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Sponge Fauna of the Apulian Marine Caves (Southern Italy): Current State of Knowledge

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Abstract: Submerged and semi-submerged marine caves are considered a European habitat of Community Interest as they preserve one of the most important biodiversity heritages in the Mediterranean and serve as refugia for endemic and/or "relict" species. Among sessile benthic taxa, caves represent significant reservoirs of sponge species richness and are well representative of the entire poriferan Mediterranean fauna. In order to assess the current knowledge of sponge species in marine caves along the Apulian coast, this study gathered data from the available literature (national and international scientific publications and grey literature) with original data, surveying 26 marine caves in the area. A total of 145 Porifera species were reported in marine caves on the Apulian coast, including 117 in the Tremiti archipelago, 33 along the Adriatic coast of Bari and 73 along the Salento Peninsula. Original data includes new records for nine species in the Corvine cave, two in the Murene cave and one in the Zinzulusa cave. Our results suggest that marine cave communities along the Apulian coast are not uniformly surveyed, being the caves of the Tremiti Islands and those of the Salento Peninsula among the best studied, while large stretches of the regional coast, although particularly rich in marine caves, are poorly investigated for their sponge fauna.

Keywords: Porifera; marine caves; Apulian coast

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1. Introduction

The rocky coastline of the Mediterranean region is known for its marine caves richness, which are often exposed to several anthropogenic pressures [1]. Although sea caves represent a relatively small portion of the marine environment, they hold great scientific and ecological importance, embodying a major reservoir of marine biodiversity and providing multiple ecosystem services [2]. Marine caves can be assigned to two main types, depending on their level of submersion: 'submerged' caves, completely below the water level, and 'semi-submerged' caves, which extend above and below the sea surface, meaning that the latter are more exposed to the high variability of physical-chemical parameters and the increased influence of hydrodynamics [1].

The composition of flora and fauna of marine caves can vary greatly; these differences mainly depend on biogeographical factors [3], as environmental gradients linked to the geomorphology, topography and depth range of each cave [4]. Although the species composition may differ, the main taxonomic groups generally exhibit similar trends in all caves. Algal species are mainly present at the entrance, where there is still enough brightness for photosynthetic processes, while animal species are mainly found in the innermost portions of the cavities. In these environments, the availability of particulate organic matter depends on the water movement from the outside, and food chains are predominantly based on secondary (detritus food chains) rather than primary (grazing food chains) production processes [5]. The absence of native primary production and the

limited and irregular supply of allochthonous nourishment make these environments ideal for studying oligotrophic systems directly in situ.

Submerged and semi-submerged marine caves host unique assemblages characterized by a rich community of filter-feeding invertebrates, including both vagile and sessile forms. Of the approximately 2000 animal taxa recorded in Mediterranean marine caves, the most abundant and species-rich phylum among the sessile organisms is that of poriferans [2,6–10]. Along with playing a crucial role in water filtration processes, sponges give sea caves their bright and variegated colors, which constitute one of the most salient attractions (i.e., underwater nature trails) for valuing marine cavities for tourism purposes. In the Mediterranean, a total of 329 sponge species have been identified from at least 185 marine caves, including 279 Demospongiae, 29 Calcarea, 20 Homoscleromorpha and one Hexactinellida, which constitute 48% of the Mediterranean sponge diversity [1,2].

Marine caves are considered an important hotspot for biodiversity in the Mediterranean Sea and worldwide, deserving further study and protection [11]. They have been found to contain unique taxa assemblages, including several exclusive benthic taxa, typical deep-sea faunal elements and a high endemism rate. Thus, the "submerged and semi-submerged sea caves" constitute one of the European Habitats of Community Interest listed in Annex I of the Habitat Directive (92/43/CEE)—code 8330, whose ecological status must be monitored and preserved in order to mitigate any human impacts and minimize potential deterioration phenomena. Additionally, they host one of the most important biodiversity heritages in the Mediterranean, play the precious role of refuge for endemic species and/or "relict" deep populations [12–17], and serve as "natural laboratories" or "deep-sea mesocosms" in the tidal zone, because, in combination with the oligotrophic characteristics of the Mediterranean Sea, they offer direct access to bathyal-like conditions at shallow and easily accessible to scuba divers depths [2,18].

According to the most recent census [1], more than 3000 marine caves have been recorded in the Mediterranean Sea. Even though they have been studied rather thoroughly, most of the information is still limited primarily due to major constraints like the time and experience needed for sampling. Furthermore, studies of cave sponge communities have not been conducted homogeneously across the Mediterranean [10,19].

Alongside the Apulian coast, southeastern Italy, sea caves are numerous in the Tremiti Islands, along the Gargano Peninsula, the Adriatic coast between Bari and Brindisi, and the Salento Peninsula (www.catasto.fspuglia.it, accessed on 30 January 2023). The benthic realm in this area has been the subject of numerous studies (e.g., [6,9,20–25]), but a detailed and updated knowledge of the submarine caves of the Apulian coast could aid in enforcing protection measures. The present work aims to provide comprehensive knowledge about the sponge fauna diversity present in the Apulian marine caves by synthesizing and updating literature and original data.

2. Materials and Methods

A bibliographic search of the indexed scientific articles relative to the sponge fauna of marine caves in the Apulian Region (Southern Italy) was conducted by keyword searching and interrogating the main databases (Web of Science, Scopus, and Google Scholar). Furthermore, articles published in journals without impact factor, grey literature available (e.g., degree thesis, abstracts at congresses, technical reports) and authors' unpublished data were considered. As a result of this search, 21 publications containing records of sponges in marine caves on the Apulian coast were found [6,9,10,21–23,25–39] (Table S1, Supplementary Materials). For each marine cave, the submerged (S) or semi-submerged (SS) typology was considered using data found in the related articles and/or in the Apulian cave register accessible online at http://www.catasto.fspuglia.it/ (accessed on 30 January 2023).

Data found referred to Apulian marine caves were grouped into three areas (Figure 1):

1. Tr: Tremiti Islands;
2. Adr: Adriatic coast near Bari;

3. Sal: Salento Peninsula.

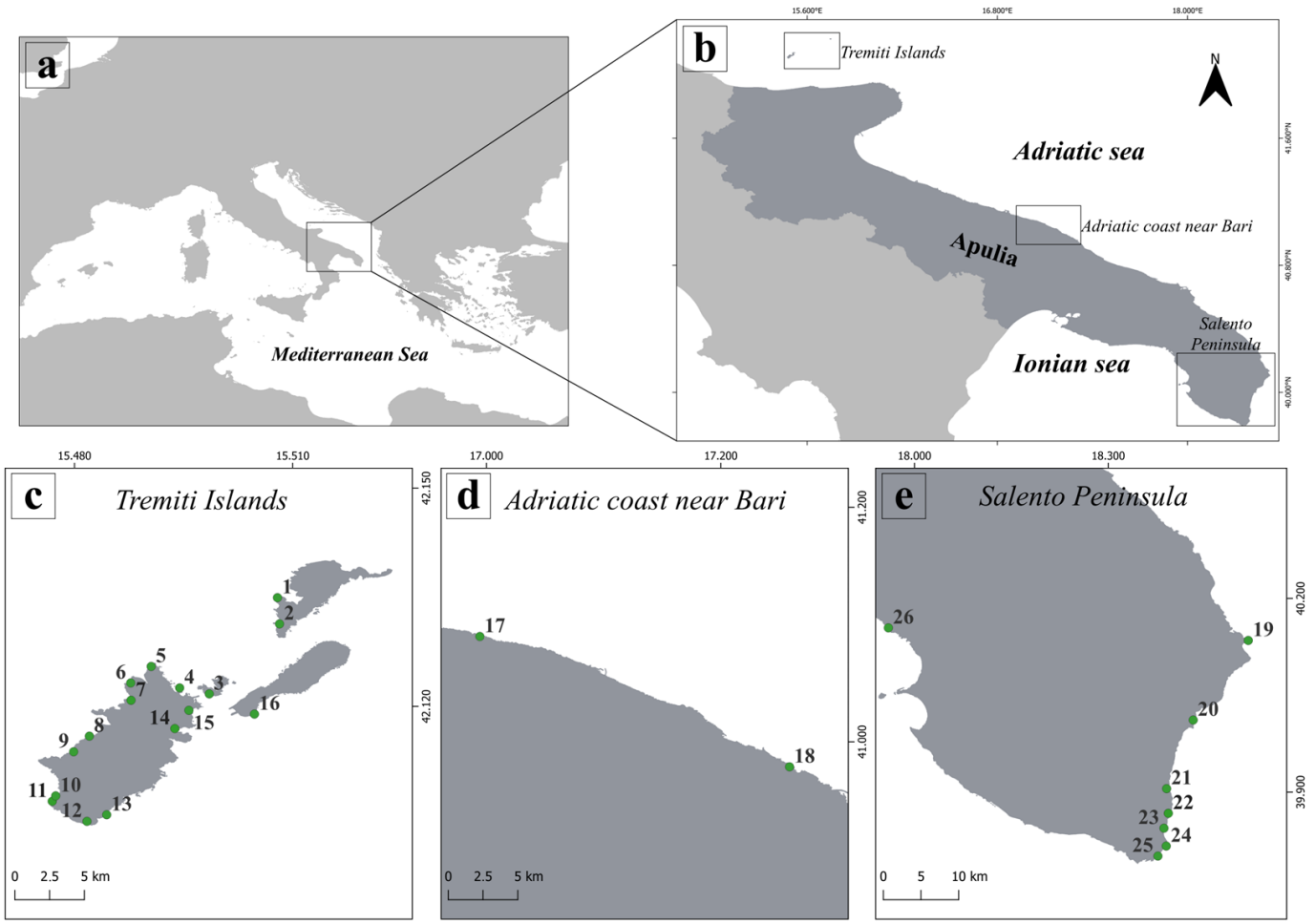

Figure 1. Map of the Apulian coast (**a**) where marine caves sponge-related studies were conducted (**b**) and location of studied marine caves at Tremiti Islands (**c**), along the Adriatic coast near Bari (**d**) and along the Salento Peninsula (**e**). 1: Elle cave; 2: Sorrentino cave; 3: Meduse cave; 4: Pagliai cave; 5: Cala Diamante cave; 6: Coccodrillo cave; 7: Cala Tonda cave; 8: Pecore cave; 9: Rondinelle cave; 10: Bue Marino cave; 11: Punta Provvidenza cave; 12: Murene cave; 13: Viole cave; 14: Cala Spido cave; 15: Arenile cave; 16: Testa di Morte cave; 17: Regina cave; 18: Torre Incine cave; 19: Lu lampiune cave; 20: Zinzulusa cave; 21: Matrona cave; 22: Sifone cave; 23: Ciolo piccola cave; 24: Marinella cave; 25: Principessa cave; 26: Corvine cave.

Since the species inventory was recorded from studies published across several decades (1961–present), taxonomic updates were necessary. All species in the checklist of the Apulian marine caves sponge fauna were checked with the World Porifera Database (WPD) [40] as part of the World Register of Marine Species (WoRMS). The nomenclature referred to the current taxonomic revision reported in the WPD. Genera and species are arranged alphabetically. Moreover, the distribution of each species in other habitats (coralligenous, lagoons or confined environments, superficial rocky environments, mesophotic, deep-sea), according to the checklist of Pansini and Longo [41] and WPD, has been added. The reports relatives to the species *Cliona nigricans* (Schmidt, 1862), *Cliona copiosa* (Sarà, 1959), and *Cliona tremitensis* (Sarà, 1961) have been kept separate from those of *Cliona viridis* (Schmidt, 1862), the currently valid name of these species, to not lose the historical data of the original report, as we believe further taxonomic studies are necessary to clarify the synonymy.

The occurrence of sponge species in marine caves of the defined areas was incorporated into a presence/absence matrix, including the total number of caves in which each species was recorded. Similarity matrices were constructed from the above-mentioned presence/absence matrix, and multivariate analyses, i.e., multidimensional (MDS) scaling and cluster analysis based on Sorensen distance, were performed. The same procedure was followed for the assemblages of each cave zone, also considering the marine cave typology (S; SS). The analysis was carried out using PRIMER v6 software packages [42].

3. Results

Although numerous studies have been conducted in recent years regarding the biotic assemblages of Apulian marine caves, only a few studies have focused on the sponge community composition [43]. On the whole, to the best of our knowledge, the analysis of the available literature allowed us to find data on the sponge fauna composition for 26 Apulian sea caves, distributed as follows: sixteen at Tremiti Islands, two along the Adriatic coast near Bari, and eight in the Salento Peninsula (Figure 1; Table 1). In addition, data related to three cavities on the Salento Peninsula that could not be attributed to any specific sea cave are provided (See Table S2, Supplementary Materials). Data mainly concerned semi-submerged caves with different spatial dimensions, covering a total of 21 caves (fourteen at Tremiti Islands, two along the Adriatic coast near Bari, and five along the Salento Peninsula), while data on sponge fauna composition of submerged sea caves regards only five caves (two at Tremiti Islands and three along the Salento Peninsula) (Table 1; Table S2, Supplementary Materials).

Table 1. Marine caves of the Apulian coast that includes data on sponge fauna composition.

Sea Cave	Cave Code	Cave Number	Typology *
Elle cave	Tr_E	1	S
Sorrentino cave	Tr_So	2	SS
Meduse cave	Tr_Me	3	SS
Pagliai cave	Tr_Pa	4	S
Cala Diamante cave	Tr_CD	5	SS
Coccodrillo cave	Tr_C	6	SS
Cala Tonda cave	Tr_CT	7	SS
Pecore cave	Tr_Pe	8	SS
Rondinelle cave	Tr_Ro	9	SS
Bue Marino cave	Tr_B	10	SS
Punta Provvidenza cave	Tr_PP	11	SS
Murene cave	Tr_Mu	12	SS
Viole cave	Tr_V	13	SS
Cala Spido cave	Tr_Sp	14	SS
Arenile cave	Tr_A	15	SS
Testa di Morte cave	Tr_TM	16	SS
Regina cave	Adr_R	17	SS
Torre Incine cave	Adr_T	18	SS
Lu lampiune cave	Sal_L	19	S
Zinzulusa cave	Sal_Z	20	SS
Matrona cave	Sal_Ma	21	SS
Sifone cave	Sal_S	22	SS
Ciolo Piccola cave	Sal_Ci	23	S
Marinella cave	Sal_M	24	SS
Principessa cave	Sal_P	25	SS
Corvine cave	Sal_Co	26	S
Miscellanea	Others		

* SS: semi-submerged; S: submerged.

Studies carried out in the Tremiti Islands sea caves mainly regarded semi-submerged benthic biocoenoses characterization [6,9,20,25,38,44–46], while only a few studies focused on submerged sea caves [6,38,47]. Among the benthic taxa analyzed in these studies, those

concerning Porifera received the most attention [6,9,10,25,26,29,34,37,38]. The first essential contribution to the sponge fauna in Tremiti sea caves was the study carried out by Sarà [6] which involved 16 superficial caves with 68 taxa of Porifera surveyed and 4 newly described species (Table 2). Moreover, the research carried out by Pulitzer-Finali [29] made a notable contribution to the knowledge of the Tremiti island's sponge caves fauna (32 species) and the description of three new species (Table 2). Subsequently, Corriero et al. [9,20] focused their research on the Bue Marino cave, which led to the description of a new species (Table 2) and a rich sponge assemblage consisting of 56 taxa. Recently, the benthic characterization of a submerged marine cave located at Capraia Island [28], made by photo/videos analysis, resulted in the identification of a total of 63 living taxa, 39 of which belonged to the phylum Porifera and among them 23 were attributable to unequivocal and currently valid species.

Table 2. List of new sponge species reported in the literature for the Apulian marine caves with their current valid nomenclature.

Species	Author	Current Valid Name	Author	Marine Cave
Cliona tremitensis	Sarà, 1961	*Cliona viridis*	(Schmidt, 1862)	Tr_Pa
Haliclona viscosa	Sarà, 1961	*Haliclona (Reniera) sarai*	(Pulitzer-Finali, 1969)	Tr_B; Tr_CT
Phloeodictyum vacuum	Sarà, 1961	*Oceanapia vacua*	(Sarà, 1961)	Tr_V
Topsentia contorta	Sarà, 1961	*Halichondria (Halichondria) contorta*	(Sarà, 1961)	Tr_B; Tr_CT
Dendrectilla tremitensis	Pulitzer-Finali, 1983			Tr_V
Rhaphisia spelaea	Pulitzer-Finali, 1983	*Myrmekioderma spelaeum*	(Pulitzer-Finali, 1983)	Tr_So; Tr_CT
Spongosorites flavens	Pulitzer-Finali, 1983			Tr_V; Tr_So; Tr_CD
Dendroxea pseudodidiscoides	Corriero et al., 1996	*Didiscus pseudodidiscoides*	(Corriero et al., 1996)	Tr_B
Higginsia ciccaresei	Pansini & Pesce, 1998			Sal_Z

Although the Apulian Adriatic coast, in particular Gargano and Bari coasts, host numerous marine cavities, only two semi-submerged caves (Regina cave and Torre Incine cave) have been the subject of taxonomic studies concerning Porifera thanks to work carried out by Labate [35] and Pulitzer-Finali [38] in the second half of the last century.

Numerous studies carried out in the Salento Peninsula marine caves (more than 40 articles) documented more than 600 animal records belonging to benthic and pelagic taxa (see [36]), with only three targeted studies on Porifera and one new species described (Table 2) [21,30].

Overall, the taxonomic revision of the literature data allowed censusing of a total of 145 sponge species (Table 3). The checklist includes eight Calcarea subdivided into three orders, six families and six genera; nine Homoscleromorpha belonging to one order, two families and five genera; and 128 Demospongiae comprising 17 orders, 45 families and 71 genera (Table 3). Within demosponges, the most represented order is Haplosclerida, with 32 species belonging to five genera and three families. Well represented is also the Keratosa order of Dictyoceratida, with 29 species, and the orders of Teractinellida and Poecilosclerida, with 26 and 23 species, respectively (Figure 2). Currently, no alien species of Porifera have been recorded in the Apulian marine caves, while eight species listed as endangered or threatened (Annex II) and regulated under the Bern and Barcelona conventions have been recorded (Table 3).

As mentioned above, taxonomic efforts on phylum Porifera research in Apulian marine caves led to the description of nine new species, five of which are currently attributable to species subject to taxonomic revisions (Table 2). Eight of these species have been described in the marine caves of the Tremiti Islands, and one species, *Higginsia ciccaresei* (Pansini and Pesce, 1998), in the Zinzulusa cave along the Salento Peninsula.

Among the 145 sponge species recorded in the Apulian sea caves, 126 were found in semi-submerged cavities and 86 in submerged ones. The Tremiti Islands marine caves host the largest number of sponge species (a total of 117), those of the Adriatic coast near Bari 33 species, while the Salento Peninsula marine caves host a total of 73 sponge species (Table 4).

Table 3. Checklist of sponge species recorded in the Apulian marine caves (Southern Italy, Central Mediterranean Sea). SS_Tr: Semi-submerged caves of Tremiti Islands; S_Tr: Submerged caves of Tremiti Islands; SS_Adr: Semi-submerged caves of Adriatic coast near Bari; SS_Sal: Semi-submerged caves of the Salento Peninsula; S_Sal: Submerged caves of the Salento Peninsula; Others: data not attributable to a specific marine cave. The underlined species are included in the lists of endangered and threatened (Annex II) and whose exploitation is regulated (Annex III) under the Bern and Barcelona convention. The references of each species in each particular cave are reported in Table S2.

	SS_Tr	S_Tr	SS_Adr	SS_Sal	S_Sal	Others
CLASS CALCAREA						
Order Baerida						
Family Petrobionidae						
Petrobiona massiliana Vacelet & Lévi, 1958		+				+
Order Clathrinida						
Family Leucaltidae						
Ascandra contorta (Bowerbank, 1866)	+	+				
Ascandra falcata Haeckel, 1872	+	+				
Family Clathrinidae						
Clathrina clathrus (Schmidt, 1864)				+	+	+
Clathrina coriacea (Montagu, 1814)	+	+	+	+		+
Family Leucettidae						
Leucetta solida (Schmidt, 1862)	+	+	+			
Order Leucosolenida						
Family Grantiidae						
Leucandra aspera (Schmidt, 1862)	+	+				
Family Syconidae						
Sycon elegans (Bowerbank, 1845)	+					
CLASS HOMOSCLEROMORPHA						
Order Homosclerophorida						
Family Oscarellidae						
Pseudocorticium jarrei Boury-Esnault, Muricy, Gallissian & Vacelet, 1995		+				
Oscarella lobularis (Schmidt, 1862)				+	+	
Family Plakinidae						
Corticium candelabrum Schmidt, 1862	+				+	+
Plakina bowerbanki (Sarà, 1960)	+	+			+	
Plakina dilopha Schulze, 1880					+	
Plakina reducta (Pulitzer-Finali, 1983)					+	
Plakina trilopha Schulze, 1880	+		+		+	+
Plakina topsenti (Pouliquen, 1972)					+	
Plakortis simplex Schulze, 1880	+		+		+	+
CLASS DEMOSPONGIAE						
Order Tetractinellida						
Family Ancorinidae						
Dercitus (*Stoeba*) *plicatus* (Schmidt, 1868)	+	+			+	
Jaspis johnstonii (Schmidt, 1862)	+			+	+	+
Stelletta grubii Schmidt, 1862			+			
Family Calthropellidae						
Calthropella (*Calthropella*) *pathologica* (Schmidt, 1868)	+					
Family Thoosidae						
Alectona millari Carter, 1879	+				+	+
Delectona madreporica Bavestrello, Calcinai, Cerrano & Sarà, 1997					+	
Thoosa mollis Volz, 1939					+	+
Family Geodiidae						
Caminella intuta (Topsent, 1892)	+					
Erylus discophorus (Schmidt, 1862	+	+	+		+	+
Geodia conchilega Schmidt, 1862	+				+	
Geodia cydonium (Linnaeus, 1767)	+		+			
Penares euastrum (Schmidt, 1868)	+			+	+	
Penares helleri (Schmidt, 1864)	+		+	+	+	+
Family Pachastrelllidae						
Triptolemma simplex (Sarà, 1959)	+					
Family Samidae						
Samus anonymus Gray, 1867	+					
Order Trachycladida						
Family Trachycladidae						
Trachycladus minax (Topsent, 1888)	+	+				

Table 3. *Cont.*

	SS_Tr	S_Tr	SS_Adr	SS_Sal	S_Sal	Others
Order Biemnida						
Family Rhabderemiidae						
Rhabderemia topsenti van Soest & Hooper, 1993	+					
Order Clionaida						
Family Clionaidae						
Cliona celata Grant, 1826	+			+	+	+
Cliona copiosa Sarà, 1959	+		+			
Cliona nigricans (Schmidt, 1862)				+	+	
Cliona rhodensis Rützler & Bromley, 1981	+			+	+	+
Cliona schmidti (Ridley, 1881)	+	+		+	+	+
Cliona tremitensis Sarà, 1961		+				
Cliona vermifera Hancock, 1867	+					
Cliona viridis Schmidt, 1862	+				+	
Pione vastifica (Hancock, 1849)						+
Family Placospongiidae						
Placospongia decorticans (Hanitsch, 1895)	+		+	+	+	+
Family Spirastrellidae						
Diplastrella bistellata (Schmidt, 1862)	+	+		+	+	
Diplastrella ornata Rützler & Sarà, 1962	+				+	+
Spirastrella cunctatrix Schmidt, 1868	+	+		+	+	+
Order Suberitida						
Family Halichondriidae						
Halichondria (*Halichondria*) *contorta* (Sarà, 1961)	+		+	+		
Halichondria (*Halichondria*) *genitrix* (Schmidt, 1870)	+					
Halichondria (*Halichondria*) *semitubulosa* (Lamarck, 1814)	+		+			
Hymeniacidon perlevis (Montagu, 1814)		+				+
Spongosorites flavens Pulitzer-Finali, 1983	+					
Family Suberitidae						
Aaptos aaptos (Schmidt, 1864)	+	+		+	+	+
Protosuberites denhartogi van Soest & de Kluijver, 2003	+					
Pseudosuberites sulphureus (Bowerbank, 1866)		+				
Terpios gelatinosus (Bowerbank, 1866)	+	+		+	+	+
Order Merliida						
Family Merliidae						
Merlia normani Kirkpatrick, 1908	+	+		+	+	+
Order Chondrillida						
Family Chondrillidae						
Chondrilla nucula Schmidt, 1862			+		+	
Order Chondrosiida						
Family Chondrosiidae						
Chondrosia reniformis Nardo, 1847	+	+	+	+	+	+
Order Poecilosclerida						
Family Acarnidae						
Acarnus tortilis Topsent, 1892	+					
Family Chondopsidae						
Batzella inops (Topsent, 1891)	+					
Family Crambeidae						
Crambe crambe (Schmidt, 1862)	+	+		+	+	+
Family Crellidae						
Crella (*Pytheas*) *sigmata* Topsent, 1925	+					
Family Esperiopsidae						
Ulosa digitata (Schmidt, 1866)				+		
Family Hymedesmiidae						
Hemimycale columella (Bowerbank, 1874)	+	+				+
Hymedesmia (*Hymedesmia*) *peachii* Bowerbank, 1882	+					+
Hymedesmia (*Hymedesmia*) *versicolor* (Topsent, 1893)	+					
Phorbas fictitius (Bowerbank, 186	+			+	+	+
Phorbas plumosus (Montagu, 1814)		+				
Phorbas tenacior (Topsent, 1925)	+	+		+	+	+
Phorbas topsenti Vacelet & Pérez, 2008	+					
Family Microcionidae						
Antho (*Antho*) *involvens* (Schmidt, 1864)		+				
Antho (*Antho*) *inconstans* (Topsent, 1925)	+					
Clathria (*Clathria*) *toxivaria* (Sarà, 1959)			+	+	+	+
Clathria (*Clathria*) *toxistyla* (Sarà, 1959)	+	+	+			
Clathria (*Microciona*) *toxitenuis* Topsent, 1925			+			

Table 3. *Cont.*

	SS_Tr	S_Tr	SS_Adr	SS_Sal	S_Sal	Others
Family Mycalidae						
Mycale (*Mycale*) *lingua* (Bowerbank, 1866)	+					
Family Myxillidae						
Myxilla (*Myxilla*) *iotrochotina* (Topsent, 1892)						+
Myxilla (*Myxilla*) *rosacea* (Lieberkühn, 1859)			+			
Family Tedaniidae						
Tedania (*Tedania*) *anhelans* (Vio in Olivi, 1792)	+					
Order Axinellida						
Family Axinellidae						
Axinella damicornis (Esper, 1794)	+	+			+	+
Axinella verrucosa (Esper, 1794)	+				+	
Family Heteoxyidae						
Myrmekioderma spelaeum (Pulitzer-Finali, 1983)	+			+	+	+
Family Raspailiidae						
Didiscus pseudodidiscoides (Corriero, Scalera-Liaci & Pronzato, 1996)	+					
Didiscus stylifer Tsurnamal, 1969				+	+	+
Eurypon vescicularis Sarà & Siribelli, 1960	+					
Raspaciona aculeata (Johnston, 1842)	+					
Family Stelligeridae						
Higginsia ciccaresei Pansini & Pesce, 1998						
Order Bubarida						
Family Bubaridae						
Bubaris vermiculata (Bowerbank, 1866)	+			+	+	
Family Desmanthidae						
Desmanthus incrustans (Topsent, 1889)	+					+
Family Dictyonellidae						
Acanthella acuta Schmidt, 1862	+	+			+	+
Dictyonella incisa (Schmidt, 1880)	+				+	+
Dictyonella marsilii (Topsent, 1893)	+					
Order Agelasida						
Family Agelasidae						
Agelas oroides (Schmidt, 1864)	+	+		+	+	+
Order Tethyda						
Family Tethyidae						
Tethya aurantium (Pallas, 1766)		+		+		
Family Timeidae						
Timea fasciata Topsent, 1934	+					
Timea stellata (Bowerbank, 1866)	+					
Timea stellifasciata Sarà & Siribelli, 1960	+					
Timea unistellata (Topsent, 1892)	+					+
Order Haplosclerida						
Family Chalinidae						
Dendrectilla tremitensis Pulitzer-Finali, 1983	+					
Dendroxea adumbrata Corriero, Scalera-Liaci & Pronzato, 1996	+					
Dendroxea lenis (Topsent, 1892)		+		+	+	+
Haliclona (*Gellius*) *angulata* (Bowerbank, 1866)				+		
Haliclona (*Gellius*) *dubia* (Babic, 1922)	+					
Haliclona (*Gellius*) *fibulata* (Schmidt, 1862)	+		+			
Haliclona (*Halichoclona*) *fulva* (Topsent, 1893)	+		+			
Haliclona (*Haliclona*) *michelei* Van Soest & Hooper, 2020	+	+	+			
Haliclona (*Halichoclona*) *parietalis* (Topsent, 1893)	+					
Haliclona (*Reniera*) *cinerea* (Grant, 1826)			+			
Haliclona (*Reniera*) *cratera* (Schmidt, 1862)	+	+	+			+
Haliclona (*Reniera*) *mediterranea* Griessinger, 1971				+		
Haliclona (*Rhizoniera*) *rosea* (Bowerbank, 1866)	+					
Haliclona (*Rhizoniera*) *sarai* (Pulitzer-Finali, 1969)	+	+		+	+	+
Haliclona (*Soestella*) *mucosa* (Griessinger, 1971)	+	+	+	+		+
Haliclona (*Soestella*) *valliculata* (Griessinger, 1971)	+			+		
Family Petrosiidae						
Petrosia (*Petrosia*) *ficiformis* (Poiret, 1789)	+	+		+	+	+
Petrosia (*Strongylophora*) *pulitzeri* Pansini, 1996				+		
Petrosia (*Strongylophora*) *vansoesti* Boury-Esnault, Pansini & Uriz, 1994				+		

Table 3. *Cont.*

	SS_Tr	S_Tr	SS_Adr	SS_Sal	S_Sal	Others
Family Phloedictyidae						
Calyx nicaeensis (Risso, 1827)	+					+
Oceanapia perforata (Sarà, 1960)				+		
Oceanapia vacua (Sarà, 1961)	+					
Order Dictyoceratida						
Family Irciniidae						
Ircinia dendroides (Schmidt, 1862)	+					
Ircinia oros (Schmidt, 1864)	+	+				
Ircinia variabilis (Schmidt, 1862)	+	+	+	+	+	+
Sarcotragus fasciculatus (Pallas, 1766)	+	+	+			+
*Sarcotragus foetidus*Schmidt, 1862	+			+	+	+
Sarcotragus pipetta (Schmidt, 1868)	+					
Sarcotragus spinosulus Schmidt, 1862	+			+	+	+
Family Thorectidae						
Fasciospongia cavernosa (Schmidt, 1862)	+	+		+	+	+
Scalarispongia proficens (Pulitzer-Finali & Pronzato, 1981)	+	+	+			
Scalarispongia scalaris (Schmidt, 1862)	+					+
Cacospongia mollior Schmidt, 1862	+	+				
Family Spongiidae						
Spongia (*Spongia*) *nitens* (Schmidt, 1862)						+
Spongia (*Spongia*) *officinalis* Linnaeus, 1759		+	+			+
Spongia (*Spongia*) *virgultosa* (Schmidt, 1868)	+	+	+	+	+	+
Family Dysideidae						
Dysidea avara (Schmidt, 1862)	+			+	+	
Dysidea fragilis (Montagu, 1818)			+			+
Dysidea incrustans (Schmidt, 1862)					+	
Pleraplysilla spinifera (Schulze, 1878)				+	+	
Order Dendroceratida						
Family Darwinellidae						
Aplysilla rosea (Barrois, 1876)			+			
Aplysilla sulfurea Schulze, 1878			+			
Order Verongiida						
Family Aplysinidae						
Aplysina cavernicola Vacelet, 1959				+		
Aplysina aerophoba (Nardo, 1833)		+				
Family Ianthellidae						
Hexadella pruvoti Topsent, 1896		+				
Hexadella racovitzai Topsent, 1896						+

Table 4. Sponge species richness of the submerged and semi-submerged sea caves studied in the three areas of the Apulian coast.

	Salento Peninsula		Adriatic Coast	Tremiti Islands	
Typology *	S	SS	SS	S	SS
No. species	57	46	33	46	102
Total	73		33	117	

* S: submerged, SS: semi-submerged.

Within the 16 Tremiti Islands marine caves, literature data found records for 14 semi-submerged (SS) caves (Tr_V, Tr_B, Tr_Mu, Tr_Pe, Tr_Ro, Tr_A, Tr-C, Tr_CT, Tr_So, Tr_Sp, Tr_TM, Tr_CD, Tr_PP, Tr_Me) and for two submerged (S) caves (Tr_Pa, Tr_E) (Table S2, Supplementary Materials). In the SS Tremiti Islands marine caves, a total of 102 sponge species have been recorded. Among them, the Bue Marino and Viole caves were the best studied and hosted a considerable number of species (63 and 70, respectively) (Figure 3) (Table S2, Supplementary Materials). No species in common to all 14 Tremiti marine caves were found, while two species (*Crambe crambe* and *Haliclona (Reniera) sarai*) were shared by nine of them, and three species (*Agelas oroides*, *Clathrina coriacea*, and *Petrosia ficiformis*) were shared by eight marine caves. On the other hand, a total of 46 sponge species have been

found in the two S marine caves. Four of these are shared by the two caves (*Diplastrella bistellata*, *Ircinia variabilis*, *Petrosia ficiformis*, and *Phorbas tenacior*).

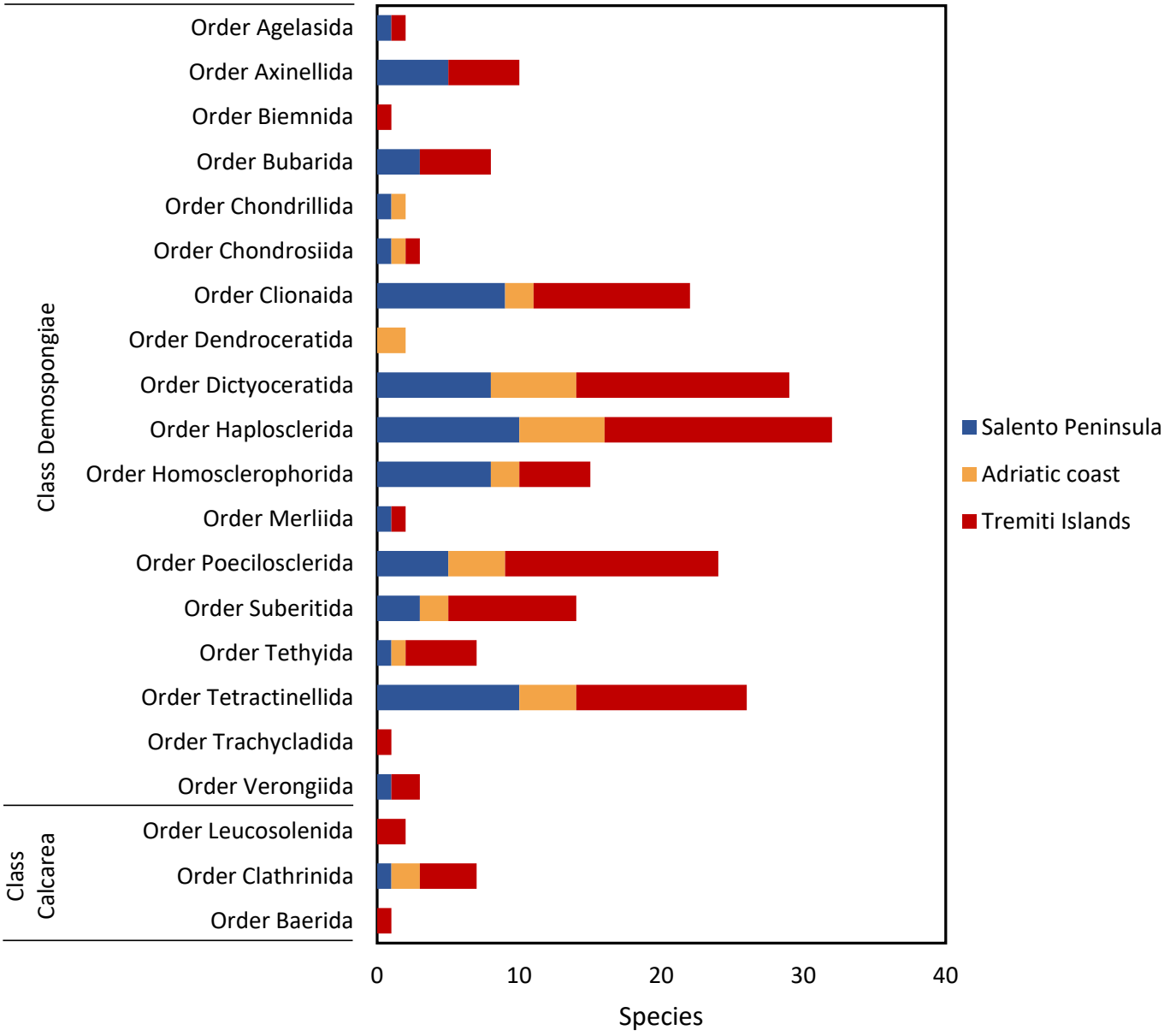

Figure 2. Histogram illustrating the contribution of the different classes and orders of Porifera in each area.

Analyzing the sponge assemblages recorded in the two semi-submerged sea caves of the Adriatic coast near Bari (Adr_R, Adr_T), of the 33 species of sponge reported, only *Ircinia variabilis* was found in both the cavities.

As regards species distribution in the marine caves of the Salento Peninsula, in the three submerged (S) marine caves (Sal_Co, Sal_Ci and Sal_L), a total of 57 sponges were reported, while in the five semi-submerged (SS) ones (Sal_P, Sal_M, Sal_S, Sal_Ma, Sal_Z) the sponges censed were 46. The S caves shared five species (*Agelas oroides*, *Petrosia ficiformis*, *Sarcotragus spinosulus* and *Spirastrella cunctatrix*), while the SS caves, excluding Sal_Z, showed only two species in common (*Petrosia ficiformis* and *Phorbas tenacior*). In this area, only the Corvine cave, a submerged marine cave located in the Porto Selvaggio Natural Park (Figure 1), has been subject to targeted sponge fauna studies (Figure 4) in which 55 species have been recorded considering both published [36] and current paper data.

Figure 3. Photographs of the sponge diversity in the Bue Marino (**a**–**c**), Viole (**d**–**f**) and Murene (**g**,**h**) caves (Tremiti Islands, Adriatic Sea). Pictures refer to a 20 × 20 cm^2. The conspicuous species were: (**a**) *Didiscus pseudodidiscoides, Jaspis johnstonii*; (**b**) *Spirastrella cunctatrix, Haliclona (Reniera) cratera, Clathrina coriacea, Cliona schmidti, Terpios gelatinosus*; (**c**) *Agelas oroides, D. pseudodidiscoides, J. johnstonii*; (**d**) *C. schmidtii, Raspaciona aculeata, T. gelatinosus*; (**e**) *J. johnstonii, H. (R.) cratera, S. cunctatrix;* (**f**) *A. oroides, S. cunctatrix;* (**g**) *C. celata, C. schmidti, Crambe crambe, S. cunctatrix;* (**h**) *Petrosia ficiformis, S. cunctatrix.* (Photo by Corriero G., 1997–1998).

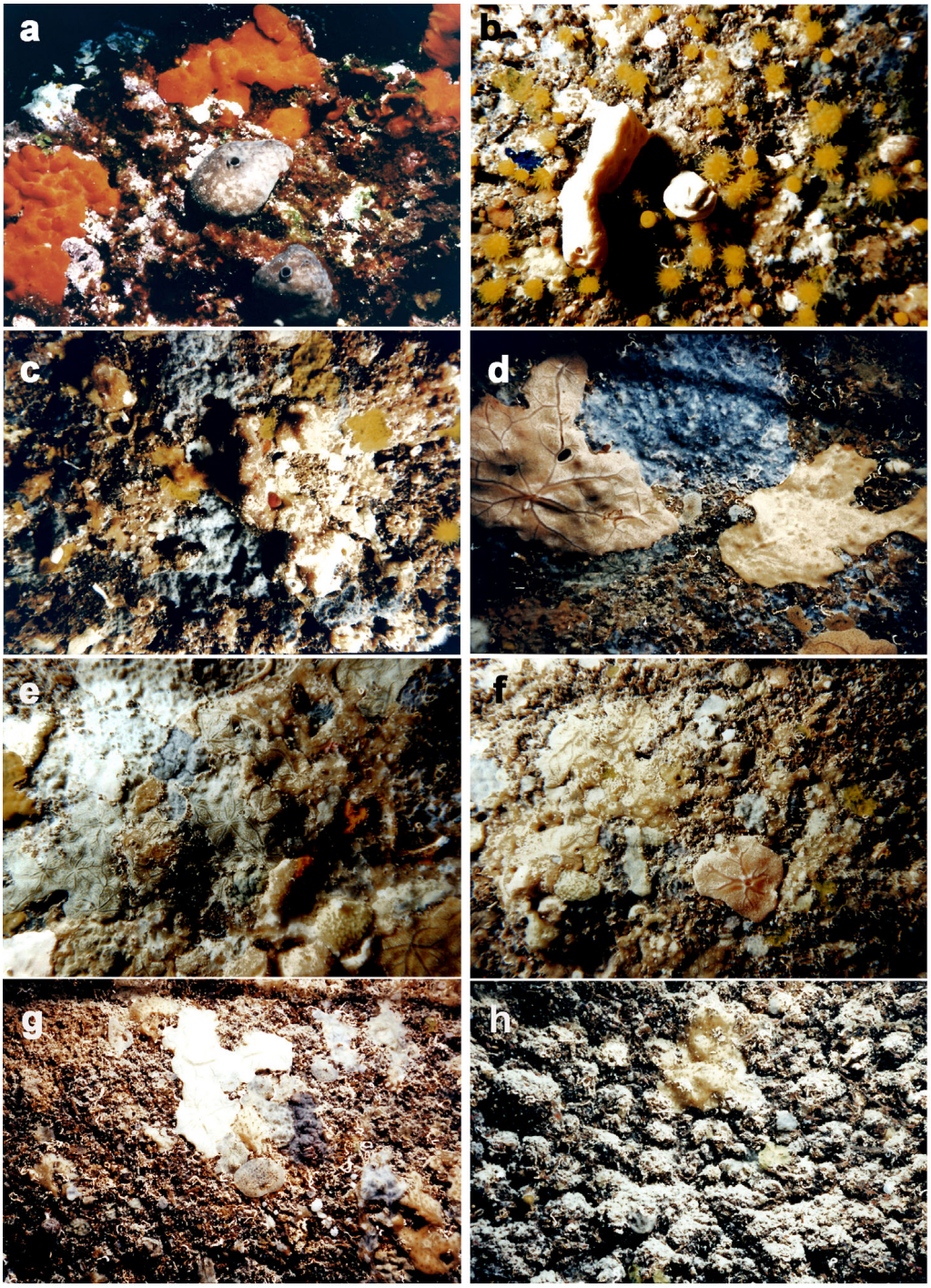

Figure 4. Photographs of the sponge diversity in the Corvine cave (Salento Peninsula, Ionian Sea). Pictures refer to a 20 × 20 cm^2. The conspicuous species were: at the entrance *Chondrosia reniformis*, *Crambe crambe* and *Cliona celata* (**a**); at 5 m from the entrance *Terpios gelatinosus*, *Agelas oroides* and *Petrosia ficiformis* (**b**); at 10 m from the entrance *Penares euastrum*, *Dendroxea lenis* and *Haliclona (Rhizoniera) sarai* (**c**); at 15 m from the entrance *Spirastrella cunctatrix*, *Diplastrella bistellata* and *D. lenis* (**d**); at 20 m from the entrance *S. cunctatrix*, *D. ornata*, *Didiscus styliferus*, *D. lenis* (**e**); at 25 m from the entrance *S. cunctatrix*, *D. ornata* and *H. (R.) sarai* (**f**); at 35 m from the entrance *Jaspis johnstonii*, *D. bistellata* and *D. lenis* (**g**); at 45 m from the entrance *J. johnstonii* and *Bubaris vermiculata* (**h**). The maximum covering value (80% circa) can be observed in the semi-dark part of the cave at 20 m from the entrance. (Photo by Longo C., February 1999).

Considering that the research effort is not comparable across each cave, the interpretation of the sponge assemblages seems to be affected by incomplete and not uniform knowledge of the Apulian marine caves' sponge fauna. Indeed, the dendrogram obtained from cluster analysis of merged data from all cave typologies (S and SS) in each considered area (Tr, Adr and Sal) showed a clear separation of sponge assemblages found in the SS_Adr caves from the others. The group comprising the S and SS caves of the Salento Peninsula showed the highest similarity (66%). The SS_Tr sponge assemblages showed 54% of similarity with the Sal group, and the S_Tr showed a similarity value of 47% with SS of the same area (Figure 5).

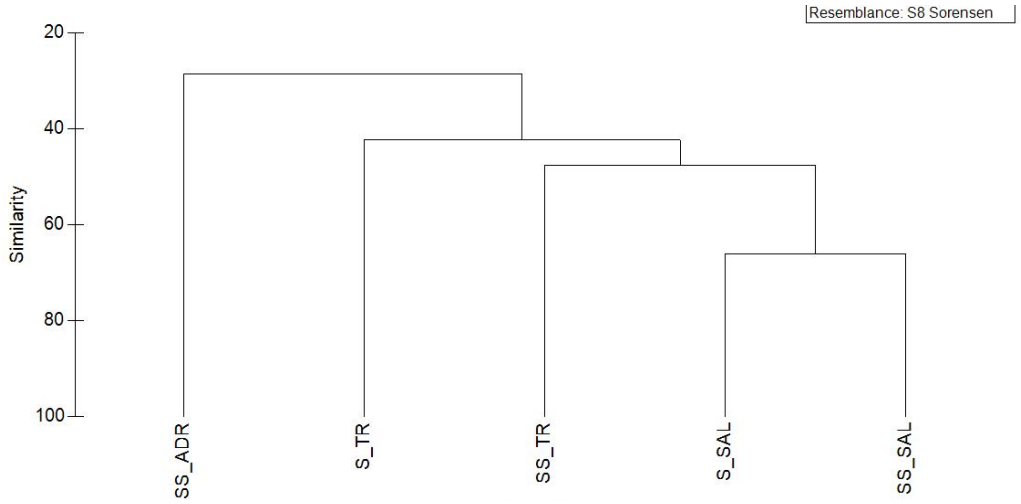

Figure 5. Cluster analysis on the sponge species presence-absence matrix based on the Sorensen similarity index. Marine caves (S: submerged; SS: semi-submerged) grouped in the three areas along the Apulian coast (TR: Tremiti Islands; ADR: Adriatic Coast near Bari; SAL: Salento Peninsula).

The comparison of the populations surveyed in the three areas identified thirteen species as shared between all the areas (*Chondrosia reniformis*, *Clathrina coriacea*, *Erylus discophorus*, *Halichondria (H.) contorta*, *Ircinia variabilis*, *Penares helleri*, *Placospongia decorticans*, *Plakina trilopha*, *Plakortis simplex*, *Sarcotragus fasciculatus*, *S. spinosulus*, *Spongia (S.) officinalis*, and *S. virgultosa*). Observations of the populations of each area reveal that nine species are present in over half of the caves on the Tremiti Islands (*Agelas oroides*, *Ascandra falcata*, *C. coriacea*, *Crambe crambe*, *Haliclona sarai*, *Petrosia ficiformis*, *Sarcotragus fasciculatus*, *Spirastrella cunctatrix*, and *S. virgultosa*), and five species in the Salento Peninsula (*A. oroides*, *I. variabilis*, *P. ficiformis*, *S. spinosulus*, *S. cunctarix*). The caves of Salento and Tremiti share 39.44% of the species, while the species exclusive to the two areas are 15.82% and 35.44% for the caves of Salento and Tremiti, respectively.

4. Discussion

The species richness of the sponge assemblages recorded in marine caves has been demonstrated in this first attempt to assess the state of knowledge of Porifera in submerged and semi-submerged caves on the Apulian coast. Based on the analysis of the available literature (articles published in national and international scientific journals and gray literature) and authors' unpublished data, the faunal composition of the sponge assemblage has been determined for a total of 26 sea caves along the Apulian coast: in particular, 16 on the Tremiti archipelago, 2 on the Adriatic coast of Bari and 8 on the Salento Peninsula. The caves of the Tremiti Islands, together with those of Salento, are among the best known in Apulia. The numerous sea caves located in the province of Bari, especially those along the coast between Torre a Mare and Monopoli and those located along the Gargano promontory, are currently unknown in terms of the biological diversity they host, although most of them are listed in the register of Apulian caves.

It is well known that Mediterranean marine caves are hot spots for sponge diversity, with more than 300 species documented so far [1,10,48]. The present faunistic assessment revealed a remarkably rich assemblage present in the Apulian sea caves, with 145 sponge species registered by now, representing 45% of the total number of sponge species known for Mediterranean marine caves. Of the sponge species recorded in the Apulian marine caves, 126 were found in semi-submerged caves and 86 in submerged ones. Moreover, the cluster analysis for the surveyed caves revealed three major groups of samples corresponding to the Adriatic, Salento Peninsula and Tremiti areas. The presence of different species explains the dissimilarities between these three groups. The caves from the three areas analyzed were characterized by a relatively diverse composition. Indeed, the faunistic census showed species richness values for each cave ranging from 33 (Adriatic caves) to 117 (Tremiti caves). Similar values for species richness have previously been reported from other Mediterranean caves [6,9,25,49–53].

A large number of the recorded species were already known as typical representatives of cave communities or, at least, had been already found in submarine caves [10], as they are typical species of sciaphilous environments, such as different species of Timeidae, *Agelas oroides*, *Petrosia ficiformis* and *Spirastrella cunctatrix*. It is to be noted, however, that a typically troglobitic species, such as *Petrobiona massilliana*, was documented only twice in this survey (Table S2, Supplementary Materials). Specifically for the Apulian region, a significant number of species were exclusively recorded in the caves of the area (14%) [41,47,54–65]. Nevertheless, the sponge assemblages known so far in Apulian marine caves include a considerable number of species that also occur in other Apulian coastal habitats (about 86%). The highest affinity values were found for species associated with coralligenous biocenoses (71% species in common) and those of superficial rocky or mesophotic environments (39% each). A lower affinity was found for species of deep Apulian ecosystems (3% of species in common) (see Table S2, Supplementary Materials). Eleven species found exclusively in Apulian marine caves have not been reported—at least so far —from habitats other than caves [40] (Table S2, Supplementary Materials), confirming the role of this habitat as a biodiversity reservoir.

Several species (59) were recorded in only one Apulian geographic area (6 exclusives of the Adriatic, 11 in Salento and 42 in Tremiti). A considerable proportion of these species (91%) were found in only one cave of the entire geographic area. For instance, in the Tremiti archipelago, no species in common with all 16 marine caves were found. This may be explained by the fact that the studied caves are characterized by diverse topographic features, which suggests that peculiar features characterize each cave. The high level of distinctiveness of marine cave assemblages has been highlighted in previous research [39], and comparable ideas have been reported in the literature: Sarà [66] emphasized that marine cave assemblages typically exhibit a high level of individuality, while Harmelin [67] proposed that populations that are well represented in certain caves but absent or rare in the adjacent ones could persist because of the relative stability of environmental conditions in the internal zones of the caves. Nevertheless, it should be noted that sponge communities differed enough to allow a clear differentiation among the three defined areas through statistical analysis. Analyses revealed that different sponge species (*Petrosia ficiformis*, *Spirastrella cunctatrix*, *Agelas oroides*, *Phorbas tenacior*, *Crambe crambe*, *Haliclona (Reniera) sarai*, and *Ircinia variabilis*) were found in at least half of the studied caves and 13 species were shared between all the areas (*Clathrina coriacea*, *Chondrosia reniformis*, *Erylus discophorus*, *Halichondria (H.) contorta*, *Ircinia variabilis*, *Penares helleri*, *Placospongia decorticans*, *Plakina trilopha*, *Plakortis simplex*, *Sarcotragus fasciculatus*, *S. spinosulus*, *Spongia (S.) officinalis*, *S. virgultosa*).

Furthermore, information from species of the author's unpublished data referred to the Corvine, Zinzulusa, and Murene caves are added to the list of species already reported in previous works. Corvine Cave is a submerged cavity among the largest ones in the entire Salento coastal area. Its development of about 50 m and its dead-end termination makes possible the existence of a series of environmental gradients which greatly condition

the communities of living organisms. A total of 55 sponge species were recorded in this cave, including 15 at the entrance and 46 inside the cave, adding 9 new species to those reported in the literature (*Bubaris vermiculata*, *Chondrilla nucula*, *Chondrosia reniformis*, *Cliona celata*, *Erylus auastrum*, *Oscarella lobularis*, *Phorbas tenacior*, *Plakina topsenti*, and *Tethya aurantium*) [36]; authors' unpublished data]. In the Zinzulusa cave, a complex anchialine cave of the Salento Peninsula, in which only *Higghinsia ciccaresei* has been reported so far, we added for the first time the record of *Terpios gelatinosus*, a frequent species in sciaphilous environments. The Murene cave (named as Gabbiani cave in grey literature) is a semi-submerged cave located on the southeastern slope of the Tremiti Island of San Domino. It consists of a single large chamber 10 m long and 8 m wide at the farthest point from the entrance. The Murene cave host 26 sponge species, 24 of them already reported in the grey literature [25,26], to which two new records were added (*Oscarella lobularis* and *Chondrilla nucula*).

In all Mediterranean biotopes, marine caves represent a hotspot of biodiversity that calls for additional scientific research and the implementation of appropriate conservation measures. The results here presented regarding the sponge assemblages of the Apulian marine caves confirm this peculiarity, where nine new sponge species have been described (*Cliona viridis*, *Halichondria (Halichondria) contorta, Oceanapia vacua*, *Haliclona (Reniera) sarai*, *Dendrectilla tremitensis*, *Myrmekioderma spelaeum*, *Spongosorites flavens*, *Didiscus pseudodidiscoides*, and *Higginsia ciccaresei*), and several "protected species of the protocol SPA/BIO" were recorded [68]. These latter species include *Aplysina aerophoba*, *Aplysina cavernicola*, *Geodia cydonium*, *Petrobiona massiliana*, *Sarcotragus foetidus*, *S pipetta*, *Spongia officinalis*, and *Tethya aurantium*. They belong to protected biocoenosis of marine caves and are designated as Habitat II.4.3, Habitat IV.3.2, and Habitat V.3.2, which, respectively, are categorized as mid-littoral caves, semi-dark caves, and dark caves [69] and constitute one of the European Habitats of Community Interest listed in Annex I of the Habitats Directive (92/43/EEC)—code 8330. Furthermore, appropriate conservation planning of these faunistic elements represents one of the challenges of the western Mediterranean protected areas following European Union directives (Natura 2000, Habitats Directive, Council Directive 92/43/EEC).

Even though numerous studies have been concerned with the assessment of benthic assemblages in Mediterranean marine caves [1], including those in the Apulia region [11,14,24–30], large stretches of regional coast, although particularly rich in marine cavities, are still unexplored. Further, the census of the sponge fauna in marine caves is characterized by non-homogeneity of sampling methods and efforts, limiting the possibilities of exhaustive comparative analysis of this biocoenosis in the whole of the Mediterranean Sea [15]. The literature overview undertaken revealed problems during the data collection process, such as lack of spatial and ecological information, several caves having the same toponyms or single sites with multiple caves; lack of information about the cave type; taxonomic inconsistencies (e.g., synonymies and possible misidentifications); and lacking or limited data concerning particular areas or taxa [70]. In order to enforce protective measures, detailed information about the submarine caves on the Apulian coast is crucial, especially for those caves that are now outside of marine protected areas. Future research should fill the geographical and biological gap of knowledge on marine caves. Reconnaissance surveys and regular monitoring activities should be undertaken in order to collect continuous data series that will provide helpful indications on the health state of the cave communities, helping to the definition of its state of conservation and the identification of the most effective management strategies.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15050641/s1; Table S1: References list regarding studies focused on marine caves sponge fauna of the Apulian coast; Table S2: List of sponge species recorded in each cave with their respective references and distribution among habitats; Table S3: List of each cave with the article in which it is referenced.

Author Contributions: Conceptualization, C.L.; methodology, C.L. and G.G.; validation, G.C. and C.L.; formal analysis, G.G. and C.L.; data curation, G.G. and F.M.; writing—original draft preparation, C.L. and G.G.; writing—review and editing, G.G. and C.L.; supervision, C.L.; funding acquisition, C.L. and G.C. All authors have read and agreed to the published version of the manuscript.

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