Pseudochrysogorgia bellona n. gen., n. sp.: a new genus and species of chrysogorgiid octocoral (Coelenterata, Anthozoa) from the Coral Sea

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ABSTRACT
A new genus and species of deep-sea Chrysogorgiidae Verrill, 1883, *Pseudochrysogorgia bellona* n. gen. n. sp., is described from colonies collected in the Coral Sea, West of New Caledonia (southwestern Pacific Ocean). These specimens bear resemblance to the genera *Chrysogorgia* Duchassaing & Michelotti, 1864 (dichotomously-subdivided branches arising from the main stem in a spiraling fashion; polyps characterized by ornamented sclerites) and *Metallogorgia* Versluys, 1902 (colony monopodial, hexagonal branching pattern). Additional material collected North of New Zealand (Otara Seamount) is used to complete the description of this new genus. Its taxonomic rank is discussed in light of morphology- and DNA-based phylogenetic inference and analysis of genetic distances among deep-sea chrysogorgiid genera.

KEY WORDS
Cnidaria,
Coelenterata,
Anthozoa,
Octocorallia,
Calcaxonia,
Chrysogorgiidae,
New Caledonia,
New Zealand,
monopodial stem,
new genus,
new species.

RÉSUMÉ
Pseudochrysogorgia bellona *n. gen, n. sp. : un genre nouveau et une nouvelle espèce d'octocorail Chrysogorgiidae (Coelenterata, Anthozoa) de la Mer de Corail.*
Un nouveau genre et une nouvelle espèce de Chrysogorgiidae Verrill, 1883 de grande profondeur, *Pseudochrysogorgia bellona* n. gen., n. sp., sont décrits à partir de colonies échantillonnées en Mer de Corail, à l'ouest de la Nouvelle-Calédonie (Pacifique sud-ouest). Ces spécimens ressemblent aux genres *Chrysogorgia* Duchassaing & Michelotti, 1864 (branches subdivisées de façon dichotomique et émergeant du tronc principal en spirale ; polypes caractérisés par des sclérites ornementés) et *Metallogorgia* Versluys, 1902 (colonie monopodiale, ramification des branches selon un motif hexagonal). Du matériel supplémentaire, prélevé au nord de la Nouvelle-Zélande (Otara Seamount), est utilisé pour compléter la description de ce nouveau genre. Son rang taxonomique est discuté à partir d'une analyse phylogénétique basée sur des données morphologiques et moléculaires, ainsi qu'à partir d'une analyse des distances génétiques entre les genres de coraux chrysogorgiidés.

MOTS CLÉS
Cnidaria,
Coelenterata,
Anthozoa,
Octocorallia,
Calcaxonia,
Chrysogorgiidae,
Nouvelle-Calédonie,
Nouvelle-Zélande,
tronc monopodial,
nouveau genre,
nouvelle espèce.

INTRODUCTION

The family Chrysogorgiidae Verrill, 1883 is distributed worldwide within a wide depth-range (10 to 3375 m; Cairns 2001). Most species (> 75%) seem restricted to deep water, inhabiting soft and hard bottoms. Although there is no published quantification of their abundance, chrysogorgiids are considered relatively common by deep-sea biologists, and often co-occur with isidids and primnoids. Recent expeditions using remotely-operated vehicles (ROVs) (MOUNTAINS-IN-THE-SEA, 2003-2004 and DEEP ATLANTIC STEPPING STONES, 2005; northwestern Atlantic) revealed chrysogorgiids as among the tallest and most majestic octocoral colonies inhabiting the Corner and New England Seamounts (Watling 2007).

While a few genera are relatively diverse, most comprise few species, and are known from only a few specimens. For instance, the genus *Chrysogorgia* Duchassaing & Michelotti, 1864 (> 60 nominal species) is one of the most speciose of the 274 alcyonacean genera, yet 12 of the 13 chrysogorgiid genera consist of fewer than 10 nominal species. This "taxonomic asymmetry" could be due to the evolutionary history of the family. However, the relatively limited number of taxonomists working on the Chrysogorgiidae, and the difficulty of obtaining specimens (most chrysogorgiids are found in the deep-sea), could significantly bias our view of the diversity within this group.

The Muséum national d'Histoire naturelle, Paris, hosts a large collection of octocorals from cruises that were aimed at describing biodiversity in the Indo-Pacific (Tropical Deep-Sea Benthos program; formerly MUSORSTOM). The present contribution is part of a larger research effort aiming at characterizing the chrysogorgiid fauna from these collections. Herein, we describe *Pseudochrysogorgia bellona* n. gen. n. sp., a new genus and species within the family Chrysogorgiidae, provide a revised dichotomous key to the common deep-sea genera of chrysogorgiid corals, and present for the first time SEM photographs for the polyps and sclerites of *Metallogorgia* Versluys, 1902, phylogenetically the closest relative of *Pseudochrysogorgia* n. gen. Comparing polyps and sclerites of *Metallogorgia* and *Pseudochrysogorgia* n. gen. will help to distinguish these genera unequivocally.

MATERIAL AND METHODS

Abbreviations

CP	chalut à perche (beam trawl);
EBISCO	Exploration de la Biodiversité et Isolement en Mer de Corail;
MNHN	Muséum national d'Histoire naturelle, Paris;
NIWA	National Institute of Water & Atmospheric Research, Wellington;
SEM	scanning-electron microscopy;
stn	station;
USNM	United States National Museum, Washington DC.

Material

This study is based on the examination of two colonies collected in October 2005 during the cruise EBISCO (Tropical Deep-sea Benthos program; French vessel NO *Alis*), organized by the MNHN. Both colonies were trawled at the same station on the Bellona Plateau, West of New Caledonia (southwestern Pacific Ocean). Colonies were preserved in 80% ethanol and are deposited at the MNHN. Additional material was provided by the NIWA Invertebrate Collection. These colonies were collected in November 2004 on Otara Seamount, on the southern end of the Kermadec Ridge, North of New Zealand. They were preserved in ethanol, and are held at the NIWA. We were not able to examine whole specimens from the NIWA collection, and therefore we were not able to assess all morphological characters. However, we could establish that polyp and sclerite morphology, and sclerite orientation were consistent with the MNHN material. In addition, DNA sequences from the mitochondrial gene *msh1* were identical. There is therefore little doubt that these specimens belong to the same taxon as the MNHN material. NIWA 16273 was preserved with an intact holdfast, which is absent from all other colonies available. This specimen was therefore included in the type series. Comparative material of *Chrysogorgia* and *Metallogorgia* was made available by the MNHN and the NIWA. These specimens are *C. admete* Bayer & Stefani, 1988 (holotype; MNHN-IC.0000-0274), *M. melanotrichos* (Wright & Studer, 1889) (NIWA 43024) and *M. macrospina* Kükenthal, 1919 (MNHN-IK-2008-1042). Polyps from MAN806-1, a specimen of *M. melanotrichos* collected on Manning Seamount (NW Atlantic) in

TABLE 1. — List of specimens examined in this study. Specimens with three associated GenBank accession numbers were used in the DNA-based phylogenetic analysis. Where there is only one GenBank accession number, it corresponds to *msh1*. The isolate corresponds to the genetic subsample maintained in the SCF Lab at UL Lafayette. Voucher in italics: type material.

Species	Isolate	Voucher	Sampling	Depth (m)	Lat.	Long.	GenBank (*msh1*, *cox1*, 18S)
Calyptrophora wyvillei Wright, 1885	LAD36	USNM 98815	20.IX.1996	1225	20.470	-157.149	EU293801, GQ868317, HM590863
Narella dichotoma Versluys, 1906	LAD12	USNM 98831	20.IX.1996	1451	20.470	-157.149	EU293800, GQ868316, HM590862
Chrysogorgia admete Bayer & Stefani, 1988	340617	*MNHN-IC. 0000-0274*	13.IV.1978	390	-22.817	167.200	
Chrysogorgia chryseis Bayer & Stefani, 1988	CR106-2		18.VIII.1993	1010	18.777	-158.247	DQ297421, GQ868308, AF052913
Iridogorgia magnispiralis Watling, 2007	KEL403-2	*YPM 38580*	19.V.2004	2311	38.779	-63.963	DQ860108, DQ860111, FJ526216
Metallogorgia macrospina Kükenthal, 1919	HAL2033-2	MNHN-IK-2008-1042	12.XI.1996	699-1280	-25.317	168.967	
Metallogorgia melanotrichos (Wright & Studer, 1889)	LYM210-1		14.VIII.2005	2143	35.194	-47.677	GQ180151, FJ268630, FJ526214
Metallogorgia melanotrichos	MAN806-1		16.V.2004	1485	38.144	-61.941	
Metallogorgia melanotrichos	NIWA 43024	NIWA 43024	11.II.1996	1292-1496	-35.366	178.553	GQ180146
Pseudochrysogorgia bellona n. gen., n. sp.	EBI 2557-1	*MNHN-IC. 2008-006*	12.X.2005	800-923	-21.117	158.500	GQ868331
Pseudochrysogorgia bellona n. gen., n. sp.	EBI 2557-2	*MNHN-IC. 2008-007*	12.X.2005	800-923	-21.117	158.500	GQ868332, GQ868310, HM590865
Pseudochrysogorgia bellona n. gen., n. sp.	NIWA 15611	NIWA 15611	9.XI.2004	1396-1462	-36.960	177.332	
Pseudochrysogorgia bellona n. gen., n. sp.	NIWA 16272	NIWA 16272	10.XI.2004	1323-1346	-36.947	177.335	
Pseudochrysogorgia bellona n. gen., n. sp.	NIWA 16273	*NIWA 16273*	10.XI.2004	1323-1346	-36.947	177.335	
Radicipes gracilis (Verrill, 1884)	100900	USNM 100900	5.XII.2000		39.883	-67.437	DQ297424, HM590861, HM590864

May 2004 at 1485 m depth, and held in our lab, were used in SEM preparations (Table 1).

MORPHOLOGY

The colonies were initially found by the authors in the collections of the MNHN in 2007, photographed and sampled for genetics. Given the genetic divergence between these specimens and other chrysogorgiids at multiple loci, the specimens were re-examined in more detail in 2008. Therefore, the photographs accompanying the manuscript correspond to the colony after removal of multiple branches for genetic analyses. Measurements (e.g., colony height) were taken directly on the colony when possible, or from photographs using the program ImageJ (Abramoff *et al.* 2004; Rasband 1997-2008) when measuring directly was not practical (e.g., measurement of angles). All measurements of sclerites were done from light microscope imagery using ImageJ. Sclerite lengths are reported as mean ± one standard deviation. Polyps

TABLE 2. Morphological characteristics of the holotype and paratype of *Pseudochrysogorgia bellona* n. gen., n. sp. Abbreviations: **n**, sample size; **rg**, range; **x̄**, mean ± one standard deviation.

Specimen	MNHN-IC.2008-006 (holotype)	MNHN-IC.2008-007 (paratype)
Colony height (cm)	36.5, stem broken at the base	37, stem broken at the base
Colony width (cm)	11.5-13	9-13
Stem diameter at the base (mm)	3	2.5
Stem diameter at the tip (mm)	1.5	1
Branch diameter at the base (mm)	n = 6, rg: 1.4-1.7, $\bar{x}$ = 1.65 ± 0.20	n = 6, rg: 1.2-1.6, $\bar{x}$ = 1.33 ± 0.16
Branch diameter at the tip (mm)	n = 6, rg: 0.3-0.7, $\bar{x}$ = 0.52 ± 0.13	n = 6, rg: 0.3-0.5, $\bar{x}$ = 0.37 ± 0.08
Branching sequence	2/7R	irregular, L
Branch anastomosis occurring?	yes, minor	yes, important
Distance between branches along the stem (cm)	n = 7, rg: 1.13-1.72, $\bar{x}$ = 1.39 ± 0.19	n = 12, rg: 0.99-1.7, $\bar{x}$ = 1.28 ± 0.24
Orthostiche distance (Versluys 1902) (cm)	9.7	8
Distance between branch nodes (mm)	n = 15, rg: 8-12, $\bar{x}$ = 9.5 ± 1.4	n = 18, rg: 7.6-12.3, $\bar{x}$ = 9.8 ± 1.6
Angle between main stem and branches (°)	rg: 90-115	rg: 100-120
Angle between branches (°)	rg: 100-120	rg: 100-130
Number of nodes / branch	n = 7, rg: 11-39, $\bar{x}$ = 23.29 ± 11.50	n = 5, rg: 10-23, $\bar{x}$ = 17 ± 5.83
Number of polyps / branch internode	0-1, never on 1st internode, occasionally on 2nd internode, always on 3rd internode	0-1, never on 1st internode, occasionally on 2nd internode, always on 3rd internode
Number of polyps / branch tip	2	1-3
Position of polyps on branch internodes	mostly equidistant from nodes	mostly equidistant from nodes
Presence of coenenchyme between polyps	yes	yes
Polyp width (mm)	n = 16, rg: 1.8-3.5, $\bar{x}$ = 2.7 ± 0.50	n = 37, rg: 1.7-3.0, $\bar{x}$ = 2.5 ± 0.37
Polyp height (mm)	n = 19, rg: 2.0-3.0, $\bar{x}$ = 2.7 ± 0.26	n = 30, rg: 1.7-3.3, $\bar{x}$ = 2.7 ± 0.42
Length of sclerites from branch coenenchyme (µm)	n = 43, rg: 115-337, $\bar{x}$ = 218 ± 66	n = 292, rg: 89-319, $\bar{x}$ = 292 ± 45
Length of sclerites from body wall (µm)	n = 235, rg: 37-626, $\bar{x}$ = 272 ± 108	n = 421, rg: 69-425, $\bar{x}$ = 199 ± 80
Length of sclerites from tentacles (µm)	n = 8, rg: 98-439, $\bar{x}$ = 273 ± 100	n = 61, rg: 20-483, $\bar{x}$ = 172 ± 99

were incubated in a solution of 5% glutaraldehyde (buffered with KH_2PO_4 and Na_2HPO_4 at pH 6.8) overnight to help anchor sclerites to the tissues. They were then exposed to 20% bleach for a few seconds to dissolve the epithelium covering the sclerites and make their arrangement more visible. Without exposure to glutaraldehyde, sclerites tended to fall off the polyp before the epithelium could successfully be removed. Polyps were then photographed using depth-of-field enhancement with a Keyence VHX-1000 digital microscope. Different polyps were dissected to separate tentacles, body wall and coenenchyme along branches, and tissues were then dissolved using bleach. Sclerites were rinsed multiple times in deionized water and mounted on SEM stubs using double-faced tape. Polyps were removed from branches, dehydrated in 100% acetone, and dried using a Denton DV-2 critical-point dryer. Digital images of sclerites and polyps were generated using a Hitachi S-3000N scanning-electron microscope.

DATA ANALYSIS

Phylogenetic inference

The phylogenetic position of *Pseudochrysogorgia* n. gen. relative to the monophyletic, deep-sea Chrysogorgiidae (see Systematics below) was assessed using morphological and genetic data. Morphological characters distinguishing deep chrysogorgiid genera were coded as unordered, binary or multistate characters (Tables 3-4). Phylogenetic trees derived from morphological data were generated in PAUP* version 4.0b10 (Swofford 1998) using maximum parsimony. The primnoid genera *Narella* Gray, 1870 and *Calyptrophora* Gray, 1866 were chosen as outgroups (for the placement of the Primnoidae relative to the Chrysogorgiidae in a genus-level molecular phylogeny of the Octocorallia, see McFadden *et al.* 2006). Characters distinguishing chrysogorgiids from primnoids were defined according to Bayer (1981).

The genetic analysis was run on a 5031-bp DNA alignment composed of the nearly complete *msh1* gene

TABLE 3. — Characters and character states used in the morphology-based phylogenetic analysis of the deep Chrysogorgiidae. A dash indicates that the character was inapplicable. Abbreviations: **CI**, consistency index.

Character	States	CI
Morphology of the colony		
1. holdfast can be dendritic	0, no; 1, yes	0.5
2. colony branching	0, whip; 1, primary branching; 2, secondary branching	0.667
3. prevalent scarring along axis in adults	–, cannot score; 0, absent; 1, present	1
4. morphology of main stem	–, cannot score; 0, dichotomous; 1, monopodial; 2, sympodial	1
5. colony shape	–, cannot score; 1, bush / planar / flabellate; 2, wide spiral; 3, cluster of branches at the distal end of the axis	0.667
Morphology of calyces		
6. coordination of polyps	0, aligned and equidistant; 1, not aligned, not always equidistant; 2, whorl	1
7. orientation of calices	0, up (distad); 1, perpendicular	0.5
8. crown can be larger than neck	0, no; 1, yes	0.5
Morphology and placement of sclerites		
9. sclerite ornamentation	0, smooth; 1, ornamented	1
10. sclerite zonation	0, no zonation; 1, zonation (tentacles / body / coenenchyme)	1
Characters to differentiate chrysogorgiids from outgroup		
11. polyp sclerites form suit of armor	0, no; 1, yes	1
12. crystal orientation in scales is radial	0, no; 1, yes	1
13. surface of axis longitudinally grooved	0, no; 1, yes	1
14. concentric layers of axis undulating in cross section	0, no; 1, yes	1

(2950 bp), a fragment of the *cox1* gene (786 bp), and a fragment of the 18S gene (1295 bp). *Calyptrophora wyvillei* Wright, 1885 and *Narella dichotoma* Versluys, 1906 were assigned as outgroup taxa. The ingroup is composed of *Chrysogorgia chryseis* Bayer & Stefani, 1988, *Iridogorgia magnispiralis* Watling, 2007, *M. melanotrichos* (LYM210-1) and *Radicipes gracilis* (Verrill, 1884). *Pseudochrysogorgia bellona* n. gen, n. sp. is represented by MNHN-IC.2008-007 (Table 1). MEGA 4 was used to construct a maximum-parsimony tree using the max-mini branch-and-bound search (Tamura *et al.* 2007). PhyML version 3.0 (Guindon & Gascuel 2003) was used to produce a maximum-likelihood tree using the GTR+G model of evolution (model selection performed in jModelTest; Posada 2008). A more detailed phylogenetic reconstruction of the Chrysogorgiidae is in preparation (Pante & France unpublished). For all phylogenetic inferences, 1000 bootstrap replicates were run to estimate node support.

Molecular divergence between genera

Genetic distance can be used as a "yardstick" to estimate divergence among and between taxonomic units (Avise 2004). In theory, if the taxonomic classification reflects evolutionary history, genetic distances within genera should be lower than genetic distances between genera. Genetic distances can therefore inform us on the appropriateness of taxonomic classification, relative to evolutionary history. Genetic distances were computed between 129 individual chrysogorgiid specimens in a pairwise manner using the Kimura 2-parameter (K2P) model of nucleotide substitution (Kimura 1980). The first 700 bp of *msh1* were used as the "genetic yardstick" (McFadden *et al.* 2010). Distributions of K2P distances were presented as frequency histograms. Computations and plotting were done in R (R Development Core Team 2010) using the package APE (Paradis *et al.* 2004).

TABLE 4. — Character matrix used in the morphology-based phylogenetic analysis, as defined by Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Narella	0	1	0	0	0	2	1	1	1	1	1	1	1	1
Calyptrophora	0	2	0	0	1	2	0	0	1	1	1	1	1	1
Radicipes	1	0	–	–	–	0	0	0	0	0	0	0	0	0
Chrysogorgia	1	2	0	2	0	1	1	1	1	1	0	0	0	0
Iridogorgia	0	1	0	1	1	0	1	0	0	0	0	0	0	0
Metallogorgia	0	2	1	1	2	1	1	0	0	0	0	0	0	0
Pseudochrysogorgia n. gen.	1	2	0	1	0	1	1	1	1	1	0	0	0	0

SYSTEMATICS

CLASSIFICATION OF *PSEUDOCHRYSOGORGIA N. GEN.* IN THE FAMILY CHRYSOGORGIIDAE

There is strong phylogenetic support for the monophyly of the common deep-sea chrysogorgiid genera, namely *Chrysogorgia*, *Metallogorgia*, *Iridogorgia* Verrill, 1883, *Rhodaniridogorgia* Watling, 2007 and *Radicipes* Stearns, 1883 (based on multiple nuclear and mitochondrial markers; Pante & France 2008: abstract). *Pseudochrysogorgia* n. gen. clusters with strong statistical support with the genera listed above, its closest relative being *Metallogorgia* (Pante & France 2008: abstract; Fig. 8). Based on the current state of knowledge on the monophyly of genera within the family Chrysogorgiidae, a new key to the common deep-sea Chrysogorgiidae is presented. This key, modified from that of Bayer & Stefani (1988), includes the recently-described *Rhodaniridogorgia* and recent observations from Mosher & Watling (2009) on variation of branching patterns with age in *Metallogorgia*. It also groups *Iridogorgia*, *Pseudochrysogorgia* n. gen. and *Metallogorgia* based on their monopodial growth.

KEY TO THE COMMON DEEP-SEA GENERA OF CHRYSOGORGIIDAE VERRILL, 1883

1. Colonies unbranched, flagelliform and spirally twisted ..... *Radicipes*
— Colonies branched. Terminal branches originating directly from the main stem or after bifurcations of primary branches 2

2. Colonies sympodial, branches originate in a regular spiral around the main stem, or forming two parallel fans at the top of a short trunk. Axial skeleton has brilliant metallic luster; flexibility variable among species ..... *Chrysogorgia*
— Colonies monopodial and not flabellate 3

3. Terminal branches undivided, arising from the outside of a golden, upward-spiraling main stem 4
— Branching in multiple planes, branches subdividing dichotomously. Axis strongly calcified, with dark, metallic luster 5

4. Main stem coiled, not wavy; presence of sclerites in the coenenchyme along branches depending on species ..... *Iridogorgia*
— Main stem wavy, not coiled; array of sclerite shapes wider than in *Iridogorgia*, sclerites consistently present in the coenenchyme along branches ..... *Rhodaniridogorgia*

5. Abundant, dichotomously-subdivided branches originate in an irregular or regular spiral around a tall, upright main stem. Distance between branches along the stem short (< 2cm) and regular. Polyps with ornamented sclerites of irregular shape, in the form of plates, scales and rods ..... *Pseudochrysogorgia* n. gen.

— Dichotomously-subdivided branches arising from the top of a tall, upright main stem. Juvenile colonies have additional branches arising around the main stem. In this case, distance between branches along the stem are wide ranging (up to 10 cm) and irregular. Older colonies typically bear scars of past side branches along the main stem. Sclerites in the form of rods and scales, with little ornamentation ..... *Metallogorgia*

Subclass OCTOCORALLIA Haeckel, 1866
Order ALCYONACEA Lamouroux, 1816
Sub-order CALCAXONIA Grasshoff, 1999
Family CHRYSOGORGIIDAE Verrill, 1883

Genus *Pseudochrysogorgia* n. gen.

TYPE SPECIES. — *Pseudochrysogorgia bellona* n. gen., n. sp.

ETYMOLOGY. — The greek prefix "pseudo", meaning "false" or "fake", is appended to *Chrysogorgia* in allusion to the morphological resemblance between this new taxon and the established *Chrysogorgia*. This resemblance is reflected by the morphology-based parsimony analysis, in which *Pseudochrysogorgia* n. gen. appears most closely related to *Chrysogorgia* rather than *Metallogorgia*, its sister taxon based on genetics (Fig. 8). Therefore, this combination was chosen over a combination involving *Metallogorgia* because misidentification of this new taxon for *Chrysogorgia* is more likely than misidentification for *Metallogorgia*. Gender is feminine.

DIAGNOSIS. — The colony is bottlebrush-shaped, and its main axis is monopodial, slightly zigzagging. Branches are subdividing dichotomously in multiple planes. Branch subdivision occurs at a relatively constant angle averaging 120°, resulting in hexagonal patterns. Over half of the polyps are leaning distad. The neck can be narrower than the head. On average, polyps are as wide as they are tall. Sclerites are slightly ornamented, in the form of plates, scales and rods. When the polyp is not leaning distad, sclerites are arranged obliquely on the polyp body. When polyps are leaning distad, sclerites are 1) mostly longitudinally arranged (parallel to the branch) on the polyp body, 2) placed obliquely in the area of the neck, and 3) longitudinally arranged on the head and along the back of the tentacles. The branch coenenchyme contains sclerites in the form of scales and plates that are mostly parallel to main branch axis.

Pseudochrysogorgia bellona n. gen., n. sp.
(Figs 1-6; Tables 1, 2)

HOLOTYPE. — **W of New Caledonia.** Bellona Plateau, EBISCO stn CP 2557 (MNHN-IC.2008-006).

PARATYPES. — **W of New Caledonia.** Bellona Plateau, EBISCO stn CP 2557 (MNHN-IC.2008-007).
N of New Zealand. Otara Seamount, stn TAN0413/41 (NIWA 16273).

ETYMOLOGY. — The specific epithet refers to the type locality. Noun in apposition.

ADDITIONAL MATERIAL EXAMINED. — Only polyps were examined (see note in Material and methods section).
N of New Zealand. Otara Seamount, stn TAN0413/35 (NIWA 15611). — stn TAN0413/41 (NIWA 16272).

DISTRIBUTION. — Known from the type locality (Bellona Plateau, Coral Sea) and Otara Seamount, at southern tip of the Kermadec Ridge (N of New Zealand). The two localities are separated by approximately 2550 km.

DIAGNOSIS. — Same as that of the genus.

DESCRIPTION

Measurements and estimates of variation in character states are detailed in Table 2. Colonies are black and matte at the base, and are characterized by a dark metallic luster (holotype and paratype NIWA16273 black; paratype MNHN-IC.2008-007 dark brown). Branching sequence, as defined for *Chrysogorgia* (e.g., Versluys 1902; Cairns 2002, 2007) is 2/7R for the holotype, and irregular for the paratypes (see Discussion). The irregular branching pattern seen on the paratype is linked to the fact that the stem bifurcates and anastomoses. The distance between branches along the stem is regular, particularly on the holotype. Coenenchyme covers most of the upper part of the stem and branches and contains numerous sclerites. The stem is stiff, robust, and significantly thicker than the base of branches along most of the colony (proximal area: stem twice as thick as branches; distal area: stem and branches equally thick). Branches are stiff and stem from the main axis at nearly right angles. Order of branching is variable, mostly between four and six; the number of nodes per branch varies between 10 and 39. Branching occurs in multiple planes. The internodal

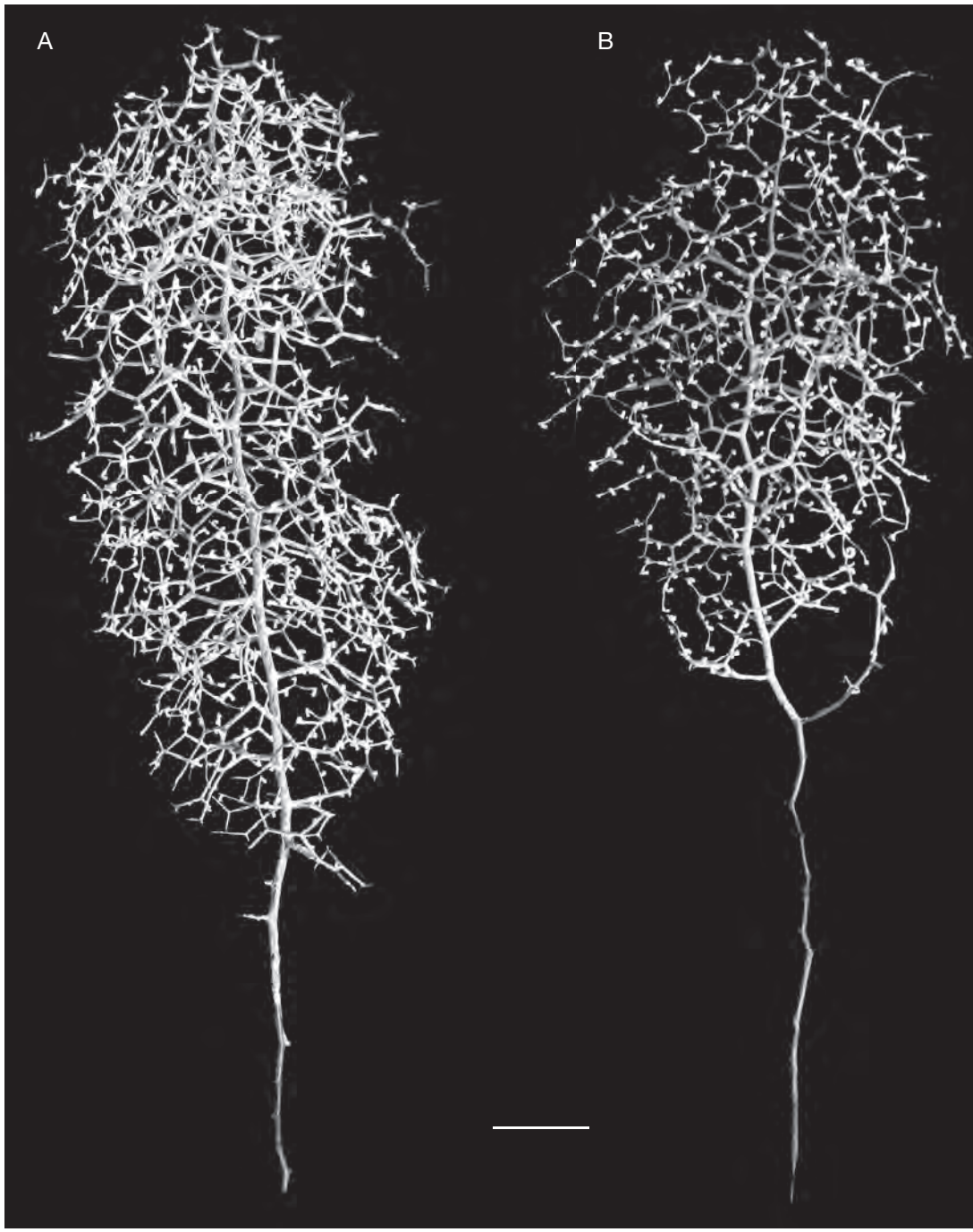

FIG. 1. — *Pseudochrysogorgia bellona* n.gen, n. sp.: **A**, holotype (MNHN-IC.2008-006); **B**, paratype (MNHN-IC.2008-007) from EBISCO stn CP 2557. Scale bar: 3 cm.

distance and the angle between subdividing branches are regular. Axial polyps were not observed on the holotype or the paratype, and polyp occurrence starts on the second branch internode. Over half of the polyps lean to one side. Polyps appear to always be leaning in the direction of branch growth. They are on average as wide as they are tall and their size varies between 1.7 and 3.5 mm. They are constricted at the neck, a character that seems to be exacerbated when polyps are left to dry. The arrangement of sclerites is detailed in the diagnosis of the genus. Sclerites do not appear tightly interlocked: while exposing polyps to bleach in an effort to remove the upper tissue layer covering the sclerites, these would fall off the polyp very rapidly (see Material and methods). All observed types of sclerites are warted; rods are more finely warted than scales. Scales have blunt extremities. Crosses (scales and rods with four rays in one plane) are rare but occur in the coenenchyme, body wall and tentacles. Most sclerites of the coenenchyme are scales and few are plates (for example, the fourth sclerite of Figure 6A is considered as a plate). While the proximal part of the polyp body wall (anthostele) is almost exclusively covered by scales, the distal part is richer in rods. The longest rods are found at the base of the tentacles, while smaller rods are found along the back of the tentacles.

Remarks

The holotype and the paratype MNHN-IC.2008-007 were associated with hydroids, which were attached at the tips of a few branches. While the sister taxon *M. melanotrichos* is found in close association with *Ophiocreas oedipus* Lyman, 1879 (Mosher & Watling 2009), no brittle stars were observed on the colonies examined (however, the symbionts might have been separated during or after sampling).

Specimens from the NIWA: NIWA15611, colony highly fragmented, main stem missing; NIWA16272, colony highly fragmented, only part of the main stem is available; NIWA16273, colony fragmented, main stem present. As NIWA16272 and NIWA16273 come from the same station (TAN0413/41), and that both lots contain branch fragments, it cannot be excluded that each lot may contain fragments from more than one colony.

Fig. 2. — Main stems of: **A**, *Chrysogorgia admete* Bayer & Stefani, 1988 (sympodial growth); **B**, *Pseudochrysogorgia bellona* n. gen., n. sp. (holotype); **C**, *Metallogorgia melanotrichos* (Wright & Studer, 1889) (NIWA43024; monopodial growth). Scale bars: 1 cm.

Bifurcation pattern of secondary branches, polyp morphology, size and spacing of the NIWA specimens is consistent with that of the MNHN specimens. However, while axial polyps were not observed on the MNHN specimens, these appear to be present on NIWA16273. In addition, polyps can be observed on first internodes (Fig. 4). While the stems

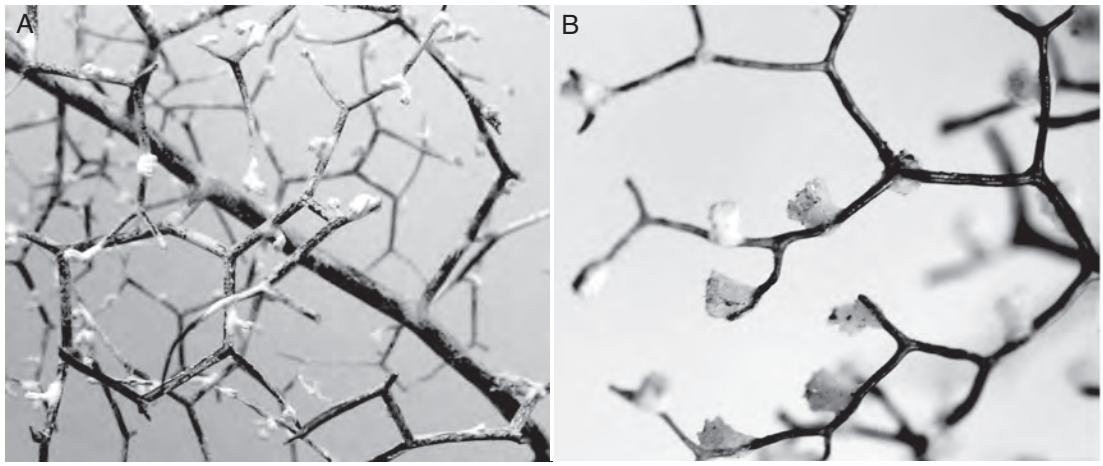

Fig. 3 — Hexagonal branching pattern in: **A**, the holotype of *Pseudochrysogorgia bellona* n. gen., n. sp.; **B**, *Metallogorgia melanotrichos* (Wright & Studer, 1889) (NIWA43024). This branching pattern is also very clearly seen in Figure 4.

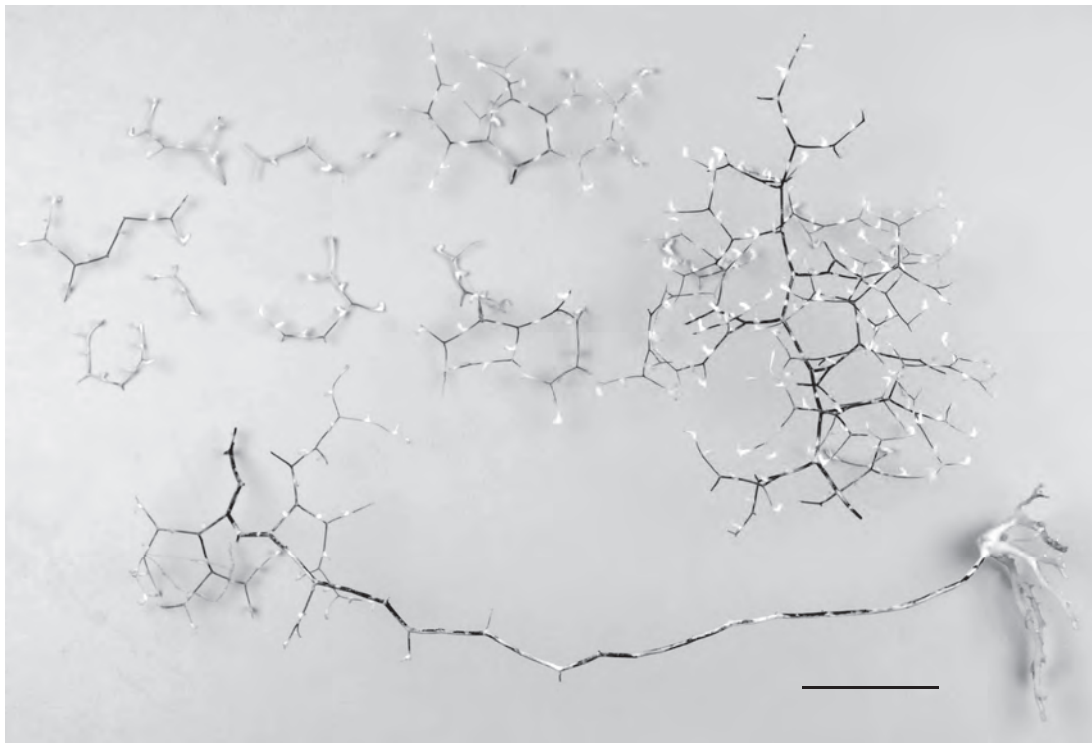

Fig. 4. — *Pseudochrysogorgia bellona* n. gen., n. sp. paratype (NIWA16273) from Otara Seamount, Kermadec Ridge. Scale bar: 3 cm.

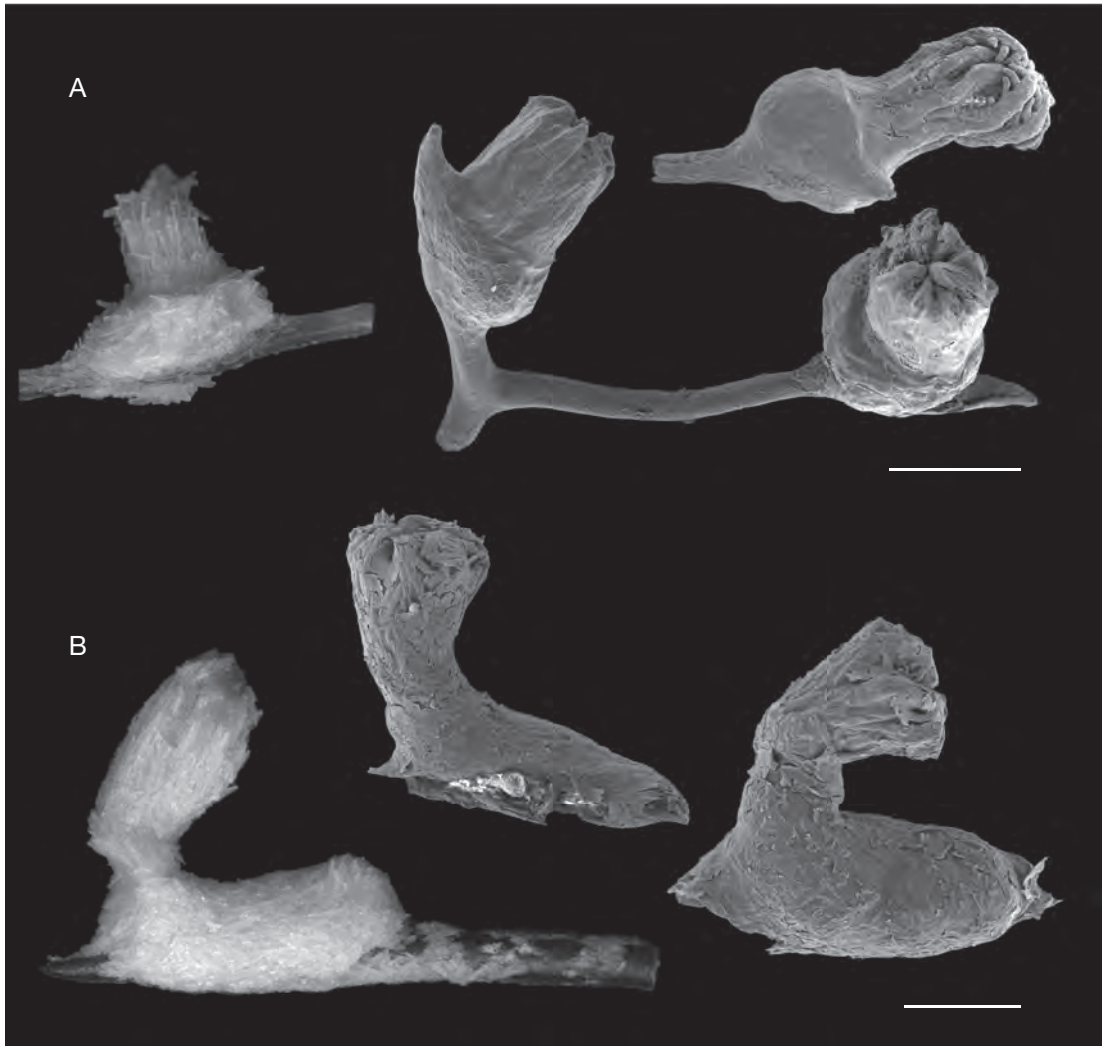

FIG. 5. — Digital (DM) and scanning-electron microscopy (SEM) images of polyps from closely-related chrysogorgiids: **A**, *Metallogorgia melanotrichos* (Wright & Studer, 1889) (MAN806-2; left: DM, right: SEM); **B**, *Pseudochrysogorgia bellona* n. gen., n. sp. (holotype; left: DM, right: SEM). Scale bars: 1 mm.

of both the MNHN type specimens were broken at the base, NIWA16273 had an intact, root-like holdfast (Fig. 4). This may indicate that the colony was collected from soft-sediments.

Polyp preparation: the speed at which sclerites fall from the polyp when exposed to bleach might depend on specimen fixation and preservation. Indeed, exposure to glutaraldehyde had the desired effect of locking sclerites into place, allowing for the digestion of the upper tissue layer. The same observation was made for *M. melanotrichos*. The described arrangement of sclerites (scales in body wall and rods in tentacles) corresponds to the "Squamosae aberrantes" (group B) as defined by Versluys (1902) for *Chrysogorgia*. Finally, polyps leaning distad have a swollen base, in which eggs can be found. This condition might be associated with the production of eggs.

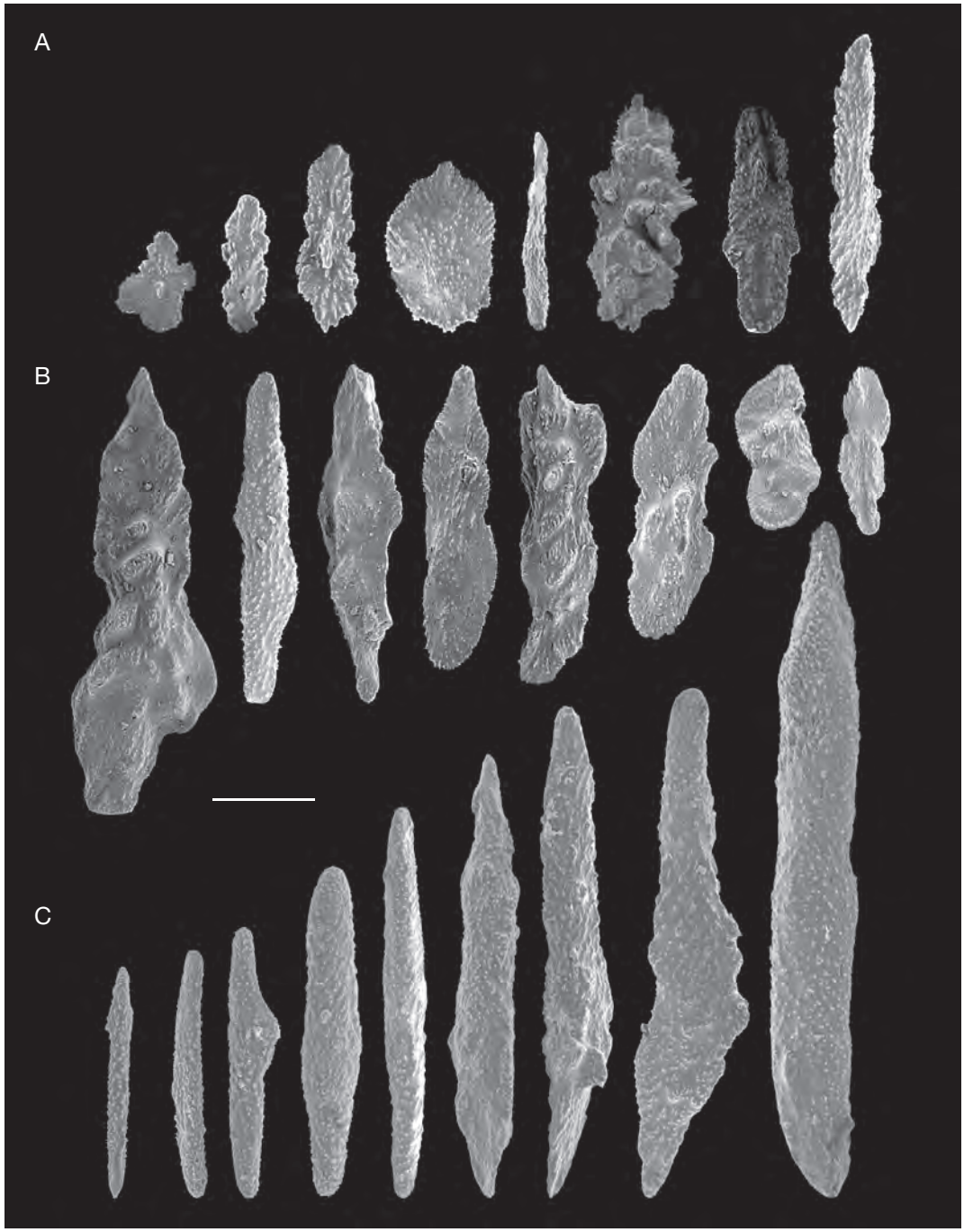

Fig. 6. — *Pseudochrysogorgia bellona* n. gen., n. sp. holotype, SEM of sclerites: **A**, branch coenenchyme; **B**, polyp body wall; **C**, tentacles. Scale bar: 100 µm.

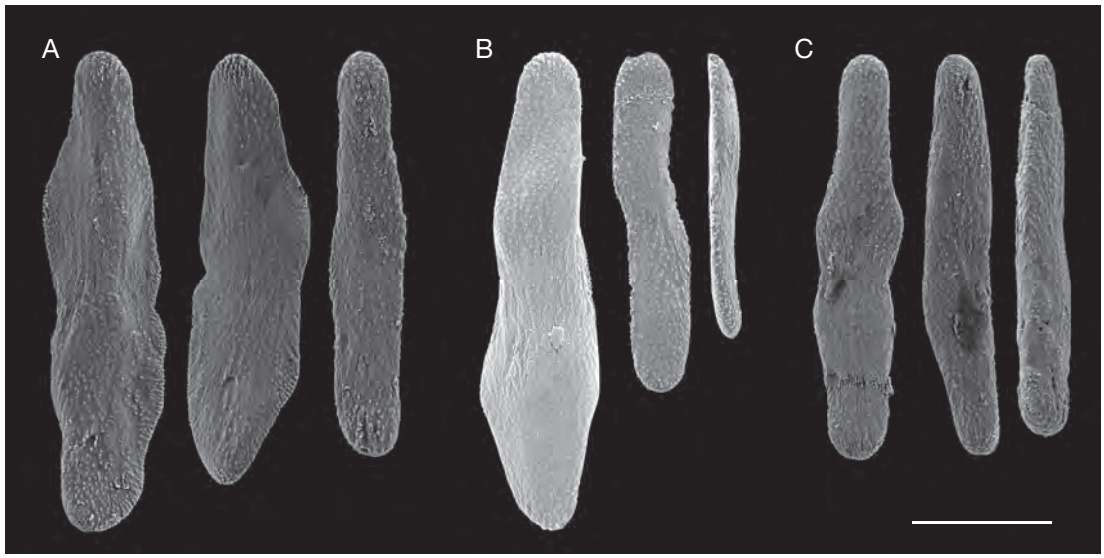

FIG. 7. — *Metallogorgia melanotrichos* (Wright & Studer, 1889) (MAN806-1), SEM of sclerites: **A**, branch coenenchyme; **B**, polyp body wall; **C**, tentacles. Scale bar: 100 µm.

DISCUSSION

SIMILARITY BETWEEN *PSEUDOCHRYSOGORGIA* N. GEN. AND OTHER CHRYSOGORGIID GENERA

Prior to this description, the different deep-sea chrysogorgiid genera were easily distinguished by major, strikingly different colony growth patterns, such as presence or absence of side branching, sympody or monopody of the main stem, and subdivision of side branches (see e.g., key to the genera of the Chrysogorgiidae in Bayer & Stefani 1988). An interesting characteristic of *Pseudochrysogorgia* n. gen. is the presence on the same colony of characters previously used to distinguish different genera. For instance, *Pseudochrysogorgia* n. gen. has abundant, bifurcating side branches along most of its stem, as does *Chrysogorgia*. The holotype of *Pseudochrysogorgia bellona* n. gen., n. sp. has a regular branching sequence, typical of *Chrysogorgia*. On the other hand, the main axis of *Pseudochrysogorgia* n. gen. is monopodial, as is *Metallogorgia*. In fact, the proximal part of the main stems of *Pseudochrysogorgia* n. gen. and full-grown *Metallogorgia* are indistinguishable, both being characterized by a dark metallic luster, heavy calcification and scars of broken branches (Fig. 2). As a consequence, *Pseudochrysogorgia* n. gen. could easily be misidentified (and indeed, the *Pseudochrysogorgia* n. gen. specimens from the NIWA were originally labelled as *Chrysogorgia*). While both *Pseudochrysogorgia* n. gen. and juvenile *M. melanotrichos* branch patterns can easily be differentiated (photographs of branching *M. melanotrichos* can be found in Mosher & Watling 2009). The main difference resides in the spacing of branches along the stem, which is regular and narrow in *Pseudochrysogorgia* n. gen. and irregular and sparse in *M. melanotrichos*.

In addition to closely examining the main stem, sclerite morphology can provide information on the specimen examined. Indeed, while *Metallogorgia* sclerites are typically rod-shaped (scales are much less abundant, typically thick and rounded) and lightly ornamented, *Pseudochrysogorgia* n. gen. sclerites have more diverse shapes (plates, scales and rods), and are significantly more ornamented. The proximal portions of *Pseudochrysogorgia* n. gen. polyps are almost exclusively composed of scales. The length of sclerites should be compared with caution. While on average *M. melanotrichos* has smaller sclerites than *P. bellona* n. gen., n. sp. (MAN806-1:

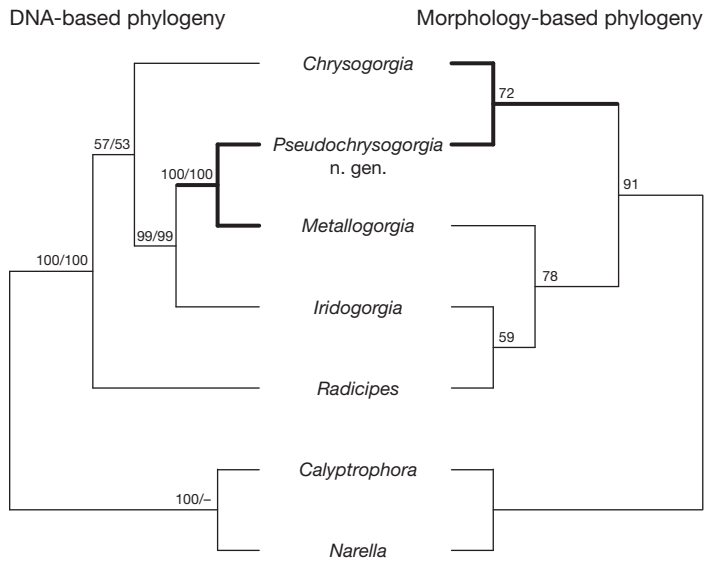

FIG. 8. — Phylogenetic trees based on genetic (left) and morphological (right) data. The morphology-based cladogram has a length of 23 steps, a consistency index of 0.7826 and a retention index of 0.7222. The DNA-based cladogram is presented with bootstrap values from maximum likelihood and maximum parsimony analyses (left and right of slash, respectively). Bold lines emphasize the relationship between *Pseudochrysogorgia* n. gen. and its closest relative, and the inconsistency between morphology- and DNA-based inference of the phylogeny.

mean 179±56 mm, range 46-304 mm, n=129), *M. macrospina* is characterized by longer sclerites (MNHN-IK-2008-1042: mean 408±197 mm, range 134-1036 mm, n=106). *Pseudochrysogorgia* n. gen. polyps tend to be more rotund than those of *Metallogorgia* and more than half are slightly angled to the branch (see description and Figure 5). To our knowledge, there are no published SEM photographs of *Metallogorgia* polyps or sclerites. For comparison, we present herein SEM pictures of typical *M. melanotrichos* polyps and sclerites (Figs 5; 7).

TAXONOMIC RANK OF *PSEUDOCHRYSOGORGIA* N. GEN.

There is no single morphological character state that could serve as a synapomorphy to distinguish *P. bellona* n. gen., n. sp. from the rest of the deep-sea Chrysogorgiidae. One can legitimately ask why this taxon should not simply be considered a new species of *Metallogorgia*. To answer this question we looked at the molecular variation between species from different genera within the family. The genetic distance between *P. bellona* n. gen., n. sp. and *M. melanotrichos* (1.897%) falls into an area of overlap between intra- and inter-generic comparisons (Fig. 9). Comparatively, distances between *P. bellona* n. gen., n. sp. and *Chrysogorgia* range between 2.9 and 4.5%. The distributions of intra- and inter-generic comparisons are both bimodal. In the first case, all distances larger than 1.454% are between *Chrysogorgia* specimens. In the second case, all distances smaller than 3.245% are exclusively between *Radicipes* and *Chrysogorgia* specimens (gray areas of Fig. 9). Pairs of *Chrysogorgia* species can therefore be more divergent than *Chrysogorgia-Radicipes* pairs. If genetic distance is used as a diagnostic tool for attributing taxonomic levels to Chrysogorgiidae species, then one of two possible changes should be made to prevent distributions of intra- and inter-generic distances from overlapping:

1. *Radicipes* and *Chrysogorgia* should be grouped as one genus. In this case, the gray area in the lower panel of Fig. 9 ceases to be, and *P. bellona* n. gen., n. sp. can be considered as a new species of *Metallogorgia*.

2. *Radicipes* and *Chrysogorgia* should be considered as two different genera, and *Chrysogorgia* should be further divided into different groups. In this case, the gray area in the upper panel of Figure 9 ceases to be, and *P. bellona* n. gen., n. sp. cannot be considered as a new species of *Metallogorgia*.

The strong morphological differences between *Radicipes* and *Chrysogorgia* restrain us from suggesting that these two genera should be grouped as one genus. In addition, molecular phylogenetics suggest that these groups form two reciprocally monophyletic groups (Pante & France unpublished). Finally, *Chrysogorgia* is known to be a very diverse taxon, and authors have previously suggested the division of this genus into three groups (the "Spiculosae", the "Squamosae typicae", and the "Squamosae aberrantes"), based on the zonation of different sclerite types (Wright & Studer 1889; Versluys 1902).

While *P. bellona* n. gen., n. sp. is more closely related to *Chrysogorgia* based on morphology, its closest relative based on genetics is *Metallogorgia* (Fig. 8). This conflicting result underlines the special status of *P. bellona* n. gen., n. sp. in the family, and suggests that incorporating this new taxon within the genus *Metallogorgia* would make a new, broadened definition of *Metallogorgia* problematic, as it would significantly overlap with the definition of *Chrysogorgia*. If *Metallogorgia* is redefined, monopody would be the only strong synapomorphy differentiating it from *Chrysogorgia*. This character, however, is difficult to assess in some cases (unpublished observations from EP).

Finally, the genetic distance between *P. bellona* n. gen., n. sp. and *M. melanotrichos*, while small compared to other inter-generic distances, is quite large when considering the currently observed variation among *Metallogorgia* specimens. DNA from 57 specimens from the Atlantic and Pacific oceans were sequenced at *msh1*, and only two genetic variants were found (Thoma *et al.* 2009; Pante & France unpublished), represented by *M. melanotrichos* and *M. macrospina*. *Metallogorgia macrospina* is rare and is represented by only two specimens. These two *Metallogorgia* haplotypes are only 0.144% divergent, and colonies can only be clearly differentiated by the size of rods on the polyp head. Similarly, the maximum genetic distance between currently known *Iridogorgia* haplotypes (n=4) is only 0.576%, compared to the 1.897% separating *P. bellona* n. gen., n. sp. from the most common *Metallogorgia* haplotype. The monophyletic clade comprising *Metallogorgia*, *Iridogorgia* and *Pseudochrysogorgia* n. gen. might evolve at a slower pace than *Chrysogorgia*. Also, species within this clade might have recently diverged (these two hypotheses are not mutually exclusive). Because *Pseudochrysogorgia* n. gen. is nested between *Iridogorgia* and *Metallogorgia* within this clade, we argue that the genetic distance separating *Metallogorgia* from *Pseudochrysogorgia* n. gen. should be interpreted in light of the small genetic distances found within the clade. In conclusion, based on these lines of evidence (problematic revision of *Metallogorgia*, incongruence between morphology-based and DNA-based phylogenies, and analyses of genetic distances), we suggest that

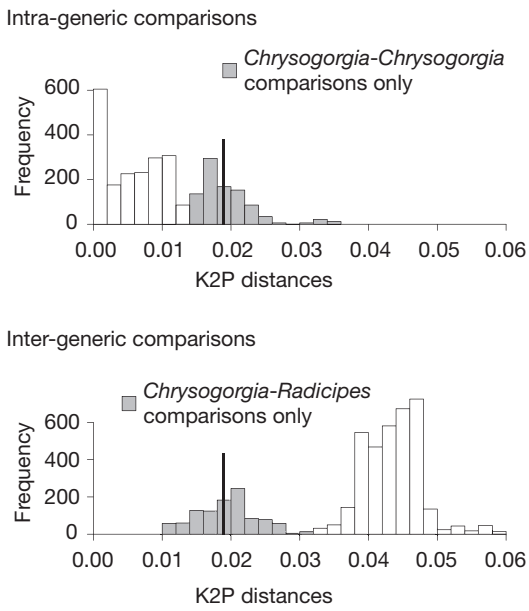

FIG. 9. — Frequency histograms of pairwise genetic distance values (K2P) across 129 chrysogorgiid specimens sequenced at the 5' end of *msh1*. Separate histograms are shown for pairwise comparisons made among congeneric individuals (top) and between individuals from different genera (bottom). The vertical black line represents the K2P distance between *Pseudochrysogorgia bellona* n. gen., n. sp. and its closest relative, *Metallogorgia melanotrichos* (Wright & Studer, 1889).

P. bellona n. gen., n. sp. deserves recognition as the type of a new genus, rather than a new species of *Metallogorgia*.

Variation in branching sequence

The type specimens of *P. bellona* n. gen., n. sp. differ significantly in branching sequence. First, side branches of the holotype arise in a dextral (R) spiral, while the MNHN paratype is characterized by a sinistral (L) spiral. In addition, branching was fairly regular for the holotype, following a 2/7R sequence (two side branches are in the same plane if they are separated by six side branches and two revolutions; in other terms, "traveling" along the main stem, it takes seven branches and two revolutions to recover the plane of a starting, reference side branch). It is noteworthy that this particular sequence has never been reported for *Chrysogorgia* (Cairns 2001, 2002, 2007). On the MNHN paratype, side branches arise irregularly around the main stem. The spiral can be interrupted by perfectly aligned, consecutive side branches, and dichotomous subdivision (and subsequent anastomosis) of the main stem. While we could not directly assess branching sequence for the NIWA paratype, branching appears to be irregular, as for the MNHN paratype (Peter Marriott and Sadie Mills, NIWA, pers. comm.).

Despite these differences in branching sequence, the holotype and MNHN paratype of *P. bellona* n. gen., n. sp. are very similar for other traits, such as spacing of side branches along the main stem, dichotomous sub-branching, and dimensions (summarized in Table 2). In addition, the three type specimens were genetically identical along a region of the mitochondrial genome spanning 3155 base pairs, crossing part of the *nad4l* and the entire *msh1* (Pante and France, unpublished). The *msh1* gene is the most variable marker available for octocorals to date, and allows discrimination of many species (McFadden *et al.*2006, 2010, and references therein). Morphological variation contrasted by lack of molecular variation could either indicate that branching sequence is not a taxonomically useful character within the genus *Pseudochrysogorgia* n. gen. and might depend on environmental factors, or that multiple, recently-diverged species exist within the genus, and the genetic marker used here is not sufficiently variable to differentiate them.

Of these two alternatives, the dependence of branching sequence on environmental variables might be the most likely. First, variable branching sequence within colonies does occur within the genus *Chrysogorgia*. Of the 59 valid species listed by Cairns (2001), six have an irregular sequence, and three have multiple but regular sequences. For example, *C. herdendorfi* Cairns, 2001 is characterized by a dominant 2/5R sequence, sometimes interrupted by a 3/8R sequence. Similarly, the spiral of *C. squamata* (Verrill, 1883) can follow a 1/5R (predominantly), 1/6R, or even a 1/7R sequence (Cairns 2001). At the scale of individual colonies, significant variation in spiral characteristics suggests environmental control of growth pattern. One hypothesis is that colonies are subjected to increased drag as they grow taller, and increased tension on the main stem disturbs the regularity of the spiral. Second, lack of congruence between variation in branching pattern and genetic data has previously been documented. For instance, lack of colony branching has long been used to distinguish *Lepidisis* Verrill, 1883 from *Keratoisis* Wright, 1869 (Isididae Lamouroux, 1812), but analyzing part of the *msh1* gene does not recover the two genera as discrete, monophyletic clades (France 2007).

Although branching sequence can be used to differentiate some species of *Chrysogorgia* (see e.g., Cairns 2001), we chose to pool both *Pseudochrysogorgia* n. gen. type specimens within the same species, based on the observations described above. Should more material become available, morphological and genetic variation within this new genus will be further tested.

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