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Revision of the central Mediterranean xerothermic cliff vegetation

Massimo Terzi, Nenad Jasprica, Danka Caković, Romeo Di Pietro

Terzi, M. (Corresponding author, massimo.terzi@ibbr.cnr.it)[1],

Jasprica, N. (nenad.jasprica@unidu.hr)[2],

Caković, D. (danka.petrovic@t-com.me)[3]

Di Pietro, R. (romeo.dipietro@uniroma1.it)[4]

[1]Institute of Bioscience and Bioresources, CNR, via Amendola 165, I-70126 Bari, Italy

[2]Institute for Marine and Coastal Research, University of Dubrovnik, P.O. Box 83, HR-20000 Dubrovnik, Croatia

[3]University of Montenegro, Faculty of Science, Department of Biology, Džorža Vašingtona bb, 81 000 Podgorica, Montenegro

[4]Department of Planning, Design and Technology of Architecture, Section Environment and Landscape, Sapienza University of Rome, Via Flaminia 72, I-00198, Rome, Italy.

Running title: **Mediterranean xerothermic cliff vegetation**

Abstract

Questions: What are the syntaxonomic and synchorological patterns of the xerothermic chasmophytic vegetation in the central part of the Mediterranean Basin? What are the diagnostic species of the high-rank syntaxa of *Asplenietalia glandulosi, Onosmetalia frutescentis* and *Centaureo dalmaticae-Campanuletalia pyramidalis*?

Location: Mediterranean coastal and subcoastal areas of southern France, Italy, Malta, Slovenia, Croatia, Bosnia and Herzegovina, Montenegro, Albania, and of mainland Greece.

Methods: The data set of 1261 published relevés was analysed using hierarchical clustering (Flexible Beta method), involving a series of data transformations. Indicator Species Analysis was used to select the best dendrogram solution and identify diagnostic taxa of the main clusters. The dendrogram was interpreted from a syntaxonomic point of view, using nomenclatural type relevés as a basis. The NMDS ordination was performed in order to visualize the floristic relationships among associations and high-rank syntaxa. MRPP was used to test for differences among alliances.

Results: The classification revealed four main clusters of relevés representing the chasmophytic vegetation of southern France, Sardinia, and the northwestern part of Italy (*Asplenienalia glandulosi*/*Asplenietalia glandulosi*), the southwestern part of Italy and Malta (*Tinguarrenalia siculae*/*Asplenietalia glandulosi*), the Adriatic Basin area (*Centaureo dalmaticae-Campanuletalia pyramidalis*) and the southern Balkans (*Onosmetalia frutescentis*). The NMDS ordination confirmed the overall pattern, while MRPP showed significant differences among the alliances of the above mentioned orders and suborders. The lists of diagnostic taxa of the high-rank syntaxa were revised according to a supra-national perspective.

Conclusions: The new syntaxonomic scheme provides a comprehensive overview of the chasmophytic vegetation of the central part of the Mediterranean Basin. This scheme mostly matches the recently published EuroVegChecklist, but exhibits also important novelties concerning the syntaxonomic position of some alliances (*Dianthion rupicolae*, *Centaureion pentadactyli*, *Arenarion bertolonii*, and *Caro-Aurinion*), and the floristic and chorological relationships among high-rank syntaxa, with new revised sets of diagnostic taxa. This revision might be useful for further small-scale phytosociological studies.

Keywords: Adriatic Basin, *Asplenietalia glandulosi*, *Asplenietea trichomanis*, *Centaureo-Campanuletalia*, Chasmophytes, Classification of vegetation, Indicator Species Analysis, Mediterranean vegetation, *Onosmetalia frutescentis*, Syntaxonomy, *Tinguarrenalia siculae*.

Nomenclature: The nomenclature of plant taxa follows Euro+Med Plantbase (http://ww2.bgbm.org/EuroPlusMed/, accessed on July 2017) and The Plant List (http://www.theplantlist.org/ accessed on October 2017) for genera not included in the Euro+Med PlantBase. The Plant list was also used for *Bituminaria*, *Campanula*, *Dianthus*, and *Iris*. For the *Galium lucidum* group, the nomenclature follows Conti & Bartolucci (2009). Syntaxonomic nomenclature follows Terzi et al. (2017) and Mucina et al. (2016) for syntaxa not included there.

Abbreviations: EVC= EuroVegChecklist (Mucina et al. 2016); IndSp = Indicator Species; IndVal = Indicator Value; ISA = Indicator Species Analysis; MRPP = Multi-response permutation procedure; NMDS = Non-metric multidimensional scaling.

Introduction

Mediterranean cliffs harbour a very specialized flora, comprising many rare and endemic taxa, and are considered a habitat worthy of protection. The Directive 92/43/EEC of the EU Commission listed calcareous and siliceous rocky cliffs with chasmophytic vegetation as habitat types 8210 and 8220, respectively.

The effective conservation of these habitats could be enhanced by a consistent classification on a supranational scale. The first phytosociological synthesis for the Mediterranean chasmophytic vegetation was provided by Meier & Braun-Blanquet (1934), who coined the class '*Asplenietales rupestris*' (recte: *Asplenietea trichomanis*), and four orders within this class. Three of these orders ('*Androsacetalia multiflorae*', '*Potentilletalia caulescentis'* and '*Asplenietalia glandulosi*') occur in Europe.

Subsequently, due to the regional floristic diversification and richness in local endemics and rare species which characterizes these vegetation types (Davis 1951), several other orders have been proposed for the chasmophytic vegetation of the Mediterranean Basin. According to the EuroVegChecklist (EVC), a recently proposed syntaxonomic classification system for the vegetation types of Europe (Mucina et al. 2016), the *Asplenietea trichomanis* include 13 orders. The *Asplenietalia glandulosi* are restricted to the limestone substrates in the thermo-mesomediterranean belt of the western Mediterranean, and are replaced by the *Centaureo dalmaticae-Campanuletalia pyramidalis* in the Adriatic coastal area, by the *Moltkietalia petraeae* towards the inland western Balkans, and by the *Onosmetalia frutescentis* in the southern Adriatic and Ionian seaboards. On siliceous substrates, the *Asplenietalia glandulosi* are replaced by the *Asplenietalia lanceolato-obovati* (Mucina & Theurillat 2015).

These orders and their subordinated alliances have been addressed in many phytosociological papers, the most influential being those of Meier & Braun-Blanquet (1934), Horvatić (1934, 1963), Braun-Blanquet et al. (1952), Rivas Goday et al. (1956), Bolòs & Molinier (1958), Rivas-Martínez (1960), Quézel (1964), Lakušić (1968), Horvat et al. (1974), Brullo & Marcenò (1979), Trinajstić (1980, 2008), Bianco et al. (1988), Martínez-Parras & Peinado (1990), Arrigoni & Di Tommaso (1991), Dimopoulous et al. (1997), Rivas-Martínez et al. (2001, 2011), Brullo et al. (2001, 2004), Rodwell et al. (2002), Brullo & Spampinato (2003), Di Pietro & Wagensommer (2008), Terzi & D'Amico (2008) and Mucina et al. (2016). However, many aspects of the floristic, synchorological and syntaxonomic relationships among these syntaxa were in most cases based on expert judgements rather than on overall statistical comparison, leading to different and sometimes contradictory interpretations. The *Asplenietalia glandulosi* range, for instance, was originally extended southwards to North Africa and eastwards to the East Adriatic coast (e.g. Meier & Braun-Blanquet 1934). On the other hand, some authors replaced the *Asplenietalia glandulosi* with other vicariant orders in Sardinia (Arrigoni & Di Tommaso 1991), North Africa and South Italy (Daumas et al. 1952) and the Adriatic area (Lakušić 1968; Trinajstić 1980).

Rivas-Martínez et al. (2001; 2011) and Costa et al. (2012) clarified the syntaxonomy and nomenclature of the chasmophytic vegetation of the Iberian Peninsula. Recent studies (Terzi & Di Pietro 2016; Terzi et al. 2017) reviewed the nomenclature of the *Asplenietalia glandulosi* and its vicariant orders in the central part of the Mediterranean Basin. This area is particularly interesting from a biogeographical viewpoint since cliff plants from both the western and eastern Mediterranean occur. The aim of this paper is to revise the syntaxonomy of the *Asplenietalia glandulosi*, *Centaureo-Campanuletalia* and *Onosmetalia frutescentis* in the central part of the Mediterranean Basin, across a wide area ranging from France to Greece. In more detail, this paper aims at: (i) identifying the syntaxonomic and synchorological relationships among the above-mentioned orders and their alliances; (ii) identifying the diagnostic species of the high-rank syntaxa under a supranational perspective.

Methods

Data set

The data set consisted of 1261 phytosociological relevés (comprising 959 taxa) of chasmophytic vegetation, already classified within the *Asplenietalia glandulosi* or in its vicariant orders. The relevés were recorded along the Mediterranean coastal and subcoastal areas of southern France, Italy, Malta, Slovenia, Croatia, Bosnia and Herzegovina, Montenegro, Albania and continental Greece (Fig. 1; Appendix S1).

In the data matrix, taxa indicated only at the genus level were omitted as well as bryophytes and lichens that were inconsistently recorded in phytosociological tables. Taxonomically closely related taxa were reported under the same tag if their differentiation among relevés in the data set was uncertain. The taxon cover-abundance scores of the original tables were transformed according to the ordinal scale of van der Maarel (1979).

Information about the plot size of the relevés in the data set, were missing for 96 relevés. The average plot size of relevés was 58.4 m^2. Extremely small (< 5 m^2) and extremely large plot sizes (> 150 m^2) were removed from the data set since they could affect the results of statistical analyses (Otýpková & Chytrý 2006). Nomenclatural type-relevés (Weber et al. 2000) were always retained.

The data set was resampled following the method proposed by De Cáceres et al. (2008; a '*resemblance-based re-sampling*' according to De Cáceres et al. 2015). The Sørensen coefficient (related to the Bray-Curtis coefficient; Kent 2012) was calculated between each pair of relevés on the basis of the presence/absence of taxa and, starting from the lowest distance value, up to the arbitrary threshold of 0.3 (see also Westhoff & van der Maarel 1978), one relevé for each pair was randomly deleted. If a nomenclatural type relevé was involved, it was always retained. The resulting data matrix consisted of 777 relevés and 925 taxa.

Relevés clustering

Taxon scores were exponentially transformed to weight the cover-abundance values according to $x' = x^y$ (van der Maarel 1979; Wildi 2010; Terzi 2015). Five data matrices were obtained by setting $y = 2$ (close to the mid-point of the percent-cover ranges of the Braun-Blanquet scale), $y = 1$ (ordinal scale), $y = 0.5$ (square root; low weight to cover), $y = 0.25$ (very low weight to cover) and $y = 0$ (presence/absence). Each transformed data matrix was subjected to hierarchical clustering by using the Flexible Beta method (β = -

0.25) in combination with Sørensen coefficient. In all, 5 dendrograms were obtained using the software PC-ORD, version 6.22 (McCune & Mefford 2011).

Indicator Species Analysis (ISA)

ISA (Dufrêne & Legendre 1997) was run for the first 15 partitioning levels of each dendrogram, the 1st level being the trivial partition with all the relevés in only one group. Since this revision focuses on high-rank syntaxa, the analysis was restricted to the first 15 partitions, further divisions dealing with minor variations (only 13 alliances are represented in the data set, Appendix S1).

In order to obtain a stronger indication, the indicator values (IndVal, Dufrêne & Legendre 1997) were calculated on the basis of the presence/absence of taxa occurring in at least three relevés (see Tichý & Chytrý 2006: 814, eq. 7). For each partitioning level, a taxon was identified as indicator species (IndSp) of a cluster if its IndVal yielded the highest value for that cluster and if it turned out to be significant ($p < 0.05$) in a Monte Carlo Test with 10,000 permutations.

The numbers of IndSp along the descending hierarchical typology of a dendrogram are considered as an ‘*objective criterion for picking the most ecologically meaningful point to prune a dendrogram from cluster analysis*’ (McCune & Grace 2002). Therefore the five dendrograms were pruned at the partitions yielding the highest number of IndSp.

In order to choose the best clustering solution, the cumulative number of IndSp of each dendrogram, from the 2nd partition up to the level at which it had been pruned, was compared with the cumulative number of IndSp counted for the same partitioning levels of the other dendrograms.

Many taxa turned out to be IndSp of more than one cluster along the hierarchical descending typology of the dendrogram. In accordance with Dufrêne & Legendre (1997), we considered as the best clustering level of an IndSp, the level for which the IndVal first reached its highest value. As a consequence, each IndSp was assigned to only one dendrogram cluster (Appendix S4). For some species, the IndVal of the first (trivial) partition with all the relevés in only one group turned out to be higher than the IndVal calculated for the following partitioning levels. These IndSp were associated with the first level of the dendrogram (Fig. 2: cluster 1t).

The syntaxonomic interpretation of the dendrogram was based on the presence in the clusters of the nomenclatural type relevés (i.e., ‘*that element of the syntaxon with which its name is permanently attached*’ Weber et al. 2000). Diagnostic taxa of each high-rank syntaxon were deduced from the IndSp associated to the relevant cluster or to its subdivisions. The phytosociological roles given to species in some influential papers on chasmophytic vegetation (Appendix S5) supported our subjective selection of IndSp in order to identify the diagnostic taxa of each syntaxon.

Non-metric multidimensional scaling (NMDS)

The floristic relationships among associations were visualized by means of NMDS using the Sørensen coefficient. Only the associations/subassociations tables composed of at least 5 phytosociological relevés were considered (Appendix S2). In few cases, more than one phytosociological table was available for the same associations/subassociations and, in these cases, we considered only one of them. For several associations/subassociations we were able to find only few relevés or none at all (in the latter case, these syntaxa were not represented in the cluster analysis). For them, if synoptic tables were available, they were added to the data matrix subjected to NMDS, substituting the Roman numerals constancy values with the central value of the relevant frequency class. In order to evaluate the syntaxonomic relationships of the *Dianthion rupicolae* and *Linarion caprariae* with the *Asplenietalia lanceolato-obovati*, three French associations belonging to the *Antirrhinion asarinae* – which is the order nomenclatural type – were added. Moreover, we added three synoptic columns representing the original diagnoses of the *Phagnalo sordidi-Asplenietum glandulosi* and its two subassociations, the *Phagnalo-Asplenietum* being the nomenclatural type of the *Asplenion glandulosi* which, in turn, is the type-alliance of the *Asplenietalia glandulosi*.

The final data matrix consisted of 87 synoptic columns and 919 taxa (Appendix S2). The NMDS ordination was performed by selecting the 'slow and thorough' autopilot mode of PC-ORD which implies a maximum of 500 iterations, an instability criterion of 10^{-8}, 250 real runs and 250 randomized runs, with six axes as starting point (McCune & Mefford 2011).

For each syntaxon represented in the NMDS ordination, the chorological spectrum weighted by taxa frequencies was calculated. Chorotypes were selected on the basis of information provided in Pignatti (1982) and Euro+Med Plantbase (Appendix S3). Joint plots with an r^2 cutoff of 0.30 were performed to display in the ordination diagram the strengths of the relationships among the ordination scores and the chorological spectra.

Multi-Response Permutation Procedure (MRPP)

MRPP (Biondini et al. 1985) was used for determining whether the alliances represented in the NMDS were significantly different from each other. Two alliances were excluded from the test: *Brassicion insularis* represented by only one association (synoptic column) and *Edraianthion tenuifolii*, to which we referred only two associations. MRPP was applied to the rank transformed distance matrix, with the Sørensen coefficient as dissimilarity measure, as implemented in the software PC-ORD, in order to enhance the correspondence of the results with the NMDS (McCune & Grace 2002; McCune & Mefford 2011).

Results

Cluster analysis

We found five dendrograms that were similar in the overall structure. The main differences relate to the position of the *Linarion caprariae*, *Centaureion pentadactyli* and various associations considered below. These differences are considered in the interpretation of results. The best clustering solution turned out to be the one obtained by using the square root transformed data matrix and it will be addressed henceforth. The highest number of IndSp was reached at the 11th level, giving 11 main clusters of relevés (Fig. 2). On the basis of the position of the type relevés, the clusters are considered as representative of the associations and alliances indicated in table 1. Further insights were obtained by considering further subdivisions of some clusters.

The first two partitions of the dendrogram separate the western associations (Fig. 2, clusters TS_{1-4} and Ag_{1-2}) from the eastern ones (clusters Ofr, CC_{1-3} and Lc+Et). Syntaxa from southwest Italy and Malta are distributed within four main clusters (Ts_{1-4}). One of them (Ts_4) includes the associations of the *Centaureion pentadactyli*; the other three clusters represent two new suballiances of the *Dianthion rupicolae*, namely the *Dianthenion rupicolae* (clusters Ts_1 and Ts_2) and *Campanulenion fragilis* (Ts_3). The associations from Sardinia (cluster Ag_1) and those from northwestern Italy and southern France (Ag_2) are grouped in the cluster 3a. On the other side of the dendrogram, the associations of the *Onosmetalia frutescentis* from Greece (cluster Ofr) are well differentiated from the others. The clusters CC_{1-3} include associations from the southeast of Italy (CC_{1-2}) and from the West Balkans (CC_3). The cluster Lc+Et includes associations sufficiently different from all the others to be classified in other orders.

ISA

Few IndSp were associated with the first partition of the dendrogram (Fig.2, cluster 1t; Appendix S4). Among them, *Asplenium ceterach* and *Sedum dasyphyllum* are class character species while others are to be considered as ingressive (*Parietaria judaica*, *Ficus carica*) or high-frequency companion species. Cluster 2a and its further subdivisions (clusters Ts_{1-4}), which represent Southwest Italy and Malta, are characterized by many IndSp, with some of them showing high IndVal. Among these taxa, there are some character species of the class (e.g., *Umbilicus rupestris*) and the *Asplenietalia glandulosi* (e.g., *Teucrium flavum*). Clusters Ag_{1-2}, representing the associations occurring in the northern part of the *Asplenietalia glandulosi* range, are characterized by many IndSp, among which the character taxa of the alliances *Asplenion glandulosi*, *Brassicion insularis* and *Centaureo-Micromerion.* On the other side of the dendrogram, the clusters 3b, 4b and 7a exhibit few IndSp, testifying to a less homogeneous composition. By contrast, the clusters Ofr (*Onosmetalia frutescentis*), CC_1 (*Asperulion garganicae*), CC_2 (*Caro-Aurinion*) and CC_3 (*Centaureo-Campanulion* and *Centaureo-Portenschlagiellion*) turned out to be floristically well differentiated, exhibiting numerous IndSp and high IndVal. Despite the floristic similarities among the alliances of the Adriatic area, there is a marked differentiation between the eastern and western alliances.

NMDS and MRPP

The NMDS ordination resulted in a three axis solution (Fig. 3), with a final stress of 16.4. The ordination explained 61.8 % of the total proportion of variance, axes 1, 2 and 3 accounting for 19.9 %, 21.6 % and 20.2 % of variance respectively.

The western alliances belonging to the *Asplenietalia glandulosi* were clearly separated from the eastern ones belonging to the *Onosmetalia frutescentis* and *Centaureo-Campanuletalia*, with the only exception of the *Campanulo-Portenschlagielletum* (Fig. 3b, n° 13 and 14). The *Antirrhinion asarinae* is distinguishable on the left side of axis 1 (Fig. 3a), as well as the two subassociations of the *Campanulo-Moltkietum* described for the Mount Lovćen, that should be classified in the *Edraianthion tenuifolii*.

Moreover, within the *Asplenietalia glandulosi*, the separation between the alliances occurring in the northern part of the order (*Asplenion glandulosi*, *Centaureo filiformis-Micromerion cordatae*, *Brassicion insularis*) and those occurring in the southern part (*Centaureion pentadactyli*, *Dianthion rupicolae*) was observed, thus confirming the results of the cluster analysis.

The west steno-Mediterranean chorotype is well represented in the *Asplenietalia glandulosi* (positive correlation with axis 3, $r^2 = 0.43$). The southern associations of the *order* (i.e., *Tinguarrenalia siculae*) exhibit higher percentages of steno-Mediterranean taxa.

The *Campanulion versicoloris* is characterized by high percentages of south-Balkan and east-steno-Mediterranean taxa (positive correlation with axis 2 of these two chorotypes: $r^2 = 0.39$ and $r^2 = 0.33$ respectively). The other relationships between ordination scores and chorological types show negative correlations of axis 2 with Italian-Balkan ($r^2 = 0.63$), Balkan ($r^2 = 0.25$) and West Balkan ($r^2 = 0.23$) types and negative correlation of axis 1 with European ($r^2 = 0.46$) and Circumboreal ($r^2 = 0.40$) types (Fig. 3).

MRPP results revealed that the alliances represented in the NMDS diagram significantly differ in species composition. Moreover, all the pairwise comparisons between alliances showed significant ($p < 0.05$) differences except (after a Bonferroni correction) comparisons involving alliances represented by 3 or 4 synoptic columns only (Appendix S7).

Syntaxonomic scheme

On the basis of the results shown above, the following syntaxonomic scheme is proposed (see also Tab. 2 and 3; Fig. 4; the order *Moltkietalia petraeae* is added to the scheme below only for the two new associations):

***Asplenietea trichomanis*.** Diagnostic taxa (D.t.): *Allosorus pteridioides*, *Asplenium ceterach*, *Asplenium ruta-muraria*, *Asplenium trichomanes*, *Capparis spinosa* aggr., *Centranthus ruber* subsp. *ruber*, *Euphorbia dendroides*, *Ephedra foeminea*, *Ficus carica*, *Melica minuta*, *Parietaria judaica*, *Phagnalon rupestre* subsp. *illyricum*, *Phagnalon rupestre* subsp. *graecum*, *Pimpinella tragium*, *Polypodium cambricum* subsp. *cambricum*, *Putoria calabrica*, *Sedum dasyphyllum*, *Teucrium flavum* subsp. *flavum*, *Umbilicus horizontalis*, *Umbilicus rupestris.*

• ***Asplenietalia glandulosi*** [syn. *Arenario bertoloni-Phagnaletalia sordidi*]. D.t.: *Antirrhinum majus, Cosentinia vellea* subsp. *vellea, Dianthus longicaulis, Dianthus siculus, Lobularia maritima* (d), *Melica minuta, Phagnalon saxatile, Teucrium flavum* subsp. *flavum.* Other taxa with high IndVal (>20): *Geranium purpureum, Juniperus phoenicea, Sedum sediforme.* Distribution: western Mediterranean Basin.

•• ***Asplenienalia glandulosi*** subord. nov. hoc loco [holotypus: *Asplenion glandulosi* Braun-Blanquet et Meier in Meier et Braun-Blanquet 1934: 23]. D.t.: *Asplenium petrarchae (Asplenium glandulosum), Brassica insularis, Chiliadenus glutinosus, Hormathophylla spinosa, Mercurialis huetii, Phagnalon sordidum.* Distribution: northern part of western Mediterranean Basin, with outposts in the Adriatic area. In the Italian Peninsula the boundary between the *Asplenienalia glandulosi* and the *Tinguarrenalia siculae* roughly lies in the Lazio Region (Central Italy).

***Asplenion glandulosi*.** D.t.: *Asplenium petrarchae, Erodium foetidum, Malva subovata, Melica amethystina.* Other taxa with high IndVal (>20): *Galium corrudifolium, Lactuca perennis, Thymus vulgaris.*

Associations: *Asplenio-Campanuletum macrorhizae*; *Diantho brachyanthi-Lavateretum maritimae*; *Hieracio stelligeri-Alyssetum spinosae*; *Melico minutae-Pseudofumarietum acaulis*; *Phagnalo sordidi-Asplenietum glandulosi.*

***Centaureo filiformis-Micromerion cordatae*.** D.t.: *Arenaria balearica* (d), *Arenaria bertolonii* (d), *Asperula pumila, Bituminaria morisiana, Centaurea filiformis, Cephalaria squamiflora* subsp. *mediterranea, Helichrysum saxatile, Hypochaeris robertia* (d), *Lactuca longidentata, Limonium morisianum, Micromeria filiformis* subsp. *cordata, Seseli praecox, Sesleria insularis* (d), *Siler montanum* subsp. *garganicum* (d). Other taxa with high IndVal (>20): *Allium subhirsutum, Arabis hirsuta, Bellium bellidioides, Brachypodium retusum, Clematis cirrhosa, Coronilla valentina, Galium lucidum, Helianthemum croceum, Quercus ilex, Rosmarinus officinalis, Stachys glutinosa, Teucrium marum.*

Associations: *Helichryso saxatilis-Cephalarietum mediterraneae*; *Laserpitio garganici-Asperuletum pumilae*.

***Brassicion insularis*.** D.t.: *Brassica insularis, Ruta divaricata.*

Association: *Asplenio rutae-murariae-Arenarietum bertolonii.*

•• ***Tinguarrenalia siculae* (Daumas et al. 1952) Galán de Mera in Pérez-Latorre et al. 1996.** D.t.: *Athamanta sicula, Ballota hispanica, Brassica fruticulosa, Euphorbia bivonae, Hypochaeris laevigata, Lomelosia cretica, Seseli bocconi, Silene fruticosa*. Other taxa with high IndVal (>20): *Hyoseris radiata, Hyparrhenia hirta, Micromeria graeca*. Distribution: southern part of western Mediterranean Basin.

***Centaureion pentadactyli*.** D.t.: *Allium pentadactyli, Centaurea pentadactyli, Crepis aspromontana, Dianthus brutius, Silene calabra.*

Associations: *Arabido collinae-Centaureetum aspromontanae*; *Centaureo pentadactyli-Dianthetum aspromontani*; *Centaureo pentadactyli-Dianthetum longicaulis*; *Centaureo pentadactyli-Dianthetum pentadactyli.*

***Dianthion rupicolae*.** D.t.: *Anthemis cupaniana, Antirrhinum siculum, Asperula rupestris, Brassica bivoniana, Brassica drepanensis, Brassica incana, Brassica macrocarpa, Brassica rupestris, Centaurea busambarensis, Centaurea panormitana* subsp. *ucriae, Centaurea panormitana* subsp. *umbrosa, Convolvulus cneorum, Cymbalaria muralis* subsp. *pubescens, Dianthus rupicola, Erucastrum virgatum, Genista gasparrinii, Glandora rosmarinifolia, Helichrysum pendulum* aggr. (species of Sicily), *Iberis semperflorens, Matthiola incana* subsp. *rupestris, Micromeria microphylla* (d), *Odontites bocconei, Pseudoscabiosa limonifolia, Seseli bocconi, Silene* *fruticosa*. Other taxa with high IndVal (>20): *Centaurea tauromenitana*, *Dianthus arrostii*, *Erica multiflora*, *Galium pallidum*.

Dianthenion rupicolae suball. nov. hoc loco [holotypus: *Scabioso creticae-Centaureetum ucriae* Brullo et Marcenò 1979: 139]. D.t.: *Anthemis cupaniana*, *Asperula rupestris*, *Brassica rupestris*, *Cymbalaria muralis* subsp. *pubescens*, *Genista gasparrinii*, *Iberis semperflorens*, *Matthiola incana* subsp. *rupestris*, *Odontites bocconei*, *Pseudoscabiosa limonifolia*, *Seseli bocconi*, *Silene fruticosa*.

Associations: *Anthemido cupanianae-Centaureetum busambarensis*; *Brassico rupestris-Centaureetum saccensis*; *Brassico villosae-Diplotaxietum crassifoliae*; *Bupleuro dianthifolii-Scabiosetum limonifoliae*; *Diantho rupicolae-Centaureetum aeolicae*; *Erucastretum virgati*; *Micromerio microphyllae-Putorietum calabricae*; *Scabiosetum creticae*; *Triadenio aegypticae-Chiliadenetum bocconei*;

Campanulenion fragilis suball. nov. hoc loco [holotypus: *Centaureo cinerariae-Campanuletum fragilis* Brullo et Marcenò 1979: 138]. D.t.: *Campanula fragilis*, *Centaurea cineraria*, *Seseli polyphyllum*. Other taxa with high IndVal (>20): *Primula palinuri*, *Athamanta ramosissima*.

Associations: *Centaureo cinerariae-Campanuletum fragilis*; *Campanulo fragilis-Portenschlagielletum ramosissimae* (uncertain syntaxonomic position).

+ ***Centaureo dalmaticae-Campanuletalia pyramidalis*.** D.t.: *Allium ampeloprasum* (d), *Aurinia leucadea*, *Aurinia sinuata*, *Campanula pyramidalis*, *Convolvulus cneorum*, *Cytisus spinescens* (d), *Dianthus tarentinus*, *Frangula rupestris* (d), *Inula verbascifolia*, *Iris illyrica*, *Leontodon apulus*, *Picris hispidissima*, *Onosma echioides* subsp. *angustifolia* (d), *Sedum hispanicum* (d), *Seseli globiferum*, *Sesleria juncifolia*, *Sonchus asper* subsp. *glaucescens* (d). Other taxa with high IndVal (>20): *Rhamnus saxatilis* subsp. *infectoria*, *Satureja montana*. Distribution: Adriatic coasts.

***Centaureo cuspidatae-Portenschlagiellion ramosissimae*.** D.t.: *Alyssoides utriculata*, *Asperula scutellaris*, *Athamanta ramosissima*, *Campanula portenschlagiana*, *Centaurea cuspidata*, *Galium firmum*, *Iris pseudopallida*, *Moltkia petraea*, *Resetnikia triquetra*, *Seseli tomentosum*, *Tanacetum cinerariifolium*, *Teucrium arduinii*.

Associations: *Campanulo pyramidalis-Moltkietum petraeae*; *Fibigio triquetrae-Cerinthetum tristis*; *Inulo verbascifoliae-Centaureetum cuspidatae*; *Micromerio kerneri-Onosmetum dalmaticae*, *Moltkio petraeae-Inuletum verbascifoliae*, *Moltkio petreae-Campanuletum lepidae*; *Moltkio petraeae-Centaureetum voraginicolae nom. inval.*; *Portenschlagiello ramosissimae-Campanuletum portenschlagianae*; *Seslerio robustae-Putorietum calabricae*; *Teucrio arduinii-Seselietum globiferi*.

***Centaureo dalmaticae-Campanulion*.** D.t.: *Aurinia petraea*, *Campanula fenestrellata* subsp. *fenestrellata*, *Campanula fenestrellata* subsp. *istriaca*, *Centaurea kartschiana* subsp. *dalmatica*, *Centaurea kartschiana* subsp. *kartschiana*, *Centaurea kartschiana* subsp. *lubenicensis*, *Centaurea ragusina*, *Clinopodium thymifolium* (d), *Euphorbia fragifera* (d), *Moehringia tommasinii*. Other taxa with high IndVal (>20): *Crithmum maritimum*.

Associations: *Asplenio lepidi-Moehringietum tommasinii*; *Aurinio petreae-Centaureetum lubenicensis*; *Campanulo pyramidalis-Centaureetum kartschianae*; *Centaureetum ragusinae*; *Crithmo maritimi-Centaureetum dalmaticae*; *Saturejo-Euphorbietum wulfenii*; *Seselio globiferi-Pseudofumarietum acaulis*; *Seslerio tenuifoliae-Scorzoneretum austriacae*; *Thalictro velebitici-Campanuletum fenestrellatae*.

***Asperulion garganicae*.** D.t.: *Asperula garganica*, *Aubrieta columnae*, *Campanula garganica* subsp. *garganica*, *Centaurea subtilis*, *Doronicum columnae* (d), *Lomelosia crenata* subsp. *dallaportae*, *Pimpinella tragium*. Other taxa with high IndVal (>20): *Festuca circummediterranea*.

Associations: *Campanulo garganicae-Aubrietetum italicae*; *Centaureetum subtilis*; *Pimpinello tragii-Inuletum verbascifoliae*; *Scabiosetum dallaportae*;

***Caro multiflori-Aurinion megalocarpae*.** Diagnostic taxa: *Aurinia saxatilis* subsp. *megalocarpa, Campanula versicolor, Centaurea brulla, Centaurea japygica, Centaurea leucadea, Centaurea nobilis, Centaurea tenacissima, Dianthus japigicus, Hellenocarum multiflorum, Leontodon intermedius, Satureja cuneifolia* (d), *Scrophularia lucida*. Other taxa with high IndVal (>20): *Prasium majus*.

Associations: *Aurinio megalocarpae-Centaureetum brullae*; *Campanulo versicoloris-Aurinietum leucadeae*; *Iberido carnosae-Athamantetum siculi*; *Piptathero holciformis-Campanuletum versicoloris.*

+ ***Onosmetalia frutescentis*.** D.t.: *Asperula arcadiensis, Asperula chlorantha, Asperula lutea, Aubrieta deltoidea, Aurinia saxatilis* subsp. *orientalis, Ballota acetabulosa, Bubon macedonicum, Campanula anchusiflora, Campanula rupestris, Campanula versicolor, Centaurea raphanina* subsp. *mixta, Centranthus ruber* subsp. *sibthorpii, Cephalaria ambrosioides, Ephedra foeminea, Hellenocarum multiflorum, Inula parnassica, Odontites linkii, Onosma frutescens, Phagnalon rupestre* subsp. *graecum, Pterocephalus perennis, Ptilostemon chamaepeuce, Saxifraga rotundifolia* subsp. *chrysosplenifolia, Scrophularia heterophylla* subsp. *heterophylla, Silene congesta, Silene gigantea, Teucrium flavum* subsp. *hellenicum, Umbilicus chloranthus.* Other taxa with high IndVal (>20): *Arabis alpina* subsp. *caucasica, Festuca jeanpertii, Fraxinus ornus, Leontodon graecus, Micromeria juliana, Phlomis fruticosa, Quercus coccifera*. Distribution: southern Balkan Peninsula.

***Campanulion versicoloris*.** Diagnostic taxa: see order.

Associations: *Asperulo arcadiensis-Hypericetum vesiculosi*; *Asperulo chloranthae-Daphnetum jasmineae*; *Asperulo chloranthae-Moltkietum petraeae*; *Inuletum rotundifoliae*; *Inulo parnassicae-Ptilostemetum chamaepeuces*; *Saxifrago chrysosplenifoliae-Athamantetum macedonicae*; *Sideritido raeseri-Alkannetum graecae*; *Stachyo candidae-Galietum boryani*.

+ ***Moltkietalia petraeae***

Edraianthion tenuifolii

- *Campanulo austroadriaticae-Moltkietum petraeae* (Tomić-Stanković ex Terzi et al. 2017 nom. corr. hoc loco) comb. nov. (= *Campanulo pyramidalis-Moltkietum petraeae* Horvatić ex Trinajstić 1964 *campanuletosum pyramidalis* Tomić-Stanković ex Terzi, Jasprica et Caković 2017: 375; *Campanula pyramidalis* has to be replaced by *Campanula austroadriatica* D. Lakušić & Kovačić [see Janković et al. 2016]), holotypus: rel. 11, tab. II, in Tomić-Stanković (1970).
- *Saxifrago crustatae-Moltkietum petraeae* (Tomić-Stanković ex Terzi et al. 2017) comb. nov. (= *Campanulo pyramidalis-Moltkietum petraeae* Horvatić ex Trinajstić 1964 *scabiosetosum graminifoliae* Tomić-Stanković ex Terzi, Jasprica et Caković 2017: 375), holotypus: rel. 6, tab. II, in Tomić-Stanković (1970).

Discussion

The EVC has the advantage of being based on a supranational perspective and, taking into consideration all European vegetation types, provides a general framework for the European area. For these reasons, we adopt the system of three orders proposed in the EVC, *Asplenietalia glandulosi*, *Centaureo-Campanuletalia* and *Onosmetalia frutescentis*. Two other orders, *Asplenietalia lanceolato-obovati* and *Moltkietalia petraeae*, are dealt with briefly in the discussion below just in order to highlight their floristic relationships with the *Asplenietalia glandulosi* and *Centaureo-Campanuletalia*, respectively.

Asplenietalia glandulosi* and *Asplenietalia lanceolato-obovati

In the central Mediterranean, the *Asplenietalia glandulosi* is represented by five alliances: *Centaureo filiformis-Micromerion cordatae*, *Asplenion glandulosi*, *Brassicion insularis*, *Centaureion pentadactyli* and *Dianthion rupicolae*.

According to the EVC, the *Dianthion rupicolae* (including the *Centaureion pentadactyli*) should be classified in the *Asplenietalia lanceolato-obovati* together with the *Antirrhinion asarinae* (the order typus), *Cheilanthion hispanicae* of the Iberian Peninsula and the *Linarion caprariae* from the Tuscan Archipelago (IT). The *Asplenietalia lanceolato-obovati* derives from the change of rank of a suborder of the *Androsacetalia vandellii* describing the low altitude Mediterranean vegetation of the siliceous cliffs (Loisel 1970). However, the nomenclatural type of the *Dianthion rupicolae*, i.e. the *Scabioso creticae-Centaureetum ucriae*, and many other, but not all, associations of this alliance were recorded on calcareous bedrock (Brullo & Marcenò 1979; Brullo et al. 2004).

Moreover, the inclusion of the *Dianthion rupicolae* and *Centaureion pentadactyli* within the *Asplenietalia lanceolato-obovati* is not supported by a solid floristic component. In fact, this order is characterized by five taxa, *Allosorus pteridioides*, *Asplenium obovatum* subsp. *billotii*, *Asplenium obovatum* subsp. *obovatum*, *Bufonia macropetala*, and *Phagnalon saxatile* (Loisel 1970; Mucina & Theurillat 2015). Three of them turned out to be IndSp in our analysis. *Allosorus pteridioides* and *Asplenium obovatum* subsp. *obovatum* are IndSp for the clusters 5b (Fig. 2: *Asplenion glandulosi*) and 10b (*Linarion caprariae*), respectively, but with a very low IndVal (<6; Appendix S4). *Phagnalon saxatile*, which is IndSp of cluster 2a (*Asplenietalia glandulosi*), is to be considered as a differential species of the *Asplenietalia lanceolato-obovati*, since it occurs in other orders and classes (e.g., *Phagnalo saxatilis-Cheilanthion maderensis*, *Asplenietalia glandulosi*, *Phagnalo saxatilis-Rumicetea indurati*). The NMDS diagram (Fig. 3) showed that the *Centaureion pentadactyli* and the *Dianthion rupicolae* are clearly separated from the *Antirrhinion asarinae* (the nomenclatural type of the *Asplenietalia lanceolato-obovati*) which, for its part, occupies an isolated left-most axis 1 position. For these reasons, the *Centaureion pentadactyli* and the *Dianthion rupicolae* are here classified in the *Asplenietalia glandulosi*. The distribution range of the *Centaureion pentadactyli* is restricted to the eastern part of southern Calabria and is even completely included within the distributional range of the *Dianthion rupicolae*. However, there are marked bioclimatic differences along the coasts of the two sides of the Calabrian Region (Brullo et al. 2001) and the character species of these two alliances turned out to be mutually exclusive (Appendix S6). For these reasons, they are here considered as two autonomous syntaxa.

On the other hand, the *Linarion caprariae* is restricted to siliceous cliffs of the Tuscan Archipelago and it lacks almost all the diagnostic taxa of the *Asplenietalia glandulosi*. For this reason we provisionally confirm the classification of this alliance in the *Asplenietalia lanceolato-obovati*. However, this order needs to be subjected to a thorough revision in order to confirm its autonomy as a distinct order (see also Pérez-Carro et al. 1989) and clarify its floristic relationships with the other chasmophytic syntaxa. Such a revision is beyond the scope of this paper.

The *Asplenietalia glandulosi* is centred in the western Mediterranean. Most of the character taxa of the order, as indicated by Meier & Braun-Blanquet (1934), Braun-Blanquet et al. (1952) and Rivas-Martínez et al. (2011: 216), have a distribution range west of the Italian Peninsula (e.g., *Chaenorhinum origanifolium* subsp. *crassifolium*, *Chiliadenus glutinosus*, *Hieracium arragonense*, *Hormathophylla spinosa*, *Mercurialis huetii*). Other character taxa (e.g., *Asplenium petrarchae*, *Phagnalon sordidum*) exhibit a distribution area which includes Italy, but these were rarely or not recorded at all in the relevés of the *Dianthion rupicolae* and *Centaureion pentadactyli*. The remaining character species, as originally indicated by the aforementioned authors, are particularly abundant in central and southern Italy (*Teucrium flavum*, *Melica minuta* and *Dianthus longicaulis*) or act as differential species for other vegetation types (*Phagnalon saxatile*, *Phagnalon rupestre*).

The results of both cluster analysis and ISA clearly show that the *Dianthion rupicolae* and the *Centaureion pentadactyli* are floristically distinguishable from the other alliances of the *Asplenietalia glandulosi*, due to their high number of endemic/subendemic and steno-Mediterranean taxa. Therefore, these results support a syntaxonomic separation of the cliff vegetation of central and southwestern Italy from that of southern France, Corsica, Sardinia and northwestern Italy. For this reason, two suborders of the *Asplenietalia glandulosi* have been considered here: *Asplenienalia glandulosi* and *Tinguarrenalia siculae*.

According to Daumas et al. (1952), in central and southern Italy, North Africa and southern Spain, the *Asplenietalia glandulosi* is substituted by the *Tinguarretalia siculae*. Some of the character species of the *Tinguarretalia siculae* and of the sole alliance included in its original diagnosis (*Rupicapnion africanae* Daumas et al. 1952) occur in southern Italy. These species are: *Athamanta sicula*, *Dianthus sylvestris* subsp. *siculus*, *Hypochaeris laevigata*, *Euphorbia bivonae*, *Hyoseris radiata*, *Polygala rupestris* (doubtfully), *Senecio squalidus* subsp. *rupestris*, *Calendula suffruticosa*, *Malva subovata* subsp. *rupestris*, and *Parietaria mauritanica*. *Athamanta sicula* [= *Tinguarra sicula*], in particular, is well represented and often dominant on calcareous cliffs of central and southern Italy (Pignatti 1982).

Other authors reduced the *Tinguarretalia siculae* to the rank of suborder of the *Asplenietalia glandulosi* (Pérez Latorre et al. 1996). Although knowledge of the chasmophytic vegetation of North Africa is fragmented and any evaluation of the coenological relationships between Italy and North Africa must remain open to further refinement, the *Dianthion rupicolae* and *Centaureion pentadactyli* are classified in the *Tinguarrenalia siculae*.

The *Dianthion rupicolae* is composed of two suballiances: *Dianthenion rupicolae* and *Campanulenion fragilis* (Tab. 2; Fig. 4; Appendix S6a). The *Campanulo-Portenschlagielletum* is provisionally classified in the *Campanulenion fragilis*. In NMDS and in some of our other dendrograms which we do not include here, this association turned out to segregate together with the *Centaureo-Campanuletalia*, so its syntaxonomic position is still to be considered uncertain.

The *Asplenienalia glandulosi* is centred in the South of France, where the nomenclatural type (*Asplenion glandulosi*), and its type association (*Phagnalo sordidi-Asplenietum glandulosi*), were originally recorded. It extends westwards into the Iberian Peninsula and eastwards into central Italy and Sardinia (Fig. 4). In Sardinia, the *Centaureo-Micromerion* develops over a wide altitudinal range, from about sea level up to over 1300 m. This has led to several species of the submontane and montane belts occurring in this alliance. Also included among the IndSp of the alliance are *Arenaria bertolonii* and *Sesleria insularis*, which were considered as the most diagnostic species of the Corsician alliance *Arenarion bertolonii* (Mucina & Theurillat 2015). This latter alliance was classified in the *Potentilletalia caulescentis* (Gamisans 1991) or in the *Arenario-Phagnaletalia* (Rodwell et al. 2002), and only recently moved to the *Asplenietalia glandulosi* (Mucina & Theurillat 2015). We were not able to find the original diagnosis of the type association of the alliance, *Asplenio rutae-murariae-Arenarietum bertolonii* (Gamisans 1975). However, Gamisans (1978: 37) indicated two relevés (although there is a possibility that these were the same relevés published twice) as lectotypes of this association. One of these relevés (relevé 2, p. 466, in Gamisans 1976) - the only one that we were able to check - was recorded at 1920 m a.s.l. The other relevés assigned to this association by Gamisans (1976), not included in our data-set, showed weak floristic similarities with the *Asplenietalia glandulosi*. Given the altitudinal range of the *Arenarion bertolonii* and following the reasoning provided by Gamisans (1976), we consider this alliance to be not included in the bioclimatic, ecological and floristic ranges of the *Asplenietalia glandulosi*.

The dendrogram cluster representing the *Asplenienalia glandulosi* also contains the relevés of the *Melico minutae-Pseudofumarietum acaulis* from Croatia. This association was originally classified within the *Asplenietalia glandulosi* because the lack of the character taxa of the *Centaureo-Campanuletalia* and the presence of *Melica minuta* (Trinajstić 1980). Subsequently, Trinajstić (2008) moved this association to the *Centaureo-Campanuletalia* on the basis of geographical considerations, but he did not give floristic arguments. Based on our results, this association is here provisionally classified in the *Asplenietalia glandulosi*.

Centaureo-Campanuletalia and *Moltkietalia petraeae*

The floristic autonomy of the chasmophytic vegetation of the North East Adriatic Region was established by Horvatić (1934), who described the new endemic coastal alliance *Centaureo-Campanulion*, classifying it in the *Asplenietalia glandulosi*. Subsequently, Lakušić (1968) described a second alliance for the southeastern Adriatic, the *Edraianthion tenuifolii*, in which he included both the coastal and inland montane chasmophytic vegetation. He classified the two alliances in the new order *Moltkietalia petraeae*. Trinajstić (1980) developed this concept and described the new order *Centaureo-Campanuletalia* for the coastal cliff vegetation of the Adriatic area in which the *Centauro-Campanulion* and *Centauro-Portenschlagiellion*, the latter replacing the *Edraianthion* in the coastal area, were included (see also Terzi & Di Pietro 2016). The

EVC followed the proposal of Trinajstić (1980) in considering a coastal order, *Centaureo-Campanuletalia*, and an inland order, *Moltkietalia petraeae*, for the montane and subalpine belts.

Lakušić' (1968) proposal to group the coastal and the inland vegetation within a single alliance and order, *Edraianthion tenuifolii* and *Moltkietalia petraeae* respectively, was presumably based on the distribution areas of some sub-mediterranean taxa that extend inland from the coast. For instance, the two subassociations of the *Campanulo pyramidalis-Moltkietum petraeae*, described for the Mount Lovćen, Montenegro (Tomić-Stanković 1970; Terzi et al. 2017), harbour several sub-Mediterranean species. Nonetheless, they belong to the *Edraianthion tenuifolii*, owing to the occurrence of diagnostic taxa, such as *Potentilla speciosa*, *Saxifraga crustata*, or *Daphne alpina*, which are typical of cool conditions. Based on our results, these two subassociations represent two autonomous units, separated from the typical *Campanulo-Moltkietum*, whose locus classicus is in the more xerothermic conditions of the Mediterranean context of the Korčula Island (Trinajstić 1964). Therefore, they are here raised to the rank of association with the names *Saxifrago crustatae-Moltkietum petraeae* and *Campanulo austroadriaticae-Moltkietum petraeae*.

The Balkan alliances of the *Centaureo-Campanuletalia* (Fig. 2, cluster CC_3) turned out to be differentiated from the southern Italian ones (clusters CC_{1-2}). The occurrence of few order character taxa on the Italian side was highlighted as early as the first work on the *Asperulion garganicae* (Bianco et al. 1988), where the main character/differential taxa of the *Centaureo-Campanuletalia* were indicated in *Inula verbascifolia*, *Aurinia sinuata*, *Sesleria juncifolia* and *Phagnalon rupestre* subsp. *illyricum*. Other local character taxa, such as *Dianthus tarentinus*, *Onosma echioides* subsp. *angustifolia*, *Cytisus spinescens* and *Leontodon apulus*, were subsequently suggested in order to distinguish the Italian range of the order (Bianco et al. 1988; Di Pietro & Wagensommer 2008; Terzi & D'Amico 2008).

The syntaxonomic position of the *Caro-Aurinion* has long been debated in the scientific literature and represents one of the most complicated points of this revision. The results of our revision support the classification of this alliance in the *Centaureo-Campanuletalia*, as already proposed in the Italian Prodromus of Vegetation (Biondi et al. 2014). However, due to some important biogeographic considerations, the *Caro-Aurinion* lies at the crossroads of three orders. Its syntaxonomic relationships with these orders, and especially with the *Onosmetalia frutescentis*, are discussed below.

Onosmetalia frutescentis

This order was described by Quézel (1964) for the xerothermic chasmophytic vegetation of the high mountains of Peloponnese, Greece. Its distribution area was subsequently extended to other parts of Greece, Turkey, Albania, Italy and northward, even up as far as Slovenia (Bianco et al. 1988; Dring et al. 2002; Šilc & Čarni 2012). The *Onosmetalia frutescentis* is not genuinely a central Mediterranean order and it was included in this revision chiefly for comparison with the rest of the syntaxa considered. According to the results of this study, the order represents an autonomous and well differentiated syntaxonomic unit and has to be restricted to the southern Balkans. The order and its sole alliance, *Campanulion versicoloris*, are characterized by a high number of taxa, more than 20, which are mostly southern Balkan taxa (Appendix S4 and S6b).

The chasmophytic vegetation of the Salento Peninsula (South East Italy) was originally classified in the *Campanulion versicoloris* and *Onosmetalia frutescentis* (Bianco et al. 1988) and later grouped in a south-east Italian endemic alliance, *Caro-Aurinion*. This alliance was included in the *Onosmetalia frutescentis* in the EVC, whereas it has also been classified in the *Asplenietalia glandulosi* (Terzi & D'Amico 2008) or in the *Centaureo-Campanuletalia* (Biondi et al. 2014). Di Pietro and Wagensommer (2008) hypothesized an Italian endemic order for this area.

The similarities between the *Caro-Aurinion* and the *Campanulion versicoloris* are mainly due to three eastern species: *Scrophularia lucida*, *Hellenocarum multiflorum* and *Campanula versicolor* (Bianco et al. 1988). In a revision of the rock cliff vegetation of Greece, Dimopolous et al. (1997) considered *Campanula versicolor* as a character species of the *Campanulion versicoloris, Hellenocarum multiflorum* as a character species of the *Asplenietea trichomanis*, whereas they did not assign any diagnostic role for *Scrophularia lucida*.

The biogeographic similarities between the Salento Peninsula and the South-West Balkans involve some other species typical of other habitats (e.g., Francini-Corti 1966; Musacchio et al. 2006; Di Pietro & Misano 2010). As already pointed out in the pioneering work by Trotter (1912), some of the southeastern taxa in the Salento Peninsula can be considered as tertiary relict taxa, their occurrence being due to geological vicissitudes which occurred during the Messinian age and earlier. During the more recent glacial-interglacial oscillations, if migrations along land-bridges between the Italian Peninsula and the Balkans occurred, they took place more in the northern and central part of the Adriatic Basin than in either the southern part or across the Strait of Otranto. The Adriatic bathymetry is characterized by shallow seafloors in the central and northern Adriatic Basin (with a Mid-Adriatic pit of 270 m of depth), whereas the maximum depths are reached in the southern part, with nearly 1200 m occurring along the Bari (IT)-Bar (ME) direction and 800 m along the Strait of Otranto. As a consequence, and long-distance dispersal excepted, the species/gene flow between the two opposite sides of the southern Adriatic Sea might have been interrupted for approximately the last five million years, or it would have had to follow an indirect land migration route.

Results of this revision clearly showed the floristic autonomy of the *Caro-Aurinion* that is characterized by numerous endemic or subendemic taxa, such as *Centaurea brulla*, *Dianthus japigicus*, *Centaurea nobilis*, *Centaurea tenacissima*, *Centaurea leucadea* and *Aurinia saxatilis* subsp. *megalocarpa*. Although the distribution area of *Aurinia saxatilis* subsp. *megalocarpa* includes both Greece and the South of Italy, in our data set, it occurred only on the Italian side being replaced by *Aurinia saxatilis* subsp. *orientalis* in Greece. Similarly, *Scrophularia lucida* emerged as a good diagnostic species for the *Caro-Aurinion*.

Campanula versicolor and *Hellenocarum multiflorum* are well represented in the southern part of the *Caro-Aurinion* range, together with *Aurinia leucadea*, principally a south Dalmatian taxon of the *Centaureo-*

Campanuletalia. These taxa lose importance in the northern part of the alliance distribution range and give way to *Aurinia saxatilis* subsp. *megalocarpa* and *Athamanta sicula*, especially in the *Iberido carnosae-Athamantetum siculi* which is intermediate between Gargano and Salento vegetation types. Therefore, the *Caro-Aurinion* comes at the crossroads of the three main orders mentioned so far.

Our dataset does not include relevés from southern Albania and western Greece and the geographical distance between relevés from Salento and those from Peloponnese could be responsible for the floristic differentiation in the dendrogram between the *Caro-Aurinion* and the *Campanulion versicoloris*. In fact, a well recognized problem dealing with chasmophytic vegetation concerns the ingression of species from the surroundings (Davis 1951; Heywood 1954), leading to a geographic aggregation of relevés on the basis of taxa with different ecological requirements. Therefore, further in depth studies on the chasmophytic vegetation of the southwestern Balkans are strongly recommended in order to resolve the synchorology of the *Onosmetalia frutescentis* at its western boundary.

Conclusions

The syntaxonomic scheme provided in this revision for the chasmophytic vegetation of the central part of the Mediterranean exhibits some important differences with respect to the EVC concerning the alliances *Dianthion rupicolae*, *Centaureion pentadactyli*, *Arenarion bertolonii*, and *Caro-Aurinion*. From a synchorological viewpoint this revision highlighted a North-South floristic differentiation within the *Asplenietalia glandulosi* and defined the distribution range of the *Centaureo-Campanuletalia* and *Onosmetalia frutescentis* more precisely.

Furthermore, this revision highlighted some critical interpretative points that might be resolved when fresh data from phytosociologically less studied areas become available. Knowledge of the cliff vegetation of North Africa is still insufficient. The same is the case for the order *Onosmetalia frutescentis*, whose distribution range turns out to be restricted to the southern Balkans, however some doubts remain as regards its western boundaries. Finally, although the *Asplenietalia obovato-lanceolati* was only marginally treated in this work, it appears that the floristic relationships between this order and the neighbouring syntaxonomic units are still unclear.

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Author contributions

MT and NJ conceived and planned the research and contributed data; MT did the analyses and led the writing; all the authors provided substantial input for the interpretation of results and critically revised the manuscript.

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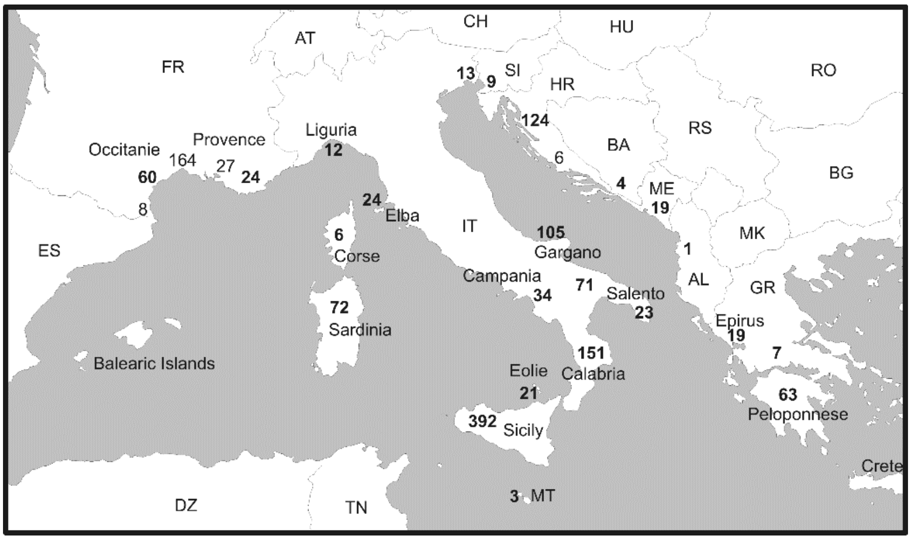

Figure 1: Map of the study area. The bold-type numerals indicate the numbers of relevés in the data set for each geographic area. Normal-type numerals represent the additional relevés summarized in synoptic columns of associations used for the NMDS ordination.

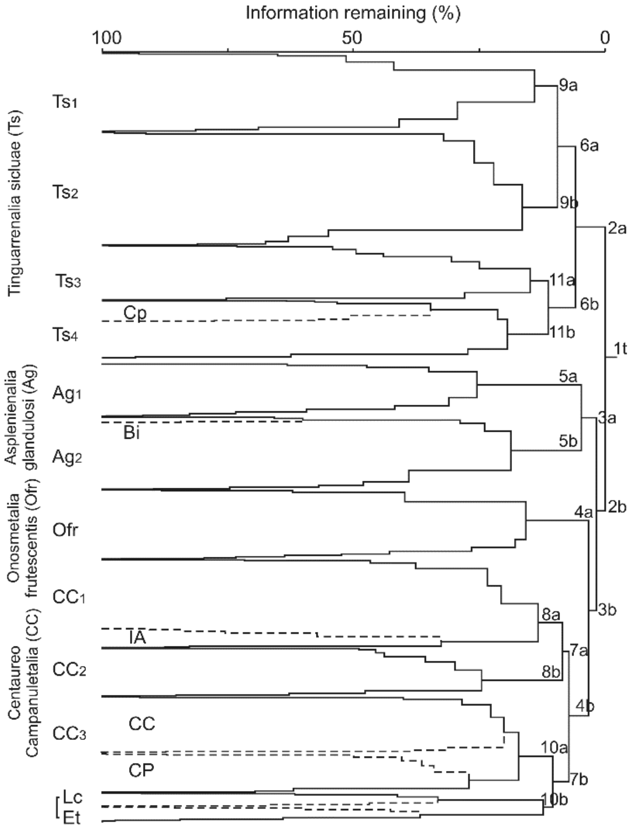

Figure 2: Cluster analysis of relevés [Flexible Beta method (Beta = - 0.25), with Sørensen coefficient, on a square-root transformed distance matrix]. The main clusters of relevés are abbreviated as follows: Ts$_{1\text{-}4}$ = *Tinguarrenalia siculae*: *Dianthion rupicolae* and *Centaureion pentadactyli* (Cp); Ag$_{1\text{-}2}$ = *Asplenienalia glandulosi*: Ag$_1$ = *Centaureo filiformis-Micromerion cordatae*; Ag$_2$ = *Asplenion glandulosi* and *Brassicion insularis* (Bi); Ofr = *Onosmetalia frutescentis*/*Campanulion versicoloris*; CC$_{1\text{-}3}$ = *Centaureo-Campanuletalia*: CC$_1$ = *Asperulion garganicae* (IA = *Iberido carnosae-Athamantetum siculi*); CC$_2$ = *Caro multiflori-Aurinion megalocarpae*; CC$_3$ = *Centaureo dalmaticae-Campanulion* (CC) and *Centaureo cuspidatae-Portenschlagiellion ramosissimae* (CP); Lc = *Linarion caprariae*; Et = *Edraianthion tenuifolii*.

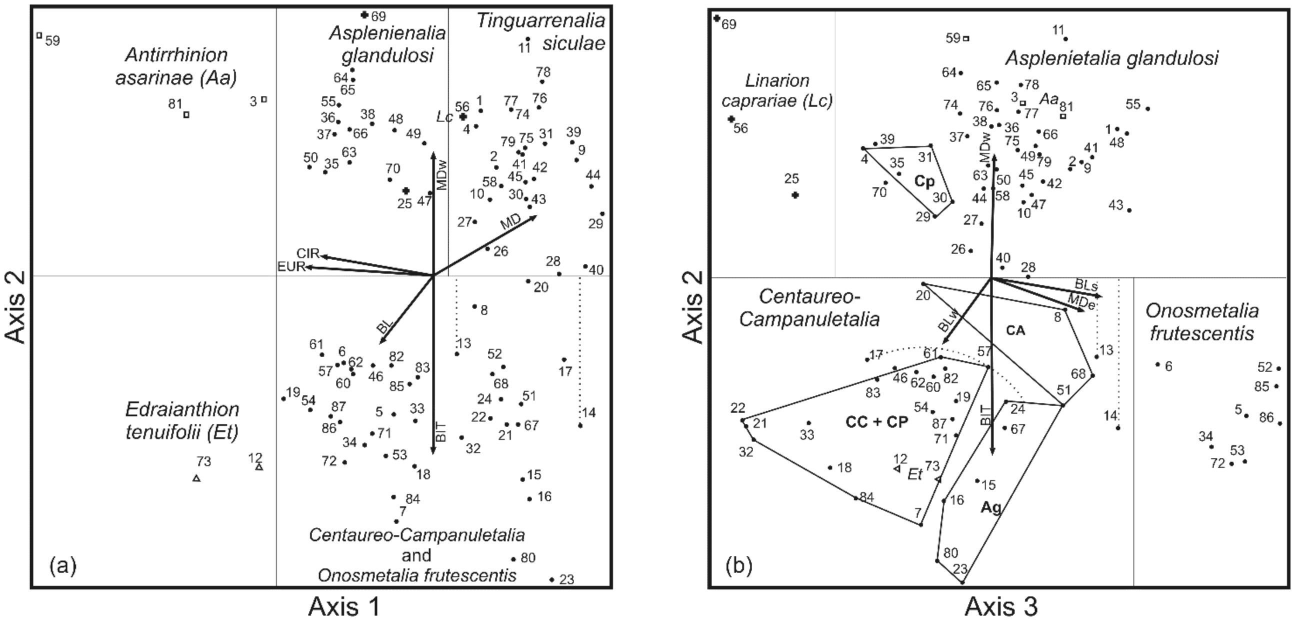

Figure 3: **NMDS ordination of associations** (see Appendix S2 for the list of associations). Axes 1, 2 and 3 account for 19.9 %, 21.6 % and 20.2 % of the variance, respectively. Syntaxa abbreviations: Ag = *Asperulion garganicae*; CA= *Caro multiflori-Aurinion megalocarpae*; CC = *Centaureo dalmaticae-Campanulion*; Cp = *Centaureion pentadactyli*; CP = *Centaureo cuspidatae-Portenschlagiellion ramosissimae*; Abbreviation of chorotypes: BIT = Italian-Balkan; BL = Balkan; BLs = south-Balkan; BLw = west-Balkan; CIR = Circumboreal; EUR = European; MD = steno-Mediterranean; MDe = east-steno-Mediterranean; MDw = west steno-Mediterranean.

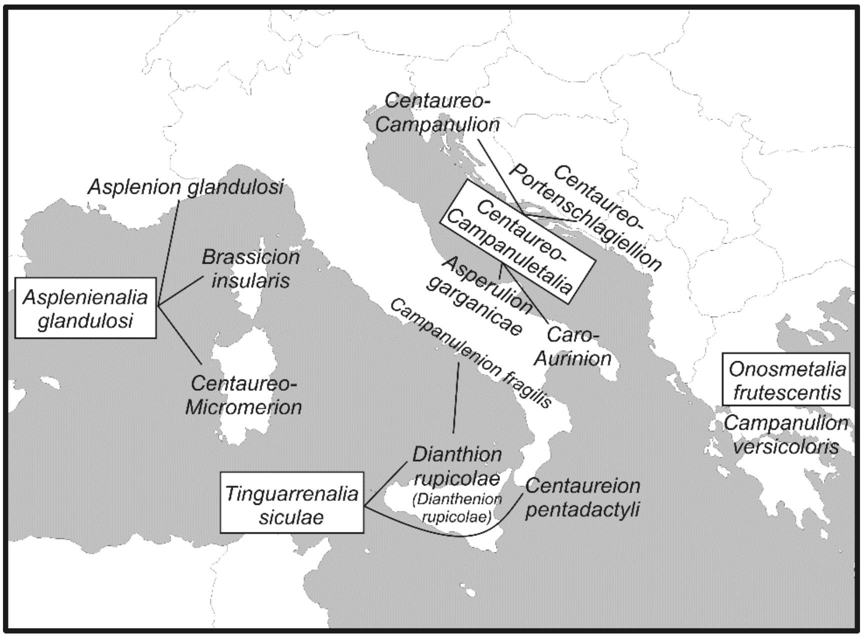

Figure 4: **Distribution map of the *Asplenienalia glandulosi*, *Tinguarrenalia siculae*, *Centaureo-Campanuletalia* and *Onosmetalia frutescentis* in the central Mediterranean.**

Table 1: Associations included in the main clusters of the dendrogram (Fig. 2). Each association was assigned to a cluster on the basis of the position in the dendrogram of its type-relevé. The associations marked with an asterisk are the nomenclatural types of the alliances reported in the last column.

cluster	associations	distribution	alliances
Cluster Ts_1	*Anthemido cupanianae-Centaureetum busambarensis*, *Bupleuro dianthifolii-Scabiosetum limonifoliae*, *Scabiosetum creticae* (*Scabioso creticae-Centaureetum ucriae* nom. illeg.*), and *Brassico rupestris-Centaureetum saccensis*.	Sicily, Egadi islands (IT)	*Dianthion rupicolae*
Cluster Ts_2	*Erucastretum virgati*, *Brassico villosae-Diplotaxietum crassifoliae* and *Micromerio microphyllae-Putorietum calabricae,* and *Triadenio aegypticae-Chiliadenetum bocconei*.	Sicily (IT) and Malta.	*Dianthion rupicolae*
Cluster Ts_3	*Centaureo cinerariae-Campanuletum fragilis* and *Campanulo fragilis-Portenschlagielletum ramosissimae*.	Calabria and Campania Regions (IT)	*Dianthion rupicolae*
Cluster Ts_4	*Diantho rupicolae-Centaureetum aeolicae*	Eolian Islands (IT)	*Dianthion rupicolae*
	Subcluster Cp: *Arabido collinae-Centaureetum aspromontanae*, *Centaureo pentadactyli-Dianthetum aspromontani*, *Centaureo pentadactyli-Dianthetum longicaulis*, and *Centaureo pentadactyli-Dianthetum pentadactyli**.	Aspromonte Massif (IT)	*Centaureion pentadactyli*
Cluster Ag_1	*Helichryso saxatilis-Cephalarietum mediterraneae* and *Laserpitio garganici-Asperuletum pumilae**.	Sardinia (IT)	*Centaureo filiformis-Micromerion cordatae*
Cluster Ag_2	*Phagnalo sordidi-Asplenietum glandulosi**, *Ruto divaricatae-Brassicetum insularis**, and three associations from central and souther Dalmatia (Croatia): *Melico minutae-Pseudofumarietum acaulis, Moltkio petraeae-Campanuletum lepidae* and *Seselio globiferi-Pseudofumarietum acaulis*. The latter two, as revealed by the NMDS, belong to the *Centaureo-Campanuletalia*.	southern France, Corsica (FR), central and southern Dalmatia (HR)	*Asplenion glandulosi, Brassicion insularis.*
Cluster Ofr	*Asperulo chloranthae-Daphnetum jasmineae*, *Asperulo arcadiensis-Hypericetum vesiculosi**, *Sideritido roeseri-Alkannetum graecae*, *Inulo parnassicae-Ptilostemetum chamaepeuces*, *Stachyo candidae-Galietum boryani*, *Inuletum rotundifoliae*, and *Saxifrago chrysosplenifoliae-Athamantetum macedonicae*.	Greece	*Campanulion versicoloris*
Cluster CC_1	*Campanulo garganicae-Aubrietetum italicae**, *Pimpinello tragii-Inuletum verbascifoliae*, *Centaureetum subtilis*, *Scabiosetum dallaportae,* and *Iberido carnosae-Athamantetum siculi* .	Gargano and Murge (IT)	*Asperulion garganicae*
Cluster CC_2	*Aurinio megalocarpae-Centaureetum brullae*, Campanulo versicoloris-Aurinietum leucadeae,* and *Piptathero-Campanuletum versicoloris*.	Salento (IT)	*Caro multiflori-Aurinion megalocarpae*
Cluster CC_3	Subcluster CC: *Aurinio petraeae-Centaureetum lubenicensis*, *Thalictro velebitici-Campanuletum fenestrellatae*, *Asplenio lepidi-Moehringietum tommasinii*, *Saturejo-Euphorbietum wulfenii*, *Campanulo pyramidalis-Centaureetum kartschianae*, *Crithmo maritimi-Centaureetum dalmaticae**, *Seslerio tenuifoliae-Scorzoneretum austriacae,* and *Centaureetum ragusinae*.	Central and northern Dalmatia (HR), Slovenia and North East of Italy	*Centaureo-Campanulion*
	Subcluster CP: *Campanulo pyramidalis-Moltkietum petraeae*, *Inulo verbascifoliae-Centaureetum cuspidatae**, *Fibigio triquetrae-Cerinthetum tristis*, *Moltkio petraeae-Inuletum verbascifoliae*, *Moltkio petraeae-Centaureetum voraginicolae* nom. inval., *Micromerio kerneri-Onosmetum dalmaticae*, *Teucrio arduinii-Seselietum globiferi* and *Seslerio robustae-Putorietum calabricae*.	Central and southern Dalmatia (HR)	*Centaureo-Portenschlagiellion*
Cluster Lc+Et	Subcluster Lc: *Centaureo aetaliae-Linarietum caprariae*, *Linario caprariae-Umbilicetum rupestris*, and *Robertio taraxacoidis-Centaureetum ilvensis** .	Tuscan Archipelago (IT)	*Linarion caprariae*
	Subcluster Et: *Campanulo pyramidalis-Moltkietum petraeae campanuletosum pyramidalis* and *C.p.-M.p. scabiosetosum graminifoliae*.	Montenegro	*Edraianthion tenuifolii*

Table 2: Abridged synoptic table of the order *Asplenietalia glandulosi* in central Mediterranean. Columns report the percentage frequencies of character and differential taxa in the associations of the alliances: column 1: *Campanulenion fragilis*; col. 2: *Dianthenion rupicolae* and *Dianthion rupicolae*; col. 3: *Centaureion pentadactyli*; col. 4: *Asplenion glandulosi*; col. 5: *Brassicion insularis*; col. 6: *Centaureo filiformis-Micromerion cordatae* (see Appendix S6a for the entire synoptic table)

columns:	1	2	3	4	5	6
number of associations:	2	9	4	5	1	2
number of relevés:	61	358	50	190	6	63
Campanulenion fragilis						
Campanula fragilis	100	11	.	.	.	.
Seseli polyphyllum	100	.	.	.	.	.
Centaurea cineraria	50	.	.	.	.	.
Dianthenion rupicolae and *Dianthion rupicolae*						
Brassica incana	100	33	.	.	.	.
Antirrhinum siculum	50	78	.	.	.	.
Dianthus rupicola	50	67	.	.	.	.
Glandora rosmarinifolia	50	22	.	.	.	.
Convolvulus cneorum	50	11	.	.	.	.
Seseli bocconi	.	67	.	.	.	.
Iberis semperflorens	.	56	.	.	.	.
Odontites bocconei	.	44	.	.	.	.
Anthemis cupaniana	.	33	.	.	.	.
Brassica rupestris	.	33	.	.	.	.
Cymbalaria muralis subsp. *pubescens*	.	33	.	.	.	.
Helichrysum pendulum aggr. (species of Sicily)	.	33	.	.	.	.
Matthiola incana subsp. rupestris	.	33	.	.	.	.
Asperula rupestris	.	22	.	.	.	.
Brassica macrocarpa	.	22	.	.	.	.
Pseudoscabiosa limonifolia	.	22	.	.	.	.
Centaurea busambarensis	.	11	.	.	.	.
Centaurea panormitana subsp. *ucriae*	.	11	.	.	.	.
Centaurea panormitana subsp. *umbrosa*	.	11	.	.	.	.
Erucastrum virgatum	.	11	.	.	.	.
Centaureion pentadactyli						
Silene calabra	.	.	100	.	.	.
Allium pentadactyli	.	.	75	.	.	.
Centaurea pentadactyli	.	.	75	.	.	.
Crepis aspromontana	.	.	50	.	.	.
Dianthus brutius	.	.	25	.	.	.
Tinguarrenalia siculae						
Ballota hispanica	100	44	50	.	.	.
Hyoseris radiata	50	78	25	.	100	50
Hypochaeris laevigata	.	78	100	.	.	.
Lomelosia cretica	.	67	50	.	.	.
Athamanta sicula	50	67	.	.	.	.
Brassica fruticulosa	.	11	25	.	.	.
Silene fruticosa	.	67	.	.	.	.
Euphorbia bivonae	.	22	.	.	.	.
Asplenion glandulosi						
Erodium foetidum	.	.	.	60	.	.
Melica amethystina	.	.	.	60	.	.

Lactuca perennis	.	.	.	40	.	.
Malva subovata	.	.	.	40	.	.
Thymus vulgaris	.	.	.	40	.	.
Brassicion insularis						
Brassica insularis	.	.	.	.	100	50
Ruta divaricata	.	.	.	.	100	.
Centaureo filiformis-Micromerion cordatae						
Arenaria balearica	.	.	.	.	.	100
Centaurea filiformis	.	.	.	.	.	100
Cephalaria squamiflora subsp. *mediterranea*	.	.	.	.	.	100
Helichrysum saxatile	.	.	.	.	.	100
Hypochaeris robertia	.	.	.	.	.	100
Micromeria filiformis subsp. *cordata*	.	.	.	.	.	100
Seseli praecox	.	.	.	.	.	100
Sesleria insularis	.	.	.	.	100	100
Siler montanum subsp. *garganicum*	.	.	.	.	.	100
Arenaria bertolonii	.	.	.	.	.	50
Asperula pumila	.	.	.	.	.	50
Bituminaria morisiana	.	.	.	.	.	50
Lactuca longidentata	.	.	.	.	.	50
Asplenienalia glandulosi						
Phagnalon sordidum	.	.	.	60	100	50
Hormathophylla spinosa	.	.	.	60	.	.
Asplenium petrarchae	50	22	.	40	.	.
Chiliadenus glutinosus	.	.	.	20	.	.
Mercurialis huetii	.	.	.	20	.	.
Asplenietalia glandulosi						
Melica minuta	50	78	.	80	100	100
Teucrium flavum subsp. *flavum*	100	89	75	60	.	.
Dianthus longicaulis	100	11	25	.	100	.
Phagnalon saxatile	50	44	75	.	.	50
Lobularia maritima	.	44	75	.	.	50
Dianthus siculus	.	11	25	.	.	100
Antirrhinum majus	.	.	.	20	.	.
Cosentinia vellea subsp. *vellea*	.	11	.	.	.	.
Asplenietea trichomanis						
Asplenium ceterach	100	67	75	100	100	100
Sedum dasyphyllum	100	78	50	100	100	100
Ficus carica	100	78	25	40	100	50
Parietaria judaica	50	67	50	40	100	50
Asplenium trichomanes	50	33	25	100	100	100
Polypodium cambricum subsp. *cambricum*	50	78	50	40	100	50
Euphorbia dendroides	100	78	75	.	.	50
Umbilicus rupestris	50	78	75	60	100	50
Capparis spinosa aggr.	.	67	25	.	.	.
Hippocrepis emerus subsp. *emeroides*	50	11	.	.	.	.
Centranthus ruber subsp. *ruber*	100	44	50	.	.	.
Phagnalon rupestre subsp. *illyricum*	50	56	.	.	.	.
Umbilicus horizontalis	.	33	75	.	.	.
Asplenium ruta-muraria	.	.	.	80	.	50
Putoria calabrica	.	11	.	.	.	.
Allosorus pteridioides	.	11	.	.	.	.

Table 3: Abridged synoptic table of the order *Onosmetalia frutescentis* and *Centaureo-Campanuletalia* in central Mediterranean. Columns report the percentage frequencies of character and differential taxa in the associations of the alliances: column 1: *Campanulion versicoloris* and *Onosmetalia frutescentis*; col. 2: *Centaureo dalmaticae-Campanulion*; col. 3: *Centaureo cuspidatae-Portenschlagiellion ramosissimae*; col. 4: *Asperulion garganicae*; col. 5: *Caro multiflori-Aurinion megalocarpae* (see Appendix S6a for the entire synoptic table). The number of relevés of the *Centaureo cuspidatae-Portenschlagiellion* is missing because this information was not provided with the original diagnosis of some associations of this alliance.

columns:	1	2	3	4	5
number of associations:	8	9	6	4	4
number of relevés:	84	76	?	81	84
Campanulion versicoloris and *Onosmetalia frutescentis*					
Campanula versicolor	100	.	.	.	75
Teucrium flavum subsp. *hellenicum*	100	.	.	.	.
Aurinia saxatilis subsp. *orientalis*	88	.	.	.	.
Onosma frutescens	88	.	11	.	.
Bubon macedonicum	75	.	.	.	.
Centaurea raphanina subsp. *mixta*	75	.	.	.	.
Centranthus ruber subsp. *sibthorpii*	75	.	.	.	.
Ephedra foeminea	75	11	56	.	.
Hellenocarum multiflorum	75	.	.	.	100
Inula parnassica	75	.	.	.	.
Phagnalon rupestre subsp. *graecum*	75	11	.	.	.
Silene congesta	75	.	.	.	.
Silene gigantea	75	.	.	.	.
Asperula lutea	63	.	.	.	.
Campanula rupestris	63	.	.	.	.
Ptilostemon chamaepeuce	63	.	.	.	.
Scrophularia heterophylla subsp. *heterophylla*	63	.	.	.	.
Aubrieta deltoidea	50	.	.	.	.
Odontites linkii	50	.	.	.	.
Asperula arcadiensis	38	.	.	.	.
Ballota acetabulosa	38	.	.	.	.
Cephalaria ambrosioides	38	.	.	.	.
Umbilicus chloranthus	38	.	11	.	.
Pterocephalus perennis	25	.	.	.	.
Saxifraga rotundifolia subsp. *chrysosplenifolia*	25	.	.	.	.
Asperula chlorantha	13	.	.	.	.
Campanula anchusiflora	13	.	.	.	.
Centaureo dalmaticae-Campanulion					
Euphorbia fragifera	.	67	11	.	.
Sonchus asper subsp. *glaucescens*	.	56	11	.	.
Aurinia petraea	.	22	.	.	.
Campanula fenestrellata subsp. istriaca	.	22	.	.	.
Clinopodium thymifolium	.	22	.	.	.
Campanula fenestrellata subsp. *fenestrellata*	.	11	11	.	.
Centaurea kartschiana subsp. *dalmatica*	.	11	.	.	.
Centaurea kartschiana subsp. *kartschiana*	.	11	.	.	.
Centaurea kartschiana subsp. *lubenicensis*	.	11	.	.	.
Moehringia tommasinii	.	11	.	.	.
Centaurea ragusina	.	11	.	.	.
Centaureo cuspidatae-Portenschlagiellion ramosissimae					

Moltkia petraea	.	.	89	.	.
Alyssoides utriculata	.	.	78	.	.
Athamanta ramosissima	13	.	78	.	.
Tanacetum cinerariifolium	.	.	78	.	.
Seseli tomentosum	.	.	67	.	.
Campanula portenschlagiana	.	.	33	.	.
Centaurea cuspidata	.	.	33	.	.
Galium firmum	.	.	33	.	.
Iris pseudopallida	.	.	33	.	.
Asperula scutellaris	.	.	22	.	.
Resetnikia triquetra	.	.	22	.	.
Teucrium arduinii	.	.	11	.	.
Asperulion garganicae					
Asperula garganica	.	.	.	100	25
Lomelosia crenata subsp. *dallaportae*	.	.	.	100	.
Pimpinella tragium	13	.	.	100	.
Campanula garganica	.	.	.	75	.
Centaurea subtilis	.	.	.	75	.
Doronicum columnae	.	.	.	75	.
Aubrieta columnae	.	.	.	25	.
Caro multiflori-Aurinion megalocarpae					
Scrophularia lucida	.	.	.	.	75
Aurinia saxatilis subsp. *megalocarpa*	.	.	.	.	75
Satureja cuneifolia	.	.	.	25	50
Centaurea brulla	.	.	.	.	50
Leontodon intermedius	.	.	.	.	25
Dianthus japigicus	.	.	.	.	25
Centaurea leucadea	.	.	.	.	25
Centaurea japygica	.	.	.	.	25
Centaurea nobilis	.	.	.	.	25
Centaurea tenacissima	.	.	.	.	25
Centaureo dalmaticae-Campanuletalia pyramidalis					
Satureja montana	.	56	67	100	75
Sesleria juncifolia	.	67	33	50	25
Inula verbascifolia	.	33	100	100	.
Sedum hispanicum	.	.	56	50	50
Aurinia sinuata	.	33	44	25	.
Aurinia leucadea	.	11	11	.	25
Campanula pyramidalis	.	100	100	.	.
Rhamnus saxatilis subsp. *infectoria*	.	.	.	100	75
Leontodon apulus	.	.	.	75	75
Dianthus tarentinus	.	.	.	75	75
Picris hispidissima	.	33	78	.	.
Allium ampeloprasum	.	56	33	.	.
Iris illyrica	.	22	67	.	.
Onosma echioides subsp. *angustifolia*	.	.	.	25	50
Frangula rupestris	13	44	22	.	.
Seseli globiferum	.	11	11	.	.
Cytisus spinescens	13	.	.	75	.
Asplenietea trichomanis					
Asplenium ceterach	75	56	100	75	75
Parietaria judaica	13	100	78	50	100
Ficus carica	38	67	44	75	100
Asplenium trichomanes	75	44	89	50	25
Teucrium flavum subsp. *flavum*	25	67	11	75	75
Sedum dasyphyllum	25	22	67	50	75
Hippocrepis emerus subsp. *emeroides*	50	78	33	25	50
Capparis spinosa aggr.	25	11	22	75	75
Athamanta sicula	13	.	.	50	75
Umbilicus horizontalis	25	.	.	.	100
Phagnalon rupestre subsp. *illyricum*	.	.	22	50	50

Melica minuta	13	.	.	25	50
Euphorbia dendroides	13	11	11	.	50
Asplenium ruta-muraria	.	33	22	.	.
Centranthus ruber subsp. *ruber*	.	.	.	25	25
Putoria calabrica	38	.	11	.	.
Polypodium cambricum subsp. *cambricum*	.	11	11	.	25
Umbilicus rupestris	.	.	.	25	.

Appendix S1: Data sources of relevés included in the dataset.

Appendix S2: Syntaxa represented in the NMDS ordination (Fig. 3).

Appendix S3: List of chorotypes used for the chorological spectra of associations.

Appendix S4: Indicator species (IndSp) associated with the clusters of relevés indicated in the dendrogram (Fig. 2).

Appendix S5: Diagnostic roles of Indicator Species, according to different literature sources.

Appendix S6a: Synoptic table of the *Asplenietalia glandulosi*.

Appendix S6b: Synoptic table of the *Onosmetalia frutescentis* and *Centaureo-Campanuletalia*.

Appendix S7: Results of MRPP (multiple response permutation procedure).