

A brief history of taxonomic research on azooxanthellate Scleractinia (Cnidaria: Anthozoa)

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Abstract.—Of the 1335 species of Scleractinia recognized at the end of 1999, 672.5 (50.3%) are azooxanthellate, i.e., devoid of zooxanthellae in their tissue. Although many exceptions occur, the majority of azooxanthellate species occur in deep water (the aphotic zone) and are solitary in habit, thus not forming reef-like structures. Four decadal-scale pulses of species descriptions punctuate the species accumulation curve of these corals. The first pulse resulted from the comprehensive revision of the Scleractinia by Milne Edwards & Haime (1848–1850), who doubled the number of species known at that time. The second pulse (starting in 1867) was caused by the discovery that corals lived in the deep-sea and were abundant and diverse in this environment. The third pulse (1898–1907) resulted from various deep-water dredging programs in the Indo-Pacific; the fourth pulse (1977–1999) resulted from even larger collections made in deeper water, as well as the existence of several full time systematists engaged in long-term comparative studies. Eighty per cent of the azooxanthellate species were described by 20 taxonomists; their individual synonymy rates are calculated, as well as references to their biographies, if any, and the museums in which they deposited most of their types. As a group, the azooxanthellates currently have a 34.1 % synonymy rate.

This brief history addresses the taxonomy of the Recent azooxanthellate Scleractinia, i.e., those species that do not have symbiotic zooxanthellae in their tissue. For the most part, a separate body of literature, a distinctive group of taxonomists, and a different method of specimen collection (i.e., deep-water dredging) have developed separately from those involved in the study of shallow-water reef corals, which justifies a separate discussion of their taxonomic histories.

A number of misconceptions surround azooxanthellate Scleractinia, one being that because they do not have to live in the euphotic zone, they are always found in deep water and thus are referred to as the “deep-water corals.” But, whereas some species occur as deep as 6328 m (Keller 1976), at least 180 species (27% of azooxanthellate

species) occur in water shallower than 40 m, some living at intertidal depths. Indeed, in the eighteenth and early nineteenth centuries, these shallow-water species were among the first azooxanthellates to be discovered and described. Another misconception is that azooxanthellates are the “solitary corals”; however, 174 species (26%) are colonial and, conversely, a number of solitary zooxanthellate species exist. Third, azooxanthellates have often been termed ahermatypic, non-reef, or non-constructural corals, but some species, such as *Tubastraea micranthus*, have large coralla that contribute to shallow-water reef structure (see Schuhmacher & Zibrowius 1985, Zibrowius 1989). On the other hand, some colonial, deep-water species, such as *Lophelia pertusa* and *Goniocorella dumosa*, form the constructional framework for deep-water

coral banks (Cairns & Stanley 1982). Finally, many think that azooxanthellates constitute a small fraction of scleractinian species richness, but, as Cairns (1999b) has shown, azooxanthellate species slightly outnumber zooxanthellates. By the end of 1999 azooxanthellates constituted 672.5 (50.3%) of the 1335 recognized species of Scleractinia.

The azooxanthellate Scleractinia are a polyphyletic, or artificial, grouping based on an ecological/physiological character: absence of zooxanthellae. Whereas some families are exclusively azooxanthellate (e.g., Flabellidae, Turbinoliidae, and Gyniidae), others are predominantly azooxanthellate (e.g., Caryophylliidae and Dendrophylliidae), or equally mixed (e.g., Oculinidae). Furthermore, some genera, such as *Madracis* and *Oculina*, contain species that are either zooxanthellate or azooxanthellate, whereas eleven species within the Scleractinia (see Cairns et al. 1999) are facultative, i.e., possessing or not possessing zooxanthellae depending on the ecological circumstances, these species counted as 0.5 for the purpose of Fig. 1.

Methods

The analyses in this paper (Fig. 1, Table 1) are based on the species list published by Cairns et al. (1999), plus subsequently discovered corrections and an update through the year 1999. Junior synonyms were not listed in that publication but were compiled for these analyses; they are not published herein. Coauthored species were counted as 0.5 for each author, except for those described by Milne Edwards & Haime, who always coauthored their species descriptions and thus are considered as one entity in Table 1.

Results

The primary result of this paper is the species accumulation curve for scleractinian corals over the last 242 years (Fig. 1). The curve shows that, following a very

slow start, the number of azooxanthellate species increased gradually, experienced four decadal-scale pulses, and only within the last two years exceeded the number of zooxanthellate species. One might assume from the almost exponential rise at the end of the graph that there is no limit in sight for the description of new species, but I still agree with my earlier prediction (Cairns 1999b) that the azooxanthellate fauna is fairly well known and that well over half of the species have been described. Most of the faunistic regions of the world have been revised based on large collections, except for the northern Indian Ocean, tropical eastern Pacific, and the rich New Caledonian region. Nonetheless, it is doubtful that the number of azooxanthellates will ever exceed 1000 species (Cairns 1999b).

This analysis also lists the 20 most prolific describers of azooxanthellate coral species (Table 1), who collectively account for 80% of the 672.5 currently recognized species. The Table not only lists the number of currently recognized species and genera they described but also the total number of species described, allowing a calculation of their individual "synonymy rate," defined as the number of junior synonyms divided by the total number of nominal species (junior and senior synonyms). Two caveats should be mentioned at this point. First, more is not necessarily better, as it is often more intellectually satisfying and more instructive to synonymize a name than to suggest another new one. Second, synonymy rates increase with time; Solow et al. (1995) suggest that it takes an average of 43 years to identify a junior synonym. Thus, low synonymy rates for late 19th century authors are probably underestimations. The synonymy rate for all azooxanthellates is 34.1% (Table 1), which is consistent with rates of some insects groups such as thrips, given as 22% by May & Nee (1995) and 39% by Solow, et al. (1995), but probably far less than that of the more common zooxanthellate corals, for which information is not now available.

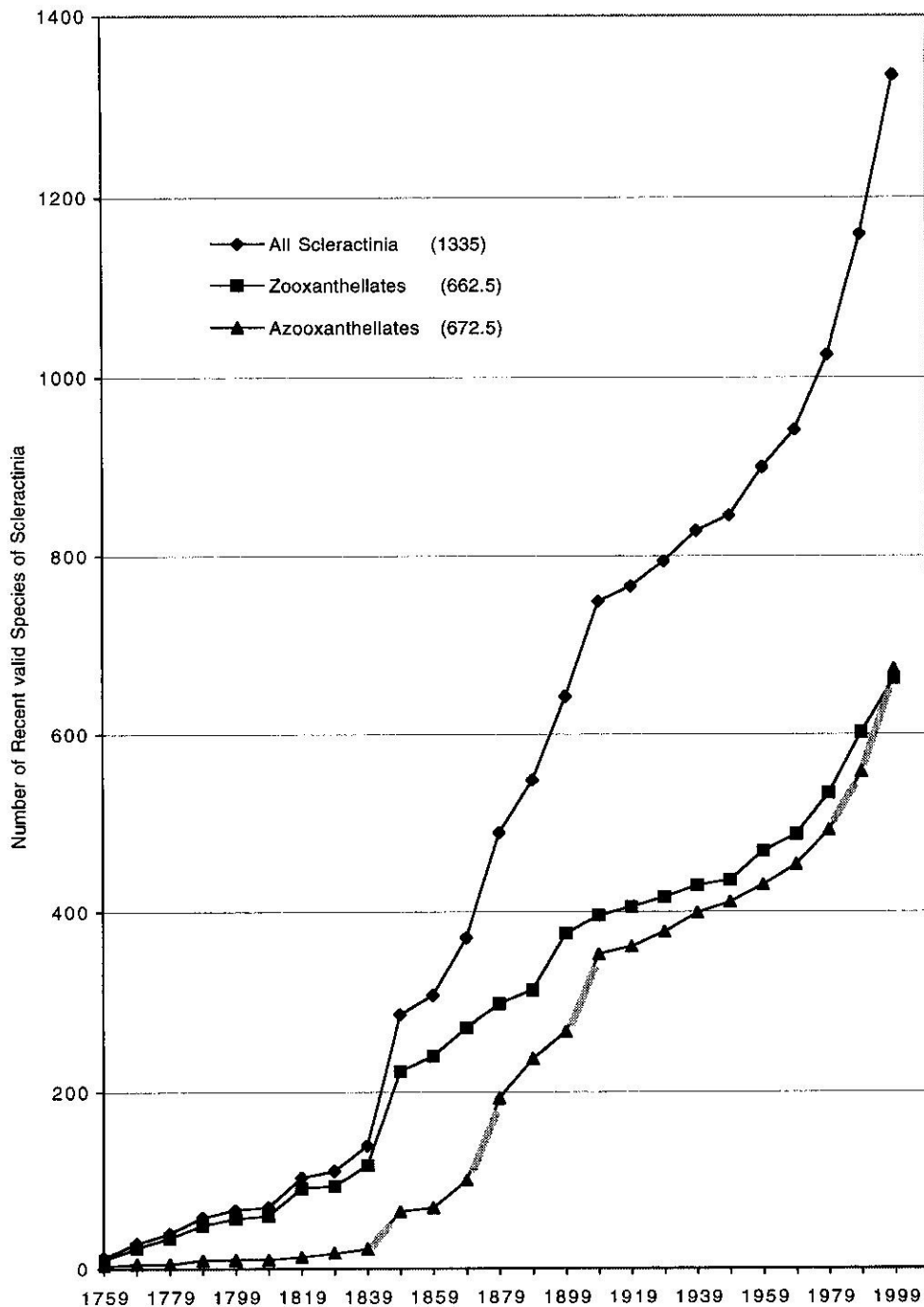


Fig. 1. Cumulative number of recognized (valid) zooxanthellate, azooxanthellate and total scleractinian species from 1759 through 1999. The four pulses of taxonomic activity are highlighted on the azooxanthellate line. The 11 facultative species (i.e., those that can be zooxanthellate or azooxanthellate) are counted as 0.5 each.

Table 1.—Number of currently recognized and total number of species described, synonymy rate, and number of currently recognized genera of Recent azooxanthellate Scleractinia proposed by the twenty most prolific authors, arranged in order of highest number of valid species. Co-authored species and genera counted as 0.5.

Author	Currently recognized species	Total species described	Junior synonyms (synonymy rate)	Currently recognized genera
Cairns	148	155	7 (4.5%)	21.5
Pourtalés	47	59	12 (20%)	8
Alcock	46	74.5	28.5 (38%)	2
Moseley	39	48	9 (19%)	2
Milne Edwards & Haime	34	64	30 (47%)	24
Zibrowius	25	27	2 (7%)	1
Duncan	22	47	25 (53%)	5
Vaughan	22	41	19 (46%)	1
Gardiner	18.5	28	9.5 (34%)	0
Wells	18	22	4 (18%)	3
Verrill	18	33	15 (45%)	1
van der Horst	16	21	5 (24%)	0
Marenzeller	15	17	2 (12%)	2
Dennant	13	18	5 (28%)	3
Squires	12	14.5	2.5 (17%)	0
Durham	11.5	25.5	14 (55%)	0.5
Tenison-Woods	10	18	8 (44%)	4
Eguchi	9.5	27.5	18 (65%)	2
Semper	7	17	10 (59%)	0
Keller	7	14	7 (50%)	0
All authors	672.5	1020.5	348 (34.1%)	117

Taxonomic History

In 1758, Carl Linnaeus (1707–1778; biography by Blunt 1971) described the first known species azooxanthellate corals: *Madrepora oculata*, *Lophelia pertusa*, and *Dendrophyllia ramea*. All are colonial forms from the northeastern Atlantic. Whereas the third species can be found in relatively shallow water, the other two are moderately deep in distribution and thus were probably accidentally snagged in fishing lines or nets and brought to Linnaeus as curiosities. The type specimens of all three appear to be lost (Zibrowius 1980).

Over the next 90 years the number of zooxanthellate corals steadily rose to over 200, but very few azooxanthellate were described, the number resting at 29 species in 1847 (Table 1). However, in the three-year period from 1848 to 1850, Henri Milne Edwards (1800–1885; see Fig. 2) and Jules Haime (1824–1856) wrote a series of four papers (1848a, 1848b, 1849, 1850) that they later synthesized in a book (Milne Ed-

wards & Haime 1857–60), in which they redescribed every coral species known to that time, fossil and Recent. This initiated the first of four decadal-scale pulses of species descriptions of azooxanthellate Scleractinia. Their work was based on the extensive collections of the Paris Museum, which included many donations of specimens from around the world, such as from the collections of Stokes and Cuming. Their contribution cannot be underestimated as it remains the only comprehensive description of all scleractinian species. They described 64 new azooxanthellate species (34 of which are still considered valid), more than doubling the previous number, and 24 new azooxanthellate genera, the latter providing a foundation for future classification of the azooxanthellate Scleractinia. All of their azooxanthellate species occurred in shallow water, which is to be expected, as these would be the species most easily collected. Forest (1996) published a short biography of H. Milne Edwards.

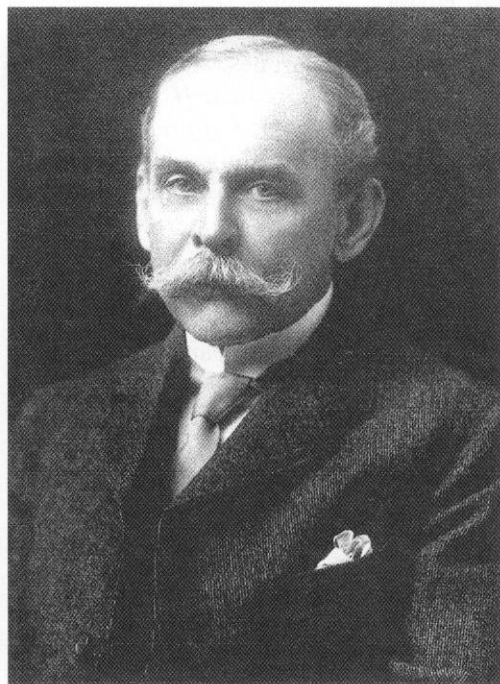


Fig. 2. Upper left: H. Milne Edwards; upper right: L. F. de Pourtalès (from Agassiz 1905); lower left: H. N. Moseley (from Bourne 1892); lower right: A. W. Alcock, circa 1917 (age 58).

Between 1867 and 1881, the second pulse of species descriptions revealed the deep-water azooxanthellate scleractinian fauna. Although the British *H. M. S. Challenger* Expedition is often credited with inaugurating deep-sea biology, it was the scientists at the Museum of Comparative Zoology (MCZ) at Harvard that first systematically dredged the deep sea in search of exotic organisms. Between 1867–1880 these researchers made over 600 deep-water stations throughout the Western Atlantic using the *U.S. Coast Survey Steamers Corwin, Bibb, Hassler, and Blake*. The corals, all new, were described by Louis F. de Pourtalès (1824–1880; see Fig. 2), who can be credited with 59 descriptions, 47 of which are still considered valid (Pourtalès 1867, 1868, 1871, 1878, 1880). Almost all of Pourtalès' types are still deposited at the MCZ, with duplicates of many at The Natural History Museum (London). Agassiz (1905) published a biography and list of publications of Pourtalès. At approximately the same time, the British *H. M. S. Lightning* (1868) and *H. M. S. Porcupine* (1869, 1870) made collections of deep-water azooxanthellate corals from the northeastern Atlantic at even greater depths than those described by Pourtalès. Peter M. Duncan (1821–1891) described many new coral species collected during these cruises (Duncan 1870, 1873, 1878), and thus can be considered as the eastern Atlantic analog of Pourtalès. Duncan's types are deposited at The Natural History Museum, London. Simultaneously with the work of Pourtalès and Duncan, the famous *Challenger* expedition (1872–1876) was making hundreds of deep-water stations during its circumnavigation of the world, especially in the rich southwestern Pacific, collecting thousands of deep-water corals that are now deposited at The Natural History Museum, London. Henry N. Moseley (1844–1891; see Fig. 2), a naturalist on board the expedition, also took charge of describing the deep-water corals. In very precise fashion and with great illustrating skill, Moseley described

48 new species (Moseley *in* Thompson 1873; Moseley 1876, 1881), 39 of them considered valid today, and made some of the few observations on the tissue of deep-water corals to date. This was, unfortunately, the only collection of deep-water Scleractinia that he studied. Moseley published a personal narrative of the cruise in 1879 (1892 revised edition); his material is deposited at The Natural History Museum, London. Bourne (1892) published a short biography of Moseley. Coincident with these investigations, Rev. Julian E. Tenison-Woods (1831–1889; publications listed in biography by Hepburn 1979) described 18 species (10 considered valid) from moderately deep-water off New South Wales and South Australia, and Theophile Studer (1878) reported several new deep-water species collected on the expedition of the *S. M. S. Gazelle* from various localities around the world. Tenison-Wood's material is deposited at the Macleayan Museum and the Australian Museum, whereas Studer's is at the Zoologisches Museum, Berlin. However, not all the additions made during this second phase were due to deep-water collecting. A. E. Verrill (1839–1926; publications listed in biography by Coe 1930) described 33 species (18 considered valid) from the shallow tropical eastern Pacific, mainly off Panama and the Galapagos, and Carl G. Semper (1832–1893) described 17 shallow-water species (7 considered valid) from shallow water in the Philippines (Semper 1872). Most of Verrill's material is deposited at the Yale Peabody Museum, whereas Semper's is deposited at the Naturhistorisches Museum, Wien (Vienna). Thus, in the span of about 15 years, the number of azooxanthellate corals roughly doubled from 100 to 200 species due to the discovery of widespread deep-water corals by the pioneering dredging programs of the United States, England, and Germany, and by personal collecting in Australia. Subsequent taxonomic research on azooxanthellate corals would be closely tied to the success of major deep-sea oceanographic ex-

peditions, which were often the object of national pride.

The third pulse of species descriptions occurred from 1898–1907 and was largely due to the efforts of Major Alfred W. Alcock (1859–1933; Fig. 2), who described the deep-water azooxanthellates collected in the northern Indian Ocean by the *Royal Indian Marine Survey Ship Investigator* (1885–1898) (Alcock 1898) and the deep-water species collected from the Dutch *H. M. S. Siboga* Expedition (1899–1900) (Alcock 1902a) in the Indonesian region. Although the *Challenger* had made some stations in the Indonesian region, the *Siboga* made 323 stations, most of them in deep water. This afforded Alcock the opportunity to describe 29 currently recognized species from this expedition, which sampled the richest region in the world for azooxanthellate corals: Indonesia and the Philippines (Cairns & Zibrowius 1997). Altogether, Alcock described 75 azooxanthellate species, 46 still considered valid, and two genera. He wrote a personal narrative of his *Investigator* cruises 1902(b) and his obituary was published by Calman & Kemp (1933). The *Investigator* specimens are purported to be deposited at the Calcutta Museum, whereas the *Siboga* types are deposited primarily at the Zoologisch Museum Amsterdam (van Soest 1979). The German *Valdivia* Deep-Sea Expedition (1898–99) was at sea at the same time as the *Siboga*, but Emil von Marenzeller (1845–1918) did not report on the corals until after Alcock, describing 17 new species, 15 of them valid today (Marenzeller 1904). They are deposited at the Zoologisches Museum, Berlin. Shortly thereafter, the United States Fish Commission Steamer *Albatross* made 403 stations in the Hawaiian Islands (1901–1902), many of them in deep water, and the corals were reported by T. Wayland Vaughan (1870–1952) in 1907. He described 16 currently recognized azooxanthellate species, and over his career, described 41 species, 22 recognized as valid today. Most of his types are deposited at the

United States National Museum (Cairns 1991a); his biography and list of publications were published by Thompson (1958) and Wells (1952). John Dennant (1839–1907) added another 18 species (13 considered valid) from miscellaneous dredging off New Zealand, Victoria, and South Australia (1902a, 1902b, 1904, 1906). Dennant's material is deposited in the Australian Museum, the National Museum of Victoria, and the South Australian Museum (Stranks 1993); an obituary notice was published in 1907 (Anonymous 1907). Thus, during this ten-year period, about 100 more species were added to the list, and, for the first time, the number of azooxanthellate species approximated that of the zooxanthellates (Fig. 1).

The next 68 years (1908–1976) produced only sporadic research on azooxanthellate corals, the number of recognized species almost reaching a plateau. During this period Cornelis J. van der Horst (1889–1951: publications and biography listed by Boschma 1951) described 22 species (16 now considered valid) between 1922 and 1938, most of them dendrophylliids collected off South Africa and in the Indian Ocean, including additional specimens from the *Siboga*, *Investigator*, and others from the 1905 Percy Sladen Trust Expedition to the Indian Ocean. Most of his specimens are deposited at The Natural History Museum, London, although the *Siboga* specimens are in the Zoologisch Museum, Amsterdam. Another significant addition to the coral list was John S. Gardiner's (1872–1946) collaboration with P. Waugh (1938, 1939) on the deep-water corals collected on the *John Murray* Expedition (1933–1934) to the northwestern Indian Ocean and Red Sea. Throughout his career, Gardiner described 28 azooxanthellate species, 18.5 of them considered valid today. His material is deposited at The Natural History Museum (London) and the Cambridge Museum of Zoology. Motoki Eguchi (1905–1978), often in collaboration with H. Yabe, also began his coral studies at about this time, de-

scribing 27.5 azooxanthellate species (9.5 now considered valid) between 1932 and 1968, all of them from his native Japanese region. His most significant papers on azooxanthellate corals were published in 1942 and 1968 (Yabe & Eguchi 1942a, b; Eguchi 1968); most of his types are deposited at the Institute of Geology and Paleontology, Tohoku (Imperial) University, Sendai. Mori (1980) published a biography and list of his many publications. The war years and those just after (1943–1953) produced very few additions to the list of azooxanthellate species, the only active researcher being J. Wyatt Durham (1907–1996), who described 25.5 species (11.5 now considered valid) from the tropical eastern Pacific, including the Galapagos Islands, based primarily on the deep-water dredging of the *Albatross* and the Allan Hancock Foundation vessels *Velero III* and *Velero IV*. The specimens described by Durham (1947) are deposited at the United States National Museum and University of California Museum of Paleontology, whereas the specimens described by Durham & Barnard (1952) were originally deposited at the Allan Hancock Foundation, but in 1990 were transferred to the Santa Barbara Museum of Natural History. Durham's co-author, J. L. Barnard, went on to become an extremely prolific amphipod taxonomist. Donald F. Squires (1927–), a student of J. W. Wells, was primarily a coral paleontologist, but during the years 1958–1966 described 14.5 Recent azooxanthellate species (12 still considered valid) from various regions around the world, including New Zealand, Victoria, Australia, the North Atlantic, and the Antarctic and Subantarctic. His most significant papers on Recent azooxanthellate corals are his revisions of *Flabellum rubrum* (see Squires 1963) and the scleractinian corals of New Zealand (Squires & Keyes 1967). Much of his material originated from the New Zealand Oceanographic Institute, Wellington (now the National Institute of Water and Atmospheric Research, NIWA), and remains de-

posited there. John W. Wells (1907–1994), also primarily a coral paleontologist and worker on zooxanthellate corals, described 22 azooxanthellate species (18 now considered valid) from a variety of localities including the Marshall Islands, Australia, Vanuatu, the Galapagos, Bermuda, and Trinidad. All of the species he described were from relatively shallow water, and all of his types are deposited at the United States National Museum (Cairns 1991a). His biography and list of publications were published by two of his students: Oliver & Cairns (1994a, 1994b).

The fourth pulse of species descriptions, which began in 1977 and continues to the writing of this manuscript, included the addition of over 200 species, which surpassed the number of zooxanthellate species for the first time. Increased accessibility to large unworked collections as well as increased access to reference specimens (types and non-types) by visitation to museums or by loan apparently triggered this latest surge. Also, some of the taxonomists working at this time have had full time to dedicate to the study of azooxanthellate corals instead of doing it part time or as an avocation. As examples of the latter, Duncan, Vaughan, Durham, Squires and Wells were primarily paleontologists; Dennant was a school inspector; Alcock a medical entomologist and surgeon-naturalist; Tenison-Woods a Catholic priest; Pourtalès worked on many other groups; and H. Milne Edwards was better known as a carcinologist than a coral worker. Regardless, Natalia B. Keller (1937–) described 14 azooxanthellate species (7 considered valid) between 1974–1982, most of them collected on the Russian oceanographic research vessels *Ob*, *Vityaz*, and *Academic Kurchatov*, usually from bathyal or trench depths around the world, including off Peru, the Kurile-Kamchatka Trench, off Cuba, and the boreal North Pacific. In fact, she has reported the deepest living scleractinian coral, *Fungiacyathus marenzelleri*, from 6328 m (Keller 1976). She also published

a set of papers on the functional morphology of deep-water scleractinians. Helmut Zibrowius (1941-) has concentrated primarily on the systematics of the eastern Atlantic azooxanthellate corals, as exemplified by his copiously illustrated dissertation on the Scleractinia of the Mediterranean and northeast Atlantic (Zibrowius 1980). However, he has also published significant papers on the symbiotic associations of azooxanthellate corals (*e.g.*, Zibrowius 1998) and on their biochemistry. To date, he has described 27 species (25 considered valid), most of his types being deposited at the Muséum National d'Histoire Naturelle, Paris. Finally, in a series of faunistic revisions beginning in 1979, I (Stephen D. Cairns, 1949-) described 155 azooxanthellate species (148 now considered valid) primarily from the following regions: western Atlantic (Cairns 1979), Antarctic (Cairns 1982), Hawaiian Islands (Cairns 1984), Philippines and Indonesia (Cairns 1989, Cairns & Zibrowius 1997), Galapagos (Cairns 1991b), southeastern Australia (Cairns & Parker 1992), southwest Indian Ocean (Cairns & Keller 1993), temperate North Pacific (Cairns 1994), New Zealand (Cairns 1995), Western Australia (Cairns 1998), and Wallis and Futuna and Vanuatu (Cairns 1999a). In most cases the material and types are deposited at the United States National Museum, but in the case of French-collected specimens, most are at the Muséum National d'Histoire Naturelle, Paris, and in the case of New Zealand-collected material, at the New Zealand Oceanographic Institute.

Summary

The number of azooxanthellate species has always lagged behind that of the zooxanthellates, primarily because they are not as accessible to collection. The majority occur in deep water and those that are found in shallow water are small and/or cryptic. However, the four pulses of species descriptions of azooxanthellates since the time of

Linnaeus eventually led to a parity of species number between the two ecological classes of Scleractinia. The first pulse is credited to the worldwide revision of the Scleractinia by Milne Edwards & Haime (1848–1850). Pourtalès, Duncan, and Moseley dominated the second pulse (1867–1881), which was directly attributable to the discovery of deep-water corals by early exploratory programs. The third pulse of descriptions (1898–1907), chiefly by Alcock, Marenzeller, and Vaughan, resulted from more intensive, often nationalist, deep-water dredging programs in the Indo-Pacific, including one of the most diverse regions for deep-water fauna: the Banda Sea. The fourth burst of descriptions (1977–1999) resulted from even larger and deeper collections, especially from Dutch, French, American, and New Zealand vessels, and researchers that were able to pursue the cause full time, *e.g.* Zibrowius and Cairns. But, despite the beauty and scientific potential of the group, the study of azooxanthellate corals has been dominated by only a handful of taxonomist over the centuries, even though they outnumber the more visible reef corals.

Acknowledgments

The immediate inspiration for this paper came from the species accumulation curve analyses of the Hydrozoa by Schuchert (1998) and the history of the Pennatulacea by Williams (1999). However, the deeper motivation for this paper, as well as my career in cnidarian systematics and my current job, can be attributed directly to Ted Bayer. I met "Dr. Bayer" in the Summer of 1970, a mere 32 years ago. I was an undergraduate between my junior and senior years, but I was determined to go to graduate school at Rosenstiel School of Marine and Atmospheric Science (then the Institute of Marine Science), University of Miami. So, along with my family, I traveled from New Orleans to Miami to pay a visit to the famous graduate school at which Dr. Bayer

worked. Wearing a suit in August in Miami, I approached the graduate student office unannounced and asked to speak to all the professors of marine biology currently in residence. Being summer, this turned out to be three people, one of them Ted. But I was warned by the secretary not to visit Dr. Bayer, because he was a very busy man and did not like to be disturbed. However, because it took little time to see the other two professors, I soon returned to the graduate office and asked for directions for finding Dr. Bayer. That day he was in the old Agassiz building, working on mollusks. I introduced myself and ending up talking to him for over an hour. He invited me back the next day to meet the department chairman, his friend and colleague, Gil Voss. Ted Bayer was very friendly and helpful to me, a complete unknown, and ultimately was probably highly instrumental in getting me accepted to the RSMAS graduate school. Although I was a student of Voss for my Master's degree, Ted Bayer lavished attention on me, ranging from marine invertebrate zoology to nomenclature to butterfly collecting to music and the opera. I finally did become his PhD student in 1973, when, at his suggestion, I began my studies of the deep-water azooxanthellate Scleractinia. Ted was also later responsible for funding my first three years at the Smithsonian, on his residual NSF grant, a favor that changed the course of my life. I will always be grateful to him for his generous and enthusiastic support of my early career and his continued support in the field of cnidarian systematics.

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