



The bryophyte vegetation of the gypsum outcrops of Sicily

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Abstract

A phytosociological study on the gypsicolous bryophyte communities of Sicily was carried out. The surveyed communities are: *Tortuletum revolventis*, *Trichostomo crispuli-Tortuletum revolventis*, *Crossidio squamiferi-Aloinetum aloidis* of the order *Barbuletalia unguiculatae*, and *Crossidio crassinervis-Tortuletum obtusatae* of the order *Tortulo brevissimae-Aloinetalia bifrontis*. The associations were examined from a synecological, synhierarchical and chorological point of view. A life form and life strategy analysis of all communities reflect the response of plant functional types towards the environmental demands. Only one life strategy dominates the communities; acrocarpous, turf-forming colonists clearly prevail on gypsum outcrops, subject to drought stress. They provide the main functional type within pioneering communities and communities of first successional stages. The keystone characters outlined ensure a successful dispersal, establishment and habitat maintenance of the species and associations.

Keywords

bryophytes, gypsum, life forms, life strategies, phytosociology, Sicilian territory

Introduction

Gypsum crops out in almost all Italian regions, with the main location on the northern border of the Apennine chain of the Emilia Romagna region and in Sicily; the last one comprises the largest gypsum outcrops with a total area of more than 1,000 km² followed by Emilia Romagna with a surface more than 100 km² (Forti and Sauro 1996). Most Italian gypsum outcrops belong to the Gessoso-Solfifera Formation (GSF) formed during the "Messinian salinity crisis" (MSC), caused by reduced water inflow from the Atlantic Ocean to the Mediterranean Sea with the consequent salt precipitation and decrease in Mediterranean level due to evaporation. Sicily, due to its geographical location in the centre of the Mediterranean, is the region where the Gessoso-Solfifera Formation crops out more extensively with the highest development in the provinces of Caltanissetta, Enna and Agrigento.

In gypsum substrates there is an incipient impoverishment of the soils, especially in arid and semi-arid areas where the high evaporation leads to a capillary rise of the gypsum towards the surface layers, inducing recrystalliza-

tion of the gypsum and the formation of crusts (Escudero et al. 2015). The gypsum crusts are inhospitable substrates to higher plants; only cyanobacteria, lichens and, with difficulty, few bryophytes can survive (Escudero et al. 2015). Gypsum has low water retention to which a high osmotic pressure of the soil solution is added which strongly reduces root absorption in higher plants (Herrero and Porta 2000), not in bryophytes which are, instead, without absorbent roots. For all these characteristics related to the type of substrate and for the environmental dryness, the plant component is poor, selected, and specialized.

Gypsum outcrops are peculiar habitats of naturalistic interest and, despite the inhospitality of the substrate, host a valuable plant diversity with many specialized and rare species, as well as some interesting communities according to the peculiar characteristics of substrate and climatic conditions.

As regards the bryoflora, the knowledge in Italy is quite good, even if not exhaustive; the contributions regard the gypsum outcrops of six sites of the Nature 2000 Network of the Emilia Romagna Region (Aleffi et al. 2014) and the main gypsum areas of Sicily (Puglisi et al. 2019); in the

last paper the functional group of gypsophily was also attributed to all surveyed species.

As concerns the bryophyte vegetation, the knowledge is limited to some gypsum areas of central Sicily (Privitera 1989); other sporadic data can be found in Lo Giudice and Bonanno (2010). Therefore, this limited knowledge, together with the interest generated by the peculiarity of the habitat, has led us to undertake an extensive investigation on the bryophyte communities colonizing the gypsum outcrops.

Methods

Study areas

The most complete succession of the Gessoso-Solfifera Formation crops out in Sicily. Here, the temporary closure of the Mediterranean Basin led to the creation of two different deposition cycles, one upper and one lower. In fact, two evaporitic successions can be recognized, laying upon pelitic facies of the Terravecchia Formation and locally on white diatomitic marls (Tripoli Formation), and covered by fine pelagic sediments (Trubi Formation), (De Waele et al. 2017). The lower evaporitic unit consists of evaporitic limestone, crystalline gypsum interlayered with gypsum marls and salts (mainly chlorides). The upper evaporitic unit consists of crystalline gypsum, primary or clastic, bioclastic limestone and, finally, clayey sands (Catalano 1986). The gypsum is poorly permeable substrate, very friable and subject to erosive processes that give a "young" character, preventing the formation of deep and advanced soils.

The Sicilian territory is characterized by a Mediterranean climate, diversified based on the altitudes and slopes. The average annual temperature is 17–18° C in the coastal areas, and 16° C in the most inland areas. Precipitation is concentrated in autumn and winter with an average of 500–700 mm/year. According to the bioclimatic classification of Rivas-Martínez et al. (2011), the bioclimate of the investigated sites is of the Mediterranean pluviseasonal oceanic, ranging from lower thermomediterranean to lower mesomediterranean thermotype and from lower dry to upper semiarid ombrotpe (Pesaresi et al. 2014).

The phanerogamic vegetation structured by gypsumophytes grow directly on gypsum outcrops or on thin layers of lithosol, poor-nutrient in low productive environments, not on the soils deriving from the gypsum where it is possible to find the scrub of the *Oleo sylvestris-Cerantonion siliquae* Br.-Bl. ex Guinochet & Drouineau 1944, probably due to predominant type bioclimate (Mediterranean sub-humid) that cause a prevalent flow-down movement of water in the soil profile and give rise to relatively fertile soils. The most important plant communities on vertical or sub-vertical gypsum rocks are *Brassica villosa* (Biv.) subsp. *tineoi* (Lojac.) Raimondo & Mazzola communities and *Diplotaxis harra* (Forssk.) Boiss subsp. *crassifolia* (Raf.) Maire communities, referable to *Dianthion rupicolae* Brullo & Marcenò 1979, and ephemeral vegetation of *Se-*

do-Ctenopsion gypsophilae Rivas Goday & Rivas-Martínez ex Izco 1974 on slightly steep gypsum outcrops with three different communities: *Filagini-Chaenorhinetum rupestris* Brullo, Marcenò, Minissale & Spampinato 1989, *Sedum gypsicola* subsp. *trinacriae* community and *Petrosedum ochroleucum* subsp. *mediterraneum* community.

Sampling methods

The phytosociological study, which follows the plant sociological method of Braun-Blanquet (1964), is based on unpublished and literature data. As regards the unpublished data, the field work was carried out during 2019–2021 years; the season of the collection was spring or late spring. The cover of each taxon is estimated according to the following values: + (<1%), 1 (1–10%), 2 (10.1–25%), 3 (25.1–50%), 4 (50.1–75%), 5 (75.1–100%).

The surveys and samplings were done on the gypsum outcrops in sites referred to the provinces of Caltanissetta, Palermo, Trapani and Agrigento. The literature data refer to sites of the Enna and Catania provinces and, partially, to Caltanissetta and Agrigento, too (Privitera 1989; Lo Giudice and Bonanno 2010; Puglisi et al. 2022). The list of the sites (Fig. 1) is reported below.

1. Rocca di Entella (municipality of Contessa Entellina), gypsum crusts, bioclimate upper thermomediterranean upper dry.
2. Castelluccio (municipality of Contessa Entellina), selenite gypsum, bioclimate upper thermomediterranean upper dry.
3. Serre di Ciminna (municipality of Ciminnà), selenite gypsum, bioclimate lower mesomediterranean upper dry.
4. S. Ninfa (municipality of S. Ninfa), selenite gypsum, bioclimate upper thermomediterranean upper dry.
5. Sutura outskirts, selenite gypsum, bioclimate upper thermomediterranean lower dry.
6. Milena hills, selenite gypsum, bioclimate upper thermomediterranean lower dry.
7. Enna outskirts (from Lo Giudice and Bonanno 2010), gypsum outcrops, bioclimate upper mesomediterranean lower subhumid.
8. Raddusa outskirts (from Lo Giudice and Bonanno 2010), gypsum outcrops, bioclimate lower mesomediterranean lower dry.

Some of the investigated sites fall within within protected areas, such as Integral Nature Reserve "Grotta di Entella" (site 1 and site 2), Oriented Nature Reserve "Serre di Ciminna" (site 3), Integral Nature Reserve "Santa Ninfa" (site 7), and/or within the SAC of Natura 2000 network: ITA020024 Rocche di Ciminna (site 3), ITA020042 Rocche di Entella (site 1 and site 2), ITA010022 Complesso Monti di Santa Ninfa – Gibellina e Grotta di Santa Ninfa (site 7).

The identification of the outcrops was carried out through the preliminary analysis of the geological map

of Sicily (Lentini and Carbone 2014); moreover, the field delimitation of the gypsum outcrops was carried out considering the vascular gypsophilous vegetation as practical guide for recognition of gypsum soil.

For the synecological analysis, life forms and life strategies of each taxon were considered. The life forms follow the concept of Mägdefrau (1982), those of the life strategies During (1979), Frey and Kürschner (1991), Kürschner and Frey (2013). For each species and category the mean percentage cover (MPC) values of the biological parameters within the association is calculated, based on the cover values (Puglisi et al. 2013, 2014, 2018).

The syntaxonomic arrangement and nomenclature follow Puglisi and Privitera (2012); the nomenclature of the taxa follows Hodgetts et al. (2020).

Results and discussion

Based on the phytosociological relevés, the investigated bryophyte vegetation is represented by xerophytic, basiphytic communities, found mostly on selenite outcrops in small depressions or concavities of rocks with accumulated soil. These communities are largely dominated by acrocarpous, small-sized mosses with a turf biotype and xero-pottioid life syndrome; conversely, the pleurocarpous mosses and liverworts are very rare. In more xeric areas, only some lichens, particularly resistant to the harshness of the chalky substrate, can be found.

From a phytosociological point of view, these pioneer bryophyte communities are referred to the class *Psoretea decipiens*. The surveyed communities are discussed below.

TORTULETUM REVOLVENTIS Marstaller 1980 (Tab. 1)

It is the most widespread and typical association characterizing the gypsum outcrops of Sicily. Its presence was highlighted in many localities with a thermomediterranean and mesomediterranean dry rarely subhumid bioclimates, such as Serre di Ciminna, Castelluccio, S. Ninfa, Sutura outskirts, Milena hills, Raddusa outskirts, and in some gypsum outcrops of Enna. The association can be defined as xerophytic, basiphytic, photophytic and strictly gypsophytic. It was found in small depressions where a thin layer of soil accumulates, as well as in the cracks between the gypsum crystals in the ambit of the association. The cover ranges from 30% to 100%; the surfaces are 20–50 dm². The association is floristically characterized by *Tortula revolvens* (Schimp.)G. Roth, occurring with high cover values only in few relevés, in the sites of Enna and Catania, in more mesic (less edaphic drought) conditions. This species is associated with some characteristics of the alliance *Grimaldion fragrantis* and a lot of species of the order *Barbuletalia unguiculatae* and class *Psoretea decipiens* with the most represented *Didymodon vinealis* and *Barbula unguiculata*. In the sites of Serre di Ciminna and S. Ninfa, in more edaphic drought conditions, it is possible to find some transgressive species of the order *Tortulo brevissimae-Aloinetalia bifrontis*, and a lichen component

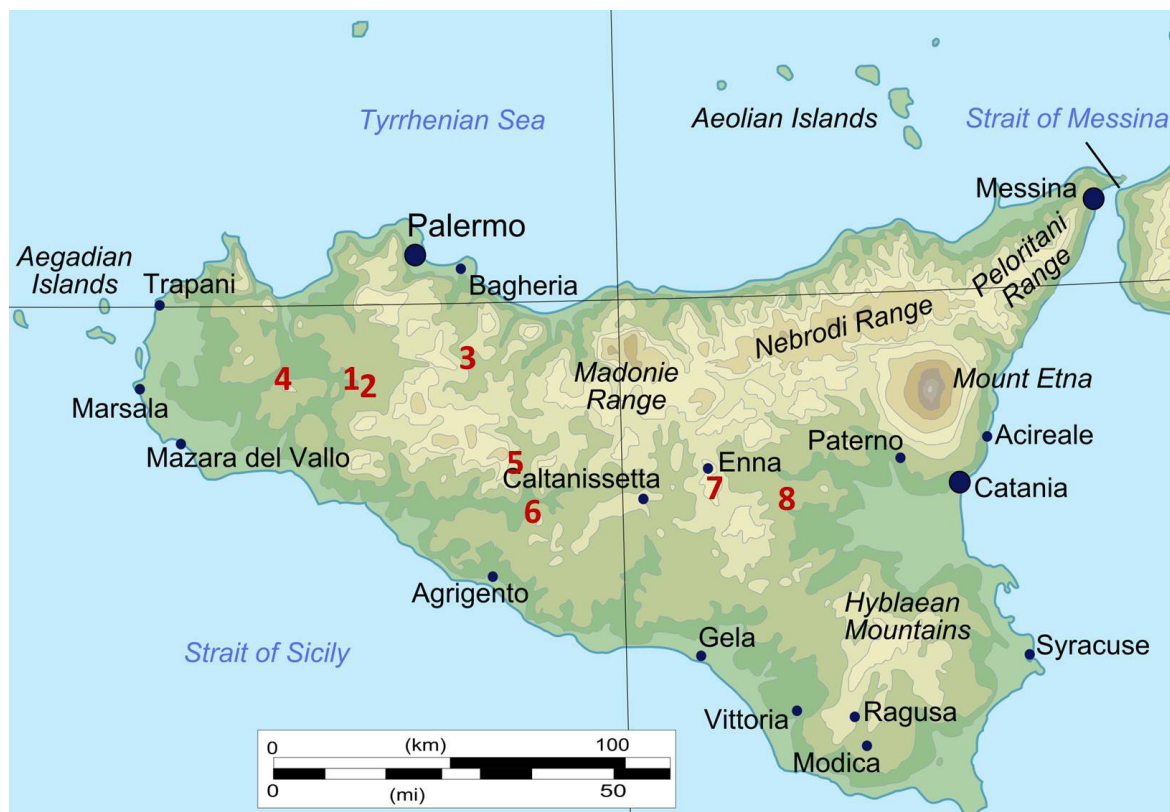


Figure 1. Location of the investigated sites.

represented by *Lathagrium cristatum* (L.) Otálora, P.M. Jørg. & Wedin and *Gyalolechia subbracteata* (Nyl.) Søchting, Frödén & Arup. Moreover, the relevés from Enna and Raddusa outskirts, characterized by the occurrence of *Encalypta vulgaris* Hedw., could represent a more mesophytic variant of the association.

Tortuletum revolventis, described for the chalky substrates of Thuringia (central Germany) (Marstaller 1980, 2008), is already known for some of the gypsum areas of central Sicily (Privitera 1989).

TRICHOSTOMO CRISPULI-TORTULETUM REVOLVENTIS Puglisi, Spampinato & Privitera 2022 (Tab. 2)

The community was found on selenite gypsum in north-western and central Sicily at Castelluccio, Sutura outskirts, Milena hills. It is a gypsicolous, terricolous, photo-sciophytic, meso-xerophilous, covering small surfaces such as concavities of rocks with a conspicuous layer of soil, making it the least pioneer among the structured communities with *Tortula revolvens*. *Trichostomo crispuli-Tortuletum revolventis* was found in the thermomediterranean dry bioclimatic belt, in more protected and less xeric conditions than *Tortuletum revolventis*. The surface cover ranges from 5 to 20 dm² and the sites are mostly flat or scarcely inclined; the cover varies between 55% and 95%.

The community is characterized by *Trichostomum crispulum* Bruch, having major cover values, and *Tortula revolvens*, constantly present. To these species a lot of characteristics of higher units (*Grimaldion fragrantis*, *Barbuletalia unguiculatae*, *Psoretea decipientis*) are associated too. This community differs from *Tortuletum revolventis* in colonizing more protected and less exposed sites, and for its less pioneering character. *Tortula revol-*

vens (incl. var. *obtusata*) is also indicated as a characteristic of *Crossidio crassinervis-Tortuletum obtusatae* Ros & Guerra 1987 and *Trichostomopso-Tortuletum obtusatae* Frey, Herrnstadt & Kürschner 1990 of the order *Tortulo brevissimae-Aloinetalia bifrontis* but differs from both for the less xeric character and the different floristic set. The community shows some affinity with the association *Trichostomo crispuli-Aloinetum aloides* from which it differs for the overall floristic composition and for the gypsophytic character.

CROSSIDIO SQUAMIFERI-ALOINETUM ALOIDIS Guerra & Varo 1981 (Tab. 3)

This association was found in the thermomediterranean and mesomediterranean bioclimatic belts at Sutura outskirts, Milena hills and Raddusa outskirts; in these sites, it colonized gypsum rocky fissures with accumulated soil. The association behaves as chasmochomophytic, basiphytic, xerophytic, photo-sciophytic. This association is not strictly linked to gypsum substrates, being found also on marl, marly-gypsum and clayey soil, limestone rocky fissures (Privitera and Puglisi 1999; Lo Giudice and Bonanno 2010), behaving as not strictly gypsophytic. The surfaces are quite small (4–6 dm²) and the cover varies between 30% and 65%. Floristically, it is characterized by *Crossidium squamiferum* (Viv.)Jur. var. *squamiferum*, a Circum-Tethyan species, and *Aloina aloides* (Koch ex Schultz) Kindb., accompanied by a set of characteristics of the alliance *Grimaldion fragrantis*, order *Barbuletalia unguiculatae* and class *Psoretea decipientis*. *Crossidio squamiferi-Aloinetum aloidis* is known in Italy only in Sicily and southern Calabria (Privitera and Puglisi 1999; Lo Giudice and Bonanno 2010).

Table 2. *Trichostomo crispuli-Tortuletum revolventis* Puglisi, Spampinato & Privitera 2022.

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Altitude (m a.s.l.)	477	477	464	464	452	452	305	305	315	345	345	210	210	195
Cover (%)	80	65	90	80	60	70	95	90	55	85	85	85	70	95
Surface (dm ²)	7	20	10	8	8	10	5	10	20	10	8	10	20	8
Inclination (°)	15	-	-	30	-	-	20	-	-	-	-	-	20	-
Exposure	SW	-	-	SE	-	-	S	-	-	-	-	-	S	-
Number of species	4	8	5	4	5	5	5	6	6	6	6	5	4	5
Char. association														
<i>Trichostomum crispulum</i>	4	2	4	4	3	3	5	4	3	4	4	4	3	4
<i>Tortula revolvens</i>	2	1	3	2	1	1	2	2	1	2	2	2	2	3
Char. alliance, order and class (<i>Grimaldion fragrantis</i>, <i>Barbuletalia unguiculatae</i>, <i>Psoretea decipientis</i>)														
<i>Trichostomum brachydontium</i>	1	1	.	+	1	.	.	1	.	1	1	1	.	+
<i>Didymon vinealis</i>	1	2	1	.	+	.	2	1
<i>Didymodon acutus</i>	.	1	+	1	.	2	.	.	+
<i>Weissia controversa</i> var. <i>controversa</i>	1	.	+	.	1	1	.	.
<i>Bryum dichotomum</i>	.	1	1	.	.	1
<i>Streblotrichum convolutum</i> var. <i>convolutum</i>	.	2	.	.	.	1
<i>Aloina ambigua</i>	1	.	+
<i>Didymon luridus</i>	1	+	.	.	.
Other species														
<i>Homalothecium sericeum</i> (Hedw.) Schimp.	+	.	+	.	1	.	.	+	1	+	.	+	+	1
<i>Tortula solmsii</i> (Schimp.) Limpr.	.	1
<i>Tortella inflexa</i> (Bruch) Broth.	.	1
<i>Petalophyllum ralfsii</i> (Wilson) Nees & Gottsche	1
<i>Tortella squarrosa</i>	+

CROSSIDIO CRASSINERVIS-TORTULETUM OBTUSATAE Ros & Guerra 1987 (Tab. 4)

This community grows on very dry, very exposed, soil with a thin layer of gypsum at Rocca di Entella in northern Sicily in the thermomediterranean dry bioclimatic belt. From an ecological point of view, it can be considered as a terricolous, thermophytic, markedly xerophytic, photophytic community. It finds its optimum in arid territories of the Mediterranean and Irano-Turanian region (García-Zamora et al. 2000). The cover is not high, ranging from 30% to 65%; the surfaces are 10 to 30 dm². Characteristic species of the association are *Tortula revolvens* and *Crossidium crassinervium*, both species with main distribution areas in the Mediterranean, Irano-Turanian and Saharo-Arabian territories. As concerns *Tortula revolvens*, in the description of the association (Ros and Guerra 1987), the characteristic species is *Tortula revolvens* var. *obtusata* Reimers, considered now a synonym of *Tortula revolvens* (Schimp.) G. Roth. To these species a set of characteristics of the alliance *Aloina bifrontis*-*Crossidium crassinervis* and order *Tortulo brevissimae*-*Aloinetalia bifrontis* are associated, such as *Dicranella howei* Renaud & Cardot, *Fossombronia caespitiformis* (Raddi) De Not. ex Rabenh. subsp. *caespitiformis*, *Didymodon tophaceus* (Brid.) Lisa subsp. *sicculus* (M.J.Cano, Ros, García-Zam. & J.Guerra) Jan Kučera, *Microbryum davallianum* (Sm.) R.H.Zander var. *davallianum*, *Tortula brevissima* Schiffn. and *Tortula atrovirens* (Sm.) Lindb. Among the other species, a group of lichens are found too, such as *Lathagrium cristatum*, *Squamarina lentigera* (Weber) Poelt and *Gyalolechia subbracteata*. From a phytosociological point of view, *Crossidium crassinervis*-*Tortuletum obtusatae* is included in the above-mentioned syntaxa, which group markedly xerophytic, photophytic communities with Mediterranean,

Irano-Turanian and Saharo-Arabian distribution. The association is signalled from Spain (Ros and Guerra 1987; Guerra et al. 1993; Moya et al. 1994; García-Zamora et al. 2000) and Israel (Frey et al. 1990), where it was found on gypsum and marl-gypsum substrates. *Crossidium crassinervis*-*Tortuletum obtusatae* is reported for the first time for the bryophyte vegetation of Italy.

Plant functional types

The plant functional types (life forms, life syndromes, morphological-anatomical keystone characters) characterizing the communities of the Sicilian gypsum substrates provide useful information on the mechanisms of habitat maintenance, establishment, re-establishment and dispersal of the species and communities (e.g., Kürschner and Frey 2013, Puglisi et al 2014, 2015, 2016a, 2016b, 201). The main characters used for the analysis (Tab. 5) are life span (avoidance vs. tolerance strategy of the gametophyte), breeding system, main reproductive effort (sexual vs. asexual reproduction) and dispersal strategies [small spores (< 25µm) providing chance dispersal vs. large spores (> 25 µm) indicating decreasing long-range dispersal and achory].

The communities show a relatively low diversity concerning plant functional types (life forms and life strategies), with a very high prevalence of the colonist strategy with MPC values of 90.7% in *Tortuletum revolvantis*, 91.0% in *Crossidium crassinervis*-*Tortuletum obtusatae*, 94.7% in *Trichostomo crispuli*-*Tortuletum revolvantis* and 95.7% in *Crossidium squamiferi*-*Aloinetum aloidis* (Tab. 6). Many investigations have shown that communities of harsh habitats, especially those of sunny sites, rocks, as

Table 3. *Crossidium squamiferi*-*Aloinetum aloidis* Guerra & Varo 1981.

Relevés number	1	2	3	4	5	6	7
Altitude (m a.s.l.)	375	380	365	380	385		
Cover (%)	40	65	40	50	30	30	40
Surface (dm ²)	4	6	5	5	5	6	6
Inclination (°)	40	30	60	40	40	30	30
Exposure	SW	SE	E	NW	SW	SW	E
Species number	6	4	5	5	3	4	6
Char. association							
<i>Aloina aloides</i> (Koch ex Schultz) Kindb.	1	.	+	1	.	.	1
<i>Crossidium squamiferum</i> var. <i>squamiferum</i>	1	3	2	2	2	2	2
Char. alliance, order and class (<i>Grimaldion fragrantis</i>, <i>Barbuletalia unguiculatae</i>, <i>Psoretea decipiensis</i>)							
<i>Didymodon vinealis</i>	2	+	.	1	+	1	.
<i>Barbula unguiculata</i>	1	.	.	1	.	+	.
<i>Didymodon luridus</i>	1	.	1
<i>Weissia controversa</i> var. <i>controversa</i>	.	1	+
<i>Aloina ambigua</i>	2
<i>Pseudocrossidium hornschiuchianum</i>	.	.	1
<i>Ptychostomum capillare</i>	1
<i>Trichostomum brachydontium</i>	1	.	.
Other species							
<i>Pseudocrossidium revolutum</i>	.	1	.	1	.	.	.
<i>Ptychostomum torquescens</i> (Bruch & Schimp.) Ros & Mazimpaka	1	.
<i>Encalypta vulgaris</i> Hedw.	+
<i>Tortula muralis</i> Hedw. supsp. <i>muralis</i>	+
<i>Ptychostomum imbricatum</i>	+

Table 4. Crossidium crassinervis-Tortuletum obtusatae Ros & Guerra 1987.

Relevé number	1	2	3	4	5	6	7	8
Altitude (m a.s.l.)	520	520	525	515	515	505	505	510
Surface (dm ²)	20	10	30	15	20	30	20	10
Cover (%)	55	65	45	60	40	50	30	45
Species number	7	7	7	8	7	8	5	4
Char. association								
<i>Tortula revolvens</i>	3	3	2	3	2	2	2	3
<i>Crossidium crassinervium</i>	1	1	2	+	1	1	1	1
Char. alliance and order (<i>Aloina bifrontis</i>-<i>Crossidium crassinervis</i>, <i>Tortulo brevissimae</i>-<i>Aloinetalia bifrontis</i>)								
<i>Tortula brevissima</i> Schffn.	1	.	+	1	1	.	+	1
<i>Dicranella howei</i>	.	+	.	1	.	1	1	.
<i>Fossombronia caespitiformis</i> subsp. <i>caespitiformis</i>	1	2	.	+	.	1	.	+
<i>Didymodon tophaceus</i> (Brid.)Lisa subsp. <i>sicculus</i> (M.J.Cano, Ros, García-Zam. & J.Guerra) Jan Kučera	+	.	1	.	1	+	.	.
<i>Microbryum davallianum</i> var. <i>davallianum</i>	+	1	.	+
<i>Tortula atrovirens</i> (Sm.) Lindb.	.	.	.	1	.	1	.	.
Char. class (<i>Psoretea decipiens</i>)								
<i>Bryum dichotomum</i>	.	.	+	1	1	.	.	1
<i>Pseudocrossidium hornschuchianum</i>	1
Other species								
<i>Pseudocrossidium revolutum</i>	.	+	.	1	1	.	1	.
<i>Aloina brevirostris</i> (Hook & Grev.) Kindb.	.	1	+	.	+	.	.	.
<i>Tortella flavovirens</i> (Bruch) Broth. var. <i>flavovirens</i>	.	.	.	1	.	2	.	.
<i>Crossidium squamiferum</i> var. <i>squamiferum</i>	1	+	.
<i>Aloina aloides</i>	1	.	.
<i>Homalothecium sericeum</i>	.	.	1
<i>Lathagrium cristatum</i> (L.) Otálora, P.M. Jørg. & Wedin	1	+	.	1	.	.	+	.
<i>Squamarina lentigera</i> (Weber)Poelt	.	.	1
<i>Gyalolechia subbracteata</i> (Nyl.) Søchting, Frödén & Arup	1	.	.	.

Table 5. Characters, life forms and life strategies of the communities. Abbreviations Life forms: Sc: solitary creeping; St: solitary thalloid; Tf turf; Tp: turf protonemal; Ts turf scattered; We weft. Life cycle: a annual/ephemeral; p pauciennial/pluriennial; pe perennial. Sexual reproduction: 1 frequent within the 1st year, 2 frequent within the 2nd – 4th year; [] data uncertain; a abundant; a/r absent or rare; f frequent; o occasional; p present. Breeding system: D dioicous; M monoicous. Asexual reproduction: a/r absent or rare; bl brood leaves; fl fragmentation of leaves/caducous leaves; Ge gemmae; Rhg rhizoid gemmae. Dispersal strategy: lr long range dispersal, sr short range dispersal. Life strategies: AnS annual shuttle; C colonists; PeS perennial shuttle species; PS perennial stayers; PaS short-lived shuttle species; as with high asexual reproductive effort; m with moderate or rare sexual and asexual reproductive effort; s with high sexual reproductive effort.

	Life forms	Life cycle	Sexual reproduction	Breeding system	Spores (Ø in µm)	Asexual reproduction	Dispersal strategy	Life strategies
<i>Aloina aloides</i>	Ts	p	f	D	15-25	a/r	sr,lr	Cs
<i>Aloina ambigua</i>	Ts	p	f	D	10-15	a/r	sr,lr	Cs
<i>Aloina brevirostris</i>	Ts	p	a/r	D	10-15	a/r	sr,lr	Cs
<i>Aloina rigida</i>	Ts	p	a/r	D	14-16	a/r	sr,lr	Cs
<i>Streblotrichum convolutum</i> var. <i>convolutum</i>	Tf	p	[2]	D	8-10	Rhg	sr,lr	Cas
<i>Barbula unguiculata</i>	Tf	p	f	D	10-14	a/r	sr,lr	Cs
<i>Brachytheciastrum velutinum</i>	We	pe	2	M	13-16	a/r	sr,lr	PSas
<i>Bryum argenteum</i>	Tf	p	1	D	8-14	g	sr,lr	Cas,s
<i>Bryum dichotomum</i>	Tf	p	a/r	D	8-16	Ge,Rhg	sr,lr	Cas
<i>Bryum radiculosum</i>	Tf	p	f	D	10-14	Rhg	sr,lr	Cas
<i>Cephaloziella baumgartneri</i>	Ms	p	f	M	8-12	Ge	sr,lr	Cas
<i>Ceratodon purpureus</i>	Tf	p	2	D	10-14	a/r	sr,lr	Cs
<i>Crossidium crassinervium</i>	Ts	p	a/r	M	9-16	a/r	sr,lr	Cm
<i>Crossidium squamiferum</i> var. <i>squamiferum</i>	Tf	p	2	M	9-22	a/r	sr,lr	Cm
<i>Dicranella howei</i>	Tf	p	a/r	D	-	Rhg	sr,lr	Cm
<i>Didymodon acutus</i>	Tf	p	o	D	9-12	Ge	sr,lr	Cas
<i>Didymodon insulanus</i>	Tf	p	a/r	D	~ 10	a/r	sr,lr	Cm
<i>Didymodon rigidulus</i>	Tuft	p	a/r	D	10-12	Ge	sr,lr	Cas
<i>Didymodon sicculus</i>	Tf	p	a/r	D	-	a/r	sr,lr	Cm
<i>Didymon luridus</i>	Tf	p	2	D	12-16	a/r	sr,lr	Cs
<i>Didymon vinealis</i>	Tuft	pe	2	D	10-13	a/r	sr,lr	Cs
<i>Encalypta vulgaris</i>	Tuft	pe	2	M	30-45	a/r	sr,lr-ac	PeSs
<i>Entosthodon convexus</i>	Tuft	a	2	-	18-26	a/r	sr,lr	F
<i>Fissidens viridulus</i>	Tf	p,pe	2	M,D	8-15	a/r	sr,lr	Cs
<i>Fossombronia caespitiformis</i> subsp. <i>caespitiformis</i>	Sc	a,p	1	M	38-56	a/r	sr,lr-ac	AnS
<i>Grimmia pulvinata</i>	Cu	p	[1]	M	8-12	a/r	sr,lr	Cpa
<i>Gymnostomum viridulum</i>	Tf	p	a/r	D	10-12	a/r	sr,lr	Cas
<i>Homalothecium aureum</i>	We	pe	o	D	14-18	a/r	sr,lr	PSm
<i>Homalothecium sericeum</i>	Mr	pe	a/r	D	11-22	a/r	sr,lr	PSm

Table 5. Continuation.

	Life forms	Life cycle	Sexual reproduction	Breeding system	Spores (\emptyset in μm)	Asexual reproduction	Dispersal strategy	Life strategies
<i>Microbryum davallianum</i> var. <i>davallianum</i>	Ts	a	a	M	31-40	a/r	sr,lr-ac	Ans
<i>Microbryum starkeanum</i>	Ts	a	a	M	19-42	a/r	sr,lr-ac	Ans
<i>Petalophyllum ralfsii</i>	St	p	f	D	40-56	a/r	sr,lr-ac	PaS
<i>Pseudocrossidium hornschuchianum</i>	Tf	p	a/r	D	8-10	a/r	sr,lr	Cm
<i>Pseudocrossidium revolutum</i>	Tf	p	a/r	D	10-14	a/r	sr,lr	Cm
<i>Ptychostomum capillare</i>	Tf	p	1	D	9-15	Rhg	sr,lr	Cs,as
<i>Ptychostomum donianum</i>	Tf	p	a/r	D	12-14	a/r	sr,lr	Cs
<i>Ptychostomum imbricatulum</i>	Tf	p	2	D	10-14	Rhg	sr,lr	Cs,as
<i>Ptychostomum torquescens</i>	Tf	p	1	D	10-16	Ge,Rhg	sr,lr	PSs,as
<i>Scleropodium touretii</i>	Mr	pe	a/r	D	11-18	a/r	sr,lr	PSm
<i>Timmiella barbuloides</i>	Tp	pe	2	M	10-13	a/r	sr,lr	PSs
<i>Tortella flavovirens</i> var. <i>flavovirens</i>	Tf	p	a/r	D	12-14	a/r	sr,lr	Cas
<i>Tortella inflexa</i>	Tp	p	a/r	D	8-10	a/r	sr,lr	Cm
<i>Tortella squarrosa</i>	Tf	p,pe	a/r	D	10-13	bl	sr,lr	PSas
<i>Tortula atrovirens</i>	Tf	p	2	M	24-28	a/r	sr,lr	Cm
<i>Tortula brevissima</i>	Ts	p	a/r	D	14-15	a/r	sr,lr	Cs
<i>Tortula muralis</i> susp. <i>muralis</i>	Tf	pe	1	M	7-14	a/r	sr,lr	Cs
<i>Tortula revolvens</i>	Tf	p	a/r	-	8-10	a/r	sr,lr	Cm
<i>Tortula solmsii</i>	Tf	pe	o	D	10-15	a/r	sr,lr	Cm
<i>Trichostomum brachydontium</i>	Tf	p,pe	a/r	D	14-18	\pm fl	sr,lr	PeSm
<i>Trichostomum crispulum</i>	Tf	p,pe	a/r	D	16-18	a/r	sr,lr	Cm
<i>Weissia condensata</i>	Tf	p	o	M	14-24	a/r	sr,lr	Cm
<i>Weissia controversa</i>	Tf	p	2	M	16-20	a/r	sr,lr	Cs

well as communities growing on anthropogenic sites and as pioneer communities (primary succession stages) are the domain of the colonists life strategy (Kürschner and Frey 2013). Colonists are characterized by a generally low gametophyte longevity (often paucennial), an often high asexual reproduction by rhizoid gemmae and leaf gemmae for a rapid establishment, a regular formation of sporophytes and the production of numerous small spores (< 25 μm in diameter). However, due to the inhospitality of the substrate, the colonist species of the gypsophytic communities show a moderate reproductive effort, with MPC values ranging from 58.4% in to 83.4% (Tab. 6).

Of no significant value are the shuttle and the perennial stayers strategies, with very low MPC incidence (Tab. 6).

Strongly correlated to the colonist strategy are the life forms turf and tuft, as typical for many acrocarpous mosses, with MPC values of the turf (including the turf scattered and turf protonemal) corresponding to 94.0% in *Tortuletum revolvantis*, 93.9% in *Trichostomo crispuli-Tortuletum revolvantis*, 88.5% in *Crossidio squamiferi-Aloinetum aloidis* and 92.3 in *Crossidio crassinervis-Tortuletum obtusatae*. The percentage of the other life forms is negligible.

Conclusion

This study has emphasized the occurrence of four communities colonizing gypsum outcrops belonging to the class *Psoretea decipiens* and to the orders *Barbuletalia unguiculatae* and *Tortulo brevissimae-Aloinetalia bifrontis*. The former order finds its optimum in the Mediterranean area up to Central European, the latter includes communities of arid and semi-arid areas of the Mediterranean and Irano-Turanian regions.

Tortuletum revolvantis, *Trichostomo crispuli-Tortuletum revolvantis* and *Crossidio squamiferi-Aloinetum aloidis* are included in the alliance *Grimaldion fragrantis*. In particular, *Tortuletum revolvantis* is the most widespread community on the gypsum outcrops of Sicily, occurring in many sites in north-western, western and central Sicily. This pioneer association is known for the gypsum steppes of Thuringia (central Germany). *Trichostomo crispuli-Tortuletum revolvantis* was found in north-western and central Sicily, showing more sciophytic, more mesic and more terricolous exigencies than *Tortuletum revolvantis*. Both communities are exclusively found on gypsum substrate. *Crossidio squamiferi-Aloinetum aloidis* is a chasmophytic community, not strictly related to gypsum outcrops, having been found also on marl and clayey substrates.

Crossidio crassinervis-Tortuletum obtusatae, the only association referred to the order *Tortulo brevissimae-Aloinetalia bifrontis*, is the most xerophytic community among those found on the Sicilian gypsum outcrops; it is found only on gypsum crusts in conditions of high brightness and very high edaphic dryness, occupying favourable topographical positions for its survival. It represents a new record for the bryophyte vegetation of Italy.

The surveyed communities are rare and interesting from a naturalistic point of view. The peculiarity of the chalky substrate and the climatic conditions impose a strong selection on the species so that only these small and particular communities, characterized by species with peculiar xero-morphic adaptations, can survive. The almost exclusive occurrence of the life syndrome colonist with moderate rep hat the life syndromes and adaptive traits indicate the response of functional types towards environmental demands (e.g., Kürschner 2004, Kürschner and Frey 2013, Puglisi et al. 2016a, Puglisi et al 2016b).

Table 6. Life forms, life strategies and reproductive strategy of taxa (MPC values in %; abbreviations see Table 5).

Life forms	<i>Tortuletum revolventis</i>	<i>Trichostomo crispuli-Tortuletum revolventis</i>	<i>Crossidio squamiferi-Aloinetum aloidis</i>	<i>Crossidio crassinervis-Tortuletum obtusatae</i>
Tf	92.9	93.5	82.3	72.8
Ts	1.1	-	6.2	19.5
Tp	-	0.4	-	-
Tuft	4.9	4.2	11.6	-
We	0.1	1.5	-	1.2
Sc	1.0	-	-	6.5
St	-	0.4	-	-
Life strategy				
Colonist	90.7	94.7	95.7	91.0
Cas	11.9	5.6	-	8.7
Cs,as	3.6	-	9.2	-
Cs	13.0	5.9	28.1	7.2
Cm	62.2	83.2	58.4	75.1
Annual shuttle	1.4	-	-	7.8
Short-lived shuttle	0.2	0.4	-	-
Perennial shuttle	7.7	3.1	2.3	-
PeSs	7.1	0.1	0.3	-
PeSm	0.6	3.0	2.0	-
Perennial stayers	-	-	2.0	1.2
PSm	-	-	-	1.2
PSas	-	-	-	-
PSs	-	-	-	-
PSs,as	-	-	2.0	-

Many gypsum outcrops are included in protected areas, which are an important factor to guarantee the persistence of species and communities with legal protection. Despite this, it is assumed a reduction or even a high extinction probability of biodiversity, due to the effects of global warming with foreseen desertification phenomena in mid-latitude areas. Therefore, further conservation measures need to be implemented and the present study can give a contribution to the conservation and management of gypsum habitats, considered to be of high naturalistic value. For this purpose, it is important that the gypsum habitats of Sicily can be recognized as Habitats of European Community interest and referred to the Habitat 1520*, including the gypsophytic bryophyte associations *Tortuletum revolventis*, *Trichostomo crispuli-Tortuletum revolventis* and *Crossidio crassinervis-Tortuletum obtusatae*.

Syntaxonomic scheme

PSORETEA DECIPIENTIS Mattick ex Follmann 1974
BARBULETALIA UNGUICULATAE von Hübschmann 1960

Grimaldion fragrantis Šmarda & Hadàc 1944

Tortuletum revolventis Marstaller 1980

Community with *Trichostomum crispulum* and *Tortula revolvens*

Crossidio squamiferi-Aloinetum aloidis Guerra & Varo 1981
TORTULO BREVISSIMAE-ALOINETALIA BIFRONTIS (Ros & Guerra 1987) ex Puglisi 2010

Aloino bifrontis-Crossidion crassinervis Ros & Guerra 1987 ex Marstaller 2006

Crossidio crassinervis-Tortuletum obtusatae Ros & Guerra 1987

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Appendixes

Appendix I: Localities and dates of the relevés

Tab. 1 - Rel. 1: Serre di Ciminna (4 March 2019, 37°52'23.38"N, 13°35'28.21"E); rels 2, 3: Serre di Ciminna (4 March 2019, 37°52'24.2"N, 13°35'31.16"E); rels 4, 5: S. Ninfa (3 March 2019, 37°46'49.97"N, 12°53'50.65"E); rels 6, 7: S. Ninfa (3 March 2019, 37°46'49.58"N, 12°53'49.21"E); rel. 8: S. Ninfa (3 March 2019, 37°46'48.37"N, 12°53'54.00"E); rels 9–13: Sutera outskirts (from Privitera 1989); rels 14–19: Milena hills (from Privitera 1989); rels 20–25: Enna outskirts (from Lo Giudice and Bonanno 2010); rels 26–29: Raddusa outskirts (from Lo Giudice and Bonanno 2010); rels 30, 31: Castelluccio (4 March 2019, 37°46'20.63"N, 13°07'11.93"E).

Tab. 2 - Rels 1, 2: Castelluccio (4 March 2019; 37°46'19.5"N, 13°07'17.2"E); rels 3, 4: Castelluccio (4 March 2019; 37°46'13.6" N, 13°07'27.6" E); rels 5, 6:

Castelluccio (4 March 2019; 37°46'17.1" N, 13°07'33.7" E); Rels 7, 8: Sutera outskirts (7 April 2020; 37°30'01.5" N, 13°45'29.6" E); rel. 9: Sutera outskirts (7 April 2020; 37°30'02.8" N, 13°45'27.9" E); rels 10, 11 Sutera outskirts (7 April 2020; 37°30'06.2" N, 13°45'20.6" E); rels 12, 13: Milena hills (7 April 2020; 37°29'49.2" N, 13°45'02.4" E); rel. 14: Milena hills (7 April 2020; 37°29'52.1" N, 13°44'56" E).

Tab. 3 - Rel. 1: Sutera outskirts (6 April 2021, 37°30'20.34"N, 13°44'34.21"E); rel. 2: Sutera outskirts (6 April 2021, 37°30'19.66"N, 13°44'31.39"E); rel. 3: Sutera outskirts (6 April 2021, 37°30'19.34"N, 13°44'38.68"E); rel. 4: Milena outskirts (6 April 2021, 37°27'24.43"N, 13°44'37.66"E); rel. 5: Milena hills (6 April 2021, 37°27'23.90"N, 13°44'35.57"E); rel. 6,7: Raddusa outskirts (from Lo Giudice and Bonanno 2010).

Tab. 4 - Rels 1, 2: Rocca di Entella (4 March 2019; 37°46'20.72"N, 13°07'19.91"E); rel. 3: Rocca di Entella (4 March 2019; 37°46'20.20"N, 13°07'21.46"E); rel. 4,5: Rocca di Entella (4 March 2019; 37°46'21.37"N, 13°07'17.20"E); rels 6, 7: Rocca di Entella (4 March 2019;

37°46'17.96"N, 13°07'22.79"E); rel. 8: Rocca di Entella (6 April 2021; 37°46'19.77"N, 13°07'20.03"E).

Appendix II: Sporadic species

Table 1 – Rel. 1: *Cephaloziella baumgartneri* (1); rel. 2: *Aloina rigida* (+), rel. 4: *Weissia condensa* (1), *Entosthodon convexus* (+); rel. 5: *Tortella flavovirens* (1), *Aloina aloides* (+); rel. 6: *Aloina aloides* (1), *Weissia condensa* (1); rel. 11: *Bryum argenteum* (1); rel. 13: *Cheilothela chloropus* (1); rel. 14: *Ceratodon purpureus* (+), *Tortella flavovirens* (+); rel. 17: *Homalothecium sericeum* (+); rel. 18: *Timmiella barbuloides* (1); rel. 19: *Timmiella barbuloides* (1); *Homalothecium sericeum* (1); *Scleropodium touretii* (+); rel. 21: *Grimmia pulvinata* (+); rel. 23: *Bryum argenteum* (+), *Homalothecium aureum* (+), *Ptychostomum torquescens* (+); rel. 24: *Homalothecium aureum* (+), *Ptychostomum torquescens* (+); rel. 30: *Petalophyllum ralfsii* (+); *Lathagrium cristatum* (1); rel. 31: *Squamarina lentigera* (1).