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A new family for the enigmatic sea pen genus *Gyrophyllum* Studer, 1891 (Octocorallia, Pennatulacea), a molecular and morphological approach

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Abstract. The description in 1891 of the sea pen genus *Gyrophyllum* Studer, 1891 and also the type species *G. hirondellei* Studer, 1891 was based on a single colony collected in the Azores Archipelago. During the 19th and 20th centuries, the family placement of this genus became controversial as the set of morphological features present in *Gyrophyllum* could justify its assignation to both the families Pennatulidae Ehrenberg, 1834 and Pteroeididae Kölliker, 1880. Deliberations over this intermediate set of characters finally ended in the reunification of the genera and species of both families under Pennatulidae by principle of priority. The use of molecular sources of information based on a series of sequencing techniques presents a different but promising phylogenetic scenario in order to go further in the understanding of pennatulacean systematics. In this paper, a complementary morphological and molecular study (multiloci sequences with three mitochondrial and one nuclear markers) based mainly on newly collected material is carried out. This study re-confirms from a molecular point of view previously published results that indicate the position of *Gyrophyllum* as being distant from *Pennatula* Linnaeus, 1758 and *Pteroeides* Herklots, 1858 (type genera of the families Pennatulidae and Pteroeididae, respectively). This fact together with the results of a detailed morphological examination strongly supports the placement of the enigmatic genus *Gyrophyllum* in a separate family: Gyrophyllidae fam. nov. and resolves the nomenclatural uncertainty at family level for this genus. Moreover, the characters previously considered useful in the distinction of the two currently recognised species *G. hirondellei* in the Atlantic and *G. sibogae* Hickson, 1916 in the Indo-western Pacific are revisited.

Keywords. Biodiversity, coral, morphology, molecular analyses, integrated approach.

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Introduction

The pennatulacean genus *Gyrophyllum* Studer, 1891 was named and described by Studer (1891: 94) for the type species *G. hirondellei* Studer, 1891, based on a single colony collected in the Azores Archipelago (eastern North Atlantic), between the islands of Pico and São Jorge. Williams (1995b: 322) pointed out the main historical vicissitudes prevalent during the 19th and 20th centuries regarding the taxonomic status considered for the two pennatulacean families Pennatulidae Ehrenberg, 1834 and Pteroeididae Kölliker, 1880. That status was definitively influenced by the different possibilities of placement of the genus *Gyrophyllum* within one or other of these families. In summary, while Studer (1891) originally placed his new genus in Pteroeididae, the presence of three-flanged sclerites was used to subsequently remove the genus from that family and to place it in Pennatulidae (Kükenthal & Broch 1911: 253), shortly afterward, however, this placement was considered as incertae sedis (Kükenthal 1915: 120) and *Gyrophyllum* was once more returned to Pteroeididae (Hickson 1916: 252; Tixier-Durivault & d'Hondt 1974a: 263, 1974b: 1420; Williams 1995a: 128). The intermediate morphological characters exhibited by *Gyrophyllum* as being somewhere between Pennatulidae (three-flanged sclerites) and Pteroeididae (siphonozooids on polyp leaves) ended in a proposal of reunification of the genera of both families under Pennatulidae by the principle of priority (see Williams 1995b), this being the most conservative proposal based on the strictly morphological outlook that prevailed at the time. However, the modern use of molecular sources of information based on sequencing of first mitochondrial genes (Dolan *et al.* 2013; Kushida & Reimer 2019) and subsequently the combination of mitochondrial and nuclear genes (e.g., García-Cárdenas *et al.* 2020; López-González & Drewery 2022) in these families presents a different and very promising phylogenetic scenario for a much-improved understanding of pennatulacean systematics overall.

McFadden *et al.* (2006) first recognised the monophyly of the order Pennatulacea in a global phylogeny of Octocorallia Haeckel, 1866, based on two mitochondrial protein coding genes, *msh1* (= *mtMutS*) and the NADH dehydrogenase subunit 2 (*ND2*). A decade ago, Dolan *et al.* (2013), carried out the first phylogenetic analysis based only on sea pens, and informally named four main clades (hereinafter as Clades I–IV) also based on *mtMutS* and *ND2*. These authors used sequences of specimens of *Gyrophyllum* from the eastern North Atlantic and the West Pacific identifying it as a monophyletic genus within Clade III. In that clade, *Gyrophyllum* was related to the genera *Funiculina* Lamarck, 1816 (fam. Funiculinidae Gray, 1870) and *Kophobelemnon* Asbjörnsen, 1856 (fam. Kophobelemnidae Gray, 1860). In this initial phylogeny only 14 sea pen genera were included in the analysis, and attention was drawn to the fact that some of these genera (*Kophobelemnon*, *Umbellula* Gray, 1870, and *Pennatula* Linnaeus, 1758, for instance) were non-monophyletic, and that most of the families currently in use in the classification of sea pens were also non-monophyletic. Dolan *et al.* (2013: 615) already pointed out that the placement of the genus *Gyrophyllun* (in Clade III) was controversial considering that the type genera of Pteroeididae (*Pteroeides* Herklots, 1858) and Pennatulidae (*Pennatula*) were located in Clades I and II, respectively. Subsequent phylogenetic proposals in a latter-day series of papers (Kushida & Reimer 2019; García-Cárdenas *et al.* 2019, 2020; López-González 2021, 2022; López-González & Drewery 2022) increased the number of genera and species, as well as the number of markers. In all recent phylogenetic studies that included *Gyrophyllum*, this genus is isolated in Clade III (at least with the genus *Kophobelemnon*, as *Funiculina* exhibited non-stable behaviour in its placement, depending on its location on the selected combination of markers used and the inference method (ML or BI), see Dolan *et al.* 2013; Kushida & Reimer 2019; García-Cárdenas *et al.* 2020; López-González & Drewery 2022). The other two supposedly allied genera in the family, *Pteroeides* and *Pennatula*, remained widely separated in Clades I and II respectively, regardless of the multiloci set of sequences and phylogenetic inference used.

As commented on above, Dolan *et al.* (2013: 614–615) had already recognised the family Pteroeididae to be separate from Pennatulidae, and also rejected the monophyly of Pteroeididae. If we want advances in the consecution of more natural classifications in the order Pennatulacea it is necessary to fill in the gaps (by the addition of more sequences from different genes and including as many pennatulacean genera and species as possible) while at the same time avoiding paraphyletic and polyphyletic situations. It is possible that polyphyletic groupings may be temporally maintained in situations where it is difficult to decide where a genus (or family) should be located in a phylogenetic hypothesis. This is of special importance where sequences attributed to a given species or genus appear in different locations in a phylogenetic hypothesis. In this case we need sequences of the type species to place a given genus, and the corresponding sequences of the type genus (including those of the type species of that genus) to place the family. We already have the *mtMutS*, *Cox1* and *28S* sequences of *Pteroeides spinosum* (Ellis, 1764), the type species of the genus *Pteroeides*. Given this, there is no doubt that the placement of the genus *Pteroeides* and family Pteroeididae within Clade I is correct.

The recent collection in the eastern North Atlantic of colonies attributable to *Gyrophyllum hirondellei*, the type species of the genus *Gyrophylum*, as well as collation of information from various museum specimens allows us to review the taxonomic placement of this orphan genus. Our study is based on complementary morphological (macroscopic examination, light microscopy, and SEM) and molecular (multiloci sequences with three mitochondrial and one nuclear markers) methods. A revision of the morphological characters in the diagnosis of the genus is presented, and those features previously considered useful in the distinction of the two currently recognised species *G. hirondellei* (in the Atlantic) and *G. sibogae* Hickson, 1916 (in the Indo-western Pacific) are discussed.

Material and methods

Sample collection

The material examined in this study was collected during several important survey programs: BIAÇORES (1971), and SCOTIA DeepEco 2020 (cruise 1420S), SCOTIA SIAMISS 2021 (cruise 0421S) and SCOTIA Deepwater Time Series 2021 (cruise 1621S). The entire colony or a fragment from each colony was fixed on board in high grade or absolute ethanol (usable for further molecular studies) while the rest of the colony was fixed in 70% ethanol (BIAÇORES samples) or fixed initially in buffered 5% sea water formalin and subsequently transferred to 70% ethanol (SCOTIA samples). The BIAÇORES expedition was organized by the Muséum national d'histore naturelle in Paris, and carried out by the vessel RV *Jean Charcot* (29 Sep.–20 Nov. 1971) in the eastern North Atlantic Ocean, mostly in the vicinity of the Azores islands. The octocoral material resultant from BIAÇORES was published by Tixier-Durivault & d'Hondt (1974b); the colony of *Gyrophyllum* examined here from that cruise was identified (according to the label into the lot) by the late Andrée Tixier-Durivault as *Gyrophyllum hirondellei*. This specimen was also successfully sequenced. The SCOTIA programs comprise a mixture of trawl and broadscale habitat mapping (camera) surveys covering parts of the Hatton-Rockall Plateau, the Hebrides Slope and Rosemary Seamount between latitudes 55–60º N over the depth range 150–2000 m (Fig. 1).

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from 11 ethanol-preserved samples of *Gyrophyllum* and 2 specimens of *Pteroeides spinosum* (see Table 1) using the E.Z.N.A. DNA kit (OmegaBiotech) following the manufacturer's instructions. Three mitochondrial regions, *mtMutS* (= *msh1*), *ND2* and *Cox1*, plus a nuclear region (*28S* ribosomal DNA) were sequenced (López-González 2021; López-González & Drewery 2022). The start of the *mtMutS* region was amplified using the primers ND42599F and

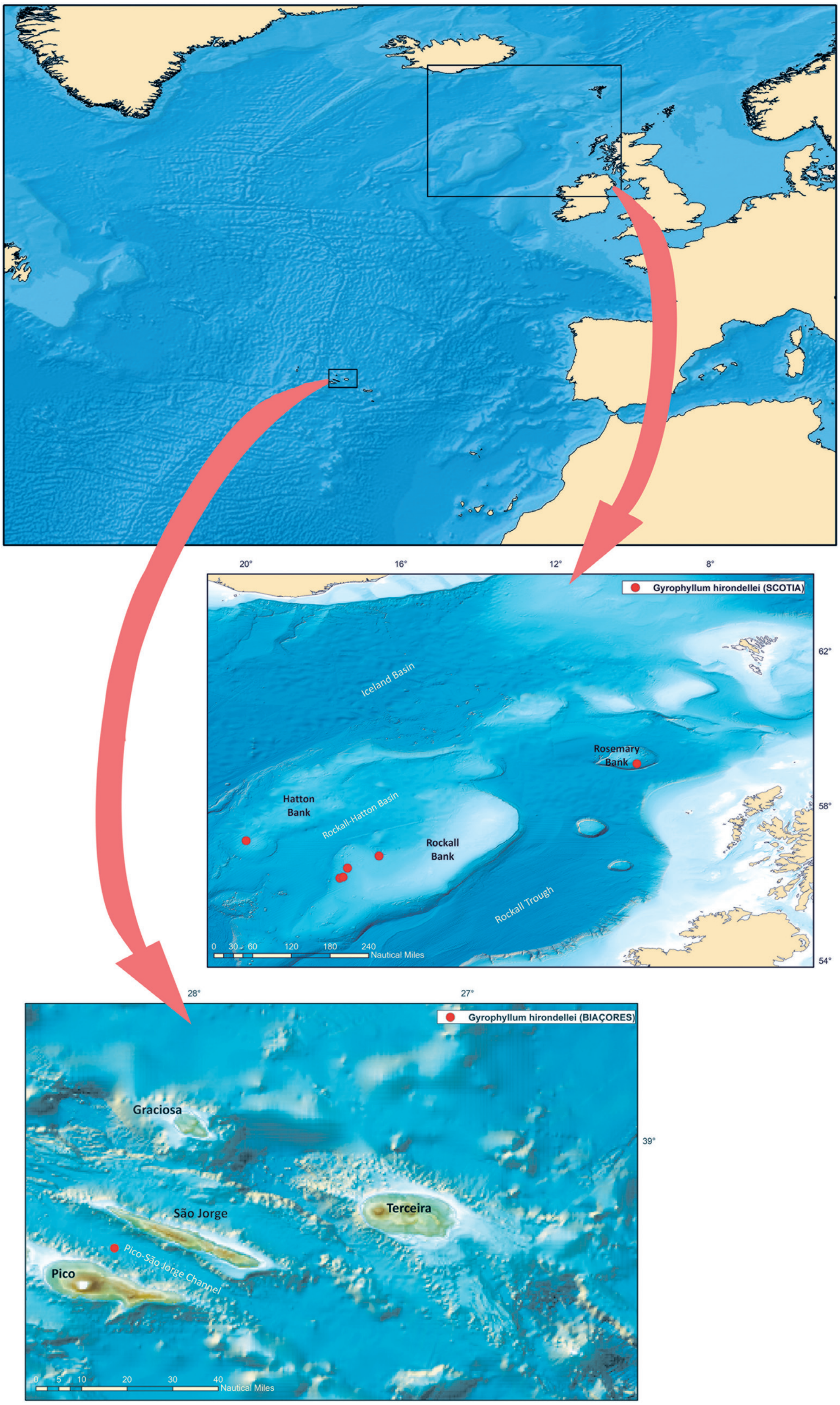

Fig. 1. Distribution of the sampling stations for *Gyrophyllum hirondellei* Studer, 1891 material examined over the course of this study.

Table 1 (continued on next two pages). Pennatulaceans included in molecular phylogenetic analyses in this paper. Species and GenBank accession numbers in bold are those sequenced for this study. Abbreviation: n.d. = no data.

species name in the tree	catalog nos / isolate / additional information	geographic area / provenance	*mtMutS*	*ND2*	*Cox1*	*28S*
Acanthoptilum gracile	34212-029	NW Pacific	JN866529	–	KF874188	–
Actinoptilum molle	RMNH Coel. 40822	n.d.	GQ342491	–	GQ342414	JX203738
Alloptilella splendida	MBM286413	Tropical W Pacific	MZ198005	–	MZ198007	MZ198009
Anthoptilum grandiflorum	NMS.Z.2019.25.16	Greenland, N Atlantic	MK919655	MK919655	MK919655	–
Anthoptilum sp. 1	NMS.Z.2019.25.1	Whittard Canyon, NE Atlantic	MK919656	MK919656	MK919656	–
Balticina cf. *finmarchica*	NMS.Z.2019.25.3	Whittard Canyon, NE Atlantic	MK919659	MK919659	MK919659	–
Balticina willemoesi	34213-026	NWFSC – west coast, NW Pacific	JN866543	–	KF874204	–
Calibelemnon hinoenma (1)	Isolate YK139	NW Pacific	MK133472	MK133667	–	–
Cavernularia pusilla	BECA OPEN-465 (G-99)	NW Mediterranean	MT968957	MZ217768	MT952706	MT951908
Cavernulina sp.	Isolate YK19	NW Pacific	MK133372	MK133567	–	–
Distichoptilum gracile	NMS.Z.2019.25.2	Whittard Canyon, NE Atlantic	MK919657	MK919657	MK919657	–
Echinoptilum macintoshi	Isolate YK22	NW Pacific	MK133373	MK133568	–	–
Funiculina sp.	FEL808611	Northern Gulf of Mexico, USA, NW Atlantic	JN227941	–	JN227949	–
Funiculina armata	NHM 2010.11 Isolate 94	NE Atlantic	KF313833	KF313807	–	–
Funiculina quadrangularis	NMS.Z.2019.25.17	Little Loch Broom, Scotland, NE Atlantic	MK919658	MK919658	MK919658	–
Gilibelemnon octodentatum	BECA OPEN-452 (G-81)	Seymour Island Antarctica	MK603841	MW863001	MK603855	MK603851
Gyrophyllum hirondellei (1)	NHM OCT.A.579 / BECA (G-128)	Azores, NE Atlantic	MT968964	MZ217769	MT952713	MT951915
***Gyrophyllum hirondellei* (2)**	BECA OPEN-659 (G-3830)	Hatton Bank, NE Atlantic	**OM641960**	**OM641973**	**OM617948**	–
***Gyrophyllum hirondellei* (3)**	NMS.Z.2022.1.3 BECA (G-3831)	South Rockall Slope, NE Atlantic	**OM641961**	**OM641974**	**OM617949**	**OM630516**
***Gyrophyllum hirondellei* (4)**	NMS.Z.2022.1.1 BECA (G-3832)	South Rockall Slope, NE Atlantic	**OM641962**	**OM641975**	**OM617950**	**OM630517**
***Gyrophyllum hirondellei* (5)**	BECA OPEN-660 (G-3833)	South Rockall Slope, NE Atlantic	**OM641963**	**OM641976**	**OM617951**	–
***Gyrophyllum hirondellei* (6)**	BECA OPEN-665 (G-3834)	South Rockall Slope, NE Atlantic	**OM641964**	**OM641977**	**OM617952**	–
***Gyrophyllum hirondellei* (7)**	NMS.Z.2022.1.2 BECA (G-3835)	South Rockall Slope, NE Atlantic	**OM641965**	**OM641978**	**OM617953**	–
***Gyrophyllum hirondellei* (8)**	NMS.Z.2022.1.4 BECA (G-4015)	West Rockall Slope, NE Atlantic	**OM641966**	**OM641979**	**OM617954**	**OM630518**
***Gyrophyllum hirondellei* (9)**	BECA OPEN-661 (G-4016)	West Rockall Slope, NE Atlantic	**OM641967**	**OM641980**	**OM617955**	–
***Gyrophyllum hirondellei* (10)**	NMS.Z.2022.1.5 BECA (G-4017)	West Rockall Slope, NE Atlantic	**OM641968**	**OM641981**	**OM617956**	**OM630519**
***Gyrophyllum hirondellei* (11)**	NMS.Z.2022.1.6 BECA (G-4018)	West Rockall Slope, NE Atlantic	**OM641969**	**OM641982**	**OM617957**	**OM630520**
***Gyrophyllum hirondellei* (12)**	BECA OPEN-662 (G-4019)	West Rockall Slope, NE Atlantic	**OM641970**	**OM641983**	**OM617958**	–
Gyrophyllum sp. (1) (2)	IO/SS/ANT/00001	Adaman Sea, E Indian Ocean	KY039182	KY039181	–	KY039183

Table 1 (continued).

species name in the tree	catalog nos / isolate / additional information	geographic area / provenance	*mtMutS*	*ND2*	*Cox1*	*28S*
Gyrophyllum sibogae (1) (3)	NTM-C014392 NOR89/535	Tasman Sea, AU, S Pacific	DQ302869	DQ302942	JX203865	JX203740
Gyrophyllum sp. (2)	NIWA 28779 Isolate 104	New Zealand, W Pacific	KF313846	KF313819	–	–
Kophobelemnon macrospinum	NTM-C014985	Tasman Sea, AU, S Pacific	DQ302865	DQ302937	GQ342429	JX203742
Kophobelemnon pauciflorum	NHM 2010.21	Crozet Islands, S Atlantic	KF313836	KF313809	–	–
Kophobelemnon sp. 1	NMS.Z.2019.25.4	Whittard Canyon, NE Atlantic	MK919660	MK919660	MK919660	–
Kophobelemnon sp. 2	NHM 2010.10 Isolate A15	Monterey, E Pacific Ocean	KF313838	KF313811	–	–
Kophobelemnon sp. 3	NMS.Z.2019.25.5	Whittard Canyon, NE Atlantic	MK919661	MK919661	MK919661	–
Kophobelemnon sp. 4	NMS.Z.2019.25.6	Whittard Canyon, NE Atlantic	MK919662	MK919662	MK919662	–
Pennatula aculeata (1)	NMS.Z.2019.25.7	Whittard Canyon, NE Atlantic	MK919663	MK919663	MK919663	–
Pennatula aculeata (2)	n.d.	Bay of Biscay, NE Atlantic	MK919664	MK919664	MK919664	–
Pennatula phosphorea (1)	BECA OPEN-453 (G-88)	Sea of the Hebrides, NE Atlantic	MK603848	MW863002	MK603858	MK882492
Pennatula phosphorea (2)	BECA OPEN-454 (G-199)	Gulf of Cadiz, NE Atlantic	MK603850	MW863003	MK603861	MK882491
Pennatula sp.1	BECA OPEN-152 (G-122)	Ross Sea, Antarctica S Atlantic	MK603849	MW863004	MK603859	MK882493
Protoptilum carpenteri	NMS.Z.2019.25.10	Whittard Canyon, NE Atlantic	MK919667	MK919667	MK919667	–
Pseudumbellula pomona	42608 c / 42609 c	Mar del Plata, Submarine Canyon, SW Atlantic	MT467665	MT467666	–	–
Pseudumbellula scotiae (1)	NMS.Z.2021.2.2 OPEN-169 (G-154B)	Hebrides Slope, NE Atlantic	MZ217756	MZ217762	MZ190838	MZ227258
Pseudumbellula scotiae (2)	NMS.Z.2021.2.3 OPEN-171 (G-156)	Hebrides Slope, NE Atlantic	MZ217757	MZ217763	MZ190839	MZ227259
Pseudumbellula sp. (4)	NHM 2009.6	Crozet Islands, S Atlantic	KF313856	KF313829	–	–
Pteroeides caledonicum	YK90	NW Pacific	MK133429	MK133624	–	–
Pteroeides spinosum (1) (5)	BECA OPEN-140 (G-98)	NW Mediterranean	MT968965	MZ217770	MT952714	MT951916
***Pteroeides spinosum* (2)**	BECA OPEN-286 (G-1703)	NW Mediterranean	**OM641971**	**OM641984**	**OM617959**	**OM630521**
***Pteroeides spinosum* (3)**	BECA OPEN-291 (G-1913)	NW Mediterranean	**OM641972**	**OM641985**	**OM617960**	**OM630522**
Ptilella grandis (1)	BECA OPEN-143 (G-92)	South Iceland, NE Atlantic	MK603844	MW863005	MK603860	MK603854
Ptilella grandis (2)	NMS.Z.2019.2.6 BECA (G-69)	Hebrides Slope, NE Atlantic	MK603843	MW863006	MK882496	MK882494
Ptilella grayi (1)	BECA (OPEN-340) (G-2591)	Rockall Bank, NE Atlantic	MW862999	MW863008	MW858344	MW862996
Ptilella grayi (2)	NMS.Z.2019.2.2 / G-20	Rockall Bank, NE Atlantic	MK603846	MW863009	MK603856	MK603853
Ptilella inflata (1)	BECA OPEN-456 (G-124)	Namibia, SE Atlantic	OL692427	OL692432	–	–
Ptilella inflata (2)	MZB 2016-0099 BECA OPEN-651 (G-3691)	Namibia, SE Atlantic	OL692428	OL692433	–	OL689086

Table 1 (continued).

species name in the tree	**catalog nos / isolate / additional information**	**geographic area / provenance**	***mtMutS***	***ND2***	***Cox1***	***28S***
Ptilosarcus gurneyi (1)	34213-020	NWFSC – west-coast, NW Pacific	JN866540	–	KF874201	–
Ptilosarcus gurneyi (2)	34210-009	NWFSC – west coast, NW Pacific	JN866521	–	KF874180	–
Renilla muelleri	n.d.	n.d.	JX023273	JX023273	JX023273	–
Renilla sp.	CSM-2010-UF4000	Gulf of Panama, E Pacific	GQ342526	–	GQ342455	–
Sclerobelemnon theseus	JAS	Colombia, W central Atlantic	DQ311679	DQ311678	–	–
Scleroptilum grandiflorum	NHM 2010.14	Mid-Atlantic Ridge, Atlantic Ocean	KF313847	KF313820	–	–
Scytalium herklotsi	USNM 1550636	Puerto Rico, NW Atlantic	MW863000	MW863011	MW858345	MW862997
Scytalium martensi	Isolate YK03	NW Pacific	MK133361	MK133556	–	–
Scytalium veneris	MBM286417	Tropical W Pacific	MZ198006	–	MZ198008	MZ198010
Solumbellula monocephalus (6)	NHM 2010.16	Indian Ocean	KF313852	KF313825	–	–
Stachyptilum dofleini	Isolate YK51	NW Pacific	MK133396	MK133591	–	–
Stylatula elongata	n.d.	n.d.	JX023275	JX023275	JX023275	–
Umbellula encrinus	NHM 2010.8	Arctic Ocean	KF313849	KF313822	–	–
Umbellula huxleyi (1)	NMS.Z.2019.25.11	Whittard Canyon, NE Atlantic	MK919668	MK919668	MK919668	–
Umbellula huxleyi (2)	BECA OPEN-161 (G-139)	NE Atlantic	MT968966	–	MT952715	MT951917
Umbellula magniflora	NHM 2010.22	Marguerite Bay, Antarctica	KF313851	KF313824	–	–
Umbellula sp. 1	NMS.Z.2019.25.12	Whittard Canyon, NE Atlantic	MK919669	MK919669	MK919669	–
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	NOCS sea pens Isolate 92	Cascais Canyon, NE Atlantic	KF313854	KF313827	–	–
Veretillum cynomorium	BECA OPEN-462 (G-90)	Alboran Sea, NW Mediterranean	MT968958	MZ217771	MT952707	MT951909
Virgularia cf. *gustaviana*	Isolate YK210	NW Pacific	MK133518	MK133713	–	–
Virgularia cf. *halisceptrum*	Isolate YK01	NW Pacific	MK133359	MK133554	–	–
Virgularia mirabilis (1)	NHM 2010.7	Sweden, NE Atlantic	KF313857	KF313830	–	–
Virgularia mirabilis (2)	NMS.Z.2019.25.15	Galway Bay, Ireland, NE Alantic	MK919673	MK919673	MK919673	–
Virgularia cf. *rumphi*	Isolate YK84	NW Pacific	MK133423	MK133618	–	–
Virgularia schultzei	RMNH Coel. 40823	n.d.	GQ342527	–	GQ342459	JX203743
OUTGROUP						
Junceella fragilis	n.d.	Taiwan, NW Pacific	KJ541509	KJ541509	KJ541509	AF263355
Viminella sp.	RMNH Coel.40032	West Papua, Indonesia, W Pacific	JX203794	–	JX203852	JX203703

(1) As *Calibelemnon* sp. in GenBank, but assigned to *Calibelemnon hinoenma* Kushida & Reimer, 2020 by Kushida & Reimer (2020).

(2) As *Gyrophyllum hirondellei* in GenBank (see Discussion part).

(3) *mtMutS* and *ND2* as *Gyrophyllum* sp. in GenBank.

(4) As *Umbellula* sp.2 ED-2013 in GenBank.

(5) As *Pteroeides griseum* (Bohadsch, 1761) in GenBank, see ICZN (1944) and Williams (1995a: 130) regarding reasons for using *P. spinosum* instead of *P. griseum.*

(6) As *Umbellula monocephalus* Pasternak, 1964 in GenBank.

MUT3458R (France & Hoover 2002; Sánchez *et al.* 2003). The start of the *ND2* region was amplified using the primers 16S47F and ND2-1418R (McFadden *et al.* 2004). *Cox1* region was amplified using the primers COII8068F and COIOCTR (McFadden *et al.* 2004; France & Hoover 2002). *28S* nuclear ribosomal gene (28S rDNA) was amplified using the primers 28S-Far and 28S-Rar (McFadden & van Ofwegen 2013). Each PCR used 1 U of MyTaq Red DNA Polymerase (Bioline), 10 µM of each primer, approximately 30 ng of genomic DNA, and was brought to a final volume of 25 µL with H_2O for molecular biology (PanReac-AppliChem). *MtMutS* PCR was carried out using the following cycle profile: initial denaturation at 95ºC for 1 min, 35 cycles of denaturation at 95ºC for 15 s, annealing at 55ºC for 15 s, and extension at 72ºC for 10 s, and a final extension at 72ºC for 5 min. The *ND2*, *Cox1*, and *28S* PCRs used the same cycle profile, however the corresponding annealing temperatures were 51ºC, 50ºC, and 58ºC respectively. PCR products were purified using ExoSAP–IT™ PCR Product Cleanup Reagent (ThermoFisher Scientific) following the manufacturer's instructions, before robust amplifications were sent to Macrogen Spain for sequencing in both directions.

Phylogenetic reconstruction

All chromatograms were visualized and sequence pairs matched and edited using Sequencher ver. 4.0. The set of new sequences and those homologous from GenBank (see Table 1) were aligned using MUSCLE (MEGA6, Tamura *et al.* 2013). Only specimens with *mtMutS* plus at least another mitochondrial sequence were included in the data-matrix. After alignment, pairwise genetic distances based on the Kimura 2-parameter (K2P) model of nucleotide substitution (Kimura 1980) were obtained in order to compare them with previous analyses at genus and family levels, following the comparisons of Pante & France (2010), Pante *et al.* (2012), López-González (2020), and López-González & Drewery (2022). In accordance with previous researchers, e.g., Dolan *et al.* (2013), Kushida & Reimer (2019), and García-Cárdenas *et al.* (2020) sequences of ellisellids from GenBank were selected as out-groups. The concatenated matrix for *mtMutS*+*ND2*+*Cox1*+*28S* sequences had 86 sequences (84 pennatulaceans and two ellisellids), and a total of 2886 positions, with 1010 variable and 760 parsimony-informative sites. The concatenated matrix including only mitochondrial markers (*mtMutS*+*ND2*+Cox1) had the same number and composition of sequences mentioned above, and a total of 2020 positions, with 637 variable and 444 parsimony-informative sites. After alignment, the best nucleotide substitution model was selected using Modeltest implemented in MEGA6, according to Akaike Information Criterion (AIC) and hierarchical likelihood ratio test (hLRT) values. The phylogeny reconstruction was obtained applying Maximum Likelihood (ML) and Bayesian inference (BI) methods. The Maximum Likelihood method was carried out in MEGA6 using the NNI (Nearest Neighbor Interchange) heuristic method and 1000 bootstrap replications. The selected nucleotide substitution models were GTR+G+I, and GTR+G for the data-set of four and three (mitochondrial only) markers, respectively. The Bayesian inference was carried out with MrBayes ver. 3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003), using the substitution model GTR+G (lset nst = 6 rates = gamma), 10^7 generations and discarding 25% of the initial trees. The stationarity of the chains and convergence of the two runs were monitored for each parameter by Tracer ver. 1.7.1 (Rambaut *et al.* 2018), determining whether the effective sample size (ESS) of all parameters was larger than 200 as recommended.

Morphological assessments

Sclerites from different colony parts were prepared for SEM study employing the standard methodology described by Bayer & Stefani (1988). Permanent mounts were made for light microscopy. Colony and sclerite terminology follow Bayer *et al.* (1983).

The presence of sclerites was corroborated by dissolving fixed tissues from all constituent parts of the colonies (e.g., the tentacles, the body and pharynx of autozooids, the siphonozooid areas on polyp leaves, the rachis, and the peduncle) in a 10% sodium hypochlorite solution. Autozooid's body and tentacles were prepared in semi-permanent mounts using clove oil as mounting medium for corroboration of the presence of sclerites and examination of their arrangement using a MOTIC B3 light microscope (Li *et al.* 2020). Microscopic slides with sclerites (permanent mounts using DPX as mounting medium) were observed under a Leica DMLB light microscope in conjunction with an OPTIKA C-P20CC digital camera and the image processing software OPTIKA PROVIEW. Sclerites were then mounted on aluminium 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. The axis of a large and a small colony obtained by SCOTIA (see Table 1) was sectioned at the rachis-peduncle limit and polished using 600, 800, 1200 and 3000 grit diamond polishing discs on a YXEC mini cutting / polishing table. Cross sections were visualized and photographed under UV light (SFA-UV stereo microscope Adapter NIGHTSEA) using a Motic SMZ-168 stereo microscope.

For comparative purposes, the overall morphology (the colony form, the sclerome and the axis cross section in combination) and the molecular information (GenBank data base) available on other sea pen genera having well-developed polyp leaves such as *Pteroeides*, *Pennatula, Ptilella* Gray, 1870, *Alloptilella* Li, Zhan & Xu, 2021, and *Scytalium* Herklots, 1858 collected during various benthic surveys and over different geographical areas and research programs [Mediterranean (INDEMARES-Cap de Creus, INDEMARES-Alborán), North Eastern Atlantic-Arctic (BIOICE, SCOTIA), North Western Atlantic (Océano Profundo 2018), and Antarctica (EASIZ, BIOROSS)] were also examined. Further information from genera having polyp leaves was obtained from the literature (Kükenthal 1915; Williams 1995a; Li *et al.* 2021, among others).

Institutional abbreviations

NMS = National Museum of Scotland, Edinburgh, UK
MNHM = Muséum national d'histoire naturelle, Paris, France
BECA = Biodiversidad y Ecología Acuática, Seville, Spain
MBARI = Monterey Bay Aquarium Research Institute, California, USA
NHM = Natural History Museum, London, UK
NOCS = National Oceanography Centre, Plymouth, UK
NTM = Museum and Art Gallery of the Northern Territory, Darwin City, Australia
RMNH = Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands
JAS = Collection of J.A. Sánchez
AMQ = Collection of A.M. Quattrini

Further abbreviation

OPEN = Octocoral PENnatulacea

Results

Phylogenetic analyses

In our *mtMutS+ND2+Cox1+28S* hypothesis (Fig. 2 left), the four main Clades I–IV observed in previously reported sea pen phylogenies were strongly supported by BI (Posterior Probability, PP 1). All multiloci sequences of colonies of *Gyrophyllum* were reunited (Bootstrap, Bst 97%, PP 1) within Clade III. The genus *Funiculina* is basally placed in Clade III, while the genus *Kophobelemnon* becomes paraphyletic. Most species of *Kophobelemnon* form the sister group of *Gyrophyllum* in a poorly supported clade (PP 0.52). The genus *Pteroeides* (fam. Pteroeididae), represented in this analysis by sequences of three colonies of its type species *P. spinosum*, is clearly placed in Clade I, the genus *Virgularia* Lamarck, 1816 (fam. Virgulariidae Verrill, 1868) being its sister group (Bst 58%, PP 0.98). On the other hand, the genus *Pennatula* (fam. Pennatulidae) forms a well-supported (Bst 89%, PP 1) terminal clade of Clade I, with

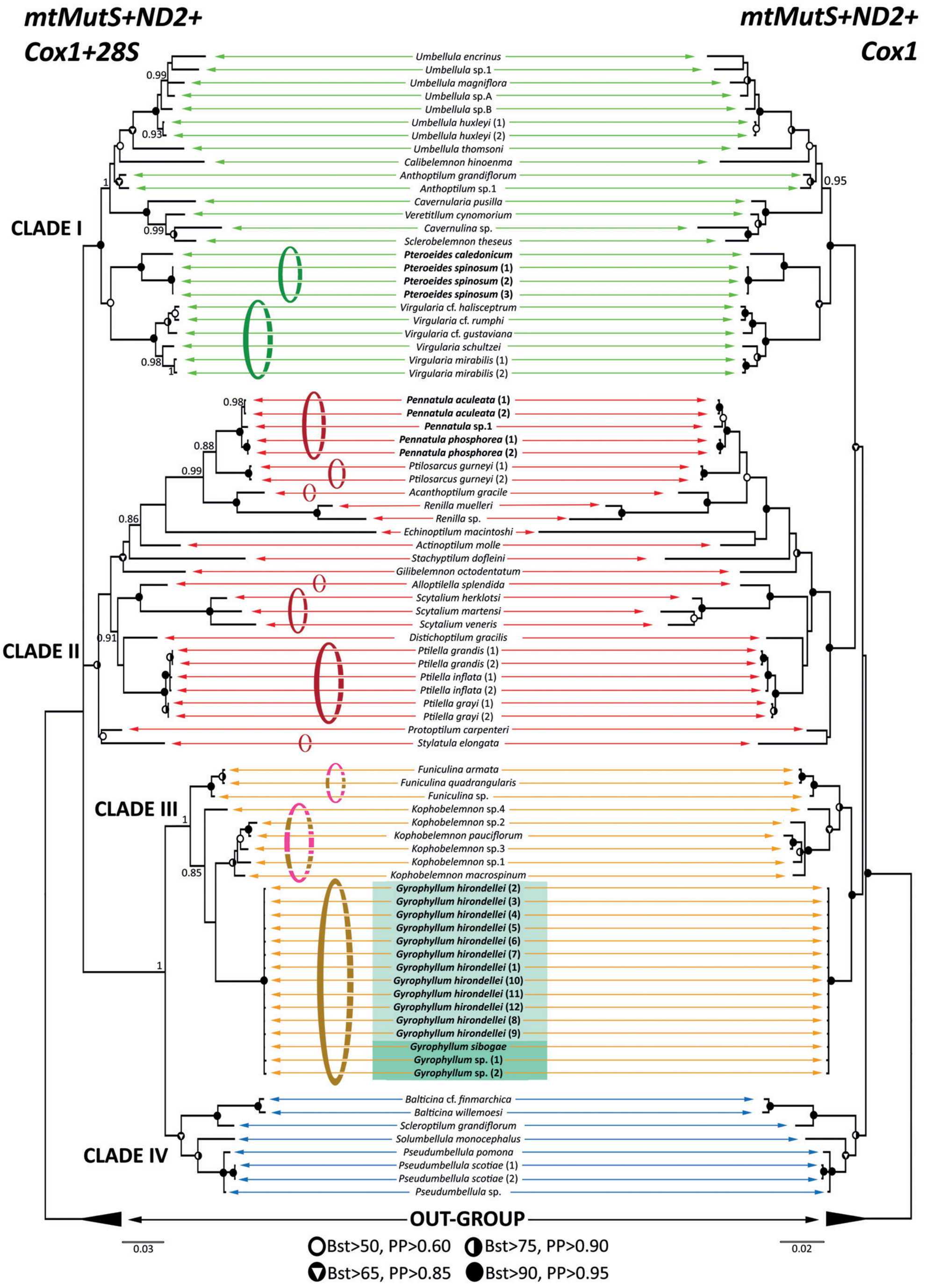

Fig. 2. Bayesian analyses showing the phylogenetic relationships of pennatulacean species (see Table 1) with the four main Clades I–IV indicated by coloured arrows. Sequences of the genus *Gyrophyllum* are in Clade III (light green are Atlantic specimens, while dark green are Indo-western Pacific specimens). The present hypotheses are based on *mtMutS*+*ND2*+*Cox1*+*28S* (left) and the concatenated set of sequences *mtMutS*+*ND2*+*Cox1* (right). Only values of Bst >50 and PP >80 have been considered to be codified according legend. When Bst was <50 but PP was >80, PP value is indicated. The trees are drawn to scale, with branch lengths measured in the number of substitutions per site. Numbers in the tree clades represent Posterior Probability values not supported by ML. Yellow rings (continuous or alternate with pink lines) delimit taxa at genus level in Clade III. Rings of continuous lines (regardless of colour) delimit taxa with polyp leaves at genus level in Clades I–IV.

Ptilosarcus Verrill, 1865 its sister group in a moderately supported clade recovered by BI (PP 0.88), but in a polytomy with *Renilla* Lamarck, 1816 and *Acanthoptilum* Kölliker, 1870 by ML inference. The sister group of *Pennatula*-*Ptilosarcus* is *Acanthoptilum*-*Renilla* in a well-supported clade (PP 0.99) by BI. In this hypothesis, Clade III is the sister group of Clade IV (PP 1) which includes the families Halipteriidae Williams, 1995 (genus *Balticina* Gray, 1870), Scleroptilidae (genus *Scleroptilum*), and Pseudumbellulidae López-González in López-González & Drewery, 2022 (genera *Pseudumbellula* López-González & Drewery, 2022 and *Solumbellula* López-González in López-González & Drewery, 2022).

In a second hypothesis that considers only the three mitochondrial markers *mtMutS*+*ND2*+*Cox1* (Fig. 2 right), all main Clades I–IV were strongly supported by BI (PP 1). Overall, the topology of this tree is quite similar to that of the four-markers tree, and supports the same hypothesis, being nearly specular in architecture. There is a slight suggestion of a possible clade between *Pennatula aculeata* Danielssen, 1860 and *Pennatula* sp1. (with a poor support Bst 53, PP 0.76), and another possible clade relating the two Indo-western Pacific species of *Scytalium*: *S. martensi* Kölliker, 1870 and *S. veneris* (Thomson & Henderson, 1806) (however, also in an unstable manner, Bst 59%, PP 0.62). All other relationships, including those in Clade III are practically identical to those observed in the *mtMutS*+*ND2*+*Cox1*+*28S* hypothesis.

Both Atlantic and Indo-western Pacific specimens share the same *mtMutS, ND2,* and *Cox1* sequences. There is a *Cox1* sequence published only in GenBank (KX179492) from a specimen attributed to *G. hirondellei* collected in the Andaman Sea that presented four mutations. In addition, a fragment of *28S* of another colony (GenBank accession number KY039183) from the same geographic area also showed some differences at the beginning and end of the sequence suggesting a possible error of reading due to irregular polymerase activity. The first author of the present paper (PJL-G) tried to locate further morphological or molecular information relating to these specimens (photographs and .ab1 files) in order to corroborate these molecular differences and study their morphology, but without success. Therefore, in the absence of a detailed morphological and molecular description of these incompletely sequenced specimens, we prefer not to use these molecular differences for future comparisons. Despite the homogeneity shown in the *mtMutS*, *ND2*, and *Cox1* genes, a preliminary comparison between our *28S* sequences (see Table 1) and those previously published from North Atlantic (MT951915) and Southwest Pacific (JX203740) specimens showed an ambiguity in position 228 of the Azorean colony (Y = T/C) due to a not completely clean reading in the chromatogram of the DNA analyzer.

Bearing in mind the phylogenetic relationships described above regarding the genus *Kophobelemnon*, K2P genetic distance based on *mtMutS* between *Gyrophyllum* and *Kophobelemnon* is 2.46% (2.17–2.80%), while *Gyrophyllum* is 2.17 % (1.85–2.33 %) distant from *Funiculina*. Furthermore, *Gyrophyllum* is 7.06% (7.06–7.08%) distant from *Pteroeides*, and 5.90% (5.89–5.90%) distant from *Pennatula*.

Taxonomy

Class Anthozoa Ehrenberg, 1834
Subclass Haeckel, 1866
Order Pennatulacea Verrill, 1865

Family **Gyrophyllidae** fam. nov.
urn:lsid: zoobank.org/act:22EA20A5-9416-4E25-9E54-212930697591

Diagnosis

As for the type genus.

Genus ***Gyrophyllum*** Studer, 1891

Gyrophyllum – Studer 1891: 94.

Gyrophyllum – Studer 1901: 34. — Roule 1905: 454. — Kükenthal & Broch 1911: 394. — Kükenthal 1915: 120. — Hickson 1916: 252. — Deichmann 1936: 286. — Tixier-Durivault & d'Hondt 1974a: 263; 1974b: 1420. — Williams 1995a: 316; 1995b: 128; 2011: 3.

non *Bathypenna* – Marion 1906: 147.

Diagnosis (modified from Williams 1995b: 128, modifications in bold)

Colonies stout and clavate, **with rachis in two parts, a distal part with polyp leaves and a proximal part without them, similar to peduncle in appearance but separated from the anchoring muscular peduncle by a thickened section showing longitudinal wrinkles**. Distal part of rachis with bilateral symmetry throughout. Axis extends throughout length of colony, **irregularly X-shaped** in cross section. Polyp leaves present, thick, fleshy, and fan-like, up to ~9 leaves per side of rachis. Autozooids up to ~50 per leaf, **usually** in two rows at the leaf margin. Anthocodiae retractile into **low** fleshy calyces **with one or two distinct fleshy blunt to pointed processes (sometimes difficult to observe, eroded?). Tentacles with two types of tentacular projections: conventional pinnulae on the lateral sides of main tentacular axis**, and filiform ones (numerous) along the oral side of tentacular axis. Siphonozooids present on both sides of polyp leaves between and below autozooids, **and on dorsal rachis' track**, not restricted to zones or pads. Sclerites elongate, three-flanged rods in polyp leaves, rachis, and peduncle, as well as short blunt rods in the tentacle axis and autozooid body (mostly longitudinally grooved or occasionally three-flanged).

Geographical and depth distribution

Indo-West Pacific (Madagascar, Malay Archipelago, Tasmanian Sea, New Zealand, India) and North Atlantic (Azores, Hatton and Rockall Banks, Rosemary Seamount, Bahamas); 520–2220 m depth (Studer 1891, 1901; Deichmann 1936; Williams 1995b: 128; Williams *et al.* 2014; present contribution).

Type species

Gyrophyllum hirondellei Studer, 1891 (by monotypy).

Gyrophyllum hirondellei Studer, 1891
Figs 3–11

Gyrophyllum hyrondellei Studer, 1891: 94.

Gyrophyllum hyrondellei – Studer 1901: 35. — Roule 1905: 456. — Kükenthal & Broch 1911: 394 (in text). — Kükenthal 1915 (in text): 120. — Hickson 1916: 252 (in text). — Thomson 1927: 56. — Deichmann 1936: 286. — Tixier-Durivault & d'Hondt 1974b: 1420. — Williams 1995a (in text).

Material examined

NORTH EASTERN ATLANTIC – **Azores** • 1 spec.; North São Miguel; 38º36.5′ N, 28º17.5′ W; depth 1260–1258 m; 26 Nov. 1971; BIAÇORES 1971 exped.; stn.139; complete colony, 158 mm in length; MNHM OCT.A.579; MNHM. – **South Rockall Slope** • 1 spec.; 56º08.71′ N, 17º34.64′ W–56º07.25′ N, 17º34.89′ W; depth 997–101 m; 29 Sep. 2020; SCOTIA 1420S; stn. S20321 #8008; complete colony, 103 mm in length; NMS.Z.2022.1.1 - BECA (G-3832); NMS • 1 spec.; 56º08.71′ N, 17º34.64′ W–56º07.25′ N, 17º34.89′ W; depth 997–101 m; 29 Sep. 2020; SCOTIA 1420S; stn.

S20321 #8009; complete colony, 78 mm in length; NMS.Z.2022.1.2 - BECA (G-3835); NMS • 1 spec.; 56º08.71′ N, 17º34.64′ W–56º07.25′ N, 17º34.89′ W; depth 997–101 m; 29 Sep. 2020; SCOTIA 1420S; stn. S20322 #8010; complete colony, 110 mm in length; NMS.Z.2022.1.3 - BECA (G-3831); NMS • 1 spec.; 56º08.83′ N, 17º29.77′ W–56º10.40′ N, 17º29.57′ W; depth 902–905 m; 29 Sep. 2020; SCOTIA 1420S; stn. S20322 #11835; 1 fragment; BECA OPEN-665 (G-3834); BECA • 1 spec.; 56º24.30′ N, 17º23.04′ W–56º22.80′ N, 17º22.72′ W; depth 761–771 m; 30 Sep. 2020; SCOTIA 1420S; stn. S20323 #8006; complete colony, 112 mm in length; BECA OPEN-660 (G-3832). – **South West Rockall Slope** • 1 spec.; 57º07.11′ N, 19º59.63′ W–57º04.87′ N, 20º00.47′ W; depth 1002–1009 m; 3 Oct. 2020; SCOTIA 1420S; stn. S20331 #7706; complete colony, 84 mm in length; BECA OPEN-659 (G-3830). – **West Rockall Slope** • 1 spec.; 56º42.59′ N, 16º30.85′ W–56º42.31′ N, 16º37.05′ W; depth 721–792 m; 14 Apr. 2021; SCOTIA 0421S; stn. S21172 #11670; complete colony, 203 mm in length; NMS.Z.2022.1.4 - BECA (G-4015); NMS • 1 spec.; 56º42.59′ N, 16º30.85′ W–56º42.31′ N, 16º37.05′ W; depth 721–792 m; 14 Apr. 2021; SCOTIA 0421S; stn. S21172 #11671; complete colony, 215 mm in length; BECA OPEN-661 (G-4016); BECA • 1 spec.; 56º42.59′ N, 16º30.85′ W–56º42.31′ N, 16º37.05′ W; depth 721–792 m; 14 Apr. 2021; SCOTIA 0421S; stn. S21172 #11672; incomplete colony, lacking peduncle; NMS.Z.2022.1.5 - BECA (G-4017); NMS • 1 spec.; 56º42.59′ N, 16º30.85′ W–56º42.31′ N, 16º37.05′ W; depth 721–792 m; 14 Apr. 2021; SCOTIA 0421S; stn. S21172 #11678; complete colony, 218 mm in length; NMS.Z.2022.1.6 - BECA (G-4018); NMS • 1 spec.; 56º42.59′ N, 16º30.85′ W–56º42.31′ N, 16º37.05′ W; depth 721–792 m; 14 Apr. 2021; SCOTIA 0421S; stn. S21172 #11801; incomplete colony, lacking peduncle; BECA OPEN-662 (G-4019); BECA. – **South East Rosemary Seamount** • 1 spec.; 59º05.85′ N, 09º52.94′ W–59º04.70′ N, 09º55.40′ W; depth 1051–1070 m; 10 Nov. 2021; SCOTIA 1621S; stn. S21553 #11834; complete colony, but peduncle eroded, 80 mm in length; BECA OPEN-663 (G-4095); Beca • 1 spec.; 59º05.85′ N, 09º52.94′ W–59º04.70′ N, 09º55.40′ W; depth 1051–1070 m; 10 Nov. 2021; SCOTIA 1621S; stn. S21553 #11833; complete colony, 121 mm in length; BECA OPEN-664 (G-4096); BECA.

Morphological description

Colonies stout and clavate, pinnate distally (Figs 3–4), up to 218 mm in length in the preserved state. Rachis in two distinct parts: distally a bilaterally symmetrical section bearing polyp leaves, and proximally a stalk of shorter length. Complete rachis is up to 110 mm in length (50.46% of overall length in the whole examined material) and up to 18 mm in width (measured at mid-length of distal rachis part, not including polyp leaves). Rachis-peduncle limit slightly prominently swollen (Figs 3–4). Peduncle up to 108 mm in length (49.54% of overall length) and up to 11 mm in width at the widest point (the limit rachis-peduncle). Rachis with up to seven fleshy polyp leaves on each side, projecting somewhat obliquely and extending ventrally upward (Fig. 3B, F). Polyp leaves placed nearly oppositely, difficult to observe in preserved and contracted state (Figs 3B, E, 4D), increasing in size along the rachis until the mid-zone to last third, then quickly decreasing in size towards the distal part. Rachis with distinctive wide dorsal (Figs 3B, E, 4C) and reduced ventral track (Figs 3F, 4B) due to accumulation of ventral portion of polyp leaves bases. Polyp leaves nearly rectangular, not triangular, maximum length ~30 mm, maximum width ~45 mm. Axis present throughout colony, X-shaped in cross section, up to 2 mm in maximum diameter at rachis-peduncle limit, becoming progressively asymmetric with age (Fig. 5A–B). Autozooids numerous, up to approximately 45–50 in the largest polyp leaves, arranged in one or two (three?) indistinct rows (Figs 3C, F, 4B, 6A–D) appearing at different levels near the atutozooid apertures along ventral edge of polyp leaf. Anthocodiae up to 3.4 mm in length (excluding tentacles) and 2.4 mm in width, completely retractile into spiculiferous, and not-always evident ‘calyces’ usually equipped with one prominent lateral blunt to pointed process (BPP hereinafter) up to 3.4 mm in length (not always present or well developed even in the same polyp leaf, see Discussion) (Figs 3C, F, 4B, 7A). Along ventral edge of polyp leaves, autozooids and spiculiferous BPPs alternate (Fig. 7). Tentacles of autozooid up to 3.5 mm in length in preserved state, with two kinds of processes, standard pinnules arranged in two lateral series (Figs 8F, 9C), and numerous filiform structures only present along the

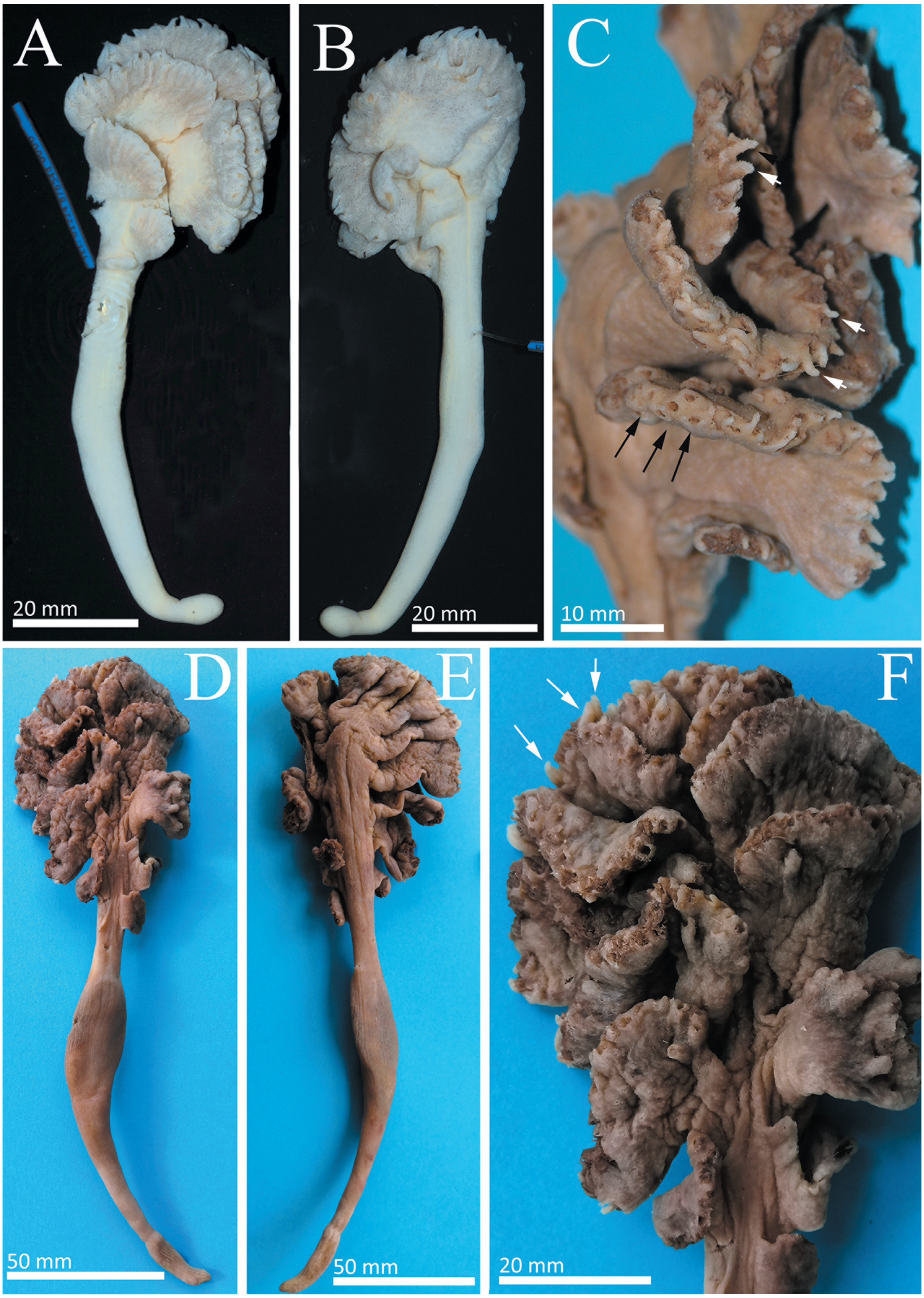

Fig. 3. *Gyrophyllum hirondellei* Studer, 1891, colonies from SCOTIA cruises. **A–B**. BECA (OPEN-660), ventral and dorsal sides, see also Fig. 4. **C**. Detail from colony NMS.Z.2022.1.6, showing parts of polyp leaves ventral edge with well-developed BPPs (white arrows) and others without BPPs (black arrows). **D–E**. Ventral and dorsal sides of the colony NMS.Z.2022.1.4. **F**. Detail from D, showing most of the proximal polyp leaves without BPPs, some can be seen on the distalmost polyp leaves (white arrows).

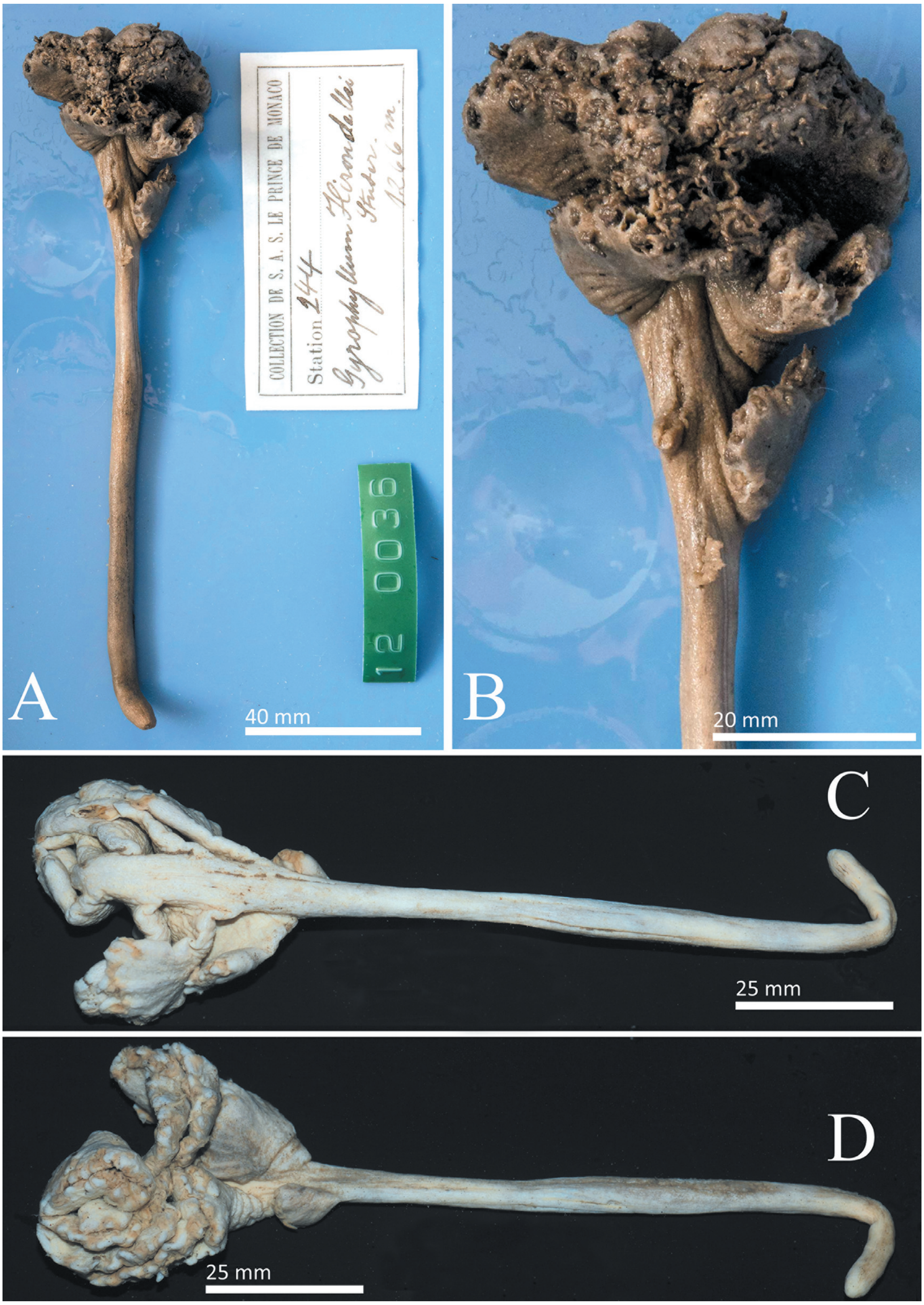

Fig. 4. *Gyrophyllum hirondellei* Studer, 1891. **A**. Holotype colony of *G. hirondellei* (MOM INV 120036) deposited in the Musée oceanographique de Monaco, ventral view. **B**. Detail from A, showing the compacted group of polyp leaves and autozooids 'calyces' without evident pointed processes. **C–D**. Dorsal and ventral view of BIAÇORES colony (MNHM OCT.A.579), see also Fig. 6A–B. Photographs A–B: Michel Dagnino.

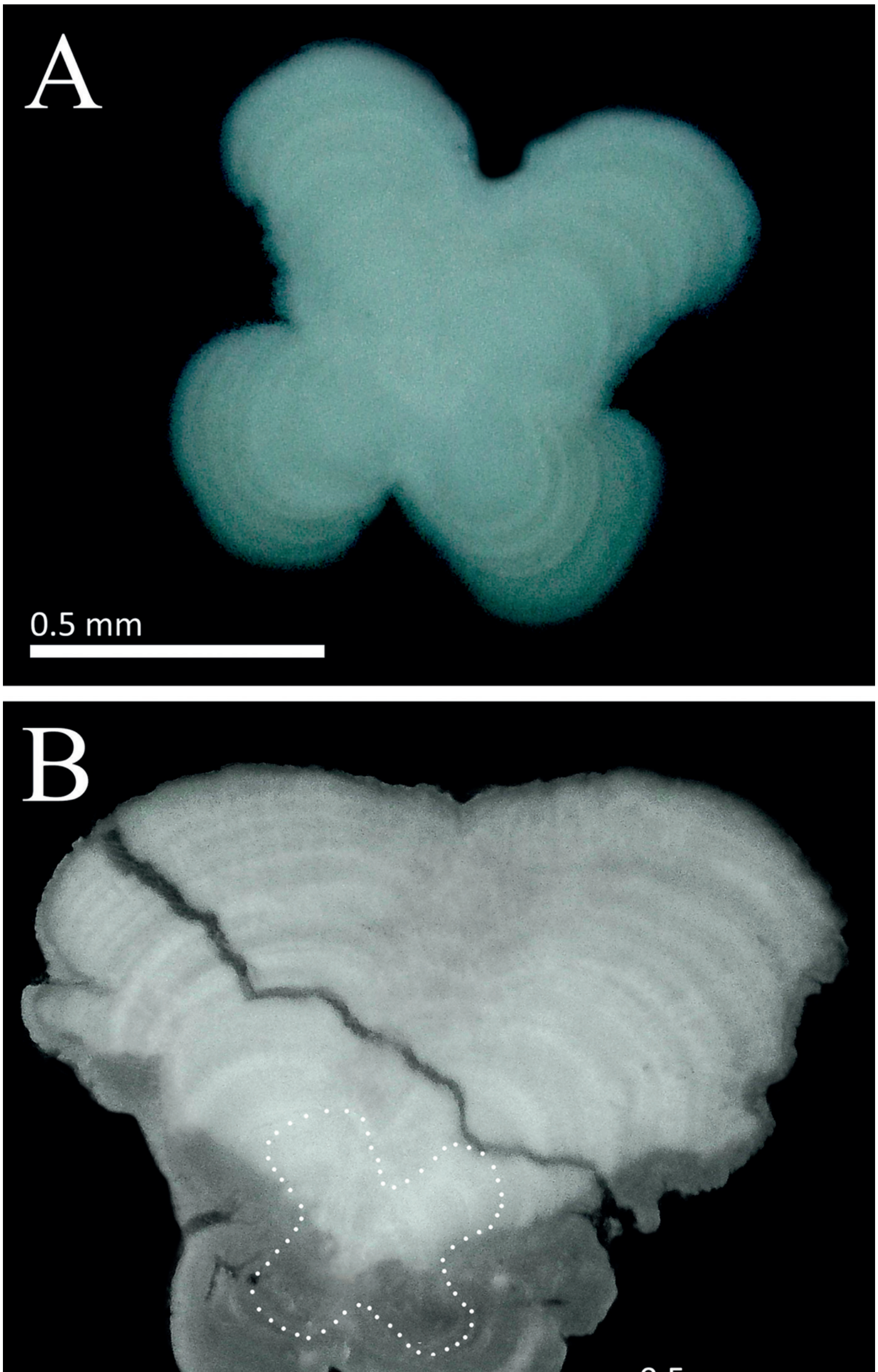

Fig. 5. *Gyrophyllum hirondellei* Studer, 1891. Cross-sections of the axis near the rachis-peduncle limit of *G. hirondellei* colonies from SCOTIA cruises. **A**. Colony BECA (OPEN-660), a colony 112 mm in total length, showing an X-shaped cross-section, with an already apparent asymmetry. If growth rings are assumed to be produced annually this specimen is ~5 years old. **B**. Colony BECA (OPEN-661), a colony 215 mm in total length, showing a highly asymmetric X-shaped cross-section and a symmetrical central core (white dots). This specimen is ~14 years old according to growth rings with the proviso above.

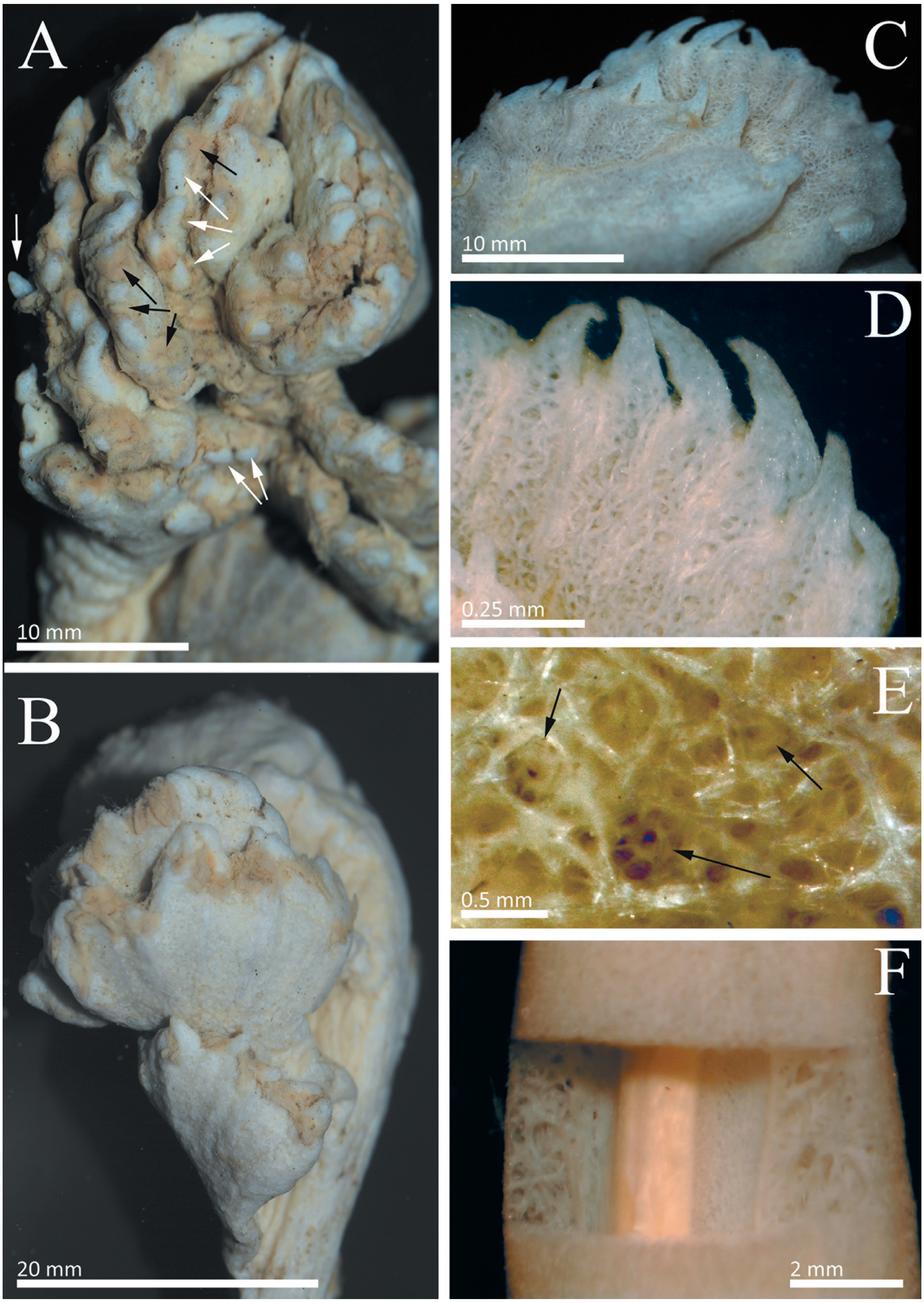

Fig. 6. *Gyrophyllum hirondellei* Studer, 1891. **A–B**. Detail of the colony MNHM OCT.A.579 in upper-ventral and lateral view, respectively, showing BPPs (white arrows) and partially retracted autozooids (black arrows). **C–D**. Detail of polyp leaves and ventral edge of a polyp leaf of the colony BECA (OPEN-660), note trabecular appearance of lateral surfaces and well developed BPPs. **E**. Detail of lateral surface of a polyp leaf, showing trabecular arrangement of sclerites and siphonozooid openings (arrowed). **F**. Partial section at rachis-peduncle limit, showing the thick trabecular wall and the axis with longitudinal groves.

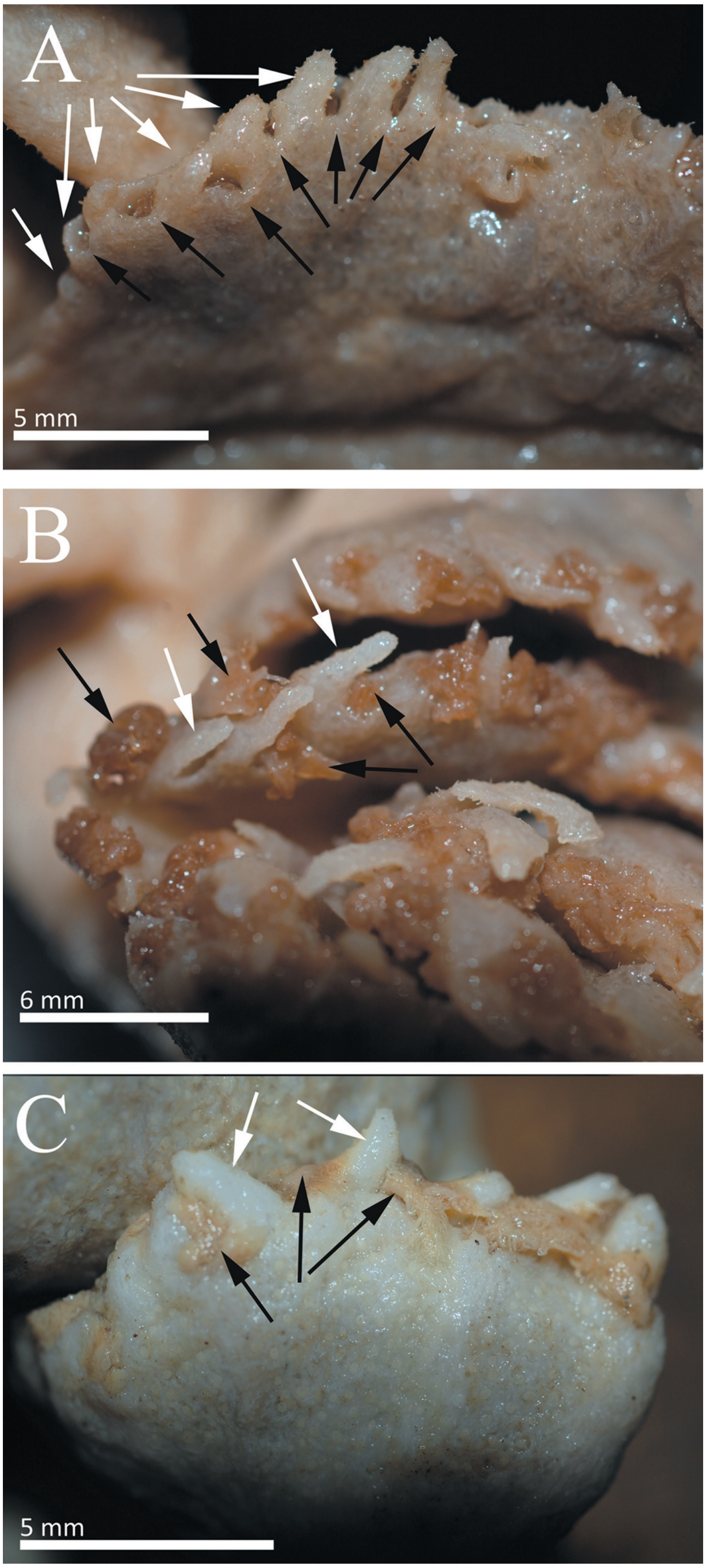

Fig. 7. *Gyrophyllum hirondellei* Studer, 1891. Details of the ventral edge of a polyp leaf, showing the apertures of an autozooid (black arrows) and a single BPP (white arrows) in differing degrees of development per autozooid. **A–B**. Colony BECA (OPEN-661). **C**. Colony MNHM OCT.A.579.

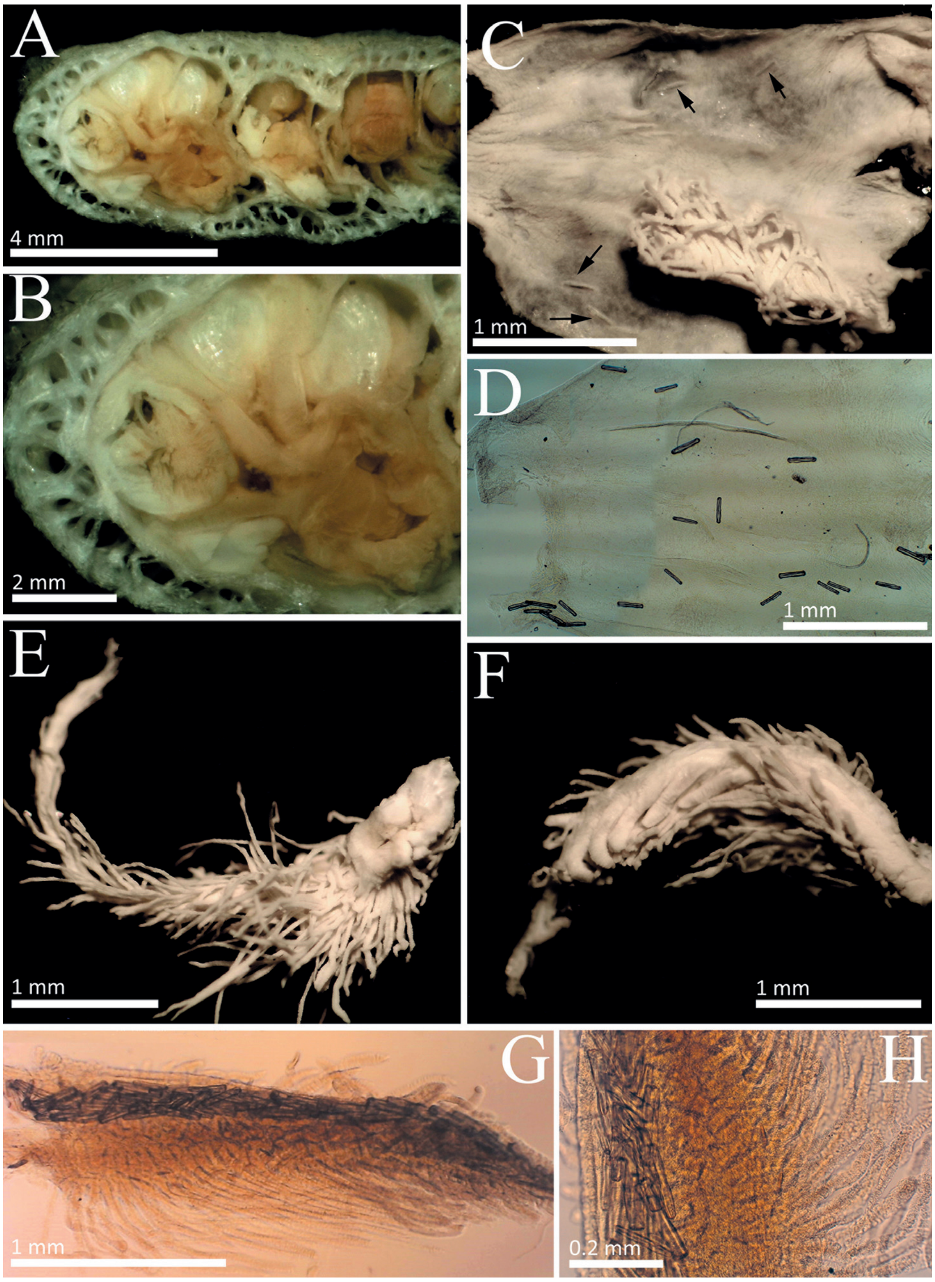

Fig. 8. *Gyrophyllum hirondellei* Studer, 1891, BECA (OPEN-660). **A**. Transversal section of a polyp leaf, showing its trabecular walls, and the thin barriers between consecutive gastrovascular cavities that are disposed in a line. **B**. Detail from A (the gastrovascular cavity on the left), showing also pharynx, mesenteria, sclerites of the tentacular axis (visible due to the transparency of oral disc), and (sectioned) one of the oral 'pouches' into which each tentacle is partially retracted. **C**. Internal view of the autozooids body wall into which the tentacular crown retracts (this becomes the outer body wall when the autozooid is extended). Note on the bottom right one of the tentacles and several sclerites (arrowed) in the thin body wall of the autozooid. **D**. Autozooid body wall treated with clove oil to clear tissue with scattered sclerites now easily observed in situ. **E**. Single tentacle in oral view (after critical point treatment) showing the numerous filiform structures. **F**. Single tentacle in lateral view (after critical point treatment) showing a series of normal pinnulae, part of the aboral side of tentacle and filiform structures. **G**. Single tentacle treated with clove oil to observe the presence and disposition of sclerites along the tentacular axis. **H**. Detail from G, also showing filiform structures.

oral axial surface (Figs 8C, E–H, 9A–C). Siphonozooids minute, 0.32–0.55 mm in diameter (average 0.46 mm, N = 20), numerous, scattered on the lateral (actually proximal and distal) sides of polyp leaves (Fig. 6E), and rachis dorsal track (more difficult to detect).

Sclerites differentially distributed in various parts of colony: densely placed in rachis, including polyp leaves, calycular BPP (Fig. 6D), and along dorsal and ventral tracks, around openings of siphonozooids (Fig. 6E), along abaxial side of tentacular axis of autozooids (Fig. 8G–H); however, much more scattered on body of autozooids (Fig. 8C–D). Sclerites present in a reticular manner on polyp leaves, observable not only on surface (Fig. 6E) but also internally. Walls between consecutive autozooids thinner than outer surrounding wall (Fig. 8A–B). Similar reticular structures visible at rachis-peduncle limit (Fig. 6F) and on penduncle. Sclerites absent in pinnules (including filiform processes), polyp body, and pharynx. No minute bodies observed in peduncle.

Sclerites from polyp body and tentacular axis as blunt tree-flanged rods up to 0.25 mm and 0.31 mm in length, respectively (Figs 8C–D, 10A). Sclerites from polyp leaves (including those surrounding siphonozooids), calycular BPPs, rachis and peduncle as elongated three-flanged rods. Those from polyp leaves up to 0.52 mm in length (Fig. 10B). Sclerites from calycular BPPs up to 0.48 mm (Fig. 10C). Sclerites from exterior surface of rachis up to 0.44 mm in length (Fig. 10D). Sclerites from inner rachis up to 0.48 mm in length (Fig. 11A). Sclerites from surface of peduncle up to 0.36 mm in length (Fig. 11B). Sclerites from inner peduncle up to 0.35 mm in length (Fig. 11C).

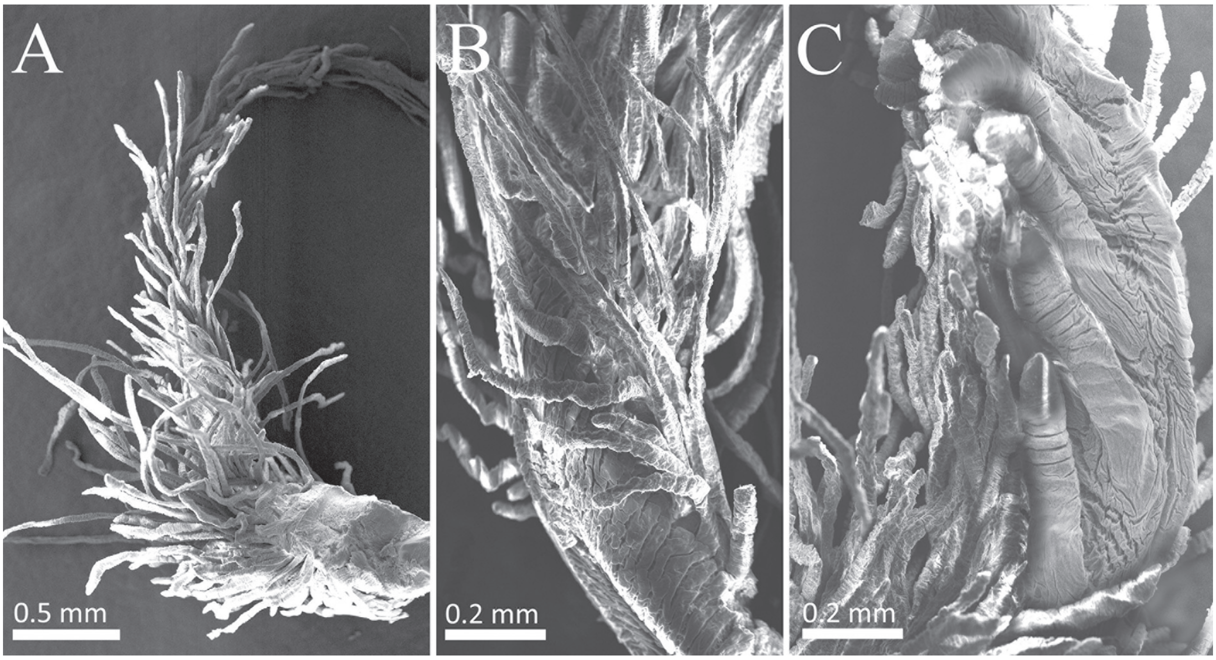

Fig. 9. *Gyrophyllum hirondellei* Studer, 1891, BECA (OPEN-660). **A**. SEM photographs of a tentacle in latero-oral view showing the numerous filiform structures. **B**. SEM photographs of a tentacle in latero-aboral view showing the naked aboral surface of tentacular axis and filiform structures. **C**. SEM photographs of a tentacle in lateral view showing digitiform normal pinnulae and, on the left, the numerous and elongate filiform structures. missing collection codes for specimens (as given in all other figs …)

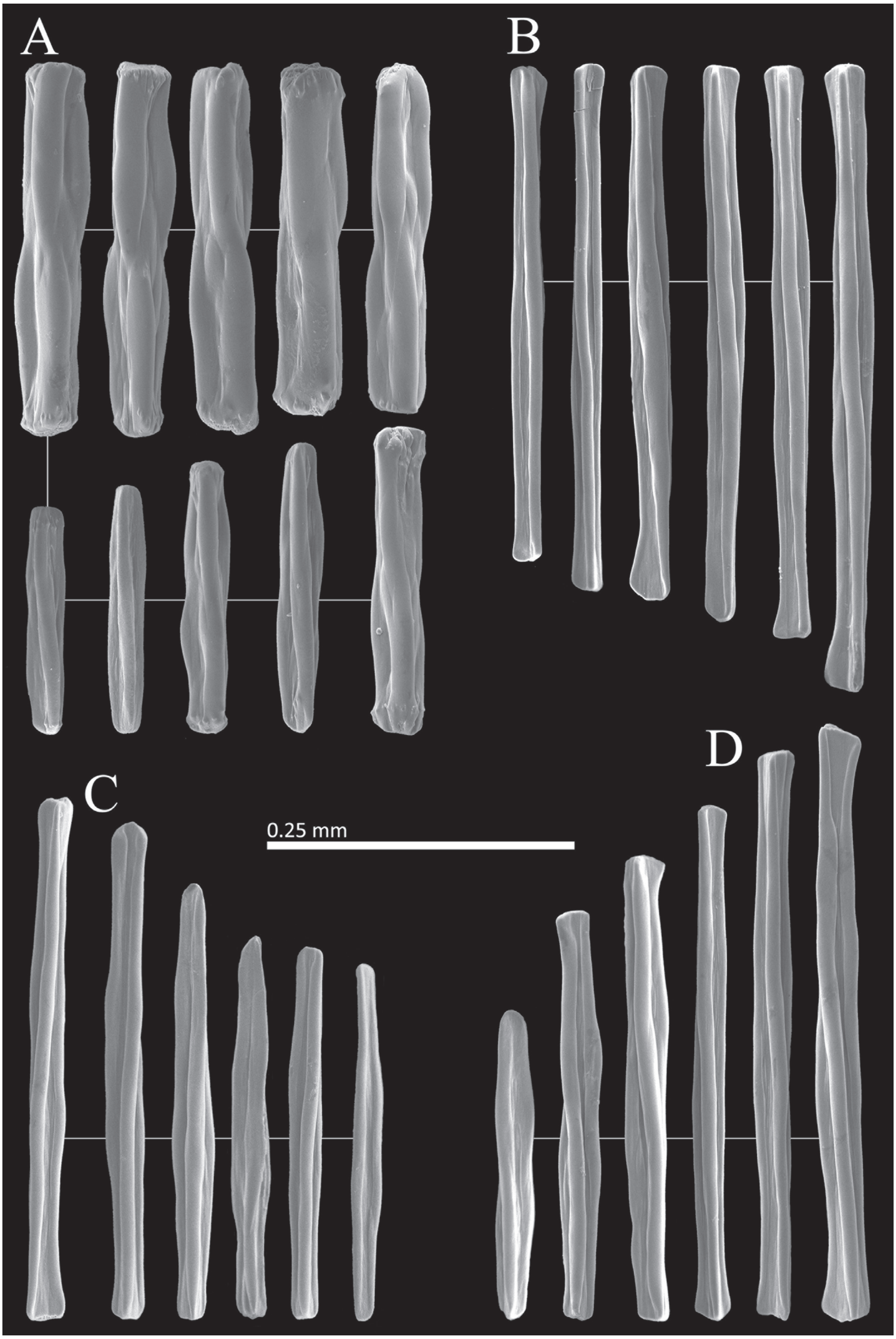

Fig. 10. *Gyrophyllum hirondellei* Studer, 1891, BECA (OPEN-660). SEM photographs of sclerites. **A**. Tentacle. **B**. Polyp leaf, siphonozooids area. **C**. Calycular pointed processes. **D**. Rachis exterior.

Colour

Freshly collected colonies were light brown at peduncle, rachis stalk and the section of rachis bearing polyp leaves dorsally, but darker brown on surfaces of polyps and calycular BPPs with the sclerites visible as whitish trabecular structures. The autozooids themselves were dark brown. Preserved colonies are whitish to light brown (Figs 3–4) while all sclerites are colourless.

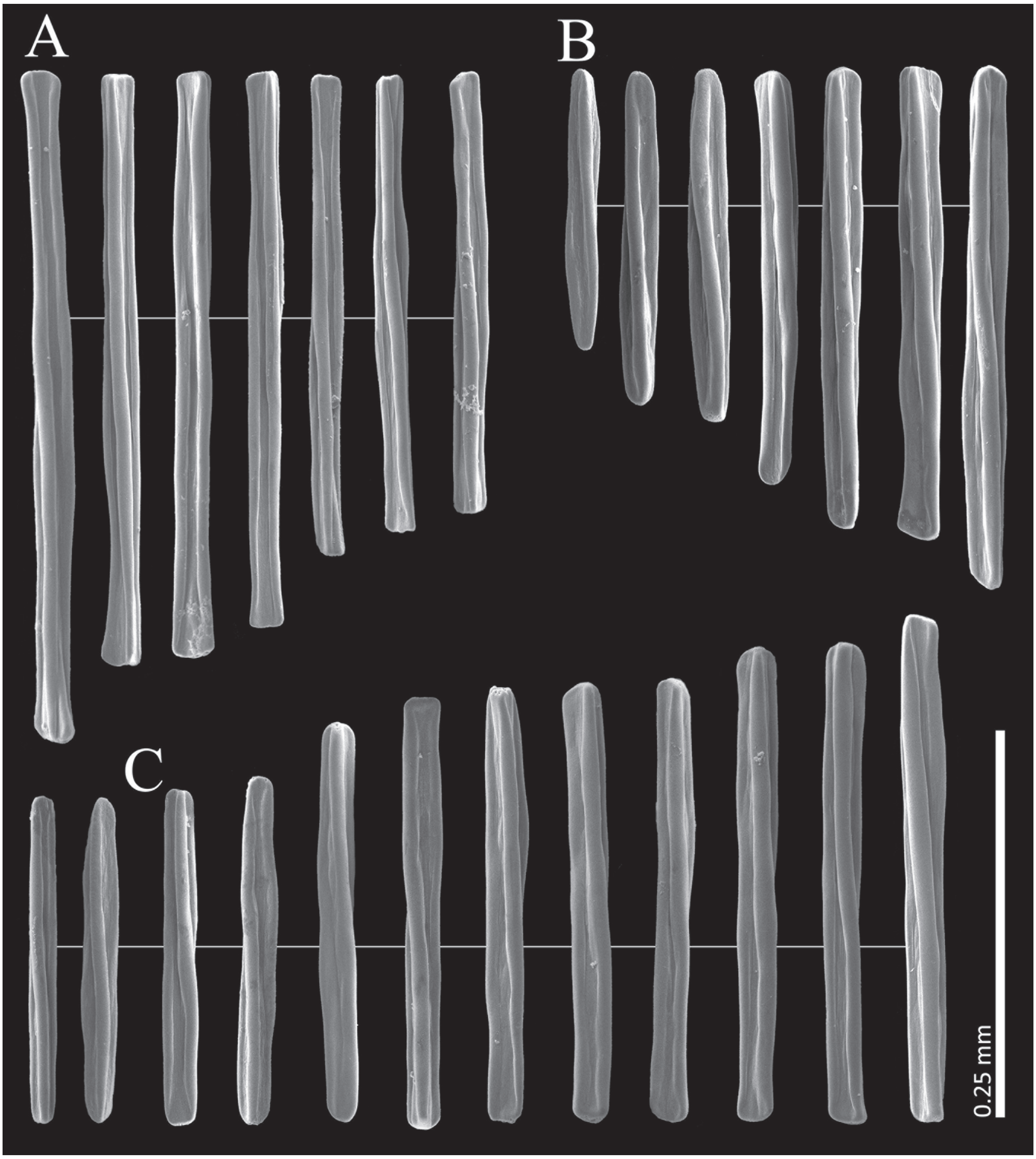

Fig. 11. *Gyrophyllum hirondellei* Studer, 1891, BECA (OPEN-660). SEM photographs of sclerites. **A**. Rachis interior. **B**. Peduncle exterior. **C**. Peduncle interior.

Geographical and depth distribution

At present, *Gyrophyllum hirondellei* is known from the North Atlantic, from Rosemary Seamount and Rockall and Hatton Banks to Azores and Bahamas, over a bathymetric range of 721–2220 m depth, the shallower records being those in reported in this paper (see Table 1) (Studer 1891; 1901; Roule 1905; Deichmann 1936; Tixier-Durivault & d'Hondt 1974b; present account).

Discussion

As reviewed above, the search for a consensual family for placement of the genus *Gyrophylum* has been challenging and a matter of dispute for some taxonomists throughout the 20th century and indeed into the beginning of the 21st. Hickson (1916: 253) even went on to point out that the presence of three-flanged sclerites was not enough to dissociate the genus from Pteroeididae, and that "I [he] should also strongly disapprove of any proposal to raise the genus to family rank".

With the respect that we must naturally have for the enormous efforts made by the taxonomists of the 20th century (e.g., Kükenthal 1915 and Hickson 1916, among others), the information currently available, reinforced by molecular data (Dolan *et al.* 2013 and Kushida & Reimer 2019 based on *mtMutS* and *ND2* mitochondrial markers; García-Cárdenas *et al.* 2020 based on *mtMutS*, *Cox1* mitochondrial and *28S* nuclear markers; López-González & Drewery 2022 and the present study based on *mtMutS*, *ND2* and *Cox1* mitochondrial markers, and *28S* nuclear marker), does not support the inclusion of *Gyrophyllum* in either Pteroeididae or Pennatulidae. The colonial morphology of *Gyrophyllum* (having polyp leaves, siphonozooids on polyp leaves (not in pads) and dorsal track of rachis, and sclerites as three-flanged rods) is clearly isolated in (and within) Clade III, although it is clearly phylogenetically related to the elongate-clavate colonies without polyp leaves (*Kophobelemnon*, fam. Kophobelemnidae) and somewhat more uncertainly to the flagelliform colonies (*Funiculina*, fam. Funiculinidae) (see Williams 1995b: 108–109, 111, figs 2b, 3i).

Until recently, eight genera were considered valid in the family Pennatulidae: *Alloptilella*, *Crassophyllum* Tixier-Durivault, 1961, *Gyrophyllum*, *Pennatula*, *Pteroeides*, *Ptilella*, *Ptilosarcus* Verrill, 1865, and *Sarcoptilus* Gray, 1848 (see Williams 1995a, 1995b; García-Cárdenas *et al.* 2019; Li *et al.* 2021; WoRMS 2022). The current molecular knowledge certainly does not support the reunification of all these genera into a single taxon at the family level (Dolan *et al.* 2013; Kushida & Reimer 2019; García-Cárdenas *et al.* 2020; López-González & Drewery 2022; this paper). Furthermore, the phylogenetic relationships of the genera in Clade II are still poorly understood. The family Pennatulidae with its type genus *Pennatula* is placed in Clade II (according to the available molecular trees, the morphological and molecular delimitation of this family is currently difficult since some of the morphologically similar genera such as *Ptilosarcus*, *Alloptilella*, and *Ptilella* are dispersed between genera having flagelliform colonies (*Distichoptillum*), bilateral colonies without polyp leaves (*Gilibelemnon*), or reniform colonies (*Renilla*)); the family Pteroeididae including *Pteroeides* is placed in Clade I (two other morphologically similar genera, *Sarcoptilus* and *Crassophyllum*, are so far unknown from a molecular point of view); and finally, the family Gyrophyllidae fam. nov. up to now including the genus *Gyrophyllum* is placed in Clade III.

This conception of the families Pennatulidae and Pteroeididae as separate was already considered by previous authors (Kölliker 1880; Kükenthal 1915; Williams 1995a). Ehrenberg (1834: 287) formulated the first diagnosis of the family initially named Pennatulinae (later on corrected to Pennatulidae by Dana 1846: 586), although at that time he also included the genera *Veretillum* Cuvier, 1798, *Pavonaria* Kölliker, 1869 (= *Funiculina*), *Umbellularia* Lamarck, 1801 (= *Umbellula*), *Scirpearia* Cuvier, 1817 (= *Virgularia* ?), *Renilla*, and *Virgularia*, all of which are currently placed in different families (see Williams 1995a). The placement of *Pennatula* and *Ptilosarcus* in the same family Pennatulidae was already recognized by Kükenthal (1915: 81, the last genus as *Leioptilus* Gray, 1860) and Williams (1995a: 125–126). The conception of a family Pteroeididae including *Pteroeoides* and *Sarcoptilus* (as *Sarcophyllum* Kölliker, 1870) was proposed by Kölliker (1880: 2), the genus *Crassophyllum* being added later when *C. cristatum* was described by Tixier-Durivault (1961). As discussed in the introductory part of this paper and extensively commented on by Williams (1995b) the family placement of the genus *Gyrophyllum* has been doubtful since its description.

Despite the proposal of unification of Pennatulidae and Pteroeididae into a single family (Williams 1995b), as commented on above, Dolan *et al.* (2013: 614–615) based on two mitochondrial markers (*mtMutS* and *ND2*) for the first time recognised (from a molecular point of view) the family Pteroeididae as separate from Pennatulidae and rejected the monophyly of Pteroeididae. Further molecular studies using three mitochondrial (García-Cárdenas *et al.* 2020) and three mitochondrial and one nuclear markers (López-González & Drewery 2021; this paper) agree with the previous statements. We present sequences of the type species of the genera *Gyrophyllum* and *Pteroeides*, establish the morphological characters both for diagnosing the family Gyrophyllidae fam. nov. and for differentiating it from Pteroeididae and Pennatulidae. The structure of the tentacles of the autozooids in *Gyrophyllum* is correctly described by LM and SEM for the first time and is shown to be quite different from that of other octocoral genera. The detailed morphological description and molecular coverage presented here along with the description of the family Gyrophyllidae fam. nov. solves the systematic placement of this orphan genus and the already known polyphyletic status of the family Pteroeididae (Dolan *et al.* 2013; Kushida & Reimer 2019; García-Cárdenas *et al.* 2020; López-González & Drewery 2022). Despite of this, the unequivocal placement of the morphologically similar genera *Sarcoptilum* and *Crassophyllum* in the family Pteroeididae must be corroborated by further molecular information.

Once we have established that the genus *Gyrophyllum* must be placed in a separate family, the question of how many species we can recognize in it and what morphological or molecular characters we could use to distinguish them is not trivial.

Studer (1891: 94) in a preliminary note described *Gyrophyllum hirondellei*, the type species of the genus, based on a single colony collected by *L'Hirondelle* in 1888 from a depth of 1266 m between the islands of Pico and São Jorge in Azores. A decade later, Studer (1901: 34) repeated his same description and provided a fine illustration of the type material (Studer 1901: pl. IV, figs 3–4) in addition. Roule (1905: 456–457), in another preliminary note reporting on the collection of additional specimens of the identical species by the *Talisman* in 1883 (in the same geographical area and over a bathymetric range of 1222–2220 m), added to Studer's original description the presence of an X-shaped axis (mentioned as "irréguliètrment quadrangulaire") (see López-González & Drewery 2022, regarding the differences between rounded, rounded-quadrangular and fully X-shaped axes in sea pens), as well as the additional presence of siphonozooids on the rachis, a feature (pointed out by this author) typically present in Pennatulidae. In a posthumous note, Marion (1906: 147) in the final lines of her manuscript mentioned a series of unidentified colonies collected by the *Talisman* in 1883, one of them from Azores (station 128, 1257 m in depth) (Marion 1906: pl. XVII, fig. 28, 28A) being a colony of *G. hirondellei* studied by Roule (1905). Among this list of non-described material one particular colony was named and illustrated as *Bathypenna elegans* (Marion 1906: pl. VI, fig. 26, 26A). Kükenthal (1915: 120) suggested the possible assignation of this material to *G. hirondellei*; however, in our opinion, the morphology of this colony shows far more similarity to *Pennatula* or *Ptilella* and as such is certainly deserving of further research if the material can still be located.

Hickson (1916: 252) proposed a second species in the genus: *G. sibogae* from the Malay Archipelago and similarly identified the presence of siphonozooids on the dorsal track of the rachis, the tentacles being provided with very long pinnules, and a calycular area with "a pair of lateral, short, stout papilliform teeth [our BPPs] (pl. VIII, fig. 48)". This last feature was the primary character proposed by Hickson to distinguish between Atlantic and Indian species (Hickson 1916: 255). The larger known colony size of *G. sibogae* in comparison to the smaller colony size of G. *hirondellei* is a continuous ontogenetic feature that should not be used itself for diagnosing species, although analysis of relative proportion data (such as the ratios rachis/peduncle length, rachis/stalk+peduncle length, total colony length/polyp leaves, etc.) from a significant number of colonies of each putative species may turn out to show that some of these ratios may be useful diagnostic features. The same can be said regarding the use of the number of polyp leaves of a colony unless this value is considered in the context of other measurements. In reference to the presence or absence of calycular BPPs, neither Studer nor subsequent researchers have observed or pointed to the existence of BPPs in the Atlantic specimens including the type material illustrated by Studer (1901: pl. IV, figs 3–4) (Fig. 4A–B in this paper). We include in our study a BIAÇORES specimen identified by Tixier-Durivault as *G. hirondellei* from Azores which exhibits well developed BPPs. As we have observed in our eastern North Atlantic material, there is considerable variation in the development of BPPs in different colonies. While BPPs are observed to be present in most colonies, a high level of intracolony variability is evident, for instance, calyces with or without BPPs are present in the same colony and even in the same polyp leaf. Hickson himself pointed out that "The absence of these teeth from a good many of the calices [in reference to the calyces of the type material of *G. sibogae*] may be due to post mortem injury but it is also possible that there is a considerable amount of variation in this respect".

Hickson (1916: 255), being fully aware of the descriptive limitations of having only a single colony available but acknowledging the possibility of intracolony variability, felt it necessary to propose as "a provisional statement" the use of colony length and presence or absence of calyx BPPs to distinguish between Atlantic (*G. hirondellei*) and Indian (*G. sibogae*) material. Nevertheless, our N Atlantic material exhibits a single BPP (sometimes reduced or absent, eroded?) on a low calyx (if it can be considered a calyx), while the Indian material described and illustrated by Hickson (1916: pl. VIII, fig. 48) clearly shows well separated, relatively high standing autozooid calyces and two BPPs per autozooid (Hickson 1916: 255). Williams (1995b) examined seven complete colonies (plus three incomplete ones) from the Tasman Sea, and although he described those as having more or less developed calycular BPPs, these structures, as illustrated (Williams 1995b: fig. 5c), showed well differentiate calyces, but not BPPs as per the illustration provided by Hickson (1916). It remains a possibility that both species may show a gradation in size of these structures due to differential development or simply as a result of the aging and/or some erosion processes. Nevertheless, it is clear that according to this study, the Atlantic form possesses a single BPP per autozooid, while the Indo-western Pacific form (as described and illustrated by Hickson) has two.

A similar and also difficult to interpret are colonies of *Gyrophyllum* collected from the Tasman Sea (Fig. 12; https://www.cmar.csiro.au/data/caab/taxon_report.cfm?caab_code=11219005), material that deserves further investigation if it becomes available for molecular and morphological study. Consultations to examine in detail other possible colonies of *G. sibogae*, as well as the holotype, have been unsuccessful to date, and we hope that this investigation can be carried out in the near future. Anyway, a better molecular and morphological characterization of *Gyrophyllum* colonies from the Indo-West Pacific would not impact on the main topic of this paper i.e., to resolve the phylogenetic placement of this genus in the phylogenetic hypotheses obtained during the last decade using a datamatrix of concatenated genes, and also when the genes are analysed separately (Dolan *et al.* 2013; Kushida & Reimer 2019; García-Cárdenas & López-González 2020; López-González & Drewery 2022; this article).

In reference to diversity, distribution and size of the sclerites in different parts of the colony, Hickson (1916: 255), who also had in his possession an Atlantic specimen of *G. hirondellei* sent by the kindly assistance of Professor Gravier, had already noted the absence of clear differences, as the sclerite shape

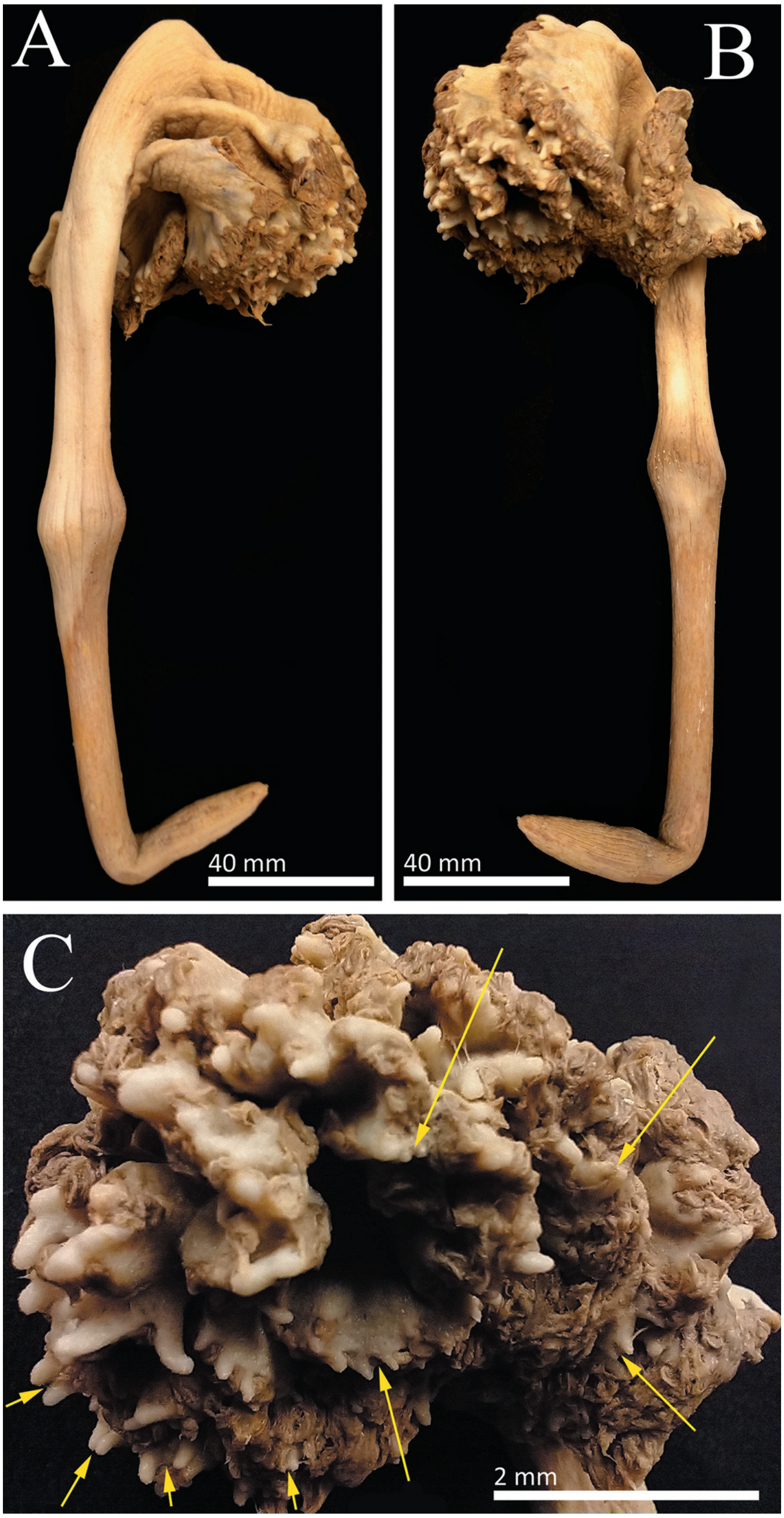

Fig. 12. *Gyrophyllum* cf. *sibogae* Hickson, 1916, colony from New Zealand waters (NIWA 158583; sampling data: NZOI Stn. P86, 31º39.498′ S, 159º9.402′ E, 610 m depth, 28 May 1977). **A**. Latero-dorsal side. **B**. Latero-ventral side. **C**. Detail showing polyp leaves ventral edges with well-developed BPPs (yellow arrows) in a double manner. These are likely to be the origin of Hickson's observations, but despite this, Indo-West Pacific colonies deserve further molecular and morphological investigations.

and distribution were the same, and the sizes clearly overlapped. Nevertheless, Hickson (1916: 255) pointed out that in *G. sibogae* short blunt rods ~0.2 mm in length are present on the tentacles and autozooid body wall below the tentacular crown, clearly different to those present in the polyp leaves (more elongated and as well as distinctly three-flanged and up to 0.5 mm in length). Thomson (1927: 57) described the polyp leave sclerites of *G. hirondellei* (Thomson referred to these as pinnules) as around ~0.5 mm in length, while those of the tentacles (~0.25 mm in length) were shorter and wider but the differences were not so marked as those in *G. sibogae*. In our eastern N Atlantic specimens the polyp body had scattered sclerites similar to those of the tentacles, up to 0.25 mm in length (average 0.20, N = 10). Our spicular study does not provide further information to distinguish Atlantic (our material) and Indo-western Pacific (Hickson 1916; Williams 1995b) specimens.

Apart from the number of BPPs per autozooid (when distinctly developed) and the degree of development of calyces, no other distinctive differences between Atlantic and Indo-west Pacific material can be discussed from a morphological point of view. It should be noted that the maximum colony length and bathymetric distribution known for these species in their respective areas are slightly different. The currently known Atlantic colonies of *G. hirondellei* had a maximum length of 218 mm (present account), and an observed bathymetric range of 721–2220 m, while Indo-western Pacific colonies of *G. sibogae* were up to 295 mm in length, and ranged 520–585 m in depth. But, can these continuous features be also usable as species discriminant? If *G. hirondellei* and *G. sibogae* are different species, the current morphological characters available are limited and the molecular markers used so far are not as useful as they have proved to be in other sea pen genera. On the other hand, perhaps these differences only suggest that we are not looking into the appropriate morphological and molecular target, and that other morphological (e.g., statistical biometric comparison), biochemical (e.g., secondary metabolites) or molecular (e.g., RADseq, microsatellite) study should be also explored before resorting to fusing both taxa into a single cosmopolitan one. Such a fusion will surely have the regrettable effect of making the scientific community forget the interesting history of these species and their authorities since the end of the 19th century and throughout the 20th century.

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