



# Influence of Frederick (Ted) M. Bayer on deep-water octocoral research

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**ABSTRACT:** The impact of Ted Bayer's research on octocorals was extraordinary and his studies will long be used by any student of the group Octocorallia. He leaves behind a legacy of 107 published papers on octocorals, in which he newly described 4 families, 1 subfamily, 48 genera, 2 subgenera, 186 species, and 10 subspecies. An annotated list of his new taxa and all of his manuscripts (including 9 unpublished) are given in an electronic supplement. Although he published on most octocoral families, his favorite groups were the deep-water calcaxonian families from the western Atlantic, central Pacific, and Antarctic; he was also an expert on the precious coral family Coralliidae. He facilitated the study of the subclass by publishing classifications of the higher taxa, an illustrated trilingual glossary of morphological terms, a key to all genera (exclusive of the Pennatulacea), and an annotated bibliography of the literature of the group. He was the first to use scanning electron microscope (SEM) images of sclerites to describe species, and perfected that technique in the use of SEM stereo pairs. He also made a significant contribution to advances in the knowledge of octocoral axial microstructure, proving that all gorgoniids have a diagnostic type of axial mineralogy. He interacted with and influenced virtually every octocoral worker in the last half of the twentieth century, co-authoring with many of them.

**KEY WORDS:** Octocorals · F. M. Bayer · Bioillustrations · Calcaxonia

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## INTRODUCTION

This paper is not meant to be an obituary or biography of Frederick (Ted) M. Bayer, but rather an analysis of his impact on the discipline of octocoral biology. (An obituary was published [*Washington Post*, October 20, 2007:B6], and several tributes to Ted on his 80th birthday were published in Cairns & Messing [2001] and Grasshoff [2001]; Ted also published a short autobiography [Bayer 2002]). His impact on the field is discussed from 5 different aspects: descriptive taxonomy, infrastructure, illustrations, mineralogy, and his students/legacy. Although Bayer wrote many papers on non-octocorallian taxa, this paper emphasizes only the octocorals.

## DESCRIPTIVE TAXONOMY

Ted Bayer was first and foremost a taxonomist—a descriptive biologist with a keen eye for distinctions

among species. During his career, which spanned 67 years (1941–2007), he published 141 papers (Supplement 1, available at [www.int-res.com/articles/suppl/m397p007\\_app.pdf](http://www.int-res.com/articles/suppl/m397p007_app.pdf)), 107 of which addressed octocorals, 75 of those pertaining to deep-water octocorals. Regarding octocorals, he newly described 4 families and 1 subfamily, 48 genera (15% of total known non-pennatulacean octocorals), 2 subgenera, 186 species (6% of the total known non-pennatulid octocorals), and 10 subspecies or forms (Supplement 2, available at [www.int-res.com/articles/suppl/m397p007\\_app.pdf](http://www.int-res.com/articles/suppl/m397p007_app.pdf)). Although some of his species have been transferred to different genera, only 3 of his genera and 4 of his species have been synonymized (Supplement 2), a remarkably low rate, notwithstanding his frequent complaint that intra- and interspecific variation within and among octocoral species respectively 'almost drove him crazy'. Although Ted published new taxa in 21 of the 29 non-pennatulacean octocoral families, he had distinct preferences and aversions within the subclass. For instance, he published only 3 short

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papers on the order Pennatulacea, and seemed to have a special preference for the gorgonacean suborder Calcaxonina, those 5 deep-water families in which the axis is solid, composed of a combination of calcium carbonate and gorgonin. He described 17 new species (11% of current total) in the Isididae, 14 new species (15%) in the Chrysogorgiidae, and 67 new species (28%), as well as 14 new genera, in the Primnoidae. Furthermore, he described 13 new species (54%) in the precious coral family Coralliidae, and was the main contributor to the short-lived (1993–1996) journal entitled *Precious Corals & Octocoral Research*, contributing 6 of the 14 articles published in that series. And, although he published on octocorals from every ocean of the world, he seemed to have a geographic preference, concentrating on taxa from the western Atlantic and western/central Pacific (particularly the Hawaiian Islands and New Caledonia), and later in his career the Antarctic region. His largest and most significant single taxonomic contribution must be considered to be the published version of his dissertation: 'The shallow-water Octocorallia of the West Indian region' (Bayer 1961), in which he described a total of 99 species, 18 of them new. In my opinion, his most significant deep-water octocoral paper is 'The Antarctic genus *Callozostrom* and its relationship to *Primnoidae* (Octocorallia, Gorgonacea: Primnoigae)' (Bayer 1996a), in which he redefined 2 difficult genera and described the new genus *Convexella*. One might add at this point that most of his 34 non-octocorallian papers pertained to mollusks, of which he described 3 new genera, 4 new subgenera, 34 new species and 2 new varieties; he was particularly interested in the deep-water slit shells—the Pleurotomariidae. He also wrote 2 papers on hemichordates and described 1 new species.

### INFRASTRUCTURE

It is relatively straightforward to enumerate Ted's papers and new taxa, but an equal or greater contribution to the discipline lay in his improvement of the scientific infrastructure of the subclass, making the group easier to study and comprehend. This was achieved in 6 seminal papers. Early in his career, Bayer was asked to write the section on Octocorallia for the *Treatise on invertebrate paleontology* (Bayer 1956). This contribution contained short diagnoses of all octocoral genera and illustrations of many, as well as a useful introduction to the biology and morphology of the subclass. Because of its comprehensive nature it was and is still considered the primary source for octocoral classification and is probably his most highly cited work. Now badly in need of revision, Ted spent many hours revis-

ing this synthesis, but never completed the task. He was the lead co-editor of the *Illustrated trilingual glossary of morphological and anatomical terms applied to Octocorallia* (Bayer et al. 1983), a compilation of the definitions and illustrations (many scanning electron microscopy [SEM] photomicrographs) of 202 descriptive terms used in describing octocorals, cross-referenced in English, German, and French. This is now an absolutely essential reference for beginners as well as experienced taxonomists, for how else could one define and see the difference between the very similar wart club and a torch, or a balloon club and a rooted head? Equally indispensable to the serious octocoral worker is the 'Key to the genera of Octocorallia exclusive of Pennatulacea, with diagnoses of new taxa' (Bayer 1981a), a serial, dichotomous key consisting of 434 couplets that included all and illustrated many of the octocorallian genera (excluding pennatulaceans) known at that time. It also included a short classification of the higher taxa which is still used today. It is the starting point for the identification of any mysterious octocoral. Equally useful, for compiling bibliographies and searching contributions of other authors, is his *Bibliography of the Octocorallia: 1469–1977* (Bayer 1981b), which meticulously lists 1441 octocoral titles, cross-referenced by subject and geographic area. Since he owned almost all of these papers and books, and knowing Ted, one can be sure the citations are accurate and complete. This list was updated and eventually placed on the web (Bayer 1996b). The bibliography, as well as *Recent advances in research on octocorals* (Bayer 1981c), were published as a result of a series of seminars given in São Paulo in February 1980, the latter an often overlooked gem that serves as a primer on how to study and illustrate octocorals. And finally, another often overlooked book chapter entitled 'Colonial organization in octocorals' (Bayer 1973a) reviews and explains in simple terms the gross morphological differences among the octocoral orders and families.

### ILLUSTRATIONS

In his brief autobiography (Bayer 2002, p. 96), Ted stated that he did not do much in his career to alleviate the deficiencies of octocoral taxonomic information, but added 'About all I can say with any satisfaction is that I have set new standards for illustrating taxonomic descriptions that should make them more accurate, and identifications much more reliable in the future.' I hope this paper will serve as a refutation of his first remark, and an endorsement of the second, in that Ted Bayer was an excellent artist, illustrator, and photographer. Even at the age of 17, his field notebooks con-

tained publication quality sketches of gastropods. All of his papers were illustrated with detailed line drawings and/or clean SEM photomicrographs. He published the first paper (Bayer 1973b) in which SEM photos were used to illustrate the sclerites of an octocoral, and then never looked back, taking over 35 000 SEM photomicrographs (from 2893 stubs) over the next 30 years, stopping only when he faced the prospect of having to change from photographic negatives to digital images. He was a great proponent of publishing stereo pairs of both SEMs of sclerites and conventional photographs of the gross morphology of colonies, a wonderful technique to see the 3-dimensional topology of a calyx and the interrelationships among adjacent sclerites. The finest example of his illustration technique may be 'The helioporacean octocoral *Epiphaxum*, recent and fossil: a monographic iconography' (Bayer 1992), which illustrates the gross morphology and microstructure of the rather small genus *Epiphaxum* and related genera in 62 plates, all images displayed in stereo view. He was also a fine histological illustrator, in which he used the laborious stipple technique, some of the best examples of this being Bayer (1974) and Cairns et al. (2007). He also worked in color, but rarely published in that medium, producing striking paintings of butterflies, and a series of 14 beautiful and scientifically accurate marine life portraits used as postage stamps in Haiti in 1973.

### MINERALOGY

A recurrent theme in Ted Bayer's research was the taxonomic and phylogenetic implications of the ultrastructure and mineral composition of the octocoral axis and sclerite. As early as 1955 (Bayer 1955), he investigated the distribution of radial versus concentric patterns of crystal orientation in axes to help define the calcaxonian families. He used the cruciform extinction pattern of sclerites (i.e. scales) as viewed under crossed Nicol filters to diagnose members of the family Primnoidae. His iconographies of the genera *Epiphaxum* (Bayer 1992) and *Corallium* (F. M. Bayer unpubl. ms 1, see Supplement 1) are filled with stereo views of microstructure, often taken at magnifications of 5000 to 15 000. Finally, later in his career (Macintyre et al. 2000 and Bayer & Macintyre 2001), he was able to show that whereas the axes and holdfasts of most octocorals are composed of either calcite or aragonite, that of the family Gorgoniidae was uniquely composed of strands of amorphous carbonate hydroxylapatite (CHAp), thus providing a diagnostic test for this family. This was clearly a fruitful and intriguing avenue of research for Bayer and one that he intended to pursue, but it now remains for future workers.

### HIS STUDENTS AND HIS LEGACY

Ted, like many descriptive taxonomists, was an independent worker, rarely co-authoring papers, especially in the first 2 decades of his career. He sometimes exhibited a rather curt demeanor, but for one persistent enough to ask questions, he was a wealth of information, and many unfinished manuscripts and tens of thousands of SEM images remain to be explored. Although he advised many graduate students in marine invertebrate taxa other than octocorals, he taught and collaborated with only 3 students on Octocorallia, unfortunately for fairly short durations with all three. He co-authored 5 publications with Katy Muzik from 1975 to 1980 (see Supplement 1) on a variety of taxa; Katy is now a marine biologist working in Okinawa. He co-authored 4 papers with Jeff Stefani from 1987 to 1989 (see Supplement 1) primarily on the deep-water calcaxonians of New Caledonia; Jeff did not continue the study of taxonomy. I consider myself to be his third and last student; we co-authored the last 12 papers of his long career (2002–2009), primarily on the primnoids of the western Atlantic and Hawaii. Ted also co-authored octocoral papers with M. Grasshoff (on ellisellids), E. Deichmann, R. W. Grigg, J. Verseveldt, D. M. Opresko, and I. G. Macintyre (on mineralogy). But, even if he did not co-author a paper with them, he had a profound influence on virtually every octocoral systematist of the last half of the twentieth century, including: P. Alderslade, E. A. Berntson, Y. Benayahu, O. Breedy, C. Castro, S. C. France, C. P. Giamonna, W. M. Goldberg, F. G. Hochberg, B. Horvath, H. R. Lasker, A. K. Matsumoto, L. P. van Ofwegen, F. A. Pasternak, J. A. Sánchez, H. Utinomi, S. T. Viada, S. A. Wainwright, and G. C. Williams.

### EPILOGUE

One way to honor a productive and influential taxonomist is to name species after him. Too many species of both gastropods and octocorals to accurately list have been named after Ted Bayer; even a hydroid was named for him by the Emperor of Japan (Hirohito 1984). Four genera have also been named in his honor: *Bayerxenia* Alderslade, 2001; *Bayericerithium* Petuch, 2001; *Bayerotrochus* Harasewych, 2002; and *Bayergorgia* Williams & López-González, 2005. When I asked his opinion about the last paper, he responded that it was a fine paper, but a terrible generic name.

*Acknowledgements.* I thank the following friends of Ted Bayer who have reviewed and made this a better paper: D. M. Opresko, K. M. Muzik, C. G. Messing, and M. S. Cairns.

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Submitted: December 24, 2008; Accepted: April 20, 2009

Proofs received from author(s): November 13, 2009