



A new deep-sea species of golden gorgonian (Octocorallia: Scleralcyonacea: Chrysogorgiidae) from Antarctic waters

Patricia Baena^{a,b,*}, Luis Martell^c, Joan J. Soto-Angel^c, Stefano Ambroso^b, Pablo J. López-González^d

^a Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta 37–49, 08003, Barcelona, Spain

^b Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona, Diagonal 645, 08028, Barcelona, Spain

^c Department of Natural History, University Museum of Bergen, University of Bergen, Bergen, Norway

^d Biodiversidad y Ecología Acuática, Departamento de Zoología, Facultad de Biología, Universidad de Sevilla, Av. de la Reina Mercedes 6, 41012, Sevilla, Spain

ARTICLE INFO

Keywords:

New species
Chrysogorgia
Octocoral
Southern ocean
Bathyal

ABSTRACT

The Southern Ocean harbours rich deep-sea ecosystems with local hotspots of benthic biodiversity. Still, many species, including deep-water octocorals, remain undescribed despite the fact that the exploration of the deep-sea has improved thanks to recent technological advances. In this context, a new species of golden gorgonian has been collected at 1407–1581 m depth during a recent cruise to Dronning Maud Land in the Eastern Weddell Sea. Currently, after recent changes in *Chrysogorgia* taxonomy, *Chrysogorgia lunae* sp. nov. (Octocorallia: Scleralcyonacea) is the only known representative of the genus in Antarctic waters. It corresponds to the "Squamosae typicae" and is characterized by a bushy colony with branching sequence of 2/5L and bell-shaped polyps. A molecular comparison with published sequences of *Chrysogorgia* species is provided based on a concatenated sequence of two mitochondrial genes, mtMutS and COI, as well as the 28S nuclear ribosomal gene.

1. Introduction

The Southern Ocean harbours rich benthic assemblages with high levels of biodiversity and endemism (Clarke and Crame, 1992; Gage, 2004; Brandt et al., 2007). This is due to the high environmental stability, low disturbance and the relative isolation of the deep-sea in Antarctic waters (Grebmeier and Barry, 1991). Benthic suspension feeders are among the major contributors to these high levels of biodiversity (Starmans et al., 1999; Orejas et al., 2000), and in particular octocorals play a key role in Antarctic deep ecosystems by providing niches for a high number of associated species (Roberts, 2006). Octocorals are sessile organisms that display three-dimensional structures that increase habitat complexity and provide refugia from predators and nursery grounds for the associated biodiversity (Jones et al., 1994; Bullimore et al., 2013; Baena et al., 2023). For these reasons, they are considered ecosystem engineers, despite the fact that they are non-reef forming species (Jones et al., 1994). Octocorals are also characterized by their long life span and slow growth (Arntz et al., 1992; Watling et al., 2011; Martínez-Dios et al., 2016). These biological traits make them highly vulnerable, as the recovery of their populations is very slow

(Bennecke et al., 2016). As a result, octocoral meadows are one of the priority groups of organisms listed as Vulnerable Marine Ecosystems (VMEs) by the Food and Agriculture Organization (FAO, 2009), and they need to be protected from potential impacts of fishing in the high seas (Auster et al., 2011).

In order to achieve effective management for marine conservation, our current knowledge of taxonomy, biology and ecology of octocorals must be expanded. Thanks to technological advancements and progress in molecular techniques, both underwater exploration and identification of species have subsequently improved (Ramírez-Llodra et al., 2010). However, although octocorals have been collected extensively in many Antarctic expeditions, they have been treated only in a handful of studies (e.g. Bayer, 1993; Cairns, 2002; Núñez-Flores et al., 2020). A large number of specimens are therefore stored in museum collections, and still remain to be analyzed.

Most octocoral families occur in the deep-sea, with highest species richness at depths greater than 200 m (Watling et al., 2011). Chrysogorgiidae Verrill, 1883 is one of these taxa. Its representatives are known worldwide, including species from Iceland to Antarctica (Madsen, 1944; Cairns, 2002). This family is an assemblage of different

* Corresponding author. Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta 37–49, 08003, Barcelona, Spain.

E-mail address: baena@icm.csic.es (P. Baena).

<https://doi.org/10.1016/j.dsr.2024.104234>

Received 13 October 2023; Received in revised form 3 January 2024; Accepted 5 January 2024

Available online 6 January 2024

0967-0637/© 2024 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC license (<http://creativecommons.org/licenses/by-nc/4.0/>).

conspicuous species that structure the benthic communities on seamounts and slopes (Thoma et al., 2009; Xu et al., 2019), both on soft and hard bottoms (Grasshoff, 1995; Watling et al., 2011; Pérez et al., 2016). Not only is the distribution of chrysogorgiids wide, but the bathymetric range of the family is also extensive, ranging from 10 m to 4492 m depth and making it one of the three major deep-sea octocoral families (Watling et al., 2011; Pante et al., 2012; Cairns, 2018). Chrysogorgiidae includes genera with stenobathic distribution –like *Metallogorgia Versluys*, 1902 and *Iridogorgia Verrill*, 1883–, and others with eurybathic distribution like *Chrysogorgia Duchassaing* and *Michelotti*, 1864 (Watling et al., 2011; Pante et al., 2012).

Verrill (1883) described Chrysogorgiidae as “some of the most interesting and beautiful of all the known gorgonians” because of their golden and iridescent branches and their elegant branching pattern. Members of this family are commonly known as “golden corals”. Recently, the scope of family Chrysogorgiidae has been modified by reducing it to eight genera instead of 21 as previously considered (McFadden et al., 2022, 2023). The currently included genera are: *Chrysogorgia* Duchassaing and Michelotti, 1864; *Iridogorgia* Verrill, 1883; *Metallogorgia Versluys*, 1902; *Pseudochrysogorgia Pante and France*, 2010; *Radicipes Stearns*, 1883; *Ramuligorgia Cairns, Cordeiro, and Xu*, 2021; *Rhodaniridogorgia Watling*, 2007; *Parachrysogorgia Xu et al.*, 2023. The type genus *Chrysogorgia* has the deepest observed distribution (4492 m depth) within the family (Watling et al., 2011; Pante et al., 2012). This genus is one of the most widespread and speciose among all octocoral genera (Cairns, 2001, 2007; Pante et al., 2012), including at least 68 valid nominal species to date (Xu et al., 2023). Many of these species have been described in the 21st century due to the increased effort in deep-sea exploration. The high phenotypic plasticity typical of this genus is often not reflected in significant genetic differences (Pante and Watling, 2012; Xu et al., 2021b). For this reason, taxonomic studies must be prudent and should have an integrative approach combining morphological and genetic analyses (e.g. Prada et al., 2008; López-González, 2022). In order to identify species of *Chrysogorgia*, a detailed examination of the branching pattern of the colonies, the polyp morphometrics, and the features of the sclerome is necessary, including observations by scanning electron microscopy (SEM) (Bayer and Stefani, 1988a; Cairns, 2001; Xu et al., 2021a). To facilitate species identification, taxonomists have traditionally categorized the species of *Chrysogorgia* into three different groups based on the nature of the sclerites observed in the polyp body wall and the tentacles (Wright and Studer, 1889; Versluys, 1902). Group A “Spiculosae” corresponds to species that have rod/spindle sclerites in the polyp body wall and tentacles; Group B “Squamosae aberrantes” is an intermediate group with scales in the body wall and rods/spindles in the tentacles; finally, Group C “Squamosae typicae” is characterized by species that have scales in both regions (Wright and Studer, 1889; Versluys, 1902; Cairns, 2001; Xu et al., 2020). A fourth group, “Spiculosae aberrantes”, was added by Cordeiro et al. (2015) for species with rods in the body wall and scales in the tentacles. Additionally, through the analysis of colony configuration, branching patterns, and sclerite morphology, Xu et al. (2023) classified the *Chrysogorgia* species into 12 distinct groups.

Cairns (2002) described the first-known species of *Chrysogorgia* within Antarctic waters, formally identified as *C. antarctica* Cairns (2002). However, a recent molecular investigation conducted by Xu et al. (2023) led to a division of the previously established morphological framework of *Chrysogorgia*. This study culminated in the creation of a novel genus, *Parachrysogorgia Xu, Zhan and Xu*, 2023. Xu et al. (2023) further expanded this taxonomic shift by relocating thirteen species, including *C. antarctica*, from genus *Chrysogorgia* to their newly established genus.

In 2019, during a Norwegian Antarctic expedition on board RV Kronprins Haakon, the deep-sea Antarctic bottoms of Dronning Maud Land (concretely the two seamounts Maud Rise and Astrid Ridge) were explored by means of Remotely Operated Vehicles (ROVs). In one of the video-transects carried out in the study area, three specimens of an

unidentified *Chrysogorgia* species were observed, and one of these specimens was collected to be analyzed in detail in the laboratory. The present paper gives a description of this golden gorgonian, providing information on colonial and sclerite morphology as well as molecular information on two mitochondrial markers (mtMutS and COI) and one ribosomal nuclear marker (28S). The results of these analyses confirm that this specimen belongs to a new species, the first one of the genus *Chrysogorgia* found in the Eastern of Weddell Sea and also the sole representative of the genus in Antarctic waters after the recent changes in chrysogorgiid taxonomy (Xu et al., 2023).

2. Materials and methods

2.1. Sample collection

The material for this study was collected during the multidisciplinary Norwegian Antarctic expedition “Dronning Maud Land” in 2019 in the same area that gives its name to the scientific cruise (Figs. 1 and 2). During this cruise, a total of five video transects were recorded in Astrid Ridge and Maud Rise by means of the ROV Aegir 6000. The transects covered a bathymetric range from 1121 to 1988 m depth. In one of these transects, specifically in Maud Rise, three colonies of an unidentified chrysogorgiid were detected, one of which was collected and subsequently fixed on board in 99% ethanol for morphological and molecular studies.

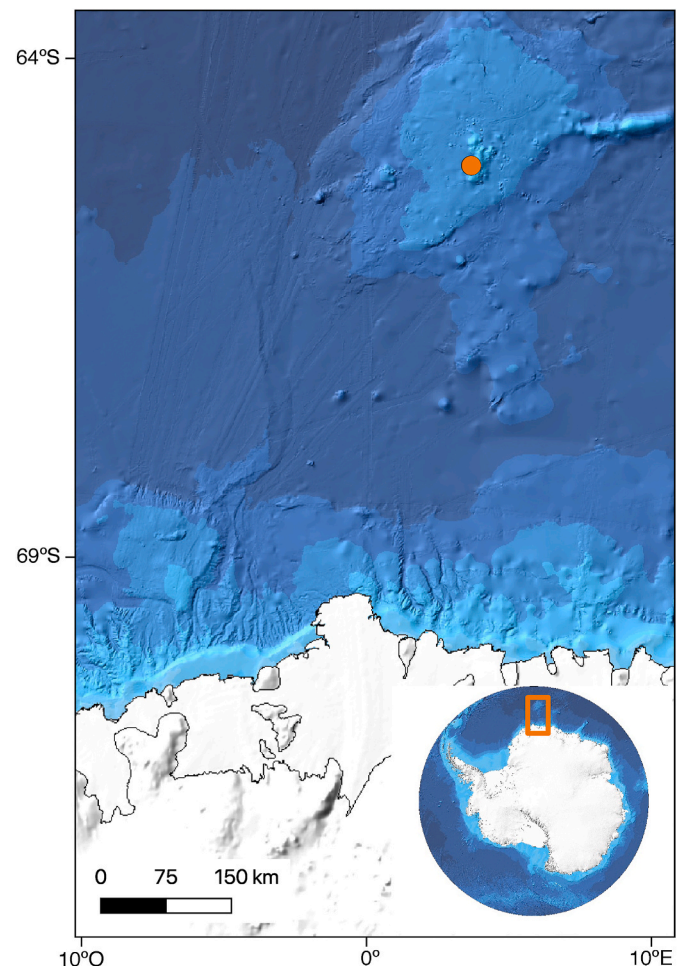


Fig. 1. Location of the collection site and type locality of *Chrysogorgia lunae* sp. nov. (Maud Rise, Eastern Weddell Sea).

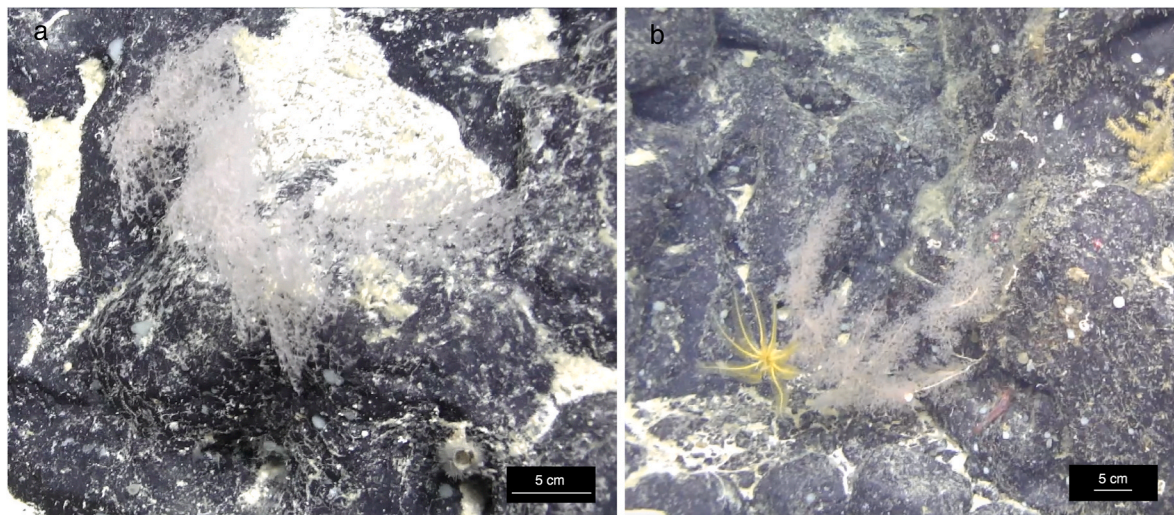


Fig. 2. In situ photograph of *Chrysogorgia lunae* sp.nov. a: holotype colony b: colony of *Chrysogorgia lunae* sp.nov. observed also in Maud Rise.

2.2. Morphological analyses

Bayer (1951) and Bayer et al. (1983) were followed for terminology and the description of the specimen. Sclerites from different colony parts (e.g. coenenchyme, polyp body, tentacles) were prepared by digestion of the tissues in a solution of sodium hypochlorite and then washed with deionized water repeatedly, let dry on slides, and finally mounted on SEM stubs using double-side carbon adhesive tape (see Bayer and Stefani, 1988b). Fragments of terminal branches with polyps were isolated and critical-point dried using an adapted hexamethyldisilazane (HMDS) protocol, limiting the immersion of octocoral fragments in this chemical to 2–3 min (Nation, 1983; Braet et al., 1997; López-González, 2020, 2021). The SEM stubs were coated with gold-palladium under a Leica ACE600, and then observed under a scanning electron microscope (SEM) Zeiss EVO SEM at the General Research Services of Microscopy at the University of Seville. In addition, different parts of the polyps and branches were prepared using clove oil and these were subsequently observed maintaining their original arrangement under an optical microscope with an OPTIKA C-P20CC digital camera and the image software OPTIKA PROVIEW. Forty sclerites of each type and colony part were measured. The material studied (holotype) has been deposited in the Invertebrate Collections of the University Museum of Bergen (UMB, Norway), while some analyzed fragments were deposited in the collection of the research team Biodiversidad y Ecología Acuática in the University of Seville (BECA).

2.3. DNA extraction, amplification and sequencing

Total genomic DNA was extracted from the ethanol (EtOH)-preserved specimen using the QIAGEN DNeasy Blood and Tissue Kit, and the E.Z.N.A. DNA kit (OmegaBiotech) following the manufacturer's protocol (spin-column protocol). The mitochondrial regions mtMutS –a homologue of the bacterial DNA mismatch repair gene mutS (=msh1)– and cytochrome *c* oxidase subunit I (COI) were sequenced, as well as a fragment of the 28S nuclear ribosomal gene (28S rDNA). Following previous studies (e.g. McFadden et al., 2011; Quattrini et al., 2013; Muthye et al., 2022; Xu et al., 2023), these regions were selected for species delimitation in order to compare with other chrysogorgiids. mtMutS was amplified using primers ND42599F (5'-GCCATTATGGTTA ACTATTAC-3') (France and Hoover, 2002) and Mut3458R (5'-TSGAGC AAAAGCCACTCC-3') (Sánchez et al., 2003). COI was amplified using primers COIIB068F (5'-CCATAACAGGACTAGCAGCATC-3') (McFadden et al., 2004) and COIOCTR (5'-TCATAGCATAGACCATACC-3') (France and Hoover, 2002). 28S was amplified using the primers 28S-Far

(5'-CACGAGACCGATAGCGAACAAGTA-3') and 28S-Rar (5'-TCATTCG ACCCTAAGACCTC-3') (McFadden and van Ofwegen, 2013). Each PCR reaction was performed using 0.15 μ l of Takara Taq DNA Polymerase (Takara Bio), 1 μ l of each primer (10 μ M) in the corresponding marker set, 2.5 μ l of 10x reaction buffer (Takara Bio), 2 μ l of dNTP mixture (Takara Bio), and 2 μ l of genomic DNA, and was brought to a final volume of 25 μ L with ddH₂O. PCR for mtMutS was carried out using the following cycle profile: initial denaturation at 94 °C for 2min, 35 cycles of denaturation at 94 °C for 30s, annealing at 55 °C for 30s, and extension at 72 °C for 30 s, and a final extension at 72 °C for 5 min. The COI and 28S PCR used the same cycle profile, but with 58 °C as annealing temperature. All PCR products were purified using ExoSAP-IT™ PCR Product Cleanup Reagent (Thermo Fisher Scientific) following the manufacturer's instructions. Strong band-yielding PCR products of COI and mtMutS were sequenced in-house at the sequencing facility of the University of Bergen, while 28S was successfully amplified at the sequencing facility of the research team BECA in the University of Seville. All of the sequences are deposited in GenBank (Table 1).

2.4. Phylogenetic reconstruction

All chromatograms were visualized and sequence pairs matched and edited using Sequencer v4.0. The sequences obtained were BLASTED (using Blastn, implemented in Blast+ 2.14.1, released August 22, 2023) and the results compared with all publicly available sequences in genus *Chrysogorgia*. This preliminary molecular identification was consistent with the morphological description of the genus (see “3. Results” section). For our phylogenetic analysis, all the available mtMutS, COI and 28S sequences of *Chrysogorgia* species and three sequenced specimens of the genus *Radicipes* (as outgroup) were obtained from GenBank (see Table 1). The specimens identified at the species level having both mitochondrial genes (mtMutS and COI) were used for a mtMutS + COI concatenated matrix including nineteen different species of *Chrysogorgia*. Six more species with only mtMutS sequenced were also included in the analyses and in the calculation of genetic distances. A total of seventeen different species that have nuclear 28S sequences available were used for a phylogenetic analysis exclusive to this marker. Mitochondrial dataset was aligned using MUSCLE, as implemented in MEGA6 (Tamura et al., 2013), while 28S nuclear dataset was aligned online in Mafft v.7 (<https://mafft.cbrc.jp/alignment/server/>) (Katoh et al., 2019).

After alignment, pairwise genetic distances based on the Kimura 2-parameter (K2P) model of nucleotide substitution (Kimura, 1980) with pairwise deletion option were obtained for the mtMutS and 28S datasets

Table 1

Octocoral species involved in the molecular comparative analyses carried out in this study. (MBM: Marine Biological Museum of Chinese Academy of Sciences; ZMBN: Department of Natural History, University Museum of Bergen, Norway. USNM: Smithsonian National Museum of Natural History).

Species	Voucher Number	GenBank Accession Number			Reference
		mtMutS	COI	28S	
<i>Chrysogorgia abludo</i> Pante and Watling (2012)	isolate NAS102-3	GQ180138	GQ868324	–	Thoma et al., 2009; McFadden et al. (2011);
<i>Chrysogorgia acanthella</i> (Wright and Studer, 1889)	MBM286357	ON221827	ON207075	ON207665	Xu et al. (2023)
<i>Chrysogorgia acanthella</i>	MBM286862	ON221828	ON207072	ON207666	Xu et al. (2023)
<i>Chrysogorgia arboriformis</i> Xu et al., 2023	MBM286465	ON221842	ON207094	ON207672	Xu et al. (2023)
<i>Chrysogorgia arboriformis</i>	MBM286466	ON221843	ON207100	–	Xu et al. (2023)
<i>Chrysogorgia artospira</i> Pante and Watling (2012)	isolate KEL619-1	GQ868346	GQ868315	–	McFadden et al. (2011)
<i>Chrysogorgia averta</i> Pante and Watling (2012)	isolate LII-10-609	KC788265	KC788235	KC788258	Quattrini et al. (2013)
<i>Chrysogorgia carolinensis</i> Xu et al., 2020	MBM286495	MW418362	–	MW418375	Xu et al. (2021b)
<i>Chrysogorgia cylindrata</i> Xu et al., 2023	MBM286460	ON221818	ON207073	–	Xu et al. (2023)
<i>Chrysogorgia cylindrata</i>	MBM286461	ON221824	ON207086	ON207667	Xu et al. (2023)
<i>Chrysogorgia cylindrata</i>	MBM286464	ON221825	ON207082	ON207668	Xu et al. (2023)
<i>Chrysogorgia delicata</i> Nutting, 1908	MBM286859	ON221829	ON207084	ON207671	Xu et al. (2023)
<i>Chrysogorgia dendritica</i> Xu et al., 2020	MBM286353	MT269888	–	–	Xu et al. (2020)
<i>Chrysogorgia fragilis</i> Xu et al., 2020	MBM286352	MN510470	–	–	Xu et al. (2020)
<i>Chrysogorgia geniculata</i> (Wright and Studer, 1889)	MBM286467	ON221845	ON207079	ON207673	Xu et al. (2023)
<i>Chrysogorgia geniculata</i>	isolate HI-015	MT558738	MT726004	–	Baco et al. (unpublished)
<i>Chrysogorgia geniculata</i>	isolate HI-018	MT558739	MT726005	–	Baco et al. (unpublished)
<i>Chrysogorgia geniculata</i>	isolate HI-037	MT558740	MT726006	–	Baco et al. (unpublished)
<i>Chrysogorgia gracilis</i> Xu et al., 2020	MBM286350	MN510472	–	ON207657	Xu et al. (2020)
<i>Chrysogorgia lunae</i> sp. nov.	ZMBN138867	OR576812	OR575174	OR574989	Present study
<i>Chrysogorgia monticola</i> Cairns (2007)	USNM 1102452	JN227989	JN227955	–	Pante et al. (2012)
<i>Chrysogorgia pendula</i> Versluys (1902)	MBM286870	ON221834	ON207074	ON207664	Xu et al. (2023)
<i>Chrysogorgia pendula</i>	MBM286359	ON221814	ON207070	ON207661	Xu et al. (2023)
<i>Chrysogorgia pendula</i>	MBM286865	ON221817	ON207080	–	Xu et al. (2023)
<i>Chrysogorgia pinnata</i> Cairns (2007)	USNM1102450	JN227988	JN227956	–	Pante et al. (2012)
<i>Chrysogorgia pinniformis</i> Xu, Zhan and Xu, 2021	MBM286504	MW085090	–	MW418372	Xu et al. (2021b)
<i>Chrysogorgia ramificans</i> Xu et al., 2019	MBM286861	ON221826	ON207077	ON207675	Xu et al. (2023)
<i>Chrysogorgia rigida</i> Versluys (1902)	MBM286356	ON221844	ON207095	ON207674	Xu et al. (2023)
<i>Chrysogorgia tenuis</i> Xu et al., 2023	MBM286858	ON221831	ON207093	ON207670	Xu et al. (2023)
<i>Chrysogorgia tricaulis</i> Pante and Watling (2012)	n.d.	OL616221	OL616221	–	Muthye et al. (2022)
<i>Chrysogorgia varians</i> Xu, Zhan and Xu, 2021	MBM286502	MW085091	–	MW418381	Xu et al. (2021b)
<i>Chrysogorgia varians</i>	MBM286440	MW418369	–	MW418383	Xu et al. (2021b)
<i>Radicipes gracilis</i> (Verrill, 1884)	USNM 100900	JN227987	HM590861	–	Pante et al. (2012)
<i>Radicipes stonei</i> Cordeiro, Cairns and Pérez, 2017	USNM:IZ:1418007	MG986912	MG986961	MG980134	Cairns and Wirshing, 2018
<i>Radicipes</i> sp.	RB-19-195	–	–	OM799018	Saso et al. (unpublished)

in order to compare them with previous studies at species level within the genus *Chrysogorgia*, following the work of Pante and France (2010), Pante et al. (2012), López-González (2020), López-González and Drewery (2022), and Xu et al. (2023).

The Maximum Likelihood approach (ML) was carried out in MEGA6 using the NNI (Nearest Neighbor Interchange) heuristic method with 1000 bootstrap replications and using the nucleotide substitution model (T92+G) (nucleotide model search implemented in MEGA6). In addition, Bayesian Inference (BI) analyses were carried out with MrBayes v3.2.6 (Huelsenbeck and Ronquist, 2001) using the substitution model GTR + G (Isetnst = 6 Rates = gamma), 10^7 generations, and discarding 25% of the initial trees. The stationary of the chains and convergence of two runs were monitored for each parameter by Tracer (v.1.7.1),

determining whether the effective sample size (ESS) of all parameters was larger than 200, as recommended (Rambaut et al., 2018).

3. Results

Subclass Octocorallia Haeckel, 1866.

Order Scleractyonacea McFadden, van Ofwegen & Quattrini, 2022.

Family Chrysogorgiidae Verrill, 1883.

Chrysogorgia Duchassaing and Michelotti, 1864.

Chrysogorgia lunae sp. nov.

3.1. Type material

ZMBN138867, Holotype, deposited in the Invertebrate Collections of the University Museum of Bergen (UMB, Norway). Antarctica, Eastern Weddell Sea, Maud Rise seamount, “Dronning Maud Land” cruise, RV Kronprins Haakon, Aegir6000 ROV, dive 05, 65°13'25.68" S, 2°30'17.64" E, 1581m depth, 28 March 2019, whole colony, ca. 25.9 cm height. Some fragments with polyps of the holotype deposited in the morphological and molecular collection of BECA under the code OCHRY5-31 (G-4101). This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN (International Code of Zoological Nomenclature). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix “<http://zoobank.org/>”. The LSID for the present publication is: urn:lsid:zoobank.org:pub:60DE6F13-2509-4776-89F4-40B6587F9458.

3.2. Diagnosis

Chrysogorgia in Versluys' (1902) group C “Squamosae typicae” group with a bushy colony, large branches pinnately branched and subdivided dichotomously, the branching sequence is 2/5L. The polyps are bell-shaped with a narrow base. The scales have different shapes and are distributed throughout the colony, including the coenenchyme and the polyp. Each pinnule has a single curved and rib-like scale. All coenenchyme and polyp body scales have minute warts on their surface. The coenenchymal sclerites usually have a central projection.

3.3. Description of the holotype

The colony corresponds to Versluys' (1902) group C “Squamosae typicae”. It is 25.9 cm in height, 20.1 cm in width, bushy, branching in different planes, and shows a golden metallic luster (Figs. 2 and 3a). Despite the complete holdfast is lacking, the colony was apparently broken during collection very close the basal-most part. As the main stem widens considerably towards the end, a discoidal shape can be expected, as it occurs in other hard-bottoms species in the genus (e.g. Xu et al. 2023). The main stem is short and circular, 3.3 mm in diameter, and is bent in a zigzag manner because it undergoes angular bending at the origin of each branch. Large branches subdivided dichotomously, irregularly and upright-directed, with its branchlets arising from the stem in a spiral, and forming a bushy colony. The lateral branchlets are subdivided dichotomously with its twigs nearly on one plane with the first branch internode at 17 mm above the supposed holdfast. The interbranch distance is 3 – 6 mm depending on how thick (or old) the main branch is. For basal branches ca. 3 mm in diameter, the interbranch distance is longer, usually, 5 – 6 mm; in thinner/younger stems (ca. 1 – 2 mm), the interbranch distance is 3 – 4 mm. The branches arise from the stem at a right angle and give rise to lateral twigs that stand at angles of 40 – 45° and end up in a dichotomous fashion. The branching sequence is 2/5L giving a spiral appearance to the axis. The orthostiche interval is 13 – 18 mm (Fig. 3d). No nematozooids (cnidal papillae) have been observed. The polyps are absent along the stem but present and well-spaced on twig internodes, arranged usually one and sometimes two in the twig internodes and two on the terminal twigs (Fig. 3b). Those polyps that are continuous on twig internodes are located at a distance of 2 – 7 mm. They are bell-shaped with a narrow base and 1.8 – 3.5 mm height (n = 40) (Figs. 3c and 4a). Thicker branches have larger polyps.

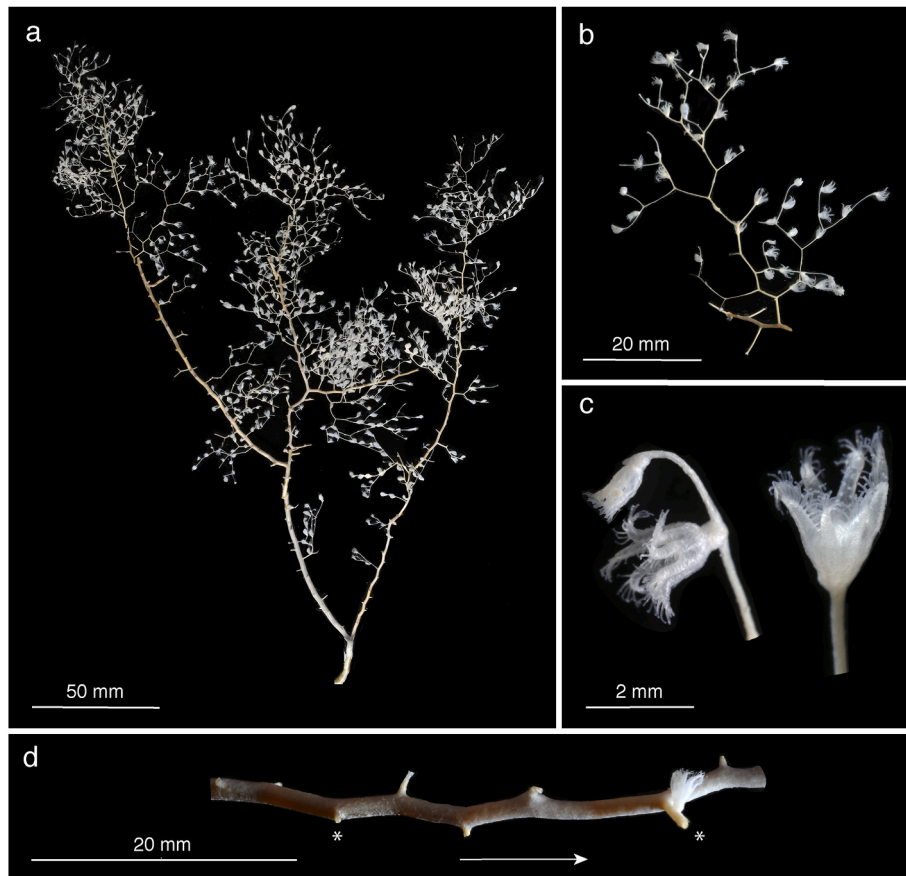


Fig. 3. *Chrysogorgia lunae* sp. nov. Holotype (ZMBN138867). a: colony. The colony was broken during collection, depicted in this photo is the reconstructed arrangement of branches. b: details of polyp arrangement on branches; c: details of bell-shaped polyps and d: details of the pattern of ramification (2/5L).

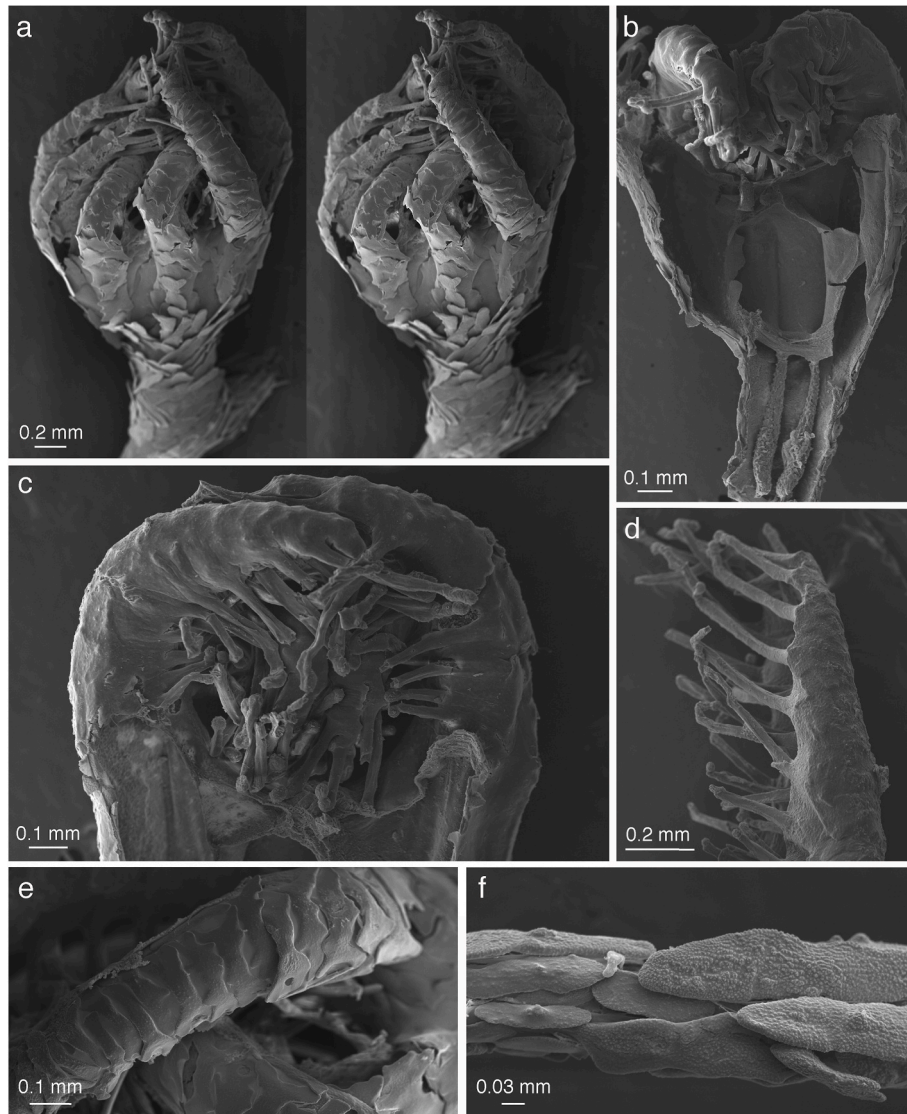


Fig. 4. *Chrysogorgia lunae* sp. nov. Holotype (ZMBN138867). SEM photographs. a: lateral vision of a polyp, stereopair; b: longitudinal section of a polyp showing contracted tentacles, pharynx and two mesenteria; c: details of contracted tentacles and pinnules; d: details of pinnules; e: sclerite arrangement in tentacles; f: sclerite arrangement in coenenchyme.



Fig. 5. *Chrysogorgia lunae* sp. nov. Holotype (ZMBN138867). SEM photographs. a: coenenchymal scales; b: basal part of the polyp; c: distal part of the polyp.

The tentacular crown is shown mostly expanded, with tentacles (1.0 – 1.4 mm long) with 18 – 20 pinnules and two rows of 9 – 10 each side of the rachis. Pinnules are slightly capitate due to the cnidae accumulation (Fig. 4b, c and 4d).

The coenenchymal sclerites are longitudinally arranged in abundance and in the sense of the growth of the branch (Fig. 4f), oval to irregularly rounded scales (Fig. 5a), up to 0.39 mm in length, and 0.09 mm in width, with prominent tubercles and minute warts on the surface, usually narrowing in the center, some scales have serrated minute edges. Also, many of them present a central projection which occurs only on one side of the sclerite. The sclerites of the polyp base are warty scales with different forms and some of them with serrated edges, longitudinally arranged and usually with a constricted middle section (Fig. 5b), up to 0.37 mm length and 0.22 mm width. The sclerites of the distal part of the polyp are asymmetric scales, some of them with minute serrated, lobed and irregular edges (Fig. 5c), up to 0.46 mm length and 0.24 mm width. The scales of the tentacular rachis occur on the aboral side, are transversally placed and they overlap slightly instead of being well separated (Fig. 4e). They present different shapes such as arched butterfly scales up to 0.32 mm in length and 0.24 mm in width, and asymmetric planar scales up to 0.42 mm in length and 0.03 mm in width (Fig. 6a and b), some of them with serrated edges like the scales present in other body parts. There is one long toothed rib-like scale on each pinnule longitudinally arranged with less prominent warts and a serrated arched side and another planar end with a few rounded lobes, up to 0.61 mm in length (Fig. 6c).

3.4. Geographic and bathymetric distribution

The holotype is the only collected colony (Figs. 2 and 3a); however, two more colonies were observed also at Maud Rise seamount during the same video transect (Figs. 1 and 2b). Both observed colonies apparently belong to the same species described here base on macroscopic characters. These colonies were observed at 1407 and 1491 m depth, thus the known bathymetric range for *Chrysogorgia lunae* is 1407–1581 m. The three colonies were observed attached to hard substrates.

3.5. Etymology

The specific epithet *lunae* is chosen in honor of the natural satellite of the Earth. The species name aims to draw an analogy between moon and deep-sea exploration, revealing landscapes akin to those from science fiction, yet entirely real. While space ignites a greater popular curiosity than the deep-sea, hidden beneath the waves are still unraveling secrets, such as new species, inviting us to explore. Perhaps, a Google search for information on the satellite might unexpectedly lead to the ocean depths, where another *luna*, moon in Spanish, takes the form of a gorgonian.

3.6. Phylogenetic analyses

The aligned datasets comprised a total of 741 nucleotide positions for mtMutS, 785 for COI, and 772 for 28S. The ML tree for mtMutS + COI clustered the sequences of the newly described species *C. lunae* sp. nov. alongside other sequences identified as *C. geniculata* and *C. arboriformis*



Fig. 6. *Chrysogorgia lunae* sp. nov. Holotype (ZMBN138867). SEM photographs of tentacular scales; a: planar scales with asymmetric shapes; b: butterfly scales with arched forms; c: pinnular scales with arched forms.

within a clade supported by a bootstrap (bst) value of 63% (Fig. 7). Conversely, the BI tree for mtMutS + COI associated the novel species with three out of a total of four specimens designated as *C. geniculata* supported by a posterior probability of 0.55 (Fig. 8). This congruence is in line with the findings from both ML and BI trees for 28S wherein *C. lunae* sp. nov. was grouped together with *C. arboriformis* in a clade sister to one specimen identified as *C. geniculata* (MBM286467) (bootstrap = 82%, posterior probability = 0.99; Figs. 9 and 10). Otherwise, in both trees based on mtMutS + COI and the two derived from 28S, it is evident that *C. lunae* sp. nov. clusters with *C. geniculata*, *C. arboriformis* and *C. rigida*, exhibiting strong supported values ranging from 89% to 100% (Figs. 7–10).

The average KP2 distance between *C. lunae* sp. nov. and any other species of *Chrysogorgia* is 0.89% for mtMutS and 8.44% for 28S. The interspecific distances for mtMutS range from 0 to 1.82% (Table 2) and for 28S range from 0.13 to 16.41% (Table 3). The mtMutS sequences of *Chrysogorgia lunae* sp. nov. are identical to those from *C. arboriformis* and three specimens identified as *C. geniculata*. Conversely, a distance of 0.15% was identified between all these sequences and a fourth specimen of *C. geniculata* (specimen MBM286467). Based on 28S, *C. lunae* sp. nov., *C. arboriformis*, and *C. geniculata* display distinct sequences (Fig. 8) with corresponding distances of 1.27% and 3.07% between the pairs *C. lunae* sp. nov.–*C. arboriformis* and *C. lunae* sp. nov.–*C. geniculata*, respectively. Following the calculated genetic distances for mtMutS and 28S and four phylogenetic trees obtained, the new described species is consistently related to *C. geniculata* and *C. arboriformis*.

4. Discussion

4.1. Geographical and bathymetric distribution of *Chrysogorgia*

The family Chrysogorgiidae is poorly represented in Antarctic waters when compared to other scleralcyonacean families such as Primnoidae, which is often dominant in Southern Ocean seabeds (Cairns and Bayer, 2009). Only two chrysogorgiid species have previously been reported in the Antarctic region, *Parachrysogorgia antarctica* (Cairns, 2002) and *Radicipes* sp. (Cairns, 2002; Watling et al., 2011; Pante et al., 2012). The majority of *Chrysogorgia* species are found in the northern Pacific Ocean and most of them in tropical latitudes (Watling et al., 2011; Pante and Watling, 2012; Cairns, 2018). Within the southern hemisphere, only two *Chrysogorgia* species, *C. lunae* sp. nov. and *C. flexilis* (Wright and Studer, 1889) have been documented beyond 45° S latitude. Specifically, the distribution of *C. flexilis* encompasses the waters surrounding Wellington Island, in the fjord region of Southern Chile; while, *C. lunae* sp. nov. stands as the singular representative of its genus in Antarctic waters. Regarding bathymetric distribution, the genus *Chrysogorgia* is eurybathic, but the majority of the species occur at depths greater than 600 m while the shallowest species (<500 m depth) have been found only at tropical and subtropical latitudes (–5°S – 34°N) (Cairns, 2001; Pante et al., 2012). In this sense, *C. lunae* sp. nov. conforms to the pattern observed so far as it was found at 1407–1581 m depth. Furthermore, like many other *Chrysogorgia* species, *C. lunae* sp. nov. has been observed on a seamount (Cairns, 2007; Pante and Watling, 2012; Xu et al., 2021b).

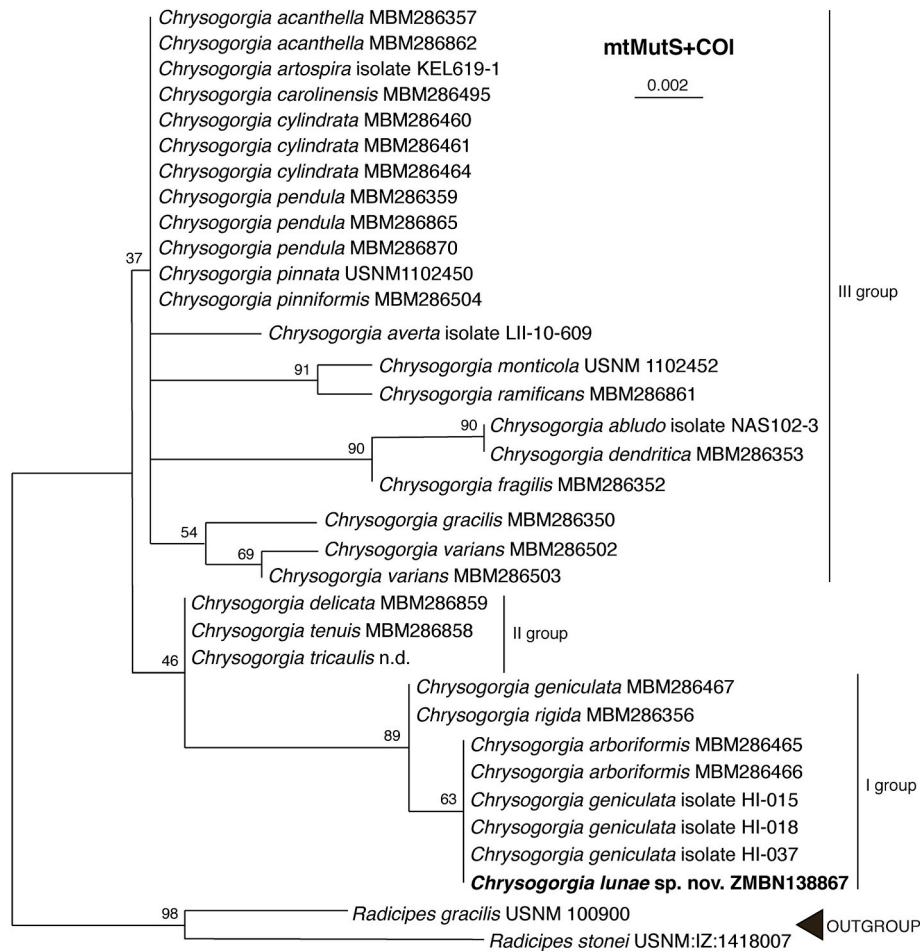


Fig. 7. Maximum likelihood (ML) tree of the MutS + COI dataset showing phylogenetic relationships between *Chrysogorgia lunae* sp. nov. and other congeners with the corresponding voucher numbers. The present hypothesis is based on the concatenated dataset comprising two markers: mtMutS + COI, along with only mtMutS sequences for *C. carolinensis*, *C. dendritica*, *C. fragilis*, *C. gracilis*, *C. pinniformis* and *C. varians*. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Supporting values of nodes as bootstrap (%)/posterior probability.

Seamounts are isolated topographic rises with environmental conditions that enhance high levels of biodiversity and endemism (Hubbs, 1959; Genin et al., 1986; Richer de Forges et al., 2000; Clark and Bowden, 2015). Following the case study of endemism of *Chrysogorgia* on seamounts by Pante et al. (2015a), there is a possibility that *C. lunae* sp. nov. may be endemic to Maud Rise or to a group of nearby seamounts. However, the current information about latitudinal and bathymetric distribution of the genus is scarce, as the majority of species have been observed only once (Pante et al., 2012). Consequently, any geographical and bathymetric comparison within the genus must be taken with caution since it represents merely a snapshot in our knowledge of chrysogorgiid distribution.

4.2. Morphological comparisons within *Chrysogorgia*

To date, twenty-one valid *Chrysogorgia* species are included in Versluys' (1902) "Squamosae typicae" group C, including *C. lunae* sp. nov. (Cairns, 2001, 2002; Pante and Watling, 2012; Xu et al., 2021b; Xu et al., 2023; this study). Only five of these species have been recorded in the southern hemisphere: *C. acanthella*, *C. axillaris* (Wright and Studer, 1889), *C. pendula*, *C. sibogae* Versluys (1902) and *C. lunae* sp. nov. (see Table 4). Of these species, besides *C. lunae* sp. nov., only *C. pendula* and *C. acanthella* have a branching sequence 2/5L. However, *C. pendula* is characterized by a typically bottle-brush colony and descending-oriented secondary branches (Versluys, 1902) while *C. lunae* sp. nov. has a bushy colony shape and ascending-oriented secondary

branches. *Chrysogorgia acanthella* resembles *C. lunae* sp. nov. in its bushy colony shape with upright-directed secondary branches; however, this species differs from *C. lunae* sp. nov. in having a stem with polyps and, in the pinnules, slender and little curved sclerites extend from the tentacles into pinnules. Conversely, in *C. lunae* sp. nov. the scales in pinnules are independent of the tentacles and are long, toothed, rib-like. On the other hand, the polyps of *C. acanthella* are pitcher-shaped while those of *C. lunae* sp. nov. are bell-shaped (Wright and Studer, 1889; Versluys, 1902; this study).

Other four "Squamosae typicae" *Chrysogorgia* species have been described with branching sequence 2/5L: *C. campanula* Madsen (1944), *C. artospira* Pante and Watling (2012), *C. cylindrata*, and *C. cavea* Kinoshita (1913), all of them occurring in the northern hemisphere (Wright and Studer, 1889; Versluys, 1902; Pante and Watling, 2012) (see Table 4). *Chrysogorgia campanula* is known from Icelandic waters and it resembles *C. lunae* sp. nov. in the presence of sclerites in the pinnules, but *C. campanula* has more than one sclerite in each pinnule while *C. lunae* sp. nov. has only one sclerite per pinnule (Madsen, 1944). *Chrysogorgia artospira* resembles *C. lunae* sp. nov. as neither of these species have polyps on the stem; however, *C. artospira* forms a bottle-brush colony in the adult stage, presents pitcher-shaped polyps, and its sclerome is characterized by smooth scales, while *C. lunae* sp. nov. has a bushy colony, bell-shaped polyps, and its sclerites are warty scales (Pante and Watling, 2012; this study). Similar to *C. lunae* sp. nov., *C. cylindrata* displays 1 or 2 terminal polyps at the tips of terminal twigs, and there are sclerites arranged in the pinnules but no scales with

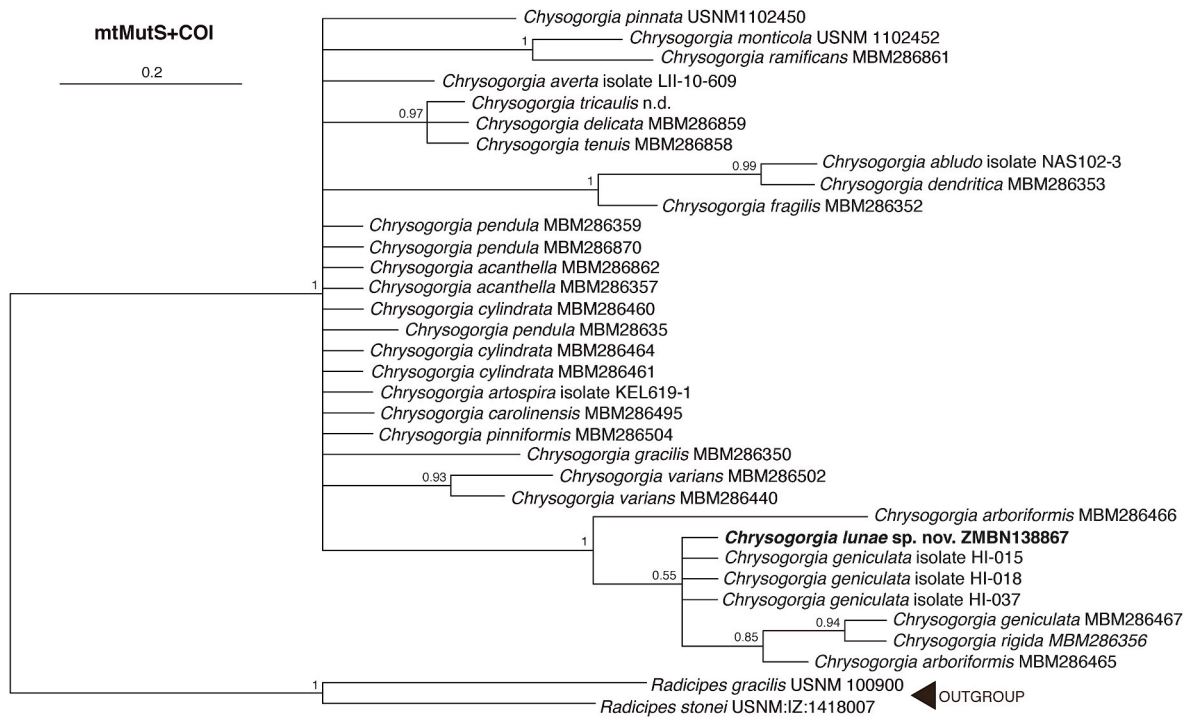


Fig. 8. Bayesian Inference (BI) tree of the MutS + COI dataset showing phylogenetic relationships between *Chrysogorgia lunae* sp. nov. and other congeners with the corresponding voucher numbers. The present hypothesis is based on the concatenated dataset comprising two markers: mtMutS + COI, along with only mtMutS sequences for *C. carolinensis*, *C. dendritica*, *C. fragilis*, *C. gracilis*, *C. pinniformis* and *C. varians*. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Supporting values of nodes as posterior probability.

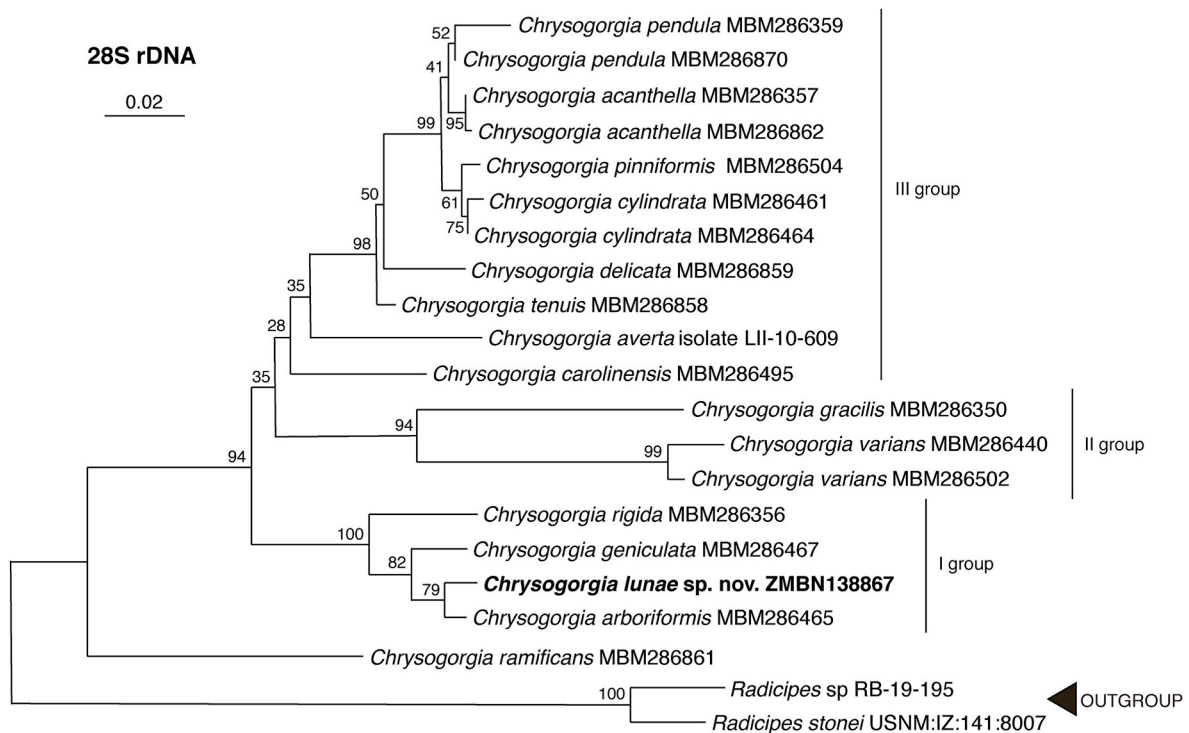


Fig. 9. Maximum likelihood (ML) tree for 28S showing phylogenetic relationships among *Chrysogorgia lunae* sp. nov. and other congeners with the corresponding voucher numbers. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Supporting values of nodes as bootstrap (%).

toothed rib-like shape. It also differs from the newly described species due to the presence of polyps on the stem and bottlebrush-shaped colonies in adults. Finally, *C. cavea* resembles *C. lunae* sp. nov. on account of a long rib-like scale within each pinnule. However, in contrast to the

new species, *C. cavea* has bottlebrush colonies in adult stage and smooth scales in stem, while *C. lunae* sp. nov. present warty texture throughout all its parts and also has prominent tubercles in the stem scales (Kükenthal, 1924; Xu et al., 2023).

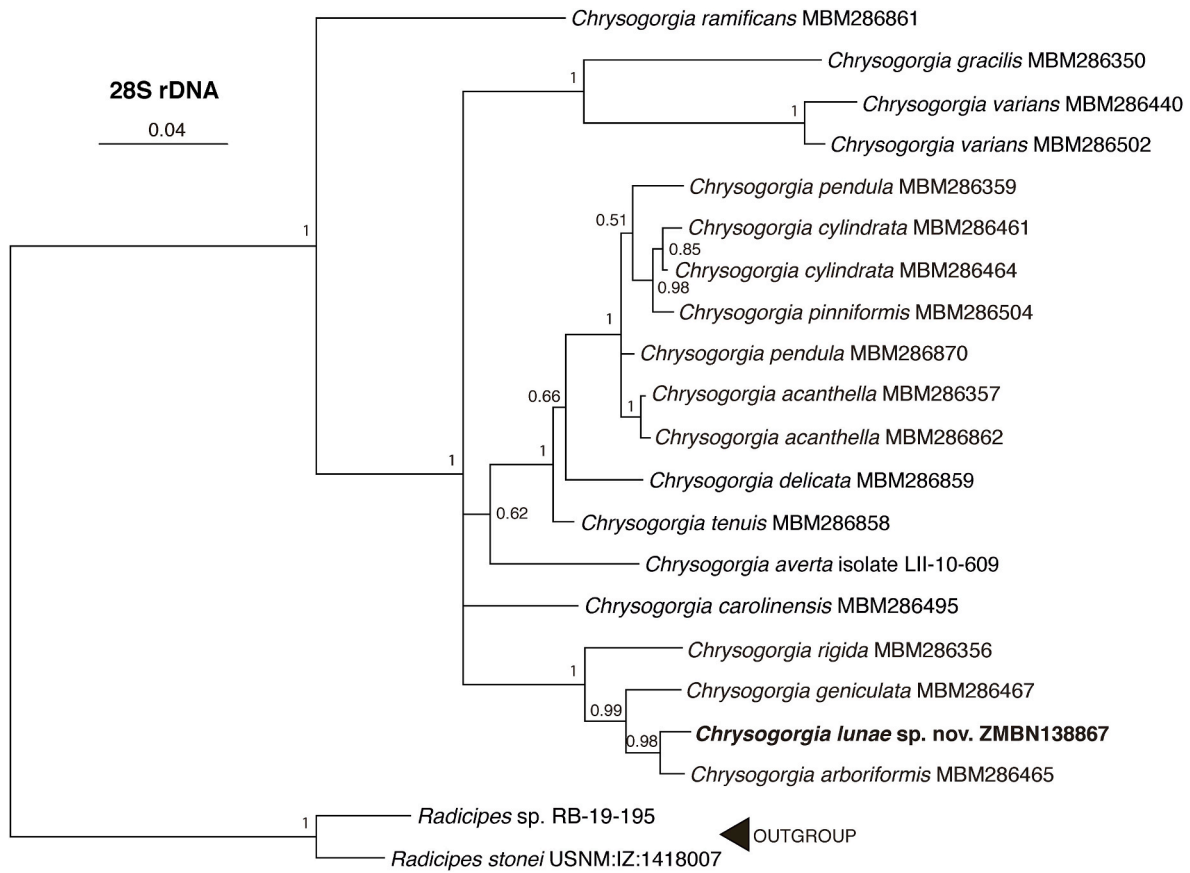


Fig. 10. Bayesian Inference (BI) tree of the 28S dataset showing phylogenetic relationships between *Chrysogorgia lunae* sp. nov. and other congeners with the corresponding voucher numbers. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Supporting values of nodes are posterior probability.

Table 2

Interspecific distances at mtMutS between *Chrysogorgia lunae* sp. nov. and select groups of *Chrysogorgia* species as delineated by the Maximum likelihood (ML) tree based on mtMutS + COI (Fig. 7).

Comparisons within	Min	Average	Max
<i>C. lunae</i> sp. nov. - I group	0	0.04	0.15
<i>C. lunae</i> sp. nov. - II group	0.74	0.77	0.83
<i>C. lunae</i> sp. nov. - III group	0.89	1.11	1.79

Table 3

Interspecific distances at 28S between *Chrysogorgia lunae* sp. nov. and select groups of *Chrysogorgia* species as delineated by the Maximum likelihood (ML) tree based on 28S (Fig. 8).

Comparisons within	Min	Average	Max
<i>C. lunae</i> sp. nov. - I group	1.27	3.03	4.74
<i>C. lunae</i> sp. nov. - II group	8.21	10.80	12.68
<i>C. lunae</i> sp. nov. - III group	7.33	8.52	9.23

4.3. Molecular analysis

Chrysogorgia lunae sp. nov. shares the complete analyzed fragments of *mtMutS* with three specimens identified as *C. geniculata* and two specimens identified as *C. arboriformis* (Table 1 of Supplementary material). The mitochondrial genomes of anthozoans evolve slowly and exhibit high conservative barcodes among congeneric species (Shearer et al., 2002; Hellberg, 2006; McFadden et al., 2017), which may explain the absence of variation between *C. lunae* sp. nov. and *C. geniculata* and *C. arboriformis*. In this sense, in a previous study case, only 70% of

different octocoral morphospecies were identified by mitochondrial genes (McFadden et al., 2011). Conversely, considering the 28S gene sequences, there are clear differences between *C. lunae* sp. nov., *C. arboriformis*, and *C. geniculata* (Figs. 9 and 10 and Table 2 of Supplementary material). The potential variability of the 28S segment will only be understood when several colonies per species are sequenced, a situation that is still far from being achieved. In the meantime, our findings suggest that 28S could potentially serve as a successful marker to discriminate *Chrysogorgia* congeners, even when mitochondrial markers do not show differences that can support other observed morphological differences. All three species included in this clade belong to “Squamosae typicae” and possess long toothed rib-like scales in pinnules (Table 5). These two morphological characteristics define group C2 as described by Xu et al. (2023), within which *C. lunae* sp. nov. is encompassed. These two characters thus seem to provide a reliable basis for intrageneric classification in *Chrysogorgia*. On the other hand, *C. geniculata* and *C. arboriformis* exhibit a 1/3L branching sequence and also both have polyps on the stem. In contrast, *C. lunae* sp. nov. has a branching sequence of 2/5L and lacks polyps on the stem. In terms of colony form, *C. arboriformis* presents a tree-like morphology, *C. geniculata* has a bottlebrush colony shape, and *C. lunae* sp. nov. is characterized by a bushy colony (Wright and Studer, 1889; Untiedt et al., 2021; Xu et al., 2023; this study).

In octocorals, further investigation is warranted for divergent sequences assigned to a specific species, a task influenced by whether these sequences belong to mitochondrial or nuclear segments (Hellberg, 2006). Mitonuclear incongruities in particular, offer a compelling avenue to explore diverse evolutionary processes including interspecific hybridization, explosive radiation, incomplete lineage sorting, or the presence of multicopy nuclear DNA segments (Vollmer and Palumbi,

Table 4
Morphological comparison of all “Squamosae typicae” *Chrysogorgia* species distributed in the southern hemisphere and four more from the northern hemisphere with 2/5L as branching sequence as well as *C. lunae* sp. nov. “-” means missing data.

Species/Characters	<i>C. lunae</i> sp. nov.	<i>C. pendula</i>	<i>C. acanthella</i>	<i>C. axillaris</i>	<i>C. sibogae</i>	<i>C. cavea</i>	<i>C. campanula</i>	<i>C. artospira</i>	<i>C. cylindrata</i>
Colony shape	Bushy	Bottlebrush	Bushy bottlebrush	Bottlebrush	Bottlebrush	Bottlebrush	Bottlebrush	Bottlebrush	Bottlebrush
Branching sequence	2/5L	2/5L	3/7L, 2/5L	1/3L	1/3L	1/3L, 2/5L	2/5L	2/5L	2/5L
Orthostiche interval	13 – 18 mm	6 – 28 mm	26 – 50 mm	8 – 9 mm	–	–	–	11 – 30 mm	5 – 30 mm
Polyps shape	Bell-shaped	Cylindrical (terminal polyps) or oval body (non-terminal polyps)	Pitcher shaped	Pitcher shaped	–	–	Trumped-shaped	Pitcher-shaped	Cylindrical (terminal polyps) or oval body (non-terminal polyps)
Polyps on the stem	Absent	Present	Present	Absent	Present	Absent	Present	Absent	Present
Polyps on terminal twigs	Often 2	Up to 4	Up to 5	1	–	–	1	1 or 2	1 or 2
Sclerites in coenenchyme	Warty scales with prominent tubercles and minute warts and narrowing in the center	Scales smooth, elongate with a medial contraction and lobed with irregular shape	Scales elongate and smooth with medial contraction, with irregular shape	Scales small, oval and irregular shape	Scales smooth, rounded or oval, some of them with irregular lobed edges	Scales smooth, elongate with serrated edges and a narrow median	Scales usually 8-shaped with a median contraction, small spines and finely denticulate edges with irregular shape	Absent	Scales smooth and slender, some of them with lobed and irregular edges
Sclerites in polyp body	Warty and asymmetric scales and a constricted middle	Scales elongate and nearly smooth with a medial contraction with irregular shape	Scales smooth and elongate with a medial contraction	Scales large with irregular and toothed edges, and little wrinkles	Scales thin with finely toothed edges	Scales slightly elongate with minute warts and serrated edges, and with a medial contraction	Scales 8-shaped with a median contraction, some of them with irregular edges	Scales smooth with rounded ends and a medial contraction	Scales smooth and elongate with a medial contraction and irregular edges and shape
Sclerites in tentacles	Arched butterfly scales and asymmetric planar scales with serrated edges	Scales nearly smooth, elongate, with irregular shape and lobed edges	Scales nearly smooth and usually irregular shape	Scales irregular with one or two large scales projecting above the base of tentacle	Scales thick, elongate with sparse fine warts, irregular shape	Scales elongate with irregular lobed edges and curved with deep lobed edges	Scales usually x-shaped	Scales smooth, flat or with idiosyncratic shapes	Scales elongate to slender, nearly smooth with irregular shape and lobed edges
Sclerites in pinnules	Toothed rib-like scales	Scales slender and slightly curved, nearly smooth or with sparse fine warts	Slender and little curved scales extend from the tentacles into pinnulae	Absent	The sclerites of the tentacles extend into the pinnules	Toothed rib-like scales	Scales long with one end forked and the other end gutter-shape	Some sclerites partially extend into the pinnules, which are otherwise sclerite-free	Scales slender and nearly smooth with minute warts
Location (depth)	Antarctica, Eastern Weddell Sea (1407–1581m)	Banda Sea, W Indian and NW Pacific, Caroline Ridge (1595m)	S Pacific, Kermadec Islands (1097m)	NW Pacific, Kermadec Islands (1097m) Philippines (150 and 186m)	Banda Sea, W Indian (204m)	NW Pacific, Japan (640–752m)	Iceland waters, Denmark Strait (2448m)	N Atlantic, New England (2253 and 1965m) and Corner Seamounts (1846 and 1650m)	NW Pacific, Caroline Ridge (1877–870m)
Reference	Present study	Versluys (1902); Xu et al. (2023)	Wright and Studer (1889); Versluys (1902); Xu et al. (2023)	Wright and Studer (1889)	Versluys (1902)	Kinoshita (1913); Kükenthal (1919); Xu et al. (2023)	Madsen (1944); Xu et al. (2023)	Pante and Watling (2012)	Xu et al. (2023)

Table 5

Morphological comparison between *Chrysogorgia lunae* sp. nov. and the genetically closely related species. All these species are included in ‘‘Squamosae typicae’’ Verluys’ (1902) group and present toothed rib-like scales in pinnules.

Species/ Characters	<i>C. lunae</i> sp. nov.	<i>C. geniculata</i>	<i>C. arboriformis</i>	<i>C. rigida</i>
Colony shape	Bushy	Bottlebrush	Tree-shaped	Bottlebrush
Branching sequence	2/5L	1/3L	1/3L	1/3L
Orthostiche interval	13 – 18 mm	10 – 11.5 mm	8 – 23 mm	12 – 13 mm
Polyyps shape	Bell-shaped	Pitcher-shaped	Expanded oval body	Conical
Polyyps on the stem	Absent	Present	Rare	Absent
Polyyps on terminal twigs	Often 2	1 or 2	Up to 7	Up to 3
Sclerites in coenenchyme	Warty scales with prominent tubercles and minute warts and narrowing in the center	Elongate and nearly smooth or with many minute warts and one or more distinct large warts	Scales slender, nearly smooth or with one or more large warts and many little warts	Scales with minute warts, many of them with a large wart on center
Sclerites in polyp body	Warty and asymmetric scales and a constricted middle	Elongate scales with irregular blunted or notched edges and with minute warts or nearly smooth	Nearly smooth scales with a medial contraction, usually with one or two broad and straight ends or irregular shape	Irregular scales with a strong medial contraction and nearly smooth
Sclerites in tentacles	Arched butterfly scales and asymmetric planar scales with serrated edges	Curved and warty scales with different shapes	Curved scales with branched, forked or irregular shapes and with many fine coarse warts	Scales curved with irregular shape and many obvious warts
Location (depth)	Antarctica, Eastern Weddell Sea (1407–1581m)	NW Pacific, Philippines (150 and 186m) and South Japan waters (630m)	NW Pacific, Caroline Ridge, (1482–1573)	NW Pacific, Caroline Ridge (522m) and Philippines waters (691m)
Reference	Present study	Wright and Studer (1889); Xu et al. (2023)	Xu et al. (2023)	Versluys (1902); Kükenhal (1919); Xu et al. (2023)

2004; Forsman et al., 2010; Bilewitch et al., 2010; McFadden et al., 2010). These factors may also contribute to the challenge of distinguishing closely related species (e.g., Soler-Hurtado et al., 2017). Our mtMutS + COI analysis revealed two divergent sequences for *C. varians*. In this specific example, nine mtMutS sequences are archived in GenBank, with eight of them being identical and just one differing by a single base. Considering the suggestion that multilocus barcodes (mtMutS + COI) can discriminate approximately 70% of octocoral morphospecies (McFadden et al., 2011), even minor discrepancies, such as those observed in mtMutS, underline the need for additional research to uncover potential species complexes (McFadden et al., 2017) or genuine mtMutS variations, as indicated in certain gorgonians (Moore et al., 2016), pending further sequencing endeavors. RADseq analyzes on a selected number of *Chrysogorgia* species (Pante et al., 2015b) are broadly consistent with mtMutS hypotheses (~70% of species recovered in well-supported clades). However, they also identify potential cryptic speciation under identical sequences of mtMutS, as well as suggesting potential variability of mtMutS. Unfortunately, detailed morphological studies and molecular information of species in this genus are rarely presented together or encompass a limited number of species (Pante and Watling, 2012; Pante et al., 2015b; Xu et al., 2023). Therefore, it is challenging to more accurately assess the information provided by currently available mitochondrial and nuclear markers (e.g., mtMutS, COI, 28S) or other promising molecular techniques (e.g., RADseq, UCE). Moreover, discrepancies in the nuclear 28S gene, as evident in our phylogenetic tree for *C. acanthella*, *C. pendula*, and *C. cylindrata* (Fig. 10), align with findings by Xu et al. (2021b, 2023). The full utility of the 28S segment remains incompletely elucidated, despite its proven higher interspecific variability, as our results demonstrate. This characteristic has reinforced the discriminatory capacity of the proposed barcode mtMutS + COI+28S (McFadden and van Ofwegen, 2012; McFadden et al., 2014). Furthermore, a more comprehensive understanding of the multicopy nuclear 28S gene in octocorals is needed, akin to what is known for other previously employed markers (Gilbert et al., 2007; Concepcion et al., 2008).

5. Conclusions

The assignment of *C. lunae* sp. nov. to the genus *Chrysogorgia* was

supported by both morphological and phylogenetic results. The known species richness of this genus has been increased especially in recent decades (e.g. Cordeiro et al., 2015; Xu et al., 2023). However, more than half of *Chrysogorgia* species occur in the deep-sea and often inhabiting locations such as seamounts, and that also hinders their study (Watling et al., 2011; Pante et al., 2012). This frequently leads to situations where species such as *C. lunae* sp. nov. are described based on a limited number of specimens. Furthermore, environmental plasticity is characteristic of octocorals, whereby certain characters like colony shape may vary depending on the growth stage, occasionally obscuring species boundaries (Untiedt et al., 2021; Xu et al., 2023). In the case of *Chrysogorgia*, some morphological features remain highly consistent thus enabling differentiation among species, as demonstrated also in our study. This appears to be the case with the growth direction of the colony (clockwise or counterclockwise), as well as the morphology of the sclerites in different parts of the colony (Versluys, 1902; Cordeiro et al., 2015; Untiedt et al., 2021; Xu et al., 2023; present study). All the aforementioned factors emphasize the strong need for further studies in *Chrysogorgia* and other deep-water octocorals.

CRediT authorship contribution statement

Patricia Baena: Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Formal analysis, Data curation. **Luis Martell:** Writing – review & editing, Resources, Methodology, Investigation, Formal analysis. **Joan J. Soto-Angel:** Writing – review & editing, Resources, Methodology, Investigation, Formal analysis. **Stefano Ambroso:** Writing – review & editing. **Pablo J. López-González:** Writing – review & editing, Supervision, Resources, Investigation, Data curation.

Declaration of competing interest

The authors affirm the absence of any known financial or personal conflicts that might have influenced the work presented in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank the captain and crew of the RV Kronprins Haakon as well as Anne Helene Solberg Tandberg, Harald Steen and his scientific crew on the 2019 Norwegian Cruise to Kong Håkons Hav, Southern Ocean. We also wish to express our gratitude to Yu Xu, Zifeng Zhan, and Kuidong Xu for all the shared sequences and contributions, to Amy Baco-Taylor for additional information of the locality of some North Pacific *Chrysogorgia* materials, and to Andreu Santín for his contribution of ideas regarding the representation of results. PB had the institutional support of the “Severo Ochoa Centre of Excellence” accreditation (CEX2019-000928-S). LM and the sequencing of phylogenetic markers were supported by the Institute of Marine Research (IMR, Norway) via the projects ‘Antarktis’ and ‘CCAMLR’ (p. no 15208 and 81021-01). SEM study, sequencing of 28S marker, phylogenetic analyses and redaction of this paper were carried out under the project CTM2017-83920-P (DIVERSICORAL) funded by the Spanish Ministry of Economy, Industry and Competitiveness. The authors would like to thank the three anonymous reviewers and the Editorial Office of DSR-I for all their valuable comments and suggestions which helped to improve the quality of an early version of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2024.104234>.

References

- Arntz, W.E., Brey, T., Gerdes, D., Gorny, M., Gutt, J., Rain, S., Klages, M., 1992. Patterns of Life History and Population Dynamics of Benthic Invertebrates under the High Antarctic Conditions of the Weddell Sea in: 25th European Marine Biology Symposium, pp. 221–230.
- Auster, P.J., Gjerde, K., Heupel, E., Watling, L., Grehan, A., Rogers, A.D., 2011. Definition and detection of vulnerable marine ecosystems on the high seas: problems with the “move-on” rule. *ICES J. Mar. Sci.* 68, 254–264. <https://doi.org/10.1093/icesjms/fsq074>.
- Baena, P., Santín, A., la Mesa, M., Riginella, E., Owsianowski, N., Gili, J.-M., Ambroso, S., 2023. Are there distribution patterns and population structure differences among demersal fish species in relation to Antarctic benthic communities? A case study in the Weddell Sea. *Polar Biol.* 46 (10), 1069–1082. <https://doi.org/10.1007/s00300-023-03184-y>.
- Bayer, F.M., 1951. A new Caribbean coral of the genus *Chrysogorgia*. *Proc. U. S. Natl. Mus.* 101, 269–273.
- Bayer, F.M., Grasshoff, M., Verseveldt, J., 1983. Illustrated Trilingual Glossary of Morphological and Anatomical Terms Applied to Octocorallia. Brill Archive.
- Bayer, F.M., Stefani, J., 1988a. A new species of *Chrysogorgia* (Octocorallia: Gorgonacea) from New Caledonia, with descriptions of some other species from the Western Pacific. *Proc. Biol. Soc. Wash.* 101, 257–279.
- Bayer, F.M., Stefani, J., 1988b. Primnoidea (Gorgonacea) de Nouvelle-Calédonie. *Bull. Mus. Natl. Hist. Nat.* 10 (A), 449–518.
- Bayer, F.M., 1993. A new scleraxonian Octocoral (Coelenterata: Anthozoa) from antarctic waters. *Precious Corals Octocoral. Res.* 2, 11–18.
- Bennecke, S., Kwasnitschka, T., Metaxas, A., Wolf-Christian, D., 2016. In situ growth rates of deep-water octocorals determined from 3D photogrammetric reconstructions. *Coral Reefs* 35, 1227–1239. <https://doi.org/10.1007/s00338-016-1471-7>.
- Bilewicz, J.P., Coates, K.A., Currie, D.C., Trapido-Rosenthal, H.G., 2010. Molecular and morphological variation supports monotypy of the octocoral *Briareum Blainville*, 1830 (octocorallia: Alcyonacea) in the Western Atlantic. *Proc. Biol. Soc. Wash.* 123, 93–112. <https://doi.org/10.2988/09-22.1>.
- Braet, F., De Zanger, R., Wisse, E., 1997. Drying cells for SEM, AFM and TEM by hexamethyldisilazane: a study on hepatic endothelial cells. *J. Microsc.* 186, 84–87. <https://doi.org/10.1046/j.1365-2818.1997.1940755.x>.
- Brandt, A., De Broeyer, C., De Mesel, I., Ellingsen, K.E., Gooday, A.J., Hilbig, B., Linse, K., Thomson, M.R.A., Tyler, P.A., 2007. The biodiversity of the deep Southern Ocean benthos. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 362, 39–66. <https://doi.org/10.1098/rstb.2006.1952>.
- Bullimore, R.D., Foster, N.L., Howell, K.L., 2013. Coral-characterized benthic assemblages of the deep Northeast Atlantic: defining “Coral Gardens” to support future habitat mapping efforts. *ICES J. Mar. Sci.* 70, 511–522.
- Cairns, S.D., 2001. Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa) Part 1: the genus *Chrysogorgia* Duchassaing & Michelotti, 1864. *Proc. Biol. Soc. Wash.* 114, 746–787.
- Cairns, S.D., 2002. A new species of *Chrysogorgia* (Anthozoa: octocorallia) from the antarctic. *Proc. Biol. Soc. Wash.* 115, 217–222.
- Cairns, S.D., 2007. Calcaxonian octocorals (Cnidaria; Anthozoa) from Eastern Pacific seamounts. *Proc. Calif. Acad. Sci.* 58, 511–541.
- Cairns, S.D., Bayer, F.M., 2009. A generic revision and middle Missouri Plains phylogenetic analysis village sites of the Primnoidea. *Smithsonian Contrib. Zool.* 629, 1–86.
- Cairns, S.D., 2018. Deep-water octocorals (Cnidaria, Anthozoa) from the Galápagos and Cocos Islands. Part 1: Suborder Calcaxonina. *ZooKeys* 1–46. <https://doi.org/10.3897/zookeys.729.21779>.
- Cairns, S.D., Cordeiro, R.T., Xu, Y., Zhan, Z., Alderslade, P., 2021. A new family and two new genera of calcaxonian octocoral, including a redescription of *Pleurogorgia militaris* (Cnidaria: Octocorallia: Chrysogorgiidae) and its placement in a new genus. *Invertebrate Systemat.* 35 (3), 282–297.
- Clark, M.R., Bowden, D.A., 2015. Seamount biodiversity: high variability both within and between seamounts in the Ross Sea region of Antarctica. *Hydrobiologia* 761, 161–180. <https://doi.org/10.1007/s10750-015-2327-9>.
- Clarke, A., Crame, J.A., 1992. The Southern Ocean benthic fauna and climate change: a historical perspective. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 338 (1285), 299–309.
- Concepcion, G.T., Crepeau, M.W., Wagner, D., Kahng, S.E., Toonen, R.J., 2008. An alternative to ITS, a hypervariable, single-copy nuclear intron in corals, and its use in detecting cryptic species within the octocoral genus *Carijoca*. *Coral Reefs* 27, 323–336. <https://doi.org/10.1007/s00338-007-0323-x>.
- Cordeiro, R.T.S., Castro, C.B., Pérez, C.D., 2015. Deep-water octocorals (Cnidaria: Octocorallia) from Brazil: family Chrysogorgiidae Verrill, 1883. *Zootaxa* 4058 (1), 81–100. <https://doi.org/10.11646/zootaxa.4058.1.4>.
- FAO, 2009. International Guidelines for the Management of Deep-Sea Fisheries in the High Seas, p. 73 (Rome, Italy).
- France, S.C., Hoover, L.L., 2002. DNA sequences of the mitochondrial COI gene have low levels of divergence among deep-sea benthic macrofauna: the importance of local ecology, the larger scale, history and the Antarctic. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 51, 1689–1708. <https://doi.org/10.1016/j.dsr2.2004.07.013>.
- Genin, A., Dayton, P.K., Lonsdale, P.F., Spiess, F.N., 1986. Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. *Nature* 322, 59–61.
- Gilbert, M.T.P., Moore, W., Melchior, L., Worebey, M., 2007. DNA extraction from dry museum beetles without conferring external morphological damage. *PLoS One* 2, e272. <https://doi.org/10.1371/journal.pone.0000272>.
- Grasshoff, M., 1995. Outlines of Coelenterate evolution based on principles of constructional morphology. In: 6th International Conference on Coelenterate Biology.
- Grebmeier, J.M., Barry, J.P., 1991. The influence of oceanographic processes on pelagic-benthic coupling in polar regions: a benthic perspective. *J. Mar. Syst.* 2, 495–518. [https://doi.org/10.1016/0924-7963\(91\)90049-Z](https://doi.org/10.1016/0924-7963(91)90049-Z).
- Hellberg, M.E., 2006. No variation and low synonymous substitution rates in coral mtDNA despite high nuclear variation. *BMC Evol. Biol.* 6, 1–8. <https://doi.org/10.1186/1471-2148-6-24>.
- Hubbs, C.L., 1959. Initial discoveries of fish faunas on seamounts and offshore banks in the eastern Pacific. *Pac. Sci.* 13, 311–316.
- Huelsbeck, J.P., Ronquist, F., 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17, 754–755. <https://doi.org/10.1093/bioinformatics/17.8.754>.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *OIKOS* 69, 373–386.
- Katoh, K., Rozewicki, J., Yamada, K.D., 2019. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings Bioinf.* 20 (4), 1160–1166. <https://doi.org/10.1093/nar/gkt389>.
- Kimura, M., 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *J. Mol. Evol.* 16, 111–120. <https://doi.org/10.1007/s00239-009-9284-8>.
- Kinoshita, K., 1913. Studien über einige Chrysogorgiiden Japans. *J. Coll. Sci. Imp. Univ. Tokyo* 33, 1–47.
- Kükenthal, W., 1919. Gorgonaria. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer “Valdivia” 1898–1899*, pp. 1–946.
- Kükenthal, W., 1924. *Coelenterata: Gorgonaria Das Tierreich*, vol. 47. Walter de Gruyter & Co., Berlin, pp. 1–478.
- López-González, P.J., 2020. A new calcaxonian genus and family for *Trichogorgia utinomii* Cordeiro, 2019 (Octocorallia, Alcyonacea): new records of a scleriteless gorgonian species from Antarctica. *Mar. Biodivers.* 50, 1–13. <https://doi.org/10.1007/s12526-020-01109-0>.
- López-González, P.J., 2021. *Scytalium herklotsi* sp. nov. (Anthozoa, Octocorallia, Pennatulacea), the first Atlantic species in the genus *Scytalium* Herklots, 1858. *Mar. Biodivers.* 51, 62.
- López-González, P.J., 2022. Molecular phylogeny and morphological comparison of the deep-sea genus *Alloptilella* Li, Zhan & Xu, 2021 (octocorallia, Pennatulacea). *Mar. Biodivers.* 54, 41. <https://doi.org/10.1007/s12526-022-01260-w>.
- López-González, P.J., Drewery, J., 2022. When distant relatives look too alike: a new family, two new genera and a new species of deep-sea *Umbellula*-like sea pens (Anthozoa, Octocorallia, Pennatulacea). *Invertebr. Systemat.* 36, 199–225. <https://doi.org/10.1071/IS21040>.
- Madsen, J., 1944. Octocorallia. Danish Ingolf-Expedition V.

- Martínez-Díos, A., Domínguez-Carrió, C., Zapata-Guardiola, R., Gili, J.M., 2016. Deep-Sea Research I New insights on Antarctic gorgonians' age, growth and their potential as paleorecords. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 112, 57–67. <https://doi.org/10.1016/j.dsr.2016.03.007>.
- McFadden, C.S., Tullis, I.D., Hutchinson, M.B., Winner, K., Sohm, J.A., 2004. Variation in coding (NADH dehydrogenase subunits 2, 3, and 6) and noncoding intergenic spacer regions of the mitochondrial genome in Octocorallia (Cnidaria: Anthozoa). *Mar. Biotechnol.* 6, 516–526. <https://doi.org/10.1007/s10126-002-0102-1>.
- McFadden, C.S., Sánchez, J.A., France, S.C., 2010. Molecular phylogenetic insights into the evolution of octocorallia: a review. *Integr. Comp. Biol.* 50, 389–410. <https://doi.org/10.1093/icb/iccq056>.
- McFadden, C.S., Benayahu, Y., Pante, E., Jana, N.T., Nevarez, P.A., Scott, C.F., 2011. Limitations of mitochondrial gene barcoding in Octocorallia. *Mol. Ecol. Resour.* 11, 19–31. <https://doi.org/10.1111/j.1755-0998.2010.02875.x>.
- McFadden, C.S., Van Ofwegen, L.P., 2012. Stoloniiferous octocorals (Anthozoa, Octocorallia) from South Africa, with descriptions of a new family of Alcyonacea, a new genus of Clavulariidae, and a new species of *Cornularia* (Cornulariidae). *Invertebr. Systemat.* 26, 331–356. <https://doi.org/10.1071/IS12035>.
- McFadden, C.S., van Ofwegen, L.P., 2013. Molecular phylogenetic evidence supports a new family of octocorals and a new genus of Alcyoniidae (Octocorallia, Alcyonacea). *ZooKeys* 346, 59–83. <https://doi.org/10.3897/zookeys.346.6270>.
- McFadden, C.S., Brown, A.S., Brayton, C., Hunt, C.B., van Ofwegen, L.P., 2014. Application of DNA barcoding in biodiversity studies of shallow-water octocorals: molecular proxies agree with morphological estimates of species richness in Palau. *Coral Reefs* 33, 275–286. <https://doi.org/10.1007/s00338-013-1123-0>.
- McFadden, C.S., Haverkort-Yeh, R., Reynolds, A.M., Halász, A., Quattrini, A.M., Forsman, Z.H., Benayahu, Y., Toonen, R.J., 2017. Species boundaries in the absence of morphological, ecological or geographical differentiation in the Red Sea octocoral genus *Ovabunda* (Alcyonacea: Xenidae). *Mol. Phylogenet. Evol.* 112, 174–184. <https://doi.org/10.1016/j.ympev.2017.04.025>.
- McFadden, C.S., Van Ofwegen, L.P., Quattrini, A.M., 2022. Revisionary systematics of Octocorallia (Cnidaria: Anthozoa) guided by phylogenomics. *Bull. Soc. Syst. Biol.* 1 <https://doi.org/10.18061/bssb.v1i3.8735>.
- McFadden, C.S., Cordeiro, R., Williams, G., van Ofwegen, L., 2023. World List of Octocorallia. *Chrysogorgiidae Verrill*, vol. 1883. Accessed through: World Register of Marine Species at: <https://www.marinespecies.org/aphia.php?p=taxdata&ls&id=125273>. on 2023-11-17.
- Moore, K., Alderslade, P., Miller, K., 2016. A taxonomic revision of the genus *Primois* Studer [& Wright], 1887 (Coelenterata: Octocorallia: Isidiidae) using morphological and molecular data. *Zootaxa* 4075 (1), 1–141. <https://doi.org/10.11646/zootaxa.4075.1.1>.
- Muthye, V., Mackereth, C.D., Stewart, J.B., Lavrov, D.V., 2022. Large dataset of octocoral mitochondrial genomes provides new insights into mt-mutS evolution and function. *DNA Repair* 110, 103273. <https://doi.org/10.1016/j.dnarep.2022.103273>.
- Nation, J.L., 1983. A new method using hexamethylsilazane for preparation of soft insect tissues for scanning electron microscopy. *Biochem. Biophys. Res. Commun.* 58, 347–351. [https://doi.org/10.1016/0014-7167\(83\)90966-8](https://doi.org/10.1016/0014-7167(83)90966-8).
- Núñez-Flores, M., Gómez-Uchida, D., López-González, P.J., 2020. Molecular and morphological data reveal three new species of *Thouarella* Gray, 1870 (Anthozoa : Octocorallia : Primnoidae) from the Southern Ocean. *Mar. Biodivers.* 50 (3), 30.
- Orejas, C., Gili, J.M., Arntz, W.E., Ros, J.D., López, P.J., Teixidó, N., Filipe, P., 2000. Benthic suspension feeders, key players in Antarctic marine ecosystems? *Contrib. Sci. (Los Angel.)* 1, 299–311.
- Pante, E., France, S.C., 2010. *Pseudochrysogorgia bellona* n. gen., n. sp.: a new genus and species of chrysogorgiid octocoral (Coelenterata, Anthozoa) from the Coral Sea. *Zoosystema* 32, 595–612. <https://doi.org/10.5252/z2010n4a4>.
- Pante, E., France, S.C., Couloux, A., Cruaud, C., McFadden, C.S., Samadi, S., Watling, L., 2012. Deep-Sea origin and in-situ Diversification of chrysogorgiid Octocorals. *PLoS One* 7, e38357.
- Pante, E., Watling, L., 2012. *Chrysogorgia* from the new England and corner seamounts : Atlantic - Pacific connections. *J. Mar. Biol. Assoc. U. K.* 92, 911–927. <https://doi.org/10.1017/S0025315411001354>.
- Pante, E., Abdelkrim, J., Viricel, A., Gey, D., France, S.C., Boisselier, M.C., Samadi, S., 2015b. Use of RAD sequencing for delimiting species. *Heredity* 114 (5), 450–459. <https://doi.org/10.1038/hdy.2014.105>.
- Pante, E., France, S.C., Gey, D., Cruaud, C., Samadi, S., 2015a. An inter-ocean comparison of coral endemism on seamounts: the case of *Chrysogorgia*. *J. Biogeogr.* 42, 1907–1918. <https://doi.org/10.1111/jbi.12564>.
- Pérez, C.D., Neves, B. de M., Cordeiro, R.T., Williams, G.C., Cairns, S.D., 2016. Diversity and distribution of Octocorallia. In: *The Cnidaria, Past, Present and Future*, pp. 1–855. <https://doi.org/10.1007/978-3-319-31305-4>.
- Prada, C., Schizas, N.V., Yoshioka, P.M., 2008. Phenotypic plasticity or speciation ? A case from a clonal marine organism. *BMC Evol. Biol.* 8 (1), 1–19. <https://doi.org/10.1186/1471-2148-8-47>.
- Quattrini, A.M., Georgian, S.E., Byrnes, L., Stevens, A., Falco, R., Cordes, E.E., 2013. Niche divergence by deep-sea octocorals in the genus *Callogorgia* across the continental slope of the Gulf of Mexico. *Mol. Ecol.* 22, 4123–4140. <https://doi.org/10.1111/mec.12370>.
- Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A., 2018. Posterior summarization in Bayesian phylogenetics using tracer 1.7. *Syst. Biol.* 67, 901. <https://doi.org/10.1093/sysbio/syy032>. –4.
- Ramírez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C.R., Levin, L.A., Martínez Arbizu, P., Menot, L., Buhl-mortensen, P., Narayanaswamy, B. E., Smith, C.R., Tittensor, D.P., Tyler, P.A., Vanreusel, A., Vecchione, M., 2010. Deep , diverse and definitely different : unique attributes of the world's largest ecosystem. *Biogeosciences* 7, 2851–2899. <https://doi.org/10.5194/bg-7-2851-2010>.
- Richer de Forges, B.R., Koslow, J.A., Poore, G.C.B., 2000. Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature* 405, 944–947. <https://doi.org/10.1038/35016066>.
- Roberts, J.M., 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science* 312 (5773), 543–547. <https://doi.org/10.1126/science.1119861>.
- Sánchez, J.A., McFadden, C.S., France, S.C., Lasker, H.R., 2003. Molecular phylogenetic analyses of shallow-water Caribbean octocorals. *Mar. Biol.* 142, 975–987. <https://doi.org/10.1007/s00227-003-1018-7>.
- Shearer, T.L., Van Oppen, M.J.H., Romanos, S.L., Wörheide, G., 2002. Slow mitochondrial DNA sequence evolution in the Anthozoa (Cnidaria). *Mol. Ecol.* 11, 2475–2487.
- Soler-Hurtado, M.M., Megina, C., Machordom, A., López-González, P.J., 2017. Foxed intra- and interspecific differentiation in *Leptogorgia* (Octocorallia: Gorgoniidae). A description of a new species based on multiple sources of evidence. *Sci. Mar.* 81, 147–157. <https://doi.org/10.3989/scimar.04509.01C>.
- Starman, A., Gutt, J., Arntz, W.E., 1999. Mega-epibenthic communities in Arctic and Antarctic shelf areas. *Mar. Biol.* 135, 269–280.
- Tamura, K., Stecher, G., Peterson, D., Filipiński, A., Kumar, S., 2013. MEGA6: molecular evolutionary genetics analysis version 6.0. *Mol. Biol. Evol.* 30, 2725–2729. <https://doi.org/10.1093/molbev/mst197>.
- Thoma, J.N., Pante, E., Brugler, M.R., France, S.C., 2009. Deep-sea octocorals and antipatharians show no evidence of seamount-scale endemism in the NW Atlantic. *Mar. Ecol. Prog. Ser.* 397, 25–35. <https://doi.org/10.3354/meps08318>.
- Untiedt, C.B., Quattrini, A.M., McFadden, C.S., Alderslade, P.A., Pante, E., Burridge, C.P., 2021. Phylogenetic relationships within *Chrysogorgia* (Alcyonacea: Octocorallia), a morphologically diverse genus of Octocoral, Revealed using a target enrichment approach. *Front. Mar. Sci.* 7 <https://doi.org/10.3389/fmars.2020.599984>.
- Versluys, J., 1902. Die gorgoniden der siboga-expedition. i. die Chrysogorgiiden. *Siboga Expeditie* 13, 1–120.
- Vollmer, S.V., Palumbi, S.R., 2004. Testing the utility of internally transcribed spacer sequences in coral phylogenetics. *Mol. Ecol.* 13, 2763–2772.
- Watling, L., 2007. A review of the genus *Iridogorgia* (Octocorallia: Chrysogorgiidae) and its relatives, chiefly from the North Atlantic Ocean. *J. Marine Biol. Assoc. United Kingdom* 87 (2), 393–402.
- Watling, L., France, S.C., Pante, E., Simpson, A., 2011. Biology of deep-water Octocorals. *Adv. Mar. Biol.* 60, 41–122. <https://doi.org/10.1016/B978-0-12-385529-9.00002-0>.
- Wright, E.P., Studer, T., 1889. Report on the alcyonaria collected by HMS "challenger" during the years 1873–1876. Report on the scientific results of the exploring voyage of HMS challenger-1873-76. *Zoology* 31.
- Xu, Y., Li, Y., Zhan, Z., Xu, K., 2019. Morphology and phylogenetic analysis of two new deep-sea species of *Chrysogorgia* (Cnidaria, Octocorallia, Chrysogorgiidae) from Kocebu Guyot (Magellan seamounts) in the Pacific Ocean. *ZooKeys* 881, 91–107. <https://doi.org/10.3897/zookeys.881.34759>.
- Xu, Y., Zhan, Z., Xu, K., 2020. Morphology and molecular phylogeny of three new deep-sea species of *Chrysogorgia* (Cnidaria, Octocorallia) from seamounts in the tropical Western Pacific Ocean. *PeerJ* 8, e8832. <https://doi.org/10.7717/peerj.8832>.
- Xu, Y., Zhan, Z., Xu, K., 2021a. Morphological and molecular characterization of five species including three new species of golden gorgonians (Cnidaria : Octocorallia) from seamounts in the Western Pacific. *Biology* 10 (7), 558.
- Xu, Y., Zhan, Z., Xu, K., 2021b. Morphology and phylogeny of *Chrysogorgia pinniformis* sp. nov. and *C. varians* sp. nov., two golden corals from the Caroline seamounts in the tropical Western Pacific Ocean. *J. Oceanol. Limnol.* 39, 1767–1789. <https://doi.org/10.1007/s00343-021-0386-5>.
- Xu, Y., Zhan, Z., Xu, K., 2023. Studies on western Pacific gorgonians (Anthozoa: Octocorallia, Chrysogorgiidae). Part 1: a review of the genus *Chrysogorgia*, with description of a new genus and three new species. *Zootaxa* 5321 (1), 1–107.