops, on rocks and stony places. It is also distributed in the lowlands of the whole Ukraine, particularly in Podillya, Kharkiv region and Crimea.

Status: *A. anthora* is a relict species with disjunctive distribution in Eurasia. It forms morphologically distinct biotypes and needs further taxonomic studies.

Threat category in Ukraine: According to the 'Red Book of Ukraine' *A. anthora* is protected as *A. jacquinii* with the category R and *A. pseudanthora* with the category VU (ZIMAN et al. 2009; KAGALO 2009). *A. jacquinii* has also been included in the 'Carpathian list of endangered species' (TASENKEVICH 2003) with category VU and according to KRICSEFALUSY & BUDNIKOV (2007) it has the status CR. We conclude that this species should gain the category VU because of the limited numbers of localities (NOVIKOFF 2010b).

Remarks: *A. anthora* is a polytypic species with high level of morphological variability, e.g. hairiness, hood shape and color of perianth. The species not only grows in the mountains but it stretches all through the Eurasian continent. Most botanists of the Ukraine and Russia described *A. anthora* within several taxa of different ranks (STEINBERG 1937; VOROSHILOV 1990; MOSYAKIN & FEDORONCHUK 1999; TZVELEV 2001). In the Ukrainian Carpathians, there are two morphotypes of *A. anthora* with yellow perianth: a) with hooked hairiness of the hood and pedicels; b) with long protruded hairiness of the hood and protruded or mixed hairiness of the pedicels (NOVIKOFF 2009a, 2010a). On the Podillyan plateau there grows a third morphotype with bluish or violet color of the perianth and hooked hairiness of hood and pedicels. The morphotype was described as *A. pseudanthora* Błocki. Some experimental works are needed to check its morphological stability on garden conditions.

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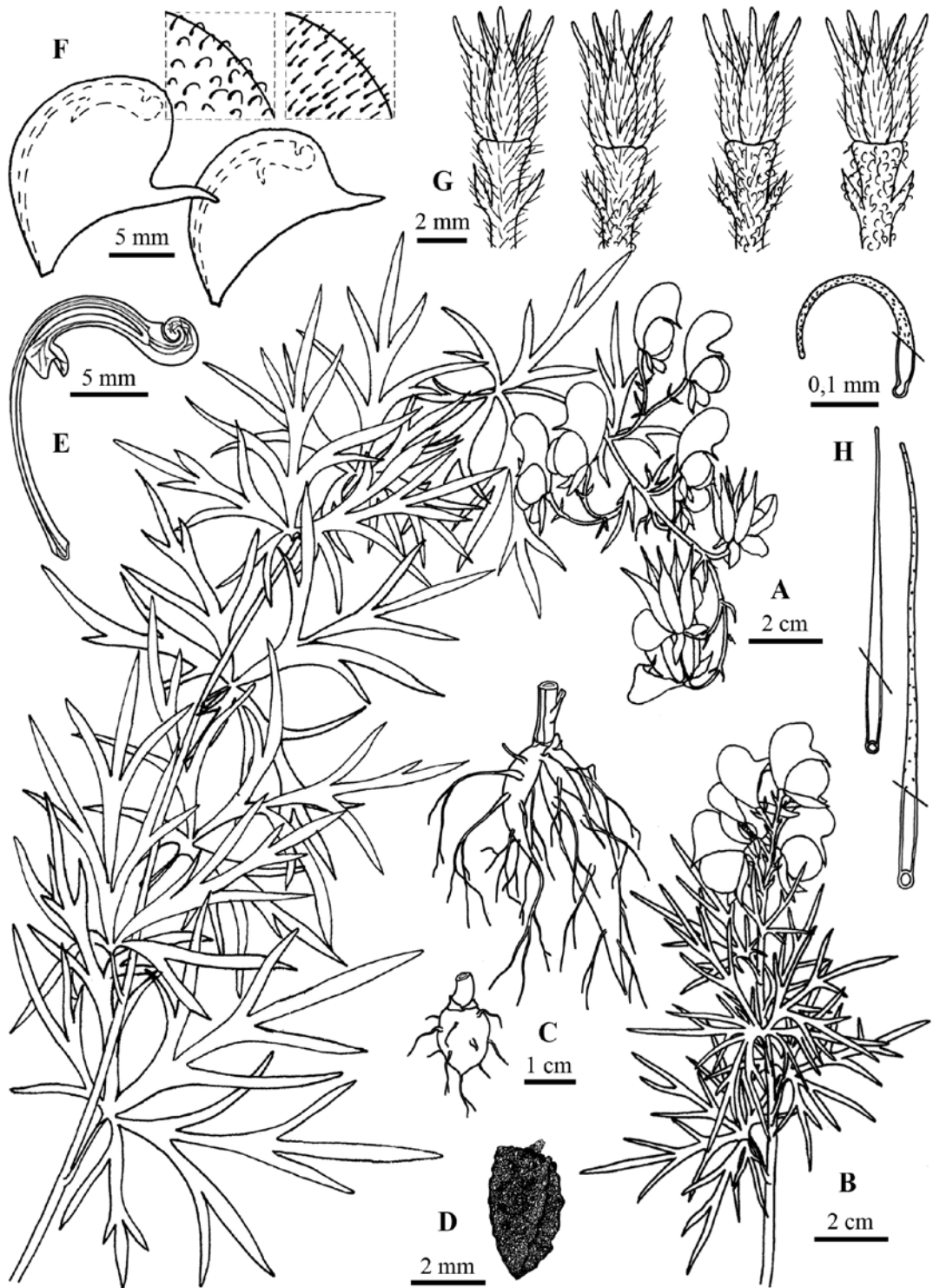


Figure 1. Subgenus *Anthora* (*Aconitum anthora*) – elongated plant from Mt. Stinka (A) and typical plant from Mt. Chyvchyn (B); tubers (C); seed (according to BOJŇANSKÝ & FARGAŠOVÁ 2007) (D); nectary (E); shape and hairiness of the hood (F); different types of pedicel hairiness (G); hooked and protuberant hairs (H).

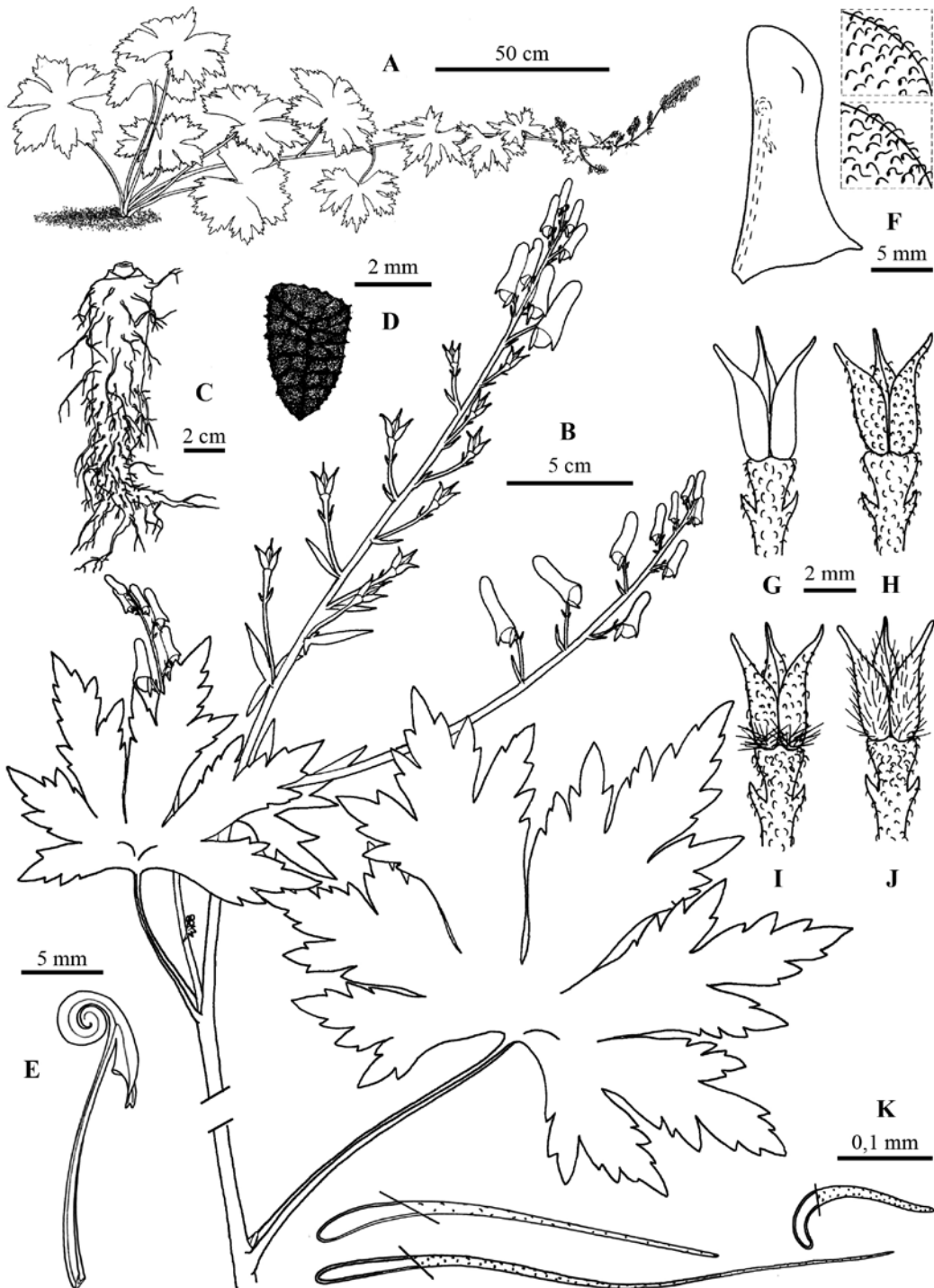


Figure 2. Subgenus *Lycoctonum* (*Aconitum lycoctonum* subsp. *lycoctonum* and *A. moldavicum*) – common view of the plants (A); fragment of shoot (B) and rhizome (C) of *A. moldavicum* from Chornohora Mts.; seed (according to BOJŇANSKÝ & FARGAŠOVÁ 2007) (D) and nectary (E) of *A. moldavicum*; shape and hairiness of the hood of *A. lycoctonum* subsp. *lycoctonum* (perianth yellow or yellowish) and *A. moldavicum* (perianth violet or bluish) (F); carpel hairiness of *A. moldavicum* subsp. *moldavicum* (G), of *A. moldavicum* subsp. *hosteanum* and *A. lycoctonum* subsp. *lycoctonum* (H), of *A. moldavicum* subsp. *simonkaianum* (I) and *A. moldavicum* subsp. *porcii* (J); hooked and protuberant hairs of *A. moldavicum* (K).

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Aconitum lycoctonum L. em. Koelle subsp. *lycoctonum*, Spicil. observ. Aconito: 23. 1788 (Fig. 2A, F, H)

Synonyms: *A. excelsior* Rchb., *A. excelsum* Rchb., *A. jacquinianum* Host., *A. rogoviczii* Wissjul., *A. septentrionale* sensu auct. flor. Carp. Occid., *A. vulparia* Rchb. ex Spreng.

Description: Semi-rosette, often with long and procumbent stem, up to 170 cm of height; rhizomes divided by particulation; stem and pedicels pubescent; leaves divided into 5–7 broad lacinas; inflorescence loose ramified, pubescent with hooked hairs; perianth yellow or yellowish, falling after blooming; hood hooked pubescent, cylindrically elongated, 2.5–3 higher than wide; 3 carpels densely pubescent; filaments dentate or not; nectary spurs coiled, not reaching the top of the hood; pedicels hooked pubescent; seeds without wings.

Distribution: In the Ukrainian Carpathians *A. lycoctonum* subsp. *lycoctonum* is known from only one locality in the Chornohora Mts., where it probably has been introduced (Fig. 6).

Status: European species.

Threat category in Ukraine: DD (NOVIKOFF 2010b).

Remarks: Just one herbarium specimen (LW 060433) collected by A. Rehman in the Skole neighborhood was found. No more information about the distribution in the Ukrainian Carpathians is known. The nearest localities of *A. lycoctonum* subsp. *lycoctonum* are in the Romanian part of the Carpathians and in the Ukrainian lowlands.

Aconitum moldavicum Hacq., Reis. Dac. Sarm. Karpathen 1: 169. 1790 (Fig. 2)

Synonyms: *A. carpathicum* (DC.) Sagorski & Schneider, *A. hosteanum* Schur., *A. lycoctonum* L. pro parte, *A. septentrionale* Koelle var. *carpaticum* DC., *Delphinium moldavicum* (Hacq.) Brândza.

Description: In general, habit similar to *A. lycoctonum*; perianth violet, dirty-violet or bluish; 3 carpels glabrous (subsp. *moldavicum*) or densely pubescent (subsp. *hosteanum* (Schur) Graebn. & P. Graebn.), with protuberant hairiness (subsp. *simonkaianum* (Gáyer) Starm.) or with protuberant hairs at the base and hooked hairs above (subsp. *porcii* Starm.).

Distribution: *A. moldavicum* subsp. *moldavicum* and subsp. *hosteanum* are distributed in the whole Eastern Carpathians. Subsp. *simonkaianum* sporadically occurs in the Chyvchyn, Hrynyava and Chornohora Mountains. Subsp. *porcii* occurs only in the Chyvchyn Mts. (Fig. 6). They grow on wet places, along torrents and rivers, in forest ecotones, etc.; mainly in the submontane and montane belts. In some cases they are found in the subalpine belt (Chyvchyn, Gorgany Mts.) in open habitats.

Status: Both *A. moldavicum* subsp. *moldavicum* and subsp. *hosteanum* are Carpathian subendemics (MITKA 2008). For the other two subspecies more chorological investigations are needed.

Threat category in Ukraine: According to KRICSEFALUSY & BUDNIKOV (2007) the typical subspecies has the status EN. We propose the status LC for *A. moldavicum* subsp. *moldavicum* and subsp. *hosteanum* and the status DD for subsp. *simonkaianum* and subsp. *porcii* (NOVIKOFF 2010b).

Remarks: *A. moldavicum* is one of the most common species of the genus, distributed in almost the whole Carpathians (it is absent, for example, in the Tatra Mts., Western Carpathians).

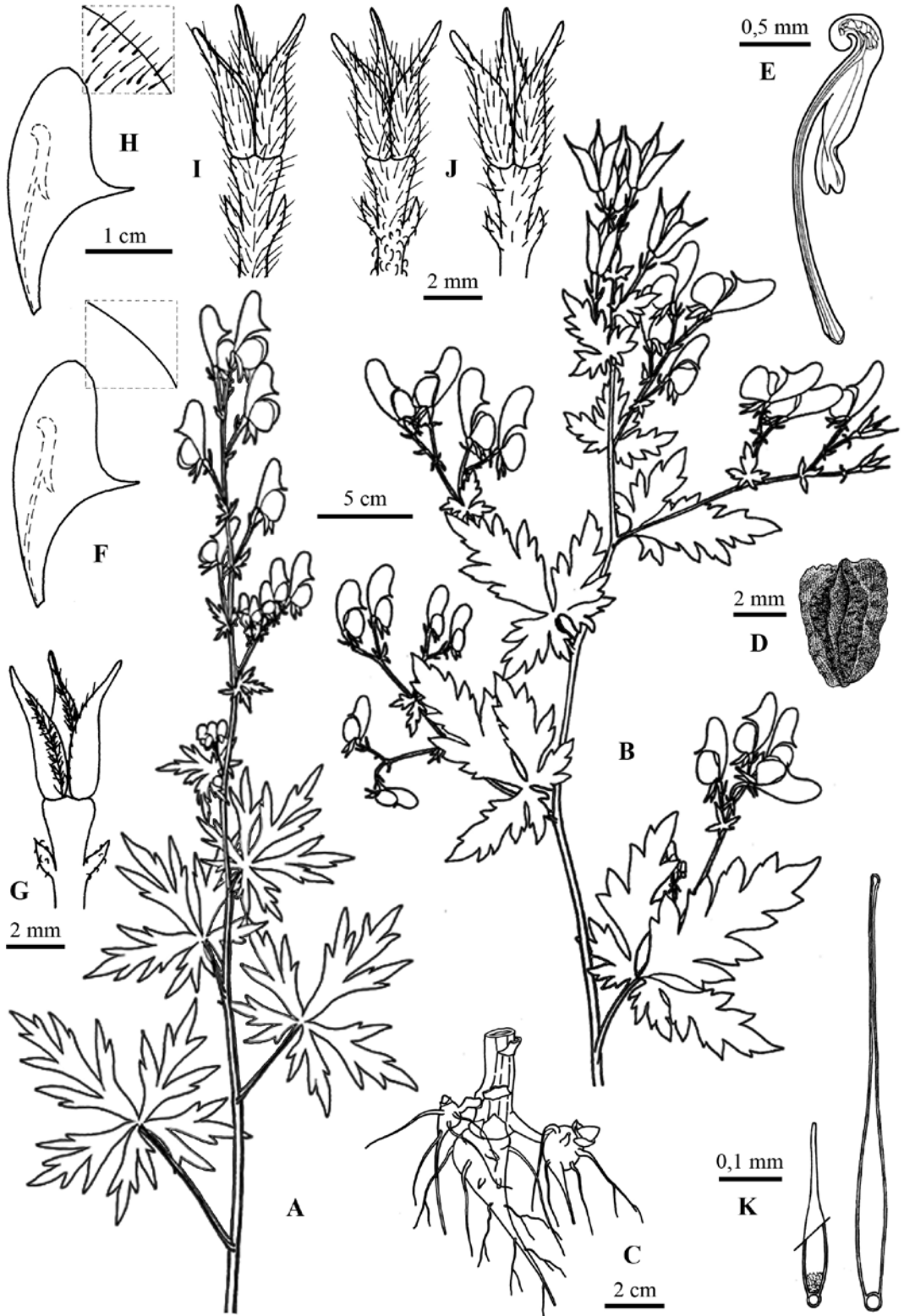


Figure 3. Subgenus *Aconitum* section *Cammarum* ('variegatum' group – *Aconitum variegatum* subsp. *variegatum* and *A. lasiocarpum*) – dwarf plant of *A. lasiocarpum* from mMt. Kukulyk, Chyvchyny (A) and elongated plant from

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Subsp. *simonkaianum* and subsp. *porcii* are very rare in the Ukrainian Carpathians. For this territory two other nothospecies were mentioned: *A. ×triste* (Rchb.) Gáyer (*A. lycoctonum* × *A. moldavicum*) and *A. ×baumgartenianum* Simonk. (*A. lasianthum* (Rchb.) Simonk. × *A. moldavicum*) (MITKA 2008). However, they haven't yet been found wether in the herbarium nor in the field.

Aconitum variegatum L. subsp. *variegatum*, Sp. Pl. 1: 532. 1753 (Fig. 3 E, G)

Synonyms: *A. album* Ait., *A. campotrichum* Gáyer, *A. cammarum* Jacq. pro parte, *A. clusii* Pohl., *A. dominii* Sill., *A. exaltatum* Rchb. pro parte, *A. gracile* Rchb., *A. hians* auct. non Rchb., *A. judenbergense* (Rchb.) Gáyer, *A. nasutum* Fisch. ex Rchb., *A. odontandrum* Wissjul. (?), *A. paniculatum* Lam. pro parte, *A. rostratum* Bernh. ex DC., *A. valesiacum* auct. flor. Carpat. Occid.

Description: Erosulate, with elongated stem, 40–160 cm of height; tubers globose with short stolons; stem and pedicels glabrous; leaves 5(7)-divided; inflorescence rigid or dense ramified, glabrous; perianth blue, bluish or with white stripes, falling; hood glabrous, conical elongated, up to 2.5 times higher than wide, with long rostrum; 3(5) carpels with hairs just on the ventral suture; filaments mostly dentate, glabrous or pubescent; nectary spurs bent or half-coiled, not reaching the top of the hood; pedicels long, glabrous; bracteoles lanceolate or spatulate, often ciliate; seeds with only one longitudinal wing.

Distribution: In the Ukrainian Carpathian mountains this species does not occur but it is expected in the Transcarpathian region. Only one specimen (LW, Woloszizak D. 17.08.1888) collected near Vorokhta (forelands of the Chornogora Mts.) is known (Fig. 7).

Status: Endemic in the European Central-Alps (MITKA 2003).

Threat category in Ukraine: According to KRICSEFALUSY & BUDNIKOV (2007) it has the status VU. We propose: DD (NOVIKOFF 2010b).

Remarks: In central and southern Europe another subspecies *nasutum* (Fisch. ex Rchb.) em. Rupr.) Götz occurs, which taxonomic status, in respect to the Caucasian taxon bearing the same name, should be clarified.

Aconitum lasiocarpum (Rchb.) Gáyer, Mag. bot. Lap. 11: 199. 1911 (Fig. 3A–E, H–J)

Synonyms: *A. beskidense* (Zapał.) Gáyer, *A. cammarum* Jacq. var. *beskidense* Zapał., *A. gracile* Rchb. pro parte, *A. nasutum* Fisch. var. *lasiocarpum* Rchb., *A. paniculatum* Lam. pro parte, *A. podolicum* (Zapał.) Vorosh., *A. toxicum* Rchb., *A. variegatum* L. subsp. *kotulae* Pawł.

Description: Similar to *A. variegatum* in general habit, but the inflorescence glandular pubescent; hood entirely glandular pubescent; 3(5) carpels entirely and densely glandular pubescent; pedicels entirely glandular pubescent (subsp. *lasiocarpum*), rarely glabrous or with solitary glandular hairs above bracteoles and with hooked hairs below bracteoles (subsp. *kotulae*); bracteoles lanceolate or spatulate, glandular pubescent or glabrous.

Skolivski Beskydy region (B); tubers (C), seed (according to BOJŇANSKÝ & FARGAŠOVÁ 2007) (D) and nectary (E) of *A. lasiocarpum*; shape and hairiness of the hood (F) and hairiness of the carpels and pedicel (G) of *A. variegatum* subsp. *variegatum*; shape and hairiness of the hood (H) and hairiness of the carpels and pedicel of *A. lasiocarpum* subsp. *lasiocarpum* (I) and *A. lasiocarpum* subsp. *kotulae* (J); glandular hairs (K).

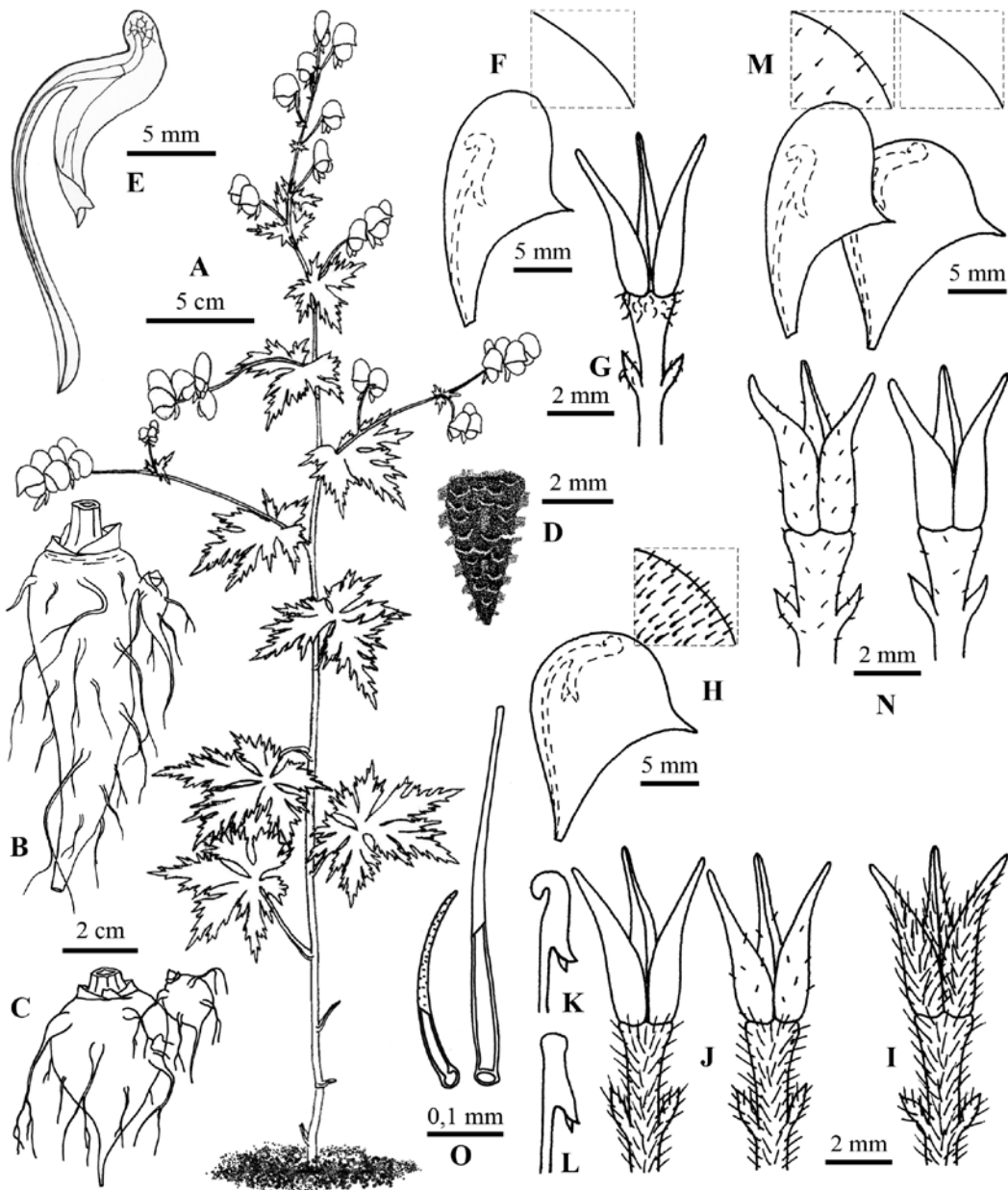


Figure 4. Subgenus *Aconitum* section *Cammarum* (*Aconitum* \times *cammarum*, *A.* \times *gayeri* and *A. degenii* subsp. *degenii*) – common view of the plants (A); tubers of *A. xcammarum* (B) and tubers of *A. xgayeri* and *A. degenii* (C); seed (according to BOJŇANSKÝ & FARGAŠOVÁ 2007) (D) and nectary (E) of *A. degenii*; shape and hairiness of the hood (F) and hairiness of the carpels and pedicel (G) of *A. xcammarum*; shape and hairiness of the hood of *A. xgayeri* and *A. degenii* subsp. *degenii* fo. *degenii* and fo. *craciunelense* (H); hairiness of the carpels and pedicel of *A. xgayeri* (I); hairiness of the carpels and pedicel of *A. degenii* subsp. *degenii* fo. *degenii* and fo. *craciunelense* (J); shape of the nectary of *A. degenii* subsp. *degenii* fo. *degenii* (K) and fo. *craciunelense* (L); shape and hairiness of the hood (M) and hairiness of the carpels and pedicel (N) of *A. degenii* subsp. *degenii* var. *intermedium*; hairs of *A. degenii* (O).

Distribution: This species often occurs in Skolivski Beskydy region, but it also grows sporadically in other regions – Svydovets, Nyzki Polonyny, Marmarosh, Chyvchyny and Hrynyava. Herbarium specimens from Chornohora and Gorgany mountains exist, but the recent condition of these

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localities is unknown (Fig. 7). It grows along streams and rivers, in wet grassland, in wet meadows of the *Calthion* alliance and in the Carpathian alder-carr *Alnetum incanae*; mostly in the montane and submontane belts, rarely in the subalpine belt (Chyvchyn Mt.).

Status: *A. lasiocarpum* subsp. *lasiocarpum* is endemic to the Eastern Carpathians and *A. lasiocarpum* subsp. *kotulae* is a Carpathian subendemic (MITKA & ZEMANEK 1997; MITKA 2000, 2002, 2003); a relict subspecies situated at the margin of the Podillya region (MELNIK & BATOCHENKO 2009).

Threat category in Ukraine: Protected according to the 'Red Book of Ukraine' and the 'Bern Convention' by the VU category. Included in the 'Carpathian list of endangered species' with the VU category (TASENKEVICH 2003) and according to KRICSEFALUSY & BUDNIKOV (2007) it has the status EN.

Remarks: *A. lasiocarpum* is a rare species which occurs sporadically, mostly in mixed populations with both subspecies. The center of distribution is in Skolivski Beskydy (the Eastern Bieszczady Mts.) in the Ukrainian Carpathians, where also white-flowering plants and plants with reduced hood occur.

***Aconitum* ×*cammarum* L. em. Fries**, Nov. Flor. Suec. 2: 171. 1828 (Fig. 4A, B, F, G)

(*A. napellus* agg. × *A. variegatum*)

Synonyms: *A. intermedium* DC., *A. napellus* subsp. *hians* sensu Dostal, *A. napellus* subsp. *linneanum* sensu Dostal, *A. ×stoerkianum* Rchb.

Description: Upright standing, erosulate plant, 60–160 cm high; tubers elongated; stem and leaves hooked pubescent; leaves 5(7), incised more than ½; inflorescence dense ramified, rarely loose, pubescent; perianth of different colour from white to violet and variegated, falling; hood glabrous, hemispherical or elongated, 1.2–2 times higher than wide; 3(4)5 glabrous carpels, sterile; filaments pubescent, dentate; nectary spurs bent or coiled, reaching the top of hood; pedicels pubescent with hooked short hairs just above the bracteoles and glabrous below.

Distribution: It is cultivated in gardens and sometimes occurs in nature in the abandoned villages.

Status: Ornamental plant.

Threat category in Ukraine: LC (NOVIKOFF 2010b).

***Aconitum* ×*gayeri* Starm.**, Stapfia 45: 41. 1996 (Fig. 4A, H, I)

(*A. degenii* × *A. lasiocarpum*)

Synonyms: *A. paniculatum* Lam. pro parte.

Description: Upright standing, erosulate plant, 60–100(160) cm high; tubers spherical, often with stolons; stem glabrous, pedicels hooked pubescent; leaves 5(7), ½–⅔ incised; inflorescence dense or loose ramified; perianth blue, falling; hood pubescent with short protruding hairs, elongated, 1.3–1.7 times higher than wide; 3 carpels densely and entirely glandular pubescent; filaments sometimes pubescent, dentate or not; nectary spurs bent or coiled, reaching the top of hood; pedicels entirely pubescent with protruding glandular hairs.

Distribution: In all regions of the Ukrainian Carpathians from montane to subalpine belts (Fig. 7). It mainly grows in the open wet places along the streams in mixed populations with *A. degenii*.

Status: Eastern Carpathians endemic (STARMÜHLER 1996).

Threat category in Ukraine: As one of the most frequent species in the section *Cammarum* DC. it is classified LC (NOVIKOFF 2010b).

Remarks: This nothospecies resembles *A. degenii* in general habit.

Aconitum degenii Gáyér subsp. *degenii*, Mag. bot. Lap. 5: 123. 1906 (Fig. 4A–E, H, J–O)

Synonyms: *A. ×hebegynum* non DC., *A. paniculatum* Lam., *A. prutense* (Zapał.) Tzvel., *A. variegatum* L. subsp. *paniculatum* (Arcang.) Greuter & Burdet., *A. variegatum* L. subsp. *kotulae* non Pawł.

Description: Hood entirely pubescent with short protruding hairs (fo. *degenii* and fo. *craciunelense* Gáyér), or glabrous (var. *intermedium* (Zapał.) Mitka); carpels glabrous; nectary spurs bent or coiled (fo. *degenii*) or capitate (fo. *craciunelense*), reaching the top of hood; pedicels entirely pubescent with protruding glandular hairs (fo. *degenii* and fo. *craciunelense*) or glabrous below the bracteoles (var. *intermedium*).

Distribution: In the whole Ukrainian Carpathians just as *A. ×gayeri* (Fig. 7).

Status: Southern Eastern Carpathians endemic (MITKA 2003).

Threat category in Ukraine: According to KRICSEFALUSY & BUDNIKOV (2007) it has the status VU. As one of the most frequent species in the section *Cammarum* DC. it is classified LC (NOVIKOFF 2010b).

Remarks: Recent phenetic studies on the *A. degenii*-*A. lasiocarpum* complex in the Eastern Carpathians (MITKA & SZAJNA 2009), supplemented by cytogenetic investigations (ILNICKI & MITKA, submitted), showed that the putative hybrid *A. ×hebegynum* DC. (*A. degenii* × *A. variegatum*) has a clear intermediate position in the morphospace defined by correspondence analysis axes. It concerns especially the helmet index. On the other hand, cytogenetic criteria (and some morphological traits including the indumentum) points to close relationships between the putative hybrid and *A. degenii*. Taking into consideration the lack of *A. variegatum* in the Eastern Carpathians, we decide to assign the putative hybridogenous *A. ×hebegynum* non DC. from the Eastern Carpathians to *A. degenii* var. *intermedium* (Zapał.) Mitka.

Aconitum firmum Rchb., Ueber. Gat. Acon.: 20. 1819 (Fig. 5A–D, H–J, M)

Synonyms: *A. acutum* Rchb., *A. hians* Host, *A. koelleianum* Rchb. var. *firmum* (Rchb.) Rchb., *A. nanum* Baumg. pro parte, *A. napellus* L. em. Skalický pro parte, *A. palmatifidum* Rchb., *A. romanicum* Wołoszcz., *A. skerisorae* Seitz non Gáyér., *A. tatrae* Borb. in Pallas.

Description: Erosulate orthotropic plants with short stem, 20–40(60) cm of height; tubers napiform; stem glabrous, pedicels rarely pubescent; leaves 5-divided, incised up to 2/3; inflorescence rigid, candle-shaped, glabrous; perianth violet or dark blue, falling; hood not elongated, 1–1.3 times higher than wide, hemispherical or crescent-shaped, glabrous; (2)3(4–5) carpels glabrous

Taxonomy and ecology of the genus *Aconitum* L. in the Ukrainian Carpathians

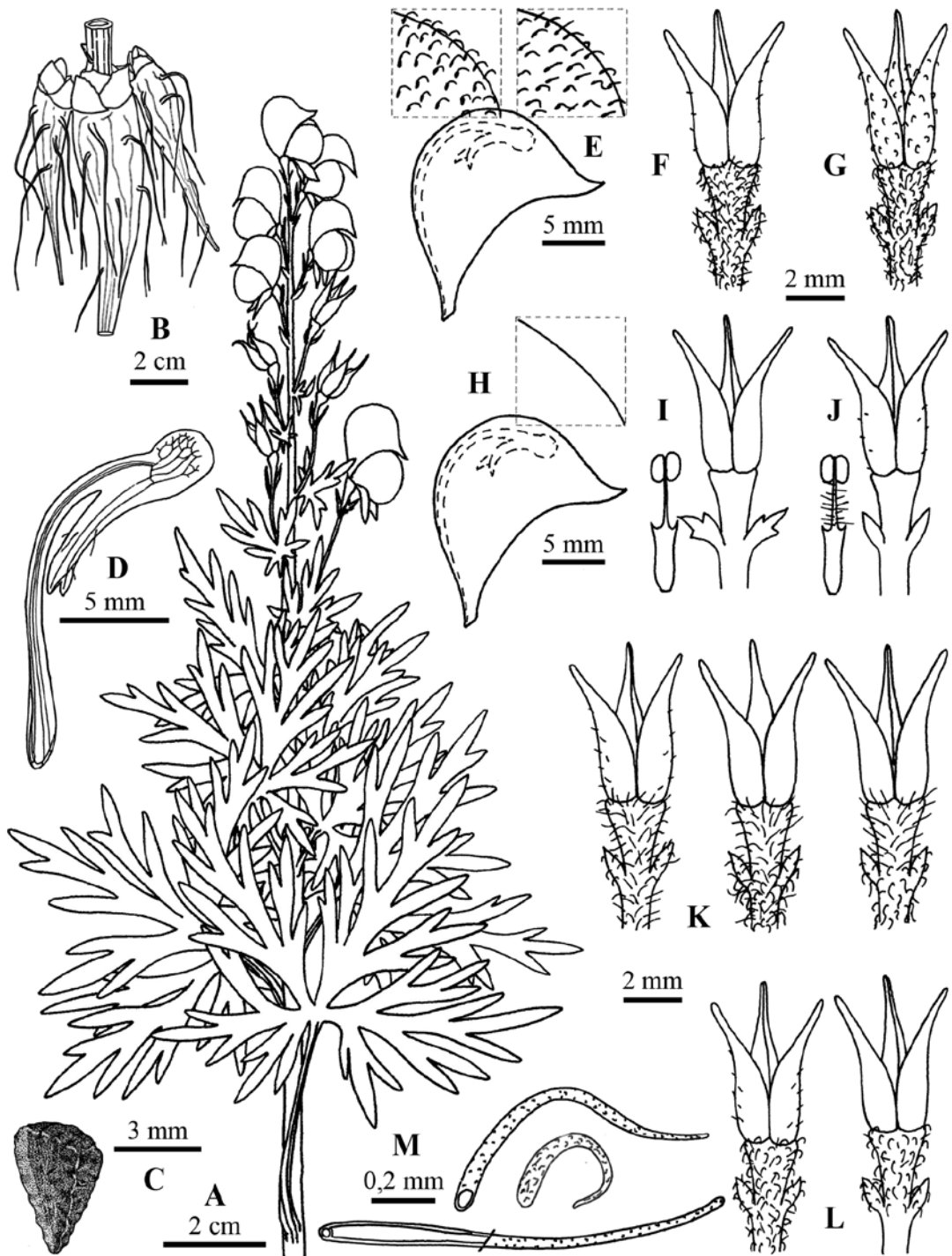


Figure 5. Subgenus *Aconitum* section *Aconitum* (*Aconitum firmum*, *A. xczarnohorens*, *A. xnanum* and *A. bucovinense*) – plant (A), tubers (B), seed (according to BOJŇANSKÝ & FARGAŠOVÁ 2007) (C) and nectary (D) of *A. firmum*; shape and hairiness of the hood of *A. bucovinense* (E); hairiness of the carpels and pedicel of *A. bucovinense* fo. *bucovinense* (F) and fo. *orthotricha* (G); shape and hairiness of the hood of *A. firmum*, *A. xczarnohorens* and *A. xnanum* (H); hairiness of the carpels, pedicel and stamens of *A. firmum* subsp. *firmum* (I) and subsp. *fissurae* (J); hairiness of the carpels and pedicel of *A. xczarnohorens* (K) and *A. xnanum* (L); hairs of *A. bucovinense* (M).

or rarely pubescent on the dorsal side; stamen filaments glabrous (subsp. *firmum*) or protruded pubescent (subsp. *fissurae* Nyárády), dentate or not; nectary spurs capitate or bent, always reaching the top of the hood; pedicels glabrous; bracteoles 3-divided (subsp. *firmum*) or lanceolate (subsp. *fissurae*); seeds with three longitudinal wings, one of them much more developed.

Distribution: In the Ukrainian Carpathians it is a rare species mostly occurring in the Chornohora and Svydovets Mts. and sporadically in the Gorgany, Nyzki Polonyny, Marmarosh

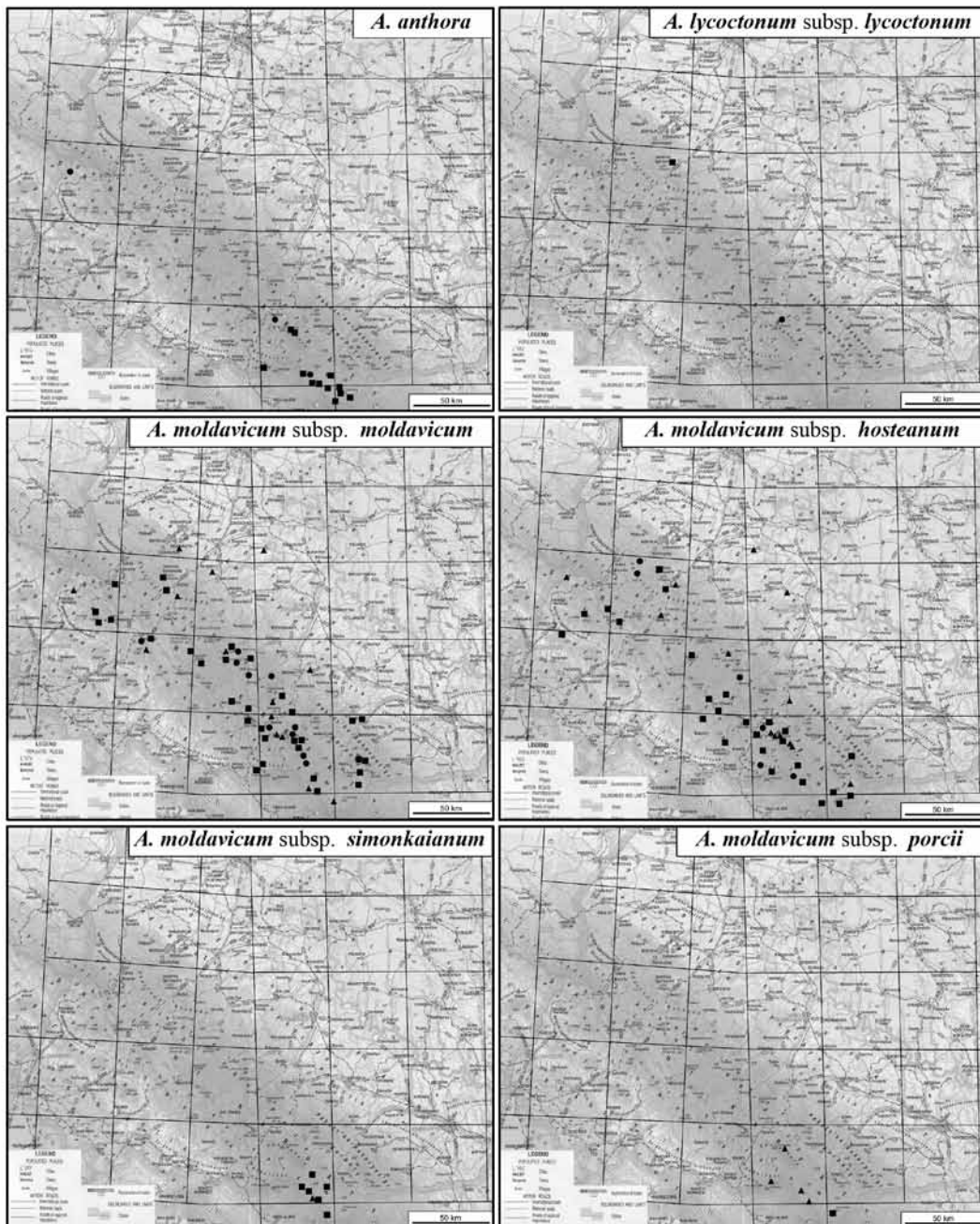


Figure 6. Distribution maps of the subgenus *Anthora* and subgenus *Lycoctonum* representatives.

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and Chyvchyny Mts. (Fig. 8). It grows in *Adenostyilion* and *Calamagrostion* communities in the subalpine and alpine belts, from where it descends sometimes along the streams into the higher montane belt.

Status: Species in the transitory area between the Western and Southern Carpathians.

Threat category in Ukraine: According to KRICSFALUSY & BUDNIKOV (2007) *A. firmum* subsp. *firmum* has the category LRnt, and *A. firmum* subsp. *fissurae* is CR. Because of the limited localities and the increasing tourist's impact, this species will probably gain the status of vulnerable VU in the next five years (NOVIKOFF 2010b).

Remarks: *A. firmum* is a typical representative of *A. napellus* agg., which occurs not only in the Carpathians, but also in the Alps and other alpid mountain ranges. Many species described within *A. napellus* agg. form probably a morphological continuum and differ mostly by the hairiness of carpels, hood and pedicels. In the Carpathians *A. firmum* is circumscribed within the two subspecies: subsp. *firmum* and subsp. *fissurae*. The first has the ecological center in the Western Carpathians, the latter – in the Southern Carpathians, where it was thought to be *A. romanicum*. In the Eastern Carpathians we probably meet the migratory routes of *A. firmum* from the Western and Southern Carpathians. The putative cline diversity of *A. firmum* along the mountain arch needs further molecular DNA and morphological studies.

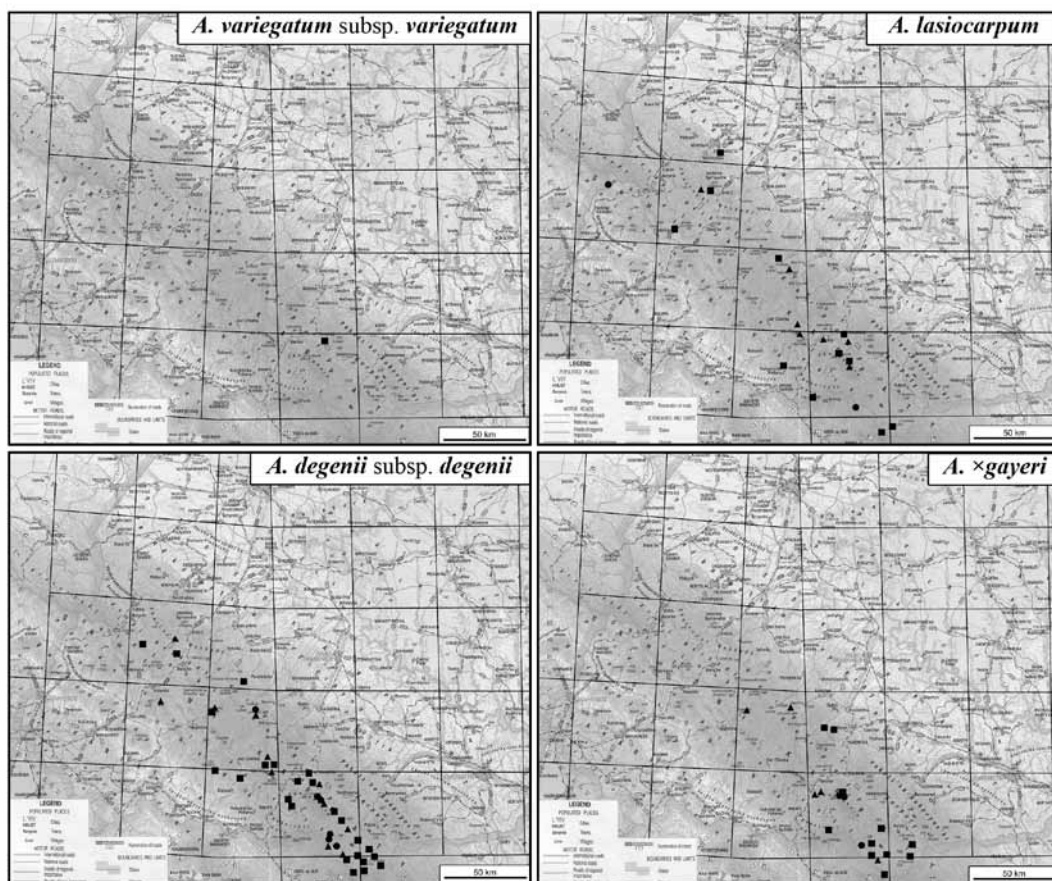


Figure 7. Distribution maps of the subgenus *Aconitum* section *Cammarum* representatives.

A. ×czarnohorensis (Zapał.) Mitka, Gen. Acon. in Poland and adj. countr.: 77. 2003 (Fig. 5H, K)
(*A. firmum* × *A. ×nanum*, MITKA 2002)

Synonyms: *A. firmum* Rchb. pro parte, *A. napellus* L. em. Skalický var. *czarnohorensis* Zapał.

Description: In general habit similar to *A. firmum*; it differs by pedicel pubescence. *A. ×czarnohorensis* has protruded or little curved hairs above bracteoles and protruded, hooked or mixed hairiness below.

Distribution: As *A. firmum*. The center of its occurrence is in the Chornohora Mts., but it also grows in the Sydovets, Gorgany, Nyzki Polonyny and Marmarosh Mts. (Fig. 8). It often occurs in mixed populations with *A. firmum* and *A. ×nanum*.

Status: Southern Eastern Carpathians endemic (MITKA 2003).

Threat category in Ukraine: The ecological conditions of populations are good but the number of mature individuals is estimated less than one thousand and the number of known localities less than ten: VU (NOVIKOFF 2010b).

Remarks: *A. ×czarnohorensis* differs from *A. ×nanum* only by pedicel pubescence which varies in both species and thus be misleading. These species mostly grow together and all of the

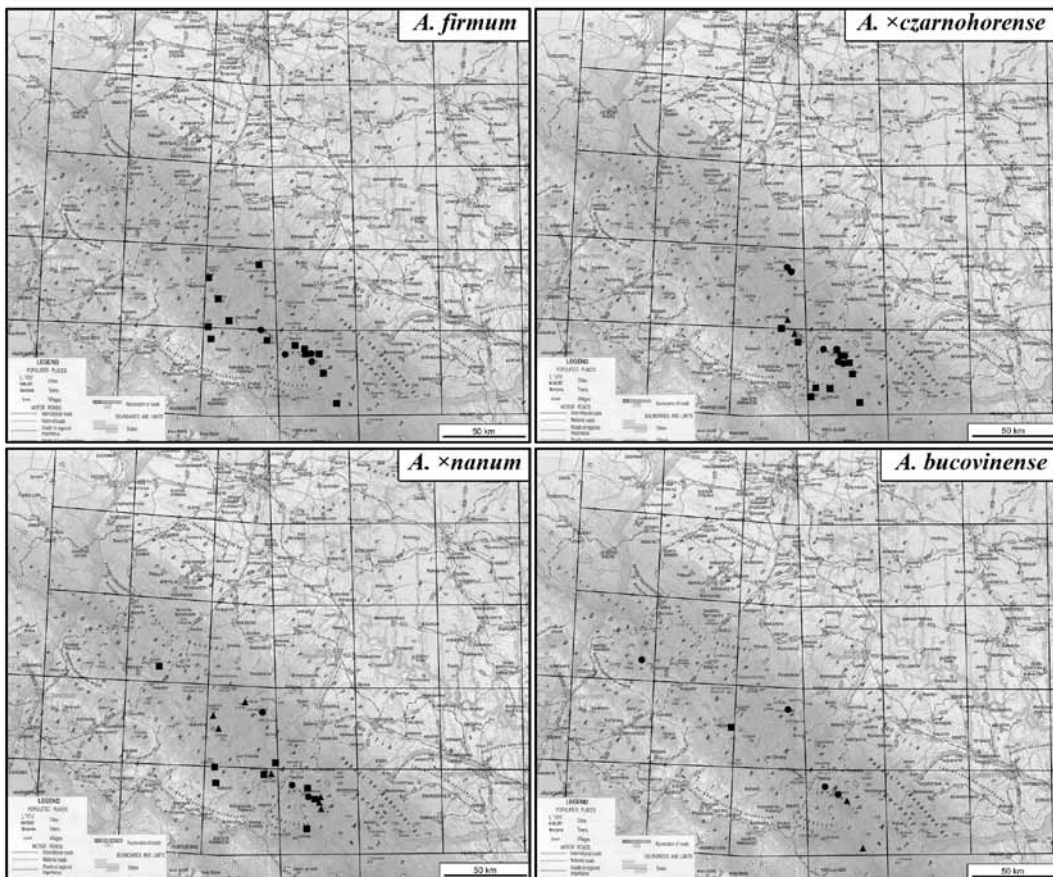


Figure 8. Distribution maps of the subgenus *Aconitum* section *Aconitum* representatives.

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known localities of *A. ×nanum* in the Ukrainian Carpathians are mixed. To check their putative hybridogenous status further DNA molecular investigations are needed.

Aconitum ×nanum (Baumg.) Simonk., Enum. Flor. Transsilv. Vesc. Crit.: 64. 1887 (Fig. 5H, L)
(*A. firmum* × *A. bucovinense*)

Synonyms: *A. firmum* Rchb. pro parte, *A. napellus* L. em. Skalický var. *nanum* Baumg., *A. tauricum* Wulf. subsp. *nanum* (Baumg.) Gáyér.

Description: In general habit similar to *A. firmum*; it differs by pedicel pubescence. *A. ×nanum* has hooked hairs with admixture of rarely protruded hairs above bracteoles and with similar or without hairiness below the bracteoles.

Distribution: It mostly occurs in the Chornohora range and then in the Skolivski Beskydy region, Svydovets, Gorgany, Nyzki Polonyny and Marmarosh Mts. (Fig. 8). It often occurs in mixed populations with *A. firmum*.

Status: Southern Eastern Carpathians endemic (MITKA 2003).

Threat category in Ukraine: DD (NOVIKOFF 2010b).

Aconitum bucovinense Zapał., Consp. Fl. Gal. Crit. 2: 230. 1908 (Fig. 5E–G)

Synonyms: *A. callibotryon* Rchb. subsp. *bucovinense* (Zapał.) Grinț., *A. firmum* Rchb. subsp. *bucovinense* (Zapał.) Graebn. & P. Graebn., *A. multifidum* non Koch ex Rchb., *A. tauricum* Wulf. in Koelle subsp. *nanum* Gáyér (non Baumg.).

Description: In general habit similar to *A. firmum*; it differs by hood and pedicels pubescence: hood densely hooked or mixed pubescent; carpels glabrous or rarely pubescent on the dorsal side (fo. *bucovinense*) or entirely and sparsely pubescent (fo. *orthotricha* Gáyér); filaments mostly pubescent; pedicels densely pubescent with mixed, protuberant and hooked hairs.

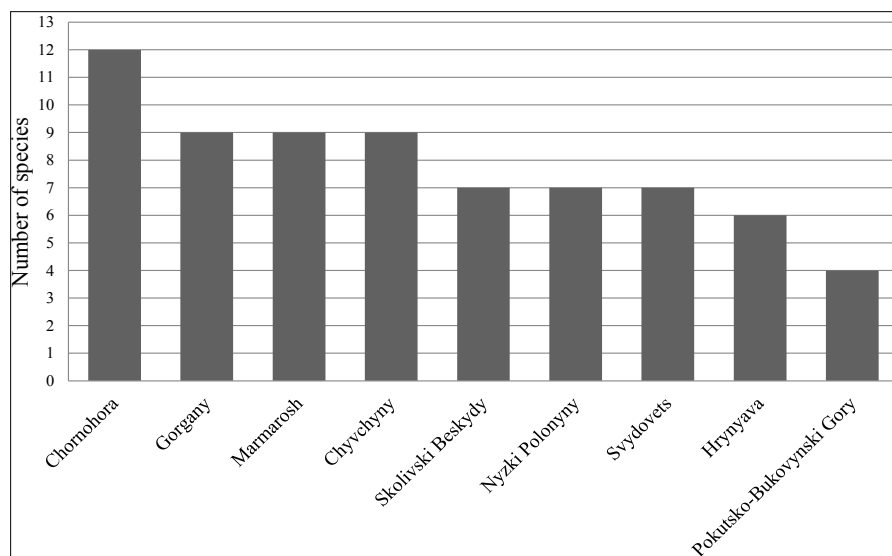


Figure 9. Distribution of the monkshoods in different regions of the Ukrainian Carpathians.

Distribution: It occurs sporadically on Mt. Pikuy (Skolivski Beskydy), in the Chornohora, Chyvchyny and Gorgany Mts. (Fig. 8). It is an alpine-subalpine species which grows mainly in open places near lakes and streams, but it also occurs on stony places and in the Carpathian alder-carr *Alnetum incanae*, etc.

Status: Southern Eastern Carpathians endemic (MITKA 2003).

Threat category in Ukraine: According to KRICSEFALUSY & BUDNIKOV (2007) it has the status EN. It is only known from four localities in the Ukrainian Carpathians, which are isolated from each other. The whole number of mature individuals does not exceed 250. All known localities are situated near the main touristic routes and thus leading to a great threat of the species: EN (NOVIKOFF 2010b). A strict protection is needed.

Discussion

Taxonomy of the 12 *Aconitum* species occurring in the Ukrainian Carpathians:

Subgen. *Anthora* (DC.) Peterm.:

Sect. *Anthora* DC.: *A. anthora* L.

Subgen. *Lycotinum* (DC.) Peterm.:

Sect. *Lycotinum* DC.:

Ser. *Lycotonia* Tamura et Lauener: *A. lycotinum* L. em. Koelle subsp. *lycotinum*, *A. moldavicum* Hacq. (subsp. *moldavicum*, subsp. *hosteanum* (Schur) Graebn. & P. Graebn., subsp. *simonkaianum* (Gáyer) Starm., subsp. *porcii* Starm.)

Subgen. *Aconitum*:

Sect. *Cammarum* DC. subsect. *Cammarum* (DC.) Rapaics:

Ser. *Variiegata* Steinberg ex Starm.: *A. variegatum* L. subsp. *variegatum*;

Ser. *Toxicum* (Rchb.) Mucher: *A. lasiocarpum* (Rchb.) Gáyer (subsp. *lasiocarpum*, subsp. *kotulae* (Pawl.) Starm. & Mitka), *A. degenii* Gáyer subsp. *degenii* (var. *intermedium* (Zapał.) Mitka, fo. *degenii*, fo. *craciunelense* Gáyer), *A. ×gayeri* Starm.;

Nothosect. *Acomarum* Starm.: *A. ×cammarum* L. em. Fries;

Sect. *Aconitum* subsect. *Aconitum*: *A. firmum* Rchb. (subsp. *firmum*, subsp. *fissurae* Nyárády), *A. ×czarnohoreense* (Zapał.) Mitka, *A. ×nanum* (Baumg.) Simonk., *A. bucovinense* Zapał. (fo. *bucovinense*, fo. *orthotricha* Gáyer).

The Ukrainian Carpathians are middle-high mountains divided into several physio-geographic regions: Skolivski Beskydy, Svydovets, Gorgany, Chornohora, Nyzki Polonyny, Marmarosh, Chyvchyny, Hrynyava and Pokutsko-Bukovynski Mts. (KONDRACKI 1978). The Chornohora Mts. are the highest and the only one with an alpine belt (KORNAŚ & MEDWECKA-KORNAŚ 2002), therefore most *Aconitum* species occur here (Fig. 9). Also interesting are the wild regions of the Chyvchyny and Marmarosh Mts., where other rare taxa like *A. anthora*, *A. moldavicum* subsp. *simonkaianum* and *A. moldavicum* subsp. *porcii* can often be found. Moreover, in the Chyvchyn range are the highest localities of *A. lasiocarpum* (W slope of Mt. Chyvchyn, 1655 m s.m.)

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and *A. moldavicum* subsp. *hosteanum* (Mt. Kukulyk, 1565 m s.m.). Other interesting regions are the Nyzki Polonyny, where an isolated, probably refugial locality of *A. anthora* (Stinka Mt., 1035 m s.m.) was found, and the Skolivski Beskydy, with a local occurrence center of *A. lasiocarpum*.

The altitudinal distribution of monkshoods in the Ukrainian Carpathians is connected with the four main ecological groups of plants. Each of them has its own optimum in the different belts. The first group is represented by *A. moldavicum* and *A. lycoctonum* from the subgenus *Lycoctonum* which grow mainly in the submontane and montane belts at altitudes from 671 m to 1270 m s.m.; they sometimes occur in the subalpine belt. They form a typical mesophytic plant group, often associated with shaded, wet habitats in the broadleaved forests. The second group includes species of the section *Cammarum* DC. which are also mesophytic but have a wider altitudinal spectrum (MITKA & ZEMANEK 1997); they occur at altitudes from 837 m to 1683 m s.m. They grow mainly along torrents and in forest ecotones in the montane belt, and they rarely occur in open wet habitats such as flood-plains. High-mountain plants of the section *Aconitum* belong to the third group. They grow at an altitudinal range from 1130 m up to 2008 m s.m. They have their ecological optimum in the subalpine and alpine belts, but they may rarely be found in the lower localities. They are xero-mesophytic and associated with wet habitats but often grow in rocky and stony places. The last, fourth group is represented by the only xerophytic species *A. anthora*, with no altitudinal relation. It is also present in the lowland flora of the Ukraine. In the Ukrainian Carpathians this species occurs mainly in the subalpine and upper part of montane belts at an altitude 1035 m to 1656 m s.m. (Fig. 10).

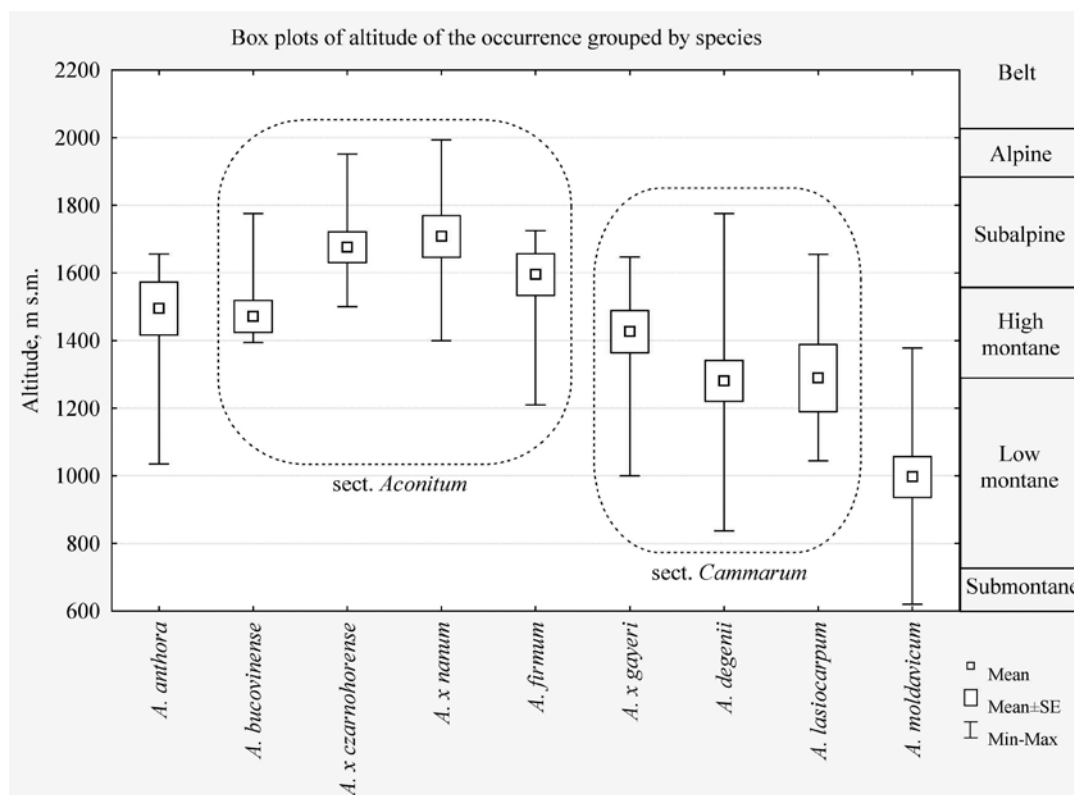


Figure 10. Altitudinal distribution of monkshoods in the Ukrainian Carpathians.

Table 1. The results of measurements of morphological features in the Ukrainian Carpathians *Aconitum* species.

	Acronym	Mean	Minimum	Maximum	Std.Dev.	CV	Std. Error
Altitude, <i>m s.m.</i>	AL	1412.46	694.00	1994.00	308.31	21.83	29.00
Plant length, <i>cm</i>	PLL	70.28	20.00	165.00	36.83	52.41	1.54
Number of inflorescence branches	NIB	3.20	0.00	19.00	3.28	102.39	0.14
Inflorescence terminal rachis length, <i>mm</i>	IRL	106.40	12.00	295.00	71.00	66.73	2.96
Leaf blade length, <i>mm</i>	LBL	75.75	18.00	248.00	41.83	55.21	1.74
Petiole length, <i>mm</i>	PL	29.76	1.50	493.00	42.28	142.05	1.76
Leaf length, <i>mm</i>	LL	105.52	20.00	723.00	79.00	74.87	3.29
Internode length, <i>mm</i>	IL	46.93	5.00	263.00	46.16	98.35	1.92
Index leaf blade/internode [LBL/IL]	IBI	2.37	0.49	8.86	1.35	56.86	0.06
Index petiole/internode [PL/IL]	IPI	71.72	3.64	371.43	51.74	72.15	2.16
Index leaf/internode [LL/IL]	ILI	3.08	0.55	12.57	1.67	54.21	0.07

The ecological groups described above are closely related to the life forms of monkshoods which have been described on the basis of the morphology of roots, shoot development and general biology. Only the members of the subgenus *Lycotconum* have rhizomes, all other species have tubers (spherical in the section *Cammarum* and elongated napiform in the sections *Aconitum* and *Acomarum*). Moreover, the investigated species have over-ground shoots of three different morphological types: a) clinopogotropic (shoots growing askew or creeping), b) apogotropic (upright standing orthotropic) with elongated internodes, c) apogotropic with brachytic internodes (ZHMYLEV et al. 2005; NOVIKOFF 2010c). The morphological shoot types are depending on the length of the plant, leaf length and length of the leaf blade, internode length and number of inflorescence branches. Together they form four biomorphological groups considered later (Tab. 1). The leaves of the first morphotype are the biggest and they have the largest blades, but leaves of the second and third morphotypes differ also in length. The first morphotype has the longest internodes, while the second morphotype has middle-sized internodes. It is interesting that *A. lasiocarpum* has internodes which are similar to the third morphotype. We suppose that it is related to the differentiation of *A. lasiocarpum* (likewise *A. variegatum*) into the two groups: dwarf plants, growing in the subalpine belt, and typical plants, growing in the montane belt. The mature plants of the first and the second morphological types are mainly multiflowered, they have ramified compound racemes, and the mature plants of the third group have rigid, simple or rarely dense ramified racemes with few flowers. Commonly, the semi-rosette, polycyclic clinopogotropic overground shoots are found only in the subgenus *Lycotconum*, while the remaining species have erosulate, monocyclic apogotropic shoots. The representatives of the section *Aconitum* have shoots with brachytic internodes, while the sections *Cammarum* and *Acomarum* have both types of apogotropic shoots.

SEREBRYAKOVA & POLYNTSEVA (1974) suggested that all of the representatives of the genus *Aconitum* belong to eleven life forms, which later (SEREBRYAKOVA 1977) joined into the two

Taxonomy and ecology of the genus *Aconitum* L. in the Ukrainian CarpathiansTable 2. Architectural models, life forms, and biomorphological groups in the Ukrainian Carpathians *Aconitum* species.

Taxa	Architectural model	Life form	Ecology	Biomorphological group	General morphology		
					Root	Shoot	Inflorescence
subg. <i>Lycocotnum</i>	Semi-rosette herbs	Perennial polycarpous herbs with indeterminate, polycyclic monocarpous overground shoot	Mesophytes	I	Perennial particulated rhizome	Clinoapogeous or apogeous with elongated internodes (in upper part)	Dense or loose ramified compound raceme
subg. <i>Aconitum</i>	sect. <i>Cammarum</i> sect. <i>Aconitum</i>	Perennial polycarpous herbs with indeterminate, monocyclic monocarpous overground shoot	Mesophytes	II	Biennial spherical tuber	Apogeous with elongated internodes	Dense or loose ramified compound raceme
			Mesophytes or mesoxerophytes	III	Biennial elongated napiform tubers	Apogeous with brachytic internodes	Rigid simple or dense ramified compound raceme
subg. <i>Anthora</i>			Mesoxerophytes or xerophytes	IV	Biennial spherical or napiform tubers	Apogeous with elongated or brachytic internodes, rarely clinoapogeous	From rigid simple to loose ramified compound raceme

main architectural models: a) perennial herbs with semi-rosette, determinate shoots (subgenus *Lycocotnum*) and b) perennial herbs with erosulate, determinate and indeterminate shoots (the remaining subgenera). It was found that all the species, including the subgenus *Lycocotnum*, have indeterminate shoots with terminal bud, which may be shift on the level below the pedicel of upper flowers (NOVIKOFF 2009b). According to another study of the life forms in the genus (BARYKINA et al. 1977a), monkshoods have only seven main life forms, which include several biomorphological groups of plants and differ mainly in root morphology.

In conclusion, the monkshoods of the Ukrainian Carpathians belong to two different architectural models and two main life forms divided into four biomorphological groups (Tab. 2). The fourth group includes *A. anthora* which is one of the most interesting species in the genus. It combines many features of the second and third group. It is worthy to note that *A. anthora* is in this respect an intermediate case – the tubers in early stages of the ontogenesis are spherical, but later they become elongated. Moreover, the number of tubers of *A. anthora* may increase and then they compound into bunch, what is also characteristic of some other Asian species (LITVINENKO 1977a, 1977b, 1981; BARYKINA et al. 1977b; ZIMAN 1983). Because of its wide geographical distribution, the various forms of the species may have short apogeous shoots, rigid inflorescences (in

high-mountain localities) or very elongated apogeotropic or even clinopogeotropic shoots and loose ramified inflorescences (in lower localities). The other significant features of *A. anthora* are: persistent perianth after blooming, unique morphology of the nectary (KOSUGE & TAMURA 1988) and seed (CAPPELLETTI & POLDINI 1984). Another species, the putative hybrid *A. ×cammarum*, is difficult to interpret, because it has an intermediate position between the second and third biomorphological group. It has elongated tubers like the species from the third group, but all other morphological features are similar to the second group. Probably, it is conditioned by the intersectional, hybridogenous origin.

Conclusion

- The genus *Aconitum* in the Ukrainian Carpathians is represented by 20 taxa (12 species) which belong to 3 subgenera – *Aconitum*, *Anthora* and *Lycocotnum*. From the total number 11 taxa are endemics and 5 taxa have a status of threatened in the wild.
- The *Aconitum* species in the territory may be divided into four ecological groups according to their optimal habitats and vertical longitudinal vegetation belts.
- The species investigated belong to the two main life forms and four biomorphological groups, mainly differentiated by root and shoot morphology.

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This paper is dedicated to Prof. Kazimierz Szczepanek, a famous scientist and distinguished investigator of the Carpathian paleoflora (Institute of Botany of the Jagiellonian University, Cracow) and to Prof. Lydia O. Tasenkevich, a distinguished researcher of the recent Carpathian flora (Department of Botany of the Ivan Franko National University, Lviv). Without their encourage this work would not have come into existence.

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