

## Original Article

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### Author for correspondence:

Gabriele Costa, E-mail: [gabrielec1987@gmail.com](mailto:gabrielec1987@gmail.com)

# Sponge community variation along the Apulian coasts (Otranto Strait) over a pluri-decennial time span. Does water warming drive a sponge diversity increasing in the Mediterranean Sea?

Gabriele Costa<sup>1</sup> , Giorgio Bavestrello<sup>1</sup>, Valerio Micaroni<sup>2,3</sup>, Maurizio Pansini<sup>1</sup>, Francesca Strano<sup>2,4,5</sup> and Marco Bertolino<sup>1</sup>

<sup>1</sup>DiSTAV, Università degli Studi di Genova, Corso Europa 26, 16132 Genova, Italy; <sup>2</sup>Avamposto MARE, Università del Salento, Via Cristoforo Colombo, s.n.c., 73039 Tricase (Lecce), Italy; <sup>3</sup>School of Biological Sciences, Victoria University of Wellington, PO Box 600, 6140 Wellington, New Zealand; <sup>4</sup>Department of Life Sciences, University of Trieste, Via Licio Giorgieri, 5, 34127 Trieste, Italy and <sup>5</sup>Department of Biology and Evolution of Marine Organisms, Anton Dohrn Zoological Station, Villa Comunale, 80121 Naples, Italy

## Abstract

Climate change and heavy anthropic pressures are giving rise to important modifications in the rocky benthic communities of the Mediterranean Sea. In particular, sponge assemblages have been deeply affected due to the susceptibility of some species to dramatic phenomena such as mass mortalities or widespread variations in the abundance of other species. For this reason, long-term biodiversity monitoring of the sponge assemblages is important for understanding the direction of changes over time. We studied the sponge fauna living off Tricase Porto (Otranto Strait) and compared its composition with the results of a study conducted in the same area 50 years ago. The comparison indicated that the sponge diversity of this area has strongly increased in the last 50 years and a large number of the sponges recorded in the old survey are still present in the recent community. This evidence matches with other results obtained from different localities of the Mediterranean Sea indicating an increase of sponge diversity, possibly due to the present water warming. The description of two new Demosponge species, *Diplastrella boeroi* sp. nov. and *Spirastrella angulata* sp. nov., is also provided.

## Introduction

The Mediterranean Sea is considered a hotspot of biodiversity with a high rate of endemism (Bianchi & Morri, 2000; Coll *et al.*, 2010). In recent decades climate change and heavy anthropic pressures are giving rise to important modifications in the rocky benthic biocoenoses of this semi-closed basin (Cerrano *et al.*, 2000; Lejeune *et al.*, 2010; Bianchi *et al.*, 2012; Di Camillo & Cerrano, 2015; Montefalcone *et al.*, 2018).

With almost 720 species (Pansini *et al.*, 2011; van Soest *et al.*, 2018), sponges are one of the most diversified group of hard bottom organisms. The effects of global changes on the Mediterranean sponge fauna were approached in several papers evidencing different trajectories of changes. In some studies sponges, mainly keratosas, were among the groups most affected by the mass mortality events observed in the Mediterranean Sea during the last decades (Gaino & Pronzato, 1991; Gaino *et al.*, 1992; Rizzello *et al.*, 1997; Pronzato, 1999; Cerrano *et al.*, 2000; Pronzato & Manconi, 2008; Garrabou *et al.*, 2009; Pronzato *et al.*, 2012). Other studies demonstrated that some species enhanced their covering during the present episode of global warming. In the Ligurian Sea it was stated that the encrusting red sponge *Crambe crambe* (Schmidt, 1862) strongly increased covering in correspondence to the disease affecting the common anthozoan *Parazoanthus axinellae* (Schmidt, 1862) (Cerrano *et al.*, 2006). In the same area a survey on a coralligenous vertical cliff, 25 years after a previous one, indicated that some species, such as *Axinella* spp. and the red encrusting sponges (*C. crambe* – *Spirastrella cunctatrix* Schmidt, 1868), strongly increased their abundance while massive species such as *Petrosia* (*Petrosia*) *ficiformis* (Poiret, 1789) and *Chondrosia reniformis* Nardo, 1847 reduced their covering (Bertolino *et al.*, 2016). More recently an increase in sponge diversity was recorded in two Ligurian marine semi-submerged caves surveyed again 50 years after the first study (Costa *et al.*, 2018). It thus is important to collect data about the trajectory of the change of different sponge communities from other regions of the Mediterranean Sea.

The coast of the Salento Peninsula (Apulia, south-east Italy) is characterized by karst cliffs rich in semi-submerged marine caves of environmental importance as emphasized by Sarà (1974) and more recently by Belmonte *et al.* (1999) and Bussotti *et al.* (2002, 2006). A large area of coralligenous outcrops characterizes the continental shelf in front of this stretch of coast (Bracchi *et al.*, 2015, 2017). This region, that accounts for more than 4% of the total Mediterranean sponge fauna (Sarà, 1960, 1969; Pulitzer-Finali, 1983; Corriero *et al.*, 2004; Longo *et al.*, 2015, 2017) was thoroughly surveyed in the period 1967–70 by Pulitzer-Finali



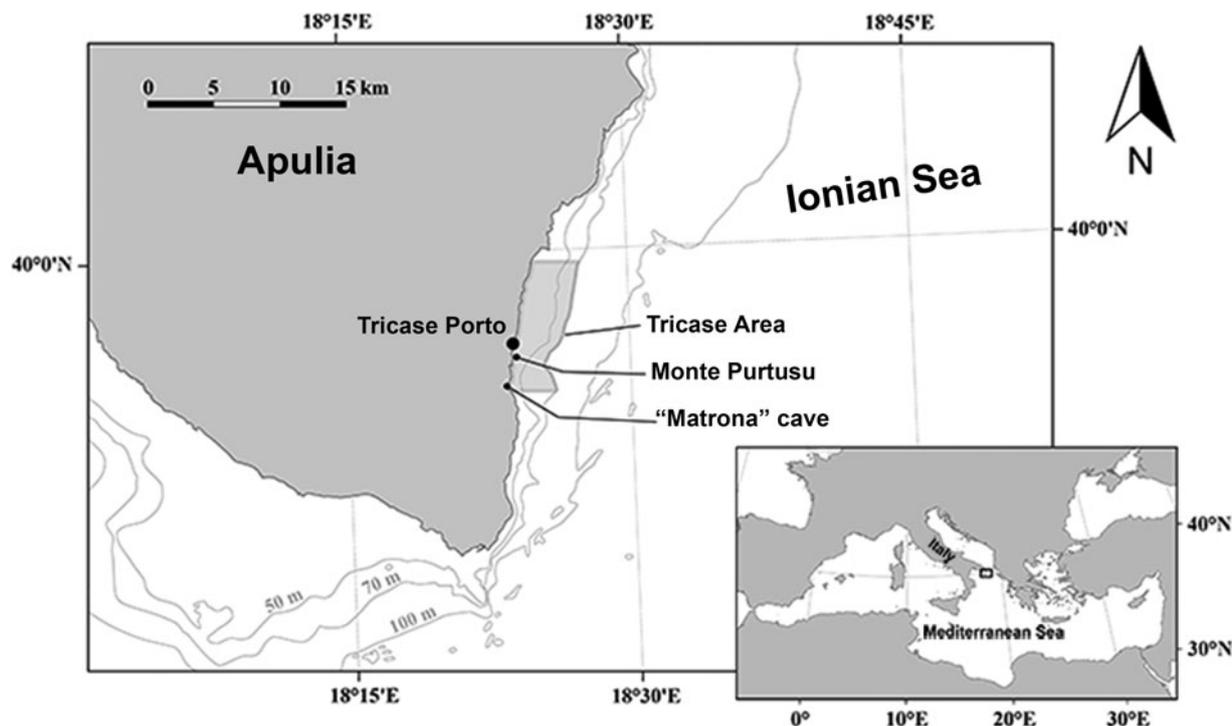


Fig. 1. Studied area in front of Tricase Porto (Otranto Canal - Ionian Sea).

(1983), particularly in the area of Tricase Porto (Otranto Strait). The rich Pulitzer-Finali reference collection (preserved at DiSTAV) of sponges offers a unique possibility to compare the present sponge fauna with that present in the same zone about 50 years ago, presumably before the onset of global warming.

The aim of this work is therefore the characterization of the sponge fauna living off Tricase Porto (Otranto Strait) and the comparison of the actual sponge fauna (2017) with that studied in the same area about 50 years ago. Special attention has been dedicated to the description of two new species recorded during the present survey.

## Materials and methods

The study area is located off Tricase Porto, just south of the narrowest point of the Otranto Strait (Figure 1). The samples were collected between June and August 2017. The sampling methods were similar to those used by Pulitzer-Finali (1983) in his faunistic collections conducted between 1967 and 1970. The focus was on coralligenous, semi-submerged caves, rocky substrate down to 40 m depth by scuba diving and deep waters to 60 m depth by trammel net and a dredge to collect coralligenous fragments.

For sampling we used the same techniques as Pulitzer-Finali (scuba diving and trammel), moreover we collected blocks of coralligenous formation by diving using hammer and chisel and we analysed them in the lab through the method described by Bertolino *et al.* (2014). Sponge samples were dried or preserved in 95% ethanol and processed by standard methods (Rützler, 1978). Taxonomic decisions are in agreement with the Systema Porifera (Hooper & van Soest, 2002), the Demosponge revision of Morrow & Cárdenas (2015) and the World Porifera Database (WPD) (van Soest *et al.*, 2018). For the two new species length and width of at least 30 spicules per type were measured. Minimum, mean (in parentheses) and maximum values of spicule dimensions are reported. Dissociated spicules and dried tissues were transferred onto stubs, sputter coated with gold and observed by a scanning electron microscope (SEM). The type

material of new species was deposited in the Museo Civico di Storia Naturale 'G. Doria' of Genova (MSNG). The type material of re-described species was deposited in the Department for Earth, Environment and Life Sciences (DiSTAV-University of Genoa).

The identified species were grouped according to their prevailing growth pattern, i.e. Massive/Erected (ME), Encrusting (En), Cavity dwelling (Cd) and Boring (Br).

## Results

During the 2017 survey, a total of 110 sponge species (including two new species (Figures 2–3)) were recorded belonging to three classes: Calcarea (2), Homoscleromorpha (7) and Demospongiae (101) (Table 1). Twenty-five species are new findings for the Ionian Sea (Table 1; Table S1). *Oceanapia perforata* (Sarà, 1960) and *Plakina reducta* (Pulitzer-Finali, 1983) have been recorded for the second time after their original descriptions. Two species are new for science and are here described together with a detailed description of *P. (S.) pulitzeri* and *P. (S.) vansoesti* which cannot be distinguished according to their external morphology (Figures 4–6). Moreover, several specimens of *Aplysina* sp. recently recorded from a semi-submerged cave on the Ligurian coast (Costa *et al.*, 2018) were recorded (Table 1). This species, living in the intertidal level, is composed of small cushion-shaped sponges, often connected by a net of stolons. The species is probably new but a genetic analysis is necessary for a definitive determination.

### SYSTEMATICS

Class DEMOSPONGIAE Sollas, 1885  
 Subclass HETEROSCLEROMORPHA Cárdenas, Pérez & Boury-Esnault (2012)  
 Order CLIONAIDA Morrow & Cárdenas, (2015)  
 Family SPIRASTRELLIDAE Ridley & Dendy, 1886  
 Genus *Diplastrella* Topsent, 1918

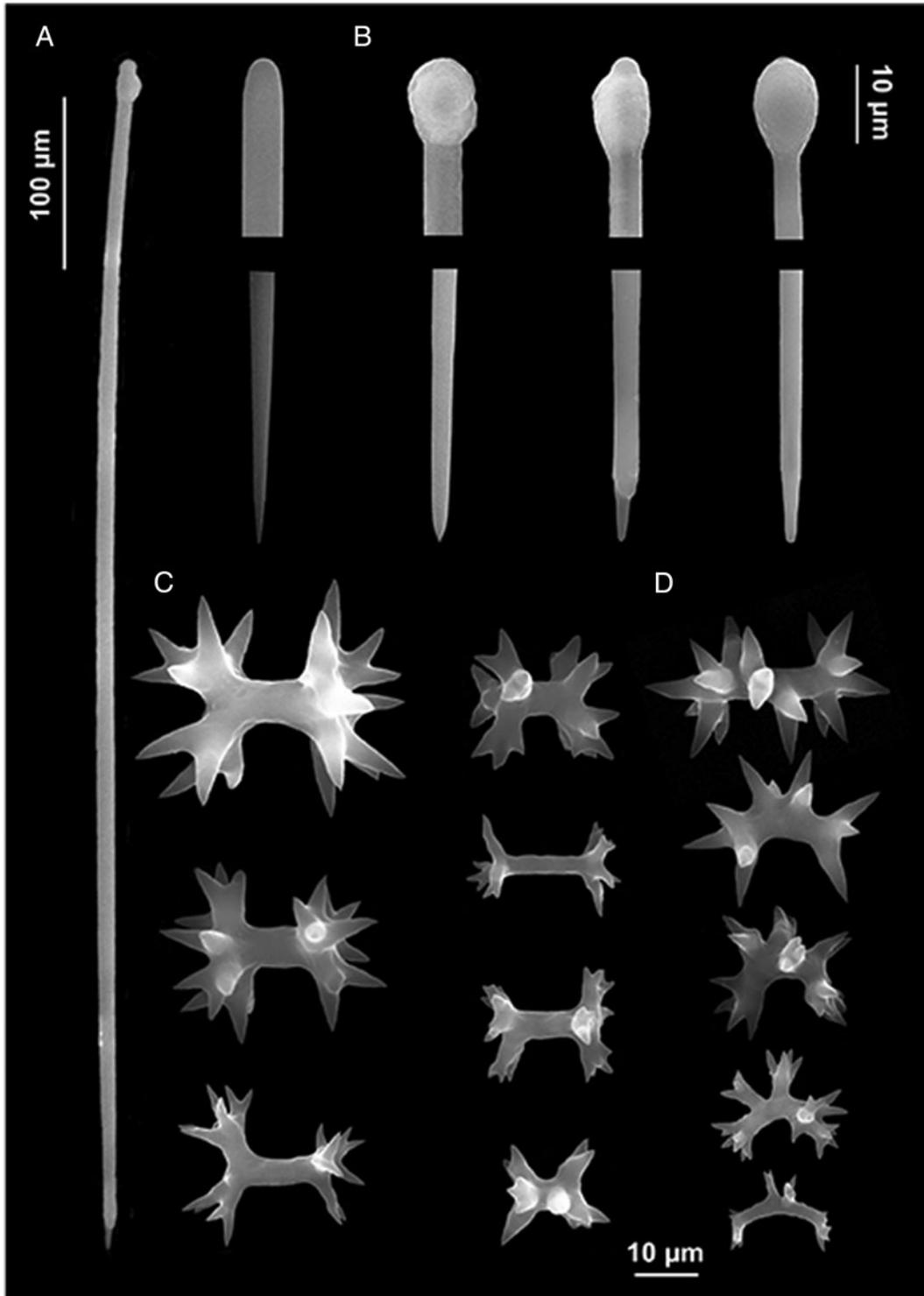


Fig. 2. *Diplastrella boeroi* sp. nov. (A) Long style; (B) style heads and tips; (C) diplasters to amphiasters; (D) spirasters.

*Diplastrella boeroi* Bertolino, Costa & Pansini, sp. nov.  
(Figure 2)

**Type material**

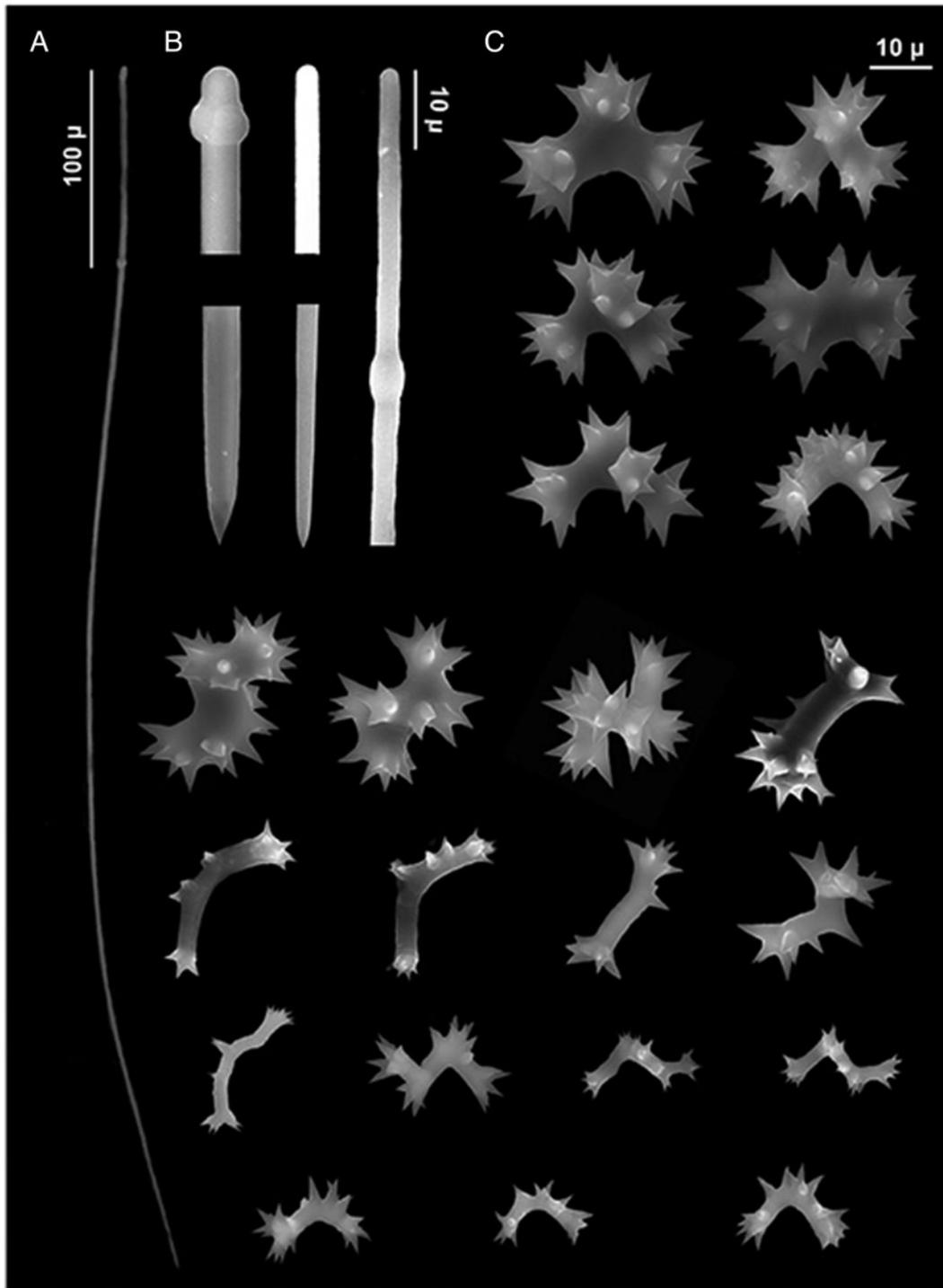
Holotype: (Specimens and slides) Tr.BL1\_48 (MSNG 60884), Ionian Sea, Tricase Porto, (Otranto Strait) 39°55'32.1"N 18° 24'00.7"E, depth 20 m, on a coralligenous concretion, 10.6.2017. Paratype: Tr.BL2\_39. Adriatic Sea, Torre Guaceto, 40° 42'57.51"N 17°48'12.61"E.

Other examined material: (Specimens and slides) Tr.BL1\_F15\_3A\_351; Tr.BL1\_F9B\_273; Tr.BL2\_39; Ionian Sea,

Tricase Porto, (Otranto Strait) 39°55'32.1"N 18°24'00.7"E, depth 20 m, on a coralligenous concretion, 10.6.2017. TG.BL1\_42; TG.BL1\_F10A\_14; Adriatic Sea, Torre Guaceto, 40° 43'00.61"N 17°48'34.50"E, depth 24 m, on a coralligenous concretion, 12.6.2017.

**Description**

The specimens are small (about 2 cm in length) and thin (1–3 mm), encrusting on coralligenous concretions. The surface is slightly hispid. The colour in life is red and fades to orange



**Fig. 3.** *Spirastrella angulata* sp. nov. (A) Long style; (B) style heads and tips; (C) spirasters.

after alcohol preservation. Live specimens are soft and show small elevated oscula.

**Skeleton.** Typical spirastrellidae structure consists of a base layer of spongin and microscleres. The tylostyles are erect, arranged in bouquets, with the heads embedded in the basal spongin layer. Some of them protrude through the sponge surface producing its hispidation. The ectosomal crust is mainly formed by diplasters.

**Spicules.** Megascleres: styles to tylostyles, straight or slightly curved, with circular or oval heads characterized by irregular or

corrugate surface. Tips may be stepped, blunt, hastate and acerate (Figure 2A, B). They measure 250 (350) 450 × 2.5 (6.25) 10 µm. Microscleres: most spicules are diplasters with a smooth shaft and regular or sometimes irregular whirls of spines, 3.5 (15.5) 27.5 × 1 (3) 5 µm (Figure 2C). Spines are often bifid. Other microscleres are spirasters that sometimes show bouquets of spines on the shaft, 9 (17) 25 × 2.5 (5) 7.5 µm (Figure 2D) (Table 2).

#### **Etymology**

The new species is named after Prof. Ferdinando Boero in recognition of his relevant contribution to biodiversity of the Salento coasts.

**Table 1.** List of sponge species collected at Tricase Porto sampled in the two periods with indication of their habit and type of habitat and the new finding for the Ionian Sea (\*)

Species	Growth habit	Coralligenous		Semi-submerged caves		Rocky substrate up to 40 m depth		Deep waters to 60 m depth	
		1967/1970	2017	1967/1970	2017	1967/1970	2017	1967/1970	2017
<i>Clathrina clathrus</i> (Schmidt, 1864)	ME						+		
<i>Sycon raphanus</i> Schmidt, 1862	ME								+
<i>Agelas oroides</i> (Schmidt, 1864)	ME	+	+			+	+		
<i>Hymerhabdia oxytrunca</i> Topsent, 1904 *	Ec		+						
<i>Prosuberites longispinus</i> Topsent, 1893	Ec	+	+						
<i>Axinella cannabina</i> (Esper, 1794)	ME							+	+
<i>Axinella damicornis</i> (Esper, 1794)	ME	+	+			+	+		
<i>Axinella rugosa</i> (Bowerbank, 1866)	ME	+							
<i>Axinella verrucosa</i> (Esper, 1794)	ME	+	+			+	+		
<i>Axinella polypoides</i> Schmidt, 1862	ME								
<i>Didiscus stylifer</i> Tsurumal, 1969	Ec	+	+						
<i>Eurypon cinctum</i> Sarà, 1960 *	Ec		+						
<i>Eurypon clavatum</i> (Bowerbank, 1866)	Ec		+						
<i>Eurypon coronula</i> (Bowerbank, 1874) *	Ec		+						
<i>Eurypon gracilis</i> Bertolino, Pansini & Calcinaï, 2013	Ec		+						
<i>Eurypon major</i> Sarà & Siribelli, 1960	Ec		+						
<i>Eurypon obtusum</i> Vacelet, 1969 *	Ec		+						
<i>Eurypon topsenti</i> Pulitzer-Finali, 1983	Ec					+			
<i>Eurypon viride</i> (Topsent, 1889)	Ec		+						
<i>Raspaciona aculeata</i> (Johnston, 1842)	Ec	+	+						
<i>Raspailia (Raspailia) viminalis</i> Schmidt, 1862 *	ME								+
<i>Halicnemia geniculata</i> Sarà, 1958 *	ME		+						
<i>Rhabderemia gallica</i> van Soest & Hooper, 1993 *	Ec		+						
<i>Rhabderemia minutula</i> (Carter, 1876)	CD		+						
<i>Bubaris carcis</i> Vacelet, 1969	Ec		+						
<i>Bubaris vermiculata</i> (Bowerbank, 1866)	Ec	+	+						
<i>Monocrepidium vermiculatum</i> Topsent, 1898 *	Ec		+						
<i>Rhabdobaris implicata</i> Pulitzer-Finali, (1983) *	ME		+						
<i>Desmanthus incrustans</i> (Topsent, 1889)	Ec		+						
<i>Acanthella acuta</i> Schmidt, 1862	ME	+				+	+		
<i>Dictyonella incisa</i> (Schmidt, 1880)	ME	+	+			+	+		
<i>Dictyonella obtusa</i> (Schmidt, 1862)	ME						+		
<i>Dictyonella</i> sp.	ME		+						
<i>Cliona amplicavata</i> Rützler, 1974 *	Br		+						
<i>Cliona burtoni</i> Topsent, 1932 *	Br		+						
<i>Cliona celata</i> Grant, 1826	Br						+		
<i>Cliona schmidtii</i> (Ridley, 1881)	Br	+	+			+	+		
<i>Cliona viridis</i> (Schmidt, 1862)	Br		+						
<i>Cliothosa hancocki</i> (Topsent, 1888)	Br		+						

(Continued)

**Table 1.** (Continued.)

Species	Growth habit	Coralligenous		Semi-submerged caves		Rocky substrate up to 40 m depth		Deep waters to 60 m depth	
		1967/1970	2017	1967/1970	2017	1967/1970	2017	1967/1970	2017
<i>Spiroxya heteroclita</i> Topsent, 1896	Br		+						
<i>Spiroxya sarai</i> (Melone, 1965)	Br		+						
<i>Diplastrella bistellata</i> (Schmidt, 1862)	Ec	+	+						
<i>Diplastrella boeroi</i> Bertolino, Costa & Pansini sp. nov.	Ec		+						
<i>Spirastrella cunctatrix</i> Schmidt, 1868	Ec	+	+						
<i>Spirastrella angulata</i> Bertolino, Costa & Pansini sp. nov.	Ec		+						
<i>Haliclona (Gellius) angulata</i> (Bowerbank, 1866)	CD			+					
<i>Haliclona (Gellius) sp.</i>	Ec					+			
<i>Haliclona (Halichocona) fulva</i> (Topsent, 1893)	Ec					+			
<i>Haliclona (Reniera) cratera</i> (Schmidt, 1862)	ME					+			
<i>Haliclona (Reniera) mediterranea</i> Griessinger, 1971	ME				+				
<i>Haliclona (Rhizoniera) sarai</i> (Pulitzer-Finali, 1969)	ME				+				
<i>Haliclona (Soestella) mucosa</i> (Griessinger, 1971) *	ME				+				
<i>Haliclona (Soestella) valliculata</i> (Griessinger, 1971) *	Ec				+				
<i>Gelliodes fibulata</i> (Carter, 1881) *	ME							+	
<i>Petrosia (Petrosia) clavata</i> (Esper, 1794)	ME		+						
<i>Petrosia (Petrosia) ficiformis</i> (Poiret, 1789)	ME	+	+	+	+	+	+		
<i>Petrosia (Strongylophora) pulitzeri</i> Pansini, (1996) *	ME				+				
<i>Petrosia (Strongylophora) vansoesti</i> Boury-Esnault <i>et al.</i> (1994) *	ME				+				
<i>Oceanapia perforata</i> Sarà, (1960) *	ME				+				
<i>Lissodendoryx (Anomodoryx) cavernosa</i> (Topsent, 1892)	CD		+						
<i>Crambe crambe</i> (Schmidt, 1862)	Ec						+		
<i>Crella sp.</i>	Ec		+						
<i>Ulosa stuposa</i> (Esper, 1794)	ME				+				
<i>Hamigera hamigera</i> (Schmidt, 1862)	Ec						+		
<i>Hemimycale columella</i> (Bowerbank, 1874)	Ec					+	+		
<i>Hymedesmia (Hymedesmia) paupertas</i> (Bowerbank, 1866) *	Ec					+			
<i>Phorbas dives</i> (Topsent, 1891)	Ec		+						
<i>Phorbas fictitius</i> (Bowerbank, 1866)	Ec		+						
<i>Phorbas tenacior</i> (Topsent, 1925)	Ec	+	+	+					
<i>Clathria (Clathria) coralloides</i> (Scopoli, 1772)	ME								+
<i>Clathria (Clathria) toxistricta</i> Topsent, 1925	Ec								+
	Ec							+	

(Continued)

Table 1. (Continued.)

Species	Growth habit	Coralligenous		Semi-submerged caves		Rocky substrate up to 40 m depth		Deep waters to 60 m depth	
		1967/1970	2017	1967/1970	2017	1967/1970	2017	1967/1970	2017
<i>Clathria (Microcionia) toxitenus</i> Topsent, 1925									
<i>Clathria (Clathria) toxivaria</i> (Sarà, 1959)	Ec		+						
<i>Mycale (Mycale) lingua</i> (Bowerbank, 1866)	Ec		+						
<i>Mycale (Mycale) massa</i> (Schmidt, 1862)	ME		+						
<i>Axinyssa aurantiaca</i> (Schmidt, 1864)	ME		+						
<i>Halichondria (Halichondria) cf. panicea</i> (Pallas, 1766)	Ec		+						
<i>Halichondria (Halichondria) contorta</i> (Sarà, 1961) *	ME				+				
<i>Spongosorites intricatus</i> (Topsent, 1892)	CD		+						
<i>Aaptos aaptos</i> (Schmidt, 1864)	ME					+	+		
<i>Protosuberites epiphytum</i> (Lamarck, 1815)	Ec	+	+						
<i>Terpios gelatinosus</i> (Bowerbank, 1866)	Ec		+				+		
<i>Tethya aurantium</i> (Pallas, 1766)	ME		+						
<i>Tethya citrina</i> Sarà & Melone, 1965	ME		+						
<i>Timea stellata</i> (Bowerbank, 1866)	CD		+						
<i>Timea unistellata</i> (Topsent, 1892)	CD		+						
<i>Ancorina cerebrum</i> Schmidt, 1862 *	CD		+						
<i>Dercitus (Stoebea) plicatus</i> (Schmidt, 1868)	CD	+	+						
<i>Jaspis incrustans</i> (Topsent, 1890)	CD		+						
<i>Jaspis johnstonii</i> (Schmidt, 1862)	CD	+	+						
<i>Stelletta grubii</i> Schmidt, 1862	CD		+						
<i>Stelletta mediterranea</i> (Topsent, 1893) *	CD		+						
<i>Stelletta stellata</i> Topsent, 1893	CD		+						
<i>Calthropella (Corticellopsis) stelligera</i> (Schmidt, 1868) *	CD						+		
<i>Calthropella</i> sp.	CD		+						
<i>Erylus discophorus</i> (Schmidt, 1862)	CD	+	+						
<i>Penares helleri</i> (Schmidt, 1864)	CD	+	+						
<i>Penares euastrum</i> (Schmidt, 1868)	CD	+	+						
<i>Geodia cydonium</i> (Linnaeus, 1767)	CD		+						
<i>Geodia conchilega</i> Schmidt, 1862	ME	+							
<i>Pachastrella monilifera</i> Schmidt, 1868	CD	+	+						
<i>Triptolemma simplex</i> (Sarà, 1959)	CD		+						
<i>Poecillastra compressa</i> (Bowerbank, 1866)	CD		+						
<i>Tetilla</i> sp.	ME		+						
<i>Alectona millari</i> Carter, 1879	Br		+						
<i>Delectona madreporica</i> Bavestrello, Calcinai, Cerrano & Sarà, 1997 *	Br		+						
<i>Chondrilla nucula</i> Schmidt, 1862	ME	+	+			+	+		
<i>Chondrosia reniformis</i> Nardo, 1847	ME	+	+				+		
<i>Aplysina aerophoba</i> (Nardo, 1833)	ME	+	+						

(Continued)

**Table 1.** (Continued.)

Species	Growth habit	Coralligenous		Semi-submerged caves		Rocky substrate up to 40 m depth		Deep waters to 60 m depth	
		1967/1970	2017	1967/1970	2017	1967/1970	2017	1967/1970	2017
<i>Aplysina cavernicola</i> Vacelet (1959)	ME								+
<i>Aplysina</i> sp.	Ec				+				
<i>Hexadella racovitzai</i> Topsent, 1896	Ec						+		
<i>Dysidea avara</i> (Schmidt, 1862)	ME		+						
<i>Dysidea fragilis</i> (Montagu, 1814)	ME		+						
<i>Dysidea incrustans</i> (Schmidt, 1862)	Ec	+							
<i>Ircinia variabilis</i> (Schmidt, 1862)	ME				+				
<i>Sarcotragus foetidus</i> Schmidt, 1862	ME						+		
<i>Sarcotragus spinosulus</i> Schmidt, 1862	ME					+	+		
<i>Spongia</i> ( <i>Spongia</i> ) <i>virgultosa</i> (Schmidt, 1868)	CD	+							
<i>Fasciospongia cavernosa</i> (Schmidt, 1862)	CD	+	+	+	+	+	+		
<i>Scalariispongia scalaris</i> (Schmidt, 1862)	ME						+		
<i>Oscarella</i> cf. <i>tuberculata</i> (Schmidt, 1868) *	ME						+		
<i>Oscarella</i> sp.	ME						+		
<i>Corticium candelabrum</i> Schmidt, 1862	ME	+	+						
<i>Plakina bowerbanki</i> (Sarà, 1960)	Ec						+		
<i>Plakina dilopha</i> Schulze, 1880 *	Ec		+						
<i>Plakina reducta</i> (Pulitzer-Finali, 1983)	Ec	+	+						
<i>Plakina trilopha</i> Schulze, 1880	Ec	+	+						
<i>Plakortis simplex</i> Schulze, 1880	Ec		+						

### Habitat

Specimens recorded at 20–25 m depth encrusting the surface of coralligenous concretions and their superficial cavities.

### Remarks

The species is assigned to the genus *Diplastrella* Topsent, 1918 according to the skeletal arrangement and the presence of diplasters. Seven species of the genus are known and two of them, *D. bistellata* (Schmidt, 1862) and *D. ornata* Rützler & Sarà, 1962, are recorded in the Mediterranean Sea. Both differ from the new species. *D. bistellata* has bigger microscleres (both spirasters and diplasters) than the new species: 45 µm in length vs 27.5 µm. *D. ornata* has large diplasters (56–76 µm) with characteristic multi-branched rays. The medium-sized ones may rarely assume the shape of thick spirasters but they do not represent a separate category of microscleres. In *D. gardineri* Topsent, 1918, a species with tropical distribution (Red Sea; Maldives; Zanzibar; Madagascar), the spirasters, 45 µm long, are much more numerous than the diplasters. *D. megastellata* Hechtel, 1965 and *D. spiniglobata* (Carter, 1879) have small asters and spheraster. *D. spirastrelloides* Van Soest, 2017 from the North Atlantic has spirasters twice as large as the new species. *D. yongmeoriensis* Kim & Sim, 2009 from the East China Sea has long and very thin spirasters similar to those found in the genus *Cliona*.

Genus *Spirastrella* Schmidt, 1868

*Spirastrella angulata* Bertolino, Costa & Pansini, sp. nov.  
(Figure 3)

### Type material

Holotype. (Specimens and slides) Tr.BL1\_37, (MSNG 60885), Tricase Porto, 39°55'32.1"N 18°24'00.7"E, depth 20 m, on a coralligenous concretion, 10.6.2017.

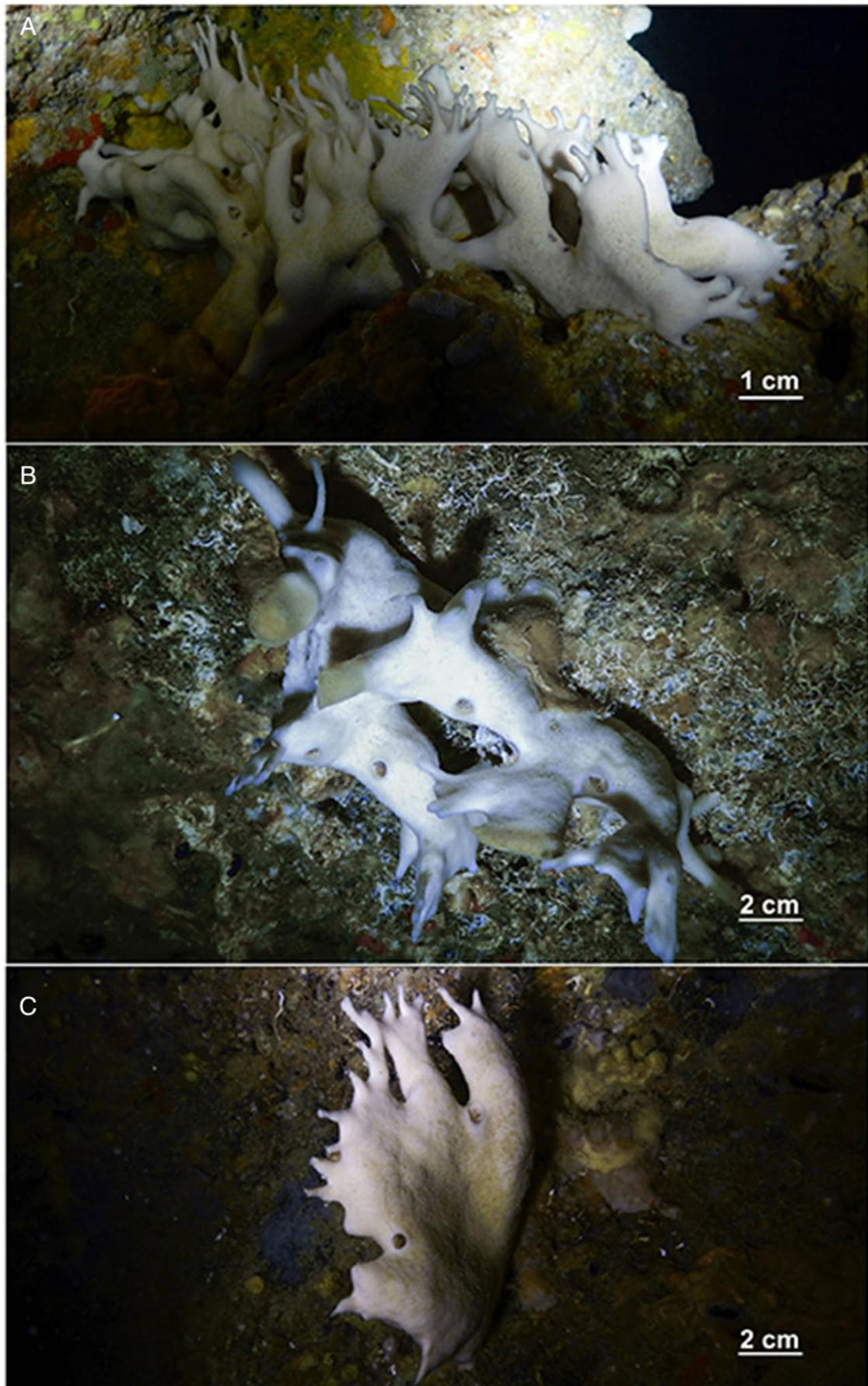
Paratypes: (Specimens and slides) Tr.BL1\_F15\_1A\_342; Tr.BL1\_F18\_3A\_441, Tricase Porto, depth 20 m, on a coralligenous concretion, 10.6.2017, dry preserved.

### Description

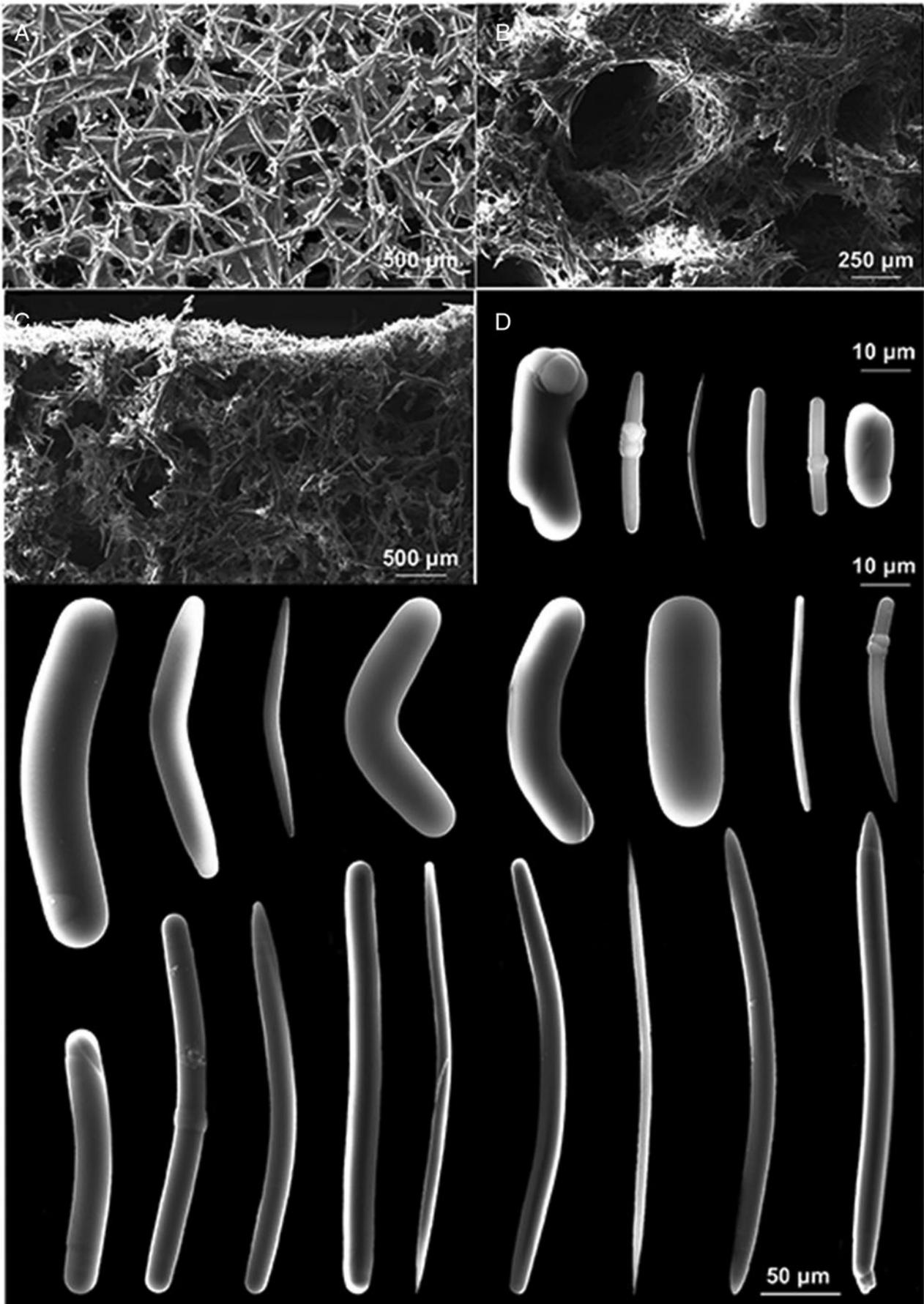
The three specimens were thinly encrusting (1–2 mm thick) on a coralligenous concretion, covering small surfaces (1–2 cm<sup>2</sup>). The colour in life is red and becomes orange in alcohol. The surface is slightly hispid. Live specimens are soft and show small elevated oscula.

**Skeleton.** The skeleton is typical of the genus *Spirastrella* with dense layers of spirasters in both ectosomal and basal choanosomal regions and bundles of a few tylostyles with the points directed outward. The smaller spirasters are concentrated at the surface, the larger ones close to the substrate, and many microscleres of both types are strewn in between. Tylostyles heads are embedded in the basal spongin layer. Some tylostyles protruding from the sponge surface cause a faint hispidation.

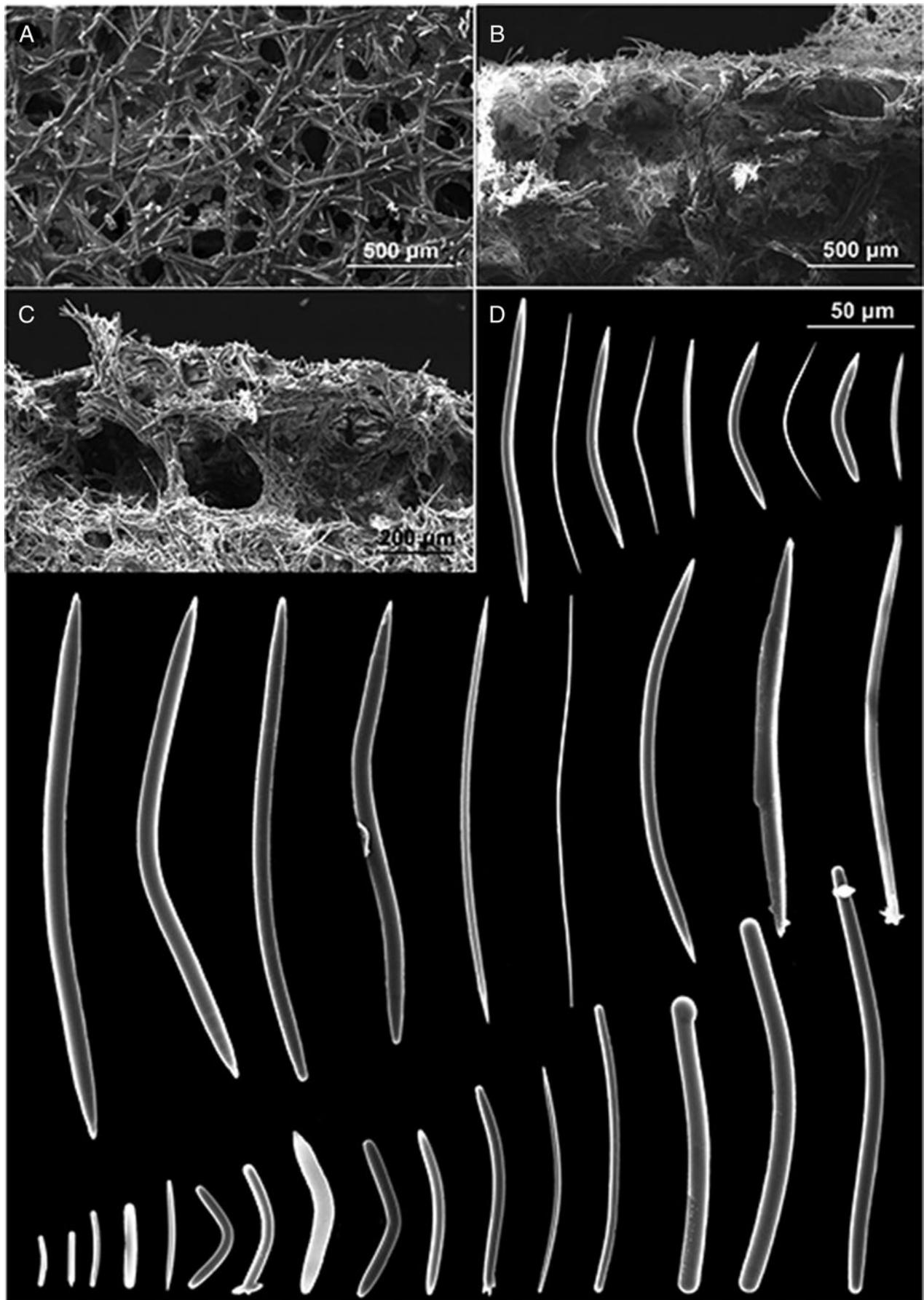
**Spicules.** Megascleres: Tylostyles to sub-tylostyles to styles, straight or curved and sometimes sinuous. Heads round to oval (sometimes showing malformations) and shafts with sharpened points (Figure 3A, B). They measure 480 (690) 900 × 5 (5.5)



**Fig. 4.** (A) *P. (Strongylophora) pulitzeri*; (B) *P. (Strongylophora) vansoesti*; (C) *P. ficiformis* with similar habit in the 'Matrona' cave at Tricase Porto.



**Fig. 5.** *P. (Strongylophora) pulitzeri*. (A) Ectosomal skeleton; (B) detail of a canal in the choanosomal skeleton; (C) choanosomal skeleton; (D) oxeas, strongyles and styles.



**Fig. 6.** *P. (Strongylophora) vansoesti*. (A) Ectosomal skeleton; (B) choanosomal skeleton; (C) detail of the choanosomal skeleton; (D) oxeas, strongyles and styles.

**Table 2.** Spicule measures of specimens of *Diplastrella boeroi* sp. nov. and *Spirastrella angulata* sp. nov.

<i>Diplastrella boeroi</i> sp. nov.	Tylostyles ( $\mu\text{m}$ )	Diplasters ( $\mu\text{m}$ )	Spirasters ( $\mu\text{m}$ )
Tr. Bl1_48	250(312.5) 375 $\times$ 2.5(5) 7.5	4(13.5) 27.5 $\times$ 2.5 (3.75)5	10(15)20 $\times$ 5(6.25)7.5
TR. Bl1_F15_3A_351	250(430) 610 $\times$ 2.5 (21.5)2.5	10(16.25) 25 $\times$ 2(3.75) 5	10(16.5) 23 $\times$ 5(6.25) 7.5
TR. Bl1_F9B_273	287.5 (313.7) 340 $\times$ 4.5(6) 7.5	3.5(14.6) 25 $\times$ 2(3.75) 5	12.5(16.25) 20 $\times$ 2.5 (3.75)5
TR. Bl2_39	287.5 (313.7) 340 $\times$ 4.5(6) 7.5	3.5(14.6) 25 $\times$ 2(3.75) 5	12.5(16.25) 20 $\times$ 2.5 (3.75)5
TG. Bl1_42	310(370) 430 $\times$ 5(7.5) 10	5(14.4)25 $\times$ 1(3.4)5	9(15.5)22 $\times$ 5(6.25)7.5
TG. Bl1_F10A_14	330(390) 450 $\times$ 5(7.5) 10	5(15)27.5 $\times$ 1(3.4)5	10(17.5) 25 $\times$ 5(6.25) 7.5
<i>Spirastrella angulata</i> sp. nov.	Tylostyles ( $\mu\text{m}$ )	Spirasters ( $\mu\text{m}$ )	
Tr. Bl1_37	500(674) 800 $\times$ 5(5.5) 7.5	7.5(18.5) 25 $\times$ 2.5 (7.5)17.5	
Tr.BL1_F15_1A_342	500(694) 900 $\times$ 5(5.5) 7.5	7.5(18.5) 25 $\times$ 2.5 (7.5)17.5	
Tr.BL1_F18_3A_441	480(660) 750 $\times$ 5(5.5) 7.5	7.5(18.5) 25 $\times$ 2.5 (7.5)17.5	

7.5  $\mu\text{m}$ . Microscleres: all the microscleres are spirasters, 7.5 (18.5) 25  $\times$  2.5 (7.5) 17.5  $\mu\text{m}$ . The spiraster axis is generally twisted, angulate and sometimes curved and often once or twice bent (Figure 3C). The conical spines, always sharp, may be more or less evenly distributed or confined to the spicule extremities. A reduction in the number of spines may be observed in some of the spicules with a thin axis (Figure 3C) (Table 2).

#### Etymology

The species is named after the peculiar shape of the small angulate spirasters.

#### Habitat

Specimens were recorded at 20–25 m depth encrusting coralligenous concretions characterized by a pillar structure.

#### Remarks

Among the 17 known species of *Spirastrella*, only *S. cunctatrix* Schmidt, 1868 is until now recorded in the Mediterranean Sea and the Eastern Atlantic. *S. cunctatrix* differs from the new species for the morphology and the size of spicules. The tylostyles of *S. angulata* sp. nov. are remarkably longer than those of *S. cunctatrix*, whereas the spirasters of *S. cunctatrix* (28–50  $\mu\text{m}$  in length) may be twice as big and different in shape from those of the new species. The two species present in the Red Sea: *S. decumbens* Ridley, 1884 and *S. pachyspira* Lévi, 1958, differ from *S. angulata* sp. nov. in the shape and size of spicules. *S. decumbens* has shorter tylostyles, *S. pachyspira* has very large spirasters up to 110  $\mu\text{m}$  in

length. The other known *Spirastrella* species have different characters in spicular complement (shape and measures) and live in geographically distant areas such as the Eastern Atlantic and the Caribbean, the Indian Ocean, the coast of Japan and a few Pacific areas.

Order HAPLOSCLERIDA Topsent, 1928

Family PETROSIIDAE van Soest, 1980

Genus *Petrosia* Vosmaer, 1885

Subgenus *Petrosia* (*Strongylophora*) Dendy, 1905

*Petrosia* (*Strongylophora*) *pulitzeri* Pansini, 1996  
(Figures 4A–5)

#### Type material

(Specimens and slides) TRP64, Tricase Porto, Ionian Sea, semi-submerged ‘Matrona’ Cave (39°54′20.02″N 18°23′25.76″E), depth 2 m, 11.6.2017.

#### Description

Massive sponge with anastomosing horizontal irregular branches and with vertical irregular digitiform processes up to 1.5–2 cm high. Scattered round oscules are 1–5 mm wide. The surface is smooth with a cribose aspect due to the presence of ostia (0.2–0.3 mm) (Figure 4A). Consistency is hard and colour is white *in vivo* and in alcohol preserved specimens.

**Skeleton.** The ectosomal skeleton is a network of irregular triangular or quadrangular meshes with sides formed by single strongyles or oxeas. At the angular points (‘corners’) of the strongyle-tracts are groups of very short strongyles which form surface nodes that produce the granular-aspect of the surface (Figure 5A). Choanosomal skeleton is a very dense, compact sub-rectangular network with small meshes formed by stout spicular tracts of closely packed strongyles and free spicules (Figure 5B, C). Toward the surface there are stout multispicular tracts formed by radiating bundles of closely packed strongyles, without visible spongin.

**Spicules.** Megascleres: oxeas, measure 30 (152.4) 300  $\times$  2 (6.1) 20  $\mu\text{m}$ ; styles measure 30 (106.7) 375  $\times$  2.5 (12.5) 20  $\mu\text{m}$  and strongyles with intermediate forms, measure 50 (162.5) 300  $\times$  2.5 (9.7) 20  $\mu\text{m}$  (Figure 5D).

#### Geographical distribution

Tyrrhenian Sea (Gulf of Naples), Aegean Sea (Crete), coasts of Turkey (Marmara Sea) (Pansini, 1996).

*Petrosia* (*Strongylophora*) *vansoesti* Boury-Esnault, Pansini & Uriz (1994) (Figures 4B–6)

#### Type material

(Specimens and slides) TRP32, Tricase Porto, Ionian Sea, semi-submerged ‘Matrona’ Cave (39°54′20.02″N 18°23′25.76″E), depth 2 m, 11.6.2017.

#### Description

Massive sponge with external morphology similar to that of *P. (Strongylophora) pulitzeri* sampled by us (Figure 4B).

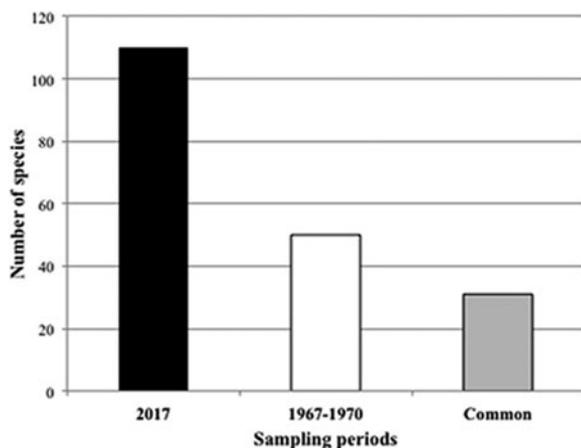
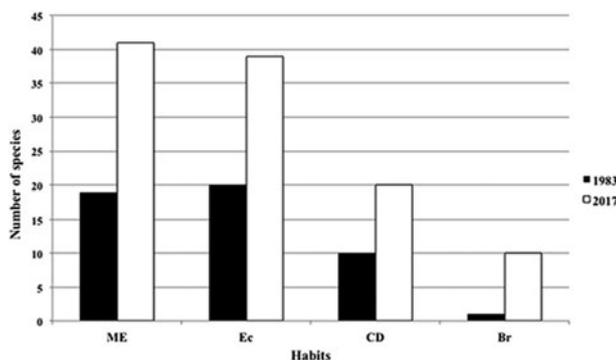
**Skeleton.** The ectosomal skeleton is a network of irregular triangular or quadrangular meshes with sides formed by single strongyles or oxeas (Figure 6A). At the angular points (‘corners’) of the strongyle-tracts are groups of very short strongyles which form surface nodes that produce the granular-aspect of the surface. Choanosomal skeleton very dense: compact sub-rectangular network of small meshes formed by stout tracts of closely packed strongyles and free spicules (Figure 6B, C). Toward the surface

**Table 3.** Morphological characters and ecology of *P. (Strongylophora) pulitzeri* Pansini, 1996 and *P. (Strongylophora) vansoesti* Boury-Esnault, Pansini & Uriz, 1994 specimens hitherto recorded in the Mediterranean Sea

Species	Shape	Colour	Surface	Consistency	Skeleton	Spicules ( $\mu\text{m}$ )	Habitat and depth
<i>P. pulitzeri</i> after the original description	Specimens: ML29 cushion-shaped CRT10 cylindrical CRT43 small incrustations Rather coarse, with rounded tubercles less than 1 mm high, or with series of low ridges arranged to form roundish meshes. Oscules are scattered, round, 1 – 2 mm wide and bordered by a low rim. Other minor vents (0.2 – 0.3 mm across) are scattered on the sponge surface.	White or yellowish	Smooth	Specimen: ML29 stony hard CRT10-CRT43 slightly softer	Ectosome as a felt-work of tangentially arranged oxeads (of different sizes), which do not form any reticulation, supported by the choanosomal spicule tracts. The choanosome is a dense reticulation of stout tracts of closely packed spicules, mostly strongyles of the bigger size, forming roundish meshes rather variable in size.	CRT10 Oxeads and strongyles with intermediate forms. (See <a href="#">Table 4</a> )	ML29 submerged cave, 15 m CRT10 submerged cave, 2 – 5 m CRT43 submerged cave, 0.5 – 1 m
<i>Petrosia (Strongylophora) vansoesti</i> after the original description	DR40-E10 DR111-48 Massive spherical An oscule 5 mm in diameter opens at the top of the sphere on a flattened area. The minor vents are grouped into small groups each corresponding to an inhaling canal.	Ochre after preservation	Smooth	Hard	Ectosomal skeleton is polygonal. Mesh of the network is 200 $\mu\text{m}$ wide on average and the bundles of the spicules constituting it, 30 – 35 $\mu\text{m}$ in diameter. This primary mesh is subdivided into smaller meshes by unispiculated lines. Choanosomal complex is also a network with an average mesh size of 340 $\mu\text{m}$ . Bundles of strongyles constituting these meshes have a diameter of 85 $\mu\text{m}$ . No visible spongin.	DR40-E10 DR111-48 Strongyles and oxeads. (See <a href="#">Table 4</a> )	Saharan upwelling within the outflow of Mediterranean seawater in the Atlantic, between 285 and 362 m.
<i>Petrosia (Strongylophora) vansoesti</i> after Voultziadou & Vafidis (2004)	Massive spherical It bears an oscule, having a diameter of 0.5 cm, in the middle of a depression, on its upper surface. Small ostia are arranged in groups around the body.	Light	Smooth	Hard	Ectosomal skeleton is made of a reticulation of spicules, while the choanosomal skeleton is characterized by thick spicule tracts, having a mean width of 200 $\mu\text{m}$ , forming meshes with a mean diameter of 500 $\mu\text{m}$ , obscured in some places by irregular masses of spicules.	Oxeads, strongyles and styles. (See <a href="#">Table 4</a> )	Cave wall at 20 m depth, Youra Island (Greece)
<i>Petrosia (Strongylophora) vansoesti</i> after Evcen & Çinar (2012)	ESFM-POR/2005-59,05.10.2005, K44 Undetermined	Undetermined	Undetermined	Undetermined	Ectosomal skeleton has a reticulation of spicules. The choanosomal skeleton has thick tracts, obscured by irregular masses of spicules in some places.	Oxeads and strongyles. (See <a href="#">Table 4</a> )	On rocks 0.1 – 3 m depth, southern Turkey coast

**Table 4.** Spicule measurements of specimens of *P. (Strongylophora) pulitzeri* and *P. (Strongylophora) vansoesti* recorded in the Mediterranean Sea

<i>Petrosia (Strongylophora) pulitzeri</i> Pansini, (1996)	Oxeas ( $\mu\text{m}$ )	Strongyles ( $\mu\text{m}$ )	Styles ( $\mu\text{m}$ )
Specimen CRT10 Pansini, (1996)	57.5(143.4)285 $\times$ 2.5(8.15)15	32.5(108.6)245 $\times$ 5(11)20	45(171)245 $\times$ 5(10.75)15
Specimen TRP64 present paper	30(152.4)300 $\times$ 2(6.1)20	30(106.7)375 $\times$ 2.5(12.5)20	50(162.5)300 $\times$ 2.5(9.7)20
<i>Petrosia (Strongylophora) vansoesti</i> Boury-Esnault, Pansini & Uriz (1994)	Oxeas ( $\mu\text{m}$ )	Strongyles ( $\mu\text{m}$ )	Styles ( $\mu\text{m}$ )
Specimen Boury-Esnault et al., 1994	54(90)140.4 $\times$ 2.7(4)5.4	21.6(128)337.5 $\times$ 8.1(12)21.6	–
Specimen Voultziadou & Vafidis (2004)	(Oxeas) 50(–)200 $\times$ 3(–)8 (Large oxeas) 200(–)320 $\times$ 20(–)32	200(–)320 $\times$ 20(–)32 (Small strongyles) 50(–)100 $\times$ 12(–)28	200(–)320 $\times$ 20(–)32
Specimen Evcen & Çinar (2012)	120(–)300 $\times$ 5(–)8	65(–)360 $\times$ 8(–)20	–
Specimen TRP32 present paper	42.5(164)242.5 $\times$ 1(5.25)12.5	50(162.14)212.5 $\times$ 5(8.6)12.5	140(190)235 $\times$ 5(8.21)12.5

**Fig. 7.** Number of sponge species recorded during the two sampling periods. The grey bar represents the species in common between the two sampling periods.**Fig. 8.** Number of sponge species recorded during the two sampling periods divided according to their habit. ME: massive habit, Ec: encrusting habit, CD: cavity dwelling habit, Br: boring habit.

there are stout multispicular longitudinal tracts formed by radiating bundles of single strongyles, closely packed, without visible spongin.

**Spicules.** Megascleres: oxeas, measure 42.5 (164) 242.5  $\times$  1 (5.25) 12.5  $\mu\text{m}$ , styles, measure 50 (162.14) 212.5  $\times$  5 (8.6) 12.5  $\mu\text{m}$  and strongyles with intermediate forms, measure 14 (190) 235  $\times$  5 (8.21) 12.5  $\mu\text{m}$  (Figure 6D).

### Geographic distribution

Saharan upwelling within the outflow of Mediterranean seawater in the Atlantic (Strait of Gibraltar), coast of Greece (Youra Island) and coast of Turkey.

### Remarks

In the Matrona Cave, three species of the genus *Petrosia* (*P. ficiformis*, *P. pulitzeri* and *P. vansoesti*) were recorded. The external morphology does not allow their specific separation (Figure 4). While the spicules of *P. ficiformis* are well known, the other two species were less studied. In Table 3 we have compared data about morphological characters and ecology of *P. (Strongylophora) pulitzeri* Pansini, 1996 and *P. (Strongylophora) vansoesti* Boury-Esnault, Pansini & Uriz, 1994 specimens hitherto recorded in the Mediterranean Sea and in Table 4 we have compared data about the spicules of our specimens with those reported by previous description. Study of the skeleton (Figure 5A–C) of *P. (Strongylophora) pulitzeri* confirms that this species can be attributed to the subgenus *Strongylophora* as suggested by Lévi & Lévi (1983), de Weerd & van Soest (1986) and Pansini (1996). *Petrosia (Strongylophora) pulitzeri* is known for the Gulf of Naples, the Island of Crete (Pansini, 1996) and the Marmara Sea (Topaloğlu, 2001). *Petrosia (Strongylophora) vansoesti* was described by Boury-Esnault et al. (1994) from the Saharan upwelling within the outflow of Mediterranean seawater in the Atlantic (Strait of Gibraltar) and later recorded on the coast of Greece (Youra Island) by Voultziadou & Vafidis (2004) and Turkey by Evcen & Cinar (2012).

### Discussion and conclusion

In recent decades, marine ecosystem composition and functioning, especially in the Mediterranean Sea, have headed toward deep modifications driven by climate variations. It is well known that the biology of marine organisms can be altered by climate changes due to both a higher frequency of short-term extreme events and long-term temperature increases (Lejeune et al., 2010).

Long-term biodiversity monitoring and observations are essential for understanding the changes over time of the marine benthic communities (Roberts, 2009; Boero et al., 2015). In this context, sponges, due to their high biodiversity and long persistence of their spicular remains, are a suitable group to check putative differences occurring over a number of temporal scales (Bertolino et al., 2016, 2017a, 2017b; Costa et al., 2018). Thanks to the data of Pulitzer-Finali (1983) recorded about 50 years before the present survey, a first comparative investigation of

the sponge assemblages present in four habitats of Tricase Porto coastal area was possible.

The number of sponge species recorded in the Tricase area was about twice that observed 50 years before in the same stretch of coast (Table 1 and Figure 7). Thirty-one species (62% of the species recorded in the period 1967–70) are shared by the two surveys (Figure 7).

The dramatic increase of the species recorded in the recent sampling is probably due to several factors. Firstly, during the recent survey we examined in detail two habitats, marine caves and deep cliffs (finding 13 and five species respectively), that were only sporadically visited by Pulitzer-Finali who found four species in each of them. Moreover, it is very likely that our survey could have been more accurate compared with that of Pulitzer-Finali which collected only discrete and large specimens. On the other hand, if we compare only the species recorded by Pulitzer-Finali in the two most species-rich habitats, the rocky cliffs and the coralligenous, we see that 64.7 and 75% of the species recorded in the period 1967–70 are present currently, indicating a significant resilience of the past communities.

Nevertheless the increase in the number of recorded species should not be considered only in relation to differences in the sampling accuracy. In the two more species-rich habitats, rocky cliffs and coralligenous, the number of species increased from 17 to 26 and from 36 to 77 respectively. This impressive increase was approximately the same in all the considered sponge growth forms (Figure 8).

Thibaut *et al.* (2005) had hypothesized that, under the recent seawater warming, the Mediterranean benthic communities experienced a strong decrease in biodiversity. Our data indicate that sponge communities do not confirm this assumption. Nevertheless, the strong increase of biodiversity recorded in the present survey may be partially biased by the more accurate sampling method (with coralligenous slices), but very likely indicates a real trend of the community. These data match well with previous evidence from other Mediterranean localities. For example, Costa *et al.* (2018) have recently shown that the number of sponge species present in semi-submerged caves of the Ligurian Sea surveyed 50 years ago is now almost doubled.

Certainly Porifera, and particularly the horny sponges, suffered many massive epidemic diseases that have brought entire populations of some species to the brink of extinction (Gaino & Pronzato, 1991; Rizzello *et al.*, 1997; Pronzato, 1999; Cerrano *et al.*, 2000; Pronzato & Manconi, 2008; Pronzato *et al.*, 2012; Di Camillo & Cerrano, 2015). Nevertheless, evidence coming from comparative studies at pluri-decennial scale, from several areas of the Mediterranean Sea, shows a clear increasing trend of sponge diversity in this period of water warming (Bianchi *et al.*, 2014; Bertolino *et al.*, 2016).

These hypotheses are in agreement with data on a millennial time span, obtained through the analysis of the spicular remains present in dated core samples of coralligenous concretions, indicating an increase of sponge diversity in correspondence with periods of increasing water temperature (Bertolino *et al.*, 2017b).

**Supplementary material.** The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315419000651>.

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**Ethical standards.** All applicable international, national and/or institutional guidelines for the care and use of animals were followed by the authors.

**Sampling and field studies.** All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities.

## References

- Belmonte G, Costantini A, Denitto F, Della Tommasa L, Miglietta MP, Onorato R, Poto M and Vetere M (1999) Indagine ecologica sulla Grotta sottomarina delle Corvine (Nardò, Lecce): dati preliminari. *Biologia Marina Mediterranea* 6, 343–346.
- Bertolino M, Calcinai B, Cattaneo-Vietti R, Cerrano C, Lafratta A, Pansini M, Pica D and Bavestrello G (2014) Stability of the sponge assemblage of Mediterranean coralligenous concretions along a millennial time span. *Marine Ecology* 35, 149–158. <https://doi.org/10.1111/maec.12063>.
- Bertolino M, Betti F, Bo M, Cattaneo-Vietti R, Pansini M, Romero J and Bavestrello G (2016) Changes and stability of a Mediterranean hard bottom benthic community over 25 years. *Journal of the Marine Biological Association of the United Kingdom* 96, 341–350. <https://doi.org/10.1017/S0025315415001186>.
- Bertolino M, Costa G, Carella M, Cattaneo-Vietti R, Cerrano C, Pansini M, Quarta G, Calcagnile L and Bavestrello G (2017a) The dynamics of a Mediterranean coralligenous sponge assemblage at decennial and millennial temporal scales. *PLoS ONE* 12. <https://doi.org/10.1371/journal.pone.0177945>.
- Bertolino M, Cattaneo-Vietti R, Costa G, Pansini M, Frascchetti S and Bavestrello G (2017b) Have climate changes driven the diversity of a Mediterranean coralligenous sponge assemblage on a millennial timescale? *Palaeogeography, Palaeoclimatology, Palaeoecology* 487, 355–363. <https://doi.org/10.1016/j.palaeo.2017.09.020>.
- Bianchi CN and Morri C (2000) Marine biodiversity of the Mediterranean Sea: situation, problems and prospects for future research. *Marine Pollution Bulletin* 40, 367–376. [https://doi.org/10.1016/S0025-326X\(00\)00027-8](https://doi.org/10.1016/S0025-326X(00)00027-8).
- Bianchi CN, Morri C, Chiantore M, Montefalcone M, Parravicini V and Rovere A (2012) Mediterranean sea biodiversity between the legacy from the past and a future of change. In Stambler N (ed.), *Life in the Mediterranean Sea: A Look at Habitat Changes*. New York, NY: Nova Science Publishers, pp. 1–55.
- Bianchi CN, Morri C and Pronzato R (2014) The other side of rarity: recent habitat expansion and increased abundance of the horny sponge *Ircinia retidermata* (Demospongiae: Dictyoceratida) in the southeast Aegean. *Italian Journal of Zoology* 81, 564–570.
- Boero F, Kraberg AC, Krause G and Wiltshire KH (2015) Time is an affliction: why ecology cannot be as predictive as physics and why it needs time series. *Journal of Sea Research* 101, 12–18. <https://doi.org/10.1016/j.seares.2014.07.008>.
- Boury-Esnault N, Pansini M and Uriz MJ (1994) Spongiaires bathyaux de la mer d'Alboran et du Golfe Ibéro-Marocain. *Mémoires du Muséum national d'histoire naturelle* 160, 1–174.
- Bracchi VA, Savini A, Basso D, Marchese F and Corselli C (2015) Coralligenous habitat in the Mediterranean Sea: a geomorphological description from remote data. *Italian Journal of Geoscience* 134, 32–40. <https://doi.org/10.3301/IJG.2014.16>.
- Bracchi VA, Basso D, Marchese F, Corselli C and Savini A (2017) Coralligenous morphotypes on subhorizontal substrate: a new categorization. *Continental Shelf Research* 144, 10–20. <https://doi.org/10.1016/j.csr.2017.06.005>.
- Bussotti S, Denitto F, Guidetti P and Belmonte G (2002) Fish assemblages in shallow marine caves of the Salento Peninsula (Southern Apulia, SE Italy). *Marine Ecology* 23, 11–20. <https://doi.org/10.1111/j.1439-0485.2002.tb00004.x>.
- Bussotti S, Terlizzi A, Frascchetti S, Belmonte G and Boero F (2006) Spatial and temporal variability of sessile benthos in shallow Mediterranean marine caves. *Marine Ecology Progress Series* 325, 109–119. <https://doi.org/10.3354/meps325109>.
- Cárdenas P, Pérez T and Boury-Esnault N (2012) Sponge systematics facing new challenges. In Becerro MA, Uriz MJ, Maldonado M and Turon X (eds), *Advances in Sponge Science: Phylogeny, Systematics, Ecology*. New York, NY: Elsevier, pp. 19–209.
- Cerrano C, Bavestrello G, Bianchi CN, Cattaneo-Vietti R, Bava S, Morganti C, Morri C, Picco P, Sara G, Schiaparelli S, Siccardi S and Sponga F (2000) A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (North-Western Mediterranean),

- summer 1999. *Ecology Letters* 3, 284–293. <https://doi.org/10.1046/j.1461-0248.2000.00152.x>.
- Cerrano C, Totti C, Sponga F and Bavestrello G** (2006) Summer disease in *Parazoanthus axinellae* (Schmidt, 1862) (Cnidaria, Zoanthidea). *Italian Journal of Zoology* 73, 355–361. <https://doi.org/10.1080/11250000600911675>.
- Coll M, Piroddi C, Steenbeck J, Kaschner K, Ben Rais Lasram F, Aguzzi J, Ballesteros E, Bianchi CN, Corbera J, Dailianis T, Danovaro R, Estrada M, Frogia C, Galil BS, Gasol JM, Gertwagen R, Gil J, Guilhaumon F, Kesner-Reyes K, Kitsos MS, Koukouras A, Lampadariou N, Laxamana E, López-Fé de la Cuadra CM, Lotze HK, Martin D, Mouillot D, Oro D, Raicevich S, Rius-Barile J, Saiz-Salinas JJ, San Vicente C, Somot S, Templado J, Turon X, Vafidis D, Villanueva R and Voultsiadou E** (2010) The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS ONE* 5. <https://doi.org/10.1371/journal.pone.0011842>.
- Corriero G, Gherardi M, Giangrande A, Longo C, Mercurio M, Musco L and Marzano CN** (2004) Inventory and distribution of hard bottom fauna from the marine protected area of Porto Cesareo (Ionian Sea): Porifera and Polychaeta. *Italian Journal of Zoology* 71, 237–245. <https://doi.org/10.1080/11250000409356578>.
- Costa G, Betti F, Nepote E, Cattaneo-Vietti R, Pansini M, Bavestrello G and Bertolino M** (2018) Sponge community variations within two semi-submerged caves of the Ligurian Sea (Mediterranean Sea) over a half-century time span. *European Journal of Zoology* 85, 382–392. <https://doi.org/10.1080/24750263.2018.1525439>.
- De Weerd WH and van Soest RWM** (1986) Marine shallow water Haplosclerida (Porifera) from the southeastern part of the North Atlantic Ocean. *Zoologische Verhandlungen* 225, 1–49.
- Dendy A** (1905) Report on the sponges collected by Professor Herdman, at Ceylon, in 1902. In Herdman WA (ed.), *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar*, 3 Supplement 18. London: Royal Society, pp. 57–246.
- Di Camillo CG and Cerrano C** (2015) Mass mortality events in the NW Adriatic Sea: phase shift from slow- to fast-growing organisms. *PLoS ONE* 10. <https://doi.org/10.1371/journal.pone.0126689>.
- Evcen A and Çinar ME** (2012) Sponge (Porifera) species from the Mediterranean coast of Turkey (Levantine Sea, eastern Mediterranean), with a checklist of sponges from the coasts of Turkey. *Turkish Journal of Zoology* 36, 460–474. <https://doi.org/10.3906/zoo-1107-4>.
- Gaino E and Pronzato R** (1991) La malattia delle spugne commerciali: considerazioni storico- economiche. *Bollettino dei Musei e Degli Istituti Biologici dell'Università di Genova* 54, 17–26.
- Gaino E, Pronzato R, Corriero G and Buffa P** (1992) Mortality of commercial sponges: incidence in two Mediterranean areas. *Bollettino di Zoologia* 59, 79–85. <https://doi.org/10.1080/11250009209386652>.
- Garrabou J, Coma R, Bensoussan N, Bally M, Chevaldonné P, Cigliano M, Diaz D, Harmelin JG, Gambi MC, Kersting DK, Ledoux JB, Lejeune C, Linares C, Marschal C, Pérez T, Ribes M, Romano JC, Serrano E, Teixido N, Torrents O, Zabala M, Zuberer F and Cerrano C** (2009) Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. *Global Change Biology* 15, 1090–1103.
- Hooper JN and van Soest RW** (2002) *Systema Porifera. A Guide to the Classification of Sponges*. Boston, MA: Springer.
- Kim MJ and Sim CJ** (2009) A new species of genus *Diplastrella* (Demospongiae: Hadromerida: Spirostrellidae) from Korea. *Korean Journal of Biological Sciences* 8, 247–250. <https://www.dbpia.co.kr/Journal/ArticleDetail/NODE01766053>.
- Lejeune C, Chevaldonné P, Pergent-Martini C, Boudouresque CF and Pérez T** (2010) Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends in Ecology & Evolution* 25(4), 250–260. <https://doi.org/10.1016/j.tree.2009.10.009>.
- Lévi C and Lévi P** (1983) Démonspogones bathyales récoltées par le N/O “Vauban” au sud de la Nouvelle Calédonie. *Bulletin du Muséum national d'histoire naturelle* 45, 931–997.
- Longo C, Cardone F, Mercurio M, Nonnis Marzano C, Pierri C and Corriero G** (2015) Spatial and temporal distributions of the sponge fauna in southern Italian lagoon systems. *Mediterranean Marine Science* 17, 174–189. <http://dx.doi.org/10.12681/mms.1426>.
- Longo C, Cardone F, Pierri C, Mercurio M, Mucciolo S, Marzano CN and Corriero G** (2017) Sponges associated with coralligenous formations along the Apulian coasts. *Marine Biodiversity* 48, 1–13. <https://doi.org/10.1007/s12526-017-0744-x>.
- Montefalcone M, De Falco G, Nepote E, Canessa M, Bertolino M, Bavestrello G, Morri C and Bianchi CN** (2018) Thirty year ecosystem trajectories in a submerged marine cave under changing pressure regime. *Marine Environment Research* 137, 98–110. <https://doi.org/10.1016/j.mar-envres.2018.02.022>.
- Morrow C and Cárdenas P** (2015) Proposal for a revised classification of the Demospongiae (Porifera). *Frontiers in Zoology* 12, 7. <https://doi.org/10.1186/s12983-015-0099-8>.
- Pansini M** (1996) *Petrosia pulitzeri* n. sp. (Porifera, Demospongiae) from Mediterranean caves. *Italian Journal of Zoology* 63, 169–172. <https://doi.org/10.1080/11250009609356126>.
- Pansini M, Manconi R and Pronzato R** (2011) *Porifera I. Calcarea, Demospongiae (Partim), Hexactinellida, Homoscleromorpha*. Bologna: Calderini-Il Sole 24 Ore.
- Pronzato R** (1999) Sponge fishing, disease and farming in the Mediterranean Sea. *Aquatic Conservation* 9, 485–493. [https://doi.org/10.1002/\(SICI\)1099-0755\(199909/10\)9:5<485::AID-AQC362>3.0.CO;2-N](https://doi.org/10.1002/(SICI)1099-0755(199909/10)9:5<485::AID-AQC362>3.0.CO;2-N).
- Pronzato R and Manconi R** (2008) Mediterranean commercial sponges: over 5000 years of natural history and cultural heritage. *Marine Ecology* 29, 146–166. <https://doi.org/10.1111/j.1439-0485.2008.00235.x>.
- Pronzato R, Ledda FD and Manconi R** (2012) Mediterranean horny sponges: How to drive a never-ending story of exploitation toward a sustainable management and conservation. In Lucas M and Borja E (eds), *Endangered Species: Habitat, Protection and Ecological Significance*. Hauppauge: Nova Science Publishers, p. 32.
- Pulitzer-Finali G** (1983) A collection of Mediterranean Demospongiae (Porifera) with, in appendix, a list of the Demospongiae hitherto recorded from the Mediterranean Sea. *Annali del Museo civico di storia naturale Giacomo Doria* 84, 445–621.
- Rizzello R, Corriero G, Scalera-Liace L and Pronzato R** (1997) Estinzione e ricolonizzazione di Spongia officinalis nello stagnone di Marsala. *Biologia Marina Mediterranea* 4, 443–444.
- Roberts C** (2009) *The Unnatural History of the Sea*. Washington, DC: Island Press.
- Rützler K** (1978) Sponges in coral reefs. In Stoddart DR and Johannes RE (eds), *Coral Reefs: Research Methods. Monographs on Oceanographic Methodologies*. Paris, UNESCO, p. 5.
- Sarà M** (1960) Poriferi del litorale dell'isola d'Ischia e loro ripartizione per ambienti. *Pubblicazioni della Stazione Zoologica di Napoli* 31, 421–472.
- Sarà M** (1969) Specie nuove di demospogge provenienti dal coralligeno pugliese. *Bollettino dei Musei e Degli Istituti Biologici dell'Università di Genova* 37, 89–96.
- Sarà M** (1974) Il popolamento delle grotte marine e sua protezione. In Società Italiana di Ecologia (eds), *Atti del IV Simposio Nazionale sulla Conservazione Della Natura*. Bari: Cacucci, pp. 51–59.
- Thibaut T, Pinedo S, Torras X and Ballesteros E** (2005) Long-term decline of the populations of Fucales (*Cystoseira* spp. and *Sargassum* spp.) in the Albères coast (France, North-western Mediterranean). *Marine Pollution Bulletin* 50, 1472–1489. <https://doi.org/10.1016/j.marpolbul.2005.06.014>.
- Topaloğlu B** (2001) Sponge fauna in the littoral zone of the Marmara Sea. *Rapports et procès-verbaux des réunions Commission Internationale pour L'Exploration Scientifique de la Mer Méditerranée* 36, 421.
- Vacelet J** (1959) Répartition générale des éponges et systématique des éponges cornées de la région de Marseille et de quelques stations méditerranéennes. *Recueil des Travaux de la Station marine d'Endoume* 16, 39–101.
- Van Soest RWM** (1980) Marine sponges from Curaçao and other Caribbean localities. Part II. Haplosclerida. *Studies on the Fauna of Curaçao and Other Caribbean Islands* 62, 1–173.
- Van Soest RWM** (2017) Sponges of the Guyana Shelf. *Zootaxa* 4217, 1–225. <https://doi.org/10.11646/zootaxa.4217.1.1>.
- Van Soest RWM, Boury-Esnault N, Hooper JNA, Rützler K, de Voogd NJ, Alvarez B, Hajdu E, Pisera AB, Manconi R, Schönberg C, Klautau M, Picton B, Kelly M, Vacelet J, Dohrmann M, Diaz MC, Cárdenas P, Carballo JL, Rios P and Downey R** (2018) *World Porifera Database*. Available at <http://www.marinespecies.org/porifera>.
- Voultsiadou E and Vafidis D** (2004) Rare sponge (Porifera: Demospongiae) species from the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom* 84, 593–598. <https://doi.org/10.1017/S002531540400952h>.