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Revision of the central Mediterranean xerothermic cliff vegetation

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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 1,261 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 also exhibits 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*

1 | 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 lists calcareous and siliceous rocky cliffs with chasmophytic vegetation as habitat types 8,210 and 8,220, 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 and 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 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 subordinate alliances have been addressed in many phytosociological papers, the most influential being those of Meier and Braun-Blanquet (1934), Horvatić (1934, 1963), Braun-Blanquet, Roussine, and Nègre (1952), Rivas Goday, Borja Carbonell, Monasterio Fernández, Fernández-Galiano, and Rivas Martínez (1956), de Bolòs and Molinier (1958), Rivas-Martínez (1960), Quézel (1964), Lakušić (1968), Horvat, Glavač, and Ellenberg (1974), Brullo and Marcenò (1979), Trinajstić (1980, 2008), Bianco, Brullo, Pignatti, and Pignatti (1988), Martínez-Parras and Peinado (1990), Arrigoni and Di Tommaso (1991), Dimopoulos, Sykora, Mucina, and Georgiadis (1997), Rivas-Martínez, Fernández-González, Loidi, Lousã, and Penas (2001), Rivas-Martínez et al. (2011), Brullo, Scelsi, and Spampinato (2001), Brullo, Marcenò, and Siracusa (2004), Rodwell et al. (2002), Brullo and Spampinato (2003), Di Pietro and Wagensommer (2008), Terzi and 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 (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, Quézel, & Santa, 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, Jasprica, & Caković, 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 biogeographic 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 to identify: (a) the syntaxonomic and synchorological relationships among the above-mentioned orders and their alliances; and (b) the diagnostic species of the high-rank syntaxa under a supranational perspective.

2 | METHODS

2.1 | 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.

2.2 | 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

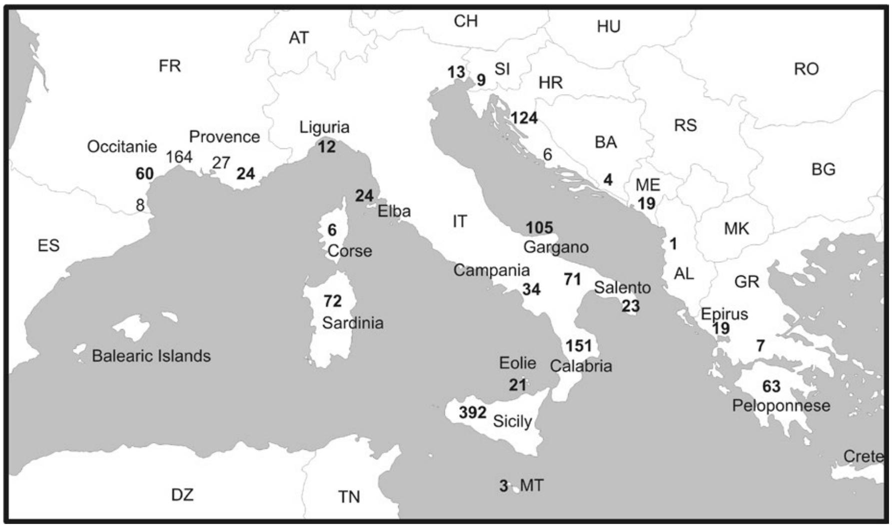

FIGURE 1 Map of the study area. The bold type numerals indicate the numbers of relevés in the data set for each geographic area. Normal type numerals represent the additional relevés summarized in synoptic columns of associations used for the NMDS ordination

Herzegovina, Montenegro, Albania and continental Greece (Figure 1, Supporting information 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, was missing for 96 relevés. The average plot size of relevés was 58.4 m^2. Extremely small (<5 m^2) and extremely large (>150 m^2) plot sizes were removed from the data set since they could affect the results of statistical analyses (Otýpková & Chytrý, 2006). Nomenclatural type-relevés (Weber, Moravec, & Theurillat, 2000) were always retained.

The data set was resampled following the method proposed by De Cáceres, Font, and Oliva (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.

2.3 | Relevés clustering

Taxon scores were exponentially transformed to weight the cover-abundance values according to $x' = x^y$ (van der Maarel, 1979; Terzi, 2015; Wildi, 2010). Five data matrices were obtained by setting $y = 2$ (close to the mid-point of the percentage 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 using the Flexible Beta method ($\beta = -0.25$) in combination with Sørensen coefficient. In all, five dendrograms were obtained using the software PC-ORD, version 6.22 (MjM Software, Gleneden Beach, OR, US).

2.4 | Indicator species analysis (ISA)

An ISA (Dufrêne & Legendre, 1997) was run for the first 15 partitioning levels of each dendrogram, the first 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; Supporting information 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 was 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 second 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 and 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

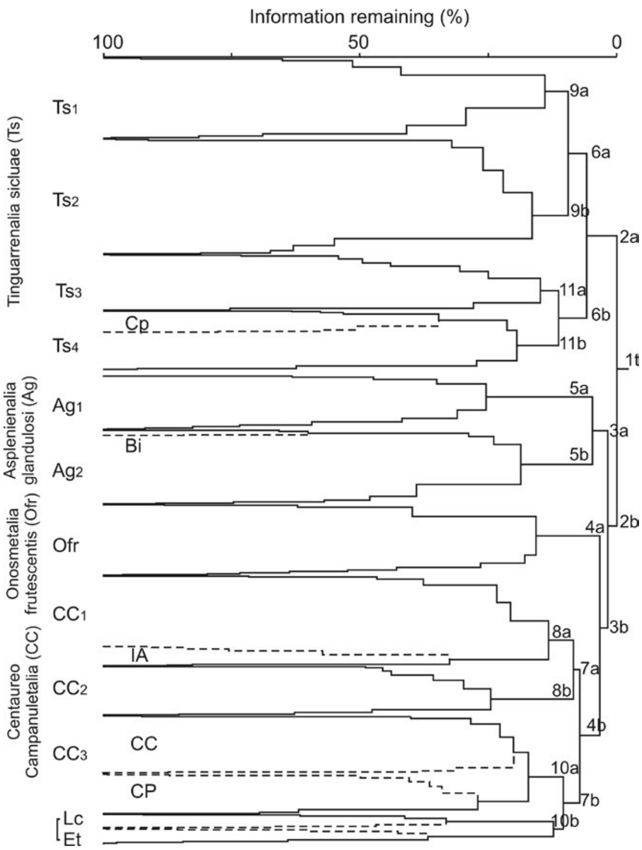

FIGURE 2 Cluster analysis of relevés [Flexible Beta method (β = −0.25), with Sørensen coefficient, on a square root-transformed distance matrix]. The main clusters of relevés are abbreviated as follows: Ts_{1-4} = *Tinguarrenalia siculae*: *Dianthion rupicolae* and *Centaureion pentadactyli* (Cp); Ag_{1-2} = *Asplenienalia glandulosi*: Ag_1 = *Centaureo filiformis-Micromerion cordatae*; Ag_2 = *Asplenion glandulosi* and *Brassicion insularis* (Bi); Ofr = *Onosmetalia frutescentis/Campanulion versicoloris*; CC_{1-3} = *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*

assigned to only one dendrogram cluster (Supporting information 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 to the first level of the dendrogram (Figure 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 (Supporting information Appendix S5) supported our subjective selection of IndSp in order to identify the diagnostic taxa of each syntaxon.

2.5 | 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 five phytosociological relevés were considered (Supporting information Appendix S2). In a 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 a 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 (Supporting information 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 (MjM Software).

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 (Supporting information Appendix S3). Joint plots with an r^2 cut-off of 0.30 were performed to display in the ordination diagram the strengths of the relationships among the ordination scores and the chorological spectra.

2.6 | Multi-response permutation procedure (MRPP)

An MRPP (Biondini, Bonham, & Redent, 1985) was used to determine 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).

3 | RESULTS

3.1 | 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 the various associations considered below. These differences are considered in the interpretation of results. The best clustering solution turned out to be that obtained using the square root-transformed data matrix and this will be addressed henceforth. The highest number of IndSp was reached at the 11th level, giving 11 main clusters of relevés (Figure 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 (Figure 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 northwest Italy and southern France (Ag_2) are grouped in 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.

3.2 | Indicator species analysis

Few IndSp were associated with the first partition of the dendrogram (Figure 2, cluster 1t; Supporting information Appendix S4). Among them, *Asplenium ceterach* and *Sedum dasyphyllum* are class character species while the others are 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, clusters 3b, 4b and 7a exhibit few IndSp, testifying to a less homogeneous composition. In 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.

3.3 | Non-metric multidimensional scaling and MRPP

The NMDS ordination resulted in a three-axis solution (Figure 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 being the *Campanulo-Portenschlagielletum* (Figure 3b, n° 13 and 14). The *Antirrhinion asarinae* is distinguishable on the left side of axis 1 (Figure 3a), as well as the two subassociations of the *Campanulo-Moltkietum* described for Mount Lovćen, which 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 (Figure 3).

The MRPP results revealed that the alliances represented in the NMDS diagram significantly differ in species composition. Moreover, all the pair-wise comparisons between alliances showed significant ($p < 0.05$) differences except (after Bonferroni correction) comparisons involving alliances represented by three or four synoptic columns only (Supporting information Appendix S7).

4 | SYNTAXONOMIC SCHEME

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

TABLE 1 Associations included in the main clusters of the dendrogram (Figure 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 southern 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 northeast 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*

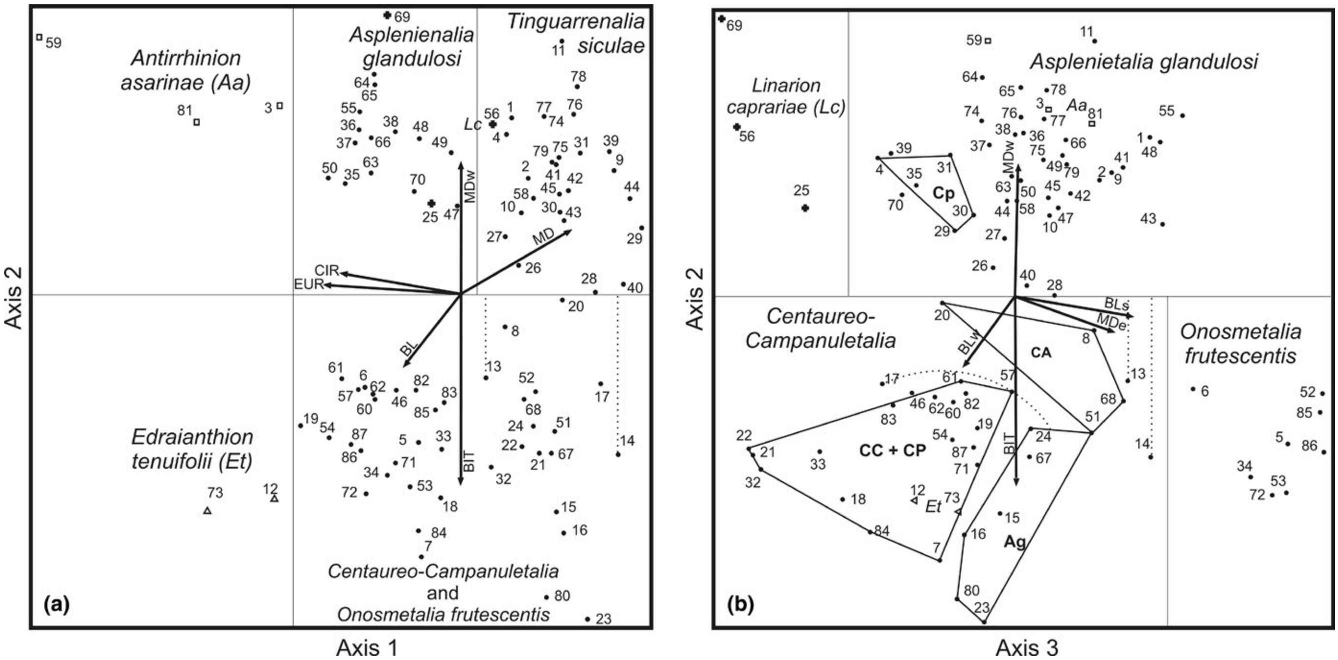

FIGURE 3 NMDS ordination of associations (see Supporting information Appendix S2 for list of associations). Axes 1, 2 and 3 (a, b) account for 19.9%, 21.6% and 20.2% of the variance, respectively. Syntaxa abbreviations: Ag = *Asperulion garganicae*; CA = *Caro multiflori-Aurinion megalocarpae*; CC = *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

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, Galán de Mera, Deil et Cabezudo 1996

TABLE 2 Abridged synoptic table of the order *Asplenietalia glandulosi* in the central Mediterranean

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		

(Continues)

TABLE 2 (Continued)

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
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

(Continues)

TABLE 2 (Continued)

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**
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				

Note. 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 Supporting information Appendix S6a for entire synoptic table).

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*.

TABLE 3 Abridged synoptic table of the orders *Onosmetalia frutescentis* and *Centaureo-Campanuletalia* in the central Mediterranean

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		

(Continues)

TABLE 3 (Continued)

Columns	1	2	3	4	5
Number of associations	**8**	**9**	**6**	**4**	**4**
Number of relevés	**84**	**76**	**?**	**81**	**84**
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		

(Continues)

TABLE 3 (Continued)

Columns	1	2	3	4	5
Number of associations	**8**	**9**	**6**	**4**	**4**
Number of relevés	**84**	**76**	**?**	**81**	**84**
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	

Note. 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 Supporting information Appendix S6a for 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.

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* D.t.: *Aurinia saxatilis* subsp. *megalocarpa*, *Campanula versicolor*, *Centaurea brulla*, *Centaurea japygica*, *Centaurea leucadea*, *Centaurea nobilis*, *Centaurea tenacissima*, *Dianthus japigicus*, *Hellenocarum*

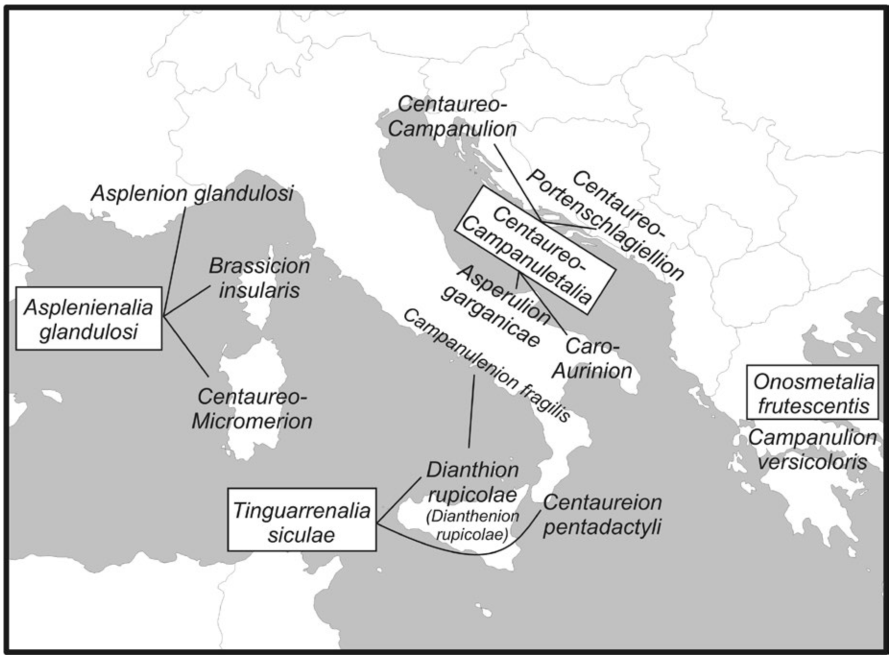

FIGURE 4 Distribution map of the *Asplenienalia glandulosi*, *Tinguarrenalia siculae*, *Centaureo-Campanuletalia* and *Onosmetalia frutescentis* in the central Mediterranean

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 et al. 2017: 375; *Campanula pyramidalis* has to be replaced by *Campanula austroadriatica* D. Lakušić & Kovačić [see Janković et al. 2016]), holotypus: rel. 11, table 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 et al. 2017: 375), holotypus: rel. 6, table II, in Tomić-Stanković (1970)

5 | 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.

5.1 | *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 clusters 5b (Figure 2: *Asplenion glandulosi*) and 10b (*Linarion caprariae*), respectively, but with a very low IndVal (<6; Supporting information 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 (Figure 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 (Italy) 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 (Supporting information 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 (Foggi et al., 2006) and it lacks almost all the diagnostic taxa of the *Asplenietalia glandulosi*. Hence, 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, Díaz, Férnández, & Salvo, 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 and 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 southwest Italy from that of southern France, Corsica, Sardinia and northwest 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* (Table 2, Figure 4, Supporting information 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 should still 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 (Figure 4). In Sardinia, the *Centaureo-Micromerion* develops over a wide altitudinal range, from about sea level to over 1,300 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 1,920 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 not to be 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 of 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*.

5.2 | *Centaureo-Campanuletalia* and *Moltkietalia petraeae*

The floristic autonomy of the chasmophytic vegetation of the northeast 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 *Centaureo-Campanulion* and *Centaureo-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 sub-alpine belts.

The proposal of Lakušić (1968) 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 Mount Lovćen, Montenegro (Terzi et al., 2017; Tomić-Stanković, 1970), harbour several sub-Mediterranean species. Nonetheless, they belong to the *Edraianthion tenuifolii*, due 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* (Figure 2, cluster CC_3) turned out to be differentiated from the southern Italian alliances (clusters $CC_{1\text{-}2}$). 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.

5.3 | *Onosmetalia frutescentis*

This order was described by Quézel (1964) for the xerothermic chasmophytic vegetation of the high mountains of the 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, >20, which are mostly southern Balkan taxa (Supporting information Appendices S4 and S6b).

The chasmophytic vegetation of the Salento peninsula (southeast Italy) was originally classified in the *Campanulion versicoloris* and *Onosmetalia frutescentis* (Bianco et al., 1988) and later grouped in a southeast 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, Dimopoulos 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 southwest Balkans involve some other species typical of other habitats (e.g., Di Pietro & Misano, 2010; Francini-Corti, 1966; Musacchio, Pellegrino, Cafasso, Widmer, & Cozzolino, 2006). As already pointed out in the pioneering work of 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 sea floors in the central and northern Adriatic Basin (with a Mid-Adriatic pit of 270 m in depth), whereas the maximum depths are reached in the southern part, at 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*, which is characterized by numerous endemic or sub-endemic 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 data set does not include relevés from southern Albania and western Greece and the geographic distance between relevés from Salento and those from the 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.

6 | 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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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

APPENDIX S1 Data sources of relevés included in the data set

APPENDIX S2 Syntaxa represented in the NMDS ordination (Figure 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 (Figure 2)

APPENDIX S5 Diagnostic roles of indicator species, according to different literature sources

APPENDIX S6 (a) Synoptic table of the *Asplenietalia glandulosi*. (b) Synoptic table of the *Onosmetalia frutescentis* and *Centaureo-Campanuletalia*

Appendix S7 Results of MRPP (multiple response permutation procedure)

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