

<https://doi.org/10.11646/zootaxa.4236.1.6>
<http://zoobank.org/urn:lsid:zoobank.org:pub:A2569FC8-0E88-416A-92A3-C61691E6FDDE>

New hexactinellid sponges from deep Mediterranean canyons

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Abstract

During the exploration of the NW Mediterranean deep-sea canyons (MedSeaCan and CorSeaCan cruises), several hexactinellid sponges were observed and collected by ROV and manned submersible. Two of them appeared to be new species of *Farrea* and *Tretodictyum*. The genus *Farrea* had so far been reported with doubt from the Mediterranean and was listed as "taxa inquirenda" for two undescribed species. We here provide a proper description for the specimens encountered and sampled. The genus *Tretodictyum* had been recorded several times in the Mediterranean and in the near Atlantic as *T. tubulosum* Schulze, 1866, again with doubt, since the type locality is the Japan Sea. We here confirm that the Mediterranean specimens are a distinct new species which we describe. We also provide 18S rDNA sequences of the two new species and include them in a phylogenetic tree of related hexactinellids.

Key words: new species, Porifera, *Farrea*, *Tretodictyum*, Cosmopolitan species, 18S rDNA, Molecular phylogeny, Red mud deposits

Introduction

The recent renewed interest for the exploration of the bathyal zone of the Mediterranean keeps revealing a higher diversity of hexactinellid sponges than previously thought (Pardo *et al.* 2011; Sitjà & Maldonado 2014; Boury-Esnault *et al.* 2015). During the survey of the NW Mediterranean deep-sea canyons, several hexactinellid sponges were observed and collected by ROV and manned submersible. In a previous paper, we have described *Sympagella delauzei* (Boury-Esnault *et al.* 2015) but two other hexactinellids were also suspected to be new species of *Farrea* and *Tretodictyum*. The genus *Farrea* had so far been reported from the Mediterranean as *F. irregularis* Bowerbank, 1876 and *F. spinulenta* Bowerbank, 1875, but this author never described the two sponges and no type-specimens are available. They are therefore listed as "taxa inquirenda" in the World Porifera Database (2016) for the two above-mentioned undescribed species. Our preliminary report (Boury-Esnault *et al.* 2015) and that of Maldonado *et al.* (2015) have mentioned the occurrence of *Farrea* sp. in Corsican canyons and off the Balearic Islands. In the Atlantic area, only 8 species are currently accepted in *Farrea* (Lopes *et al.* 2011), although 22 names can be found in the literature. This is largely due to the fact that 10 species from Bowerbank (1875; 1876) and Schmidt (1880) were never described and thus also remain "taxa inquirenda" (Table 1a). In the NE Atlantic, four species are accepted, one of them being the "cosmopolitan" species *Farrea occa* Bowerbank, 1862 (type species of the genus *Farrea*), the type specimen of which comes from Comoros (Western Indian Ocean, Reiswig 2002) (Table 1b).

The species *Tretodictyum tubulosum* Schulze, 1886 (type-species of the genus *Tretodictyum*) has been reported several times in the Mediterranean (Schulze 1900; Vacelet 1969; Vamvakas 1970; Zibrowius 1985; Longo *et al.* 2005; Boury-Esnault *et al.* 2015; Maldonado *et al.* 2015) and in the near Atlantic (Topsent 1928; Boury-Esnault *et al.* 1994; Dohrmann *et al.* 2008) (Table 2a). However the type-locality of this species is the NW Pacific (Japan Sea), which casts a doubt on this identification for specimens collected in the Atlanto-Mediterranean area (Vacelet 1969; Dohrmann *et al.* 2008). These doubtful assignments to *T. tubulosum* are the only ones reported for the Atlantic area in this genus, and the six other *Tretodictyum* species are all from the Indo-Pacific area (Table 2b).

TABLE 1A. Species names of the genus *Farrea* found in the literature for the NE Atlantic (upper table) and W Atlantic (lower table), their taxonomic status, and their reported distribution.

Species	Taxonomic status	Distribution
<i>Farrea occa</i> Bowerbank, 1862	Accepted	Cosmopolitan, Indian Ocean (type-locality Comoros), Antarctic, NE Atlantic, SW Atlantic, NW Pacific, SW Pacific
<i>Farrea irregularis</i> Bowerbank, 1876	Taxon inquirendum	NE Atlantic, W Mediterranean, Algerian Coast
<i>Farrea laminaris</i> Topsent, 1904	Accepted	NE Atlantic, Azores, Canaries, Madeira
<i>Farrea spinulenta</i> Bowerbank, 1875	Taxon inquirendum	Mediterranean, Tunisian Plateau, Gulf of Sidra
<i>Farrea weltneri</i> Topsent, 1901	Accepted	NE Atlantic, Azores
<i>Farrea woodwardi</i> (Kent, 1870)	Accepted	NE Atlantic, Portugal
<i>Farrea foliascens</i> Topsent, 1906	Accepted	NE Atlantic, Azores
<i>Farrea aculeata</i> Schulze, 1899	Accepted	Tropical NW Atlantic
<i>Farrea campossinus</i> Lopes, Hajdu & Reiswig, 2011	Accepted	SW Atlantic
<i>Farrea deanea</i> Schmidt, 1880	Taxon inquirendum	Tropical NW Atlantic, Caribbean
<i>Farrea facunda</i> (Schmidt, 1870)	Unaccepted	Tropical NW Atlantic, Caribbean
<i>Farrea gassioti</i> Bowerbank, 1875	Taxon inquirendum	Tropical NW Atlantic, Gulf of Mexico
<i>Farrea herdendorfi</i> Duplessis & Reiswig, 2004	Accepted	NW & SW Atlantic
<i>Farrea inermis</i> Bowerbank, 1876	Taxon inquirendum	Tropical NW Atlantic, Caribbean
<i>Farrea infundibularis</i> (Carter, 1877)	Unaccepted	Tropical NW Atlantic, Caribbean
<i>Farrea laevis</i> Bowerbank, 1875	Taxon inquirendum	Tropical NW Atlantic, Caribbean
<i>Farrea parasitica</i> Bowerbank, 1875	Taxon inquirendum	Tropical NW Atlantic, Caribbean
<i>Farrea perarmata</i> Bowerbank, 1876	Taxon inquirendum	Tropical NW Atlantic, Caribbean
<i>Farrea pocillum</i> Bowerbank, 1875	Taxon inquirendum	Tropical NW Atlantic, Caribbean
<i>Farrea robusta</i> Bowerbank, 1875	Taxon inquirendum	Tropical NW Atlantic, Caribbean
<i>Farrea spinifera</i> Bowerbank, 1875	Taxon inquirendum	Tropical NW Atlantic, Caribbean

TABLE 1B. Records of *Farrea occa* in the literature. Type locality in bold. MEOW: Marine Ecoregions of the World (Spalding *et al.* 2007). NA: not available.

Source	Ocean	MEOW region	Latitude	Longitude	Depth m
Topsent 1901	Antarctic	Amundsen/Bellinghausen Sea	-71.233S	-89.233W	450
Topsent 1892	NE Atlantic	Azores Canaries Madeira	38.396N	-30.858W	927
Topsent 1904	"	"	38.1N	-26.217W	3018
Topsent 1928	"	"	39.417N	-31.367W	1229
Burton 1954	"	"	28.417N	-13.233W	NA
Burton 1928	"	N Atlantic Lower Bathyal Province	61.733N	-27W	887
Boury-Esnault <i>et al.</i> 1994	"	Saharan upwelling	35.611N	-6.751W	826
Lopes <i>et al.</i> 2011	SW Atlantic	Lower Bathyal Basin (Campos Basin)	-22.35S	-39.97W	1150
Bowerbank 1862	Indian Ocean	Western & Northern Madagascar	-11.833S	43.167E	NA
Dendy & Burton 1926	"	South India & Sri Lanka	7.291N	76.908E	1440
"	"	Andaman & Nicobar	11.616N	92.233E	494
Lévi & Lévi 1989	Central Indo-Pacific	Eastern Philippines	13.033N	122.617E	1100
Carter 1885	NW Pacific	Central Kuroshio Current	35.066N	139.75E	NA
Schulze 1887	"	"	35.216N	139.383E	NA
Reiswig & Kelly 2011	SW Pacific	Kermadec Islands	32.605 S	179.602W	1175

TABLE 2A. Records of *Tretodictyum tubulosum* in the literature previous to the recent reports of Boury-Esnault *et al.* (2015) and Maldonado *et al.* (2015). Type locality in bold. MEOW: Marine Ecoregions of the World (Spalding *et al.* 2007). NA: not available.

Source	Ocean	MEOW region	Latitude	Longitude	Depth m
Schulze 1886	NW Pacific	Central Kuroshio Current	35.250N	139.433E	NA
Ijima 1927	"	Gulf of Tonkin	17.733N	110.433E	216
"	"	Palawan/North Borneo	5.718N	119.667E	522
Wilson 1904	NE Pacific	Eastern Galapagos	0.267N	-90.358W	1008
"	"	Panama Bight	4.050N	-81.517W	1645
Dohrmann <i>et al.</i> 2008	NE Atlantic-Mediterranean	Celtic Seas (Rockall)	55.499N	-15.798W	581
Topsent 1928	"	Cape Verde	15.283N	-23.05W	875
Boury-Esnault <i>et al.</i> 1994	"	Alboran Sea	35.434N	-4.301W	390-400
"	"	"	35.935N	-5.569W	534-560
Schulze 1900	"	W Mediterranean Tyrrhenian Sea	40.581N	14.433E	NA
Longo <i>et al.</i> 2005	"	Ionian Sea	39.462N	18.402E	738-809
Zibrowius 1985	"	Ionian Sea (Apulian escarpment)	38.5N	19.45E	2180-2644
"	"	Ionian Sea (Malta escarpment)	36.417N	15.58E	1916-2539
Vamvakas 1970	"	Aegean Sea, Gulf of Athens (Epidaurus hollow)	37.667N	23.2E	207
Vacelet 1969	"	W Mediterranean (Cassidaigne canyon)	42.983N	5.367E	320
"	"	W Mediterranean (Cassidaigne canyon)	42.883N	5.333E	500
"	"	W Mediterranean (off Blauquieres bank)	43.033N	5.617E	340

TABLE 2B. Species names of the genus *Tretodictyum* found in the literature, their taxonomic status and their reported distribution.

Species	Taxonomic status	Distribution
<i>Tretodictyum tubulosum</i> Schulze, 1886	Accepted	NW Pacific, Japan Sea, NE Pacific, NE Atlantic, Mediterranean
<i>Tretodictyum amchitkensis</i> Reiswig & Stone, 2013	Accepted	N Pacific, Aleutian Islands
<i>Tretodictyum cocosensis</i> Reiswig, 2010	Accepted	Tropical E Pacific, Cocos Islands
<i>Tretodictyum minor</i> (Dendy & Burton, 1926)	Accepted	Indian Ocean, Andaman and Nicobar Islands
<i>Tretodictyum montereyense</i> Reiswig, Dohrmann, Pomponi & Wörheide, 2008	Accepted	NW Pacific, California
<i>Tretodictyum pumicosum</i> Ijima, 1927	Accepted	Indopacific, Banda Sea
<i>Tretodictyum schrammeni</i> Ijima, 1927	Accepted	Indopacific, Banda Sea

The present descriptions of new species of *Farrea* and *Tretodictyum* from the Mediterranean, obviously different from their Indopacific relatives, highlights the necessity to take the problem of so-called “cosmopolitan” species in consideration in Hexactinellida, just as it has been done in the three other Poriferan classes.

Material and methods

Observation and collection sites (Table 3 and Fig. 1). Still and video images of the two new hexactinellid species were obtained from the cameras of ROVs and submersibles deployed during several deep-sea cruises: CYLYCE

cruise (IFREMER) at the Ile Rousse Canyon in 1997; A HERMES-MARUM cruise at the Cassidaigne canyon in 2009 (information communicated by A. Freiwald), the MedSeaCan cruises at canyons and rocky banks of the coasts of continental France (2008–2009), the CorSeaCan cruises at canyons and rocky banks of the western coast of Corsica (2010), the ROV-3D cruise to the Valinco and Les Moines canyons in SW Corsica (2014) and an ALTEO cruise at the Cassidaigne canyon (2016). Already published information from several OCEANA cruises (2010–2014) off the Balearic Islands (Boury-Esnault *et al.* 2015; Maldonado *et al.* 2015) were also considered. Most of the specimens observed were not collected and their identification is based on similarities of external characters with the sampled specimens. These identifications appear rather safe, given the distinctive body shape, aspect and colour of the two species and the low diversity of hexactinellids in the Mediterranean. Specimens of each new species were collected by the manipulator arm of the ‘Achille’ ROV (COMEX S.A.) during the ROV-3D cruise. The new species of *Farrea* was collected in July 2014 in the Valinco Canyon (SW Corsica) at 383 m depth. After recovery on board, most of the specimen was preserved in 95% ethanol while smaller pieces were frozen at -20°C and fixed in 2.5% glutaraldehyde. Two specimens of the new species of *Tretodictyum* were collected the same day in the Valinco Canyon at 397 m depth. They were preserved in 95% ethanol while smaller pieces have been frozen (-20°C) and fixed in 2.5% glutaraldehyde. The type-specimens are deposited in the Museum National d’Histoire Naturelle, Paris (MNHN); the remaining material is preserved in collections of the Station Marine d’Endoume, Marseille (SME), where paratypes are numbered 490 and 491.

TABLE 3. Distribution of *Farrea bowerbanki* n. sp. and *Tretodictyum reiswigi* n. sp. as reported in the literature and observed here during HERMES-MARUM, MedSeaCan, CorSeaCan, ROV-3D and ALTEO cruises on still pictures and videos (see Material & Methods). Sites of material collection in bold. Records from the literature allocated with doubts to *Tretodictyum tubulosum* and *Farrea occa*, and which we here allocate to the new species. NA: not available.

Species	Source	Station name	Latitude	Latitude	Depth (m)
<i>Farrea bowerbanki</i> n. sp.	This work	Stoechades canyon	43.14N	6.680E	683
		Ajaccio canyon	41.770N	8.65E	442
		Valinco canyon	41.661N / 41.694N	8.744E / 8.796E	378–426
		Cassidaigne canyon	43.117N / 43.127N	5.471E / 5.489E	478–663
	Maldonado <i>et al.</i> 2015	Emile Baudot Jr. seamount	38.715N	2.604E	495
<i>Tretodictyum reiswigi</i> n. sp.	This work	Planier canyon	43.088N / 43.103N	5.204E / 5.210E	365–484
		Cassidaigne canyon	43.043N / 43.136N	5.428E / 5.547E	380–632
		Toulon canyon	42.950N	6.069E	456
		Méjean rocky bank	43.393N	7.023E	392–393
		Cannes canyon	43.498N	7.023E	354–393
		Nice canyon	43.565N	7.198E	560–565
		North Centuri canyon	43.006N / 43.046N	9.251E / 9.268E	340–552
		South Centuri canyon	42.941N / 42.980N	9.253E / 9.310E	384–545
		St Florent canyon	42.761N / 42.816N	9.159E / 9.307E	285–520
		Ile-Rousse canyon	42.711N / 42.833N	8.97E / 8.951E	243–370
		Calvi canyon	42.613N / 42.627N	8.724E / 8.743E	272–392
		Galeria canyon	42.446N / 42.486N	8.561E / 8.603E	316–460
		Porto canyon	42.261N / 42.36N	8.515E / 8.626E	199–456
		Cargese canyon	42.109N / 42.118N	8.569E / 8.573E	427–543
		Sagone canyon	42.041N	88.679E	438
		Ajaccio canyon	41.759N / 41.880N	8.507E / 8.708E	356–507
		Valinco canyon	41.657N / 41.698N	8.723E / 8.838E	312–444

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TABLE 3. (Continued)

Species	Source	Station name	Latitude	Latitude	Depth (m)
		Les Moines canyon	41.746N	8.740E	186–491
Boury-Esnault <i>et al.</i> 2015	El Loquet Bank		38.639N	0.948E	300
		Bank de La Nau	38.558N	0.633E	497
		Emile Baudot escarpment	39.037N	2.982E	253
Maldonado <i>et al.</i> 2015	Emile Baudot Jr. seamount		38.715N	2.604E	495
		Emile Baudot South seamount	38.623N	2.437E	600
Vacelet 1969	Cassidaigne canyon		42.983N	5.367E	320–350
	Cassidaigne canyon		42.883N	5.333E	500
	Blauquieres rocky bank		43.033N	5.617E	340
Schulze 1900	Tyrrhenian Sea, Galli Islands, Amalfi coast		40.581N	14.433E	NA
Vamvakas 1970	Aegean Sea, Gulf of Athens		37.667N	23.2E	207
Longo <i>et al.</i> 2005	Ionian Sea, Cape S. Maria di Leuca		39.462N	18.402E	738–809
Zibrowius 1985	Ionian Sea, Apulian escarpment		38.5N	19.45E	2180–2644
	Ionian Sea, Malta escarpment		36.417N	15.58E	1916–2539
Boury-Esnault <i>et al.</i> 1994	Alboran Sea		35.435N	-4.301W	390–340
	Alboran Sea		35.935N	-5.57W	534–560
Topsent 1928	Cape Verde		15.283N	-23.05W	875
Dohrmann <i>et al.</i> 2008	Celtic Seas, Rockall		55.499N	-15.798W	581

Spicule and skeleton preparation. Skeletal architecture was studied by light microscopy on whole mounts or on sections, hand-cut or 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). 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). About 20–30 measurements were made for each type of spicule. Minimum, maximum and mean sizes are provided.

Molecular characterization. One piece of an ethanol-preserved specimen of each species was used for DNA extraction using QIAamp DNA Mini kit (Qiagen). PCR amplifications of ca 1900 bp of the 18S ribosomal DNA (18S) were conducted with primers 18S D and 18S G as in Gazave *et al.* (2010). Consensus sequences were obtained after cloning PCR products, assembling and editing sequences with BioEdit 7.0.9 (Hall 1999). Sequences were deposited in the European Nucleotide Archive (ENA—EMBL) under accession numbers LT627560–LT627561.

Sequences were manually aligned with other 18S sequences of Hexactinellida recovered from nucleotide databases to build phylogenetic trees. Phylogenetic reconstructions were estimated through the Neighbour-joining

(NJ) method as implemented in CLUSTALX 2.1 (Larkin *et al.* 2007), which was then used as a starting tree for a Maximum likelihood (ML) analysis (HKY85 substitution model) as implemented in PhyML 3.0 with Smart Model Selection (Guindon *et al.* 2010). With both methods, bootstrap support was assessed over 1000 replicates.

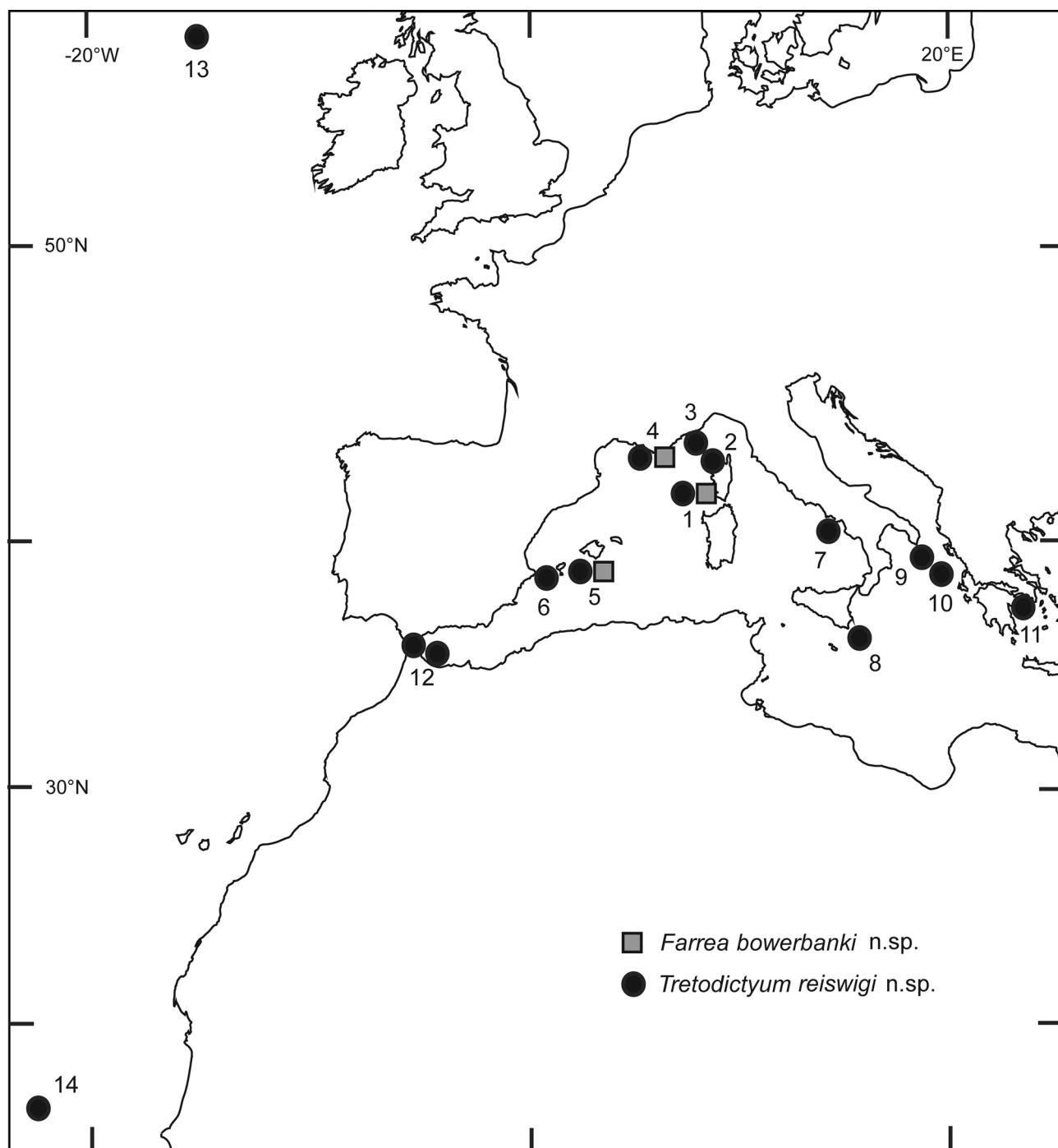


FIGURE 1. Distribution map of the two new species *Farrea bowerbanki* (grey squares) and *Tretodictyum reiswigi* (black circles) based on recent observations and collections as well as on literature records (see Table 3). 1. SW Corsican canyons (including Valinco canyon, the type locality of the two new species); 2. NW Corsican canyons; 3. French Riviera canyons and deep rocky banks; 4. Provence canyons and deep rocky banks; 5. Emile Baudot escarpment and seamounts; 6. El Loquet and de la Nau banks; 7. Galli Islands; 8. Malta escarpment; 9. Cape Santa Maria di Leuca; 10. Apulian escarpment; 11. Gulf of Athens; 12. Alboran Sea; 13. Rockall bank; 14. Cape Verde Islands.

Description

Hexactinellida Schmidt, 1870

Hexasterophora Schulze, 1886

Hexactinosida Schrammen, 1912

Sceptrulophora Mehl, 1992

Farreidae Gray 1872

***Farrea* Bowerbank, 1862**

***Farrea bowerbanki* n. sp. Boury-Esnault, Vacelet & Chevaldonné**

Type-specimen. Sample VAL2-ACH-P15_ECH01. MNHN-HJV-03

Type-locality. Valinco Canyon, SW Corsica (Western Mediterranean), 383 m, 41.66148N / 8.7953E, 31/07/2014.

Comparative material. Slides from specimens of the Ibero-Moroccan Gulf (BALGIM Cruise, 1984, Stn CP91-13, 34.3675N –7.417W, 945 m).

External morphology. Several specimens were observed on ROV pictures and videos or by direct observations from the manned submersible ‘Remora 2000’ (Comex) in 2009, 2010, 2014 and 2016 (Fig. 1, 2 and 4, Table 3). A complete specimen, designated as holotype, has been collected in 2014. The holotype (Fig. 2A, 2C) is 15 cm high, with a diameter of about 20 cm at its widest part. The body is formed by a branching and anastomosing system of tubes attached to the rocky substrate by a small basal plate, 2 cm in diameter. Two main tubes, 2 cm in diameter, arising from the basal plate, divide and merge several times, with distally infundibular openings 5–8 cm wide. The shape of these openings is reminiscent of a flower corolla. The thickness of the tube wall is about 1–2 mm. Color in life is white, with the basal plate and a short common basal part of the tubes, deep grey. The sponge is very fragile, and several parts of the tubes are broken on the preserved holotype which was very difficult to collect in a good state of preservation by the ROV. The other specimens observed, such as shown in Figures 2B, 4A, 4B and 4D, have the same general shape, varying in size from a few centimeters to 40 cm. Several observed specimens were composed of a white living part and of a dead skeleton, colored in grey due to the deposit of mud.

Skeleton. The skeleton framework is a typical farreoid dictyonal type with smooth beams and spined spurs (Fig. 2D, 2F). Dictyonalia are formed in more than one layer. The meshes are mostly rectangular, sometimes square or triangular (Fig. 2E), with dictyonal beams 168–430/35–50 µm in size. The spurs are 90–210 µm in length, always spined and most often curved (Fig. 2F).

Spicules

- Uncinates (Fig. 2K), very thin, often slightly curved, with spines strongly recurved, more numerous and longer (up to 2 µm long) on one third: 738–1350/5–10 µm (mean 989.8/6.8 µm).
- Pentactins (Fig. 2G), similar on dermal and atrial sides, frequently with a vestigial 6th ray; tangential rays smooth on the outer and lateral surface; proximal ray and tip of the tangential rays microspined: tangential rays 100–270 µm (mean 220 µm), proximal ray 172–225 µm (mean 204 µm), vestigial 6th ray 5–11 µm (mean 6.4 µm).
- Pileate-anchorate clavules (Fig. 2I, 2J), 192–345/1–2 µm (mean 246/1.26 µm) in length; diameter of the head 7–27.5 (mean 15.9 µm) with claws 2.5–16 µm (mean 5.7 µm) in length but sometimes vestigial.
- Microscleres onychasters (Fig. 2H), sometimes oxyhexasters, finely spinose, with primary rays dividing into three secondary rays with extremities bearing small recurved spines, *i.e.* onychoid (onychasters), more rarely sharp (oxyhexasters). Diameter 75–105 µm (mean 87.5 µm), the primary rays always shorter than the secondary ones, 12–17.5 µm (mean 14.8 µm) versus 25–35 µm (mean 28.3 µm).
- Some very rare microhexactins present, rays smooth, 40–45 µm long.

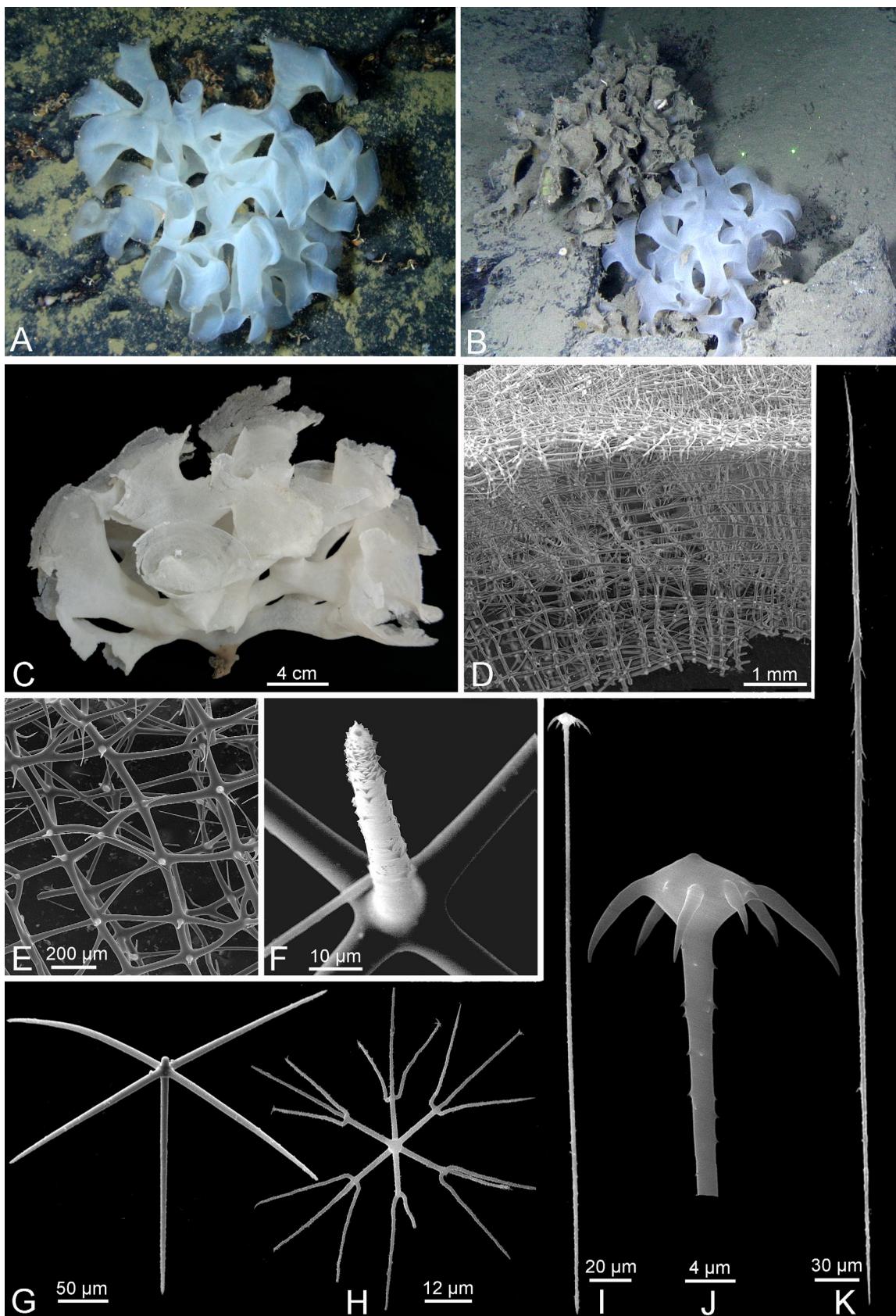


FIGURE 2. *Farrea bowerbanki* n. sp. A: In situ view of the holotype before collection, Valinco canyon, Corsica, 383 m. B: Another specimen from the Valinco canyon, Corsica, at 425 m, next to a dead individual. The green dots in the center are laser beams 6 cm apart. C: preserved holotype. D, E: dictyonal framework near the base. F: beams and spur of a dictyonalium. G: pentactin. H: onychexaster. I, J: clavule. K: uncinate. A, B: Photos courtesy of AAMP.

Distribution. The type locality is the Valinco canyon on the south-western coast of Corsica, at 41.66148N / 8.7953E and 383 m depth. Several other specimens (Fig. 2B) were observed in this canyon between 378 and 426 m, where the species is exceptionally common. Other, isolated specimens were observed on still and video images in other Mediterranean canyons: Stoechades Canyon, 43.14 N 6.680E at 683 m, Ajaccio Canyon, 41.778N 8.65E at 442 m. However it is most common in the Cassidaigne canyon (Fig. 4A, 4B, 4D) where this species occurs in high densities between 478 and 663 m, although these areas are heavily impacted by red-mud discharge from an aluminum plant (Bourcier & Zibrowius 1972). For the time being this species has only been reported from the Mediterranean Sea.

Etymology. The species name, *bowerbanki*, refers to the British spongologist James Scott Bowerbank who was the first to report *Farrea* from the Mediterranean Sea. Unfortunately he did not provide a proper description of the species (Lopes *et al.* 2011).

Remarks. *Farrea bowerbanki* shares with all other *Farrea* described so far a typical farreoid dictyonal skeleton, the presence of clavules, uncinates and pentactine megascleres and microhexasters as microscleres. The new species is mainly characterized by its shape, especially the size of the tubes, with distally infundibular openings. It is also distinct by the shape of the pentactins which are mostly smooth except at the end of the rays which bear a very short spination (Fig. 2G). This character is shared with *Farrea mexicana* Wilson 1904 from the northeastern Pacific (Cortezian Marine Ecoregion) (Lopes *et al.* 2011) which differs mainly by the shape of the anchorate clavules. Most of the other *Farrea*, including the type species *F. occa*, as well as specimens from the Ibero-Moroccan Gulf (Boury-Esnault *et al.* 1994), possess pentactines with tuberculated tangential rays. The NE Atlantic species *F. weltneri* and *F. woodwardi* differ by the presence of discohexasters, *F. herdendorfi* by the presence of thimbleate clavules and heavily spined pentactins, *F. foliascens* by the presence of umbellate clavules and heavily spined pentactins and *F. laminaris* by the absence of tubes and a laminated shape as well as spined pentactins (Lopes *et al.* 2011). All specimens allocated to the Atlantic area need to be revised in order to document the exact distribution of *Farrea occa*, as already suggested by Ijima (1927) (Table 1b).

Tretodictyidae Schulze, 1886

Tretodictyum Schulze, 1886

Tretodictyum reiswigi n. sp. Boury-Esnault, Vacelet & Chevaldonné

Type-specimen. Sample VAL2-ACH-P15-ECH02. MNHN-HJV-04,

Type-locality. Valinco Canyon (Western Mediterranean) 41.662N/8.795E, 397 m, 31/07/2014.

Other material (available in SME collection): Sample CS-ACH-P03-ECH06b, a small fragment encrusting a brachiopod shell, Cassidaigne canyon (W Mediterranean) 43.047N/5.397E, 370 m, 28/10/2009. Sample VAL-ACH-P12-ECH01, small fragments, Valinco Canyon, Corsica, 41.663N/8.795E, 444 m, 24/08/2010. Sample from CYLYCE cruise, dive 12 of Cyana submersible, fragments of two tubes, Ile Rousse Canyon, NW Corsica, 42.833N/8.953E, 320 m, 25/05/1997, Slides from specimens of BALGIM Cruise, R/V Cryos, Alboran Sea, Station CP135-168, 35.435N/-4.301W and DR152-257, 35.935N/-5.569W, 390–560m, May–June 1984.

External morphology. The sponge is formed by several tubes more or less coalescent, expanding from a narrower base of attachment to the substrate. The tubes are most often arranged in a single or a double line (Fig. 3), with each line formed by up to 12 tubes. The maximum size estimated from ROV images is ca 15 x 7 x 5 cm, with tubes either entirely joined or free for up to 5 cm. The tubes are 1–2.2 cm in diameter with a central canal 0.55–0.65 cm in diameter. The wall of the tubes is ca 3 mm thick. The surface is pierced by numerous small depressions. The color is pure white in living or freshly dead specimens, grey in dead skeletons due to sediment deposits. Specimens with both living parts and dead skeletons have often been observed (Fig. 3B). The consistency is hard, but the sponge is easily broken.

Numerous observations of sponges with very similar external characters have been made between 199 and 632 m depth from submersible and ROV dives, for examples Fig. 3A, 3B; Fig. 4B, 4C, 4D (Table 3). Their identification to the same species is made with great confidence.

Skeleton. The main skeleton is a dictyonal framework of square meshes with 200–300 µm sides and beams 30–60 µm thick, with tubercles arranged in rows. Megascleres are dermal and parenchymal hexactins.

Strongyloscopules are present in dermal and atrial surfaces. Microscleres are oxyhexactins and two types of hexasters.

Spicules

- Hexactins with unequal rays (Fig. 3I): basal rays with few spines, 115–750 x 9–15 µm, (mean length: 322.5 µm). Lateral rays 80–180 x 6–15 µm, mean length 117.4 µm. Apical rays, shorter and generally more spinose than the other rays, 60–90 x 7–15 µm, mean length 80 µm.
- Hexactins with equal or sub-equal rays (Fig. 3G, 3H), less numerous and less spinose, rays 60–150 x 5–8 µm, mean length 110 µm.
- Strongyloscopules (Fig. 3L), 510–870 x 3.5–4.5 µm (mean length for 30 measurements: 668.3 µm), branches 60–110 µm (mean: 79.8 µm).
- Uncinates (Fig. 3F), straight or slightly curved, very thin, with long points. 190–590 x 2.4–2.6 µm (mean length for 30 measurements: 378.27 µm).
- Oxyhexactins, rare, sometimes with one ray divided, 45–100 µm in diameter (mean: 75.3 µm).
- Oxyhexasters (Fig. 3K), very numerous, with primary rays divided in two secondary rays along an open angle, with a cover of small spines: 55–100 µm in diameter (mean: 77 µm).
- Tylohexasters (Fig. 3J), less abundant and larger than oxyhexasters, with primary rays divided in secondary rays along a closed angle most often in three, sometimes in 2, 4 or 6, rarely one primary ray not divided. All rays covered by small spines, more numerous on secondary rays. The end of secondary rays is only slightly enlarged: 70–130 µm in diameter (mean: 92 µm).

These spicule characters are in good agreement with those given for specimens from Gibraltar and the Alboran Sea identified as *T. tubulosum* (Boury-Esnault *et al.* 1994), in which however the tylohexasters have not been reported; a re-examination of the slides of the two specimens described in this publication has shown that tylohexasters are very rare, but present. The specimen from Cylyce cruise in Corsica differs only by subtle spicule characters, such as tylohexasters up to 150 µm in diameter and oxyhexasters having sometimes 2 or 3 rays not divided.

Distribution. Our review of recent research cruise observations indicates that the sponge occurs from 186 to 632 m depth in most of the western Corsican canyons, in five French continental canyons (Planier, Cassidaigne, Toulon, Cannes and Nice canyons) and on the Méjean Rocky Bank (Table 3). Vacelet (1969) had already mentioned this species under the name *Tretodictyum tubulosum* at the Cassidaigne canyon and near the Blauquières bank (320–500 m, Table 2). It has also been reported under this name off the Amalfi coast of Italy, off the Balearic Islands, in the Ionian Sea and in the Gulf of Athens between 207 and 809 m depth (Schulze 1900; Vamvakas 1970, Longo *et al.* 2005; Boury-Esnault *et al.* 2015; Maldonado *et al.* 2015), with possible deeper occurrence (according to identifications from underwater pictures) on deep-sea cliffs in the Ionian Sea (Eastern Mediterranean) between 2064 and 2644 m depth (Zibrowius 1985). The sponge is always attached to vertical or subvertical rocky surfaces, more rarely on small rocks isolated in the mud. It may be very common on these vertical surfaces. For instance, a density of 30 living specimens and 4 dead skeletons per square meter has been estimated from pictures in parts of Saint Florent canyon in Corsica at 285 m. A similar high density of living and dead specimens has been observed on cliffs covered by brown-red sediment in Cassidaigne canyon, ca 480 m depth (*e.g.* Fig 4C) in areas exposed to “red muds” discharged by an aluminium plant (Bourcier & Zibrowius 1972).

Etymology. The species name refers to Henry Reiswig, who contributed so much to the knowledge of Hexactinellida.

Remarks. *Tretodictyum tubulosum*, first described from Japan (Enoshima, Sagami Bay) by Schulze (1886), and later redescribed by Schulze (1887) under the name *Hexactinella tubulosa*, has been reported with doubt several times from areas very distant from its type locality. It has been also recorded in the NE Pacific, Galapagos and Pacific coast of Panama (Wilson 1904), the NE Atlantic from Cape Verde (Topsent 1928) to the Rockall bank (Dohrmann *et al.* 2008) and the Mediterranean from Alboran to Aegean Seas (Schulze 1900; Vacelet 1969; Vamvakas 1970; Zibrowius 1985; Boury-Esnault *et al.* 1994; Longo *et al.* 2005) (Table 2b). Such a very large distribution is however unlikely. Our specimens from the European area confirm that they clearly differ from *T. tubulosum* from Sagami Bay (Japan). Their spicule complement differs from that of *T. tubulosum* (as summarized

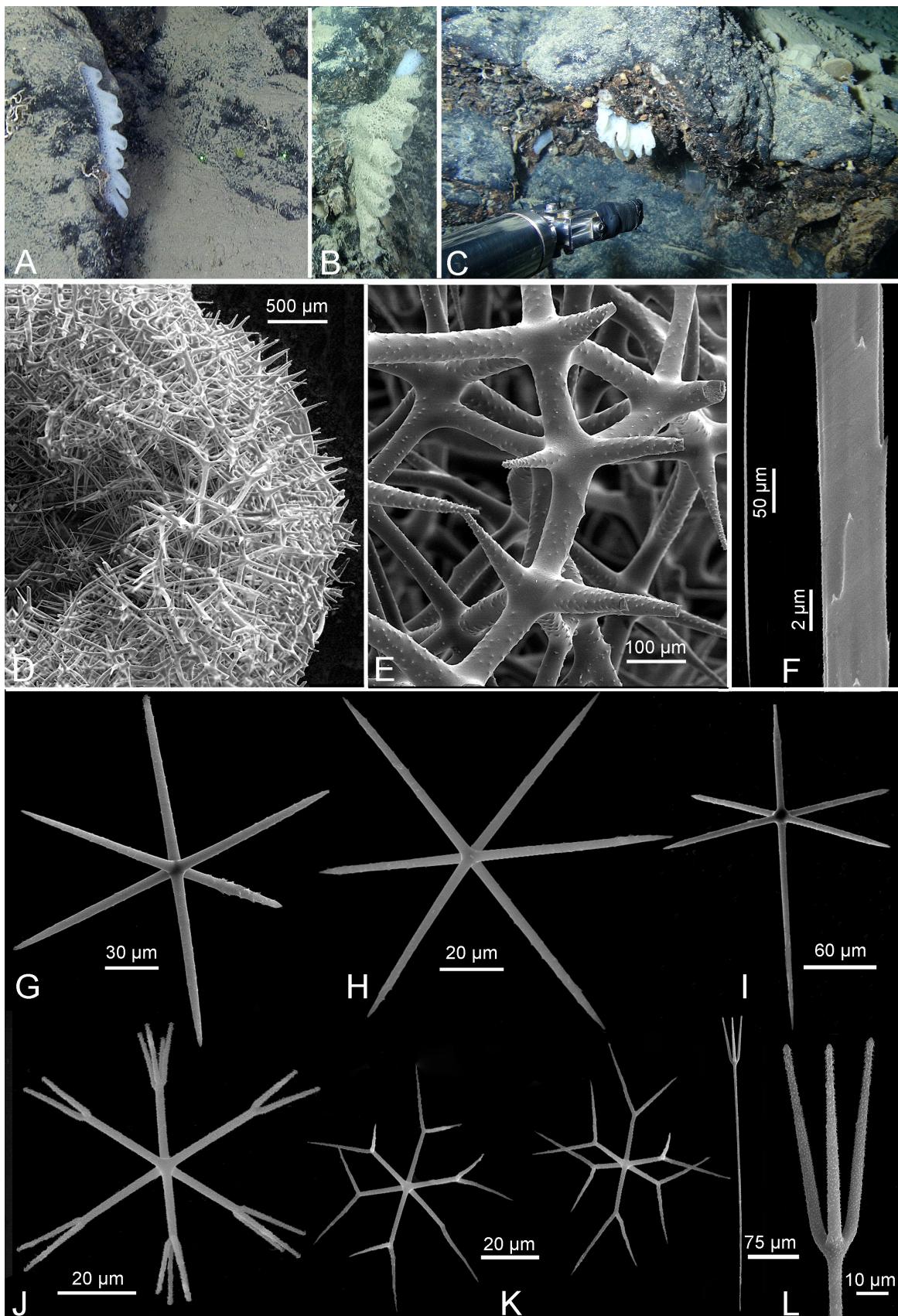


FIGURE 3. *Tretodictyum reiswigi* n. sp. A: Live specimen in Valinco Canyon, Corsica, 592 m. B: Mostly dead specimen with a single living tube (upper right), Cargese Canyon, Corsica, 536 m. C: Holotype, collected in Valinco Canyon, Corsica, 397 m. D, E: dictyonal framework. F: uncinate. G, H: hexactins with equal rays. I: hexactin with one longer ray. J: tylohexaster. K: oxyhexasters. L: strongyloscopule. A, B, C: Photos courtesy of AAMP.

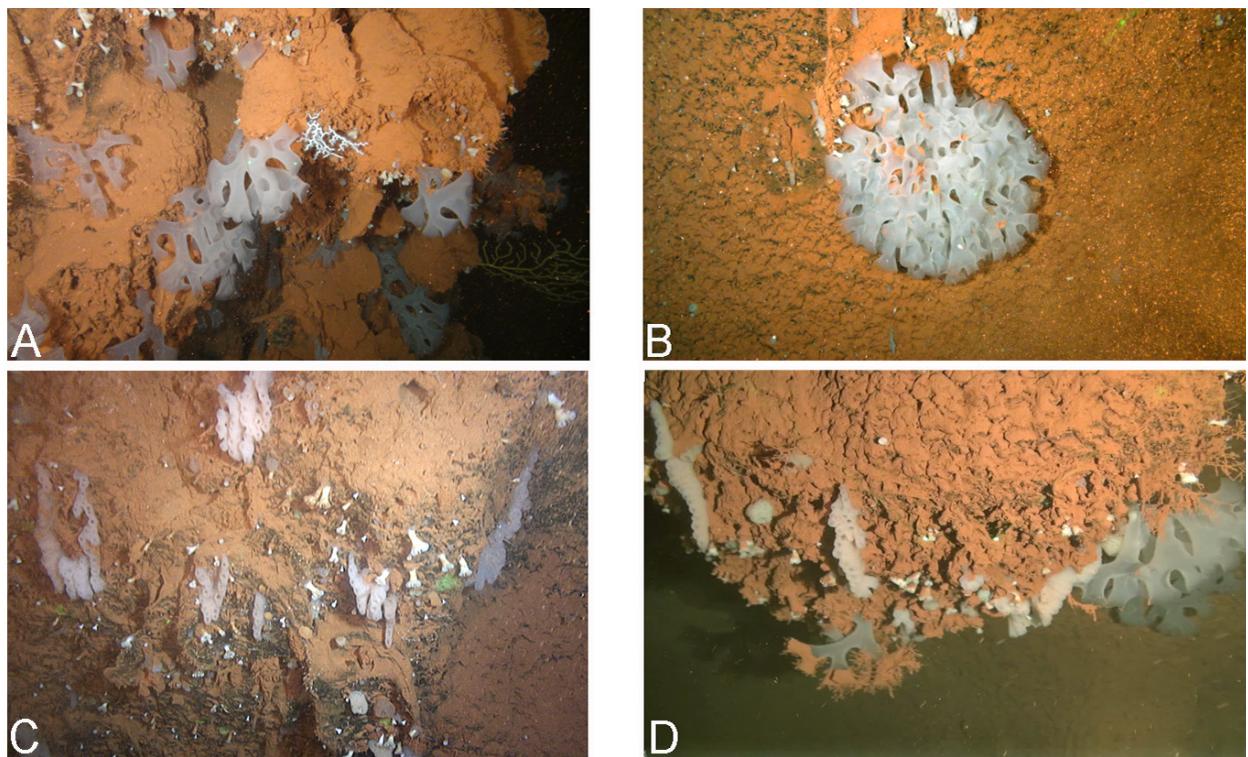


FIGURE 4. *Farrea bowerbanki* n. sp. and *Tretodictyum reiswigi* n. sp. at the Cassidaigne canyon (Provence, NW Mediterranean), in areas exposed to industrial red mud discharge for decades. A: The highest density of *F. bowerbanki* observed so far, growing on (sub-fossil?) shells of the bivalve *Neopycnodonte zibrowii*, 580 m. In the center, the cold-water scleractinian coral *Madrepora oculata*. B: An isolated specimen of *F. bowerbanki*, ca 30 cm in diameter, and small specimens of *T. reiswigi*, at 536 m. C: High density of live *T. reiswigi* with a dead skeleton in the center, ca 480 m. D: Live specimens of *T. reiswigi* and *F. bowerbanki* at 521 m. The one on the lower left is apparently partly dead, as the distal parts accumulate red mud. A, B, D: Photos courtesy of COMEX S.A. C: Photo courtesy of MARUM - Center for Marine Environmental Sciences, University of Bremen, Germany.

from literature in Reiswig 2002), by having two types of hexactins instead of one pentactin and also by differences in the hexaster microscleres, including the presence of tylohexasters. The DNA sequences obtained here suggest that the Mediterranean specimens and those from the NE Atlantic (Rockall Bank, Celtic Sea), obtained by Dohrmann *et al.* (2008), may belong to the same species, *T. reiswigi*. Among *Tretodictyum*, this new species, the only one reported in the Atlantic-Mediterranean area, differs by its characters not only from *T. tubulosum* as discussed above, but also from the other species reported from the Indo-Pacific area. The presence of tylohexasters differentiates the new species from *T. tubulosum*, but also from *Tretodictyum minor* (Dendy & Burton 1926) (Indian Ocean), *T. pumicosum* and *T. shrammeni* Ijima, 1927 (NE Pacific) and *T. montereyense* Reiswig *et al.*, 2008 (NW Pacific); in addition, *T. minor* and *T. montereyense* are lamellar instead of tubular. The other species having discohexasters more or less similar to the tylohexasters of the new species, *T. cocosensis* Reiswig, 2010 (tropical Eastern Pacific) and *T. amchitkensis* Reiswig & Stone, 2013 (N. Pacific), have discohexasters with 4–7 secondary rays and differ by a lamellar shape and several spicule characters, such as pentactins or pinular hexactins.

Discussion

Geographical distribution. As the exploration capabilities of the deep sea increase over time, the hexactinellid sponge fauna of the Mediterranean does not seem to be as poor as once suspected, now counting 8 valid species. By themselves, the recent efforts deployed by the MedSeaCan and CorSeaCan cruises have allowed the description of three new hexactinellid species, *Sympagella delaizei* (Boury-Esnault *et al.* 2015), *Farrea bowerbanki* n. sp. and *Tretodictyum reiswigi* n. sp. (this paper).

Farrea bowerbanki has some noteworthy populations especially in 3 canyons of the SW coast of Corsica and

in Cassidaigne Canyon off the Provence coast (Figure 1; Table 3). It appears to also be present on one of the Emile Baudot seamounts in the Balearic Sea (Maldonado *et al.* 2015). The specimen reported as *Farrea occa* in the Ibero-Moroccan Gulf does not belong to the new species and is likely a new Atlantic species. For the time being the new species *F. bowerbanki* seems to be restricted to the Mediterranean Sea.

Tretodictyum reiswigi has been collected in many of the canyons studied during MedSeaCan and CorSeaCan cruises, and has been also recorded in the Aegean, Ionian and Tyrrhenian Seas (Schulze 1900; Vamvakas 1970; Zibrowius 1985; Longo *et al.* 2005), the Balearic Sea (Maldonado *et al.* 2015) and the Alboran Sea (Boury-Esnault *et al.* 1994). Furthermore, this species is not restricted to the Mediterranean area since it has also been collected at Rockall (Celtic Sea) and the Cape Verde Islands (Topsent 1928; Dohrmann *et al.* 2008).

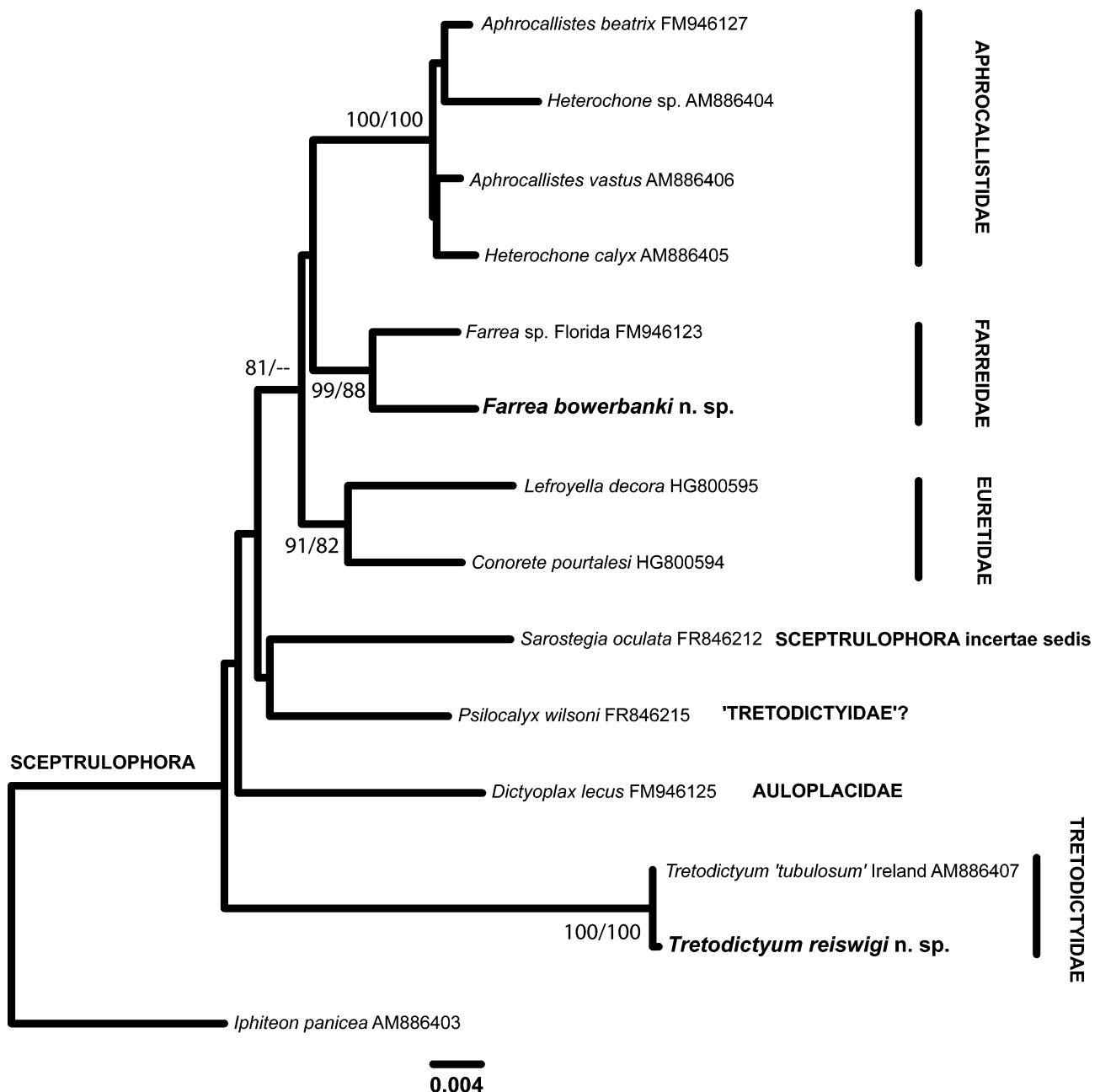


FIGURE 5. Placement of the two new species *Farrea bowerbanki* and *Tretodictyum reiswigi* in a phylogenetic tree (here NJ topology presented, see text) inferred from 18S rDNA sequences of Sceptrulophora (Hexactinellida) currently available in DNA databases at this partition. Bootstrap support (>80%) is presented as percentages for 1000 replicates (NJ/ML). The tree is rooted with *Iphiteon panicea*. Scale bar: genetic distance.

It seems that studying in more details, and with more material, so-called “cosmopolitan” sponge species results in discovering cryptic species. Since the 1990’s, several examples have demonstrated that species of the Poriferan classes Calcarea, Homoscleromorpha and Demospongiae with a very wide geographical distribution resulted from over-conservative systematics (Solé-Cava *et al.* 1991; Klautau *et al.* 1999; Lazoski *et al.* 2000; Boury-Esnault & Solé-Cava 2004). These cosmopolitan species were very often the type species of a genus—*e.g.* *Oscarella*, *Plakina*, *Spirastrella*, *Chondrilla*, *Chondrosia* etc. In Hexactinellida, perhaps because material is not easily collected, several such species with wide distributions are still accepted (Ijima 1927; Vacelet 1969; Reiswig 2002; Dohrmann *et al.* 2008; Lopes *et al.* 2011) and have not yet been thoroughly and critically reviewed. They are also type-species of genera, such as *e.g.* *Aphrocallistes*, *Farrea*, *Tretodictyum, etc. The present descriptions of new species of *Farrea* and *Tretodictyum* from the Mediterranean, obviously different from their Indopacific relatives, highlight the necessity to take this problem into consideration in Hexactinellida, just as it has been done in the three other Poriferan classes.*

18S rDNA phylogeny. Support from DNA sequences is useful when dealing with such “cosmopolitan” distributions, therefore we provided 18S rDNA barcodes for the new species. Sequences recovered from our samples were 1870 bp for *Farrea bowerbanki* **n. sp.** and 1938 bp for *Tretodictyum reiswigi* **n. sp.** Unfortunately, it was not possible to compare them with, for instance, samples from the type localities of *Farrea occa* or *Tretodictyum tubulosum*, which are not available. Our sequences were aligned with 13 other sequences of hexactinellids of the suborder Sceptrulophora available from nucleotide databases that encompassed the same part of the gene. It was also possible to build a much shorter alignment (1162 bp) with 6 additional sequences only available at the 5’ end of the gene. The outgroup was *Iphiteon panicea* as in Reiswig & Dohrmann (2014). ML and NJ reconstruction methods produced trees with the same, consistent topology (NJ shown for the long 14-sequence alignment on Figure 5, but with bootstrap support from both methods). Trees produced with the short 20-sequence alignment (not shown) did not provide further information of great significance, except when detailed below. *F. bowerbanki* **n. sp.** forms a highly supported clade with the only other *Farrea* available in the database, “*Farrea* sp. MD-2008” from Florida (Dohrmann *et al.*, 2009). With the short alignment, decreased bootstrap support (80%) makes it delicate to infer their relationship with other genera in Farreidae such as *Aspidoscopulia* and *Lonchiphora*. Farreidae are however recovered as weakly monophyletic (80%) when adding these taxa. There is good support with the long alignment to consider Euretidae as a monophyletic group too (Fig. 5), which is still true when adding *Verrucocoeloidea liberatorii* from the shorter alignment (85%), whereas Reiswig & Dohrmann (2014) recovered this family as weakly paraphyletic. Aphrocallistidae are always (short and long alignments) found monophyletic with 100% bootstrap support (Fig. 5). As pointed out by Reiswig & Dohrmann (2014), the position of *Sarostegia oculata* in the Sceptrulophora tree is not well supported. The sequence of *T. reiswigi* **n. sp.** goes in a well defined group with “*T. tubulosum*” from Rockall Bank off Ireland (Dohrmann *et al.* 2008) and *Hexactinella carolinensis* (100% bootstrap support in the short alignment). The placement of *Psilocalyx wilsoni* as a Tretodictyidae, on the other hand, is not clearly supported by our data, although it was clearly recovered as such by Reiswig & Dohrmann (2014) with a larger dataset. The two sequences of *Tretodictyum* are 100% identical (not accounting for ambiguities) which is a good indication that the two specimens from Corsica and Ireland likely belong to a single species, *T. reiswigi* **n. sp.** Dohrmann *et al.* (2008) already indicated that their sample might belong to a new species different from the Pacific *T. tubulosum*. On the other hand, *F. bowerbanki* **n. sp.** and the *Farrea* from Florida display 1.4% nucleotide divergence (27/1870 bp). This divergence is not compatible with intraspecific variability in hexactinellid 18S rDNA (Boury-Esnault *et al.* 2015; Dohrmann *et al.* 2008; 2009; 2012a; b) and clearly suggests that the Florida specimen does not belong to *F. bowerbanki* **n. sp.** The relationship between this *Farrea* from Florida and *F. occa* or other described species remains to be studied. In general, adding more taxa and more characters (*e.g.* full 18S rDNA length) to the Sceptrulophora DNA dataset is warranted to obtain a more accurate view of their relationships, especially at generic and familiar levels.

Ecology. The ecology of the new hexactinellids described herein as well as that of *Sympagella delaizei* is rather contrasted and interesting. During the MedSeaCan and CorSeaCan expeditions, *T. reiswigi* was found almost everywhere a rocky, vertical substrate occurred between 300 and 500 m, the preferred depth range of this species (Table 3). It was the most commonly observed hexactinellid. On the contrary, *S. delaizei* was rare and mostly observed at only one station, in the Valinco canyon off SW Corsica, on rather sub-horizontal rocky surfaces (Boury-Esnault *et al.* 2015). The other closest known stations in the Aegean and Alboran Seas are quite far apart. Yet another situation prevails for *F. bowerbanki* which is rare across the NW Mediterranean (*e.g.* Ajaccio and

Stoechades canyons) but can be common at Valinco canyon and even abundant (hundreds observed) at Cassidaigne canyon, on sub-vertical or overhanging rocky surfaces. It has not been possible to apprehend the environmental particularities of each of these stations, but it is worth noting that the Valinco canyon is the only one to display all three species. It is possibly a rather pristine canyon with low human impacts (Fourt *et al.* 2014). It is also possible that the local water circulation patterns make it a particularly favorable site for hexactinellids. The Cassidaigne canyon is another peculiar setting, with abundant *F. bowerbanki* and *T. reiswigi* populations, and where currents and a particular topography create a powerful upwelling (Albérola & Millot 2003) believed to enhance the biomass and biodiversity encountered in all parts of the canyon. This is where the highest densities of *F. bowerbanki* were observed (Fig. 4) although the observations of the denser beds were within an area directly impacted by red mud disposal. It is impossible at this stage to state whether it is particularly unfortunate to have discharged this industrial waste at such a rare hexactinellid hot spot, or whether these two species, especially *F. bowerbanki* are exceptionally resistant to such human-induced disturbance. It should be noted that dead skeletons of the two species are commonly observed in their living position (Fig. 2B, 4C). Also, our 2014 survey, attempting to return to hexactinellid sponges accurately positioned with the ROV in 2010, mostly failed to recover live individuals, whereas new sponges were commonly observed. As recently proposed by Kahn *et al.* (2016), all these observations possibly mean that the growth and colonization dynamics of hexactinellids may not be as slow as anticipated.

Acknowledgements

We thank the COMEX crew for their professionalism and dedication in documenting and collecting specimens. Caroline Rocher and Marjorie Selva at SCBM (IMBE) provided much appreciated technical advice and Marine Remize helped processing specimens on board. André Freiwald shared useful information and photographs from the Cassidaigne Canyon. We thank F. Orsini and P. Thibault for allowing us to use the pictures and distribution data from the monitoring program of the Gardanne aluminium plant discharge at sea, carried out in the Cassidaigne Canyon with COMEX SA by GIS Posidonie and CREOCEAN for ALTEO. The French Marine Protected Areas Agency (AAMP) was the main sponsor of the MedSeaCan and CorSeaCan cruises, with the particular involvement of Pierre Watremez and Boris Daniel. The ROV-3D cruise to SW Corsica canyons in 2014 was made possible by a partnership involving AAMP, the Calanques National Park (PNC) and COMEX. We thank the two anonymous reviewers for their very useful comments.

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