

Scleractinia, Octocorallia and Antipatharia of Bermuda's Reefs and Deep-Water Coral Communities: A Taxonomic Perspective Including New Records

Jan M. Locke, Jaret P. Bilewitch, and Kathryn A. Coates

Introduction

Ongoing research continues to reveal more diversity and endemism in Bermuda's coral reefs and coral communities than previously recognized (Sterrer 1986, 1998). Deeper water biota in both Bermuda and the Greater Caribbean are poorly explored relative to shallow water, but new Bermudian records are presented here for both deep and shallow coral communities. The few deep water collections made within the Bermuda Exclusive Economic Zone (EEZ) indicate the presence of many species, including tropicals and species with ranges extending into temperate regions.

The Bermuda Natural History Museum (BAMZ) holds incomplete collections of Bermudian species and important collections, e.g., type specimens, are held in several major museums, including the Natural History Museum, United Kingdom (NHMUK), Smithsonian National Museum of Natural History (USNM), Harvard University Museum of Natural History (Museum of Comparative Zoology) and the Yale Peabody Museum (YPM).

Short histories of the exploration of diversity of primary reef taxa, scleractinians and octocorallians, are presented. Where the details of historic studies are reported, the species names used in the original documents are presented along with the current, accepted, name for the species; where possible. The current name will normally follow the original Bermuda name, bracketed. Current usages have been checked against the World Register of Marine Species (WoRMS) database (Appeltans et al. 2012) and the Integrated Taxonomic Information System (ITIS Retrieved August 10, 2011, <http://www.itis.gov>), and the primary literature.

J.M. Locke (✉) • K.A. Coates
Marine Ecology Section, Department of Conservation Services,
17 North Shore Road, Hamilton Parish FL 04, Bermuda
e-mail: jml100@gmail.com; kathryn.coates@dilke.com

J.P. Bilewitch
School of Biological Sciences, University of Queensland,
Brisbane, QLD 4072, Australia
e-mail: jbilewitch@gmail.com

Shallow-Water Zooxanthellate Scleractinia

History of Species Documentations

Most of Bermuda's shallow-water scleractinian diversity was recognized by the end of the nineteenth century. Contributions of AE Verrill are apparent in many of the early studies of the islands' species diversity, including his comprehensive works on the Bermuda islands (1900–1907). Prior to these, Verrill (1864) published the initial record of Bermudian Scleractinia naming *Diploria cerebriformis* Milne Edwards and Haime, 1849 (= *Diploria labyrinthiformis* Linnaeus, 1758), *Isophyllia dipsacea* Agassiz, MS (= *Isophyllia sinuosa* [Ellis and Solander, 1786]) and *Isophyllia rigida* Verrill (later corrected to *Mussa rosula* Verrill, 1907 [= *I. sinuosa*]) (Verrill 1907:230). A more comprehensive list for Bermuda published by JM Jones (1868) [mis-referenced as 1869 by Verrill 1900] added *Oculina diffusa* Lamarck, 1816, *Oculina varicosa* Lesueur, 1821, *Oculina valenciennesi* Milne Edwards and Haime, 1850, *Siderastrea radians* (Pallas, 1766), *Mycedium fragile* Dana (= *Agaricia fragilis* [Dana, 1846]), and *Porites clavaria* Lamarck, 1816 (= *Porites porites* [Pallas, 1766]). *Maeandrina cerebriformis* Lamarck (= *D. labyrinthiformis* Linnaeus, 1758) was also included but had been previously documented. Verrill identified most of the specimens included by Jones (1868) and, in Verrill's words, the collection was "incomplete" (1900:551). Dana's (1872:114) species list, also compiled with Verrill's assistance, noted the presence of *Oculina pallens* Ehrenburg, 1834 (= *O. diffusa* Lamarck, 1816), which agreed with previous accounts considering current synonymies. In 1871, Pourtalès noted that specimens of both *Lithophyllia cubensis* Milne Edwards and Haime (= *Scolymia cubensis* Milne Edwards and Haime, 1849) and *Isophyllia multilamella* Pourtalès (= *I. sinuosa*) from Bermuda were in the collections of the Museum of Comparative Zoology at Harvard College. In 1877, Brüggemann's work on specimens housed at the British Museum, now the Natural History Museum, United

Kingdom, noted *Scolymia lacera* as occurring in Bermuda based on Pourtalès' collections. The occurrence of this species in Bermuda has not been documented elsewhere.

In 1886, Quelch reported on the shallow-water corals collected during the HMS Challenger Expedition (1872–1876). He documented the first specimens of *Maeandrina strigosa* Dana (= *Diploria strigosa* [Dana, 1846]), *Astraea ananas* Ellis and Solander and *Astraea coarcta* Duchassaing and Michelotti (both = *Favia fragum*) and *Madracis decactis* (Lyman, 1859). Other species Quelch listed that have since been synonymized are *Isophyllia strigosa* Duchassaing and Michelotti (= *I. sinuosa*), *Isophyllia knoxi* Duchassaing and Michelotti (= *I. sinuosa*), *Isophyllia cylindrica* Duchassaing and Michelotti (= *I. sinuosa*), *Isophyllia australis* Edwards and Haime (= *I. sinuosa*), *Isophyllia fragilis* Dana (= *I. sinuosa*), *Oculina speciosa* Milne Edwards and Haime (= *O. diffusa*), *Oculina bermudensis* Duchassaing and Michelotti (= *O. valenciennesi*), *Siderastrea galaxea* Ellis and Solander (= *S. radians*), *Maeandrina labyrinthica* Ellis and Solander (= *D. labyrinthiformis*), *Diploria cerebriformis* Lamarck (= *D. labyrinthiformis*), and *Maeandrina sinuossima* Milne Edwards and Haime (= *D. labyrinthiformis*). The following of Quelch's records are of dubious validity and uncertain synonymy, *Oculina coronalis* n.sp. (suggested to be *O. diffusa* [J.W. Wells, pers. comm. to S. Cairns, 1977]; observation of type material would confirm this) and *Isophyllia marginata* Quelch (= ? *I. sinuosa*) (see Verrill 1907:229). Besides the species obtained by the Challenger, Quelch (1886) noted in his report that both *Lithophyllia cubensis* Milne Edwards and Haime, 1857 (= *Scolymia cubensis*) and *Lithophyllia lacera* Pallas (= *Scolymia lacera* [Pallas, 1766]) as well as *Isophyllia multilamella* Pourtalès (= *I. sinuosa*) and *Isophyllia spinosa* Edwards and Haime (= *I. sinuosa*) were known to occur in Bermuda. These claims were undoubtedly based on the publications of Pourtalès (1871) and Brüggemann (1877). Quelch's (1886) collection is housed at the NHMUK and his report doubled previous species accounts; however Verrill (1900) synonymized certain species, including six *Isophyllia* species, reducing this number considerably.

The following year Rathburn (1887) recorded *Porites astraeoides* Lamarck, 1816 (sic, *Porites astreoides*) as occurring on Bermuda's reefs. In 1888, Heilprin noted the occurrence of *Diploria stokesii* Milne Edwards and Haime, 1849 (= *D. labyrinthiformis*), *Isophyllia guadeloupensis* Pourtalès (= ? *I. sinuosa*; see Verrill 1900:223) and *Oculina recta* Quelch (of dubious validity and uncertain synonymy). Of the 19 species now recognized in Bermuda, eight were considered spurious or mere varieties (Verrill 1900) reinforcing previous accounts but not expanding what was known. In 1900, Verrill added *Orbicella annularis* Dana (= *Montastraea annularis* [Ellis and Solander, 1786]), *Orbicella cavernosa* (= *Montastraea cavernosa* [Linnaeus, 1767]), *Plesiastraea goodei* Verrill, 1900 (= *Stephanocoenia intersepta* [Esper, 1795]) and *Siderastrea siderea* (Ellis and Solander, 1786); at this point, 17 valid coral

species had been recorded for Bermuda. Verrill (1901a, 1907) reported *Mussa (Symphyllia) annectens* sp. nov. and *Mussa rosula* sp. nov. (both = *I. sinuosa*) from Bermuda. The latter had been misidentified in 1864 as *I. rigida* (see Verrill 1907:230).

Over 50 years passed before the full complement of Bermuda's known diversity was documented again. In 1966, Laborel conducted the most recent comprehensive field survey of species, reporting both *Meandrina meandrites* (Linnaeus, 1758) and *Dichocoenia stokesi* Milne Edwards and Haime, 1848 for the first time. He noted that he could not find *Siderastrea siderea* and the occurrence of *Isophylliastrea rigida* (sic, *Isophyllastrea rigida*) (= *Isophyllia rigida* [Dana, 1848]) was questionable. In 1978, Dryer and Logan, list *Madracis mirabilis* (= *Madracis auretenra* Locke, Weil and Coates, 2007) as occurring in Bermuda. Although the solitary coral species *S. cubensis* and *S. lacera* were mentioned by Quelch (1886) (and mistakenly thought by Verrill [1907] to be young *Mussa* [= *Isophyllia*]), *S. cubensis* was not noted again in the literature until 1985 by Fricke and Meischner. *Scolymia lacera* has not been documented since Quelch (1886), and his report of the species may be the result of misinterpretation of prior literature; Brüggemann's specimen is the key to solving this question.

Current Studies of Shallow-Water Zooxanthellate Scleractinia

The most current previously published inventory of Bermuda's scleractinian species is Cairns et al. (1986). Changes to that list as presented here are due to the synonymy of *Stephanocoenia michelinii* with *Stephanocoenia intersepta*, revision of the genus *Montastraea* and revival of *Montastraea franki* (Weil and Knowlton 1994), description of *Madracis auretenra* and re-evaluation of all shallow-water specimens identified as *Madracis mirabilis* (Locke et al. 2007), and a new record of *Phyllangia americana americana* (Logan 1988).

Based upon Cairns et al. (1986), the reference collection at BAMZ, literature reviews, and personal observations (J.M. Locke), a total of 20 species of valid zooxanthellate scleractinian corals are currently well documented for Bermuda's shallow waters (Locke 2009) (Table 14.1). Records have been verified from specimens deposited in Bermuda and at other museums.

Other, recent, novel records of extant shallow-water zooxanthellate coral species in Bermuda are dubious. Veron (2000) reported 25 species of zooxanthellate corals as occurring in Bermuda based on historical records; the following of which are unsubstantiated: *Diploria clivosa*, *Eusmilia fastigiata*, *Isophyllia rigida*, *Manicina areolata*, *Mycetophyllia lamarckiana*, and *Astrangia poculata*. A few new distribution records for Bermuda (Venn et al. 2009; Frade et al. 2010) are

Table 14.1 Current list of valid shallow-water zooxanthellate scleractinian species in Bermuda

Species
Family Agariciidae
<i>Agaricia fragilis</i> Dana, 1846
Family Astrocoeniidae
<i>Stephanocoenia intersepta</i> Lamarck, 1816
Family Faviidae
<i>Diploria labyrinthiformis</i> (Linnaeus, 1758)
<i>Diploria strigosa</i> (Dana, 1846)
<i>Favia fragum</i> (Esper, 1795)
<i>Montastraea cavernosa</i> Linnaeus, 1767
<i>Montastraea franksi</i> (Gregory, 1895)
Family Meandrinidae
<i>Dichocoenia stokesi</i> Milne Edwards and Haime, 1848
<i>Meandrina meandrites</i> (Linnaeus, 1758)
Family Mussidae
<i>Isophyllia sinuosa</i> (Ellis and Solander, 1786)
<i>Scolymia cubensis</i> (Milne Edwards and Haime, 1849)
Family Oculinidae
<i>Oculina diffusa</i> (Lamarck, 1816)
<i>Oculina varicosa</i> (Lesueur, 1821)
<i>Oculina valenciennesi</i> Milne Edwards and Haime, 1850
Family Pocilloporidae
<i>Madracis auretenra</i> Locke, Weil and Coates, 2007
<i>Madracis decactis</i> (Lyman, 1859)
Family Poritidae
<i>Porites porites</i> (Pallas, 1766)
<i>Porites astreoides</i> Lamarck, 1816
Family Siderastreidae
<i>Siderastrea radians</i> (Pallas, 1766)
<i>Siderastrea siderea</i> (Ellis and Solander, 1786)

also untenable due to a lack of archived and supporting materials (including specimens and taxonomically useful images, A. Venn, pers. comm., 2009); these are: *Madracis carmabi*, *Madracis formosa* (Bermuda extracts indistinguishable genetically from extracts from specimens from other countries that were identified, when collected, as *M. carmabi*, *M. formosa*, *M. senaria* and *M. pharensis*, in Frade et al. 2010), and *Madracis senaria* (no sequence obtained from Bermuda extracts, in Frade et al. 2010).

Shallow-Water Azooxanthellate Scleractinia

Six species of azooxanthellate corals are currently known from Bermuda's shallow waters. The earliest published record is of *Astrangia solitaria* (Lesueur, 1817) listed in Smith (1948) although it might have been recognized in 1877 by GB Goode (see Verrill 1901a:183). Otherwise the first notable records of azooxanthellate corals in Bermuda were made by Wells (1972) who reported *A. solitaria* as well as *Coenocyathus goreau* Wells, 1972, *Guynia annulata* Duncan,

Table 14.2 Current list of valid azooxanthellate scleractinian coral species in Bermuda

Species
Family Caryophylliidae
<i>Caryophyllia ambrosia ambrosia</i> Alcock, 1898
<i>Caryophyllia sarsiae</i> Zibrowius, 1974
<i>Coenocyathus goreau</i> Wells, 1972 ^a
<i>Deltocyathus calcar</i> Pourtalès, 1874
<i>Deltocyathus eccentricus</i> Cairns, 1979
<i>Deltocyathus italicus</i> (Michelotti, 1838)
<i>Deltocyathus moseleyi</i> Cairns, 1979
<i>Desmophyllum dianthus</i> (Esper, 1794)
<i>Lophelia pertusa</i> Linnaeus, 1758
<i>Oxysmia rotundifolia</i> (Milne Edwards and Haime, 1848)
<i>Paracyathus pulchellus</i> (Philippi, 1842)
<i>Phyllangia americana americana</i> Milne-Edwards and Haime 1849 ^a
<i>Soleosmia variabilis</i> Duncan, 1873
<i>Tethocyathus cylindraceus</i> (Portalès, 1868)
Family Dendrophylliidae
<i>Enallopsammia rostrata</i> (Portalès, 1878)
<i>Rhizopsammia bermudensis</i> Wells, 1972 ^a
Family Flabellidae
<i>Javania cailleti</i> (Duchassaing and Michelotti, 1864)
<i>Polymyces wellsii</i> Cairns, 1991
Family Fungiacyathidae
<i>Fungiacyathus symmetricus</i> (Portalès, 1871)
Family Guyniidae
<i>Guynia annulata</i> Duncan, 1872 ^a
Family Oculinidae
<i>Madrepora carolina</i> (Portalès, 1871)
<i>Madrepora oculata</i> Linnaeus, 1758
Family Pocilloporidae
<i>Madracis asperula</i> Milne-Edwards and Haime, 1849
<i>Madracis myriaster</i> (Milne Edwards and Haime, 1849)
Family Rhizangiidae
<i>Astrangia solitaria</i> (Lesueur, 1817) ^a
<i>Colangia immersa</i> Pourtalès, 1871 ^b
Family Stenocyathidae
<i>Stenocyathus vermiformis</i> (Portalès, 1868)
Family Turbinoliidae
<i>Deltocyathoides stimpsonii</i> (Portalès, 1871)

^aKnown in Bermuda from shallow depths (0–3 m)

^bKnown from both shallow and deep depths

1872 (range 3–653 m) and *Rhizopsammia bermudensis* Wells, 1972 from reef cavities (0–6 m). Thus far, *Rhizopsammia bermudensis* is known only from Bermuda (Wells 1972; Cairns 2000) (Fig. 14.1). *Colangia immersa* Pourtalès, 1871 also inhabits reef cavities and although only collected from 6 to 8 m depths in Bermuda, this species has been reported from depths up to 347 m (Cairns et al. 1986; Cairns 2000). *Phyllangia americana americana* Milne-Edwards and Haime, 1849, first recorded from Bermuda by Logan (1988), commonly colonizes submerged man-made objects at depths up to 53 m (Cairns 2000) (Table 14.2).

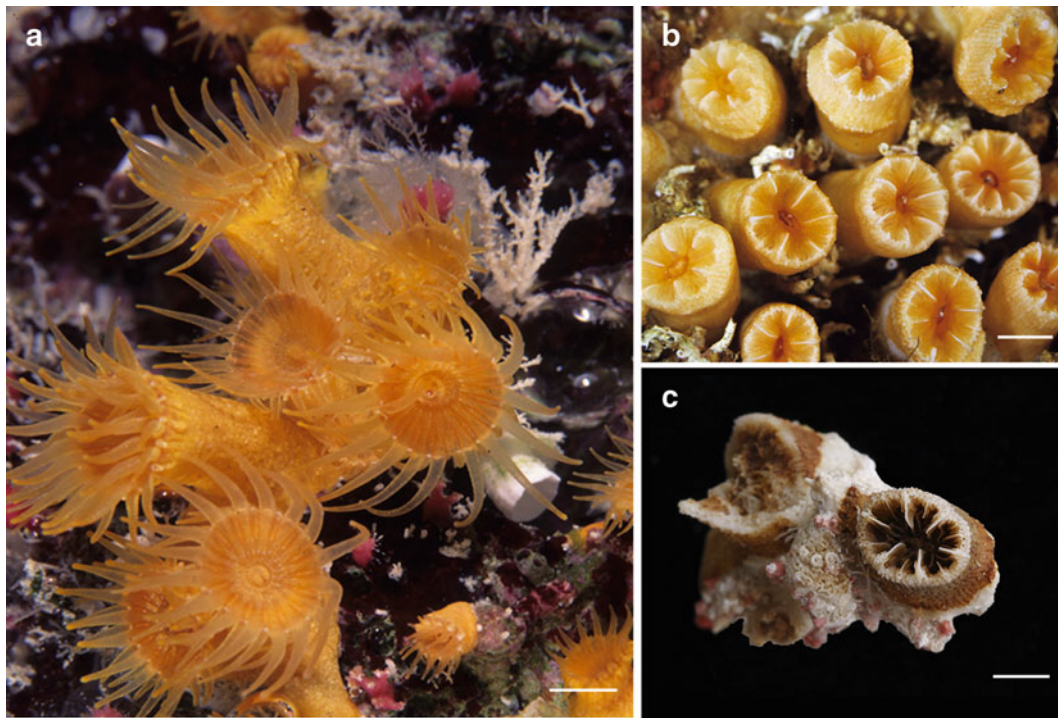


Fig. 14.1 Bermuda's only endemic coral *Rhizopsammia bermudensis* (a) in situ within a reef cavity at Eastern Blue Cut, with polyps extended and (b) with polyps withdrawn. (c) Bermuda Natural History Museum

specimen BAMZ 2009 266 013 collected from Eastern Blue Cut, 6 m. All scales equal 5 mm (Photo's a and b: I Murdoch, Photo c: L Greene)

The cryptic habitats occupied by these solitary and smaller species are poorly studied and further investigation may increase the number of known species. Records have been verified from BAMZ collections.

Deep-Water Scleractinia

Forays into the deep marine environments surrounding the Bermuda Pedestal and the seamounts within Bermuda's EEZ began with the deep-water dredging conducted during the HMS Challenger Expedition, and resumed over a century later with the submersible exploration of Fricke and Meischner (1985); the Royal Ontario Museum, Bermuda Underwater Institute-SDL Cruise (1997); the Ocean Projects Ltd-Innovator Cruise (2006); the Ocean Genome Legacy-Pacific Guardian Cruise (2007); and the Bermuda Institute for Ocean Science (BIOS)-Octopus Cruise (2007).

Collectively, these expeditions acquired azooxanthellate scleractinian specimens at depths from 55 m to 1,966 m. Many species are known only from single collections. The Bermuda specimens are housed at BAMZ, NHMUK, USNM, and Hessisches Landesmuseum (HLM), Darmstadt.

History of Species Documentations

The earliest records of deep-sea Scleractinia from Bermuda are those of Moseley (1881) from the HMS Challenger Expedition. He reported *Madracis asperula* Milne Edwards and Haime, 1849 (55 m), *Axohelia dumetosa* Pourtalès, 1874 (= *Madracis myriaster* [Milne Edwards and Haime, 1849]) (796 m), *Deltocyathus italicus* Milne-Edwards and Haime (1,966 m) (see Cairns 1979), *Deltocyathus italicus* var. *calcar* (= *Deltocyathus calcar* Pourtalès, 1874) (366 m), *Caryophyllia communis* Moseley, 1881 (= *Caryophyllia ambrosia ambrosia* Alcock, 1898) (1,262 m), *Caryophyllia cylindracea* Reuss? (=species indeterminate, S. Cairns, pers. comm., 2012) (796 m), and *Bathyaectis symmetrica* Moseley, 1881 (= *Fungiacyathus symmetricus* [Portalès, 1871]) (1,966 m). The whereabouts of Moseley's single specimen of *D. italicus* var. *calcar*, "off Bermuda 200 fms", is unknown (S. Cairns and A. Cabrinovic [NHMUK], pers. obs.) and the lot of specimens included in Moseley's *D. italicus* has been determined by Cairns (1979) to consist of *D. italicus*, *Deltocyathus moseleyi* Cairns, 1979 and *Deltocyathus eccentricus* Cairns, 1979 (S. Cairns, pers. comm., 2012). To date, the deepest collection record for a living specimen for the Bermuda EEZ is 1,966 m from the

report of Moseley (1881). Of the species listed by Moseley, only *M. myriaster* has been observed in and collected from Bermuda waters since the HMS Challenger Expedition.

A century later Fricke and Meischner (1985) explored Bermuda's mesophotic zone and provided the first photographs of corals living in Bermuda's deeper reef habitats. As well as revealing 13 zooxanthellate coral species living at depths between 30 m and 78 m their efforts documented new azooxanthellate records of *Madrepora carolina* (Pourtalès, 1871), *Oxysmilia rotundifolia* (Milne Edwards and Haime, 1848) and an unidentified species of *Polycyathus*. The latter two have not been observed again in Bermuda.

More recent studies of North Atlantic Scleractinia with bathymetric ranges extending below 200 m, report, cumulatively, 19 species occurring in Bermuda (Cairns 2000; Cairns and Chapman 2001; Dawson 2002). Of these, *Premocyathus cornuformis* (Pourtalès, 1868) and *Caryophyllia ambrosia caribbeana* Cairns 1979 were incorrectly listed for Bermuda (S. Cairns, pers. comm., 2012); in contrast, *Caryophyllia ambrosia ambrosia* Alcock, 1898 (= *Caryophyllia communis* in Moseley [1881]) was omitted from the list. The location data for *C. ambrosia ambrosia* and *C. ambrosia caribbeana* in Cairns (1979:58) do not support the occurrence of either subspecies in Bermuda. However, Moseley's (1881) record of *Caryophyllia communis*, considered by S. Cairns (pers. obs., pers. comm., 2012) to be a synonym of *C. a. ambrosia*, is evidence of the presence of this species. As of 2002 there were 17 known azooxanthellate coral species in Bermuda with bathymetric ranges exceeding 200 m. Although listed in Cairns and Chapman (2001), there are no confirmable records of collections of *Javania cailleti* (Duchassaing and Michelotti, 1864) prior to 2007 (BIOS-Octopus Cruise).

New Records of Species Diversity

Collections at BAMZ and USNM include species not documented in the literature as occurring in Bermuda. The following species were identified by Stephen Cairns (Smithsonian Institution) and represent new records for Bermuda: *Madrepora oculata* (221 m), *Tethocyathus cylindraceus* (Pourtalès, 1868) (354 m), *Polymyces wellsii* Cairns, 1991 (850 m), *Javania cailleti* (340 m), *Stenocyathus vermiciformis* (Pourtalès, 1868) (700–900 m) and *Deltocyathoides stimpsonii* (Pourtalès, 1871) (850 m). These new records are the first documentation of the families Flabellidae, Stenocyathidae, and Turbinoliidae (Table 14.2) in Bermuda. The identifications of the following specimens have not been resolved: *Carophyllia* sp. (USNM 1114321, USNM 1129938) (354 m, 700–920 m), *Caryophyllia* n. sp. (BAMZ 2011.276.005) (850 m), and *Tethocyathus* n. sp. (USNM 1158159) (850 m) from Family Caryophyllidae. This family is represented in Bermuda by several other species.

These new records increase the number of known Bermuda deep-water azooxanthellate Scleractinia from 17 to 23 species and from 7 to 10 families (Table 14.2). The majority of these species occur in deep water (>200 m). Two of these species are known to inhabit depth ranges (~300–654 m) greater than 200 m in the western Atlantic, but thus far have only been found in Bermuda in shallow waters (<3 m). This, coupled with the 102 deep-water species of azooxanthellates currently known in the western Atlantic (Cairns 2000), indicates that a good understanding of Bermuda's deep-water Scleractinia diversity still eludes us.

Shallow-Water Octocorallia

History of Species Documentation

The documentation of shallow-water octocorals in Bermuda has a long and rich history, beginning in the nineteenth century. The earliest overview was produced by Verrill (1864), who included *Pterogorgia acerosa* Ehrenberg, 1834 (= *Antillologorgia acerosa* [Pallas, 1766]), *Rhipidogorgia flabellum* Valenciennes, 1855 (probably *Gorgonia ventalina* Linnaeus, 1758), *Plexaura homomalla* (Esper, 1792) and *Plexaura crassa* Lamouroux, 1816 (= *Pseudoplexaura porosa* [Houttuyn, 1772]). Shortly thereafter, Jones (1868) added *Plexaura flexuosa* Lamouroux, 1812 and *Pterogorgia americana* Ehrenberg, 1834 (= *Antillologorgia americana* [Gmelin, 1791]) to Verrill's list. Heilprin (1889) listed *Plexaurella dichotoma* (Esper, 1791), *Plexaura purpurea* (Pallas, 1766) (possibly a morphotype of *P. flexuosa*?) and *Eunicea pseudo-antipathes* (Lamarck, 1816), but the latter two taxa are of dubious validity and uncertain synonymy (see Verrill 1900:568, 1907:317).

The extensive effort of the Challenger Expedition in the nineteenth century surprisingly added nothing to the known shallow-water octocoral diversity, although it did yield new deep-sea records from the area (see section below). Wright and Studer (1889) mention only three shallow water species from Bermuda in their expedition report: *Plexaura valencianesi* (= *P. flexuosa*), *P. crassa* (= *P. porosa*), and *G. flabellum* (= *G. ventalina*); all of which were already documented by Jones (1868).

The twentieth century brought the greatest contributions to our knowledge of Bermudian octocoral diversity. Addison E. Verrill was, in his later years, involved in significant expansions of octocoral records in Bermuda. He added *Gorgonia turgida* (Ehrenberg, 1834) (= *Eunicea clavigera* Bayer, 1961) in Verrill (1869), *Gorgonia citrina* Esper, 1794 (= *Pterogorgia citrina* [Esper 1792]), *Eunicea grandis* Verrill, 1900 (= *E. calyculata* [Ellis and Solander, 1786]), *Muricea muricata* (Pallas, 1766) and *Eunicea rousseaui* Milne-Edwards and Haime, 1857 (= *E. tourneforti* forma *typica* Milne Edwards

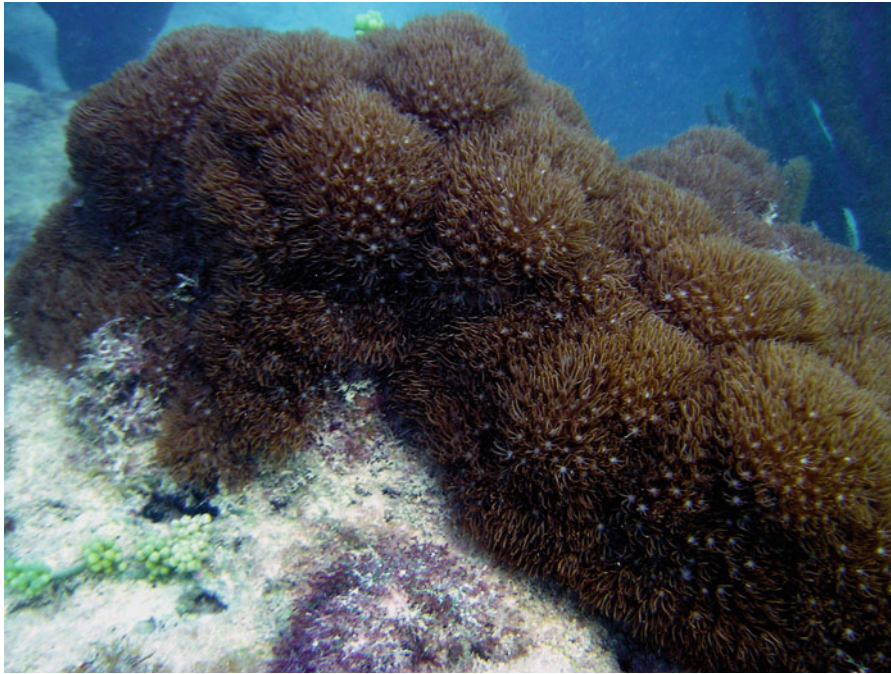


Fig. 14.2 The encrusting form of *Briareum asbestinum* insitu at Paget Island. In Bermuda, the species is known only from certain islands located in the northeastern region. (Photo: LP Holland, JP Bilewitch)

and Haime, 1857) in Verrill (1900) and *Eunicea atra* Verrill, 1901 (= *E. tourneforti* forma *atra*) in Verrill (1901c) and finally *Plexaura esperi* Verrill, 1907 (= *Pseudoplexaura flagellosa*) in Verrill (1907). It is noteworthy that his collections (currently housed at YPM) also include the earliest known Bermudian specimen of the encrusting form of the scleraxonian *Briareum asbestinum* (Pallas, 1766), although it was not recognized in these collections and identified until the 1990s (E. Lazo-Wasem, pers. comm. 2008). Verrill also makes mention of *Plexaura flavida* (Lamarck, 1815) (= *Muriceopsis flavida* [Lamarck, 1815]) in Bermuda, although he seems doubtful about the record; as he states “I have seen a few specimens from Bermuda, but have not found it myself” (Verrill 1907:305). This genus has not otherwise been reported from this region and no collections that include specimens from Bermuda are currently known.

After Verrill (1907), there was no summary of Bermudian octocorals for more than 50 years, until Frederick M. Bayer’s comprehensive study of the western Atlantic in the 1960s. Bayer (1961) examined existing museum and personal collections and listed 18 species as present in Bermuda. Except for *M. muricata*, his list included all previously recorded species as well as new records of *Pseudoplexaura wagnaari* (Stiasny, 1941), *Muricea atlantica* (Kükenthal, 1919), *Eunicea succinea* (Pallas, 1766), *Eunicea fusca* Duchassaing and Michelotti, 1860, his newly-described *Eunicea clavigera* (previously recorded in Bermuda as

Gorgonia turgida by Verrill [1869], see above) and a dubious record of *Eunicea laciniata* Duchassaing and Michelotti, 1860.

Several species have been added to records from Bermuda since Bayer’s study, but these represent occasional reports for single taxa rather than comprehensive reviews. For instance, the encrusting form of *Briareum asbestinum* (Pallas, 1766) (= *B. polyanthes* [Duchassaing and Michelotti, 1860], *sensu* Bilewitch et al. [2010]) was first noted as being present in Bermuda in a report on novel biochemical metabolites by Grode et al. (1983). Despite being an obvious shallow-water species (Fig. 14.2), its restricted distribution was likely responsible for it being previously overlooked. *Briareum asbestinum* has only been recorded in Bermuda from several small islands at the northeastern end of the archipelago: Paget Is., Governor’s Is., the south side of Higg’s Is., the northeastern end of Smith’s Is. and on St. David’s Is. at the entrance to Smith’s Sound (Hammond 2001; J.P. Bilewitch, unpubl. data).

The penultimate modern list of octocorals in Bermuda is found in the seminal description of Bermudian marine fauna and flora by Sterrer (1986). Aside from the previous records, the section on the Octocorallia (Cairns et al. 1986) adds *Plexaurella nutans* (Duchassaing and Michelotti, 1860) and *Muricea laxa* Verrill, 1864 to the known species in the islands, while omitting *E. succinea* and the questionable record of *E. laciniata*. If we include *E. succinea* and all other verifiable accounts, this would form a list of 20 shallow-water species known for Bermuda up to the 1980s.

New Records of Species Diversity

The most recent report of shallow-water octocorallian diversity in Bermuda has been produced through a combination of studies on museum collections by J.P. Bilewitch and extensive field surveys by L.P. Holland—both of which were completed in 2008. An unpublished report on these efforts (Bilewitch 2008) includes the taxa listed by Cairns et al. (1986) and adds five new species—*Eunicea knighti* Bayer, 1961, *Muricea pinnata* Bayer, 1961, *Muricea* cf. *waltonsmithi* Bayer, 1994, *Plexaurella grisea* Kunze, 1916 and *Leptogorgia* cf. *setacea* (Pallas, 1766) (Table 14.3).

The current list for Bermuda contains octocoral taxa for which there are reliable field records and for which identifiable specimens are held in the collections of BAMZ, USNM or YPM (Cairns et al. 1986; Bilewitch 2008; L.P. Holland, unpubl. data). All included species are considered valid but many require further taxonomic investigation and revision. In particular, *Eunicea knighti*, here reported as a new record for Bermuda, possesses overlapping character variation with *Eunicea calyculata* that can make intermediate forms difficult to identify (Bayer 1961). Likewise, *Muricea pinnata* and *Muricea waltonsmithi* intergrade with one another, and with *Muricea laxa* (Bayer 1994), again allowing only tenuous identifications for some specimens.

The identity of *Leptogorgia* cf. *setacea*, Bermuda's only shallow-water azooxanthellate octocoral, is deserving of further taxonomic investigation (Fig. 14.3). The only colonies found in Bermuda, from the Great Sound, are usually unattached, possess polyps in biserial rows, and have characteristic disk spindle sclerites (Bayer 1961). However, the colonies appear to lack anthocodial sclerites and the lateral branching exceeds that described for *L. setacea* (J.P. Bilewitch, unpubl. data). Additional taxonomic analysis might show that the Bermudian variety is a distinct, new species. This would make it the only known endemic octocoral species from Bermuda.

The extent of the distribution of the rarer species of shallow-water Octocorallia in Bermuda remains largely unknown and the recent addition of so many new octocoral species records for the region (Bilewitch 2008) presents the possibility of even more undocumented taxa in shallow reef or inshore waters. The fortuitous discovery of the *L.* cf. *setacea* population (K.A. Coates and S.A. Manuel, pers. obs. 2008) during systematic surveys of the marine benthic habitats of Bermuda has revealed a second species of octocoral, other than *B. asbestinum*, with a greatly restricted distribution in Bermuda. Both *B. asbestinum* and *L.* cf. *setacea* are known only from isolated localities, but other small, undocumented populations may exist. Both species occupy non-reef habitats that are not frequently explored by either scientific or recreational divers, so that these species are unlikely to be encountered. *Briareum asbestinum* is found on the subtidal rocky shores of a few northeastern islands and *L.* cf. *setacea* is found in the silty

Table 14.3 Current list of valid shallow-water octocoral species in Bermuda

Species
Briareidae
<i>Briareum asbestinum</i> (Pallas, 1766)
Gorgoniidae
<i>Gorgonia ventalina</i> Linnaeus, 1758
<i>Leptogorgia</i> cf. <i>setacea</i> (Pallas, 1766)
<i>Antillogorgia acerosa</i> (Pallas, 1766)
<i>Antillogorgia americana</i> (Gmelin, 1791)
<i>Pterogorgia citrina</i> (Esper, 1792)
Plexauridae
<i>Eunicea calyculata</i> (Ellis and Solander, 1786)
<i>Eunicea clavigera</i> Bayer, 1961
<i>Eunicea fusca</i> Duchassaing and Michelotti, 1860
<i>Eunicea knighti</i> Bayer, 1961
<i>Eunicea tourneforti</i> Milne Edwards and Haime, 1857
<i>Eunicea tourneforti</i> forma <i>atra</i> Verrill, 1901
<i>Muricea atlantica</i> (Kükenthal, 1919)
<i>Muricea laxa</i> Verrill, 1864
<i>Muricea muricata</i> (Pallas, 1766)
<i>Muricea pinnata</i> Bayer, 1961
<i>Muricea</i> cf. <i>waltonsmithi</i> Bayer, 1994
<i>Plexaura flexuosa</i> Lamouroux, 1821
<i>Plexaura homomalla</i> (Esper, 1792)
<i>Plexaurella dichotoma</i> (Esper, 1791)
<i>Plexaurella grisea</i> Kunze, 1916
<i>Plexaurella nutans</i> (Duchassaing and Michelotti, 1860)
<i>Pseudoplexaura flagellosa</i> (Houttuyn, 1772)
<i>Pseudoplexaura porosa</i> (Houttuyn, 1772)
<i>Pseudoplexaura wagnaari</i> (Stiasny, 1941)

substrate of turbid, low-visibility waters in the Great Sound. Clearly, the diversity of some types of habitats is significantly underexplored compared to typical reef habitats, and these are deserving of comprehensive and structured studies.

Deeper-Water Octocorallia

History of Species Documentations

The documentation of deep-water octocoral records in Bermuda begins with the HMS Challenger Expedition, which reports *Sympodium armatum* Wright and Studer, 1889 (validity unknown) and *Acanella simplex* (Verrill, 1883) (= *Lepidisis simplex* [Verrill, 1883]) midway between Bermuda and Challenger Bank (Wright and Studer 1889:32, 273).

Verrill (1901c:53, 1907:317) was first to report a mesophotic species from the region—*Verrucella grandis* Verrill, 1901c (= *Ellisella grandis* [Verrill, 1901c]), collected from about 30 m on the northern fore-reef terrace. Over 30 years later, this

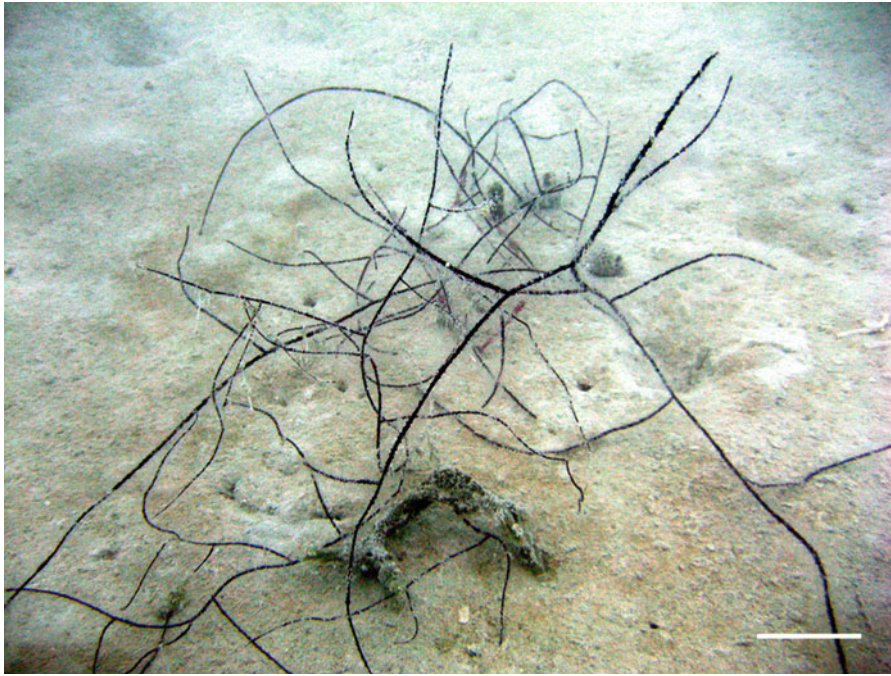


Fig. 14.3 Bermuda's only shallow-water azooxanthellate octocoral, *Leptogorgia* cf. *setacea*, was discovered in Bermuda's Great Sound in 2008. Scale equals 5 cm (Photo: LP Holland)

species was noted again (as *Scirpearia grandis* [Verrill, 1901c]) at 66 m in the same vicinity (Deichmann 1936).

The shallow-water study of Bayer (1961: Fig. 101) reports the deep-water genus *Scleracis* Kükenthal, 1919 for Bermuda. However, *Scleracis* was omitted in Cairns et al. (1986), which instead lists one pennatulacean, *Sclerobelemnon* cf. *theseus* Bayer, 1959, one nidaliid alcyonacean, *Nidalia occidentalis* Gray, 1835 and mentions three species of ellisellid but specifically names only *Ellisella barbadensis* (Duchassaing and Michelotti, 1864). Most recently, Cairns and Bayer (2003, 2004) describe *Narella alvinae* Cairns and Bayer, 2003 and add records of *Narella versluysi* (Hickson, 1909) and *Candidella imbricata* (Johnson, 1862) from Bermuda.

Current Studies of Species Diversity

A report to the Bermuda Zoological Society by Bilewitch (2008) lists the known species of deep-sea octocorals present in Bermuda (amended herein to include 33 species in total; Table 14.4). Except for Wright and Studer's (1889) questionable record of *Lepidisis simplex* (Verrill, 1883), all listed species are represented in one of the collections of BAMZ, YPM, or USNM. This expands upon the list of Cairns et al. (1986), which included only five deep-sea octocorals among the Pennatulacea, Nidaliidae and Ellisellidae. The most recent records belong to the Primnoidae (seven spp.), the Isididae (four spp.) and a chrysogorgiid— all calcaxonians. One species

of clavulariid telestacean, *Telestula septentrionalis* Madsen, 1944 is also added based on two specimens in the USNM, collected from Muir Seamount to the northeast of Bermuda. Among the Holaxonia, seven records are added for the Paramuriceidae, one to the Keroididae, one to the Gorgoniidae and four to the Plexauridae.

Of the genera in Tables 14.3 and 14.4, only *Antillogorgia*, *Plexaurella*, *Muricea* and *Eunicea* are represented in both shallow and deep waters and *Plexaurella nutans* and *Antillogorgia acerosa* are the only species broadly recorded from 1 m to 55 m depth. Interestingly, Bayer (1961:129, 191) describes *Muricea elongata* Lamouroux, 1821 as an inshore species in the Caribbean whereas in Bermuda it has not been recorded from less than 45 m. This discrepancy could be due to taxonomic confusion or to the effects of localized environmental differences.

The specimen of the rare isidid *Chelidonisis aurantiaca* Studer, 1890, currently curated at BAMZ, is a noteworthy record. The species is represented by very few specimens from localities as disparate as Ireland and the Gulf of Mexico (Deichmann 1936; Bayer and Stefani 1987). Although Verrill mentions an unconfirmed record from Florida (see Bayer and Stefani [1987:984–985] for discussion), the BAMZ record is likely the first and only specimen from the Atlantic. Whether the Bermudian specimen represents the Caribbean subspecies *C. aurantiaca mexicana* (like most shallow-water octocoral taxa), the European subspecies *C. aurantiaca aurantiaca* or an intermediate of the two remains to be determined.

Table 14.4 Current list of valid deep-water octocoral species in Bermuda

Species
Order Alcyonacea
Suborder Alcyoniina
Nidaliidae
<i>Nidalia occidentalis</i> Gray, 1835
Nephtheidae
<i>Gersemia rubiformis</i> (Ehrenberg, 1834)
Suborder Calcaxonia
Ellisellidae
<i>Ellisella atlantica</i> (Toeplitz, 1929)
<i>Ellisella barbadensis</i> (Duchassaing and Michelotti, 1864)
<i>Ellisella grandis</i> (Verrill, 1901)
<i>Nicella gracilis</i> Cairns, 2007
Chrysogorgiidae
<i>Chrysogorgia fewkesii</i> Verrill, 1883
Primnoidae
<i>Callogorgia gracilis</i> (Milne Edwards and Haime, 1857)
<i>Callogorgia verticillata</i> (Pallas, 1766)
<i>Candidella imbricata</i> (Johnson, 1862)
<i>Narella alvinae</i> Cairns and Bayer, 2003
<i>Narella versluysi</i> (Hickson, 1909)
<i>Narella bellissima</i> (Kükenthal, 1915)
<i>Thouarella (Euthouarella) grasshoffi</i> Cairns, 2006
Isididae
<i>Keratoisis flexibilis</i> (Pourtalès, 1868)
<i>Chelidonisis aurantiaca</i> Studer, 1890
<i>Lepidisis caryophyllia</i> Verrill, 1883
<i>Lepidisis simplex</i> (Verrill, 1883)
Suborder Holaxonia
Gorgoniidae
<i>Antillogorgia acerosa</i> (Pallas, 1766)
Keroeidae
<i>Thelogorgia vossi</i> Bayer, 1991
Paramuriceidae
<i>Bebryce parastellata</i> Deichmann, 1936
<i>Muriceides kükenthali</i> (Broch, 1912)
<i>Scleracis guadalupensis</i> (Duchassaing and Michelotti, 1860)
<i>Scleracis petrosa</i> Deichmann, 1936
<i>Thesea citrina</i> Deichmann, 1936
<i>Placogorgia cf. intermedia</i> (Thomson, 1927)
<i>Placogorgia tenuis</i> (Verrill, 1883)
Plexauridae
<i>Eunicea pinta</i> Bayer and Deichmann, 1958
<i>Lytreaia plana?</i> (Deichmann, 1936)
<i>Muricea elongata</i> Lamouroux, 1821
<i>Plexaurella nutans</i> (Duchassaing and Michelotti, 1860)
Order Pennatulacea
Suborder Sessiliflorae
Kophobelemnidae
<i>Sclerobelemnon theseus</i> Bayer, 1959
Order Telestacea
Clavulariidae
<i>Telestula septentrionalis</i> Madsen, 1944

Table 14.5 Current list of valid Antipatharia species in Bermuda

Species
Family Myriopathidae
<i>Cupressopathes gracilis</i> (Thomson and Simpson, 1905)
<i>Tanacetipathes hirta</i> (Gray, 1857)
<i>Tanacetipathes tanacetum</i> (Pourtalès, 1880)
<i>Tanacetipathes thamnea</i> (Warner, 1981)
Family Antipathidae
<i>Antipathes atlantica</i> Gray, 1857
<i>Antipathes furcata</i> Gray, 1857
<i>Stichopathes lutkeni</i> Brook, 1889
<i>Stichopathes cf. spiessi</i> Opresko and Genin, 1990
Family Schizopathidae
<i>Parantipathes tetrasticha</i> (Pourtalès, 1868)

Antipatharia: Deep and Deeper Water

Six families of Antipatharia or black corals are reported in the greater Caribbean Region (Opresko and Sanchez 2005). For Bermuda, nine species are known (exclusive of three specifically undetermined specimens: *Tanacetipathes* sp. BAMZ 2007.258.034 and USNM 77485 and *Stichopathes* sp. USNM 99863) from five genera and three families, Antipathidae, Myriopathidae and Schizopathidae (Table 14.5). These records are based on Cairns et al. (1986) and collections held at the BAMZ and the USNM, and include two new records for Bermuda. The new records, based on specimens collected during the Pacific Guardian Cruise in 2007 (identified by DM Opresko), are of *Stichopathes cf. spiessi* Opresko and Genin, 1990 from 784.9 m, BAMZ 2007.258.011, and *Parantipathes tetrasticha* (Pourtalès, 1868) from 778.4 m, BAMZ 2007.258.013. Bermuda was not included within the distributional region of the recent guide to Caribbean Antipatharia (Opresko and Sanchez 2005) but based on the authors' criteria the majority of Bermuda's species are shallow-water black corals (depth range: 50–72 m) with a few exceptions.

Conclusion

Knowledge of two aspects of biological diversity underlie any plans to conserve and manage ecosystems: what species occur and where they occur. From these basics, we develop hypotheses and research programs on what controls distribution of individual species and species groups – such research spans the gamut of major fields of biology and relies on input from physical and chemical oceanography and from palaeogeography, climatology and many other fields of science.

We are fortunate that the diversity of Bermuda's corals has been extensively studied by natural historians and taxo-

onomic specialists since the mid-nineteenth century and there is a well-laid foundation for future studies. Unfortunately, and not for Bermuda alone, only précised versions of taxonomic foundations have been presented and consulted in many recent research programs. This leads to unnecessarily inaccurate representations of both what is present and where species occur and this restricts any understanding of what controls their presence.

In foundation studies for Bermuda, shallow water environments have received the majority of attention and it is clear that some taxa have been more comprehensively studied than others. Further field investigations and studies of pre-existing, well-curated collections can add substantially to our basic knowledge, the latter is exemplified here by the new records of Scleractinia, Octocorallia and Antipatharia.

Competence in taxonomy is a limiting factor in many field studies, but good record keeping and well-curated specimens can overcome this barrier, as in the case of the new record for Bermuda of *Leptogorgia cf setacea*. New distribution and species records cannot be based on unsubstantiated field observations, and at some point taxonomic specialists are needed to interpret the many forms of data used to determine species identity, from molecules to morphology. Bermuda's coral reef environment is monitored by the Bermuda Government (Departments of Conservation

Services [DCS] and Environmental Protection [DEP]) both internally and in collaboration with the NGO's, the Bermuda Zoological Society with DCS (Bermuda Reef Ecosystem Analysis and Monitoring) and the Bermuda Institute of Ocean Sciences (BIOS) with DEP (Marine Environmental Program). The current efforts, given better developed taxonomic protocols, have the potential to rapidly move forward understanding of diversity and functioning of Bermuda's coral reef environments and associated habitats.

The number of experienced and trained taxonomists has diminished in the past few decades. Although the advent of automated DNA sequencing in the 1980s revived research interests in systematics through a molecular biological approach, this has done little to cultivate understanding of proper taxonomic process (e.g., the ICZN Code) and morphology-based familiarity with taxa. Rather, molecular systematics has often attempted to circumvent problematic issues, such as morphological plasticity, rather than provide a better understanding of them. Although the genetic delineation of species boundaries represents a powerful tool for taxonomic classification, it should be used in conjunction with detailed morphological diagnoses of taxa, rather than attempting to obviate an intimate understanding of morphology and the processes that drive remarkable phenotypic variation.

Confusing Records of Scleractinia for Bermuda

Isophyllia rigida (Dana, 1848): A Complex History of Misidentification

Confusion about the presence of *Isophyllia rigida* in Bermuda has a long history, beginning with Verrill's original misidentification of some specimens of *Isophyllia* (referred to, at that time, as *Mussa*) in 1864. Subsequent reports of *I. rigida* were based on communication with or the literature of AE Verrill prior to his published recognition of this error in 1907. He (Verrill 1907:230) notes that, after viewing Dana's type of *I. rigida*, held at Yale University, he decided the species named in his 1864 paper was not *I. rigida* but a distinct species, *Mussa rosula* Verrill, 1907. This last species has since been synonymized with *I. sinuosa*. Labrel (1966) did not find *I. rigida* in Bermuda, and there are no other substantial, more

recent, records. Perhaps recent species lists for Bermuda, that include *I. rigida* (e.g., Veron 2000), have relied on out-dated information and not on deposited specimens. *Isophyllia sinuosa* is well-documented and represented in collections for Bermuda.

Siderastrea siderea: A Question to Pursue

Currently considered rare, *Siderastrea siderea* was initially observed in Bermuda by Verrill (1900); however, Labrel (1966) did not find it. Verrill's specimens of *S. siderea* from Castle Harbor, Bermuda, are deposited at the Yale Peabody Museum (YPM 006787, YPM 008228). There are also three specimens from Bermuda, including a fossil specimen, deposited at the Smithsonian National Museum of Natural History (USNM 64392 [Pleistocene], USNM 1142515, USNM 16363) and one specimen (Fricke and Meischner 1985) at the Hessisches

(continued)

(continued)

Landesmuseum (HLM), Darmstadt, FRG (Federal Republic Germany) (HLM, Fri Be-6). Verrill (1901b:152) says that “Bermudian specimens that have been referred to the species *Siderastrea siderea* ...[as far as he has observed are not the typical form, and] ... may be an extreme variety of *Siderastrea radians*. The calices are not so large nor so deep as in the Florida form, nor are the septa so numerous (about 42–48).” Logan (1988) stated that virtually all Bermudian *Siderastrea* belonged to *radians*; however earlier, Dryer and Logan (1978) had reported *S. siderea* from northwest reefs in Castle Harbour. The presence of *S. siderea* is debatable (Laborel 1966; Logan 1988; W. Sterrer and S.R. Smith, pers. comm., 2008) and an in depth study, including fieldwork and observation of new material and deposited specimens is warranted. The large colonies of *S. siderea* common to Florida, the Bahamas and Caribbean are not known to occur in Bermuda.

Montastraea annularis* and *Montastraea franksi

Records of *M. annularis* in Bermuda predate or are based in literature that predates a recent revision of several species in the genus (Weil and Knowlton 1994), and almost certainly are incorrect. Early accounts of *M. annularis* are found in Verrill (1900, 1901a, b, 1907), Smith (1948), Squires (1958), and Cairns et al. (1986), among others. Weil and Knowlton (1994) redescribed *M. annularis* sensu stricto and resurrected and amended the descriptions of two older taxa, *Montastraea faveolata* (Ellis and Solander, 1786), and *M. franksi* (Gregory, 1895). Based on these new, and accepted, descriptions, it is recognized that *M. franksi* is common on Bermuda reefs, along with *M. cavernosa*, and also that it has probably been regularly misidentified as *M. annularis*. Nonetheless, to confirm that there is no objective basis for records of *M. annularis* in Bermuda, it is important to re-examine historical collections from Bermuda.

Acknowledgements Stephen Cairns and Dennis Opresko, National Museum of Natural History, Smithsonian Institution, assisted with the identification of specimens for new species records for Bermuda; Andrew Cabrinovic, Natural History Museum, United Kingdom and Lisa Greene, Bermuda Natural History Museum assisted with collection information; Alison Green, Bermuda Natural History Library and Michel Paon, Dalhousie University Libraries provided access to taxonomic resources; and Wolfgang Sterrer has worked for many years on documenting Bermuda’s marine biodiversity. This is a contribution of the Bermuda Biodiversity Project BBP#201.

References

- Appeltans W, Bouchet P, Boxshall GA, De Broyer C, de Voogd NJ, Gordon DP, Hoeksema BW, Horton T, Kennedy M, Mees J, Poore GCB, Read G, Stöhr S, Walter TC, Costello MJ. (eds) (2012) World register of marine species (WoRMS). <http://www.marinespecies.org>. Accessed 21 July 2012
- Bayer FM (1961) The shallow-water Octocorallia of the West Indian Region. Martinus Nijhoff, The Hague
- Bayer FM (1994) A new species of the gorgonacean genus *Muricea* (Coelenterata: Octocorallia) from the Caribbean Sea. *Precious Corals Octocoral Res* 3:23–27
- Bayer FM, Stefani J (1987) New and previously known taxa of isidid octocorals (Coelenterata: Gorgonacea), partly from Antarctic waters. *Proc Biol Soc Wash* 100:937–991
- Bilewitch JP (2008) Octocoral biodiversity in Bermuda. Report for the Bermuda Zoological Society, Bermuda, BAMZ #1915
- Bilewitch JP, Coates KA, Currie DC, Trapido-Rosenthal HG (2010) Molecular and morphological variation supports monotypy of the octocoral *Briareum* Blainville, 1830 (Octocorallia: Alcyonacea) in the western Atlantic. *Proc Biol Soc Wash* 123:93–112
- Brüggemann F (1877) Notes on stony corals in the collection of the British museum. III. A revision of the recent solitary Mussaceae. *Ann Mag Nat Hist* 20:300–313
- Cairns SD (1979) The deep-water Scleractinia of the Caribbean and adjacent waters. *Stud Fauna Curaçao* 57:1–341
- Cairns SD (2000) A revision of the shallow-water azooxanthellate scleractinia of the western Atlantic. *Nat Hist Carib Reg* 75:1–240
- Cairns SD, Bayer FM (2003) Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 3: the genus *Narella* Gray, 1870. *Proc Biol Soc Wash* 116:617–648
- Cairns SD, Bayer FM (2004) Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 5: the genera *Plumarella* Gray, 1870; *Acanthoprinnia* n. gen.; and *Candidella* Bayer, 1954. *Proc Biol Soc Wash* 117:447–487
- Cairns SD, Chapman RE (2001) Biogeographic affinities of the North Atlantic deep-water Scleractinia. In: Proceedings of the first international symposium on deep-sea corals, Ecology Action Centre and Nova Scotia Museum, Halifax, pp 30–57
- Cairns SD, den Hartog JC, Arneson C, Rützler K (1986) Class Anthozoa (Corals, Anemones). In: Sterrer W (ed) Marine fauna and flora of Bermuda. A systematic guide to the identification of marine organisms. Wiley, New York, pp 159–194
- Dana JD (1872) Corals and coral islands. Dodd and Mead, New York
- Dawson JP (2002) Biogeography of azooxanthellate corals in the Caribbean and surrounding areas. *Coral Reefs* 21:27–40
- de Pourtalès LF (1871) Deep sea corals, vol IV, *Illust Cat Museum of Comparative Zoology*. Printed for the Museum of Comparative Zoology, Cambridge, MA
- Deichmann E (1936) The alcyonaria of the western part of the Atlantic Ocean. *Mem Mus Comp Zool* 53:1–317
- Dryer S, Logan A (1978) Holocene reefs and sediments of Castle Harbour, Bermuda. *J Mar Res* 36:399–425
- Frade PR, Reyes-Nivia MC, Faria J, Kaandorp JA, Luttkhiuzen PC, Bak RPM (2010) Semi-permeable species boundaries in the coral genus *Madracis*: introgression in a brooding coral system. *Mol Phyl Evol* 57:1072–1090
- Fricke H, Meischner D (1985) Depth limits of Bermudan scleractinian corals: a submersible survey. *Mar Biol* 88:175–187
- Grode SH, James TR, Cardellina JH II (1983) Briantein Z, a new polyfunctional diterpene from the gorgonian *Briareum polyanthes*. *Tetrahedron Lett* 24:691–694

- Hammond MP (2001) Range, distribution, and dispersion of a recent colonist, the gorgonian *Briareum polyanthes*, in St. Georges Harbour, Bermuda. Report for the Bermuda Aquarium Museum and Zoo, BAMZ #1102
- Heilprin A (1888) Contributions to the natural history of the Bermuda Islands. *Proc Acad Nat Sci Phil* 40:302–328
- Heilprin A (1889) The Bermuda Islands: a contribution to the physical history and zoology of the somers archipelago. Heilprin A, Philadelphia
- Jones JM (1868) Contributions to the natural history of the Bermudas. Coralliaria. *Trans Nova Scotia Inst Nat Sci* 2(2):7–16
- Laborel J (1966) Contribution à l'étude des Madreporaires des Bermuda (systématique et répartition). *Bull Mus Nat Hist Nat* 38:281–300
- Locke JM (2009) *Madracis auretenra* (Scleractinia: Pocilloporidae) – testing our knowledge of systematics, biology and connectivity in the western North Atlantic. Ph.D. dissertation, University of Puerto Rico, Mayagüez
- Locke JM, Weil E, Coates KA (2007) A newly documented species of *Madracis* (Scleractinia: Pocilloporidae) from the Caribbean. *Proc Biol Soc Wash* 120:214–226
- Logan A (1988) Holocene reefs of Bermuda. Sedimenta IX. Comparative Sedimentology Laboratory, University of Miami, Miami Beach
- Moseley HN (1881) Report on certain hydroid, alcyonarian, and madreporian corals procured during the voyage of H.M.S. Challenger. In: Thomson CW, Murray J (eds) Report on the scientific results of the voyage of the H.M.S. Challenger, vol 2. Royal Stationery Office, London
- Opresko DM, Genin A (1990) A new species of antipatharian (Cnidaria: Anthozoa) from seamounts in the eastern North Pacific. *Bull Mar Sci* 46:301–310
- Opresko DM, Sanchez JA (2005) Caribbean shallow-water black corals (Cnidaria: Anthozoa: Antipatharia). *Carib J Sci* 41:492–507
- Quelch JJ (1886) Report on the reef corals collected by H.M.S. Challenger during the years 1873–76. In: Thomson CW, Murray J (eds) Report on the scientific results of the Voyage of the H.M.S. Challenger, vol 16. Royal Stationery Office, London
- Rathburn R (1887) Annotated catalogue of the species of *Porites* and *Synaraea* in the United States National Museum, with a description of a new species of *Porites*. *Proc US Nat Mus* 10:354–366
- Smith PGW (1948) Atlantic reef corals. A handbook of the common reef and shallow-water corals of Bermuda, Florida, the West Indies and Brazil. University of Miami Press, New York
- Squires DF (1958) Stony corals from the vicinity of Bimini, Bahamas, British West Indies. *Bull Am Mus Nat Hist* 115:215–262
- Sterrer WE (ed) (1986) Marine fauna and flora of Bermuda: a systematic guide to the identification of marine organisms. Wiley, New York
- Sterrer WE (1998) How many species are there in Bermuda? *Bull Mar Sci* 62:809–840
- Venn AA, Weber FK, Loram JE, Jones RJ (2009) Deep zooxanthellate corals at the high latitude Bermuda seamount. *Coral Reefs* 28:135
- Veron JEN (2000) Corals of the world. Australian Institute of Marine Science, Townsville
- Verrill AE (1864) List of the polyps and corals sent by the museum of comparative zoology to other institutions in exchange, with annotations. *Bull Mus Comp Zool Harvard* 1:29–60
- Verrill AE (1869) Critical remarks on the halcyonoid polyps with descriptions of new species in the museum of Yale college. No. 4. *Am J Sci Arts* 48:419–429
- Verrill AE (1900) Additions to the Anthozoa and Hydrozoa of the Bermudas. *Trans Conn Acad Arts Sci* 10:551–572
- Verrill AE (1901a) Comparisons of the Bermuda, West Indian, and Brazilian coral faunae. *Trans Conn Acad Arts Sci* 11:169–206
- Verrill AE (1901b) Variations on the nomenclature of Bermudian, West Indian, and Brazilian Reefs corals, with notes on various Indo-Pacific corals. *Trans Conn Acad Arts Sci* 11:63–168
- Verrill AE (1901c) Additions to the fauna of the Bermudas from the Yale expedition of 1901, with notes on other species. *Trans Conn Acad Arts Sci* 11:15–62
- Verrill AE (1907) The Bermuda Islands. Part IV. Geology and paleontology and Part V. An account of the coral reefs. *Trans Conn Acad Arts Sci* 12:45–348
- Weil E, Knowlton N (1994) A multi-character analysis of the Caribbean coral *Montastraea annularis* (Ellis and Solander, 1786) and its two sibling species, *M. faveolata* (Ellis and Solander, 1786), and *M. franksi* (Gregory, 1895). *Bull Mar Sci* 54:151–175
- Wells JW (1972) Some shallow water ahermatypic corals from Bermuda. *Postilla* 156:1–10
- Wright EPW, Studer T (1889) Report on the Alcyonaria collected by H.M.S. Challenger during the years 1873–1876. In: Thomson CW, Murray J (eds) Report on the scientific results of the voyage of the H.M.S. Challenger, vol 31. Royal Stationery Office, London