Research article

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.

**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 *Gyrophyllum* (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
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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 temporarily 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 Gyrophyllum, 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’histoire 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 55–60° 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.

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(1) As Calibelemnon sp. in GenBank, but assigned to Calibelemnon hinoennma 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.

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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 H₂O 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), 10⁷ 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, Pitilella Gray, 1870, Allocitiella 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 Haliptreriidae 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.


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


**Material examined**

NORTH EASTERN ATLANTIC – Azores • 1 spec.; North São Miguel; 38°36.5′ N, 28°17.5′ 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.; 56°08.71′ N, 17°34.64′ W–56°07.25′ N, 17°34.89′ 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.; 56°08.71′ N, 17°34.64′ W–56°07.25′ N, 17°34.89′ W; depth 997–101 m; 29 Sep. 2020; SCOTIA 1420S; stn.
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S20321 #8009; complete colony, 78 mm in length; NMS.Z.2022.1.2 - BECA (G-3835); NMS • 1 spec.; 56°08.71′ N, 17°34.64′ W–56°07.25′ N, 17°34.89′ 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-3834); NMS • 1 spec.; 56°08.83′ N, 17°29.77′ W–56°10.40′ N, 17°29.57′ W; depth 902–905 m; 29 Sep. 2020; SCOTIA 1420S; stn. S20322 #11835; 1 fragment; BECA OPEN-665 (G-3834); BECA • 1 spec.; 56°24.30′ N, 17°23.04′ W–56°22.80′ N, 17°22.72′ W; depth 761–771 m; 30 Sep. 2020; SCOTIA 1420S; stn. S20331 #7706; complete colony, 112 mm in length; BECA OPEN-660 (G-3832). – South West Rockall Slope • 1 spec.; 57°07.11′ N, 19°59.63′ W–57°04.87′ N, 20°00.47′ 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.; 56°42.59′ N, 16°30.85′ W–56°42.31′ N, 16°37.05′ 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.; 56°42.59′ N, 16°30.85′ W–56°42.31′ N, 16°37.05′ 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.; 56°42.59′ N, 16°30.85′ W–56°42.31′ N, 16°37.05′ 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.; 56°42.59′ N, 16°30.85′ W–56°42.31′ N, 16°37.05′ 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.; 56°42.59′ N, 16°30.85′ W–56°42.31′ N, 16°37.05′ 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.; 59°05.85′ N, 09°52.94′ W–59°04.70′ N, 09°55.40′ 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); Bec • 1 spec.; 59°05.85′ N, 09°52.94′ W–59°04.70′ N, 09°55.40′ 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) appearing at different levels near the autozooid 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 hirondelai 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 peduncle. 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 ...)

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Fig. 10. *Gyrophyllum hirondellei* Studer, 1891, BECA (OPEN-660). SEM photographs of sclerites. 
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 *Gyrophyllum* 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 Pteroideidae or Pennatulidae. The colonial morphology of *Gyrophyllum* (having polyp leaves, siphonozoooids 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. Funiculiniidae) (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*, *Pteroideis*, *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 (*Distichoptilum*), bilateral colonies without polyp leaves (*Gilibelemnon*), or reniform colonies (*Renilla*)); the family Pteroideidae including *Pteroideis* 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 Pteroideidae 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 
equivocal 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 “irrégulièrement 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 BIACORES 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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