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When distant relatives look too alike: a new family, two new genera and a new species of deep-sea *Umbellula*-like sea pens (Anthozoa, Octocorallia, Pennatulacea)

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ABSTRACT

Among octocorals, colonies of the deep-sea pennatulacean genus *Umbellula* Gray, 1870 are some of the most instantly recognisable forms. Historically however, species identification in this genus has been usually based on few morphological characters with very little knowledge of associated intraspecific variability. This fact, combined with the very limited access to these deep-sea organisms, has resulted in numerous uncertainties about the true characters that should be used in species determination and recognition of synonyms and questionable species. Recent phylogenetic analyses based on mitochondrial and nuclear DNA markers has shown to be an excellent complementary source of information to morphological examination, being able to detect incongruent taxonomic assignments in classifications based only on morphological characters. Molecular analyses can reveal the presence of paraphyletic or polyphyletic groupings of taxa that may then be the subject of further research integrating morphological and molecular techniques. This paper addresses the existence of a set of specimens initially assigned to the genus *Umbellula* Gray, 1870 but that have been shown to be distantly related to the type species *Umbellula encrinus* (Linnaeus, 1758) based on molecular phylogenetic hypotheses. Phylogenetic analyses based on four genetic markers, three mitochondrial (*mtMutS*, *ND2*, *Cox1*) and one nuclear (*28S*), validate the definition of a new family (Pseudumbellulidae fam. nov.) and two new genera (*Pseudumbellula* gen. nov. and *Solumbellula* gen. nov). These analyses also justify the segregation of some of the morphological characters previously included in the diagnosis of the genus *Umbellula* and the monotypic family Umbellulidae Kölliker, 1880. Moreover, a new species, *Pseudumbellula scotiae* sp. nov. is described and illustrated with material from the North Eastern Atlantic and compared with congeners. Additionally, the well-known but atypical species *Umbellula monocephalus* Pasternak, 1964 is transferred and described here as *Solumbellula monocephalus* (Pasternak, 1964), comb. nov., based on both molecular data and morphology.

Keywords: deep sea, Integrated approach, new taxa, Octocorallia, Pennatulacea, *Pseudumbellula* gen. nov., Pseudumbellulidae fam. nov., sea pen, *Solumbellula* gen. nov., taxonomy, *Umbellula*.

Introduction

Colonies of the sea pen genus *Umbellula* Gray, 1870 are distributed worldwide and represent some of the most recognisable forms among the deep-sea macrobenthos (Tyler 2002; Baker *et al.* 2012; among others). However, current species identification in this genus is based on very few morphological characters (Kükenthal 1915; Broch 1958) and limited knowledge on intraspecific variability, resulting in numerous named species falling into synonymy or being considered of questionable validity (see Broch 1957, 1958), most of these compiled in databases such as WoRMS (Cordeiro *et al.* 2021). More recently, the use of molecular markers as an additional source of information in the order Pennatulacea has provided new understanding of the phylogenetic relationships among sea pen species (Dolan *et al.* 2013; Kushida and Reimer 2019). The continuous addition of new mitochondrial and nuclear sequences of sea pens during recent years allows us to observe taxonomic assignments that are incompatible with phylogenetic history (García-Cárdenas *et al.* 2019, 2020).

Dolan *et al.* (2013) first pointed out the non-monophyly of the traditional suborders (Sessiliflorae and Subselliflorae) of Pennatulacea, and that of some of the main pennatulacean families, Umbellulidae among these. *Umbellula* seems to be clearly distinguishable from all other genera of sea pens (Williams 1995) but molecular studies focusing on sea pens have shown the polyphyletic nature of this genus (Dolan *et al.* 2013; Kushida and Reimer 2019; Risaro *et al.* 2020), but without taxonomic resolution. These studies, based on two mitochondrial markers *mtMuts* and *ND2*, showed that *Umbellula* sequences were located in two different clades (Clade I and Clade IV). McFadden *et al.* (2014) suggested that the integration of both mitochondrial and nuclear markers (such as the proposed barcode for octocorals *mtMutS*, *Cox1* and *28S*) would be more informative than the use of mitochondrial markers alone. This multilocus approach has now been used for phylogenetic approaches in various octocoral groups including sea pens (García-Cárdenas *et al.* 2020) and confirms the conclusion that the suborders Sessiliflorae and Subselliflorae and those of some of the well-known sea pen families and genera (e.g. *Umbellula*, *Pennatula*), are non-monophyletic (García-Cárdenas *et al.* 2020).

By contrast, complementary research can contribute important advances in the understanding of the processes of divergence and evolution within pennatulaceans. These investigations are not only based on DNA sequencing, but also on the presence of patterns in the arrangement of genes (see also Brugler and France 2008; Uda *et al.* 2011; Brockman and McFadden 2012; Pante *et al.* 2013). Hogan *et al.* (2019) documented the first complete sea pen mitogenomes, including four *Umbellula* species, and defined three different gene orders in Pennatulacea, one of them completely new and two previously known in Alcyonacea (the ancestral one and one found in bamboo corals). Furthermore, these authors found a bipartite genome in one of the *Umbellula* species (two circular molecules of 13 and 5 kbp). These findings are only a few examples of new discoveries where molecular studies have proven essential for improved understanding of this particular group of octocorals.

The research in this paper is based on macro- and microscopic examination of morphological characters and a phylogenetic reconstruction using sequences of three mitochondrial (*mtMutS*, *ND2* and *Cox1*) markers and one nuclear (*28S*) marker. This study explores the placement of some sequences and specimens previously attributed to the genus *Umbellula* but that are distinctly separated from the sequences of the type species *Umbellula encrinus* (Linnaeus, 1758) and related forms. The results lead us to conclude that some species from the eastern North Atlantic and the Southern Ocean need to be reclassified in new taxa that are formally described here.

Materials and methods

Sample collection

The material examined in this study was collected during three important survey programs: PROSPEC (1996), BENGAL (1997–1998) and SCOTIA Deepwater Time Series program (1998–present). The PROSPEC program explored the Hébrides Terrace at stations located between 55–56°N and 10–9°W, at 1000- and 2000-m depth. The BENGAL (High resolution temporal and spatial study of the BENthic biology and Geochemistry of an eastern North Atlantic Abyssal Locality) program encompassed six cruises to the Porcupine Abyssal Plain (PAP) in the north-eastern Atlantic, centred on 48°50′N, 16°30′W, south-west of Ireland at a depth of ~4840 m (Billett and Rice 2001). The SCOTIA program is an ongoing biannual trawl survey covering the Hebrides Slope between latitudes 55 and 60°N over the depth range 500–2000 m.

The BENGAL and PROSPEC cruises utilised an Agassiz trawl (BENGAL at 4810–4850-m depth PROSPEC at 1000 to 1579 m) and a random stratification survey design to cover the study area. During SCOTIA cruises, specimens were collected using demersal fish trawl with both the cod end and the full body of the trawl being thoroughly searched for macrobenthos after each deployment. Details of the sampling stations where the materials studied in this paper were collected are shown in Table 1 (see also Fig. 1).

Pennatulacean colonies were sorted, labelled and fixed on board, in either 100% ethanol or in buffered formalin (5% in seawater). For specimens fixed in formalin, colonies were further preserved in 70% ethanol following the fixation period. Colonies or fragments fixed in 100% ethanol were suitable for further molecular studies.

Morphological study

The presence of sclerites was corroborated by dissolving fixed tissues from all parts of the colonies (pinnulae, main tentacle axis, pharynx, polyp body, siphonozooid areas, stem and peduncle) in a 10% sodium hypochlorite solution. Microscopic slides with sclerites were observed under a Leica DMLB light microscope in conjunction with an OPTIKA C-P20CC digital camera and the image processing software OPTIKA PROVIEW. Preparations of the sclerites were mounted on stubs, coated with gold–palladium under a Leica ACE600 High Vacuum Sputter Coat and observed with a Zeiss EVO Scanning Electron Microscope at the General Research Services of Microscopy of the University of Seville.

Table 1. Main data of the cruises and sampling station where the material described in this paper was collected.

Cruise	Station	Area and coordinates; Star-Stop	Depth (m)	Date
PROSPEC	CPH-10	Hebrides Terrace; 55°18′N,10°15′W	1579	12 July 1996
BENGAL 3	13200(94)	Porcupine Abyssal Plain; 48°47′N,16°32′W	4847–4851	26 July 1997
BENGAL 5	13368(48)	Porcupine Abyssal Plain; 48°45′N,16°32′W	4845–4848	17 March 1998
BENGAL 5	13368(53)	Porcupine Abyssal Plain; 48°49′N,16°20′W	4842–4846	20 March 1998
BENGAL 6	13627(24)	Porcupine Abyssal Plain; 48°52′N,16°42′W	4839	5 October 1998
SCOTIA	S11448	Hebrides Slope; 56°14.84′N, 9°21.82′W; 56°11.34′N, 9°22.76′W	1010–1080	5 September 2011
SCOTIA	S11450	Hebrides Slope; 56°5.50′N, 9°48.69′W; 56°8.00′N, 9°52.23′W	1786–1800	5 September 2011
SCOTIA	S12439	Hebrides Slope; 56°4.92′N, 9°51.48′W; 56°7.02′N, 9°54.32′W	1850–1868	17 September 2012
SCOTIA	S12453	Hebrides Slope; 57°21.50′N, 9°41.59W; 57°18.61′N, 9°38.94W	1510–1523	20 September 2012
SCOTIA	S13313	Hebrides Slope; 56°6.87′N, 9°52.46′W; 56°3.70′N, 9°50.78′W	1832–1840	20 September 2013
SCOTIA	S17332	Hebrides Slope; 56°6.63′N, 9°52.24′W; 56°3.42′N, 9°50.43′W	2025–2026	21 September 2017
SCOTIA	S17315	Donegal Slope; 55°16.13′N, 10°11.43′W; 55°12.91′N, 10°12.09′W	1255–1262	16 September 2017
SCOTIA	S19348	Donegal Slope; 55°15.49′N, 10°20.96′W; 55°13.92′N, 10°22.71′W	1859–1875	4 October 2019
SCOTIA	S17313	Donegal Slope; 55°16.99′N, 10°18.60′W; 55°18.10′N, 10°17.60′W	1766–1830	16 September 2017

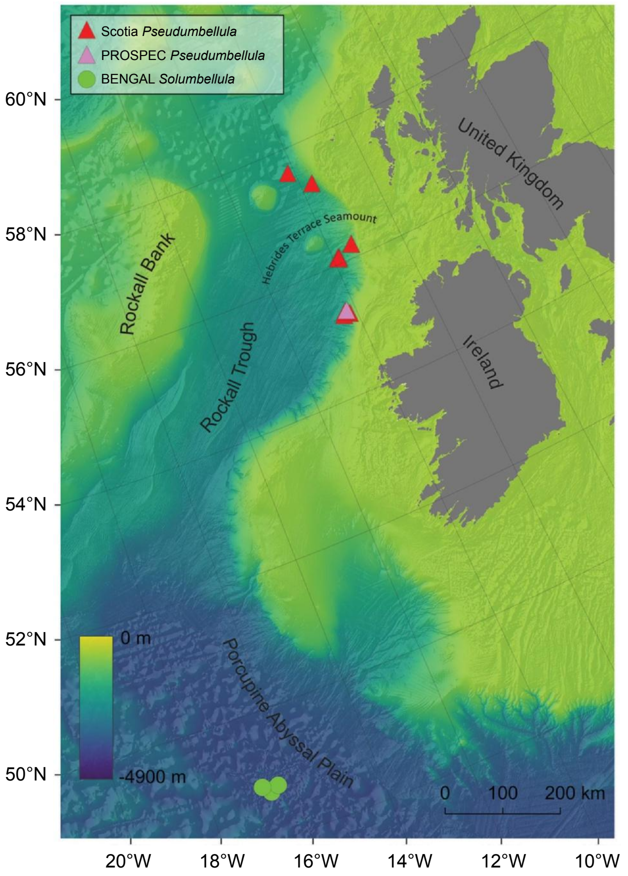

Fig. 1. Distribution of the sampling stations for *Pseudumbellula scotiae* sp. nov. (red triangles) and *Solumbellula monocephalus* (Pasternak, 1964) com, nov. (green circles) material examined over the course of this study with the various survey programs involved indicated. Map © Crown copyright.

For comparative purposes, the morphology (overall colony and axis cross section) of other *Umbellula* specimens collected during various benthic surveys and over different geographical areas and research programs [Antarctica (EASIZ, ANDEEP, BIOROSS), North Eastern Atlantic–Arctic (BIOICE, SCOTIA)] were also examined. The axis of colonies from the *Umbellula*-like genera discussed in this paper were sectioned and polished using 600-, 800-, 1200- and 3000-grit diamond polishing discs on a mini cutting and polishing table YXEC. Cross-sections were visualised and photographed under UV light (SFA-UV Stereomicroscope Adaptor NIGHTSEA) using a stereomicroscope Motic SMZ-168.

DNA extraction and PCR procedures

Total genomic DNA was extracted from ethanol (EtOH)-preserved material using the E.Z.N.A. DNA kit (Omega-Biotech) following the manufacturer's instructions. The *mtMutS*, *ND2* and *Cox1* mitochondrial regions and the nuclear *28S* were sequenced for comparative purposes. The start of the *mtMutS* region was amplified using the primers ND42625F and MUT3458R (Sánchez *et al.* 2003; McFadden *et al.* 2006). *ND2* was amplified using the primers 16S647F and ND21418R (McFadden *et al.* 2004). *Cox1* region was amplified using the primers COII8068F and COIOCTR (France and Hoover 2002; McFadden *et al.* 2004). *28S* nuclear ribosomal gene (*28S* rDNA) was amplified using the primers *28S*-Far and *28S*-Rar (McFadden and van Ofwegen 2013). Each PCR used 1 U of MyTaq Red DNA Polymerase (Bioline), 10 µM of each primer and ~30 ng of genomic DNA, being brought to a final volume of 25 µL with molecular grade H_2O. *MtMutS* PCR was carried out using the following cycle profile: initial denaturation at 94°C for 2 min, 35 cycles of denaturation at 94°C for 15 s, annealing at 55°C for 15 s, extension at 72°C for 10 s and a final extension at 72°C for 5 min. The *ND2*, *Cox1* and *28S* PCR used the same cycle profile, however the corresponding annealing temperatures were 51, 50 and 58°C respectively. PCR products were purified using ExoSAP–IT PCR Product Cleanup Reagent (ThermoFisher Scientific) following the manufacturer's instructions before strong amplifications were sent to Macrogen Europe for sequencing in both directions. Purified products were electrophoresed on an ABI PRISM 3730xl Genetic Analyser.

Phylogenetic analyses

All chromatograms were visualised, and sequence pairs matched and edited using Sequencher (ver. 4.0, Gene Codes, Ann Arbor, MI, USA). The set of new sequences and those homologous from GenBank (see Table 2) were aligned using MUSCLE (in MEGA, ver. 6.0, see https://www.megasoftware.net/; Tamura *et al.* 2013). After alignment, pairwise genetic distances based on the Kimura 2-parameter (K2P) model of nucleotide substitution (Kimura 1980) were obtained to compare these with previous analyses at genus and family levels, following the comparisons of Pante and France (2010), Pante *et al.* (2012), and López-González (2020).

In accordance with the molecular phylogenies of Dolan *et al.* (2013) and Kushida and Reimer (2019) sequences of ellisellids from GenBank were selected as out-groups. The concatenated matrix for *mtMutS* + *ND2* + *Cox1* + *28S* sequences had 2849 bases, consisting of 61 pennatulacean plus five ellisellid sequences as out-group. Individual markers (*mtMutS*, *ND2*, *Cox1*, *28S*) were also examined; the number of bases and number of sequences in the different datasets for pennatulacean + out-group were: 704 bases and 61 + 5 sequences for *mtMutS*, 541 bases and 53 + 2 sequences for *ND2*, 775 bases and 40 + 3 sequences for *Cox1*, and 829 bases and 20 + 1 sequences for *28S*. The phylogenetic reconstructions were obtained applying Maximum Likelihood (ML) and Bayesian inference (BI) methods. The best nucleotide substitution model was selected using Modelltest implemented in MEGA (ver. 6) according to Akaike Information Criterion (AIC) and hierarchical likelihood ratio test (hLRT) values (T92 + G for multi-loci and most of the individual markers, except for *Cox1*, where model T92 + G + I was selected by the software, MEGA, ver. 6; Tamura 1992). Maximum likelihood method (ML) was implemented in MEGA (ver. 6.0), using the NNI heuristic method (Nearest Neighbour Interchange) and 1000 bootstrap replications (Felsenstein 1985). The Bayesian Inference was carried out in MrBayes program (ver. 3.1.2, see https://nbisweden.github.io/MrBayes/download.html; Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003), using the model GTR + G (lset nst = 6 rates = gamma), 10^7 generations and discarding 25% of the initial trees. The stationarity of the chains and the convergence of the two runs were monitored for each parameter by Tracer (ver. 1.7.1, see https://github.com/beast-dev/tracer/releases/tag/v1.7.2; Rambaut *et al.* 2018) to ensure the effective sample size (ESS) of all parameters was larger than 200 as recommended.

Deposition of materials

The material examined for this study has been deposited in the National Museum of Scotland (NMS), in the Museu de Zoologia in Barcelona (MZB) and in the collection of the research group Biodiversidad y Ecología Acuática at the University of Seville (BECA).

Nomenclatural remark

The genus name *Umbellula* has been widely utilised in several important taxonomic papers (e.g. Kükenthal 1915; Hickson 1916; Broch 1957, 1958; among many others) within the ecological, biological, bionomic and biochemical literature of deep-sea fauna over the last century mainly due to the apparent distinctive morphology (e.g. Tyler *et al.* 1995; Baker *et al.* 2012; Bessho-Uehara *et al.* 2020, among many others). Despite the fact that a different spelling and authority (*Ombellula* Cuvier, 1798) would have priority (see Kükenthal 1915, p. 130; Williams 1995, p. 119), the genus name *Umbellula* was the subject of a successful proposal of conservation (Bayer and Grasshoff 1997) whereby the junior synonym was formally accepted. For these reasons, and because the species described in this paper have been reported in the literature in the genus *Umbellula*, the new names here proposed at genus and family levels are created using the root-*umbellula* that will link future findings and research with previously published information.

Nomenclatural acts

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the International Commission on Zoological Nomenclature (ICZN). The ZooBank Life Science Identifiers (LSID) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix 'http://zoobank.org/'. The LSID for this publication is urn:lsid:zoobank.org:pub:755CA87C-6613-4E8D-8272-88D8F14A268A.

Abbreviations

BECA, Biodiversidad y Ecología Acuática; MZB, Museu de Zoologia de Barcelona; MOTUs, molecular operational taxonomic units; NMS, National Museum of Scotland; SEM, Scanning Electron Microscopy; stn, sampling station; SO, Southern Ocean.

Table 2. Pennatulaceans included in molecular phylogenetic analyses in this paper.

Species name in the tree	Abbreviation	Catalog numbers; Isolate; additional information	Geographic area/provenance/ Cruise	*mtMutS*	*ND2*	*Cox1*	*28S*
Acanthoptilum gracile	*A.grac*	34212–029	NWFSC-west coast	JN866529	–	KF874188	–
Actinoptilum molle	*A.mol*	RMNH Coel. 40822	n.d.	GQ342491	–	GQ342414	JX203738
Anthoptilum grandiflorum	*A.gran*	NMS.Z.2019.25.16	Greenland	MK919655	MK919655	MK919655	–
Anthoptilum sp. 1	*A.sp1*	NMS.Z.2019.25.1	Whittard Canyon	MK919656	MK919656	MK919656	–
Balticina cf. *finmarchica*[A]	*B.fin*	NMS.Z.2019.25.3	Whittard Canyon	MK919659	MK919659	MK919659	–
Balticina willemoesi[A]	*B.wil*	34213–026	NWFSC-west coast	JN866543	–	KF874204	–
Calibelemnon hinoenma[B]	–	YK139	NW Pacific	MK133472	MK133667	–	–
Cavernularia pusilla	*C.pus*	BECA(OPEN-465); G-99	NW Mediterranean	MT968957	**MZ217768**	MT952706	MT951908
Cavernulina sp.	*Cavnl*	Isolate YK19	NW Pacific	MK133372	MK133567	–	–
Distichoptilum gracile	*D.gra*	NMS.Z.2019.25.2	Whittard Canyon	MK919657	MK919657	MK919657	–
Echinoptilum macintoshi	*E.mac*	Isolate YK22	NW Pacific	MK133373	MK133568	–	–
Funiculina quadrangularis	*F.qua*	NMS.Z.2019.25.17	Little Loch Broom, Scotland	MK919658	MK919658	MK919658	–
Gilibelemnon octodentatum	*G.oct*	BECA(OPEN-452); G-81	Seymour Island–Antarctica	MK603841	MW863001	MK603855	MK603851
Gyrophyllum hirondellei	*G.hir*	MNHM OCT.A.579; G-128	BIAÇORES	MT968964	**MZ217769**	MT952713	MT951915
Gyrophyllum sibogae[C]	*G.sib*	NTM-C014392; NOR89/535	Tasman Sea–Australia	DQ302869	DQ302942	JX203865	JX203740
Kophobelemnon macrospinum	*K.mac*	NTM-C014985	Tasman Sea–Australia	DQ302865	DQ302937	GQ342429	JX203742
Kophobelemnon pauciflorum	*K.pau*	NHM 2010.21	Crozet Islands–Atlantic Ocean S	KF313836	KF313809	–	–
Kophobelemnon sp. 3	*K.sp3*	NMS.Z.2019.25.5	Whittard Canyon	MK919661	MK919661	MK919661	–
Kophobelemnon sp. 4	*K.sp4*	NMS.Z.2019.25.6	Whittard Canyon	MK919662	MK919662	MK919662	–
Pennatula aculeata	*P.acu*	NMS.Z.2019.25.7	Whittard Canyon	MK919663	MK919663	MK919663	–
Pennatula phosphorea	*P.pho*	BECA(OPEN-453)(G-88)	Sea of the Hebrides, NE Atlantic	MK603848	MW863002	MK603858	MK882492
Protoptilum carpenteri	*P.car*	NMS.Z.2019.25.10	Whittard Canyon	MK919667	MK919667	MK919667	–
***Pseudumbellula scotiae*-1, HOLOTYPE**	–	NMS.Z.2021.2.2; OPEN-169 (G-154B)	Hebrides Slope	**MZ217756**	**MZ217762**	**MZ190838**	**MZ227258**
***Pseudumbellula scotiae*-2, PARATYPE**	–	NMS.Z.2021.2.3; OPEN-171 (G-156)	Hebrides Slope	**MZ217757**	**MZ217763**	**MZ190839**	**MZ227259**
***Pseudumbellula scotiae*-3**	–	NMS.Z.2021.1.1; BECA(OPEN-648); G-3599	Hebrides Slope	**MZ217758**	**MZ217764**	**MZ190840**	**MZ227260**

(*Continued on next page*)

Table 2. (*Continued*)

Species name in the tree	Abbreviation	Catalog numbers; Isolate; additional information	Geographic area/provenance/Cruise	*mtMutS*	*ND2*	*Cox1*	*28S*
***Pseudumbellula scotiae*-4**	–	NMS.Z.2021.1.2; BECA(OPEN-649); G-3600	Donegal Slope	**MZ217759**	**MZ217765**	**MZ190841**	**MZ227261**
***Pseudumbellula scotiae*-5**	–	NMS.Z.2021.1.3; BECA(OPEN-645); G-3596	Donegal Slope	**MZ217760**	**MZ217766**	**MZ190842**	**MZ227262**
***Pseudumbellula scotiae*-6**	–	NMS.Z.2021.1.4; BECA(OPEN-646); G-3597	Donegal Slope	**MZ217761**	**MZ217767**	**MZ190843**	**MZ227263**
Pseudumbellula 'sp. 2-RH'[D]	–	NMS.Z.2019.25.13	Porcupine Bank, Ireland	MK919670	MK919670	MK919670	–
Pseudumbellula pomona	–	42608 c; 42609 c	Mar del Plata Submarine Canyon, SW Atlantic	MT467665	MT467666	–	–
Pseudumbellula 'sp. 2-ED'[E]	–	NHM 2009.6	Crozet Islands–Atlantic Ocean S	KF313856	KF313829	–	–
Pteroeides caledonicum	*P.cal*	YK90	NW Pacific	MK133429	MK133624	–	–
Pteroeides spinosum[F]	*P.spi*	BECA(OPEN-140); G-98	NW Mediterranean	MT968965	**MZ217770**	MT952714	MT951916
Ptilella grandis	*P.gran*	BECA(OPEN-143); G-92	South Iceland, NE Atlantic	MK603844	MW863005	MK603860	MK603854
Ptilella grayi	*P.grey*	NMS.Z.2019.2.2; G-20	Rockall Bank–NE Atlantic	MK603846	MW863009	MK603856	MK603853
Ptilosarcus gurneyi	*P.gur*	34213–020	NWFSC-west coast	JN866540	–	KF874201	–
Renilla muelleri	*R.mue*	n.d.	n.d.	JX023273	JX023273	JX023273	–
Sclerobelemnon theseus	*S.the*	JAS	Colombia	DQ311679	DQ311678	–	–
Scleroptilum grandiflorum	*S.gra*	NHM 2010.14	Mid-Atlantic Ridge–Atlantic Ocean	KF313847	KF313820	–	–
Scytalium herklotsi	*S.her*	USNM 1550636	Puerto Rico–NW Atlantic	MW863000	MW863011	MW858345	MW862997
Scytalium martensi	*S.mar*	Isolate YK03	NW Pacific	MK133361	MK133556	–	–
Solumbellula monocephalus[G]	–	NHM 2010.16	Indian Ocean	KF313852	KF313825	–	–
Stachyptilum dofleini	*S.doe*	Isolate YK51	NW Pacific	MK133396	MK133591	–	–
Stylatula elongate	*S.elo*	n.d.	n.d.	JX023275	JX023275	JX023275	–
Umbellula encrinus	–	NHM 2010.8	Arctic Ocean	KF313849	KF313822	–	–
Umbellula huxleyi-1	–	NHM 2010.17	Atlantic Ocean NE	KF313850	KF313823	–	–
Umbellula huxleyi-2	–	NMS.Z.2019.25.11	Whittard Canyon	MK919668	MK919668	MK919668	–
Umbellula huxleyi-3	–	BECA(OPEN-161); G-139	Atlantic Ocean NE	MT968966	–	MT952715	MT951917
Umbellula magniflora	–	NHM 2010.22	Marguerite Bay-Antarctica	KF313851	KF313824	–	–
Umbellula sp. 1	–	NMS.Z.2019.25.12	Whittard Canyon	MK919669	MK919669	MK919669	–

(*Continued on next page*)

Table 2. (*Continued*)

Species name in the tree	Abbreviation	Catalog numbers; Isolate; additional information	Geographic area/provenance/ Cruise	*mtMutS*	*ND2*	*CoxI*	*28S*
Umbellula sp. A	–	BECA(OPEN-464); G-57	Antarctica	MT968967	–	MT952716	
Umbellula sp. B	–	BECA (OPEN-463); G-127	Antarctica	MT968968	–	MT952717	MT951918
Umbellula thomsoni[B]	–	NOCS sea pens Isolate 92	Cascais Canyon–Atlantic Ocean NE	KF313854	KF313827	–	–
Umbellula thomsoni[C,H]	–	NHM 2010.19	Crozet Islands, South Indian Ocean S	KF313853	KF313826	–	–
Veretillum cynomorium	*V.cyn*	BECA(OPEN-462); G-90	Alboran Sea–INDEMARES-Alboran	MT968958	**MZ217771**	MT952707	MT951909
Virgularia mirabilis[B]	*V.mir1*	NHM 2010.7	Sweden–Atlantic Ocean NE	KF313857	KF313830	–	–
Virgularia mirabilis[C]	*V.mir2*	NMS.Z.2019.25.15	Galway Bay, Ireland	MK919673	MK919673	MK919673	–
Virgularia schultzei	*V.sch*	RMNH Coel. 40823	n.d.	GQ342527	–	GQ342459	JX203743
Virgularia cf. *gustaviana*	*V.gus*	Isolate YK210	NW Pacific	MK133518	MK133713	–	–
Virgularia cf. *halisceptrum*	*V.hal*	Isolate YK01	NW Pacific	MK133359	MK133554	–	–
Virgularia cf. *rumphi*	*V.rum*	Isolate YK84	NW Pacific	MK133423	MK133618	–	–
OUT-GROUP							
Ctenocella schmitti	–	JAS-238	NW Atlantic	JN227995	–	FJ2686281	–
Nicella sp.	–	AMQ-2013	NW Atlantic	KC788269	–	KC788231	–
Nicella sp. 2	–	NTM-C014406	n.d.	DQ302863	DQ302935	–	–
Verrucella sp. 2	–	NTM-C014982	Tasman Sea, Australia	DQ302864	DQ302936	–	–
Viminella sp.	–	RMNH Coel.40032	West Papua, Indonesia	JX203794	–	JX203852	JX203703

Species and GenBank accession numbers in bold are those sequenced for this study. Abbr., species' abbreviations in Fig. 15 and 16. Abbreviations: AMQ, Collection of A. M. Quattrini; BECA, Biodiversidad y Ecología Acuática (Seville, Spain); JAS, Collection of J. A. Sánchez; n.d., no data; NHM, Natural History Museum in London; NMS, National Museum Scotland Smithsonian (Scotland, UK); NOCS, National Oceanography Centre (Plymouth, UK); NTM, Museum and Art Gallery of the Northern Territory (Darwin city, Australia); NWFSC, North-west Fisheries Science Center (Seattle, USA); MBARI, Monterey Bay Aquarium Research Institute (California, USA); MNHM, Muséum National d'Histoire Naturelle (Paris, France); RMNH, Rijksmuseum van Natuurlijke Historie (Leiden, Netherlands).

[A] Previously cited in the genus *Halipteris* Kölliker, 1869, see Pérez *et al.* (2021).

[B] As *Calibelemnon* sp. in GenBank, but assigned to *Calibelemnon hinoenma* by Kushida and Reimer (2020).

[C] *mtMutS* and *ND2* as *Gyrophyllum* sp. in GenBank.

[D] As *Umbellula* sp. 2 RH-2019 in GenBank. As this sequence is from GenBank and we have not examined the sequenced colony, we prefer let the identification of this material as 'cf.'.

[E] As *Umbellula* sp. 2 ED-2013 in GenBank.

[F] As *Pteroeides griseum* in GenBank, see International Commission on Zoological Nomenclature (1944) and Williams (1995, p. 130) for reasons for the using of *P. spinosum* instead of *P. griseum*.

[G] As *Umbellula monocephalus* in GenBank.

[H] As *Umbellula thomsoni* in GenBank. It is doubtful that this sequence from a Southern Ocean colony belonged to *U. thomsoni*, as the type material of *U. thomsoni* was collected between Cape San Vicente (Portugal) and Madeira, 35°20′N 13°04′W in 2125 fathoms (~3886 m deep) (see von Kölliker 1874, p. 16, 1880, p. 189). The other sequence attributed to *Umbellula thomsoni* considered in this molecular comparison came from Cascais Canyon (SW Lisboa, Portugal), ~440 km distant from the type locality of *Umbellla thomsoni*. Uncorrected *p*-distance (*mtMutS*) between the two sequences attributed to *U. thomsoni* is 0.6%. It is not the intention of the present paper to revise the *Umbellula* species included in Clade I, but it is unlikely that both sequences and materials are conspecific.

Taxonomy

Subclass **OCTOCORALLIA** Haeckel, 1866

Order **PENNATULACEA** Verrill, 1865

Family **PSEUDUMBELLULIDAE** López-González, fam. nov.

Diagnosis

Colonies with a long and slender stalk. Symmetry of rachis bilateral. Conspicuous axis present throughout the colony, rounded in cross-section, in some parts nearly quadrangular (never with longitudinal grooves). Autozooids solitary or in a terminal cluster, not numerous (<15). Anthocodiae non-retractile, calyces absent. Siphonozooids on the rachis, among the base of autozooids, and below the terminal cluster (or single autozooid) on the upper part of the stem. Sclerites always present, as knobby three-flanged (rarely smooth), monoaxial spindles or rods (distinctly large) and rough ovals or rods.

Type genus: Pseudumbellula López-González and Drewery, gen. nov., here designated.

Remarks

Although a revision based on additional molecular and morphological information of the species in the family Umbellulidae is still pending, the family Pseudumbellulidae fam. nov. is well justified from a molecular and morphological point of view, and segregates species previously considered as *Umbellula* with a round to rounded quadrangular axis (never with longitudinal grooves) and that bear a sclerome including distinctly large monaxial rods and knobby three-flanged rods.

In accordance with the genetic distances and morphological differences discussed here, two new genera are proposed in Pseudumbellulidae fam. nov.: *Pseudumbellula* López-González and Drewery, gen. nov. and *Solumbellula* López-González, gen. nov.

Nomenclatural statement

A LSID number was obtained for the new family: urn:lsid:zoobank.org:act:3F8224DF-2306-4FAE-943B-C4F0711C242D.

Genus ***Pseudumbellula*** López-González and Drewery, gen. nov.

Diagnosis

Pseudumbellulid with a terminal cluster of <15 autozooids. Sclerites mainly as knobby three-flanged tentacles with distinctly large monoaxial rods, peduncle with rough ovals or rods.

Type species: Pseudumbellula scotiae López-González and Drewery, sp. nov., here designated.

Nomenclatural statement

A LSID number was obtained for the new genus: urn:lsid:zoobank.org:act:E97DEF4B-D70A-456C-9358-C850ECA19F1D.

Etymology

The prefix of the new genus is from the Greek ψεῦδο (false) due to the broadly similar morphological appearance to the umbellulid genus *Umbellula*. Gender feminine.

Nominal species

At present, at least five named species should be included in *Pseudumbellula* gen. nov.: *P. durissima* (Kölliker, 1880), comb. nov., *P. crassiflora* (Roule, 1905), comb. nov., *P. aciculifera* (J. S. Thomson, 1915), comb. nov., *P. pomona* (Risaro, Williams, Pereyra & Lauretta, 2020), comb. nov. and *Pseudumbellula scotiae* López-González and Drewery, sp. nov. Despite having an overall *Umbellula*-like appearance, all these species share the morphological characters listed in the diagnosis of *Pseudumbellula* (see above): the combination of an axis rounded in cross-section and a sclerome composed of knobby three-flanged rods, monoaxial rods (sometimes distinctly large) being a unifying character for this genus. Moreover, the molecular information available from (at least) three species (see below) strongly suggests that these can no longer be maintained under the genus *Umbellula*.

According to some authors (e.g. Nutting 1912; Kükenthal 1915; Broch 1958; Grasshoff 1972), two other species could be considered uncertain synonyms of *P. durissima: Umbellula dura* Thomson and Henderson, 1906 (south of Andaman Island, 10°06′N 92°29′E, ∼1289-m depth, see also Thomson and Henderson 1906, p. 93), and *Umbellula eloisa* Nutting, 1912 (south Japan, ∼33°25.25′N 135°30.48′E, ∼1097-m depth, see also Nutting 1912, p. 43). In the case of *Umbellula dura*, Kükenthal (1915, p. 56) treated the species separately but indicated that this was very close to *U. durissima*, whereas Broch (1958, p. 252) listed this directly as a synonym. As for *Umbellula eloisa*, Nutting himself doubted if this could be *Umbellula durissima* (Nutting 1912, p. 44), as did Kükenthal (1915, pp. 56–57). In both cases, as the different authors throughout the last century harboured doubts about the distinctive characters of these species from a purely morphological point of view (the only available source of information at this time), we prefer to be conservative and maintain this doubtful status until a complete description, preferably including molecular information, is carried out.

According to our molecular analyses (see below), a published sequence from the Southern Ocean (Crozet Island) clearly belongs to the genus *Pseudumbellula* gen. nov. However a detailed morphological study of that colony is needed for a reliable species assignation.

Species of this genus are distributed in the Indian, Atlantic and Southern Oceans, and have been recorded at a depth range of between 1033 and 3282 m (von Kölliker 1880; Roule 1905; Thomson 1915; Risaro *et al.* 2020; present paper).

Pseudumbellula scotiae López-González and Drewery, sp. nov.

Material examined

Holotype: NMS.Z.2021.2.2, SCOTIA cruise, stn S11448: 1 whole colony.

Paratype: NMS.Z.2021.2.3, SCOTIA cruise, stn S11450: 1 whole colony.

Additional material examined

BECA (OPEN-287), PROSPEC cruise, stn CPH-10: 1 whole colony. BECA (OPEN-353, G-2645), SCOTIA cruise, stn S12453: 1 fragment. BECA (OPEN-354, G-2646), SCOTIA cruise, stn S12439: 1 fragment. BECA (OPEN-355, G-2647), SCOTIA cruise, stn S13313: 1 fragment. NMS.Z.2021.1.1, SCOTIA cruise, stn S17332: 1 whole colony, a fragment is deposited in BECA (OPEN-648, G-3599). NMS.Z.2021.1.2, SCOTIA cruise, stn S17315: 1 whole colony, a fragment is deposited in BECA (OPEN-649, G-3600). NMS.Z.2021.1.3, SCOTIA cruise, stn S17348: 1 whole colony, a fragment is deposited in BECA (OPEN-645, G-3596). NMS.Z.2021.1.4, SCOTIA cruise, stn S17313: 1 whole colony, a fragment is deposited in BECA (OPEN-646, G-3597).

Description of the holotype

Colony 680 mm long (Fig. 2*a*), with a terminal group of ten autozooids, bilateral, with 'dorsal' side free of autozooids with the shape of the internal axis evident longitudinally beneath the epidermis (Fig. 2*b*). Peduncle 160 mm (~23.5% of total colony length), not excessively bulbous in preserved state. Rachis composed of a long stalk of 410 mm (~60%)

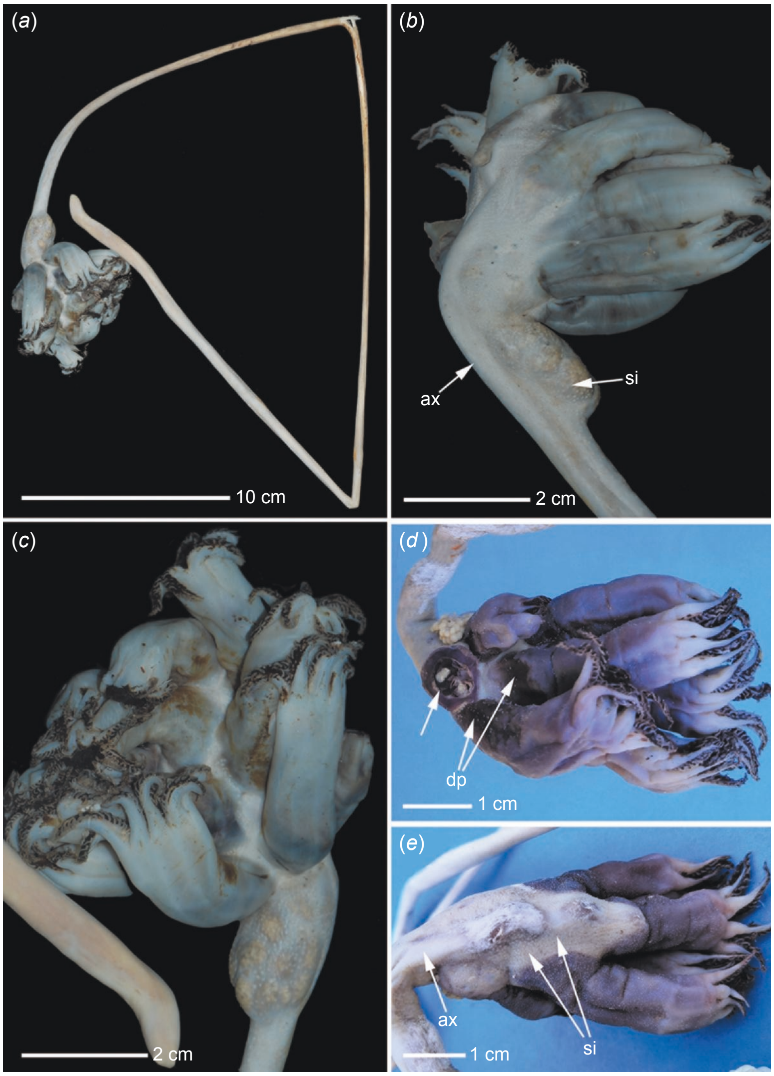

Fig. 2. *Pseudumbellula scotiae* sp. nov., holotype (NMS.Z.2021.2.2): (*a*) whole colony; (*b*) latero-dorsal view of terminal cluster of polyps showing the presence of internal axis (ax) and advanced reproductive state at the proximal part of terminal cluster with numerous siphonozooids (si); (*c*) ventral view of terminal cluster of polyps. Preserved colony NM.Z.2021.1.1 photographed a few months after collection: (*d*) ventral view of terminal cluster of polyps showing the purple tone on the body of the autozooids, small dark patches on body surface (dp), and dark-purple oral areas of tentacles; white arrow indicates polyp removed for molecular analyses; (e) dorsal view of terminal cluster of polyps showing the internal presence of axis (ax) and dorsal area with minute siphonozooids as yellow spots (si).

and a terminal group of autozooids of 110 mm (~16.5%). Lower part of the terminal cluster of polyps distinctly swollen (Fig. 2*b*, *c*, 3*c*), probably partly due to an advanced state of maturity. Axis rounded in cross-section, 3 mm at the widest point. Holotype specimen female.

Autozooids relatively short and robust (Fig. 2*c*, 3*a*, *b*), up to 37.5 mm high and 12 mm wide, almost cylindrical, with an apparently smooth surface. Body wall of autozooids, up to 0.65 mm thick, not translucent due to a thick mesogloeal layer. Pharynx elongated and wrinkled (Fig. 3*d*, *e*). Tentacles relatively short with a distinct thick mesogloeal base and a reduced longitudinal internal cavity clearly displaced to oral side (Fig. 3*f*–*i*). In preserved state, pinnulae thick and relatively short, closely placed in a single line (Fig. 3*j*), up to 19 in number on each side of main tentacle axis.

Siphonozooids (0.4–0.6 mm in diameter) numerous among autozooid bases and below autozooids' cluster (Fig. 3*c*), sparse along elongate stalk.

Sclerites in all parts of the colony. Three kinds of sclerites: distinctly large monoaxial rods with numerous points and longitudinal furrows (Fig. 4*a*), knobby three-flanged rods (Fig. 4*b*–*d*, 5), and ovals to oval-rods with more or less pointed ornamentation (Fig. 6). Without large surface sclerites on body of autozooids or aboral side of main tentacular axis.

Sclerites of main tentacular axis in two types, one with two distinct size categories: large monoaxial rods (Fig. 4*a*) up to 0.39 mm long and elongate knobby three-flanged rods (Fig. 4*b*) up to 0.13 mm long inside a thick mesogloeal tentacular axis (Fig. 3*g*). Tentacle surface with short knobby

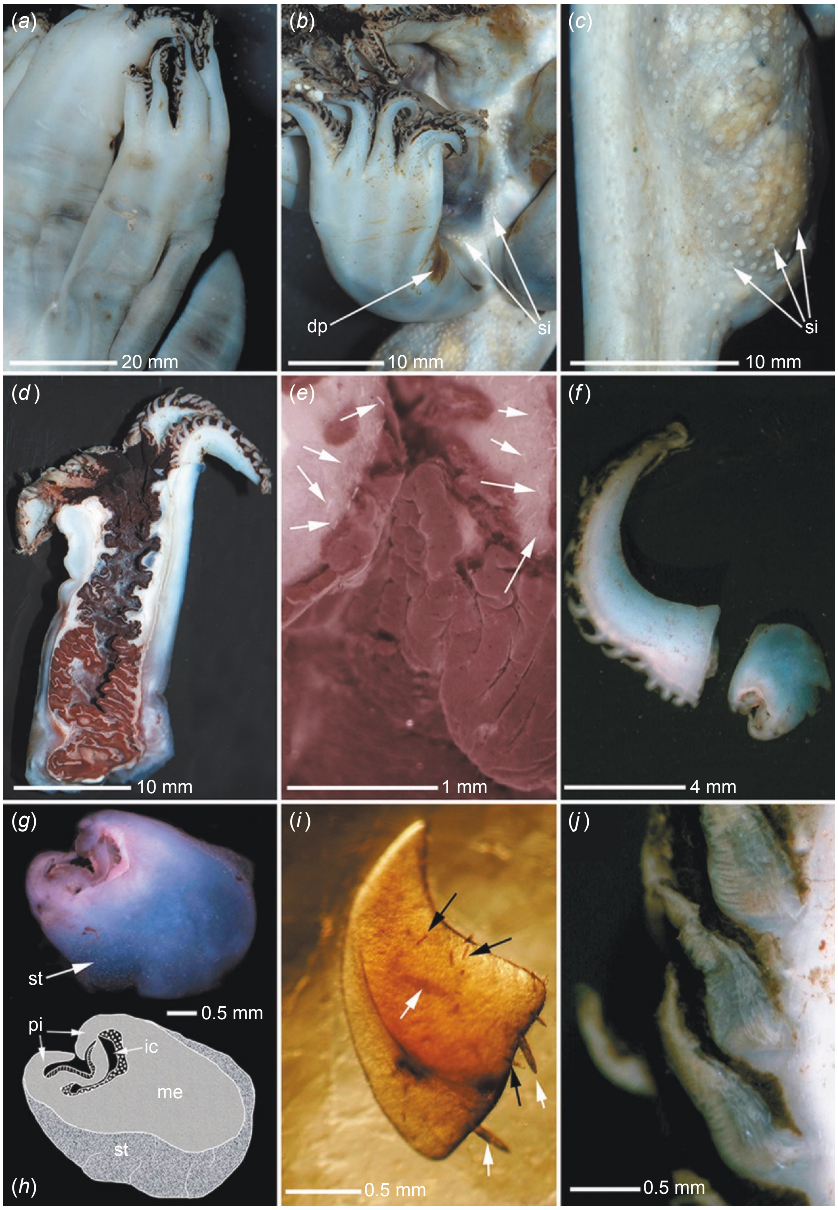

Fig. 3. *Pseudumbellula scotiae* sp. nov., holotype (NMS.Z.2021.2.2): (*a*, *b*) details of autozooids, showing robust polyp bodies with short and robust tentacles, as well as the dark colour in preserved state of the oral areas of tentacles, siphonozooids among autozooid's bases (si) and of small patches on body surface (dp); (*c*) basal part of the cluster of autozooids showing the axis on the left, the swollen areas due to reproductive products, and well distributed siphonozooids as white spots (si); (*d*) longitudinal section of an autozooid showing dark coloured oral area (oral disc and tentacles) and pharynx; (e) detail of part of the sectioned pharynx showing the well dispersed distribution of the sclerites (arrows); (*f*) detail of a tentacle, showing the relatively short length and thick basal part, along with a transversal section of the base showing the thick mesogloeal aboral layer; (*g*) detail from (*f*) cross section of a tentacle at the basal part, showing the thick mesogloela aboral layer (me), surface of tentacle (st) with its small sclerites (arrows) (see Fig. 4*c*), internal canal (ic), and pinnules (pi); (*h*) schematic diagram to clarify part (*g*), using the same abbreviations and signals; (*i*) mesoglea of the basal part of tentacle during digestion in commercial bleach (sodium hypochlorite solution), showing large monoaxials sclerites (See Fig. 4*a*) embedded inside the mesoglea, and the smaller knobby three-flanged ones (see Fig. 4*b*); (*j*) a group of pinnulae, short and showing the packed sclerites (see Fig. 4*d*) arranged along the pinnulae axis.

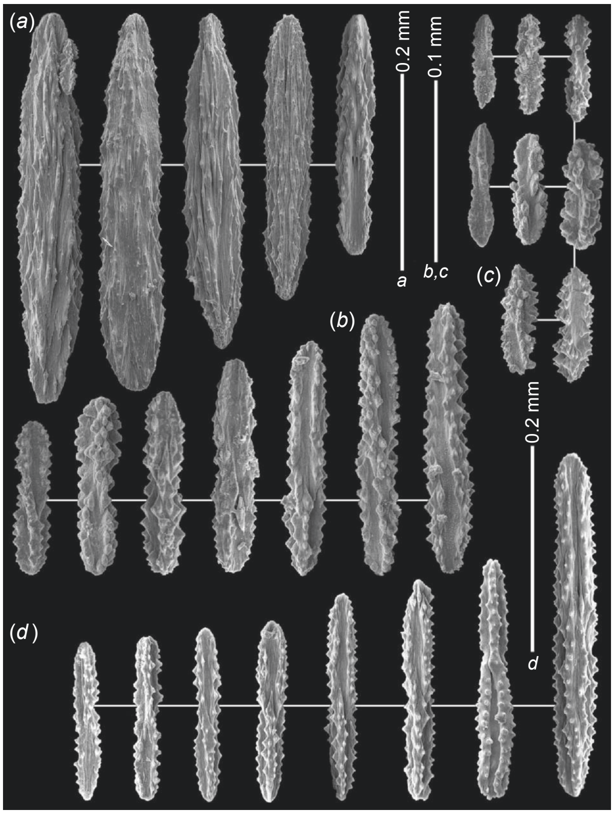

Fig. 4. *Pseudumbellula scotiae* sp. nov., holotype (NMS.Z.2021.2.2): (*a*) large monoaxial sclerites embedded inside aboral mesogloeal layer of tentacles; (*b*) knobby three-flanged sclerites embedded inside aboral mesogloeal layer of tentacles; (*c*) short knobby three-flanged sclerites of the aboral surface of tentacles; (*d*) knobby three-flanged sclerites of pinnulae.

three-flanged rods (Fig. 4*c*) up to 0.075 mm long. Pinnulae with knobby three-flanged rods (Fig. 2*k*) (Fig. 3*j*, 4*d*) up to 0.26 mm long, on aboral side.

Body of autozooid with numerous minute knobby three-flanged rods (Fig. 5*a*) only, up to 0.08 mm long, densely packed in all directions. Pharyngeal tissue with far less abundant sclerites (Fig. 3*e*) as knobby three-flanged rods (Fig. 5*b*) up to 0.1 mm long. Siphonozooids fields down and among autozooids with knobby nodulous three-flanged rods (Fig. 5*c*) up to 0.1 mm long.

Elongate stalk (rachis) with pointed to knobby rods to ovals with deep furrows on the surfaces (Fig. 6*a*) up to 0.18 mm long. Peduncle sclerites similar to those from rachis but larger (up to 0.18 mm long) and somewhat smoother (Fig. 6*b*).

Colour

All preserved specimens are milky to dirty white in colour (Fig. 2, 7), with some dark areas among autozooid bodies. Pharynx with a thick brown to reddish-brown epidermis (Fig. 3*b*). A dark coloured epidermis is also present on the oral disc including the tentacles and the pinnules (Fig. 2, 3). Preserved colonies photographed a few months after collection (Fig. 2*d*, *e*) retained a purple tone on the body of the autozooids, a lighter tone on the aboral side of tentacles, small dark patches on the body surface of the autozooids, and dark purple on the oral areas of tentacles, whereas the dorsal area of terminal cluster of autozooids, the elongated stalk and peduncle are lighter in colour, and the minute siphonozooids may be identified as yellowish spots.

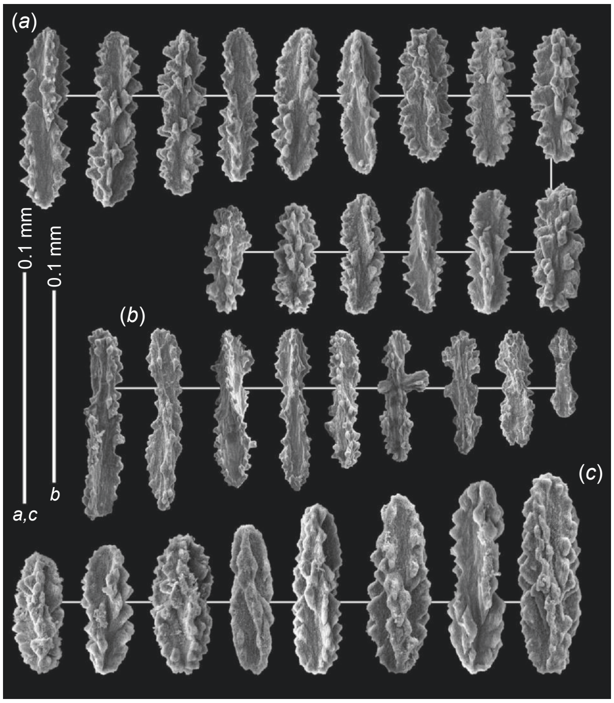

Fig. 5. *Pseudumbellula scotiae* sp. nov., holotype (NMS.Z.2021.2.2): (*a*) knobby three-flanged sclerites of polyp body of autozooids; (*b*) knobby three-flanged sclerites of pharynx; (*c*) knobby three-flanged sclerites of siphonozooid areas.

Variations

The other complete colonies examined mainly follow the same morphological characters as described above for the holotype. The paratype NMS.Z.2021.2.3 (Fig. 7*a*, *b*) is 700 mm long and like the holotype has ten autozooids. The basal part of the antozooid cluster is somewhat less enlarged, with autozooids up to 31 mm long and 13 mm wide. The colony BECA (OPEN-287) (Fig. 7*c*, *d*) from PROSPEC cruise is observed to be smaller at 530 mm, with only four polyps but otherwise with the same general characteristics as the holotype. Part of the remaining material corresponds to polyps fixed on board for molecular study with the remainder of each colony not being retained. These morphological features of these polyps are in agreement with those from the whole colonies examined, and all four molecular markers sequenced here were found to be

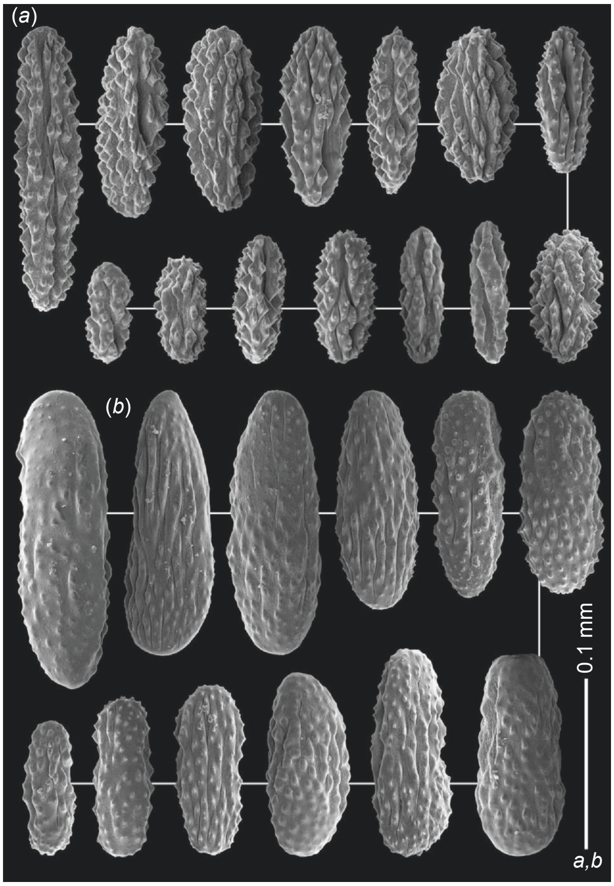

Fig. 6. *Pseudumbellula scotiae* sp. nov., holotype (NMS.Z.2021.2.2): (*a*) pointed ovals to rods of stem part of rachis; (*b*) scarcely pointed ovals to rods of peduncle.

identical to those of the holotype and paratype colonies. In the present paper we use these fragments to corroborate genetic characterisation and to provide additional data on the geographic and bathymetric distribution of this new species. Other colonies collected from SCOTIA cruises also agree with type materials having 5–13 autozooids up to 29 mm long and total lengths of 635–812 mm.

Etymology

The specific epithet *scotiae* is chosen in recognition of the great sampling effort of the MRV Scotia survey program in the deep waters to the west of Scotland, the work of which has allowed numerous specialists the opportunity to combine morphological and molecular tools to review the taxonomy of rarely encountered deep sea species and to further the systematics for many groups of benthic organisms.

Distribution

The examined material of *Pseudumbellula scotiae* sp. nov. was collected from the Hebrides-Donegal Slope (eastern North Atlantic), between 1010 and 2026 m deep (Fig. 1). Specimens attributable to this species from Porcupine Seabight and Goban Spur (reported in Dolan's 2008 PhD thesis as *Umbellula aciculifera*) show an overlapping bathymetric distribution, between 1357.5- and 1789.5-m depth).

Genus ***Solumbellula*** López-González, gen. nov.

Diagnosis

Pseudumbellulid with a single extremely large terminal autozooid. Sclerites mainly as monoaxial spindles and rods, distinctly large and sparsely knobby three-flanged rods. The latter present at the rachis-peduncle limit and on at least the upper part of peduncle.

Nomenclatural statement

A LSID number was obtained for the new genus: urn:lsid:zoobank.org:act:B779F715-941F-48DC-8066-22965BB28E3C.

Type species: *Umbellula monocephalus* Pasternak, 1964, here designated.

Etymology

The prefix of the new genus is from Latin *sôlus, a, um* (single, exclusive or singular) due to the presence of a single extremely large autozooid, a feature only shared by the soft-coral genus *Bathyalcyon* Versluys, 1906 (see Bayer 1993) and we use the root-*umbellula* as commented on above. Gender feminine.

Nominal species

At present, *Solumbellula* gen. nov. is considered monotypic, including only the species *Solumbellula monocephalus* (Pasternak, 1964), comb. nov., distributed in the Indian and Atlantic Oceans between 3910 and 4851 m deep (Pasternak 1964; Grasshoff 1972; present paper) (see also Discussion below).

Solumbellula monocephalus (Pasternak, 1964), comb. nov.

Umbellula monocephalus Pasternak, 1964, p. 193, fig. 2–4 — Tiefenbacher (2001, p. 1, fig. 1); López-González and Williams (2011, p. 313, in species list); Risaro *et al.* (2020, in text).

Umbellula thieli Grasshoff, 1972, p. 5, fig. 4–8.

Material examined

BECA (OPEN-110), BENGAL 5 cruise, stn 13368(53): 2 colonies. BECA (OPEN-69), BENGAL 3 cruise, stn 13200(94): 2 colonies. NMS.Z.2021.2.1, BENGAL 3 cruise, stn 13200(94): 1 colony. BECA (OPEN-655), BENGAL 5 cruise, stn 13368(48), 1 colony. MZB 2021–1031, BENGAL 5 cruise, stn 13368(48), 1 colony. BECA (OPEN-38), BENGAL 6, stn 13627(24): 1 colony.

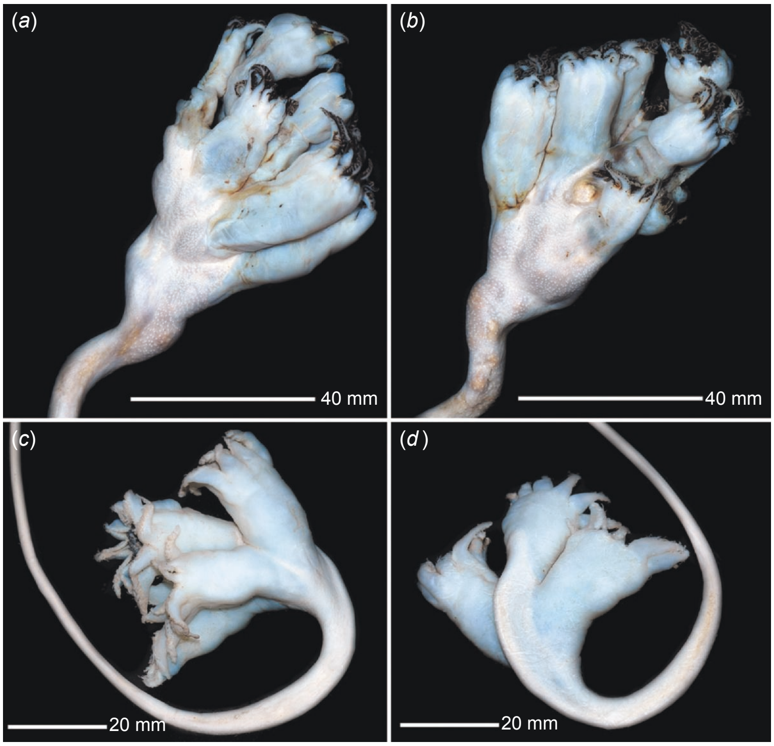

Fig. 7. *Pseudumbellula scotiae* sp. nov., paratype (NMS.Z.2021.2.3): (*a*) dorso-lateral view; (*b*) ventro-lateral view. Specimen from PROSPEC cruise (BECA OPEN-287): (*c*) ventro-lateral view; (*d*) dorso-lateral.

Description of the examined material

Colonies with a single extremely large and laterally flattened terminal autozooid (Fig. 8, 9), up to 180 mm long and 45 mm wide, with tentacles of up to 65 mm long and 10–14 pinnulae of up to 10 mm. Basal part of autozooids tapering proximally or swelling due to accumulation of reproductive products. Lateral sides of autozooid body with eight 'tongue-like' fields of numerous siphonozooids (0.6–0.8 mm in diameter) as distinctly elevated bands (Fig. 8*a–c*). Stem elongated, curved and more or less flexible distally, but thicker, rigid and straight proximally. Intact peduncles not properly observed. Greatest thickness of axis at rachis-peduncle limit. Axis rounded in cross section, 6 mm at the widest part.

Colonies with abundant sclerites in all parts, especially on polyp body (Fig. 8–10) and tentacles (Fig. 10*a–c*). Four kinds of sclerites: distinctly large monoaxial rods with an irregular contour and ends (Fig. 11*a*), monoaxial rods with a low thorny surface (e.g. Fig. 12, 13), monoaxial flattened rods with a low thorny surface (Fig. 14*b*), and smooth to sparsely knobby three-flanged rods (Fig. 14*d*). Young (smaller) colonies apparently more densely spiculated than large ones (Fig. 9, 10*c*).

Main tentacular axis with large monaxial rods with a low thorny surface (Fig. 11*a*) up to 2.4 mm long, also with smaller forms usually more pointed distally, especially those from the proximal parts of tentacles (Fig. 12*a*) up to 1.8 mm long. Pinnulae, up to 17 in number on each side of main tentacle axis, with distinctly large monoaxial rods with irregular contour and ends (Fig. 11*b*) up to 2.3 mm long and also smaller forms with pointed ends.

Polyp body with elongated rods with low thorny surfaces (Fig. 12*b*) up to 1.1 mm long. Pharynx with monoaxial rods (Fig. 13*b*) up to 0.45 mm long. 'Tongue-like' fields of siphonozooids with monoaxial low thorny rods (Fig. 12*a*) up to 1.2 mm long, but typically smaller.

Swollen basal part of autozooid with elongated rods (Fig. 13*c*) up to 0.68 mm long. Stem with sclerites along the longitudinal axis (Fig. 10*e, f*) distinctly more robust than those from the autozooid base (Fig. 13*d*), up to 0.72 mm long.

Proximal part of rachis with large monoaxial rods with rounded ends, flattened in the largest forms (Fig. 14*a, b*) up to 0.72 mm long, 0.15 mm wide and 0.06 mm in thickness. Occasionally with some sclerites in the form of crosses. Transition region between rachis and peduncle with largest sclerites, these becoming progressively less abundant towards upper part of peduncle and being gradually replaced by smaller smooth to sparsely knobby three-flanged rods (Fig. 10*g–j*, 14*c, d*) up to 0.17 mm long, occasionally in the form of crosses.

Colour

Preserved specimens are dirty white to cream in colour.

Distribution

The material described here was collected from the Porcupine Abyssal Plain, between 4845 and 4851 m deep (see also the

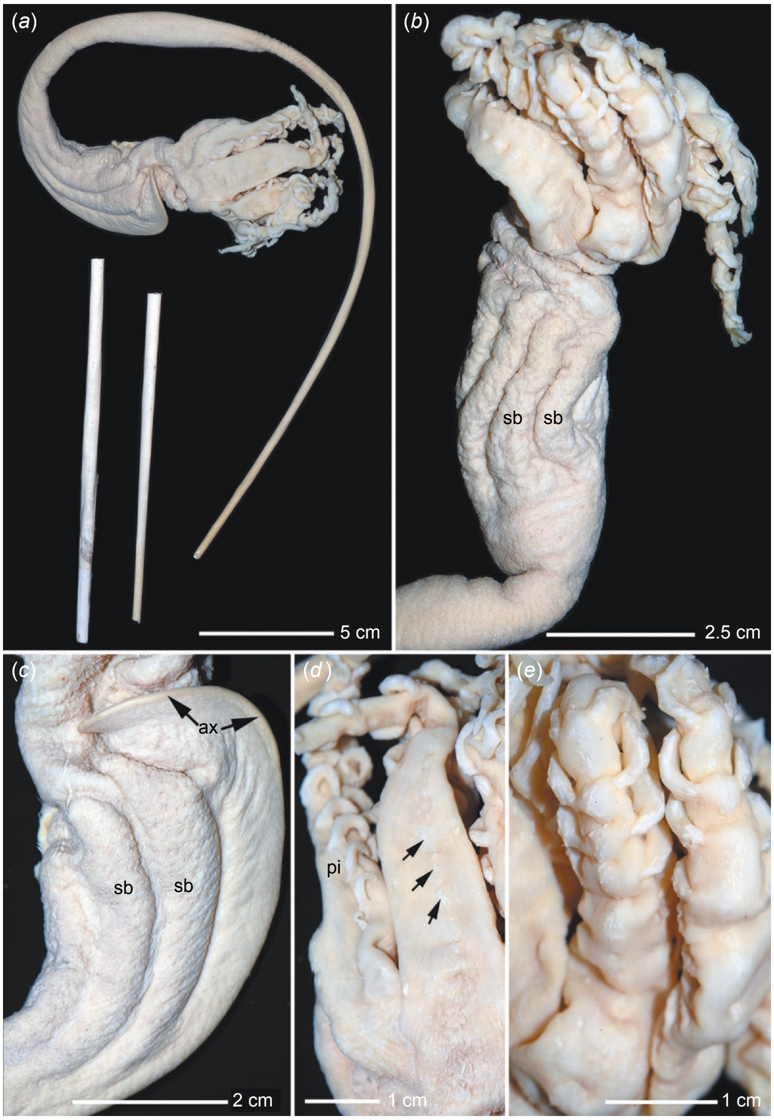

Fig. 8. *Solumbellula monocephalus* (Pasternak, 1964), comb. nov., (*a*) the largest colony from the lot BECA (OPEN-110), showing the extremely large single autozooid, the flexible axis at the upper part of the rachis and the straight and thick stem at the lower part of the rachis-peduncle limit; (*b*) colony NMS.Z.2021.2.1 showing the ventral side of the single autozooid and the 'tongue-shaped' elevated bands of siphonozooids (sb) and large tentacles; (*c*) left lateral side of the autozooid from the colony in (*a*) showing the bands of siphonozooids (sb) and the terminal portion of the axis (ax) recurved on the dorsal part of the polyp; (*d*) basal part of the aboral side of tentacles from the colony in (*a*), showing large sclerites along the middle longitudinal tentacular axis (arrows), as well as the separated pinnulae (pi); (e) mid part of tentacles and highly spiculated pinnulae from colony in (*b*).

general distribution summary above). Previously recorded occurrences in the Atlantic Ocean are those of Grasshoff (1972) 3956–4002 m deep (33°46′N, 15°33′W) North-Eastern Madeira Island, Broch (1957) 4474–4430 m deep (2°26′N, 39°26′W) off Brazilian coasts in the Equatorial Eastern Atlantic.

Phylogenetic analyses

Following the nomenclature of the same clades used in the previously cited papers on phylogeny of sea-pens, our current analyses based on *mtMutS* + *ND2* + *Cox1* + *28S*, agree well with these previous proposals: Clades I to III are well supported (Bst, 96–99; PP, 1), whereas Clade IV is moderate to poorly supported by ML (Bst, 60) but strongly supported by BI (PP 0.99) (see Fig. 15). Both phylogenetic hypotheses (ML and BI) showed the same topology among and within the main clades (including Clade IV). In these hypotheses, the genus *Umbellula* is a taxon in Clade I, whereas the two genera here considered to be part of the new family Pseudumbellulidae fam. nov., are placed in Clade IV.

Clade IV is formed by two main clades: *Balticina* spp. and *Scleroptilum* are sister groups, and the proposed family Pseudumbellulidae fam. nov. with two subclades corresponding to the two new genera described here. The genus *Solumbellula* gen. nov. is only represented by mitochondrial sequences (*MutS* and *ND2*) from a single Indian specimen of *S. monocephalus*, whereas the genus *Pseudumbellula* gen. nov. includes three species: a Southern Ocean (Crozet Island) specimen, considered here as *Pseudumbellula* sp., *Pseudumbellula pomona* comb. nov. (SW Atlantic), and sequences of six specimens of *Pseudumbellula scotiae* sp. nov. (plus an additional sequence from GenBank, as *Umbellula* sp. 2, likely conspecific with *P. scotiae* sp. nov.) all from the eastern North Atlantic. Molecular information was obtained from most of the examined colonies and

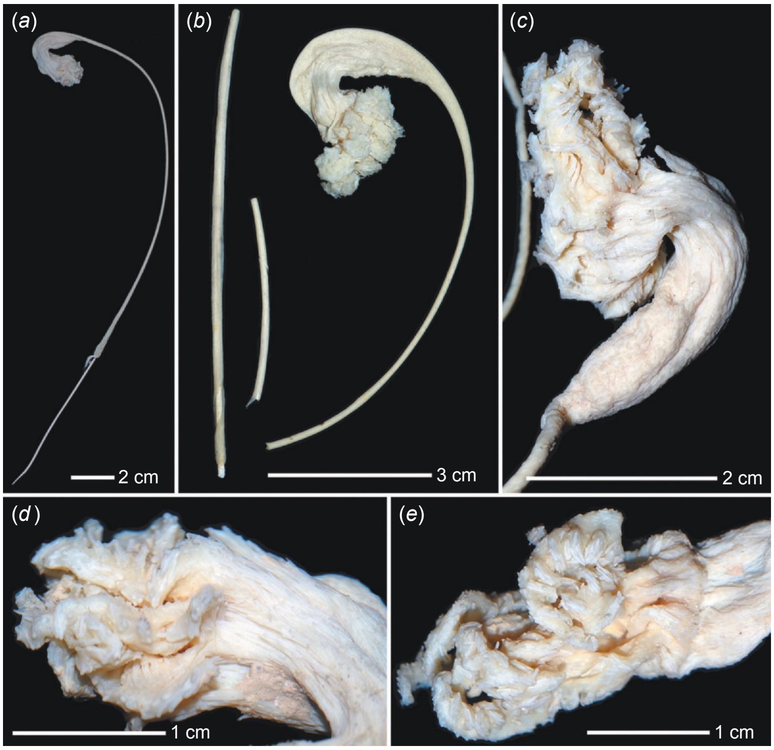

Fig. 9. *Solumbellula monocephalus* (Pasternak, 1964), comb. nov., (*a*–*c*) lateral view of young colonies from lots BECA (OPEN-69), BECA (OPEN-38), and BECA (OPEN-110) respectively; (*d*) terminal autozooid, lateral view (lot BECA (OPEN-69); (e) terminal autozooid, ventral view (lot BECA (OPEN-69).

fragments of *Pseudumbellula scotiae* sp. nov. We were unable to include any other specimens of *Solumbellula monocephalus* comb. nov. in our molecular study because, apart from the specimen yielding the abovementioned sequence, all our available specimens of *S. monocephalus* were initially fixed in formalin before being transferred to 70% ethanol.

When the four molecular markers are analysed separately (Fig. 16), Clades I–IV are easily identifiable in *mtMutS*, *Cox1* and *28S*, whereas basal resolution at the main Clades level is not always observable in *ND2*. In all resulting phylogenetic hypotheses, the sequences of *Umbellula* (Clade I) are distinctly distant from the sequences of *Pseudumbellula* gen. nov. and *Solumbellula* gen. nov. (both in Clade IV), and these last two genera are reunited as Pseudumbellulidae fam. nov. (lacking *Cox1* and *28S* information for *Solumbellula* gen. nov.).

In the *mtMutS* tree, Clades I–III are strongly supported, whereas Clade IV is less supported (Bst, 56; PP, 0.81). A sequence belonging to the genus *Calibelemnon* merges within the *Umbellula* species, between the sclerite-less and the sclerite-bearing *Umbellula* groups. This affinity is not present in the *ND2* tree (where sequences of both sclerite-less and the sclerite-bearing *Umbellula* species are also included), and no molecular information is available for *Calibelemnon* for *Cox1* or *28S* markers. This affinity deserves further research and more complete molecular coverage. The family Pseudumbellulidae fam. nov. is well defined and moderately supported (Bst, 63; PP, 0.7) (see Discussion).

In the *ND2* tree, the family Umbellulidae (now without *Calibelemnon*) is well defined and supported, although the lack of basal resolution at the level of the four main Clades in this hypothesis partially disorganises the component of Clade I. Clade II is however better defined and supported (PP, 0.99). Clades III and IV also show a lack of basal reunification, except for the family Pseudumbellulidae (PP, 0.94).

In the *Cox1* tree, the basal resolution of Clades I and II are not completely separated. However, Umbellulidae is well defined and supported, whereas Pseudumbellulidae fam. nov. is again well separated from *Umbellula*, and related to *Balticina* and (now) *Funiculina*. No sequences of *Scleroptilum* are available for *Cox1* or *28S*. No *Cox1* sequences are available for *Solumbellula* gen. nov.

In the *28S* tree, despite the much lower number (20) of sequences available for our matrix, as compared to the other three markers (61 sequences for *mtMutS*, 53 for *ND2*, or 40 for *Cox1*), the four main Clades are identifiable. Clade I is partially poorly defined basally, but Clade II (PP, 0.98) and particularly Clades III and IV are well defined and supported. Again, *Umbellula* sequences are distinctly distant from *Pseudumbellula* gen. nov. sequences. No *28S* sequences are available for *Solumbellula* gen. nov.

K2P genetic distances based on *mtMutS* between Pseudumbellulidae fam. nov. and Umbellulidae ranged from 5.7 to 9.0%. Distances between *Pseudumbellula* gen. nov. and *Solumbellula* gen. nov. ranged from 2.0 to 2.3%, whereas those between the three *Pseudumbellula* species ranged from 0.3 to 0.6%.

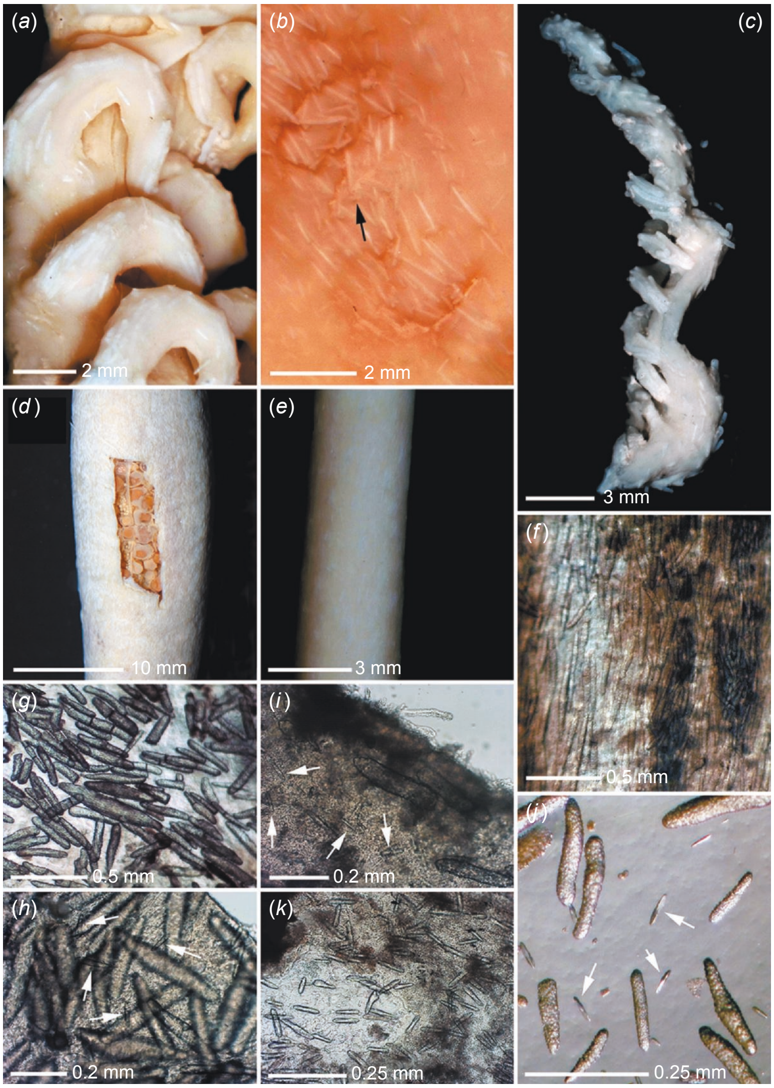

Fig. 10. *Solumbellula monocephalus* (Pasternak, 1964), comb. nov., (*a*) colony NMS.Z.2021.2.1 detail of a group of pinnulae, showing the large sclerites on the aboral side and other smaller ones on the lateral side; (*b*) middle aboral side of tentacles, showing large and smaller sclerites along the longitudinal margin in one of the largest colonies examined, from Fig. 8*c*; (*c*) colony from lot BECA (OPEN-69), a separate tentacle from one of the young colonies, where the spiculation (in comparison to that in a large colony) is apparently more intense; (*d*) lower portion of the autozooid from the large colony of lot BECA OPEN-110 (female) showing its advanced reproductive state; (*e*) detail of the stem, in which longitudinally arranged sclerites can be seen; (*f*) a section of the stem wall partially digested in sodium hypochlorite solution showing arrangement of sclerites; (*g–j*) series of images in the transition from the stem (rachis) where large monoaxial sclerites dominate to upper part of peduncle, where only small smooth to poorly knobby three-flanged sclerites are present. Smaller sclerites in the intermediate phases are indicated with arrows.

Artificial key to the *Umbellula*-like genera discussed in this paper (see also Table 3, Fig. 17)

(1) See Fig. 17 for distinction between X-shaped and rounded or rounded–quadrangular cross sections. (2) Pending a review of the *Umbellulla* species in Clade I, here we can find at least: *Umbellula encrinus* (Linnaeus, 1758) (type species), *U. magniflora* Kölliker, 1880, *U. carpenteri* Kölliker, 1880, and other species used in the phylogenetic hypotheses in this paper, such as *Umbellula* sp. A, and *Umbellula* sp. B (see Kükenthal 1915, p. 47, Dolan *et al.* 2013, present comparative material, see Table 2 and Fig. 17*a–d*). (3) Here we can find *Umbellula thomsoni* (Kölliker, 1874) and similar forms (*U. guentheri* Kölliker, 1880 and *U. hemigymna* Pasternak, 1975); this is also a group requiring revision, and sclerites must be illustrated by SEM (Bayer *et al.* 1983, fig. 98, 100 showed a couple of sclerites of a specimens identified as *Umbellula guentheri*) (see von Kölliker 1874, p. 13, 1880, p. 18; Pasternak 1975, p. 163; Dolan *et al.* 2013, present comparative material, Table 2 and Fig. 17*e*). (4) Here we include materials identified as *Umbellula huxleyi* Kölliker, 1880 and *U. spicata* Kükenthal, 1902 (see von Kölliker 1880, p. 21; Kükenthal 1902, p. 594; Dolan *et al.* 2013, present comparative material, see Table 2 and Fig. 17*f*).

1. Axis cross section X-shaped (with four longitudinal grooves)(1)......2
   Axis cross section rounded to rounded-quadrangular (never with longitudinal grooves)(1)..3
2. Sclerites completely absent...........................*Umbellula (partim)*(2)
   Sclerites present in all parts of the colony (in the terminal cluster of polyps and autozooid bodies these sclerites are three-flanged spindles or rods with serrate edges, never knobby)..........
   ....*Umbellula (partim)*(3)
3. Sclerites completely absent...........................*Umbellula (partim)*(4)
   Sclerites present in all parts of the colony.....................................4
4. Mature colonies with a few autozooids, <15 in number, but more than a single very large one; sclerites as monoaxial spindles or rods, knobby three-flanged rods, and rough ovals or rods (this last at the main stem and peduncle)............*Pseudumbellula* gen. nov.
   Mature colonies with a single very large autozooid; sclerites mainly as large monoaxial spindles or rods, small (<200 µm) sparsely knobby three-flanged rods at the lower part of rachis and upper part of the peduncle...*Solumbellula* gen. nov.

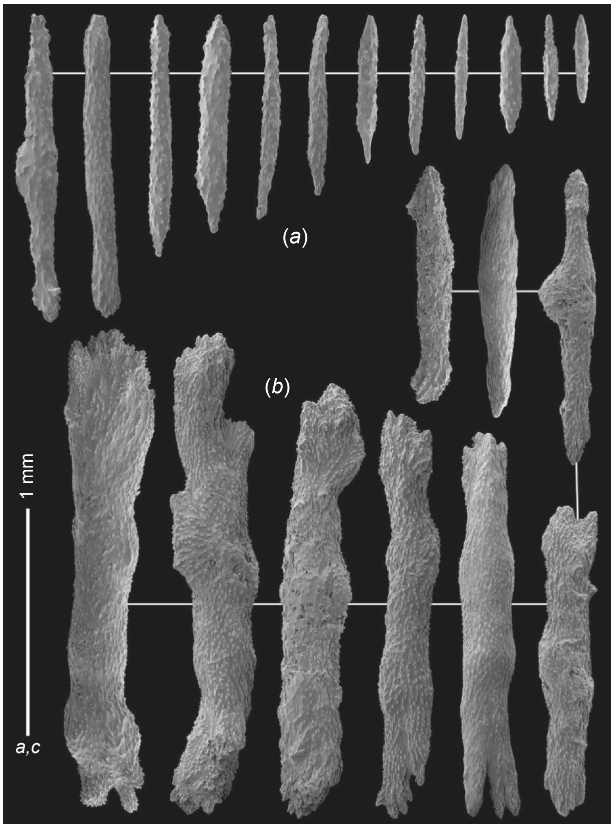

Fig. 11. *Solumbellula monocephalus* (Pasternak, 1964), comb. nov., large colony from lot BECA (OPEN-110) in Fig. 8*a*. (*a*) monoaxial sclerites from aboral side of tentacles; (*b*) large monoaxial sclerites from pinnulae.

Discussion

On Pseudumbellulidae

The need to describe the family Pseudumbellulidae fam. nov. is clearly evidenced in our phylogenetic hypothesis (Fig. 15) based on a multilocus dataset (see above) and even when each marker is analysed separately (Fig. 16), despite varying levels of resolution in each case. The existence of a small number of divergent sequences significantly distant from those of *Umbellula* species (Clade I) has been recognised for ca. a decade (Dolan *et al.* 2013; Kushida and Reimer 2019; García-Cárdenas *et al.* 2020). The opportunity to consult newly collected specimens from the eastern North Atlantic in a complementary morphological and molecular approach allows us: (1) to recognise that the characteristic *Umbellula*-like form appeared more than once in the evolution of sea pens, and (2) to segregate a set of morphological features (mainly at the sclerome level) to be considered in the diagnosis of the new family. In the dataset matrix used for this study (see Table 2), Pseudumbellulidae fam. nov. (considering all species of both genera, *Pseudumbellula* gen. nov. and *Solumbellula* gen. nov.) and Umbelluliidae

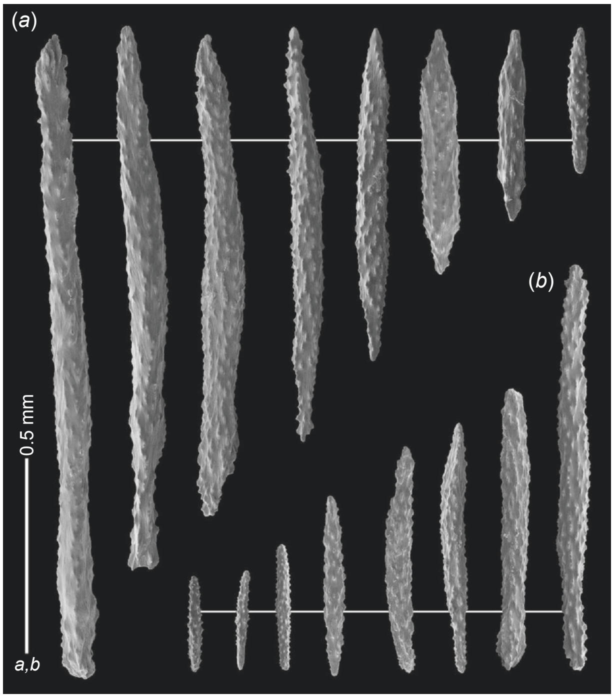

Fig. 12. *Solumbellula monocephalus* (Pasternak, 1964), comb. nov., large colony from lot BECA (OPEN-110) in Fig. 8*a*. (*a*) monoaxial sclerites from the basal part the aboral side of tentacles; (*b*) moaxial sclerites from the body wall of the autozooid.

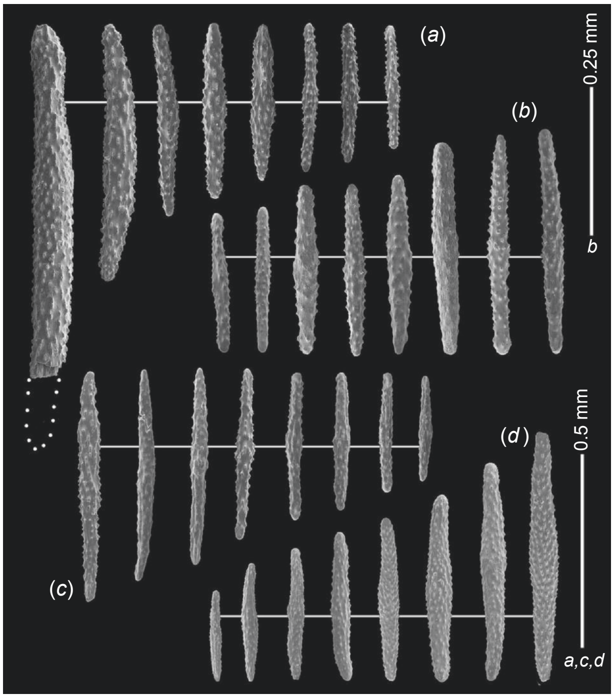

Fig. 13. *Solumbellula monocephalus* (Pasternak, 1964), comb. nov., large colony from lot BECA (OPEN-110) in Fig. 8*a*. (*a*) monoaxial sclerites from siphonozooids 'tongue bands'; (*b*) monoaxial sclerites from the pharynx; (*c*) monoaxial sclerites from the upper part of the stem (lowest part of the autozooid); (*d*) monoaxial sclerites from the stem (see also Fig. 9*f*).

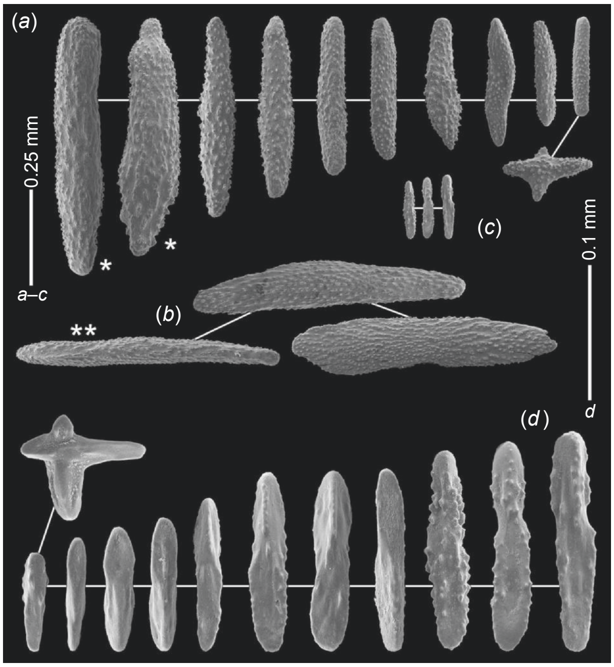

Fig. 14. *Solumbellula monocephalus* (Pasternak, 1964), comb. nov., sclerites from rachis-peduncle limit. (*a*) large monoaxial rods with rounded ends from colony BECA (OPEN-655), flattened in the largest forms (*); (*b*) large monoaxial rods with rounded ends from colony MZB 2021–1031, flattened in the largest forms (*), in lateral view (**); (*c*) sparsely knobby three-flanged rods from colony BECA (OPEN-655), notice these are illustrated at the same magnification than the large monoaxial rods; (*d*) sparsely knobby three-flanged rods (and a cross) from colony BECA (OPEN-655), three of them from (*a*) notice these are illustrated here in a different scale.

(considering all species of *Umbellula* in Clade I) differ in 19 bases in *mtMutS*, 8 bases in *ND2*, 9 bases in *Cox1* and 158 bases in *28S*. This is unlikely to be the final step in resolving the uncertain status and relationships of *Umbellula* species. However this nomenclatural act is necessary to advance the systematics of the order Pennatuacea in the light of the new and ever-increasing molecular information.

Thus, *Umbellula*-like forms with sclerites are present in two well-separated Clades (I and IV). The sclerite-bearing species in Clade I have an axis X-shaped in cross-section whereas the axis of those in Clade IV is rounded to rounded–quadrangular. However, both lineages possess three-flanged spindles or rods. In *Umbellula* (Clade I), these have serrate edges (see SEM sclerite images by Bayer *et al.* 1983, fig. 98, 100 of *Umbellula guentheri* Kölliker, 1870), whereas in Clade IV (Pseudumbellulidae fam. nov.) these sclerites are knobby (see Fig. 4*b–d*, 5, 14*d*).

The support of a *Solumbellula–Pseudumbellula* clade is relatively poor in the ML framework (Bst, 60%) but strongly supported by BI (PP, 0.99). We consider that in the absence of additional *Solumbellula* sequences (*Cox1*, *28S*) from the only known specimen (we are using four markers in *Pseudumbellula*) and the lack of complementary sequenced *Solumbellula* specimens from the Indian and most especially from the Atlantic Oceans, the present proposal is the most conservative at this time. This proposal is also supported by: (1) the similar morphological colonial growth form (number of autozooids aside); (2) the presence of similar distinctly large monoaxial and knobby nodulous three-flanged sclerites in both *Pseudumbellula* and *Solumbellula*; and (3) the morphological differences between these and the other genera (and families, namely Balticinidae and Scleroptilidae) in Clade IV. The sister group of Pseudumbellulidae fam. nov. is a *Balticina–Scleroptilum* clade. Species of the genus *Balticina* (Fam. Halipteridae) possess long, slender and whip-like colonies, with retractile autozooids in spiculate calyces placed on numerous elevated and obliquely orientated ridges (see additional information in Williams 1995, p. 120). By contrast, species of *Scleroptilum* (Fam. Scleroptilidae) possess slender and delicate colonies, with non-retractile autozooids arranged singly or in pairs along the rachis (see additional information in Williams 1995, p. 115). Moreover, the genetic distance (*mtMutS*, K2P) between *Balticina* and *Scleroptilum* is 2.9%, whereas that between the two *Balticina* species used here, *B. finmarchica* and *B. willemoesi* (Atlantic and Eastern Pacific specimens respectively) is 0.3%. The genetic distances between Balticinidae (*Balticina*) and Pseudumbellulidae fam. nov. ranged from 4.7 to 5.9%, and those between Scleroptilidae (*Scleroptilum*) and the new proposed family ranged from 3.6 to 4.6% (we must note that the genetic distance between Pseudumbellulidae fam. nov. and Umbellulidae ranges from 5.7 to 9.0%).

On *Pseudumbellula* spp.

Among the species previously considered to belong to the genus *Umbellula* and here transferred to the genus *Pseudumbellula* gen. nov. is *Umbellula durissima*, a strongly spiculiferous species as described by von Kölliker (1880, p. 16). The type specimen of *U. durissima* shows bilateral symmetry, large wart-like siphonozooids mainly distributed on a (rhomboidal in shape) dorsal upper section of the rachis, the axis round in cross section with four autozooids (two large and two undeveloped) and large clearly visible surface sclerites on the body and tentacles of the autozooids of 2.0 to 2.85 mm long. The type material of this species was collected in the North Pacific Ocean (south of Yeddo, Japan) at ~1024-m depth. At present, all published records place this species in the deep seas of the Indian Ocean; however, some of the records attributed to this species are considered doubtful, as are the many names in the list of synonyms (Kükenthal 1915) for this species. Despite this, the overall appearance of the terminal group of autozooids, the distinctive siphonozoids and the large clearly visible sclerites on the body of the autozooids, and the main tentacular axis distinctly differentiate the von Kölliker (1880, p. 16) species from *Pseudumbellula scotiae* sp. nov.

During the Talisman cruise along the eastern North Atlantic coasts in 1883 (see Dolan 2020) a few colonies of a sea pen with an *Umbellula*-like morphology were collected between 2000- and 2125-m depth. One of these *Umbellula*-like colonies was also included in a fine artistic colour illustration of a deep-sea landscape by Filhol (1885, plate 2), published as part of the popularisation of the deep-sea fauna collected during this cruise by the expedition participants. These colonies were formally described as *Umbellula crassiflora* by Roule (1905) in a short note on the preliminary results of the sea pen fauna collected during the Talisman cruise along the Atlantic Moroccan coasts. Despite the somewhat brief morphological description provided and the lack of illustrations, the details of both the sclerite morphology and the structure of the polyps are in agreement with our description of *Pseudumbellula*. A decade

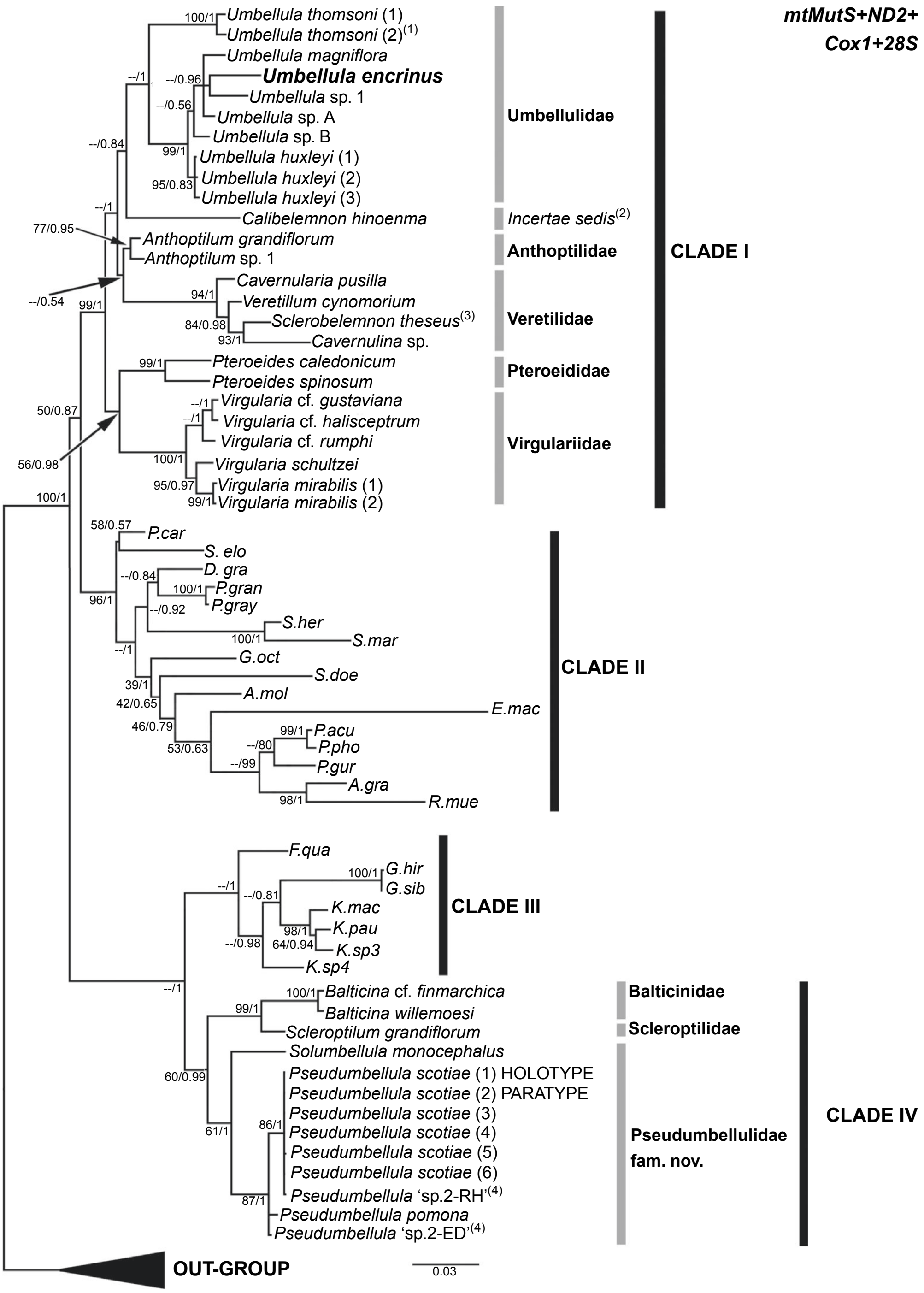

Fig. 15. (*Caption on next page*)

after Roule's (1905) note however, this species was considered as *species dubia* by Kükenthal (1915, p. 56) and since that time has been simply forgotten or occasionally listed among the synonyms of *Umbellula thomsoni* (see Broch 1958, p. 253; Pasternak 1964, p. 192, 1975, p. 161). The type material of *U. crassiflora* is deposited in the Museum National d'Histoire Naturelle in Paris, and the stout polyps and relatively short tentacles with thick basal parts (*épais a leur base*, as described by Roule 1905) are very distinctive features of this species, as are the large (>2.5 mm) superficial sclerites on the aboral side of the tentacles (visit the images of the type material of this species in the repository of the MNHN collections: https://science.mnhn.fr/institution/mnhn/collection/ik/item/2000-331?listIndex=2&listCount=7). Although the type material of *Umbellula crassiflora* is in need of a morphological and molecular re-description (assuming the type material is suitable for DNA extraction of high enough quality), this clearly differs from *Pseudumbellula scotiae* sp. nov.; the large surface sclerites present on the aboral side of the tentacles in the former are absent in the new species proposed here, where the largest sclerites in the tentacle are embedded into the mesoglea (Fig. 3*h*) and do not reach more than 0.4 mm long (Fig. 4*a*).

Eastern North Atlantic colonies belonging to the species described here as *Pseudumbellula scotiae* sp. nov. were also reported by Dolan (2008) in her PhD thesis (University of Southampton Institutional Repository). Dolan (2008) identified her material as *Umbellula aciculifera* Thomson, 1915. This is mentioned here because of the current wide distribution of documents in institutional electronic repositories. Dolan's (2008) PhD thesis is referenced in the present paper as recommended by the University of Southampton for this type of document. We consider *U. aciculifera* as a valid species; however, our knowledge of this species is currently restricted to the type material (see below).

Umbellula aciculifera was described by J. S. Thomson (1915), however Broch (1958, p. 253) considered this name a synonym of *Umbellula thomsoni* and since that time this subordinate placement has been repeated by subsequent prominent authors (Pasternak 1962, 1964, 1970, 1975, 1993; Williams 1990). The description of *Umbellula aciculifera* was based on a single specimen collected SW of Cape Point (South Africa) that is deposited in the Iziko Museums of South Africa (formerly South African Museum, registration code: SAM-H1166). The only further description and illustration of this type material in existence is that carried out by Williams (1990, p. 81) who identified the material as *Umbellula thomsoni*, as previously proposed by Broch (1958). The assignation of *U. aciculifera* under *U. thomsoni* may be rooted in the interpretation at the time of what should be described as a quadrangular axis (i.e. that with four more or less flat or slightly convex sides) and what should be described as an X-shaped axis (i.e. that with four sides possessing more or less deep longitudinal grooves). The latter form is known to be present in several species of the genus *Umbellula* (both those with and without sclerites) and (more or less developed) in other sea pen genera such as *Funiculina* (see Manuel 1981, p. 53) and *Porcupinella* (see López-González and Williams 2011, p. 312). In our diagnosis above, the axis of *Pseudumbellula* species never possesses deep longitudinal grooves and, while the cross section may vary slightly from rounded to quadrangular (with four sides more or less convex as illustrated by Williams 1990, fig. 22), this never exhibits an X-shaped form. *Pseudumbellula aciculifera* (Thomson, 1915), comb. nov. differs from *P. scotiae* sp. nov. by the general shape of the terminal group of authozooids, the

Fig. 15. Molecular analysis by Bayesian inference method (BI). Only the relevant Clades I and IV are shown non-collapsed (see Discussion). Relationship of the family Pseudumbellulidae and the genera *Pseudumbellula* gen. nov. and *Solumbellula* gen. nov. in Clade IV. The placement of *Umbellula encrinus*, type species of the genus *Umbellula*, is emphasised in bold in Clade I. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Bootstrap and posterior probability (Bst/PP) are indicated in each node, where (–) indicates that particular node has no supporting value in one of the inference methods. See Table 2 for additional information on the sequenced specimens used in these comparisons. Only the species constituting Clades I and IV (where the families Umbellulidae and Pseudumbellulidae discussed in this paper are included) are indicated in expanded form, all other species in Clades II and III are abbreviated according to Table 2. In Clades II and III, non-monophyletic situations at genus or family level are not indicated as different revisionary researches are ongoing, and species or specimens must be investigated with complete morphological and molecular coverage before other nomenclatural changes can be proposed (López-González, Drewery and Williams, in prep.). Notes: (1) It is doubtful that both sequences belong to *Umbellula thomsoni*; this particular material from Crozet Islands (SO) deserves further research (see also note 7 in Table 2). (2) The family placement of the genus *Calibelemnon* is controversial, being considered in Chunellidae by Williams (1995, p. 115), and in Scleroptilidae by Williams and Alderslade (2011) whereas Kushida and Reimer (2019, 2020) pointed out the polyphyletic status of this las family, the type genus of which *Scleroptilum*, is in Clade IV. In this sense, sequences of the genus *Chunella* are required to ascertain if *Calibelemnon* should return to Chunellidae or rather if it should be considered in a different suprageneric unit at family level according to the available names and literature dealing with the genus *Calibelemnon*. (3) The genus *Sclerobelemnon* has traditionally been considered in the family Kophobelemnidae (*Kophobelmenon* is placed in all published phylogenies in Clade III and also here) however, as in previous papers (Kushida and Reimer 2019, García-Cárdenas *et al.* 2020, fig. S2), *Sclerobelemnon* merges among veretilid genera, thus the family Veretilidae can only be considered monophyletic if *Sclerobelemnon* is included within it. Obviously, it is preferable to keep the family Veretilidae monophyletic than to retain doubts about the placement of *Sclerobelemnon* (and a paraphyletic Veretilidae). It is desirable that in the near future this sequenced material be fully described from a morphological point of view and, if possible, molecular information completed (*Cox1* and *28S* sequences are not available). (4) The status of these unidentified sequenced specimens are briefly discussed in the text (see Discussion).

relative proportions of the length and width of the autozooids and the shape of the tentacles (see Williams 1990, fig. 22 compared to Fig. 2, 3 in this paper). Moreover, both species also differ in respective scleromes (e.g. main tentacle axis, pinnules and polyp body). *Pseudumbellula aciculifera* is a distinctive spiculiferous species, as noted by

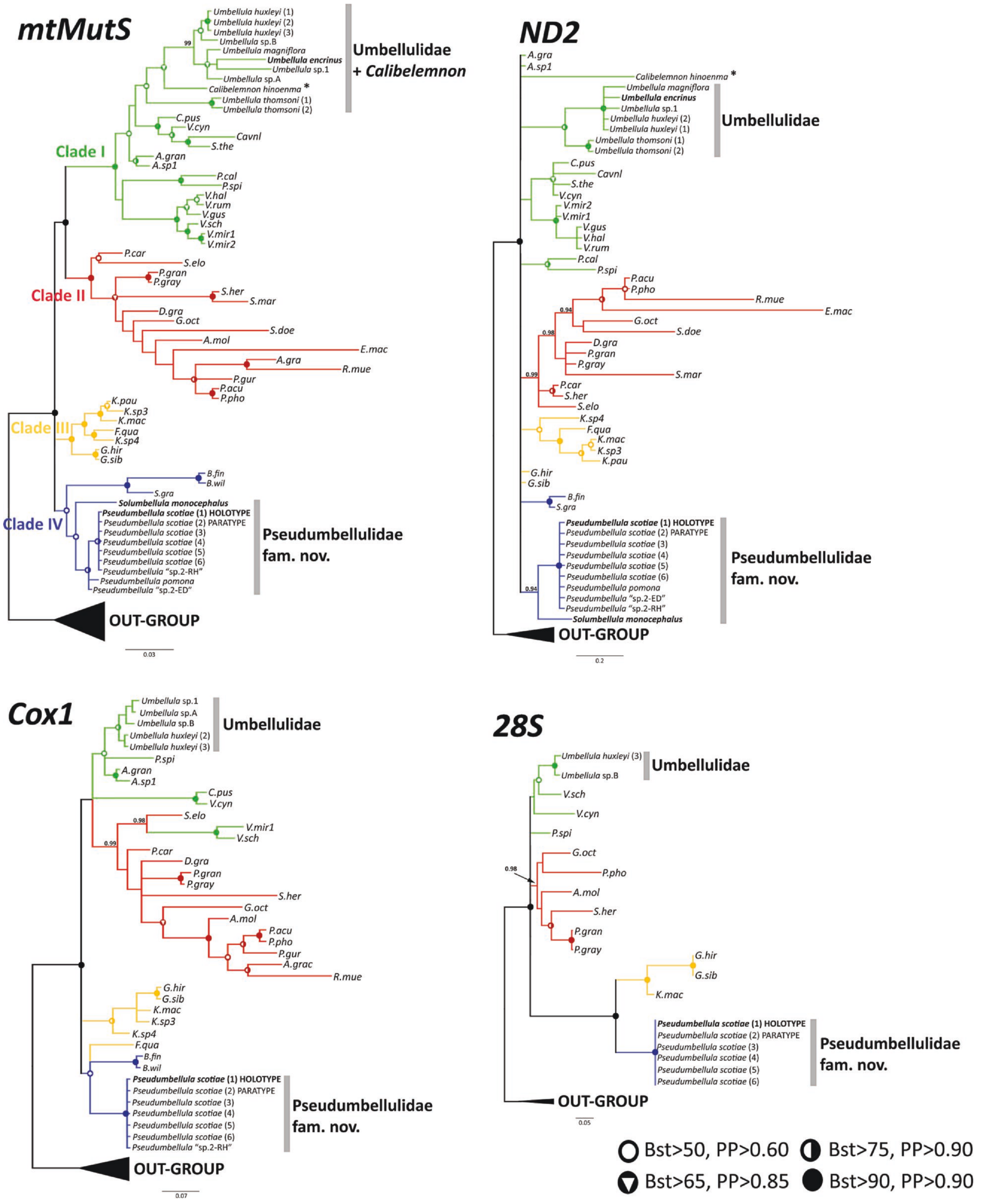

Fig. 16. (*Caption on next page*)

Williams (1990) with distinct large monoaxial sclerites of up to 1.3 mm long (rather than < 0.4 mm as in our new species) and rods of > 0.6 mm in the pinnules (rather than < 0.3 mm long knobby three-flanged rods in our new species). Moreover, polyp body sclerites are < 0.05 mm in Thomson's (1915) species, but up to ~0.08 mm in *P. scotiae* sp. nov. Finally, the sclerites of the peduncle appear to be rougher and slightly shorter (up to 0.11 mm long) in *P. aciculifera* (see Williams 1990, fig. 23A–D) than in *P. scotiae* sp. nov. (> 0.17 mm long, Fig. 6*b*). There is no molecular information on *Pseudumbellula aciculifera*.

Another species recently described in the genus *Umbellula* from the SW Atlantic, *Umbellula pomona* Risaro, Williams, Pereyra & Lauretta, 2020, should also be ascribed to the genus *Pseudumbellula* gen. nov. following our diagnosis. *Pseudumbellula pomona* (Risaro, Williams, Pereyra & Lauretta, 2020), comb. nov. also clearly differs from *P. scotiae* sp. nov. by the general shape of the terminal group of authozooids, the relative proportions of the length and width of the autozooids and the tentacle shape (see Risaro *et al.* 2020, fig. 8 compared to Fig. 2, 3 in this paper). Moreover, both species also show distinct differences in scleromes (e.g. main rachis, pinnules and polyp body). The main axis tentacle sclerites in *P. pomona* belong to a single type (rods) however, according to the original authors, these are in two size categories, the larger ranging in size from 0.9 to 1.5 mm long and the smaller from 0.5 to 0.7 mm long. However, in *P. scotiae* sp. nov. there are two sclerite types (rods and knobby three-flanged rods) of which both types are located embedded in the thick axial mesoglea but only one on the aboral surface of tentacles. In the tentacular mesoglea, the largest are rods < 0.4 mm with a distinctly low thorny surface, whereas a second type are knobby three-flanged rods < 0.15 mm. The second size category of knobby three-flanged rods occurs on the surface of the tentacles, these are < 0.08 mm. The pinnulae of both species show

Table 3. Comparative table of the *Umbellula*-like genera discussed in this paper whose some morphological features are segregated in two different families according to the molecular information (see also Fig. 15).

	Umbellulidae Kölliker, 1880	**Pseudumbellulidae fam. nov.**	
Characteristics	***Umbellula* Gray, 1870**	***Pseudumbellula* gen. nov.**	***Solumbellula* gen. nov.**
Maximum known number of autozooids	>50	<15	1
Terminal group (or single) autozooid's symmetry	Radial/bilateral	Bilateral	Bilateral
Sclerites	Absent or present^A	Present	Present
Sclerite's morphology (if present): Autozooid, siphonozooids and common tissues of terminal part of rachis: Rachis' stem and peduncle:	Three-flanged needles or rods with serrate edges. Rough ovals to rods with angular prominences.	Knobby three-flanged, monoaxial rods (somewhat distinctly large), and Rough ovals to rods with rounded or pointed prominences.	Monoaxial spindles and rods (somewhat distinctly large) Rachis' stem with monoaxial spindles and rods (somewhat distinctly large), and sparsely knobby three-flanged rods at the rachis-peduncle limit
Axis cross-section	X-shaped (with longitudinal grooves)^A or rounded	Rounded to nearly quadrangular, never with longitudinal grooves	Rounded to nearly quadrangular, never with longitudinal grooves
Clade in published phylogenetic hypotheses^A	Clade I	Clade IV	Clade IV

It is necessary to mention that a review of the species of the genus *Umbellula* (currently only those located in Clade I) is still pending, and that the delimitation of possible new groupings will require a more important contribution of molecular data of different putative species, as well as a careful update of the morphological descriptions of that sequenced materials.

[A] Currently, in the genus *Umbellula*, the presence of sclerites (three-flanged needles and rods with serrate margins) is linked to an axis with X-shaped cross-section, whereas sclerites-less *Umbellula* species can show X-shaped or rounded cross-sections. Moreover, the possession of an X-shaped cross-section is not unique to sclerites-bearing *Umbellula* species.

Fig. 16. Molecular analysis by Bayesian inference method (BI) of the four molecular markers separately. The family Pseudumbellulidae and the genera *Pseudumbellula* gen. nov. and *Solumbellula* gen. nov. are in Clade IV. The placement of type species of the genera *Umbellula*, *Pseudumbellula* gen. nov., and *Solumbellula* gen. nov. are emphasised in bold. The trees are drawn to scale with branch lengths measured in the number of substitutions per site. Where a number is present in the tree it indicates a particular high value from PP or Bst, whereas the topology in ML is not exactly as in BI. See Table 2 for additional information on the sequenced specimens used in these comparisons. Asterisks (*) indicate the position of the available sequences of *Calibelemnon* (see Phylogenetic analyses section for additional comments). Only the species of the families Umbellulidae and Pseudumbellulidae fam. nov., and the genus *Calibelemnon* are indicated in expanded form, all other species in the trees are abbreviated according to Table 2.

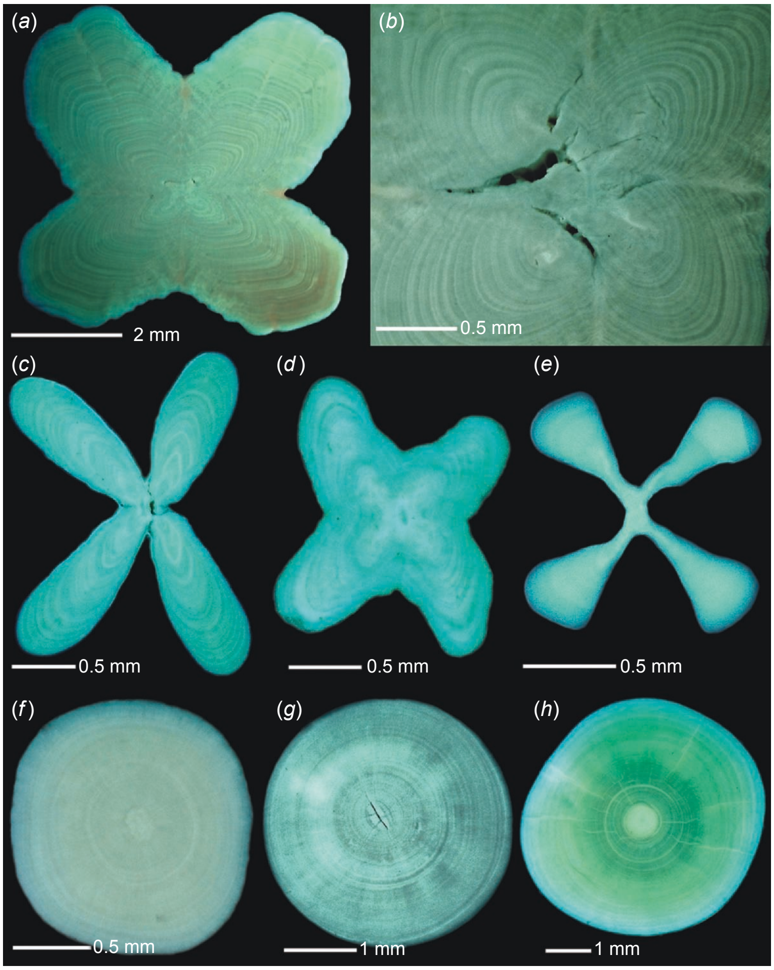

Fig. 17. Cross-sections of the axis near the rachis-peduncle limit of *Umbellula*, *Pseudumbellula* gen. nov. and *Solumbellula* gen. nov. species. Growth rings are visualised and photographed under UV light. (*a*) *Umbellula encrinus* (BECA OPEN-658), from BIOICE cruise in North Atlantic-Arctic waters, complete cross-section; (*b*) *Umbellula encrinus* (BECA OPEN-657), same cruise program and geographic area as (*a*) detail of the internalmost core showing the alternation of multiple growth rings; (*c*) *Umbellula carpenteri* (BECA OPEN-627), from EASIZ cruises in Antarctic waters, complete cross-section; (*d*) *Umbellula* sp. B (BECA OPEN-103), same cruise program and geographic area as (*c*); (e) *Umbellula* cf. *thomsoni* (BECA OPEN-88), from ANDEEP program in Antarctic waters; (*f*) *Umbellula* cf. *huxleyi* (BECA OPEN-170), from Scotia cruise program in North Atlantic waters; (*g*) *Pseudumbellula scotiae* sp. nov., paratype (NMS.Z.2021.2.3/BECA OPEN-171), from Scotia program in North Atlantic waters; (*h*) *Solubellula monocephalus* comb. nov. (BECA OPEN-110), from BENGAL program in North Atlantic waters. See Discussion for additional morphological details and differences among these *Umbellula*-like species or specimens, two of them assigned here to the new proposed family Pseudumbellulidae fam. nov., in the genera *Pseudumbellula* gen. nov. (*g*) and *Solumbellula* gen. nov. (*h*).

similar three-flanged rods, however these are slightly larger and somewhat more pointed than knobby in the SW Atlantic species compared to those of the new species (up to ~0.32 mm in the former but up to ~0.27 mm long in the latter) (see Risaro *et al.* 2020, fig. 7, and Fig. 4 in this paper). Rachis sclerites of *P. pomona* are spindles, some of these are more or less three-flanged up to 0.4 mm long, whereas those from the upper part of the rachis (around the basal area of the autozooids) of *P. scotiae* sp. nov. are knobby three-flanged rods up to 0.28 mm. There is no information about stem or pharyngeal sclerites from *P. pomona*. The genetic analyses above also clearly differentiate *P. pomona* and *P. scotiae* sp. nov. Risaro *et al.* (2020, fig. 9), in discussing the phylogenetic relationships of *Umbellula pomona* (based on *mtMutS* and *ND2*), also detected the polyphyletic status of the genus *Umbellula* pointed out in previous papers (Dolan *et al.* 2013; Kushida and Reimer 2019). In this case the species of *Umbellula* were separated into two clades: '*Umbellula* clade I' (within Clade I of our phylogeny) including the type species *Umbellula encrinus* and '*Umbellula* clade II' (within Clade IV of our phylogeny) where *Umbellula pomona* was related to the sequences *U. monocephalus* and *Umbellula* sp. 2 of Dolan *et al.* (2013). Risaro *et al.* (2020, p. 137) also suggested that following a more revisionary study a new genus for '*Umbellula* clade II' would have to be proposed.

Sequences of two unidentified species that are deposited in GenBank and attributed to the genus *Umbellula*, and here placed in the genus *Pseudumbellula* gen. nov., deserve further comments. First, a colony collected off Porcupine Bank and very close to our study area (*Umbellula* sp. 2 in Hogan *et al.* (2019), GenBank Accession number of the complete mitochondrial genome MK919670) that we consider most likely conspecific with *P. scotiae* sp. nov. is included in the phylogeny as *Pseudumbellula* 'sp. 2-RH'. The second unidentified *Pseudumbellula* species was collected from off the Crozet Islands in the Southern Ocean (*Umbellula* sp. 2 in Dolan *et al.* 2013, KF313856 and KF313829) and is included as *Pseudumbellula* 'sp. 2-ED' in our tree (Fig. 15). Until a detailed morphological description of this Southern Ocean colony is completed, assigning this specimen to any known species will not be possible. However, this specimen may prove to represent *P. aciculifera* or be an undescribed species. The information in GenBank suggests that the specimen is deposited in the Natural

History Museum in London but the registration code given ('NHM Sea Pens 2009.6') is not a regular registration code of that museum and despite extensive efforts, the specimen has not been located.

On *Solumbellula* spp.

The only available sequences from the single species currently recognised to belong in this genus are from a colony of *Solumbellula monocephalus* comb. nov. from the Indian Ocean, the geographic area of the type material (see Pasternak 1964; Dolan *et al.* 2013). Although specimens from the Atlantic were examined as part of this study, the fixation method (formalin) used rendered molecular comparison impossible. This Atlantic material was described as *Umbellula thieli* by Grasshoff (1972), who at that point was not aware of Pasternak's paper, but who also established the synonymy himself in his papers a decade later (Grasshoff 1982*a*, 1982*b*). The synonym of *U. thieli* was due to the material showing the same general colonial morphology, with a single large autozooid and the lack of clear differences in morphology, size ranges and distribution of sclerites.

Molecular studies are often splitting species that are historically considered cosmopolitan or in general very widely distributed. Material of these species has often been identified only by morphological characters that until recently have been the only available source of differentiation. If Atlantic colonies of *Solumbellula* from the Porcupine Abyssal Plain become available for sequencing in the future, a second species would be considered in this genus if these demonstrate sufficient genetic divergence from Indian Ocean material. This putative second species, in which the present examined material should be included, should be ascribed to *Solumbellula thieli* (Grasshoff, 1972).

General remarks

According to Broch (1957, 1958), 'certainly too many species have been described within this [*Umbellula*] genus', but perhaps the main problem is the lack of knowledge about the intraspecific variability of the relatively low number of morphological characters used in the description. The combination of the few main opposite morphological features in historical use (with sclerites or without sclerites, axis round-quadrangular or axis quadrangular with deep longitudinal grooves) has defined four main species groups. However, *Umbellula* species were further differentiated by sometimes subtle details on the number, sizes and ordination of the autozooids, and the thickness of the axis (Broch 1958) that were the only available characters at that time. The number of named species in the genus *Umbellula* (and monotypic family Umbellulidae) reached ~60 of which most are considered synonyms, *incertae sedis*, *nomen dubium* or *species inquerenda* (e.g. Kükenthal 1915; Williams 1995; see also compilation of this type of information in WoRMS databases by Cordeiro *et al.* 2021).

Apart from the phylogenetic relationships of the genus *Umbellula* obtained using the *18S* marker (Berntson *et al.* 1999, 2001) that are difficult to explain, the use of *mtMutS* (=*msh1*) during the last decades and subsequent multi-locus comparisons (McFadden *et al.* 2006) placed the genus *Umbellula* within a monophyletic Pennatulacea clade. The analyses of mitochondrial genes such as *mtMutS* + *ND2* (Dolan *et al.* 2013; Kushida and Reimer 2019; Risaro *et al.* 2020), or matrices of two mitochondrial and one nuclear marker such as *mtMutS* + *Cox1* + *28S* concatenated (García-Cárdenas *et al.* 2019, 2020) has highlighted incongruences between the traditional classification based on morphology and the different phylogenetic trees generated. The main results of these investigations included the following: (1) the two main groups of sea pens, Sessiliflorae and Subselliflorae are non-monophyletic; (2) some of the most important or widely distributed families such as Pennatulidae, Virgulariidae and Umbellulidae are non-monophyletic; (3) most of the genera (with the exception of a few such as *Umbellula* or *Veretillum*) including more than a single species in the analyses were monophyletic; and (4) many of the generic and family relationships need to be revisited in the light of combined morphological and molecular studies.

Current DNA sequencing analyses allow us to identify phylogenetically related groups of species and focus our research on these monophyletic MOTUs separately using morphological and molecular tools. The present paper deals with a grouping of species distantly related from the genus *Umbellula* (species whose genetic data indicate these are closely related to the type species *Umbellula encrinus*). The existence of divergent sequences attributed to the genus *Umbellula* has already been mentioned over the last decade in various papers dealing with the phylogenetic relationships of pennatulaceans (Dolan *et al.* 2013; Kushida and Reimer 2019; García-Cárdenas *et al.* 2020). This study sheds light on this small group of species and resolves the taxonomy and placement within the systematics of pennatulaceans.

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Data availability. Supplemental data for this article can be accessed in public databases (GenBank) and examined materials are deposited in the various museums and institutions detailed above.

Conflicts of interest. The authors declare that they have no conflicts of interest.

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