Systematics and Biodiversity

ISSN: 1477-2000 (Print) 1478-0933 (Online) Journal homepage: https://www.tandfonline.com/loi/tsab20

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To cite this article: Marcelo V. Kitahara , Stephen D. Cairns & David J. Miller (2010) Monophyletic origin of *Caryophyllia* (Scleractinia, Caryophylliidae), with descriptions of six new species, Systematics and Biodiversity, 8:1, 91-118, DOI: 10.1080/14772000903571088

To link to this article: https://doi.org/10.1080/14772000903571088

Systematics and Biodiversity (2010), **8(1)**: 91–118

Taylor & Francis
Taylor & Francis Group

Research Article

Monophyletic origin of *Caryophyllia* (Scleractinia, Caryophylliidae), with descriptions of six new species

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(Received 11 May 2009; revised 29 October 2009; accepted 16 December 2009)

The genus *Caryophyllia* Lamarck, 1816 is the most diverse genus within the azooxanthellate Scleractinia comprising 66 Recent species and a purported 195 nominal fossil species. Examination of part of the deep-sea scleractinian collection made by the Paris Museum off New Caledonia and part of the material collected by CSIRO off Australian waters revealed the occurrence of 23 species of *Caryophyllia*, of which six are new to science. All new records, including the new species, are described, and synonyms, distribution, type locality, type material and illustration are provided for each species. An identification key to all Recent species of *Caryophyllia* is presented. In addition, the validity of the genus *Caryophyllia* was investigated by phylogenetic analyses of a dataset consisting of partial mitochondrial 16S rRNA sequences from 12 species assigned to this genus together with seven species representing some of the most morphologically similar caryophylliid genera, and 14 non-caryophyllid species representing 14 scleractinian families. Irrespective of the method of analysis employed, all of the *Caryophyllia* species formed a well-supported clade together with *Dasmosmilia lymani* and *Crispatotrochus rugosus*. Although based on a subset of the Recent *Caryophyllia* species, these results are consistent with *Caryophyllia* being a valid genus, but call for a reexamination of *Dasmosmilia* and *Crispatotrochus*.

Keywords: 16S rRNA, Australia, azooxanthellate, *Caryophyllia*, deep-sea, New Caledonia, phylogenetic analysis, Scleractinia

Introduction

The family Caryophylliidae Dana, 1846 is represented by 89 valid genera. Of those, 38 are only known as fossil records, with the oldest fossil record dating from the Jurassic (about 180 Mya). The other 51 Recent valid genera of this family are ubiquitous through all oceans of the world, being recorded from shallow (Cairns *et al*., 2005) to deep (Squires, 1959) waters, from coastal Antarctic (Cairns, 1982) to the Arctic Circle (Roberts *et al.*, 2003). Representatives of this family include the largest colonial azooxanthellate species of coral, e.g. *Lophelia pertusa* (Linnaeus, 1758), one of the primary deep-water coral bank constructors (Cairns & Stanley, 1982), attaining more than 35 m in height and several km wide, to some of the smallest ones, e.g. *Coenocyathus parvulus* (Cairns, 1979), which is less than 1 cm in CD.

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The trabecular wall structure of every caryophylliid begins as a marginotheca, but transforms into a septo- or parathecal wall later in ontogeny; these more mature wall structures usually have well-developed costae (Stolarski, 1995), and occasionally non-trabecular calcium carbonate is deposited on the exterior of the corallum in the form of tectura or even epitheca (e.g. *Tethocyathus* Kühn, 1933) (Cairns, 2002). According to Wells (1956), this family is characterized as: 'solitary or colonial; colony formation usually by extratentacular (rarely intratentacular) budding, forming phaceloid or dendroid colonies; costae commonly covered by tectura or epitheca; septa exsert; columella formed by curled trabecular laths, solid, spongy, or absent; pali or paliform lobes common; endothecal dissepiments developed in some groups'.

Within this family, the exclusively azooxanthellate genus *Caryophyllia* is common worldwide and consists of 66 Recent valid species (Appendix 1, see supplementary material which is available on the Supplementary content tab of the

ISSN 1477-2000 print / 1478-0933 online

DOI: 10.1080/14772000903571088

Published online 22 Mar 2010

article's Informaworld page at http://www.informaworld.com/mpp/uploads/kitahara_et_al._supplementary_information.pdf), being the most diverse Recent genus of azooxanthellate corals. All representatives of this genus are solitary, including forms firmly attached to the substrate, such as *Caryophyllia berteriana* Duchassaing, 1870, and others that detach at an early stage, such as *Caryophyllia ambrosia* Alcock, 1898, to continue a free life form on soft bottoms (sand or mud).

With the first fossil record from the Upper Jurassic (Vaughan & Wells, 1943) and today predominantly collected between 0–2700 m, the first *Caryophyllia* was described 15 years before the description of the genus as *Madrepora cyathus* (Ellis & Solander, 1786) (= *Caryophyllia cyathus*), which was selected by Stokes & Broderip (1828) as the type species for the genus. According to Zibrowius (1980), this species was already well known and commonly collected in the Mediterranean Sea. In the same study, *Caryophyllia smithii* Stokes & Broderip (1828) was described based on specimens collected from southwestern England. Not surprisingly, *C. smithii* is the *Caryophyllia* with the highest number of synonyms, totalling 14 between the years 1828 to 1878.

Described as *Acanthocyathus grayi*, *C.* (*A.*) *grayi* (Milne Edwards & Haime, 1848), it is often collected in Pacific waters and has previous records from the Indian Ocean. However, no information regarding type material deposition or type locality were provided by the species authors. Two years after the description of *C. grayi*, *Caryophyllia berteriana* Duchassaing, 1850 was described based on a specimen collected off Guadeloupe, differentiated from *C. cyathus* by Duchassaing (1850) by its pali disposition. Continuing his studies on the *Caryophyllia* from the Caribbean Sea, Duchassaing (1870) described *C. corona* and *C. protei*, both species collected off the Antilles at 60 and 100 m, respectively. However, since the original description no one has examined or even mentioned these species, being both considered as *nomen oblitum* in the present study. Using the stony corals deposited at the British Museum, Kent (1871) described *Acanthocyathus spiniger* Kent, 1871 (= *Caryophyllia (A.) spinigera*) from specimens collected in Japanese waters. In a study of the corals dredged during the expeditions of H.M.S. *Porcupine* from the North Atlantic between 1869 and 1870, for the first time scleractinians were reported below 2000 m (Duncan, 1873). During these expeditions 'hempen tangles' were employed instead of the crushing dredge, which resulted in the collection of 14 new species of Scleractinia, including four valid species of *Caryophyllia*: *C. abyssorum* Duncan, 1873; *C. atlantica* (Duncan, 1873); *C. seguenzae* Duncan, 1873; and *C. calveri* Duncan, 1873. In the same study, the genus *Ceratocyathus* was synonymized as *Caryophyllia*. Using the material collected by the Hassler Expedition off Barbados and the Blake Expedition off Florida, Pourtalès described *C. antillarum* Pourtalès, 1874, and *C. polygona* Pourtalès, 1878, and followed with the second study of the H.M.S. *Porcupine* material that included the description of *Caryophyllia inornata* (Duncan, 1878).

One of the largest additions to the genus was made during 1881 with the material collected worldwide during the voyage of H.M.S. *Challenger* between the years 1873–1876, resulting in seven species being described: *C. dentata* (Moseley, 1881); *C. lamellifera* Moseley, 1881; *C. paucipalata* Moseley, 1881; *C. profunda* Moseley, 1881; *C. rugosa* Moseley, 1881; *C. spinicarens* (Moseley, 1881); and *C. transversalis* Moseley, 1881. Subsequently, Marenzeller published a study about the turbinoliids from Japanese waters, describing *C. japonica* Marenzeller, 1888, which today is one of the *Caryophyllia* species with the greatest depth range (77–1680 m). The penultimate study from the 19th century describing species belonging to this genus was published using the material collected off Indian waters by H.M.S. *Investigator* during the years 1881–1893. Scleractinians described in those studies included: *Caryophyllia ambrosia* Alcock, 1898, *C. cinticulata* (Alcock, 1898), and *C. paradoxa* (= *C. paradoxus* Alcock, 1898). Finally, the last description of a Recent *Caryophyllia* in the 19th century was based on a fossil (Pleistocene) specimen from California named *C. arnoldi* Vaughan, 1900, being the only specimen of this species to have an unattached pedicel (Cairns, 1994).

The beginning of the 20th century was very rich for *Caryophyllia* descriptions (40 species); Lieut.-Col. Alfred Alcock named *C. ephyala* Alcock, 1901, *C. quadragenaria* Alcock, 1902 and *C. scobinosa* Alcock, 1902, the last one having a very widespread distribution, being reported from the western south Atlantic, western Indian Ocean, Indo-Pacific and Pacific Ocean. Subsequently, *C. antarctica* Marenzeller, 1904 and *C. diomedeae* Marenzeller, 1904 were described from specimens collected by the Valdivia Expedition. Before the First World War, another three species were described: *C. planilamellata* Dennant, 1906 from Australian waters, and *C. hawaiiensis* Vaughan, 1907 and *C. octopali* Vaughan, 1907 from Hawaiian waters. After a gap of more than 30 years without new species known from the genus, Gardiner & Waugh (1938), studying the material collected by the John Murray Expedition, described *C. grandis* Gardiner & Waugh, 1938, *C. mabahithi* Gardiner & Waugh, 1938 and *C. sewelli* Gardiner & Waugh, 1938. During the years 1939 and 1967 (probably due to the Second World War), only *C. alaskensis* Vaughan, 1941 was described.

The last pulse of descriptions of new species of *Caryophyllia* started with *C. jogashimaensis* Eguchi, 1968, *C. sarsiae* Zibrowius, 1974 and *C. horologium* Cairns, 1977, followed by revisions of large collections of azooxanthellate corals deposited in museums, and especially revisions of all previous data. Species described from the western Atlantic include *C. ambrosia caribbeana* Cairns, 1979, *C. barbadensis* Cairns, 1979, *C. corrugata* Cairns,

1979 and *C. zopyros* Cairns, 1979. Subsequently, during the 1980s, studies from the eastern North Atlantic Ocean increased the number of species from this genus including the descriptions of *C. alberti* Zibrowius, 1980 and *C. foresti* Zibrowius, 1980. Studying specimens collected from Antarctic and sub-Antarctic waters, two species with depth range between 406 to 814 m were described: *C. eltaninae* Cairns, 1982, and *C. squiresi* Cairns, 1982. These two species along with *C. antarctica* are probably the southernmost records for the genus. After these descriptions from the southern ocean, almost all subsequent descriptions of *Caryophyllia* were based on specimens collected from Pacific or Indo-Pacific region, the only exception being *C. balaenacea* Zibrowius & Gili, 1990, and *C. valdiviae* Zibrowius & Gili, 1990, collected from Walvis Ridge and/or South Africa, south eastern Atlantic, and *C. crypta* Cairns, 2000 from Caribbean waters. The others 16 Pacific or Indo-Pacific species are: *C. marmorea* Cairns, 1984; *C. quangdongensis* Zou, 1984; *C. zanzibarensis* Zou, 1984; *C. perculta* Cairns, 1991; *C. solida* Cairns, 1991; *C. ralphae* Cairns, 1995; *C. cornulum* Cairns & Zibrowius, 1997; *C. crosnieri* Cairns & Zibrowius, 1997; *C. karubarica* Cairns & Zibrowius, 1997; *C. octonaria* Cairns & Zibrowius, 1997; *C. secta* Cairns & Zibrowius, 1997; *C. unicristata* Cairns & Zibrowius, 1997; *C. decamera* Cairns, 1998; *C. stellula* Cairns, 1998; *C. abrupta* Cairns, 1999; and *C. huinayensis* Cairns, Haussermann & Forsterra, 2005, the last *Caryophyllia* described to date (Appendix 1, see supplementary material).

As a result of the examination of part of the collections made by the MNHN from New Caledonia, CSIRO from Australian waters and *C. transversalis* deposited at WAM (Appendix 2, see supplementary material), 23 species of *Caryophyllia* were identified. The present study reports all new records of this genus, providing updated synonymies, type locality, type material, description, distribution and illustrations of all species examined, including the description of six new species collected during the expeditions: MNHN – PrFo; Halipro I; Bathus 3; Bathus 4; Norfolk 1; and Norfolk 2, and CSIRO – SS0197; SS0105; SS0207; and NORFANZ. Also, an identification key for all species pertaining to the genus is proposed.

Until now, no phylogenetic analysis had been performed of any caryophylliid genera, which constitute by far the most diverse family of azooxanthellate Scleractinia. However, recent molecular studies (Romano & Palumbi, 1996; Romano & Cairns, 2000; Le Goff-Vitry *et al.*, 2004) suggested that the family is unnatural or polyphyletic, having representatives grouping with the two big scleractinian clades: the robust and complex corals, in more than two separated clades.

Our study of the *Caryophyllia* from New Caledonia and the new records from Australian waters combine morphological descriptions and genetic data, and therefore has the following aims: (1) comprehensive morphological descriptions of all *Caryophyllia* from New Caledonia waters, including five new species; (2) a report of the first records of four species of *Caryophyllia* in Australian waters, including a new species; and (3) a reconstruction of the phylogenetic relationships based on partial 16S rRNA sequences of the genus *Caryophyllia*, supporting its monophyletic status.

Materials and methods

Between 1993 and 2003, French expeditions collected and preserved more than 2700 specimens of deep-water scleractinians (ranging in depth from 170 to 1434 m) from approximately 135 stations off New Caledonia from 18°00′S, 160°00′E to 26°00′S, 170°00′E (Figs 1–6) (Appendix 2, see supplementary material). Also, between 1997 and 2007, Australian expeditions collected hundreds of azooxanthellate scleractinians from Pacific and Indian Ocean waters. The examination of these specimens revealed the occurrence of 23 species belonging to the genus *Caryophyllia*, all of them being fully described herein. Additionally, for each new record a complete citation synonym, type locality, type material, new records, distribution and illustrations are provided.

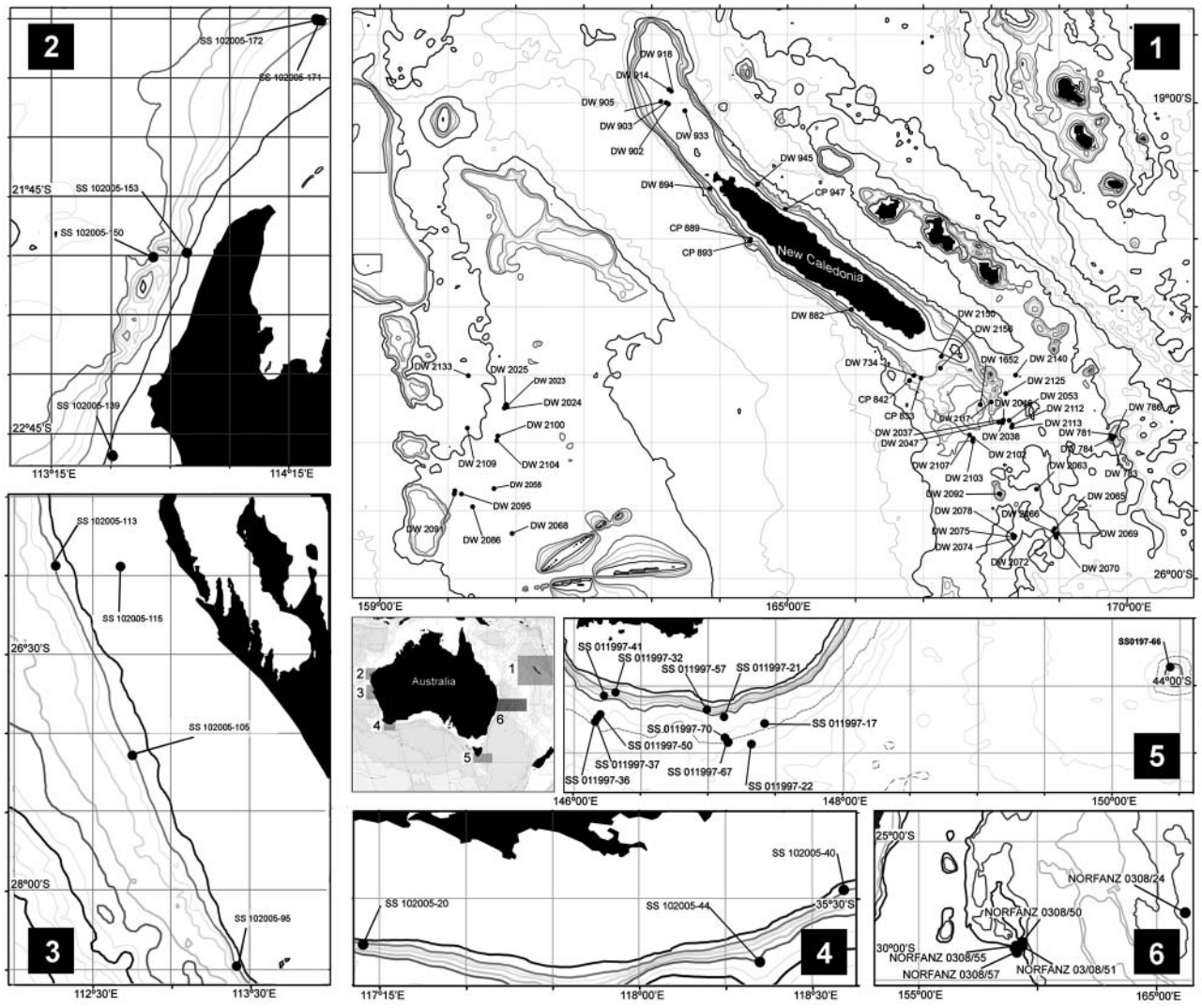
Measurements and counts follow Wells (1956), Zibrowius (1980) and Cairns (1979, 2000). The basic morphological terminology used is explained by Vaughan & Wells (1943), Wells (1956), Alloiteau (1957) and Cairns (1982) and in case of septal formula by Cairns (1989).

All specimens examined are deposited primarily at the Muséum National d'Histoire Naturelle, Paris (MNHN), the National Museum of Natural History, Washington, DC (USNM), the Australian Museum, Sydney (AMS) or at the Western Australian Museum, Perth (WAM).

Abbreviations

The following abbreviations for morphological characters were used: **CD:** calicular diameter; **GCD:** greater calicular diameter; **HT:** height of corallum; **LCD:** lesser calicular diameter; **PD:** pedicel diameter; **Sx:** septa of cycle designated by numerical subscript; Sx > **Sy:** septa of cycle x wider than those of cycle y; and **Px:** pali before the septal cycle designated by numerical subscript.

The following abbreviations for institutions were used: **AMS:** Australian Museum, Sydney; **CSIRO:** Australian Commonwealth Scientific and Research Organization; **IO:** Institute of Okeanology, Moscow; **MCZ:** Museum of Comparative Zoology, Harvard University, Cambridge; **MNHN:** Muséum National d'Histoire Naturelle, Paris; **NHM:** The Natural History Museum, London; **NMV:** National Museum of Victoria, Melbourne; **NMW:** Nationaal Natuurhistorisches Museum, Wien; **NZOI:** New Zealand Oceanographic Institute, Wellington (now National Institute of Water & Atmospheric Research); **POLIPI:** Politbang Oseanologi (National Institute of Oceanology), Jakarta; **TIUS:** Institute of Geology and Paleontology, Tohoku (Imperial)



Figs 1–6. Map of the stations with occurrence of *Caryophyllia* examined in the present study: 1, New Caledonia region; 2 and 3, Western Australian region; 4, southern Western Australian region; 5, Tasmania region; 6; southwestern Pacific region.

University, Sendai; **USNM:** United States National Museum (now National Museum of Natural History – NMNH), Washington, DC; and **ZMA:** Zöologisch Museum, Amsterdam.

DNA preparation, amplification and sequence analyses

Tissue was collected from a whole mesentery using forceps when the species was large or an entire sector (including the skeleton) was taken when the species was too small to collect only the mesentery. Genomic DNA was extracted using the DNeasy Tissue Kit of QIAGEN following the manufacturer's instructions. For each species the concentration of genomic DNA extracted was measured in Nanodrop 1000 (Thermo Scientific), and when necessary an aliquot of the genomic DNA was diluted or concentrated to achieve the final concentration of 25 ng/ul.

Using the primers developed by Le Goff-Vitry *et al*. (2004) (LP16SF 5′-TTGACCGGTATGAATGGTGT and LP16SR 5′-TCCCCAGGGTAACTTTTATC) a fragment of the mitochondrial 16S rRNA ranging between 290 to 303 bp according to the species being amplified. Reactions were carried out in 50 μl, with 5 μl of 10× PCR Buffer, 5 μl of 2 mM dNTP, 3 μl of 25 mM MgCl2, 2 μl of each primer (10 mM each), 0.3 μl of Taq polymerase, and 5 μl of template. PCR conditions used were: a denaturation first step of 95°C for 5 min, followed by 35 cycles of 30 s at 94°C, 30 s at 50°C, and 45 s at 72°C, followed by

10 min at 72°C. When the amplification of the 16S failed, a new reaction using the Clontech Advantage-2 Kit with the same template, primers and PCR conditions were performed following the manufacturer's instructions. All cycles were performed using Bio-Rad DNA engine (Peltier Thermal Cycler). The PCR products were then purified using Mo-Bio Ultra Clean (PCR Clean Up) spin columns, and then submitted to the Macrogen (Korea) sequencing facility to be sequenced using ABI3730XL (Applied Byosystems). Sequence were verified and manipulated with Sequencher ver. 4.8 (Gene Codes Corporation). A Blast search was performed on GenBank for each sequence and the matching homologous *Caryophyllia* sequences were retained for subsequent alignment. Using this protocol, two previously published sequences were added to the alignment (*C. ambrosia* and *C. inornata*). Based on morphological similarity, another seven 16S rRNA sequences (three first-time sequenced plus four retrieved from GenBank) (Appendix 3, see supplementary material) belonging to seven different caryophylliid genera were added to the analyses. For those species for which more than one specimen was sequenced, all sequences were aligned and only the consensus sequence was used. Intending to include a large representation of non-caryophylliids to the analysis, additional 14 16S rRNA sequences representing 14 scleractinian families were retrieved from GenBank and added to the alignment.

Sequences were initially aligned in ClustalW (EBI) using the default settings. The resulting alignment was then manually refined using JalView version 8.0 (Clamp *et al.*, 2004), totalling 448 bp and 33 species in the final alignment. Using the final alignment, the General Time Reversible with gamma distribution (GTR+G) model of DNA substitution was determined by the hierarchical likelihood ratio test implemented in MrModeltest (Nylander, 2004) as the best model for the data. Phylogenetic analyses were performed using PhyML (Guindon & Gascuel, 2003) for maximum likelihood (ML) and MrBayes version 3.1.2 (Huelsenbeck & Ronquist, 2001) for the Bayesian inference (BI). The maximum likelihood analyses were performed under the GTR model with a non-parametric Shimodaira–Hasegawa-like procedure, and also with 100 bootstrap replicates. For the Bayesian inference, two runs each of 10 million generations were calculated with topologies saved at each 1000 generations, with the average standard deviation of split frequencies between runs converging to 0.003. A quarter of the 10 000 topologies were discarded as burn-in, and the remaining used to calculate the posterior probability.

Results

Taxonomic

Order Scleractinia Bourne, 1900
Suborder Caryophylliina Vaughan & Wells, 1943
Family Caryophylliidae Dana, 1846
Genus ***Caryophyllia*** Lamarck, 1816

Diagnosis. Corallum solitary, attached or free: if attached, corallum cylindrical, trochoid, or ceratoid; if free, corallum usually cornute. Calice circular, elliptical, or compressed; thecal edge spines present on species having compressed coralla. Septal symmetry variable, but hexameral symmetry with four cycles of septa most common (Cairns, 1991). One crown of pali present before penultimate or rarely the antipenultimate cycle of septa. Columella fascicular, composed of several twisted laths. Exclusively azooxanthellate and common in deep water.

Caryophyllia (*Caryophyllia*) Lamarck, 1816

Diagnosis. *Caryophyllia* in which the calice is circular to elliptical (not compressed), and which do not have thecal edge spines or crests (Cairns, 1994).
Type species. *Madrepora cyathus* Ellis & Solander, 1786, by subsequent designation (Broderip, 1828).

Caryophyllia *(Acanthocyathus)*
Milne Edwards & Haime, 1848

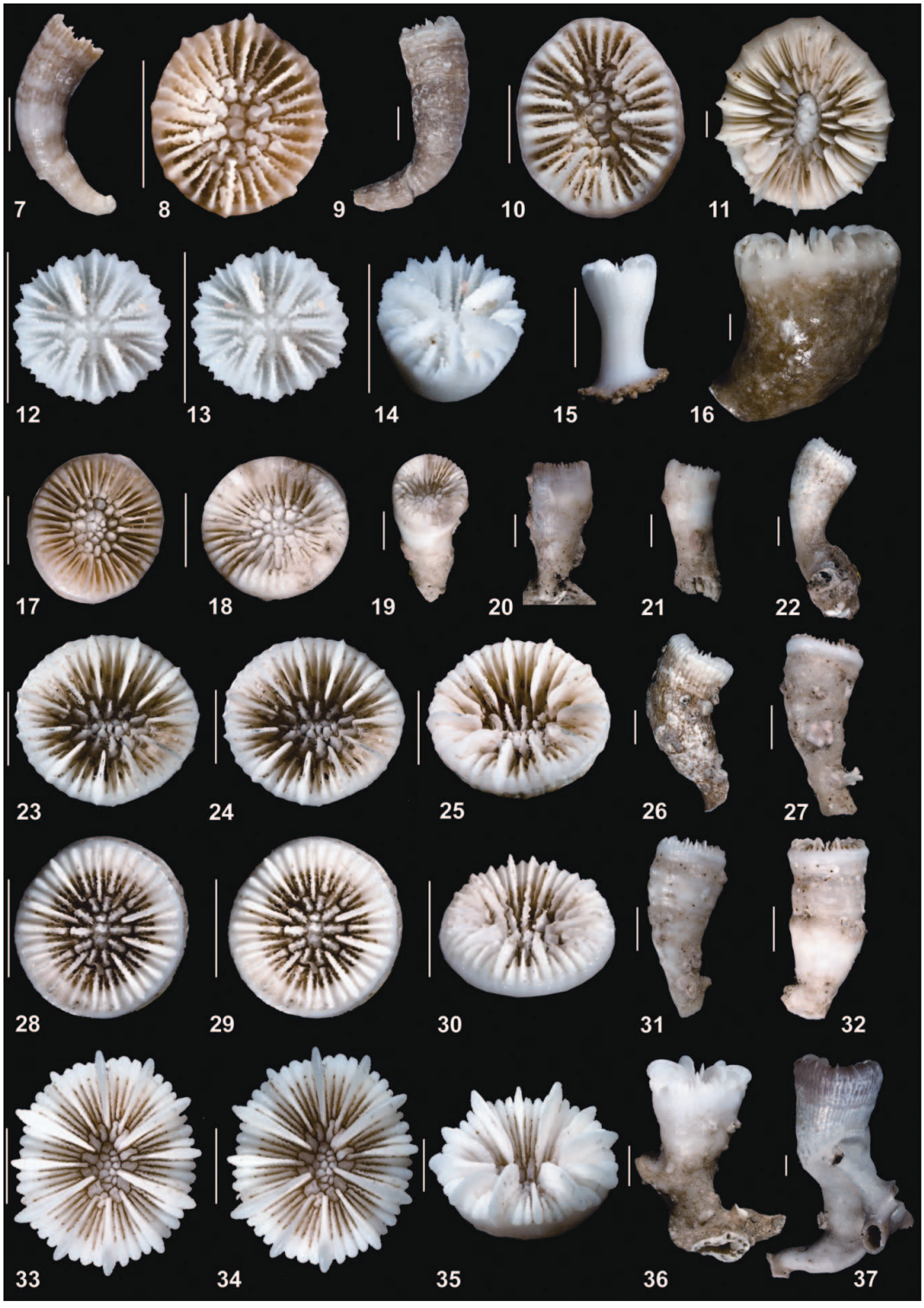
Diagnosis. *Caryophyllia* having coralla with edge spines or crests.
Type species. *Acanthocyathus grayi* Milne Edwards & Haime, 1848, by subsequent designation (Milne Edwards & Haime, 1850: xiii).

Caryophyllia abrupta Cairns, 1999
(Figs 7–10)

Caryophyllia abrupta Cairns, 1999: 71–72, figs 5d–e.
TYPE MATERIAL: The holotype and 33 paratypes are deposited at the MNHN (uncatalogued?), and 22 paratypes are at the USNM (USNM 98606 to 98612).
TYPE LOCALITY: Musorstom 7 stn. 535 (12°29.6′S, 176°41.3′W–Waterwitch Bank), 340–470 m.
NEW RECORDS: MNHN-IC.2009-0067 (8) and USNM 1130994 (5) (Bathus 3, stn. DW 786, 13 specimens); MNHN-IC.2009-0068 (Bathus 4, stn. DW 914, 2 specimens); MNHN-IC.2009-0069 (6) and USNM 1130995 (5) Bathus 4, stn. DW 918, 11 specimens).
DISTRIBUTION: New Caledonia, 600–699 m; Wallis and Futuna region (Cairns, 1999), 305–650 m; Vanuatu (Cairns, 1999), 300–400 m.

Description

Corallum ceratoid, curved between 45 and 90° usually in the plane of GCD, and free. Largest New Caledonian specimens (DW 918) 9.0 × 7.1 mm in CD and 27.5 mm in height. Base always open, having a small circular scar of less than 2 mm in diameter displaying 8 major septa. Calice circular to elliptical, with serrate calicular edge. Theca



Figs 7–37. ***Caryophyllia abrupta*** (MNHN-IC.2009–0067): 7, lateral view; 8, calicular view. (MNHN-IC.2009–0069) 9, lateral view; 10, calicular view. ***Caryophyllia atlantica*** (TMAG-K3827): 11, calicular view; 16, lateral view. ***Caryophyllia aspera*** sp. nov. (MNHN-IC.2009–0083–Holotype): 12 and 13, stereo pair calicular view; 14, oblique calicular view; 15, lateral view. ***Caryophyllia cinticulata*** (USNM 1131001): 17, calicular view; 20, lateral view. (MNHN-IC.2009–0082): 18, calicular view; 19, oblique calicular view; 21, lateral view. ***Caryophyllia concreta*** sp. nov. (USNM 1130993–Paratype): 22, lateral view. (MNHN-IC.2009-0057–Holotype): 23 and 24, stereo pair of calicular view; 25, oblique calicular view; 26, lateral view. (MNHN-IC.2009-0058–Paratype): 27, lateral view; 28 and 29, stereo pair of calicular view; 30, oblique calicular view. (MNHN-IC.2009–0059–Paratype): 31, lateral view. (MNHN-IC.2009–0060–Paratype): 32, lateral view. ***Caryophyllia crosnieri*** (MNHN-IC.2009–0041): 33 and 34, stereo pair of calicular view; 35, oblique calicular view; 36, lateral view. ***Caryophyllia diomedeae*** (TMAG-K3818): 37, lateral view. Scale bars represent 5 mm.

smooth or bearing small granules, especially in the lower 2/3 of corallum. Costae equal in width, flat, and separated by shallow, thin striae, which are more visible near calice. Rejuvenescence common. Coralla of most specimens cream to yellowish-brown.

Septa usually octamerally arranged in three cycles (8:8:16 [32 septa]) according to formula: S1 > S2 ≥ S3. However, two specimens from the station DW 914 and specimens from station DW 918, have septa decamerally arranged (10:10:20 [40 septa]). Eight exsert (up to 2 mm) primary septa with highly sinuous axial edges extend 3/5 distance to columella. S2 least exsert septa but only slightly smaller than S1, and have very sinuous axial edges. Sometimes S2 more sinuous than S1. A pair of S3 fuses to adjacent S1 forming small triangular lancets. S3 equal to or slightly smaller than S2, having slightly sinuous axial edges. A crown of 8–10 very sinuous lamellar pali encircle the well-developed columella. Fossa ranging from shallow to moderately deep, containing a fascicular columella formed by 2–6 twisted, linearly arranged elements.

REMARKS: Among the 66 previously described Recent species of *Caryophyllia*, only two propagate by transverse division: *C. secta* and *C. abrupta*. However, *C. abrupta* is distinguished by the octamerally or decamerally arranged septa versus the consistent hexameral symmetry of *C. secta*.

Caryophyllia aspera sp. nov.
(Figs 12–15)

HOLOTYPE: MNHN-IC.2009-0083 (Norfolk 2, stn. DW 2117).

PARATYPE: MNHN-IC.2009-0084 (Norfolk 2, stn. DW 2117, 1 specimen).

TYPE LOCALITY: 23°24′S, 168°00′E (New Caledonia), 400 m.

DISTRIBUTION: Same as type locality.

ETYMOLOGY: The species is named *aspera* (Latin *asper* = rough, harsh, uneven) referring to the roughness of the septal and palar faces observed in this species.

Description

Corallum ceratoid, straight, and fixed through a robust pedicel (PD:GCD = 0.57–0.6) that expands into a thin encrusting base. Larger specimen (paratype) 5.4 × 4.8 mm in CD, 3.3 mm in PD, and 10.4 mm in height. Calice elliptical and calicular edge serrate. Theca covered with narrow transverse ridges. Costae absent or slightly ridged near calicular edge. Corallum white.

Septa hexamerally arranged in four incomplete cycles according to formula: S1 > S2 > S3 > S4. S1 thick, highly exsert (up to 1 mm), with straight and thickened axial edges that fuse to columella. S2 less exsert, 1/2 to 3/4 width of S1, and with sinuous axial edges. S3 less wide and exsert than S2, also with slightly sinuous axial edges. Sometimes at calicular edge, S3 fuse to adjacent S1. When a half system is complete (5 septa), S4 rudimentary and only present near calicular edge, fusing to adjacent S1, and pali indistinguishable from columellar elements. However, when S4 are absent (half-system with 3 or 4 septa), a wide paliform lobe with highly sinuous outer edge is present before S2, easily distinguishable from columellar elements. Septal and palar faces bear several high and sharp pointed granules, giving the impression of a rough texture.

Fossa shallow, containing a well-developed columella usually fused into a mass. Columella composed of 2 or 3 slightly twisted but highly granular pillars.

REMARKS: Among the six Recent congeners that have theca covered with transverse ridges, three have hexamerally arranged septa and are sympatric in New Caledonian waters: *C. aspera* sp. nov., *C. corrugata* and *C. lamellifera*. *C. aspera* sp. nov. is distinguished by having septal and palar faces that are highly granular. Another species commonly collected in New Caledonian and Australian waters having transverse ridge theca and about the same size of *C. aspera* is *C. rugosa*. In the present study *C. rugosa* is reported having octamerally arranged septa (common condition), but also found with decameral and hexameral symmetry (see *C. rugosa* description). However, *C. aspera* sp. nov. differs in septal sinuosity (S1 with straight axial edge versus very sinuous in *C. rugosa*), and also in the roughness of septal and palar faces (very granular in *C. aspera* sp. nov. and not granular in *C. rugosa*).

Caryophyllia atlantica (Duncan, 1873)
(Figs 11 and 16)

Bathycyathus atlanticus Duncan, 1873: 318, pl. 48, figs 1–2. *Caryophyllia laevicostata* Moseley, 1881: 134, pl. 1, fig. 1. *?Caryophyllia panda* Alcock, 1902a: 91.–Alcock, 1902b: 9, pl. 1, figs 3, 3a. *Caryophyllia alcocki* Vaughan, 1907: 73–74, pl. V, figs 1a–b. *Caryophyllia atlantica*.–Zibrowius, 1980: 56–57, pl. 20, figs A-K.–Cairns, 1991: 12.–Cairns, 1995: 47–48, pl. 8d, e.–Cairns, 1998: 376.–Cairns *et al.*, 1999: 20.–Cairns, 2004: 277. *Caryophyllia profunda*.–Squires & Keyes, 1967: 23 (in part). *?Caryophyllia pacifica* Keller, 1981a: 16–17, pl. 1, figs 2a–b.–Keller, 1981b: 33, pl. 1, figs 1a–b.

TYPE MATERIAL: According to Zibrowius (1980), the lecto- and paralectotype of *B. atlanticus* are deposited at NHM (1882.12.10.132).

TYPE LOCALITY: 39°39′N, 9°43′W (off Portugal), 1355–2000 m.

NEW RECORDS: TMAG-K3827 (SS022007, stn. 50, 1 specimen).

DISTRIBUTION: Australia (Cairns, 1998; Cairns, 2004; present study), 193–1230 m; eastern Atlantic including Portugal (Duncan, 1873), Morocco, Madeira Archipelago, Azores, Mediterranean Sea (Zibrowius, 1980), 860–2165 m; Ceram Sea (Alcock, 1902b), 776–2165 m; Marcus-Necker Ridge (Keller, 1981a), 1420 m; Hawaii (Vaughan,

1907 as *C. alcocki*), 1602 m; New Zealand (Squires & Keyes, 1967 as *C. profunda*; Cairns, 1995), 1004–1474 m.
DIAGNOSIS: Corallum ceratoid, curved, extremely robust, and presumably attached. Specimen examined 39.0 × 34.0 mm in CD, and 36.0 mm in height (base broken). Calice elliptical with serrate calicular edge. Theca porcellaneous, slightly granular, and slightly ridged C1. Corallum white encircling the calice and tinted brown in direction of pedicel. Septa arranged in three size classes and 17 sectors (17:17:34 [68 septa]) according to formula: S1 > S3 > S2. Wide (up to 5 mm) and slightly sinuous pali present before S2. Columella elongate composed of a fused mass of twisted elements.
REMARKS: This species described as *Bathycyathus atlanticus* Duncan, 1873, and over a century later transferred to the genus *Caryophyllia* (Zibrowius, 1980), has an interesting disjunct distribution, being reported from the eastern Atlantic (including Mediterranean Sea), western Pacific (from Japanese to New Zealand waters), and Indian Ocean (just Indonesia and western Australia regions). The skeletal morphology of the specimen briefly described above agrees with the New Zealand specimens described by Cairns (1995) especially in the high number of septal sectors. Among their congeners, *C. atlantica* can be distinguished by the robustness of the corallum, the presence of three septal size classes (usually with 16–18 sectors), S3 > S2, and straight axial edges of the S1.

Caryophyllia cinticulata (Alcock, 1898)
(Figs 17–21)

Thecocyathus cinticulatus Alcock, 1898: 17–18, pl. ii, figs 5, 5a. *Trochocyathus cincticulatus*.–Gardiner, 1904: 99, 103–104, pl. II, fig. 2.–Squires, 1961: 17.–Cairns *et al*., 1999: 24.
TYPE MATERIAL: The type species is purported to be deposited at the Calcutta Museum, India (see Alcock, 1898: prefatory note).
TYPE LOCALITY: off Maldives, 384 m.
NEW RECORDS: MNHN-IC.2009-0081 (1) and USNM 1131001 (1) (Norfolk 1, stn. DW 1652, 2 specimens). MNHN-IC.2009-0082 (Norfolk 2, stn. DW 2023, 1 specimen).
DISTRIBUTION: New Caledonia (from 23°26.1′S, 167°50.3′E to 23°27′S, 167°51′E), 282–378 m; Maldives (Alcock, 1898), 384 m; South Africa (33°2′59″S, 27°56′59″E) (Gardiner, 1904).

Description

Corallum ceratoid to subcylindrical, robust, fixed, and with elliptical and slightly serrate calicular edges. Largest specimen examined (DW 1652) 10.5 × 9.7 mm in CD, 7 mm in PD, and 20 mm in height. Pedicel robust (PD:GCD = 0.65–0.8) expanding into a large encrusting base. Theca glistens, covered with thin, rounded, transverse ridges from outer septal edges to base. However, some specimens have transverse ridges best developed on lower half of corallum. Costal granules absent, however, some intercostal striae detectable and dividing the transverse ridges. Width of costae marked between two striae equal for all cycles. Corallum colour variable, two specimens display calicular edge and mid corallum slightly yellowish-brown, bisected by a white belt. Another two specimens display faint vertical pigmented strips in one side of the corallum.

Septa decamerally arranged in three cycles (10:10:20 [40 septa]) according to the formula: S1 > S2 > S3. However, one specimen (DW 1652) has 44 septa in 11 systems and a corresponding 11 pali. S1 less than 1.5 mm exsert, with vertical and sinuous axial edges fusing to columella low in fossa. S2 only slightly less exsert and smaller than S1, also having vertical and sinuous axial edges. S3 least exsert septa, and with slightly sinuous axial edges. All septal faces covered with quite small low and rounded granules. Upper edge of each S1 sometimes has small short carinae oriented perpendicular to trabecula. A well-developed pali before each S2 forms a crown encircling the fascicular columella. Pali with highly sinuous outer and less sinuous axial edges and ornately carinate faces, giving the pali the appearance of even greater sinuosity. Fossa of moderate depth containing a columella recessed well below pali. Columella composed of 5–9 twisted elements often fused basally.
REMARKS: Of the 66 previously described species of *Caryophyllia* (Supplementary information 1), only a small group of six have circumferential transverse ridges on the theca: *C. rugosa*, *C. lamellifera*, *C. corrugate*, *C. cinticulata* and *C. aspera* sp. nov., the others having theca ranging from porcellanous to granular and/or longitudinally ridged, i.e. costate. *Caryophyllia cinticulata* is distinguished from its congeners that have transversely ridged theca by its decameral septal symmetry, adult size larger than 10 mm in GCD, S3 smaller than S2, and extremely sinuous axial edges of S1 and S2. Only the second time collected since its original description in 1898, *C. cinticulata* has a disjunct distribution, being reported from temperate waters off South Africa, and tropical waters off Maldives and New Caledonia.

Caryophyllia concreta sp. nov.
(Figs 22–32)

HOLOTYPE: MNHN-IC.2009-0057 (Norfolk 2, stn. DW 2024).
PARATYPES: MNHN-IC.2009-0058, MNHN-IC.2009-0059, MNHN-IC.2009-0060, MNHN-IC.2009-0061, MNHN-IC.2009-0062, MNHN-IC.2009-0063, and USNM 1130992 (4) (Norfolk 2, stn. DW 2024, 10 specimens); MNHN-IC.2009-0064 and USNM 1130993 (Norfolk 2, stn. DW 2037, 2 specimens); MNHN-IC.2009-0065 (Norfolk 2, stn. DW 2133, 1 specimen).

TYPE LOCALITY: 23°28′S, 167°51′E (New Caledonia), 370–371 m.
DISTRIBUTION: New Caledonia (from 23°01′S, 168°18′E to 23°40′S, 167°41′E), 215–570 m.
ETYMOLOGY: The species name *concreta* (Latin: *concretus*, thick, hard, stiff) refers to the very thick theca found in this species.

Description

Corallum trochoid to ceratoid, straight to slightly curved, having a robust pedicel (PD:GCD = 0.44–0.53) that is firmly attached by a thin encrusting base. Largest specimen (DW 2037) 11.3 × 10.2 mm in CD, 6 mm in PD and 27.6 mm in height (base is broken). Calice circular to slightly elliptical (GCD:LCD = 0.09–1.1). Theca extremely thick, glistening with low rounded granules or heavily encrusted. Costae poorly developed or absent, especially in younger specimens. However, in larger specimens costae unequal (C1 slightly thinner than C2–3), flat, and separated by thin and shallow intercostal striae. Costae fade/disappear in direction of pedicel. Rejuvenescence common. Corallum white to yellowish-brown.

Septa symmetry appears to have a correlation with calicular diameter: specimens with GCD < 10 display septa decamerally arranged in 3 cycles (10:10:20 [40 septa]) according to formula: S1 > S2 ≥ S3, but two larger (GCD > 10) specimens collected from station DW 2037 have 11 and 12 primaries respectively. S1 largest and most exsert septa, extending 4/5 distance to columella with slightly sinuous axial edges. S2 slightly more exsert and larger than S3, otherwise S2 equal in width to S3. Axial and upper edges of S2 sinuous, extending only 1/4 to 1/2 distance to columella. S3 equal to slightly smaller than S2, with slightly sinuous axial edges. Ten to 12 well-developed and sinuous lamellar pali present before S2, forming a crown encircling the fascicular columella. Septa and pali lateral faces bear several tall granules, especially in smaller specimens.

Fossa of moderate depth containing a fascicular columella composed of 3–8, aligned to the GCD, twisted elements.
REMARKS: *Caryophyllia concreta* sp. nov. appears to be unique among *Caryophyllia* due to its extremely thick theca, and septa that are arranged in three cycles. Small specimens have a thick 'belt' or thickening below the calicular edge, making the calicular edge slightly smaller than this area. The different septal symmetry observed in this species probably is related to ontogenetic differences, with systems being added until 12 primaries are present.

Caryophyllia crosnieri Cairns & Zibrowius, 1997
(Figs 33–36)

Caryophyllia elongata Cairns in Cairns & Keller, 1993: 236–237, pl. 4, figs A–B [junior homonym of *C. clavus* var. *elongata* Duncan, 1873: 311–312 (= *C. smithii* Stokes & Broderip, 1828)].–Cairns, 1995: 52, pl. 10, figs. d-f.–Cairns, 1999: 70, figs A–B. *Caryophyllia crosnieri* Cairns & Zibrowius, 1997: 87, 89.–Cairns, 1999: 70, figs 5a, b.–Cairns *et al*., 1999: 20.–Cairns, 2004: 277.
TYPE MATERIAL: The holotype of *C. elongata* is deposited at the IO (V-2716), Moscow.
TYPE LOCALITY: 33°17′S, 44°55′E (Madagascar Plateau), 630–680 m.
NEW RECORDS: MNHN-IC.2009-0041 (2) and USNM 1130986 (1) (Norfolk 2, stn. DW 2024, 4 specimens). MNHN-IC.2009-0042 (Norfolk 2, stn. DW 2112, 2 specimens).
DISTRIBUTION: New Caledonia (Cairns & Zibrowius, 1997; and present study), 165–1434 m (but more common between 165 and 640 m); Madagascar Plateau (Cairns & Keller, 1993), 630–680 m; New Zealand (Cairns, 1995), 165–590 m; Philippines and Indonesia (Cairns & Zibrowius, 1997), 206–330 m; Australian seamounts, and north eastern and western coasts (Cairns, 1998; 2004), 133–1400 m; Wallis and Futuna, 550–600 m; and Vanuatu region (Cairns, 1999), 366–536 m.

Description

Corallum ceratoid, straight to slightly curved, and attached by a robust pedicel (PD:GCD = 0.5–0.71). Largest specimen examined (DW 2024) 12.8 × 11.9 mm in CD, 6.5 mm in PD and 22.6 mm in height, but base is broken. Theca granular and porcellanous. Costae flat to slightly convex separated by thin, shallow striae near calicular edge, however, sometimes C1–2 ridged and sinuous. Corallum yellowish-brown (including septa, pali and columella), but darker near calicular edge. Base and pedicel white.

Septa hexamerally arranged in four cycles (6:6:12:24 [48 septa]) according to formula: S1 > S2 > S4 ≥ S3. S1 highly exsert, extending to columella with straight and slightly convex upper edge, which becomes vertical deeper in fossa. S2 less exsert and narrower than S1, having slightly sinuous axial edges. S3 least exsert septa and equal or slightly smaller than S4. Upper edge of S3 oblique, becoming vertical at same level of the upper edge of P3. Axial edge of S3 sinuous. S4 dimorphic: those adjacent to S1 wider than S3, and those adjacent to S2 equal in width to S3. Upper, outer edge of S4 fuses to adjacent S1 or S2 forming low triangular lancets at calicular edge. Septal faces covered with blunt triangular granules, which sometimes fuse forming small carinae perpendicular to plane of septa. A well-developed and sinuous pali (P3) separated by a moderately deep notch present before each S3. Sometimes lateral palar faces bear short carinae.

Fossa deep, containing a fascicular columella aligned in axis of GCD and composed of 7 to 12 highly twisted elements that always terminate lower in fossa than palar crown.

REMARKS: *Caryophyllia crosnieri* is distinguished from its New Caledonian and Australian congeners by having well-developed S1 that separate a pair of pali, or, as observed by Cairns & Zibrowius (1997), by having small 'paired' pali.

Caryophyllia diomedeae Marenzeller, 1904
(Figs 37–46)

Caryophyllia diomedeae Marenzeller, 1904: 79–80, pl. 1, fig. 2.–Durham & Barnard, 1952: 10, 82, pl. 9, fig. 43.–Cairns, 1991: 11–13, pl. 4, figs c-e.–Cairns, 1995: 49–50, pl. 9, figs a-d.–Cortés, 1997: 330.–Cairns & Zibrowius, 1997: 88.–Koslow & Gowlett-Holmes, 1998: 38.–Cairns, 1999: 74.–Cairns *et al*., 1999: 20.–Piñón, 1999: 20, 81.–Cairns, 2004: 264, 277, 328.–Cairns *et al*., 2005: 17, 25, 28, figs 2D–E.–González-Romero *et al*., 2008: 1–2, fig. 1. *Caryophyllia profunda*.–Cairns, 1982: 17–19 (in part: Eltanin-1403). *Caryophyllia sarsiae*.–Cairns & Parker, 1992: 19–20, figs 5c, e, f.

TYPE MATERIAL: One syntype is deposited at the USNM (22083).

TYPE LOCALITY: Albatross stn. 3358 (6°30′N, 81°44′W, 1043 m–Pacific coast of Panama).

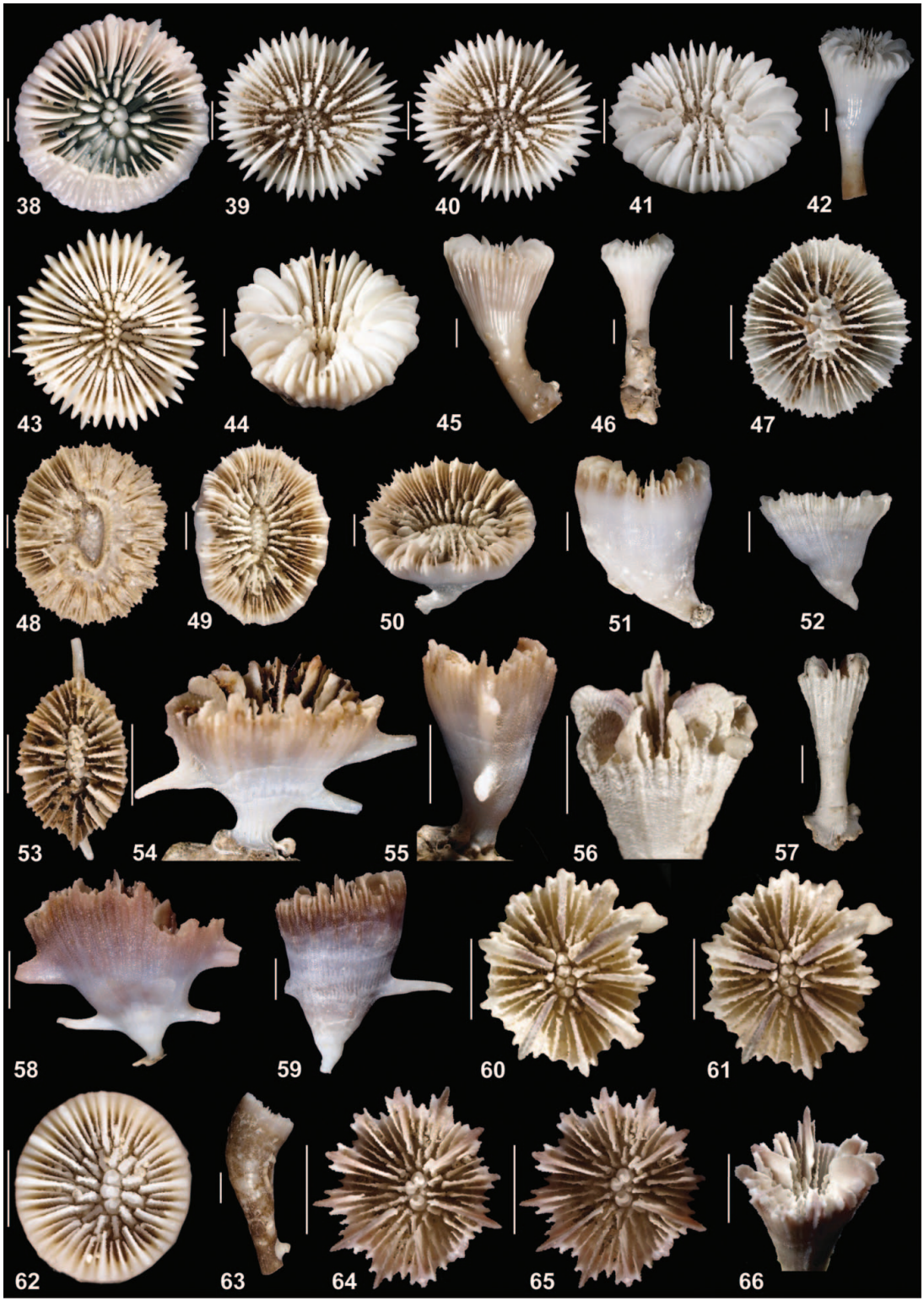
NEW RECORDS: MNHN-IC.2009–0003 (Bathus 3, stn. CP 833, 1 specimen). MNHN-IC.2009–0004 (Bathus 4, stn. DW 914, 1 specimen). MNHN-IC.2009–0005 (Norfolk 2, stn. DW 2046, 2 specimens). MNHN-IC.2009–0006 (Norfolk 2, stn. DW 2047, 2 specimens). MNHN-IC.2009–0007 (Norfolk 2, stn. DW 2063, 1 specimen). MNHN-IC.2009–0008 (Norfolk 2, stn. DW 2065, 3 specimens). MNHN-IC.2009–0009 (Norfolk 2, stn. DW 2068, 3 specimens). MNHN-IC.2009–0010 (8) and USNM 1130978 (4) (Norfolk 2, stn. DW 2069, 12 specimens). MNHN-IC.2009–0011 (Norfolk 2, stn. DW 2070, 3 specimens). MNHN-IC.2009–0012 (Norfolk 2, stn. DW 2074, 5 specimens). MNHN-IC.2009–0013 (Norfolk 2, stn. DW 2075, 3 specimens). MNHN-IC.2009–0014 (6) and USNM 1130979 (2) (Norfolk 2, stn. DW 2078, 8 specimens). MNHN-IC.2009–0015 (Norfolk 2, stn. DW 2086, 9 specimens). MNHN-IC.2009–0016 (Norfolk 2, stn. DW 2091, 1 specimen). MNHN-IC.2009–0017 (Norfolk 2, stn. DW 2100, 1 specimen). MNHN-IC.2009–0018 (14) and USNM 1130980 (4) (Norfolk 2, stn. DW 2102, 18 specimens). MNHN-IC.2009–0019 (12) and USNM 1130981 (4) (Norfolk 2, stn. DW 2103, 16 specimens). MNHN-IC.2009–0020 (Norfolk 2, stn. DW 2104, 1 specimen). MNHN-IC.2009–0021 (Norfolk 2, stn. DW 2107, 9 specimens). MNHN-IC.2009–0022 (Norfolk 2, stn. DW 2156, 1 specimen). TMAG-K3815 (SS011997, stn. ??, 4 specimens). TMAG-K3816 (6) and MTQ a61479 (4) (SS011997, stn. 17, 10 specimens). TMAG-K3817 (SS011997, stn. 22, 7 specimens). TMAG-K3818 (6) and MTQ a61480 (4) (SS011997, stn. 57, 10 specimens). TMAG-K3819 (4) and MTQ a61481 (1) (SS011997, stn. 67, 5 specimens). TMAG-K3820 (25) and MTQ a61482 (5) (SS011997, stn. 70, 30 specimens). WAM Z21463 (1) and MTQ a61454 (1) (SS102005, stn. 44, 2 specimens). TMAG-K3821 (SS022007, stn. 21, 1 specimen). TMAG-K3822 (SS022007, stn. 36, 3 specimens). TMAG-K3823 (SS022007, stn. 37, 4 specimens). TMAG-K3824 (SS022007, stn. 41, 2 specimens). TMAG-K3825 (SS022007, stn. 66, 3 specimens). AM-G.17614 (Norfanz: stn. 51, 1 specimen).

DISTRIBUTION: New Caledonia and Australia regions, 336–1786 m; off Pacific Panama (Marenzeller, 1904), 1043 m; Cocos and Galapagos Islands (Cairns, 1991), 245–806 m; New Zealand (Cairns, 1982; 1995), 660–1200 m; northeastern Atlantic from the Mediterranean to the Azores; Bermuda; Cook Islands (Cairns, 1995), 1585 m; Philippines and Indonesia (Cairns & Zibrowius, 1997), 300–885 m; off southeastern and western Australia (Cairns, 1998; 2004), 600–900 m; Vanuatu (Cairns, 1999), 475–799 m; off northern Pacific from 0° to 31°N (Piñón, 1999; González-Romero *et al*., 2008), 55–2086 m; off northern Chile (Cairns *et al*., 2005), 1760 m.

Description (based on New Caledonian specimens)

Corallum ceratoid, always attached through a robust pedicel reinforced by concentric layers of stereome (or tectura), which expands into a thin encrusting base. Coralla usually straight or slightly curved near base, but some specimens, especially when fixed to *Solenosmilia variabilis*, display different shapes. Pedicel up to 11.0 mm in diameter. Largest New Caledonian specimen examined (DW 2066) 25.1 × 21.1 mm in CD, 6.3 mm in PD and 30.9 mm in height (base broken). Calice slightly elliptical with jagged margins. Theca thick and porcellanous, however expression of costae quite variable. Some specimens have scarce or no indication of costae; some have low and rounded, equal costae separated by shallow grooves; whereas others have C1 and C2 ridged and more prominent than C3 and C4 especially near the calicular edge. Costal granules not common, but when present 3 or 4 (sometimes fused) can be counted across each costa. Corallum white to yellowish-brown, normally darker near base.

Septa hexamerally arranged in four complete cycles (6:6:12:24 [48 septa]) according to formula: S1–2 > S3 ≥ S4. S1–2 very exsert (up to 3.2 mm) especially in larger coralla, with rounded upper edges, and vertical, sinuous axial edges extending about 3/5 distance to columella. Paliferus S3 about 1/2 to 3/4 the exsertness of S1–2, with very sinuous lower axial edges that extend about halfway to columella. Each S3 is separated from their respective P3 by a deep notch (∼1 mm wide). S4 least exsert septa and equal in width to S3 in smaller coralla, but smaller in larger specimens having only slightly sinuous axial edges. Axial and



Figs 38–66. ***Caryophyllia diomedeae*** (TMAG-K3818): 38, calicular view. ***Caryophyllia diomedeae*** (MNHN-IC.2009–0016): 39 and 40, stereo pair of calicular view; 41, oblique calicular view; 42, lateral view. (MNHN-IC.2009–0015): 43, calicular view; 44, oblique calicular view; 45, lateral view. (MNHN-IC.2009–0003): 46, lateral view. ***Caryophyllia grandis*** (WAM Z21467): 52, lateral view; 47, calicular view; 48, calicular view. (WAM Z21466): 49, calicular view; 50, oblique calicular view; 51, lateral view. ***Caryophyllia grayi*** (WAM Z21471): 53, calicular view; 54, lateral view; 55, lateral view of the LCD. (WAM Z21470): 58, lateral view; 59, lateral view. ***Caryophyllia hawaiiensis*** (MNHN-IC.2009–0043): 56, oblique calicular view; 57, lateral view; 60 and 61, stereo pair of calicular view. ***Caryophyllia laevigata*** (MNHN-IC.2009–0023–Holotype): 62, calicular view; 63, lateral view. ***Caryophyllia lamellifera*** (MNHN-IC.2009–0044): 64 and 65, stereo pair of calicular view; 66 oblique calicular view. Scale bars represent 5 mm.

outer edges of P3 very sinuous and lateral faces granular, forming a distinctive crown around the columella. Septal faces smooth above calicular edge, becoming granular below it.

Fossa of moderate depth containing a fascicular columella composed of 3 to 18 twisted elements aligned in the plane of GCD.

REMARKS: Among the species belonging to the genus *Caryophyllia*, *C. diomedeae* groups with species that are fixed and contain four complete septal cycles, which is the most common morphologic pattern within the genus. *C. diomedeae* can be distinguished from the other species from New Caledonia and Australian regions by the presence of a complete fourth septal cycle, well-developed pali before the penultimate septal cycle, and a septal formula of S1–2 > S3 ≥ S4. However, due to the broad distribution reported for this species (see Distribution), some intraspecific morphological variations are observed especially in costae, septal exsertness and size of corallum. Some specimens collected off New Caledonia could be confused with *C. stellula*, but differ in having always an attached corallum, and a PD:GCD > 0.2.

Caryophyllia grandis Gardiner & Waugh, 1938
(Figs 47–52)

Caryophyllia grandis Gardiner & Waugh, 1938: 177, pl. 1, fig. 2.–Cairns, 1991: 12.–Cairns & Keller, 1993: 234.–Cairns & Zibrowius, 1997: 96, figs 9g–h.–Cairns, 1998: 376.–Cairns *et al*., 1999: 20.–Cairns, 2004: 277.

TYPE MATERIAL: Four syntypes are deposited at NHM (1950.1.9.211–215).

TYPE LOCALITY: 4°58′42″N, 73°16′24″E (west side of Fadiffolu Atol, Maldives Islands), 494 m.

NEW RECORDS: WAM Z21466 (SS102005, stn. 95, 1 specimen). WAM Z21467 (SS102005, stn. 171, 1 specimen).

DISTRIBUTION: Australia, 399–431 m; Indonesia (Cairns & Zibrowius, 1997), 251–567 m; Malaysia (???); from South Africa to western Sumatra (???), 183–595 m.

DIAGNOSIS: Corallum up to 50 mm in GCD, usually free and curved. C1–3 slightly ridged or absent. Upper theca and septal faces light beige, but lower theca white or discoloured. Septa usually hexamerally arranged in 5 cycles (S1–3 > S4 > S5). S5 more exsert than S4, fusing with their adjacent S1–3 forming highly exsert lancets. Twenty-four P4, which are usually narrower than S4 they border, form a crown encircling a fascicular columella composed of broad, twisted elements.

REMARKS: The examination of the two specimens collected off western Australian waters does not add to our knowledge of morphological variation. However, images from freshly collected specimens from Australian waters show that even with the low amount of tissue present in this species, just above the pali the tissue exhibits a green fluorescent colour, and below the pali the tissue is orange.

Caryophyllia grayi (Milne Edwards & Haime, 1848)
(Figs 53–55, 58–59)

Acanthocyathus grayi Milne Edwards & Haime, 1848: 293, pl. 9, fig. 2.–Alcock, 1898: 15.–van der Horst, 1931: 6.–Umbgrove, 1938: 264–265.–Umbgrove, 1950: 641–642, pl. 81, figs 27–32.–Wells, 1984: 209, pl. 2, figs 5–9.–Zou, 1988: 76, figs 8–9. *Caryophyllia grayi*.–Cairns, 1994: 49, pl. 21i–k.–Cairns & Zibrowius, 1997: 97–98, figs 7c, f, i.–Cairns, 1998: 377.–Cairns, 1999: 76.–Cairns *et al*., 1999: 20.–Cairns, 2004: 276.

TYPE MATERIAL: Syntype is deposited at NHM (1840.9.29.42).

TYPE LOCALITY: Not stated.

NEW RECORDS: WAM Z21469 (SS102005, stn. 115, 3 specimens). WAM Z21470 (SS102005, stn. 139, 1 specimen). WAM Z21471 (4) and MTQ a61469 (1) (SS102005, stn. 153, 5 specimens).

DISTRIBUTION: Japan (Cairns, 1994), 37–490 m; Philippines and Indonesia (Cairns & Zibrowius, 1997), 50–268 m; Wallis and Futuna region (Cairns, 1999), 125–360 m; South Africa; Australia (Cairns, 2004; present study), 100–166 m.

DIAGNOSIS (based on Australian specimens)
Corallum ceratoid, compressed (GCD:LCD = 1.3–1.5), and usually attached to a small object by a slender pedicel 1.5–1.8 mm in diameter or secondarily unattached. Thecal edges rounded, the concave (or one of the edges) edge having 1 to 3 elongate spines, and the other edge bearing 2 to 5 elongate spines, but an equal number of spines not observed. Edge spines circular to elliptical in cross section. Costae rounded, not ridged. Septa usually arranged in 14 sectors. Primary septa highly exsert, forming small calicular lancets. Pairs of S4 sometimes present in end half-systems. A crown of 14 pali (P2) encircle the fascicular elongated columella.

REMARKS: Comparisons between the Japanese specimens described by Cairns (1994) and the Australian specimens available for the present study show that the latter have primary septa with sinuous axial edges, in contrast to the Japanese specimens that have straight axial edges. Otherwise, they are practically indistinguishable. Among its congeners, *C. grayi* can be identified by the asymmetrical arrangement of the edge spines on both thecal edges, and a corallum with usually more than 56 septa (14 pali). *C. grayi* is more fully described by Cairns (1994).

Caryophyllia hawaiiensis Vaughan, 1907
(Figs 56–57, 60–61)

Caryophyllia hawaiiensis Vaughan, 1907: 76, pl. 5, figs 4a, b.–Cairns, 1984: 11. Cairns, 1991: 12.–Cairns,

1995: 44–45, pl. 7, figs d–f.–Cairns & Zibrowius, 1997: 93.–Cairns, 1999: 69–70.–Cairns *et al*., 1999: 20.–Cairns, 2004: 277.–Cairns, 2006: 47.
TYPE MATERIAL: Four syntypes are deposited at the NMNH (USNM 20749–20750).
TYPE LOCALITY: 21°04′05″N, 157°10′35″W (off Molokai, Hawaiian Islands), 168–388 m.
NEW RECORDS: MNHN-IC.2009–0043 (1) and USNM 1130987 (1) (Bathus 4, stn. DW 902, 2 specimens).
DISTRIBUTION: New Caledonia, 341–351 m; Hawaii (Vaughan, 1907; Cairns, 1984), 44–388 m; Japan (Cairns, 1995), 128–174 m; New Zealand and Australia (Cairns, 1995; 2004), 126–279 m; Philippines and Indonesia (Cairns & Zibrowius, 1997), 97–170 m; Wallis and Futuna, and Vanuatu region (Cairns, 1999), 252–300 m; South China Sea.

Description

Corallum ceratoid to trochoid, straight to slightly curved, and firmly attached by a robust pedicel that expands into a thin encrusting base (PD:GCD = 0.32–0.34). Largest specimen examined 9.5 × 7.8 mm in CD and 21.6 mm in height. Theca coarsely granular and all costae ridged. C1–2 more prominent but narrower than C3–4, and extending further in direction of the pedicel. Corallum usually white, however upper and axial edges of S1–2 slightly yellowish-brown.

Septa pentamerally arranged in four complete cycles (5:5:10:20 [40 septa]) according to formula: S1 > S2 > S4 > S3. Septal exsertness and sinuosity following the same pattern of *C. lamellifera*, however, in *C. hawaiiensis* S4 is/are wider than S3. Twelve well-developed pali (P3) form a palar crown encircling the columella.

Fossa of moderate depth containing a fascicular columella consisting of 3–12 twisted elements.
REMARKS: Within the New Caledonian *Caryophyllia* group, *C. hawaiiensis* is distinguished by the presence of highly exsert S1 (which are larger than S2), and S4 that are larger than S3. However, according to Cairns (1995) this species has even with a tendency toward pentameral symmetry and a total of 40 septa, eventually specimens with 11 pali and 44 septa (Hawaiian Islands) and 12 pali and 48 septa (New Zealand) occur as well.

Caryophyllia laevigata sp. nov.
(Figs 62–63)

HOLOTYPE: MNHN-IC.2009–0023 (Norfolk 2, stn. DW 2066).
PARATYPES: MNHN-IC.2009–0024, MNHN-IC.2009–0025, USNM 1130982 (2) (Bathus 3, stn. DW 781, 4 specimens). MNHN-IC.2009–0002 (3) and USNM 1130977 (1) (Bathus 3, stn. DW 783, 4 specimens). MNHN-IC.2009–0026 (Bathus 3, stn. DW 784, 1 specimen). MNHN-IC.2009–0027, MNHN-IC.2009–0028, MNHN-IC.2009–0029, MNHN-IC.2009–0030, MNHN-IC.2009–0031, MNHN-IC.2009–0032 and USNM 1130983 (3) (Bathus 3, stn. DW 786, 9 specimens). MNHN-IC.2009–0033 (Norfolk 2, stn. DW 2025, 1 specimen). MNHN-IC.2009–0034 (Norfolk 2, stn. DW 2058, 1 specimen). MNHN-IC.2009–0035 (Norfolk 2, stn. DW 2066, 1 specimen). MNHN-IC.2009–0036, MNHN-IC.2009–0037 and USNM 1130984 (2) (Norfolk 2, stn. DW 2069, 4 specimens). MNHN-IC.2009–0038 and USNM 1130985 (Norfolk 2, stn. DW 2102, 2 specimens). MNHN-IC.2009–0039 (Norfolk 2, stn. DW 2107, 1 specimen). MNHN-IC.2009–0040 (Norfolk 2, stn. DW 2113, 1 specimen).
TYPE LOCALITY: 25°17′S, 168°55′E (Banc Athos, New Caledonia), 834–870 m.
DISTRIBUTION: New Caledonia (from 23°27′S, 167°51′E to 25°20′S, 168°58′E), 410–1032 m.
ETYMOLOGY: The species name *laevigata* (Latin: *laevigatus* = smooth, slippery) refers to the porcellanous theca present in this species.

Description

Corallum ceratoid, usually curved up to 45° or only slightly bent in the axis of the GCD, and attached by a robust pedicel (PD:GCD = 0.29–0.63), which expand into a thin encrusting base, but most specimens examined have a broken base. Holotype 9.9 × 9.1 mm in CD, 5 mm in PD and more than 35.0 mm in height. Calice always elliptical with GCD:LCD between 1.07 and 1.14 (the smaller ratio is related to smaller specimens) with a serrate calicular edge. Theca smooth and porcellanous, bearing very low and rounded granules. Costae usually poorly defined or absent. If present, all costae flat to slightly ridged (especially near calicular edge), with C1 slightly narrower than C2–4. All costae separated by extremely thin and shallow intercostal striae. Theca usually yellowish-brown near calicular edge with lower part of corallum lighter; however, specimens completely white or completely yellowish-brown also present.

Septa hexamerally arranged in four complete cycles (6:6:12:24 [48 septa]) according to formula: S1–2 > S4 ≥ S3, however, smaller specimens have S3 ≥ S4. Primaries and secondaries equal in width and exsertness (up to 1.2 mm exsert), extending 1/2 to 3/5 distance to columella with sinuous axial edges. Tertiaries equal to or slightly less exsert than quaternaries (S4 usually fuses to adjacent S1 above calicular edge forming low lancets), being slightly wider in small specimens, and smaller in mature coralla. Axial edge of tertiaries very sinuous, but quaternaries only slightly sinuous. A tall and sinuous palus is present before each tertiary, forming a well-developed crown encircling

the columella, and terminate higher in fossa than columellar elements. All septal and palar faces bear tall pointed granules.

Fossa of moderate depth, containing a fascicular columella composed of an elongate field of 2–9 twisted and closely spaced elements.

REMARKS: *Caryophyllia laevigata* sp. nov. is grouped morphologically within the largest group of *Caryophyllia*, i.e., species having hexameral symmetry in four complete cycles. However, it can be distinguished by the presence of the following characters: porcellanous theca, S4 usually larger than S3 (especially in mature coralla), and slightly (instead of highly) exsert S1–2. *C. laevigata* sp. nov. may be confused with *C. diomedeae*, and in fact they are probably sister species, being differentiated especially by the septal exsertness, size of adult corallum (GCD < 11 mm in *C. laevigata* sp. nov. and usually > 20 mm in *C. diomedeae*), and corallum colour (most *C. diomedeae* are completely white and darker near the base, and *C. laevigata* sp. nov. is usually darker near calicular edge).

Caryophyllia lamellifera Moseley, 1881
(Figs 64–68)

Caryophyllia lamellifera Moseley, 1881: 140–141, pl. 1, figs 7a, b.–Hutton, 1904: 315.–Cairns, 1991: 12.–Cairns, 1995: 51–52, pl. 9, fig. i, pl. 10, figs a–c.–Cairns & Zibrowius, 1997: 90.–Cairns, 1999: 74–75.–Cairns *et al*., 1999: 20.–Cairns, 2004: 278.

TYPE MATERIAL: Two uncataloged syntypes are deposited at NHM.

TYPE LOCALITY: *Challenger* stn. 170: 29°55′S, 178°14′W (Kermadec Ridge), 1152 m.

NEW RECORDS: MNHN-IC.2009–0044 (Bathus 4, stn. DW 882, 1 specimen). AM-G.17615 (Norfanz 0308, stn. 24, 1 specimen).

DISTRIBUTION: New Caledonia, 250–350 m; New Zealand (Cairns, 1995), 89–1152; Australia (Cairns, 1995; 2004, and present study), 143–164 m; Philippines and Indonesia (Cairns & Zibrowius, 1997), 100–300 m; Wallis and Futuna region, and Vanuatu (Cairns, 1999), 180–516 m.

Description (based on New Caledonia specimens)

Corallum small, ceratoid to trochoid, with circular to elliptical calice, and attached by a pedicel (PD:GCD = 0.32–0.47) which expands into a thin encrusting base. Specimen examined (DW 882) 12.2 × 10.5 mm in CD, but has a broken pedicel. Costae inconspicuous, each separated by very shallow and narrow intercostal striae disappearing toward pedicel. Theca covered with closely spaced, rounded on edge, transverse ridges. Ridges continuous and best developed on lower part of the corallum. Corallum white to reddish-brown near calicular edge.

Septa hexamerally arranged in four complete cycles (6:6:12:24 [48 septa]), according to formula: S1–S2 > S3 > S4. S1–S2 equally exsert (up to 2 mm), extending about 80% distance to columella, with rounded upper edges, and vertical and slightly sinuous axial edges. Higher cycles progressively less exsert and wide. However, S4 almost as exsert as S2, fusing to adjacent S1 above calicular edge forming tall triangular lancets. Axial edge of S3 very sinuous, and S4 straight to slightly sinuous. Twelve well-developed pali, each separated from their corresponding S3 by a V notch, form a palar crown encircling columella. Fossa of moderate depth containing a fascicular columella consisting of 3–12 twisted elements.

REMARKS: Among the six species of *Caryophyllia* that have theca covered with transverse ridges (sometimes as aligned granules), *C. lamellifera* is most easily distinguished by its lack of costae, S1 = S2, S3 > S4, septal symmetry, and septal exsertness (especially the primaries).

Caryophyllia oblonga sp. nov.
(Figs 69–71)

HOLOTYPE: MNHN-IC.2009–0085 (Norfolk 2, stn. DW 2053).

PARATYPES: MNHN-IC.2009–0086 (1) and USNM 1131003 (1) (Norfolk 2, stn. DW 2072, 2 specimens).

TYPE LOCALITY: 23°40′S, 168°16′E (off New Caledonia), 670–708 m.

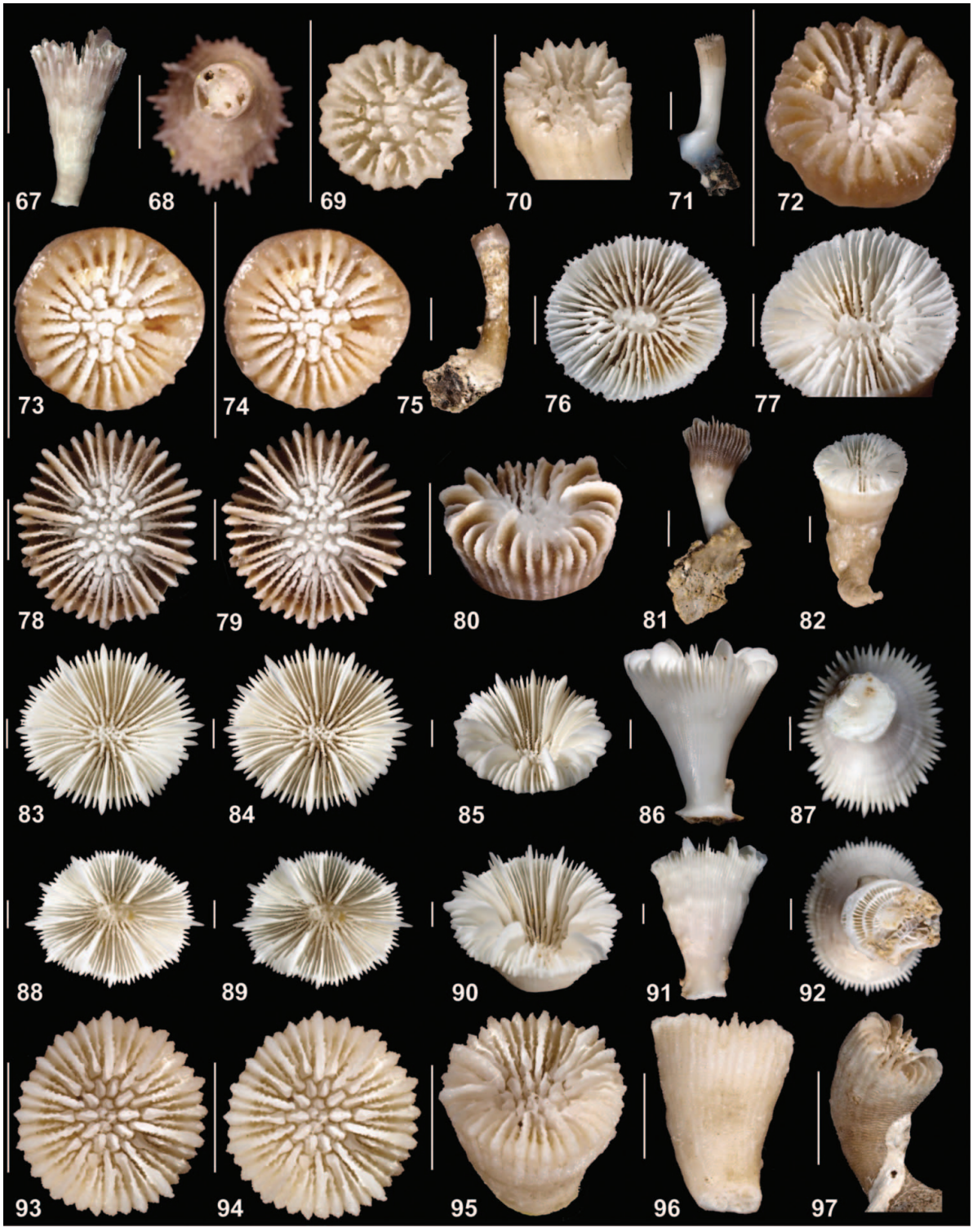
DISTRIBUTION: New Caledonia (from 23°40′S, 168°16′E to 25°21′S, 168°57′E), 670–1005 m.

ETYMOLOGY: The species is named *oblonga* (Latin *oblongus* = longer than broad, having an elongate shape) referring to the elongate corallum of this species.

Description

Corallum elongate, ceratoid, straight to slightly curved, and attached by a robust pedicel (PD:GCD = 0.43–0.71) that expands into a thin encrusting) base. Holotype 4.1 × 4.0 mm in CD, 15.5 mm in height and 2.9 mm in PD. Calice circular (GCD:LCD = 1.0–1.04), with serrate calicular margin. Theca porcellanous, bearing low rounded granules. Costae unequal in width: C1 and C2 slightly ridged; C3 flat and slightly broader than C1 and C2; when present, C4 only distinguishable near calicular edge. Costae separated by very shallow intercostal striae, extending from calicular edge to pedicel. Corallum white to cream.

Septa hexamerally arranged in four incomplete cycles (6:6:12:x) according to formula: S1 > S2 > S3 > S4. S1 thicker than other septa, up to 1 mm exsert, extending about 3/5 distance to columella with moderately sinuous and vertical axial edges. S2 slightly narrower and less exsert than S1, with highly sinuous axial edges. S3 1/2 to 3/4 width



Figs 67–97. ***Caryophyllia lamellifera*** (MNHN-IC.2009–0044): 67, lateral view; 68, detail of a broken base. ***Caryophyllia oblonga*** sp. nov. (MNHN-IC.2009–0085–Holotype): 69, calicular view; 70, oblique calicular view; 71, lateral view. ***Caryophyllia octopali*** (MNHN-IC.2009–0066): 72, oblique calicular view; 73 and 74, stereo pair of calicular view; 75, lateral view. ***Caryophyllia planilamellata*** (WAM Z21464): 76, calicular view; 77, oblique calicular view; 82, lateral view. ***Caryophyllia quadragenaria*** (MNHN-IC.2009–0070): 78 and 79, stereo pair of calicular view; 80, oblique calicular view; 81, lateral view. ***Caryophyllia ralphae*** (MNHN-IC.2009–0077): 83 and 84, stereo pair calicular view; 85, oblique calicular view; 86, lateral view; 87, broken base. ***Rhizosmilia robusta*** (DW 2124): 88 and 89, stereo pair calicular view; 90, oblique calicular view; 91, lateral view; 92, broken base. ***Caryophyllia rugosa*** (MNHN-IC.2009–0055): 93 and 94, stereo pair of calicular view; 95, oblique calicular view; 96, lateral view. (MNHN-IC.2009–0056): 97, lateral view. Scale bars represent 5 mm.

of S2, with slightly sinuous axial edges. S4 rudimentary and present only near calicular edge. A crown composed of 6 pali stands before the S2 encircling the columella. Pali extremely sinuous, occupying the space between a pair of S1 (pali better developed in holotype). Pali of paratypes indistinguishable from columellar elements.

Fossa shallow to moderately deep, containing a fascicular columella composed of several twisted laths.

REMARKS: Not many species of *Caryophyllia* have an elongate, subcylindrical corallum with small calicular diameter. Among the ones that do, *Caryophyllia oblonga* sp. nov. is most similar to *C. marmorea*, but is easily distinguished by its septal symmetry (octameral in *C. marmorea*).

Caryophyllia octopali Vaughan, 1907
(Figs 72–75)

Caryophyllia octopali Vaughan, 1907: 74–75, pl. 5, fig. 4.–Cairns, 1984: 11.–Cairns, 1991: 12.–Cairns & Zibrowius, 1997: 92.–Cairns *et al*., 1999: 20.–Cairns, 2006: 47.

TYPE MATERIAL: The holotype and paratypes are deposited at NMNH (USNM 20746 and 20747, respectively).

TYPE LOCALITY: *Albatross* stn. 3827 and 3828 (South of Molokai, Hawaii), 513–678 m.

NEW RECORDS: MNHN-IC.2009–0066 (Norfolk 2, stn. DW 2025, 1 specimen).

DISTRIBUTION: New Caledonia, 410–443 m; Hawaiian Islands (Vaughan, 1907; Cairns, 1984), 457–627 m.

Description

Corallum elongate to subcylindrical, straight to slightly curved, and attached by a robust pedicel (PD:GCD = 0.65) that expands into a thin encrusting base. Largest specimen examined 4.5 mm in CD, 18.1 mm in height and 2.9 mm in PD. Calice circular, theca smooth and porcellanous near calice. Costae flat, not well defined, and more conspicuous near pedicel and lower corallum, where they are equal in width and separated by very shallow and narrow intercostal striae. Upper 3 mm of corallum, including upper and outer septal edges, reddish-brown, and lower part display an opaque yellowish-brown colour. Axial septal edges, pali and columellar elements white.

Septa octamerally arranged in three incomplete cycles (four S3 usually missing from end half-systems, totalling 28 septa), according to formula: S1 > S2–S3. S1 less than 1 mm exsert, with rounded upper edge and moderately sinuous axial edges that almost reach columella. S2 least exsert septa (< 0.5 mm), also with moderately sinuous axial edges, and extending about 3/4 width of S1. S3 equal to or slightly wider than S2, with less sinuous axial edges. At calicular edge, each S3 fuses to its adjacent S1 forming very low calicular lancets that rise higher than the S2. All septal faces highly granular. Each S2 bears a sinuous 0.5 mm wide palus. Fossa shallow. Columella fascicular composed of three twisted elements.

REMARKS: Among the four previously described *Caryophyllia* that lack transversely ridged theca, and with octamerally arranged septa with tertiaries equal to or wider than their secondaries (*C. octopali*, *C. barbadensis*, *C. marmorea* and *C. octonaria*), *C. octopali* is distinguished by its non-granular pali, PD:GCD ≥ 0.5, and elongate to subcylindrical corallum. The new records of this species extend its occurrence from the Hawaiian Islands to the southwestern Pacific.

Caryophyllia planilamellata Dennant, 1906
(Figs 76–77, 82)

Caryophyllia planilamellata Dennant, 1906: 157–158, pl. 6, figs 4a, b.–Howchin, 1909.–Squires, 1961: 18.–Veron, 1986: 605.–Cairns, 1991: 12.–Cairns & Parker, 1992: 17–19, figs 4g–i.–Stranks, 1993: 20.–Cairns *et al*., 1999: 20.–Cairns, 2004: 278. *Caryophyllia cyathus*.–Hoffmeister, 1933: 14, pl. 4, figs 4–5.–Squires, 1961: 18. *Caryophyllia clavus*.–Wells, 1958: 262, 265, pl. 1, figs 12–13.–Squires, 1961: 18.

TYPE MATERIAL: The holotype is deposited at the NMV (F41521).

TYPE LOCALITY: Cape Jaffa (220–549 m) or off Beachport (201 m), South Australia (Stranks, 1993).

NEW RECORDS: WAM Z21464 (6) and MTQ a61449 (3) (SS102005, stn. 20, 9 specimens). WAM Z21465 (SS102005, stn. 40, 1 specimen). TMAG-K3826 (1) and MTQ a61442 (1) (SS022007, stn. 32, 2 specimens).

DISTRIBUTION: Australia (Cairns & Parker, 1992; Cairns, 1998; Cairns, 2004; present study), 128–1220 m.

DIAGNOSIS: Corallum ceratoid to cornute, gradually tapering to a curved pedicel. Calice slightly elliptical (GCD:LCD between 1.05–1.14). Theca porcellanous composed of equal flat costae that bear low rounded granules. Septa arranged in three size-classes according to the formula: S1 > S2 > S3. Specimens examined have about 80 septa (20:20:40), and consequently 20 well-developed pali (P2). Primary septa moderately exsert, extending about 3/5 distance to columella, with straight vertical axial edges. Paliferus secondaries less exsert and about 2/3 width of primaries, bearing straight to slightly sinuous axial edges. Tertiaries slightly less exsert and wide than secondaries with straight axial edges. Fossa shallow, containing a robust and fascicular columella.

REMARKS: Even more than a century after the description of *C. planilamellata*, this species is reported only from Australian waters, and can be distinguished from its congeners by the absence of spines and transverse division, and the presence of three septal size classes, S2 > S3, and more than 18 pali. Sometimes specimens can be weakly attached

to the substratum. Freshly collected specimens have orange tentacles.

Caryophyllia quadragenaria Alcock, 1902
(Figs 78–81)

Caryophyllia quadragenaria Alcock, 1902a: 91–92.–Alcock, 1902b: 10, pl. 1, figs 4, 4a.–Keller, 1981a: 18.–Cairns, 1991: 12.–Cairns, 1994: 46–47, pl. 20, figs c–h, pl. 51, figs c–d.–Cairns, 1995: 45–46, pl. 7, figs g–h.–Cairns & Zibrowius, 1997: 88, 93.–Cairns, 1998: 375.–Cairns, 1999: 73.–Cairns *et al*., 1999:20.–Cairns, 2004: 278.–González-Romero *et al*., 2008: 1–2, fig. 2. *Caryophyllia scobinosa*.–Yabe & Eguchi, 1942: 119 (in part). *Caryophyllia scobinosa decapali* Yabe & Eguchi, 1942: 120, 149, pl. 10, figs 6, 7.–Eguchi, 1968: C33–34.–Eguchi & Miyawaki, 1975: 56.–Cairns, 1991: 12. *Caryophyllia profunda*.–Squires & Keyes, 1967: 23 (in part). *Caryophyllia decapali*.–Grygier, 1983: 420.–Zibrowius & Grygier, 1985: 120, figs 10, 11.

TYPE MATERIAL: Two syntypes of *C. quadragenaria* are deposited at the ZMA (Coel. 5534, and Coel. 5529). The holotype and paratypes of *C. scobinosa decapali* are deposited at the TIUS (holotype catalogue number 53640).

TYPE LOCALITY: *C. quadragenaria: Siboga* stns 90, 251 and 289 (Makassar Strait, Banda, and Timor Seas), 54–281 m. *C. scobinosa decapali*: *Soyo Maru*-210 (33°29′N, 135°28′E–Kii Strait, Japan), 165 m.

NEW RECORDS: MNHN-IC.2009–0070 (PrFo, stn. ??, 2 specimens). MNHN-IC.2009–0071 (Bathus 4, stn. DW 894, 1 specimen). MNHN-IC.2009–0072 (Norfolk 2, stn. DW 2025, 1 specimen). MNHN-IC.2009–0073 (2) and USNM 1130996 (1) (Norfolk 2, stn. DW 2117, 3 specimens). MNHN-IC.2009–0074 (2) and USNM 1130997 (2) (Norfolk 2, stn. DW 2150, 4 specimens).

DISTRIBUTION: New Caledonia, 245–443 m; Japan, East China Sea, and Eastern Channel of Korea (Cairns, 1994), 70–422 m; New Zealand (Cairns, 1995), 77–198 m; Indonesia (Cairns & Zibrowius, 1997), 112–385 m; Western Australia (Cairns, 1998), 154–201 m; Wallis and Futuna, and Vanuatu regions (Cairns, 1999), 314–430 m; eastern North Pacific (González-Romero *et al*., 2008), 986–1669 m.

Description

Corallum ceratoid to subcylindrical, fixed, straight to slightly curved, and attached by a narrow pedicel (PD:GCD = 0.35–0.5), which expands into a thin encrusting base. Largest New Caledonian specimen examined (PrFo) 9.2 × 8.5 mm in CD, 16.9 mm in height and 3.5 mm in PD. Calice circular to slightly elliptical, with calicular margin vaguely serrate, especially in specimens in which a pair of S3 fuses to their adjacent S1 at calicular edge. Theca thick, costae equal in width, slightly ridged and separated by moderately deep furrows near calicular edge. Near pedicel costae become flat and less prominent, being virtually indistinguishable. All costae covered with low rounded granules. Corallum white and reddish-brown near calicular edge.

Septa decamerally arranged in three cycles (10:10:20 [40 septa]) according to the formula: S1 > S2≥ S3 or S1 > S3 ≥ S2. Primary septa up to 1 mm exsert, extending 4/5 distance to columella and having vertical slightly sinuous axial edges. Size of S2 in relation to S3 quite variable, the examined specimens having: S2 > S3, S2 = S3 and S2 < S3, however, the complement S2 ≥ S3 is more common. Secondaries about 0.7 width of primaries, with highly sinuous axial edges, but less exsert than tertiaries. Axial edges of tertiaries only slightly sinuous and upper outer edges fuse to adjacent primaries forming low triangular lancets. Each secondary bears a well-developed and highly sinuous pali that projects well above columellar elements. Ten P2 encircle the fascicular columella composed of 3–11 ornately twisted elements.

REMARKS: With a broad latitudinal range in western Pacific waters and also with records in Indian Ocean, *C. quadragenaria* is distinguished from its decameral congeners by having sinuous pali axial edges, theca granular and PD:GCD between 0.22 and 0.39. A brief comparison with *C. perculta* is provided in the discussion of that species.

Caryophyllia ralphae Cairns, 1995
(Figs 83–87)

Caryophyllia ralphae Cairns, 1995: 48–49, pl. 8, figs f-i.–Cairns *et al.*, 1999:20.–Cairns, 2004: 278.

TYPE MATERIAL: The holotype is deposited at the NZOI (now NIWA, H-623). Three paratypes are deposited at AMS (G15500) and other at USNM (94006).

TYPE LOCALITY: 22°43′S, 159°16′E (northern Lord Howe Seamount Chain), 328 m.

NEW RECORDS: MNHN-IC.2009–0075 (Norfolk 2, stn. DW 2038, 1 specimen). MNHN-IC.2009–0076 (3) and USNM 1130998 (2) (Norfolk 2, stn. DW 2091, 5 specimens). MNHN-IC.2009–0077 (3) and USNM 1130999 (2) (Norfolk 2, stn. DW 2092, 5 specimens). MNHN-IC.2009–0078 (Norfolk 2, stn. DW 2095, 2 specimens). MNHN-IC.2009–0079 (2) and USNM 1131000 (1) (Norfolk 2, stn. DW 2125, 3 specimens). MNHN-IC.2009–0080 (Norfolk 2, stn. DW 2140, 1 specimen).

DISTRIBUTION: New Caledonia, 270–896 m; Australia (Cairns, 1995), 328 m.

Description

Corallum ceratoid, robust, flared distally, straight to slightly curved, and attached by a robust pedicel enlarged by concentric layers of stereome (PD:GCD = 0.25–0.42). Calice always elliptical and jagged. Theca thick and smooth, covered with low rounded granules (3 or 4 across width of a costa) that sometimes fuse, forming short transverse ridges

but never larger than costal width. Near calicular edge, all costae ridged and separated by deep intercostal furrows. In direction of pedicel costae become flat and poorly defined. Corallum white.

Septa hexamerally arranged in five cycles according to formula: S1 ≥ S2 > S3 ≥ S4 ≥ S5. However, a full fifth cycle (96 septa) not observed. S1 thick, extending 4/5 distance to columella, up to 5 mm exsert, with rounded upper edges, and straight to slightly sinuous vertical axial edges. S2 less exsert than S1, having sinuous axial edges. S3 3/4 width of S2, up to 3 mm exsert, with moderately sinuous axial edges. S4 3/4 width of S3 and only slightly less exsert. However, if a pair of S5 is present, S4 enlarged to S3 size. S5 usually enlarge to S4 size, and in all specimens examined S5 present only flanking one S4 per half-system. To summarize: each half-system usually have 1 S1, 1 S2, 1 S3, 2 S4 (1 equal to S3), and 2 S5 (1 enlarged to S4 size). The middle septa within each half-system (S5) is slightly smaller than the S5 adjacent to its S1. Each S3 bears a narrow and sinuous pali (P3). When a half-system has 1 S4 enlarged to S3 size, the lower axial edge of S4 fuses to the P3 and the P3 seems to migrate between the S2 and the accelerated S4. All septal and palar faces covered with numerous pointed granules.

Fossa deep, containing a slightly twisted papillose columella composed of few granular elements, and aligned in the axis of GCD.

REMARKS: One of the most distinctive species of *Caryophyllia* especially due to the large size in adult stage, *C. ralphae* can be grouped with another three species that are characterized by having pali before the antipenultimate septal cycle: *C. paucipalata*, *C. capensis* and *C. eltaninae* (Lesser Antilles, off South Africa, and off South Georgia, respectively). *C. ralphae* is distinguished by its highly exsert septa and very deep fossa. However, *C. ralphae* can easily be confused with *Rhizosmilia robusta*, both having about the same adult corallum size, septal symmetry and exsertness, colour and fossa depth. But *R. robusta* can be differentiated by the presence of concentric rings of partitioned chambers resembling polycyclic development in the base cross section, the pedicel/base of *C. ralphae* being completely solid. Figures 88 to 92 are provided for comparison between these two caryophylliid species.

Caryophyllia rugosa Moseley, 1881
(Figs 93–97)

Caryophyllia rugosa Moseley, 1881: 141–143, pl. 1, figs 8a–b.–Kock, 1889: 10–20, 7 figs.–Faustino, 1927: 70–71, pl. 8, figs 12–14.–Wells, 1954: 469, pl. 177, figs 5–6.–Cairns, 1984: 11–13, pl. 2, figs A–B, pl. 4, fig. I.–Cairns, 1991: 12. –Cairns & Keller, 1993: 236, pl. 3, fig. 1.–Cairns, 1994: 47, pl. 20, fig. i, pl. 21, fig. a.–Cairns, 1995: 43–44, pl. 6, fig. h, pl. 7, figs a–c.–Cairns & Zibrowius, 1997: 91–92.–Cairns, 1998: 375.–Cairns, 1999: 71.–Cairns *et al*., 1999:20.–Cairns, 2004: 264, 278.–Cairns, 2006: 47.–Ogawa, 2006:105, 109. *Caryophyllia paraoctopali* Yabe & Eguchi, 1941: 150, pl. 10, fig. 12.

TYPE MATERIAL: The syntypes of *C. rugosa* are deposited at NHM (? uncatalogued).

TYPE LOCALITY: *Challenger* stns 192 and 201 (Banda and Sulu Seas), 187–230 m.

NEW RECORDS: MNHN-IC.2009–0054 (3) and USNM 1130990 (1) (Bathus 4, stn. DW 902, 4 specimens). MNHN-IC.2009–0055 (Norfolk 2, stn. DW 2063, 1 specimen). MNHN-IC.2009–0056 (2) and USNM 1130991 (1) (Norfolk 2, stn. DW 2117, 3 specimens). AM-G.17616 (Norfanz, stn. 55, 1 specimen). AM-G.17617 (1) and MTQ a61485 (1) (Norfanz, stn. 57, 2 specimens).

DISTRIBUTION: New Caledonia, 212–724 m; Hawaiian region (Cairns, 1984), 137–439 m; off Zululand, Mozambique, Kenya and Maldives (Cairns & Keller, 1993), 95–250 m; Japan and East China Sea (Cairns, 1994), 71–240 m; New Zealand (Cairns, 1995), 142–508 m; Philippines and Indonesia (Cairns & Zibrowius, 1997), 137–581 m; Australia (Cairns, 1998; 2004, and present study), 180–330 m; Wallis and Futuna, and Vanuatu region (Cairns, 1999), 286–580 m.

Description

Corallum small, ceratoid to trochoid, and attached by a robust pedicel (PD:GCD > 0.5), which expands into a large encrusting base. Largest specimen examined (DW 2063) 8.5 × 7.7 mm in CD and 4.3 mm in PD, but base is broken. Costae covered with narrow, well-defined transverse ridges. Circumferential ridges split and rejoin around corallum, being present from encrusting base to septal projection above calicular edge. In some specimens ridges more prominent 2–4 mm below calice. Corallum white to light cream.

Septa octamerally arranged in three cycles (8:8:16 [32 septa]) according to formula: S1 > S2 > S3. However, one specimen (DW 2063) has decameral symmetry (10:10:20 [40 septa]), and another three (DW 2053) have hexameral symmetry (6:6:12:24 [48 septa]). S1 most exsert septa (up to 1.5 mm), extending about 3/5 distance to columella. Higher septal cycles progressively less exsert and wide. Axial edges of all septa sinuous, especially those of S1 and S2. A well-developed ring of 8 to 12 (usually 8) quite sinuous pali encircle the fascicular columella, which is composed of few twisted elements.

REMARKS: This small, cryptic, but commonly collected species of *Caryophyllia* is easily distinguished from its congeners by the presence of transverse ridges in the theca, and the extremely sinuous septa and pali. The normal condition of septal arrangement of this species is octameral, however, three specimens with hexamerally arranged septa are noted in the present study.

Caryophyllia scobinosa Alcock, 1902
(Figs 113 and 117)

Caryophyllia cultrifera Alcock, 1902a: 89–90.–Alcock, 1902b: 7–8, figs 1, 1a.–Faustino, 1927: 67–68, pl. 8, figs 8–9.–Veron, 1986: 905. *Caryophyllia scobinosa* Alcock, 1902a: 90.–Alcock, 1902b: 8, pl. 1, figs 2, 2a.–Faustino, 1927: 68–69, pl. 8, figs 10–11.–Yabe & Eguchi, 1942: 119–120 (in part).–Utinomi, 1965: 254.–Eguchi, 1965: 285.–Keller, 1981a: 17, fig. 2.–Cairns, 1991: 12.–Cairns & Keller, 1993: 235.–Cairns, 1994: 45–46, pl. 20, figs a–b (in part).–Cairns, 1995: 52–53, pl. 10, figs g–i, pl. 11, figs a–c.–Cairns & Zibrowius, 1997: 94.–Cairns, 1999: 75.–Cairns *et al*., 1999:20.–Kitahara, 2007: 498, 507, 510, fig. 2K.–Kitahara *et al*., 2008: 16, fig. 2D.–Cairns, 2004: 278. *Caryophyllia* cf. *scobinosa*.–Utinomi, 1956: 42.

TYPE MATERIAL: Six syntypes of *C. scobinosa* are deposited at the ZMA (Coel. 574, 575), and the holotype of *C. cultrifera* is also deposited at ZMA (Coel. 1180).

TYPE LOCALITIES: *C. scobinosa: Siboga* stns. 45 and 102 (Flores and Sulu Seas), 535–794 m. *C. cultrifera*: *Siboga* stn. 101 (Sulu Sea), 1270 m.

NEW RECORDS: MNHN-IC.2009–0088 (1) and USNM 1131004 (1) (Bathus 2, stn. DW 734, 2 specimens). MNHN-IC.2009–0089 (22) and USNM 1131005 (10) (Bathus 4, stn. CP 842, 32 specimens). MNHN-IC.2009–0090 (Bathus 4, stn. DW 905, 1 specimen). MNHN-IC.2009–0091 (Halipro I, stn. CH 78, 1 specimen). MNHN-IC.2009–0092 (Norfolk 2, stn. DW 2103, 1 specimen). WAM Z21468 (3) and MTQ a61467 (2) (SS102005, stn. 150, 5 specimens). AMG.17619 (Norfanz, stn. 51, 1 specimen).

DISTRIBUTION: New Caledonia, 354–830 m; Australia (Cairns, 1995; 2004; present study), 296–2450 m; Tanzania, Madagascar Plateau, Sulu Sea, Celebes Sea, off Tonga and Samoa (Cairns, 1995), 535–1270 m; Philippines and Indonesia (Cairns & Zibrowius, 1997), 253–1270 m; Wallis and Futuna, and Vanuatu regions (Cairns, 1999), 715–900 m; Brazil (Kitahara, 2007), depth unknown.

Description (based on New Caledonian specimens)

Corallum solitary, cornute, free, and usually curved 90° in the plane of GCD. Unattached pedicel usually eroded, but if intact pointed and about 1 mm in diameter. Largest specimen examined (DW 2103) 15.5 × 12.9 mm in CD, and 15.4 mm in height. Costae usually absent (especially in adult corolla), but if present C1 and C2 slightly more ridged than others. Ridges near calicular edge sometimes slightly sinuous. C3 and C4 flat. Costae separated by shallow striae, and covered with numerous low rounded granules, more conspicuous in lower half of corallum. Juvenile specimens normally entirely white, however, theca of adult specimens has two distinct colours: white in the first 5 mm from calicular edge, and discoloured in direction of pedicel.

Almost all specimens examined have hexamerally arranged septa in four cycles (or five incomplete cycles) according to the formula: S1–2 > S3 ≥ S4> S5. However, some specimens have heptamerally arranged septa in 14 sectors and thus 14 pali. These two different septal patterns were observed in specimens collected in the same stations and having the same size. S1–2 highly exsert (up to 2–2.5 mm), with rounded upper edge, and vertical and slightly sinuous axial edge. S1 and S2 fuse to columella deep in fossa. S3 least exsert septa (less than 1 mm), with moderately sinuous axial edges each of which bear a paliform lobe. S4 slightly smaller to same size of S3, but each S4 fuses to adjacent S1 or S2 at calicular edge forming rectangular lancets. A crown of 12–14 well-developed pali encircles columella. Pointed granules cover all septa and palar faces. Columella fascicular, composed of 5–9 twisted elements aligned in 1 or 2 rows in the plane of GCD.

REMARKS: *Caryophyllia scobinosa* is distinguished from the other Indo-Pacific unattached species of *Caryophyllia* previously described (*C. ambrosia*, *C. mabahithi*, *C. planilamellata*, *C. cornulum*, *C. stellula* and *C. grandis*), by the presence in the adult corallum of 48–72 septa (not 96 as in *C. ambrosia* and *C. grandis*); 12 to 14 pali; and in having an extremely jagged calicular margin.

Caryophyllia sp. A.
(Figs 98–102)

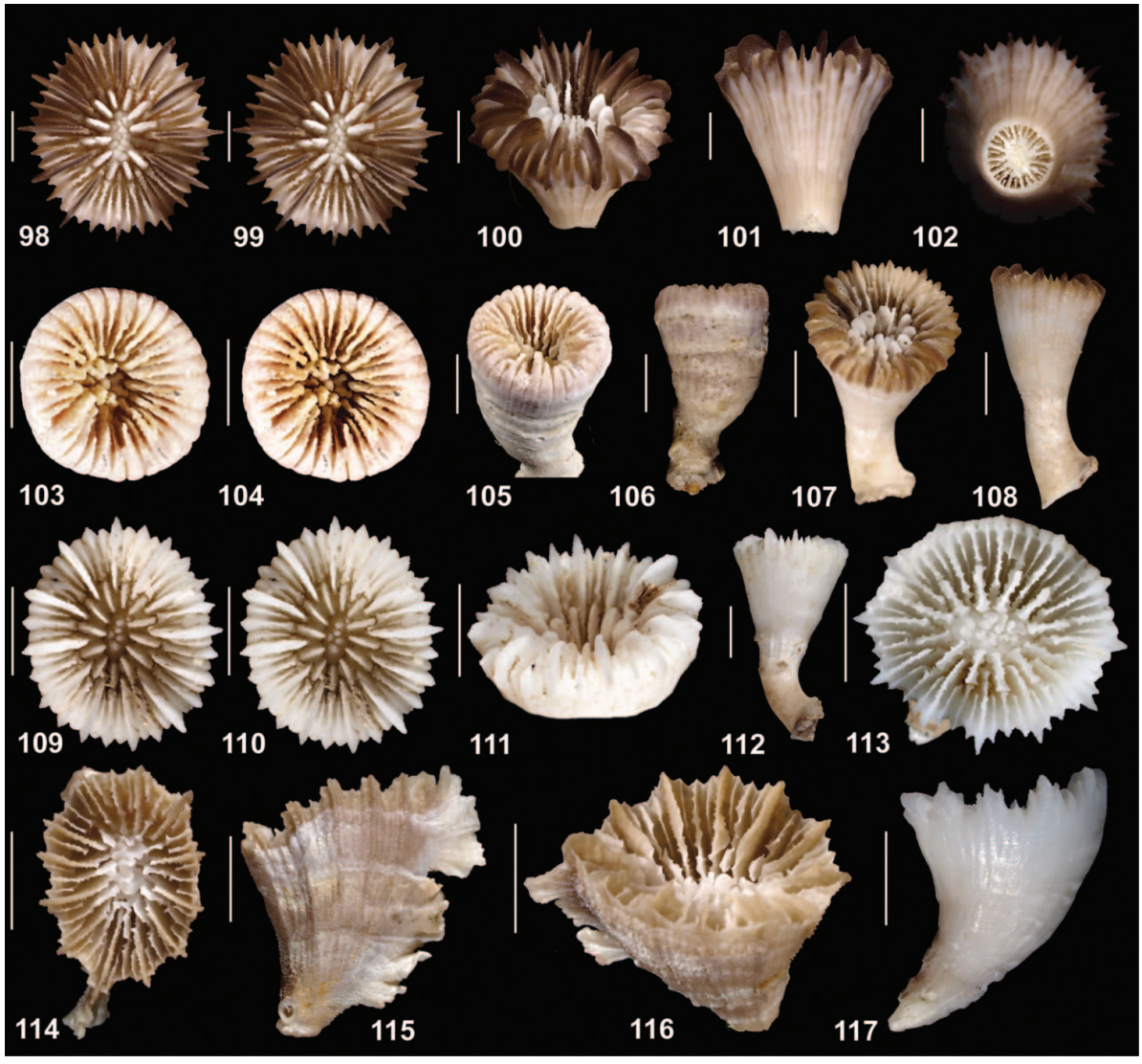
MATERIAL EXAMINED: MNHN-IC.2009–0087 (Bathus 4, stn. CP 889, 1 specimen).

DISTRIBUTION: Known only from the single specimen (21°00.83′S, 164°27.34′E) off New Caledonia, 416–433 m.

Description

Corallum ceratoid, straight, presumably fixed (base broken), and slightly flared distally. Calice elliptical: 18.5 mm in GCD and 14.0 mm in LCD (GCD:LCD = 0.76). Theca thick and covered with 5–7 (usually aligned) low, rounded granules across width of each costa. Intercostal striae absent, C1–3 slightly ridged especially near calicular edge. Corallum cream coloured, but C1–4, S1–2, and outer and upper edges of S3–4 dark brown. Columellar elements and pali completely white.

Septa hexamerally arranged in four complete cycles (6:6:12:24 [48 septa]) according to formula: S1–2 > S3 > S4. Upper edge of S1–2 rounded and highly exsert (up to 3.5 mm) and axial edge sinuous and slightly inclined, extending about 2/3 distance to columella. S1–2 fuses to columella deep in fossa. S3 up to 2 mm exsert, about 0.9 width of S1–2, and have highly sinuous vertical axial edges. S4 usually least exsert septa, but usually fusing to adjacent S1 and S2 above calicular edge, forming low lancets. Upper and axial edges of S4 slightly sinuous, extending 2/5 distance to columella. All septal faces covered with low



Figs 98–117. ***Caryophyllia*** sp. A (MNHN-IC.2009–0087): 98 and 99, stereo pair of calicular view; 100, oblique calicular view; 101, lateral view; 102, broken base view. ***Caryophyllia tangaroae*** sp. nov. (AM-G.17618–Holotype): 103 and 104, stereo pair calicular view; 105, oblique calicular view; 106, lateral view. ***Caryophyllia versicolorata*** sp. nov. (MNHN-IC.2009–0045–Holotype): 107, oblique calicular view; 108, lateral view. (MNHN-IC.2009–0053–Paratype): 109 and 110, stereo pair of calicular view; 111, oblique calicular view; 112, lateral view. ***Caryophyllia scobinosa*** (MNHN-IC.2009–0089): 113, calicular view; 117, lateral view. ***Caryophyllia unicristata*** (MNHN-IC.2009–0094): 114, calicular view; 115, lateral view; 116, oblique calicular view. Scale bars represent 5 mm.

rounded granules arranged in rows oblique to trabecula, and in some S1–2, granules fused into low and short carinae. Below 1–2 mm of septal upper edge the granules are white. Twelve slightly sinuous, well-developed lamellar pali (P3) with inclined outer edge and vertical axial edge present before S3.

Fossa of moderate depth containing a fascicular columella composed of 12 small twisted ribbons.

REMARKS: The specimen described above is almost indistinguishable from *C. lamellifera* but does not have transverse thecal ridges, which are diagnostic for that species. Otherwise, septal symmetry and exsertness are the same. However, the skeleton colour pattern is indistinguishable from some specimens of *C. versicolorata* sp. nov. Although probably representing an undescribed taxa, more material is needed to fully describe this species.

Caryophyllia tangaroae sp. nov.
(Figs 103–106)

HOLOTYPE: AM-G.17618 (Norfanz, stn. 50).

TYPE LOCALITY: 29°07′44″S, 158°35′26″E (Australia), 505–900 m.

DISTRIBUTION: Same as type locality.

ETYMOLOGY: The species is named *tangaroae* in honour of the RV *Tangaroa* (NIWA), for the numerous research expeditions undertaken into deep waters of the southern Pacific and Indian Oceans.

Description

Corallum ceratoid, small, slightly curved, and attached through a small pedicel (PD:GCD = 0.48), which expands into a thin and small encrusting base. Holotype 9.7 × 9.4 mm in CD, 18.3 mm in height and 4.7 mm in PD. Calice slightly elliptical, with calicular margin vaguely serrate. Theca thick, costae visible only near calicular edge. Lower part of corallum covered with stereome or eroded. Costae equal in width and covered with low rounded granules, usually 3–5 across width of each costa. Corallum beige to white.

Septa octamerally arranged in three complete cycles (8:8:16 [32 septa]) according to formula: S1 > S2 > S3. Primary septa up to 1 mm exsert, their sinuous axial edges almost reaching the columella deep in fossa. Secondaries slightly less wide and exsert than primaries, also having sinuous axial edges. Tertiaries least exsert septa and only 2/3 width of secondaries. Axial edges of S3 slightly sinuous. Tall and wavy pali present before each S2. All septa and palar faces bear tall granules sometimes fused as small carinae perpendicular to trabeculae.

Fossa of moderate depth containing a columella formed by 1 twisted element.

REMARKS: Even with only one specimen available, *Caryophyllia tangaroae* sp. nov. is very distinctive among the five congeners previously described that have octamerally arranged septa (*C. barbadensis*, *C. marmorea*, *C. octopali*, *C. rugosa* and *C. octonaria*), being distinguished by the following characters: corallum shape; PD:GCD < 0.5; corallum ceratoid; and pali not or only slightly granular (not as in *C. barbadensis* and *C. marmorea*, which present granular or carinate palar faces).

Caryophyllia unicristata Cairns & Zibrowius, 1997
(Figs 114–116)

Caryophyllia unicristata Cairns & Zibrowius, 1997: 101–102, figs 9d, e.–Cairns, 1998: 337.–Cairns *et al*., 1999:20.–Cairns, 2004: 277.

TYPE MATERIAL: The holotype is deposited at the MNHN (uncatalogued), and the paratypes are deposited at: MNHN (28 paratypes distributed in 4 lots), POLIPI (8 paratypes distributed in 3 lots), and USNM (97038 [1], 97040 [75], 97041 [3]).

TYPE LOCALITY: Karubar stn. 76, 8°49′S, 131°36′E (South of Tanimbar Islands), 400 m.

NEW RECORDS: MNHN-IC.2009–0093 (1) and USNM 1131006 (1) (Bathus 4, stn. CP 893, 2 specimens). MNHN-IC.2009–0094 (9) and USNM 1131007 (5) (Bathus 4, stn. CP 967, 14 specimens). WAM Z21472 (SS102005, stn. 105, 8 specimens). WAM Z21473 (SS102005, stn. 113, 4 specimens). WAM Z21474 and MTQ a61474 (20) (SS102005, stn. 171, > 200 specimens). WAM Z21475 and MTQ a61477 (20) (SS102005, stn. 172, > 200 specimens).

DISTRIBUTION: New Caledonia, 386–620 m; Arafura Sea, Indonesia (Cairns & Zibrowius, 1997), 251–477 m; Australia (Cairns, 1998; 2004; present study), 302–477 m.

Description (based on New Caledonia specimens)

Corallum cornute, usually curved 45–90° in the plane of GCD, and free in adult stage, but commonly collected with scars of previous attachment, or even attached to octocorals, gastropod shells, and dead coral skeletons. Calice elliptical with one side meeting in a sharp angle (not rounded). Largest specimen examined (CP 893) 14.4 × 10.3 mm in CD, 1 mm in PD and 19.2 mm in height. Theca covered with tall pointed granules. Costae well defined with C1–2 slightly ridged, especially near calice. Principal C1 in the convex edge of the corallum always sinuously crested. C3–4 slightly convex but not ridged, bearing 1 or 2 granules across their width. Intercostal striae shallow and thin. Corallum usually yellowish-brown when collected dead, and slightly reddish-brown when alive. C1–2 and upper outer edge of S1–2 darker than the rest of the coralla.

Septa of most specimens decamerally arranged in three cycles (5:5:10 [30 septa]) according to formula: S1 > S2 > S3, however, 5 specimens have hexameral symmetry arranged in four cycles (6:6:12:24 [48 septa]), 1 has heptameral symmetry in three cycles (7:7:14 [28 septa]), and one has octameral symmetry arranged in three cycles (8:8:16 [32 septa]). S1 up to 1.6 mm exsert, extending about 4/5 distance to columella, and have slightly sinuous axial edges. S2 least exsert septa, 3/5 width of S1, with moderately sinuous axial edges, being separated from their sinuous pali by a deep narrow notch. A pair of S3 fuses to adjacent S1 forming rectangular lancets. S3 more exsert but less sinuous than S2. Septal faces covered with tall and pointed granules arranged in rows perpendicular to trabecula. Pali terminate higher than columellar elements.

Fossa of moderate depth containing a fascicular columella aligned in the axis of GCD, being composed by 1–9 twisted elements.

REMARKS: Among the *Caryophyllia* that bear edge spines or lateral crests, *C. unicristata* is easily distinguished by the presence of a highly sinuous crest only on the convex thecal edge.

Caryophyllia versicolorata sp. nov.
(Figs 107–112)

HOLOTYPE: MNHN-IC.2009–0045 (Norfolk 2, stn. DW 2037).

PARATYPES: MNHN-IC.2009–0046 (Bathus 4, stn. DW 822, 1 specimen). MNHN-IC.2009–0047, MNHN-IC.2009–0048, MNHN-IC.2009–0049 and

USNM 1130988 (3) (Norfolk 2, stn. DW 2037, 6 specimens). MNHN-IC.2009–0050, MNHN-IC.2009–0051 and USNM 1130989 (Norfolk 2, stn. DW 2053, 3 specimens). MNHN-IC.2009–0052 (Norfolk 2, stn. DW 2109, 1 specimen). MNHN-IC.2009–0053 (Norfolk 2, stn. DW 2133, 1 specimen).

TYPE LOCALITY: 23°40′S, 167°41′E (New Caledonia), 517–570 m.

DISTRIBUTION: New Caledonia (from 22°02.43′S, 165°56.24′E to 23°47′S, 168°17′E), 215–708 m.

ETYMOLOGY: The species is named *versicolorata* (Latin: *versicolor* = of various colours, variegated) alluding to the two very distinct colours present in the septa and C1–3 (brown pigmented) and the pali and columellar elements (white).

Description

Corallum ceratoid, straight to slightly curved, slightly flared distally, and attached by a thin encrusting base (PD:GCD = 0.33–0.44). Holotype 9.0 × 8.5 mm in CD, 3.8 mm in PD and 20.1 mm in height. Largest specimen examined (DW 2109) 12.3 × 10.5 mm in CD, 4.1 mm in PD and 30.2 mm in height. Calice always slightly elliptical, with serrate edges. Theca moderately thick, covered with thin transverse ridges. Ridges present from outer septal edge to pedicel, but more developed in lower part of corallum. Equal and flat costae sometimes present near calice, separated by thin, shallow intercostal striae; however, some specimens have slightly ridged C1–2. Well-preserved specimens have costae near calicular edge, and septa brown pigmented, white pali and columellar elements, and rest of the corallum cream.

Septa always hexamerally arranged in four complete cycles (6:6:12:24 [48 septa]) according to formula: S1 ≥ S2 > S3 > S4. S1 most exsert (up to 1.5 mm), extending half distance to columella with slightly sinuous axial edges. Higher septal cycles progressively less exsert and wide (but S2 sometimes as wide as S1). Axial edge of S3 highly sinuous. Before each S3 is a well-developed, tall, rounded, lamellar (slightly sinuous) palus (P3), together forming a well-defined crown of 12 elements. Each palus terminates well above columellar elements.

Fossa of moderate depth, containing a fascicular columella composed of 4–10 twisted rods aligned with the axis of GCD.

REMARKS: Among the six previously described species of *Caryophyllia* with transversely ridged theca, *C. versicolorata* is unique in having: septa hexamerally arranged in four complete cycles, septa only slightly exsert, C1–3 and S1–3 usually pigmented dark-brown, and white pali and columellar elements. *C. versicolorata* has morphological characters that link it to *C.* sp. A, (described below) and *C. lamellifera*, but can be distinguished by the low S1 exsertness.

Key to the Recent valid species of *Caryophyllia*

1a, Corallum bears edge spines or lateral crests ..... ***Caryophyllia*** *(Acanthocyathus)* (2)
1b, Corallum does not bear edge spines or lateral crests ..... ***Caryophyllia*** *(Caryophyllia)* (10)
2a, Coralla having edge spines .....(3)
2b, Coralla having lateral crests .....(7)
3a, Spines present on convex thecal edge, and sometimes only one spine present on concave thecal edge .....(4)
3b, Spines present on both thecal edges .....(5)
4a, Septa hexamerally arranged ..... ***C. dentata***
4b, Septa decamerally arranged ..... ***C. decamera***
5a, Thecal face spines present ..... ***C. spinigera***
5b, Thecal face spines absent .....(6)
6a, Septa arranged in 12 sectors (48 septa) with 12 pali ..... ***C. quangdongensis***
6b, Septa usually arranged in 14 sectors (56 septa) with 14 pali ..... ***C. grayi***
7a, Only convex side of the corallum having carinate thecal edge ..... ***C. unicristata***
7b, Both thecal edges bear crests ..... (8)
8a, GCD:LCD >1.75 ..... ***C. zanzibarensis***
8b, GCD:LCD < 1.70 ..... (9)
9a, Rounded primary costae; 14 primary septa ..... ***C. karubarica***
9b, Ridged primary costae; 12 primary septa ..... ***C. spinicarens***
10a, Transverse division present .....(11)
10b, Transverse division absent .....(12)
11a, Septa octamerally arranged ..... ***C. abrupta***
11b, Septa hexamerally arranged ..... ***C. secta***
12a, Corallum unattached (usually ceratoid) ..... (13)
12b, Corallum attached (ceratoid, trochoid, or subcylindrical) .....(23)
13a, Adult corallum with 96 or more septa ..... (14)
13b, Adult corallum with less than 96 septa (usually 48–72) (15)
14a, S4 wider than S5; pedicel may be present ..... (73)
14b, S5 equal to or wider than S4; pedicel absent ..... ***C. ambrosia***
15a, Adult stage with 3 septa size classes ..... (16)
15b, Adult stage with 4 or 5 septa size classes ..... (18)
16a, S2 wider than S3 ..... (17)
16b, S2 equal to or less wide than S3 ..... (19)
17a, Septa arranged octamerally (32 septa); 8 pali present ..... ***C. mabahithi***
17b, Septa arranged in many cycles (more than 80 septa); 18–24 pali present ..... ***C. planilamellata***
18a, Septa little exsert; S1 > S3 ≥ S2 ..... ***C. cornulum***
18b, S1 and S3 highly exsert; S1 > S2–S3 ... ***C. valdiviae***
19a, Pali equal or wider than the paliferus septa ..... ***C. horologium***

19b, Pali smaller than septa ..... (20)
20a, Last septal cycle more exsert than penultimate, usually fusing to primaries forming triangular lancets above calicular edge .....(21)
20b, Septa not exsert or all cycles equally exsert .... (22)
21a, Adult stage with small (< 25 mm) GCD; 12–16 pali ..... ***C. scobinosa***
21b, Adult stage with large (> 35 mm) GCD; > 20 pali .. .. ***C. seguenzae***
22a, Corallum small (GCD < 12 mm); curved up to 90°; all septa sinuous ..... ***C. stellula***
22b, GCD > 13 mm; base rarely curved more than 40°; S1, S2 with straight axial edges ..... ***C. squiresi***
23a, Theca covered with transverse ridges ..... (24)
23b, Theca granular or glisten; longitudinal costae usually present .....(29)
24a, Axial edge of S1 straight; septa and pali highly granular ..... ***C. aspera***, sp. nov.
24b, All septa with sinuous axial edges (S1 usually only slightly sinuous) ..... (25)
25a, Septa hexamerally arranged in four cycles ..... (26)
25b, Septa octamerally or decamerally arranged in three cycles ..... (28)
26a, S1 highly exsert ..... (27)
26b, S1 slightly exsert; septal colour usually different from colour of pali and columellar elements ....***C. versicolorata*** sp. nov.
27a, S1>S2; S3>>S4; C1–3 usually ridged .... ***C. corrugata***
27b, S1 = S2; S3 > S4; C1–3 not ridged, but sometimes pigmented ..... ***C. lamellifera***
28a, Columellar elements easily distinguished from pali . .....***C. rugosa***
28b, Columellar elements not clearly separated from pali ..... ***C. cinticulata***
29a, Pali before antipenultimate cycle of septa ..... (30)
29b, Pali before penultimate cycle of septa ..... (31)
30a, Septa pentamerally arranged (40 septa and 5 pali present) ..... ***C. paucipalata***
30b, Septa hexamerally arranged in four or five cycles ... .(74)
31a, Septa octamerally arranged ..... (32)
31b, Septa pentamerally, hexamerally, heptamerally, or decamerally arranged .....(35)
32a, Pali very granular or bearing short horizontal carinae .....(33)
32b, Pali not granular ..... (34)
33a, Corallum subcylindrical; axial edges of all septa sinuous ..... ***C. barbadensis***
33b, Corallum ceratoid; axial edge of S3 relatively straight ..... ***C. marmorea***
34a, PD:GCD = 0.26–0.45; corallum not elongate .. (72)
34b, PD:GCD > 0.5; corallum elongate and subcylindrical .....***C. octopali***
35a, Septa arranged decamerally ..... (36)
35b, Septa arranged pentamerally, hexamerally, or heptamerally .....(41)
36a, Septal faces high granular or carinate .....(37)
36b, Septal faces smooth to slightly granular .....(38)
37a, Long and obliquely oriented carinae present on lower axial septal faces; pali wide ..... ***C. perculta***
37b, Septal faces granular, but carinae absent; pali narrow ..... ***C. zopyros***
38a, Axial edge of pali straight to slightly sinuous .... ***C. solida***
38b, Axial edge of pali highly sinuous .....(39)
39a, PD:GCD ≥ 0.44; theca porcellanous covered by very low, rounded granules ..... (40)
39b, PD:GCD = 0.22–0.39; theca granular; fossa of moderate depth .....***C. quadragenaria***
40a, Theca very thick; calicular diameter smaller than diameter below calice ..... ***C. concreta*** sp. nov.
40b, Theca normal; calicular diameter larger than diameter of the rest of corallum ..... ***C. antillarum***
41a, Septa arranged pentamerally ..... ***C. hawaiiensis***
41b, Septa arranged hexamerally or heptamerally ....(42)
42a, S1 > S2 in width .....(43)
42b, S1 = S2 in width .....(53)
43a, Axial edge of S1 straight .....(44)
43b, Axial edge of S1 slightly to very sinuous .....(48)
44a, Last septal cycle extends equally or further than penultimate (usually S4 ≥ S3) .....(45)
44b, Penultimate septal cycle wider than last septal cycle .....(47)
45a, Septa arranged in three size classes, and 14–16–18 sectors ..... ***C. atlantica***
45b, Septa hexamerally arranged in four cycles, and thus 12 sectors .....(46)
46a, Axial edge of all septa straight to slightly sinuous .. .. ***C. polygona***
46b, Axial edge of S3 more sinuous than axial edges of S1, S2 and S4 ..... ***C. balaenacea***
47a, 12 pali present; pedicel robust; S1 slightly more exsert than S2 ..... ***C. inornata***
47b, 14 pali usually present; pedicel slender; S1 well exserted ..... ***C. transversalis***
48a, Theca porcellanous, not costate, and covered with low granules ..... (49)
48b, Costae present, usually C1 and C2 slightly ridged near calice ..... (51)
49a, Pali thin (0.4–0.5 mm); pali separated from their corresponding septa by a wide gap equal to or greater than its own width ..... ***C. solida***
49b, Pali with more than 1 mm in width ..... (50)
50a, S4 equal to or wider than S3 (S4 ≥ S3) . ***C. crosnieri***
50b, S3 wider than S4 (S3 > S4) ..... ***C. diomedeae***
51a, S1 = S2 in width; S1 as thick as S2 .. ***C. diomedeae***
51b, S1 > S2 in width; S1 thicker than other septa .. (52)

52a, Fossa shallow; S4 rudimentary .. ***C. oblonga*** sp. nov.
52b, Fossa deep; S4 fuse to S1 above calicular edge forming lancets ..... ***C. crypta***
53a, Axial edge of S1 straight ..... (54)
53b, Axial edge of S1 usually slightly sinuous ..... (59)
54a, Pali (P3) not sinuous ..... (55)
54b, Pali (P3) sinuous ..... (56)
55a, Adult stage with five cycles of septa; 16–23 pali present ..... ***C. profunda***
55b, Adult stage with four cycles of septa; 12–14 pali present ..... ***C. sewelli***
56a, Pedicel robust (PD:GCD > 0.5) ..... ***C. arnoldi***
56b, Pedicel slender (PD:GCD < 0.5) ..... (57)
57a, S4 more exsert than S3 ..... ***C. smithii***
57b, S4 less exsert than S3 ..... (58)
58a, S1–2 1.5–2.1 mm exsert; S4 only slightly less wide than S3 ..... ***C. japonica***
58b, S1–2 less than 1 mm exsert; S4 about 3/4 width of S3 ..... ***C. alaskensis***
59a, Highest septal cycles equal to or wider than penultimate in adult specimen ..... (60)
59b, Last septal cycle smaller than penultimate in adult specimen ..... (62)
60a, S1 highly exsert (up to 2.1 mm); sometimes septa decamerally arranged ..... ***C. calveri***
60b, S1 only slightly exsert; septa always hexamerally arranged ..... (61)
61a, Theca not glisteny; P3 usually 1/2 (or larger) width of S3; P3 bear carinae ..... ***C. alberti***
61b, Theca glisten; P3 less than 1/2 width of S3; P3 with pointed granules instead of carinae ..... ***C. laevigata***
62a, 14 or more pali present ..... (63)
62b, 13 or less pali present ..... (64)
63a, Corallum robust (GCD up to 30 mm); > 20 pali present ..... ***C. cyathus***
63b, Corallum small (GCD < 13 mm); < 20 pali present ..... ***C. jogashimaensis***
64a, Axial edge of S4 straight ..... (65)
64b, Axial edge of S4 sinuous (usually slightly sinuous) . ..... (67)
65a, In adult stage paliferus septa much more wide than pali (septa more than 3 times wider than pali) . ***C. sarsiae***
65b, Paliferus septa less than 3 times width of pali .. (66)
66a, Calicular margin not lanceted; S3 as exsert as S1–2 . ..... ***C. huinayensis***
66b, Calicular margin slightly lanceted; S3 less exsert than S1–2 ..... ***C. ephyala***
67a, Only 10 pali present ..... ***C. abyssorum***
67b, 12 or more pali present ..... (68)
68a, Septal faces ornamented with carinae and squared-off granules ..... ***C. antarctica***
68b, Septal faces not ornamented with carinae ..... (69)
69a, C1–3 sharply ridged from calice to pedicel ..... ***C. horologium***
69b, C1–3 slightly ridged only near calicular edge .. (70)
70a, Columella not arranged in one or two rows aligned with GCD (usually arranged in an elliptical field) ..... ***C. foresti***
70b, Columella usually arranged in one or two rows aligned with GCD ..... (71)
71a, Septal granules high and blunt, sometimes fusing into short, oblique carinae ..... ***C. berteriana***
71b, Septal granules do not form carinae, and usually are low and rounded ..... ***C. diomedeae***
72a, Primary septa highly exsert (1.7–2.2 mm) ..... ***C. octonaria***
72b, Primary septa only slightly exsert (up to 1 mm) ..... ***C. tangaroae*** sp. nov.
73a, Pali present before antipenultimate septal cycle ..... ***C. eltaninae***
73b, Pali present before penultimate septal cycle ..... ***C. grandis***
74a, S1 more exsert than S2 ..... ***C. ralphae***
74b, S1 as exsert as S2 ..... ***C. eltaninae***
C. paradoxa* not included due to the high variability of the species.

Phylogenetic analysis

To test the hypothesis that *Caryophyllia* is a valid genus, 16S rRNA sequences were obtained from 12 *Caryophyllia* species, 7 representatives of morphologically related caryophylliid genera, and 14 representatives of non-caryophyllid families (Appendix 3, see supplementary material). In a broad view, the 'complex' and 'robust' scleractinian clades were well resolved, with representatives of the Fungiacyathidae, Flabellidae, Turbinoliidae, Poritidae, Dendrophylliidae, Acroporidae and Agariciidae grouping as the 'complex' corals, and the other families present in our analyses grouping as the 'robust' corals. With the exception of *Polycyathus* Duncan, 1876 and *Rhizosmilia* Cairns, 1978, all of the Caryophylliidae used are solitary. Each caryophyllid genera examined bear pali or paliform lobes (with exception of *Crispatotrochus* Tenison-Woods, 1878), have a corallum resembling that of at least one *Caryophyllia* species, have septotheca that are usually costate, characteristically have columellar elements, and have septa that are exserted to some degree. The 12 *Caryophyllia* species included in the analyses capture most of the range of morphological variation within the genus, with the following characters being represented: attached and free species; presence or absence of thecal spines, crests or transverse ridges; differences in septal symmetry; different numbers of pali; and corallum robustness. Results of the Bayesian inference (BI) are shown as Figure 118 and summarized below. The maximum-likelihood results using Shimodaira–Hasegawa-like procedure and 100 bootstrap replicates are not shown due to poorly supported distal nodes.

However, each of the methods of phylogenetic analyses recovered a strongly supported clade containing all

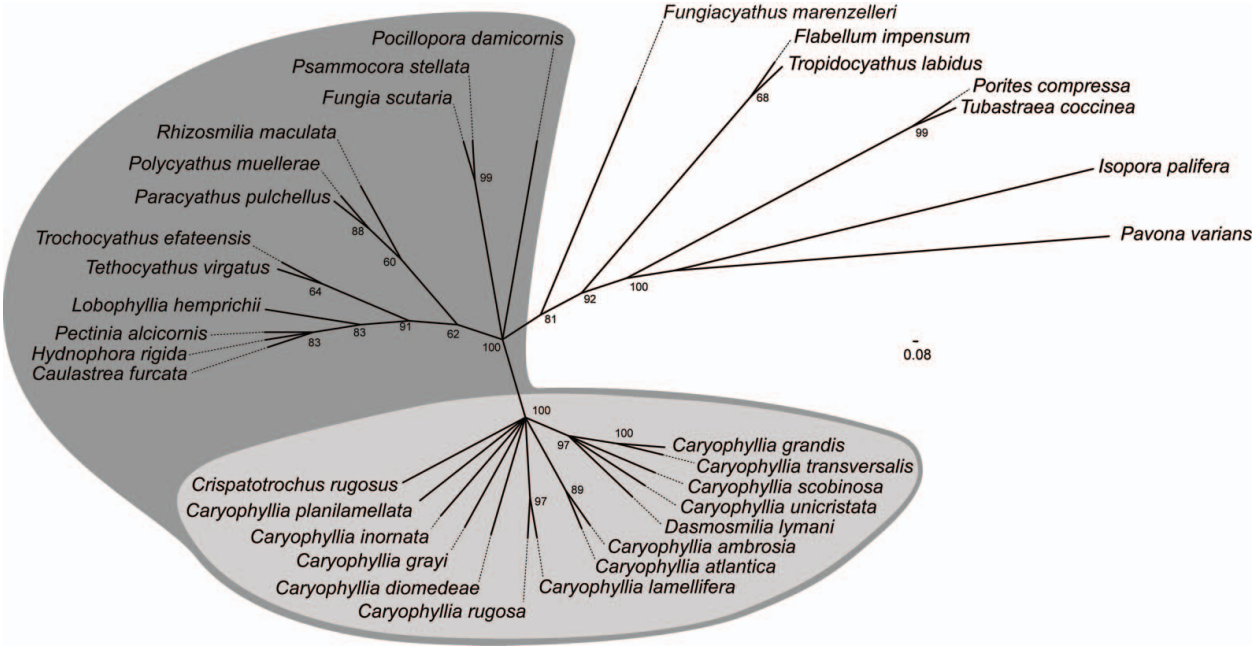


Fig. 118. Unrooted cladogram generated from partial 16S rRNA gene from 19 species of Caryophylliidae and 14 non-caryophylliid scleractinians showing their phelogenetic relationships. Numbers on branches show posterior probability calculated based on Bayesian inference. Light shaded area shows the *Caryophyllia* clade, and the dark shaded area shows the 'robust' corals clade.

12 *Caryophyllia* species together with representatives of two morphologically similar caryophyllid genera: *Crispatotrochus* and *Dasmosmilia* Pourtalès, 1880. The major difference between *Caryophyllia* and *Crispatotrochus* is the absence of pali or paliform lobes in the latter, suggesting the possibility of secondary loss of this morphological character. By contrast, *Dasmosmilia* has paliform lobes before all but the last septal cycle (a morphological character shared with *Rhizosmilia*, *Paracyathus* Milne Edwards & Haime, 1848, *Polycyathus*, *Tethocyathus* Kühn, 1933, and *Trochocyathus* Milne Edwards & Haime, 1848), and grouped with four different *Caryophyllia* species. One of the major differences between *Dasmosmilia lymani* (Pourtalès, 1871) and all of the other species included in our analyses is its reproductive strategy (parricidal budding resulting in unattached coralla with an open/fractured base or base still attached to inner theca of parent coralla), a characteristic probably acquired due to the low amount of hard substrata available in the habitat of this species, or the brooding of non-swimming larvae that colonize the first part of the skeleton without tissue cover.

Discussion

The *Caryophyllia* species examined fell into two subclades formed by: (1) *C. unicristata*, *C. grandis*, *C. transversalis* and *C. scobinosa*; and (2) the other eight species examined. Each subclade contains some species with attached adult stages and some free-living species. For example, the unattached species *C. unicristata* and *C. scobinosa* groups with the attached species *C. transversalis* in the first subclade, and *C. ambrosia* groups with the presumably attached *C. atlantica* in the second. Likewise, even though the presence/absence of spines or crests is often used to distinguish *Caryophyllia* subgenera, these features may have multiple origins, as the two species from the subgenus *Acanthocyathus* included in the analyses, *C. (A.) grayi* (spinose) and *C. (A.) unicristata* (crested) were split between the two subclades. On the other hand, some morphological characters do correlate with the groupings within the *Caryophyllia* clade; for example, the two species examined that have transverse ridges covering the theca (*C. rugosa* and *C. lamellifera*) fall into the second subclade with high posterior probability.

Another implication is that *C. ambrosia* and *C. scobinosa* may not be as closely related as was assumed on the basis of morphology implying that their similar morphology may reflect convergence driven by their occupying similar ecological niches. Consistent with this, *C. ambrosia* and *C. scobinosa* overlap both in distribution (particularly in the Pacific) and depth range.

Although the analyses presented here are of limited scope, two groupings of species external to the

Caryophyllia clade are worthy of comment and probably are representatives of an undescribed family once they appear relatively distant in relation to *Caryophyllia*. First, the phylogeny presented here suggests that *Tethocyathus* and *Trochocyathus* may be sister genera as this clade has strong posterior probability support. A second implication of our analyses is that the genera *Paracyathus*, *Polycyathus* and *Rhizosmilia maculata* may be closely related. The morphological similarity of *Paracyathus* and *Polycyathus* has previously been commented on, and *Polycyathus senegalensis* Chevalier, 1966 was characterized by Hubbard & Wells (1986) as a 'quasicolonial *Paracyathus pulchellus* (Philippi, 1842) with smaller corallites'. However, whilst agreeing on the similarity of the genera, Cairns (2000) showed that *Polycyathus* forms a true colony. In this case, colonial and solitary genera group together, which is consistent with the hypothesis that coloniality may have evolved on multiple occasions.

When testing the validity of a taxonomic group, one should ideally include as many as possible of the known species (Barraclough & Nee, 2001). However, in the case of molecular phylogenetics of deep-sea corals this is presently unrealistic, as older museum material is often preserved in ways that are incompatible with DNA based analyses. The genus *Caryophyllia* is particularly challenging because fresh material is rarely collected—this is particularly true for the small solitary species. Although based on only 12 of the 73 Recent *Caryophyllia* species, the analysis presented here supports the monophyly of the genus, but does not necessarily imply that all of the species currently assigned to this genus belong there. These analyses also call for a re-evaluation of the genera *Dasmosmilia* and *Crispatotrochus*.

Acknowledgements

We would like to thank Professor Dr Karen Miller and Dr Felicity Mcennulty for the loan of material collected off south and western Australia: the 1997 survey (SS01997) was conducted by the Australian CSIRO Marine Research with funding from the Fisheries Research and Development Corporation (FRDC) and Environment Australia (now the Australian Government Department of Environment, Water, Heritage and the Arts); the 2005/2007 cruises (SS102005 and SS022007) were funded by the Australian CSIRO (Commonwealth Scientific and Industrial Research Organization) Wealth from Oceans Flagship with the assistance of the Australian Government Department of the Environment, Water, Heritage and the Arts; and the NORFANZ cruise was a collaboration between Australia's National Oceans Office (now the Australian Government Department of Environment, Water, Heritage and the Arts), Australia's CSIRO Marine and Atmospheric Research, New Zealand's Ministry of Fisheries and New Zealand's National Institute of Water and Atmospheric Sciences. We also thank Dr Carden Wallace and Mrs Barbara Done for the logistic help with the loans. We are grateful to Dr Pierre Lozouet, Dr Aude Andouche and Dr Philippe Bouchet for providing part of the material used in the present study. The first author is very thankful to Mr James Robinson and Mr Dustin Edge for the technical assistance. The first author also thanks the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the PhD scholarship.

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