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Phytogeographic and syntaxonomic diversity of wall vegetation (*Cymbalario-Parietarietea diffusae*) in southeastern Europe

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ABSTRACT

Walls represent globally distributed, locally extensive, artificial ecosystems. Wall vegetation is still poorly known in the Mediterranean and Temperate regions of southeastern Europe. The aim of this study is to classify and describe chasmophytic vegetation of walls, covering southeastern Europe from Slovenia to North Macedonia. From a total 463 phytosociological relevés, we identify and describe 12 distinct species – poor to moderately rich vegetation units using TWINSPAN evaluated by NMDS, and indicator values. The vegetation units are included within three alliances from two macroclimate regions: (1) vegetation of cool-temperate Europe of the *Cymbalario-Asplenion* alliance, and (2) Mediterranean vegetation of the *Galio valantiae-Parietarion judaicae* and *Artemisio arborescentis-Capparidion spinosae* alliances. The southernmost limit of the *Cymbalario-Asplenion* was determined in Central Bosnia. The presence of the *Artemisio arborescentis-Capparidion spinosae* in the eastern Adriatic is highlighted.

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Introduction

Walls are temporary man-made habitats with strong and continuous anthropogenic influences (Segal 1969; Francis 2011). These influences have an effect on a range of plant species that are able to colonize this habitat type. Studies of vegetation on old city walls and on buildings and various monuments in different parts of Europe showed that this vegetation is composed of species from natural rocky habitats or ruderal and seminatural flora in the vicinity, and often occurs in the form of large hanging carpets composed of a few species with extensive cover (Lundholm and Marlin 2006; Ceschin et al. 2016). From a more practical standpoint, wall vegetation colonizes monumental and archaeological stonework in particular, causing conservation problems (Lisci and Pacini 1993).

Walls generally show characteristics similar to rocky surfaces occurring in natural environments (Segal 1969), and some authors classify the wall and rocky rupicolous chasmophytic vegetation in the class *Asplenietea trichomanis* (e.g. Pignatti 1953; Mucina 1993, for a literature review see Brullo and Guarino 1998). However, various ecological conditions segregate walls from rocks. Walls are habitats characterized by smaller dimensions and more extreme fluctuations of microclimate, a great variety of building material and the presence of a binding material (e.g. calcareous mortar or concrete), poor soil deposition, less heterogeneity in micro-habitats, and location in areas with anthropogenic disturbances (cf. Duchoslav 2002).

Wall vegetation has been studied in some European countries during recent decades: in Italy (Hruška 1987; Gamper and Bacchetta 2001; Brullo and Guarino 2002; Świerkosz 2012), France (Géhu 2005, 2006; de Foucault 2014), Austria (Brandes 1989; Mucina 1993), the Czech Republic (Duchoslav 2002; Kolbek et al. 2015 and references therein) and Slovakia (Kolbek et al. 2015). Segal (1969) and Brandes (1992a, 1992b) compared flora and vegetation on walls of southern, western and central Europe, while Brullo and Guarino (1998) classified wall vegetation in a wider, pan-European, context. However, the interpretations of data are in general various and frequently conflicting. Moreover, in all the syntaxonomical ranks, a confused proliferation of invalid names and synonyms has been noticed leaving unresolved the coenological overlaps among the syntaxonomic schemes proposed by different authors (e.g. Rivas-Martínez 1978, 2003; Rivas-Martínez et al. 1999; Świerkosz 2004; Biondi et al. 2014). Several doubts about the attribution of the phytosociological relevés to a particular association have also been reported and

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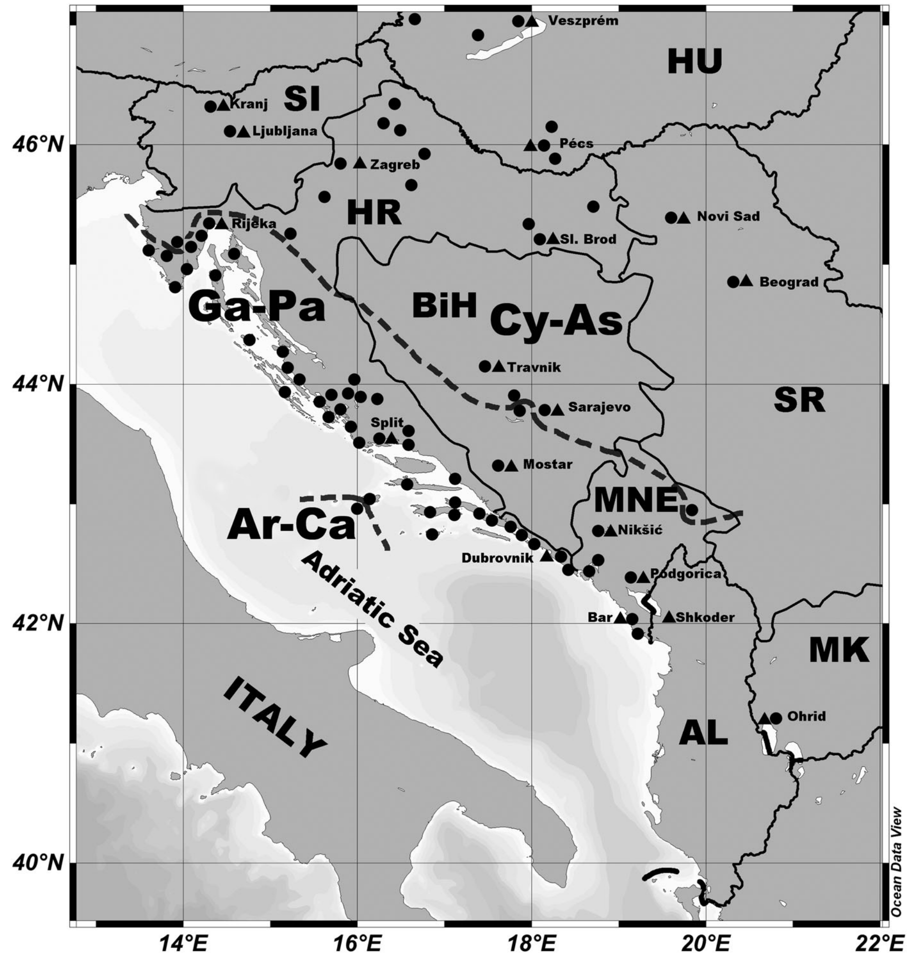

Figure 1. Distribution of relevés of the vegetation units in the Balkans and Hungary (40°–48° N and 13°–21° E). ▲: Map of surveyed meteorological stations (see Supplementary Appendix S1), ●: Location of sampling sites (see Supplementary Appendix S2). Lines denote the limit of the alliances: Cy-As = *Cymbalario-Asplenion*; Ga-Pa = *Galio valantiae-Parietarion judaicae*; Ar-Ca = *Artemisio arborescentis-Capparidion spinosae*. Country abbreviations: AL = Albania; BIH = Bosnia and Herzegovina; HR = Croatia; HU = Hungary; MK = North Macedonia; MNE = Montenegro; SI = Slovenia; SR = Serbia.

frequently different vegetation units are grouped under the same name (Brullo and Guarino 1998).

More recently, Mucina et al. (2016) proposed a syntaxonomic scheme for thermophilous chasmophytic vegetation of walls of the Mediterranean and the winter-mild atlantic to subcontinental regions of temperate Europe, Middle East and North Africa. This vegetation has been included in the class *Cymbalario-Parietarietea diffusae* with a single order *Tortulo-Cymbalarietalia*, and differentiating the two groups of alliances: (1) temperate (*Cymbalario-Asplenion*), and (2) Mediterranean (*Galio valantiae-Parietarion judaicae*, *Artemisio arborescentis-Capparidion spinosae* and *Parietario judaicae-Hyoscyamion aurei*).

Among the southeastern European countries, thermophytic vegetation of walls has been reported, mostly within a wider syntaxonomic overview, for the territory of Slovenia (Šilc and Košir 2006; Šilc 2009; Šilc and Čarni 2012), Croatia (Trinajstić 1994, 2008, 2010; Škvorc et al. 2017), Bosnia and Herzegovina (Lakušić et al. 1977), Montenegro (Blečić and Lakušić 1976), Serbia (Jovanović et al. 1986; Lakušić et al. 2005) and Albania (Dring et al. 2002), and some communities are also mentioned in a vegetation survey of Hungary (Borhidi et al. 2012). Until now, a total synthesis of phytosociological data of wall communities in the area has not been completed.

The aims of this paper are: (1) to provide new phytosociological relevés for lesser known areas in the Mediterranean (i.e. the eastern Adriatic coast) and temperate regions of the southeast European countries (the inland Dinarides, the Pannonian region), (2) to evaluate diversity and chorology of wall vegetation based on the available published and recently collected data, (3) to compare them with the major vegetation types recognised in the traditional expert-based classification, (4) to refine the European Vegetation Classification (EVC, Mucina et al. 2016) at the association level for southeastern Europe.

Study area

The investigated area is located between 40° 48′ and 47° 37′ N and between 13° 41′ and 20° 26′ E (Figure 1) and includes the southeastern European countries Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Montenegro, Albania, North Macedonia, and in the southern and western part of Hungary. The territory in focus has a complex structure, since it comprises parts of the southern hillsides of the Eastern Alps and the Pannonian basin, the eastern Adriatic Sea islands and coast, and central part of the Eastern Dinarides (Dinaric Alps). The territory is classified as the Euro-Siberian region, i.e. the Eastern Alpine, the Apennine-Balkan and the Pannonian-Carpathian provinces, and the Mediterranean region with the Adriatic province (Rivas-Martínez et al. 2004).

According to Köppen's climate classification (Köppen and Geiger 1954; Sträβser 1998; Merkel 2018) the eastern Adriatic islands and coast mostly lie within the Csa climate zone, i.e. the *Quercetea ilicis* vegetation zone, where the climate is typically Mediterranean: mild and rainy winters, warm and dry summers, and an extended period of sunshine throughout the year (Supplementary Appendix S1). Sub-Mediterranean cities belong to the Cfa climate zone, i.e. the vegetation of the low-altitude calcareous thermophilous oak and oriental hornbeam forests (*Carpinion orientalis*, *Quercetea pubescentis*). The Cfb climate zone extends to most of the area investigated with different natural potential vegetation within the class *Quercetea pubescentis* or *Carpino-Fagetea sylvaticae* (Supplementary Appendix S1, *sensu* Jovanović et al. 1986). The majority of relevés from Hungary originated from the coline region of southern and western Hungary, where the natural zonal vegetation consists of sub-Mediterranean type of deciduous forests dominated by *Quercus pubescens*, *Q. cerris*, *Q. petraea*, *Carpinus betulus* and *Fagus sylvatica*, which are related to the forests of the Balkans (Zólyomi 1973; Borhidi et al. 2012). Hereafter we refer for simplicity to this region as southeastern Europe.

Material and methods

Data source and analysis

This study is based on a dataset consisting of 463 phytosociological relevés sharing 390 plant taxa, carried out according to the Braun-Blanquet approach (Westhoff and van der Maarel 1980) (Figure 1, Supplementary Appendix S2). Forty-five relevés were used from the available literature, and 418 are new and were mostly collected in the period from 2014 to 2018 (Supplementary Appendices S2 and S3). For most vegetation plots we recorded slope, exposure, vegetation cover and a complete list of vascular taxa. Bryophyte taxa were omitted in the data matrix due to inconsistent records in phytosociological tables, while whenever possible moss cover was estimated.

Only vegetation on vertical wall surfaces with joints (fissures) was investigated. The base of walls (i.e. vertical surface up to 30 cm above ground) and the horizontal wall tops were not included in the survey. The wall bases due to their increased moisture and nutrient content are usually occupied by plants of nearby vegetation, while the horizontal wall tops are slightly different microhabitats characterized by higher soil accumulation (shallow skeletal soil). The range of sampling stands includes all types of walls (i.e. isolated walls in courtyard, fortification, city walls, walls of disintegrated buildings, monuments, etc.).

The plot size is indicated for 98% of the relevés. The average plot size of relevés was 14 m^2 (SD ± 16 m^2) with minimum and maximum values of 1 m^2 and 120 m^2, respectively. The mode of a set of plot size data was 6 m^2.

The system of characterizing species and the nomenclature of higher taxa were derived from Mucina et al. (2016), and Brullo and Guarino (1998, 2002). Nomenclatural decisions concerning new syntaxa follow the third edition of the International Code of Phytosociological Nomenclature (Weber et al. 2000).

Data on climatic variables for selected cities were collected from Climate-data.org (Merkel 2018), except for the Vis Archipelago where data from the meteorological station at the town of Komiža (the island of Vis, for 1998–2017, Meteorological and Hydrological Service of Croatia) were used.

Statistical analysis

The relevés were stored in TURBOVEG format (Hennekens and Schaminée 2001). The Braun-Blanquet scale was transformed by TURBOVEG to cover percentages as follows: 5 = 88%, 4 = 68%, 3 = 38%, 2 = 13%, 1 = 3% and + = 2%. Classification of the dataset was carried out by TWINSPAN (Hill 1979), run under the JUICE software (Tichý 2002). TWINSPAN pseudospecies cut levels for species abundances were set to 0-5-25 percentage scale units. Initially, six levels of division were chosen and the minimum group size for division was set to three relevés. Each division was evaluated individually, and the optimal number of vegetation units was determined by expert judgement, taking into account differences in ecology and biogeography.

To check the differentiation of the obtained vegetational groups Non-Metric Multidimensional Scaling (NMDS) performed on a dissimilarity matrix of Bray–Curtis and based on square-root transformed percentage cover values were used. The final stress for two *a priori* chosen dimensions was 0.21. NMDS was performed using the R package 'vegan' (https://cran.r-project.org/web/packages/vegan) operated through the JUICE software (Tichý 2002).

Pignatti's indicator values were used for ecological interpretation of vegetation patterns (Pignatti et al. 2005). Unweighted mean indicator values were calculated for each relevé using JUICE software (Tichý 2002).

Diagnostic species of vegetation units were determined by calculating fidelity using the phi (Φ) coefficient. Only species with $\Phi > 0.4$ and a probability under random expectation of the observed pattern of species occurrence lower than 0.001 (Fisher's exact test) were considered diagnostic. Species with $\Phi > 0.6$ were considered as highly diagnostic. To calculate fidelity, the number of relevés for each order or alliance was virtually standardized to equal size (Tichý and Chytrý 2006).

Results

Classification and ordination

Based on TWINSPAN, 12 main vegetation units (clusters, communities) included within three main groups (Figure 2, Supplementary Appendices S2 and S4) were identified: (1) the chasmophytic vegetation of sunny walls of the subcontinental regions of cool-temperate Europe of the *Cymbalario-Asplenion* alliance on the left side of the ordination diagram

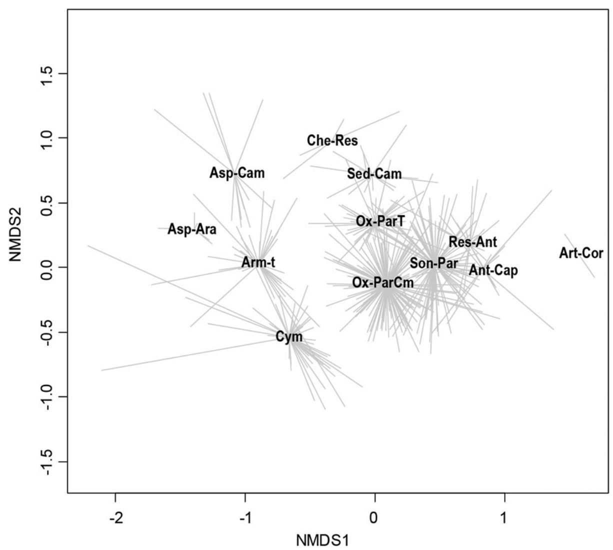

Figure 2. NMDS ordination diagram with projected cluster membership of the relevés. Community abbreviations: Che-Res = *Chenopodium album-Reseda lutea* community; Asp-Cam = *Asplenio rutae-murario-Campanuletum rotundifoliae*; Asp-Ara = *Asplenium trichomanes-Arabis hirsuta* community; Arm-t = *Asplenietum rutae-murario-trichomanis*; Cym = *Cymbalarietum muralis*; Sed-Cam = *Sedo dasyphilli-Campanuletum austroadriaticae*; Ox-ParT = *Oxalido corniculatae-Parietarietum judaiace typicum*; Ox-ParCm = *Oxalido corniculatae-Parietarietum judaiace cymbalarietosum muralis*; Son-Par = *Soncho tenerrimi-Parietarietum judaiace*; Res-Ant = *Resedo albae-Anthirrinetum majoris*; Ant-Cap = *Antirrhinum majus-Capparis orientalis* community; Art-Cor = *Artemisia arborescens-Coronilla valentina* community.

(communities Che-Res, Asp-Cam, Asp-Ara, Arm-t, Cym), and (2) thermomediterranean chasmophytic vegetation of limestone walls of the Western Mediterranean *Galio valantiae-Parietarion judaicae* alliance in an intermediate position on the diagram (communities Sed-Cam, Ox-ParT, Ox-ParCm, Son-Par, Res-Ant, Ant-Cap). On the right side of the ordination diagram, (3) the relevés (community Art-Cor) from the Central Mediterranean *Artemisio arborescentis-Capparidion spinosae* alliance are clearly separated from those of the *Galio-Parietarion* communities.

Based on these results, a set of diagnostic, constant and dominant taxa were proposed (Table 1, Supplementary Appendix S4).

Indicator values

Generally, two groups of vegetation units i.e. (1) the temperate *Cymbalario-Asplenion*, and (2) Mediterranean *Galio valantiae-Parietarion judaicae* and *Artemisio arborescentis-Capparidion spinosae* alliances are quite well differentiated. Indicator values show that the highest light intensity is characteristic of the *Artemisia arborescens-Coronilla valentina* community, followed by *Antirrhinum majus-Capparis orientalis* community and *Resedo albae-Anthirrinetum majoris*, while both *Oxalido corniculatae-Parietarietum judaicae* subassociations (*typicum*, *cymbalarietosum muralis*) and *Soncho tenerrimi-Parietarietum judaicae* show the greatest range (Figure 3). In contrast, the lowest indicator value for light was observed for the *Asplenium trichomanes-Arabis hirsuta* community. With respect to temperature, a similar relationship among the communities was shown. With regard to moisture, the highest values were found for the *Asplenium trichomanes-Arabis hirsuta* community and *Cymbalarietum muralis* association, while the lowest were for the *Antirrhinum majus-Capparis orientalis* and *Artemisia arborescens-Coronilla valentina* communities. The communities differed in relation to substrate reaction. The highest reaction value was for the *Asplenio rutae-murario-Campanuletum rotundifoliae* association and *Asplenium trichomanes-Arabis hirsuta* community, whereas the lowest were noted for *Oxalido corniculatae-Parietarietum judaicae cymbalarietosum muralis* and *Soncho tenerrimi-Parietarietum judaicae*. The latter had the greatest range. The communities differed considerably in relation to nutrients. High values were found for the *Asplenietum rutae-murario-trichomanis* and *Cymbalarietum muralis*, and the lowest for the *Antirrhinum majus-Capparis orientalis* community.

Endemic and non-native taxa

The association *Sedo dasyphilli-Campanuletum austroadriaticae*, and *Antirrhinum majus-Capparis orientalis* and *Artemisia arborescens-Coronilla valentina* communities include endemic taxa, mostly belonging to the group of Illyrian-Adriatic endemics (*Seseli globiferum* Vis., *Stachys menthifolia* Vis., *Teucrium arduinii* L., *Campanula austroadriatica* D.Lakušić & Kovačić, etc.) or local stenoendemic taxa (e.g. *Asperula visianii* Korica) (*sensu* Nikolić et al. 2015).

Regarding non-native taxa (based on proportion of neophytes), their contribution to total wall flora was 6.6%, and appeared at low frequencies in both *Cymbalario-Asplenion* and *Galio-Parietarion* alliances. Among them, various *Erigeron* L. taxa were the most common.

Discussion

Based on results, we classified the clusters obtained into 12 communities of three different alliances. The following syntaxonomic scheme is here proposed:

Class: *Cymbalario-Parietarietea diffusae* Oberd. 1969
Order: *Tortulo-Cymbalarietalia* Segal 1969
Alliance: *Cymbalario-Asplenion* Segal 1969

- *Chenopodium album-Reseda lutea* community
- *Asplenio rutae-murario-Campanuletum rotundifoliae* Jasprica, Škvorc et Purger ass. nov. hoc loco, Appendix 1
- *Asplenium trichomanes-Arabis hirsuta* community
- *Asplenietum rutae-murario-trichomanis* Kuhn 1937
- *Cymbalarietum muralis* Görs *ex* Oberd. 1977

Alliance: *Galio valantiae-Parietarion judaicae* Rivas-Mart. *ex* de Bolòs 1967

- *Sedo dasyphilli-Campanuletum austroadriaticae* Jasprica, Škvorc et Kovačić ass. nova hoc loco, Appendix 1
- *Oxalido corniculatae-Parietarietum judaicae* (Braun-Blanq., Roussine et Nègre 1952) Segal 1969 subass. *typicum*
- *Oxalido corniculatae-Parietarietum judaicae* subass. *cymbalarietosum muralis* Brullo et Guarino 1998

Table 1. Combined synoptic table of frequencies and fidelities of communities belonging to the Southeastern Europe wall vegetation.

Community	Che-Res	Asp-Cam	Asp-Ara	Arm-t	Cym	Sed-Cam	Ox-ParT	Ox-ParCm	Son-Par	Res-Ant	Ant-Cap	Art-Cor
No. of relevés	4	12	5	33	48	15	50	172	93	20	9	2
Reseda lutea L.	*75*	42	40	3	17	.	2	.	5	.	.	.
Chenopodium album L.	*50*	8	.	3	12	.	.	.	1	.	.	.
Campanula rotundifolia L.	.	*75*	.	.	.	.	.	.	.	.	.	.
Minuartia glaucina Dvořáková	.	*58*	.	.	.	.	.	.	.	.	.	.
Sedum album L.	.	*50*	.	9	6	33	33	.	.	.	.	.
Arabidopsis arenosa (L.) Lawalrée	.	*42*	40	.	2	.	.	.	.	.	.	.
Fragaria vesca L.	.	.	*80*	.	.	.	.	.	.	.	.	.
Linaria vulgaris Mill.	.	.	*60*	.	.	.	.	.	.	.	.	.
Arabis hirsuta (L.) Scop.	.	.	*40*	.	.	.	.	.	.	.	.	.
Epilobium lanceolatum Sebast. & Mauri	.	.	*40*	.	2	.	.	.	.	.	.	.
Verbascum thapsus L.	.	.	*40*	.	2	.	.	.	.	.	.	.
Thymus pulegioides L.	.	.	*40*	3	.	.	.	.	.	.	.	.
Agrostis sp.	.	.	*40*	.	.	.	.	.	.	.	.	.
***Asplenium ruta-muraria* L. [Cy-As]**	.	67	100	*88*	46	13	29	6	5	.	.	.
Cymbalaria muralis P.Gaertn., B.Mey. & Scherb.	.	.	.	34	*90*	.	8	76	34	10	33	.
Sonchus asper (L.) Hill	.	.	.	.	*31*	.	.	.	.	.	.	.
Campanula austroadriatica D.Lakušić & Kovačić	.	.	.	.	.	*73*	2	1	8	10	11	.
Poa bulbosa L.	.	.	.	.	.	*60*	14	2	1	.	.	.
Sedum dasyphyllum L.	.	.	.	.	.	*47*	12	3	17	.	11	.
Micromeria juliana (L.) Benth. ex Rchb.	.	.	.	.	.	*47*	6	3	28	20	22	.
Satureja montana L.	.	.	.	.	.	*33*	.	2	4	15	22	.
Leontodon crispus Vill.	.	.	.	.	.	*33*	.	1	2	5	.	.
***Asplenium ceterach* L. [Ga-Pa]**	.	.	.	.	2	87	*90*	62	46	20	22	.
Geranium rotundifolium L.	.	.	.	.	.	20	*39*	3	11	5	.	
Saxifraga tridactylites L.	.	.	.	.	.	13	*31*	8	3	10	.	
***Parietaria judaica* L. [Ga-Pa]**	.	.	.	.	.	73	88	*93*	97	100	78	.
***Sonchus tenerrimus* L. [Ga-Pa]**	.	.	.	.	.	.	18	23	*33*	.	.	
Reichardia picroides (L.) Roth	.	.	.	.	6	20	.	4	37	*65*	11	50
Sonchus asper (L.) Hill ssp. *glaucescens* (Jord.) Ball	.	.	.	.	.	13	.	1	4	*65*	22	.
Reseda alba L.	.	.	.	.	.	.	.	.	5	*45*	.	.
Dittrichia viscosa (L.) Greuter	.	.	.	.	.	13	.	.	8	*40*	11	.
Inula verbascifolia (Willd.) Hausskn.	.	.	.	.	.	.	2	8	9	*40*	.	.
Capparis orientalis Veill.	.	.	.	.	.	7	4	10	6	15	*100*	100
Antirrhinum majus L.	100	8	.	25	.	.	6	13	41	70	*78*	.
***Coronilla valentina* L. [Ar-Ca]**	.	.	.	.	.	.	.	.	.	.	.	*100*
***Artemisia arborescens* L. [Ar-Ca]**	.	.	.	.	.	.	.	.	.	.	.	*100*
***Convolvulus cneorum* L. [Ar-Ca]**	.	.	.	.	.	.	.	.	.	.	.	*100*
Other most abundant species												
***Chelidonium majus* L. [Cy-As]**	50	8	40	50	44	7	8	3	.	.	.	.
Petrorhagia saxifraga (L.) Link	.	42	.	13	6	47	4	2	8	15	.	50
Hedera helix L.	50	.	40	58	6	13	4	5	10	10	.	.
Ficus carica L.	.	.	.	.	2	20	4	17	20	15	11	50
Sonchus oleraceus L.	50	.	.	6	13	7	6	1	6	10	.	.
***Arenaria leptoclados* (Rchb.) Guss. [Ga-Pa]**	25	.	.	19	.	13	39	23	18	10	.	.
***Asplenium trichomanes* L. [Cy-As]**	.	50	80	59	38	47	41	31	4	5	.	.
Silene vulgaris (Moench) Garcke ssp. *vulgaris*	.	8	.	3	6	27	.	.	2	20	.	100
Catapodium rigidum (L.) C.E.Hubb.	.	.	.	.	.	20	6	6	28	25	.	.
Anisantha madritensis (L.) Nevski	.	.	.	.	.	20	24	13	20	25	.	.
Anisantha sterilis (L.) Nevski	.	8	.	.	6	13	6	1	3	15	.	.
***Geranium purpureum* Vill. [Ga-Pa]**	.	.	.	.	.	27	29	20	28	20	11	.
Clinopodium nepeta (L.) Kuntze	.	.	.	3	.	20	2	4	13	15	11	.
Campanula pyramidalis L.	.	.	.	.	.	.	4	11	12	5	11	.
Mercurialis annua L.	.	.	.	3	.	7	8	3	17	5	11	.
Medicago lupulina L.	25	.	20	9	6	.	.	.	1	.	.	.
Sedum hispanicum L.	.	.	.	6	4	20	14	.	2	.	.	.
Lactuca serriola L.	.	.	.	9	17	13	4	2	6	.	.	.
Hordeum murinum L.	25	.	.	.	8	.	2	1	2	5	.	.
Erigeron annuus (L.) Desf.	.	.	20	9	13	.	.	1	1	5	.	.
Oxalis corniculata L.	.	.	.	.	2	.	2	2	14	5	.	.

Only species with phi values >0.3 and a frequency >30% in at least one group are included. Italicized values indicate diagnostic species with high ($\Phi \geq 0.4$) fidelity to particular clusters. At the end of the table frequencies of additional 20 most abundant species are shown. Diagnostic species of the alliances *Cymbalario-Asplenion* (Cy-As), *Galio valantiae-Parietarion judaicae* (Ga-Pa) and *Artemisio arborescentis-Capparidion spinosae* (Ar-Ca) are indicated in bold. Community abbreviations: Che-Res = *Chenopodium album-Reseda lutea* community; Asp-Cam = *Asplenio rutae-murario-Campanuletum rotundifoliae*; Asp-Ara = *Asplenium trichomanes-Arabis hirsuta* community; Arm-t = *Asplenietum rutae-murario-trichomanis*; Cym = *Cymbalarietum muralis*; Sed-Cam = *Sedo dasyphilli-Campanuletum austroadriaticae*; Ox-ParT = *Oxalido corniculatae-Parietarietum judaiace typicum*; Ox-ParCm = *Oxalido corniculatae-Parietarietum judaiace cymbalarietosum muralis*; Son-Par = *Soncho tenerrimi-Parietarietum judaiace*; Res-Ant = *Resedo albae-Anthirrinetum majoris*; Ant-Cap = *Antirrhinum majus-Capparis orientalis* community; Art-Cor = *Artemisia arborescens-Coronilla valentina* community.

- *Soncho tenerrimi-Parietarietum judaicae* Jasprica, Škvorc, Pandža et Milović ass. nov. hoc loco, Appendix 1
- *Resedo albae-Anthirrinetum majoris* Trinajstić 2008
- *Antirrhinum majus-Capparis orientalis* community

Alliance: *Artemisio arborescentis-Capparidion spinosae* Biondi, Blasi et Galdenzi in Biondi et al. 2014

- *Artemisia arborescens-Coronilla valentina* community

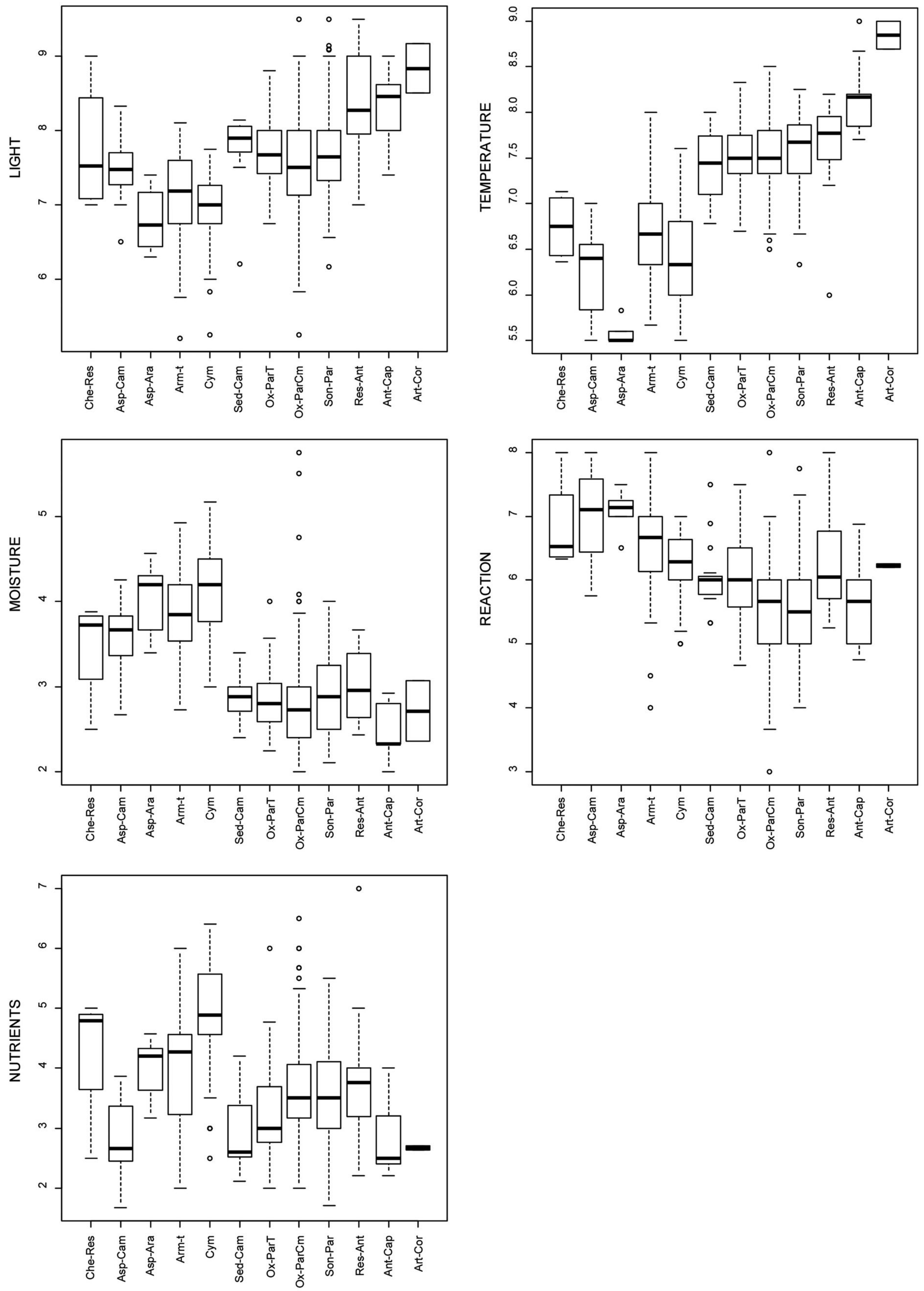

Figure 3. Relationships of the defined vegetation communities to environmental factors expressed by Pignatti indicator values (Pignatti et al. 2005). Median values, quartiles and ranges are shown. Community abbreviations: Che-Res = *Chenopodium album-Reseda lutea* community; Asp-Cam = *Asplenio rutae-murario-Campanuletum rotundifoliae*; Asp-Ara = *Asplenium trichomanes-Arabis hirsuta* community; Arm-t = *Asplenietum rutae-murario-trichomanis*; Cym = *Cymbalarietum muralis*; Sed-Cam = *Sedo dasyphilli-Campanuletum austroadriaticae*; Ox-ParT = *Oxalido corniculatae-Parietarietum judaiace typicum*; Ox-ParCm = *Oxalido corniculatae-Parietarietum judaiace cymbalarietosum muralis*; Son-Par = *Soncho tenerrimi-Parietarietum judaiace*; Res-Ant = *Resedo albae-Anthirrinetum majoris*; Ant-Cap = *Antirrhinum majus-Capparis orientalis* community; Art-Cor = *Artemisia arborescens-Coronilla valentina* community.

There are several interpretations concerning these vegetation alliances that have been attributed to different syntaxonomic ranks and/or units (cf. Brandes 1989; Sádlo 2009; etc.). For example, the *Cymbalario-Asplenion* was classified within the class *Asplenietea trichomanis*, i.e. in the order *Parietarietalia* (Tzonev et al. 2009; Šilc and Čarni 2012) or the *Tortulo-Cymbalarietalia* (Borhidi et al. 2012). In Italy, the alliance *Artemisio arborescentis-Capparidion spinosae* is included within the order *Capparidetalia spinosae* (Biondi et al. 2014). Here, we follow the EuroVegChecklist (EVC) standardized classification systems (Mucina et al. 2016) where only three alliances of the *Tortulo-Cymbalarietalia* for the whole of Mediterranean Europe are separated into temperate (*Cymbalario-Asplenion*) and Mediterranean groups of alliances.

This study shows that the distribution of alliances in general effectively matches the bioclimatic classification of territories (Köppen and Geiger 1954; Sträβser 1998). Two groups of the vegetation units for most indicator values also showed a high degree of concordance with two main macroclimates. In the study, the communities of the *Cymbalario-Asplenion* alliance characterize cool and mostly shady habitats with the highest humidity. They find their ecological optimum within the Temperate climate (Cfa, Cfb) in the zone of natural vegetation of the *Aremonio-Fagion*, *Erythronio-Carpinion* (*Carpino-Fagetea sylvaticae*) and *Fraxino orni-Ostryion* and *Quercion pubescenti-petraeae* (*Quercetea pubescentis*) (Borhidi 1964; Marinšek et al. 2013; Stupar et al. 2016; Supplementary Appendix S1). The southern limit of the alliance distribution in a west-east direction follows a line from the inland part of the Istrian Peninsula towards Central Bosnia, North Montenegro and the territory of Serbia (Figure 1). In Italy, the southern limit of the alliance distribution was found in North and Central Italy (Hruška 1987; Brullo and Guarino 2002), while in the Balkans it extents to southern Bulgaria and Albania, respectively (Mucina and Kolbek 1989; Dring et al. 2002).

Among the communities of the *Cymbalario-Asplenion* alliance, and according to the indicator values, *Asplenium trichomanes-Arabis hirsuta* community occurred (inland Croatia) in the coolest and shadiest habitats with highest humidity. In particular, numerical analysis (see also Table 1, Supplementary Appendix S4) shows that this community, along with others of the alliance, has a floristic link with the class *Asplenietea trichomanis* due to the presence of *Asplenium trichomanes* L., *A. ceterach*, L., etc. In this study, a large number of taxa were chasmophytes, but their habitats of origin are cliffs, scree slopes and rocks, and walls act as a form of 'analogue habitat' for cliff specialists (Lundholm and Richardson 2010).

The taxa from ruderal and agrestal communities (*Chenopodium album* L., *Epilobium lanceolatum* Sebast. & Mauri, etc.) or from natural and semi-natural vegetation (*Fragaria vesca* L., *Campanula rotundifolia* L., etc.) occurred frequently in several communities (i.e. *Chenopodium album-Reseda lutea* community, *Asplenio rutae-murario-Campanuletum rotundifoliae*, *Asplenium trichomanes-Arabis hirsuta* community, *Resedo albae-Anthirrinetum majoris*, etc.; Table 1, Supplementary Appendix S2). Although very few investigations have specifically dealt with the relationship between wall plants and their environment of origin, a wall environment favours disturbance-tolerant species (ruderals) (for details see Ceschin et al. 2016). This suggests that wall species have similar ecological and coenological features in both habitats. Indeed, Duchoslav (2002) and Francis and Hoggart (2009) both found that competitor and ruderal life strategies were most frequent among wall flora. However, the ruderal character of these communities and the connection between these vegetation forms needs further investigation (Świerkosz 2004). In this study most relevés were collected in urban regions, and walls were extensive in area, variable in type, and colonising species were often moved to preserve the integrity of the wall structure. A strong relationship between floristic composition and wall location type has not been recognized.

In this study, the proportion of non-native taxa (based on proportion of neophytes, *sensu* Müller 2010) in both the *Cymbalario-Asplenion* and *Galio-Parietarion* alliances was low (6.6% of total wall flora). A wide range of proportions of neophytes (3-91%) in wall assemblages has been reported in the literature (de Neef et al. 2008; Francis 2011). Further, this information and a detailed knowledge of the association richness or diversity and endemic rates might be useful also, for example, for conservation purposes.

In comparison to the *Cymbalario-Asplenion*, the *Galio-Parietarion* is more thermophilous i.e. lies within Mediterranean (Csa) and Temperate (Cfa) climates. Taxa such as *Parietaria judaica* L., *Arenaria leptoclados* (Rchb.) Guss., *Sonchus tenerrimus* L., *Campanula austroadriatica* D.Lakušić & Kovačić, *Reichardia picroides* (L.) Roth, etc., point to a relation with the *Carpinion orientalis* and *Fraxino orni-Quercion ilicis* or *Oleo-Ceratonion siliquae* alliances. In the studied area, the communities of the *Galio-Parietarion* are distributed along the eastern Adriatic, in eury- and sub-Mediterranean areas, with the exception of the *Oxalido corniculatae-Parietarietum judaicae cymbalarietosum muralis* which was also found on the warmer and dryer habitats in Bosnia. This is not surprising as the central part of Bosnia is influenced by the Mediterranean climate through deep karstic Herzegovinian canyons and valleys, which generally have a north-south direction (cf. Lovrić et al. 2002; Stupar et al. 2015).

Owing to their particular ecology and floristic composition, three new associations are described here. The first, *Asplenio rutae-murario-Campanuletum rotundifoliae* from Hungary is distinct from the *Cymbalario muralis-Campanula rotundifolia* community (originally not classified) previously described in France (Brandes 1992a: 323). The latter almost completely lacks the character species of *Cymbalario-Asplenion*. The second, *Soncho tenerrimi-Parietarietum judaiace,* which is widespread along the eastern Adriatic coast and relatively rich in ruderals showed an intermediate position for most of the ecological factors among the *Galio-Parietarion* communities. This association contains some typical taxa of less thermophilous conditions, exhibits a wide range in herb cover layer and number of taxa. The third, the moderately thermophilous *Sedo dasyphilli-Campanuletum austroadriaticae* association from South Croatia, Montenegro and Albania is characterized by sub-endemic *Campanula* *austroadriatica* D.Lakušić & Kovačić whose habitat is restricted to the area from the lower Neretva River to northern Albania. Due to the presence and cover values of the *Sedum dasyphyllum*, the association shows some similarities with *Sedo dasyphylli-Ceterachetum offcinarum* Hruška ex Brullo et Guarino reported from Italy (Brullo and Guarino 1998). This was in particular shown for some relevés originating from the towns of Knin and Rijeka, here also included in the *Sedo dasyphilli-Campanuletum austroadriaticae*. In our study, due to the presence of *C. austroadriatica*, the flowering stands are much more noticeable, physiognomically more robust than previous community and occur in more thermophilous conditions.

Alongside the *Soncho tenerrimi-Parietarietum judaicae* association, *Resedo albae-Anthirrinetum majoris* and *Antirrhinum majus-Capparis orientalis* communities are the most thermophilous within the *Galio-Parietarion*, and can mediate with the *Artemisio arborescentis-Capparidion spinosae*. The classification of the *Artemisia arborescens-Coronilla valentina* community to the *Artemisio arborescentis-Capparidion spinosae* alliance, here described by only two relevés, was motivated by the occurrence and dominance of *Capparis orientalis* Veill. and *Artemisia arborescens* L. (Biondi et al. 1994, 2014). Škvorc et al. (2017) were the first to recognize the occurrence of the *Artemisio arborescentis-Capparidion spinosae* alliance restricted to the most thermophilous habitats on the eastern Adriatic i.e. within the thermo-Mediterranean vegetation belt of the *Oleo-Ceratonion siliquae*. The distribution of this alliance should also be extended to the Montenegrin coast where *A. arborescens* was found on the walls facing towards the sea in the old town of Budva (Pulević 2005). This perennial community, already noted for the western Adriatic, requires more in-depth studies to determine its correct syntaxonomic position.

In this study, previously reported associations from South Croatia (*Cymbalario-Crithmetum maritimi* Segal 1969, *Centaureetum ragusinae* Horvat ex Terzi et al. 2017, *Linario-Erigeronetum karvisikianus* Segal 1969 and *Adianto-Parietarietum judaicae* Segal 1969) (Jasprica and Kovačić 2013; Jasprica et al. 2017) and the northeastern Adriatic (e.g. Gamper and Bacchetta 2001) were not differentiated as separate communities. The proposed reasons are as follows: (1) weak floristic differentiation of some communities may be caused by the rates of colonization of the walls by plant taxa from neighbouring ecosystems (Duchoslav 2002), (2) many wall plot samples do not fit well with the phytosociological communities probably because of the cosmopolitan nature of many urban floras (Guggenheim 1992; Shimwell 2009) (3) some associations (*Centaureetum ragusinae*) have been attributed to other vegetation (Terzi et al. 2017), and the interface between them (e.g. *Crithmo-Staticetea* and *Asplenietea trichomanis*) is not completely known (Terzi et al. 2019). Świerkosz (2012) also showed that some of the associations distinguished by Brullo and Guarino (1998) in their pan–European synthesis cannot be confirmed as separable units. In general, the vegetation classification systems developed for larger areas and, particularly, species-poor to moderately rich vegetation, may include some inconsistencies (e.g. Landucci et al. 2015).

In sum, this study makes a contribution to the interpretation of the poorly known vegetation diversity of the chasmophytic wall vegetation in this part of southeastern Europe. The most significant result of this paper lies in information on the alliances distribution in the area and the quantitative data it provides about wall vegetation, description of some new syntaxa and discussion of them in the European syntaxonomic framework of the EVC. Several syntaxonomic interpretative problems regarding the interface between the *Cymbalario-Parietarietea diffusae* and neighbouring vegetation have arisen. These have not figured prominently and deserve further investigation.

Nomenclature

The nomenclature of plant taxa follows the Euro + Med PlantBase (Euro + Med 2006–2018), except for *Mentha* × *verticillata* L., *Reynoutria* × *bohemica* Chrtek & Chrtková and *Sedum palmeri* S.Watson where World Flora Online was used (WFO 2018) (Supplementary Appendix S2). The syntaxonomical system (the EuroVegChecklist) proposed by Mucina et al. (2016), and followed by Škvorc et al. (2017) was applied.

Author contributions

N.J. and Ž.Š. equally contributed to the manuscript and shared primary authorship. They conceived and planned the research; Ž.Š. made the data analyses; N.J. led the writing. All authors made the phytosociological relevés and critically revised the manuscript.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Appendix 1: Holotypes of the new syntaxa

***Asplenio rutae-murario-Campanuletum rotundifoliae* Jasprica, Škvorc et Purger ass. nov. hoc loco** [the town of Sümeg, Hungary; Holotypus (marked with asterisk*): rel. no. 9 of Supplementary Appendix S2; Plot size: 8 m^2; Cover herb layer: 50%; Cover moss layer: 10%; Sloping: 90°; Exposition: NE; Number of the vascular taxa: 9; Date: 4 October 2018 by D. Purger; *Poa pratensis* L. (1), *Campanula rotundifolia* L. (2), *Artemisia campestris* L. (+); *Chelidonium majus* L. (+), *Sedum album* (1), *Asplenium ruta-muraria* (+), *Asplenium trichomanes* L. (1), *Erysimum diffusum* Ehrh. (+), *Urtica dioica* L. (+)].

***Sedo dasyphilli-Campanuletum austroadriaticae* Jasprica, Škvorc et Kovačić ass. nov. hoc loco** [the town of Shkodër, Kalaja e Rozafës, Albania; Holotypus (marked with asterisk*): rel. no. 107 of Supplementary Appendix S2; Plot size: 9 m^2; Cover herb layer: 50%; Cover moss layer: 0%; Sloping: 90°; Exposition: S; Number of the vascular taxa: 16; Date: 16 July 2017 by N. Jasprica; *Sedum dasyphyllum* L. (+), *Convolvulus althaeoides* L. (1), *Aethionema saxatile* (L.) W.T.Aiton (+), *Campanula austroadriatica* D.Lakušić & Kovačić (3), *Galium lucidum* All. (+), *Micromeria juliana* (L.) Benth. ex Rchb. (+), *Catapodium rigidum* (L.) C.E.Hubb. (+), *Sedum album* L. (+), *Satureja montana* L. (+), *Reichardia picroides* (L.) Roth (+), *Petrorhagia saxifraga* (L.) Link (+), *Asplenium ceterach* L. (2), *Parietaria judaica* L. (1), *Asplenium trichomanes* L. (+), *Koeleria splendens* C.Presl (+), *Chondrilla juncea* L. (+)].

***Soncho tenerrimi-Parietarietum judaiace* Jasprica, Škvorc, Pandža et Milović ass. nov. hoc loco** [the city of Pula, The Istrian Peninsula, Croatia; Holotypus (marked with asterisk*): rel. no. 408 of Supplementary Appendix S2, Plot size: 12 m^2; Cover herb layer: 50%; Cover moss layer: 10%; Sloping: 90°; Exposition: N; Number of the vascular taxa: 18; Date: 2 July 2016 by M. Pandža, M. Milović and N. Jasprica; *Lactuca serriola* L. (+), *Veronica cymbalaria* Bodard (+), *Sonchus tenerrimus* L. (1), *Arenaria leptoclados* (Rchb.) Guss. (+), *Anisantha madritensis* (L.) Nevski (+), *Geranium purpureum* Vill. (+), *Asplenium ceterach* L. (+), *Parietaria judaica* L. (+), *Asplenium trichomanes* L. (2), *Scrophularia peregrina* L. (1), *Crepis neglecta* L. (+), *Crepis sancta* (L.) Bornm. (+), *Veronica arvensis* L. (+), *Vulpia bromoides* (L.) Gray (+), *Cardamine hirsuta* L. (+), *Sedum ochroleucum* Chaix (+), *Piptatherum miliaceum* (L.) Coss. (+), *Mercurialis annua* L. (+)].