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Living genera of sea pens (Coelenterata: Octocorallia: Pennatulacea): illustrated key and synopses

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An illustrated dichotomous key and synopses of the 32 genera of living pennatulacean octocorals are presented, which incorporate new morphological and distributional data from the examination of recently collected material. In addition, a key to the 15 extant families, lists of valid genera, synonyms, and a table of comparative characters are also included. Lastly, a revised classification and phylogenetic considerations are presented. Preliminary investigations indicate that the traditional higher classification scheme of the Pennatulacea is inadequate for reasons of paraphyly and intermediate taxa, that tend to negate precise distinctions between some of the nominal higher taxa. Of the approximately 436 described species of sea pens worldwide, only 186 (or 43%) are estimated to be valid. In addition, several undescribed species have recently been discovered, and others will no doubt be discovered in the future. It is therefore estimated that the extant pennatulacean fauna of the world comprises approximately 200 species in 32 genera.

ADDITIONAL KEY WORDS:—Pennatulaceans – diagnoses – distributions – classification – phylogeny.

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INTRODUCTION

Sea pens, or pennatulaceans, are a highly specialized group of anthozoan coelenterates. They are benthic sessile animals that are adapted exclusively for living partly imbedded in fine to medium or relatively coarse sediments such as sand, mud, or abyssal ooze deposits. Sea pens are encountered in all of the

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world's seas and at virtually all depths (intertidal to over 6100 meters). Many deeper water species have near cosmopolitan distributions in such habitats (Williams, 1992: 363, 373).

Unlike other octocorals, sea pen colonies are formed from a single large polyp—the oozooid. Lateral budding of the body wall of the oozooid gives rise to all secondary zooids that comprise the colony. The oozooid has a fleshy proximal portion, the peduncle, which anchors the colony in soft substrata via burrowing by means of peristaltic contractions against the hydrostatic pressure of the peduncle. The daughter polyps are contained on a distal portion of the oozooid—the rachis. These are usually dimorphic (rarely trimorphic), consisting of large autozooids with well-developed tentacles, smaller siphonozooids with tentacles reduced or absent, and in some forms mesozooids (as in the genus *Pennatula*)—intermediate in form between autozooids and siphonozooids (Williams, 1990: 34). Eleven genera have well-developed polyp leaves—lateral processes emanating from opposite sides of the rachis—each containing several to many polyps. Several pennatulacean species were originally called sea pens or sea feathers (the German 'seefedern') because of their resemblance to quill pens.

It has been hypothesized that sea pens arose from alcyonacean ancestors in the shallow-water tropics, and subsequently diversified and spread to temperate and polar latitudes, as well as deeper water (Williams, 1993). The pennatulacean fossil record is considered to be restricted to the Cretaceous and Tertiary, with questionable or controversial records from earlier geological periods.

Recently acquired material from a variety of sources and from a wide geographical base has allowed for the refining and reassessment of the systematics of pennatulacean genera. Bayer (1981) published a key to the genera of octocorals excluding the pennatulaceans. The present paper is an attempt to fill in this gap and to provide revised diagnoses, detailed distributional information, and summaries of nominal species, based largely on recently procured specimens. Kükenthal (1915) provided the most recent comprehensive account of the Pennatulacea. Bayer (1956) provided a brief survey of the Pennatulacea including fossil genera. Hickson (1916) and Williams (1990) have made detailed regional surveys which have included a great deal of taxonomic information on virtually the entire group.

Dichotomous keys to the families and genera are provided and precede the synoptic account. Synopses of the genera and illustrations of the taxa are grouped together systematically for convenience of comparison. Each synopsis includes a generic synonymy, diagnostic characteristics, distribution and depth data, type species, a summary of nominal species and there recorded distributions, and references. Special taxonomic problems are covered under the heading 'Remarks'. Comprehensive lists of valid taxa as well as synonyms and misspelled names in the literature are also presented. Diagnoses of the families are provided by Kükenthal (1915), Hickson (1916), and most recently by Williams (1990). The familial arrangement presented here follows that of Hickson (1916) for the most part. The terminology used throughout the present work conforms to that of Bayer, Grasshoff and Verseveldt (1983). All figures are by the author.

The number of valid species listed under the heading 'Nominal species' in each genus are only estimates as many genera are in need of revision—which will invariably involve the study of type specimens. The estimates were arrived at by reviewing the literature (including Kükenthal, 1915 and Hickson, 1916)

and by examination of museum specimens and recently collected material. Of the approximately 436 described species of pennatulaceans, only 186 (or 43%) are here considered to be valid.

METHODS

Material has been collected recently from a variety of sources and geographic regions from 1984 to 1993. SCUBA and dredging operations off the east coast of South Africa between the Mozambique border and the eastern Cape Province have yielded fresh specimens representing many taxa, as has SCUBA collecting in Papua New Guinea, Okinawa, Taiwan, the Philippines, Malaysia, Panama, the Gulf of California and the Gulf of Mexico. Trawling off the western coast of southern Africa between the Angola/Namibia border and the western Cape Province, as well as trawling and use of a Remote Operational Vehicle off the central California coast, have produced a wealth of newly acquired material. Other material has been acquired for examination from western and southern Australia, New Zealand and Great Britain. The extensive collections of the California Academy of Sciences (representing the Indo-Pacific and eastern Pacific) and the South African Museum (representing southern Africa and the subantarctic) were also studied. Specimens representing one or two species for every genus were examined. The material examined is housed in the collections of the California Academy of Sciences, Moss Landing Marine Laboratories (California), South African Museum, National Museum of Natural History (Paris), and the Western Australian Museum. Material was preserved in 70% ethanol.

MATERIAL EXAMINED

Abbreviations are as follows: CAS (California Academy of Sciences, San Francisco, California); MLML (Moss Landing Marine Laboratories, Moss Landing, California); SAM (South African Museum, Cape Town); NMNH (National Museum of Natural History, Paris); WAM (Western Australian Museum, Perth); MBARI ROV (Monterey Bay Aquarium Research Institute, Remote Operational Vehicle, Monterey, California).

Acanthoptilum gracile (Gabb, 1864), MLML-C0039, California, Marin County, Tomales Bay, 11 m, 20 July 1971, J. W. Nybakken, 1 colony. *Actinoptilum molle* (Kükenthal, 1910), SAM-H3339, South Africa, Cape Province, Algoa Bay, 16 m, 17 May 1984, G. C. Williams, 3 colonies. *Amphiacme abyssorum* (Kükenthal, 1902), SAM-H3737, South Africa, Natal Province, off Port Durnford, 1000–1200 m, SAM RV *Meiring Naude* cruises, 2 colonies. *Anthoptilum grandiflorum* (Verrill, 1879), MLML-C0100, California, Monterey County, Monterey Bay, 1034–1107 m, 18 November 1975, E. Anderson & G. McDonald, 1 colony. *Anthoptilum murrayi* Kölliker, 1880; CAS-009459, Alaska, Bering Sea, Bowers Bank, 1068 m, 3 June 1906, USS *Albatross*, 1 colony. *Calibelemnon indicum* (Thomson & Henderson, 1906), SAM-H3734, South Africa, Natal Province, off Cape Vidal, 740 m, 27 May 1975, SAM RV *Meiring Naude* cruises, many colonies. *Cavernularia malabarica* Fowler, 1894, CAS-002392, Pakistan, Karachi region, off Kemari, 27–30 m, F. B. Steiner, 12 colonies. *Cavernulina darwini* (Hickson, 1921), CAS-088056, El Salvador, Pacific coast, off La Union, 11 July 1932, 1 colony. *Chunella gracillima* Kükenthal, 1902,

SAM-H3735, South Africa, Natal, off Port Durnford, 1000–1200 m, 25 May 1976, SAM RV *Meiring Naude* cruises, 8 colonies. *Crassophyllum cristatum* Tixier-Durivault, 1961; NMNH-St. 51, off Moita Seca, Angola, 44 m, 25 October 1948, 1 colony. *Distichoptilum gracile* Verrill, 1882, CAS-088057, California, Farallon Islands, 2900 m, 30 July 1991, Farallones Oceanic Research Expedition, 1 fragment of a colony. SAM-H3263, South Africa, Cape Province, Off Table Bay, 2744 m, 27 August 1959, Division of Sea Fisheries, several colonies. *Echinoptilum echinatum* (Kükenthal, 1910), SAM-H3684, South Africa, Transkei, off Qora River, 400–420 m, 12 July 1984, G. C. Williams, RV *Meiring Naude*. *Funiculina quadrangularis* (Pallas, 1766), SAM-H4187, South Africa, Natal Province, off Cape Vidal, 200 m, 11 June 1988, G. C. Williams, RV *Meiring Naude*, 1 colony. *Gyrophyllum sibogae* Hickson, 1916, South Australian Museum-TH11844, Australia, Tasmania, off Richardson Point, 520 m, 20 October 1984, W. Zeidler, CSIRO 'Soela' Cruise, 7 colonies. *Halipteris californica* (Moroff, 1902), MLML-C0107, California, Monterey County, off Point Sur, 549–567 m, 28 February 1978, N. J. Anu, 5 colonies. *Kophobelemnon affine* Studer, 1894, CAS-088058, California, Farallon Islands, 2795–2865 m, 27 July 1991, Farallones Oceanic Research Expedition, 1 colony. *Lituaria hicksoni* J. A. Thomson & Simpson, 1909, CAS-088059, Taiwan, Taiwan Strait, 60 m, February 1972, F. B. Steiner, 2 colonies. *Malacobelemnon* sp., SAM-H4195, South Africa, Natal, Leven Point, 50–60 m, 9 June 1988, G. C. Williams, RV *Meiring Naude*, several colonies. *Ombellula lindahli* Kölliker, 1875, CAS-088069, California, Monterey Submarine Canyon, January 1992, G van Dykhuizen, MBARI ROV, 1 colony. *Pennatula phosphorea* Linnaeus, 1758, CAS-088060, California, Farallon Islands, 2790–2825 m, 28 July 1991, Farallones Oceanic Research Expedition, 3 colonies. *Protoptilum* sp., CAS-088061, California, Farallon Islands, 2300–2550 m, 29 July 1991, Farallones Oceanic Research Expedition, 1 colony. CAS-088066, California, Farallon Islands, 2900 m, 30 July 1991, Farallones Oceanic Research Expedition, 1 colony. *Pteroeides* sp., CAS-088071, Papua New Guinea, Madang region, Pig Island, 6–27 m, 27 November 1990, G. C. Williams, 5 colonies. CAS-088062, Papua New Guinea, Madang region, Pig Island, 4.6 m, 5 June 1992, T. M. Gosliner, 1 colony. *Pteroeides spinosum* (Ellis, 1764), CAS-088063, Mediterranean Sea, France, Banyuls-sur-Mer, 35 m, 15 October 1992, R. J. Mooi & B. David, RV *Nereis*, 1 colony. *Ptilosarcus undulatus* (Verrill, 1865), CAS-088065, Mexico, Baja California Sur, off Isla Requeson, 15 m, 5 October 1992, G. Metz, 3 colonies. CAS-013015, Mexico, Baja California Sur, La Paz, 22 March 1940, E. F. Ricketts, 6 colonies. *Ptilosarcus gurneyi*, CAS-088064, California, Channel Islands, San Nicolas Island, 27 August 1932, 1 colony *Renilla amethystina* Verrill, 1864, CAS-000896, California, Orange County, Newport Bay, January 1930, G. E. MacGinitie, 2 colonies. *Sarcoptilus grandis* Gray, 1860, WAM-68-59, Australia, Western Australia, Albany, 4.6 m, 12 January 1959, 1 colony. *Sclerobelemnon* sp. CAS-088067, Papua New Guninea, Madang region, Pig Island, 10–16 m, 10 June 1992, G. C. Williams, 8 colonies. *Scleroptilum grandiflorum*, NMNH-Biogas 5/DS 66, off Bay of Biscay, France, 3480 m, 12 June 1974, 1 colony. *Scytaliopsis djiboutiensis* Gravier, 1906, SAM-H3711, South Africa, Transkei, off Qora River, 450-460 m, 14 July 1984, G. C. Williams, RV *Meiring Naude*, 1 colony. *Scytalium* sp., SAM-H4133, South Africa, Natal, Kosi River Mouth, 48 m, 8 June 1987, G. C. Williams, RV *Meiring Naude*, 2 colonies. CAS-088068, Taiwan, Taiwan Strait, 30–50 m, 5 May 1972, F. B. Steiner, 6 colonies. *Stachyptilum superbum* Studer, 1894, CAS-024641, Oregon, Lincoln County, off Newport, 750 m, 4 September 1962, A. G. Carey, RV *Acona*, 1 colony. *Stylatula elongata* Gabb, 1862, CAS- 008887, California, San Francisco Bay, 18 March 1912, USS *Albatross*, 2 colonies. *Veretillum* spp., CAS-088070, Papua New Guinea, Madang region, Pig Island, 15–27 m, 27 November 1990, G. C. Williams, 6 colonies. CAS-088072, Papua New Guinea, Madang region, Pig Island, 6–21 m, 27 November 1990, G. C. Williams, 7 colonies. *Virgularia schultzei* Kükenthal, 1910, SAM-H3338, South Africa, Cape Province, Algoa Bay, 16 m, 17 May 1984, G. C. Williams, 1 colony.

KEY TO THE FAMILIES OF PENNATULACEA

1 Adjacent autozooids free, not fused to any degree 2
– Proximal portions of adjacent autozooids fused to some degree, forming polyp leaves or raised ridges, or joined only at the bases 12
2 Colonies cordate/foliate; rachis greatly flattened, lying on surface of substratum ..... Renillidae
– Colonies cylindrical, capitate, clavate, or elongate; rachis erect, not lying on substratum 3
3 Autozooids distributed evenly and on all sides of rachis, or proximal portion of rachis with a single longitudinal furrow or V-shaped region devoid of polyps 4
– Autozooids confined to a terminal cluster, or arranged biserially along rachis, or in whorls of two to four arranged sparsely along rachis, or arranged on three sides of rachis with a naked dorsal tract along entire length of rachis 5
4 Autozooids without calyces ..... Veretillidae
– Autozooids with non-retractile bifurcated calyces ..... Echinoptilidae
5 Autozooids arranged in a terminal cluster at the end of a long slender stalk ..... Ombellulidae
– Autozooids arranged along the sides of the rachis 6
6 Colonies cylindrical or clavate with distal portion often somewhat wider than rest of colony. Polyps arranged biserally and not in oblique rows, or disposed on three sides of rachis with a naked dorsal tract along the entire length of the rachis .....Kophobelemnidae
– Colonies elongate and narrow with uniform thickness, or if clavate then polyps arranged in oblique rows. Polyps arranged biserally or in isolated pairs or whorls 7
7 Colonies without sclerites. Polyps arranged biserally without calyces ..... Anthoptilidae
– Colonies with or without sclerites, and polyps arranged in pairs or whorls of 2–4, without calyces; or colonies with sclerites, and polyps arranged biserally, with calyces 8
8 Rachis with or without sclerites. Polyps arranged in pairs or whorls of 2–4, without calyces 9
– Rachis with sclerites. Polyps arranged biserally, with calyces 10
9 Rachis with spindles or rods (<0.10 mm) .....Scleroptilidae
– Rachis without sclerites or with minute irregularly-shaped rods (>0.05 mm) ..... Chunellidae
10 Autozooids tubular with calyces having eight conspicuous terminal teeth; siphonozooids and autozooids morphologically similar ..... Funiculinidae
– Calyces with zero to eight terminal teeth; siphonozooids and autozooids very different morphologically 11
11 Polyps arranged in oblique or transverse rows along the rachis; colonies often somewhat clavate .....Stachyptilidae
– Autozooids arranged in one to three longitudinal rows along the rachis; colonies elongate, not clavate .....Protoptilidae
12 Autozooids disposed on raised ridges or pads that are obliquely arranged along the rachis 13
– Autozooids disposed on conspicuous polyps leaves that emanate laterally

along the rachis in two opposite longitudinal series 14
13 Rachis with sclerites. Polyps with bifurcated calyces ..... Halipteridae
– Rachis without sclerites. Polyps without calyces ..... Anthoptilidae
14 Autozooids tubular with spiculiferous calyces having one, two or eight terminal teeth ..... Pennatulidae
– Autozooids without spiculiferous calyces 15
15 Autozooids united to form thin, often translucent polyp leaves; peduncle often slender and vermiform; rachis rodshaped; siphonozooids often present on rachis ..... Virgulariidae
– Autozooids contained on large, opaque, often thick polyp leaves; peduncle thick; rachis feather-shaped; siphonozooids restricted to polyp leaves ..... Pteroeididae

KEY TO THE GENERA OF PENNATULACEA

1 Polyps arise directly from the surface of the rachis (Figs 1–4) 2
– Polyps arise from lateral processes of the rachis, which may be in the form of inconspicuous raised ridges or conspicuous polyp leaves (Figs 5, 6) 21
2 Symmetry of colony radial throughout (Fig. 1A–E) 3
– Symmetry of colony bilateral in the lower part of the rachis or bilateral throughout the entire rachis (Figs 1G, 2–4).....7
3 Polyps with two-toothed calyces (Fig. 1F) ..... *Actinoptilum*
– Polyps without calyces (Fig. 1A–D) 4
4 Sclerites are smooth spindles, rods, or ovals (Fig. 7D) ..... *Cavernularia*
– Sclerites are primarily rods or plates, smooth or rough with denticles or tubercules, or with bilobed or branched ends 5
5 Sclerites are rods or plates, mostly conspicuously bilobed or branched at the ends (Fig. 7C) ..... *Cavernulina*
– Sclerites are mostly plates, irregularly-shaped, bone-shaped, or biscuit-shaped, finely denticulated to tuberculated or smooth, but not conspicuously bilobed or branched at the ends 6
6 Sclerites include tuberculated capstan-like forms or broad irregular plates, often rough with tubercles or terminal denticles, as well as smooth bone-shaped platelets; interior of peduncle without minute otolith-shaped ovals (Fig. 7A) ..... *Lituaria*
– Sclerites are either flat plates with smooth rounded ends and mostly constricted in the middle, or irregularly-shaped plates often rough with fine denticulation or tubercles; interior of peduncle with numerous minute otolith-like bodies (Fig. 7B) ..... *Veretillum*
7 Only proximal portion of rachis shows bilateral symmetry (Fig. 1G) ..... *Echinoptilum*
– Entire rachis shows bilateral symmetry (Figs 2–4) 8
8 All polyps arranged in a terminal cluster or with a single large polyp at the end of a long naked stalk (Fig. 4E) ..... *Ombellula*
– Polyps not arranged in a terminal cluster 9
9 Colonies cordate/foliate and flattened (Fig. 2A). Axis absent ..... *Renilla*
– Colonies not flattened but rather clavate or long and thin with uniform thickness. Axis present 10
10 Colonies cylindrical or clavate with distal portion often somewhat wider

than the rest of the colony. Polyps longitudinally disposed, not arranged in oblique rows (Fig. 2B–D) 11
– Colonies long and thin with uniform thickness (vermiform), or if clavate then polyps arranged in oblique rows (Figs 3, 4A–D) 13
11 Colonies without sclerites .....*Malacobelemnon*
– Colonies with sclexites 12
12 Sclerites are plate-shaped or bone-shaped (Fig. 8B) .....*Sclerobelemnon*
Sclerites are three-flanged needles and spindles (Fig. 8C) .....*Kophobelemnon*
13 Colonies without sclerites. Polyps arranged biserally, without calyces (Fig. 3C) .....*Anthoptilum*
– Colonies with or without sclerites, and polyps in whorls of 2–4, without calyces; or colonies with sclerites, and polyps arranged biserally, with calyces 14
14 Polyps without calyces. Polyps arranged in several isolated pairs or whorls along the rachis (Fig. 4A–D) 15
– Polyps with calyces. Polyps arranged biserially along the sides of the rachis (Fig. 3A, E, I) 18
15 Colonies with a single terminal rudimentary or fully developed polyp (Fig. 4C & D) 16
– Colonies without a terminal polyp (Fig. 4A & B) 17
16 Terminal polyp fully developed (Fig. 4D) .....*Amphiacme*
– Terminal polyp rudimentary (Fig. 4C) .....*Chunella*
17 Rachis with spindles or rods (0.10–0.36 mm), inconspicuously or distinctly three-flanged (Fig. 9A) .....*Scleroptilum*
– Rachis without sclerites or with minute irregularly-shaped rods (>0.05 mm), which are not three-flanged .....*Calibelemnon*
18 Calyces with eight terminal teeth. Siphonozooids appear morphologically similar to autozooids (Fig. 3I & J) .....*Funiculina*
– Calyces with zero to eight terminal teeth. Siphonozooids morphologically very different from autozooids 19
19 Polyps arranged in longitudinal rows (Fig. 3B & F) 20
– Polyps arranged in oblique or transverse rows along the rachis (Fig. 3G & H) .....*Stachyptilum*
20 Polyps arranged in two alternate or suboposite longitudinal series with no polyps on the ventral surface. Calyces usually with two to six terminal teeth (Fig. 3A & B) .....*Distichoptilum*
– Polyps arranged in one to three longitudinal series with some polyps present on the ventral surface. Calyces with zero to eight terminal teeth (Fig. 3E & F) .....*Protoptilum*
21 Polyps present on raised ridges or pads that are obliquely arranged along the rachis (Figs 3D & 5B) 22
– Polyps present on well-defined polyp leaves that emanate laterally in two opposite longitudinal series (Fig. 5C & L, 6) 23
22 Colonies with sclerites, autozooids with calyces (Fig. 5A & B) .....*Halipteris*
– Colonies without sclerites, autozooids without calyces (Fig. 3C & D) .....*Anthoptilum*
23 Polyps are united to form thin polyp leaves, peduncle often slender and vermiform, rachis rod-shaped (Fig. 5C–L) 24
Polyps are contained on large often thick polyp leaves, peduncle thick, rachis

feather-shaped (Fig. 6) 28
24 Sclerites present in the rachis and polyp leaves 25
– Sclerites absent in the rachis and polyp leaves 27
25 Needle- or spindle-shaped sclerites present in the rachis or polyp leaves 26
– Only small plate-shaped sclerites scattered in the rachis and polyp leaves (Fig. 9I) ..... *Scytalium*
26 Needle-like sclerites form a strong fan-shaped armature at the base of each polyp leaf (Fig. 5D) ..... *Stylatula*
– Spindle-like sclerites form a weak cluster at the base of each polyp leaf, or spindles present in autozooids with basal cluster absent (Fig. 5F) ..... *Acanthoptilum*
27 Polyps of a single polyp leaf are of equal size (Fig. 5J) ..... *Virgularia*
– Polyps on the inner portion of each polyp leaf are smaller in size than those of the outer portion of the leaf (Fig. 5L) ..... *Scytaliopsis*
28 Sclerites are three-flanged spindles and irregularly-grooved rods, or oval plate-like sclerites and finger biscuits (Fig. 10A–C) 29
– Sclerites are smooth or irregularly-grooved spindles, needles, or rods (Fig. 10D–F) 31
29 Rachis excluding polyp leaves conspicuously wider than peduncle, colony excluding leaves clearly clavate in appearance. Peduncle conspicuously longer than rachis. Polyp leaves thick and fleshy, not densely spiculated, few in number (>10 per side) (Fig. 6F & G) ..... *Gyrophyllum*
– Rachis excluding polyp leaves not conspicuously wider than peduncle, colony excluding leaves not clearly clavate in appearance. Peduncle shorter than or equal to length of rachis. Polyp leaves thin, densely spiculated, numerous (<10 per side) 30
30 Calyces with eight teeth (Fig. 6B) ..... *Pennatula*
– Calyces with one or two teeth (Fig. 6D & E) ..... *Ptilosarcus*
31 Polyp leaves without needle-shaped sclerites. Rachis and polyp leaf sclerites are spindles, elongate rods, or short flattened rods. Siphonozooids restricted to a swollen pad at base of each polyp leaf, absent from surfaces of polyp leaves (Fig. 6K) ..... *Sarcoptilus*
– Polyp leaves with needle-shaped sclerites. Siphonozooids crowded and forming a zone, which covers the entire proximal portion of the polyp leaves (Fig. 6I & M) 32
32 Needle-like sclerites of the polyp leaves form strong rays. Rachis sclerites are rods (Fig. 6I) ..... *Pteroeides*
– Needle-like sclerites of the polyp leaves do not form rays. Rachis sclerites absent (Fig. 6M) ..... *Crassophyllum*

APHABETICAL LIST OF PENNATULACEAN GENERA CONSIDERED VALID

Acanthoptilum Kölliker, 1870
Actinoptilum Kükenthal in Kükenthal & Broch, 1911
Amphiacme Kükenthal, 1903
Anthoptilum Kölliker, 1880
Calibelemnon Nutting, 1908
Cavernularia Valenciennes in Milne Edwards & Haime, 1850
Cavernulina Kükenthal & Broch, 1911
Chunella Kükenthal, 1902
Crassophyllum Tixier-Durivault, 1961
Distichoptilum Verrill, 1882

Echinoptilum Hubrecht, 1885
Funiculina Lamarck, 1816
Gyrophyllum Studer, 1891
Halipteris Kölliker, 1870
Kophobelemnon Asbjørnsen, 1856
Lituaria Valenciennes in Milne Edwards & Haime, 1850
Malacobelemnon Tixier-Durivault, 1965
Ombellula Cuvier, 1798
Pennatula Linnaeus, 1758
Protoptilum Kölliker, 1872
Pteroeides Herklots, 1858
Ptilosarcus Verrill, 1865
Renilla Lamarck, 1816
Sarcoptilus Gray, 1848
Sclerobelemnon Kölliker, 1872
Scleroptilum Kölliker, 1880
Scytaliopsis Gravier, 1906
Scytalium Herklots, 1858
Stachyptilum Kölliker, 1880
Stylatula Verrill, 1864
Veretillum Cuvier, 1798
Virgularia Lamarck, 1816

SYNONYMS AND MISSPELLED GENERIC NAMES OF PENNATULACEA

(synonyms are listed on the left with the valid genera to which they belong shown in parentheses; *=misspelled names or transcription errors)

**Acanthoptilon* Traquar 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 (*Kophobelemnon*)
Benthoptilum Verrill, 1885 (*Anthoptilum*)
**Benthoptillum* Haddon in Zoological Record 22, 1885 (*Anthoptilum*)
Cladiscus Koren & Danielssen, 1877 (*Virgularia*)
Clavella Gray, 1870 (*Lituaria*)
Crinillum Harting, Miguel & Hoeven, 1861 (*Ombellula*)
Crispella Gray, 1870 (*Pteroeides*)
Deutocaulon Marshall & Fowler, 1888 (*Virgularia*)
Dübenia Danielssen & Koren, 1884 (*Stylatula*)
Encrinus Lamarck, 1801 (*Ombellula*)
Fusticularia Simpson, 1905 (probably synonymous with *Cavernularia* according to Kükenthal, 1915)
**Godefroyia* Leuckart, 1872 (*Pteroeides*)
Godeffroyia Kölliker, 1870 (*Pteroeides*)
Göndul Koren & Danielssen, 1883 (*Halipteris*)
Gunneria Danielssen & Koren, 1884 (*Kophobelemnon*)
Halisceptrum Herklots, 1863 (*Virgularia*)
Helicoptilum Nutting, 1912 (*Distichoptilum*)
Herklotsia Gray, 1860 (*Renilla*)
Juncoptilum Thomson & Henderson, 1905 (*Distichoptilum*)
**Leioptilum* Verrill, 1865 (*Ptilosarcus*)
**Leioptillum* 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 & Danielssen, 1877 (*Halipteris*)
Lygus Herklots, 1858 (*Virgularia*)
Mesobelemnon Gravier, 1907 (considered synonymous with *Sclerobelemnon* by Hickson, 1916)
Microptilum Kölliker, 1880 (*Halipteris*)
Norticina Gray, 1870 (*Halipteris*)
Ombellulaires Cuvier, 1817 (*Ombellula*)
Ombellularia Lamarck, 1836 (*Ombellula*)
Osteocella Gray, 1870 (*Halipteris*)
Parabelemnon (probably synonymous with *Cavernularia*)
Pavonaires Cuvier, 1827 (*Funiculina*)
Pavonaria Schweigger, 1820 (*Funiculina*)
Pavonaria Kölliker, 1869 (*Halipteris*)
Penna Bohadsch, 1761 (*Pennatula*, in part) (name unavailable as the work was suppressed by ICZN)
Phosphorella Gray, 1870 (*Pennatula*)
Policella Gray, 1870 (*Veretillum*)

Prochunella Balss, 1909 (*Calibelemnon*)
Protocaulon Kölliker, 1880 (*Virgularia*)
**Pteroides* Pfeffer, 1886 (*Pteroeides*)
Pteromorpha Herklots, 1858 (*Pteroeides*)
Ptilella Gray, 1870 (*Pennatula*)
Renila Schweigger, 1820 (*Renilla*)
Renillina Gray, 1860 (possibly a young example of the alcyoniid soft coral *Sarcophyton* according to Kükenthal, 1915)
Sarcobelemnon Herklots, 1858 (*Cavernularia*)
Sarcophyllum Kölliker, 1870 (*Sarcoptilus*)
Sceptonidium Richiardi, 1869 (*Virgularia*)
Stephanoptilum Roule, 1905 (*Anthoptilum*)
Stichoptilum Grieg, 1887 (*Halipteris*)
Struthiopteron Broch, 1910 (*Pteroeides*)
Stylobelemnon Kölliker, 1872 (*Cavernularia*)
Stylobelemnoides J. A. Thomson & Henderson, 1905 (possibly synonymous with *Cavernularia*)
Svava Danielssen & Koren, 1884 (*Virgularia*)
Svavopsis Roule, 1908 (*Virgularia*)
Thesioides J. A. Thomson & Henderson, 1906 (*Anthoptilum*)
Trichoptilum Kölliker 1880 (*Funiculina*)
Umbellaria Schweigger, 1820 (*Ombellula*)
**Umbellula* Gray, 1870 (*Ombellula*)
Umbellularia Lamarck, 1801 (*Ombellula*)
**Verrilia* Lutken in Zoological Record 10, 1873 (*Halipteris*)
Verrillia Stearns, 1873 (*Halipteris*)
Vorticella Linnaeus, 1767 (*Ombellula*, in part)

SYNOPSES OF THE GENERA OF PENNATULACEA

Order Pennatulacea Verrill, 1865

Family Veretillidae Herklots, 1858

Lituaria Valenciennes MS in Milne Edwards & Haime, 1850 (Figs 1A, 7A)

Pennatula (*non* Linnaeus, 1758) Pallas, 1766: 179 (in part).
Veretillum (*non* Cuvier, 1798) Lamarck, 1816: 420 (in part).
Lituaria Valenciennes MS in Milne Edwards & Haime, 1850: 84. Gray, 1870: 33. Kölliker, 1872a: 135. J. A. Thomson & Simpson, 1909: 31.1. Balss, 1910: 73. Kükenthal, 1915: 7. Hickson, 1916: 42. Light, 1921: 247. Williams, 1990: 49.
Clavella Gray, 1870: 33. Kölliker, 1872a: 144. J. A. Thomson & Simpson, 1909: 311. Balss, 1910: 78. Hondt, 1984b: 636 (discussion of reasons for synonymy). *Type species*. *C. australasiae* Gray, 1870.

Diagnosis. Colonies cylindrical to clavate. Radial symmetry throughout length of rachis. Axis present in the rachis, sometimes with longitudinal furrows or outgrowths. Polyp leaves absent. Autozooids evenly distributed on surface of rachis. Anthocodiae retractile into rachis, permanent calyces absent. Siphonozooids densely-set between the autozooids. Sclerites mostly short (>0.20 mm long) tuberculated capstan-like forms or irregularly-shaped broad plates, many of which are finely tubercated or have denticles on the ends. Other sclerites are rods, crosses, and smooth bone-shaped or biscuit-shaped plates. Interior of peduncle without minute otolith-like ovals. Polyps with or without sclerites.

Distribution and depth. Indo-West Pacific (southeastern Africa, India, Mergui and Andaman Archipelagos, Malay Archipelago, Philippines, southern China, Taiwan, Japan, Papua New Guinea, and Australia); 3–150 m in depth.

Type species. *Pennatula phalloides* Pallas, 1766 (by subsequent designation—d'Hondt, 1984: 638); Indian Ocean (nonspecific type locality).

Nominal species. Ten nominal species, all of which are considered here as valid: *Lituaria amoyensis* Koo, 1935 (Taiwan Strait); *L. australasiae* (Gray, 1860) (Northern Australia); *L. breve* Light, 1921 (Philippines); *L. habereri* Balss, 1910 (Japan); *L. hicksoni* Thomson & Simpson, 1909 (India); *L. kuekenthali* Light, 1921 (Philippines); *L. molle* Light, 1921 (Philippines); *L. phalloides* (Pallas, 1: 66) (Indian Ocean); *L. philippinensis* Light, 1921 (Philippines); *L. valenciennesi* d'Hondt, 1984 (Eastern Indian Ocean and Western Pacific).

Remarks. According to Hondt (1984b: 636), *Lituaria phalloides* Valenciennes MS in Milne Edward & Haime, 1850 and *Pennatula phalloides* Pallas, 1766 represent two different species. She established Pallas's species as the type of the genus *Lituaria* and gave the new name *Lituaria valenciennesi* for Valenciennes's species, which was erroneously designated as *Lituaria phalloides* by Kölliker, 1872 and Kükenthal, 1915.

References for species identification. Light, 1921; Hondt, 1984b.

Cavernulina Kükenthal & Broch, 1911
(Figs 1B, 7C)

Cavernularia (non Valenciennes in Milne Edwards & Haime, 1850) J. A. Thomson & Simpson, 1909: 302 (in part). Hickson, 1916: 52, 54 (in part).

Cavernulina Kükenthal & Broch, 1911: 172 Kükenthal, 1915: 9. Williams, 1989: 307. 1990: 48.

Diagnosis. Cylindrical to clavate in shape. Radial symmetry throughout length of rachis. Axis present. Polyp leaves absent. Autozooids distributed evenly over entire surface of rachis. Anthocodiae retractile directly into rachis; permanent calyces absent. Siphonozooids numerous between autozooids. Rachis sclerites are mainly rods with bilobed or branched ends, >0.4 mm long. Peduncle sclerites are smooth rods and spindles, mostly bilobed or branched at the ends, >0.2 mm long. Polyps without sclerites:

Distribution and depth. Indo-Pacific and eastern Pacific (southeastern Africa, India, Indonesia, Ryukyu Islands, New Caledonia, Baja California, El Salvador, Ecuador, Galapagos Archipelago); 30–62 m in depth.

Type species. *Cavernulina cylindrica* Kükenthal & Broch, 1911 (by monotypy); type locality Amboina (Malay Archipelago).

Nominal species. Four described species, all considered valid: *Cavernulina cylindrica* Kükenthal & Broch, 1911 (Malay Archipelago); *C. darwini* (Hickson, 1921) (eastern Pacific); *C. grandiflora* Hondt, 1984b (New Caledonia); *C. orientalis* Thomson & Simpson, 1909 (India to western Pacific).

Remarks. The distinction between *Cavernulina* and *Cavernularia* is based on the presence of sclerites that are branched or bilobed at the ends in the former and unbranched in the latter. An initial comparative examination of material representing both genera shows the distinction to be not well-defined. Some rachis sclerites of *Cavernulina obesa* and *C. malabarica* are conspicuously branched at the ends (Hondt, 1984b: 631, 633), while some rachis sclerites in species of *Cavernulina* such as *C. grandiflora* are clearly unbranched (Hondt, 1984b: 628). It seems that certain species of both genera contain varying proportions of branched to unbranched sclerites. I therefore consider the genus *Cavernulina* to be of dubious validity. However, I have retained the distinction between the genera here, as I have examined very few specimens of material that can be

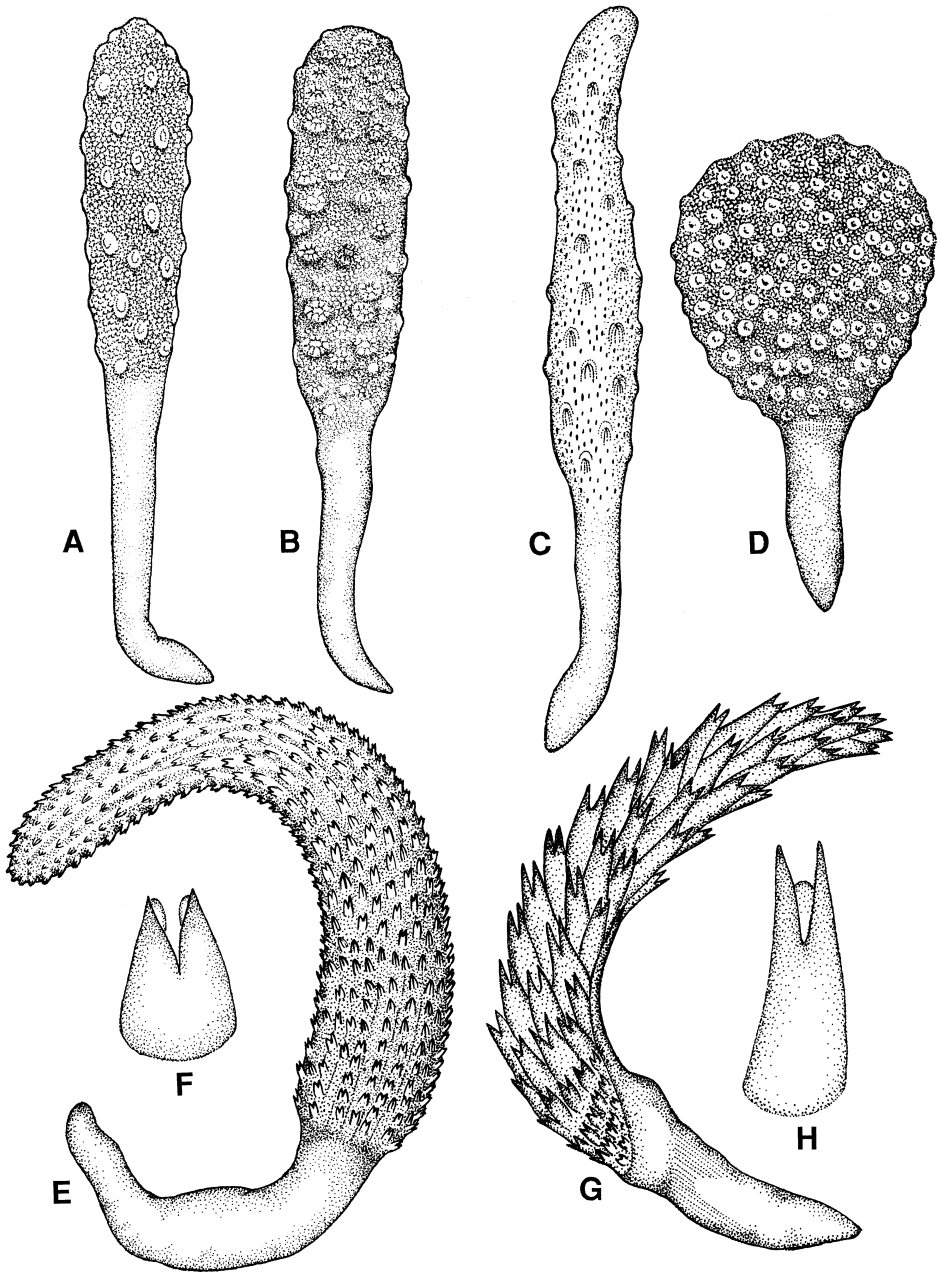

Figure 1. Colonies A, *Lituaria hicksoni*, 80 mm. B, *Cavernulina darwini*, 55 mm. C, *Veretillum manillensis*, 120 mm. D, *Cavernularia malabarica*, 25 mm. E, *Actinoptilum molle*, 150 mm. F, *Actinoptilum molle*, calyx of a retracted autozooid, 1.2 mm. G, *Echinoptilum echinatum*, 70 mm. H, *Echinoptilulm echinatum*, calyx of a retracted autozooid, 3 mm.

allocated to *Cavernulina*. A comparison of types and the examination of more material representing both genera is necessary before a synonymy can be made.

References for species identification. Hondt, 1984b.

Veretillum Cuvier, 1798
(Figs 1C, 7B)

Pennatula (*non* Linnaeus, 1758) Pallas, 1766: 177 (in part).
Alcyonium (*non* Linnaeus, 1758) Linnaeus, 1767: 342 (in part).
Veretillum Cuvier, 1798: 675. Herklots, 1858: 26. Gray, 1870: 33. Kölliker, 1872a: 324. Balss, 1910: 79. Kükenthal & Broch, 1911: 175. Kükenthal, 1915: 11. Hickson, 1916: 46. Williams, 1990: 47.
Policella Gray, 1870: 33. Kölliker, 1872a: 138. Balss, 1910: 79. Kükenthal & Broch, 1911: 170. Kükenthal, 1915: 10. *Type species*. *P. australis* Gray, 1870.

Diagnosis. Colonies cylindrical or slightly clavate. Radial symmetry throughout length of rachis. Axis variable in length, from well-developed to absent. Polyp leaves absent. Autozooids evenly distributed over entire surface of rachis. Anthocodiae retractile into rachis, calyces absent. Siphonozooids numerous between the autozooids, sometimes in longitudinal rows. Surface sclerites are small (>0.15 mm) irregularly-shaped plates with varying amounts of fine denticulation or tuberculation, or bone-shaped or biscuit-shaped plates, smooth and rounded on the ends and usually constricted in the middle, densely to sparsely distributed. Interior sclerites of the peduncle are minute otolith-like ovals (>0.03 mm long), usually numerous. Sclerites may be absent from the rachis altogether. Polyp sclerites present or absent.

Distribution and depth. Eastern Atlantic and Indo-West Pacific (southern Europe, Mediterranean Sea, along the west coast of Africa to Namibia, southern Mozambique, Andaman and Merqui Archipelagos, Western Australia, Malay Archipelago, Philippines, and Papua New Guinea), 6–220 m in depth.

Type species. *Pennatula cynomorium* Pallas, 1766 (by subsequent monotypy—Cuvier, 1798); type locality Europe.

Nominal species. Eighteen described species have been referred to this genus, of which perhaps seven are valid: *Veretillum australis* (Gray, 1870) (Western Australia); *V. cynomorium* (Pallas, 1766) (Eastern Atlantic from southern Europe to western Africa and Indian Ocean from southern Mozambique); *V. leloupi* Tixier-Durivault, 1960 (southern Mozambique); *V. malayense* Hickson, 1916 (Malay Archipelago); *V. manillensis* (Kölliker, 1872) (Eastern Indian Ocean and western Pacific); *V. tenuis* (Marshal & Fowler, 1889) (Eastern Indian Ocean); *V. vanderbilti* Boone, 1938 (Philippines).

Remarks. Kükenthal (1915: 7) differentiates *Policella* from *Veretillum* by the absence of sclerites in the polyps of *Policella*. The amount of polyp spiculation is a variable character in many octocoral species, and in my opinion does not justify the establishment of a separate genus.

References for species identifications. Hickson, 1916.

Cavernularia Valenciennes in Milne Edwards & Haime, 1850
(Figs 1D, 7D)

Veretillum (*non* Cuvier, 1798) Philippi, 1835: 277. Gray, 1870: 28.
Cavernularia Valenciennes in Milne Edwards & Haime, 1850: 84. Kukenthal & Broch, 1911: 180 (Lit.!). Kükenthal, 1915: 12. Hickson, 1916: 50. Williams, 1989: 304. 1990: 41.
Sarcobelemnon Herklots, 1858: 25. *Type species: S. elegans* Herklots, 1858.

Stylobelemnon Kölliker, 1872a: 336. Balss, 1910: 79. *Type species: S. pusillum* Kölliker, 1872.

?Fusticularia Simpson, 1905: 561. Balss, 1910: 80. Kükenthal, 1915: 18. *Type species: F. herdmani* Simpson, 1905.

?Parabelemnon J.A. Thomson & Simpson, 1909: 307. Kükenthal, 1915: 17. *Type species: P. indicum* Thomson & Simpson, 1909.

?Stylobelemnoides J.A. Thomson & Henderson, 1905: 325. Kükenthal, 1915: 18. *Type species: S. herdmani* Thomson & Henderson, 1905.

Diagnosis. Cylindrical, clavate, or capitate in shape. Radial symmetry throughout length of rachis. Axis absent, rudimentary, or conspicuous. Polyp leaves absent. Autozooids distributed evenly over entire surface of rachis. Anthocodiae retractile directly into rachis; permanent calyces absent. Siphonozooids numerous between autozooids. Sclerites are smooth spindles, rods, or ovals. Interior sclerites of the peduncle are often minute ovals. Polyps with or without sclerites.

Distribution and depth. Eastern Atlantic and Indo-Pacific (southern Europe, Mediterranean Sea, along the west coast of Africa to Namibia, east coast of Africa from South Africa to Tanzania, India, Pakistan, Indonesia, Taiwan, Truk, Japan, Papua New Guinea, Australia, New Caledonia and the Marquesas); 3–320 m in depth.

Type species. *Cavernularia obesa* Valenciennes in Milne Edwards & Haime, 1850 (by monotypy); Indian Seas (nonspecific type locality).

Nominal species. At least 20 described species that have been referred to this genus, 13 of which are here considered valid: *Cavernularia capitata* Williams, 1989 (South African east coast); *C. chuni* Kükenthal & Broch, 1911 (Borneo); *C. clavata* Kükenthal & Broch, 1911 (Taiwan); *C. dayi* Tixier-Durivault, 1954 (South African east coast); *C. dedeckeri* Williams, 1989 (South African east coast); *C. elegans* (Herklots, 1858) (African west coast); *C. glans* Kölliker, 1872 (India, China, Japan); *C. habereri* Moroff, 1902 (Japan); *C. luetkeni* Kölliker, 1872 (Bay of Bengal); *C. malabarica* Fowler, 1894 (India); *C. mirifica* Tixier-Durivault, 1963 (Senegal, Gambia); *C. obesa* Valenciennes in Milne Edward & Maime, 1850) (Indo-Pacific); *C. pusilla* (Philippi, 1835) (Mediterranean, Senegal).

References for species identifications. Williams, 1989.

Family Echinoptilidae Hubrecht, 1885

Actinoptilum Kükenthal in Kükenthal & Broch, 1911
(Figs 1E & F, 7E)

Cavernularia (*non* Valenciennes in Milne Edwards & Haime, 1850) Hickson, 1900: 89, 92.

Actinoptilon Kükenthal, 1910: 56.

Actinoptilum Kükenthal in Kükenthal & Broch, 1911: 201. Kükenthal, 1915: 20. Williams, 1990: 58.

Actinoptinum Day *et al.*, 1970: 17 (incorrect spelling for *Actinoptilum*).

Diagnosis. Colonies cylindrical and sausage-shaped. Rachis radially symmetrical throughout. Axis absent. Polyp leaves absent, autozooids emanating directly from rachis. Autozooids with permanent bifurcated calyces, bird-beaked shaped; terminal teeth short (>2.0 mm long with acute tips. Anthocodiae retractile

into calyces. Siphonozooids crowded between autozooids, with minute bifurcated calyces. Sclerites include three-flanged spindles in the calyces and rachis, small ovals or platelets in the polyp walls, and finger-biscuitlike forms and minute ovals in the peduncle.

Distribution. Southern Africa (west coast of South Africa to southern Mozambique); 12–333 m in depth.

Type Species. *Actinoptilon molle* Kükenthal, 1910 (by monotypy); type locality South Africa.

Nominal Species. A monotypic genus: *Actinoptilum molle* (Kükenthal, 1910) (southern Africa).

References for species description. J. S. Thomson, 1915; Williams, 1990.

Echinoptilum Hubrecht 1885
(Figs 1G & H, 7F)

Echinoptilum Hubrecht 1885: 512. Balss, 1910: 37. Kükenthal & Broch, 1911: 196. Kükenthal, 1915: 18. Hickson, 1916: 57. Williams, 1990: 50.

Actinoptilon Kükenthal, 1910: 54 (in part). *Species designated: A. echinatum* Kükenthal, 1910.

Diagnosis. Colonies digitiform, sometimes distinctly curved. Distal portion of rachis is usually radially symmetrical while proximal portion shows distinct bilateral symmetry. Axis absent. One side of colony with a longitudinal furrow or groove forming an inverted V-shaped area in the proximal portion of the rachis, which is devoid of polyps. Polyp leaves absent. Autozooids present on all sides of the rachis except in the region of the longitudinal furrow, sometimes arranged in indistinct oblique rows. Anthocodiae retractile into conspicuous bifurcated calyces with prominent acute-tipped teeth. Siphonozooids are numerous at the bases of autozooids, also with bifurcate spiculiferous calyces. Sclerites are three-flanged needles, spindles, or rods of the calyces and rachis, as well as broad spindles, rods and ovals of the surface of the peduncle, which may be longitudinally grooved but not conspicuously three-flanged. Minute ovoid bodies are present in the interior of the peduncle.

Distribution and depth. Indo-Pacific (east coast of Africa from Somalia to Transkei, Malay Archipelago, Japan, Hawaii); 50–628 m in depth.

Type species. *Echinoptilum macintoshii* Hubrecht, 1885 (by monotypy); type locality Japan.

Nominal species. Six described species, with number of valid species questionable: *Echinoptilum asperum* Hickson, 1916 (Malay Archipelago); *E. echinatum* (Kükenchal, 1910) (east coast of Africa); *E. elongatum* Hickson, 1916 (Malay Archipelago); *E. macintoshi* Hubrecht, 1885 (southeastern Africa, Japan, Hawaii); *E. minimum* Hickson, 1916 (Malay Archipelago); *E. roseum* Hickson, 1916 (Malay Archipelago).

References for species identification. Hickson, 1916; Williams, 1990.

Family Renillidae Gray, 1870

Renilla Lamarck, 1816
(Figs 2A, 8A)

Pennatula (non Linnaeus, 1758) Pallas, 1766: 374 (in part).

Renilla Lamarck, 1816: 428. Ehrenberg, 1834: 289. Milne Edwards, 1857: 219.

Herklots, 1858: 27. Gray, 1860: 24. Müller, 1864: 352. Kölliker, 1871: 85. Eisen, 1876: 3. Kükenthal & Broch, 1911: 205. Kükenthal, 1915: 21

Herklotsia Gray, 1860: 25. 1870: 37. *Type species: H. edwardsii* (Herklots, 1858).

Diagnosis. Colonies dorso-ventrally compressed, round, ovoid or heart-shaped. The vermiform peduncle gives rise to the cordate/foliate rachis. The rachis is bilaterally symmetrical throughout. Axis absent. Polyp leaves absent. Autozooids arranged on the dorsal surface of the rachis, randomly distributed or often in rows radiating out from the midline. Anthocodiae retractile directly into the rachis, calyces absent, although 5–7 triangular teeth may be present at the base of each polyp. Siphonozooids minute and numerous, contained on the dorsal surface of the rachis between the autozooids. Sclerites are three-flanged spindles and rods of the rachis and stout spindles or oval-shaped rods of the peduncle, smooth or indistinctly three-flanged.

Distribution and depth. Pacific and Atlantic coasts of North, Central, and South America (southern California to Chile including the Gulf of California and the Galapagos Islands, and Cape Hatteras to Argentina including the Caribbean Sea and Gulf of Mexico); 0–70 m in depth.

Type species. *Pennatula reniformis* Pallas, 1766 (by subsequent monotypy: Cuvier, 1830); type locality east coast of North America.

Nominal species. Approximately 17 described species have been referred to this genus, of which at least four may be valid: *Renilla amethystina* Verrill, 1861 (southern California to Peru); *R. edwardsi* Herklots, 1858 (South America); *R. muelleri* Schultze in Kölliker, 1872 (Gulf of California to Peru, Gulf of Mexico to Argentina); *R. reniformis* (Pallas, 1766) (North Carolina to Patagonia).

Remarks. A single collection of six specimens of *Renilla* sp. indet. was recently made by M. Telford (University of Toronto) from Scotland, following the El Niño warming event of the early 1980s. This represents the first verified record of the genus outside of the New World.

References for species identification. Kükenthal, 1915.

Family Kophobelemnidae Gray, 1860

Kophobelemnon Asbjørnsen, 1856
(Figs 2B, 8C)

Kophobelemnon Asbjørnsen, 1856: 81. Herklots, 1858: 23. Kölliker, 1872: 118. Danielssen & Koren, 1884: 58. Jungersen, 1904: 68. J. A. Thomson & Henderson, 1909: 270. Balss, 1910: 24. Kükenthal & Broch, 1911: 219. Kükenthal, 1915: 29. Hickson, 1916: 71. Williams, 1990: 64.

Bathyptilum Kölliker, 1872: 200. *Type species: B. carpenterii* Kölliker, 1872.

Gunneria Danielssen & Koren, 1884: 58. *Type species: G. borealis* Danielssen & Koren, 1884.

Diagnosis. Colonies elongate and cylindrical to slightly clavate or short, stout and distinctly clavate. Distal end rounded and knob-like or distinctly pointed. Rachis shows bilateral symmetry throughout, although not always distinctly so. Axis thin, round to slightly quadrangular in transverse section. Polyp leaves absent. Autozooids 2–50 in number, arranged biserially along rachis. Anthocodiae mostly not retractile, calyces absent. Siphonozooids numerous, often with minute

spiculated calyces, arranged on areas of rachis not occupied by autozooids. Sclerites are densely set and are spindles and rods, mostly three-flanged, sometimes ornamented with tubercles.

Distribution and depth. Nearly cosmopolitan distribution (Atlantic Ocean from Europe to southwestern Africa, Mediterranean Sea, Caribbean Sea, southeastern Africa, Malay Archipelago, Japan, Kuril Trench, and eastern Pacific from California to Panama); 36–4400 m in depth.

Type species. *Pennatula stellifera* Müller, 1776 (*Kophobelemnon mülleri* Asbjørsen, 1856 = *Kophobelemnon stelliferum* (Müller, 1776) by monotypy); type locality northern Atlantic Ocean.

Nominal species. Twenty-four described species are referable to this genus, of which nine may be valid: *Kophobelemnon affine* Studer, 1894 (Panama and California); *K. heterospinosum* Kükenthal, 1910 (Malay Archipelago); *K. hispidum* Nutting, 1912 (Japan); *K. irregulatus* Keller, Pasternak & Naumov, 1975 (Caribbean Sea); *K. leucharti* Cecchini, 1917 (Mediterranean Sea); *K. macrospinosum* J. A. Thomson, 1927 (North Atlantic and North Pacific); *K. molanderi* Pasternak, 1975 (Antarctic Peninsula); *K. pauciflorum* Hickson, 1916 (Malay Archipelago); *K. stelliferum* (Müller, 1776) (Atlantic and Pacific Oceans).

References for species identification. Hickson, 1916; Cecchini, 1917; J. A. Thomson, 1927; Keller et. al., 1975, Pasternak, 1975. Kükenthal, 1915.

Sclerobelemnon Kölliker, 1872
(Figs 2C, 8B)

Sclerobelemnon Kölliker, 1872: 117, 131. J. A. Thomson & Henderson, 1906: 89. J. A. Thomson & Simpson, 1909: 279. Balss, 1910: 24. Kükenthal & Broch, 1911: 318. Kükenthal, 1915: 27. Hickson, 1916: 77.

Mesobelemnon Gravier, 1907: 159. 1908: 228. Kükenthal & Broch, 1911: 217. Kükenthal, 1915: 27. *Type species: M. gracile* Gravier, 1908.

Diagnosis. Colonies narrow and arrow-shaped or stout and club-shaped. Symmetry of rachis is bilateral throughout, although not always distinctly so. Axis conspicuous throughout extent of colony. Polyp leaves absent. Autozooids arranged in two to 20 longitudinal rows along the rachis, in two longitudinal series. Anthocodiae retractile directly into rachis, permanent spiculiferous calyces absent. Siphonozooids often form minute swellings and are sparsely to densely distributed on the rachis between or below the autozooids, often arranged in short longitudinal rows. Scerites are plates or minute ovals or rods, often irregularly-shaped or biscuit-shaped, the margins sometimes ornamented with denticles. Sclerites are not three-flanged.

Distribution and depth. Indo-West Pacific and western Atlantic (Gulf of Mexico, Trinidad, Surinam, Red Sea, Indian Ocean, Australia, Papua New Guinea, Malay Archipelago, Philippines, Taiwan, and Japan); 10–472 m in depth.

Type species. *Sclerobelemnon schmeltzii* Kölliker, 1872 (by monotypy); type locality Taiwan.

Nominal species. Eight described and apparently valid species: *Sclerobelemnon burgeri* (Herklots, 1858) (Indo-West Pacific); *S. elongatum* Hickson, 1916 (Malay Archipelago); *S. gracile* (Gravier, 1908) (Red Sea); *S. gravieri* Hickson, 1916

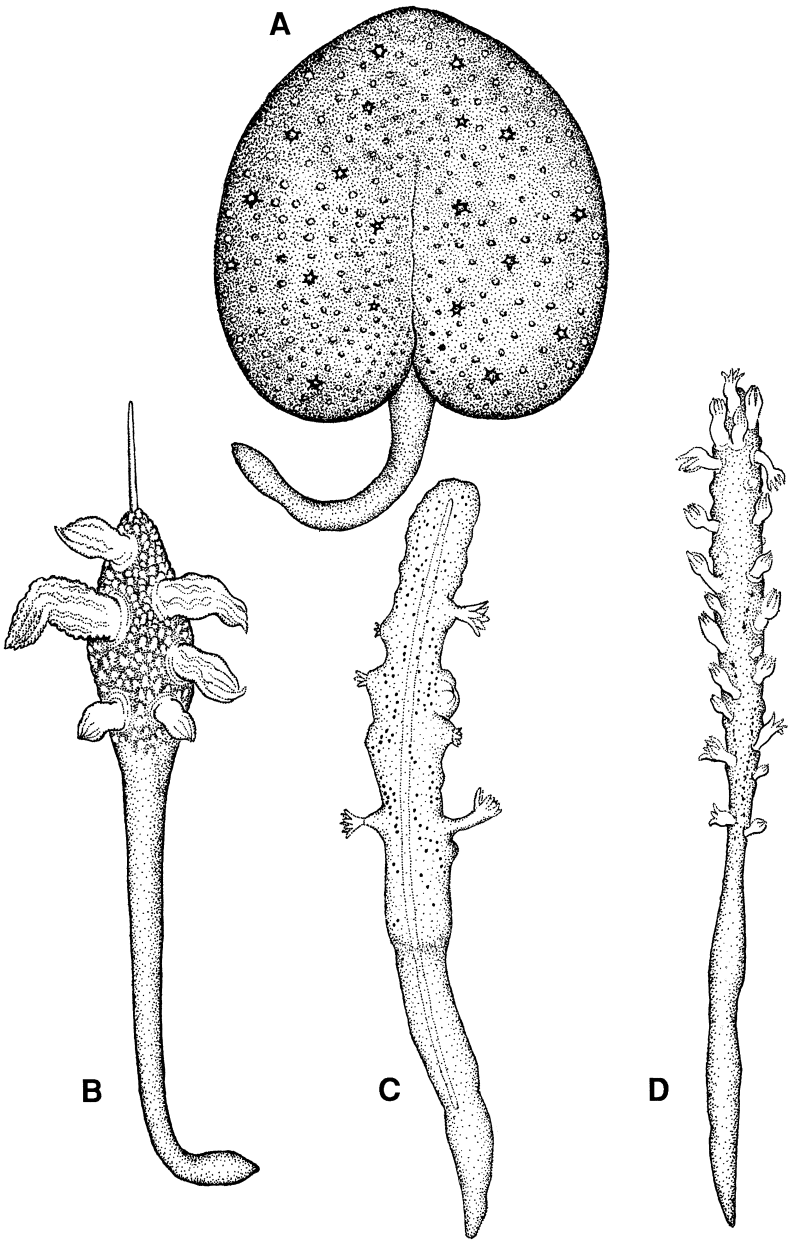

Figure 2. Colonies A, *Renilla amethystina*, 60 mm. B, *Kophobelemnon affine*, 80 mm. C, *Sclerobelemnon* sp., 60 mm. D, *Malacobelemnon* sp., 102 mm.

(Malay Archipelago); *S. kollikeri* Thomson & Henderson, 1906 (Indian Ocean); *S. magniflorum* Hickson, 1916 (Malay Archipelago); *S. schmeltzi* Kölliker, 1872 (Indo-West Pacific); *S. theseus* Bayer, 1959 (Gulf of Mexico, Trinidad, and Surinam).

References for species indentification. Hickson, 1916; Bayer, 1959.

Malacobelemnon Tixier-Durivault, 1965
(Figs 2D, 8D)

Malacobelemnon Tixier-Durivault, 1965: 712.

Diagnosis. Colonies stout and cylindrical to slightly clavate. Symmetry of rachis bilateral throughout, although not always distinctly so. Axis short, thin, and fattened or long, thick, and quadrangular. Polyp leaves absent. Autozooids arranged irregularly in two longitudinal series. Anthocodiae retractile directly into rachis or into fleshy and bulbous basal portions of the polyps, which do not form permanent calyces. Siphonozooids sparsely distributed in short longitudinal or oblique rows on the rachis between the autozooids, and may also be present on the rachis below the lower-most autozooids as well as on the side of the rachis opposite the autozooids. Sclerites absent altogether except for minute otolith-like ovals, which may be present in the peduncle.

Distribution and depth. Western Indian and western Pacific Oceans (southeastern Africa and eastern Australia); 42–60 m in depth.

Type species. *Malacobelemnon stephensoni* Tixier-Durivault, 1965 (by monotypy); type locality southern Queensland (Australia).

Nominal species. One described species: *Malacobelemnon stephensoni* Tixier-Durivault, 1965 (Australia); possibly one undescribed species from South Africa.

References for species description. Tixier-Durivault, 1965.

Family Funiculinidae Gray, 1870

Funiculina Lamarck, 1816
(Figs 3I & J, 8F)

Funiculina Lamarck, 1816: 422. Herklots, 1858: 8. Kölliker, 1872: 250. Jungersen, 1904: 49. Balss, 1910: 32. Kükenthal & Broch, 1911: 241. Kükenthal, 1915: 34. Hickson, 1916: 94. Manuel, 1981: 53. Williams, 1990: 71. 'Pavonaires' Cuvier, 1817: 85.

'Pavonaires' Cuvier, 1817: 85. *Types species*: *P. antennina* Cuvier, 1817.

Pavonaria Schweigger, 1820: 435. *Designated species: P. antennina*.

Leptoptilum Kölliker, 1880: 27. *Type species: L. gracile* Kölliker, 1880.

Trichoptilum Kölliker, 1880: 29. *Type species: T. brunneum* Kölliker, 1880.

Diagnosis. Colonies elongate, often thin and whip-like. Symmetry of rachis is bilateral throughout. Axis extends through entire length of colony, quadrangular in transverse section. Polyp leaves absent. Autozooids biserial and longitudinally placed along rachis, arranged irregularly or in indistinct oblique rows. Anthocodiae retractile into tubular calyces with eight conspicuous terminal teeth. Siphonozooids relatively large and conspicuous, often resembling small autozooids, very sparsely distributed on the rachis between autozooids. Sclerites are densely distributed and are three-flanged spindles, rods, and ovoids or plates. Autozooids are heavily armed with spindles.

Distribution and depth. Cosmopolitan distribution (Indo-Pacific, eastern Pacific, Mediterranean Sea, and Atlantic Ocean); 60–2600 m in depth.

Type species. *Pennatula guadrangularis* Pallas, 1766 (by subsequent monotypy: Milne Edwards & Haime, 1857); type locality Europe.

Nominal species. There are nine described species referable to this genus, three cf which are considered valid: *Funiculina armata* Verrill, 1879 (Indian Ocean and

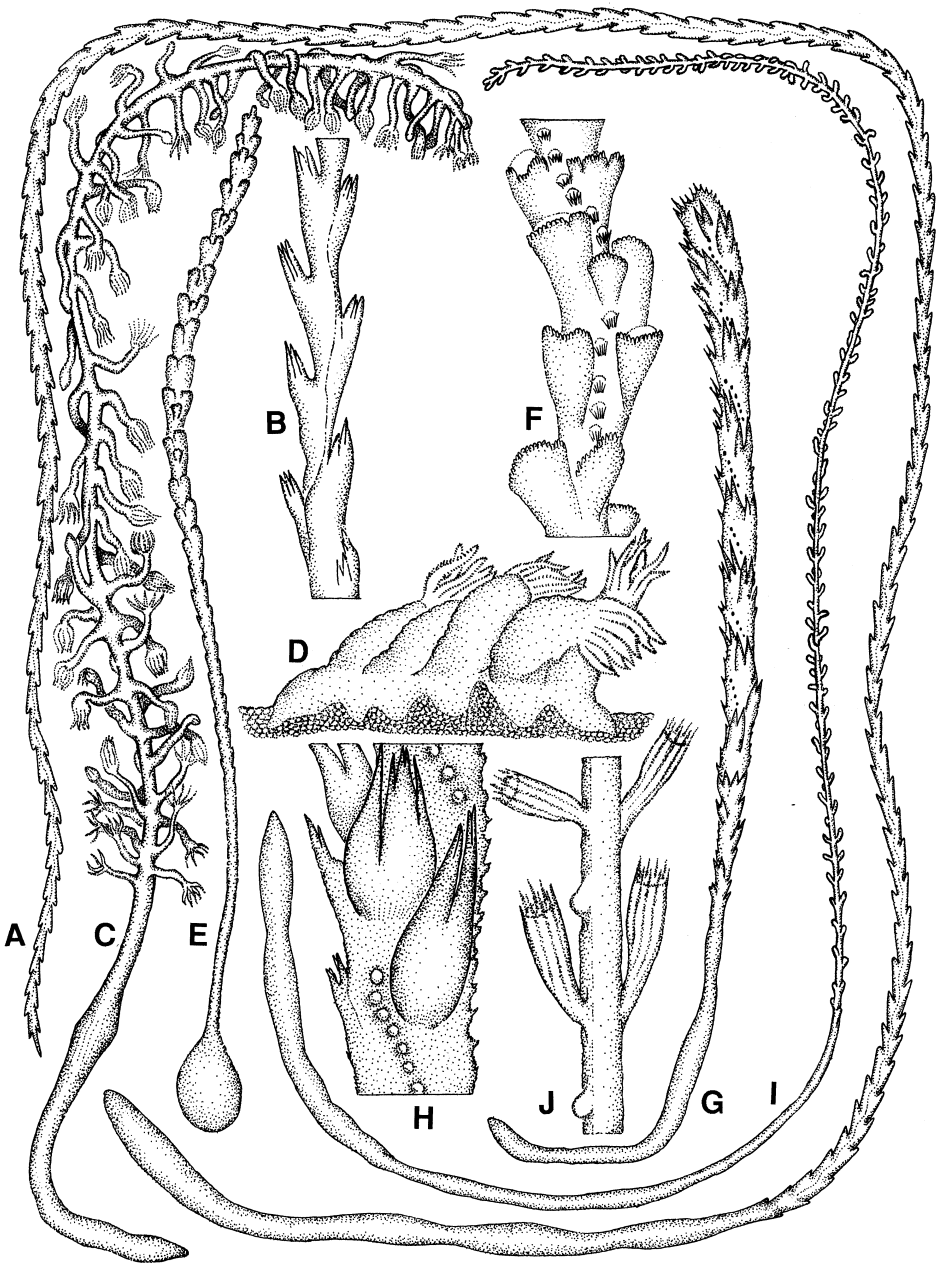

Figure 3. Colonies. A, *Distichoptilum gracile*, 700 mm. B. *Distichoptilum gracile*, portion of rachis showing autozooid calyces, 14 mm (portion shown). C, *Anthoptilum murrayi*, 350 mm. D, *Anthoptilum grandiflorum*, portion of rachis showing group of autozooids with siphonozooids at base, 14 mm (portion shown). E, *Protoptilum* sp., 120 mm. F, *Protoptilum* sp., portion of rachis showing autozooid calyces and smaller siphonozooids, 5.6 mm (portion shown). G, *Stachyptilum superbum*, 100 mm. H, *Stachyptilum superbum*; portion of rachis showing placement of autozooids and smaller siphonozooids, 5.8 mm (portion shown). I, *Funiculina guadrangularis*, 350 mm. J, *Funiculina guadrangularis*, portion of rachis showing placement of autozooids and siphonozooids, 5 mm (portion shown).

western Atlantic)—colonies rigid, not coiled; *F. parkeri* Kükenthal, 1909 (southern California)—colonies slender and flexible, spirally coiled, without broad plate-like sclerites in the peduncle; *F. quadrangularis* (Pallas, 1776) (Atlantic and Indo-Pacific)—colonies slender and flexible, spirally coiled, with broad plate-like sclerites in the peduncle.

References for species identification. Kükenthal, 1915; Manuel, 1981; Williams, 1990.

Family Protoptilidae Kölliker, 1872

Distichoptilum Verrill, 1882
(Figs 3A & B, 8H)

Distichoptilum Verrill, 1882: 362. Jungersen, 1904: 62. Kükenthal & Broch, 1911: 255. Kükenthal, 1915: 39. Hickson, 1916: 101. Williams, 1990: 72.

Juncoptilum J. A. Thomson & Henderson, 1905: 555. *Type species*: *J. alcocki* Thomson & Henderson, 1905.

Helicoptilum Nutting, 1912: 51. *Type species*: *H. rigidum* Nutting, 1912.

Diagnosis. Colonies elongate, slender, and whip-like. Symmetry of rachis is bilateral throughout. Axis present throughout length of colony. Polyp leaves absent. Autozooids arranged bilaterally along rachis, opposing polyps alternately or subopposite disposed. The surfaces of the rachis between the longitudinal polyps rows are free of autozooids. Anthocodiae retractile into permanent spiculiferous calyces. Calyces with two to six obscure to distinct terminal teeth. Calyces with axial sides appressed to lateral margin of rachis. Siphonozooids 2–3 on the rachis directly above each autozooid. Sclerites are three-flanged spindles or rods of the calyces, rachis, and peduncle.

Distribution and depth. Near cosmopolitan distribution (Indo-Pacific, eastern Pacific, and Atlantic Oceans); 650–4300 m in depth.

Type species. *Distichoptilum gracile* Verrill, 1882 (by monotypy); type locality eastern North America.

Nominal species. Three described species referable to this genus, with one recognized as valid (*): *Juncoptilum alcocki* (Sri Lanka); **Distichoptilum gracile* Verrill, 1882 (Cosmopolitan); *Helicoptilum rigidum* Nutting, 1912 (Japan).

Remarks. *Helicoptilum* was originally distinguished from *Distichoptilum* by the absence of sclerites in the tentacles. The two genera seem to be similar in all other respects. I suspect that the presence or absence of anthocodial sclerites (as in other octocorals), can be accommodated by the expression of phenotypic variation within a single species.

References for species description. Hickson, 1916; Williams, 1990.

Protoptilum Kölliker, 1872
(Figs 3E & F, 8G)

Protoptilum Kölliker, 1872: 192 (p. 370 in consecutively paginated edition). 1880: 28. Jungersen, 1904: 51. Balss, 1910: 34. Kükenthal & Broch, 1911: 256. Kükenthal, 1915: 37. Hickson, 1916: 97.

Diagnosis. Colonies long and slender. Rachis bilaterally symmetrical throughout. Axis extends throughout entire length of colony. Polyp leaves absent. Autozooids arranged in rows of 1–3 along opposite sides of the rachis. Individual autozooids may be scattered on the rachis between the lateral rows. Anthocodiae retractile into spiculated calyces, which usually have 3–8 terminal teeth (or teeth sometimes absent altogether). Siphonozooids more than 2–3 per autozooid, often numerous and congested around autozooids. Sclerites of the tentacles, calyces, rachis, and peduncle are three-flanged needles, spindles, rods or ovals.

Distribution and depth. Northern Atlantic, Indo-Pacific, and eastern Pacific (northern Europe, east coast of North America to Puerto Rico and the Gulf of Mexico, Somalia, Malay Archipelago, Japan, Hawaii, and California); 250–4000 m in depth.

Type species. *Protoptilum carpenterii* Kölliker, 1872 (by monotypy); type locality North Atlantic Ocean.

Nominal species. Thirteen described species, perhaps six of which can be considered as valid: *Protoptilum carpenteri* Kölliker, 1872 (North Atlantic); *P. celebense* Hickson, 1916 (Malay Archipelago); *P. cyaneum* Kükenthal, 1910 (East Africa); *P. denticulatum* Jungersen, 1904 (North Atlantic); *P. smitti* Kölliker, 1872 (North Atlantic); *P. thomsoni* Kölliker, 1872 (North Atlantic and Gulf of Mexico); possibly one undescribed species from California.

References for species identifications. Kükenthal, 1915; Hickson, 1916.

Family Stachyptilidae Kölliker, 1880

Stachyptilum Kölliker, 1880
(Figs 3G & H, 8I)

Stachyptilum Kölliker, 1880: 11. Kükenthal & Broch, 1911: 260. Kükenthal, 1915: 41.

Diagnosis. Colonies stout and clavate or slender, firm or spongy in texture. Symmetry of rachis is bilateral throughout. Axis present throughout length of colony. Polyp leaves absent. Autozooids arranged in oblique rows in two longitudinal series along the rachis. Each row is disposed alternately to a corresponding row on the other side of the rachis. Anthocodiae three to several per row, retractile into densely-spiculated calyces. Calyces indistinctly toothed or with two to three long terminal teeth. Siphonozooids mostly in oblique rows between the rows of autozooids, often with calyces formed by fan-shaped arrays of sclerites. Sclerites are three-flanged needles and spindles of the polyp calyces and rachis, while oval- or rodshaped plates may be present in the peduncle. Rods sometimes contained in the tentacles.

Distribution. Pacific Ocean (Malay Archipelago, Japan, and Oregon to central America); 36–950 m in depth.

Type species. *Stachyptilum macleari* Kölliker, 1880 (by monotypy); type locality between Ceram and New Guinea.

Nominal species. Three described and apparently valid species: *Stachyptilum dofleini* Balss, 1909 (Japan)—rachis thick and spongy; *S. macleari* Kölliker, 1880 (Malay Archipelago and Japan)—rachis slender, calyces not clearly toothed; *S. superbum*

Studer, 1894 (Pacific Coast of North and Central America)—rachis slender, calyces conspicuously toothed.

References for species identifications. Kükenthal, 1915.

Family Scleroptilidae Jungersen, 1904

Scleroptilum Kölliker, 1880
(Figs 4A, 9A)

Scleroptilum Kölliker 1880: 30. Balss, 1910: 24. Kükentahl & Broch, 1911: 267. Kükenthal, 1915: 43. Williams, 1990: 75.

Diagnosis. Colonies slender, delicate. Symmetry of rachis is bilateral throughout. Axis present throughout entire length of colony, round in transverse section. Polyp leaves absent. Autozooids arranged singly or in pairs along rachis, sparsely distributed with regions of bare rachis evident between polyps. Autozooids of each pair mostly arranged subopposite ly on rachis. Anthocodiae non-retractile, without calyces. Siphonozooids are very sparsely distributed on rachis between or immediately above and below the autozooids. Sclerites of the polyps, rachis and peduncle are rods and spindles, which may be distinctly to inconspicuously three-flanged. Sclerites present in the tentacles.

Distribution and depth. Scattered distribution in the Atlantic, Indian, and Pacific Oceans; 510–4200 m in depth.

Type species. *Scleroptilum grandiflorum* Kölliker, 1880 (by monotypy); type locality east of Japan in the northwest Pacific.

Nominal species. Three described species, with one considered valid (*): *Scleroptilum durissimum* Kölliker, 1880 (northern Pacific); *S. gracile* Verrill, 1884 (New England); **S. grandiflorum* Kölliker, 1880 (northern Pacific and northern Atlantic). In addition, one undescribed species has recently been collected from the southwestern Indian Ocean.

References for species description. Kükenthal & Broch, 1911; Kükenthal, 1915.

Family Chunellidae Kükenthal, 1902

Calibelemnon Nutting, 1908
(Figs 4B, 9B)

Protocaulon (non Kölliker, 1880): Thomson & Henderson, 1906: 85. *Species designated*: *P. indicum* Thomson & Henderson, 1906.

Calibelemnon Nutting, 1908: 562. Balss, 1910: 70. Kükenthal, 1915: 44. Williams, 1990: 75.

Prochunella Balss, 1909: 426. *Type species: P. indica* (Thomson & Henderson, 1906).

Diagnosis. Colonies thin and delicate. Rachis with bilaterial symmetry throughout. Axis present throughout length of colony, quadrangular in cross section. Polyp leaves absent. Autozooids usually in 5–15 pairs, each pair separated by bare intervals of rachis. Autozooids of each pair arranged oppositely. Anthocodiae non-retractile, without calyces. Siphonozooids sparsely distributed on rachis. Sclerites absent or restricted to minute oval bodies or rods in the peduncle and reduced, irregularly-shaped rods (>0.05 mm) in the rachis.

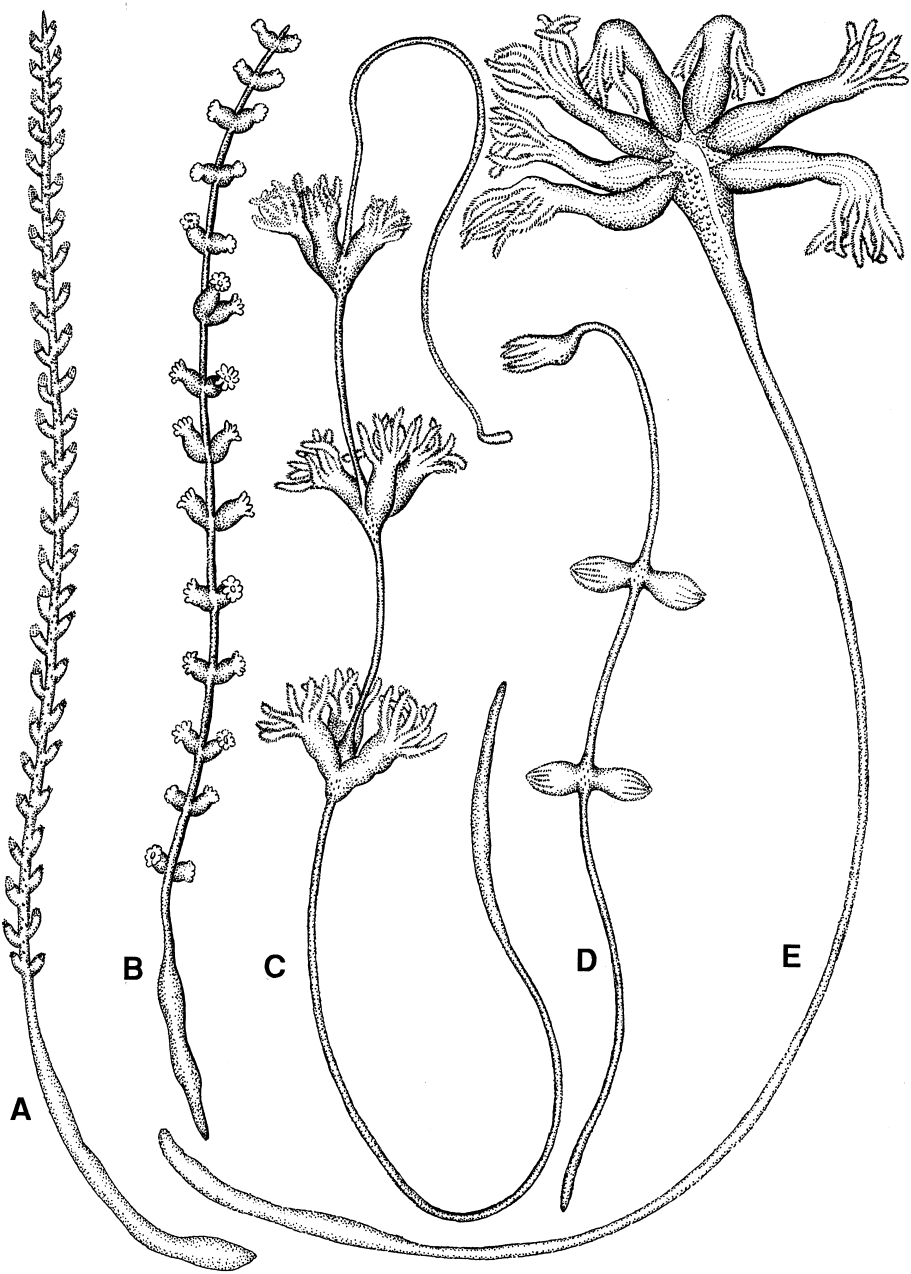

Figure 4. Colonies. A, *Scleroptilum grandiflorum*, 42 mm. B, *Calibelennon indicum*, 105 mm. C, *Chunella gracillima*, 430 mm. D, *Amphiacme abyssorum*, 200 mm. E, *Umbellula lindahli*, 250 mm.

Distribution and depth. Indo-Pacific (southeastern Africa, Indian Ocean, Japan, and Hawaii); 100–1275 m in depth.

Type Species. Calibelemnon symmetricum Nutting, 1908 (by original designation); type locality Hawaii.

Nominal Species. Three described species, with at least the latter two considered

valid: *Calibelemnon hertwigi* (Balss, 1909) (Japan); *C. indicum* (Thomson & Henderson, 1906) (southeastern Africa to Japan), without sclerites in the rachis; *C. symmetricum* Nutting, 1908 (Hawaii), with reduced sclerites in the rachis.

References for species descriptions. Nutting, 1908; Kükenthal, 1915.

Amphiacme Kükenthal, 1903
(Figs 4D, 9D)

Amphianthus Kükenthal, 1902: 303.

Amphiacme Kükenthal, 1903: 275. 1915: 46. Kükenthal & Broch, 1911: 276. Williams, 1990: 78.

Diagnosis. Colonies elongate, slender, and delicate, peduncle and rachis 1–3 mm in diameter. Rachis bilaterally symmetrical throughout. Axis present throughout colony, quadrangular in cross section. Polyp leaves absent. Autozooids arranged in 2–4 pairs along the rachis, well separated by intervals of naked rachis. Anthocodiae non-retractile. Calyces absent. Terminal autozooid well developed, bilaterally symmetrical to somewhat asymmetrical, with a ventral keel. Siphonozooids minute, situated on the ventral keel of the terminal autozooid and also on the rachis between each pair of autozooids. Sclerites absent except for minute ovals (>0.02 mm in length) in the peduncle.

Distribution and depth. The eastern African coast and western Indian Ocean (border of Kenya/Tanzania to Natal and Madagascar); 818–1200 m in depth.

Type Species. *Amphianthus abyssorum* Kükenthal, 1902 (by monotypy); type locality border of Kenya and Tanzania.

Nominal Species. A monotypic genus: *Amphiacme abyssorum* (Kükenthal, 1902) (eastern Africa and Madagascar).

Remarks. The name *Amphianthus* Kükenthal, 1902 is preoccupied by *Amphianthus* Hertwig, 1882 (Actiniaria: Hormathiidae) (Kükenthal, 1903).

References for species description. Kükenthal & Broch, 1911; Williams, 1990.

Chunella Kükenthal, 1902
(Figs 4C, 9C)

Chunella Kükenthal, 1902: 302. 1915: 45. Kükenthal & Broch, 1911: 271. Kükenthal, 1915: 45. Hickson, 1916: 110. Williams, 1990: 76.

Diagnosis. Colonies elongate and slender. Bilaterally symmetrial throughout extent of rachis. Axis present throughout length of colony, quadrangular in cross section. Polyp leaves absent. Autozooids in whorls of one to four along rachis, each whorl separated by intervals of bare rachis. Anthocodiae non-retractile, calyces absent. Terminal autozooid highly reduced (rudimentary). Siphonozooids minute and sparsely scattered on rachis adjacent to autozooid whorls. Sclerites are absent except for minute ovals of the peduncular interior.

Distribution and depth. Indo-West Pacific (African east coast from Kenya/Tanzania border and Natal, as well as Malay Archipelago to Irian Jaya); 818–1200 m in depth.

Type species. *Chunella gracillima* Kükenthal, 1902 (by monotypy); type locality East Africa.

Nominal species. Three nominal but probably only one valid species (*), based

on the number of polyps per whorl: *Chunella biflora* Hickson, 1916 (Malay Archipelago), with two polyps per whorl; **C. gracillima* Kükenthal, 1902 (eastern African coast), with three polyps per whorl; *C. guadriflora* Kükenthal & Broch, 1911 (East Africa) with four polyps per whorl.

Remarks. Williams (1990: 78) noted the variation of polyp number per whorl and the possibility that the three described species may in fact be conspecific.

References for species descriptions. Kükenthal & Broch, 1911; Williams, 1990.

Family Ombellulidae Williams nom. nov.
(corrected spelling of Umbellulidae Kölliker, 1880)

Ombellula Cuvier, 1798
(Figs 4E, 9E)

Hydra marina arctica Ellis, 1753: 305.
Isis Linnaeus, 1758: 800 (in part).
Pennatula Pallas, 1766: 335 (in part).
Vorticella Linnaeus, 1767: 1317 (in part).
Ombellula Cuvier, 1798: 675, 706.
Encrinus Lamarck, 1801: 379. *Type species: E. caputmedusae* Lamarck, 1801.
Umbellularia Lamarck, 1801: 380. 1816: 436. 1836: 677. Kölliker, 1872: 203. *Type species: U. groenlandica* Lamarck, 1801.
'Ombellulaires' Cuvier, 1817: 86.
Umbellaria Schweigger, 1820: 434.
Ombellularia Lamarck, 1836: 676.
Crinillum Harting, Miquel & Hoeven, 1861: 294. Kölliker, 1872: 202. *Type species: C. siedenburgi* Harting, Miquel & Hoeven, 1861.
Umbellula Gray, 1870: 39. Kölliker, 1875: 11. Kölliker, 1880: 16. Danielssen & Koren, 1884: 13. J. A. Thomson & Henderson, 1906: 92. Kükenthal & Broch, 1911: 282.
Kükenthal, 1914: 630. 1915: 47. Hickson, 1916: 116.
Broch, 1957: 350. 1958a: 267. 1958b: 251. Grasshoff, 1982: 956. Williams, 1990: 81.

Diagnosis. Colonies with a long and slender stalk and a terminal cluster of polyps. Symmetry of rachis is bilateral. The conspicuous axis is present throughout the colony, round to quadrangular in cross-section. Polyp leaves absent. Autozooids restricted to a terminal cluster containing one to forty polyps. Anthocodiae non-retractile, calyces absent. Siphonozooids present on the rachis at the base of the autozooids and below the terminal cluster on the upper part of the stem. Sclerites are present in only three species, totally absent in all other species. Sclerites when present are spindles, rods, ovoid rods, or needles, which are three-flanged or round in cross-section, surfaces often rough with numerous low knobby tubercles. Sclerites may be present in the tentacles, walls of the autozooids, and pedundle.

Distribution and depth. Cosmopolitan distribution (Atlantic, Indian, Pacific, Arctic, and Southern Oceans); 210–<6100 m depth.

Type species. *Isis encrinus* Linnaeus, 1758 (by subsequent designation: Danielssen & Koren, 1884); type locality Greenland.

Nominal species. Forty-two described species are assignable to this genus, of

which at least nine are probably valid: Three species with sclerites are *Ombellula durissima* (Kölliker, 1880) (Indo-Pacific), with many polyps, sclerites and axis round in cross section; *O. monocephalus* (Pasternak, 1964) (Indian and Atlantic Oceans), with one polyp; and *O. thomsoni* (Kölliker, 1874) (Indo-Pacific and Atlantic), with many polyps, three-flanged sclerites, and rectangular axis. There are also six species without sclerites: *O. encrinus* (Linnaeus, 1758) (Arctic Ocean); *O. hemigymna* (Pasternak, 1975) (Caribbean Sea); *O. huxleyi* (Kölliker, 1880) (Northeastern Atlantic and Northwestern Pacific); *O. lindahli* (Kölliker, 1874) (Cosmopolitan); *O. pellucida* (Kükenthal, 1902) (Indian Ocean); and *O. spicata* (Kükenthal, 1902) (Indian Ocean).

Remarks. The name *Umbellula*, used originally by Gray and subsequently by other authors, is a misspelling of *Ombellula* Cuvier, 1798. Even though *Umbellula* has been used since 1870, *Ombellula* is the correct original spelling for this genus, as there is no evidence of transcription error or other inadvertent error as reported by authors such as Kükenthal (1915: 130). For reasons of long-term and widespread usage a reasonably good case might be made before the ICZN to rule under plenary powers that *Ombellula* is an incorrect original spelling for *Umbellula* (F. M. Bayer, personal communication). However, for reasons of priority, I have chosen here to use the original name as proposed by Cuvier.

References for species identification. Broch, 1958b; Grasshoff, 1972 & 1982; Williams, 1990.

Family Anthoptilidae Kölliker, 1880

Anthoptilum Kölliker, 1880
(Figs 3C & D, 8E)

Virgularia (non Lamarck, 1816) Verrill, 1879: 239.

Anthoptilum Kölliker, 1880: 13. Verrill, 1883: 5. Jungersen, 1904: 65. Thomson & Henderson, 1906: 91. Kükenthal & Broch, 1911; 232. Kükenthal, 1915: 32. Hickson, 1916: 138. Grasshoff, 1982: 954. Williams, 1990: 68.

Benthoptilum Verrill, 1885: 510. Stephens, 1909: 19. *Type species: B. sertum* Verrill, 1885.

Stephanoptilum Roule, 1905: 455. *Type species: S. intermedium* Roule, 1905.

Thesioides J. A. Thomson & Henderson, 1906: 91. *Type species: T. inermis* Thomson & Henderson, 1906.

Diagnosis. Colonies elongate and whip-like. Rachis symmetry is bilateral throughout. Axis present throughout length of colony, round to somewhat quadrangular in transverse section. Polyp leaves absent. Autozooids numerous and elongate, either arranged individually along sides of the rachis or in oblique rows situated in two longitudinal series along the rachis. Anthocodiae non-retractile with calyces absent. Adjacent autozooids of a particular oblique row sometimes united at their bases. Siphonozooids minute and numerous on the rachis between the groups of autozooids. Sclerites absent except for minute ovals in the interior of the stalk.

Distribution and depth. Near cosmopolitan distribution (Indo-Pacific, northern and eastern Pacific, Atlantic, and Arctic Oceans); 155–3150 m in depth.

Type Species. *Virgularia grandiflora* Verrill, 1879 (by subsequent designation: Kölliker, 1880); type locality northern Atlantic Ocean.

Nominal Species. Nine described species with at least two of these considered valid: *Anthoptilum grandiflorum* (Verrill, 1879) (cosmopolitan), with polyps arranged in oblique rows and adjacent polyps fused at base; *A. murrayi* Kölliker, 1880 (North Atlantic and North Pacific), with polyps separate, not fused.

References for species identification. Kükenthal, 1915; Hickson, 1916; Deichmann, 1936; Williams 1990.

Family Halipteridae Williams nom. nov.
(replaces Pavonaridae Jungersen, 1904 by priority)

Halipteris Kölliker, 1869
(Figs 5A & B, 9F)

Virgularia (non Lamarck, 1816) Koren & Danielssen, 1847: 269.
Halipteris Kölliker, 1869: 124. Williams, 1990: 95.
Pavonaria Kölliker, 1869: 123 (non Schweigger, 1820). Kükenthal & Broch, 1911: 305. Kükenthal, 1915: 60. *Type species: P. finmarchica* (Sars, 1851).
Balticina Gray, 1870: 13. *Type species: B. finmarchica* Gray, 1870.
Norticina Gray, 1870: 13. *Type species: N. christi* Gray, 1870.
Osteocella Gray, 1870: 40. *Type species: O. cliftoni* Gray, 1870.
Verrillia Stearns, 1873: 148 (subgenus of *Pavonaria* Kölliker, 1869). *Type species: Pavonaria (Verrillia) blakei* Stearns, 1873.
Lygomorpha Koren & Danielssen, 1877: 99. *Type species: L. sarsii* Koren & Danielssen, 1877.
Microptilum Kölliker, 1880: 26. *Type species: M. willemoesi* Kölliker, 1880.
Göndul Koren & Danielssen, 1883: 19. *Type species: G. mirabilis* Koren & Danielssen, 1883.
Stichoptilum Grieg, 1887: 15, 21. *Type species: S. arcticum* Grieg, 1875.

Diagnosis. Colonies long, slender, and whip-like. Rachis is bilaterally symmetrical throughout. Axis extends throughout colony length, round to quadrangular in cross section. Polyp leaves present in mature colonies as raised ridges. Autozooids disposed in many oblique rows along two longitudinal series. Adjacent autozooids often united at their bases forming raised ridges, which emerge from opposite sides of the rachis. Anthocodiae retractile into calyces with two terminal teeth. Siphonozooids are sparsely scattered on the rachis between the oblique rows of autozooids. Sclerites are densely-set three-flanged spindles in the calyces, and smooth rods in the peduncle. Tentacles often with three-flanged rods.

Distribution and depth. Near cosmopolitan distribution (Atlantic Ocean from the North Atlantic to Patagonia and western Africa, Pacific Ocean from Japan and California, Indian Ocean from southeastern Africa and the Andaman Islands, and the Subantarctic from Marion/Prince Edward Islands); 36–1950 m in depth.

Type species. *Halipteris christii* (Koren & Danielssen, 1847) (by subsequent monotypy: Kölliker, 1869); type locality northern Atlantic Ocean. *Nominal species*. Sixteen described species referable to this genus of which six may possibly be valid: *Halipteris africana* (Studer, 1879) (African west coast); *H. californica* (Moroff, 1902) (California); *H. christii* (Koren & Danielssen, 1847) (Northern Atlantic);

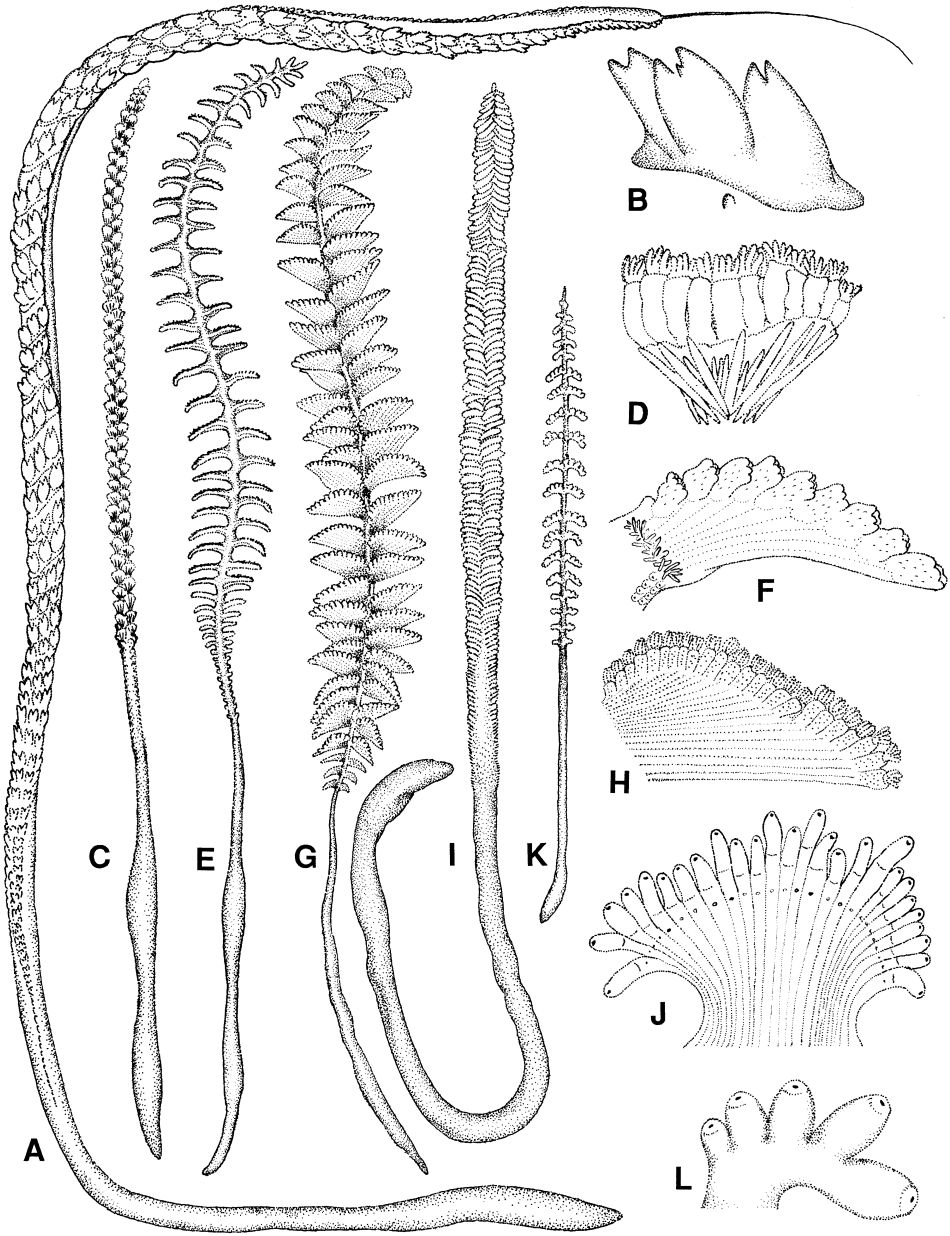

Figure 5. Colonies. A, *Halipteris californica*, 420 mm. B, *Halipteris californica*; a single row of autozooid calyces forming a raised ridge, with one siphonozooid at the base, 6 mm (row shown). C, *Stylatula elongata*, 115 mm. D, *Stylatula elongata*, a single polyp leaf with basal armature, 2 mm—(greatest linear dimension of leaf shown). E, *Acanthoptilum gracile*, 200 mm. F, *Acanthoptilum gracile*; a single polyp leaf showing autozooids with a cluster of sclerites and smaller siphonozooids at the base, 8 mm—(greatest linear dimension of leaf shown). G, *Scytalium* sp., 300 mm. H, *Scytalium* sp., a single polyp leaf showing autozooids, 12 mm—(greatest linear dimension of leaf shown). I, *Virgularia schultzei*; 230 mm. J, *Virgularia schultzei*; a single polyp leaf showing autozooids and smaller siphonozooids, 8 mm—(greatest linear dimension of leaf shown). K, *Scytaliopsis djiboutiensis*, 100 mm. L, *Scytaliopsis djiboutiensis*; a single polyp leaf showing gradation in size of autozooids, 4 mm—(greatest linear dimension of leaf shown).

H. finmarchica (Sars, 1851) (Northern Atlantic); *H. heptazooidea* Acuña & Zamponi, 1992 (Subantarctic); *H. willemoesi* Kölliker, 1870 (Pacific Ocean).

Remarks. A good deal of confusion concerns the proper generic name for this genus. Kükenthal (1915: 60), Deichmann (1936: 279), Bayer (1956: 228), and Williams (1990: 97) have commented on this problem. Gray (1870: 13) described *Balticina* for *B. finmarchica* and *Norticina* for *N. christii.* Kükenthal, 1915: 60) correctly considered both of these to be synonyms of *Pavonaria* Kölliker, 1869. Deichmann (1936: 279) pointed out that the name *Pavonaria* was originally used by Schweigger (1820) and is correctly a synonym of *Funiculina.* Kölliker (1869) introduced the name *Halipteris* on page 124 (along with *Pavonaria* on page 123) but did not apply either name to particular species until 1870. Deichmann selected *Balticina* Gray, 1870 as the proper name for the genus, because of its age priority over *Pavonaria* Kölliker, 1870, but she did not mention the simultaneous introduction of *Halipteris* by Kölliker. In my opinion, the use of *Halipteris* in 1869 (even though not applied to a particular species) gives priority to this name.

Kükenthal (1915: 60) included this genus in a separate subfamily of the family Virgulariidae. In my opinion, the lack of well-developed polyp leaves and the presence of densely spiculated polyp calyces, justifies the segregation of *Halipteris* in a separate family, following Jungersen (1904).

References for species identification. Kükenthal, 1915.

Family Virgulariidae Verrill, 1868

Stylatula Verrill, 1864
(Figs 5C & D, 9G)

Stylatula Verrill, 1864: 30. Kölliker, 1870: 556. Jungersen, 1904: 37. Balss, 1910: 42. Kükenthal & Broch, 1911: 315. Kükenthal, 1915: 67.

Dübenia Koren & Danielssen, 1877: 92. Type species: *D. abyssicola* Koren & Danielssen, 1877.

Diagnosis. Colonies long and slender, often vermiform. Bilateral symmetry throughout rachis. Axis present throughout entire colony, mostly round in cross section. Polyp leaves present, short, densely arranged on rachis. Each polyp leaf subtended by a strong fan-like armature of long white sclerites. Autozooids 5–30 per polyp leaf, with anthocodiae retractile into bulbous basal portions of polyps. Siphonozooids absent from polyp leaves, arranged on the rachis between the leaves. Sclerites are elongate, partly or entirely three-flanged, somewhat flattened needles of the polyp leaf armature. These may be broad and rounded at one end, tapering and pointed at the other. In addition, the calyx-like proximal portions of the polyps may contain spindles. Sclerites from other parts of the colony are absent, except for extremely minute oval bodies which may be present in the interior of the peduncle.

Distribution and depth. Northern and western Atlantic and eastern Pacific Oceans (northern Europe and the east coasts of North and South America to Argentina including the Gulf of Mexico and Caribbean Sea, and British Columbia to Panama including the Gulf of California); 0–1020 m in depth.

Type Species. Virgularia elongata (Gabb, 1862) (by subsequent designation: Verrill, 1864); type locality California.

Nominal species. Twelve described species assignable to the genus, nine of which are apparently valid: *Stylatula antillarum* Kölliker, 1872 (Gulf of Mexico and Caribbean Sea); *S. brasiliensis* (Gray, 1870) (Brazil); *S. diadema* Bayer, 1959 (Surinam); *S. darwini* Kölliker, 1870 (Brazil, Argentina, Patagonia); *S. elegans* (Danielssen, 1860) (North Atlantic); *S. elongata* (Gabb, 1862) (Pacific Coast of North and Central America); *S. gracilis* (Verrill, 1864) (California, Panama); *S. kinbergi* Kölliker, 1870 (locality unknown); *S. lacazi* Kölliker, 1870 (locality unknown).

References for species identifications. Kükenthal, 1915.

Acanthoptilum Kölliker, 1870
(Figs 5E & F, 9H)

Acanthoptilum Kölliker, 1870: 569. Balss, 1910: 41. Kükenthal, 1915: 63. Bayer; 1957: 382.

Diagnosis. Colonies long, slender, and somewhat feather-shaped. Rachis bilaterally symmetrical throughout. Axis present throughout length of colony. Polyp leaves present, often sickle-shaped, biseriate along rachis, mostly 3–8 mm long and 1–3 mm wide, numerous and mostly crowded with extent of naked rachis between leaves usually not exceeding the length of a single leaf. Four to nine autozooids per polyp leaf, grading larger distally. Anthocodiae retractile into permanent calyces, which are sparsely spiculated and may have several indistinct rounded terminal teeth. Siphonozooids minute, in one or two longitudinal rows on the rachis between the polyp leaves. In most species, three-flanged spindles at the base of each polyp leaf form an irregular cluster or armature. Other sclerites of the calyces, rachis, and peduncle are three-flanged spindles or small to minute ovals or rods.

Distribution and depth. North America (California and the Gulf of Mexico); 3–529 m in depth.

Type Species. *Acanthoptilum pourtalesii* Kölliker, 1870 (by monotypy); type locality Gulf of Mexico.

Nominal Species. Seven nominal species, all of which are apparently valid: *Acanthoptilum album* Nutting, 1909 (California); *A. agassizii* Kölliker, 1872 (Gulf of Mexico); *A. annulatum* Nutting, 1909 (California); *A. gracile* (Gabb, 1863) (central California: Tomates Bay to Monterey Bay); *A. oligacis* Bayer, 1957 (Gulf of Mexico); *A. pourtalesii* Kölliker, 1870 (Gulf of Mexico); *A. scalpelifolium* Moroff, 1902 (southern California).

References for species identification. Kükenthal, 1915.

Scytalium Herklots, 1858
(Figs 5G & H, 9I)

Scytalium Herklots, 1858: 14. Kölliker, 1870: 573. J.A. Thomson & Simpson, 1909: 282. Balss, 1910: 48. Kükenthal & Broch, 1911: 310. Kükenthal, 1915: 65. Hickson, 1916: 202.

Diagnosis. Colonies elongate and slender to more stout and robust. Bilateral symmetry throughout rachis. Axis present throughout colony, mostly quadrangular in cross section. Polyp leaves present, thin and fleshy with the broadest part

of each leaf being where it joins with the rachis. Autozooids tubular. Anthocodiae numerous along margins of polyp leaves, retractile into bulbous or tubular basal portions of the polyps, forming spiculiferous calyces. Siphonozooids arranged on the rachis between the polyp leaves. Sclerites are exclusively small ovalshaped plates, distributed in the rachis, peduncle, polyp leaves, and proximal portions of autozooids.

Distribution and depth. Indo-West Pacific (Red Sea, southeastern Africa, Indian Ocean, Malay Archipelago, Philippines, China, Taiwan, Japan); 18–100 m in depth.

Type species. *Scytalium sarsii* Herklots, 1858 (by monotypy); type locality unknown.

Nominal species. Six nominal species assignable to the genus, three of which are considered here as valid: *Scytalium tentaculatum* Kölliker, 1880 (Philippines), with a digitiform process on each calyx; *S. martensi* Kölliker, 1870 (Indian Ocean, China, Japan), with a naked ventral region along the rachis; *S. sarsi* Herklots, 1858 (Indian Ocean, Philippines, Red Sea), without a naked ventral region on the rachis.

References for species identification. Hickson, 1916.

Virgularia Lamarck, 1816
(Figs 5I & J, 9J)

Pennatula (non Linnaeus, 1758: 818) Linnaeus, 1758: 819 (in part).

Virgularia Lamarck, 1816: 429. Herklots, 1858: 11. Richiardi, 1869: 63. Koren & Danielssen, 1877: 101. Kölliker, 1880: 9. Kükenthal & Broch, 1911: 323. Kükenthal, 1915: 71. Williams, 1990: 87.

Lygus Herklots, 1858: 11. *Type species*: *L. mirabilis* Herklots, 1858.

Halisceptrum Herklots 1863: 33. Leuckant, 1872: 281. Kölliker, 1880: 9. *Type species*: *H. gustavianum* Herklots, 1863.

Sceptonidium Richiard, 1869: 63. *Type species: S. mosambicanum* Richiardi, 1869.

Cladiscus Koren & Danielssen, 1877: 101. Danielssen & Koren, 1884: 57. *Type species: C. gracilis* Koren & Danielssen, 1877.

Protocaulon Kölliker, 1880: 26. *Type species: P. molle* Kölliker, 1880.

Svava Danielssen & Koren, 1884: 6. Marshall & Fowler, 1887: 481. *Type species: S. glacilis* Danielssen & Koren, 1884.

Deutocaulon Marshall & Fowler, 1888: 453. *Type species: D. hystricis* Marshall & Fowler, 1888.

Svavopsis Roule, 1908: 181. *Type species: S. elegans* Roule, 1908.

Diagnosis. Colonies long, slender, and vermiform, or more stout, robust, and rigid. Bilateral symmetry of rachis throughout. Axis extends througout most of the length of the colony, sometimes extending beyond the apex of the rachis, mostly round in cross-section. Polyp leaves present, relatively short and often congested, or sometimes with intervals of bare rachis between adjacent leaves. Tubular autozooids fused for most of their length to form relatively thin polyp leaves. Autozooids three to one hundred or more per polyp leaf. Anthocodiae retractile into bulbous fleshy proximal portions of polyps, thus forming fleshy calyces. Siphonozooids sparsely distributed on the polyp leaves below the free parts of the autozooids or more commonly on the rachis between polyp leaves. Sclerites absent except for minute oval bodies in the interior of the peduncle.

Distribution and depth. Widespread distribution in the Atlantic, Indian and Pacific Oceans (Europe, Mediterranean Sea, and the east coasts of North and South America including the Gulf of Mexico, southern Africa, Red Sea, Andaman Islands, Australia New Zealand, Malay Archipelago, New Guinea, Philippines, Taiwan, Okinawa, Japan, Hawaii, and west coast of North America from California to the Galapagos Islands); 0–1100 m in depth.

Type species. *Pennatula mirabilis* Linnaeus, 1758 (by subsequent monotypy: Lamarck, 1816); type locality North Atlantic Ocean.

Nominal species. Fifty-six described species are referable to this genus, of which probably no more than 20 are valid. Some of the most common and well-known species include: *Virgularia gustaviana* (Herklots, 1863) (Indo-West Pacific); *V. juncea* (Pallas, 1766) (Eastern Indian Ocean and Australian Region); *V. mirabilis* (Linnaeus, 1758) (Atlantic and southwestern Indian Oceans); *V. presbytes* Bayer, 1955 (North Carolina to Brazil and the Gulf of Mexico); *V. schultzei* Kükenthal, 1910 (Southern Africa).

Remarks. Deichmann (1936: 272) provides a good summary of the confusion in the literature regarding the authorship and identity of the type species *Virgularia mirabilis*.

References for species identification. Kükenthal, 1915.

Scytaliopsis Gravier, 1906
(Fig. 5K & L)

Scytaliopsis Gravier, 1906: 293. 1908: 237. Kükenthal, 1915: 67. Williams, 1990: 94.

Diagnosis. Colonies shaft-like and rigid, feather-like. Symmetry of rachis is bilateral throughout. Axis extends throughout length of colony, round in cross section. Polyp leaves present, in 15–20 pairs arranged along rachis with conspicuous areas of bare rachis between each pair of leaves. Autozooids usually four or five per leaf. Adjacent autozooids show a gradation of size from smaller innermost to larger outermost. Anthocodiae retractile into bulbous, calyx-like proximal portions of the polyps. Siphonozooids sparse and inconspicuous, usually two present on the rachis between or just below each pair of polyp leaves. Sclerites absent altogether.

Distribution and depth. Western Indian Ocean (Red Sea and southeastern Africa); up to 460 m in depth.

Type species. *Scytaliopsis djiboutiensis* Gravier, 1906 (by original designation); type locality Djibouti (Red Sea).

Nominal species. Apparently one described and valid species: *Scytaliopsis djiboutiensis* Gravier, 1906 (Djibouti and South Africa).

References for species description. Gravier, 1906; Williams, 1990.

Family Pennatulidae Ehrenberg, 1834

Pennatula Linnaeus, 1758
(Figs 6A & B, 10A)

Pennatula Linnaeus, 1758: 818. Pallas, 1787: 200 (in part). Lamarck, 1816: 424. Herklots, 1858: 15. Kölliker, 1869: 230. Gray, 1870: 19. Leuckart, 1872:

280. Balss, 1910: 32. Kükenthal & Broch, 1911: 348. Kükenthal, 1915: 81. Hickson, 1916: 181. Williams, 1990: 100.

Penna Bohadsch, 1761: 98 (in part) (non binominal: name unavailable as work was suppressed by ICZN).

Leioptilus Gray, 1860: 22. 1870: 21 (in part). Type species: *L. fimbriatus* Gray, 1860.

Phosphorella Gray, 1870: 20. Type species: *P. phosphorea* (Linnaeus, 1758).

Ptilella Gray, 1870: 21. Type species: *P. borealis* Gray, 1870.

Diagnosis. Colonies feather-shaped in appearance. Symmetry of rachis is bilateral throughout. Axis present throughout length of colony. Polyp leaves present, usually large and conspicuous, deltoid, sickle-shaped, or fan-shaped. Autozooids arranged in one or more rows along margins of polyp leaves. Anthocodiae retractile into permanent spiculiferous calyces. Calyces tubular, mostly provided with eight terminal teeth. Siphonozooids confined to the rachis, which may extend between the polyp leaves. Mesozooids may also be present on rachis or on margins of polyp leaves opposite the autozooids. Sclerites are three-flanged needles of the calyces, inconspicuously three-flanged rods of the surface of the peduncle, and small ovals in the interior of the peduncle (mostly >0.1 mm long).

Distribution and depth. Near cosmopolitan distribution (Atlantic Ocean, Mediterranean Sea, Indo-Pacific, eastern Pacific, and Southern Oceans); 18–2825 m in depth.

Type Species. *Pennatula phosphorea* Linnaeus, 1758 (by monotypy); unspecified type locality.

Nominal species. Thirty-five described species are referable to this genus, of which perhaps fourteen are to be considered as valid: *Pennatula aculeata* Danielssen, 1860 (North Atlantic); *P. argentina* Acuña & Zamponi, 1992 (Patagonia); *P. delicata* Tixier-Durivault, 1966 (Madagascar); *P. fimbriata* Herklots, 1858 (Japan, Philippines); *P. grandis* Ehrenberg, 1834 (North Atlantic); *P. indica* Thomson & Henderson, 1906 (Indian Ocean); *P. inflata* Külenthal, 1910 (Africa and Subantarctic); *P. moseleyi* Kölliker, 1880 (Southeastern Australia); *P. murrayi* Kölliker, 1880 (Indo-West Pacific); *P. naresi* Kölliker, 1880 (Japan); *P. pearceyi* Kölliker, 1880 (Indo-West Pacific, Japan); *P. phosphorea* Linneaus, 1758 (Cosmopolitan); *P. prolifera* Jungersen, 1904 (North Atlantic); *P. rubra* (Ellis, 1761) (Mediterranean Sea).

References for species identification. Kükenthal, 1915; Tixier-Durivault, 1966.

Ptilosarcus Verrill, 1865
(Figs 6C–E, 10B)

Leioptilus (non Gray, 1860: 22. 1870: 22, (in part)) Gray, 1870: 21 (in part). Kükenthal, 1915: 94

Sarcoptilus Gray, 1840: 45 (in part). Gray, 1860: 23 (in part).

Leioptilum Verrill, 1865: 182. Leuckart, 1872: 281. Kölliker, 1870: 247, 252. Balss, 1910: 58. Kükenthal & Broch, 1911: 386 (misspelling).

Ptilosarcus Verrill, 1865: 183. Leuckart, 1872: 281. Nutting, 1909: 689.

Leioptillum Verrill, 1868: 381 (misspelling).

Lioptilum Pfeffer, 1886: 55 (misspelling).

Diagnosis. Colonies stout and feather-shaped. Rachis is bilaterally symmetrical

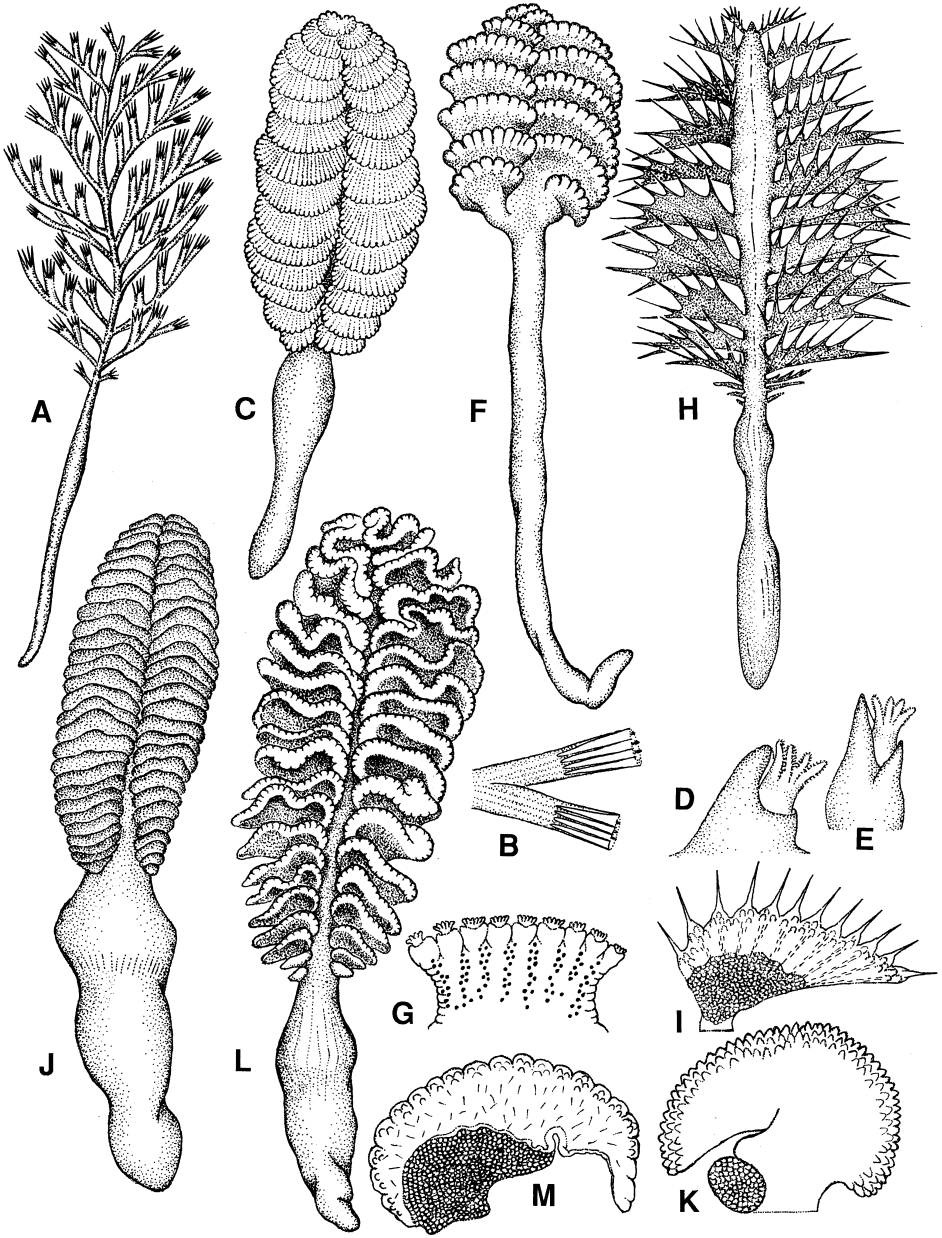

Figure 6. Colonies. A, *Pennatula phosphorea*; 90 mm. B, *Pennatula phosphorea*; two autozooids showing calyces with retracted anthocodiae, 6 mm—(greatest linear dimension shown). C, *Ptilosarcus undulatus*, 50 mm. D, *Ptilosarcus undulatus*; a single autozooid showing calyx with partly retracted anthocodia; calyx is 0.5 mm in height. E, *Ptilosarcus gurneyi*; a single autozooid showing calyx with partly retracted anthocodia; calyx is 0.75 mm in height. F, *Gyrophyllum sibogae* Hickson, 1916, 210 mm. G, *Gyrophyllum sibogae*; a single polyp leaf showing distal autozooids with smaller siphonozooids on the face of the leaf, 35 mm—(greatest linear dimension shown). H, *Pteroeides* sp., 130 mm. I, *Pteroeides spinosum*; a single polyp leaf showing rays of needle-like sclerites, distal autozooids, and congested proximal zone of siphonozooids, 30 mm—(greatest linear dimension of leaf shown). J, *Sarcoptilus grandis*, 110 mm. K, *Sarcoptilus grandis*; a single polyp leaf showing distal autozooids and basal globular pad with siphonozooids, 20 mm = (maximum diameter of leaf shown). L. *Crassophyllum cristatum*, 200 mm. M, *Crassophyllum cristatum*; a single polyp leaf showing needle-like sclerites, distal autozooids, and proximal zone of siphonozooids; 32 mm = (greatest diameter of leaf shown).

throughout. Axis extends length of colony. Polyp leaves present, kidney-shaped, margins often sinuous. Autozooids crowded on distal margins of polyp leaves. Anthocodiae retractile into calyces that are mostly spiculiferous, usually with one or two indistinct to very conspicuous terminal teeth. Siphonozooids numerous in two longitudinal tracts along rachis, clumped or continuous, not present on polyp leaves. Sclerites are three-flanged needles and spindles or longitudinally grooved oval-shaped plates and rods of the calyces and polyp leaves, as well as smooth and relatively large ovals of the peduncle (up to 0.25 mm in length). Some sclerites may contain amber-coloured chitin according to Shapeero (1969).

Distribution and depth. Eastern Pacific Ocean (west coast of North America from the Gulf of Alaska to Peru); 0–68 m in depth.

Type species. *Sarcoptilus gurneyi* Gray, 1860 (by subsequent monotypy: Verrill, 1865); type locality California.

Nominal species. Ten described species are referable to the genus, two of which are considered valid: *Ptilosarcus gurneyi* (Gray, 1860) (Alaska to southern California), with two calyx teeth and siphonozooids not arranged in clumps; *P. undulatus* (Verrill, 1865) (Gulf of California to Peru), with one calyx tooth and siphonozooids arranged in clumps. *P. sinuosus* (Gray, 1860) from New Guinea is here considered a dubious species.

Remarks. The *Leioptilus* of Gray, 1860 and 1870 (in part) is synonymous with *Pennatula*, and the *Sarcoptilus gurneyi* of Gray, 1860 is incorrectly placed in the valid but different genus *Sarcoptilus* Gray, 1848, according to Batie, 1972. Therefore *Ptilosarcus* is the correct generic designation. Batie (1972) provides a detailed history of synonymy for this genus.

References for species identifications. Batie, 1972.

Family Pteroeididae Kölliker, 1880

Gyrophyllum Studer, 1891
(Figs 6F & G, 10C)

Gyrophyllum Studer, 1891: 94. 1901: 34. Roule, 1905: 454. Kükenthal, 1915: 120. Hickson, 1916: 252.

?*Bathypenna* Marion, 1906: 147. *Type species*: *B. elegans* Marion, 1906.

Diagnosis. Colonies stout and clavate with peduncle longer than rachis. Rachis shows bilateral symmetry throughout. Axis extends throughout length of colony, round in cross section. Polyp leaves present, thick, fleshy, and fan-like, 6–9 leaves per side of rachis. Autozooids 20–50 per leaf, in two rows at the leaf margin. Anthocociae retractile into fleshy calyces with or without two fleshy lobe-like teeth. Siphonozooids are present on both sides of the polyp leaves between and below the autozooids, not restricted to zones or pads. Sclerites are elongate three-flanged rods of the polyp leaves, rachis, and peduncle, as well as short blunt rods of the tentacles that are mostly longitudinally grooved or sometimes three-flanged.

Distribution and depth. Widespread distribution (north Atlantic, Madagascar, Malay Archipelago, and Tasmania); 520–2220 m in depth.

Type species. *Gyrophyllum hirondellei* Studer, 1891 (by monotypy); type locality North Atlantic Ocean.

Nominal species. Two species: *Gyrophyllum hirondellei* Studer, 1891 (North Atlantic),

without calyx teeth; *G. sibogae* Hickson, 1916 (Malay Archipelago, Madagascar, Tasmania), with calyx teeth.

References for species identifications. Hickson, 1916.

Sarcoptilus Gray, 1848
(Figs 6J & K, 10F)

Sarcoptilus Gray, 1848: 45 (in part). Gray, 1860: 23 (in part).

Sarcophyllum Kölliker, 1870: 224. Leuckart, 1872: 280. Kükenthal & Broch, 1911: 441. Kükenthal, 1915: 117. *Type species: S. australe* Kölliker, 1870.

Pteroeides (non Herklots, 1858) Balss, 1910: 60 (in part).

Diagnosis. Colonies stout and feather-like. Symmetry of rachis is bilateral throughout. The axis extends throughout the length of the colony, round in cross section. Polyp leaves present, rounded on the margins, mostly fan-shaped or kidney-shaped. Polyp leaves without rays. Autozooids congested on the margins and distal portions of the polyp leaves. Anthocodiae small, retractile into their basal portions, forming calyx-like swellings. Siphonozooids restricted to swollen pads at the base of each polyp leaf where the polyp leaves join the rachis, with proximal surfaces of polyp leaves devoid of siphonozooids altogether. In addition, mesozooids may be present on the distal ventral portion of the rachis in a single longitudinal row or scattered. Sclerites are smooth, not three-flanged; spindles or rods of the polyp leaves do not form rays, long needles absent; rods or flattened rods are present in the rachis; small ovoid or biscuit-shaped rods or plates may occur in the peduncle.

Distribution and depth. Southern Australia (Western Australia, South Australia, New South Wales) and New Zealand; 0–145 m in depth.

Type species. *Sarcoptilus grandis* Gray, 1848 (by monotypy); type locality Australia.

Nominal species. Six described species, five of which are valid: *Sarcoptilus bollonsi* (Benham, 1906) (New Zealand); *S. grandis* Gray, 1848 (Southern Australia); and three recently described species from southern Australia (William, in press).

References for species identification. Williams (in press).

Crassophyllum Tixier-Durivault, 1961
(Figs 6L & M, 10E)

Crassophyllum Tixier-Durivault, 1961: 428.

Diagnosis. Colonies stout, robust, and fleshy. Symmetry of rachis bilateral throughout. Axis extends throughout most of the length of the colony, round in cross section. Polyp leaves present, nearly round in shape, thick and fleshy, 20–36 leaves per side, each leaf arranged in close proximity to adjacent leaves. Each polyp leaf contains 180–250 autozooids in 5–6 rows. Anthocodiae retractile into polyp leaf or into rounded calyces that are not densely spiculated. Siphonozooids appear as a band on the upper portion of the rachis as far down as the third to sixth polyp leaf, as well as in a congested zone in the proximal half of each polyp leaf. Sclerites are smooth, not three-flanged, and include needles from the surfaces of the polyp leaves, smooth rods from the polyp zone and surface of the peduncle, and small ocals sometimes present in

the peduncle. The needle-like sclerites are scattered and do not form rays on the surfaces of the polyp leaves. Sclerites are absent from the rachis.

Distribution and depth. Mediterranean Sea and west coast of Africa (northern Aegean Sea, Zaire and northern Angola); 30–650 m in depth.

Type Species. *Crassophyllum cristatum* Tixier-Durivault, 1961 (by monotypy); type locality Angola.

Nominal species. Two described species, both considered valid: *Crassophyllym cristatum* Tixier-Durivault, 1961 (equatorial West Africa), with *c*. 20 polyp leaves per side; *C. thessalonicae* Vafidis & Koukouras, 1991 (Aegean Sea), with *c*. 35 polyp leaves per side.

References for species identification. Vafidis & Koukouras, 1991.

Pteroeides Herklots, 1858
(Figs 6H & I, 10D)

Penna Bohadsch, 1761: 98 (in part) (non binominal — name unavailable: work suppressed by ICZN).

Pteroeides Herklots, 1858: 19. Kölliker, 1872: 124. Gray, 1870: 24. Leuckart, 1872: 277. Kükenthal & Broch, 1911: 395. Kükenthal, 1915: 97. Hickson, 1916: 219. Hondt, 1984a: 3. Williams, 1990: 106.

Pteromorpha Herklots, 1858: 18. *Type species*: *P. crispa* Herklots, 1858.

Argentella Gray, 1870: 22. *Type species: A. elegans* (Herklots, 1858).

Crispella Gray, 1870: 25. *Type species: C. sieboldii* (Herklots, 1858).

Godeffroyia Kölliker, 1870. 222. *Type species: G. elegans* (non Herklots, 1858) Kölliker, 1870.

Godefroyia Leuckart, 1872: 280 (misspelling).

Pteroides Pfeffer, 1886: 53 (misspelling).

Struthiopteron Broch, 1910: 63. Kükenthal & Broch, 1911: 436. Kükenthal, 1915: 116. *Type species*: *S. elegans* Broch, 1910.

Diagnosis. Colonies mostly stout and feather-like. Symmetry of rachis is bilateral throughout. Axis is present throughout length of colony. Polyp leaves present, well-developed and rigid due to the presence of one to many supporting rays composed of long needle-like sclerites. Accessory leaves may be present between the main leaves. Anthocodiae of autozooids are retractile into the fleshy distal portion of the polyp leaves or into rounded calyces that are not densely spiculated. Siphonozooids minute, numerous and crowded in a conspicuous proximal zone of each polyp leaf. Sclerites are smooth (not three-flanged) needles, spindles or rods of the polyp leaves, rachis, and peduncle. The ends of some needles may be very finely tuberculated.

Distribution and depth. Eastern Atlantic, Mediterranean Sea, and Indo-West Pacific (Europe, Mediterranean, west coast of Africa, east coast of Africa, Madagascar, Indian Ocean, Australia, Malay Archipelago, Philippines, New Guinea, China, Taiwan, Okinawa, Japan, New Zealand, and New Caledonia); 9–320 m in depth.

Type species. *Pennatula spinosa* Ellis, 1764 (by subsequent monotypy: Herklots, 1858); type locality, Europe; *Penna grisea* Bohadsch, 1761 is not admissible since Bohadsch, 1761 is suppressed by ICZN.

Nominal species. Approximately 87 described species and six subspecies are referable to this genus, of which at least 25 species are probably valid. Some

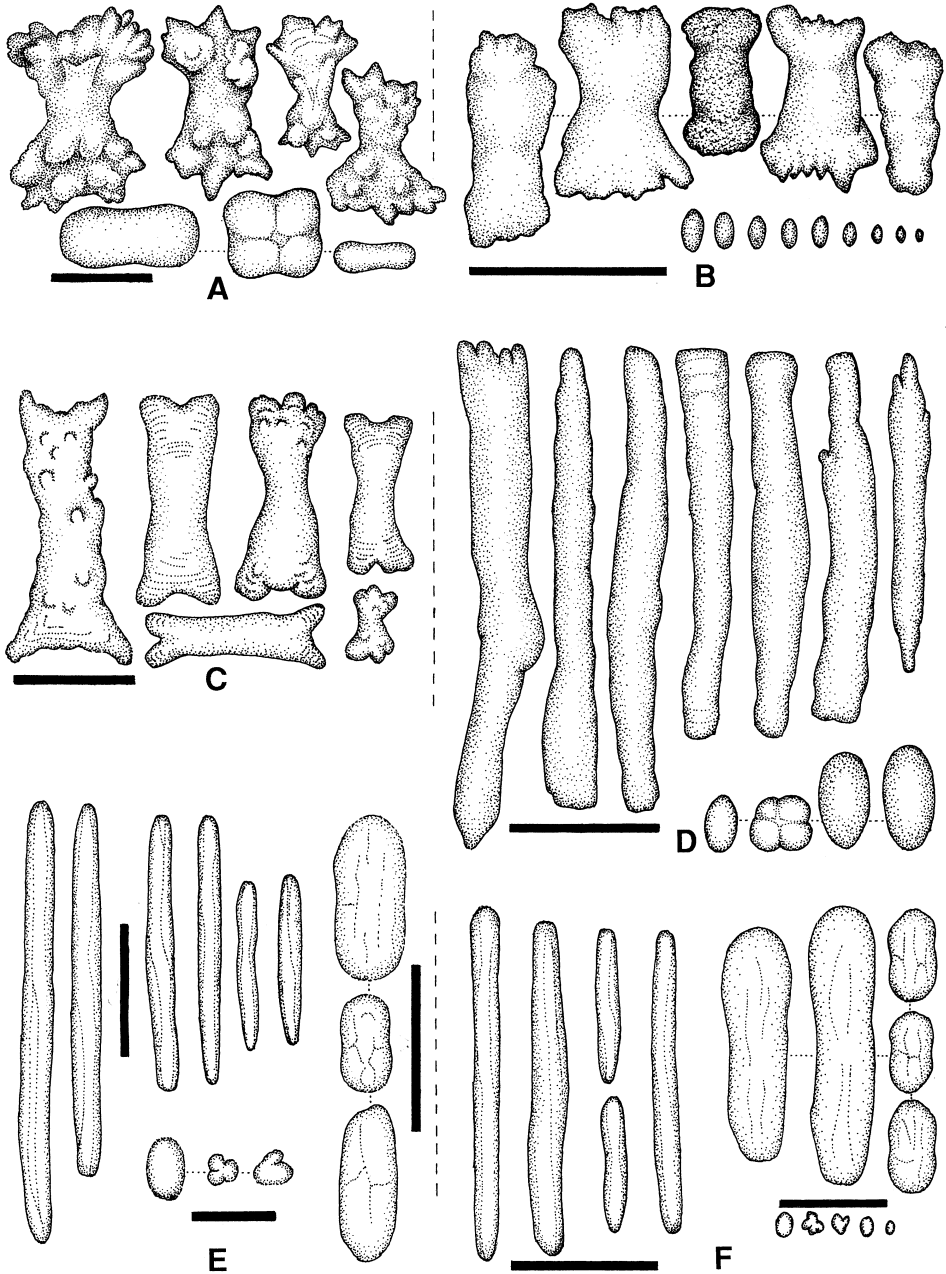

Figure 7. Sclerites. A, *Lituaria hicksoni*; top row, surface of rachis; bottom row, surface of peduncle; scale bar = 0.05 mm. B, *Veretillum* sp.; top row, surface of rachis and peduncle; bottom row, interior of peduncle; scale bar = 0.1 mm. C, *Cavernulina darwini*; surface of rachis; scale bar = 0.1 mm. D, *Cavernularia malabarica*; top row, surface of rachis; bottom row, surface of peduncle; scale bar = 0.1 mm. E, *Actinoptilum molle*; left, calyx and rachis sclerites, scale bar = 0.2 mm; right, surface of peduncle, scale bar = 0.1 mm; bottom centre, interior of peduncle, scale bar = 0.02 mm. F, *Echinoptilum echinatum*; left, calyx and rachis, scale bar = 0.2 mm; top right, peduncle surface, scale bar = 0.05 mm; bottom right, peduncle interior, scale bar = 0.05 mm.

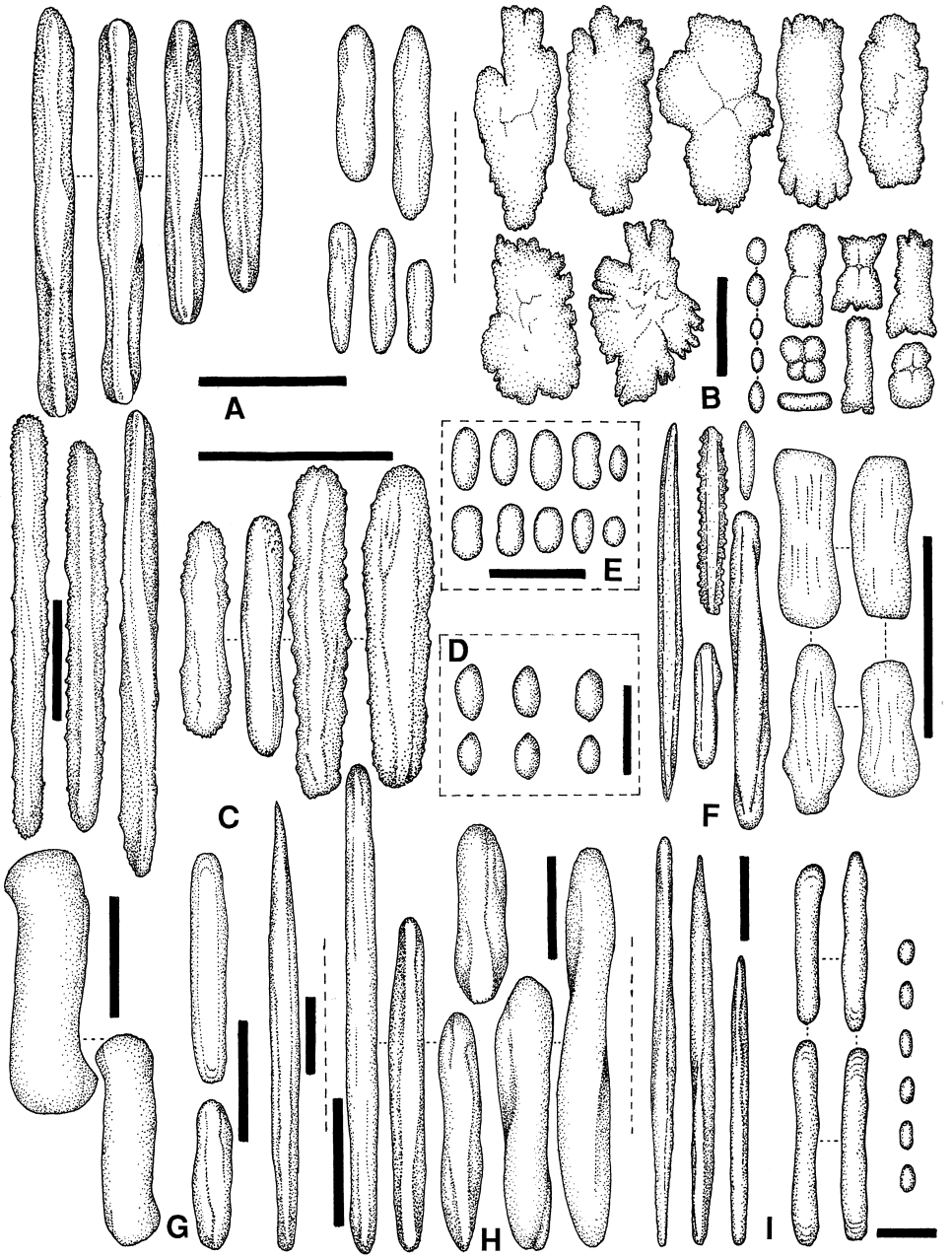

Figure 8. Sclerites. A, *Renilla amethystina*; left, surface of rachis; right, surface of peduncle, scale bar = 0.1 mm. B, *Sclerobelemnon* sp.; top and left, surface of rachis; bottom center, peduncle interior; bottom right, peduncle surface; scale bar = 0.05 mm. C, *Kophobelemnon affine*; left, rachis surface, scale bar = 0.1 mm; right, peduncle surface, scale bar = 0.1 mm. D, *Malacobelemnon* sp., peduncle surface scale bar = 0.02 mm. E, *Anthoptilum grandiflorum*; peduncle interior, scale bar = 0.05 mm. F, *Funiculina quadrangularis*; left, polyps and rachis (spindle on far left is 0.4 mm in length), for all others, scale bar = 0.05 mm; right, surface of peduncle. G, *Protoptilum* sp.; left, surface of tentacles, scale bar = 0.1 mm; right, calyx and rachis, scale bars = 0.1 mm. H, *Distichoptilum gracile*; left, calyx and rachis, scale bar = 0.1 mm; top center, surface of tentacle, length of sclerite = 0.09 mm; right, surface of peduncle, scale bar = 0.05 mm. I, *Stachyptilum superbum*; left, surface of calyx, scale bar = 0.2 mm; centre, surface of peduncle, scale bar = 0.3 mm; right interior of peduncle, scale bar = 0.3 mm.

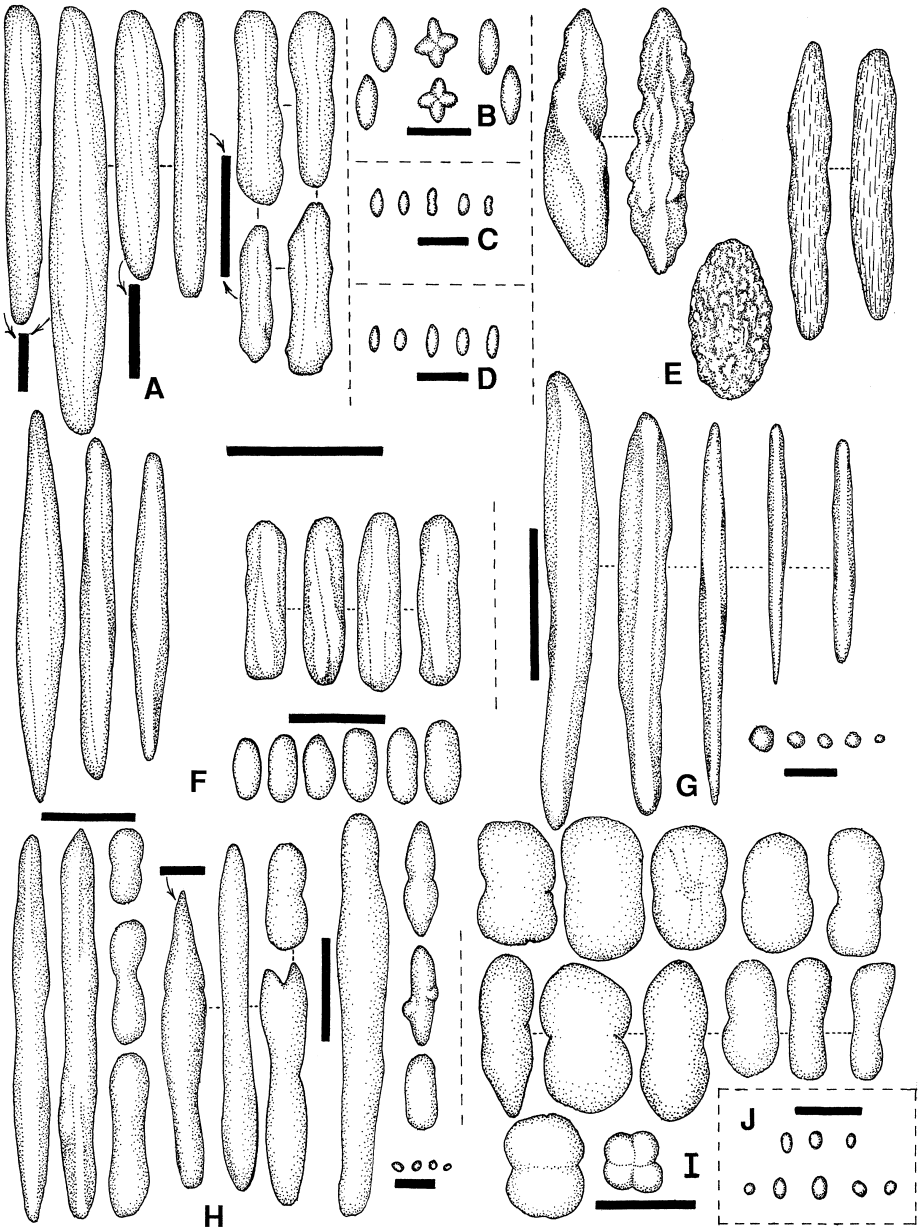

Figure 9. Sclerites. A, *Scleroptilum grandiflorum*; left, polyps and rachis; right, peduncle; scale bars, left = 0.05 mm, centre = 0.2 mm, right = 0.1 mm. B, *Calibelemnon indicum*; peduncle interior, scale bar = 0.03 mm. C, *Chunella gracillima*; peduncle interior, scale bar = 0.04 mm. D, *Amphiacme abyssorum*; peduncle interior, scale bar = 0.04 mm. E, *Umbellula thomsoni*; left, surface of polyp wall, 0.05 and 0.06 mm in length; bottom centre, surface of peduncle, 0.09 mm in length; right, surface of tentacle, 0.10 and 0.08 mm in length. F, *Halipteris californica*; left, surface of calyx; top right, surface of tentacle, scale bar for both = 0.3 mm; bottom right, surface of peduncle, scale bar = 0.05 mm. G, *Stylatula elongata*; top row, polyp leaf armature, scale bar 0.5 mm; bottom right, peduncle interior, scale bar = 0.01 mm. H, *Acanthoptilum gracile*; left, surface of rachis, scale bar = 0.05 mm; left centre, polyp leaf armature, scale bar = 0.1 mm; right centre, surface of polyp leaf, scale bar = 0.05 mm; right, surface of peduncle, scale bar = 0.05 mm; bottom right, interior of peduncle, scale bar = 0.02 mm. I, *Scytalium* sp.; top row, surface of rachis; middle row, surface of polyp leaves and polyps, bottom row, surface of peduncle, scale bar = 0.02 mm. J, *Virgularia schultzei*; interior of peduncle, scale bar = 0.02 mm.

common and well-known species include: *Pteroeides caledonicum* Kölliker, 1869 (New Caledonia and Malay Archipelago); *P. esperi* Herklots, 1858 (Indo-West Pacific); *P. sagamiense* Moroff, 1902 (Japan); *P. spinosum* (Ellis, 1764) (European Atlantic and the Mediterranean Sea).

Remarks. *Penna* Bohadsch, 1761 is considered a synonym of *Pennatula* Linnaeus, 1758, according to Kükenthal, 1915: 81, but the name is invalid because Bohadsch, 1761 was suppressed by ICZN for nomenclatural purposes.

References for species identifications. Leuckart, 1872; Kükenthal, 1915; Hickson, 1916.

DISCUSSION

Classification and phylogeny

The recent collection of a large amount of new material representing many taxa of wide geographic and bathymetric scope, has allowed for the detailed examination of many specimens of pennatulaceans. This material, coupled with the techniques of modern phylogenetics, has lead to a reassessment of the classification and phylogenetic relationships of the group. Kükenthal & Broch (1911), Kükenthal (1915), and Hickson (1916) represent the last major works concerning the systematics and evolution of the Pennatulacea. A modern phylogenetic assessment has been initiated with the publication of the first preliminary cladistic analysis of the group (Williams, 1993).

The identification and comparison of characters of many taxa of pennatulaceans has shown that the higher classification scheme of Kükenthal (1915) regarding the subordinal, familial and subfamilial levels is problematic and largely inadequate. Some families recognized by Kükenthal, Hickson and other authors of this century are shown to be paraphyletic taxa. In addition, detailed examination of many specimens has indicated that justification for certain discontinuities between previously recognized taxa either do not exist or are of a tenuous nature. For example, the distinction between the Pennatulidae and Pteroeididae was based on the occurrence of three-flanged sclerites in the former and cylindrical sclerites in the latter (Kükenthal, 1915: 80). The existence of *Gyrophyllum*, which is similar to the pteroeidids by the presence of thick fleshy polyp leaves containing siphonozooids and sparsely or non-spiculated calyces, but also with three-flanged sclerites that are characteristic of the pennatulids, was obviously an enigma to Kükenthal (1915: 120) as he considered the taxon a "Gen. incertae sedis" at the end of his treatment of the two families. Hickson (1916: 253) was of the opinion that *Gyrophyllum* shows stronger affinities to the Pteroeididae than to the Pennatulidae. His placement thus negates the distinction between the two families as delineated by Kükenthal. The intermediate nature of *Gyrophyllum* precludes precise definitions for the two families. In addition, preliminary cladistic analysis suggests that the six genera formerly assigned to the two families (*Pennatula* and *Ptilosarcus* in the Pennatulidae, and *Gyrophyllum*, *Pteroeides*, *Crassophyllum* and *Sarcoptilus* in the Pteroeididae) can more prudently be viewed to represent a single holophyletic taxon, making the retaining of two families of nominal importance only.

Kükenthal (1915: 6) and Kükenthal & Broch (1911: 153–154) developed a higher classification scheme of two suborders and six sections (equivalent to

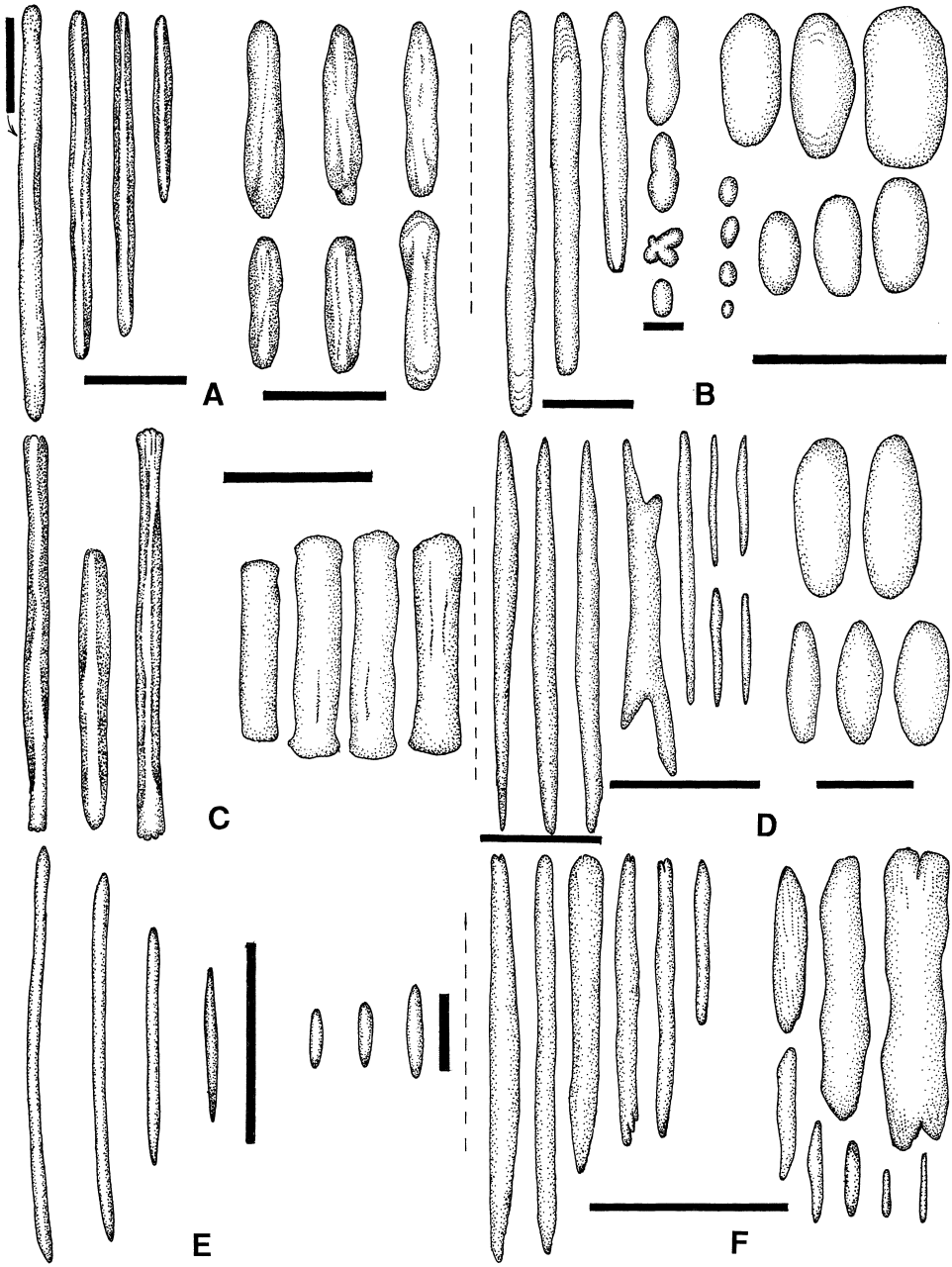

Figure 10. Sclerites. A, *Pennatula phosphorea*; left, surface of calyx, scale bar = 0.2 mm; right, surface of peduncle, scale bar = 0.1 mm. B, *Ptilosarcus undulatus*; left, surface of polyp leaf, scale bars = 0.1 mm and 0.02 mm; right, peduncle sclerites, scale bar = 0.1 mm. C, *Gyrophyllum sibogae*; left, surface of rachis; right surface of tentacles, scale bar for both = 0.1 mm. D, *Pteroeides griseum*; left, surface of polyp leaf, scale bars = 0.5 mm and 0.3 mm; right, surface of peduncle, scale bar = 0.05 mm. E, *Crassophyllum cristatum*; polyp leaf, scale bar = 1.0 mm; peduncle, scale bar = 0.2 mm. F, *Sarcoptilus grandis*; left, surface of polyp leaf; right surface of peduncle, scale bar for both = 0.5 mm.

Table 1. Comparative characters for the genera of Pennatulacea (X = present; * present or absent; BL = bilateral; R = radial; S = spiculiferous; F = fleshy; RR = raised ridges, not distinct polyp leaves).

Genus	Axis	Symmetry	Polyp Leaves	Three-Flanged Sclerites	Permanent Calyces	Depth (m)
Acanthoptilum	X	BL	X	X	S	3–529
Actinoptilum		R		X	S	12–333
Amphiacme	X	BL				818–1200
Anthoptilum	X	BL				155–3150
Calibelemnon	X	BL				100–1275
Cavernularia	*	R				3–320
Cavernulina	X	R				30–62
Chunella	X	BL				818–1200
Crassophyllum	X	BL	X		F	30–650
Distichoptilum	X	BL		X	S	650–4300
Echinoptilum		R or BL		X	S	50–628
Funiculina	X	BL		X	S	60–2600
Gyrophyllum	X	BL	X	X	F	520–1266
Halipteris	X	B	RR	X	S	36–1950
Kophobelemnon	X	BL		X		36–4400
Lituaria	X	R				3–150
Malacobelemnon	X	BL				42–60
Ombellula	X	BL		*		210–>6100
Pennatula	X	BL	X	X	S	18–2825
Protoptilum	X	BL		X	S	250–4000
Pteroeides	X	BL	X		S or F	9–320
Ptilosarcus	X	BL	X	X	S	0–68
Renilla		BL		X		0–70
Sarcoptilus	X	BL	X		S?	0–145
Sclerobelemnon	X	BL				10–472
Scleroptilum	X	BL		X		510–4200
Scytaliopsis	X	BL	X		F	up to 460
Scytalium	X	BL	X		S	18–180
Stachyptilum	X	BL		X	S	36–950
Stylatula	X	BL	X	X	S or F	0–1020
Veretillum	*	R				6–220
Virgularia	X	BL	X		F	0–1100

superfamily rank). The suborders are the Sessiliflorae for taxa with polyps emanating directly from the rachis and the Subselliflorae for taxa with polyps disposed on polyp leaves or raised ridges. The sections are based on growth form, whether radiate, foliate, biserial, verticillate, rush-shaped and feather-shaped. Respectively, the names applied to these taxa are Pennatulina radiata, Pennatulina foliata, Pennatulina biserialia, Pennatulina verticillata, Pennatulina junciformia, and Pennatulina penniformia. Preliminary cladistic investigation suggests that the Sessiliflorae be considered a paraphyletic taxon since it is based on the symplesiomorphy of polyps arising directly from the rachis and thus does not contain all descendants from a common ancestor. The Subselliflorae, on the other hand, is an holophyletic clade, as it is based on the synapomorphy of polyp leaves, and includes all descendents of a single clade. Kükenthal & Broch's section 'Pennatulina foliata' (genus *Renilla*) represents an autapomorphic clade as only its members and no others share a foliate growth form, and thus it is here considered a natural group. Justification for maintaining the other sections is questionable based on preliminary analysis, and thus the traditional higher classification scheme should be viewed as having nominal value only.

Hickson (1916: 34) did not recognize any higher classification scheme above the familial level. Considering the present incomplete status of knowledge concerning the Pennatulacea and the problems associated with defining natural taxa of higher rank, I find Hickson's simpler classification scheme to be the most useful.

Four genera that have been recognized in several previous treatments and which find synonymy in the present work are *Policella*, *Mesobelemnon*, *Helicoptilum*, and *Struthiopteron*. Justification for distinguishing each of these taxa was based on a single variable, nebulous, or insignificant character that in my opinion forms insufficient grounds for separation on each count.

Hickson considered *Amphiacme* and *Calibelemnon* to be synonymous with *Chunella* as he recognized no adequate morphological distinction between the three genera. In the present work, these three genera are retained but are considered closely related: *Calibelemnon* without a terminal polyp, *Amphiacme* with a well-developed and functional terminal polyp, and *Chunella* with a rudimentary or vestigial terminal polyp.

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