

Ecology and niche assembly of *Campanula tommasiniana*, a narrow endemic of Mt Učka (Liburnian karst, north-western Adriatic)

BOŠTJAN SURINA^{1,2*}, ANDREJ MARTINČIČ³

¹ Faculty of Mathematics, Natural Sciences and Information Technologies, University of Primorska, Glagoljaška 8, SI-6000 Koper, Slovenia

² Natural History Museum Rijeka, Lorenzov prolaz 1, 51000 Rijeka, Croatia

³ Zaloška cesta 78a, SI-1000 Ljubljana, Slovenia

Abstract – *Campanula tommasiniana* is a typical chasmophyte occupying calcareous rock crevices and cracks along a wide range of ecological gradients, demonstrating a high degree of ecological plasticity and stress tolerance with regards to abiotic factors. Generally, three ecologically and floristically distinct groups of stands were recognized and typified according to a sigmatistic approach: (a) *Seslerio juncifoliae-Campanuletum tommasinianae* ass. nov., with stands occupying higher elevated sites fully exposed to sun and strong winds; (b) *Seslerio autumnalis-Campanuletum tommasinianae* ass. nov., representing stands predominantly developed within thermophytic beech stands, semi- to fully-shaded by the tree canopy; (c) *Cystopteris fragilis-Campanuletum tommasinianae*, sciophytic, stands adapted to moisture and cold with high frequency and coverage of bryophytes. Results of DCA analyses using a unimodal model suggest that *Campanula tommasiniana* is primarily a plant of open and exposed sites of higher elevation despite being most frequently found in rock crevices within thermophytic and altimontane beech forests.

Key words: *Campanula tommasiniana*, Campanulaceae, Dinaric Alps, ecology, endemic species, Liburnian karst, Mt. Učka, phytosociology

Introduction

The kaleidoscopic complexity of topographic, climatic and geological conditions in the Mediterranean results in a high degree of overall biodiversity and a rapid species turnover. The flora of the Mediterranean is, for example, the species-richest area in the Old World. Although the Mediterranean region represents less than 1.5% of the land area of the world, its flora comprises around 30,000 species and subspecies of flowering plants (QUEZÉL 1985, GREUTER 1991), more than 160 species of ferns, and hosts approximately 10% of all known species of ferns and flowering plants on Earth (BLONDEL and ARONSON 1999). Around 80%

* Corresponding author, e-mail: bostjan.surina@prirodoslovni.com

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of all endemic taxa are to be found in the area (GOMEZ-CAMPO 1985). However, the main reason for such a high degree of biodiversity of flowering plants in Mediterranean is not the overall species richness of the area, but the high number of endemics, many of them restricted to one or only a few known localities with specifics in ecology (e.g., geology, soil type, relief, etc.) or geography (e.g., islands, mountains). Here, almost every island, regardless of its size, hosts at least some (indigenous) endemic taxa. Ecologically similar to islands, mountains promote speciation events too, which may result in there being up to 42% of endemics among the higher plants (MEDAIL and VERLAQUE 1997), although this rate may vary a lot (BLONDEL and ARONSON 1999).

One of the many local or regional endemics of the genus *Campanula* along the Adriatic coast (for the review see KOVAČIĆ 2004, PARK et al. 2006) is the chasmophytic *C. tommasiniana* Koch (in F. Schultz, Arch. Fl. Fr. et Allemagne 6. Cent., 229, 1852), a narrow endemic of Mt. Učka, located above Kvarner Bay in the Liburnian karst (north-western Adriatic). Along with *Edraianthus wettsteinii* subsp. *lovcenicus* and *E. dinaricus* (Campanulaceae), two narrow endemics of Mt Lovćen, above Kotor Bay, and Mt Mosor in central Dalmatia (WETTSTEIN 1887, JANCHEN 1910, MAYER and BLEČIĆ 1969, LAKUŠIĆ et al. 2009), respectively, and a few predominantly island populations of ambiguous taxonomic rank, e.g., *Centaurea friderici*, *C. kartschiana*, *C. cuspidata* (Asteraceae; e.g., TEYBER 1913, GINZBERGER and TEYBER 1921, GINZBERGER 1921, LOVRIĆ 1971, RADIĆ 1981, LOVRIĆ 1992), *Brassica incana* (Brassicaceae; e.g., GINZBERGER 1921) and *Asperula staliana* (Rubiaceae; e.g., KORICA 1975, LOVRIĆ and KORICA 1981, KORICA 1986) aggregates in north-western Adriatic and Dalmatia, *C. tommasiniana* is one of the most range-restricted taxa among the all adriatide (sensu TROTTER 1912), occupying an area of only 6.5 km² (SURINA 2013).

The data on ecology and niche assembly of *Campanula tommasiniana*, despite its being a prominent narrow endemic, are surprisingly scarce. According to HORVATIĆ (1963b), *C. tommasiniana* is a chasmophyte growing in calcareous rock crevices within thermophytic beech forests of the association *Seslerio autumnalis-Fagetum*, building an association *Campanuletum tommasinianae-justinianae*. However, results of a detailed survey of its distribution range and habitat preferences (SURINA 2013) suggest its great ecological plasticity, for it thrives in rock crevices of rocky outcrops and cliffs as well as within various types of forest stands (e.g., associations *Fraxino ornii-Quercetum ilicis*, *Quercu-Carpinetum orientalis*, *Aristolochio luteae-Quercetum pubescentis*, *Seslerio autumnalis-Ostryetum*, *Seslerio autumnalis-Fagetum* and *Ranunculo platanifolii-Fagetum*) along the whole elevational (vegetational) profile of the mountain's eastern slopes (for detailed comments on vegetation profiles see ŠUGAR 1970, 1984). On western slopes, in contrast to the eastern, it rarely descends below 1000 m a.s.l. While commenting on the site ecology of *Leontopodium alpinum* on Mt. Učka, *C. tommasiniana* (as *C. waldsteiniana*!) has been recorded within the alliance *Micromerion croaticae* (ŠUGAR 1971).

With our research we aimed to get insights into site ecology, habitat preferences and niche assembly of *Campanula tommasiniana*.

Research area

The Učka mountain range rises above Kvarner Bay; between the Poklon pass (920 m a.s.l.) and Plomin Bay it forms a distinct ridge in a north-south direction along the north-eastern Istrian coast (NE Adriatic). The mountain's highest peaks, Vojak (1396 m

a.s.l.), Suhi vrh (1332 m a.s.l.) and Plas (1285 m a.s.l.), are located in its northern part, which is generally much higher than its southern part. While the macrorelief of the mountain is rather simple, characterized by a prominent ridge, forming distinct eastern and western slopes of the mountain, the microrelief is diversified, being the most picturesque with the solitary limestone towers and cliffs in the Vela draga canyon and beyond the peak Plas on the mountain's western slopes. Some precipitous rock faces are to be found on the eastern slopes as well; the most distinct are those located north of the Grdi breg slope, east of Vojak peak, the eastern rock face of the Suhi vrh peak and the south-western rock face of Argun peak. According to geological maps (ŠIKIĆ et al. 1963, ŠIKIĆ et al. 1967) and explanatory texts (ŠIKIĆ and POLŠAK 1973, ŠIKIĆ and PLENIČAR 1975), Lower and Upper Cretaceous limestones and dolomites prevail in the area. Along the Lovranska draga valley, limestones and dolomites are intercepted by Quaternary sediments, marlstones and sandstones, conglomerates, breccias and foraminiferan limestones. As indicated by various but pronounced climatogenic vegetation types along an elevational gradient of the mountain, the climate is diverse. The foothills are rather warm with mean annual temperatures between 14–15 °C, while the values gradually decrease with increasing elevation, being only 4–6 °C at the summits (ZANINOVIĆ 2008). The higher elevations of the mountain receive from 2000 to 2500 mm of precipitation yearly, which is the highest amount of precipitation in Istria (GAJIČ-ČAPKA et al. 2008). However, despite being positioned on the Adriatic coast, the eastern foothills of the mountain receive still more than 1500 mm of precipitation yearly (ibid.). The precipitation regime is a Mediterranean one.

Mt. Učka is one of the most renowned botanical sites in the Adriatic area (TOPIĆ et al. 2009) with a remarkable tradition of botanical exploration (e.g., BRANA 2012, TRINAJSTIĆ and PAVLETIĆ 2012). As a consequence, the mountain's flora is rather well known, although the data on vegetation are somewhat scarce. From a biogeographical aspect and according to ŠUGAR (1970, 1984, but with phytosociological nomenclature according to VUKELIĆ 2012), vegetation types along an elevational profile of the mountain belong to two phyto-geographical regions: (a) Mediterranean, further divided into eumediterranean (ass. *Fraxino orni-Quercetum ilicis*), submediterranean (ass. *Quercus-Carpinetum orientalis*), both restricted to a narrow elevational belt on the mountain's foothills, and epimediterranean (ass. *Aristolochio luteae-Quercetum pubescentis*) zones, and (b) Eurosibiric-Northamerican region, with paramediterranean (ass. *Seslerio autumnalis-Fagetum*) and illyric (altimontane beech forests, ass. *Ranunculo platanifolii-Fagetum*) zones, both covering majority of the mountain range. Within eumediterranean and submediterranean subzones, stands with dominating *Laurus nobilis* in a tree layer (*Fraxino orni-Quercetum ilicis* fac. *Laurus nobilis* and *Quercus-Carpinetum orientalis lauretosum nobilis*) are well developed locally on deeper and moister soils (HORVATIĆ 1963a, PELCER 1983). In comparison to other eastern Adriatic mountain ranges of the Dinaric Alps, the outstanding features of Mt. Učka are the homogenous and extensive forests both from the inland (western) and seaward (eastern) sides. Since 1999, the natural and cultural heritage of the area has been protected within Učka Nature Park (NARODNE NOVINE 1999).

Materials and methods

In summer 2011, we recorded 112 relevés with *Campanula tommasiniana* through the whole distribution range of the species. The cover-abundance estimates were made accord-

ing to the Domin scale (sensu DAHL and HADAČ 1941) and the plot size used for sampling averaged 9 m² (the standard plot size for chasmophytic and scree stands, but see also CHYTRY and OTÝPKOVÁ 2003). Details of the phytosociological parameters of sites are given in Appendix 1 to On-line Supplement Tabs. 2–4. With each relevé, light conditions were roughly estimated as: open sites (no shading), semi-open sites (medium shading) and fully covered sites (full shading) by the canopy of the nearby forest vegetation. A complete floristic inventory is given in table 4, while taxa occurring only once in the analyses are listed in Appendix 2 to On-line Supplement Tabs. 2–4. The nomenclature and taxonomic source for the names of vascular plants was Flora Europaea (TUTIN et al. 2001), while the names of bryophytes were in agreement with the Catalogue of Mosses of Slovenia (MARTINČIČ 2003) and the Annotated Checklist of Slovenian Liverworts and Hornworts (MARTINČIČ 2011). All collected and identified bryophytes are stored in the herbarium of the Natural History Museum Rijeka (NHMR). Raunkiær's life forms (RAUNKIAER 1907), subsequently revised and modified by MÜLLER-DOMBOIS and ELLENBERG (1974), were adopted from PIGNATTI (2005) for vascular plants and HILL and PRESTON (1998), DÜLL et al. (1999) and MARTINČIČ (1966, 2003) for the bryophytes. Syntaxonomic groups in Tab. 4 were assigned primarily according to Flora alpina (AESCHIMANN et al. 2004), while in some cases we followed our own criteria. Coverage index ($D_{\%}$, e.g. SURINA 2005) was calculated for life forms (Tab. 1) and each taxon (Tab. 4), respectively. Prior to numerical analysis, the original cover-abundance values for individual taxa were transformed accordingly (CURRAL 1987). Groups of vegetation types were ascertained using cluster and ordination analyses with the help of the programme package PAST (HAMMER et al. 2001). The arrangement of relevés was done according to the results of cluster analysis and diagnostic groups of species were tested by means of the SIMPER analysis (On-line Supplement Tabs. 1–4), an algorithm implemented in the programme package PAST, and constrained ordination analyses using species fit (of 25%) as an inclusion rule, characterized as the quality of the description of the »behaviour« of species values, derived from the particular combination of ordination axes (LEPŠ and ŠMILAUER 2003). In order to explain the variation in niche assembly by specific environmental and structural (phytosociological) parameters, unconstrained (DCA) and constrained (RDA, CCA) ordination analyses were performed, using the CANOCO computer programme (BRAAK TER and ŠMILAUER 2002). In order to determine the lengths of gradients, DCA analyses, detrended by segments, were initially performed and the models (linear, unimodal) used accordingly. The statistical significance ($p < 0.02$) of the site parameters was tested using the Monte Carlo test, with 499 permutations. Only the significant parameters were then analyzed together, with the aim of producing a general view of the environmental impact on floristic composition and structure of stands. For estimating the general environmental affinities of the relevés, indicator values (co-variables) for vascular plants were assigned according to PIGNATTI (2005) and passively projected into the ordination diagrams. The environmental value in a relevé (EV_w) was estimated as the weighted average of the indicator values of all present species, their abundances being used as weights (LEPŠ and ŠMILAUER 2003). The Kruskal–Wallis non-parametric test was used to test whether samples were taken from groups with equal median environmental values and a post-hoc test was carried out using Mann-Whitney's pairwise comparisons. While defining the syntaxa we followed the sigmatistic-Braun-Blanquet approach (BRAUN-BLANQUET 1928), subsequently improved by WESTHOFF and VAN DER MAAREL (1973), and based on a revised association concept proposed by WILLNER (2006).

Tab. 1. Stand parameters of chasmophytic niche assemblages with *Campanula tommasiniana* on Mt. Učka (NW Adriatic)

Groups of assemblages	SjC				SaC		CfC
	S	GM	GS	C	S	M	
Elevation (m)*	1116 (760–1216)	1237 (1188–1296)	1260 (1140–1316)	1258 (965–1380)	405 (396–420)	1033 (827–1355)	1143 (47–1375)
stoniness	70 (50–80)	80 (70–90)	70 (60–80)	70 (30–90)	45 (40–70)	60 (40–80)	50 (20–70)
Coverage (%)*							
herb layer	30 (20–50)	20 (10–30)	25 (20–40)	30 (10–40)	35 (30–50)	25 (10–40)	30 (10–40)
moss layer	1 (0–10)	1	1 (1–10)	8 (1–40)	35 (1–40)	20 (1–40)	40 (30–70)
No. of vascular plants per rel.*	12 (8–17)	9 (6–17)	10,5 (6–20)	9 (6–15)	15 (11–23)	10 (5–21)	10 (4–16)
No. of bryophytes per rel.*	7 (0–13)	2 (1–8)	4 (0–8)	8 (4–10)	7,5 (6–14)	11 (5–16)	11 (6–17)
Total no. of vascular plants	46	45	45	52	45	81	54
Total no. of bryophytes	25	18	20	29	26	47	50
Life forms (no. of taxa/D%)							
Hemicryptophytes	24 (52%)/89.2	26 (58%)/66.2	24 (53%)/71.3	62 (31%)/76.2	18 (40%)/46.4	54 (67%)/76.2	65 (35%)/79.9
Phanerophytes	9 (20%)/11.3	6 (13%)/3.2	4 (9%)/3.3	5 (10%)/2.1	18 (40%)/38.5	12 (15%)/5.2	7 (13%)/1.4
Chamaephytes	6 (13%)/27.8	9 (20%)/27.5	12 (27%)/20.9	8 (16%)/12.7	6 (13%)/12.5	4 (5%)/4.9	/
Geophytes	6 (13%)/12.3	3 (7%)/4	2 (4%)/3.1	4 (8%)/4.1	3 (7%)/2.6	7 (9%)/9.1	8 (15%)/5.2
Therophytes	1 (2%)/3.3	1 (2%)/1.4	3 (7%)/1.4	2 (4%)/4.1	/	4 (5%)/4.6	4 (7%)/13.3
No. of relevés	9	17	18	14	25	23	

Tab. 2. Overall average dissimilarities (lower left hand corners) and taxa contribution (up to 50% of overall dissimilarities, upper right hand corners) between the three general types of chasmo-phytic niche assemblages with *Campanula tommasiniana* on Mt Učka (NW Adriatic) according to SIMPER analysis. Taxa abbreviations as in table 4 and text below. Syntaxa are explained in the text following figure 3.

Syntaxa	SjC	CfC	SaC
SjC		Nec cri (5.5), Cte mol (4.6), Ses jun (3.6), Asp tri (2.5), Cys fra (2.3), Cym mur (2.1), Pla str, Hom phy, Myc mur, Cam tom (2), Ath tur (1.7), Glo cor, Rad com (1.4), Tor tor, Sil sax, Sch sp, Asp rtm (1.3), Hom ser, Ara alp (1.2)	Ses jun (4), Nec cri (2.8), Ano vit (2.5), Pla str (2.3), Hom ser (2.2), Asp tri, Cam tom (2), Nec bes, Cte mol (1.9), Ses aut (1.8), Ath tur, Hom phi (1.7), Glo cor, Sch sp, Asp rtm (1.5), Tor tor, Sil sax (1.4), Mic thy, Por pla, Nec com (1.2), Sat mon (1.1), Cyc pur (1)
CfC	80.44		Nec cri (3.1), Cte mol (2.8), Ano vit (2), Cys fra (1.8), Hom ser (1.7), Pla str, Cym mur, Hom phi (1.6), Nec bes (1.5), Ses aut, Cam tom, Myc mur (1.3), Asp rtm, Tor tor (1.2), Rad com, Sch sp, Pse alb, Nec com (1.1), Por pla, Asp tri, Ara alp, Fis dub, Cyc pur (1)
SaC	78.63	65.92	

Results

Niche selection and floristic assembly of stands

Campanula tommasiniana, inhabiting calcareous rock crevices and cracks from low elevated sites (47 m) to mountain tops (1390 m), is an edificatory vascular plant for chasmo-phytic assemblages. The total floristic assembly of stands, covering 10–80% (Me=35%) of the sampling plots, counts for 155 taxa of vascular plants and 77 taxa of bryophytes (two of them are lichenicolous fungi), with a median number of 12 (min=6, max=23) and 8 (min=0, max=17) taxa per plot, respectively (Tab. 4, On-line Supplement Tabs. 2–4). The coverage and number of taxa of vascular plants and bryophytes varies a lot between the sites (Tab. 1) and depends heavily on site ecology. Among the vascular plants, typical chasmo-phytes occur in more than one third of the relevés: *Campanula tommasiniana* (100%), *Asplenium ruta-muraria* (71), *A. trichomanes* (65), *Sesleria juncifolia* (57), *Athamanta tur-bith* (46) and *Cymbalaria muralis* (40), while among bryophytes the most frequent were *Tortella tortuosa* (71), *Ctenidium molluscum* (54), *Schistidium* sp. (54), *Neckera crispa* (51), *Homalothecium sericeum* (50), *H. philippeanum* (36) and *Plasteurhynchium striatulum* (35; Tab. 4). In number and coverage of vascular plant taxa, hemicryptophytes completely prevail and represent more than a half of all registered vascular plant taxa ($D_{\%}=46.4\text{--}89.2$), followed by phanerophytes (18%, $D_{\%}=1.4\text{--}38.5$), geophytes (15%, $D_{\%}=2.6\text{--}12.3$), therophytes (5%, $D_{\%}=0\text{--}13.3$) and chamaephytes (3%, $D_{\%}=0\text{--}27.8$).

Cluster and SIMPER analyses

Application of various algorithms and (dis)similarity measures yields very similar clustering topology. A dendrogram of chasmo-phytic stands from Mt. Učka shows two

groups of relevés (Fig. 1). In cluster »A«, 97 taxa of vascular plants, 34 taxa of bryophytes and 2 taxa of lichenicolous fungi are surveyed. Beside *Campanula tommasiniana*²⁻⁵(100%), *Sesleria juncifolia*³⁻⁶(90), *Asplenium ruta-muraria*⁺³(71) and *Athamanta turbith*⁺⁶(69) completely prevail (Tab. 4, On-line Supplement Tabs. 2-4). Other relatively frequent vascular plants are *Silene saxifraga* subsp. *hayekiana*⁺³(55), *Micromeria thymifolia*¹⁻³(48), *Asplenium trichomanes*¹⁻⁴(40) and *Scrophularia laciniata*⁺³(36). The most frequent bryo-

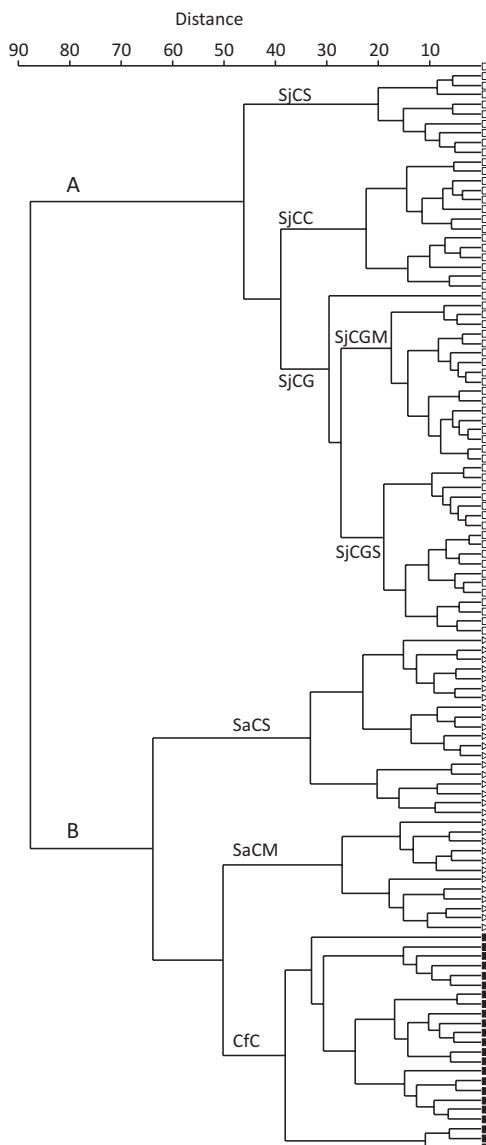


Fig. 1. Dendrogram of chasmophytic assemblages with *Campanula tommasiniana* on Mt. Učka (NW Adriatic; Ward's method, Euclidean distances). Syntaxonomy is explained in the text following figure 3.

phytes are *Tortella tortuosa*¹⁻³(79), *Schistidium* sp.¹⁻³(45) and *Homalothecium sericeum*¹⁻³(38). In cluster »A« the following taxa occur exclusively: *Globularia cordifolia*²⁻⁴(57), *Senecio abrotanifolius*¹⁻³(29), *Stachys subcrenata*¹⁻³(26), *Arabis scopoliana*¹⁻³(19), *Sempervivum tectorum*⁺³(16), *Rosa pimpinellifolia*⁺²(14%), *Euphrasia illyrica*⁺³(12), *Campanula marchesettii*¹⁻³(10), *C. cochleariifolia*⁺²(10), *Rhannus saxatilis*¹⁻³(9), *Gentiana lutea* subsp. *symphyandra*⁺²(9), *Teucrium arduinii*¹⁻⁴(9), *Satureja subspicata* subsp. *liburnica*⁺²(7), *Primula auricula*¹⁻⁴(5), *Leontopodium alpinum*¹⁻²(5) and others, while *Silene saxifraga* subsp. *hayekiana*, *Sedum album*¹⁻³(16), *Micromeria thymifolia*, *Hieracium bupleuroides*¹⁻³(31), *Scrophularia laciniata*, *Allium saxatile* subsp. *tergestinum*⁺³(24), *Teucrium montanum*⁺³(24), *Saxifraga paniculata*¹⁻³(16) occur almost exclusively. Bryophytes, found relatively frequently only in this cluster, are *Tortella densa*²⁻³(10), *Ditrichium flexicaule*²⁻³(17), while *Syntrichia ruralis* var. *ruralis*¹⁻³(16) and *Scapania aspera*¹⁻³(7) occur in cluster »A« almost exclusively. Cluster »A« further divides into three sub-clusters: (a) SjCG (On-line Supplement Tab. 2, rel. 10–44) is characterized by high frequency and coverage of *Globularia cordifolia*²⁻⁴(89) and *Hieracium bupleuroides*¹⁻³(43), and the two groups of stands: *Micromeria thymifolia*²⁻³(94), *Scrophularia laciniata*⁺³(56; SjCGM) and *Stachys subcrenata*¹⁻³(59), *Tortella densa*²⁻³(35; SjCGS), respectively (rel. 10–27, 28–44 in On-line Supplement Tab. 2); (b) SjCC (On-line Supplement Tab. 2, rel. 45–58), characterized by high constancy, frequency and coverage of bryophytes, specially *Ctenidium molluscum*¹⁻⁴(93), *Neckera crispa*¹⁻⁴(36) and *Fissidens dubius*¹⁻³(43); (c) SjCS (On-line Supplement Tab. 2, rel. 1–9), where *Sedum album*¹⁻³(89), *Satureja montana* subsp. *variegata*³⁻⁵(67) and *Syntrichia ruralis* var. *ruralis*¹⁻³(56) occur almost exclusively.

Cluster »B« represents less homogenous but more diverse floristic assembly; a total of 130 taxa of vascular plants and 56 taxa of bryophytes are registered. Along the *Campanula tommasiniana*²⁻⁶(100), the most frequent vascular plants are: *Asplenium trichomanes*²⁻⁵(100), *A. ruta-muraria*²⁻⁴(96), *Cymbalaria muralis*²⁻⁴(91), *Mycelis muralis*⁺³(87), *Cystopteris fragilis*²⁻⁴(83), *Geranium robertianum*¹⁻³(57), *Plagiochilla porelloides*¹⁻³(43), *Cyclamen purpurascens*²⁻³(39), *Valeriana tripteris*¹⁻³(39), *Senecio fuchsii*⁺³(35), *Pseudofumaria alba*¹⁻⁷(30), *Saxifraga rotundifolia*²⁻⁴(30), *Adenostyles glabra*¹⁻³(30), *Sesleria juncifolia*⁺³(30). In comparison to cluster »A«, bryophytes are much more frequent and abundant in cluster »B«. The most common taxa are *Ctenidium molluscum*³⁻⁸(100), *Neckera crispa*³⁻⁸(96), *Schistidium* sp.¹⁻³(65), *Homalothecium philippeanum*³⁻⁵(57), *Plasteurhynchium striatum*¹⁻⁵(57), *Radula complanata*¹⁻³(57), *Tortella tortuosa*¹⁻³(52), *Fissidens dubius*¹⁻⁴(48), *Porella platyphylla*¹⁻³(45), *Neckera complanata*¹⁻⁴(39), *Pseudoleskeela catenulata*¹⁻⁴(39), *Bryum* sp.¹⁻³(35), *Homalothecium sericeum*¹⁻⁴(35), *Anomodon viticulosus*¹⁻⁵(30), *Cololejeunea calcarea*¹⁻⁴(30), *Pedinophyllum interruptum*³(30), *Mnium thomsonii*²⁻³(30) etc. In cluster »B«, *Mycelis muralis*, *Plagiochila porelloides*¹⁻³(43), *Mnium thomsonii*, *Quercus ilex*¹⁻²(13), *Galeobdolon flavidum*⁺³(26) occur exclusively, while *Cystopteris fragilis*, *Arabis alpina*¹⁻³(52), *Coronilla emeris* subsp. *emeroides*²⁻³(19), *Asparagus acutifolius*¹⁻²(19), *Hedera helix*¹⁻³(13) occur almost exclusively. Here, three floristically well defined sub-clusters are recognized: (a) SaCM (On-line Supplement Tab. 4, rel. 7–31), representing floristic assemblages characterized by the presence and high coverage of *Homalothecium sericeum*¹⁻⁵(84), *Sesleria autumnalis*¹⁻⁵(68) and *Neckera besseri*¹⁻⁶(52), *Cyclamen purpurascens*⁺³(72), *Galeobdolon flavidum*⁺³(32) and *Mycelis muralis*⁺³(48); (b) SaCS (On-line Supplement Tab. 4, rel. 1–6), a group of floristically quite distinct stands with high frequency, coverage and (almost) exclusive occurrence of *Coronilla emeris* subsp. *emeroides*²⁻³(100), *Asparagus acutifolius*¹⁻²(100), *Quercus ilex*¹⁻²(66), *Hedera helix*¹⁻³(66), *Lep-*

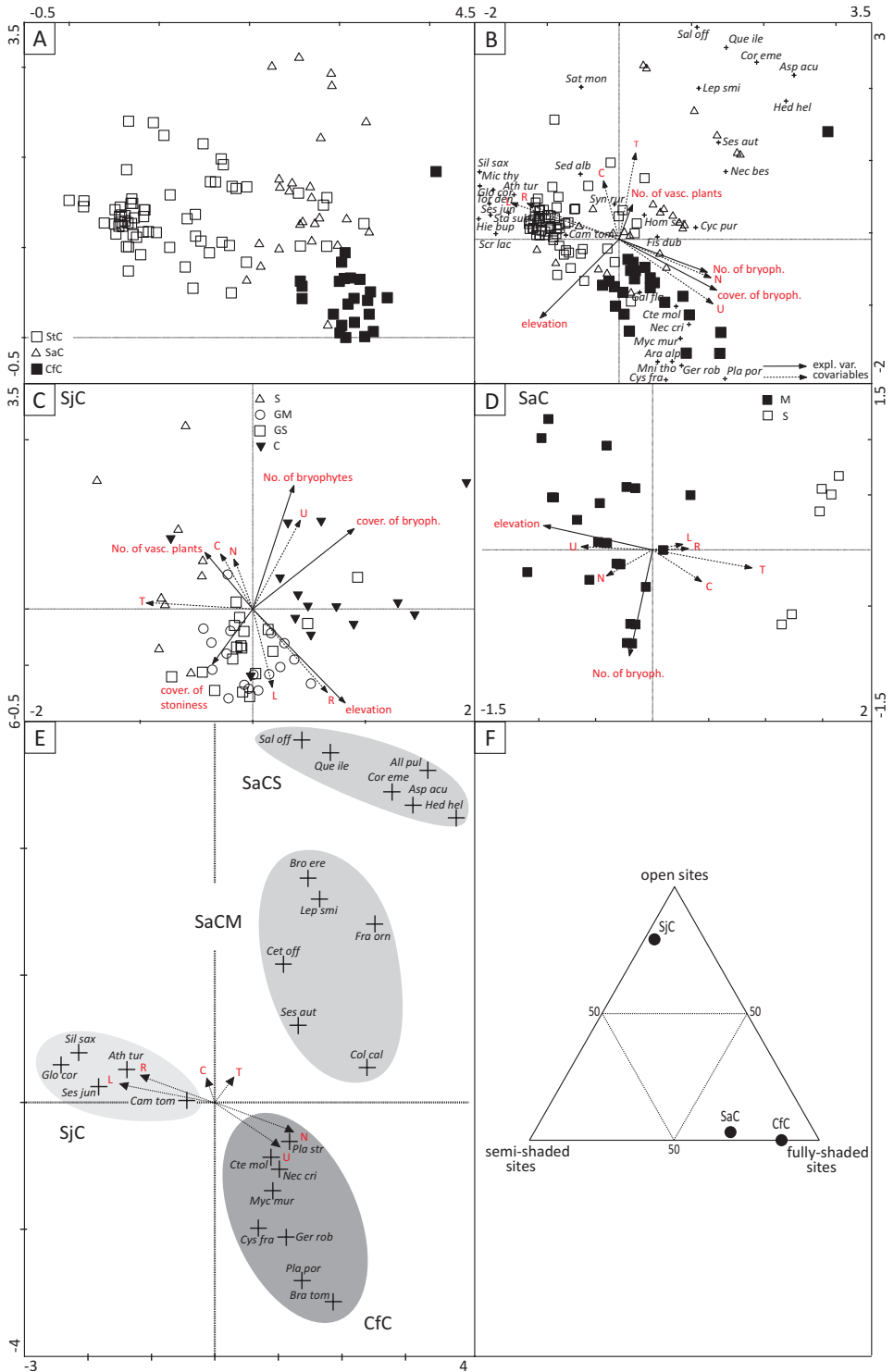
*todon smithii*³⁻⁶(66) and *Salvia officinalis*¹⁻²(50); (c) CfC, stands characterized by exclusiveness, highest frequency and coverage of *Mycelis muralis*⁺³(87), *Cystopteris fragilis*²⁻⁴(83), *Geranium robertianum*¹⁻³(57), *Arabis alpina*¹⁻³(52), *Plagiochila porelloides*¹⁻³(43) and *Mnium thomsonii*²⁻³(30; On-line Supplement Tab. 3).

Floristically, the cluster CfC which is the most different from cluster SjC (80.44%); the taxa that contribute most to dissimilarity are *Sesleria juncifolia*, *Asplenium trichomanes*, *Cystopteris fragilis*, *Cymbalaria muralis*, *Mycelis muralis*, *Athamanta turbith*, *Globularia cordifolia*, *Asplenium ruta-muraria*, *Silene saxifraga* subsp. *hayekiana* and *Arabis alpina* among the vascular plants, while among the bryophytes there are *Necera crispa*, *Ctenidium molluscum*, *Homalothecium philippeanum*, *H. sericeum*, *Radula complanata*, *Tortella tortuosa* and *Schistidium* sp. (Tab. 2). Cluster CfC differs significantly less from cluster SaC (65.92%) and the taxa that contribute most to dissimilarity are *Neckera crispa*, *Ctenidium molluscum*, *Anomodon viticulosus* and many other bryophytes, while among the vascular plants the most important differential taxa are *Cystopteris fragilis*, *Cymbalaria muralis*, *Sesleria autumnalis*, *Mycelis muralis*, *Asplenium trichomanes*, *A. ruta-muraria*, *Arabis alpina* and *Cyclamen purpurascens*. The average dissimilarity between clusters SjC and SaC is 78.63%, and the most important differential taxa are *Sesleria juncifolia*, *S. autumnalis*, *Asplenium trichomanes*, *A. ruta-muraria*, *Globularia cordifolia* etc. among vascular plants, and *Neckera crispa*, *N. besseri*, *Anomodon viticulosus*, *Plasteurhynchium striatulum*, *Ctenidium molluscum* etc. among bryophytes.

Specifically, groups of assemblages within the cluster SjC (SjCS, SjCGM, SjCGS and SjCC (Fig. 1) appear to be floristically most similar with overall average dissimilarities ranging between 55.61 (between SjCGM and SjCGS) and 72.82% (between SjCS and SjCGS; On-line Supplement Tab. 1). Average dissimilarities between the cluster CfC and all the other groups of assemblages are in general high (72.26–84.52%), while the most distinct group of assemblages is represented by the group SaCS with the highest recorded dissimilarities (86.5% to SjCGM, 86.38% to SjCGS and 80.37% to SjCC). SaCS shows the lowest dissimilarity to SaCM (70.56%).

Ecology and vegetation typology of stands

Cluster topology (Fig. 1) reflects the ecology of chasmophytic assemblages well (Fig. 2). Cluster »A« (SjC) includes stands of sunny and exposed rocky outcrops and cliffs, while cluster »B« represents stands fully- (CfC) to semi-shaded (SaC) by the tree canopy (Fig. 2F). Unconstrained ordination analysis (Fig. 2A) explains 25.3% of variance along the first axis, where assemblages preferring sunny and exposed sites (SjC) are located on the left, while those occupying shaded and moist rock crevices (SaC, CfC) are on the lower right side of the diagram. The ecology of chasmophytic assemblages is even better reflected in results of constrained ordination analyses (Figs. 2B–F). CCA analysis of all assemblages (Fig. 2B) yields coverage ($F = 5.56$) and number of bryophyte taxa (2.42), elevation (5.47) and number of vascular plants (1.85) as statistically significant explanatory variables ($p < 0.002$). In coverage and number of respective bryophyte taxa assemblages of the cluster CfC, and partly of SaC dominate. These stands prefer sciophytic, moist, nutrient-rich and higher-elevated sites. In contrast, assemblages of cluster SjC, depauperate in number and coverage of bryophyte taxa, prefer open sites along the broad elevational range. Assemblages of the cluster SaC seem to be ecologically somewhat intermediate, preferring semi-



or fully shaded sites most commonly within thermophytic beech forests of the association *Seslerio autumnalis-Fagetum*. Elevation is negatively correlated with the number of vascular plant taxa, where a group of SaC assemblages from lower elevated sites is well differentiated from all other stands in floristic richness, distinct composition as well as most thermophytic site conditions.

Using an inclusion rule in order to define a subset of species that fit the quality criterion of representing the percentage of variability in species values explained by the explanatory variables, the following groups of species are identified (Fig. 2E): *Sesleria juncifolia*, *Athamanta cretensis*, *Silene saxifraga* subsp. *hayekiana*, *Globularia cordifolia* and *Campanula tommasiniana* for the group SjC; *Cystopteris fragilis*, *Mycelis muralis*, *Neckera crispa*, *Ctenidium molluscum*, *Geranium robertianum*, *Plagiochila porelloides*, *Brachythecum tommasinii* and *Plasteurhynchium striatulum* for the group CfC; *Sesleria autumnalis*, *Fraxinus ornus*, *Ceterach officinarum*, *Leptodon smithii*, *Bromus erectus* and *Cololejeunea calcarea* for the group SaCM, and *Quercus ilex*, *Salvia officinalis*, *Coronilla emerus* subsp. *emeroides*, *Allium pulchellum* subsp. *carinatum*, *Asparagus acutifolius* and *Hedera helix* for the group SaCS.

The results of the non-parametric test for equal medians of environmental values of chasmophytic assemblages (Tab. 3) show significant differences ($p < 0.05$) in both site parameters and Pignatti's indicator values (Tab. 3). Generally, moisture (U, $H=87.94$) and light conditions (L, 84.91) show the highest probability of non-equal medians of environmental values in the studied assemblages, followed by soil reaction (R, 80.78), coverage of bryophytes (76.61), nutrients (N, 67.85) and elevation (50.82). Post-hoc pairwise comparisons suggest that stands from the cluster »A« (SjC) significantly differ from all the other groups in light conditions, moisture, soil reaction, amount of nutrients and coverage of bryophytes. On the other hand, group CfC differs significantly from all the other groups in moisture and soil reaction, while the group SaC represents relatively mesophytic assemblages. According to initial cluster, and subsequent unconstrained and constrained ordination analyses, further easily recognized groups of assemblages are recognized based on specifics in site ecology and floristic assembly. Within the group SjC, a subset of stands SjCS, characterized by the presence and high coverage of *Sedum album*, *Satureja montana*

Fig. 2. Unconstrained and constrained analyses of chasmophytic assemblages with *Campanula tommasiniana* on Mt. Učka (NW Adriatic) according to site parameters and Pignatti's indicator values. **A** – DCA diagram, length of gradient 4.071, eigenvalues 0.533, 0.340, 0.212, 0.159; cumulative percentage variance of species data: 6.4, 10.6, 13.1, 15.0; **B** – CCA diagram according to site parameters and Pignatti indicator values; eigenvalues: 0.429, 0.362, 0.151, 0.122; cumulative percentage variance of species data: 5.2, 9.6, 11.4, 12.8; **C** – CCA diagram of stands of the assemblage group SjC; eigenvalues: 0.284, 0.248, 0.164, 0.140; cumulative percentage variance of species data: 5.4, 10.1, 13.3, 15.9; **D** – CCA diagram of stands of the assemblage group SaC; eigenvalues: 0.386, 0.231, 0.297, 0.257; cumulative percentage variance of species data: 8.8, 14.1, 20.9, 26.8; **E** – CCA diagram of species-environmental data using inclusion rule (25%) option; **F** – ternary plot for the three types of assemblages according to light condition of sites. Full lines – explanatory variables: site parameters (elevation, number of vascular plants, number of bryophytes, coverage of bryophytes, coverage of stoniness); dashed lines – co-variables: passively projected Pignatti indicator values (L – light conditions, T – temperature, R – soil reaction, C – continentality, U – moisture, N – nutrients). Syntaxonomy is explained in the text following figure 3.

Tab. 3. Results of Kruskal-Wallis tests and Mann-Whitney's pairwise comparisons (post-hoc tests) of environmental affinities of the studied groups of chasmophytic assemblages with *Campanula tommasiniana* on Mt. Učka (NW Adriatic), based on environmental data, phytosociological parameters and Pignatti's indicator values

parameter	Syntaxa	Mann-Whitney's pairwise comparisons Bonferroni corrected/uncorrected						Kruskal-Wallis test H/p	
		SjCS	SjCGM	SjCGS	SjCC	CfC	SaCS		SaCM
Elevation	SjCS		0.0001	0.0001	0.0001	0.1159	0.002	0.6103	50.82/p < 0.05
	SjCGM	0.0001		0.904	0.4871	0.0025	0.0004	0.0001	
	SjCGS	0.01432	1		0.6768	0.0074	0.0001	0.0002	
	SjCC	0.0198	1	1		0.0251	0.0001	0.0001	
	CfC	1	0.5219	0.1539	0.5279		0.0001	0.0057	
	SaCS	0.0376	0.0085	0.0085	0.0130	0.0161		0.0001	
	SaCM	1	0.0016	0.0001	0.0078	0.1195	0.0038		
Cover. (%) of bryoph.	SjCS		0.0499	0.4075	0.0363	0.0001	0.075	0.0001	76.61/p < 0.05
	SjCGM	1		0.0801	0.0001	0.0001	0.0001	0.0001	
	SjCGS	1	1		0.0001	0.0001	0.0001	0.0001	
	SjCC	0.7628	0.0003	0.0133		0.0001	0.2373	0.0019	
	CfC	0.0002	0.0001	0.0001	0.0001		0.136	0.0001	
	SaCS	1	0.0079	0.1817	1	1		0.4016	
	SaCM	0.0026	0.0001	0.0001	0.0403	0.0001	1		
L	SjCS		0.0015	0.0025	0.2439	0.0001	0.0018	0.0001	84.91/p < 0.05
	SjCGM	0.0309		0.0983	0.0027	0.0001	0.0001	0.0001	
	SjCGS	0.0534	1		0.0276	0.0001	0.0001	0.0001	
	SjCC	1	0.0573	0.5788		0.0001	0.0001	0.0001	
	CfC	0.0001	0.0001	0.0001	0.0001		0.1386	0.3069	
	SaCS	0.0376	0.0086	0.0085	0.0130	1		0.3442	
	SaCM	0.0012	0.0001	0.0001	0.0001	1	1		

Tab. 3. – continued

parameter	Syntaxa	Mann-Whitney's pairwise comparisons Bonferroni corrected/uncorrected						Kruskal-Wallis test H/p	
		SjCS	SjCGM	SjCGS	SjCC	CfC	SaCS		SaCM
R	SjCS		0.0001	0.0001	0.0025	0.0003	0.5169	0.1682	80.78/p < 0.05
	SjCGM	0.0042		0.1734	0.0289	0.0001	0.0011	0.0001	
	SjCGS	0.0001	1		0.0001	0.0001	0.0001	0.0001	
	SjCC	0.052	0,6078	0,0037		0.0001	0.0057	0.0004	
	CfC	0,0066	0,0001	0,0001	0,0002		0,0098	0,0001	
	SaCS	1	0,0235	0,0097	0,1203	0,2048		0,7172	
	SaCM	1	0,0003	0,0001	0,0009	0,0273	1		
N	SjCS		0.4502	0.5714	0.9246	0.0004	0.0445	0.0001	67.85/p < 0.05
	SjCGM	1		0.4485	0.5656	0.0001	0.0018	0.0001	
	SjCGS	1	1		0.9209	0.0001	0.0063	0.0001	
	SjCC	1	1	1		0.0001	0.0012	0.0002	
	CfC	0.0001	0.0001	0.0001	0.0002		0.067	0.9122	
	SaCS	0.9436	0.0384	0.1325	0.2475	1		0.1110	
	SaCM	0.0039	0.0004	0.0009	0.0004	1	1		
U	SjCS		0.0019	0.0983	0.1472	0.0001	0.008	0.0001	87.94/p < 0.005
	SjCGM	0.0407		0.0313	0.0001	0.0001	0.0004	0.0001	
	SjCGS	1	0.6571		0.0023	0.0001	0.0001	0.0001	
	SjCC	1	0.0012	0.0608		0.0001	0.2479	0.0001	
	CfC	0.0003	0.0001	0.0001	0.0001		0.0004	0,001	
	SaCS	0.1682	0.0085	0.0085	1	0.0088		0,012	
	SaCM	0.0011	0.0001	0.0006	0.0014	0.0213	0.0252		

SjCS – *Seslerio juncifoliae*-*Campanuletum sedetosum*; SjCGM – *Seslerio juncifoliae*-*Campanuletum globularietosum* var. *Micromeria thymifolia*; SjCGS – *Seslerio juncifoliae*-*Campanuletum globularietosum* var. *Stachys subcrenata*; CfC – *Cystopteri fragilis*-*Campanuletum*; SaCS – *Seslerio autumnalis*-*Campanuletum* var. *Salvia officinalis*; SaCM – *Seslerio autumnalis*-*Campanuletum* var. *Mycelis muralis*. L – light conditions, R – soil reaction, N – nutrients, U – moisture. Values in bold are statistically significant.

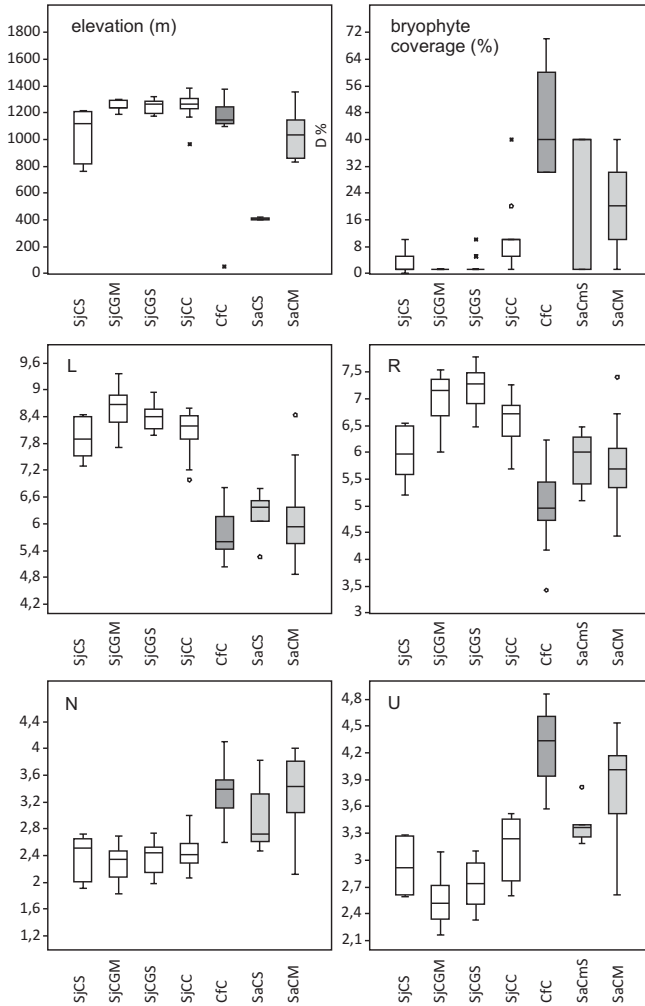


Fig. 3. Box plots of environmental parameters (elevation, coverage of bryophytes) and Pignatti's indicator values (L – light conditions, R–soil reaction, N – nutrients, U – moisture) of floristically distinct chasmophytic assemblages with *Campanula tommasiniana* on Mt. Učka (NW Adriatic). Syntaxonomy (x-axis) is explained in the text below.

subsp. *variegata* and *Syntrichia ruralis* var. *ruralis*, prefers warmer, open to semi shaded and significantly lower-elevated sites and relatively lower soil pH reaction in an otherwise broad elevational range (Tab. 3, Figs. 2C, 3). SjCC subset is characterized by a significantly higher number and coverage of bryophytes, particularly *Ctenidium molluscum*, *Neckera crispa* and *Fissidens dubius* and prefers moister rock crevices in higher elevated sites. The two subsets, SjCGM and SjCGS, respectively, although differing well floristically, show the only significant differentiation in site moisture where the subset SjCGM, characterized by the presence and high coverage of *Globularia cordifolia*, *Hieracium bupleuroides*, *Micromeria thymifolia* and *Scrophularia laciniata*, prefers slightly dryer and more exposed sites. Among the explanatory variables, four statistically significant parameters are identified by

CCA analysis (Fig. 2B) : coverage (F=2.69) and number (1.80) of bryophytes, elevation (2.70) and number of vascular plants (2.00). Two subsets of assemblages is are recognized within the group SaC (Fig. 2D, Tabs.1, 3): SaCS, characterized by the exclusive occurrence, high frequency and coverage of *Coronilla emerus* subsp. *emeroides*, *Asparagus acutifolius*, *Quercus ilex*, *Hedera helix* and *Salvia officinalis*, developed on significantly drier and lower elevated sites; and SaCM, where the differential group of taxa is represented by *Cyclamen purpurascens*, *Galeobdolon flavidum* and *Mycelis muralis*, species otherwise frequent in the beech forest understorey. Here, CCA analysis (Fig. 2D) gives only elevation (F = 2.64) and number of bryophytes (1.74) as statistically significant explanatory variables.

Hemicyptophytes achieve the highest coverage in group StS and the lowest in groups SjCC and CfC (Tab. 1). Chamaephytes are most abundant in groups SjC, while they are absent in group CfC. In number and coverage of phanerophytes, the group SaCS departs significantly from all the other groups. Accordingly, no therophytes were surveyed in this group.

Syntaxonomy, nomenclature and typification of the syntaxa

We propose three new associations, seven new lower ranked syntaxa and the following classification scheme:

- Asplenietea trichomanis* Br.-Bl. et Maire 1934 corr. Oberd. 1977
- Potentilletalia caulescentis* Br.-Bl. in Br.-Bl. et Jenny 1926
- Potentillion caulescentis* Br.-Bl. in Br.-Bl. et Jenny 1926
- Physoplexido-Potentillenion caulescentis* Theurillat in Theurillat et al. 1995
- Seslerio juncifoliae-Campanuletum tommasinianae* ass. nov. (**SjC**)
- sedetosum albae* subass. nov. (**SjCS**)
- globularietosum cordifoliae* subass. nova (**SjCG**)
- var. *Micromeria thymifolia* var. nova (**SjCGM**)
- var. *Stachys subcrenata* var. nova (**SjCGS**)
- ctenidietosum mollusci* subass. nova (**SjCC**)
- Moehringion muscosae* Horvat et Horvatić 1962
- Seslerio autumnalis-Campanuletum tommasinianae* ass. nova (**SaC**)
- (=*Campanuletum tommasinianae-justiniana*e Horvatić 1960 nom. nud.)
- var. *Salvia officinalis* (**SaCS**)
- var. *Mycelis muralis* (**SaCM**)
- Cystopteri fragilis-Campanuletum tommasinianae* ass. nova (**CfC**)

Characteristic group of taxa for the association *Seslerio juncifoliae-Campanuletum* are *Campanula tommasiniana*, *Sesleria juncifolia*, *Athamanta turbith* and *Silene saxifraga* subsp. *hayekiana* (Tab. 4, On-line Supplement Tab. 2); differential group of taxa for the subassociation *sedetosum* are *Sedum album*, *Satureja montana* subsp. *variegata* and *Syntrichia ruralis* var. *ruralis*; differential group of taxa for the subassociation *globularietosum* are *Globularia cordifolia* and *Hieracium bupleuroides* (*Micromeria thymifolia*, *Scrophularia laciniata* and *Stachys subcrenata*, *Tortella densa* for the variants *Micromeria thymifolia* and *Stachys subcrenata*, respectively); differential group of taxa for the subassociation *ctenidietosum mollusci* are *Ctenidium molluscum*, *Neckera crispa* and *Fissidens dubius*. A characteristic group of taxa for the association *Seslerio autumnalis-Campanuletum* are

Tab. 4. Synoptic table of chasmophytic syntaxa with *Campanula tommasiniana* on Mt. Učka (NW Adriatic)

Association			SjC						CfC		SaC					
Subassociation			S		G		C				S		M			
Variant					M		S									
Characteristic and differential groups of taxa																
PPc	Cam tom	<i>Campanula tommasiniana</i>	100	¹⁹	100	¹²	100	¹³	100	¹⁵	100	¹⁴	100	¹³	100	¹⁸
ES	Ses jun	<i>Sesleria juncifolia</i>	44	⁹	100	¹⁵	100	¹⁶	93	¹⁵	30	²	.		20	²
PPc	Ath tur	<i>Athamanta turbith</i>	78	¹³	53	⁴	72	⁶	79	⁸	9		.		36	²
PPc	Sil sax	<i>Silene saxifraga</i> subsp. <i>hayekiana</i>	67	⁷	76	⁸	72	⁶	.		.		.		4	¹
KC	Sed alb	<i>Sedum album</i>	89	¹⁰	.		.		7	²	.		.		20	¹
Ss	Sat mon	<i>Satureja montana</i>	67	⁸	18	¹	6	¹	14	²	.		83	⁷	24	²
B	Syn rur	<i>Syntrichia ruralis</i> var. <i>ruralis</i>	56	¹⁰	12	³	.		14	²	.		.		24	²
ES	Glo cor	<i>Globularia cordifolia</i>	.		88	⁹	89	⁹	14	¹	.		.		.	
Pc2	Hie bup	<i>Hieracium bupleuroides</i>	11	²	35	²	50	⁴	14	²	.		.		4	¹
PPc	Mic thy	<i>Micromeria thymifolia</i>	44	⁶	94	¹⁰	17	¹	36	³	.		.		4	¹
AT	Ser lac	<i>Scrophularia laciniata</i>	33	²	53	⁴	17	¹	43	³	.		.		12	¹
Ss	Sta sub	<i>Stachys subcrenata</i>	.		12	²	56	⁵	21	²	.		.		.	
B	Tor den	<i>Tortella densa</i>	.		.		33	¹⁰	
B	Cte mol	<i>Ctenidium molluscum</i>	11	²	18	⁵	11	³	93	¹³	100	¹⁴	50	⁷	64	⁶
B	Nec cri	<i>Neckera crispa</i>	22	⁴	6	²	17	⁴	64	⁹	96	¹⁵	17	²	76	¹⁰
B	Fis dub	<i>Fissidens dubius</i>	.		.		11	²	43	⁶	48	³	50	⁴	24	²
FS	Myc mur	<i>Mycelis muralis</i>		87	⁷	.		48	⁴
CF	Cys fra	<i>Cystopteris fragilis</i>	.		.		.		7	¹	83	⁸	.		8	²
Tr	Ara alp	<i>Arabis alpina</i>	.		.		.		14	²	52	⁴	.		.	
B	Pla por	<i>Plagiochila porelloides</i>		43	³	.		.	
B	Mni tho	<i>Mnium thomsonii</i>		30	²	.		.	
B	Hom ser	<i>Homalothecium sericeum</i>	22	⁵	35	¹¹	39	¹²	50	⁷	35	³	83	⁸	84	⁸
Qp	Ses aut	<i>Sesleria autumnalis</i>	11	¹	6	¹	.		14	²	22	¹	100	⁶	60	⁶
	Nec bes	<i>Neckera besseri</i>	22	³	6	¹	.		.		13	²	50	⁹	52	⁵

Tab. 4. – continued

		Association		SjC				CfC		SaC						
		Subassociation		G		S		C		S		M				
		Variant		M		S		C		S		M				
Co	Cor eme	<i>Coronilla emerus</i> subsp. <i>emeroides</i>	4	1	100	8	.				
PRa	Asp acu	<i>Asparagus acutifolius</i>	4	1	100	6	.				
Qi	Que ile	<i>Quercus ilex</i>	67	3	.				
QF	Hed hel	<i>Hedera helix</i>	4	1	67	3	.				
B	Lep smi	<i>Leptodon smithii</i>	11	2	12	3	.	.	.	67	8	8	2			
Ss	Sal off	<i>Salvia officinalis</i>	50	2	.	.			
AF	Cyc pur	<i>Cyclamen purpurascens</i>	22	2	6	1	.	7	2	39	3	33	1	72	4	
FS	Gal fla	<i>Galeobdolon flavidum</i>	9	1	.	.	32	2	
Other vascular plants																
AT	Asp tri	<i>Asplenium trichomanes</i>	67	10	35	3	22	2	50	4	100	11	83	6	92	11
AT	Asp rtm	<i>Asplenium ruta-muraria</i>	100	8	76	7	44	3	79	7	96	8	17	2	64	6
GS	Tha min	<i>Thalictrum minus</i>	33	2	12	2	44	4	29	2	4	1	33	2	12	1
CrP	Cym mur	<i>Cymbalaria muralis</i>	33	2	24	1	11	1	50	3	91	8	.	.	32	3
BV	Rha rup	<i>Rhamnus rupestris</i>	33	5	18	1	6	1	7	2	.	.	33	2	16	2
EP	Cal var	<i>Calamagrostis varia</i>	22	2	24	2	11	2	14	2	9	2	.	.	8	2
Ss	Gal luc	<i>Galium lucidum</i>	44	2	12	2	6	1	29	3	.	.	33	1	.	.
GS	Ant ram	<i>Anthericum ramosum</i>	11	2	.	.	17	2	29	3	9	1	17	2	24	2
Ss	All ter	<i>Allium saxatile</i> subsp. <i>tergestinum</i>	22	2	18	1	39	2	14	2	24	2
ES	Ran car	<i>Ranunculus carinthiacus</i>	.	.	6	1	11	1	36	2	22	2	.	.	8	1
Qp	Sor ari	<i>Sorbus aria</i>	11	1	.	.	11	1	7	1	.	.	17	2	4	1
FB	Teu mon	<i>Teucrium montanum</i>	22	2	18	2	50	4	33	2	.	.
Qp	Fra orn	<i>Fraxinus ornus</i>	11	1	4	1	50	5	20	2
Qp	Ost car	<i>Ostrya carpinifolia</i>	44	3	7	1	.	.	50	2	16	2
AT	Sax pan	<i>Saxifraga paniculata</i>	.	.	6	1	22	1	29	2	4	1
	Car ten	<i>Carduus tenuiflorus</i>	11	1	35	2	17	2	8	1

Tab. 4. – continued

Association			SjC				CfC		SaC					
Subassociation			S	G	S	C			S	M				
Variant			M											
VP	Hie mur	<i>Hieracium murorum</i>	.	.	6	¹	14	²	.	17	²	16	¹	
LPs	Ros dum	<i>Rosa dumalis</i>	44	²	.	.	7	¹	4	¹	.	8	¹	
Pc1	Ker sax	<i>Kernera saxatilis</i>	.	12	²	6	¹	.	9	²	.	8	¹	
Tr	Sen rup	<i>Senecio rupestris</i>	11	¹	.	.	7	²	4	¹	.	8	¹	
AT	Cet off	<i>Ceterach officinarum</i>	56	⁶		67	⁶	28	²
	Eup ill	<i>Euphrasia illyrica</i>	11	²	.	11	²	29	²	
ES	Sen abr	<i>Senecio abrotanifolius</i>	.	29	²	22	²	57	⁴	
CF	Pse alb	<i>Pseudofumaria alba</i>	22	¹	30	⁴	.	12	²	
VP	Val tri	<i>Valeriana tripteris</i>	14	²	39	³	.	20	²	
	Thy sp	<i>Thymus</i> sp.	.	35	³	28	²	7	¹	
AT	Sem tec	<i>Sempervivum tectorum</i>	.	12	²	17	²	29	²	
Qp	Ara tur	<i>Arabis turruta</i>	4	¹	33	²	36	²
FB	Bro ere	<i>Bromus erectus</i> agg.	7	¹	.		67	³	8	²
PP	Ade gla	<i>Adenostyles glabra</i>	7	¹	30	²	.	16	²	
Ss	Cam mar	<i>Campanula marchesettii</i>	11	²	12	²	17	¹	
CF	Moe mus	<i>Moehringia muscosa</i>	22	²	9	²	.	20	¹	
Tr	Pel all	<i>Peltaria alliacea</i>	33	²	.	.	7	¹	.		.	12	¹	
EP	Bup sal	<i>Bupthalmum salicifolium</i>	.	6	²	.	14	²	.		.	12	²	
QF	Poa nem	<i>Poa nemoralis</i>	7	²	13	²	.	8	¹	
BV	Rha sax	<i>Rhamnus saxatilis</i>	.	6	¹	17	¹	7	²	
ES	Gen sym	<i>Gentiana lutea</i> subsp. <i>symphyandra</i>	.	12	²	6	¹	14	²	
VP	Cle alp	<i>Clematis alpina</i>	.	6	¹	.	7	²	.		.	4	¹	
AT	Asp vir	<i>Asplenium viride</i>	7	¹	13	²	.	4	¹	
QF	Car dig	<i>Carex digitata</i>	11	¹	4	¹	.	8	¹	
M	Gal mol	<i>Galium mollugo</i>	11	¹	.	.	7	¹	.		.	4	¹	

Tab. 4. – continued

		Association	SjC				CfC		SaC		
		Subassociation	S	M	G	S	C			S	M
		Variant									
CP	Cle vit	<i>Clematis vitalba</i>	7 ¹	.	.	17 ²	.
MA	Ver alb	<i>Veratrum album</i>	.	6 ¹	.	.	.	4 ¹	.	.	4 ¹
Tr	Ger mac	<i>Geranium macrorhizum</i>	44 ⁶	4 ¹
PPc	Ara sco	<i>Arabis scopoliana</i>	.	.	39 ³	29 ³
TA	Ger rob	<i>Geranium robertianum</i>	57 ⁴	.	.	12 ¹
MA	Sax rot	<i>Saxifraga rotundifolia</i>	30 ³	.	.	4 ²
Tr	Teu aur	<i>Teucrium arduinii</i>	33 ³	12 ¹
MA	Sen fuc	<i>Senecio fuchsii</i>	35 ²	.	.	20 ²
FB	Car hum	<i>Carex humilis</i>	50 ²	.	8 ¹
GS	Ros pim	<i>Rosa pimpinellifolia</i>	.	12 ²	33 ²
PPc	Cam jus	<i>Campanula justiniana</i>	26 ²	.	.	4 ¹
EP	All eri	<i>Allium ericetorum</i>	33 ²	4 ¹
PRa	Jun oxy	<i>Juniperus oxycedrus</i>	33 ²	.	4 ¹
Tr	Cam coc	<i>Campanula cochleariifolia</i>	.	.	17 ¹	21 ²
Pc1	Pri aur	<i>Primula auricula</i>	.	.	6 ¹	14 ²
AT	Pol vul	<i>Polypodium vulgare</i> agg.	13 ²	.	.	8 ²
Ss	Sat lib	<i>Satureja subspicata</i> subsp. <i>liburnica</i>	.	12 ¹	11 ²
Qp	Euo ver	<i>Euonymus verrucosus</i>	11 ¹	20 ²
QF	Gal syl	<i>Galium sylvaticum</i>	9 ¹	.	.	16 ²
VP	Las kra	<i>Laserpitium krapfii</i>	9 ¹	.	.	16 ²
FB	All pul	<i>Allium carinatum</i> subsp. <i>pulchellum</i>	4 ¹	.	33 ¹	.
Sc	Lig seg	<i>Ligusticum seguerii</i>	22 ²	6 ¹
ES	Leo alp	<i>Leontopodium alpinum</i>	.	.	6 ¹	14 ²
QF	Pyr pir	<i>Pyrus piraster</i>	11 ¹	17 ²	.
PPc	Cam pyr	<i>Campanula pyramidalis</i>	17 ²	4 ¹

Tab. 4. – continued

	Association	Subassociation	S		SjC		C	CfC		SaC	
			S	M	G	S		S	M		
							Variant				
Qp	Ace obt	<i>Acer obtusatum</i>	11	1	4	1
ES	Phy orb	<i>Phyteuma orbiculare</i>	.	6	1	6	1
AF	Cal gra	<i>Calamintha grandiflora</i>	4	1	4	1
FS	Fag syl	<i>Fagus sylvatica</i>	4	1	4	1
MA	Tha aqu	<i>Thalictrum aquilegifolium</i>	4	1	4	1
AP	Lam mac	<i>Lamium maculatum</i>	22	4
KC	Sed sex	<i>Sedum sexangulare</i>	11	2
	Eup sp	<i>Euphorbia</i> sp.	11	1
O	Lil bul	<i>Lilium bulbiferum</i>	11	1
M	Lot cor	<i>Lotus corniculatus</i>	11	1
AF	Rha fal	<i>Rhamnus fallax</i>	11	1
FB	Glo wil	<i>Globularia willkomii</i>	.	12	2
FB	Dor ger	<i>Dorycnium germanicum</i>	.	6	1
	Fes sp	<i>Festuca</i> sp.	.	6	1
Ps	Jun com	<i>Juniperus communis</i> subsp. <i>communis</i>	.	6	1
FS	Lab alp	<i>Laburnum alpinum</i>	.	6	1
FB	Mel cil	<i>Melica ciliata</i>	.	6	1
AT	Dia syl	<i>Dianthus sylvestris</i> agg.	.	.	.	11	1
Ss	Gen syl	<i>Genista sylvestris</i>	.	.	.	6	1
PPc	Dap alp	<i>Daphne alpina</i>	.	.	.	6	1
Pc2	Pot cau	<i>Potentilla caulescens</i>	.	.	.	6	1
EP	Epi atr	<i>Epipactis atrorubens</i>	7	1	.	.
ES	Eri pol	<i>Erigeron polymorphus</i>	7	1	.	.
FS	Mer per	<i>Mercurialis perennis</i>	13	2	.	.
FS	Epi mon	<i>Epilobium montanum</i>	9	1	.	.

Tab. 4. – continued

		Association	SjC				CfC		SaC		
		Subassociation	S	M	G	S	C				
		Variant							S	M	
AT	Sed his	<i>Sedum hispanicum</i>	4	1	.	.
TA	Ace pse	<i>Acer pseudoplatanus</i>	9	1	.	.
MA	Aco var	<i>Aconitum variegatum</i>	4	1	.	.
Tr	Ant fum	<i>Anthriscus fumarioides</i>	4	1	.	.
TA	Aru dio	<i>Aruncus dioicus</i>	4	1	.	.
	Hier sp	<i>Hieracium</i> sp.	4	1	.	.
TA	Pol acu	<i>Polystichum aculeatum</i>	4	1	.	.
Qp	Tam com	<i>Tamus communis</i>	4	1	.	.
QP	Cot cog	<i>Cotinus coggygria</i>	17	2
Qp	Mel mel	<i>Melittis melissophyllum</i>	33	2
	Rub sp2	<i>Rubus</i> sp.	33	2
PRa	Lon etr	<i>Lonicera etrusca</i>	17	1
Co	Vio sco	<i>Viola alba</i> subsp. <i>scotophylla</i>	33	1
Sc	Aet sax	<i>Aethionema saxatile</i>	17	2
PPc	Cam istr	<i>Campanula fenestrellata</i> subsp. <i>istriaca</i>	17	2
Ss	Cen rup	<i>Centaurea rupestris</i>	17	2
Ss	Cre cho	<i>Crepis chondrylloides</i>	17	2
R	Hel ita	<i>Helichrysum italicum</i>	17	2
CrP	Par jud	<i>Parietaria judaica</i>	17	2
GS	Peu cer	<i>Peucedanum cervaria</i>	17	2
Qp	Que pub	<i>Quercus pubescens</i>	17	2
QF	Ros arv	<i>Rosa arvensis</i>	17	2
	Rub sp1	<i>Rubus</i> sp.	17	2
	Rub ulm	<i>Rubus ulmifolius</i>	17	2
Qp	Dig lae	<i>Digitalis laevigata</i>	16 ²

Tab. 4. – continued

		Association		SjC					CfC		SaC						
		Subassociation		S		G		C									
		Variant		M		S				S		M					
FB	Dia mon	<i>Dianthus monspessulanus</i>		8	2				
Qp	Mer ova	<i>Mercurialis ovata</i>		12	2				
FB	Lin cat	<i>Linum catharticum</i>		4	1				
Qp	Cam per	<i>Campanula persicifolia</i>		4	1				
VP	Ros pen	<i>Rosa pendulina</i>		4	1				
TG	Vin hir	<i>Vincetoxicum hirundinaria</i>		8	1				
FB	Ara hir	<i>Arabis hirsuta</i>		4	1				
Qp	Cni sil	<i>Cnidium silaifolium</i>		4	1				
Tr	Cys mon	<i>Cystopteris montana</i>		4	1				
AF	Eup car	<i>Euphorbia carniolica</i>		4	1				
Qp	Hyp mon	<i>Hypericum (montanum?)</i>		4	1				
FB	Koe pyr	<i>Koeleria pyramidata</i>		4	1				
M	Leo his	<i>Leontodon hispidus</i>		4	1				
	Ros sp	<i>Rosa</i> sp.		4	1				
FS	Sal glu	<i>Salvia glutinosa</i>		4	1				
AT	Sed max	<i>Sedum maximum</i>		4	1				
Qp	Tan cor	<i>Tanacetum corymbosum</i>		4	1				
B	Bryophytes and lichens																
	Tor tor	<i>Tortella tortuosa</i>		67	9	82	31	78	21	86	13	52	4	67	7	72	6
	Sch sp	<i>Schistidium</i> sp.		44	6	47	17	50	15	36	4	65	5	33	3	68	6
	Hom phi	<i>Homalothecium philippeanum</i>		22	5	6	2	17	4	43	7	57	6	33	4	52	6
	Tor nit	<i>Tortella nitida</i>		33	6	18	5	17	5	7	2	4	1	50	5	20	2
	Bry sp	<i>Bryum</i> sp.		44	6	6	2	6	2	29	3	35	2	17	2	24	2
	Hyp cup	<i>Hypnum cupressiforme</i> var. <i>cupressiforme</i>		11	2	6	2	6	2	21	2	4	1	33	3	24	2

Tab. 4. – continued

	Association Subassociation Variant	SjC								CfC		SaC	
		S		G		C				S	M		
			M	S		S							
Pla str	<i>Plasteurhynchium striatulum</i>	11	² 6	¹ .		7	¹ .	57	⁶ .	50	⁶ 80	⁸ .	
Enc str	<i>Encalypta streptocarpa</i>	11	² 12	⁴ .		29	⁴ .	17	¹ .	33	³ 24	² .	
Por pla	<i>Porella platyphylla</i>	11	² .	. .		14	² .	13	¹ .	33	³ 48	⁴ .	
Wei sp	<i>Weissia</i> sp.	.	. .	6	² .	14	² .	4	¹ .	33	³ 20	¹ .	
Pse cat	<i>Pseudoleskeela catenulata</i>	.	. .	6	² .	14	² .	39	³ .	17	² 4	² .	
Ano vit	<i>Anomodon viticulosus</i>	33	⁷	30	³ .	33	⁴ 68	⁸ .	
Ort cup	<i>Orthotrichum cupulatum</i>	44	¹⁰ 18	⁶	4	¹ .	.	36	³ .	
Rad com	<i>Radula complanata</i>		29	⁴ .	57	⁵ .	17	² 36	² .	
Col cal	<i>Cololejeunea calcarea</i>		14	² .	30	² .	50	⁵ 8	¹ .	
Nec com	<i>Neckera complanata</i>		7	¹ .	39	² .	17	² 56	⁵ .	
Dit fle	<i>Ditrichum flexicaule</i>	11	² .	. .	28	⁸ 29	⁴	
Sca sp	<i>Scapania</i> sp.	17	⁵ 7	² .	4	¹	
Wei con	<i>Weissia controversa</i> var. <i>controversa</i>	22	³ 6	²	4	¹ .	
Hyp lac	<i>Hypnum cupressiforme</i> var. <i>lacunosum</i>	.	. .	6	² 11	³	4	¹ .	
Enc vul	<i>Encalypta vulgaris</i>	11	² 7	¹ .	9	¹	
Nec pen	<i>Neckera pennata</i>	13	² .	17	¹ 8	¹ .	
Ort ano	<i>Ortotrichum anomalum</i>	4	¹ .	33	² 4	¹ .	
Myu jul	<i>Myurella julacea</i>	.	. .	6	¹ .	. .	7	¹ .	13	² .	.	.	
Sco cir	<i>Scorpiurum circinatum</i>	4	¹ .	33	⁵ .	.	
Sca asp	<i>Scapania aspera</i>	6	² 21	⁴	
Ped int	<i>Pedinophyllum interruptum</i>	30	³ .	.	4	¹ .	
Ano att	<i>Anomodon attenuatus</i>	9	² .	.	4	¹ .	
Tor fra	<i>Tortella tortuosa</i> var. <i>fragillifolia</i>	11	²	8	² .	
Bra tom	<i>Brachythecium tommasinii</i>	22	² .	.	8	¹ .	
Cir cra	<i>Cirriphyllum crassinervium</i>	22	² .	.	4	¹ .	

Tab. 4. – continued

	Association Subassociation Variant	S		SjC G		C		CfC		SaC		
		S	M	S	S	C	CfC	CfC	S	M		
Sci flo	<i>Eurhynchium flotowianum</i>	7	²	.	.	.	4	¹
Ort int	<i>Orthothecium intricatum</i>	4	¹	.	4	¹
Fru dil	<i>Frullania dilatata</i>	4	¹	.	4	¹
Lep sp	<i>Leptogium</i> sp.	22	³
Tor bre	<i>Tortella tortuosa</i> var. <i>brevifolia</i>	11	²
Fis tax	<i>Fissidens taxifolius</i> ssp. <i>taxifolius</i>	11	²
Tor mur	<i>Tortulla muralis</i> var. <i>muralis</i>	11	²
Gri pul	<i>Grimmia pulvinata</i>	.	.	.	6	²
Cam elo	<i>Campylium elodes</i>	.	.	.	6	²
Bar cro	<i>Barbula crocea</i>	14	²
Ort sp	<i>Ortotrichum</i> sp.	7	²
Dis cap	<i>Distichium capillaceum</i>	7	¹
Jun sub	<i>Jungermannia subulata</i>	7	²
Mni mar	<i>Mnium marginatum</i>	13	²	.	.	.
Apo pub	<i>Apometzgeria pubescens</i>	4	²	.	.	.
Pla cus	<i>Plagiomnium cuspidatum</i>	4	²	.	.	.
Pla und	<i>Plagiomnium undulatum</i>	4	²	.	.	.
Tha alo	<i>Thamnobryum alopecurum</i>	4	²	.	.	.
Thu tam	<i>Thuidium tamariscinum</i>	4	²	.	.	.
Euc ver	<i>Eucladium verticillatum</i>	4	¹	.	.	.
Eur str	<i>Eurhynchium striatum</i>	4	¹	.	.	.
Mni ste	<i>Mnium stellare</i>	4	¹	.	.	.
Hom lut	<i>Homalothecium lutescens</i>	4	¹	.	.	.
Bra sta	<i>Brachythecium starkei</i>	4	¹	.	.	.
Eur sch	<i>Eurhynchium schleicheri</i>	4	¹	.	.	.

Tab. 4. – continued

	Association Subassociation Variant	SjC				CfC		SaC	
		S	M	G	C			S	M
				S					
Met con	<i>Metzgeria conjugata</i>	4	¹	.	.
Sol sac	<i>Solorina saccata</i>	4	¹	.	.
Syn mon	<i>Syntrichia montana</i>		17	²
Leu sci	<i>Leucodon sciuroides</i>		20	²
Bar sp	<i>Barbula</i> sp.		4	¹
Bra sal	<i>Brachythecium salebrosum</i>		4	¹
Pre qua	<i>Preissia quadrata</i>		4	¹
Hyp and	<i>Hypnum andoi</i>		4	¹
Hyp jut	<i>Hypnum jutlandicum</i>		4	¹
Pte fil	<i>Pterigynandrum filiforme</i>		4	¹
Sca aeq	<i>Scapania aequiloba</i>		4	¹
Weï bra	<i>Weissia brachycarpa</i>		4	¹

AF-Aremonii-Fagion; **AP**-Aegopodium podagrariae; **B**-Bryophytes and lichens; **BV**-Berberidion; **CF**-Cystopteridion fragilis; **Co**-Carpinion orientalis; **CP**-Crataego-Prunetea; **CrP**-Centrantho rubri-Parietarion; **EP**-Erico-Pinetea; **FB**-Festuco-Brometea; **GS**-Geranium sanguinei; **LPS**-Ligustro-Prunenion spinosae; **Pc1**-Potentilletalia caulescentis; **PP**-Petasition paradoxii; **PPc**-Physoplexido-Potentillion caulescentis; **QF**-Querco-Fagetea; **Qi**-Quercetea ilicis; **Qp**-Quercetalia pubescentis; **ES**-Elyno-Seslerietea; **KC**-Koelerio-Corynepherea; **M**-Mollinio-Arrhenatheretea; **MA**-Mulgedio-Aconitetea; **Ss**-Satureijon subspicatae; **Pc2**-Potentillion caulescentis; **O**-Origanetalia vulgaris; **PRa**-Pistacio-Rhamnetea alaterni; **Ps**-Prunetalia spinosae; **R**-Rosmarinetea; **Sc**-Stipetalia calamagrostis; **AT**-Asplenietea trichomanis; **FS**-Fagetalia sylvaticae; **TA**-Tilio-Acerion; **TG**-Trifolio-Geranietea; **TR**-Thlaspietea rotundifolii; **Tr**-Thlaspietalia rotundifolii; **VP**-Vaccinio-Piceetea.

SjCS – *Seslerio juncifoliae*-*Campanuletum sedetosum*; **SjCGM** – *Seslerio juncifoliae*-*Campanuletum globularietosum* var. *Micromeria thymifolia*; **SjCGS** – *Seslerio juncifoliae*-*Campanuletum globularietosum* var. *Stachys subcrenata*; **CfC** – *Cystopteridi fragilis*-*Campanuletum*; **SaCS** – *Seslerio autumnalis*-*Campanuletum* var. *Salvia officinalis*; **SaCM** – *Seslerio autumnalis*-*Campanuletum* var. *Mycelis muralis*.

Campanula tommasiniana, *Sesleria autumnalis*, *Homalothecium sericetum* and *Neckera besseri* (Tab. 4, On-line Supplement Tab. 4); a differential group of taxa for the variant *Salvia officinalis* are *Coronilla emerus* subsp. *emeroides*, *Quercus ilex*, *Asparagus acutifolius*, *Hedera helix*, *Leptodon smithii* and *Salvia officinalis*, and for the variant *Mycelis muralis*: *Cyclamen purpurascens*, *Mycelis muralis* and *Galeobdolon flavidum*. A characteristic group of taxa for the association *Cystopteris fragilis*-*Campanuletum* are *Campanula tommasiniana*, *Mycelis muralis*, *Cystopteris fragilis*, *Geranium robertianum*, *Arabis alpina*, *Plagiochila porelloides* and *Mnium thomsonii* (Tab. 4, On-line Supplement Tab. 3). Characteristic and differential taxa for the newly described syntaxa are indicated in Fig. 2B.

Sesleria juncifoliae-*Campanuletum tommasinianae* ass. nov. *globularietosum cordifoliae* subass. nova var. *Micromeria thymifolia* var. nova. Nomenclatorial type for the association, subassociation and variant (*holotypus*): Croatia, NW Adriatic, Liburnian karst, Mt. Učka, eastern slope; elev. 1287 m, exp. ESE, incl. 90°; relevé area: 8 m², coverage of the relevé area: vascular plants-10%, bryophytes-1%; calcareous rocky outcrop not shaded by the tree canopy (rel. no 22 in On-line Supplement Tab. 2): *Sesleria juncifolia* 3, *Campanula tommasiniana* 2, *Globularia cordifolia* 2, *Homalothecium sericeum* 2, *Micromeria thymifolia* 2, *Saxifraga paniculata* 2, *Scrophularia laciniata* 2, *Silene saxifraga* subsp. *hayekiana* 2, *Thymus* sp. 2, *Tortella nitida* 2, *Athamanta turbith* 1, *Carduus tenuiflorus* 1, *Hieracium bupleuroides* 1, *Syntrichia ruralis* var. *ruralis* 1.

Sesleria juncifoliae-*Campanuletum tommasinianae* *globularietosum cordifoliae* var. *Stachys subcrenata* var. nova. Nomenclatorial type for the variant (*holotypus*): Croatia, NW Adriatic, Liburnian karst, Mt. Učka, western slope; elev. 1278 m, exp. SSW, incl. 90°; relevé area: 10 m², coverage of the relevé area: vascular plants-20%, bryophytes-1%; calcareous rocky outcrop not shaded by the tree canopy (rel. no 38 in On-line Supplement Tab. 2): *Campanula tommasiniana* 4, *Sesleria juncifolia* 4, *Asplenium ruta-muraria* 3, *Athamanta turbith* 3, *Ditrichium flexicaule* 3, *Globularia cordifolia* 3, *Tortella densa* 3, *T. tortuosa* 3, *Schistidium* sp. 3, *Senecio abrotanifolius* 2, *Silene saxifraga* subsp. *hayekiana* 2, *Stachys subcrenata* 2, *Teucrium montanum* 2, *Carduus tenuiflorus* 1, *Sempervivum tectorum* 1, *Primula auricula* 1.

Sesleria juncifoliae-*Campanuletum tommasinianae* *sedetosum albae* subass. nova. Nomenclatorial type for the subassociation (*holotypus*): Croatia, NW Adriatic, Liburnian karst, Mt. Učka, eastern slope; elev. 760 m, exp. NE, incl. 85°; relevé area: 20 m², coverage of the relevé area: vascular plants-20%, bryophytes-10%; calcareous rock not shaded by the tree canopy (rel. no. 3 in On-line Supplement Tab. 2): *Campanula tommasiniana* 4, *Sesleria juncifolia* 4, *Allium saxatile* subsp. *tergestinum* 3, *Anomodon viculosus* 3, *Asplenium ruta-muraria* 3, *Athamanta turbith* 3, *Ceterach officinarum* 3, *Ctenidium molluscum* 3, *Ditrichium flexicaule* 3, *Homalothecium sericeum* 3, *Hypnum cupressiforme* var. *cupressiforme* 3, *Leptodon smithii* 3, *Neckera besseri* 3, *N. crispa* 3, *Orthotrichum cupulatum* 3, *Schistidium* sp. 3, *Silene saxifraga* subsp. *hayekiana* 3, *Syntrichia ruralis* var. *ruralis* 3, *Tortella tortuosa* 3, *Rhannus rupestris* 2, *Sedum album* 2, *Allium ericetorum* 1, *Asplenium trichomanes* 1, *Satureja montana* subsp. *variegata* 1.

Sesleria juncifoliae-*Campanuletum tommasinianae* *ctenidietosum mollusci* subass. nova. Nomenclatorial type for the subassociation (*holotypus*): Croatia, NW Adriatic, Liburnian karst, Mt. Učka, eastern slope; elev. 1235 m, exp. SE, incl. 85°; relevé area: 10 m², coverage of the relevé area: vascular plants-40%, bryophytes-10%; calcareous rock not shaded by the

tree canopy (rel. no. 45 in On-line Supplement Tab. 2): *Calamagrostis varia* 4, *Sesleria juncifolia* 4, *Asplenium ruta-muraria* 3, *A. trichomanes* 3, *Athamanta turbith* 3, *Campanula tommasiniana* 3, *Galium corrudifolium* 3, *Anthericum ramosum* 2, *Bryum* sp. 2, *Ctenidium molluscum* 2, *Cymbalaria muralis* 2, *Euphrasia illyrica* 2, *Fissidens dubius* 2, *Homalothecium sericeum* 2, *Micromeria thymifolia* 2, *Neckera crispa* 2, *Saxifraga paniculata* 2, *Schistidium* sp. 2, *Scrophularia laciniata* 2, *Sedum album* 2, *Senecio abrotanifolius* 2, *Syntrichia ruralis* var. *ruralis* 2, *Tortella tortuosa* 2, *Homalothecium philippeanum* 1, *Hypnum cupressiforme* var. *cupressiforme* 1, *Ranunculus carinthiacus* 1, *Silene saxifraga* subsp. *hayekiana* 1, *Thalictrum minus* 1, *Gentiana lutea* subsp. *symphyandra* +.

Seslerio autumnalis-Campanuletum tommasinianae var. *Mycelis muralis* ass. and var. nova. Nomenclatorial type for the association and the variant (*holotypus*): Croatia, NW Adriatic, Liburnian karst, Mt. Učka, western slope; elev. 1055 m, exp. E, incl. 85°; relevé area: 16 m², coverage of the relevé area: vascular plants-40%, bryophytes-30%; calcareous rock fully shaded by the tree canopy (rel. no. 28 in On-line Supplement Tab. 4): *Anomodon viticulosus* 5, *Neckera crispa* 5, *Campaula tommasiniana* 4, *Pseudofumaria alba* 4, *Asplenium trichomanes* 3, *Ctenidium molluscum* 3, *Cyclamen purpurascens* 3, *Galeobdolon flavidum* 3, *Geranium robertianum* 3, *Homalothecium sericeum* 3, *Mercurialis ovata* 3, *Moehringia muscosa* 3, *Mycelis muralis* 3, *Neckera besseri* 3, *N. complanata* 3, *Plasteurhynchium striatulum* 3, *Porella platyphylla* 3, *Valeriana tripteris* 3, *Arabis turrta* 2, *Athamanta turbith* 2, *Brachythecium tommasinii* 1, *Galium sylvaticum* 1, *Hypnum cupressiforme* var. *cupressiforme* 1, *Laserpitium krapfii* 1, *Radula complanata* 1, *Senecio fuchsii* 1, *Sesleria autumnalis* 1, *S. juncifolia* 1, *Ceterach officinarum* +, *Peltaria alliacea* +.

Seslerio autumnalis-Campanuletum tommasinianae var. *Salvia officinalis* var. nova. Nomenclatorial type for the variant (*holotypus*): Croatia, NW Adriatic, Liburnian karst, Mt. Učka, eastern slope; elev. 396 m, exp. SE, incl. 90°; relevé area: 18 m², coverage of the relevé area: vascular plants-30%, bryophytes-1%; calcareous rock semi shaded by the tree canopy (rel. no. 1 in On-line Supplement Tab. 4): *Campanula tommasiniana* 4, *Coronilla emerus* subsp. *emeroides* 3, *Homalothecium sericeum* 3, *Leptodon smithii* 3, *Satureja montana* subsp. *variegata* 3, *Schistidium* sp. 3, *Teucrium montanum* 3, *Tortella nitida* 3, *Weissia* sp. 3, *Arabis turrta* 2, *Asparagus acutifolius* 2, *Asplenium trichomanes* 2, *Bromus erectus* agg. 2, *Ceterach officinarum* 2, *Juniperus oxycedrus* 2, *Ostrya carpinifolia* 2, *Rhamnus rupestris* 2, *Sesleria autumnalis* 2, *Galium corrudifolium* 1, *Hedera helix* 1, *Neckera besseri* 1, *Ortotrichum anomalum* 1, *Quercus ilex* 1, *Salvia officinalis* 1, *Thalictrum minus* 1.

Cystopteris fragilis-Campanuletum tommasinianae ass. nova. Nomenclatorial type for the association (*holotypus*): Croatia, NW Adriatic, Liburnian karst, Mt. Učka, eastern slope; elev. 1297 m, exp. NE, incl. 90°; relevé area: 12 m², coverage of the relevé area: vascular plants-40%, bryophytes-60%; calcareous rock fully shaded by the tree canopy (rel. no. 3 in On-line Supplement Tab. 3): *Neckera crispa* 7, *Pseudofumaria alba* 7, *Campanula tommasiniana* 6, *Ctenidium molluscum* 6, *Anomodon viticulosus* 4, *Brachythecium tommasinii* 4, *Homalothecium sericeum* 4, *Mnium marginatum* 4, *Plasteurhynchium striatulum* 4, *Saxifraga rotundifolia* 4, *Arabis alpina* 3, *Asplenium trichomanes* 3, *Bryum* sp. 3, *Cymbalaria muralis* 3, *Cystopteris fragilis* 3, *Geranium robertianum* 3, *Mnium thomsonii* 3, *Mycelis muralis* 3, *Neckera pennata* 3, *Pedinophyllum interruptum* 3, *Plagiochila porelloides* 3, *Pseudoleskeela catenulata* 3, *Schistidium* sp. 3, *Asplenium ruta-muraria* 2, *Adenostyles glabra* 1, *Anomodon attenuatus* 1, *Epilobium montanum* 1, *Neckera complanata* 1,

Discussion

Niche assembly and ecology

Campanula tommasiniana inhabits rock crevices that are remarkably diverse in the number of vascular plants and bryophytes. The number of coverage vascular plants vs. bryophytes varies substantially and depends much on microsite conditions; bryophytes prevail over vascular plants in fully shaded and moist microsities, e.g. in group of assemblages CfC (*Cystopteridi-Campanuletum*), while in open and exposed sites (SjC – *Seslerio juncifoliae-Campanuletum*), vascular plants completely prevail over bryophytes. In our survey, one new bryophyte, *Tortella densa*, was recorded for Croatia for the first time and the finding was reported in detail elsewhere (SURINA and MARTINČIĆ in ELLIS et al. 2012).

In comparable studies (but inferred from a different number of samples/relevés; bryophytes and lichens excluded) botanists found a considerably lower number of vascular plant taxa in niche assemblies of chasmophytic narrow endemics. For example: PIGNATTI and PIGNATTI (1978), for *Campanula morettiana*, restricted to the Italian Dolomites, in an elevational range between 1730–2450 m, recorded 38 taxa of vascular plants in 15 relevés (5–15 per rel., median=8), while the accompanying flora of geographically even more restricted *Moehringia tommasinii* (Caryophyllaceae) from northern Istria, in an elevational range between 150–360 m, numbers 32 taxa of vascular plants recorded in 9 relevés (4–13 per rel., median=11) (MARTINI 1990). However, in a detailed study on the phytosociological characteristics of the sites of *Moehringia villosa* (DAKSKOBLER 2000), restricted to the southern Julian Alps and the adjacent Prealps, 156 taxa of vascular plants in 88 relevés (5–30 per rel., median=15) sampled in an elevational range between 430–1830 m were recorded, which is comparable to the results of our study. Both *Campanula tommasiniana* and *Moehringia villosa* occupy rock crevices of relatively broad elevational range, forming floristically and ecologically well characterized but different syntaxa. According to the results of an extensive study (LAVERGNE et al. 2004), endemic taxa compared to widespread congeners differ in a number of ecological characteristics (their habitat in terms of abiotic and community characteristics) and biological traits (floral traits and the size and maternal fertility of individual plants), but not in levels of herbivory and levels of ecophysiological traits (specific leaf area, leaf dry matter content, leaf nitrogen concentration, and rates of photosynthesis). The principal component of the difference concerns the occurrence of endemic taxa in rocky and steep slopes in low, open habitats rather than forest vegetation (compare GROVE and RACKHAM 2003, QUEZÉL and MEDAIL 2003), with low species richness, regardless of geological bedrock. Highly specialized conditions in the physical environment select for these differences in small, ecologically and taxonomically isolated (endemic) populations, since rock crevices and screes experience a range of microclimatic conditions that are very different from both level rocky terrain and horizontal landscapes with soil. However, *Campanula tommasiniana*, despite being almost an obligate chasmophyte (see SURINA 2013), indicates a remarkable ability to adapt to various abiotic factors, but a relatively low number of taxa per microsite suggests low biotic competitiveness. In contrast to the similarly rich floristic assembly of *Moehringia villosa*, the niche assembly of *Campanula tommasiniana* constitutes only three taxa of vascular plants, all rockdwellers: *Campanula tommasiniana*, *Asplenium trichomanes*, *A. ruta-muraria*), occurring in more than 50% of all samples, which additionally speaks for its high abiotic plasticity and niche differentiation. The most important ecological gradients in shaping the floristic assemblies are light

conditions and moisture. According to field diagnostics, results of numerical and statistical analyses based on groups of characteristic and differential taxa among vascular plants, bryophytes as well as site ecology, three floristically and ecologically well defined groups of assemblages are identified. The assemblage Sj-C – *Seslerio juncifoliae-Campanuletum* is the most homogenous in terms of floristical composition, while the assemblage CfC – *Cystopteri-Campanuletum* has the most uniform site ecology. This reflects also the life form spectrum, where chamaephytes, adapted to open sites, do not thrive at all in the assemblage *Cystopteri-Campanuletum*.

Our research proved the high diagnostic values of bryophytes for the delimitation of groups of assemblages based on floristic composition. Several taxa occur exclusively or almost exclusively in floristically and ecologically well differentiated groups of assemblages. However, their diagnostic values for site conditions are less significant, a fact already stressed and discussed by SURINA and MARTINČIĆ (2012).

Results of our analyses suggest that *Campanula tommasiniana* is a chasmophyte of open and exposed habitats in the altimontane to subalpine vegetation belt, a similar niche preference (see HORVAT 1931) also for the closely related (see PARK et al. 2006, LIBER et al. 2008) but allopatric *C. waldsteiniana*, another endemic of the north-western Dinaric Alps.

Campanula tommasiniana experiences a range of microclimatic conditions along ecological gradients building three floristically and ecologically well defined and differentiated groups of chasmophytic assemblages, suggesting its high ecological plasticity and abiotic stress tolerance. Hence, the reason for its limited range, restricted to an area of 6–7 km², remains a puzzling question. Another stenoendemic, *Hladnikia pastinacifolia* (Apiaceae), a monotypic species with even narrower distribution area, restricted to a few localities of the Trnovski gozd plateau in north-western Dinaric Alps (MAYER 1960, ČUŠIN 2004), colonizes an even broader range of habitats – stony grasslands, rock crevices and screes (ŠAJNA et al. 2012), reflecting an ability to adapt to a variety of both abiotic and biotic factors. Nevertheless, *H. pastinacifolia*, like *Campanula tommasiniana*, remains confined to an extremely narrow distribution area, despite the many available habitats in the vicinity, also without any reasonable explanation.

Nomenclatorial and synsystematic issues

Stands with *Campanula tommasiniana* were first mentioned by HORVATIĆ (1944), who recognized its diagnostic value and distinct floristic assemblages, naming the association *Campanuletum tommasinianae* Horvatić 1944. In the 1960s Horvatić mentioned and cited the association's name as *Campanuletum tommasinianae-justiniana* Horvatić 1960 (HORVATIĆ 1960, 1963b). He found *Campanula tommasiniana*, *C. justiniana*, *Hieracium bifidum* and *H. amplexicaule* subsp. *petraeum* (recte *H. bupleuroides*) to be regionally characteristic taxa for the association occurring on calcareous cliffs and blocks within the thermophytic beech forests of the association *Seslerio autumnalis-Fagetum*. He classified it within the alliance *Moehringion muscosae*. To that end, TRINAJSTIĆ (2008) in his Plant Communities of Croatia, without giving a specific reason, found the valid publication for the association Horvatić's treatise from 1963. However, neither a supplementary analytical and/or synoptic table nor designation of a type relevé were provided, and both botanists failed to describe the association according to the rules of phytosociological nomenclature (compare WEBER et al. 2000). Beside purely nomenclatorial issues, our results show significantly more com-

plex problems in syntaxonomics of communities with *Campanula tommasiniana*. Since three groups of assemblages are easily recognized, both floristically and ecologically, and even classified in two different alliances, we find the validation of the name and the description of additional syntaxa based on a sound association concept (WILLNER 2006), and following the rules of phytosociological nomenclature (WEBER et al. 2000), to be fully justified. While we find the differentiation and status of the newly described syntaxa not questionable, their syntaxonomic position within higher ranked syntaxa remains problematic. Hence our proposal is still only preliminary since it is evident that earlier attempts (e.g., HORVAT 1962, HORVATIĆ 1963b, TRINAJSTIĆ 1980, TRINAJSTIĆ 2008) at stabilization of a chasmophytic syntaxonomic system in the northern Adriatic do not suffice, and therefore a thorough numerical revision is required.

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