

JUL 26 1999

Index Pennatulacea
Annotated Bibliography and Indexes of the Sea Pens
(Coelenterata: Octocorallia) of the World 1469–1999

by

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A reasonably comprehensive bibliography of the living and fossil pennatulacean Octocorallia is presented, with the goal of including all published accounts regarding the biology of the sea pens. This compilation of approximately 1000 citations represents 530 years of published research. Complete unabbreviated citations for periodicals are used throughout. Many of the citations are annotated with descriptive notes. Taxonomic, geographic, and field-of-study indexes to the literature are included, as well as a synopsis of historical periods in the study of the Pennatulacea.

TABLE OF CONTENTS

Introduction	21
Acknowledgments	22
Historical Account	23
Pre-Linnean Period (1469–1757)	23
The Linnean Period (1758–1858)	25
The Darwinian Period (1859–1899)	25
The Early Twentieth Century (1900–1949)	25
The Late Twentieth Century (1950–1999)	29
Synonyms and misspelled generic names of Pennatulacea	29
Taxonomic Index	33
Geographic Index	47
Africa – southern	47
Africa – western	47
Arctic Ocean	47
Australia – southern	47
Australia – western	47
Indo-Pacific (including the Red Sea)	47
Japan	48
New Zealand	48
North America – Pacific	48
North Atlantic and Mediterranean (Europe and eastern North America)	48
Pacific Ocean – northern	48
South America (Atlantic)	48
South America (Pacific)	48

PLATE 1



Umbellula antarctica
After Kükenthal & Broch, 1911

Southern Oceans (Antarctica and the subantarctic)	49
Western Tropical Atlantic and Caribbean	49
Worldwide	49
Subject Index	49
Behavior	49
Bibliography	49
Biography (Regarding Authors of Pennatulacean Research)	49
Bioluminescence	49
Corals (Pre-Linnean General Natural History)	50
Ecology and Biotic Interactions	50
General Natural History and General Biology	51
Histology	51
History of Science (Regarding Coelenterates and/or Sea Pens)	51
Molecular Biology and Genetics	51
Morphology and Ultrastructure	51
Natural Products Chemistry, Biochemistry, and Toxicology	51
Paleontology (Mesozoic and Cenozoic Fossil Taxa)	52
Paleontology (Vendian Frondlike Fossil Taxa)	52
Photography (Color Photographs of Living Sea Pens)	52
Phylogeny, Cladistics, Evolution, and Biogeography	52
Physiology and Cell Biology	52
Polymorphism, Phenotypic Variability, and Biodiversity	53
Quoted Passages	53
Reproductive and Developmental Biology	53
Taxonomy, Distributional and Bathymetric Records	53
Bibliography	54

INTRODUCTION

The pennatulaceans, commonly known as sea pens and sea pansies, are a highly specialized and distinct group of sessile benthic coelenterates. They are distributed throughout the world's oceans from the polar seas to the tropics, and at all depths from the intertidal (certain virgulariids) to over 6200 meters (Umbellulidae, Pl. 1). Morphologically, sea pens are highly diverse and exhibit morphological changes as evolutionary events within different lineages. Examples are bilateral symmetry, concentration and localization of feeding polyps, the development of lateral processes as polyp leaves or ridges, and the reduction in the number and size of sclerites. As octocorallian coelenterates, pennatulaceans are characterized by having eight pinnate tentacles surrounding the mouth of each polyp, and eight mesenteries. Unlike other octocorals, however, mature colonies develop from a single large polyp (the oozoid) that produces secondary zooids by lateral budding of its body wall. Also unique to the Pennatulacea, is the unbranched muscular peduncle, which anchors the animal by peristaltic contractions into soft substrata such as sand, mud, or abyssal ooze. The secondary polyps (larger autozooids for feeding and reproduction, and smaller siphonozooids for internal water circulation) are restricted to the distal rachis, which is also unbranched but may have laterally-produced polyp leaves.

The ability to inhabit soft substrata has allowed several abyssal-dwelling sea pens to have nearly cosmopolitan distributions. Despite these very widespread geographic ranges, pennatulacean species diversity in the deep-sea is relatively low, and may be attributable to a combination of factors including: relatively low energy input and depauperate productivity in the abyssal environment, coupled with a relative lack of ecological diversity.

Thirty-two genera in fifteen families of living pennatulaceans are currently recognized. Of the 436 nominal species names described in the literature, approximately one half are currently considered valid. Major monographic works on the Pennatulacea include Kükenthal (1915), Hickson (1916), and Williams (1990, 1995a).

The sparsely-represented pennatulacean fossil record extends back to the Cretaceous Period and consists primarily of virgulariid fossil taxa in the genera *Graphularia* and *Virgularia*. Bayer (1956:228) observed that fossils of *Graphularia* closely resemble the axial structure of the genus *Stylatula*, and the two may be congeneric. Problematic and controversial frondlike taxa that resemble pennatulid sea pens are described from the Vendian Period of the late Precambrian. In fact, the coming of age of Precambrian paleobiology in the 1980s has produced a wealth of publications dealing with the Ediacaran or Vendian biota. Many of the Vendian frondlike taxa have been allied with the Pennatulacea by various authors, but these interpretations remain highly disputatious. Because of the importance of recent fossil discoveries, which have helped to bridge the gap between fossil biotas of the Precambrian and the Cambrian, many of the references on these Vendian pennatulacean-like organisms are included here, but the coverage should in no way be considered comprehensive.

The goal of this work is to produce a bibliography of all published works pertaining in part or in full to the pennatulacean octocoral coelenterates. Although no work of this kind can claim to be absolutely comprehensive, this bibliography can at least be considered reasonably complete, certainly more so than any previously-published, similar work. The fine bibliography of octocorals by Bayer (1996) concentrates on taxonomic works for all of the Octocorallia, but does not claim to be inclusive for Pennatulacea or fields of study outside of taxonomy.

The following annotated and alphabetical bibliography to the Pennatulacea of the world is derived from a variety of sources—primarily the Zoological Record (1864–1998), as well as the author's research library. Other sources include Bayer (1981), Bayer (1996), and Hickson (1916). My annotations are in square brackets at the end of many of the citations.

This work is intended for a variety of users including professional biologists, biology students, fisheries biologists and marine resource managers.

The intent of the presentation is to make this work as user friendly as possible. In order to facilitate this goal, full citations are given for the vast majority of the references listed, as abbreviations for periodical publications have proved in the past to be confusing, inconsistent, or often unusable.

The Melvyl System, library data base of the University of California, [<http://www.melvyl.ucop.edu>] was used extensively to acquire complete citations for periodicals. Other sources used for abbreviations and complete citations of periodicals include the List of Serial Publications in the BM(NH) Library, the World List of Scientific Periodicals 1900–1960, and Biosis Serial Sources.

For the most recently-recognized, valid species names of Pennatulacea, see Williams (1995a, 1997f).

ACKNOWLEDGMENTS

I am grateful to Larry Currie (Librarian, California Academy of Sciences, San Francisco), who was instrumental in providing expertise and in locating several references.

I thank Leen van Ofwegen (Nationaal Natuurhistorisch Museum, Leiden), Phil Alderslade (Museum and Art Gallery of the Northern Territory, Darwin), Frederick Bayer (National Museum of Natural History, Washington, D. C.), and Michael Ghiselin (California Academy of Sciences) for their valuable contributions and comments.

I especially thank Alan Leviton (California Academy of Sciences) for his interest and patience, regarding many hours spent at the computer preparing the figures.

HISTORICAL ACCOUNT

Pre-Linnean Period (1469–1757)

In writing about the history of research regarding pennatulacean bioluminescence, E. Newton Harvey (1952:170), related the following, “Although the Romans knew of sea pens, referring to them as ‘Penna marina,’ the sea feather, or as ‘Mentula alata,’ the winged penis, the ability to luminesce does not appear to have been recorded. Probably the first mention of luminous sea pens comes to us in the famed ‘De lunariis’ and the ‘Historia Animalium’ of Conrad Gesner, published in the middle sixteenth century.”

The earliest published accounts describing aspects of the natural history of octocorals, including the sea pens, are Pliny the Elder (1469), Guillaume Rondelet (1554, 1555), Conrad Gesner (1555, 1558) (Pl. 2), Ferrante Imperato (1599), and Captain Lancaster (1601). Other noteworthy pre-Linnean works dealing at least in part with the Octocorallia are those of Francisci Erasmi (1668), Paolo Boccone (1674), Hans Sloane (1707), Jacques Barrelier (1714), Herman Boerhaave (1720, 1727), Christlob Mylius (1753, 1754), and John Ellis (1753, 1755).

Pennatulacean bioluminescence is at least mentioned by François Boussuet (1558), Caspar Bauhin (1620, 1671), Ulisse Aldrovandi (1642, 1648), Johann Bauhin (1650–51), and Thomas Shaw (1738–46).

Louis Agassiz (1860) praised the perspicacity of early workers such as Rondelet and Gesner, who first established the animal nature of the “acalephs” (many of the taxa that we now regard as coelenterates), departing from the earlier views of Aristotle and Pliny, who compared them to plants (the “zoöphytes”).

Pertaining to Rondelet, Agassiz (1860:8) stated, “. . . we are chiefly indebted to Rondelet for contributions to the natural history of the Acalephs. He was, indeed, not only better acquainted with the inhabitants of the Mediterranean than all his predecessors, but he knew them even more accurately than any naturalist that lived before the present century.”

In his praise of sixteenth century naturalists, Agassiz (1860:10) continues, “It has been a source of constant delight for me, while perusing the works of the earlier naturalists, to sympathize with the genial spirit and the earnestness that pervade their writings, so free from egotism, and animosity against their fellow-students. Their devotion to their studies is equal to the spirit of reverence with which they look upon nature; and it is disgraceful to our age, that we must contrast with such dispositions the ill-will, the jealousies, the quarrels for priority, and the profanation, which pervade the discussions of certain modern authors. Moreover, in a systematic point of view, the great naturalists of the sixteenth century deserve to be studied more fully than they have been thus far. It is astonishing, for instance, to see how near Rondelet, in discussing the views of Aristotle upon the affinities of animals, came to perceiving their true affinities, and their natural classification . . .”

A good example of the evolution of thought in natural history is exemplified by various views regarding the nature of corals in the seventeenth and eighteenth centuries. The concept of corals as “zoöphytes,” transitional between plants and animals, was established by the Roman scholars Sextus Empiricus and Pliny the Elder (Caius Plinius Secundus), based on Aristotle’s notion of the gradation from plants to higher animals. This undoubtedly served to propagate a state of confusion for nearly two thousand years—the false view that corals as living beings share the natures of both animals and plants (Agassiz, 1860:6–7). Paolo Boccone (1670) and John Woodward (1695) emphasized the inanimate aspect of corals and regarded them as stones, while L. F. Marsigli (1725) considered them to be plants, and the coral polyps as “flowers of the coral.” It was the perceptive observer, Jean-André Peyssonnel (1753), who first recognized the animal nature of corals and their affinities to other coelenterates, after observing the contraction, expansion and movement of the tentacles of coral polyps (Hyman 1940:365).

PLATE 2



Conrad Gesner (1516-1565). Courtesy
Kraig Adler, Cornell University.



Carl von Linné (Linnaeus) (1707-1778). Courtesy
Picture Collection, California Academy of Sciences.



Peter Simon Pallas (1741-1811). Courtesy
Kraig Adler, Cornell University.



Lazzaro Spallanzani (1729-1799). Courtesy
Michael Ghiselin, California Academy of Sciences.

The Linnean Period (1758–1858)

The publication of the 10th edition of *Systema Naturae* by Linnaeus (Carl von Linné 1758) (Pl. 2) is accepted as the starting point for our contemporary system of binominal nomenclature. Linnaeus named the genus *Pennatula*, from which the ordinal name Pennatulacea is derived. Other contributors during the Linnean Period include William Borlase (1758), Job Baster (1759–65); Joannes Baptist Bohadsch (1761); John Ellis (1764); Peter Simon Pallas (1766) (Pl. 2), first monographer of the “zoophytes”; Pieter Boddaert (1771); I. Lepechin (1781); John Ellis and Daniel Solander (1786); Lazzaro Spallanzani (1796) (Pl. 2); Georges Cuvier (Pl. 3), originally Jean Léopold Nicolas Frédéric Cuvier (1797), who named the genera *Umbellula* and *Veretillum*; Jean Baptiste Pierre Antoine de Monet de Lamarck (1816) (Pl. 3), who named the genera *Funiculina*, *Renilla*, and *Virgularia*; Tilesius von Tilenau (1819); S. della Chiaje (1827, 1841–44); M. W. Rapp (1827); H.-M. Ducrotay de Blainville (1834); Christian Gottfried Ehrenberg (1834a) (Pl. 3), who introduced the family name Pennatulina, later corrected by Dana, 1846 to Pennatulidae; Fredrich Sigismund Leuckart (1841); James Dwight Dana (1846) (Pl. 3), who corrected the familial name of Ehrenberg to Pennatulidae; George Johnston (1847); John Edward Gray (1840–1873), who named the genus *Sarcoptilus* in 1848; Henri Milne Edwards (Pl. 4) and Jules Haime (1850), who named the fossil genus *Graphularia*; Achille Valenciennes (1850), who named the veretillid genera *Litularia* and *Cavernularia*; P. Chr. Asbjørnsen (1856), who named the genus *Kophobelemnion*; and Jan Adrianus Herklots (1858) (Pl. 4), who named the genera *Scytalium* and *Pteroeides*.

The Darwinian Period (1859–1899)

The publication of the *Origin of Species* by Charles Darwin (1859) initiated what is here referred to as the Darwinian Period.

The pre-eminent author of the Pennatulacea during this period was Rudolf Albert von Kölliker, who produced major descriptive taxonomic works between 1865 and 1880. Kölliker described the sea pens of the *H. M. S. Challenger* Expedition, in which thirty species were described. Kölliker also named the genera *Acanthoptilum*, *Anthoptilum*, *Halipteris*, *Protoptilum*, *Sclerobelemnion*, *Scleroptilum*, and *Stachyptilum*. Other noteworthy contributions during this period include Pieter Bleeker (1859) (Pl. 4), who described several species of *Pteroeides*; William More Gabb (1859–1864) (Pl. 4); Jan Adrianus Herklots (1863); Josua Lindahl (1874); Johan Koren and Daniel C. Danielssen (1847–1884); Addison Emery Verrill (1865–1882), who named the genera *Distichoptilum*, *Ptilosarcus*, and *Stylatula*, and introduced the name Pennatulacea in 1865 as a subordinal name, later elevated to ordinal status by Studer, 1887a; Sir Charles Wyville Thomson (1874), chief scientist of the *H. M. S. Challenger* Expedition (Pl. 5); Robert Edward Carter Stearns (1873–1883) (Pl. 5); Ambrosius Arnold Willem Hubrecht (1885) (Pl. 5), who named the genus *Echinoptilum*; G. Herbert Fowler (1888, 1894); A. Milnes Marshall (1883a, 1883b); A. Milnes Marshall and G. Herbert Fowler (1887, 1889); and A. Milnes Marshall and William P. Marshall (1882); T. H. Tizard et al. (1885); and Théophile Studer (1891), who named the genus *Gyrophyllum*.

The Darwinian Period produced numerous studies of evolutionary relationships for many groups of organisms. Important works pertaining to pennatulacean phylogeny during this time included R. A. von Kölliker (1870, 1880), Gottlieb von Koch (1878), and A. Milnes Marshall (1887).

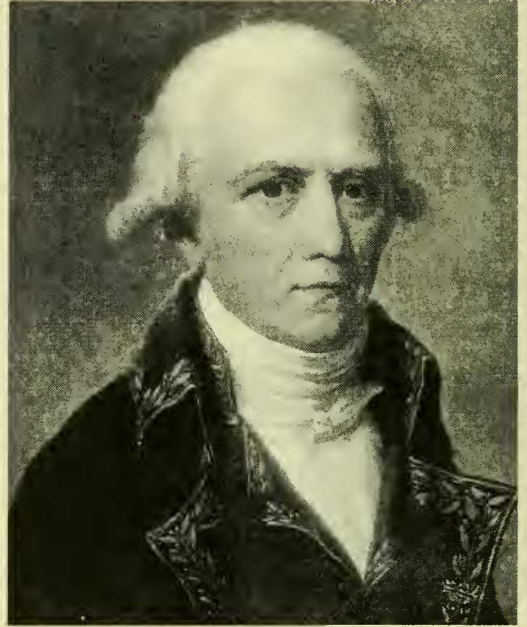
The Early Twentieth Century (1900–1949)

Significant contributions in octocorallian systematics (including pennatulaceans) during the early part of the Twentieth Century include Hector F. E. Jungersen (1904, 1907, 1917); Charles Gravier (1906), who named the genus *Scytaliopsis*; Charles Cleveland Nutting (1908), who named the genus *Calibelemnion*; Heinrich Balss (1909, 1910); Hjalmar Broch (1910–1961); Willy Kükenthal (1902–1925) (Pl. 6), who named the genera *Actinoptilum*, *Amphiacme*, and *Chunella*; W. Kükenthal and H. Broch (1911), who named the genus *Cavernulina*; Sydney John Hickson (1883–1940);

PLATE 3



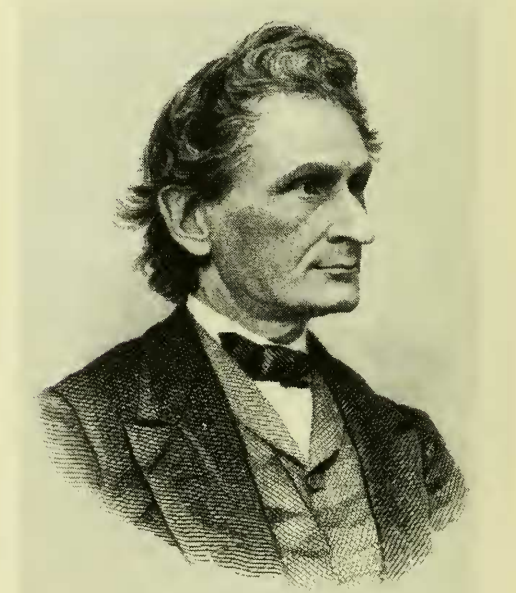
Baron Georges Cuvier (1769-1832). Courtesy
GS Myers/AE Leviton Portrait File in Natural
History, California Academy of Sciences.



Jean Baptiste Pierre Antoine de Monet de Lamarck (1744-
1829). Courtesy GS Myers/AE Leviton Portrait File in
Natural History, California Academy of Sciences.



Christian Gottfried Ehrenberg (1795-1876). Courtesy
of the Linnean Society of London.

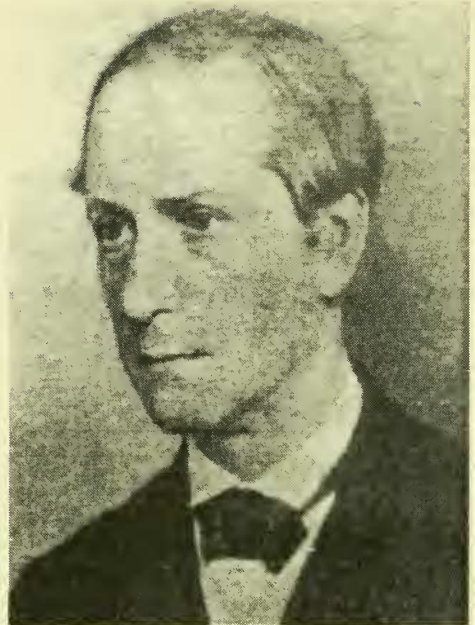


James Dwight Dana (1813-1895). Courtesy
Smithsonian Institution Archives.

PLATE 4



Henri Milne Edwards (1800-1885).
Courtesy Nationaal Natuurhistorisch Museum, Leiden.



Jan Adrianus Herklots (1820-1872).
Courtesy Nationaal Natuurhistorisch Museum, Leiden.

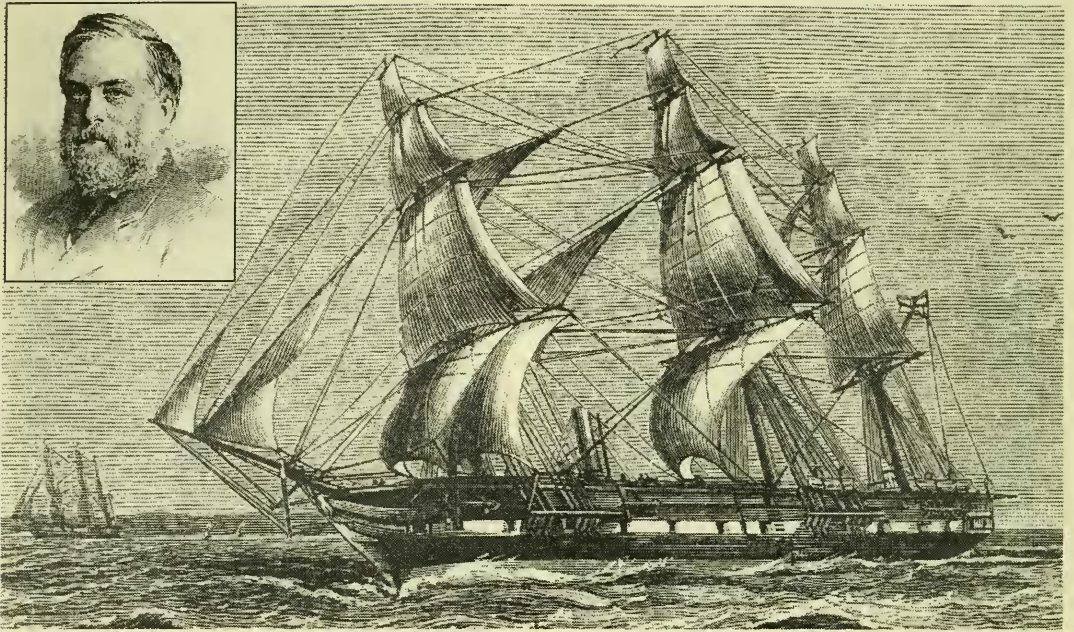


Pieter Bleeker (1819-1878). Courtesy
Nationaal Natuurhistorisch Museum, Leiden.

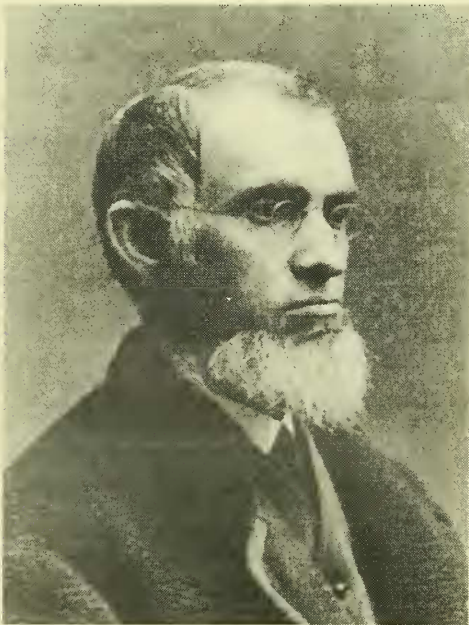


William Gabb (1839-1878). Courtesy Department of
Invertebrate Zoology and Geology, California
Academy of Sciences.

PLATE 5



HMS Challenger (1872–1876), Sir Charles Wyville Thomson, Chief scientist (inset).
After “Voyage of the Challenger,” Narrative, Vol. 1 (1885) and “The Atlantic,” Vol. 1 (1877) respectively.



Robert Edwards Carter Stearns (1827-1909). Courtesy Bancroft Library, University of California, Berkeley.



Ambrosius Arnold Willem Hubrecht (1853-1915).
Courtesy Nationaal Natuurhistorisch Museum, Leiden.

Elisabeth Deichmann (1936, 1941) (Pl. 6); and J. Arthur Thomson (1905–1931). The latter published in collaboration with several co-authors including George Crane, Doris L. Mackinnon, Nita I. Rennet, W. D. Henderson, James Ritchie, and James J. Simpson. F. M. Bayer (pers. comm.) stated, “Deichmann . . . is the 20th Century link with the 19th Century in octocoral systematics. Her Blake report (1936) is pivotal for the western Atlantic.”

It was during this period that the proposal was introduced by Libbie Henrietta Hyman (1940:365) to abandon the name “Coelenterata” of Rudolph Leuckart in favor of “Cnidaria,” introduced by Berthold Hatschek. This argument has apparently convinced many zoologists to substitute a name long in use with a more recently created one. Hyman stated, “Leuckart (1847) clearly grasped the fundamental differences between the two great radiate groups, the coelenterates and the echinoderms, and separated them. creating the name Coelenterata. Leuckart’s Coelenterata, however, included the sponges and the ctenophores The proper splitting of Leuckart’s Coelenterata was achieved by Hatschek (1888), who recognized three phyla: Spongiaria, Cnidaria, and Ctenophora. We therefore consider Cnidaria to be the most suitable name for the phylum”

The acceptance of this line of reasoning is both unnecessary and inconsistent. As an example, Ernst Haeckel’s “Scyphozoa” originally included both the Scyphozoa and the Anthozoa, yet the name Scyphozoa is still retained by most zoologists. This is just one example of a major animal group in which the name has long usage and is still recognized today, even though it originally encompassed more taxa than are now accepted.

The Late Twentieth Century (1950–1999)

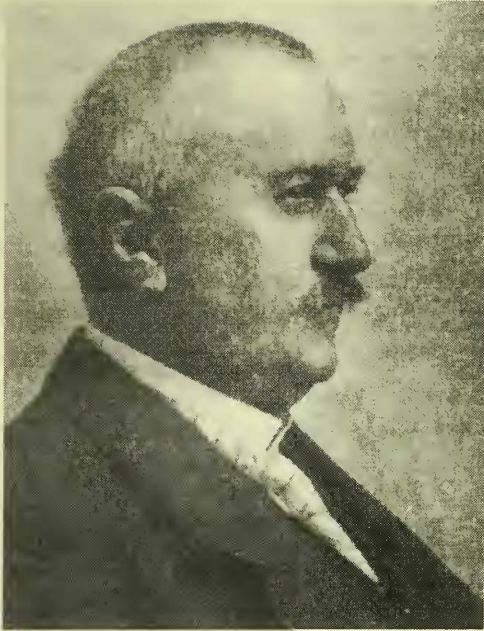
Previous to this period, publications on the Pennatulacea dealt predominantly with descriptive taxonomy or general natural history (particularly bioluminescence). This most recent period has produced a flourishing of works in fields of study other than taxonomy—including behavior, ecology, morphology, physiology, cell biology, natural products biochemistry, and evolutionary biology. Important contributions in systematics during this period include Frederick M. Bayer (1955–1996) (Pl. 6); Huzio Utinomi, also known as Fujio Hiro (1956–1982) (Pl. 6); Manfred Grasshoff (1972–1991); F. M. Bayer, M. Grasshoff, and Jakob Verseveldt (1983); F. M. Bayer and M. Grasshoff (1997); Marie-José d’Hondt (1984); Andrée Tixier-Durivault (1954–1987), who named the genera *Crassophyllum* and *Malacobelemnion*; and Gary C. Williams (1986–1999). The latter author introduced cladistic methodology to the study of evolutionary relationships in the Pennatulacea.

SYNONYMS AND MISSPELLED GENERIC NAMES OF PENNATULACEA

Revised from Williams, 1995a:101; synonyms are listed on the left with the valid genera to which they belong shown in parentheses; * = misspelled names or transcription errors; ** = see Bayer and Grasshoff, 1997.

- **Acanthoptilon* Traquair in Zoological Record 7, 1870 (*Acanthoptilum*)
- Actinoptilon* Kükenthal, 1910 (*Actinoptilum*)
- **Actinoptinum* Day et al., 1970 (*Actinoptilum*)
- Amphianthus* Kükenthal, 1902 (*Amphiacme*)
- Argentella* Gray, 1870 (*Pteroeides*)
- Balticina* Gray, 1870 (*Halipteris*)
- Bathypenna* Marion, 1906 (possibly synonymous with *Gyrophyllum* according to Kükenthal, 1915)
- Bathyptilum* Kölliker, 1872 (*Kophobelemnion*)
- Benthoptilum* Verrill, 1885 (*Anthoptilum*)
- **Benthoptillum* Haddon in Zoological Record 22, 1885 (*Anthoptilum*)
- Cladiscus* Koren and Danielssen, 1877 (*Virgularia*)

PLATE 6



Willy Kükenthal (1861-1922). Courtesy
Nationaal Natuurhistorisch Museum, Leiden.



Elizabeth Deichmann (1896-1975). Courtesy
Frederick M. Bayer, Smithsonian Institution.



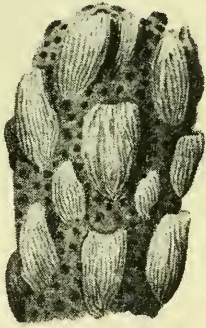
Frederick M. Bayer

Huzio Utinomi

Courtesy Frederick M. Bayer, Smithsonian Institution.

- Clavella* Gray, 1870 (*Lituaria*)
Crinillum Harting, Miquel and Hoeven, 1861 (*Umbellula*)
Crispella Gray, 1870 (*Pteroeides*)
Deutocaulon Marshall and Fowler, 1888 (*Virgularia*)
Dübenia Danielssen and Koren, 1884 (*Stylatula*)
Encrinus Lamarck, 1801 (*Umbellula*)
Fusticularia Simpson, 1905 (probably synonymous with *Cavernularia* according to Kükenthal, 1915)
 **Godefroyia* Leuckart, 1872 (*Pteroeides*)
Godeffroyia Kölliker, 1870 (*Pteroeides*)
Göndul Koren and Danielssen, 1883 (*Halipterus*)
Gunneria Danielssen and Koren, 1884 (*Kophobelemnon*)
Halisceptrum Herklots, 1863 (*Virgularia*)
Helicoptilum Nutting, 1912 (*Distichoptilum*)
Herklotsia Gray, 1860 (*Renilla*)
Juncoptilum Thomson and Henderson, 1905 (*Distichoptilum*)
 **Leioptilum* Verrill, 1865 (*Ptilosarcus*)
 **Leioptilum* Verrill, 1868 (*Ptilosarcus*)
Leioptilus Gray, 1860 (*Pennatula*)
Leioptilus of authors other than Gray, 1860 (*Ptilosarcus*)
Leptoptilum Kölliker, 1880 (*Funiculina*)
 **Lioptilum* Kölliker, 1872 (*Ptilosarcus*)
Lygomorpha Koren and Danielssen, 1877 (*Halipterus*)
Lygus Herklots, 1858 (*Virgularia*)
Mesobelemnon Gravier, 1907 (considered synonymous with *Sclerobelemnon* by Hickson, 1916)
Microptilum Kölliker, 1880 (*Halipterus*)
Norticina Gray, 1870 (*Halipterus*)
Ombellulaires Cuvier, 1817 (*Umbellula*)
 ***Ombellula* Cuvier, 1797 (*Umbellula*)
Ombellularia Lamarck, 1836 (*Umbellula*)
Osteocella Gray, 1870 (*Halipterus*)
Parabelemnon Thomson and Simpson, 1909 (possibly synonymous with *Cavernularia* according to Kükenthal, 1915) (Pl. 7)
Pavonaires Cuvier, 1817 (*Funiculina*)
Pavonaria Schweigger, 1820 (*Funiculina*)
Pavonaria Kölliker, 1869 (*Halipterus*)
Penna Bohadsch, 1761 (*Pennatula*, in part) (name unavailable as the work was suppressed by ICZN)
Phosphorella Gray, 1870 (*Pennatula*)
Policella Gray, 1870 (*Veretillum*)
Prochumella Balss, 1909 (*Calibelemnon*)
Protocaulon Kölliker, 1880 (*Virgularia*)
 **Pteroides* Pfeffer, 1886 (*Pteroeides*)
Pteromorpha Herklots, 1858 (*Pteroeides*)
Ptilella Gray, 1870 (*Pennatula*)
 **Renilla* Schweigger, 1820 (*Renilla*)
Renillina Gray, 1860 (possibly a young example of the alcyoniid soft coral *Sarcophyton* according to Kükenthal, 1915)
Sarcobelemnon Herklots, 1858 (*Cavernularia*)

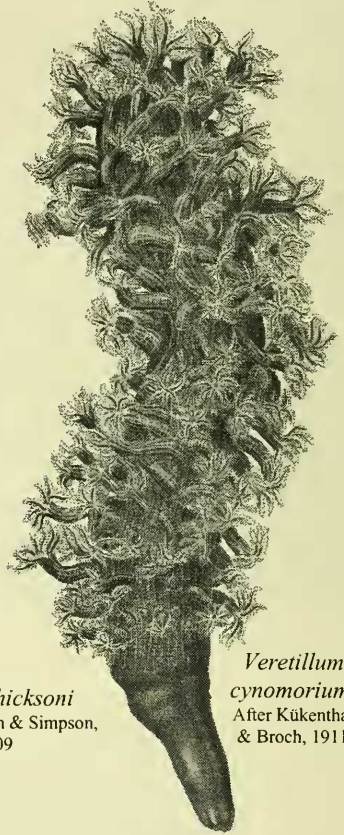
PLATE 7



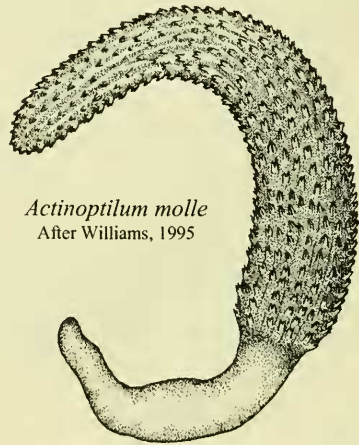
Parabelemnites indicum
After Thomson & Simpson,
1909



Lituaria hicksoni
After Thomson & Simpson,
1909



Veretillum cynomorium
After Kükenthal
& Broch, 1911



Actinoptilum molle
After Williams, 1995

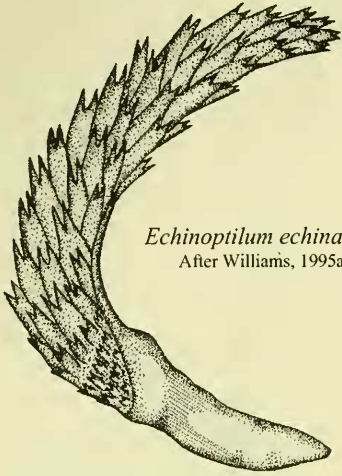
- Sarcophyllum* Kölliker, 1870 (*Sarcoptilus*)
Sceptonidium Richiardi, 1869 (*Virgularia*)
Stephanoptilum Roule, 1905 (*Anthoptilum*)
Stichoptilum Grieg, 1887 (*Halipteris*)
Struthiopteron Broch, 1910 (*Pteroeides*)
Stylobelemnion Kölliker, 1872 (*Cavernularia*)
Stylobelemnoides J. A. Thomson and Henderson, 1905 (possibly synonymous with *Cavernularia* according to Kükenthal, 1915)
Svava Danielssen and Koren, 1884 (*Virgularia*)
Svavopsis Roule, 1908 (*Virgularia*)
Thesioides J. A. Thomson and Henderson, 1906 (*Anthoptilum*)
Trichoptilum Kölliker, 1880 (*Funiculina*)
Umbellaria Schweigger, 1820 (*Umbellula*)
Umbellularia Lamarck, 1801 (*Umbellula*)
 **Verrilia* Lütken in Zoological Record 10, 1873 (*Halipteris*)
Verrillia Stearns, 1873 (*Halipteris*)
Vorticella Linnaeus, 1767 (*Umbellula*, in part)

TAXONOMIC INDEX

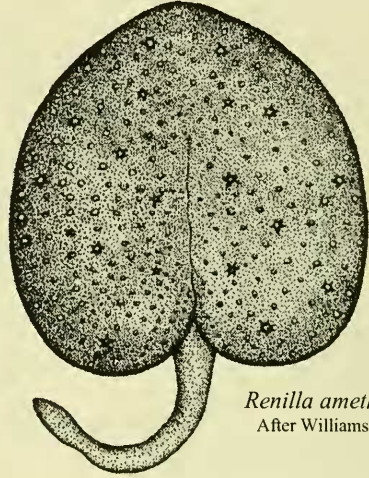
Original descriptions and other selected taxonomic references—restricted primarily to taxa considered valid by Williams (1995a, 1997f, and the present work); † = fossil taxa; ‡ = taxa with both living and fossil representation.

- Acanthoptilum* Kölliker, 1870
 [See also Balss (1910); Bayer (1957); Kükenthal (1915); Williams (1995a)]
Acanthoptilum album Nutting, 1909
Acanthoptilum agassizi Kölliker, 1872
Acanthoptilum annulatum Nutting, 1909
Acanthoptilum gracile (Gabb, 1863)
Acanthoptilum oligacis Bayer, 1957
Acanthoptilum pourtalesii Kölliker, 1870
Acanthoptilum scalpelifolium Moroff, 1902
Actinoptilum Kükenthal in Kükenthal and Broch, 1911
 [See also Kükenthal (1910, 1915); Williams (1990, 1995a)]
Actinoptilum molle (Kükenthal, 1910) (Pl. 7)
Amphiacme Kükenthal, 1903
 [See also Hickson (1916); Kükenthal (1902a, 1915); Kükenthal and Broch (1911); Williams (1990, 1995a)]
Amphiacme abyssorum (Kükenthal, 1902)
Anthoptilum Kölliker, 1880 (Pl. 9, 10)
 [See also Grasshoff (1982a, 1982b); Hickson (1916); Kükenthal (1915); Kükenthal and Broch (1911); Williams (1990, 1995a)]
Anthoptilum grandiflorum (Verrill, 1879) (Pl. 9)
Anthoptilum murrayi Kölliker, 1880
 †*Bensonularia* Hamilton, 1958
 †*Bensonularia spatulata* Hamilton, 1958 [Eocene of New Zealand]
Calibelemnon Nutting, 1908
 [See also Balss (1910); Hickson (1916); Kükenthal (1915); Williams (1990, 1995a)]

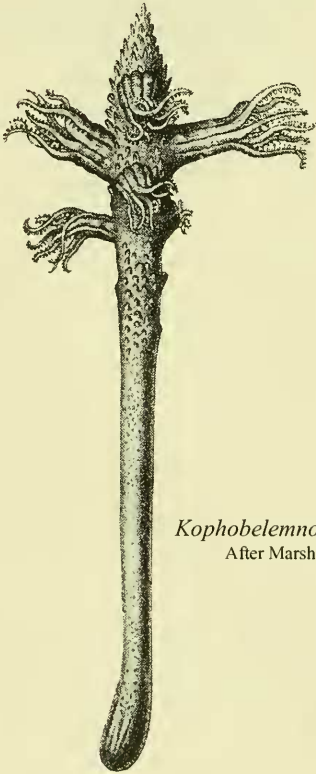
PLATE 8



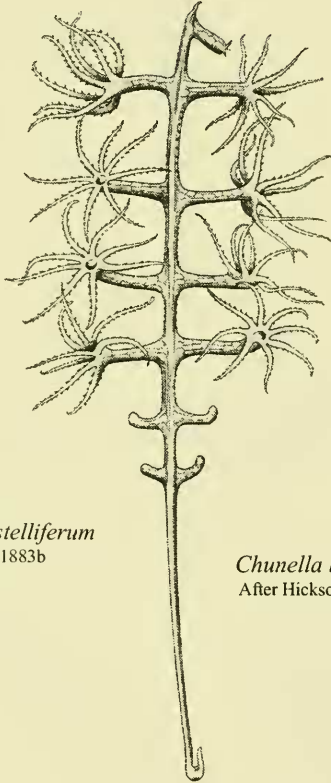
Echinoptilum echinatum
After Williams, 1995a



Renilla amethystina
After Williams, 1995a



Kophobelemnon stelliferum
After Marshall, 1883b



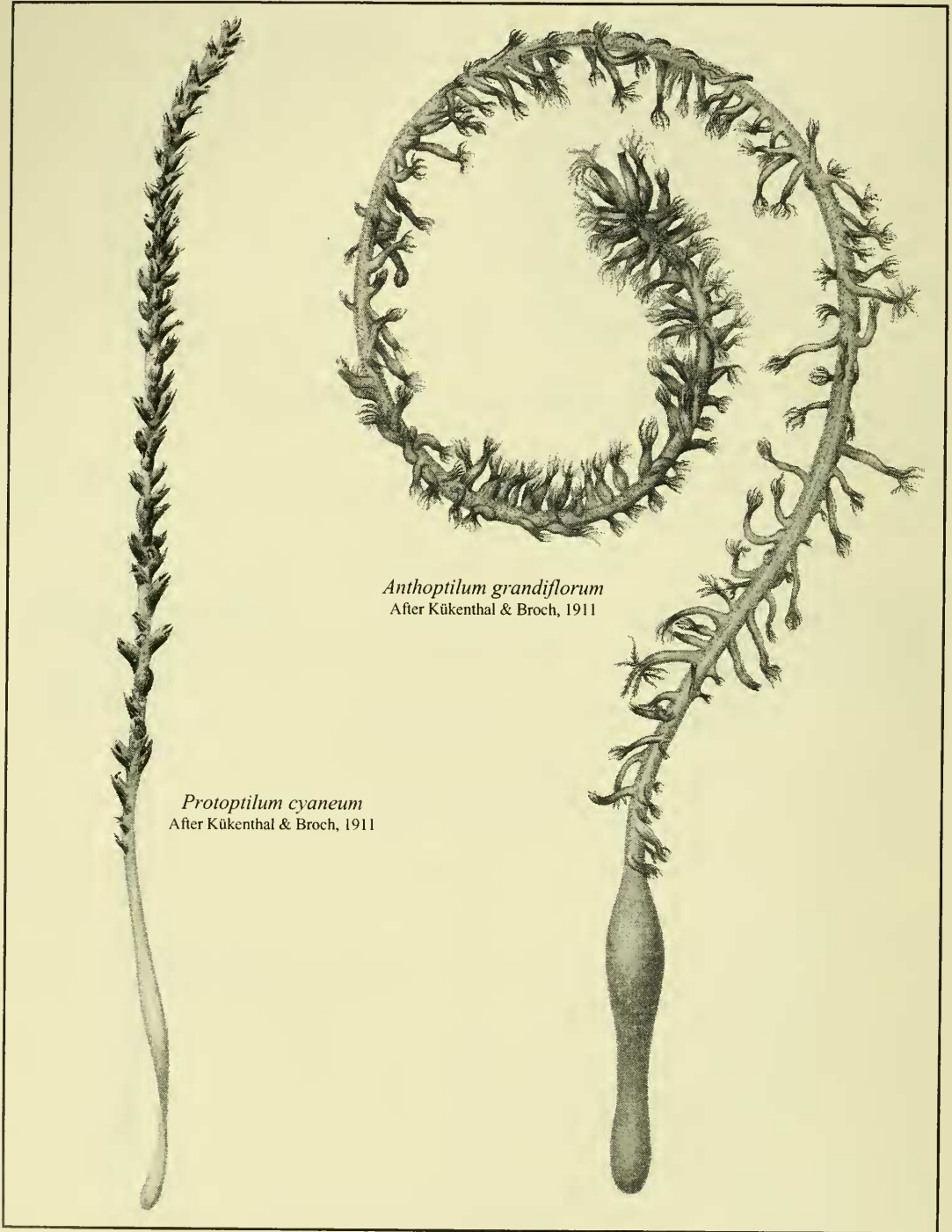
Chunella biflora
After Hickson, 1916



Umbellula thomsoni
After Tizard et al., 1885

- Calibelemnon hertwigi* (Balss, 1909)
Calibelemnon indicum (Thomson and Henderson, 1906)
Calibelemnon symmetricum Nutting, 1908
Cavernularia Valenciennes in Milne Edwards and Haime, 1850
 [See also Hickson (1916); Hondt (1984b); Kükenthal (1915); Lopez-Gonzalez, Gili, and Williams (in press); Williams (1989b, 1990, 1995a)]
Cavernularia capitata Williams, 1989
Cavernularia clavata Kükenthal and Broch, 1911
Cavernularia chuni Kükenthal and Broch, 1911
Cavernularia dayi Tixier-Durivault, 1954
Cavernularia dedeckeri Williams, 1989
Cavernularia elegans (Herklots, 1858)
Cavernularia glans Kölliker, 1872
Cavernularia habereri Kölliker, 1872
Cavernularia huetkeni Kölliker, 1872 (also spelled *C. lütkeni* and *C. lutkeni*)
Cavernularia malabarica Fowler, 1894
Cavernularia mirifica Tixier-Durivault, 1963
Cavernularia obesa Valenciennes in Milne Edwards and Haime, 1850
Cavernularia pusilla (Philippi, 1835)
Cavernulina Kükenthal and Broch, 1911
 [See also Hickson (1916); Hondt (1984b); Kükenthal (1915); Williams (1989b, 1990, 1995a)]
Cavernulina cylindrica Kükenthal and Broch, 1911
Cavernulina darwini (Hickson, 1921)
Cavernulina grandiflora Hondt, 1984b
Cavernulina orientalis Thomson and Henderson, 1909
Chunella Kükenthal, 1902 (Pl. 8)
 [See also Kükenthal (1915); Kükenthal and Broch (1911); Hickson (1916); Williams (1990, 1995a, 1997c)]
Chunella gracillima Kükenthal, 1902
Crassophyllum Tixier-Durivault, 1961
 [See also Williams (1995a, 1995d)]
Crassophyllum cristatum Tixier-Durivault, 1961
Crassophyllum thessalonicae Vafidis and Koukouras, 1991
Distichoptilum Verrill, 1882
 [See also Hickson (1916); Kükenthal (1915); Kükenthal and Broch (1911); Williams (1990, 1995a)]
Distichoptilum gracile Verrill, 1882
Echinoptilum Hubrecht, 1885
 [See also Balss (1910); Hickson (1916); Kükenthal (1915); Kükenthal and Broch (1911); Sachs (1913); Williams (1990, 1995a)]
Echinoptilum asperum Hickson, 1916
Echinoptilum echinatum (Kükenthal, 1910) (Pl. 8)
Echinoptilum elongatum Hickson, 1916
Echinoptilum macintoshi Hubrecht, 1885
Echinoptilum minimum Hickson, 1916
Echinoptilum roseum Hickson, 1916
Funiculina Lamarek, 1816
 [See also Balss (1910); Herklots (1858); Hickson (1916); Jungersen (1904); Kölliker (1872); Kükenthal (1915); Kükenthal and Broch (1911); Williams (1990, 1995a)]

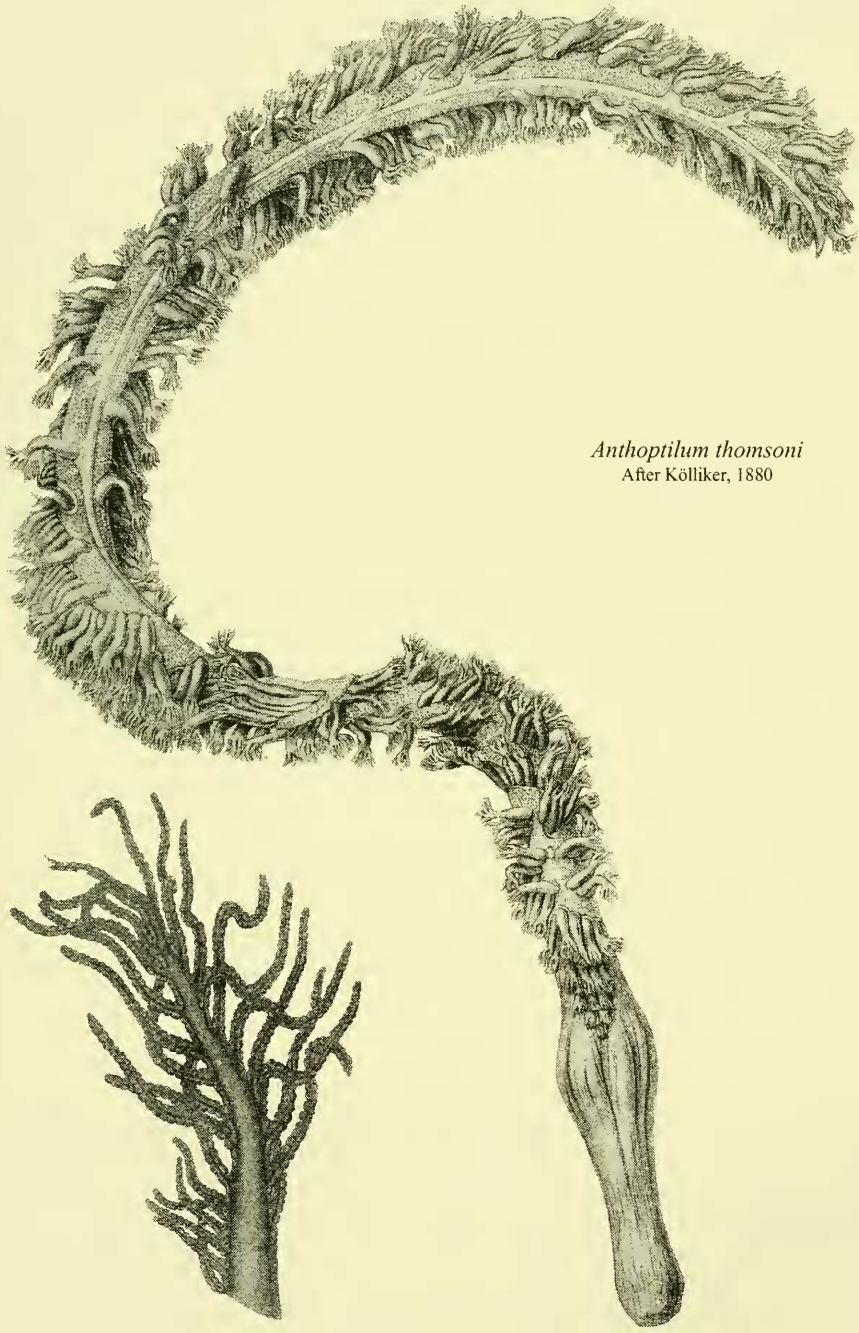
PLATE 9



Anthoptilum grandiflorum
After Kükenthal & Broch, 1911

Protoptilum cyaneum
After Kükenthal & Broch, 1911

PLATE 10



Anthoptilum thomsoni
After K lliker, 1880

- Funiculina armata* Verrill, 1879
Funiculina parkeri Kükenthal, 1909
Funiculina quadrangularis (Pallas, 1766)
†*Graphularia* Milne Edwards and Haime, 1850
†*Graphularia ambigua* (Morton, 1830) [Cretaceous/Tertiary of southeastern North America]
[See also Shapiro and Ramsdell (1965)]
†*Graphularia badenia* Strand, 1928
†*Graphularia belgica* Vincent (1893) [Eocene of Belgium]
†*Graphularia crecelii* Andrée, 1912 [Oligocene of Germany]
†*Graphularia desertorum* Kuhn, 1949
†*Graphularia groenwalli* Nielsen, 1914 [Cretaceous of Denmark]
†*Graphularia incerta* Malaroda, 1951 [Oligocene of Italy]
†*Graphularia irregularis* Nielsen, 1914 [Cretaceous of Denmark]
†*Graphularia kalimnae* Chapman and Crespin, 1928 [Tertiary of Australia]
†*Graphularia longissima* Squires, 1958 [Cretaceous/Tertiary of New Zealand]
†*Graphularia meijeri* Voight, 1958
†*Graphularia nigra* Malaroda, 1951 [Oligocene of Italy]
†*Graphularia quadrata* Voigt, 1958
†*Graphularia salisburgensis* Traub, 1938 [Paleocene of Austria]
†*Graphularia* sp. [Eocene of Hungary]
†*Graphularia sulcata* Nielsen, 1914 [Cretaceous of Denmark]
[See also Kolosvary (1949)]
†*Graphularia wetherelli* Milne-Edwards and Haime, 1850 [Eocene of England]
[See also Davis (1936)]
†*Graphularia?* *yamakawai* Yabe and Sugiyama, 1937 [Pleistocene of Japan]
Gyrophyllum Studer, 1891
[See also Hickson (1916); Kükenthal (1915); Roule (1905); Studer (1901); Williams (1995a, 1995d)]
Gyrophyllum hironellei Studer, 1891
Gyrophyllum sibogae Hickson, 1916 (Pl. 14)
Halipterus Kölliker, 1869
[See also Williams (1990, 1995a)]
Halipterus africana (Studer, 1879)
Halipterus californica (Moroff, 1902)
Halipterus christii (Koren and Danielssen, 1847)
Halipterus finmarchica (Sars, 1851)
Halipterus heptazooidea Acuña and Zamponi, 1992
Halipterus willemoesi Kölliker, 1870
Kophobelemnion Asbjørnsen, 1856
[See also Balss (1910); Danielssen and Koren (1884); Herklots (1858); Hickson (1916); Jungersen (1904); Kölliker (1872); Kükenthal (1915); Kükenthal and Broch (1911); Thomson and Simpson (1909); Williams (1990, 1995a)]
Kophobelemnion affine Studer, 1894
Kophobelemnion heterospinosum Kükenthal, 1910
Kophobelemnion hispidum Nutting, 1912
Kophobelemnion irregulatus Keller, Pasternak and Naumov, 1975
Kophobelemnion leucharti Cecchini, 1917
Kophobelemnion macrospinosum J. A. Thomson, 1927
Kophobelemnion molanderi Pasternak, 1975

- Kophobelemnon pauciflorum* Hickson, 1916
Kophobelemnon stelliferum (Müller, 1776) (Pl. 8)
Lituaria Valenciennes in Milne Edwards and Haime, 1850
 [See also Balss (1910); Gray (1870); Hickson (1916); Hondt (1984b); Light (1921); Kölliker (1872); Kükenthal (1915); Thomson and Simpson (1909); Williams (1990, 1995a)]
Lituaria amoyensis Koo, 1935
Lituaria australasiae (Gray, 1860)
Lituaria breve Light, 1921
Lituaria habereri Balss, 1910
Lituaria hicksoni Thomson and Simpson, 1909 (Pl. 7)
Lituaria kuekenthali Light, 1921
Lituaria molle Light, 1921
Lituaria phalloides (Pallas, 1766)
Lituaria philippinesis Light, 1921
Lituaria valenciennesi Hondt, 1984
Malacobelemnon Tixier-Durivault, 1965
 [See also Williams (1995a)]
Malacobelemnon stephensoni Tixier-Durivault, 1965
 †*Octobasis* Malecki, 1982 [Upper Cretaceous of Poland]
 †*Pavonaria portisi* Angelis, 1895? [Tertiary of Italy]
 †*Pavonaria? singularis* Malaroda, 1951 [Oligocene of Italy]
Pennatula Linnaeus, 1758 (Pl. 12, 13)
 [See also Balss (1910); Gray (1870); Herklots (1858); Kölliker (1869); Lamarck (1816); Leuckart (1872); Hickson (1916); Kükenthal (1915); Kükenthal and Broch (1911); Williams (1990, 1995a, 1995d)]
Pennatula aculeata Danielssen, 1860
Pennatula argentina Acuña and Zamponi, 1992
Pennatula delicata Tixier-Durivault, 1966
Pennatula fimbriata Herklots, 1858
Pennatula grandis Ehrenberg, 1834
Pennatula indica Thomson and Henderson, 1906
Pennatula inflata Kükenthal, 1910 (Pl. 13)
Pennatula mollis Alder, 1867 (considered a junior synonym of *Pennatula phosphorea* by Cornelius and Garfath, 1980, after examination of the two well-preserved syntypes)
Pennatula phosphorea Linnaeus, 1758 (Pl. 13)
Pennatula prolifera Jungersen, 1904
Pennatula rubra (Ellis, 1764)
 †*Pennatulites* Nelli, 1903
 †*Pennatulites manzonii* Nelli, 1903 [Miocene of Italy]
 †*Prographularia* Frech, 1890
 †*Prographularia tradica* Frech, 1890 [Triassic]
Protoptilum Kölliker, 1872
 [See also Balss (1910); Hickson (1916); Jungersen (1904); Kölliker (1880); Kükenthal (1915); Kükenthal and Broch (1911); Williams (1995a)]
Protoptilum carpenteri Kölliker, 1872
Protoptilum celebense Hickson, 1916
Protoptilum cyaneum Kükenthal, 1910 (Pl. 9)
Protoptilum denticulatum Jungersen, 1904
Protoptilum smitti Kölliker, 1872

Protoptilum thomsoni Kölliker, 1872

Pteroeides Herklots, 1858 (Pl. 14)

[See also Gray (1870); Hickson (1916); Hondt (1984a); Kölliker (1872); Kükenthal (1915); Kükenthal and Broch (1911); Leuckart (1872); Williams (1990, 1995a, 1995d)]

Pteroeides acutum Tixier-Durivault, 1966

‡ *Pteroeides argenteum* (Ellis and Solander, 1786) [Tertiary of Kei Islands]

[See also Bayer (1955a)]

Pteroeides bankanense Bleeker, 1859

Pteroeides bestae Hondt, 1984

Pteroeides breviradiatum Kölliker, 1869

Pteroeides caledonicum Kölliker, 1869

Pteroeides carnosum Tixier-Durivault, 1972

Pteroeides crossieri Tixier-Durivault, 1966

Pteroeides densum Tixier-Durivault, 1966

Pteroeides duebeni Kölliker, 1869

Pteroeides dofleini Balss, 1909

Pteroeides durum Kölliker, 1872

Pteroeides esperi Herklots, 1858

Pteroeides flexuosum Tixier-Durivault, 1966

Pteroeides humesi Tixier-Durivault, 1966

Pteroeides hymenocaulon Bleeker, 1859

Pteroeides isosceles J. S. Thomson, 1915

Pteroeides jungerseni Broch, 1910

Pteroeides laboutei Hondt, 1984

Pteroeides latissimum Kölliker, 1869

Pteroeides lusitanicum Broch, 1910

Pteroeides malayense Hickson, 1916

Pteroeides morbusus Tixier-Durivault, 1961

Pteroeides oblongum Gray, 1860

Pteroeides sagamiense Moroff, 1902

Pteroeides sparmanni Kölliker, 1869

Pteroeides spicatum Tixier-Durivault, 1972

Pteroeides spinosum (Ellis, 1764)

Pteroeides tenerum Kölliker, 1869

Pteroeides timorense Hickson, 1916

Pteroeides triangulum Tixier-Durivault, 1972

Ptilosarcus Verrill, 1865

[See also Leuckart (1872); Nutting (1909); Verrill (1865); Williams 1995a, 1995d)]

Ptilosarcus gurneyi (Gray, 1860)

Ptilosarcus undulatus (Verrill, 1865)

Renilla Lamarck, 1816 (Pl. 8)

[See also Ehrenberg (1834); Eisen (1876); Gray (1860); Herklots (1858); Kölliker (1871b); Kükenthal (1915); Kükenthal and Broch (1911); Müller (1864); Williams (1995a); Zamponi and Pérez (1996); Zamponi, Pérez, and Capitoli (1997)]

Renilla koellikeri (also spelled *R. kollikeri* or *R. köllikeri*) Pfeffer, 1886

Renilla muelleri (also spelled *R. mulleri* or *R. mülleri*) Kölliker, 1872

Renilla musaica Zamponi and Pérez, 1995

Renilla octodentata Zamponi and Pérez, 1995

Renilla reniformis (Pallas, 1766)

Renilla tentaculata Zamponi, Pérez, and Capitoli, 1997

Sarcoptilus Gray, 1848

[See also Williams (1995a, 1995c, 1995d)]

Sarcoptilus bollonsi (Benham, 1906)

Sarcoptilus grandis Gray, 1848

Sarcoptilus nullispiculatus Williams, 1995

Sarcoptilus rigidus Williams, 1995

Sarcoptilus shaneparkerii Williams, 1995

Sclerobelemnon Kölliker, 1872

[See also Balss (1910); Hickson (1916); Kölliker (1872); Kükenthal (1915); Kükenthal and Broch (1911); Thomson and Henderson (1906b); Williams (1995a, 1995d)]

Sclerobelemnon burgeri (Herklots, 1858)

Sclerobelemnon elongatum Hickson, 1916

Sclerobelemnon gracile (Gravier, 1908)

Sclerobelemnon gravieri Hickson, 1916

Sclerobelemnon koellikeri Thomson and Henderson, 1906

Sclerobelemnon magniflorum Hickson, 1916

Sclerobelemnon schmelzi Kölliker, 1872

Sclerobelemnon theseus Bayer, 1959

Scleroptilum Kölliker, 1880

[See also Balss (1910); Kükenthal (1915); Kükenthal and Broch (1911); Williams (1990, 1995a)]

Scleroptilum grandiflorum Kölliker, 1880

Scytaliopsis Gravier, 1906

[See also Gravier (1908); Kükenthal (1915); Williams (1990, 1995a)]

Scytaliopsis djiboutiensis Gravier, 1906

Scytaliopsis ghardagensis (?Gravenhorst, 1821) (also spelled *S. ghardaqana*; a probable *nomen nudem* since it is unclear whether this citation represents an original description of a new taxon, or merely the use of an unsubstantiated name)

[See also Atiya (1994); Schuhmacher and Hinterkircher (1996)]

Scytalium Herklots, 1858

[See also Balss (1910); Hickson (1916); Kölliker, 1870; Kükenthal (1915); Kükenthal and Broch (1911); Thomson and Simpson (1909); Williams (1995a)]

Scytalium balssi Hickson, 1916

Scytalium martensi Kölliker, 1870

Scytalium sarsii Herklots, 1858

Scytalium tentaculatum Kölliker, 1880 (Pl. 11)

Stachyptilum Kölliker, 1880

[See also Kükenthal (1915); Kükenthal and Broch (1911); Williams (1995a)]

Stachyptilum dofleini Balss, 1909

Stachyptilum macleari Kölliker, 1880

Stachyptilum superbum Studer, 1894

Stylatula Verrill, 1864

[See also Balss (1910); Jungersen (1904); Kölliker (1870); Kükenthal (1915); Kükenthal and Broch (1911); Williams (1995a)]

Stylatula antillarum Kölliker, 1870

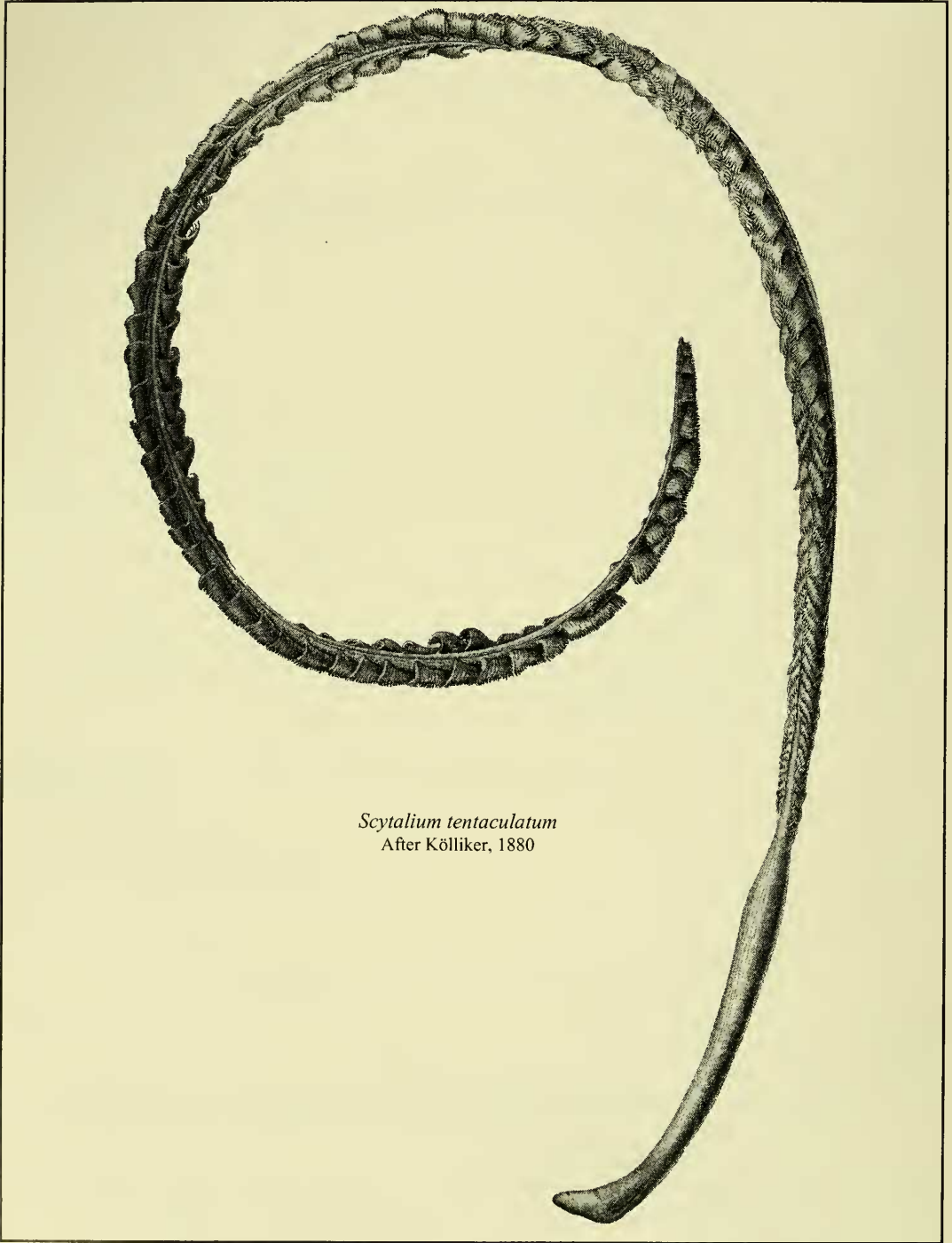
Stylatula brasiliensis (Gray, 1870)

Stylatula darwini Kölliker, 1870

Stylatula diadema Bayer, 1959

Stylatula elegans (Danielssen, 1860)

PLATE 11



Scytalium tentaculatum
After Kölliker, 1880

PLATE 12

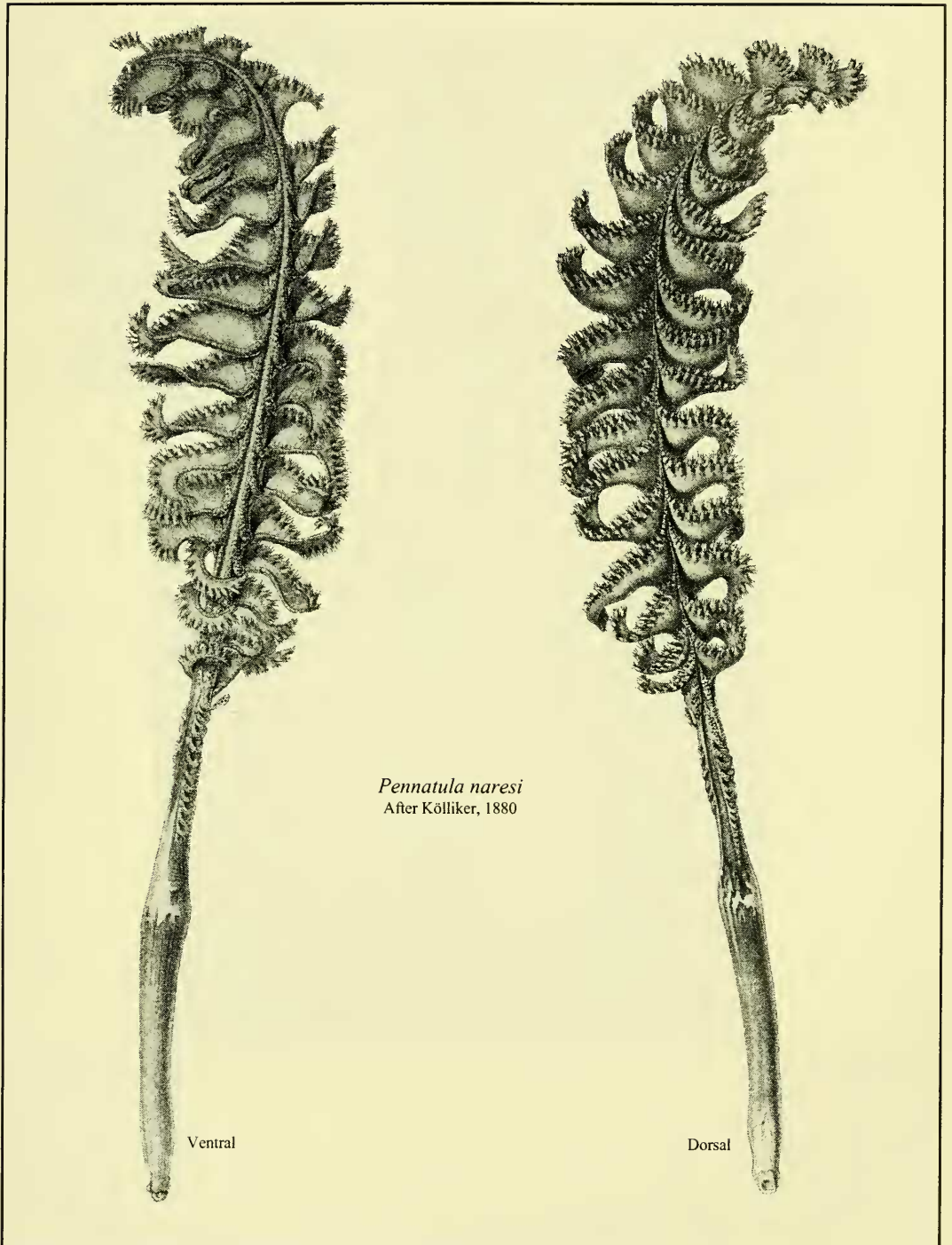
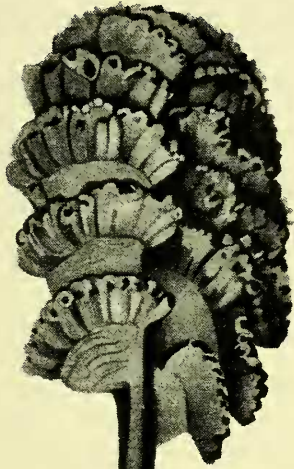


PLATE 13

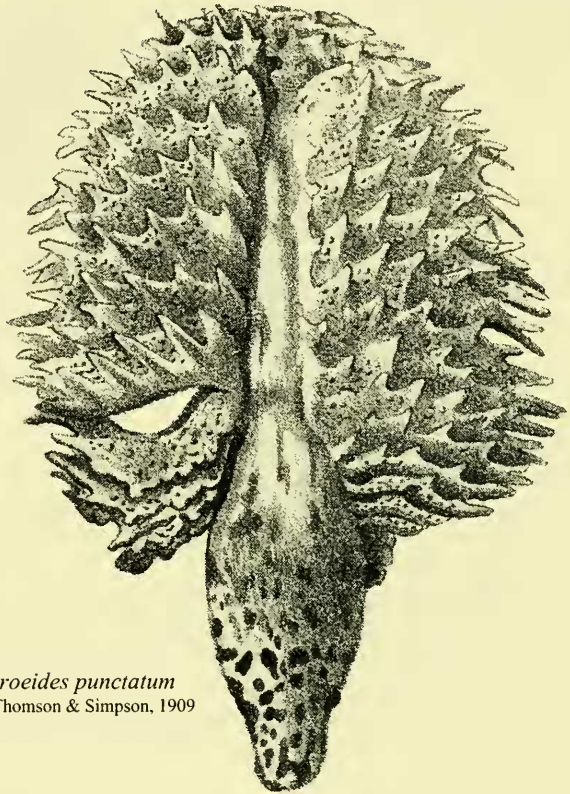


Virgularia schultzei, upper left; *Virgularia schultzei*, lower left; *Pennatula inflata*, center; *Pennatula phosphorea*, right.
After Kükenthal & Broch, 1911

PLATE 14



Gyrophyllum sibogae
After Hickson, 1916



Pteroeides punctatum
After Thomson & Simpson, 1909

Stylatula elongata (Gabb, 1862)

Stylatula gracilis (Gabb, 1864)

Stylatula kinbergi K  lliker, 1870

Stylatula lacazi K  lliker, 1870

Stylatula polyzoidea Zamponi and P  rez, 1996

Umbellula Cuvier, 1797 (see Bayer and Grasshoff, 1997) (Pl. 1, 8)

[See also Broch (1957, 1958a); Cuvier (1800); Ellis (1753, 1755); Grasshoff (1971, 1973, 1982a, 1982b); Heezen and Hollister (1971); Hickson (1916); K  lliker (1875, 1880); K  kenthal (1902b, 1915); K  kenthal and Broch (1911); Lamarck (1801); Mylius (1755); Pasternak (1975); Williams (1990, 1993b, 1995a, 1997a, 1997c); Williams and Rogers (1989)]

Umbellula durissima K  lliker, 1880

Umbellula encrinus Linnaeus, 1758

Umbellula hemigymina Pasternak, 1975

Umbellula huxleyi K  lliker, 1880

Umbellula lindahli K  lliker, 1874

Umbellula monocephalus Pasternak, 1975

Umbellula pellucida K  kenthal, 1902

Umbellula spicata K  kenthal, 1902

Umbellula thomsoni K  lliker, 1874 (Pl. 8)

Veretillum Cuvier, 1797

[See also Balss (1910); Gray (1870); Herklots (1858); Hickson (1916); K  kenthal (1915); K  kenthal and Broch (1911); Williams (1990, 1995a)]

Veretillum australis (Gray, 1870)

Veretillum cynomorium (Pallas, 1766) (Pl. 7)

Veretillum leloupi Tixier-Durivault, 1960

Veretillum malayense Hickson, 1916

Veretillum manillensis (K  lliker, 1872)

Veretillum tenuis (Marshall and Fowler, 1889)

Veretillum vanderbilti Boone, 1938

Virgularia Lamarck, 1816

[See also Herklots (1858); K  lliker (1880); Koren and Danielssen (1877); K  kenthal (1915); K  kenthal and Broch (1911); Richiardi (1869); Williams 1990, 1995a)]

Virgularia abies K  lliker, 1870

Virgularia brochi K  kenthal, 1915

Virgularia bromleyi K  lliker, 1880

Virgularia densa Tixier-Durivault, 1966

Virgularia galapagensis Hickson, 1930

Virgularia glacialis K  lliker, 1870

Virgularia gracillima K  lliker, 1880

Virgularia gustaviana (Herklots, 1863)

Virgularia halisceptrum Broch, 1910

Virgularia juncea (Pallas, 1766)

Virgularia kophameli May, 1899

Virgularia loveni Utinomi, 1971

Virgularia mirabilis (M  ller, 1776)

Virgularia patagonica (a probable *nomen nudem* since an original description cannot be found and a type specimen has not been located)

[See also Barrattini and Ureta, 1960; Darwin, 1860]

Virgularia patachonica (see *Virgularia patagonica*)

- ‡ *Virgularia presbytes* Bayer, 1955a [Tertiary of Trinidad]
 [See also Bayer (1957); Belém and Figueiredo Alvarenga (1973)]
Virgularia reinwardti Herklots, 1858
Virgularia rumphi Kölliker, 1870
Virgularia schultzei Kükenthal, 1910 (Pl. 13)
Virgularia tuberculata Marshall, 1883

GEOGRAPHIC INDEX

- Africa – eastern (see Indo-Pacific)
 Africa – northern (see North Atlantic and Mediterranean)
 Africa – southern
 Branch et al. (1994); Broch (1939, 1940); Day (1974b); Day et al. (1970); Molander (1929); J. S. Thomson (1915, 1917, 1924); Tixier-Durivault (1954, 1960); Williams (1987, 1989a, 1989b, 1990, 1992, 1993a); Williams and Rogers (1989).
 Africa – western
 Broch (1910a; 1914b, 1958b); Buchanan (1955); Dollfus (1938); López-González et al. (in press); Molander (1929); Pax and Müller (1954); Studer (1878); Tixier-Durivault (1961b, 1963); Williams (1987, 1989b, 1990, 1992).
 Africa – Atlantic (see Africa – western)
 Antarctica (see Southern Oceans)
 Arctic Ocean
 Broch (1913c, 1955, 1956); Jungersen (1907, 1915, 1917); Lindahl (1874c); Madsen (1948); May (1900); Mylius (1753, 1754); Pasternak (1980); Verrill (1922); Yashnov (1948).
 Asia – northeastern (see Pacific Ocean – northern; or Japan)
 Atlantic – eastern (see North Atlantic and Mediterranean or Africa – western)
 Atlantic – northern (see North Atlantic and Mediterranean)
 Atlantic – western temperate (see North Atlantic and Mediterranean or South America – Atlantic)
 Atlantic – western tropical (see Western Tropical Atlantic and Caribbean)
 Australia – eastern (see Indo-Pacific)
 Australia – northern (see Indo-Pacific)
 Australia – southern
 Broch (1910c); Briggs (1915); Godfrey (1943); Gray (1848); McCoy (1892); Pasternak (1966); Utinomi (1971); Utinomi and Shepherd (1982); Williams (1995c).
 Australia – western
 Broch (1910c); Williams (1995c).
 Caribbean Sea (see Western Tropical Atlantic and Caribbean)
 Cosmopolitan (see Worldwide)
 East Africa (see Africa – eastern)
 East Asia (see Indo-Pacific)
 Eastern Australia (see Indo-Pacific)
 Eastern Pacific – western North America (see North America – Pacific)
 Eastern Pacific – western South America (see South America – Pacific)
 Europe (see North Atlantic and Mediterranean)
 Indo-Pacific (including Red Sea*)
 Alcock (1902); Allen and Steene (1994); *Atiya (1994); Briggs (1915); Clastres et al. (1984); Colin and Arneson (1995); Dinamani (1965); Fowler (1894); Gosliner et al. (1996); Gravely (1941); *Gravenhorst (1821); *Gravier (1906a, 1906b, 1906c, 1907a, 1908, 1912a); Hickson (1905); Hondt (1984a, 1984b); Hornell (1922); Humes (1978); Imahara (1991); Koo (1935).

1940); *Kükenthal (1913b); Light (1921); *Magnus (1966); A. M. Marshall and Fowler (1889); Mather and Bennet (1993); Nakasone and Yu (1987); Nutting (1908); Pasternak (1964); Ridley (1883); Roule (1908); Sankolli and Neelakantan (1971); *Schuhmacher and Hinterkircher (1996); Simpson (1905); J. A. Thomson (1905); J. A. Thomson and Crane (1909a, 1909b); J. A. Thomson and Henderson (1905a, 1905b, 1906a, 1906b); Tixier-Durivault (1960, 1965, 1966, 1972); Tixier-Durivault and Hondt (1974a); Utinomi (1956b).

Japan

Balss (1910); Fisher (1874); Hubrecht (1885); Kumano (1937); Moroff (1902b); Nutting (1912); Okutani (1969); Stearns (1883); Stimpson (1855); J. A. Thomson and Rennet (1927); Utinomi (1956a, 1958, 1961, 1964).

Mediterranean Sea (see North Atlantic and Mediterranean)

New Zealand

Benham (1906, 1907); Dendy (1897); Hamilton (1958); Hutton (1904); Powell (1947); Williams (1995c).

North America – temperate Atlantic (see North Atlantic and Mediterranean)

North America – Pacific

Allen (1969); Anonymous (1898); Batic (1972); Belcik (1977); Blake (1872, 1873); Brusca (1980); Dawson (1872); Fautin et al. (1987); Flora and Fairbanks (1966); Gabb (1862, 1864); Gotshall (1987, 1994); Gotshall and Laurent (1979); Hartman (1960); Hickson (1930a); Hochberg and Ljubenkov (1998); Human (1973); Johnson and Snook (1935); Kerstitch (1989); Kozloff (1974, 1983, 1987); Kükenthal (1913a); Lam et al. (1982); Nutting (1909); Ricketts et al. (1985); Sclater (1872, 1873); Shimek (1998); Stearns (1873a); Strathmann (1988); Studer (1894); Verrill (1865, 1868a, 1868b).

North Atlantic and Mediterranean (Europe and eastern North America)

Abel (1963); Alder (1862); Alder (1863); Altuna-Prados (1994); Andrée (1912); Angelis (1895?); Arculeo et al. (1990); Atkinson (1989); Broch (1913a, 1914a, 1953); Baluk and Pisera (1984); Bellini (1905); Berenguier (1954); Broch (1953); Demir (1952); Dyer et al. (1981); Eckelbarger et al. (1998); Ellis (1753, 1755, 1764); Field (1949); Fischer (1889); Forbes and Goodsir (1851); Gili and Pagès (1987); Gili et al. (1987); Grasshoff (1981, 1982a, 1982b, 1989); Grieg (1887, 1892, 1893, 1896); Jahn (1970); Keller et al. (1975); Koren and Danielssen (1847, 1856, 1874, 1877, 1883, 1884); Kramp (1932, 1933, 1950); Lacaze-Duthiers (1891); Langton et al. (1990); Lindahl (1874a, 1874b, 1874c); Luther and Fiedler (1961); Madsen (1948); Manuel (1981); Marion (1906); Mylius (1753, 1754); Nobre (1931); Patterson (1986); Pax (1936); Pax and Müller (1953, 1955a, 1955b, 1955c, 1959, 1962); Pérès and Picard (1958); Perrier (1936); Rice et al. (1992); Riedl (1963, 1983); Rossi (1971); Roule (1905); Rowe (1971); Sars (1846, 1851); Stephens (1909); Tixier-Durivault and Lafargue (1968); Vafidis and Koukouras (1991); Vafidis et al. (1994); Verrill (1878, 1879, 1882a, 1882b, 1884a, 1884b, 1885a).

Northern Pacific (see Pacific Ocean – northern)

Pacific Ocean – eastern (see North America – Pacific)

Pacific Ocean – northern

Blake (1872, 1873); Broch (1935); Pasternak (1960, 1961a, 1970); Rho and Song (1976, 1977).

Pacific Ocean – western (see Indo-Pacific)

South America (Atlantic)

Bartini and Ureta (1960); Acuña and Zamponi (1992);); Belém and Figueiredo Alvarenga (1973); Darwin (1860); Pasternak (1975b, 1993); Sanchez (1994); Tommasi et al. (1972); Zamponi and Perez (1996); Zamponi et al. (1997).

South America (Pacific)

Pasternak (1975b); Pérez (1996); Zuñiga (1948).

Southeast Asia (see Indo-Pacific)

Southern Asia (see Indo-Pacific)

Southern Africa (see Africa – southern)

Southern Australia (see Australia – southern)

Southern Oceans (Antarctica and the subantarctic)

Acuña and Zamponi (1992); Branch and Williams (1993); Kükenthal (1912a); May (1900); Pasternak (1961b, 1962); J. A. Thomson and Rennet (1931); Zamponi and Perez (1995a, 1995b).

Subantarctic (see Southern Oceans)

West Africa (see Africa – western)

Western Australia (see Australia – western)

Western Tropical Atlantic and Caribbean

Bayer (1957, 1959, 1961); Cairns, Hartog, and Arneson (1986); Deichmann (1936a, 1936b); Fowler (1888); Kaplan (1982, 1988); Keller et al. (1975); Pasternak (1975a); Sanchez (1994); Voss (1976).

Worldwide

Bayer (1956); Kükenthal (1915); Williams (1995a, 1997e, 1997f).

SUBJECT INDEX

NOTE: The largest percentage, approximately 37%, of the citations listed pertain to taxonomy and geographic records (see Fig. 1).

Anatomy (see Morphology and Ultrastructure)

Behavior

P. A. V. Anderson (1976); P. A. V. Anderson and Case (1975); Buisson (1974, 1976, 1980, 1988); Darwin (1860); Couet (1979); Dickinson (1978); Hoare and Wilson (1977); Kastendiek (1975a, 1975b, 1976); Lancaster (1601); Langton et al. (1990); Mori (all citations); Mori and Ondo (1957); Mori and Tanase (1973); Pantin (1950); Pavans de Ceccatty and Buisson (1965); Takada and Mori (1956, 1957).

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Bayer (1981a, 1996); Hickson (1916); Kükenthal (1915); D. W. Thompson (1885); Williams (1990).

Biography (Regarding Authors of Pennatulacean Research)

Boeseman (1973); Forest (1996); Fransen et al. (1997); Gardiner (1940); Holthuis (1993, 1995); Smit (1979); Zimmer (1925).

Bioluminescence

Agassiz (1850); Aldrovandi (1642, 1648); Anctil et al. (1982); J. M. Anderson and Cormier (1978); J. M. Anderson et al. (1974, 1978); P. A. V. Anderson and Case (1975); Awad and Anctil (1993a, 1993b); Batie (1972); C. Bauhin (1620, 1671); J. Bauhin (1650-51); Bilhaut (1975a, 1975b); Blainville (1834); Boussuet (1558); Buck (1973); Chiaje (1827); Charbonneau (1981); Cormier (1978); Davenport and Nicol (1956); DeLuca et al. (1976); Dittrich (1888); Ehrenberg (1834c); Ellis (1764); Forbes (1847); Forbes and Goodsir (1851); Germain and Anctil (1988); Gesner (1555, 1558); Grant (1827, 1829); Grober (1990a, 1990b); Hart et al. (1979); Harvey (1917, 1920, 1940, 1952); Hastings (1968, 1983); Hastings and Morin (1969); Herdman (1913a); Herring (1978, 1991); Hori and Cormier (1973); Hori et al. (1972, 1973); Imperato (1599); Korotneff (1887); Kreiss and Cormier (1967); Krukenberg (1887, 1888); Mangold (1910); N. B. Marshall (1979); Matern (1984); Matthews

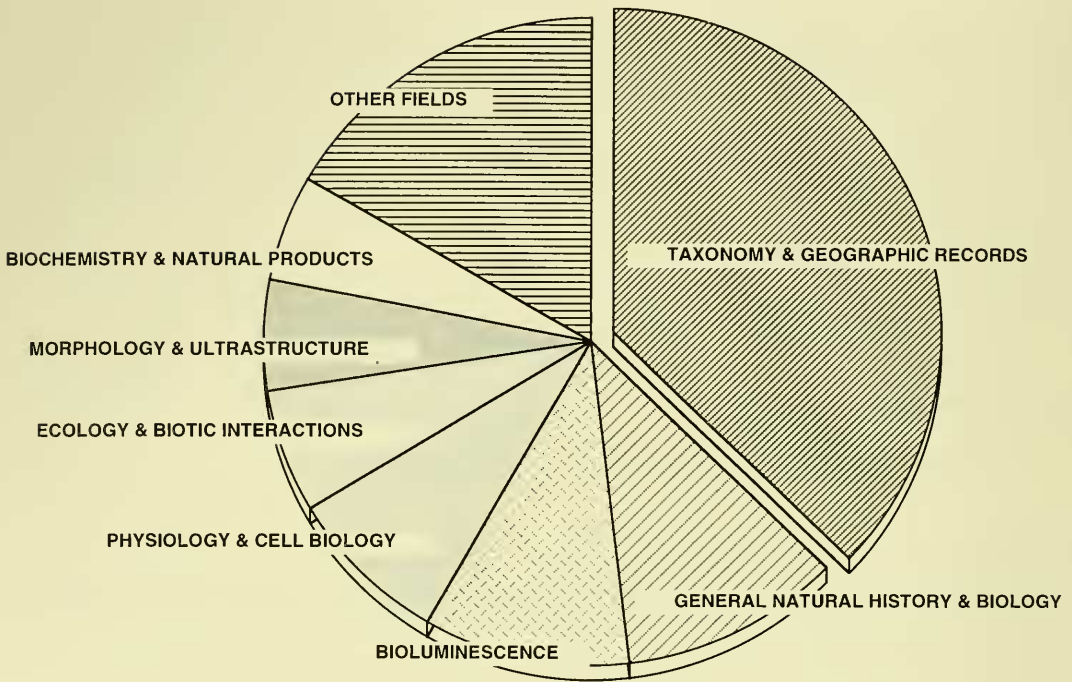


FIGURE 1. Quantitative analysis of the literature by field of study.

et al. (1977); Morin (1974, 1976, 1998); Neelson et al. (1986); Nicol (1955a, 1955b, 1955c, 1958); Panceri (1871b, 1871c, 1872a, 1872b, 1872c); Parker (1920c); Péron (1804); Pratje (1923); Rapp (1827); Royal Society (1870); Satterlie and Case (1979); Shaw (1838–46); Shimomura and Johnson (1975, 1979); Soares and Sawaia (1975); Spallanzani (1784, 1796); Spurlock and Cormier (1975); Tilesius von Tilenau (1819); Titschack (1965, 1966); Tizard et al. (1885); Wampler et al. (1971, 1973); Ward (1979); Ward and Cormier (1978a, 1978b); Williams (1990); Wyville Thomson (1874).

Corals (Pre-Linnean General Natural History)

Boccone (1670); Marsigli (1725); Peyssonnel (1753); Rondelet (1554-1555); Woodward (1695).

Ecology and Biotic Interactions

P. K. Anderson (1989); Atkinson (1989); Bertsch (1968, 1982); Best (1988); Birkeland (1969, 1971, 1974); Brafield (1969); Creed and Coull (1984); Davis (1978); Davis et al. (1982); Dawydoff (1930, 1938); Day (1974a); Dube and Ball (1971); Fager (1968); Fujita and Ohta (1988); ; Gili et al. (1987); Gilluly (1970); Gosliner et al. (1996); Hornell (1922); Howson and Davies (1991); Humes (1978); Jones (1960); Kastendiek (1975a, 1975b, 1976, 1982); Lam et al. (1982); Laubier (1972); Magnus (1966); Mariscal and Bigger (1977); McDonald and Nybakken (1978); Miyajima (1897, 1900); Mori (all citations); Mori and Ondo (1957); Mori and Tanase (1973); Nakasone and Yu (1987); Okutani (1969); Ramesh et al. (1985); Rittschof et al. (1986, 1988); Rowe (1971); Sankolli and Neelakantan (1971); Shepherd (1983); Shimek (1998); Short and Trower (1986); Standing et al. (1984); Thompson et al. (1988); Tyler et al. (1995).

General Natural History and General Biology

Alcock (1902); Allen (1969); Arculeo et al. (1990); Arndt (1912); R. D. Barnes (1987); R. S. K. Barnes et al. (1988); Bayer (1973, 1981a); Bayer et al. (1983); Bayer and Owre (1968); Bellomy (1974); Bourne (1900); Branch et al. (1994); Brusca and Brusca (1990); Colin and Arneson (1995); Coleman and Teague (1973); Cooke (1889); Dakin (1953); Dalyell (1848); Darwin (1860); Delage and Hérouard (1901); Donovan (1995); Dunn (1982); Faulkner and Chesher (1979); Fosså and Nilsen (1995); Frische (1991); Gage and Tyler (1991); Gesner (1565); Hadi (1994); Hardy (1967); Gosliner et al. (1996); Gotshall (1987, 1994); Gotshall and Laurent (1979); Gravier (1912b); Haeckel (1904); Hardy (1965, 1967); Heezen and Hollister (1971); Hickson (1906, 1909, 1930b); Huxley (1907); Hyman (1940); Johnson and Snook (1935); Kaplan (1982, 1988); Kerstitch (1989); Koren and Danielssen (1877); Kozloff (1974, 1983, 1987, 1990); Kükenthal (1923-1925); Lancaster (1601); Luther and Fiedler (1961); Lutz (1986); Lydekker (no date); MacGinitie (1938); MacGinitie and MacGinitie (1968); N. B. Marshall (1979); W. P. Marshall (1895); Mather and Bennet (1993); Meglitsch (1972); Milne and Milne (no date); Milne Edwards and Haime (1857); Ming (1993); Modeer (1786); H. B. Moore (1937); Moseley (1872); Moss (1878); Mylius (1753, 1754); Nordgaard (1905); Omori (1991); Pearse et al. (1987); Philippi (1835); Pimentel (1967); Ricketts et al. (1985); Riedl (1963); Ricketts et al. (1985); Rondelet (1554-1555); Rumphius (1705); Schechter (1959); Schömann (1949); Schuhmacher and Hinterkircher (1996); Sclater (1872, 1873); Smith (1964); Smith and Carlton (1975); Sphon (1964); Sprung and Delbeek (1997); Thurston (1890); Tilesius (1812); Tizard et al. (1885); Tixier-Durivault (1987); A. Trembley (1744); Tyler and Zibrowius (1992); Utinomi (1956a, 1964); Voss (1976); Wilkins and Birkholz (1986); Williams (1986, 1993a, 1995a, 1997c); Wyville Thomson (1874); Zim and Ingle (1955).

Histology

Hasama (1944); Kölliker (1865); Korotneff (1887); Lyke (1965); Niedermeyer (1913, 1914); Titschack (1970).

History of Science (Regarding Coelenterates and/or Sea Pens)

Agassiz (1860); Bayer (1981a); Hickson (1916); Hyman (1940); Shapiro and Ramsdell (1965); Williams (1993b, 1995a, 1997c).

Molecular Biology and Genetics

Lorenz et al. (1991).

Morphology and Ultrastructure

Alonso (1979); Beklemishev (1969a, 1969b); Buisson (1970); Buisson and Franc (1969); Bujor (1901); Chia and Crawford (1977); Crawford and Chia (1974); Bullough (1950); Dunkelberger and Watabe (1972, 1974); Fautin and Mariscal (1991); S. Franc (1979); S. Franc et al. (1971, 1974, 1985); Franzén (1967); Germain and Anctil (1988); Hickson (1883); Ivester and Dunkelberger (1971); Jungersen (1888a, 1888b); Koch (1878, 1889, 1890); Kölliker (1865, 1871b, 1872, 1874); Korotneff (1887); Ledger and Franc (1978); Lenhoff et al. (1971); Lightbown (1918); Lyke (1965); Mariscal (1974, 1979); Mariscal and Bigger (1977); Marks et al. (1949); Niedermeyer (1911, 1912); Panceri (1870); Parker (1919); Roule (1907); Satterlie et al. (1976); Shapeero (1969); Spurlock and Cormier (1975); Titschack (1966, 1968, 1970); P. Trembley (1941, 1942); Watabe and Dunkelberger (1979); Wilbur (1976); Wilson (1884).

Natural Products Chemistry, Biochemistry, and Toxicology

Anctil (1987, 1989a, 1989b); Anctil et al. (1982, 1984, 1991); J. M. Anderson and Cormier (1978); J. M. Anderson et al. (1974, 1978); P. A. V. Anderson (1976); Awad and Anctil (1993a,

1993b); Bernheimer and Arigad (1981); Bullock (1970); Charbonneau (1981); Clastres et al. (1984); Coan and Travis (1970); Datta et al. (1990); DeLuca et al. (1976); Fu et al. (in press); Goswami et al. (1995); Grimmelikhuijzen and Groeger (1987); Grimmelikhuijzen et al. (1987); Harmon et al. (1984); Hart et al. (1979); Hori and Cormier (1973); Hori et al. (1972, 1973); Huang and Mir (1972); Jones et al. (1979); Karkhanis and Cormier (1971); Keifer et al. (1986); Kittredge et al. (1962); Kreiss and Cormier (1967); Morin (1976); Kumar et al. (1990); Lorenz et al. (1991); Mackie (1987); Pani and Anctil (1994); Shapeero (1969); Shimomura and Johnson (1975, 1979); Standing et al. (1984); Thompson et al. (1988); Tillet-Barret et al. (1992); Vanderah and Djerassi (1977); Vidal et al. (1992); Waele et al. (1987); Wampler et al. (1971); Wekell (1974, 1978); Wratten et al. (1977a, 1977b).

Paleontology (Mesozoic and Cenozoic Fossil Taxa)

Andrée (1912); Angelis (1895?); Baluk and Pisera (1984); Bayer (1955a, 1955b, 1956); Bradley (1980, 1981); Branco (1885); Chapman and Crespín (1928); Davis (1936); Fowler (1911); Frech (1890); Gabb (1859, 1861); Gregorio (1890); Hamilton (1958); Häntzschel (1958); Howell (1947); Kolosvary (1949); Kuhn (1949); Malaroda (1951); Malecki (1982); Milne Edwards and Haime (1850); Morton (1830, 1834); R. C. Moore (1956); Nelli (1903); Nielsen (1914); Shapiro and Ramsdell (1965); Roemer (1880); Squires (1958); Strand (1928); Traub (1938); P. Trembley (1941, 1942); Valenciennes (1850); Vincent (1893); Voigt (1958); Yabe and Sugiyama (1937).

Paleontology (Vendian Frondlike Fossil Taxa)

Arthur (1997); Bergström (1989, 1991); Buss and Seilacher (1994); Conway Morris (1991, 1993); Deng and Chen (1981); Dzik (1991); Fedonkin (1992, 1996); Glaessner (1958a, 1958b, 1959, 1961, 1984); Glaessner and Daily (1959); Glaessner and Wade (1966); Jenkins (1985, 1992); Jenkins and Gehling (1978); Lewin (1984); Liu (1981, 1983); Richter (1955); Runnegar (1992); Seilacher (1989); Simonetta and Conway Morris (1991); Weiguo (1986); Williams (1995b, 1997c, 1997d); Wright (1997).

Photography (Color Photographs of Living Sea Pens)

Allen and Steen (1994); Branch et al. (1994); Colin and Arneson (1995); Faulkner and Chesher (1979); Gosliner et al. (1996); Fosså and Nilsen (1995); Gotshall (1987, 1994); Gotshall and Laurent (1979); Kerstitch (1989); Ming (1993); Nishimura (1992); Schumacher and Hinterkircher (1996); Shimek (1998); Sprung and Delbeek (1997); Weinberg (1996); Williams (1990, 1996); Wilkins and Birkholz (1986).

Phylogeny, *Cladistics, Evolution, and Biogeography

Altuna-Prados (1994); Bergström (1989, 1991); Bourne (1900); Broch (1913b); Conway Morris (1991); Grasshoff (1973, 1991); Hickson (1916, 1930b); Kinoshita (1912); Koch (1878); Kölliker (1869-72, 1872, 1880); Kükenthal (1912b, 1914, 1915a, 1921); Kükenthal and Broch (1910, 1911); A. M. Marshall (1883b); Niedermeyer (1913); Patterson (1986); Williams (1992, *1993b, 1995a, *1995b, *1995d, 1997a, 1997b, *1997c, 1997d, 1997e).

Physiology and Cell Biology

Anctil (1987, 1989a, 1989b); Anctil et al. (1982, 1984, 1991); J. M. Anderson and Cormier (1978); J. M. Anderson et al. (1974); P. A. V. Anderson (1976); P. A. V. Anderson and Case (1975); Awad and Anctil (1993a, 1993b); Bilhaut and Pavans de Ceccatty (1971a, 1971b); Brafield (1969); Brafield and Chapman (1967); Case and Morin (1966); Chapman (1972); Child (1951); Buck and Hanson (1967); Buisson (1964, 1969, 1971a, 1971b, 1973, 1976, 1979, 1988); Carlgren (1940); Charbonneau (1981); Crawford and Chia (1974); Dickinson (1978); J. M. Franc (1979); S. Franc (1970, 1973, 1979, 1980); Hagiwata et al. (1981); Honjo (1940); Imafuku (1973, 1975, 1976); Ivester

(1977); Korotneff (1887); Krukenberg (1887); Ledger and Franc (1978); A. R. Moore (1926); Mori (all citations); Mori and Ondo (1957); Mori and Tanase (1973); Musgrave (1909); Nicol (1955b, 1955c); Parker (1920a, 1920b); Pavans de Ceccatty and Buisson (1964a, 1964b, 1965); Pavans de Ceccatty et al. (1963); Pratt (1909); Satterlie et al. (1976, 1980); Senut and Franc (1985); Takada and Mori (1956, 1957); Titschack (1965, 1966, 1968, 1970); Umbriaco et al. (1990); Waele et al. (1987).

Polymorphism, Phenotypic Variability, and Biodiversity

Hickson (1903b, 1903c); Human (1973); Jaworski (1939); A. M. Marshall (1883); Pasternak (1989); Williams (1992, 1993b, 1997b).

Quoted Passages

Agassiz (1860); Harvey (1952); Hyman (1940); Lankaster (1601); N. B. Marshall (1979); Péron (1804); C. W. Thomson (1874); Shapiro and Ramsdell (1965) quoted under Gregorio (1890); Tizard et al. (1885), Williams (1993b).

Reproductive and Developmental Biology (including Growth Stages and Regeneration)

Birkeland (1969, 1971); Chia and Crawford (1973); Dalyell (1839); Delage and Hérouard (1901); Eckelbarger et al. (1998); Franzén (1967); Jungersen (1888a, 1888b); Korschelt (1936); Lacaze-Duthiers (1865, 1887); Mori and Tanase (1973); Roule (1932); Satterlie and Case (1979); Strathmann (1988); Tarent and Tarent (1980); Torrey (1901); Tyler et al. (1995); Willemoes-Suhm (1875); Wilson (1880, 1881, 1882a, 1882b, 1883b, 1903).

Taxonomy, Distributional and Bathymetric Records

Abel (1963); Acuña and Zamponi (1992); Alder (1861, 1862, 1863, 1867); Allen (1969); Anonymous (1898); Arculeo et al. (1990); Arndt (1912); Asbornsen (1856); Atiya (1994); Atkinson (1989); Balss (1909, 1910, 1911); Barattini and Ureta (1960); Barreira y Castro (1990); Batie (1972); Bayer (1955b, 1956, 1957, 1959, 1961); Bayer and Grasshoff (1997); Belcik (1977); Belem and Alvarenga (1973); Belyaev (1972); Benham (1906, 1907); Boone (1933, 1938); Branch et al. (1994); Branch and Williams (1993); Broch (all citations); Buchanan (1955); Cairns, Hartog, and Arneson (1986); Carpine and Grasshoff (1985); Castro (1981); Colin and Arneson (1995); Costa Soares (1979); Cuvier (1797, 1800); Dana (1846); Danielssen and Koren (1884); Dawson (1966); Deichmann (1936a, 1936b, 1941); Ehrenberg (1834a, 1834b); Ellis and Solander (1786); Erhardt and Moosleitner (1995); Fautin et al. (1987); Fowler (1888, 1894); Fu et al. (in press); Gabb (1862, 1864); Gili (1986); Gili and Pagès (1987); Gosliner et al. (1996); Gotshall (1987, 1994); Gotshall and Laurent (1979); Grasshoff (all citations); Gravenhorst (1821); Gravier (all citations); Gray (all citations); Hartman (1960); Herklots (1858, 1863); Hickson (1890, 1894, 1900, 1903a, 1904, 1905, 1907, 1911, 1914, 1916, 1921, 1922, 1930a, 1936, 1937, 1940); Hoare and Wilson (1977); Hochberg and Ljubenkov (1998); Hondt (1984a, 1984b); Hubrecht (1885); Imahara (1991); Jahn (1970); Johnston (1847); Jungersen (1904, 1905, 1907, 1915, 1917); Kölliker (all citations); Koo (1935, 1940); Koren and Danielssen (1847, 1856, 1874, 1877, 1883, 1884); Kükenthal (all citations); Kramp (1932, 1933, 1950); Kumano (1937); Lacaze-Duthiers (1891); Lamarck (1816, 1836); Langton et al. (1990); Lepechin (1781); Leuckart (1841); Leunis (1886); Light (1921); Lindahl (1874a, 1874b, 1874c); Linnaeus (1758, 1767); Lopez-Gonzalez et al. (in press); Madsen (1948); Manuel (1981); A. M. Marshall (1883b); A. M. Marshall and Fowler (1888); A. M. Marshall and Marshall (1882); May (1899, 1900); Milne Edwards and Haime (1850, 1857); Molander (1929); Moroff (1902a, 1902b); O.F. Müller (1776); F. Müller (1866); Naumov (1955); Nobre (1931); Norman (1867); Nutting (1908, 1909, 1912); Pallas (1766, 1787); Panceri (1871a); Pasternak (all citations); Pax (1936); Pax and Müller (1955b, 1955c, 1962); Pérez (1996); Pfeffer (1886); Poche (1914, 1915a, 1915b); Quoy and Gaimard (1827); Rho and Song (1976, 1977); Richiardi (1869); Richmond (1997); Ridley (1883);

Riedl (1963, 1983); Riveros Zunica (1948); Robertson (1887); Rossi (1971); Roule (1905, 1906, 1908); Sachs (1913); Sars (1846,1851); M. Schultze (1871); F. E. Schulze (1875); Simpson (1905); Stearns (1873a, 1873b, 1873c, 1874, 1882, 1883); Stephens (1909); Stiasny (1937, 1938); Stimpson (1855); Studer (all citations); J. A. Thomson (1905, 1927); J. A. Thomson and Crane (1909a, 1909b); J. A. Thomson and Henderson (1905a, 1905b, 1906a, 1906b); J. A. Thomson and Mackinnon (1911); J. A. Thomson and Rennet (1927, 1931); J. A. Thomson and Ritchie (1906); J. A. Thomson and Simpson (1909); J. S. Thomson (1915, 1917, 1924); Tilesius (1826); Tixier-Durivault (all citations); Tixier-Durivault and Hondt (1974a, 1974b); Tixier-Durivault and Lafargue (1968); Utinomi (all citations); Utinomi and Shepherd (1982); Vafidis and Koukouras (1991); Van Soest (1977); Verrill (all citations); Waterman (1950); Williams (all citations); Wiktor (1974); Yashnov (1948); Zamponi and Pérez (1995a, 1995b,1996); Zamponi et al. (1997); Zuñiga (1948).

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