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Some light shed on stenoendemic *Galium transcarpaticum* (Rubiaceae) from the Ukrainian Carpathians

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Abstract

Galium transcarpaticum was described in 1979 as a stenoendemic occurring exclusively in the Ukrainian Carpathians. Since then, little has been contributed to its taxonomy and distribution, and only a few specimens have been collected. We successfully isolated DNA and amplified nuclear (*ITS*) and plastid (*trnH-psbA*, *atpB-rbcL*, *trnL* (c-d), and *trnL* (e-f)) markers from *G. transcarpaticum* isotype specimens deposited at the LWS herbarium. The obtained results do not allow delimiting *G. transcarpaticum* as an independent species, but rather place it within *G. mollugo*. Hence, the new combination *Galium mollugo* subsp. *transcarpaticum* (Stojko & Tasek.) A.V. Novikov, Nachychko & Zinenko.

Keywords: *Galium*, Rubiaceae, Ukrainian Carpathians, taxonomy, herbarium DNA

Introduction

Galium transcarpaticum Stojko & Tasek. (Rubiaceae Juss.) is a problematic species, a representative of polymorphic *G. mollugo* s.l. delimited based on the complex of variable morphological features, i.e., lack of pubescence, oblanceolate leaves with acute apex and indented margin, and the brown to blackish color of the stamens (Stojko and Tasek 1979). Originally, it was described by Ukrainian botanists Stepan Stojko (1920–2020) and Lydia Tasek (b. 1948) as an Eastern Carpathian endemic. However, since the species description, no occurrences have been reported outside the Ukrainian Carpathians. Consequently, Kliment et al. (2016) designated it as an Eastern Carpathian endemic occurring exclusively in the Ukrainian Carpathians.

In the original description, Stojko and Tasek (1979) noted that *Galium transcarpaticum* belongs to the *G. mollugo* complex and is morphologically closest to *G. suberectum* Klokov. The last one was later nested within *G. album* Mill. as a subspecies (i.e., *G. album* subsp. *suberectum* (Klokov) Michalk.) and reported as also having glabrous and oblanceolate leaves (Michalková 1993a, 1993b). Gynda (2004) noted that *G. transcarpaticum* differs from *G. album* subsp. *suberectum* based on the flower, pedicel, and leaf size. However, no clear distinguishing size limits were provided. Besides this, Gynda (1993, 2004) indicated *G. transcarpaticum* as a diploid ($2n = 2x = 22$) while *G. suberectum* as a tetraploid ($2n = 4x = 44$).

Although *Galium transcarpaticum* is often cited as an endemic species represented in the flora of the Ukrainian Carpathians (e.g., Kobiv 2010; Chorney 2011; Tasenkevich et al. 2025), only a few specimens were collected since its description and deposited at the herbaria KW (holotype), LWS (isotypes), KWHA, and CHER (see Thiers 2026 for herbarium acronyms). In the “Flora of the Ukrainian Carpathians” (Chopyk and Fedoronchuk 2015), *G. transcarpaticum* is not listed at all. Instead, it is mentioned in a recent checklist by Fedoronchuk and Shyian (2025), with reference to the old herbarium material and the initial publication by Stojko and Tasenkevich (1979).

The lack of clear delimiting characteristics of *Galium transcarpaticum* led to uncertainty about its taxonomic status and raised questions about whether it represents an independent species or an intraspecific morph within the *G. mollugo* complex.

At the herbarium LWS, we were able to sample herbarium material of *Galium transcarpaticum* and *G. mollugo* L., collected by Lydia Tasenkevich herself. Therefore, these specimens represent authentic material, allowing for the distinction of *G. transcarpaticum* from *G. mollugo* by Lydia Tasenkevich, one of the authors of the description of the former species. Unfortunately, we were unable to obtain authentic material of *G. album* subsp. *suberectum* as the rules of the KW herbarium, where it is stored, do not allow such destructive sampling. At the same time, the LWS herbarium does not contain such authentic specimens. Here, we present our brief outcomes and considerations based on the combined analysis of nuclear and several plastid markers.

Material and Methods

For molecular analysis, the material (5–10 leaves) has been sampled from six herbarium specimens of *Galium transcarpaticum* (three isotypes, two specimens from the locus classicus, and one specimen from the surrounding mountain area) and three specimens of *G. mollugo*, deposited at the LWS herbarium and collected in the Ukrainian Carpathians (Supplement 1). The material was homogenized in a ceramic mortar with an excessive amount of lysis buffer. The total DNA has been isolated from the herbarium material using the EURx GeneMATRIX Plant & Fungi DNA Purification Kit. Then the nuclear (*ITS*), and plastid (*trnH-psbA*, *atpB-rbcL*, *trnL* (c-d), *trnL* (e-f), *trnC-ycf6*, and *rpoB-trnC*) regions were amplified using the primers and programs listed in Supplement 2. Amplification success was analyzed using the electrophoresis in the agarose gel. As a result, five DNA regions, (i.e., *ITS*, *trnH-psbA*, *atpB-rbcL*, *trnL* (c-d), and *trnL* (e-f)) were successfully amplified for three *G. transcarpaticum* and three *G. mollugo* specimens (Supplement 1). For successfully amplified samples, the standard Sanger sequencing was performed by an outsourcing company (Macrogen). Additional sequences for *G. aparine* L. (served as an outgroup), as well as for *G. mollugo* and *G. album* (served as comparative reference sequences), were downloaded from the GenBank service (see Supplement 1 for the records details). The obtained sequences were aligned and concatenated using Geneious Prime.

The Bayesian Inference analysis was performed using MrBayes 3.2.6 in the PhyloSuite 2 environment (Zhao et al. 2025). Two matrices were applied independently: (a) with nucleotide sequences only and (b) a partitioned dataset consisting of nucleotide characters (positions 1–1801) and 0/1 coded indels (positions 1802–1807). For the gap analysis, the concatenated sequences were initially processed with FastGap 1.2 (Borchsenius 2009). After that, only informative gaps were selected and built into the partitioned dataset. For the nucleotide partition, the GTR+ Γ substitution model was applied. The indel partition was analyzed as standard discrete morphological characters using variable coding and gamma-distributed rate variation. Model parameters were unlinked across partitions. Two million generations of Markov chain Monte Carlo were run with four chains and a temperature parameter of 0.2, sampling trees every 1000 generations. The first 500 sampled trees were discarded as burn-in

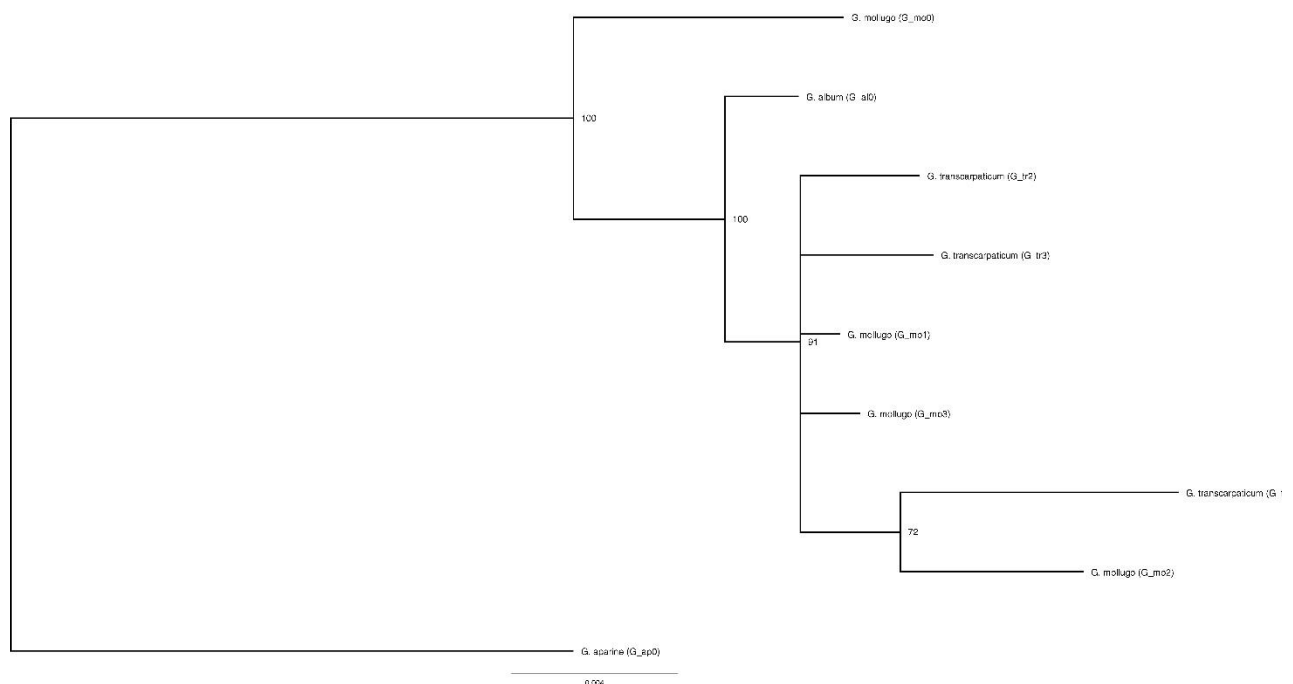
prior to constructing the majority-rule consensus tree and estimating posterior probabilities. The obtained trees were visualized using FigTree v1.4.4 software (Rambaut 2018).

Morphological analysis has been performed on the specimens deposited in the LWS herbarium using the standard ruler, caliper, and stereomicroscope Kern OZM-983. The distribution map was visualized using QGIS 3.10.2 and was based on consolidated data from the LWS, KWHA, and CHER herbaria.

Results and Discussion

The DNA extracted from the herbarium material, especially that exposed to regular high-temperature treatments for years, as in the LWS herbarium, is often degraded (Staats et al. 2011; Porrelli et al. 2026). This generally raises concerns about working with such material, increases the workload, and limits the application of standard molecular markers. Therefore, in our research, we focused on the application of markers resulting in sequences up to 1 kbp in length. We were unsuccessful in amplification of *trnC-ycf6* and *rpoB-trnC* plastid regions. However, other applied markers worked well with most of the treated specimens.

The received fragment of the *ITS* sequence (223 bp) failed to distinguish between Ukrainian *Galium transcarpathicum* and *G. mollugo*. Similarly, a 304 bp sequenced fragment of the *trnH-psbA* spacer did not show any differences between Ukrainian *G. mollugo* and *G. transcarpathicum* samples. The *trnL-F* region amplified with c-d (520 bp) and e-f (389 bp) primers did not show meaningful differences between *G. transcarpathicum* and *G. album*, or between *G. transcarpathicum* and *G. mollugo*, consistently placing them in the same clade with very little internal structure. The only observed differences of *G. transcarpathicum* from *G. mollugo* have been observed in the 634 bp sequence of *atpB-rbcL* chloroplast spacer, containing one unique insertion (in the position 54829 of *G. mollugo* plastid complete genome NC_036970.1) and two deletions in the positions 54971 and 55075. While indels are not considered informative characters by most phylogenetic algorithms, they represent here three independent evolutionary events and an apomorphy of the *G. transcarpathicum* lineage. Therefore, in addition to the traditional analysis of nucleotide sequences (Fig. 1A), we performed combined Bayesian analysis of nucleotide sequences and indels (Fig. 1B).



A

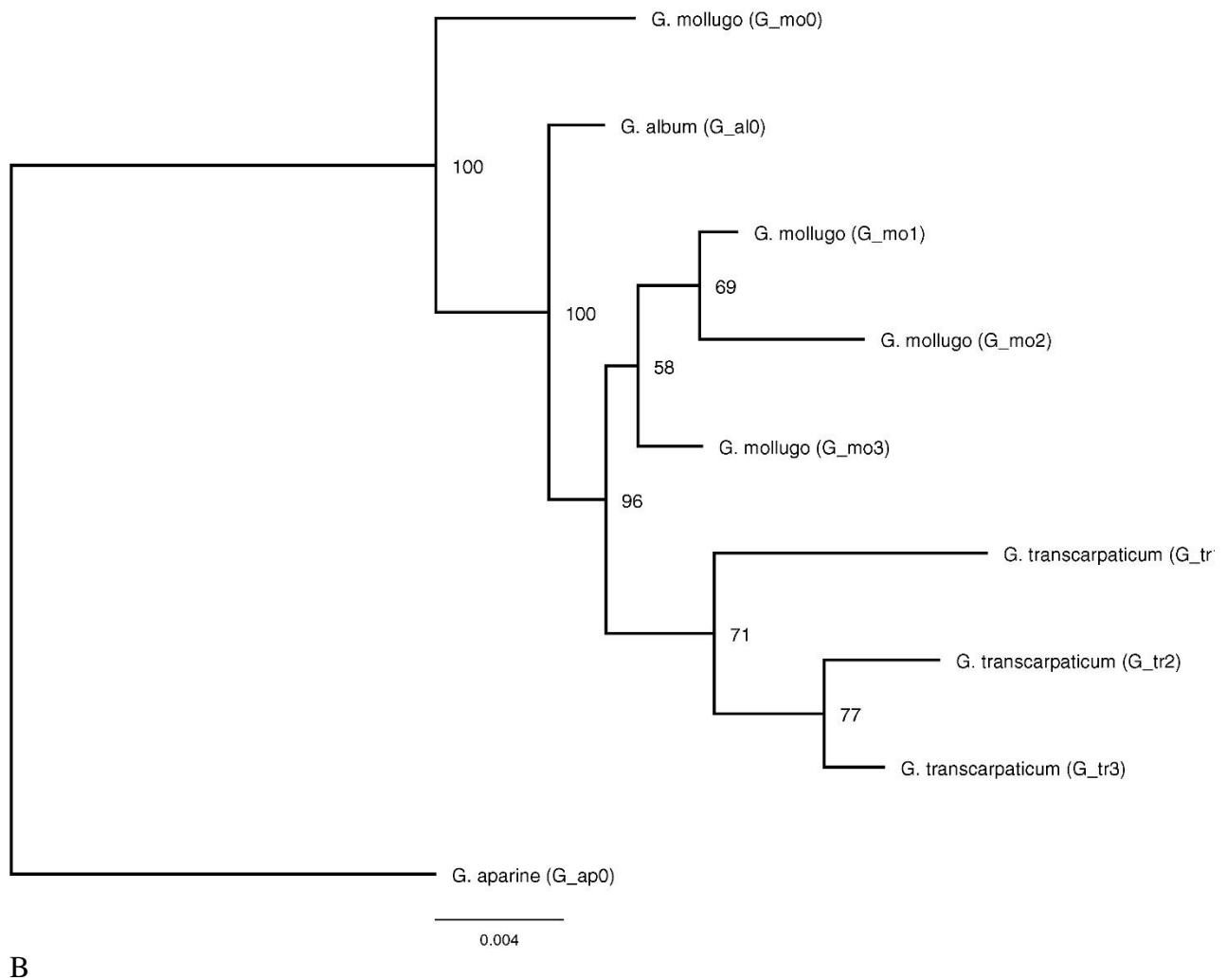


Figure 1. The results of Bayesian analysis of *Galium transcarpaticum*: A – nucleotide data only; B – nucleotide data combined with coded indels.

In the Bayesian analysis based solely on nucleotide substitutions, *Galium transcarpaticum* was not recovered as a monophyletic group, as its accessions were intermixed with representatives of *G. mollugo* specimens from the Ukrainian Carpathians. This result indicates very close molecular affinity between the two taxa and does not support clear species-level separation. After the inclusion of coded indel characters, the tree topology slightly changed, but the overall result remained the same. All sampled accessions of *G. transcarpaticum* formed a clade distinct from the clade of Ukrainian *G. mollugo*. However, support for the *G. transcarpaticum* clade was moderate (PP = 0.71), while the strong support value (PP = 0.96) was gained for the clade containing both *G. mollugo* and *G. transcarpaticum*. Thus, although coded indels provide additional phylogenetic signal and suggest some molecular differentiation of *G. transcarpaticum*, this evidence remains limited and does not allow for confirming *G. transcarpaticum* as an independent species.

Morphological analysis showed that specimens of *Galium transcarpaticum* share most of the characters with *G. mollugo* (Supplement 3). The difference was found in several characters, which, nevertheless, slightly overlap or make a continuum with *G. mollugo* (Table 1). In particular, *G. transcarpaticum* plants are generally smaller, with shorter, narrower basal leaves, but have a higher number of leaves per node, larger flowers, and larger fruits. Mature fruits of *G. transcarpaticum* are normally dark brown, while fruits of *G. mollugo* are slightly brighter, reddish-brown. It is also important to note that *G. transcarpaticum* is attributed to open lime outcrops in the montane belt,

while *G. mollugo* has a much wider ecological amplitude and is normally associated with eutrophic moister habitats (e.g., meadows, forest glades, forest edges, etc.).

Table 1. Comparative assessment of *Galium transcarpaticum* and *G. mollugo* in the Ukrainian Carpathians.

Characters	<i>G. transcarpaticum</i>		<i>G. mollugo</i>	
	Protologue (Stojko and Tasenkevich 1979)	Analyzed specimens	Description of Michalková (1993b)	Analyzed specimens
Main shoot length	(15–) 30–40 (–45) cm	25–34 cm	(40–) 60–70 (–140)	60–140 cm
Nr of leaves per whorl	6– (7–9) –10	6–8	5–7 (based on illustration)	5–6
Basal leaves length	0.5–1.0 cm	1.0–1.2 cm		1.2–3.0 cm
Basal leaves width		1.1–1.5 mm		1.6–3.4 mm
Perianth diameter	3.5–5.5 mm	2.5–3.7 mm	(2.3–) 2.4–2.7 (–3.5) mm	1.7–2.5 mm
Fruit length	Up to 2 mm	1.0–1.8 mm	(0.9–) 1.0–1.2 mm	0.9–1.2 mm
Fruit color	Dark brown	Dark brown	Reddish-brown	Reddish-brown
Substrate	Lime outcrops	Lime outcrops	Eutrophic moister alluvial soils	Eutrophic moister soils

Considering the general results of the molecular analysis presented here, as well as the shared distribution range (Fig. 2), diploid chromosome number, and overall morphological similarity, we conclude that *Galium transcarpaticum* should be treated within *G. mollugo*. At the same time, the presence of diagnostic indels, distinct ecological preferences (particularly its association with limestone outcrops), and the morphological peculiarities summarized in Table 1 support its recognition at the subspecies level. Therefore, we propose the following new combination: *G. mollugo* subsp. *transcarpaticum* (Stojko & Tasenk.) A.V.Novikov, Nachychko & Zinenko.

***Galium mollugo* subsp. *transcarpaticum* (Stojko & Tasenk.) A.V.Novikov, Nachychko & Zinenko, comb.nov.**

Basionym

Galium transcarpaticum Stojko & Tasenk., Ukrayins'k. Bot. Zhurn. [Ukr. Bot. J.] 36(6): 594. 1979.

Type material

RSS Ucrainae, Carpati Orientales Ucrainici, Jugum Poloninense, districtus Transcarpatia, pagus Velika Ugolyka, rupes calcarea in loco Velikij Grebenj, 820 m, in clivis austrooccidentalibus (Stojko and Tasenkevich 1979). Holotype: KW. Isotypes: LWS 017273, LWS 112550, LWS 112551.

Distribution and habitat

Ukrainian Carpathians. Open lime outcrops in the upper mountainous vegetation belt at the elevations of 800–1100 m a.s.l. Xerothermic and mesophytic calcareous communities.

Selected specimens examined

RSS Ucrainae, Carpati Orientales Ucrainici, Jugum Poloninense, distr. Transcarpatia, pagus Velika Ugoljka, rupes calcarea, in loco Velikiy Grebinj, 820 m, in clivis austro-occidentalibus: 1976-07-27 Stoyko S.M. & Tassenkevich L.O. (Holotype – KW; Isotypes – LWS 112550, LWS 112551). Zakarpattia region, Tiachiv district, Uholka forestry of Carpathian State Reserve, lime slope of Hrebin, 820 m a.s.l., SW slope: 1976-07-27 Stoyko S.M. & Tassenkevich L.O. (Isotype LWS 017273). Zakarpattia region, Tiachiv district, Uholka massif of the Carpathian Nature Reserve. Lime rocks: 1988-06-22 Melnyk V.I. (KWHA, 5 unnumbered specimens). Zakarpattia region, village Dilove, urochysche Kizi, lime slope: 1980-08-27 Tassenkevich L.O. (LWS 088718). Zakarpattia region, Velikiy Bychkiv MK, urochysche Kuziy, lime rocks Sokolyne Berdo: 1991-08-11 Tassenkevich L.O. (LWS 088716). Zakarpattia region, Tiachiv district, Uholka forestry, lime rock Hrebin, 820 m: 1988-07-28 Tassenkevich L.O. (LWS 088715). Zakarpattia region, Tiachiv district, Carpathian Reserve, village Mala Uholka, lime rock Kopytsia: 1990-07-06 Tassenkevich L.O. (LWS 088714). Zakarpattia region, Tiachiv district, Carpathian Reserve, lime rock Chury, village Mala Uholka: 1990-07-06 Tassenkevich L.O. (LWS 088712). Zakarpattia region, Tiachiv district, Mala Uholka, Chur, Carpathian Reserve, lime slopes: 1990-07-06 Tassenkevich L.O. (LWS 088713). Chernivtsi region, Putyla district, Chyvchyny, urochysche Chorniy Dil, Mt. Velikiy Kamin: 1978-07-14 Tassenkevich L.O. (LWS 007239, LWS 007240). Zakarpattia region, Tiachiv district, Uholka forestry, lime rock Hrebin, 900 m a.s.l.: 1978-07-26 Tassenkevich L.O. (LWS 017268). Zakarpattia region, Tiachiv district, Uholka forestry of Karpathian State Reserve, lime rock Velikiy Hrebin, 1050 m a.s.l., top, SW slope: 1979-08-13 Tassenkevich L.O. (LWS 017274). Zakarpattia region, Tiachiv district, Uholka forestry of Karpathian State Reserve, lime rock Hrebin, 900 m a.s.l., SE slope: 1978-07-26 Tassenkevich L.O. (LWS 017268, LWS 017270, LWS 017271, LWS 017272, LWS 017275, LWS 017276). Zakarpattia region, village Dilove, urochysche Kizi, lime rocks: 1980-08-27 Tassenkevich L.O. (LWS 017277, LWS 017278, LWS 017279, LWS 017280). Zakarpattia region, Tiachiv district, Karpathian State Reserve, village Mala Uholka, lime rock Velikiy Hrebin: 1990-07-08 Tassenkevich L.O. (LWS 016632). Chernivtsi region, Putyla district, Chyvchyny Mts., Mt. Velikiy Kamin, the summit: 1994-08-21 Chorney I.I. (CHER, unnumbered). Chernivtsi region, Putyla district, Chyvchyny Mts., Mt. Velikiy Kamin: 1991-07-18 Chorney I.I. (CHER, unnumbered). Chernivtsi region, Putyla district, Chyvchyny Mts., Chorniy Dil mountain range, Mt. Velikiy Kamin: 2003-09-21 Chorney I.I. et al. (CHER, unnumbered). Chernivtsi region, Putyla district, Chyvchyny Mts., Mt. Velikiy Kamin: 2004-08-10 Chorney I.I. et al. (CHER, unnumbered).

Key to the species of *Galium mollugo* agg. in the Ukrainian Carpathians

1	Stems few; ascendent or decumbent; glabrous or rarely slightly hairy at the base and/or in the nodes. Leaves oblanceolate to narrowly obovate; glabrous or rarely with sparse hairs underneath; cauline leaves up to 0.7 cm wide. Inflorescences lax.	2
–	Stems usually numerous; erect or ascendent; glabrous or pubescent, usually becomes glabrescent in direction toward the apex. Leaves oblong to obovate; pubescent,	3

	rarely glabrous; cauline leaves up to 0.4–0.5 cm wide. Inflorescences dense.	
2	Stems normally 60–70 cm long, often much longer. Leaves 5–7 per whorl; basal leaves 1.2–3.0 (–3.5) cm long and 1.6–3.4 (–4.0) mm wide. Perianth (1.7–) 2.4–2.7 (–3.5) mm in diameter. Fruits (0.9–) 1.0–1.2 mm long, reddish-brown.	<i>G. mollugo</i> subsp. <i>mollugo</i> (incl. <i>G. kernerianum</i> Klokov and <i>G. pseudomollugo</i> Klokov)
–	Stems up to 40 (–45) long. Leaves 6–8 per whorl; basal leaves (0.5–) 1.0–1.2 cm long and 1.1–1.5 mm wide. Perianth 2.5–3.7 (–5.5) mm in diameter. Fruits 1.0–1.8 (–2.0) mm long, dark brown.	<i>G. mollugo</i> subsp. <i>transcarpaticum</i>
3	Slender plants. Stem glabrous or sparsely hairy at the base and nodes. Stems 50–100 cm long; branched; lateral branches patent. Leaves oblong to oblanceolate; glabrous or rarely slightly hairy beneath. Pedicels patent or erect.	4
–	Robust plants. Stem sparsely hairy at the base and nodes, rarely glabrescent. Stems 40–80 cm long; weakly branched; lateral branches extended and patent. Leaves narrowly obovate; usually pubescent from both sides, very rarely glabrous. Pedicels patent. Inflorescences with numerous flowers.	<i>G. album</i> subsp. <i>pycnotrichum</i> (Heinr. Braun) Krendl
4	Leaves oblong or oblanceolate; glabrous or rarely slightly hairy beneath; cauline leaves (1.4–) 1.7–2.0 (–2.5) cm long and 0.2–0.3 (–0.4) cm wide. Pedicels patent. Inflorescences with numerous flowers.	<i>G. album</i> subsp. <i>album</i>
–	Leaves narrowly oblanceolate; glabrous; cauline leaves (0.9–) 1.2–1.5 (–1.8) cm long and 0.1–0.2 (–0.3) cm wide. Pedicels erect. Inflorescences with few flowers.	<i>G. album</i> subsp. <i>suberectum</i> (Klokov) E. Michálek.

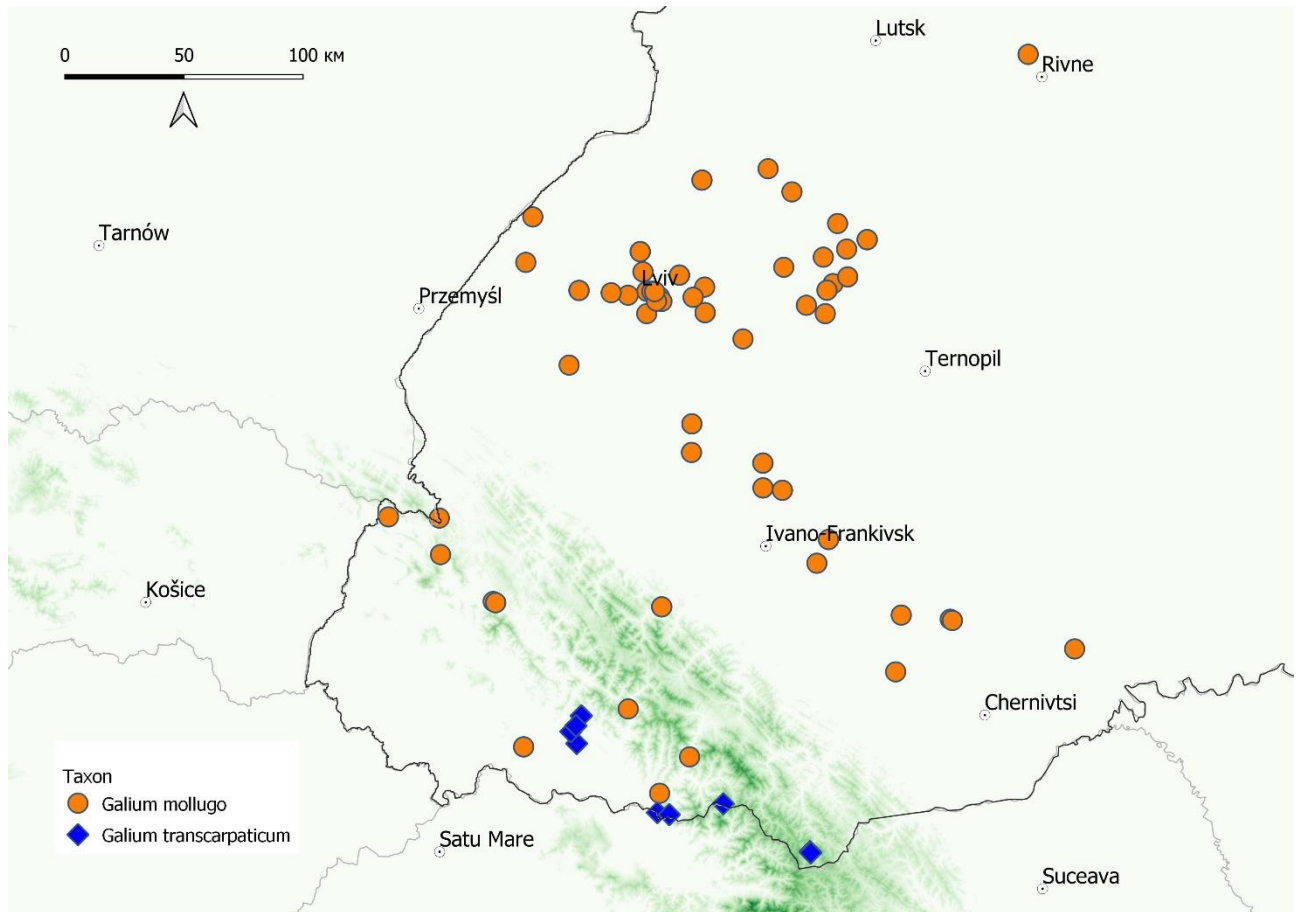


Figure 2. Distribution of *Galium transcarpaticum* and *G. mollugo* in the Ukrainian Carpathians and adjacent lowlands based on the herbarium data.

Conclusions

The conducted molecular analyses demonstrated very close affinity between *Galium transcarpaticum* and *G. mollugo*. The nucleotide dataset alone did not support the monophyly of *G. transcarpaticum*. Although several unique indels indicate some degree of molecular differentiation, the obtained evidence remains insufficient to confirm *G. transcarpaticum* as an independent species. Therefore, the taxon is more likely to represent a geographically and/or morphologically differentiated infraspecific lineage within the *G. mollugo* complex, possibly at the rank of subspecies or variety.

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