

Hidden in the crowd: re-evaluation of the generic status of the Antarctic sea pen *Kophobelelemnion pauciflorum* (Anthozoa: Octocorallia: Pennatulioidea), a molecular and morphological approach

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Summary: Our understanding of Antarctic octocoral diversity is still far from complete. Newly collected specimens of the Antarctic sea pen *Kophobelelemnion pauciflorum* Molander, 1929 have allowed a detailed morphological and molecular description of the species. The results of this study, including the diversity and complete distribution of the sclerome, the distribution of autozooids and siphonozooids and the sequences of three mitochondrial markers (mtMutS, COI and ND2) and one nuclear marker (28S) contribute to knowledge of the complex relationships of the genera *Kophobelelemnion* Asbjørnsen, 1856 and *Funiculina* Lamarck, 1816, which were initially traced in some recent works on the taxonomy and phylogeny of this highly derived group of octocorals. The sequences attributed to the genus *Kophobelelemnion* were divided into three different groups. Two of these groups are recognized here simply as *Kophobelelemnion* I and *Kophobelelemnion* II, pending further morphological and molecular review. The sister group of *Kophobelelemnion* I was the genus *Funiculina*. The third group, corresponding to *K. pauciflorum* sequences, is here assigned to a new genus, *Scotiabelemnion* gen. nov. The family delimitation and the relationships of the families Kophobelemnidae Gray, 1860, Funiculinidae Gray 1860 and Gyrophyllidae López-González, Drewery and Williams, 2022 are discussed. Finally, it is proposed to merge Kophobelemnidae into Funiculinidae, leaving only two families within Clade III, Funiculinidae and Gyrophyllidae.

Keywords: Southern Ocean; biodiversity; corals; new genus; *Scotiabelemnion*; morphological and molecular approach.

Oculto entre la multitud: reevaluación del estatus genérico de la pluma de mar antártica *Kophobelelemnion pauciflorum* (Anthozoa: Octocorallia: Pennatulioidea), un enfoque molecular y morfológico.

Resumen: Nuestro conocimiento sobre la diversidad de octocorales antárticos está aún lejos de ser completo. Especímenes recientemente recolectados de la pluma de mar antártica *Kophobelelemnion pauciflorum* Molander, 1929 han permitido una descripción morfológica y molecular detallada de esta especie. Los resultados de este estudio, como la diversidad y distribución completa del escleroma, la distribución de autozooides y sifonozooides, y las secuencias de tres marcadores mitocondriales (mtMutS, COI, ND2) y un marcador nuclear (28S), contribuyeron a revelar las complejas relaciones de los géneros *Kophobelelemnion* Asbjørnsen, 1856 y *Funiculina* Lamarck, 1816, un hecho inicialmente encontrado en algunos trabajos recientes sobre la taxonomía y filogenia de este grupo de octocorales altamente derivado. Las secuencias atribuidas al género *Kophobelelemnion* se dividieron en tres grupos diferentes. Dos de estos grupos se reconocen aquí simplemente como *Kophobelelemnion* I y *Kophobelelemnion* II, a la espera de una mayor revisión morfológica y molecular. El grupo hermano de *Kophobelelemnion* I fue el género *Funiculina*. El tercer grupo, correspondiente a las secuencias de *K. pauciflorum*, se asigna aquí a un nuevo género, *Scotiabelemnion* gen. nov. Se discute la delimitación familiar y las relaciones de las familias Kophobelemnidae Gray, 1860, Funiculinidae Gray 1860, y Gyrophyllidae López-González, Drewery y Williams, 2022. Finalmente, se propone fusionar Kophobelemnidae y Funiculinidae, dejando solo dos familias dentro del Cado III, Funiculinidae y Gyrophyllidae.

Palabras clave: Océano Austral; biodiversidad; corales; nuevo género; *Scotiabelemnion*; enfoque morfológico y molecular.

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INTRODUCTION

Current molecular phylogenetic studies often act as a kind of earthquake on the bases of the morphology-based systematics for many marine invertebrate groups, making it difficult at some points to reconcile traditional hierarchical classifications (based solely on morphological characters) and phylogenetic hypothesis (based on the analyses of a set of sequences of different markers, complete mitochondrial sequences, or a variety of next generation sequencing methods) (Havermans et al. 2010, Morrow et al. 2013, O'Hara et al. 2017, Polisenio et al. 2020; among many others). It is desirable to use an integrating vision in which the sources of morphological and molecular information do not compete but rather collaborate to achieve more natural classifications (e.g. Di Camillo et al. 2018, Gómez Daglio and Dawson 2019).

As in many other groups of marine invertebrates, the recently resurrected superfamily Pennatuloidea is not exempt from the lack of agreement between traditional classifications and the phylogenetic hypotheses based on DNA sequencing (e.g. Dolan et al. 2013, Kushida and Reimer 2019, García-Cárdenas et al. 2020). Molecular phylogeny is capable of detecting poly- and paraphyletic situations, whether at the species, genus or family level, which must be resolved from the nomenclatural point of view for the best stability of sea pen classification (García-Cárdenas et al. 2019, López-González and Drewery 2022, López-González et al. 2022, McFadden et al. 2022). These classifications and nomenclature are the basis for many other disciplines, including ecology and physiology, and for the correct establishment of policies for the maintenance of biodiversity and the maintenance of services of the earth's ecosystems (Worm et al. 2006, Palumbi et al. 2009, Sanitha and Madeswaran 2020, Lotze 2021, among many others).

The existence of a number of qualitative morphological steps (e.g. with or without calyces, with or without polyp leaves, with or without sclerites) made it apparently quite easy to identify a given specimen to the genus level. However, a lack of understanding of the variability of some morphological characters made it much more difficult to assign them to one of the numerous named species, probably also because of the lack of precision of diagnostic features in the original literature. The pennatuloid genera *Pennatula* Linnaeus, 1758, *Virgularia* Lamarck, 1816, *Pteroeides* Herklots, 1858, *Umbellula* Gray, 1870 and *Kophobelemnion* Asbjørnsen, 1856 are good examples of this.

Recent cases of polyphyletic situations detected by molecular studies have been found in the genera *Pennatula* and *Umbellula* (Dolan et al. 2013, Kushida and Reimer 2019, García-Cárdenas et al. 2019). These cases required a further examination to segregate a number of morphological characters that were previously considered diagnostic of a single taxonomic unit. In recent years, the genus *Pennatula* has been divided into three, *Pennatula*, *Ptilella* Gray, 1870 and *Alloptilella* Li, Zhan and Xu, 2021 (see García-Cárdenas et al.

2019, Li et al. 2021, López-González 2022), while the genus *Umbellula* has been divided not only into three different genera, but also into two different families, *Umbellulidae* K  lliker, 1880 (with the sole genus *Umbellula*), and *Pseudumbellulidae* L  pez-Gonz  lez in L  pez-Gonz  lez and Drewery 2022 (with the genera *Pseudumbellula* L  pez-Gonz  lez and Drewery, 2022 and *Solumbellula* L  pez-Gonz  lez in L  pez-Gonz  lez and Drewery 2022) (see L  pez-Gonz  lez and Drewery 2022).

The true diversity of the genus *Kophobelemnion* is still far from being known, despite the apparently short list of species included in WoRMS, this list being supplemented by several proposed synonyms, *nomen dubia* and uncertain species (K  kenthal 1915; McFadden et al. 2024). The genus *Kophobelemnion* is often reported in ecological, biomedical, biochemical and descriptive community papers as "unidentified species", mainly because of the difficulty of obtaining a precise species assignment (Belcik 1977, Robert et al. 2015, Marchese et al. 2021, Bessho-Uehara et al. 2020, among many others), or attributed to the type species *Kophobelemnion stelliferum* (M  ller, 1776) (Utinomi 1958, Pasternak 1970, Gili 1987, Williams 1990, Rice et al. 1992, Mastrototaro et al. 2013, De Clippele et al. 2015, Matsumoto et al. 2007, among many others). The main problem in reporting type species is that some of them are apparently recognized in various seas and oceans, which leads them to be considered widely distributed or even cosmopolitan. This occurs in some of the most widely reported genera, including *Funiculina* Lamarck, 1816, *Distichoptilum* Verrill, 1882, *Anthoptilum* K  lliker, 1880, *Virgularia*, *Pennatula* and *Kophobelemnion* (see Williams 1995). The demonstration that some type species really have a wide distribution or are cosmopolitan is a pending issue (see comments on *Pennatula phosphorea* Linnaeus, 1758 in Garc  a-C  rdenas and L  pez-Gonz  lez 2019: 265).

The first sequences (the mitochondrial mutS-like protein DNA mismatch repair gene [mtMutS] and the NADH dehydrogenase subunit 2 gene [ND2] of a species of *Kophobelemnion* [*K. macrospinum*, from the Tasman Sea]) were published by McFadden et al. (2006), showing a high affinity with another genus of sea pen, *Gyrophyllum* Studer, 1891. Subsequent authors added additional sequences to their phylogenetic proposals and specifically focused their studies on Pennatulacea. Dolan et al. (2013: Fig. 1), based on mtMutS and ND2, detected for the first time four main clades (initially unofficially named 1 to 4, later on labelled I to IV). The same authors detected for the first time the relationships of the genera *Kophobelemnion*, *Gyrophyllum* and *Funiculina*, which were reunited in Clade III (Dolan et al. 2013: Fig. 1), as well as the possible polyphyletic nature of the genus *Kophobelemnion*, by adding four additional species from Atlantic and Pacific localities in a phylogenetic tree based on the markers mtMutS and ND2. The same conclusions were drawn by Kushida and Reimer (2019), also showing an unstable placement of the genus *Funiculina* within Clade III. Hogan et al. (2019) added complete mitochondrial

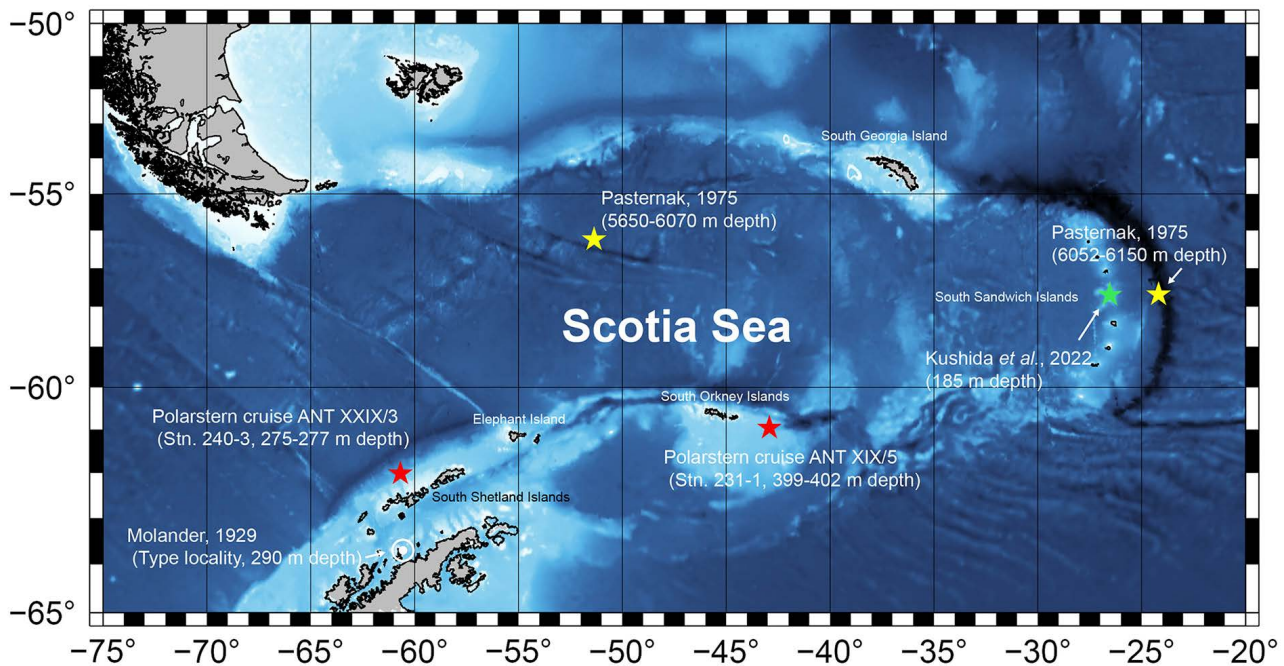


Fig. 1. – Distribution of the known sampling stations where *Scotiabelemnion* specimens have been collected. Map Google Earth: data SIO, NOAA, U.S. Navy, NGA, GEBCO, Image Landsat/Copernicus; data LDEO-Columbia, NSF, NOAA, Image U.S. Geological Survey. Molander and Porlarstern specimens are considered here as *Scotiabelemnion pauciflorum* comb. nov. Kushida et al. (2022) specimens are identified here only to the genus level as *Scotiabelemnion* sp. (see discussion). Pasternak's (1975) specimens collected from the abyssal-hadal limit and upper hadal zones are also considered to be in the genus *Scotiabelemnion*, but species identity remain doubtful until molecular studies can be performed (see Discussion).

sequences of three additional species from Whittard Canyon (NE Atlantic). García-Cárdenas et al. (2020) carried out the first concatenated analyses of two mitochondrial (mtMutS and cytochrome c oxidase I [COI]) and a nuclear gene (28S), including new sequences of these markers for species of the three genera in Clade III, *Kophobelemnion* (2 spp. from NE and SE Atlantic), *Gyrophyllum* (1 sp.) and *Funiculina* (2 spp.). These authors also showed the unstable placement of *Funiculina* when this set of markers is used, because the maximum likelihood (ML) model supported Clade III, whereas the Bayesian influence (BI) one did not. López-González et al. (2022), carried out their phylogenetic analyses using three mitochondrial markers (mtMutS, COI and ND2) and one nuclear one (the 28S nuclear ribosomal gene) to describe a new family for the genus *Gyrophyllum*, resulting in a Clade III composed of the sea pen families Funiculinidae, Kophobelemonidae and Gyrophyllidae. In the latter paper (using four markers, and using only the three mitochondrials as well), the authors also supported the paraphyletic nature of *Kophobelemnion*, as in Dolan et al. (2013) and Kushida and Reimer (2019). Hogan et al. (2023) provided knowledge of the phylogenetic relationships of sea pens via sequences of whole mitochondrial genomes, but included only *Kophobelemnion* and *Funiculina* sequences, lacking information from the genus *Gyrophyllum* at that time.

Recently, Kushida et al. (2022) carried out a phylogenetic analysis using three mitochondrial markers

(mtMutS, COI, and ND2), adding to Clade III sequences of four additional *Kophobelemnion* species from Japanese waters and mtMutS and COI sequences of two colonies tentatively identified as *Pennatulacea* sp. from Antarctic waters (collected in the Antarctic Circumnavigation Expedition 2016–2017) (Reg No. WAM Z44543, WAM Z43174). The latter unidentified species was placed in the ML tree between two compact sets of *Kophobelemonion* sequences, again indicating the paraphyletic nature of this genus. The colonies of these two divergent sequences were also characterized by the lack of an internal axis.

In parallel, morphologically similar colonies to the *Pennatulacea* sp. sequenced by Kushida et al. (2022) were under molecular and morphological study by one of the authors of this paper (P.J.L.-G), with material collected in the South Shetland Islands and near the South Orkney Islands during two cruises on board the RV *Polarstern* (LAMPOS-ANT XIX/3 in 2002, and ECOWED-ANT XXIX/3 in 2013). The morphology of this material agrees with the species *Kophobelemnion pauciflorum* Molander, 1929, later renamed by Pasternak (1975) as *Kophobelemnion molanderi* to avoid homonymy with *K. pauciflorum* Hickson, 1916 (see Hickson 1916: 72, Molander 1929: 48, Pasternak 1975: 102).

The present study, starting from the phylogenetic hypotheses proposed by Kushida et al. (2022), together with additional morphological and molecular studies of the colonies collected during the *Polarstern* cruises

strongly suggests that *K. pauciflorum* must be placed in a different genus. This paper offers an updated detailed morphological description of this species, as well as the most comprehensive molecular analyses and discussion at genera and family level of the sequenced pennatulaceans reunited in Clade III. In this paper a new genus is formally described to accommodate the material attributed to *Kophobelemnon molanderi* Pasternak, 1975 (= *Kophobelemnon pauciflorum* Molander, 1929), examined here from a molecular and morphological point of view. The diversity and originality of Southern Ocean octocorals is once again increasing, in this case with the addition of a new genus of sea pen, thanks to the study of newly collected materials from an integrative perspective.

MATERIAL AND METHODS

Sample collection

The material studied was collected on the tip of the Antarctic Peninsula, South Shetland Islands, near the South Orkney Islands, the South Sandwich Islands and the Scotia Sea (Fig. 1) on board the R/V *Polarstern* on the cruises ANT XIX/5 (LAMPOS, 3 April to 5 May 2002) and ANT XXIX/3 (22 January to 18 March 2013) sponsored by the Alfred Wegener Institut für Polar- und Meeresforschung (Bremerhaven) under the auspices of the Scientific Committee for Antarctic Research.

Octocoral colonies were collected using Agassiz trawls in the Bransfield Strait and South Shetland Islands area (Fig. 1). The octocorals were fixed on board in hexamethylenetetramine-buffered 10% formalin-seawater for morphological examination, or directly in absolute ethanol for further molecular studies.

DNA extraction and PCR procedures

Total genomic DNA was extracted from ethanol (EtOH)-preserved material using the E.Z.N.A. DNA kit (OmegaBiotech) following the manufacturer's instructions. The mtMutS, ND2 and COI mitochondrial regions and the nuclear 28S were sequenced. The start of the mtMutS region was amplified using the primers ND42625F and MUT3458R (McFadden et al. 2006; Sánchez et al. 2003). ND2 was amplified using the primers 16S647F and ND21418R (McFadden et al. 2004). The COI region was amplified using the primers COII8068F and COIOCTR (McFadden et al. 2004; France and Hoover 2002). The 28S nuclear ribosomal gene (28S rDNA) was amplified using the primers 28S-Far and 28S-Rar (McFadden and van Ofwegen 2013). Each PCR used 1 U of MyTaq Red DNA Polymerase (Bioline), 10 µM of each primer and approximately 30 ng of genomic DNA, being brought to a final volume of 25 µL with molecular grade H₂O. MtMutS PCR was carried out using the following cycle profile: initial denaturation at 94°C for 2 min, 35 cycles of denaturation at 94°C for 15 s, annealing at 55°C for 15 s, extension at 72°C for 10 s and a final extension at

72°C for 5 min. The ND2, COI and 28S PCR used the same cycle profile, but the corresponding annealing temperatures were 51°C, 50°C and 58°C respectively. The PCR products were purified using ExoSAP-ITTM PCR Product Cleanup Reagent (ThermoFisher Scientific) following the manufacturer's instructions before strong amplifications were sent to Macrogen Europe for sequencing in both directions. The purified products were electrophoresed on an ABI PRISM® 3730xl Genetic Analyzer.

Phylogenetic analyses

All chromatograms were visualized and sequence pairs were matched and edited using Sequencher v4.0. A preliminary BLAST search identified our sequences close to the genera *Kophobelemnon*, *Funiculina* and *Gyrophyllum*, all them within the informally named Clade III. This relationship was also in an ML comparison based only on mtMutS (~400 pennatuloid sequences, not shown). Therefore, for the present study, we will only include sequences of Clade III to avoid repeating trees and discussions between clades already included in other recently published studies (e.g. Dolan et al. 2013, Kushida and Reimer 2019, Kushida et al. 2022, García-Cárdenas et al. 2020).

The set of new sequences and the homologous ones from GenBank belonging to related genera and species of sea pens within Clade III (Table 1) were aligned using MUSCLE (MEGA6, Tamura et al. 2013). After alignment, pairwise genetic distances based on the mtMutS marker and the Kimura 2-parameter (K2P) model of nucleotide substitution (Kimura 1980) were obtained to compare them with previous analyses at genus and family levels, following the comparisons of Pante et al. (2012), López-González (2020) and López-González and Drewery (2022).

In accordance with previously published molecular phylogenies on pennatuloids (e.g. Dolan et al. 2013, Kushida and Reimer 2019, García-Cárdenas et al. 2020, López-González and Drewery 2022), sequences of ellisellids from GenBank were selected as outgroups. Three data sets of sequences were analysed: mtMutS separately, the three mitochondrial genes mtMutS+ND2+COI, and the last one with the addition of the nuclear gene 28S. The matrix including only the mtMutS sequences had 689 bases. The concatenated matrix including only the three mitochondrial sequences had 2014 bases. The concatenated matrix for the mtMutS+ND2+COI+28S sequences had 2814 bases. All data matrices had 26 pennatuloid plus three ellisellid sequences.

The phylogenetic reconstructions were obtained by applying the BI and ML methods. The best nucleotide substitution model was selected using Modeltest (Darriba et al. 2012) according to the Akaike information criterion and hierarchical likelihood ratio test (hLRT) values (T92 for all the data matrices). ML was implemented in MEGA6 using the NNI heuristic method (nearest neighbour interchange) and 1000 bootstrap replications (Felsenstein 1985). The BI was carried

Table 1. – Pennatuloids included in molecular phylogenetic analyses in this paper. Species and GenBank accession numbers in bold are those sequenced for this study. Due to the paraphyletic status of the genus *Kophobelemnon*, the grouping *Kophobelemnon* I (K.I) or *Kophobelemnon* II (K.II) is indicated after the specimen name (see also Fig. 10). Abbreviations: BECA, Biodiversidad y Ecología Acuática, Seville, Spain; NMS, National Museum of Scotland, Edinburgh, UK; NSMT, National Museum of Nature and Science, Tsukuba, Japan; WAMZ, Western Australian Museum, Perth, Australia; MNHM, Muséum national d’histoire naturelle, Paris, France; NHM, Natural History Museum, London, UK; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands; OPEN, Octocoral PENnatulacea collection in BECA; *, mtMutS and ND2 as *Gyrophyllum* sp. in GenBank; **, as Pennatulacea sp. in GenBank; ***, as *Kophobelemnon macrospinum* in GenBank and McFadden et al. 2006 probably a writing error, as it is reported as *K. macrospinum* in Dolan et al, 2013, and no species description as *K. macrospinum* has been found in the literature.

Species name in the tree	Catalog nos. / isolate /additional information	Geographic area/provenance	mtMutS	ND2	CoxI	28S	References
<i>Funiculina</i> sp.	FEL808611	Northern Gulf of Mexico, USA, NW Atlantic	JN227941	-	JN227949	-	Pante et al. 2012
<i>Funiculina armata</i>	NHM 2010.11 Isolate 94	NE Atlantic	KF313833	KF313807	-	-	Dolan et al. 2013
<i>Funiculina quadrangularis</i>	NMS.Z.2019.25.17	Little Loch Broom, Scotland, NE Atlantic	MK919658	MK919658	MK919658	-	Hogan et al. 2019
<i>Gyrophyllum hirondellei</i> (1)	MNHM OCT.A.579 BECA (G-128)	Azores, NE Atlantic	MT968964	MZ217769	MT952713	MT951915	García-Cárdenas et al. 2020, López-González and Drewery 2022
<i>Gyrophyllum hirondellei</i> (2)	NMS.Z.2022.1.3 BECA (G-3831)	South Rockall Slope, NE Atlantic	OM641961	OM641974	OM617949	OM630516	López-González et al. 2022
<i>Gyrophyllum</i> sp. (2)	NIWA 28779 Isolate 104	New Zealand, W Pacific	KF313846	KF313819	-	-	Dolan et al. 2013
<i>Gyrophyllum sibogae</i> (1)*	NTM-C014392 NOR89/535	Tasman Sea, AU, S Pacific	DQ302869	DQ302942	JX203865	JX203740	McFadden et al. 2006, McFadden and van Ofwegen 2012
<i>Kophobelemnon</i> sp. 1 –ED (K.I-A)	NHM Sea Pens 2010.13 isolate 91	Sweden, Koster Channel, NE Atlantic	KF313837	KF313810	-	-	Dolan et al. 2013
<i>Kophobelemnon</i> sp. 4 (K.I-B)	NMS.Z.2019.25.6	Whittard Canyon, NE Atlantic	MK919662	MK919662	MK919662	-	Hogan et al. 2019
<i>Kophobelemnon</i> sp. (K.I-C)	ANT59 (Lavrov,D.V)	unknown locality	OL616244	OL616244	OL616244	-	Muthye et al. 2022
<i>Kophobelemnon</i> sp. (K.I-D)	YK318 NSMT-Co 1767	Tanabe Bay, Wakayama, Japan	ON603965	ON603949	ON586713	-	Kushida et al. 2022
<i>Kophobelemnon</i> sp. (K.I-E)	YK298 NSMT-Co 1766	Shimoda, Shizuoka, Japan	ON603961	ON603946	ON586710	-	Kushida et al. 2022
<i>Kophobelemnon</i> sp. (K.I-F)	YK319 NSMT-Co 1768	Tanabe Bay, Wakayama, Japan	ON603966	ON603950	ON586714	-	Kushida et al. 2022
<i>Kophobelemnon macrospinum</i> *** (K.II-A)	NTM-C014985	Tasman Sea, AU, S Pacific	DQ302865	DQ302937	GQ342429	JX203742	McFadden et al. 2006, McFadden and van Ofwegen 2012
<i>Kophobelemnon pauciflorum</i> (K.II-B)	NHM 2010.21	Crozet Islands, S Atlantic	KF313836	KF313809	-	-	Dolan et al. 2013
<i>Kophobelemnon</i> sp. 2 –ED (K.II-C)	NHM 2010.10 Isolate A15	Monterey, E Pacific Ocean	KF313838	KF313811	-	-	Dolan et al. 2013

Species name in the tree	Catalog nos. / isolate /additional information	Geographic area/ provenance	<i>mtMutS</i>	<i>ND2</i>	<i>CoxI</i>	28S	References
<i>Kophobelemnon</i> sp. 3 (K.II-D)	NMS.Z.2019.25.5	Whittard Canyon, NE Atlantic	MK919661	MK919661	MK919661	-	Hogan et al. 2019
<i>Kophobelemnon</i> sp. 1 (K.II-E)	NMS.Z.2019.25.4	Whittard Canyon, NE Atlantic	MK919660	MK919660	MK919660	-	Hogan et al. 2019
<i>Kophobelemnon</i> sp. A (K.II-F)	BECA OPEN-141 (G-97)	NE Atlantic	MT968962	PP898428	MT952711	MT951913	García-Cárdenas et al. 2020, this paper
<i>Kophobelemnon</i> sp. B (K.II-G)	BECA OPEN-151 (G-121)	SE Atlantic	MT968963	PP898429	MT952712	MT951914	García-Cárdenas et al. 2020, this paper
<i>Kophobelemnon</i> sp. 3 –ED (K.II-H)	NIWA Sea Pens 28827 Isolate 102	New Zealand, W Pacific	KF313839	KF313812	-	-	Dolan et al. 2013
<i>Kophobelemnon</i> sp. (K.II-I)	YK263	Kumamo Nada, Mie, Japan	ON603955	ON603941	ON586706	-	Kushida et al. 2022
<i>Scotiabelemnon pauciflorum</i> comb. nov. (1)	BECA OPEN-121 (G-337)	South Shetland Islands, Antarctica	PP898424	PP898426	PP896679	PP901974	this paper
<i>Scotiabelemnon pauciflorum</i> comb. nov. (2)	BECA OPEN-122 (G-330)	South Shetland Islands, Antarctica	PP898425	PP898427	PP896680	PP901975	this paper
<i>Scotiabelemnon</i> sp. (1)**	WAMZ44543	Candlemas Island, Antarctica	ON603970	-	ON586718	-	Kushida et al. 2022
<i>Scotiabelemnon</i> sp. (2)**	WAMZ43174	Candlemas Island, Antarctica	ON603971	-	ON586719	-	Kushida et al. 2022
OUTGROUP							
<i>Junceella fragilis</i>	n.d.	Taiwan, NW Pacific	KJ541509	KJ541509	KJ541509	AF263355	Chen et al. 2000, Wu et al. 2016
<i>Ellisella</i> sp.	YK122	Palau, NW Pacific	MK133457	ON586722	MK133652	-	Kushida and Reimer 2019, Kushida et al. 2022
<i>Viminella</i> sp.	RMNH Coel.40032	W Papua, Indonesia, W Pacific	JX203794	-	JX203852	JX203703	McFadden and van Ofwegen 2012

out in the MrBayes v3.1.2 program (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003), using the model GTR+G (lset nst=6 rates=gamma) with 10^7 generations, discarding 25% of the initial trees. The stationarity of the chains and the convergence of the two runs were monitored for each parameter by Tracer (v.1.7.1) (Rambaut et al. 2018) to ensure that the effective sample size of all parameters was larger than 200, as recommended.

Morphological study

Colonies were dissected under a Motic MSZ168 stereomicroscope, and fragments from different part of the colonies were prepared for corroboration of the presence of sclerites and sclerite preparation for light microscopy and scanning electron microscope obser-

vation. Fragments of different parts (tentacles, anthocodia, etc.) were prepared in clove oil to observe sclerite arrangement in a Leica DMLB light microscope with an OPTIKA C-P20CC digital camera and the OPTIKA PROVIEW image software. The same procedure was carried out to observe sexual products and to sex selected dissected colonies. Sclerites (selecting the largest to smallest of all possible morphological types) from different parts of the colony were mounted on stubs, coated with gold-palladium under a Leica ACE600 and observed with a Zeis EVO SEM at the General Research Services of Microscopy at the University of Seville.

Deposition of materials

The material examined for this study has been deposited in the Museu de Zoologia in Barcelona (MZB)

and in the collection of the Biodiversidad y Ecología Acuática (BECA) research group at the University of Seville.

Nomenclatural acts

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank Life Science Identifiers (LSID) can be resolved, and the associated information can be viewed through any standard web browser by appending the LSID to the prefix “<http://zoobank.org/>”. The LSID for this publication is <https://zoobank.org/References/D8EEA0C1-C8F5-4BE2-9454-EFA268199A39>

RESULTS

Taxonomy

Class OCTOCORALLIA Haeckel, 1866
Order Scleralcyonacea McFadden, van Ofwegen and Quattrini, 2022
Superfamily Pennatuloidae Ehrenberg, 1834

Remarks

McFadden et al. (2022) recently proposed that the order Pennatulacea Verrill, 1865, which includes at least 15 families (see also López-González et al. 2022), should be abandoned in favour of a superfamily Pennatuloidae McFadden, van Ofwegen and Quattrini, 2022 in a new octocoral order named Scleralcyonacea McFadden, van Ofwegen and Quattrini, 2022. This proposal builds on previous analyses on mtMutS+ND2 (McFadden et al. 2006), further discussions on calcareous systematics (Williams 2019), and analyses of ultraconserved exons and loci and mtMutS (McFadden et al. 2022). The consideration of the previous order Pennatulacea as the superfamily Pennatuloidae is retained here to avoid the paraphyly of the recently described order Scleralcyonacea (see McFadden et al. 2022). However, from a nomenclatural point of view, once the taxonomic category order is proposed to be removed for this grouping, the subordinate category superfamily (a rank of the family group) is regulated under the ICZN (1999) according to the Article 36.1 Statement of the Principle of Coordination applied to family-group names. “A name established for a taxon at any rank in the family group is deemed to have been simultaneously established for nominal taxa at all other ranks in the family group; all these taxa have the same type genus, and their names are formed from the stem of the name of the type genus [Art. 29.3] with appropriate change of suffix [Art. 34.1]. The name has the same authorship and date at every rank.” This means that the authorship of this superfamily corresponds to Ehrenberg, 1834, because it was he who created the family Pennatulidae based on the type genus *Pennatula* according to Article 36.1, following the Principle of Coordination.

Family Funiculinidae Gray, 1860

Diagnosis (amended from Williams, 1990: 64, 69)
Colonies clavate to whip-like; with autozooids arranged bilaterally along rachis, sometimes in somewhat oblique series, rarely distally reunited, with or without spiculiferous calyces; siphonozooids on the rachis, with or without calyces; axis, present, rarely absent; sclerites, when present, three-flanged, tuberculate rods and plates. According to the current molecular knowledge, with a distinctive combination of nucleotide sequence in mtMutS (position 148-C, insertion 177-185, 203-C, 208-T, 225-T, 255-C, 358-C, 626-G, 688-A), ND2 (432-C, 537-C), and COI (273-A, 388-G) within Clade III, where the family Gyrophyllidae is also included.

Type genus

Funiculina Lamarck, 1816.

Genus *Scotiabelemnon* gen. nov.

Diagnosis

Funiculinid with a terminal cluster of a few (3-4) upwardly directed autozooids. Siphonozooids in two sets, in short longitudinal lines at the rachis-peduncle limit, and as a distal dome over autozooids bases. Axis absent. Sclerites mainly as large monoaxial rods with points and longitudinal furrows, scarcely tuberculate platelets, knobbly three-flanged rods, plus smooth to nearly smooth indistinctly tree-flanged needles (siphonozooid field), and ovals to oval-rods with irregular knobbly ornamentation (rachis and peduncle). According to the current molecular knowledge, with a distinctive combination of nucleotide sequence in mtMutS (position 72-T, 93-A, 117-A, 289-G, 438-G, 463-G), ND2 (209-C, 309-G), and COI (255-T, 387-T, 396-T) within Funiculinidae.

Type species

Kophobelemnon pauciflorum Molander, 1929.

Nomenclatural statement

An LSID number was obtained for the new genus: <https://zoobank.org/NomenclaturalActs/27f06b9c-6c7f-4e81-bb87-4187b4184c70>

Etymology

The new genus is named by combining *Scotia* in reference to the Scotia Sea and surrounding archipelagos, the currently known range of distribution of the type species after the works of Molander (1929), Pasternak (1975) and this paper, and the Greek word *belemnon* (dart or javelin), a common suffix used in naming sea pen genera after the general shape of the colony. Gender neuter.

Nominal species

Scotiabelemnon pauciflorum (Molander, 1929).

Remarks on nominal species in *Scotiabelemn* gen. nov.

Specimens sequenced by Kushida et al. (2022) as Pennatulacea sp. are here considered as *Scotiabelemn* sp. mainly because of molecular differences in the COI mitochondrial marker and some spicular differences (Kushida and Reimer, pers. comm.) (see also phylogenetic approach part in this paper). Paradoxically, Pasternak (1975) correctly executed a nomenclatural act denoting the homonymy between *Kophobelemn pauciflorum* Molander 1929 and *Kophobelemn pauciflorum* Hickson, 1916, providing a new name to Molander species whose type material retained the consideration of the name bearer. However, the erection of the genus *Scotiabelemn* gen. nov. and the transfer of *K. molanderi* (= *K. pauciflorum* Molander) to it make the use of *K. molanderi* Pasternak unnecessary, as there are no other species using the specific epithet *pauciflorum* in *Scotiabelemn* gen. nov. Therefore, the correct name for the material examined here and the type species of this new genus should be *Scotiabelemn pauciflorum* (Molander, 1929). The present paper suggests that the diversity of the genus *Scotiabelemn* gen. nov. could include more than a single species. Molander's and our present material was collected in shallower waters (200–402 m depth) than the abyssal-hadal and upper hadal (5650–6150 m depth) specimens described by Pasternak (1975) collected from South Sandwich Islands and the northern Scotia Sea, for which no molecular data are available. Moreover, even Pasternak (1975: 102–103) himself indicated that the deep-sea water colonies are significantly different from the shallow ones (они значительно отличаются от мелководных), and that tentacular sclerites are only present in the tentacular axis, unlike in Molander's and our specimens described here, which also have sclerites in the pinnulae (see below). This is a diagnostic characteristic at the species level that is frequently used in sea pens. For these reasons, we prefer to keep the potential synonymy of Pasternak's specimens with a question mark.

Scotiabelemn pauciflorum (Molander, 1929) comb. nov.

Kophobelemn pauciflorum Molander, 1929: 80.
Kophobelemn molanderi Pasternak, 1975: 102 (substitution name for *K. pauciflorum* Molander, 1929 invalidated by homonymy).
(?) *Kophobelemn molanderi* Pasternak, 1975: 102 (South Sandwich Islands and northern Scotia Sea specimens).
non *Kophobelemn pauciflorum* Hickson, 1916: 72.

Material examined

Newly collected material: MZB 2024-3405, ANT XIX/5 – LAMPOS, Stn. 231-1, 22 Apr 2002, Agassiz trawl, 43°27.42'W 60°59.19'S, 399–402 m depth, 1 whole colony, 32 mm in length. BECA(OPEN-667), ANT XIX/5 – LAMPOS, Stn. 231-1, 22 Apr 2002, Agassiz trawl, 43°27.42'W 60°59.19'S, 399–402 m depth, 1 colony in two pieces, 10 mm in length, male. BECA(OPEN-122, G-330), ANT XXIX/3 – ECOWED, Stn 240-3, 9 Mar 2013, Agassiz trawl, 62°7.05'S 60°34.12'W 275–277 m depth, 1 whole colony, 36 mm in length. BECA(OPEN-121, G-337), ANT XXIX/3 – ECOWED, Stn 240-3, 9 Mar 2013, Agassiz trawl, 62°7.05'S 60°34.12'W 275–277 m depth, 1 whole colony in two halves, 38 mm in length, female.

Description

Colonies varied from 10 to 38 mm in length (Figs 2A, B; 4B, D), with a terminal group of up to 4 autozooids (largest studied colony, Fig. 2A left), usually 3 autozooids from 10 mm in colony length (Figs 4C–D). Colonies without a clearly distinguishable symmetry pattern (Fig. 2B). Internal axis completely absent (Figs 3D, 4D). Peduncle (calculated in the largest colonies) 33%–40% of total colony length, not excessively bulbous in living and preserved state. Rachis composed of a stalk 60%–77% of total colony length, where relatively large autozooids appear distally (although gastrovascular cavities run internally along most of the rachis length, Fig. 3D). Lower part of the stalk cylindrical to conical widening distally. Terminal cluster of polyps distinctly swollen (Figs 2A–C, 3D, 4). Colony of 38 mm in total length developing numerous oocytes, up to 900 µm in diameter (Figs 3D, 5A). Colony of 10 mm in total length developing numerous spermatid cysts, up to 360 µm in diameter (Figs 4B, D, 5B, C).

Autozooids relatively short and robust (Figs 2A–C, 3B, 4), partially extended in preserved state (also in just collected material, Figs 2A–C), up to 4.5 mm in height (without tentacle length, probably much larger in fully extended state) and 4.0 mm in width, almost cylindrical, with an apparently smooth surface. Introvert folded in preserved state (Fig. 3C). Pharynx elongated and wrinkled. Tentacles relatively large and robust (Fig. 3B, C), up to 8 mm in preserved state. Pinnulae thick and relatively short, closely placed in a single line (Fig. 3B, C), up to 2.5 mm in length in preserved state, and up to 16 in number on each side of main tentacle axis.

Siphonozooids (0.2–0.5 mm in diameter) in two sets, at the basal part of rachis along intermittent longitudinal rows of 4–14 zooids (Fig. 2A, B, D), and numerous as a distal dome among the autozooid bases (Figs 2C, 4A, C).

Sclerites in all parts of the colony. Five kinds of sclerites: distinctly large monoaxial rods with numerous points and longitudinal furrows (Fig. 6A₁, 7A₁), scarcely tuberculate platelets (Fig. 8A₂), smooth to nearly smooth indistinctly tree-flanged needles (Fig. 8A₁), knobbly three-flanged rods (Figs 7B₂, C₂), and ovals to oval-rods with irregular knobbly ornamentation (Figs 8B, 9).

Sclerites of main tentacular axis (Fig. 6A) in two types: large monoaxial rods up to 0.42 mm in length (Fig. 6A₁) and elongate knobbly three-flanged rods up to 0.19 mm in length (Fig. 6A₂). Pinnulae with scarcely tuberculate platelets (Fig. 6B₁), knobbly three-flanged rods (Fig. 6B₂) and intermediate forms (Fig. 6B₃), all three up to 0.21 mm in length.

Distal part of body of autozooid with large monoaxial rods up to 0.35 mm in length (Fig. 7A₁) and knobbly three-flanged rod, some of them nearly smooth, up to 0.18 mm in length (Fig. 7A₂). Lower part (introvert) with the same sclerome but slightly smaller, large monoaxial rods up to 0.29 mm in length (Fig. 7B₁) and knobbly three-flanged rods up to 0.18 mm in length (Fig. 7B₂). Pharyngeal tissue with the same compo-

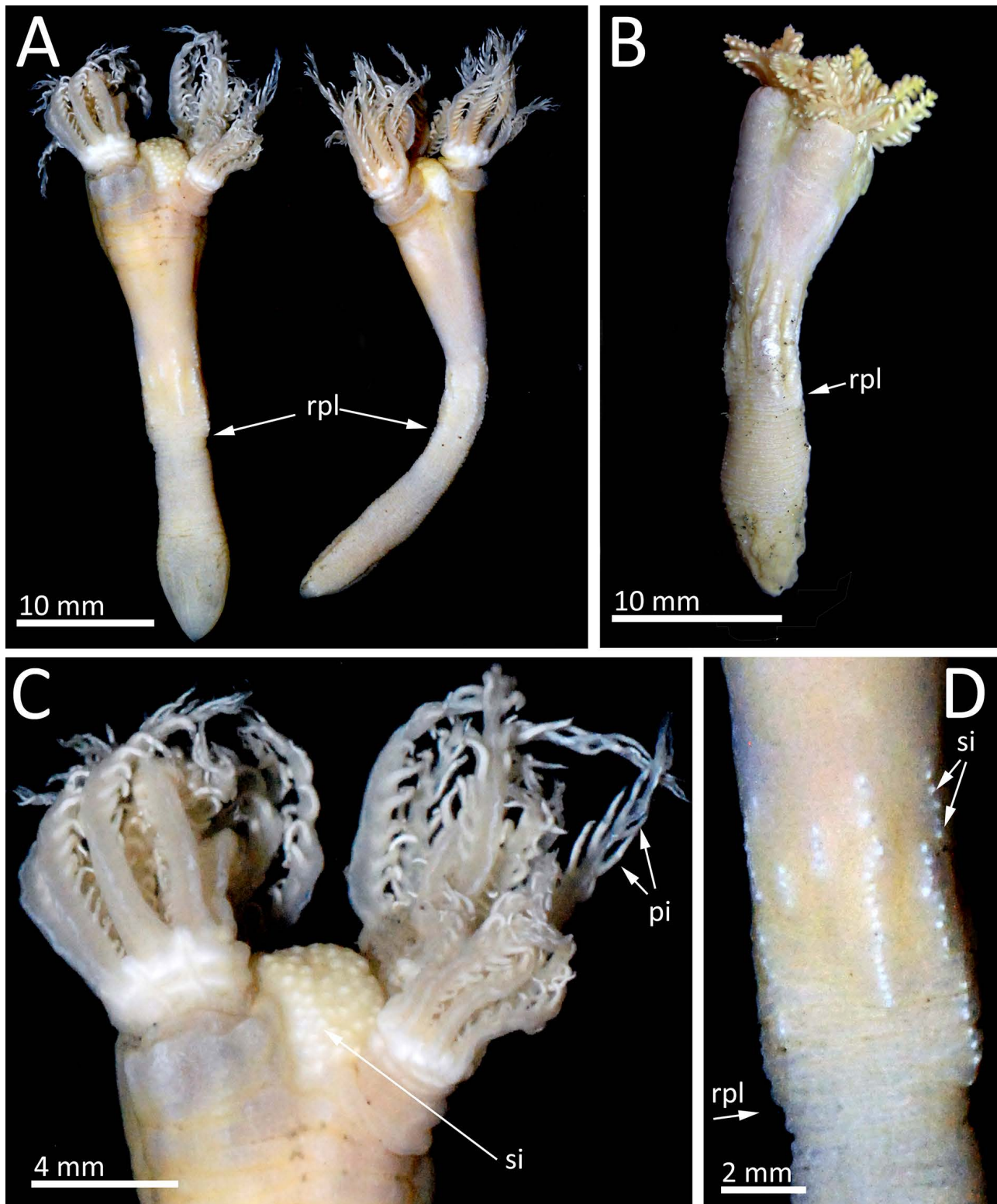


Fig. 2. – *Scotiabelemnnon pauciflorum* comb. nov. (A), two living colonies collected during ANT XXIX/3 cruise (BECA OPEN-121 on the left; BECA OPEN-122 on the right); (B), living colony collected during ANT XIX/5 cruise (MZB 2024-3405); (C), detail of the distal part of the colony BECA OPEN-121, showing three of the four partially extended autozooids and distal dome of siphonozoids; (D), detail of rachis peduncle limit of colony part of colony BECA OPEN-121, showing the short longitudinal rows of siphonozoids. Abbreviations: pinnulae (pi), rachis peduncle limit (rpl), siphonozoids (si).

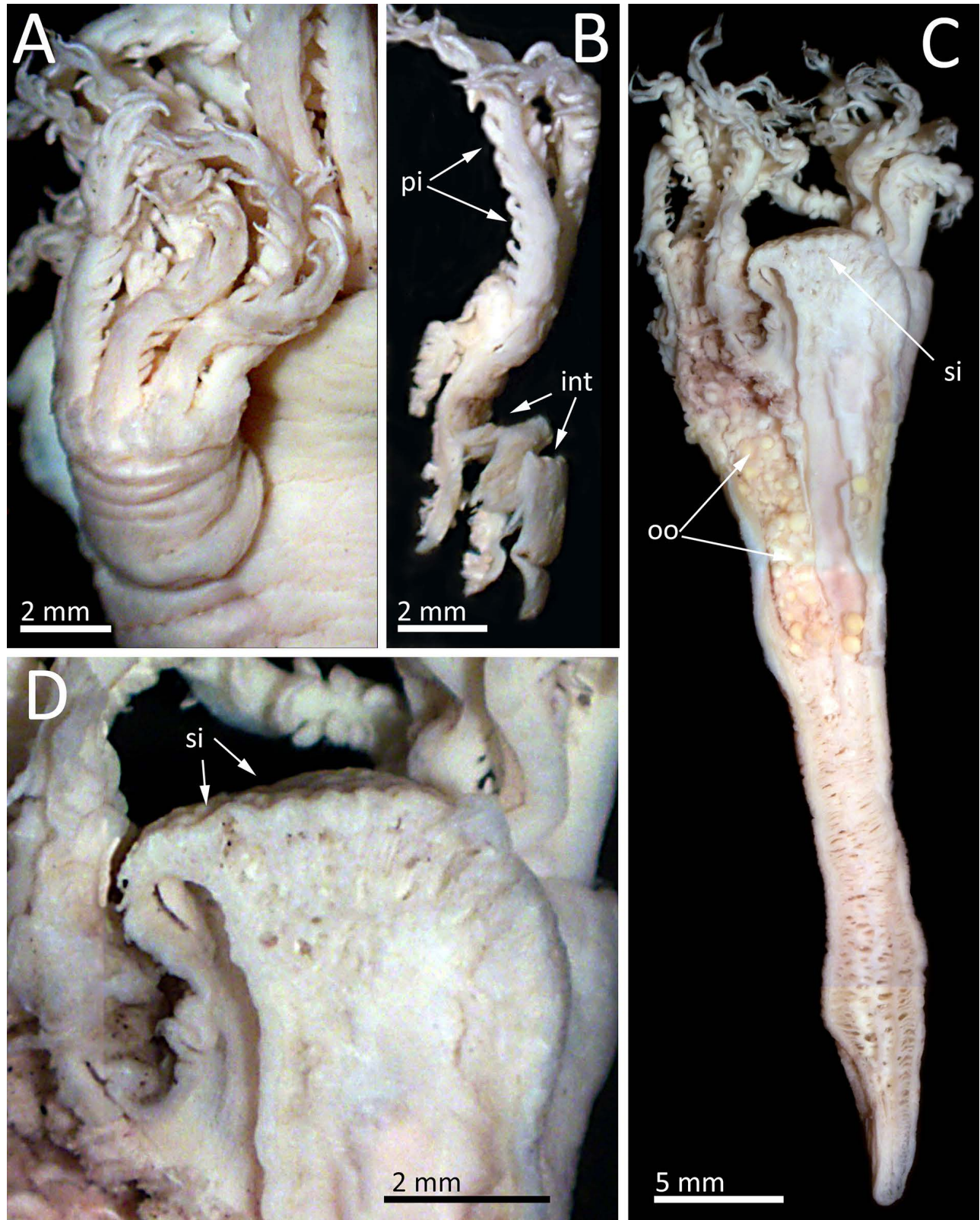


Fig. 3. – *Scotiabelemnon pauciflorum* comb. nov. Colony BECA OPEN-121: (A), partial extended autozooids; (B), detail of a couple of tentacles dissected including folded introvert; (C), colony dissected longitudinally, showing the large gastrovascular cavities with developing oocytes, the distal dome of siphonozooids and the lack of internal axis; (D), Detail of distal dome with siphonozooids. Abbreviations: introvert (int), oocytes (oo), pinnulae (pi), siphonozooids (si).

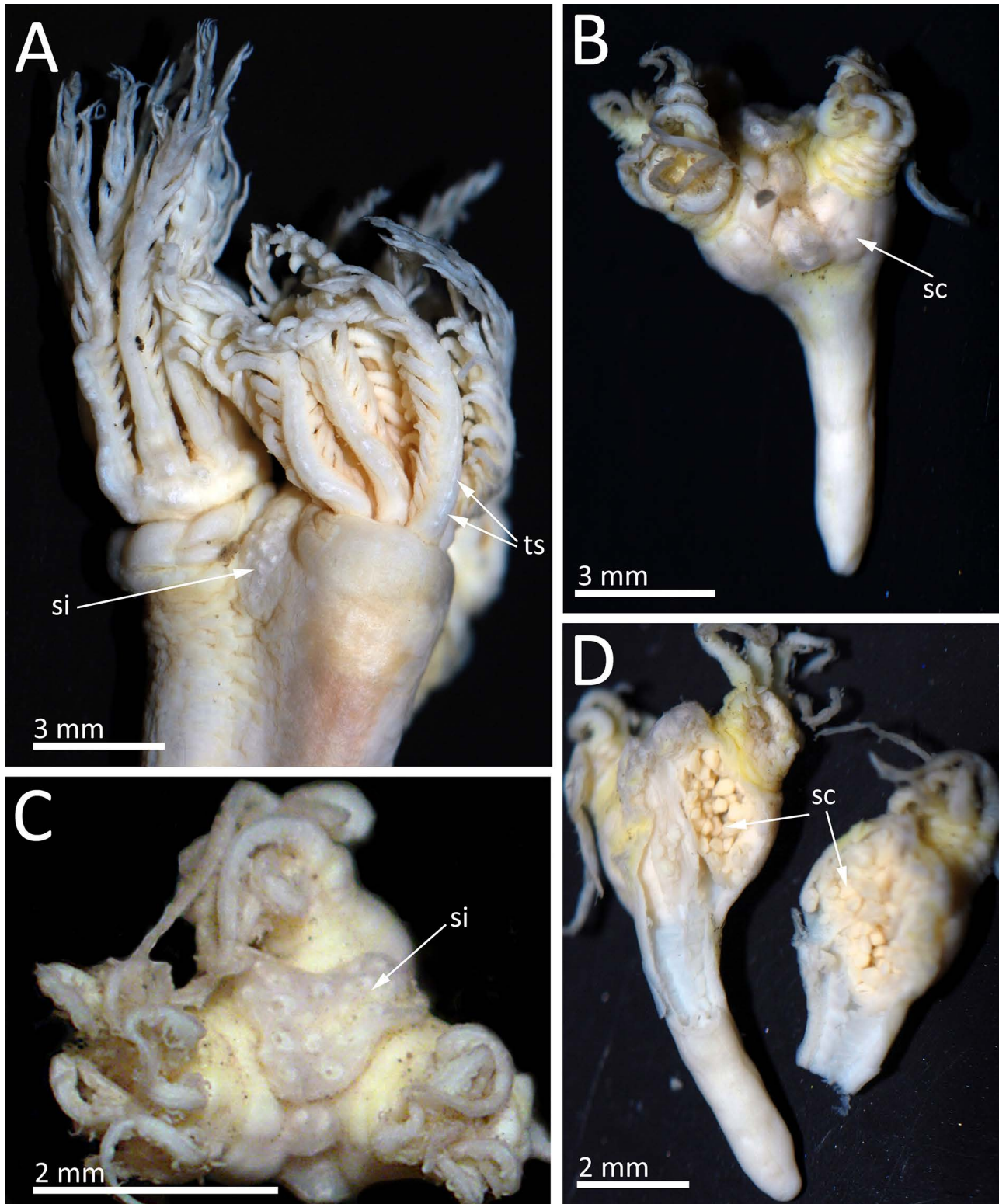


Fig. 4. – *Scotiabelelmonn pauciflorum* comb. nov. (A), detail of the distal part of the colony BECA OPEN-122, showing sclerites (as white marks) of the aboral side of tentacles and siphonozooids distally; (B), the smaller collected colony (BECA OPEN-667) in lateral view, 10 mm in length, showing spermatic cysts because of transparency of the autozoid wall; (C), detail of the same colony as in (B) in apical view, showing distal dome of siphonozooids and the three autozoids; (D), the same colony as in (B) partially dissected, showing the gastrovascular cavity of one of the autozoids with numerous spermatic cysts. Abbreviations: pinnulae (pi), spermatic cysts (sc), siphonozooids (si), tentacular sclerites (ts).

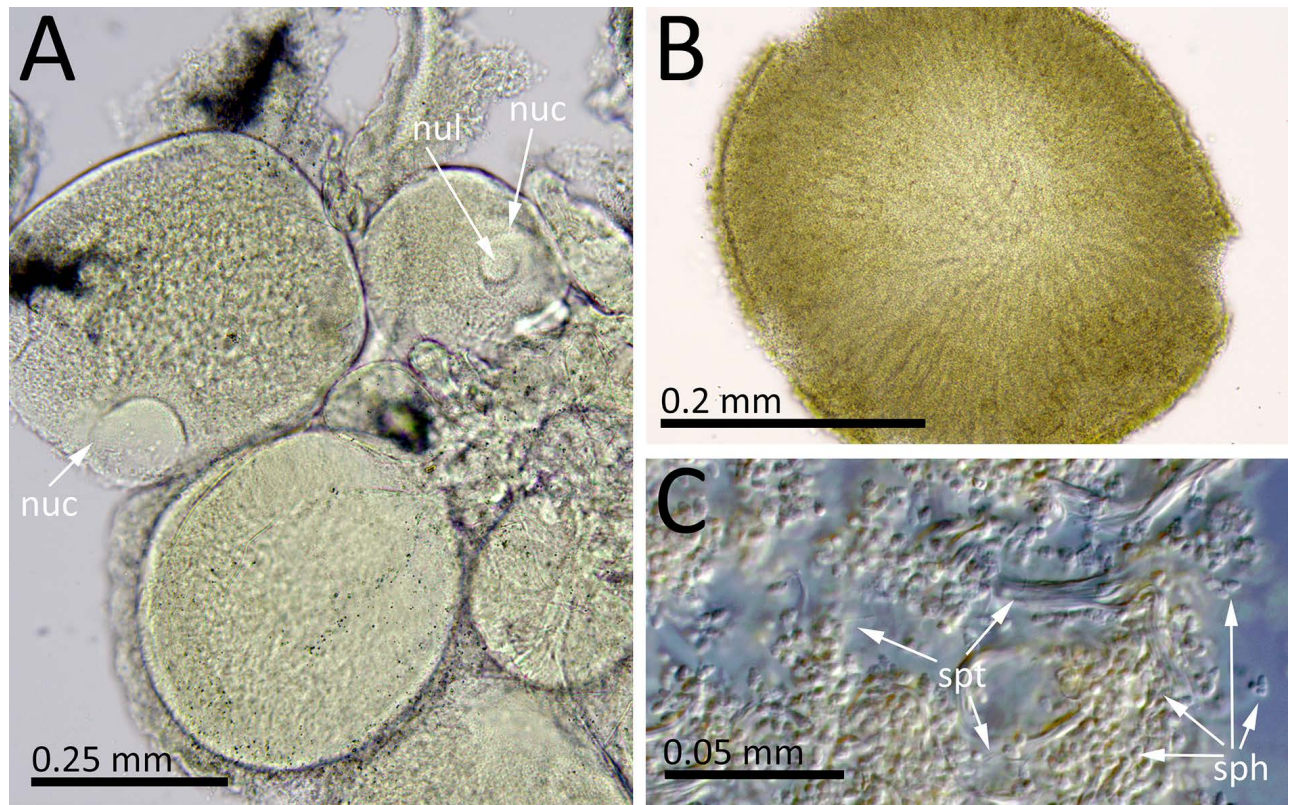


Fig. 5. – *Scotiabelemnnon pauciflorum* comb. nov. (A), group of developing oocytes from colony BECA OPEN-121, showing nucleus limits and nucleolus; (B), spermatid cyst from colony BECA OPEN-667, showing the typical radial arrangement of developing sperm heads and also the central space where the tails of the mature spermatozoa accumulate; (C), sperm heads and tails of mature sperms obtained by squash preparations of spermatid cysts of colony BECA OPEN-667. Abbreviations: nucleolus (nuc), nucleus limit (nuc), sph sperm heads (sph), sperm tails (spt).

sition as polyp body wall, but slightly thinner, large monoaxial rods up to 0.27 mm in length (Fig. 7C₁) and knobbly three-flanged rods (somewhat transitional in appearance to large monoaxial rods) up to 0.21 mm in length (Fig. 7C₂).

Siphonozooids field among autozooids with smooth to nearly smooth indistinctly tree-flanged needles up to 0.4 mm in length (Fig. 8A₁), scarcely tuberculate platelets up to 0.24 mm in length (Fig. 8A₂) and short knobbly three-flanged rods up to 0.14 mm in length (Fig. 8A₃).

Rachis ovals to oval-rods with irregular knobbly ornamentation up to 0.18 mm in length (Fig. 8B). Peduncle sclerites similar to those from rachis but with smoother ornamentation, up to 0.16 mm in length (Fig. 9).

Colour

Living colonies dirty white to fleshy in colour (Fig. 2A, B); yellowish to orange colour in some colonies because of oocyte development. Siphonozooids as minute white spots (in both sets, those along the intermittent longitudinal rows and those at the distal dome); distal part of anthocodia (without tentacles) and pinnulae also distinctly whitish, while introvert is translucent probably because of a thinner body wall, allowing the

observation by transparency of sexual products (Fig. 2B). Preserved specimens are milky to dirty white or yellowish in colour (Figs 3, 4)

Distribution

Scotiabelemnnon pauciflorum (Molander, 1929) comb. nov. is distributed along the tip of Antarctic Peninsula: Bransfiel Strait (Molander 1929), South Shetland island (this paper), and near South Orkney Islands (this paper), between 200 and 402 m depth.

Phylogenetic approach

In the hypothesis using only mtMutS (Fig. 10 left), Clade III showed a strongly supported family Gyrophyllidae (bootstrap [Bst] 99%, posterior probability [PP] 1) as the sister group of a moderately-supported polytomy grouping of taxa including *Kophobelemnnon s.l.* and *Funiculina* sequences (Bst 77%, PP 0.79). Regardless of whether the BI or ML method was used, four groups were clearly differentiated: three of them correspond to species identified as belonging to the genus *Kophobelemnnon* (Bst 96 to 100%, PP 0.99 to 1, see below), while the fourth is composed of *Funiculina* species (Bst 74%, PP 0.88 to 1). In this tree, *Funiculina* sequences are reunited with a set of *Kophobelemnnon* sequences, here informally named *Kophobelemnnon* I

(Bst 91%, PP 0.99). Another set of *Kophobelemnon* sequences, here informally named *Kophobelemnon* II, was also distinctly separated (Bst 96%, PP 0.97 to 1), and the fourth grouping reunited sequences (Bst 99%, PP 1) of those colonies identified as *Kophobelemnon*

pauciflorum (present study) and Pennatulacea sp. sequences (GenBank accession numbers ON603970 and ON603971), all these considered here within the genus *Scotiabelemnon* gen. nov.

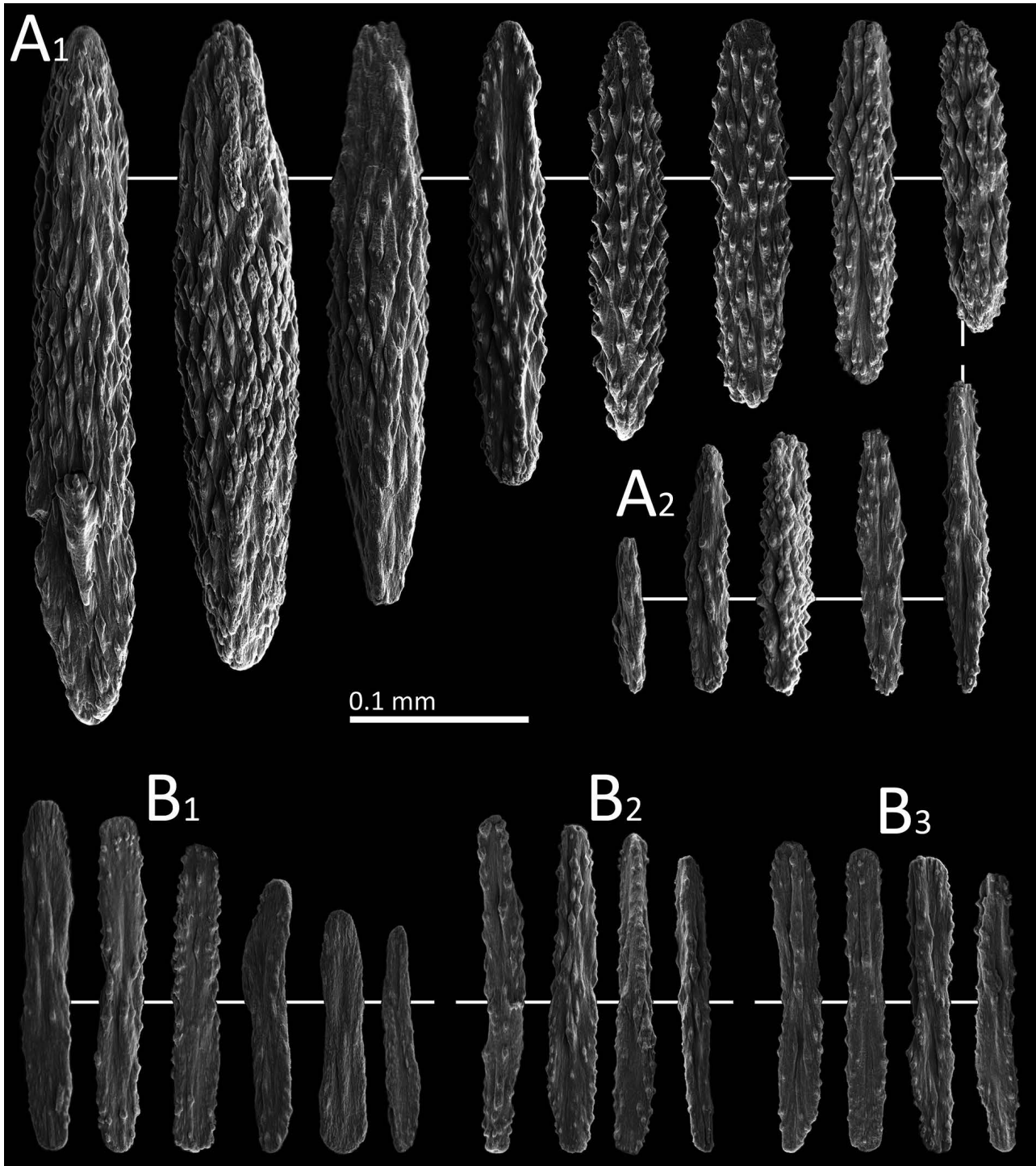


Fig. 6. – *Scotiabelemnon pauciflorum* comb. nov. (BECA OPEN-121). (A) sclerites from tentacular axis, (A₁) monoaxial rods, and (A₂) knobbly three-flanged sclerites; (B) sclerites from pinnulae, (B₁) scarcely tuberculate platelets, (B₂) knobbly three-flanged rods, and (B₃) intermediate forms. Sclerites from the same colony part connected by a continuous white line. Different sclerite types from the same part of the colony separated by a short gap.

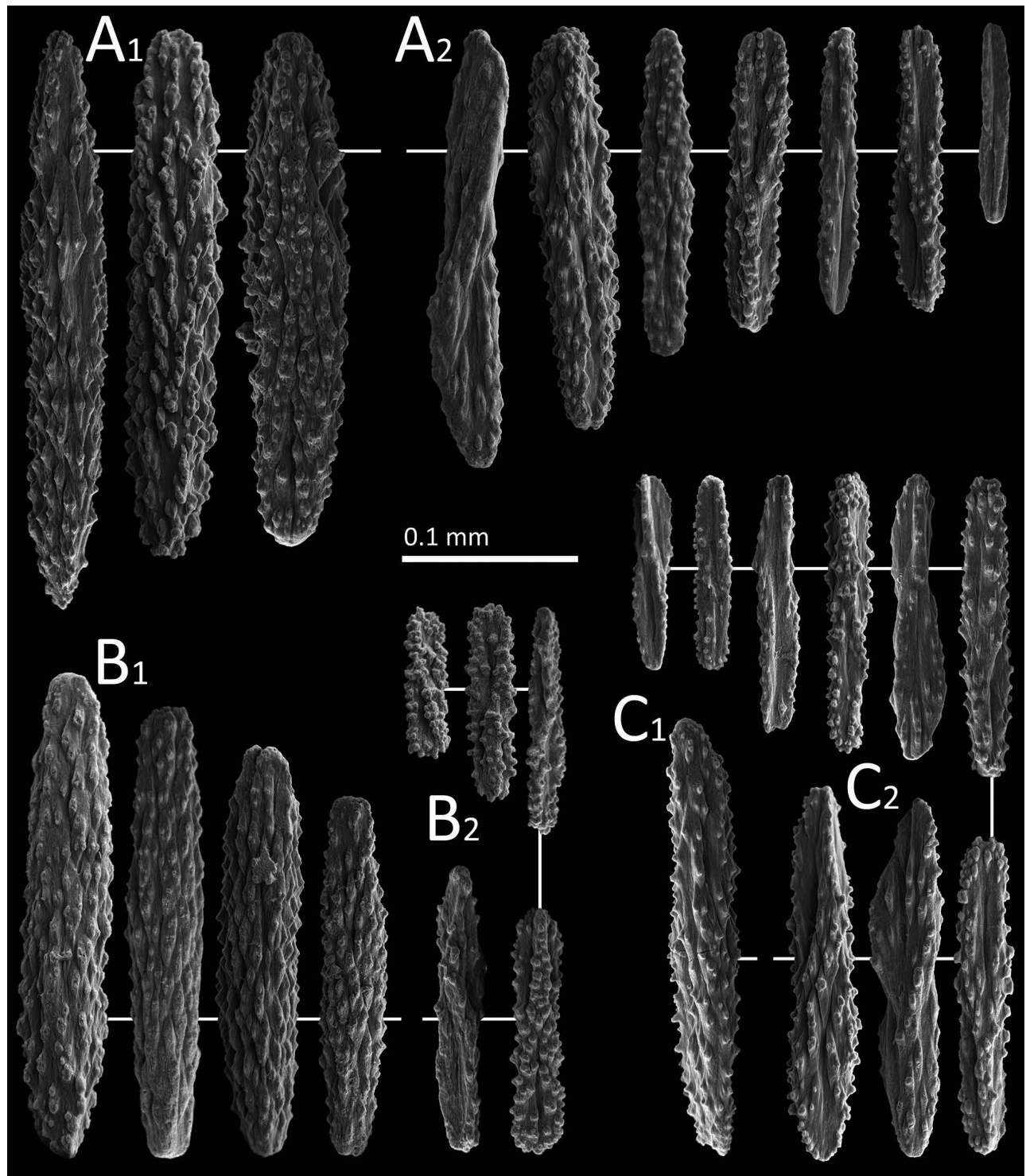


Fig. 7. – *Scotiabelemnnon pauciflorum* comb. nov. (BECA OPEN-121). (A) sclerites from autozoid's body distally, (A₁) monoaxial rods (A₂) knobby three-flanged sclerites; (B) sclerites from autozoid's body proximally, (B₁) monoaxial rods, and (B₂) knobby three-flanged rods; (C) sclerites from autozoid's pharynx, (C₁) monoaxial rod, and (C₂) knobby three-flanged rods. Sclerites from the same colony part connected by a continuous white line. Different sclerite types from the same part of the colony separated by a short gap.

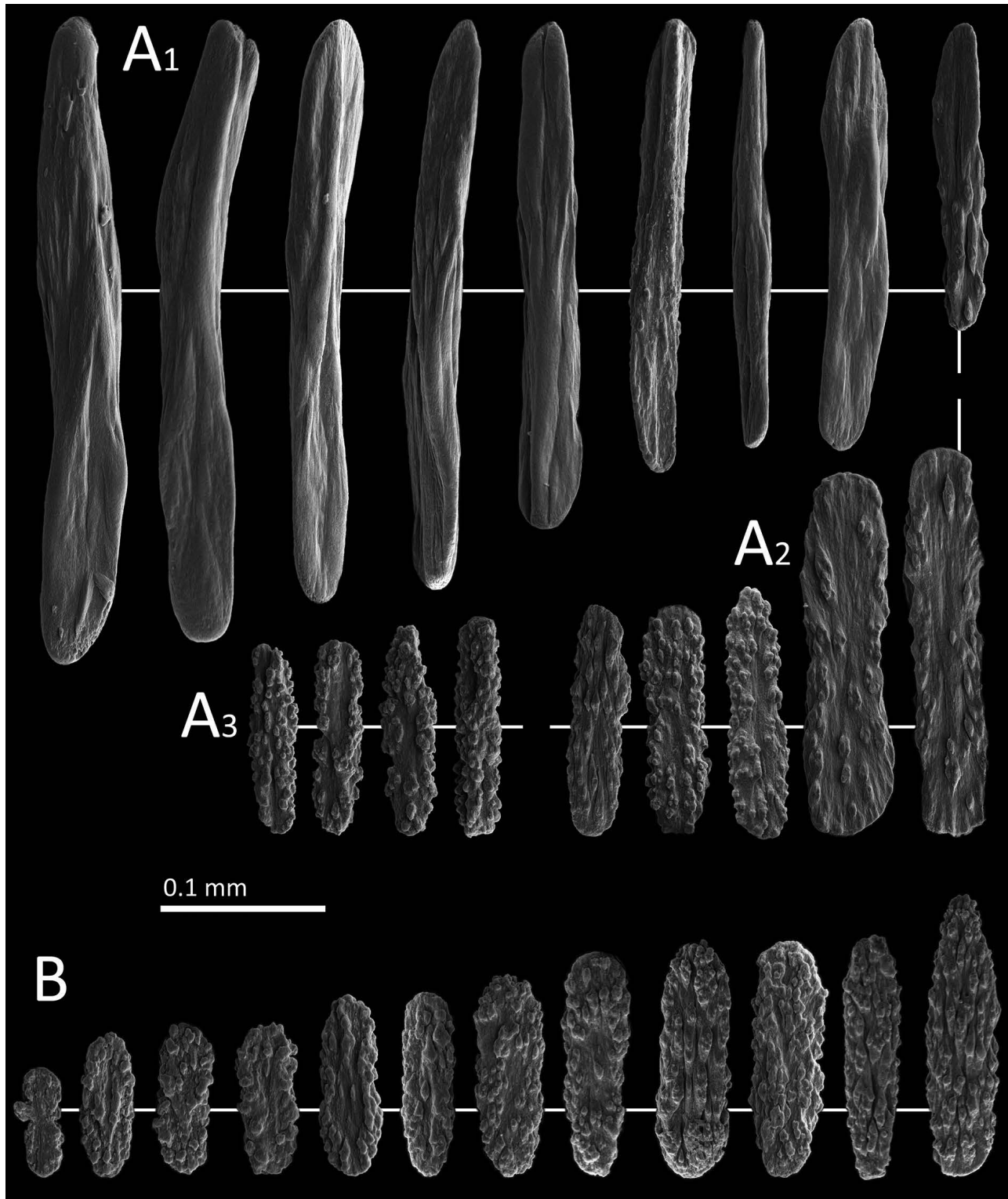


Fig. 8. – *Scotiabelemnnon pauciflorum* comb. nov. (BECA OPEN-121). (A) sclerites from siphonozoid field, (A₁) smooth to nearly smooth indistinctly tree-flanged needles, (A₂) scarcely tuberculate platelets, and (A₃) short knobbly three-flanged rods; (B) sclerites from rachis. Sclerites from the same colony part connected by a continuous white line. Different sclerite types from the same part of the colony separated by a short gap.

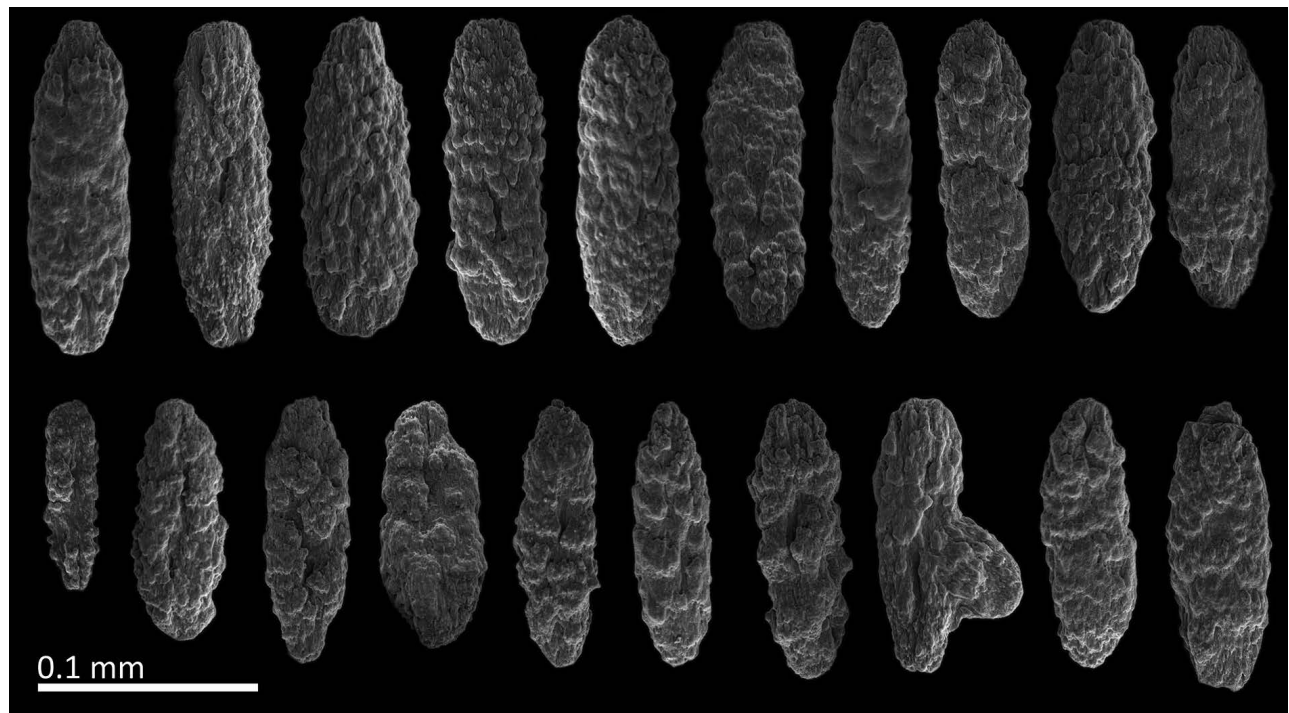


Fig. 9. – *Scotiabelemnnon pauciflorum* comb. nov. (BECA OPEN-121). Sclerites from peduncle, ovals to oval-rods.

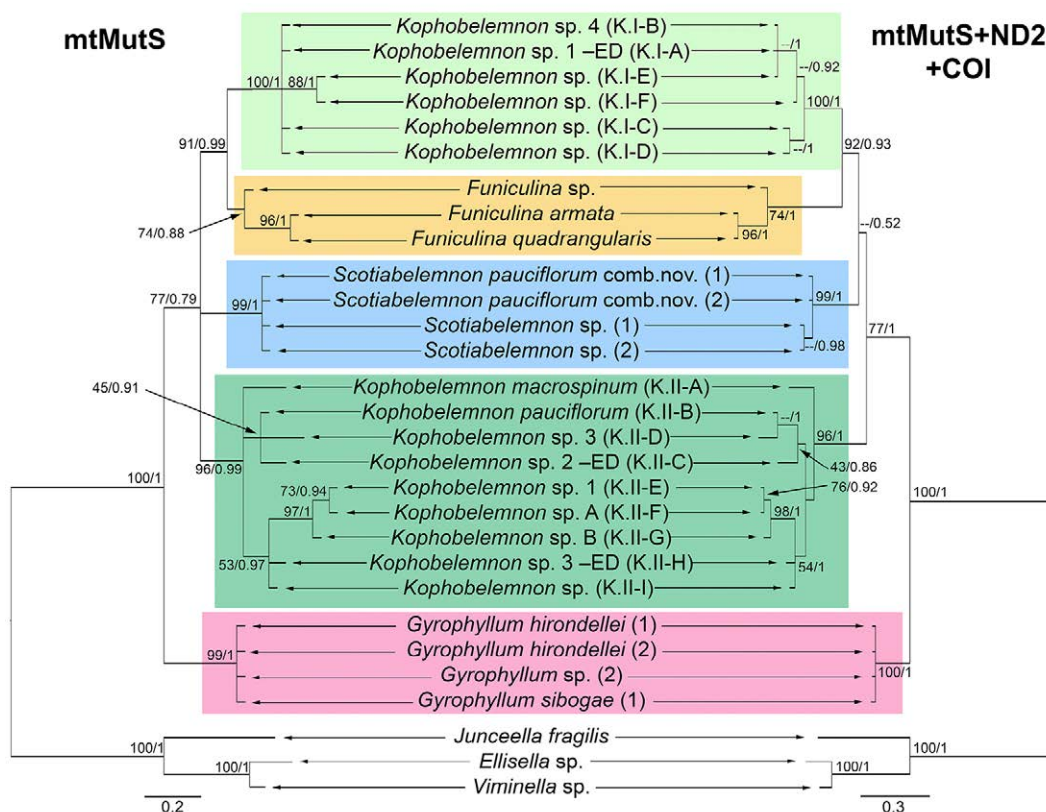


Fig. 10. – Bayesian analysis showing the phylogenetic relationships of *Scotiabelemnnon pauciflorum* comb. nov. and other related genera and species of sea pens within Clade III. The present hypotheses are based on mtMutS (left) and the concatenated set of mitochondrial sequences mtMutS+ND2+COI (right). Bootstrap and posterior probability values (Bst/PP) are indicated in each node. *Kophobelemnnon* lineages I and II are indicated in each species as “K.I” and “K.II”, respectively. *Kophobelemnnon* lineage I is highlighted in light green, while *Kophobelemnnon* lineage II is highlighted in dark green. See Table 1 for complete list of species and GenBank accession numbers.

In the mtMutS+ND2+COI hypothesis (Fig. 10 right), based on all of the mitochondrial markers examined here, Clade III again showed a strongly supported family Gyrophyllidae (Bst 100%, PP 1) as the sister group of the above grouping of taxa (here considered in the reformulated family Funiculinidae), including *Kophobelemnon* s.l. *Scotiabelemnon* gen. nov. and *Funiculina* sequences (Bst 77%, PP 1). Regardless of whether the BI or ML method was used, four groups were clearly differentiated in Funiculinidae: two of them correspond to species identified as belonging to the genus *Kophobelemnon* (lineages I and II), the third reunited *Scotiabelemnon* gen. nov. sequences, and the fourth is composed of *Funiculina* sequences.

In the third hypothesis including also the nuclear 28S markers (Fig. 11), the ML and BI methods showed initially different topologies. Concerning basal clades, the ML tree (Fig. 11 right) had a similar topology to that shown in the mtMutS tree (Fig. 2 left), and the genus *Gyrophyllum* arose from the more basal node of Clade III. However, the BI tree (Fig. 11 left) seemed to be more affected by the poor 28S coverage in Clade III, and the genus *Funiculina* arose from the more basal node of Clade III. 28S sequences are available only

in 6 of the 22 species in Clade III, representing 7 of the 29 sequences in our analyses. Three 28S sequences are only available from the group informally called here *Kophobelemnon* II, two for one of the species of *Scotiabelemnon*, and none from *Kophobelemnon* I or *Funiculina*. Further efforts appear to be needed to complete the coverage of 28S and to discuss a more reliable four-marker hypothesis exploring possible internal relationships in Clade III. In any case the usefulness of 28S for resolving taxa at genus and family levels is debatable because of the observed mito-nuclear incongruences (see Discussion).

Mean K2P genetic distances between groups were relatively homogeneous, *Scotiabelemnon* gen. nov. was 1.7% distant from *Funiculina* but 2.1% distant from all three other groupings (*Kophobelemnon* I, *Kophobelemnon* II and *Gyrophyllum*). The K2P mean genetic distances within groups were 0.0% (*Gyrophyllum*), 0.4% (*Funiculina*), 0.2% (*Kophobelemnon* I), 0.9% (*Kophobelemnon* II) and 0.0% (*Scotiabelemnon* gen. nov.).

The MtMutS sequence of *Scotiabelemnon pauciflorum* comb. nov. was 0.0% distant from the homologous sequence from colonies identified as Pennatulacea sp.

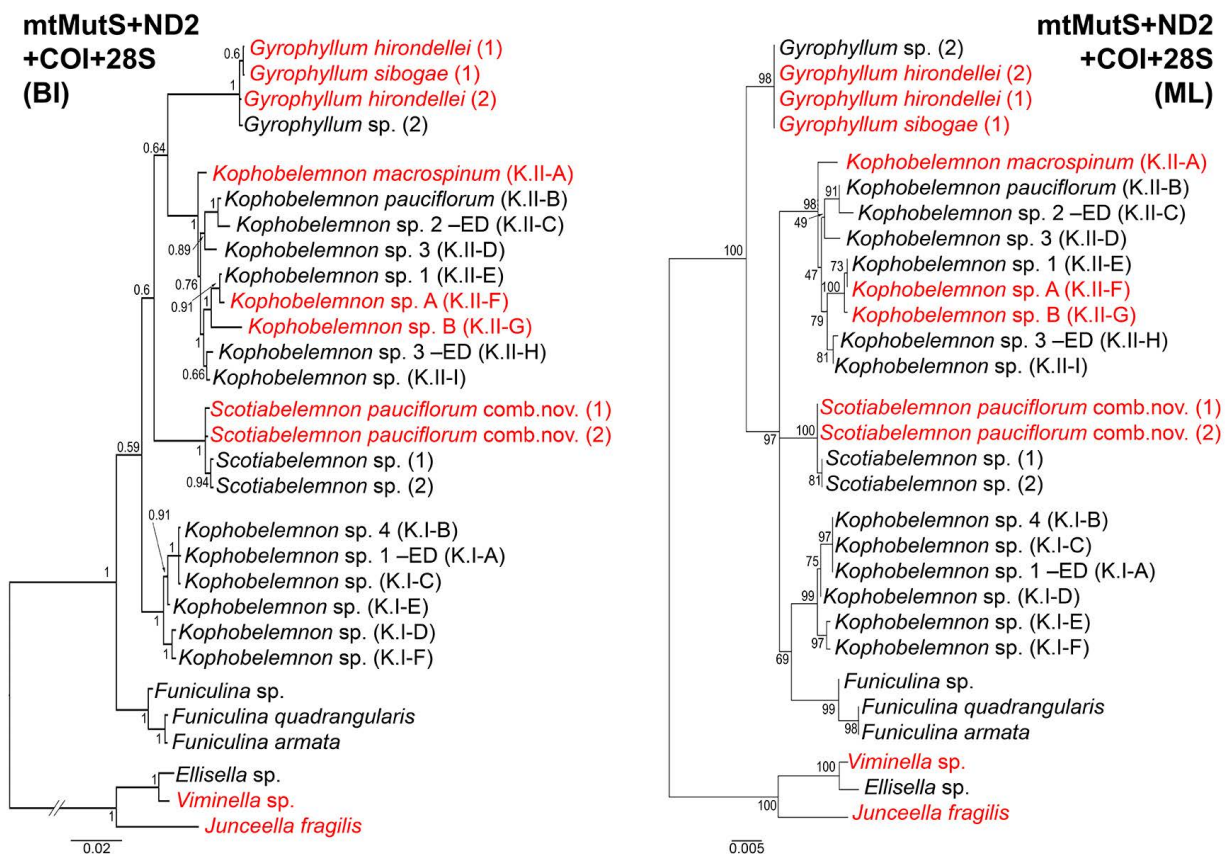


Fig. 11. – Bayesian inference (left) and maximum likelihood (right) analyses showing the phylogenetic relationships of *Scotiabelemnon pauciflorum* comb. nov. and other related genera and species of sea pens within Clade III. The present hypotheses are based on the concatenated dataset of mitochondrial sequences mtMutS+ND2+COI and nuclear 28S (those specimens in red). Posterior probability (PP) and bootstrap (Bst) values are indicated in each node. *Kophobelemnon* lineages I and II are indicated in each species as “K.I” and “K.II”, respectively. See Table 1 for complete list of species and GenBank accession numbers.

(GenBank Accession numbers for mtMutS ON603970 and ON603971), denoting that, at least, they all belong to the same genus. Differences in the COI sequences suggest that more than one species of *Scotiabelemn* gen. nov. could be present in the study area.

DISCUSSION

Remarks on the family Kophobelemonidae

The family Kophobelemonidae was described by Gray (1860) as the tribe Kophobelemonieae to accommodate club-shaped colonies with polyps in longitudinal rows on the ventral surface, at the time to include only the genus *Kophobelemon*.

From a morphological point of view, the family Kophobelemonidae included three genera: *Kophobelemon* Asbjørnsen, 1856, *Sclerobelemon* K  lliker, 1872 and *Malacobelemon* Tixier-Durivault, 1966 (Williams 1995, McFadden et al. 2024). Because of the relative simplicity and poorly defined morphological characters (cylindrical to clavate colonies, with or without sclerites, autozooids in longitudinal rows with bilateral symmetry but not always clearly defined) the first molecular analyses that included more than the type genus (*Kophobelemon*) suggested that this family is more of a taxonomic repository than a natural unit.

McFadden et al. (2006) first included sequences of *Kophobelemon* and *Sclerobelemon* species in a single tree (McFadden et al. 2006: Fig. 2), showing a large genetic distance between the two genera, the former aligned with *Gyrophyllum* (later named as Clade III) and the latter related to *Pteroeides* (later named as Clade I). Subsequent phylogenetic studies focusing on pennatulaceans added more sequences but showed the same scenario, a phylogenetic tree with four main clades in which these two genera are widely separated (Dolan et al. 2013, Kushida and Reimer 2019, Garc  a-C  rdenas et al. 2020). Kushida and Reimer (2019) showed that Veretillid genera and *Sclerobelemon* formed a clade, with robust support from analyses utilizing the mtMutS and ND2 region. Furthermore, L  pez-Gonz  lez and Drewery (2022), in a four molecular marker phylogenetic analysis, stated that “*Sclerobelemon* merges among veretillid genera, thus the family Veretillidae can only be considered monophyletic if *Sclerobelemon* is included within it”, a placement that is also supported by phylogenetic hypothesis based on mtMutS and ND2 analysed separately (L  pez-Gonz  lez and Drewery 2022: 218 and Fig. 15–16).

The genus *Malacobelemon* Tixier-Durivault, 1966 is still a question mark. This genus was based on *M. stephensoni* Tixier-Durivault, 1966, a species with few usable morphological characteristics that has never been collected again, and no molecular information of it is available. More recently, L  pez-Gonz  lez et al. (2009) described a second species in this genus because of its morphological simplicity, and trying to be conservative in the systematics of sea pens, the species was included in this genus as *M. daytoni* L  pez-Gonz  lez, Gili and Fuentes, 2009. However, the first amplifications

of newly collected material of *M. daytoni* showed it to be highly divergent (L  pez-Gonz  lez unpublished data), while a deeper whole mitochondrial study is in preparation (Figueroa and L  pez-Gonz  lez, in prep.). Thus, even considering that *M. daytoni* was correctly assigned to the genus *Malacobelemon*, the pertinence of this genus to the old family Kophobelemonidae or to the here reformulated Funiculinidae remains doubtful and tentative.

L  pez-Gonz  lez et al. (2022) concluded Clade III to be composed of three families: Funiculinidae (with the genus *Funiculina*), Kophobelemonidae (including at that time only the genus *Kophobelemon*) and Gyrophyllidae (with the genus *Gyrophyllum*). All these genera were the type genus of their respective families, although some sequences in the genus *Kophobelemon* were distinctly divergent. According to the current molecular knowledge and available sequenced genera and species (Dolan et al. 2013, Kushida and Reimer 2019, Garc  a-C  rdenas et al. 2019, L  pez-Gonz  lez and Drewery 2022, L  pez-Gonz  lez et al. 2022, Hogan et al. 2023), it seems that evolutionary hypotheses can be divided into at least four, this paper representing a fifth because of the introduction of *Scotiabelemn* gen. nov. (Fig. 12):

Hypothesis 1 had *Gyrophyllum* as the basal taxon of Clade III and nested *Kophobelemon* and *Funiculina* (Dolan et al. 2013, Kushida and Reimer 2019, Garc  a-C  rdenas et al. 2020 [ML]). When *Kophobelemon* I and II can be differentiated (mainly thanks to the amount of sequenced specimens included in the analysis), *Funiculina* is usually grouped with *Kophobelemon* I distally. This topology is observed when mtMutS is analysed alone (by BI or ML) and when mtMutS is part of a concatenated dataset of mitochondrial markers only (by BI).

Hypothesis 2 did not support the large Clade III (Garc  a-C  rdenas et al. 2019 [BI]). 28S is included in a concatenated four-marker data set analysed by BI.

Hypothesis 3 had *Funiculina* as the basal taxon of Clade III and nested *Kophobelemon* and *Gyrophyllum* (L  pez-Gonz  lez and Drewery 2022, L  pez-Gonz  lez et al. 2022). *Gyrophyllum* is grouped with *Kophobelemon* II sequences distally. This occurs when 28S is included as the fourth marker.

Hypothesis 4 had *Gyrophyllum* as the basal taxon of Clade III and nested *Funiculina* and *Kophobelemon* sequences (L  pez-Gonz  lez and Drewery 2022). This topology occurs when only the three mitochondrial markers are analysed. *Kophobelemon* I and II are distinct and located distally with respect to *Funiculina*. A derived version of this hypothesis (as 4* in Fig. 12) is in Kushida et al. (2022), where a couple of divergent sequences based on specimens from the South Sandwich Islands (Antarctic waters) as Pennatulacea sp. were included in the analysis (P in Fig. 12). Pennatulacea sp. are related to *Kophobelemon* II distally. These sequences are considered in this paper to belong to *Scotiabelemn* gen. nov.

Hogan et al. (2023) utilized only *Kophobelemon* and *Funiculina* for phylogenetic trees utilizing mito-

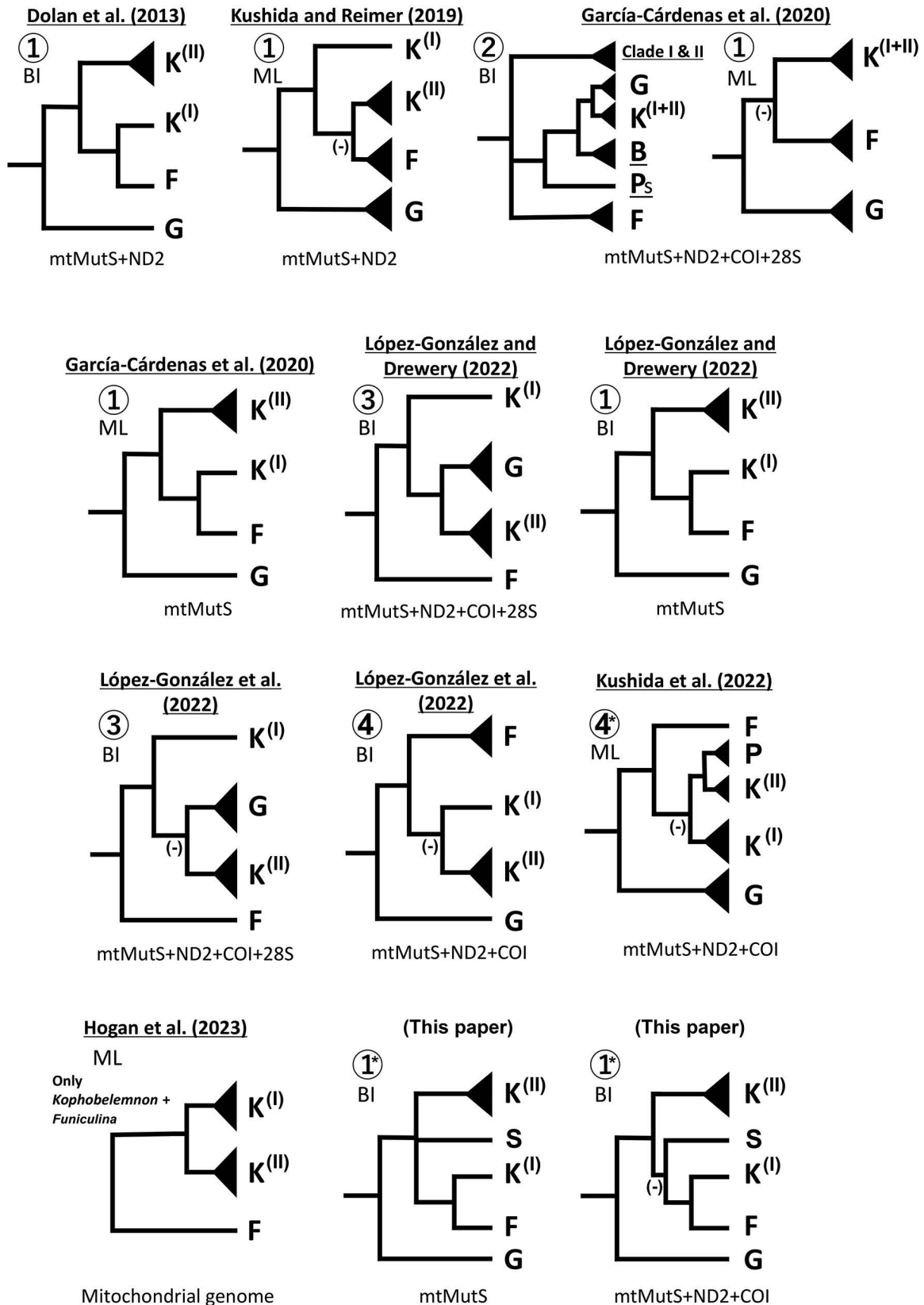


Fig. 12. – Schematic diagram of hypotheses about the Clade III relationships in past studies. Each number with a circle indicates the hypothesis number. Names of each taxon expressed by the initials of genus name; S, *Scotiabelemnnon*; K, *Kophobelemnnon* (lineages I and II are also indicated); F, *Funiculina*; G, *Gyrophylum*; B, *Balticina*; P, *Pennatulacea* sp.; Ps, *Pseudumbellula*. (-) indicates low support of that clade; *, indicates a variant of a given hypothesis. BI or ML, indicate Bayesian inference and maximum likelihood, respectively. Each line under the initials indicates the memberships not within Clade III.

chondrial genome, and it was difficult to discuss the phylogenetic hypothesis within their Clade III as *Gyrophyllum* and potential *Scotiabelemnnon* gen. nov. data were not available.

All phylogenetic trees in this study supported Hypothesis 1 (derived as 1* by the inclusion of *Scotiabelemnnon* gen. nov. sequences). *Gyrophyllum* is the basal taxon of Clade III and nested *Kophobelemnnon* s.l., *Scotiabelemnnon* gen. nov. and *Funiculina* (this paper, see Figs 10, 12). Basal relationships of these last three genera are still uncertain, but *Funiculina* is always grouped with *Kophobelemnnon* I distally, while it is poorly suggested that *Scotiabelemnnon* gen. nov. could be their sister group.

The genera *Funiculina* and *Gyrophyllum* have an unstable location when 28S is included in the analyses, likely affected by evolutionary differences between the mito-nuclear region (see Quattrini et al. 2023, Hogan et al. 2023) and the poor coverage of this marker in our datamatrix (only 6 of the 26 in Clade III are available). The inclusion of nuclear 28S in the mitochondrial marker data set in combination with the inference model used resulted in different taxa combinations (BI placed as basal *Gyrophyllum* when 28S is not included, but *Funiculina* when 28S is incorporated in the data matrix, while ML usually places *Gyrophyllum* as the basal taxon in Clade III, with and without 28S in the data matrix). Incomplete taxonomic and molecular coverage, especially at the 28S marker, probably also affects the results for a reliable four-marker hypothesis (see above).

In this paper, which includes the broadest coverage of *Kophobelemnnon* and *Funiculina* sequences, the pennate colony forms of the family Gyrophyllidae are clearly differentiated from the flagelliform and clavate colony forms (*Funiculina* and *Kophobelemnnon* s.l.+*Scotiabelemnnon* gen. nov., respectively). The sister group of Gyrophyllidae is a polytomy (mtMutS) bringing together four subclades, three of them with relatively low basal resolution, which includes sequences from *Kophobelemnnon*, *Scotiabelemnnon* gen. nov. and *Funiculina*. Among these four groups, the sequences initially attributed to *Kophobelemnnon* represent three of them, the fourth being *Funiculina* sequences. One of these *Kophobelemnnon* clusters is described here as the genus *Scotiabelemnnon* gen. nov., while the other two are simply named here as *Kophobelemnnon* I and II.

The observed stronger support of *Kophobelemnnon* I clade to the *Funiculina* clade (Bst 91, PP 0.99 in mtMutS; Bst 92, PP 0.93 in mtMutS+ND2+COI;) than to *Kophobelemnnon* II and *Scotiabelemnnon* gen. nov. raises additional discussions concerning the delimitation of the families involved. Surprisingly, *Scotiabelemnnon* gen. nov. is closer to *Funiculina* spp. (in K2P genetic distance) than to other sequenced specimens attributed to the genus *Kophobelemnnon* I or II. In any event, Gyrophyllidae and Funiculinidae become monophyletic, but Kophobeleminidae (*Kophobelemnnon* s.l. + *Scotiabelemnnon* gen. nov.) become paraphyletic, *Kophobelemnnon* I being closer to *Funiculina* spp. than to other putative species of *Kophobelemnnon* in *Kophobelem-*

non II. The proposal of this paper to avoid paraphyly of Kophobeleminidae is the reunion of *Funiculina*, *Kophobelemnnon* s.l. and *Scotiabelemnnon* gen. nov. in a single family, Funiculinidae. It is therefore proposed to consider only two families in Clade III, Gyrophyllidae and Funiculinidae.

The family name, Funiculinidae Gray 1860 must be used, applying the principle of priority (ICZN 1999: Article 52.3). In 1860 Gray inserted into our sea pen literature as tribe names Funiculininae (Gray 1860: 20) and Kophobelemininae (Gray 1860: 23), and these names were elevated to family rank by Gray in 1870, as Funiculinidae (Gray 1870: 12) and Kophobeleminidae (Gray 1870: 27), using the appropriate suffix to accommodate the original names to the new taxonomic category.

On the new reformulated family Funiculinidae

The current conception of this family is the result of the merge of the monotypic family Funiculinidae with the family Kophobeleminidae (see Williams 1990 for previous separate morphological diagnoses) because of the close molecular relationships of their type genera *Funiculina*, and *Kophobelemnnon* s.l., as well as the new genus proposed here, *Scotiabelemnnon* gen. nov. As molecular systematics comes to redefine the boundaries between taxonomic categories previously considered stable, morphological diagnoses of several octocoral families become less morphologically diagnostic than ever, sometimes being merely informative about the morphological diversity of the taxa included in them (see McFadden et al. 2022).

In the present paper we propose a diagnosis for the family Funiculinidae that complements morphological information with those molecular characteristics that currently distinguish the two families considered within Clade III, Funiculinidae Gray 1860 and Gyrophyllidae López-González, Drewery and Williams 2022. Obviously, as with any type of characteristics included in the diagnosis of a taxon, morphological and molecular information must be updated to cover the variability of the taxa considered in it at any given time.

In the present study, we considered with certainty three nominal genera in this reformulated family Funiculinidae: *Funiculina*, *Kophobelemnnon* and *Scotiabelemnnon* gen. nov. Considering that the genus *Kophobelemnnon* is in urgent need of revision, and that at least an additional genus name (new or resurrected from old literature) will be added once a reliable revision of these species is carried out.

Other genera previously considered in Kophobeleminidae, such as the genera *Sclerobelelemnnon* and *Malacobelelemnnon*, have been discussed above. Sequences of *Sclerobelelemnnon* are strongly attracted to genera in the family Veretillidae Herklots, 1858 (see García-Cárdenas and López-González 2020, López-González and Drewery 2022), so its morphological features are not considered in this reformulated family Funiculinidae. As discussed above, the inclusion of *Malacobelelemnnon* in the family Funiculinidae is tentative until reliable molecular information on its type species becomes available.

On the genera *Kophobelemnon* and *Scotiabelemnon* gen. nov.

The genus *Kophobelemnon* was erected by Asbjørnsen (1856) for the species *Kophobelemnon muelleri* Asbjørnsen, 1856, a junior synonym of *Pennatulula stellifera* Müller, 1776. Once diversity of pennatuloid genera was expanded during the 19th century, *P. stellifera* was subsequently transferred from *Pennatulula* Linnaeus, 1758 to *Veretillum* Cuvier, 1798, *Umbellularia* Lamarck, 1801 and *Funiculina*, and was finally accommodated in *Kophobelemnon* (Kükenthal and Broch 1911: 224, Kükenthal 1915: 29).

From a morphological point of view, the genus *Kophobelemnon* is characterized by the following characters: 1) colonies elongate and cylindrical to slightly clavate or short, stout and distinctly clavate; 2) distal end rounded and knob-like or distinctly pointed; 3) rachis with bilateral symmetry throughout, although not always distinctly so; 4) axis thin, round to slightly quadrangular in cross section; 5) polyp leaves absent, autozooids up to approx. 50 in number, arranged biserially along rachis; 6) anthocodiae mostly not retractile, calyces absent; 7) siphonozooids numerous, often with minute spiculated calyces, on areas of rachis not occupied by autozooids; and 8) sclerites densely set, spindles and rods, mostly three-flanged, sometimes ornamented with tubercles (Williams 1995: 108-109).

Obviously, there is a strong morphological similarity between the colonies of the two *Kophobelemnon* lineages (I and II), but only one can retain the genus name. In this case we prefer not to decide here which genus name must be used for each of these two *Kophobelemnon* groupings yet, because these nomenclatural acts should only be carried out after a deep morphological and molecular study in which morphological features are explored and segregated and molecular differences have been established by the analysis of solitary genes or concatenated gene datasets (see Fig 12; Dolan et al. 2013, Kushida and Reimer 2019; Kushida et al. 2022; López-González and Drewery 2022; this paper). In this case, the genus name *Kophobelemnon* must be retained when *Kophobelemnon muelleri* Asbjørnsen, 1856, the type species of the genus [today recognized as *Kophobellemon stelliferum* (Müller, 1776)], is correctly recognized. Rather than being an easy task, this step is a challenge. Müller (1776) described in his *Zoologiae danicae prodromus, seu animalium danicae et norvegiae indigenarum* the species *Pennatulula stellifera* based on material from an imprecise locality from the northern seas, whereas in both main *Kophobelemnon* lineages (I and II) specimens from the northeastern Atlantic have been sequenced. At this time, the sequenced specimen *Kophobelemnon* sp. 1-ED seems to be the geographically closest to the type locality of *K. muelleri* (= *Kophobellemon stelliferum*), although this fact may not be a decisive criterion. This sequence (MutS GenBank accession number KF313837) is placed in the here unofficially named *Kophobelemnon* I lineage. This lineage is also present in other localities of the northeastern Atlantic and western Pacific, while the *Kophobelemnon*

II lineage is present in the northeastern Atlantic and the western and eastern Pacific.

Morphological features of *Scotiabelemnon molderi* comb. nov. can be used for a diagnostic description of a new genus, even though these features were previously considered to be included within the morphological variability of the genus *Kophobelemnon*. Apart from the molecular differences, the genus *Scotiabelemnon* gen. nov. is differentiated from *Kophobelemnon* s.l. in the following set of characters: 1) siphonozooids in two sets, short longitudinal lines over rachis-peduncle limit and as a distal dome among the few autozooid bases; 2) autozooids placed distally and upwardly directed (including gastrovascular cavities), and 3) absence of axis. As chronologically described above, the genus *Kophobelemnon* was quickly recognized as a para- or polyphyletic taxon (Dolan et al. 2013, Kushida and Reimer 2019, García-Cárdenas et al. 2020, López-González and Drewery 2022, López-González et al. 2022). Moreover, the last phylogenetic hypotheses by Kushida et al. (2022) included sequences of additional species attributed here to the genus *Scotiabelemnon* gen. nov. This fact suggests that the diversity of this last genus is still unknown, and its placement in the phylogenetic trees reinforces the current paraphyletic nature of the genus *Kophobelemnon*.

Final statement

In the current scenario, Linnaean taxonomy (understood as the discipline that regulates how to name a hierarchical set of subordinate taxonomic categories) and phylogenetic hypotheses (generated after the analysis of an ever-increasing amount of molecular information) should find a conciliatory space to achieve a better and useful view of the tree of life. Undoubtedly, the addition of new sequences, even when taxa are only identified at the genus level, greatly helps to outline the limits of higher taxonomic units and to recognize para- or polyphyletic taxa (species, genus, or families) previously named on the basis of morphological characters. The nomenclatural problems produced by the inconsistencies observed in the phylogenetic trees should be progressively resolved through the complete description of the affected taxa in a combined morphological and molecular study, which is ultimately called integrative taxonomy (Di Camillo et al. 2018, Gómez Daglio and Dawson 2019).

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

ETHICAL APPROVAL

All applicable international, national or institutional guidelines for animal testing, animal care and use of animals were followed by the authors.

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DATA AVAILABILITY

The data generated and analysed during this study are deposited in public repositories (GenBank, <https://www.ncbi.nlm.nih.gov/genbank/>).

AUTHORSHIP CONTRIBUTION STATEMENT

P.J. López González: Conceptualization, formal analysis, investigation, visualization, writing—original

draft, writing—review & editing. **Y. Kushida:** Investigation, visualization, writing—review & editing.

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Note: During the period our paper was in press, McFadden et al. (2024) published an errata to their 2022 paper, in order to correctly perform the nomenclatural acts proposed that year, and to follow ICNZ rules. Therefore, the new taxa proposed in 2022 are not nomenclaturally available. In their 2024 Erratum, nothing is mentioned about the authorship of the superfamily Pennatuloidea, which was attributed in WoRMS to these authors since the publication of their 2022 paper, but was corrected to Ehrenberg, 1834 simultaneously with the acceptance of our paper. In this short period, at least two papers were affected using Pennatuloidea McFadden, van Ofwegen and Quattrini, 2022 (Giusti et al. 2024, Kushida et al. 2024).