

Mediterranean hexactinellid sponges, with the description of a new *Sympagella* species (Porifera, Hexactinellida)

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An overview is proposed of the hexactinellid sponge fauna of the Mediterranean Sea, including the description of a new species of Sympagella, S. delauzei sp. nov., collected by ROV during the exploration of deep-sea canyons of the NW Mediterranean and of deep banks and seamounts of the Alboran Sea. The type species of Sympagella, S. nux, is redescribed from specimens from the type locality. An 18S rDNA sequence of the new species was obtained and included in a phylogenetic tree of related hexactinellids. Some modifications to the classification of Rossellidae are proposed according to the new morphological and molecular data obtained during this study: the genera Caulophacus, and Caulophacella are accordingly moved from Rossellinae to Lanuginellinae.

Keywords: Porifera, glass sponges, deep Mediterranean, new species, integrative taxonomy, 18S rDNA, *Sympagella*

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INTRODUCTION

The Mediterranean Sea has long been considered to be a very poor habitat for hexactinellid sponges mainly due to the relatively high temperature (~13°C) of its deep waters and the rather recent history of its deep-sea fauna. During the Pleistocene though, the hexactinellid fauna seems to have been important and fossilized skeletons from this period have been found in the south of Crete (1500–2000 m) and in the South Ionian Sea (Cyrenian escarpment; Zibrowius, 1981, 1985). This is certainly related to the Ice Age conditions providing colder waters more appropriate for an important hexactinellid fauna. As a consequence of this present poverty, few studies have been dedicated to the Mediterranean hexactinellid fauna. In 1985, eight species were cited from the Mediterranean area in a review on hexactinellid species (Zibrowius, 1985), to which one (*Hyalonema thomsoni* Marshall, 1875) was later added from the Catalan coast by Uriz & Rosell (1986, 1990) (Table 1). Three of these species are north-eastern Atlantic species: *Asconema setubalense* Kent, 1870 described from the coast of Portugal, restricted to the Alboran Sea in the Mediterranean (Vacelet, 1961; Pardo *et al.*, 2011; Sitjà & Maldonado, 2014), *Pheronema carpenteri* (Thomson, 1869) locally abundant in the muddy bathyal zone (Vacelet, 1969) and *Hyalonema thomsoni*. *Oopsacas minuta* Topsent, 1927, described from one incomplete specimen from the Gibraltar Strait, was much later discovered to be an inhabitant of some particular shallow, dark caves in the north-western

Mediterranean and in the Adriatic (Vacelet *et al.*, 1994; Bakran-Petricioli *et al.*, 2007) where it constitutes large populations. The species has never been found outside the Mediterranean Sea. Two species mentioned by Bowerbank (1876), *Farrea irregularis* and *Farrea spinulenta*, are nowadays considered as *taxa inquirenda* (Van Soest *et al.*, 2014) since they lack a proper description. Three other species recorded in the Mediterranean are believed to be cosmopolitan: *Tretodictyum tubulosum* Schulze, 1886 (type-locality temperate north-west Pacific, Japan), *Aphrocallistes beatrix* Gray, 1868 (Central Indo-Pacific, Malacca Strait) and *Sympagella nux* Schmidt, 1870 (Tropical West Atlantic, Florida). Even if the true cosmopolitan nature of these species has been questioned (Vacelet, 1969), no recent work has been undertaken to test it.

With the development of new techniques of investigation in the deep sea (submersibles and ROVs) a revival of interest for the bathyal zone has recently established that hexactinellid species appear much more frequent than previously thought in the deep Mediterranean (Pardo *et al.*, 2011; Sitjà & Maldonado, 2014).

Two series of research cruises 'MedSeaCan' and 'CorSeaCan' were organized by the French Marine Protected Areas Agency (AAMP) from November 2008 to August 2010, to explore the canyons of the NW Mediterranean continental French coast from the Rech Lacaze-Duthiers in the west to the Canyon of Nice in the east and along the western coast of Corsica from the Centuri Canyon in the north to Les Moines Canyon in the south (Fourt *et al.*, 2014). Explorations and sampling were conducted with the ROV 'Achille' and the manned submersible Remora 2000 (COMEX Company). Data on the distribution of hexactinellid species collected or identified on video during these cruises are

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Table 1. Distribution of hexactinellid species in the Mediterranean

Species	Authorship	Type locality	Mediterranean distribution	Depth (m)	References
<i>Asconema setubalense</i>	Kent(1870)	NE Atlantic (Portugal Coast)	Alboran Sea	175–200	Vacelet (1961)
			Algerian coast: 35°44'N 1°32'W Alboran Sea Banco de Djibouti Alboran Sea Banco des Cabliers	335–460	Vacelet (1961) Pardo <i>et al.</i> (2011) Sitjà & Maldonado (2014)
<i>Aphrocallistes beatrix</i>	Gray, 1858	Malacca Strait	Alboran Sea: 35°56'07"N 5°34'07"E	534–560	Boury-Esnault <i>et al.</i> (1994)
<i>Farrea irregularis</i>	Bowerbank (1876)	<i>taxon inquirendum</i>	Algerian coast: 43°43'05N 8°43'07E		Bowerbank (1876)
<i>Farrea spinulenta</i>	Bowerbank (1875)	<i>taxon inquirendum</i>	Libyan coast (Tripoli)		Bowerbank (1875)
<i>Hyalonema thomsoni</i>	Marshall (1875)	NE Atlantic Shetland Islands	Western Mediterranean:	1545–1580	Uriz & Rosell (1986)
			Western Mediterranean: 40°31'04"N 1°46'05"E 40°20'49"N 1°53'03"E	1716–1759	Uriz & Rosell (1990)
<i>Oopsacas minuta</i>	Topsent (1927)	Gibraltar Strait	Gibraltar Strait	924	Topsent (1928)
			NW Mediterranean 3PPs cave	25	Boury-Esnault <i>et al.</i> (1994)
			Adriatic Sea		Bakran-Petricioli <i>et al.</i> (2007)
<i>Pheronema carpenteri</i>	Thomson (1869)	NE Atlantic (Scotland Coast)	Tyrrhenian Sea	1103	
			East of Corsica	660–820	Vacelet (1960)
			Canal de Corse	2170	Topsent (1928)
			Canal de Corse	335–367	Vacelet (1960)
			Banc de Méjean	600–700	Vacelet (1960)
			Saint Tropez Golf	440–860	Vacelet (1960)
			Alboran Sea: 35°56'06"N 3°07'09"W	380–386	Boury-Esnault <i>et al.</i> (1994)
<i>Sympagella 'nux'</i>	Schmidt (1870)	West Atlantic : Florida	Aegean Sea, Cyclades	444–414	Schulze (1900)
			Alboran Sea: 35°35'03"N 3°45'01"W	480	Boury-Esnault <i>et al.</i> (1994)
			Galli Islands (Amalfi)		Schulze (1887)
<i>Tretodictyum tubulosum</i>	Schulze (1886)	East Pacific: Japan	Banc des Blauquières	340	Vacelet (1969)
			Canyon de la Cassidaigne	306–500	Vacelet (1969)
			Ionian Sea: escarp. Apulien 38°30'N 19°27'E	2180–2541	Zibrowius (1985)
			Ionian Sea: escarp. Malte 36°25'N 15°35'E	1916–2539	Zibrowius (1985)
			Alboran Sea: 35°26'05"N 4°18'04"W	390–400	Boury-Esnault <i>et al.</i> (1994)
			Alboran Sea: 35°56'07"N 5°34'07"W	534–560	Boury-Esnault <i>et al.</i> (1994)

here reported. Among the species collected, a new species of stalked hexactinellid much alike *Caulophacus* Schulze, 1886 or *Sympagella* Schmidt, 1870 was collected in the Valinco Canyon (SW coast of Corsica). With the help of additional specimens sighted and collected by the OCEANA organization in the Alboran Sea, a morphological and molecular study has been undertaken on what appears to be a new species of *Sympagella*. A redescription of the type species of the genus, *Sympagella nux* and a revision of the classification of *Sympagella* and *Caulophacus* are also here proposed.

MATERIALS AND METHODS

Collection sites

Our reference specimen of *Sympagella nux* came from the type locality and is in the collection of Harbor Branch

Oceanographic Institute (HBOI) under the number 200706081006. It is redescribed in the present work.

Specimens of the new species of *Sympagella* were collected in August 2010 by the articulated arm of the ROV 'Achille' (Comex) in the Valinco Canyon 41°41'14"N 8°47'27"E (SW Corsica – Sample VAL-ACH-P3_ECH01) at 188 m depth and by a Saab Seaeye Falcon DR ROV (OCEANA) in the Alboran Sea on the Avempace bank 36°23'51"N 03°58'03"W at 388 m (Figure 1).

Spicule and skeleton preparation

The skeletal architecture was studied by light microscopy on whole mounts, hand-cut tangential sections or thick polished sections obtained by sawing specimens embedded in Araldite with a low-speed saw using a diamond wafering blade, and wet-ground on polishing discs (Boury-Esnault *et al.*, 2002).

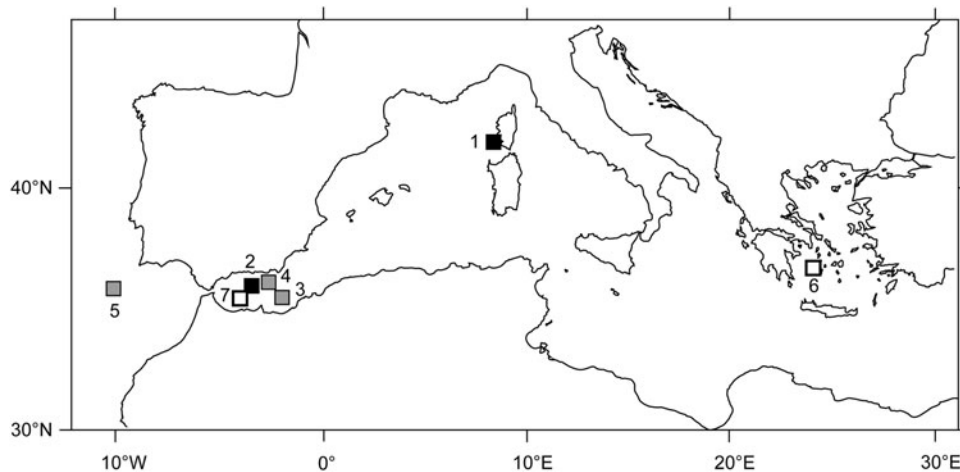


Fig. 1. Distribution map of *Sympagella delauzei* sp. nov., with recent collection sites (black squares), recent video observations (grey squares) and past collection sites from the literature (white squares). (1) Valinco Canyon, Corsica (type locality – 188 m); (2) Avempace Bank, Alboran Sea (paratype – 388 m); (3) Cabliers Bank, Alboran Sea (320–403 m); (4) Chella Bank, Alboran Sea (363–432 m); (5) Gorringer Bank, Ibero-Moroccan Gulf (350–474 m); (6) Between Serifos and Milos, Cyclades Islands (414 m); (7) Near Tofino Bank, Alboran Sea (480 m).

For the study of spicules, a rapid method adapted from classical methods was used for both light and scanning electron microscopy (SEM). A small piece of sponge was boiled in a few drops of nitric acid on a microscopic glass slide, renewing the acid two or three times before complete drying. After drying and enough cooling to avoid breakage of the slide, the slide was rinsed with several drops of distilled water and drained. Boiling in nitric acid and rinsing were repeated if necessary to obtain a sufficiently clean slide. The slide was then either mounted in Araldite for light microscopy or sputter-coated with gold–palladium, then observed under a Hitachi S570 SEM (Vacelet, 2006).

Molecular phylogeny

The specimen of the new *Sympagella* from Valinco Canyon (Sample ID #VAL-ACH-P3) has been preserved in ethanol 95% after recovery on board. One piece was used for DNA extraction using QIAmp DNA Mini kit (Qiagen). PCR amplification of 1876 bp of the 18S ribosomal DNA (18S) was conducted with primers 18S D and 18S G as in Gazave *et al.* (2010). A consensus sequence was obtained after cloning PCR products, assembling and editing sequences with BioEdit 7.0.9 (Hall, 1999). The sequence was deposited in the European Nucleotide Archive (ENA – EMBL) under accession number LN624216.

Our sequence was manually aligned with other 18S sequences of Hexactinellida recovered from nucleotide to build a phylogenetic tree. Phylogenetic reconstruction was estimated through the Neighbour-joining (NJ) method as implemented in CLUSTALX 2.1 (Larkin *et al.*, 2007), and with the Maximum likelihood (ML) method as implemented in PhyML 3.0 (Guindon *et al.*, 2010). With both methods, bootstrap support was assessed over 1000 replicates.

RESULTS

Description of the species
Hexactinellida Schmidt, 1870
Hexasterophora Schulze, 1886

Lyssacinosa Zittel, 1877
Rossellidae Schulze, 1885
Lanuginellinae Gray, 1872
Sympagella Schmidt, 1870

Type species: *Sympagella nux* syntype MCZ PORa-6790;
Type locality: off Sand Key and off American Shoal, Florida,
180–225 m.

DIAGNOSIS

Body is saccular, funnel-like, tubular or mushroom-like, basi-phytic, with long or short stalk. Choanosomal spicules are diactins and hexactins. Dermalia are pinular hexactins and/or pentactins. Atrialia are pinular hexactins or pentactins. Hypodermalia and sometimes hypoatrialia, if present, are pentactins. Microscleres are strobiloplumicomes and various combinations of discohexasters, onychasters, hexasters, hemi-hexasters, hemionychasters and tylohexasters (corrected from Tabachnick, 2002).

Redescription of the type species of the genus

Sympagella nux Schmidt, 1870

Material studied: specimen HBOI voucher no. 200706081006 collected by A. Wright, D. Liberatore & J. Rob; identified by S. Pomponi (Figure 2A, B).

Locality: Florida; Pourtales Terrace, South of Marathon, near UM Multibeam Site 23, Bioherm, East Slope; latitude 24°14'22"N; longitude 81°00'46"W; 1666 m depth; under an overhang.

Other material examined: HBOI voucher no. 199411141003 Turks & Caicos; Providenciales Island 1.25 Nautical Miles W of Island; latitude 21°49'23"N; longitude 72°22'13"W; 2827 m depth; large boulder rock outcrop; identifier H.M. Reisswig.

EXTERNAL SHAPE

Group of at least 50 white urn-shaped stalked specimens (Figure 2A), under an overhang. The body of the specimens is 2–4.5 cm high and 2–4 cm in diameter; the peduncle is 5–10 cm long and 3–4 mm wide (Figure 2B). A single large

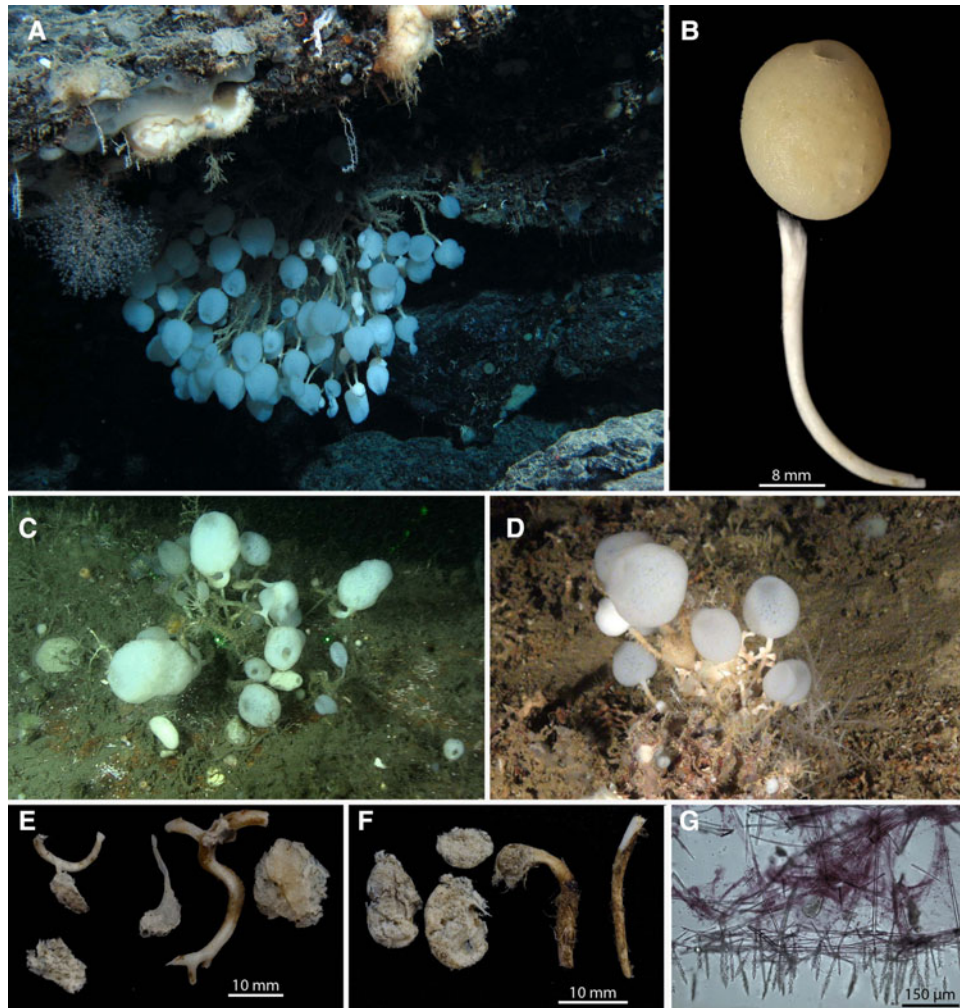


Fig. 2. *Sympagella nux* and *Sympagella delauzei* sp. nov. *in situ* and after collection. (A) *Sympagella nux* under an overhang, Pourtales terrace (HBOI *in situ* photo); (B) Specimen studied of *S. nux* (HBOI photo); (C) *Sympagella delauzei* sp. nov. from Valinco Canyon (AAMP *in situ* photo); (D) *Sympagella delauzei* sp. nov. from Avempace Bank (Alboran sea) (OCEANA *in situ* photo); (E) Specimen studied of *Sympagella delauzei* sp. nov. from Valinco Canyon; (F) Specimen studied of *Sympagella delauzei* sp. nov. from Alboran Sea; (G) Organization of the ectosome of *Sympagella delauzei* sp. nov.; the pinular pentactine dermalia lay on a layer of pentactine hypodermalia.

osculum about 6 mm in diameter is present at the top of the specimens.

SKELETON

The ectosomal skeleton is composed of a layer of pinular pentactine dermalia which lay on a layer of smooth pentactine hypodermalia; around the atrial cavity is a layer of pinular hexactine atrialia. The choanosomal skeleton is composed of hexactins and two kinds of diactins. The skeleton of the stalk consists of diactins with rough inflated extremities linked by spiny synapticula which form rectangular meshes.

SPICULE TYPES

Dermalia: pinular pentactins (Figure 3A): pinular ray 100–165 μm long, 5–10 μm and 13–25 μm wide respectively at the basis and at the most inflated spined part (mean 120/7.3/27 μm); tangential rays slightly spined 65–105/4–8.8 μm (88/5.40 μm) and a rudimentary basal ray 3–5 μm (3.9 μm).

Gastralia: pinular hexactins (Figure 3B): pinular ray 144–676/12–26.6 μm (mean 333.7/16.6 μm); the other rays are slightly spiny, tangential ray 92.4–186.3/5.8–10.3 μm

(mean 134.4/7.8 μm), distal ray 115.2–151.8/4.8–11.4 μm (mean 134.4/7.5 μm).

Hypodermalia: smooth pentactins (Figure 3C): tangential ray 310–538/12–39 μm (mean 412.2/28.2 μm), proximal ray often slightly curved 520–740/20–41 μm (637/30 μm).

Choanosomal hexactins (Figure 3D): smooth rays 700–1200/30–75 μm (mean 935/46 μm).

Choanosomal diactins of two size classes (Figure 3E): 620–1350/10–18 μm (mean 1008/12.9 μm) and 1755–3913/27–40 μm (mean 2907/30.7 μm) showing four vestigial rays in the middle.

Discohexasters (Figure 3F): 70–85 μm in diameter with the primary star about 2.5–3 μm in diameter and very thin terminal rays 35–40/1.4–1.6 μm , the disc at the extremities of the rays being about 5–7 μm in diameter.

Strobiloplumicomeres (Figure 3G): 35–42 μm in diameter (mean 40 μm); the primary star is about 3–5.5 μm in diameter. The terminal rays are 14–15.6 μm in length, the width is 0.2–0.4 μm at the point of attachment to the primary swelling and 0.7–0.9 μm at the extremity.

Diactins of the peduncle with rough inflated extremities: 2106–5000/15–50 μm (mean 3416/31 μm).

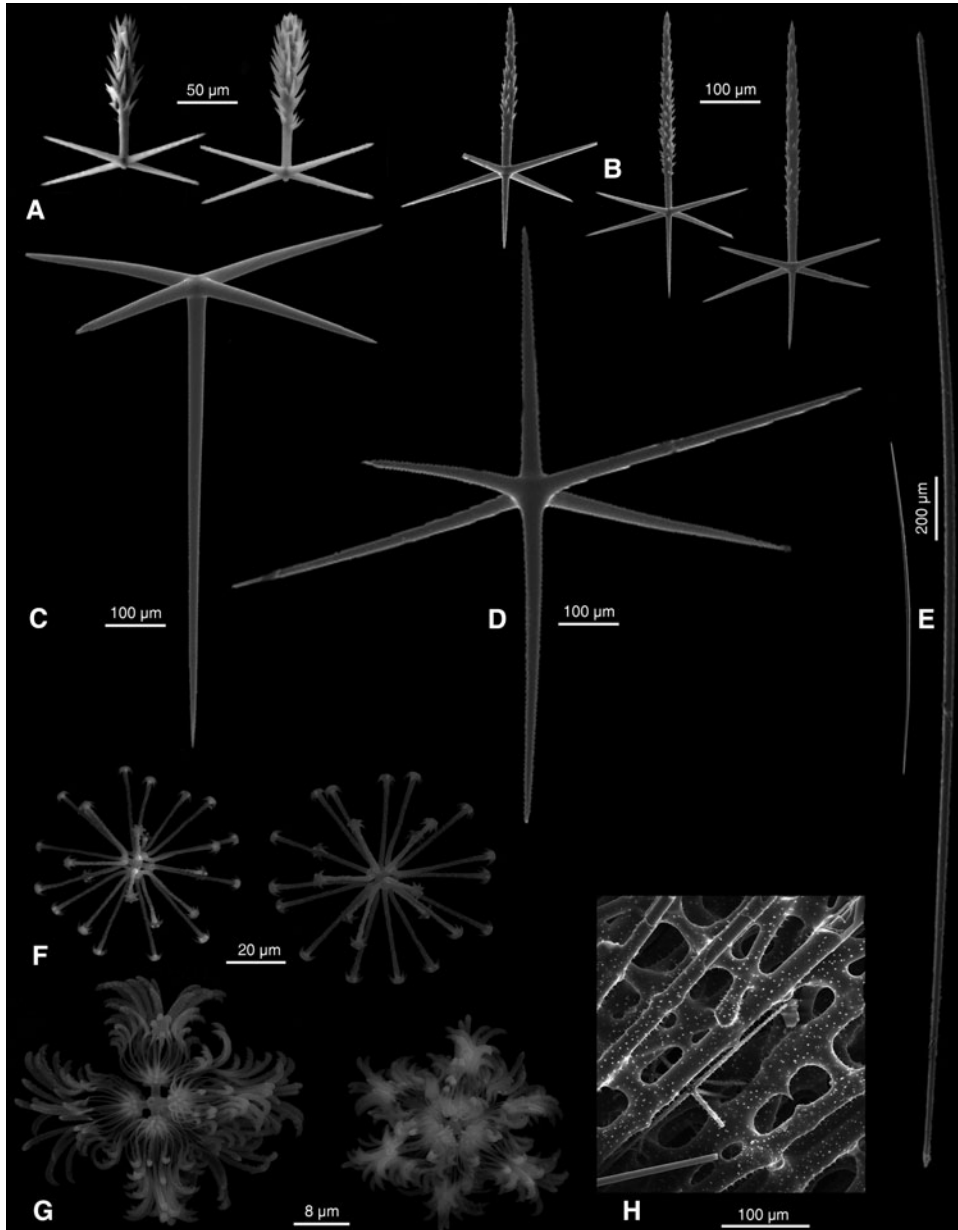


Fig. 3. Scicules of *Sympagella nux* from Pourtales terrace (SEM). (A) Pinular pentactins; (B) Pinular hexactins; (C) Smooth hypodermalia pentactin; (D) Choanosomal hexactin; (E) Choanosomal diactins of two size classes; (F) Discohexasters; (G) Strobiloplumicomeres; (H) Synapticulate skeleton of the peduncle with spiny secondary silica layer.

Synapticula (Figure 3H): the meshes of the synapticula are rectangular 55–75/40–45 μm (mean 63/42 μm), the spines which cover the synapticula are about 7.5 μm in length.

DISTRIBUTION

Sympagella nux was described by Schmidt, 1870 off Sand Key and off American Shoal, Florida, NW tropical Atlantic, 180–225 m. The specimen studied here came exactly from the type locality called nowadays Pourtales Terrace but deeper than Schmidt's specimen. All the occurrences from other Atlantic localities (Table 2) need to be checked.

Description of the new species

Sympagella delauzei Boury-Esnault, Vacelet, Reiswig, Chevaldonné sp. nov.

Holotype VAL-ACH-P3_ECH01 (Figure 2C, E): Valinco Canyon, Corsica: 41°41'14"N 8°47'27"E, 188 m; 18 October 2010. The type specimen is deposited in the Muséum national d'Histoire naturelle de Paris (MNHN) under the number MNHN H.JV-01.

Paratype: Specimen from Avempace Bank, Alboran Sea (Figure 2D, F) 36°23'51"N 03°58'03"W at 388 m; 14 July 2011, deposited in the MNHN in Paris under the number MNHN H.JV-02.

Other material: Balgim collection (NBE personal collection) Station DW 128, Alboran Sea, 35°35'03"N 3°45'01"W, 480 m (Boury-Esnault *et al.*, 1994).

EXTERNAL SHAPE

White urn-shaped stalked specimens have been observed on rocks at 188 m depth. The population observed is composed

Table 2. World distribution of *Sympagella* species

Species	Authority	Locality	Latitude	Longitude	Depth (m)	Source
<i>Sympagella nux</i>	Schmidt 1870	North Atlantic Ocean				
	Schmidt 1870	Florida off Sand Key			180–225	Schmidt (1870)
		North American coast	37–40°N	69–74°W	128–410	Schulze (1899)
		Cape Verde Islands			183–235	Schulze (1887)
		Azores: Sao Miguel Station 569			27	Topsent (1904)
		Azores: S Pico Station 597			523	Topsent (1904)
		Atlantic Spain – Portugal Coast				Milne-Edwards (1881)
		Mediterranean: Aegean Sea			414–444	Schulze (1900)
		Namibia	24°18'00"S	13°28'21"E	322	Uriz (1988)
		24°04'03"S	13°38'07"E	152	Uriz (1988)	
<i>delauzei</i> sp. nov.		Mediterranean Sea				
		W Corsica Valinco Canyon	41°41'14"N	8°47'27"E	188	present paper
		Alboran Sea				
		Avempace Bank	36°23'51"N	3°58'03"W	388	present paper
		Avempace Bank	36°23'50"N	3°58'10"W	386–394	video Aguilar
		Avenzoar Bank	36°29'10"N	2°24'46"W	396	video Aguilar
		Chella Bank	36°31'46"N	2°54'56"W	432	video Aguilar
		Chella Bank	36°32'34"N	2°52'48"W	363	video Aguilar
		Catifas Bank	35°52'33"N	2°34'40"W	379–395	video Aguilar
		Cabliers Bank	35°47'38"N	2°15'12"W	320–403	video Aguilar
		Tofino Bank	35°35'03"N	3°45'01"W	480	Boury-Esnault <i>et al.</i> (1994) (as <i>S. nux</i>)
		North-east Atlantic Ocean				
		Gorringe Bank				
		Gorringe Bank 1	36°30'45"N	11°26'48"W	474	video Aguilar
	Gorringe Bank 2	36°30'50"N	11°28'32"W	350	video Aguilar	
	North Mid-Atlantic Ridge					
<i>cooki</i>	Tabachnick & Menshenina 2013		54°19'30"N	36°01'06"W	2620–2676	Tabachnick & Menshenina (2013)
<i>ecomari</i>	Tabachnick & Menshenina 2013		53°58'46"N	36°11'30"W	2500	Tabachnick & Menshenina (2013)
		Pacific Ocean				
<i>anomala</i>	Ijima 1903	N-W Pacific, Sagami Bay			430–522	Ijima (1903)
		N-W Pacific, Philippines	12°53'N	122°26'E	1650–1660	Lévi & Lévi (1989)
<i>cantharellus</i>	Lendenfeld (1915)	S-E Pacific, Peru	5°41'07"S	82°59'07"W	4063	Lendenfeld (1915)
		N-W Pacific, Kuriles Islands			5045	Koltun (1970)
<i>clavipinula</i>	Tabachnick & Lévi 2004	SW Pacific, Norfolk Ride	25°45'38"S	167°14'67"E	680–780	Tabachnick & Lévi (2004)
		Indian Ocean				
<i>gracilis</i>	(Schulze, 1903)	Timor Island	10°30'S	126°30'E	421	Schulze (1903)
<i>johnstoni</i>	(Schulze, 1886)	South Indian Ocean	46°41'S	38°10'E	570	Schulze (1887)
<i>multihexastera</i>	Tabachnick <i>et al.</i> 2008	W Australia off Rowley shoals	17°28'S	118°53'E	405	Tabachnick <i>et al.</i> (2008)

of about 40 individuals often grouped in tufts. The body of the individual specimens is 17–51 mm high and 14–42 mm in diameter (mean 32/23 mm). The stalk is 17–34 mm long and 1.7–2.5 mm wide (mean 25/2.3 mm). A single large osculum 5–8 mm in diameter is present at the top of the specimens (Figure 2C).

SKELETON

The ectosomal skeleton is composed of a layer of pinular pentactine dermalia which lay on a layer of smooth pentactine hypodermalia (Figure 2G); around the atrium cavity is a layer of pinular hexactine/pentactine atrialia. The choanosomal skeleton consists of large smooth hexactins and flexuous diactins. The peduncle consists of diactins linked by slightly

spined synapticula which form rectangular meshes, and some spiny pentactins, hexactins and monactins.

SPICULE TYPES

Dermalia: pinular pentactins (Figure 4A): Pinular ray 74–128 µm long, 2–5 µm and 7–12 µm wide respectively at the basis and at the most inflated spined part; tangential rays slightly spined 45–67/1.1–4 µm and a rudimentary basal ray 2.4–7/1–1.6 µm.

Gastralia: pinular hexactins (Figure 4B): Pinular ray 92–232 µm long, 3.3–5 µm and 6.4–8.4 µm wide respectively at the basis and at the most inflated spined part (mean 140.71/4.4/6.2 µm); tangential rays slightly spined 43–120/2–5.2 µm (mean 80/3.4 µm); proximal slightly spined ray 30–122/1.8–5.2 µm (mean 83/3 µm).

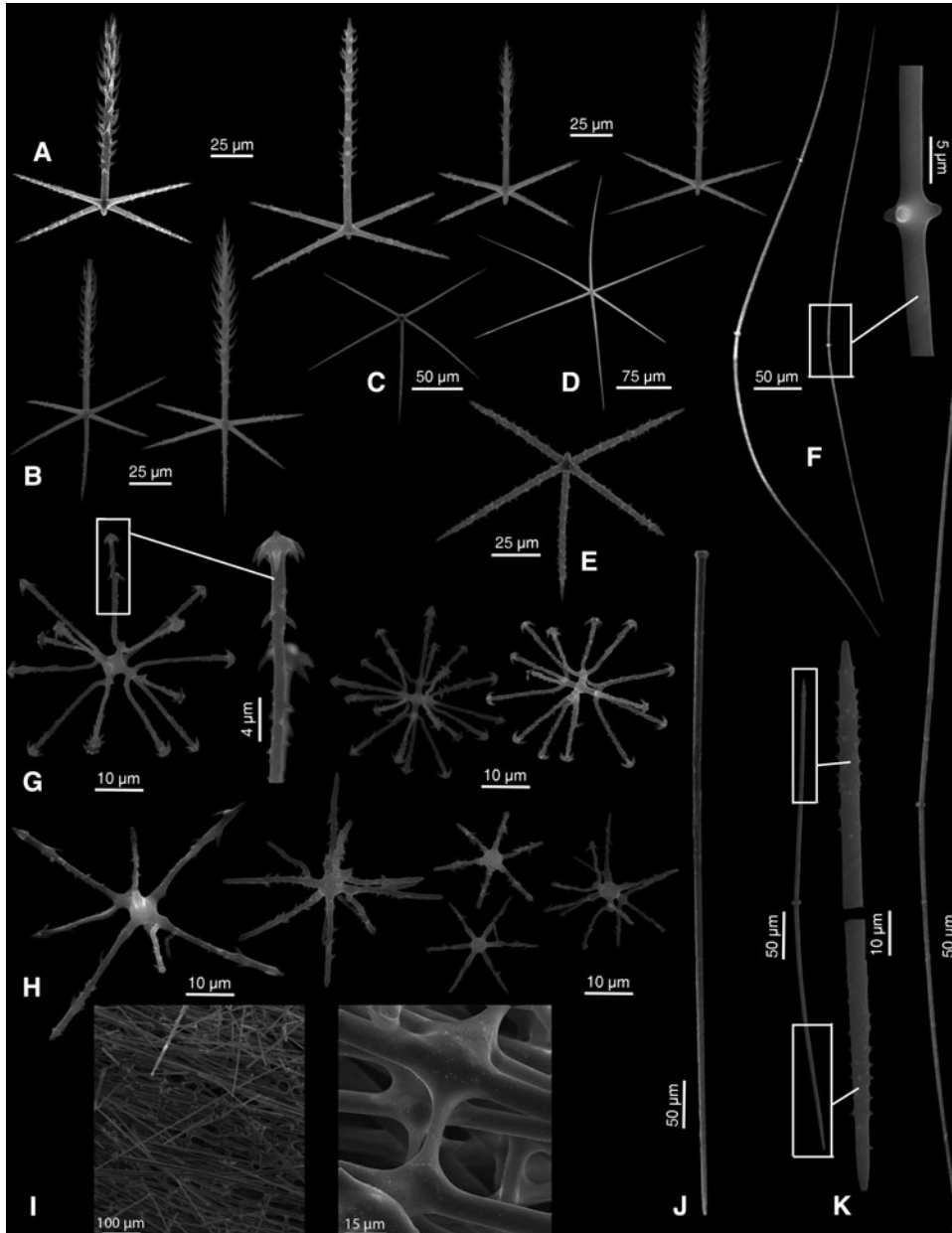


Fig. 4. - Spicules of *Sympagella delauzei* sp. nov. from Valinco Canyon (Corsica) (SEM). (A) Pinular pentactins; (B) Pinular hexactins; (C) Smooth hypodermalia pentactin; (D) Choanosomal hexactin; (E) Spiny pentactin from the peduncle; (F) Thin flexuous choanosomal diactin with enlarged middle segment; (G) Discohexasters with enlarged terminal ray; (H) Microhexactins; (I) Skeleton of the peduncle with inset of synapticula; (J) Monactin; (K) Diactins of the peduncle with enlarged ends.

Hypodermalia: smooth pentactins (Figure 4C): Tangential rays 185–470/4.4–12.7 μm (mean 284.8/7.2 μm); proximal ray often slightly curved 190–549.5/3.6–13.7 μm (mean 345.8/8 μm).

Choanosomal hexactins (Figure 4D): 168.3–435/2.6–9.7 μm (mean 323.3/6.9 μm).

Spiny pentactins and hexactins (Figure 4E): Rays 60–125/5 μm (mean 87.5/5 μm) particularly abundant in the peduncle.

Choanosomal diactins (Figure 4F): The choanosomal diactins are flexuous within the middle traces of four vestigial rays 539–760/2.5–3.7 μm (mean 631.7/3.1 μm).

Discohexasters (Figure 4G): 25–75 μm in diameter (mean 42.7 μm) with a primary star 1.4–2.5 μm in diameter,

terminal rays I 1–2 μm long and ray II 11.2–24.9/0.5–1 μm long (mean 19.5/0.7 μm), the disc at the extremities being about 3 μm in diameter.

Microhexactins (Figure 4H): 9–66.9 μm (mean 41.3 μm) in diameter and rays 4–33.4/0.5–1.3 μm (mean 21.2/0.9 μm) spiny and very irregular, in some cases secondary links between two adjacent rays.

Synapticula (Figure 4I): the meshes formed by synapticula are rectangular 45–120/4.2–25.2 μm (mean 80.8/13.2 μm), they are barely spiny.

Monactins of the peduncle (Figure 4J): 355–650/5–8 μm (mean 491/6.6 μm), ‘tylostyle-like’ spicules, the head being constituted by four vestigial rounded knobs. They seem to be diactins which have developed only one ray.

Diactins of the peduncle of two size classes (Figure 4K): I – 920–2875/5–10 µm (mean 2001/8.6 µm) with slightly spiny sharp extremities and II – 370–870/5–10 µm (mean 618.3/7 µm) with spiny blunt extremities, both showing four vestigial knobs in the middle.

DISTRIBUTION

The type locality is the Valinco Canyon on the south-western coast of Corsica 41°41'14"N 8°47'27"E at 188 m depth. Other specimens come from the Alboran Sea where the species is common: Avempace Bank, 36°23'51"N 03°58'03"W at 388 m (paratype), and near the Tofino Bank, 35°35'03"N 03°45'01"W, 480 m, described by Boury-Esnault *et al.* (1994) under the name *Sympagella nux*. The species has been identified with a reasonable certainty from additional videos and pictures in other locations (Table 2 and Figure 1) in the Alboran Sea, such as Cabliers Bank (35°50'49"N 02°18'14"W) and Chella Bank (36°31'13"N 02°50'44"W) as well as in the Atlantic Ibero-Moroccan Gulf (Gorrige Bank, 36°05'42"N 09°54'00"W).

ETYMOLOGY

This species is dedicated to Henri-Germain Delauze, founder of the COMEX Company, a pioneer in deep submarine exploration always fascinated by the beauty of marine life.

DISCUSSION

18S rDNA phylogeny

A 1876 bp sequence of 18S rDNA was recovered from our sample of *Sympagella delauzei* sp. nov. It was aligned with 18S rDNA sequences of other hexactinellids available from nucleotide databases, mostly coming from Dohrmann *et al.* (2008, 2009, 2012a, b). ML and NJ reconstruction methods produced trees with the same, robust topology (NJ shown on Figure 5, but with bootstrap support from both methods) clearly showing that *S. delauzei* falls within the family Rossellidae, as currently defined. More precisely, as already shown in Dohrmann *et al.* (2012a, b), there is a very good bootstrap support (93 and 91% for ML and NJ respectively) for a group of rossellids that includes *Caulophacus* + *Lophocalyx* + *Caulophacella* + *Sympagella*, which is reminiscent of the former subfamily Caulophacinae Schulze, 1886. This group displays a diagnostic 18 bp deletion in position 667. In more details, the new species is distinctively grouped with *Sympagella nux* with maximum bootstrap support, which supports the generic allocation of our specimen to *Sympagella* rather than *Caulophacus*, *Caulophacella* Lendenfeld, 1915 or *Lophocalyx* Schulze, 1887. Moreover it also provides evidence that our specimens are not conspecific with *S. nux* as available in GenBank. Indeed the two 18S rDNA sequences differ by a dozen base pairs and two indels, which is not compatible with intraspecific variability in hexactinellid 18S rDNA (Dohrmann *et al.*, 2008, 2009, 2012a, b).

Comparison of *S. delauzei* with the Atlantic *Sympagella* spp.

Sympagella delauzei shares with all other *Sympagella* described so far, a stipitate body with a large atrium which opens in a

single osculum, an ectosomal skeleton constituted by pinular pentactins which lay on a layer of smooth pentactins, a surface of the atrium covered by a layer of pinular hexactins, a choanosomal skeleton made of smooth hexactins and diactins, and a skeleton of the peduncle constituted by diactins linked by synapticula. The most abundant microsclere type is a discohexaster present in the type species of the genus and most other species. The main difference between *S. delauzei* and other *Sympagella* species is the absence of strobiloplumicome and the presence instead of microhexactins. Most of the spicules of *S. delauzei* are smaller and the spines of the synapticulate stalk are thinner than those of *S. nux*. The presence of monactins in the peduncle is unusual. The specimen from the Alboran Sea identified as *S. nux* by Boury-Esnault *et al.* (1994) is identical to the new species here described and also lacks strobiloplumicome; it must therefore be considered as a specimen of *S. delauzei*. Schulze (1900) had identified *Sympagella nux* from a broken specimen collected in the Cyclades (between Serifos and Milos, Aegean Sea, east Mediterranean). He had underlined that the pinular pentactins and hexactins are very weak, and the presence of abnormal oxyhexactins. The specimen has all other characteristics of *S. nux* and especially the strobiloplumicome. This description matches that of the new Mediterranean species except for the presence of strobiloplumicomes. Two hypotheses can therefore be proposed: either (i) the specimen of Schulze belongs to a second Mediterranean species of *Sympagella* or (ii) it belongs to *S. delauzei* which can sometimes produce strobiloplumicomes depending on environmental conditions such as the silica content in the sea, as it happens for example in the Mediterranean demosponge *Crambe crambe* (Maldonado *et al.*, 1999).

Tabachnick & Menshenina (2013) described two species from the mid-Atlantic ridge: *S. cooki* that they differentiate by the absence of discohexasters, and *S. ecomari* which differs by a set of microsclere types consisting of strobiloplumicomes and discohexasters only. The latter species *S. ecomari* has been described only from fragments and perhaps will need to be redescribed with better preserved specimens.

Loss of strobiloplumicomes

Tabachnick (1999, 2002) has abandoned the family Caulophacidae due to the fact that 'the taxon Caulophacidae has no unique or specific features which distinguish it from Rossellidae' (Tabachnick, 1999). He has allocated the different genera of former Caulophacidae in the subfamilies Rossellinae for *Caulophacus*, *Caulodiscus* and *Caulophacella* and Lanuginellinae for *Sympagella*. However, the characters shared by *Sympagella*, *Caulophacus*, *Caulodiscus* and *Caulophacella* are numerous and this is even reflected in the definition of the genera given by Tabachnick (2002, pp. 1503 and 1465).

Three subfamilies are currently recognized within Rossellidae: (1) Lanuginellinae for species which share the presence of strobiloplumicomes, (2) Rossellinae for species without strobiloplumicome or discocaster, both recognized by Tabachnick (2002, p. 1491), and (3) Acanthascinae resurrected recently by Reisinger & Stone (2013) for Rossellidae with discocasters.

It does not seem parsimonious to strictly define a subfamily on the presence or absence of one type of microsclere (Dohrmann *et al.*, 2012b). The loss of spicule types is much

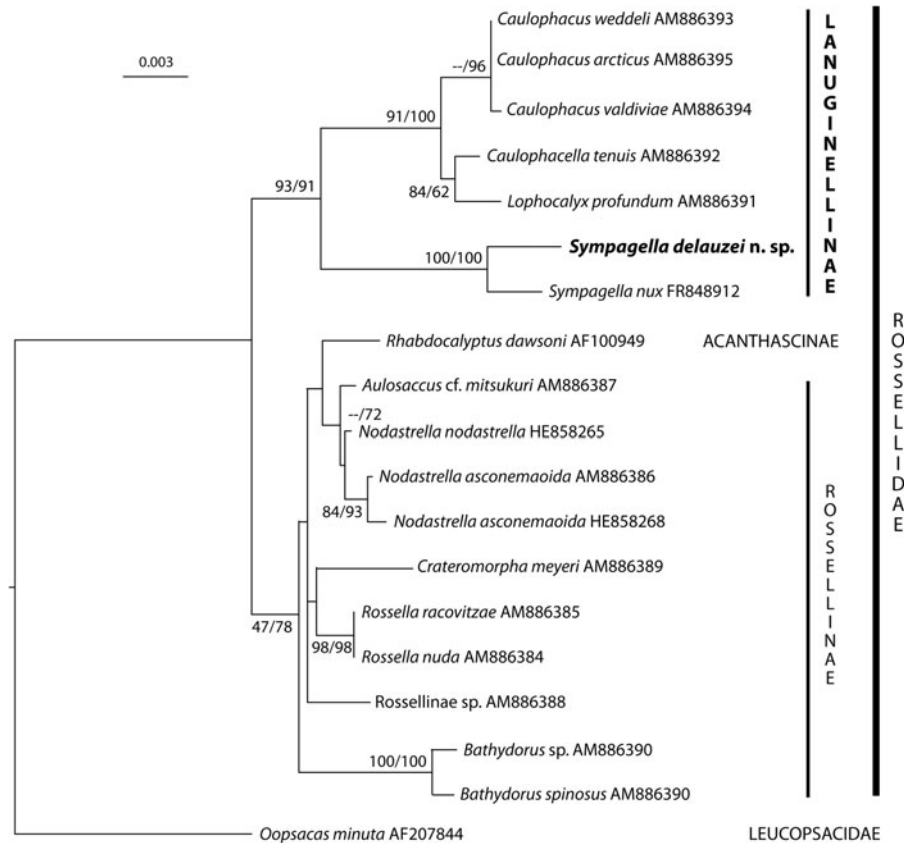


Fig. 5. Neighbour joining and Maximum likelihood phylogenetic reconstructions of the relationships between *Sympagella delauzei* sp. nov. and available Rossellidae from GenBank (accession numbers reported after taxon name) produced the same topology. NJ tree shown here is rooted with *Oopsacas minuta*. Bootstrap values (% over 1000 replicates) are shown at main nodes for ML and NJ respectively. Scale bar: genetic distance.

more frequent than expected in Porifera and must be clearly distinguished from the absence of a character (e.g. Cárdenas *et al.*, 2012 for more references). The strong relationship between *S. nux* and *S. delauzei* in our molecular tree (Figure 5) clearly supports the loss of strobiloplumicome in the Mediterranean species. Such a loss of microsclere is not an exception in *Sympagella*, since *S. cooki* has lost the discohexasters (Tabachnick & Menshenina, 2013). Even in the subfamily Lanuginellinae, the genus *Mellonympha* has a type species (*M. velata* Thomson, 1873) with strobiloplumicome and another one *M. mortenseni* (Burton, 1928) which lacks strobiloplumicome.

Figure 5 also shows the close relationship between the *Sympagella* clade and a second clade containing *Caulophacus*, *Caulophacella* and *Lophocalyx* species, which confirms previous results (Dohrmann *et al.*, 2012a, b). As already underlined by Dohrmann *et al.* (2012b), this is in agreement with earlier classification. We propose, for the time being, to allocate *Caulophacus* (with its subgenus *Caulodiscus*) and *Caulophacella* to the subfamily Lanuginellinae, here strongly supported by our molecular tree (Figure 5, bootstrap support >90%).

Emended diagnosis for Lanuginellinae (revised from Tabachnick, 2002):

Rossellidae with strobiloplumicomes, or if these are absent, the concerned group(s) share so many morphological

characters with a group bearing strobiloplumicomes that their common ancestry with loss of that spicule is most parsimonious: specifically *Sympagella* and *Caulophacus* share basiphytous attachment, long hollow peduncle composed of diactins fused by synapticula, smooth body without prostalia, pinular hexactins and pentactins as dermalia and atrialia, hypodermalia and hypoatrialia (when present) as pentactins or hexactins, choanosomal diactins and hexactins, discohexasters as the most common microsclere (excluding strobiloplumicomes). DNA sequence analysis supports this diagnosis.

Remarks: In forming this new diagnosis of the subfamily Lanuginellinae, we favour the suggestion by Janussen *et al.* (2004) that *Caulophacella* ought to be moved to subgenus status within *Caulophacus*. We accept this as a proposal, and if not so considered by others, we here make the formal proposal that *Caulophacella* be moved to a subgenus of *Caulophacus*. Our move of *Caulophacus* from Rossellinae to Lanuginellinae includes all subgenera of *Caulophacus*.

However it would be necessary to proceed to a molecular phylogenetic analysis of all genera of this subfamily to test its monophyly. A molecular study of all Rossellidae genera would also be important to understand the relationships between the subfamilies and the genera of this large group.

Distribution of *Sympagella* species (Table 2)

Ten species of *Sympagella* have been described so far (Table 2): three from the Indian Ocean (Schulze, 1887, 1903; Tabachnick *et al.*, 2008); three in the Pacific Ocean

Table 3. Distribution of hexactinellid species observed during MedSeaCan and CorSeaCan cruises and OCEANA cruises.

Species	Authority	Location	Latitude	Longitude	Depth (m)	Type of record
<i>Tretodictyum</i> cf. <i>tubulosum</i>	Schulze (1886)	Canyon du Planier	43°05'16"N 43°06'09"E	5°12'17"E/5°12'37"E	365–484	video
		Canyon de la Cassidaigne	43°02'35"N 43°08'09"E	5°23'49"E/5°29'39"E	380–632	video
		Canyon de Toulon	42°57'02"N	6°04'08"E	456	video
		Hauts fonds de Méjean	43°23'35"N	7°01'23"E	392–393	video
		Canyon de Cannes	43°29'53"N	7°01'22"E	359	video
		Canyon de Nice	43°33'55"N	7°11'54"E	560–565	video
		Canyon de Centuri N	43°00'23"N/43°02'47"N	9°14'45"E/9°16'04"E	397–552	video
		Canyon de Centuri S	42°56'28"N/42°58'47"N	9°15'12"E/9°18'35"E	384–545	video
		Canyon de St Florent	42°45'40"N/42°48'59"N	9°09'34"E/9°18'25"E	285–520	video
		Canyon de l'Île-Rousse	42°42'41"N	8°58'12"E	325–370	video
		Canyon de Calvi	42°36'48"N 42°37'37"N	8°43'28"E 8°44'34"E	272–432	video
		Canyon de Galeria	42°26'46"N 42°29'10"N	8°33'41"E 8°36'10"E	316–460	video
		Canyon de Porto	42°15'40"N 42°21'36"N	8°30'53"E 8°37'34"E	199–456	video
		Canyon de Cargese	42°06'34"N 42°07'06"N	8°34'10"E 8°34'22"E	427–537	video
		Canyon de Sagone	42°02'27"N	8°40'44"E	438	video
		Canyon d'Ajaccio	41°45'32"N 41°52'49"N	8°30'24"E 8°42'28"E	360–507	video
		Canyon de Valinco	41°39'26"N 41°41'53"N	8°43'22"E 8°50'16"E	312–444	collected
		El Loquet Bank	38°38'20"N	0°56'52"E	300	video
		El Banc de La Nau	38°33'28"N	0°39'48"E	497	video
		Emile Baudot escarpment	39°02'13"N	2°58'57"E	253	video
Emile Baudot seamount	38°42'47"N	2°36'23"E	522	video		
Emile Baudot seamount	38°37'24"N	2°26'05"E	571	video		
<i>Farrea</i> sp.		Canyon des Stoehades	43°08'24"N	6°40'47"E	683	video
		Canyon d'Ajaccio	41°46'12"N	8°39'00"E	442	video
		Canyon de Valinco	41°39'38"N	8°47'35"E	425	video
<i>Asconema setubalense</i>	Kent (1870)	Chella Bank	36°31'10"N	2°53'25"W	200–470	video
		Cabliers Bank	35°49'09"N	2°15'40"W	270–415	video
		Catifas Bank	35°49'50"N	2°34'28"W	370–465	video
		Avempace Bank	36°23'36"N	3°58'21"W	340–390	video

(Ijima, 1903; Lendenfeld, 1915; Koltun, 1970; Lévi & Lévi, 1989; Tabachnick & Lévi, 2004); and four in the Atlantic Ocean. However until very recently it was considered that *S. nux* was the only Atlantic *Sympagella*. Tabachnick & Menshenina (2013) then have described two species from the mid-Atlantic ridge (*S. cooki* and *S. ecomari*). With the species described here, four species are now recognized in the Atlantic and Mediterranean. However all the reported occurrences of *S. nux* in the Azores Islands, Cape Verde Islands and Namibia will have to be checked with regards to *S. delauzei*.

Distribution of hexactinellid species in the canyons of the French Mediterranean coast and in the Alboran Sea

Table 3 summarizes the recent findings of hexactinellids during the French research cruises MedSeaCan/CorSeaCan and by Spanish research cruises in the Alboran Sea. Four species have been observed among the 29 canyons explored along the French Mediterranean coast. *Tretodictyum* cf. *tubulosum* was the most abundant, being observed in 6/17 canyons of the French continental coast, 11/12 Corsican canyons (Table 3) and at three seamounts of the Alboran Sea. *Oopsacas minuta* which displays a large population at the 3PP cave (Boury-Esnault & Vacelet, 1994) has not been positively identified in the nearby canyons. In the Valinco Canyon in Corsica, one undescribed species of *Farrea* was present, not

far from the new species of *Sympagella*. Both *Tretodictyum* and *Farrea* species have recently been collected and will soon be studied in more details for a proper description and to solve their identification. *Asconema setubalense* is abundant in the Alboran Sea (four seamounts), but has not been collected at any other location in the Mediterranean Sea (Table 3).

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