

Vegetation of calcareous petrifying springs (*Lycopodo europaei-Cratoneurion commutati*) in Western Ukraine in the central and southeastern European context

Vegetation von Kalktuffquellen (*Lycopodo europaei-Cratoneurion commutati*) in der Westukraine im mitteleuropäischen und südosteuropäischen Kontext

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Abstract

Calcareous petrifying tufa springs of the *Lycopodo europaei-Cratoneurion commutati* alliance are rare and threatened habitats of significant conservation importance. Comprehensive knowledge of their vegetation variability is critical for informed conservation plans; however, data from Eastern and Southeastern Europe remain largely insufficient. This study aims to bring novel data from Western Ukraine and provide a unified classification of the *Lycopodo europaei-Cratoneurion commutati* alliance in Western Ukraine and adjacent countries (Czech Republic, Poland, Slovakia) reaching up to Southeastern Europe (Bulgaria, Greece, Montenegro, Romania, Serbia). We analysed an stratified and cleaned data set of 129 relevés using unsupervised and semi-supervised classification (ISOPAM, k-means). The analyses resulted in five clusters which correspond with the following syntaxa: i) *Eucladietum verticillati*, ii) *Brachythecio rivularis-Cratoneuretum commutati typicum*, iii) *Brachythecio rivularis-Cratoneuretum commutati rhynchostegietosum riparioidis* subass. nova, iv) *Cochleario pyrenaicae-Cratoneuretum commutati*, and v) *Pinguiculo hirtiflorae-Cratoneuretum commutati* ass. nova. While the *Cochleario pyrenaicae-Cratoneuretum commutati* was identified only in Slovakia and the *Pinguiculo hirtiflorae-Cratoneuretum commutati* only in the Balkans, the other three syntaxa were widespread and occurred among others in Ukraine. The communities differed in their mean indicator values for temperature and light. Our synthesis provides the first unified classification of the *Lycopodo europaei-Cratoneurion commutati* alliance for Southeastern Europe.

Keywords: Calcareous petrifying springs, Central Europe, classification, Southeastern Europe, tufa springs, Western Ukraine

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Calcareous petrifying springs are fed by water rich in calcium bicarbonate and carbon dioxide. When the water emerges at the surface, carbon dioxide is released, causing calcium carbonate to precipitate and form deposits known as tufa, travertine or calcite. The combination of high alkalinity, permanent water availability, and ongoing calcium carbonate deposition creates stressful conditions for plant growths, while simultaneously offering a competitive advantage to species adapted to these habitats by excluding non-adapted species. As a result, the plant communities that occur in this environment are highly specialized (Horsák et al. 2017, Bartošová et al. 2019, Cantonati et al. 2020, de Mars et al. 2024, Lyons & Kelly 2025), and thus, the sites are highly significant for biodiversity protection.

Calcareous petrifying spring vegetation have been already studied and classified in Western and Central Europe (Hadač 1983, Rodwell 1991, Hinterlang 1992, 2017, Zechmeister 1993, Zechmeister & Mucina 1994, Siebum et al. 1995, Valachovič 2001, Matuszkiewicz 2007, Hájková & Hájek 2011, Rivas-Martínez 2011, Lyons & Kelly 2017, de Foucault 2018). However, in Eastern Europe, descriptions of such vegetation are scarce (but see Didukh et al. 2018), indicating a significant knowledge gap.

Calcareous petrifying springs have been assigned to different syntaxa in the past. Koch (1928) described the *Cratoneurion commutati* alliance, which represents the oldest valid alliance name for calcareous springs dominated by *Palustriella commutata* (*Cratoneuron commutatum*), or ecologically similar moss species. This alliance was typified based on material from the alpine zone of the Alps, where *Palustriella falcata* (*Cratoneuron falcatum*) prevails. Hadač (1983) additionally described the *Lycopodo europaei-Cratoneurion commutati* alliance from lower elevations where *P. commutata* s. str. and *Cratoneuron filicinum* prevail. Since then, the definition of the *Cratoneurion commutati* has been restricted to communities above the timberline (e.g. Valachovič 2001, Mucina et al. 2016, Peterka et al. 2023). In contrast to the restricted concept of *Cratoneurion commutati*, communities of the *Lycopodo europaei-Cratoneurion commutati* lack high-mountain species. Instead, they persist in shaded forests, grassland or reed beds and therefore include vascular plant taxa characteristic of these habitats. Moreover, calcicole spring bryophytes that also grow on limestone rocks are found in these communities: *Eucladium verticillatum*, *Didymodon tophaceus*, *Pellia endiviifolia*, *Fissidens gracilifolius* and *Preissia quadrata*. Carbonate deposits at lower elevations are generally thicker and more compact than those in high-mountain *Cratoneurion commutati* springs. At higher altitudes, the formation of such deposits may be completely inhibited by lower hydrogencarbonate concentrations and lower air temperatures (Singh et al. 2023). In the first pan-European classification of springs (Zechmeister & Mucina 1994), these low-elevation calcareous springs were assigned to the *Adiantion* alliance i.e. Mediterranean communities of shaded wet or water-splashed rocks and walls, yet still being included into the *Montio-Cardaminetea* class. In the European checklist of higher-rank syntaxa, Mucina et al. (2016) accepted a separate class *Adiantetea* Br.-Bl. et al. 1952 for Mediterranean communities in wet or water-splashed rocks, while communities of low-elevation calcareous petrifying springs were considered as *Lycopodo europaei-Cratoneurion commutati* alliance within the *Montio-Cardaminetea* class. The recent European syntaxonomical schemes of spring vegetation of the *Montio-Cardaminetea* (Mucina et al. 2016, Peterka et al. 2023) hence classify petrifying springs into the two alliances: the *Cratoneurion commutati* Koch 1928 includes heliophilous calcareous springs

in the subalpine to alpine vegetation belts and the *Lycopodo europaei-Cratoneurion commutati* Hadač 1983 sciophilous to heliophilous calcareous springs spanning from the lowlands to submontane/montane belt. Whenever fen species of the class *Scheuchzerio-Caricetea fuscae* form a substantial part of the community the vegetation is classified within the alliance *Caricion davallianae* (Hájek et al. 2021). This classification of calcareous petrifying springs according to phytosociological criteria is, however, inconsistently applied in individual countries (Hájková & Hájek 2011). Moreover, the classification of calcareous springs has not been conducted yet at the association level on the European level.

Because of the lack of vegetation data from calcareous springs from the southern parts of Eastern Europe, we aimed at the vegetation diversity of these habitats in Ukraine, focusing on the species composition of both bryophytes and vascular plants. The limited data from Eastern Europe partially result from the natural rarity of this habitat which is uncommon in flat regions in general and especially in agricultural lowlands. Our aim is to classify the Ukrainian relevés within the broader context of Central and Southeastern Europe, as as relying solely on limited local data lead to biased results. Moreover, compiling a geographically broader dataset enables a more robust and critical synthesis of the vegetation. This approach allowed us to classify the vegetation of Ukrainian petrifying springs in a broader context and more validly. The main objectives of this study are (1) to present original vegetation data from Ukrainian tufa springs, (2) classify this data in a broader geographical context, and (3) interpret the results from ecological and biogeographical perspectives.

2. Materials and Methods

2.1 Study area in Ukraine

The study area in Ukraine encompasses the 250-km canyon-like Dniester River Valley, located in the northeast of the Ukrainian Carpathians. It forms part of the southwestern Podillia Upland and the Khotyn Upland in western Ukraine, extending from N 48.980°, E 25.072° to N 48.586°, E 27.151° (Herenchuk 1973). The canyon of the Dniester River Valley is composed by Mesozoic limestone, marl, sandstone, and dolomite as well as Miocene gypsum and Cretaceous chalk limestone. Springs emerge primarily at the contact zones of porous deposits of Upper Cretaceous (Cenomanian) and Miocene (Sarmatian) deposits and dense, impermeable Devonian or Silurian limestone aquifers (Volik 2007, Didukh et al. 2018). Carbonate precipitation is promoted by enhanced carbon dioxide outgassing driven by high summer temperatures (July averages of 18–19 °C), and a prolonged period with daily temperatures above 14 °C. Warm microclimate conditions may further stimulate tufa formation (Herenchuk 1973). An annual precipitation of 520–590 mm ensures sufficient water discharge. The data set from the Dniester River Valley in Ukraine was expanded with vegetation data from other regions of Central and Southeastern Europe. We included additional plots from lowland to montane calcareous petrifying springs stored in the Czech National Phytosociological Database (Chytrý & Rafajlová 2003), the European Mire Vegetation Database (Peterka et al. 2015) and the Slovak Vegetation Database (Šibík 2012) as well as our private databases, which are in most cases also archived in the European Vegetation Archive. These data originate from Kornaš & Medvecká-Kornaš (1967), Coldea (1991), Hájek (2000), Valachovič & Kochjarová (2000), Hrivnák et al. (2005), Kliment et al. (2008), and Dítě et al. (2016). Finally, the dataset was further enlarged by our own (M.H., P.H.) unpublished relevés from the Balkan peninsula, Slovakia, Poland, Romania and Ukraine (2000–2021). Plots originally assigned by their authors to *Lycopodo europaei-Cratoneurion commutati* alliance, as well as plots classified within this alliance in the recent synthesis of spring vegetation (Peterka et al. 2023), were also included.

The initial dataset included 196 relevés, in which we harmonised species names according to the Euro+Med Database (Euro+Med 2023) for vascular plants, Hodgetts et al. (2020) for bryophytes, and the Index Fungorum for lichens. Taxa identified only at the genus level were excluded. The delimitation of species aggregates follows Peterka et al. (2023). Trees and shrubs were removed prior to resampling and unsupervised classification (see below).

We conducted a heterogeneity-constrained random (HCR) resampling (Lengyel et al. 2011) within a geographical grid of 3 minutes latitude and 5 minutes longitude to ensure uniform sampling density. In grid cells containing more than five relevés, the five most distinct relevés were selected based on Bray-Curtis dissimilarity calculated from square-rooted percentage cover values of species. Following the HCR procedure, 129 relevés remained and used in subsequent analyses. Plot sizes averaged 7 m² ranging from 0.3 to 25 m².

As a final step, we removed ten relevés which behaved as outliers in the first run of the analyses and obviously do not represent the *Montio-Cardamineteta* vegetation rather than *Caricion davallianae* fens, *Cratoneuron decipiens* high-mountain springs, and wetlands in which reed taxa dominated over spring bryophytes.

2.2 Unsupervised classification and expert system processing

For the initial classification, we used the ISOPAM algorithm (Schmidtlein et al. 2010) as it is the most suitable method for reducing noise caused by incidental non-spring species, which are common in this type of vegetation. The ISOPAM algorithm was calculated using R 4.4.2 in the JUICE 7.1 environment (Tichý 2002).

We run the ISOPAM algorithm repeatedly using different number of clusters. A five-cluster solution yielded the most interpretable with regard to habitat ecology and existing syntaxonomical schemes: (i) a cluster of the most shaded springs typically dominated by *Palustriella* and *Cratoneuron* species; (ii) a cluster of springs usually dominated by taxa whose ecological niche extends beyond *Montio-Cardamineteta* springs, such as *Rhynchostegium riparioides* or *Hydroambystegium tenax*; (iii) a cluster of semi-shaded to open springs lacking forest species, characterised by light-demanding taxa such as *Cochleria pyrenaica*, *Pinguicula vulgaris*, *Carex flava* and *Parnassia palustris*; (iv) a cluster of springs dominated by *Eucladium verticillatum* rather than pleurocarpus mosses; (v) a cluster characterised by *Pinguicula hirtiflora* and sub-mediterranean taxa. In parallel, we applied several other unsupervised classification methods, with the number of clusters set by the Optimclass method (Tichý et al. 2010) showing similar results (not shown) and the sharpest differentiation of vegetation units by diagnostic taxa at the level of five clusters (not shown).

To ensure that our final classification corresponds as closely as possible to the existing syntaxonomical scheme, we proceeded with semi-supervised classification approach comprising the following steps. First, we defined the cores of recognised vegetation types using formal criteria in order to capture the traditionally recognised associations roughly corresponding with each cluster: (1) the *Brachythecio rivularis-Cratoneuretum*, defined either by the presence of *Palustriella commutata* in combination with at least two taxa from the species group defined by the COCKTAIL method (Bruehlheide & Chytrý 2000, Kočí et al. 2003) including *Geranium robertianum*, *Brachythecium rivulare* and *Pellia endiviifolia*, or by a dominance of *Palustriella commutata* exceeding 50% cover together with at least one species from this group; (2) springs with *Rhynchostegium riparioides*, defined by the dominance of *Rhynchostegium riparioides* a cover of at least < 5%, and with cover equal to or exceeding that of *Palustriella commutata*; (3) the *Cochleario pyrenaicae-Cratoneuretum commutati*, defined by the dominance of *Cochlearia pyrenaica* with a cover of at least 5%. (4) the *Eucladietum verticillati*, defined by a cover of *Eucladium verticillatum* exceeding that of *Palustriella commutata* (5) the Balkan springs, defined by the presence of *Pinguicula hirtiflora*. After setting these cores, which comprised 42% of the data set, the remaining relevés were assigned to the existing cores or, where compositionally distinct, to newly emerging clusters using a semi-supervised k-means approach based on Hellinger-transformed cover values (Legendre & Legendre 1998). Whenever more than five clusters emerged, the additional clusters consisted only of one or two outlying relevés from shaded springs formed the additional clusters. Therefore, the level of five clusters, corresponding with the number of

cores, was retained. As a final step, the cluster representing *Rhynchosstegium*-dominated springs was cleaned manually refined: relevés lacking its diagnostic species were reassigned to the *Brachythecio rivularis*-*Cratoneuretum commutati* cluster.

Diagnostic species for the individual clusters were identified based on the *phi* coefficient with virtually standardized cluster sizes (Chytrý et al. 2002, Tichý & Chytrý 2006). We applied a fidelity threshold of *phi* = 0.25 in combination with Fisher's exact test ($p < 0.05$). Species with *phi* > 0.5 are indicated in bold in the text. Constancy thresholds of 25% and 50% were used to distinguish constant and highly constant species; species with constancy > 50% are likewise shown in bold.

To explore environmental differences among the clusters, we calculated Ellenberg-type indicator values calculated as unweighted means of vascular plant indicator values for light, temperature, soil reaction and nutrients (Tichý et al. 2023), as well as indicator values for water level based on both vascular plants and bryophytes (Hájek et al. 2020). Differences in mean indicator values among clusters were tested using the Kruskal-Wallis non-parametric test, followed by pairwise Mann-Whitney tests with Bonferroni correction. All analyses were conducted in Past 4 (Hammer et al. 2001).

To visualize the position of the clusters along compositional gradients, Detrended correspondence analysis (DCA) was performed in Canoco 5 (Šmilauer & Lepš 2014). To interpret the first two ordination axes ecologically, we calculated Spearman's rank correlations between axes with EIV values. Maps were created in ArcGIS 10.8.2. The following sources were used as basemaps: World Imagery (<https://services.arcgis.com>).

3. Results

3.1 Cluster analysis

Our classification resulted in five clusters, defined by the following species:

Cluster 1

9 relevés (Table 1, Fig. 1–2)

Diagnostic species: *Blackstonia perfoliata*, *Briza media*, *Carex distans*, *C. paniculata*, *Cirsium appendiculatum*, *Dactylorhiza maculata* agg., *Didymodon tophaceus*, *Epilobium parviflorum*, *Epipactis palustris*, *Equisetum ramosissimum*, *Holcus lanatus*, *Juncus articulatus*, *J. inflexus*, *Lathyrus pratensis*, *Linum catharticum*, *Molinia caerulea* agg., *Ononis spinosa*, *Parnassia palustris*, *Philonotis calcarea*, *Pinguicula hirtiflora*, *Schedonorus arundinaceus*, *Trifolium pratense*, *Tussilago farfara*.

Constant species: *Agrostis stolonifera*, *Briza media*, *Carex distans*, *C. paniculata*, *Cirsium appendiculatum*, *Dactylorhiza maculata* agg., *Didymodon tophaceus*, *Epilobium parviflorum*, *Holcus lanatus*, *Juncus articulatus*, *J. inflexus*, *Molinia caerulea* agg., *Ononis spinosa*, *Palustriella commutata* agg., *Parnassia palustris*, *Philonotis calcarea*, *Pinguicula hirtiflora*, *Tussilago farfara*.

This cluster comprises exclusively our original relevés from the Pindus Mountains in Greece. It is characterised by the frequent occurrence of *Pinguicula hirtiflora*, alongside species typical of calcareous springs (*Palustriella commutata*, *Philonotis calcarea*, as well as some light-demanding species overlapping to calcareous fens (e.g. *Blysmus compressus*, *Carex flacca*, *Parnassia palustris*), which contribute to the highest mean EIVs for light. Balkan and sub-Mediterranean species with an ecological optimum outside of springs and fens also occur in this cluster (e.g., *Blackstonia perfoliata*, *Cirsium appendiculatum*). While our data originate from Greece, similar non-fen spring vegetation featuring *Pinguicula hirtiflora* and *Palustriella commutata* has also been observed in Albania, eastern Montenegro, and Herzegovina (L. Shuka, D. Stešević, P. Lazarević & D. Milanović, unpubl. data).

Table 1. A shortened synoptic table shows the percentage constancy of species in five clusters. Diagnostic species are sorted by decreasing fidelity measured with the phi-coefficient. Species with a *phi*-value greater than 0.25 are considered diagnostic and shaded by light grey colour; species with a *phi*-value greater than 0.5 are considered highly diagnostic and shaded by dark grey colour. Species highly diagnostic or diagnostic in one cluster are accepted as diagnostic for associations. Species with a constancy of 15% or less in all individual columns are not shown in the table.

Tabelle 1. Stetigkeitstabelle der fünf unterschiedenen Cluster. Diagnostische Arten sind nach abnehmender Treue auf Basis der Phi-Koeffizienten sortiert. Hellgrau hinterlegte Arten mit einem *Phi*-Wert größer als 0,25 sind diagnostisch, dunkelgrau hinterlegte Arten mit einem *Phi*-Wert größer als 0,5 sind hochgradig diagnostisch. Arten mit 15 % Steigkeit oder weniger in einer Spalte sind nicht angezeigt.

Cluster ID	1	2	3	4	5
Number of relevés	9	76	15	7	18
Range of relevé area (m ²)	2–10	0.3–25	2–12	4–16	1–16
Mean relevé area (m ²)	7	7	5	9	5
Ass. <i>Pinguiculo hirtiflorae</i>-Cratoneuretum commutati					
<i>Pinguicula hirtiflora</i>	78	.	.	.	.
<i>Juncus articulatus</i>	89	5	.	14	.
<i>Carex distans</i>	67	.	.	.	6
<i>Briza media</i>	56	.	.	.	.
<i>Dactylorhiza maculata</i> agg.	56	1	.	.	.
<i>Ononis spinosa</i>	44	.	.	.	.
<i>Cirsium appendiculatum</i>	44	.	.	.	.
<i>Carex paniculata</i>	44	1	.	.	.
<i>Holcus lanatus</i>	44	1	.	.	.
<i>Tussilago farfara</i>	89	18	.	29	22
<i>Epilobium parviflorum</i>	67	11	.	29	.
<i>Epipactis palustris</i>	33	.	.	.	.
<i>Blackstonia perfoliata</i>	33	.	.	.	.
<i>Trifolium pratense</i>	33	.	.	.	.
<i>Schedonorus arundinaceus</i>	33	.	.	.	.
<i>Parnassia palustris</i>	56	1	.	29	6
Ass. <i>Brachythecio rivularis</i>-Cratoneuretum commutati subass. <i>Brachythecio rivularis</i> - <i>Cratoneuretum commutati typicum</i>					
<i>Geranium robertianum</i>	.	46	33	.	11
<i>Plagiomnium undulatum</i>	.	30	40	.	6
Subass. <i>Brachythecio rivularis</i>-Cratoneuretum commutati rhynchostegietosum riparioidis					
<i>Rhynchostegium riparioides</i>	.	3	73	.	.
<i>Hygroamblystegium tenax</i>	.	3	53	.	6
Ass. <i>Cochleario pyrenaicae</i>-Cratoneuretum commutati					
<i>Cochlearia pyrenaica</i>	.	.	.	86	.
<i>Mentha longifolia</i>	11	13	7	86	.
<i>Deschampsia cespitosa</i>	.	12	.	86	22
<i>Carex flava</i> agg.	.	11	.	71	28
<i>Potentilla erecta</i>	.	.	.	57	.
<i>Festuca heterophylla</i>	.	.	.	43	.
<i>Pinguicula vulgaris</i> agg.	.	.	.	43	.

Cluster ID	1	2	3	4	5
Ass. <i>Eucladietum verticillati</i>					
<i>Eucladium verticillatum</i>	22	25	7	14	100
All. <i>Lycopodo europaei-Cratoneurion commutati</i>/Ord. <i>Montio-Cardaminetalia</i>					
<i>Philonotis calcarea</i>	44	8	13	.	.
<i>Apopellia endiviifolia</i>	11	46	67	14	44
<i>Ptychostomum pseudotriquetrum</i> agg.	33	42	2	86	33
<i>Carex flacca</i>	33	7	.	29	22
<i>Didymodon tophaceus</i>	44	11	.	.	17
<i>Conocephalum conicum</i>	.	21	2	.	.
<i>Bellidiastrum michelii</i>	.	.	.	.	17
<i>Cratoneuron filicinum</i>	33	3	4	29	33
<i>Palustriella commutata</i> agg.	100	84	2	100	67
Cl. <i>Montio-Cardaminetia</i>					
<i>Caltha palustris</i>	.	16	.	.	.
<i>Cardamine amara</i> agg.	.	29	13	14	.
<i>Brachythecium rivulare</i>	11	38	4	43	6
<i>Chaerophyllum hirsutum</i>	.	18	.	14	.
<i>Chrysosplenium alternifolium</i>	.	5	33	.	.
Other taxa with high frequency					
<i>Agrostis stolonifera</i>	67	41	60	57	28
<i>Eupatorium cannabinum</i>	11	26	13	86	50
Other taxa					
<i>Lactuca muralis</i>	.	22	13	.	17
<i>Veronica beccabunga</i>	.	21	7	.	11
<i>Urtica dioica</i>	.	14	40	.	6
<i>Ranunculus repens</i>	.	16	20	14	6
<i>Equisetum arvense</i>	11	12	7	43	11
<i>Molinia caerulea</i> agg.	56	5	.	.	39
<i>Marchantia polymorpha</i>	.	9	20	29	6
<i>Calliergonella cuspidata</i>	11	11	.	29	6
<i>Equisetum palustre</i>	22	9	.	14	.
<i>Juncus inflexus</i>	44	3	7	29	6
<i>Mentha aquatica</i>	.	5	27	.	11
<i>Bidens frondosa</i>	.	5	7	.	28
<i>Aneura pinguis</i>	22	9	.	.	.
<i>Festuca rubra</i> agg.	22	4	.	29	6
<i>Carex panicea</i>	.	4	.	43	6
<i>Lycopus europaeus</i>	.	4	.	.	22
<i>Linum catharticum</i>	33	4	.	.	6
<i>Sesleria caerulea</i>	.	1	.	14	22
<i>Leontodon hispidus</i>	11	.	.	29	6
<i>Calamagrostis varia</i>	.	3	.	29	.
<i>Primula farinosa</i>	.	.	.	29	6
<i>Lathyrus pratensis</i>	22	.	.	.	.
<i>Equisetum ramosissimum</i>	22	.	.	.	.



Fig. 1. Examples of *Lycopodo europaei-Cratoneurion commutati* communities from the study area. **a)** *Pinguicula hirtiflorae-Cratoneuretum commutati* in the Cijevna river gorge (Montenegro), **b)** *Brachythecio rivularis-Cratoneuretum commutati typicum* on travertine rocks in Strypa river valley near Rukomysh village (Ukraine), **c)** *Brachythecio rivularis-Cratoneuretum commutati rhyncho-stegietosum riparioidis* on travertine rocks in the Dniester river valley near Deleva village (Ukraine), **d)** *Cochleario pyrenaicae-Cratoneuretum commutati* near Bukovinka in the Velká Fatra Mts., **e)** *Eucladietum verticillati* on travertine rocks on Dniester river valley near Isakiv village (Ukraine). (Photos: a) D. Stešević, 30/06/2025; b) S. Nyporko, 12/06/2023; c) S. Nyporko, 01/08/2023; d) M. Hájek, 26/05/2019; e) S. Nyporko, 01/08/2023).

Abb. 1. Beispiele für *Lycopodo europaei-Cratoneurion commutati*-Gesellschaften aus dem Untersuchungsgebiet. **a)** *Pinguicula hirtiflorae-Cratoneuretum commutati* in der Cijevna-Flussschlucht (Montenegro), **b)** *Brachythecio rivularis-Cratoneuretum commutati typicum* auf Travertinfelsen im Strypa-Flusstal bei Rukomysh (Ukraine), **c)** *Brachythecio rivularis-Cratoneuretum commutati rhyncho-stegietosum riparioidis* auf Travertinfelsen im Dniester-Flusstal bei Deleva (Ukraine), **d)** *Cochleario pyrenaicae-Cratoneuretum commutati* bei Bukovinka in den Velká-Fatra-Bergen, **e)** *Eucladietum verticillati* auf Travertinfelsen im Dniester-Flusstal bei Isakiv (Ukraine). Für die Bildautoren siehe die englische Abbildungsunterschrift.

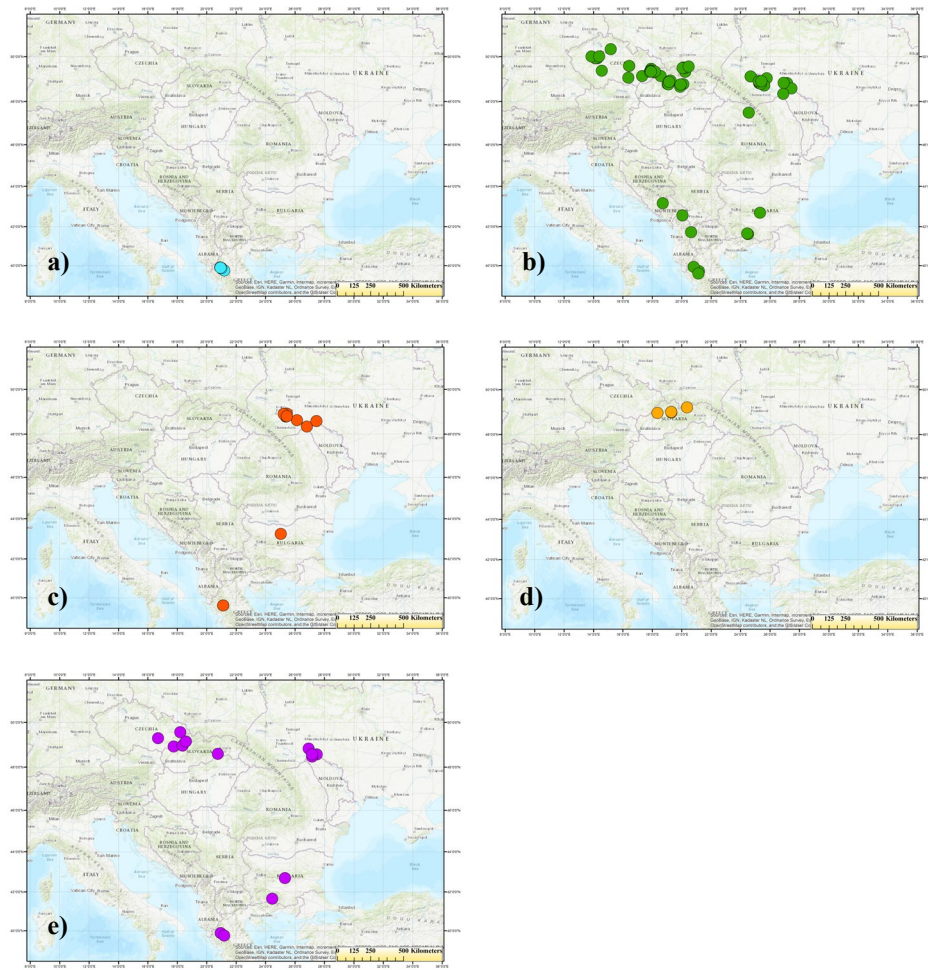


Fig. 2. Spatial distribution of the relevés belonging to the *Lycopodo europaei*-*Cratoneurion commutati*. **a)** *Pinguicula hirtiflorae*-*Cratoneuretum commutati*, **b)** *Brachythecio rivularis*-*Cratoneuretum commutati typicum*, **c)** *Brachythecio rivularis*-*Cratoneuretum commutati rhynchostegietosum riparioidis*, **d)** *Cochleario pyrenaicae*-*Cratoneuretum commutati*, **e)** *Eucladietum verticillati*.

Abb. 2. Räumliche Verteilung der Aufnahmen der Gesellschaften des *Lycopodo europaei*-*Cratoneurion commutati*. **a)** *Pinguicula hirtiflorae*-*Cratoneuretum commutati*, **b)** *Brachythecio rivularis*-*Cratoneuretum commutati typicum*, **c)** *Brachythecio rivularis*-*Cratoneuretum commutati rhynchostegietosum riparioidis*, **d)** *Cochleario pyrenaicae*-*Cratoneuretum commutati*, **e)** *Eucladietum verticillati*.

Cluster 2

76 relevés (Table 1, Fig. 1–2)

Diagnostic species: *Caltha palustris*, *Geranium robertianum*.

Constant species: *Agrostis stolonifera*, *Apopellia endiviifolia*, *Brachythecium rivulare*, *Geranium robertianum*, *Palustriella commutata* agg., *Ptychostomum pseudotriquetrum* agg.

This community occurs at an elevations ranging from 120 to 1500 m a.s.l. and typically colonizes rocks with slopes of 60–90°. The vegetation is usually shaded. Relevés originate from Slovakia, Czech Republic, Romania, Bulgaria, North Macedonia, Montenegro, Greece, and Ukraine (Fig. 2b). In western Ukraine, this vegetation was found within Dniester River Valley within the Chernivtsi, Ternopil, and Ivano-Frankivsk regions occurring in deciduous forests at an elevation at 120–255 m a.s.l. on cascade, stream crust, and dam types of tufa developed on Devonian sandstones. Along with cluster 3, this community is characterised by higher nutrient demanding vascular plants compared to the other clusters.

Cluster 3

15 relevés (Table 1, Fig. 1–2)

Diagnostic species: *Chrysosplenium alternifolium*, *Hygroamblystegium tenax*, *Rhynchostegium riparioides*, *Urtica dioica*.

Constant species: *Agrostis stolonifera*, *Apopellia endiviifolia*, *Brachythecium rivulare*, *Cratoneuron filicinum*, *Hygroamblystegium tenax*, *Plagiomnium undulatum*, *Rhynchostegium riparioides*, *Urtica dioica*.

This community occurs at 112–1000 m a.s.l. in shaded locations with slopes of 5–60° within the forest zone. In contrast to the previous cluster, relevés of this community include nutrient-demanding bryophytes such as *Rhynchostegium riparioides*, *Hygroamblystegium tenax*, *Cratoneuron filicinum*, *Plagiomnium undulatum*, and *Oxyrhinchium hians*, rather than *Palustriella commutata*. For the vascular plant layer, the mean Ellenberg indicator values for nutrients were the highest among all clusters, though not significantly different from the cluster 2. The vegetation of this cluster has been recorded in Ukraine and Czech Republic, Slovakia, Bulgaria, and Greece (Fig. 2c). In western Ukraine, it occurs within the Dniester River Valley and its tributaries in Kmlenytskyi, Ternopil and Ivano-Frankivsk regions in deciduous forests at an elevation of 110–280 m a.s.l. on dam type tufa formed on Devonian sandstones.

Cluster 4

7 relevés (Table 1, Fig. 1–2)

Diagnostic species: *Calamagrostis varia*, *Carex flava* agg., *C. panicea*, *Cochlearia pyrenaica*, *Deschampsia cespitosa*, *Equisetum arvense*, *Eupatorium cannabinum*, *Festuca heterophylla*, *Mentha longifolia*, *Pinguicula vulgaris* agg., *Potentilla erecta*, *Primula farinosa*, *Ptychostomum pseudotriquetrum* agg.

Constant species: *Agrostis stolonifera*, *Brachythecium rivulare*, *Carex flava* agg., *C. panicea*, *Cochlearia pyrenaica*, *Deschampsia cespitosa*, *Equisetum arvense*, *Eupatorium cannabinum*, *Festuca heterophylla*, *Mentha longifolia*, *Palustriella commutata* agg., *Pinguicula vulgaris* agg., *Potentilla erecta*, *Ptychostomum pseudotriquetrum* agg.

This cluster comprises relevés with *Cochlearia pyrenaica* and *Palustriella commutata* and has been recorded only in two regions of Slovakia. The first region is located at northeastern foothills of the Great Fatra Mountains (Bukovinka, Bukovina and Jazierske

travertíny sites), and the second in the Spiš basin at eastern foothills of the High Tatra Mountains (Dítě et al. 2016). Elevations range from 380 to 730 m a.s.l., and slopes from 10° to 80°. The sites are relatively open, favoring light-demanding species generally limiting shade-tolerant species. At the Bukovinka site in the Great Fatra Mountains, the community is developed at the interface with fen vegetation, but occurs on thick, hard tufa that is not intermixed with peat. Nevertheless, the proximity to fen habitats, good light conditions, and low nutrient availability allow some fen species – such as *Parnassia palustris*, *Primula farinosa*, and *Carex flava* agg. – to appear in the relevés. In addition to relevés from the Great Fatra and High Tatra Mountains, one relevé from the Strážovské Mountains lacking *Cochlearia pyrenaica* was included in this cluster, likely due to the presence of light-demanding species.

Cluster 5

18 relevés (Table 1, Fig. 1–2)

Diagnostic species: *Bellidiastrum michelii*, *Bidens frondosa*, *Eucladium verticillatum*, *Lycopus europaeus*.

Diagnostic species do not occur in Ukraine: *Bellidiastrum michelii*.

Constant species: *Apopellia endiviifolia*, *Eucladium verticillatum*, *Eupatorium cannabinum*, *Molinia caerulea* agg., *Palustriella commutata* agg.

This community, characterised by the dominance of *Eucladium verticillatum*, occurs at elevations of 115–1400 m a.s.l. on slopes facing from east to south-west. It occupies open, sun-exposed tufa rocks, mainly with inclinations of 40–80°. Based on the highest mean Ellenberg indicator values for reaction in vascular plants, this community prefers springs with the most intense tufa precipitation. Relevés of this cluster have been recorded in Ukraine (one relevé), Slovakia, Czech Republic, Bulgaria, and Greece (Fig. 2e). In Ukraine, the community was observed only in the Dniester River Valley within the Khmelyntskyi region at 115 m a.s.l. occurring on cascade-type tufa over Devonian sandstone bedrock.

3.2 Floristic gradients in relation to the classification and environmental conditions

In the DCA, along axes 1 and 2, clusters 1 and 3–4 formed clearly distinct outgroups, while cluster 2 was located in the center, partially overlapping with clusters 3–5 (Fig. 3). The first DCA axis ranging from cluster 1 to 3 was most strongly negatively correlated with mean Ellenberg indicator values for light and positively correlated with mean Ellenberg indicator values for nutrients and temperature. The second axis, ranging from cluster 2 to the moss-dominated cluster 5, was primarily correlated with temperature and reaction. Mean Ellenberg indicator values for light, nutrients, temperature and reaction differed significantly among clusters (Fig. 3): cluster 1 showed the highest light values, clusters 2–3 the highest nutrient values, and cluster 5 the highest reaction values. No significant differences were observed for temperature or water level.

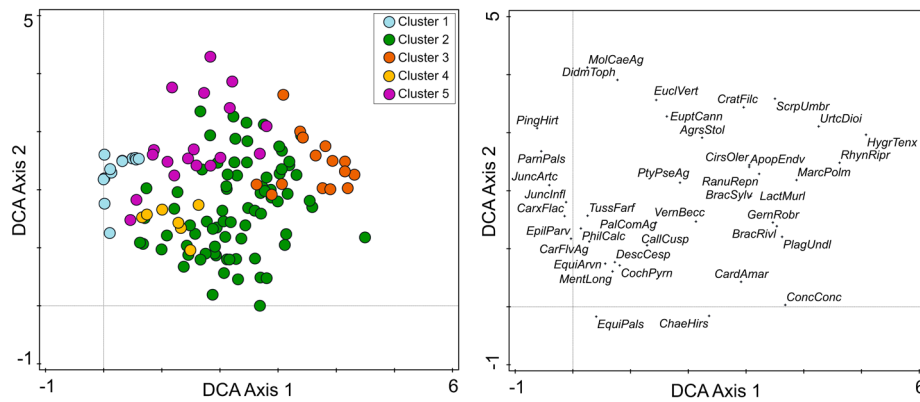


Fig. 3. DCA ordination of the *Lycopodo europaei*-*Cratoneurion commutati* associations. Eigenvalue axis 1: 0.586 (3.4% explained variation), axis 2: 0.446 (2.6%), axis 3: 0.347 (2.0%). 40 species with the largest weight are shown. Cluster 1 – *Pinguicula hirtiflorae*-*Cratoneurion commutati*, cluster 2 – *Brachythecio rivularis*-*Cratoneurion commutati typicum*, cluster 3 – *Brachythecio rivularis*-*Cratoneurion commutati rhynchostegietosum riparioidis*, cluster 4 – *Cochleario pyrenaicae*-*Cratoneurion commutati*, cluster 5 – *Eucladium verticillati*.

Abb. 3. DCA-Ordination der Assoziationen des *Lycopodo europaei*-*Cratoneurion commutati*. Eigenwert Achse 1: 0,586 (3,4 % erklärte Varianz), Achse 2: 0,446 (2,6 %), Achse 3: 0,347 (2,0 %). Diejenigen 40 Arten mit dem größten Gewicht sind gezeigt. Für die den Clustern entsprechenden Assoziationen siehe die englische Abbildungsunterschrift.

Abbreviations: AgrsStol = *Agrostis stolonifera*, ApopEndv = *Apopellia endiviifolia*, BracRivl = *Brachythecium rivulare*, BracSylv = *Brachypodium sylvaticum*, CallCusp = *Calliergonella cuspidata*, CardAmar = *Cardamine amara*, CarFlvAg = *Carex flava* agg., CarxFlac = *C. flacca*, ChaeHirs = *Chaerophyllum hirsutum*, CirsOle = *Cirsium oleraceum*, CochPyr = *Cochlearia pyrenaica*, ConcConc = *Conocephalum conicum*, CratFilc = *Cratoneuron filicinum*, DescCesp = *Deschampsia cespitosa*, DidmToph = *Didymodon tophaceus*, EpilParv = *Epilobium parviflorum*, EquiArvn = *Equisetum arvense*, EquiPals = *E. palustre*, EuclVert = *Eucladium verticillatum*, EupatCann = *Eupatorium cannabinum*, GernRobr = *Geranium robertianum*, HygrTenx = *Hygroamblystegium tenax*, JuncArtc = *Juncus articulatus*, JuncInfl = *J. inflexus*, LactMurl = *Lactuca muralis*, MarcPolm = *Marchantia polymorpha*, MentLong = *M. longifolia*, MolCaeAg = *Molinia caerulea* agg., PalComAg = *Palustriella commutata* agg., ParnPals = *Parnassia palustris*, PhilCalc = *Philonotis calcarea*, PingHirt = *Pinguicula hirtiflora*, PlagUndl = *Plagiomnium undulatum*, PtyPseAg = *Ptychostomum pseudotriquetrum* agg., RanuRepn = *Ranunculus repens*, RhynRipr = *Rhynchostegium riparioides*, ScrpUmbr = *Scrophularia umbrosa*, TussFarf = *Tussilago farfara*, UrtcDioi = *Urtica dioica*, VernBecc = *Veronica beccabunga*

4. Discussion

4.1 Interpretations

4.1.1 Syntaxonomical interpretations and proposed syntaxonomical scheme

Three of the identified clusters correspond well with traditionally recognized associations, whereas two others do not, despite being clearly delineated by the initial unsupervised methods. One of these clusters, characterized by *Rhynchostegium riparioides*, is compositionally similar to the *Brachythecio rivularis-Cratoneuretum commutati* and lacks exclusive diagnostic species. Consequently, we formally describe it as a new subassociation. The second cluster is well delimited biogeographically and compositionally and includes the exclusive diagnostic species *Pinguicula hirtiflora*. Accordingly, we formally describe this vegetation as a new association.

Overall, we propose the following syntaxonomical scheme with association numbers corresponding to the number of clusters:

Montio-Cardaminetea Br.-Bl. et Tx 1943

Montio-Cardaminetalia Pawlowski 1928 (Syn. *Cardamino-Cratoneuretalia* Maas 1959)

Lycopodo europaei-Cratoneurion commutati Hadač 1983

1. *Pinguiculo hirtiflorae-Cratoneuretum commutati*, ass. nova hoc loco
2. *Brachythecio rivularis-Cratoneuretum commutati* Dierßen 1973, *Brachythecio rivularis-Cratoneuretum commutati typicum*
3. *Brachythecio rivularis-Cratoneuretum commutati rhynchostegietosum riparioidis* subass. nova hoc loco
4. *Cochleario pyrenaicae-Cratoneuretum commutati*. Th. Müller 1961
5. *Eucladietum verticillati* Allorge ex Braun 1968

4.1.2 Nomenclatural types

***Brachythecio rivularis-Cratoneuretum commutati rhynchostegietosum riparioidis* subass. nova**

Holotypus *hoc loco* (Supplement E1 & E2, relevé No 6)

Locality: Skomorokhy village, Ternopil region, Ukraine. N 48.91780, E 25.40510. Authors: I. Vasheniak and S. Nyporko. Date of recording: 13.06.2023. Plot size: 4 m². Elevation: 232 m. Aspect: 172°. Slope: 60°. Total vegetation cover (E): 50%. Herb layer (E₁): 10%. Bryophyte layer (E₀): 40%.

E₁: *Aegopodium podagraria* 1, *Cardamine amara* agg. +, *Chrysosplenium alternifolium* +, *Galium aparine* 1, *Geranium robertianum* 1, *Lactuca muralis* +, *Myosoton aquaticum* +, *Poa nemoralis* +, *Poa palustris* 1; E₀: *Apopellia endiviifolia* 1, *Brachythecium rivulare* 2, *Cratoneuron filicinum* 3, *Hygroamblystegium tenax* 1, *Marchantia polymorpha* +, *Palustris triella commutata* 1, *Plagiomnium undulatum* +, *Rhynchostegium riparioides* 1 (cover code: Braun-Blanquet scale, old).

***Pinguicula hirtiflorae*-*Cratoneuretum commutati* ass. nova**

Holotypus *hoc loco* (Supplement E1 & E2, relevé No 17)

Locality: 1.5 km SE of Elatochori village, Greece. N 39.86055, E 20.98750. Authors: M. Hájek., P. Hájková. Date of recording: 04.07.2000. Plot size: 2 m². Elevation: 1000 m, Aspect: Not available. Slope: 20°. Total vegetation cover (E): 60%. Herb layer (E₁): 40%. Bryophyte layer (E₀): 50%.

E₁: *Agrostis stolonifera* 2a, *Blackstonia perfoliata* +, *Briza media* +, *Carex distans* r, *Dactylorhiza saccifera* +, *Epilobium parviflorum* +, *Epipactis palustris* +, *Equisetum palustre* 1, *E. ramosissimum* 2a, *Holcus lanatus* 1, *Juncus articulatus* +, *J. inflexus* 1, *Ononis spinosa* 2a, *Pinguicula hirtiflora* 1, *Pinus* sp. +, *Salix purpurea* +, *Schedonorus arundinaceus* 1, *Trifolium ochroleucon* +, *Tussilago farfara* +; E₀: *Didymodon tophaceus* 2a, *Eucladium verticillatum* 2a, *Palustriella commutata* 3 (cover code: Braun-Blanquet scale, new).

4.1.3 Ecological interpretation of the principal floristic gradients

The first DCA gradient extend from the *Pinguicula hirtiflorae*-*Cratoneuretum commutati* to the *Brachythecio rivularis*-*Cratoneuretum commutati rhynchostegietosum riparioidis* with the other syntaxa inbetween. The former association showed the lowest indicator values for nutrients (EIV-N) and the latter sccociation the highest. In addition, mean EIV-N was strongest strongest correlated with the first DCA axis. We therefor conclude that nutrients were the strongest driver for vegetation differentiation in our study. Temperature and elevation were also correlated with the first axis, reflecting climatic differences mainly between Ukraine and Southeastern Europe. Interestingly, the mean indicator value for light was negatively correlated with the first DCA axis, indicating a shift from well-lit conditions at lower axis values toward comparatively more shaded conditions at higher values. It should be noted that the unmeasured, but presumably higher, discharge and water flow velocity in the *Brachythecio rivularis*-*Cratoneuretum commutati rhynchostegietosum riparioidis* may also strongly contribute to the differentiation of the vegetation.

The second DCA axis correlates with Ellenberg indicator values for light, temperature, and reaction (pH). It separates moss-rich communities on consolidated calcareous tufa with *Eucladium verticillatum* and *Didymodon tophaceus* from communities with higher biomass of vascular plants (*Caltha palustris*, *Cardamine amara*, *Chaerophyllum hirsutum*) and shade-tolerant bryophytes (*Conocephalum conicum*), which develop on less intensely tufaceous substrates and represent transitional stages between the *Brachythecio rivularis*-*Cratoneuretum commutati* and other spring communities.

The third axis correlates positively with Ellenberg indicator values for nutrients and partly differentiates vegetation of strongly tufaceous springs – from the low-productive *Eucladietum verticillati* to the more productive *Brachythecio rivularis*-*Cratoneuretum commutati rhynchostegietosum riparioidis* with nutrient-demanding species such as *Mentha aquatica*, *Scrophularia umbrosa*, and *Marchantia polymorpha*.

4.2 General syntaxonomical overview

4.2.1 *Lycopodo europaei-Cratoneurion commutati* communities in Central and South-eastern Europe

While the higher-rank classification of calcareous springs at the alliance level and above is approaching consensus (Mucina et al. 2016, Peterka et al. 2023), relatively few studies have addressed classifications at lower hierarchical levels. Within the alliance *Lycopodo europaei-Cratoneurion commutati*, Dierßen (1973) described the association *Brachythecio rivularis-Cratoneuretum commutati* from shaded springs of the Weser River Uplands in NW-Central Germany from about 200 m a.s.l. Open low-elevation springs have sometimes been classified as *Cratoneuretum filicino-commutati* (Kuhn 1937) Oberdorfer 1977. However, according to the Code of Phytosociological Nomenclature (Theurillat et al. 2021), this is a homotypic synonym of the *Brachythecio rivularis-Cratoneuretum commutati* Dierßen 1973 (i.e. *nomen superfluum*), because Oberdorfer (1977) included the older name *Brachythecio rivularis-Cratoneuretum commutati* Dierßen 1973 among synonyms of *Cratoneuretum filicino-commutati*, and Kuhn's original description is invalid, as he referred to a "community" (*Gesellschaft*), rather than formally describing an association. For these reasons, the name *Cratoneuretum filicino-commutati* is synonymous to the name *Brachythecio rivularis-Cratoneuretum commutati*, and open low-elevation springs should be classified under other associations.

In our study, two clusters exhibited a higher number of light-demanding taxa. The *Pinguicula hirtiflorae-Cratoneuretum commutati* is clearly delimited within the *Lycopodo-Cratoneurion* alliance and includes the exclusively diagnostic taxon *Pinguicula hirtiflora*. This taxon occasionally transitions to fens, but less frequently than *P. vulgaris* or *P. balcanica*, showing a clear optimum on hard substrates such as wet rocks or compact tufa. Although it occurs at higher elevations than other associations of the alliance, this association lacks most taxa diagnostic of *Cratoneurion commutati* such as *Bellidiastrum michelii*, *Arabis soyeri*, *Saxifraga aizoides*, *Pinguicula alpina*, *Tofieldia calyculata* and *Carex frigida* (compare Peterka et al. 2023) and was predominantly classified as *Lycopodo-Cratoneurion commutati* in the previous pan-European synthesis (Peterka et al. 2023). When continued succession associated with peat accumulation continues, the community develops into the *Caricion davallianae* alliance. The second cluster comprising light-demanding and even fen taxa was interpreted as *Cochleario pyrenaicae-Cratoneuretum commutati*. This association has also been reported from Slovakia by previous authors (Valachovič & Kochjarová 2000, Valachovič 2001, Kliment et al. 2008, Dítě et al. 2016). The association was originally described from Germany, where Hinterlang (2017) reported its occurrence in light-exposed, strongly calcareous, nutrient-poor springs. In Ukraine, the diagnostic taxon *Cochlearia pyrenaica* occurs at a single site whose description (Yurechko 2019) suggests that the vegetation with *C. pyrenaica* belongs to fen communities. In the Eastern Carpathians, near the Ukrainian border, the populations formerly sometimes identified as *C. pyrenaica* were found to belong to the separate taxon *C. borzeana* (Kochjarová et al. 2019). We therefore conclude that the *Cochleario pyrenaicae-Cratoneuretum commutati* does not occur in Ukraine.

Another association name which may refer, at least in part, to light-demanding vegetation of calcareous springs was introduced by Kornaś & Medwecka-Kornaś (1967), who validly described the *Cardamino-Cratoneuretum* from an elevational range of 800–1245 m a.s.l. in the Gorce Mountains (Poland). Its diagnostic species – *Ptychostomum pseudotriquetrum*, *Cardamine amara*, *Palustriella commutata* – represent a similar set of diagnostic

taxa as in the case of *Brachythecio rivularis-Cratoneuretum commutati*. In terms of overall species composition, this association represents a transitional vegetation type between the high-mountain springs of *Cratoneurion commutati* and the low-elevation springs of *Lycopodo europaei-Cratoneurion commutati*. Like the *Cratoneurion commutati*, it is characterized by a low amount of precipitated carbonate. Warmth-demanding species that prefer solid carbonates, such as *Eucladium verticillatum*, *Fissidens gracilifolius*, or *Didymodon tophaceus* are absent. At the same time, some montane – but not alpine – taxa occur (e.g. *Chaerophyllum hirsutum*, *Epilobium alsinifolium*, *Petasites albus*, *P. kablikianus*, *Stellaria nemorum*, *Viola biflora*). Our analysis did not provide support for distinguishing this association in our dataset, with most relevés assigned to the *Brachythecio rivularis-Cratoneuretum commutati*. If the *Cardamino-Cratoneuretum* were treated as a heterotypic synonym of the *Brachythecio rivularis-Cratoneuretum commutati*, it would constitute an older and therefore valid name. Nevertheless, because montane springs corresponding to *Cardamino-Cratoneuretum* were underrepresented in our dataset, we consider such a decision premature and continue to recognize the rationale for distinguishing between the two latter associations.

Regarding shade-tolerant communities, they clearly divided into two types: those dominated strongly by *Eucladium verticillatum* at the most extreme sites – very calcium-rich, with hard tufas up to 90 degrees of inclination; the *Eucladietum verticillati* association, and the more widespread community of shaded springs – the *Brachythecio rivularis-Cratoneuretum commutati*. The latter corresponds to the central association concept by Dierschke (1988). Our results, however, provide clear support for recognizing two distinct subassociations within the *Brachythecio rivularis-Cratoneuretum commutati*.

In addition to the typical subassociation, the subassociation *rhynchostegietosum riparioidis* is formally described here. This community represents the transition between the *Montio-Cardaminetea* and *Platyhypnidio-Fontinalietea antipyreticae* Philippi 1956 – the latter traditionally described as a bryocoenosis (i.e., moss community based on very small plots, excluding vascular plants), and treated syntaxonomically independently of other Braun-Blanquet system syntaxa (Mucina et al. 2016). The diagnostic species of *Platyhypnidio-Fontinalietea antipyreticae* largely overlap with those of *Montio-Cardaminetea* and are strongly represented within this cluster including *Brachythecium rivulare*, *Rhynchostegium riparioides*, and *Marchantia polymorpha*.

Because these communities contain vascular plants typical of freshwater wetlands, including springs and streams (e.g. *Agrostis stolonifera*, *Berula erecta*, *Mentha aquatica*) and considering the plot sizes used in our study, we opted to classify them within the *Montio-Cardaminetea*. Similarly, Lyons & Kelly (2017) identified the same vegetation type in Ireland, using a comparable sampling approach, classifying it only at the community level (*Brachythecium rivulare-Platyhypnidium riparioides* tufaceous streams and flushes), rather than as an association. The diagnostic species largely overlap between Ireland and Southeastern to Eastern Europe, indicating an oceanic-submediterranean distribution and supporting recognition of this vegetation as a formally defined syntaxonomic unit. Because the diagnostic species of this cluster largely coincide with those of the *Brachythecio rivularis-Cratoneuretum commutati*, and no taxon occurs frequently enough to serve as an exclusive diagnostic species, we decided not to treat it as separate association. However, we suggest that depauperate variants of this vegetation type – lacking *Cratoneuron/Palustriella* species and vascular plants with affinity to springs – be classified within the moss communities of *Platyhypnidio-Fontinalietea antipyreticae* Philippi 1956.

4.2.2 *Lycopodo europaei-Cratoneurion commutati* communities in Western Ukraine

The three out of five communities delimited in this study and commented in the previous chapter occur in Western Ukraine in the Dniester Valley. Generally, all calcareous petrifying springs in the Dniester Valley are dominated by bryophytes and do not contain characteristic calcicole vascular plants (e.g. *Adiantum capillus-veneris*, *Blackstonia perfoliata*) unlike the analogue communities in sub-Mediterranean habitats. The vascular plants that occur in these springs are characteristic mainly of lowland wet grasslands (e.g. *Agrostis stolonifera*, *Lysimachia vulgaris*, *Molinia caerulea* agg.) and occur predominantly in spring fringes where they may cover more than 20% of surface. Contrary to other investigated regions, invasive plants (*Amorpha fruticosa*, *Bidens frondosus*, *Galinsoga quadriradiata*) also occurred in the calcareous petrifying springs in the Dniester Valley. Further differences against the Carpathians are that the calcareous petrifying springs in lowland western Ukraine occupy mainly cascade and dam tufas and contrary to Carpathians (Hájek et al. 2021) do not create mosaics with calcareous fens. Instead, they frequently occur in vertical locations on the steep walls, where only bryophytes can occur (Volic 2005, 2007).

The most specific communities in lowland western Ukraine, according to our analysis, belong to the *Brachythecio-Cratoneuretum rhynchostegietosum riparioidis* subassociation, where *Cratoneuron filicinum* occurs instead of *Palustriella commutata* which is more characteristic for the typical subassociation. We even frequently recorded the lack of *Palustriella commutata* in the above-mentioned communities. Notably, *Palustriella commutata* is a rare species in the lowland springs in Ukraine and is more typical of the mountainous regions (Virchenko & Nyporko 2022). Unexpectedly, the *Eucladietum verticillati* association as defined in our study appeared not widely distributed in the Dniester Valley unlike highly diagnostic species (*Eucladium verticillatum*) of this association (Zerov & Partyka 1975). According to our results, most localities of *Eucladium verticillati* occur in the Carpathian and Balkan Mountains (300–1400 m a.s.l.) and at the low-elevation level in Dniester Valley (Ukraine). Supposedly, these communities have formed only in isolated spots in the plains in the most extreme conditions, preventing the occurrence of nutrient-demanding species that characterise *Brachythecio rivularis-Cratoneuretum commutati rhynchostegietosum riparioidis* subassociation. Such places are rare and endangered. Furthermore, Didukh (2019) reported the occurrence of similar communities named as *Eucladio-Adiantetum capilli-veneris* association from the Crimean Mountains (Ukraine) within the *Adiantetea* class that could be considered as the *Eucladietum verticillati* association.

4.2.3 Habitat and ecological preferences of the *Lycopodo europaei-Cratoneurion commutati* communities

Communities of sciophilous to heliophilous calcareous springs of the *Lycopodo europaei-Cratoneurion commutati* occur on tufa substrates characterized by high calcium concentrations and elevated values of pH and alkalinity (Hadač 1983, Hájková & Hájek 2011, Peterka et al. 2023). Based on ecological indicator values, the differentiation of calcareous petrifying spring vegetation in Central to Southeastern Europe is primarily driven by light, nutrient availability and soil reaction (Table 2, Fig. 4). These factors appear to play a key role in structuring the vegetation of petrifying springs across Europe (Spitale et al. 2012, Lyons & Kelly 2017, 2025, Grootjans et al. 2021, Seiler et al. 2021).

Table 2. Spearman correlations between the DCA axes and environmental variables. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. The strongest correlations are highlighted in bold.

Tabelle 2. Spearman-Korrelationen zwischen den DCA-Achsen um Umweltvariablen. *** $p < 0,001$; ** $p < 0,01$; * $p < 0,05$. Die stärksten Korrelationen sind fett hervorgehoben.

Variable	axis 1	axis 2	axis 3
EIV Water level ($n = 129$)	-0.06 n.s.	-0.10 n.s.	-0.22*
EIV Light ($n = 121$)	-0.71***	0.18*	-0.22*
EIV Temperature ($n = 121$)	0.37***	0.60***	-0.09 n.s.
EIV Nutrients ($n = 125$)	0.73***	0.16 n.s.	-0.09 n.s.
EIV Soil reaction ($n = 127$)	-0.05 n.s.	0.49***	0.21*
Elevation ($n = 120$)	-0.58***	-0.38***	-0.04 n.s.

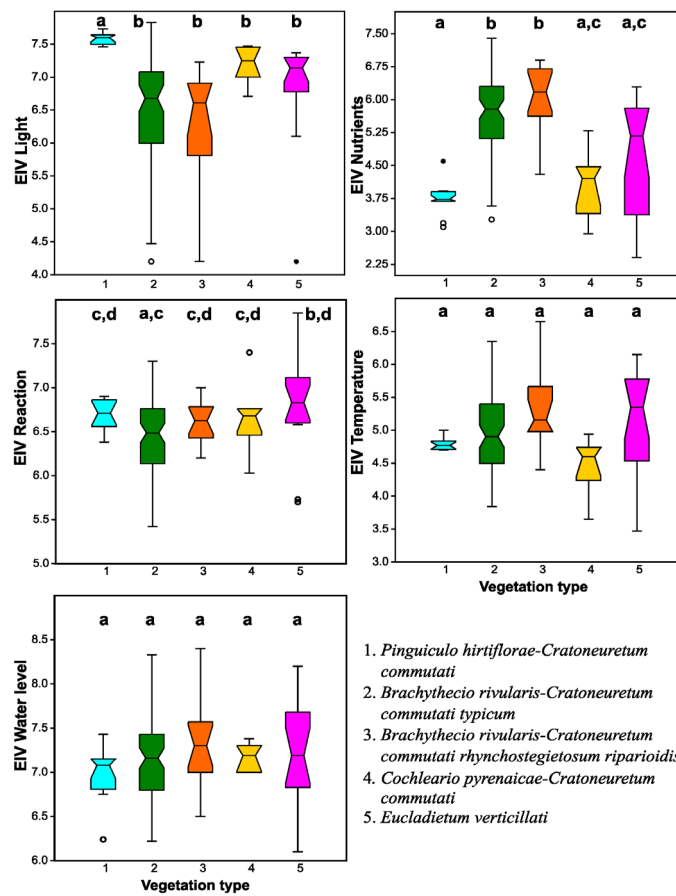


Fig. 4. Mean indicator values for light, nutrients, reaction, temperature, and moisture of five communities of the alliance *Lycopodo europaei*-*Cratoneurion commutati*. Boxplots show medians, interquartiles, extreme values, and outliers. Different letters indicate significant differences. Pairwise Mann-Whitney test with Bonferroni correction.

Abb. 4. Mittlere Zeigerwerte für Licht, Nährstoffe, Reaktion, Temperatur und Feuchtigkeit von fünf Gesellschaften des Verbands *Lycopodo europaei*-*Cratoneurion commutati*. Boxplots mit Medianen, Interquartilen, Extremwerten und Ausreißern. Unterschiedlichen Buchstaben zeigen signifikante Unterschiede an. Paarweise Mann-Whitney-Tests mit Bonferroni-Korrektur.

The *Brachythecio rivularis-Cratoneuretum commutati rhynchostegietosum riparioidis* showed the highest nutrient indicator values, although these did not differ significantly from the typical subassociation. It should be noted that indicator values for nutrients are not available for bryophytes (Tichý et al. 2023), so the calculation was based solely on vascular plants. When focusing on the bryophyte layer, the effect of increased nutrient availability in this subassociation becomes more apparent. Recent studies (de Mars et al. 2024, Lyons & Kelly 2025) demonstrate that diagnostic taxa of petrifying springs, such as *Palustriella commutata* and *Philonotis calcarea*, occur in waters extremely poor in nitrates and phosphates, whereas more generalistic taxa typical of *Rhynchostegietosum riparioidis* – including *Brachythecium rivulare*, *Cratoneuron filicinum*, *Rhynchostegium riparioides*, and *Oxyrrhynchium hians* – tend to indicate nutrient-enriched waters.

The heliophilous calcareous springs of the *Pinguiculo hirtiflorae-Cratoneuretum commutati*, *Cochleario pyrenaicae-Cratoneuretum commutati* and *Eucladietum verticillati* occur on the well-developed, open, sun-exposed, and often steep tufa cliffs. These communities exhibit the highest mean ecological values for light, although the difference was statistically significant compared to the *Brachythecio rivularis-Cratoneuretum commutati* only in the case of the *Pinguiculo hirtiflorae-Cratoneuretum commutati* (Fig. 4). According to Lyons & Kelly (2017, 2021), springs supporting *Eucladium verticillatum*, *Didymodon tophaceus*, and *Apopellia endiviifolia* occur on steep to vertical tufa surfaces with relatively high rates of tufa precipitation compared to the other communities of the *Lycopodo europaei-Cratoneurion commutati*. In Ukraine, however, these light-demanding and nutrient-deficient springs are either absent or extremely rare, often transitioning into *Brachythecio-Cratoneuretum rhynchostegietosum riparioidis* communities.

4.2.4 Implications for nature conservation and habitat management

Vegetation of calcareous petrifying springs is among the most threatened habitat types in Europe (Lyons & Kelly 2017, 2025, Grootjans et al. 2021, de Mars et al. 2024). Despite their inclusion in the EU Habitats Directive as habitat type 7220* “Petrifying springs with tufa formation” (Council Directive 92/43/EEC) and in the Bern Convention as C2.12 “Hard water springs” (Bern Convention 1979), conservation assessments and management measures are often applied uniformly, overlooking their pronounced ecological and floristic heterogeneity (Schaminée et al. 2016).

Our unified classification of the *Lycopodo europaei-Cratoneurion commutati* alliance highlights this heterogeneity by distinguishing five ecologically and functionally distinct vegetation units. These units differ in light availability, nutrient status, hydrological stability, and intensity of carbonate precipitation – factors known to structure calcareous petrifying spring vegetation (Spitale et al. 2012, Lyons & Kelly 2017, Peterka et al. 2023).

The *Brachythecio rivularis-Cratoneuretum commutati* represents the most widespread association of shaded calcareous petrifying springs. In contrast, the newly described sub-association *Brachythecio rivularis-Cratoneuretum commutati rhynchostegietosum riparioidis* is typically associated with high-flow spring outlets and small waterfalls. These communities are particularly sensitive to reductions in discharge or partial drying of spring outlets, which may rapidly trigger vegetation changes and lead to the degradation of habitat type 7220* (Lyons & Kelly 2017, 2025, de Mars et al. 2024).

In contrast, the more light-demanding associations – *Eucladietum verticillati*, *Cochleario pyrenaicae-Cratoneuretum commutati* and *Pinguiculo hirtiflorae-Cratoneuretum commutati* – are restricted to open tufa cliffs with intensive carbonate precipitation and low nutrient

availability. These communities support a high proportion of habitat specialists and are particularly sensitive to shading, nutrient enrichment and hydrological disturbance, including reduced discharge or physical damage to tufa-forming surfaces (Hinterlang 2017, Grootjans et al. 2021, de Mars et al. 2024).

Recognizing these five associations within habitat type 7220* enables conservation practitioners to identify priority sites, assess degradation pathways, and implement site-specific management measures. Such measures include maintaining open conditions, preventing nutrient enrichment, and preserving natural discharge regimes by avoiding water abstraction, piping or other hydrological modifications of spring outlets. Additional pressures comprise drainage and land-use changes in the spring catchment, as well as direct physical modification or destruction of spring outlets (Grootjans et al. 2021). This differentiation is especially important in Eastern Europe, where lowland calcareous petrifying springs are embedded in intensively used landscapes and increasingly impacted by eutrophication and, as our study shows, by invasion of alien or nutrient-demanding native plants.

In Ukraine, where calcareous petrifying springs face under strong anthropogenic pressure and occur partly in military-occupied regions, including Crimea, the proposed classification provides a robust basis for habitat assessment, prioritization and reporting within the Emerald Network/Natura 2000. This framework supports more effective national-level conservation of habitat 7220* (Schaminée et al. 2016, Didukh et al. 2018).

Erweiterte deutsche Zusammenfassung

Einleitung – Kalktuff- und Travertinquellen zeichnen sich durch hohe pH-Werte, einen konstanten Wasserfluss und vor allem Ausfällung von Calciumcarbonat aus. Sie beherbergen hochspezialisierte Lebensgemeinschaften und haben daher eine hohe Naturschutzbedeutung. Die Vegetation dieser Quellen in West- und Mitteleuropa wurde bereits klassifiziert (Hadač 1983, Rodwell 1991, Hinterlang 1992, 2017, Zechmeister 1993, Siebum et al. 1995, Valachovič 2001, Matuszkiewicz 2007, Hájková & Hájek 2011, Rivas-Martínez 2011, Lyons & Kelly 2017, de Foucault 2018), während aus Osteuropa bislang nur wenige Informationen vorlagen (Didukh et al. 2018).

Untersuchungsgebiet – Das Untersuchungsgebiet erstreckt sich über einen rund 250 km langen Abschnitt des Dnistertals in der Westukraine (N 48,9804°, E 25,0718° bis N 48,5855°, E 27,1511°), nordöstlich der Ukrainischen Karpaten. Dieser alte Canyon besteht vor allem aus paläozoischen Sedimentgesteinen aus dem Devon, aber auch aus känozoischen Schichten. Die Kalktuffquellen liegen meist an den Kontaktzonen silurischer Kalke oder porösen kreidezeitlichen und miozänen Ablagerungen und undurchlässigen devonischen Schichten, die als Aquifer wirken. Die klimatischen Bedingungen sind mit Jahresniederschlägen von 520–590 mm und Julitemperaturen von 18–19 °C für die Tuffbildung geeignet. Um eine verzerrte Klassifikation zu vermeiden, werteten wir unsere Vegetationsdaten zusammen mit Daten aus Zentral- und Südosteuropa aus.

Methoden – Der initiale Datensatz von 196 Vegetationsaufnahmen wurde durch stratifiziertes Resampling auf 129 Aufnahmen reduziert. Es wurden Aufnahmen integriert, die dem *Lycopodo europaei-Cratoneurion commutati* zugeordnet waren, sowie Parzellen, die in der Synthese der Quellvegetation von Peterka et al. (2023) demselben Verband zugeordnet waren. Zur Verringerung von Unterschieden in der Probendichte führten wir eine heterogenitätsbeschränkte Zufallsauswahl durch (Lengyel et al. 2011). Anschließend verwendeten wir den ISOPAM-Algorithmus (Schmidtlein et al. 2010), wobei die optimale Anzahl der Cluster mithilfe von OptimClass bestimmt wurde (Tichý et al. 2010). In den nächsten Schritten nutzten wir formale Definitionen der Assoziationen, die den Clustern entsprachen, und schließlich die halb-beaufsichtigte k-means-Methode, um die verbliebenen Aufnahmen zu klassifizieren. Diagnostische Arten für die einzelnen Cluster wurden auf Basis des Phi-Koeffizienten

geschätzt (Chytrý et al. 2002) und mit einem Fisher-Exakt-Test auf Signifikant ($p < 0,05$) überprüft. Ellenberg-Zeigerwerte wurden verwendet, um Umweltunterschiede zwischen den Clustern zu untersuchen (Hájek et al. 2020, Tichý et al. 2023). Um die Klassifikation im Kontext von Umweltbedingungen zu visualisieren diente eine *Detrended Correspondence Analysis* (DCA).

Ergebnisse – Wir unterschieden fünf Cluster, die syntaxonomisch wie folgt interpretiert wurden: (i) *Pinguiculo hirtiflorae-Cratoneuretum commutati*, (ii) *Brachythecio rivularis-Cratoneuretum commutati typicum*, (iii) *Brachythecio rivularis-Cratoneuretum commutati rhynchostegietosum riparioidis*, (iv) *Cochleario pyrenaicae-Cratoneuretum commutati* und (v) *Eucladietum verticillati*. Zwei der Syntaxa werden formal neu beschrieben. Drei der Gesellschaften wurden in der Ukraine nachgewiesen. Die einzelnen Gesellschaften unterschieden sich hinsichtlich ihrer Zeigerwerte für Nährstoff, Temperatur und Licht.

Diskussion – Die neu beschriebene Assoziation *Pinguiculo hirtiflorae-Cratoneuretum commutati* repräsentiert offene Kalktuffquellen des westlichen Balkans mit submediterran und balkanisch verbreiteten Arten. Die neu beschriebene Subassoziation *Brachythecio rivularis-Cratoneuretum commutati rhynchostegietosum riparioidis* ist dagegen subatlantisch-submediterran verbreitet. Beide Subassoziationen des *Brachythecio rivularis-Cratoneuretum commutati* zeichnen sich zudem durch höhere Nährstoff-Zeigerwerte als in den anderen Gesellschaften aus und zeigen tendenziell geringere Licht-Zeigerwerte, dieser „Unterschied“ ist jedoch nicht signifikant. Im lokalen Untersuchungsgebiet des Dnistertals in der Ukraine dominierten hingegen schattentolerante und besser nährstoffversorgte Gesellschaften mit häufigem Vorkommen von Generalisten und sogar Neophyten.

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Author contributions

I.V. conceived the idea, recorded relevés in the field together with S.N. and Y.D., identified the bryophytes, and carried out the classification under supervision by M.H. and Y.D. P.H. and T.P. performed statistical analyses. I.V., T.P., P.H., and M.H. drafted the manuscript which was read and revised by all authors. All authors approved the final version for publication.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Phytosociological table of new syntaxa of calcareous petrifying springs.

Anhang E1. Pflanzensoziologische Tabelle neuer Syntaxa der Kalk-Tuffquellen.

Supplement E2. Header data for relevés described within new syntaxa of calcareous petrifying springs.

Anhang E2. Kopfdaten der Vegetationsaufnahmen, die als neue Syntaxa der Kalk-Tuffquellen beschrieben wurden.

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Supplement E1. Phytosociological table of new syntaxa of calcareous petrifying springs. Diagnostic species of *Brachythecio rivularis-Cratoneuretum rhynchostegietosum riparioides* and *Pinguiculo hirtiflorae-Cratoneuretum commutati* are sorted by deacresing fidelity and marked by frame.

Anhang E1. Pflanzensoziologische Tabelle neuer Syntaxa der Kalktuffquellen. Diagnostische Arten des *Brachythecio rivularis-Cratoneuretum rhynchostegietosum riparioides* und des *Pinguiculo hirtiflorae-Cratoneuretum commutati* sind nach abnehmender Treue sortiert und durch einen Rahmen markiert.

Cluster ID	1										3														
Relevé number	1	2	3	4	5	6*	7	8	9	10	11	12	13	14	15	16	17*	18	19	20	21	22	23	24	
Ass. <i>Pinguiculo hirtiflorae-Cratoneuretum commutati</i>																									
<i>Pinguicula hirtiflora</i>	2	+	2	3	3	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Juncus articulatus</i>	2	1	.	1	1	+	2	+	2																
<i>Carex distans</i>	.	+	1	+	+	r	.	1	.																
<i>Briza media</i>	+	+	1	.	.	+	.	+	.																
<i>Dactylorhiza saccifera</i>	.	+	.	.	.	+	1	+	r																
<i>Ononis spinosa</i>	.	+	+	.	.	2	.	1	.																
<i>Cirsium appendiculatum</i>	.	2	.	.	r	.	.	+	r																
<i>Carex paniculata</i>	2	2	.	.	+	.	3	.	.																
<i>Holcus lanatus</i>	.	.	+	.	.	1	.	+	+																
<i>Tussilago farfara</i>	1	1	r	1	+	+	.	2	2																
<i>Epilobium parviflorum</i>	1	+	+	.	.	+	+	.	1																
<i>Epipactis palustris</i>	.	.	.	.	1	+	+	.	.																
<i>Blackstonia perfoliata</i>	.	.	+	+	.	+	.	.	.																
<i>Trifolium pratense</i>	+	+	1	.	.	.	.	.	.																
<i>Schedonorus arundinaceus</i>	.	.	.	.	.	1	+	+	.																
<i>Parnassia palustris</i>	+	.	2	1	2	.	2	.	.																
Subass. <i>Brachythecio rivularis-Cratoneuretum commutati rhynchostegietosum riparioidis</i>																									
<i>Geranium robertianum</i>	.	.	.	.	.	.	.	.	.	+	r	.	.	.	.	.	1	.	.	.	+	+	.	.	
<i>Plagiomnium undulatum</i>	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	+	.	+	1	.	.	.	.	
<i>Rhynchostegium riparioides</i>	.	.	.	.	.	.	.	.	.	5	5	4	3	5	3	2	1	+	3	2	.	.	.	.	
<i>Hygroamblystegium tenax</i>	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	1	2	.	2	2	5	3	1	
All. <i>Lycopodo europaei-Cratoneurion commutati</i>, Ord. <i>Montio-Cardaminetalia</i>																									
<i>Philonotis calcarea</i>	.	2	1	+	.	.	.	.	5	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.
<i>Apopellia endiviifolia</i>	.	.	.	2	.	.	.	.	.	+	+	1	2	.	2	1	1	.	.	1	2	5	.	.	
<i>Ptychostomum pseudotriquetrum</i>	.	2	+	+	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	1	
<i>Carex flacca</i>	.	.	.	1	.	.	+	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Didymodon tophaceus</i>	1	2	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Conocephalum conicum</i>	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	1	.	.	.	
<i>Eucladium verticillatum</i>	.	.	.	2	.	2	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	
<i>Cratoneuron filicinum</i>	2	+	.	.	.	.	1	.	.	.	1	.	1	.	.	5	3	.	.	.	.	1	+	.	
<i>Palustriella commutata</i>	3	3	5	4	5	3	5	5	2	.	.	3	1	.	3	.	.	.	.	.	.	.	.	.	
Cl. <i>Montio-Cardaminetea</i>																									
<i>Cardamine amara</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	
<i>Brachythecium rivulare</i>	.	.	.	.	.	.	.	.	+	.	.	.	+	1	.	.	2	+	.	.	1	1	.	.	
<i>Rhizomnium punctatum</i>	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Chrysosplenium alternifolium</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	1	.	.	+	1	.	.	
<i>Cardamine acris</i> agg.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	
Other taxa																									
<i>Agrostis stolonifera</i>	2	1	2	+	.	2	.	1	.	1	.	.	+	.	.	+	1	1	1	5	.	+	3	.	
<i>Eupatorium cannabinum</i>	.	.	.	+	.	.	.	.	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	
<i>Urtica dioica</i>	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	+	1	1	+	.	+	.	
<i>Ranunculus repens</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	1	.	
<i>Molinia caerulea</i> s.s.	1	2	+	.	2	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Marchantia polymorpha</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	3	.	.	.	.	
<i>Juncus inflexus</i>	2	1	.	.	.	1	.	.	2	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	
<i>Mentha aquatica</i>	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	2	1	.	.	1	.	

Taxa rarely occurred within dataset:

E1: *Adiantum capillus-veneris* (15: 1), *Aegopodium podagraria* (17: 1), *Amorpha fruticosa* (24: +), *Angelica sylvestris* (9: 1), *Bellis perennis* (23: +), *Berula erecta* (19: 3), *Bidens frondosa* (24: +), *Blysmus compressus* (5: r), *Brachypodium pinnatum* (4: +), *B. sylvaticum* (13: +), *Bromus hordeaceus* (9: r), *Chelidonium majus* (20: 1; 21: +), *Cirsium oleraceum* (19: 3), *Clematis vitalba* (8: +), *Epilobium hirsutum* (19: 1), *Equisetum arvense* (3: +; 13: +), *E. palustre* (6: 1; 8: 1), *E. ramosissimum* (3: 1; 6: 2), *Eriophorum latifolium* (7: 1), *Festuca rubra* s.l. (4: 1; 7: 1), *Fragaria viridis* (8: 1), *Galium aparine* (17: +), *G. palustre* (19: +), *Geum rivale* (20: +), *Glechoma hirsuta* (10: 1), *Gymnadenia conopsea* s.l. (*Gymnadenia densiflora* (Wahlenb.) A. Dietr.) (2: r), *Hedera helix* (5: +), *Helosciadium nodiflorum* (3: 2), *Hieracium prenanthoides* (8: 1), *Hypericum tetrapterum* (3: +), *Isolepis setacea* (4: +), *Kernera saxatilis* (2: +), *Lactuca muralis* (15: +; 17: +), *Lamium galeobdolon* (22: 1), *Lathyrus pratensis* (1: +; 7: 1), *Linum catharticum* (8: 1), *Lotus corniculatus* (2: r), *Lysimachia nummularia* (23: 1), *L. vulgaris* (20: +), *Lythrum salicaria* (19: 1), *Mentha longifolia* (1: +; 13: +), *Myosoton aquaticum* (17: +; 21: +), *Neottia ovata* (7: r), *Odontites vernus* (8: +), *Poa nemoralis* (17: +; 21: +), *P. palustris* (14: +; 17: 1), *Potentilla reptans* (19: +), *Schedonorus pratensis* (3: +), *Scirpoides holoschoenus* (5: 2), *Scrophularia umbrosa* (19: 1), *Trifolium hybridum* (9: 2), *T. ochroleucon* (6: +), *Valeriana sambucifolia* (16: +),
E0: *Aneura pinguis* (5: +; 7: +), *Calliergonella cuspidata* (7: 1), *Campylium stellatum* agg. (7: 2), *Conardia compacta* (21: +), *Cyrtomnium hymenophylloides* (10: +), *Dicranella varia* (1: +), *Didymodon fallax* (24: +), *Fissidens rivularis* (15: 1), *Gymnocolea inflata* (4: +), *Oxyrrhynchium hians* (11: 1), *Philonotis marchica* (22: 1), *Plagiomnium affine* (16: +), *Ptychostomum torquescens* (5: 1).

Supplement E2. Header data for relevés describing new syntaxa of calcareous petrifying springs.

Anhang E2. Kopfdaten der Vegetationsaufnahmen, die als neue Syntaxa der Kalktuffquellen beschrieben wurden.

Relevé number	Name of syntaxon	Country	Location	Author	Date of recording	Relevé area (m ²)	Altitude	Aspect (°)	Slope (°)	Cover total (%)	Cover herb layer (%)	Cover moss layer (%)	Longitude	Latitude	Dataset
1	<i>Pinguiculo hirtiflorae-Cratoneuretum commutati</i>	Greece	Kousta Mt. (1731 m a.s.l.), northern slopes, between Skamnéli and Makrino villages	Hájek M., Hájková P.	03.07.2000	3	1450	NA	2	70	45	60	20.90917	39.90278	private data Hájek, Hájková
2	<i>Pinguiculo hirtiflorae-Cratoneuretum commutati</i>	Greece	Kousta Mt. (1731 m a.s.l.), northern slopes, between Skamnéli and Makrino villages	Hájek M., Hájková P.	03.07.2000	10	1400	NA	40	80	30	70	20.90917	39.90278	private data Hájek, Hájková
3	<i>Pinguiculo hirtiflorae-Cratoneuretum commutati</i>	Greece	Flambourari, 3 km SE of the village to Limni Aoon	Hájek M., Hájková P.	04.07.2000	2	1100	NA	50	95	40	95	21.01028	39.83222	private data Hájek, Hájková
4	<i>Pinguiculo hirtiflorae-Cratoneuretum commutati</i>	Greece	between Metsovo and Anthochori	Hájek M., Hájková P.	05.07.2000	4	1000	NA	50	80	50	80	21.17472	39.74917	private data Hájek, Hájková
5	<i>Pinguiculo hirtiflorae-Cratoneuretum commutati</i>	Greece	1.5 km SE of Elatochori village, by the road to Dilako	Hájek M., Hájková P.	04.07.2000	3	1000	NA	1	80	60	80	20.98639	39.87139	private data Hájek, Hájková
6*	<i>Pinguiculo hirtiflorae-Cratoneuretum commutati</i> , NR	Greece	1.5 km SE of Elatochori village, by the road to Dilako	Hájek M., Hájková P.	04.07.2000	2	1000	NA	20	60	40	50	20.98750	39.86055	private data Hájek, Hájková
7	<i>Pinguiculo hirtiflorae-Cratoneuretum commutati</i>	Greece	northern slopes of Kousta Mt. (1731 m a.s.l.), between Skamnéli and Makrino villages	Hájek M., Hájková P.	03.07.2000	15	1450	NA	2	95	80	90	20.90917	39.90278	private data Hájek, Hájková
8	<i>Pinguiculo hirtiflorae-Cratoneuretum commutati</i>	Greece	0.5 km S of Dilako village	Hájek M., Hájková P.	04.07.2000	10	900	NA	2	95	30	95	20.98778	39.86055	private data Hájek, Hájková
9	<i>Pinguiculo hirtiflorae-Cratoneuretum commutati</i>	Greece	Kousta Mt. (1731 m a.s.l.), SE slopes, by the path to Makrino village	Hájek M., Hájková P.	03.07.2000	4	1400	NA	30	95	40	90	20.92806	39.88544	private data Hájek, Hájková
10	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i>	Ukraine	Dolzhok valley, Chernelytsia village, Ivano-Frankivsk region	Vasheniak I., Nyporko S.	03.08.2023	4	220	41	61	50	10	40	25.43590	48.81400	private data Vasheniak Iuliia
11	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i>	Bulgaria	Predbalkan, Devetashko Plato - Krushuna	Hájek M., Hájková P.	20.06.2004	12	240	NA	85	90	1	90	25.02667	43.24972	Private data Hájek, Hájková
12	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i>	Greece	canyon Hroussia between Kalarites and Syrrako, old fountain in the village	Hájek M., Hájková P.	08.07.2000	5	900	NA	80	95	NA	95	21.11306	39.59556	Private data Hájek, Hájková
13	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i>	Greece	Syrrako village, Ioannina region	Hájek M., Hájková P.	08.07.2000	2	1100	NA	90	80	1	80	21.10479	39.59522	Private data Hájek, Hájková
14	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i>	Ukraine	Stripa valley, Skomorohky village, Ivano-Frankivsk region	Vasheniak I., Nyporko S.	13.06.2023	4	232	172	60	60	10	60	25.40510	48.91780	private data Vasheniak Iuliia
15	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i>	Greece	canyon Hroussia between Kalarites and Syrrako, old fountain in the village	Hájek M., Hájková P.	08.07.2000	8	1000	NA	90	90	1	90	21.11167	39.59500	Private data Hájek, Hájková
16	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i>	Ukraine	Ternava valley, Kytaigorod village, Khmelnytskyi region	Vasheniak I., Nyporko S.	11.06.2023	4	159	258	60	60	10	60	26.81020	48.63492	private data Vasheniak Iuliia
17*	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i> , NR	Ukraine	Stripa valley, Skomorohky village, Ivano-Frankivsk region	Vasheniak I., Nyporko S.	13.06.2023	4	232	172	60	50	10	40	25.40510	48.91780	private data Vasheniak Iuliia
18	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i>	Ukraine	Stripa valley, Rusyliv village, Ivano-Frankivsk region	Vasheniak I., Nyporko S.	13.06.2023	4	260	109	60	50	10	40	25.42113	48.95314	private data Vasheniak Iuliia
19	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i>	Ukraine	Potik valley, Vilhivtsi village, Ivano-Frankivsk region	Vasheniak I., Nyporko S.	02.08.2023	4	261	8	2	50	10	40	25.37280	48.80140	private data Vasheniak Iuliia
20	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i>	Ukraine	Dniester valley, Kunysivtsi village, Ivano-Frankivsk region	Vasheniak I., Nyporko S.	02.08.2023	4	245	352	78	50	10	40	25.36900	48.81350	private data Vasheniak Iuliia
21	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i>	Ukraine	Dniester canyon, Pyzhivka village, Khmelnytskyi region	Vasheniak I., Nyporko S.	11.06.2023	4	127	157	61	60	10	60	27.15390	48.58551	private data Vasheniak Iuliia
22	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i>	Ukraine	Dniester valley, Deleva village, Ivano-Frankivsk region	Vasheniak I., Nyporko S.	01.08.2023	4	189	49	83	50	10	40	25.23070	48.91600	private data Vasheniak Iuliia
23	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i>	Ukraine	Dolzhok valley, Chernelytsia village, Ivano-Frankivsk region	Vasheniak I., Nyporko S.	03.08.2023	4	282	51	28	50	10	40	25.43590	48.81320	private data Vasheniak Iuliia
24	<i>Brachythecio rivularis-Cratoneretum commutati rhynhostegietosum riparioidis</i>	Ukraine	Dniester canyon, Pyzhivka village, Khmelnytskyi region	Vasheniak I., Nyporko S.	11.06.2023	4	112	71	61	60	10	60	27.15531	48.58571	private data Vasheniak Iuliia