PROC. BIOL. SOC. WASH.
94(3), 1981, pp. 902–947

KEY TO THE GENERA OF OCTOCORALLIA EXCLUSIVE OF PENNATULACEA (COELENTERATA: ANTHOZOA), WITH DIAGNOSES OF NEW TAXA

Frederick M. Bayer

Abstract.—A serial key to the genera of Octocorallia exclusive of the Pennatulacea is presented. New taxa introduced are *Olindagorgia,* new genus for *Pseudopterogorgia marcgravii* Bayer; *Nicaule,* new genus for *N. crucifera,* new species; and *Lytreia,* new genus for *Thesea plana* Deichmann. *Ideogorgia* is proposed as a replacement name for *Dendrogorgia* Simpson, 1910, not Duchassaing, 1870, and *Helicogorgia* for *Hicksonella* Simpson, December 1910, not Nutting, May 1910. A revised classification is provided.

Introduction

The key presented here was an essential outgrowth of work on a general revision of the octocoral fauna of the western part of the Atlantic Ocean. The far-reaching zoogeographical affinities of this fauna made it impossible in the course of this study to ignore genera from any part of the world, and it soon became clear that many of them require redefinition according to modern taxonomic standards. Therefore, the type-species of as many genera as possible have been examined, often on the basis of original type material, and a fully illustrated generic revision is in course of preparation as an essential first stage in the redescription of western Atlantic species. The key prepared to accompany this generic review has now reached a stage that would benefit from a broader and more objective testing under practical conditions than is possible in one laboratory. For this reason, and in order to make the results of this long-term study available, even in provisional form, not only to specialists but also to the growing number of ecologists, biochemists, and physiologists interested in octocorals, the key is now presented in condensed form with minimal illustration.

In using the key, it must be kept in mind that some common species have been repeatedly described under different names, and many others have been assigned to the wrong genera. The key cannot reconcile the generic identification reached for any given specimen with the existing literature. One cautionary example, perhaps a typical one, is the genus *Heterogorgia.* None of the species described in that genus by Nutting (1910) in his *Siboga* monograph will key out to the genus *Heterogorgia,* because most of them are species of *Echinogorgia*—some of them valid species by default, others already described by earlier authors. Other species of *Echinogorgia* were described in still other genera in the same paper, and most of those placed in *Echinogorgia* actually belong in such genera as *Villogorgia* and *Menella*.

Although the key includes all common and well-known genera, some that may be valid are omitted for the present owing to incomplete information about them. Three new generic taxa are introduced, and one very common genus is included even though no available name applicable to it has yet been found in the literature. It is probable that some poorly-known genus established with inadequate description and no illustration will be found to apply to it. Several genera that have been treated as junior synonyms or as subgenera by previous authors are here restored to valid generic status on the basis of characters that warrant recognition, and it is possible that several more will be validated when comparative studies have been completed.

The serial key format employed here is a departure from the usual practice in octocorals, and was selected because morphologically similar forms are more closely grouped than is the case in the usual dichotomous format. It is essentially an outline key with the character statements serially numbered and printed without indentation, with the number of the alternate character statement appearing in parentheses. The key has been composed in a single long series not only to accommodate investigators with a limited working knowledge of octocoral systematics, but also because several of the traditional families are so ambiguous that it is impossible to break the key up by families in any defensible way. Where families are sufficiently well defined, they are noted at appropriate points in the key, but several are not mentioned.

Because the pennatulacean material available to me for study is not adequate for improving the summary of that order published by Kükenthal (1915), those genera are not included. I have, however, with considerable misgivings included the "soft coral" genera even though I have not had access to original type-material, because there is no comprehensive review of them comparable to Kükenthal's accounts of the gorgonians (1924) and sea pens (1915). My sources have been the original descriptions and later amplifications chiefly of Kükenthal, Tixier-Durivault and Utinomi, together with such collections as are at my disposal. This part of the key will no doubt be found full of faults, but if it serves to stimulate a reappraisal and a redescription of the "alcyonacean" genera it will have served a useful purpose.

It was not originally my intention to include illustrations in this preliminary version of the key, as the expanded version will be accompanied by diagnoses, synonymies, and scanning electron micrographs of sclerites and other skeletal structures and, wherever necessary, drawings of anthocodial armature and other features not adaptable to portrayal by SEM. As the project progressed, however, it became clear that at least some illustrations would be necessary to clarify verbal statements. Accordingly, some figures have been inserted at various points in the key. In selecting them, I have no doubt erred in the direction of scantiness, as it is not possible to illustrate every point where the user might go astray. In some major taxa where the characters seem quite straightforward, there are no illustrations at all, and in others I may have illustrated the obvious, but I have tried to illustrate those key statements that seemed most likely to prove troublesome to investigators not familiar with the organisms and with the rather subjective terminology that has been traditional in their description. The inconsistent appearance of the figures results from their selection from diverse sources. Some are from my own published papers, some from the work of other authors, and some drawn especially for this paper. In the interests of economy, pen and ink drawings have been used throughout in preference to scanning electron micrographs.

Key to Genera

1(4). Skeleton primarily non-spicular aragonite, formed as distinct corallites containing polyps, united by ribbonlike stolons or common coenosteum (HELIOPORACEA).

2(3). Corallites connected basally only by ribbonlike stolons, skeleton not massive, white; mesogloea of polyps containing sparsely distributed sclerites of calcite (Lithotelestidae) .... *Epiphaxum* Lonsdale, 1850

3(2). Corallites united by massive coenosteum, blue; mesogloea of polyps without sclerites (Helioporidae) .... *Heliopora* Blainville, 1830

4(1). Skeleton when present primarily spicular calcite, sometimes with a more or less calcified scleroproteinous axial support.

5(8). Solitary octocorals, polyps never forming colonies by vegetative budding.

6(7). Polyps large, up to 3.5 cm tall (Fig. 1); sclerites are spindles (Taiaroidae) .... *Taiaroa* Bayer & Muzik, 1976

7(6). Polyps smaller, less than 2 cm tall; sclerites are radiates and irregularly branched forms (Haimeidae) .... *Hartea* Wright, 1864[1]

8(5). Polyps forming colonies by vegetative budding.

9(22). Filaments of all septa but the asulcal pair rudimentary or absent in adult polyps; tentacles with pinnules in multiple

---

[1] This genus may have been based upon a founder polyp of *Sarcodictyon* (pers. comm., Mr. R. L. Manuel).

rows on each side; sclerites, if present, minute (mostly 0.02–0.03 mm, rarely up to about 0.1 mm), flattened, ovate rods or disks, often absent altogether (Xeniidae).

10(15). Polyps retractile.
11(12). Polyps dimorphic .... *Fungulus* Tixier-Durivault, 1970
12(11). Polyps monomorphic.
13(14). Colonies membranous .... *Sympodium* Ehrenberg, 1834
14(13). Colonies forming upright, digitate lobes .... *Efflatounaria* Gohar, 1934
15(10). Polyps not retractile.
16(17). Colonies membranous .... *Anthelia* Larmarck, 1816
17(16). Colonies forming upright lobes.
18(19). Lobes digitate, polyps generally distributed, not limited to terminal capitulum .... *Cespitularia* Milne Edwards & Haime, 1850
19(18). Lobes capitate, polyps concentrated on well-defined capitulum.
20(21). Polyps always monomorphic .... *Xenia* Lamarck, 1816
21(20). Polyps dimorphic, at least when breeding .... *Heteroxenia* Kölliker, 1874
22(9). Filaments fully developed and permanently retained on all 8 septa; tentacles with pinnules in a single row on each side; sclerites usually present, of diverse form.
23(434). Colonies usually firmly attached to solid substrate by a spreading holdfast, sometimes anchored in soft substrate by rootlike projections of axial skeleton or of colonial coenenchyme; polyps monomorphic or dimorphic.
24(197). Skeleton consists only of sclerites, free or more or less firmly cemented together by horny or calcareous material, but sometimes absent entirely.
25(182). Colonies with no internal axial support, or one of loosely bound sclerites.
26(63). Polyps connected only at their bases, neither immersed in common coenenchyme nor joined to one another laterally.
27(28). Calcareous skeleton lacking; stolons and polyps invested by thin, horny perisarc (Cornulariidae) .. *Cornularia* Lamarck, 1816
28(27). Calcareous skeleton composed of sclerites present in addition to horny perisarc.
29(56). Proximal part of gastric cavity open to base of polyps, not filled with mesogloea containing sclerites ("intrusion tissue").
30(53). Colonies arise from stolons that are ribbonlike or simple sheets not divided into two coenenchymal layers.
31(48). Sclerites of stolons and anthosteles not inseparably fused but may form clumps locally.

32(41). Anthocodiae retractile into tall, cylindrical anthosteles arising from ribbonlike, often anastomosing stolons.
33(34). Polyps simple, not producing lateral daughters, arising from stolons usually of ribbonlike or reticular form .... *Clavularia* Blainville, 1830
34(33). Tall axial polyps produce numerous daughters from their lateral walls.
35(36). Anthocodiae not retractile, oral region covered by infolded tentacles during contraction; colonies richly arborescent, polyps of last order very short; white .... *Coelogorgia* Milne Edwards & Haime, 1857
36(35). Anthocodiae fully retractile into anthosteles.
37(38). Sclerites of body walls slender, often branching and interlocking, sometimes fusing into smaller or larger clumps, ornamented with thorns and prickles; white (Fig. 2) .... *Carijoa* F. Müller, 1867
38(37). Sclerites of body walls coarse, blunt spindles, sculpture of outer surface often rounded, smoother and coarser than that of inner surface; red, orange, rarely white (Fig. 3).
39(40). Wall of axial polyp with multiple rings of solenia .... *Paratelesto* Utinomi, 1958
40(39). Wall of axial polyp with one ring of solenia .... *Telesto* Lamouroux, 1812
41(32). Polyps retractile directly into stolons, producing at most only low, conical or short, cylindrical anthosteles.
42(45). Sclerites are tuberculate rods or spindles.
43(44). Sclerites are blunt spindles or rods of moderate size (less than 0.5 mm) with complex tubercles, more or less clearly derived from 6- and 8-radiates (Fig. 4); anthocodiae with few or no sclerites, fully retractile into scarcely projecting anthosteles in ribbonlike stolons that occasionally form a wide membrane; red, pink or yellow .... *Sarcodictyon* Forbes, 1847[2]
44(43). Sclerites are spindles of large size (1 mm) with small and rather simple tubercles or thorns; anthocodiae armed with distinct transverse crown and 8 points of converging spindles below the tentacles, retractile into low but distinct anthosteles, often preserved exsert; stolons commonly membranous; white .... *Trachythela* Verrill, 1922
45(42). Sclerites are large, flattened plates.
46(47). Calices bluntly conical, walls covered by few large plates,

---

[2] Synonym: *Rolandia* Lacaze-Duthiers, 1900.

apertures closed by triangular plates forming distinct operculum; stolons thin, ribbonlike; red (Fig. 5) .... *Tesseranthelia* Bayer, 1981

47(46). Calices bluntly conical, or short cylinders with walls covered by numerous plates of decreasing size but not forming differentiated operculum; stolons ribbonlike or sheetlike; white (Fig. 6) .... *Scleranthelia* Studer, 1878

48(31). Sclerites of stolons and anthosteles rigidly and inseparably fused.

49(50). Polyps short, simple, with low, conical anthosteles; red .... *Cyathopodium* Verrill, 1868

50(49). Polyps tall, producing secondary polyps more or less abundantly from high, cylindrical anthosteles.

51(52). Axial polyps commonly producing shorter lateral polyps; anthocodiae with sclerites in both rachis and pinnules of tentacles .... *Stereotelesto* Bayer, 1981

52(51). Axial polyps infrequently producing shorter lateral polyps; anthocodiae with sclerites below tentacles in 8 septal and 8 interseptal rows, tentacles and pinnules without sclerites .... *Bathytelesto* Bayer, 1981

53(30). Colonies arise from stolons forming multilayered sheets or platforms.

54(55). Sclerites solidly fused except in anthocodiae; colonies forming rounded clumps of large size, transversely partitioned by stolonic platforms; red .... *Tubipora* Linnaeus, 1758

55(54). Sclerites not fused; colonies matlike, spreading, stolons composed of multiple irregular layers but not regularly successive platforms; purple or violet .... *Pachyclavularia* Roule, 1908

56(29). Proximal part of gastric cavity filled in with mesogloea containing sclerites.

57(58). Polyps producing daughters to form sympodial colonies (Pseudocladochonidae) .... *Pseudocladochonus* Versluys, 1907

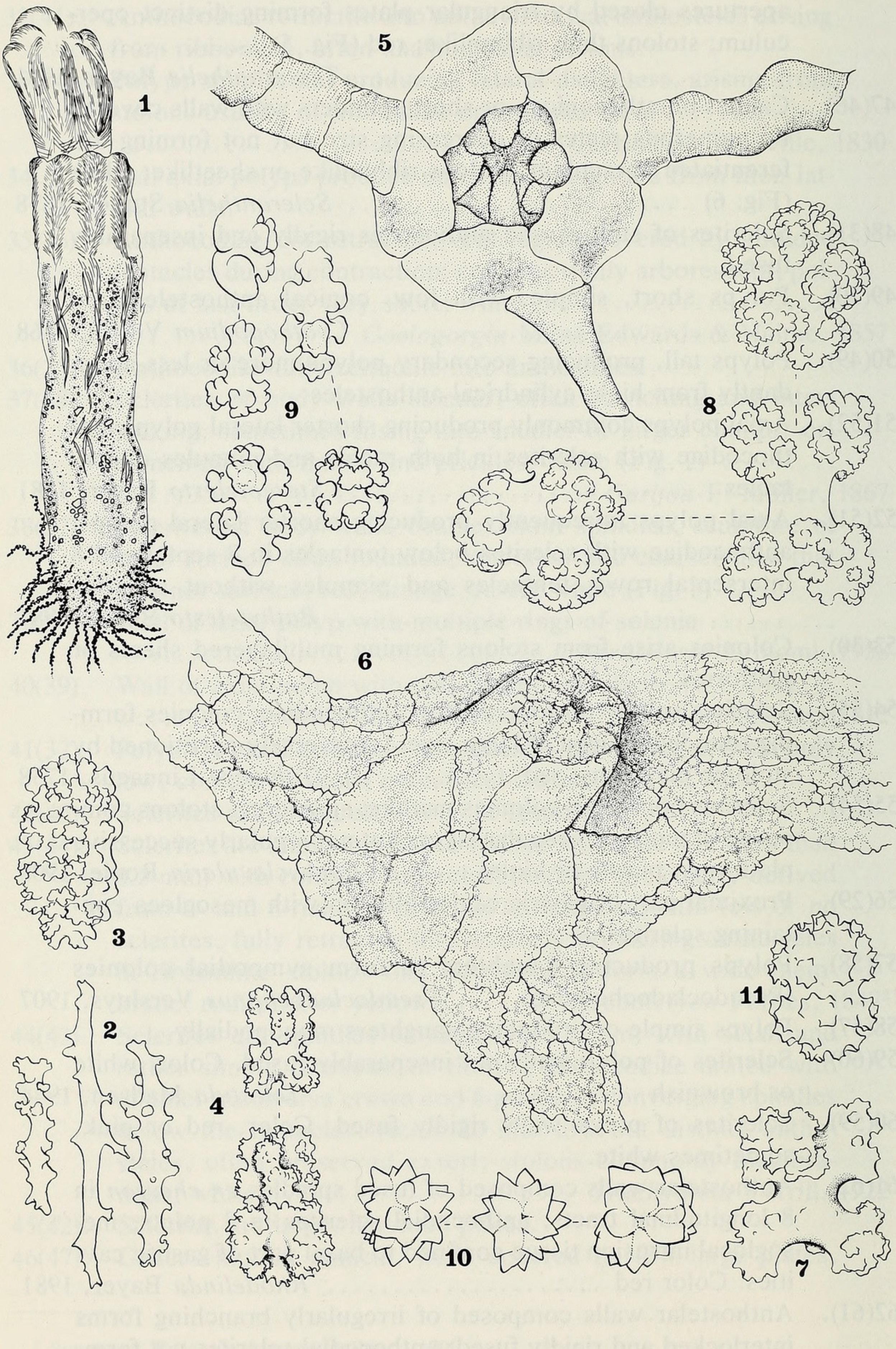
58(57). Polyps simple or producing daughters monopodially.

59(60). Sclerites of polyp walls not inseparably fused. Color, white or brownish .... *Telestula* Madsen, 1944

60(59). Sclerites of polyp walls rigidly fused. Color, red or pink, sometimes white.

61(62). Anthostelar walls composed of fused spindles *en chevron* in 8 longitudinal tracts; anthocodial sclerites in 8 points; mesogloeal intrusion tissue confined to basal part of gastric cavities. Color red .... *Rhodelinda* Bayer, 1981

62(61). Anthostelar walls composed of irregularly branching forms interlocked and rigidly fused; anthocodial sclerites not form-


1
2
3
4
5
6
7
8
9
10
11

ing 8 points; basal spicular intrusion of gastric cavities more extensive. Color, white or pinkish .. *Scyphopodium* Bayer, 1981

63(26). Polyps either partially united laterally or immersed in common coenenchyme.

64(65). Polyps partially united laterally by scanty coenenchyme, new polyps arising at various levels, together forming slender, upright clusters arising from encrusting base .... *Protodendron* Thomson & Dean, 1931

65(64). Polyps immersed in extensive common coenenchyme, forming membranous, lobate or arborescent colonies that may be large or massive.

66(67). Colonies with one dominant axial polyp with very long gastric cavity, having thick coenenchymal walls in which are embedded numerous short lateral polyps, forming flattened, usually unbranched bladelike capitulum arising from a slender sterile stalk attached to annelid tubes or other small objects .... *Pseudogorgia* Kölliker, 1870

67(66). No dominant axial polyp, regardless of colonial shape.

68(97). Coenenchyme divided into inner (medullar) and outer (cortical) layers, gastric cavities of polyps chiefly confined to cortical layer, not extensively penetrating medulla.[3]

69(94). Polyps monomorphic.

70(73). Colonies forming thick, encrusting sheets without conspicuous upright lobes or branches.

71(72). Sclerites predominantly 6-radiates (Fig. 7); surface of coenenchyme purplish red .... *Erythropodium* Kölliker, 1865

72(71). Sclerites mostly irregularly warted, blunt spindles; polyps retracting into hemispherical calices; reddish purple or orange thoughout .... *Anthopodium* Verrill, 1872

73(70). Colonies producing upright lobes or digitate processes, or arborescent structures.

[3] Forms with this array of characters comprise the greater part of the suborder Scleraxonia in the system of Kükenthal.

←

Figs. 1–11. 1, *Taiaroa tauhou* Bayer & Muzik, polyp, ×3; 2, *Carijoa riisei* (Duch. & Mich.), sclerites, ×105; 3, *Telesto sanguinea* Deichmann, sclerite, ×105; 4, *Sarcodictyon catenatum* Forbes, sclerites, ×140; 5, *Tesseranthelia rhodora* Bayer, calyx, ×25; 6, *Scleranthelia rugosa* (Pourtalès), calyx, ×25; 7, *Erythropodium caribaeorum* Duch. & Mich., sclerite, ×275; 8, *Titanideum frauenfeldii* (Kölliker), sclerites, ×275; 9, *Paragorgia* spp., sclerites, ×275; 10, *Asterospicularia randalli* Gawel, sclerites, ×275; 11, *Minabea* sp., sclerite, ×250.

74(75). Colonies lobate or digitate; medulla penetrated by solenia throughout but not separated from cortex by longitudinal boundary canals, sclerites coarse spindles sometimes branched as tripods, purple in medulla, white and/or purple in cortex .... *Briareum* Blainville, 1830

75(74). Colonies digitate or arborescent, medulla little penetrated by solenia, chiefly proximally, separated from cortex by boundary canals.

76(77). Medullar sclerites smooth, fusiform, branching, often anastomosing; colonies arborescent, fanshaped or bushy (Subergorgiidae) .... *Subergorgia* Gray, 1857

77(76). Medullar sclerites mostly long spinous rods or needles, intermixed with more or less abundant tuberculated spindles or rods that may have processes more or less branched; sclerites may fuse in larger or smaller clumps, but not throughout length of medulla.

78(83). Cortical sclerites include radiate forms.

79(80). Cortical sclerites are exclusively radiates (Fig. 8) .... *Titanideum* Verrill, 1863

80(79). Cortical sclerites include blunt, closely tuberculate spindles or oval bodies as well as radiate forms.

81(82). Non-radiate sclerites of cortex are stubby, oval bodies about 0.15 mm long .... *Homophyton* Gray, 1866

82(81). Non-radiate sclerites of cortex are blunt tuberculate spindles or rods up to 0.5 mm long ...... *Diodogorgia* Kükenthal, 1919

83(78). No radiate sclerites in cortex.

84(85). Colonies digitate, clavate, rarely if ever branching; cortex highly vesicular .... *Tripalea* Bayer, 1955

85(84). Colonies branched, often richly so; cortex not vesicular.

86(87). Trunk and/or main branches hollow, tubular; colonies either affixed to hard substrate by spreading holdfast, or anchored in soft substrate by spatulate expansion of trunk .... *Solenocaulon* Gray, 1862

87(86). Trunk and branches not hollow, tubular.

88(89). Polyps widely scattered on all sides, forming distinctly projecting but short, cylindrical calices, anthocodiae commonly preserved exsert; branches round, slender, producing tangled colonies often without evident main stem .... *Anthothela* Verrill, 1879

89(88). Polyps crowded, fully retractile into coenenchyme or forming at most only low, bluntly conical or hemispherical calices; branches more or less flattened, colonies arborescent, with conspicuous main stem.

90(91). Polyps fully retractile into edges of conspicuously flattened terminal branches; branch tips not fistulose .... *Alertigorgia* Kükenthal, 1908
91(90). Polyps usually forming inconspicuous or low hemispherical calices; branch tips fistulose.
92(93). Polyps crowded on three sides of branchlets and on front of large branches and trunk .... *Semperina* Kölliker, 1870
93(92). Polyps biserial, generally absent from front and back of colony .... *Iciligorgia* Duchassaing, 1870
94(69). Polyps dimorphic. Colonies upright, arborescent; cortical sclerites 6-, 7- and 8-radiate capstans, often more or less strongly modified as double clubs or "opera glasses"(Fig. 9) medullar sclerites long, spinose, branching rods (Paragorgiidae).
95(96). Cortex separated from medulla by a distinct ring of boundary canals; sclerites colorless .... *Sibogagorgia* Stiasny, 1937
96(95). Cortex not separated from medulla by a ring of boundary canals; cortical sclerites commonly pink or red, medullar sclerites colorless or pink .... *Paragorgia* Milne Edwards & Haime, 1857
97(68). Coenenchyme not divided into inner and outer layers, gastric cavities of polyps extending throughout.
98(105). Polyps arranged in clusters or on branches that are retractile within common coenenchymal trunk.
99(100). Polyps in small clusters retractile within short, cylindrical trunks united in series by ribbonlike stolons .... *Maasella* Poche, 1914
100(99). Polyps on branches retractile within stout columnar trunk attached to or embedded in substrate; trunks solitary (Fig. 12).
101(102). Polyps widely spaced on ends of twigs comprising a loosely branched polyparium; trunk soft-walled (Fig. 12a) .... *Paralcyonium* Milne Edwards & Haime, 1850
102(101). Polyps crowded on numerous fingerlike branches and retractile within well-defined calices strengthened by abundant sclerites.
103(104). Polyps monomorphic. Sclerites predominantly spindles .... *Studeriotes* Thomson & Simpson, 1909
104(103). Polyps dimorphic. Sclerites predominantly capstans (Fig. 12b) .... *Carotalcyon* Utinomi, 1952
105(98). Polyps not in clusters or on branches retractile within common trunk.

106(171). Polyps scattered or in clusters on branchlets or lobes of arborescent or lobate but not massive colony.

107(108). Sclerites are small, stellate bodies similar to those of didemnid tunicates (Fig. 10) .... *Asterospicularia* Utinomi, 1951

108(107). Sclerites of various shapes but not stellate, or absent altogether.

109(134). Colonies capitate or digitate, branching little or not at all.

110(123). Polyps monomorphic.

111(112). Anthosteles distally flared to form a broad, octagonal collar into which the anthocodiae can be withdrawn (Fig. 13); sclerites are spiny spindles .... *Agaricoides* Simpson, 1905

112(111). Anthosteles not flared to form wide collar.

113(114). Polyps not retractile, with supporting bundle of spindles along one side, forming cluster at top of undivided trunk .... *Coronephthya* Utinomi

114(113). Polyps retractile, without supporting bundle, generally distributed on distal part of trunk.

115(120). Colonies digitate.

116(117). Colonial stalk covered by distinct horny cuticle; sclerites are minute oval or rounded platelets . *Ceratocaulon* Jungersen, 1892

117(116). Colonial stalk without conspicuous cuticle; sclerites not minute platelets.

118(119). Sclerites are thorny spindles, sometimes clubbed .... *Bellonella* Gray, 1862

119(118). Sclerites are double spindles ..... *Metalcyonium* Pfeffer, 1888[4]

120(115). Colonies capitate.

121(122). Sclerites are coarse, tuberculate spindles; polyps retract into conical calices formed by converging sclerites .... *Nidalia* Gray, 1834

122(121). Sclerites are capstans or thorny spheres .... *Metalcyonium* Pfeffer, 1888

123(110). Polyps dimorphic.

124(125). Colonies consist of a single large, cylindrical autozooid with many siphonozooids embedded in its wall .... *Bathyalcyon* Versluys, 1906

125(124). Colonies consist of many autozooids and siphonozooids in a capitulum borne on a sterile stalk.

126(127). Sclerites totally absent .... *Malacacanthus* J. Stuart Thomson, 1910

---

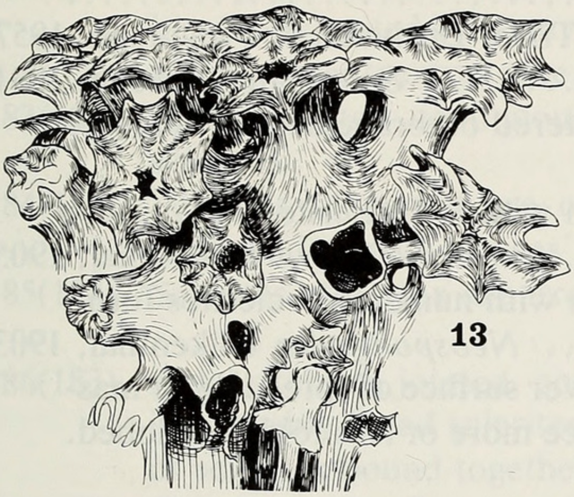
[4] Utinomi (1964, JARE Sci. Rept. (E)23:7) recognized *Metalcyonium* only for capitate forms, considering Pfeffer's digitate type to be *Alcyonium*.

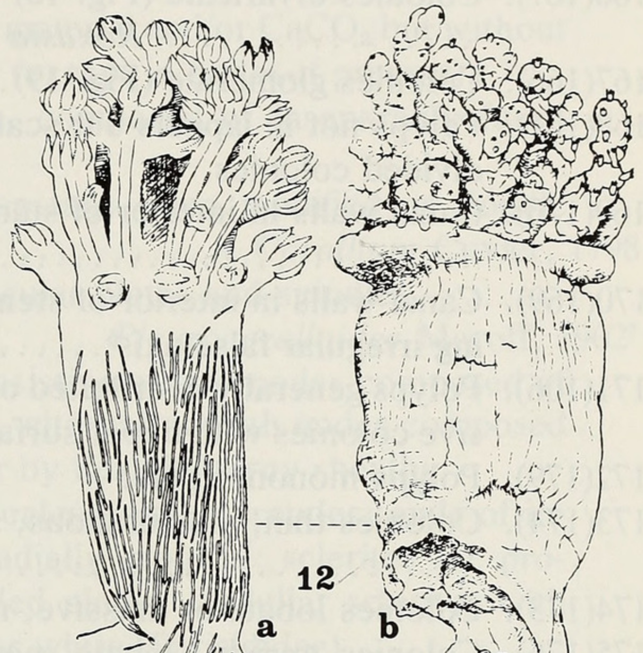
127(126). Sclerites always present in coenenchyme.
128(131). Capitulum digitate; polyps without sclerites.
129(130). Sclerites are clubs about 0.25 mm long .... *Acrophytum* Hickson, 1900
130(129). Sclerites are capstans up to 0.1 mm long (Fig. 11) .... *Minabea* Utinomi, 1957
131(128). Capitulum rounded or spheroidal, not digitate; polyps with sclerites.
132(133). Sclerites are capstans, double stars and thorny spindles; capitulum mushroom-shaped, sharply delimited from sterile stalk .... *Anthomastus* Verrill, 1878
133(132). Sclerites are large, tuberculate spindles; capitulum not sharply delimited from sterile stalk .... *Nidaliopsis* Kükenthal, 1906
134(109). Colonies repeatedly branching or multilobate.
135(138). Polyps retractile.
136(137). Colonies low, branches lobate; polyps weakly armed .... *Gersemia* Marenzeller, 1877
137(136). Colonies tall, branches slender; polyps strongly armed with well-formed crown and points ... *Siphonogorgia* Kölliker, 1874
138(135). Polyps not retractile.
139(156). Polyps without supporting bundle of spindles.
140(143). Colonial form umbellate (Fig. 14).
141(142). Polyps with strong armature of spindles *en chevron* forming 8 points but without transverse collaret; sclerites of coenenchyme few to many, either abundant small capstans or sparse spindles about 2.5 mm long, sometimes totally absent .... *Umbellulifera* Thomson & Dean, 1936
142(141). Polyps weakly armed with blunt, flattened rods in converging double rows; coenenchymal sclerites are capstans and tuberculate rods of small size (up to 0.12), rather sparse .... *Duva* Koren & Danielssen, 1883
143(140). Colonial form not umbellate.
144(147). Polyps situated on small terminal twigs ("lappets" or "catkins") (Fig. 15).
145(146). Coenenchyme with abundant leaf-clubs .... *Capnella* Gray, 1869
146(145). No leaf clubs .... *Litophyton* Forskål, 1775
147(144). Polyps scattered or in clusters on twigs and branches.
148(149). Cylindrical branches radiate outward from summit of short sterile stalk (Fig. 16) .... *Daniela* von Koch, 1891
149(148). Branches not radiating outward from summit of short sterile stalk, but originating at various levels in colony.
150(155). Colonies lobular, sterile trunk short, inconspicuous.

151(152). Polyps and branches with an outer layer of small (0.05–0.12 mm, flattened, tuberculate rods overlying larger, slender spindles up to 0.8 mm long ...... *Scleronephthya* Studer, 1887
152(151). No outer layer of small sclerites.
153(154). Sclerites of polyps arranged *en chevron* in 8 double rows forming conspicuous longitudinal ridges (Fig. 17); coenenchyme with capstans and clubs ... *Pseudodrifa* Utinomi, 1961
154(153). Sclerites of polyps not in 8 double rows forming longitudinal ridges; coenenchyme with irregular spindles and capstans .. .. *Drifa* Danielssen, 1887
155(150). Colonies not lobular.
156(157). Sterile stems arising from common base subdivide into sterile primary and secondary branches producing slender branchlets and twigs bearing scattered polyps; sclerites are curved spindles with projections taller on convex side and needles chiefly in twigs and branches, and small double stars, "brackets" and 4-rayed forms with 2 rays longer in basal parts; tentacles with small, finely granulated, lobed scales .... *Lemnalia* Gray, 1868
157(156). Sterile stems arising from common base produce digitate branches that subdivide at most only once, bearing polyps crowded on distal parts; sclerites are spindles, some thorny, some nearly smooth .... *Paralemnalia* Kükenthal, 1913
158(139). Polyps with supporting bundle of spindles.
159(160). Polyps arise directly from summit of sterile trunk .... *Coronephthya* Utinomi, 1966
160(159). Polyps arise from branches.
161(168). Polyps in lappets (catkins) or bundles on branchlets of abundantly ramified colonies.
162(163). Polyps in lappets (catkins) .... *Nephthea* Audouin, 1826
163(162). Polyps in bundles on branchlets.
164(165). Form of colonies umbellate (Fig. 14) .... *Morchellana* Gray, 1862
165(164). Form of colonies not umbellate.

→

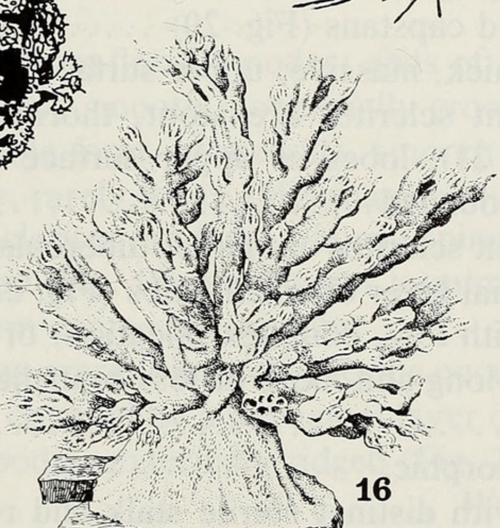
Figs. 12–19. 12, Colonies with retractile polyp-bearing branches: a, *Paralcyonium spinulosum* (delle Chiaje) (after Stiasny, 1941); b, *Carotalcyon sagamianum* Utinomi (after Utinomi, 1952); 13, *Agaricoides alcocki* Simpson, anthosteles of syntype, British Museum (Nat. Hist.), ×3; 14, Umbellate growth form, diagrammatic (after Thomson & Dean, 1931); 15, Catkins of *Litophyton*; 17, *Pseudodrifa nigra* (Pourtalès), 3 contracted polyps, scale = 1 mm; 18, Divaricate growth form, diagrammatic (after Thomson & Dean, 1931).

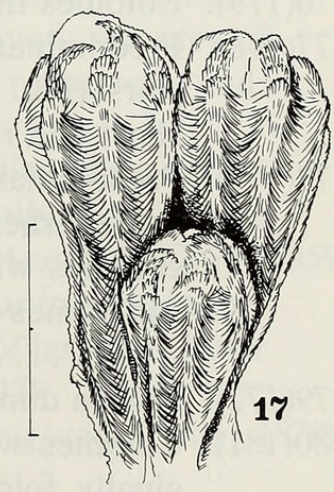

13

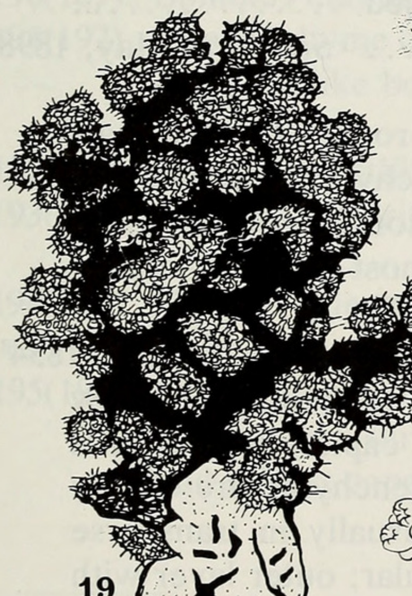


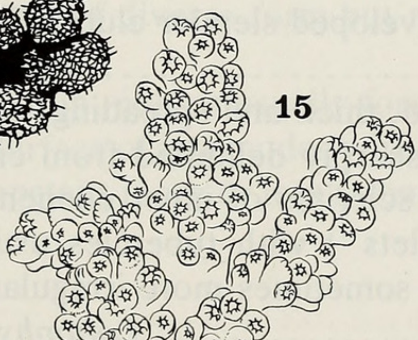
12

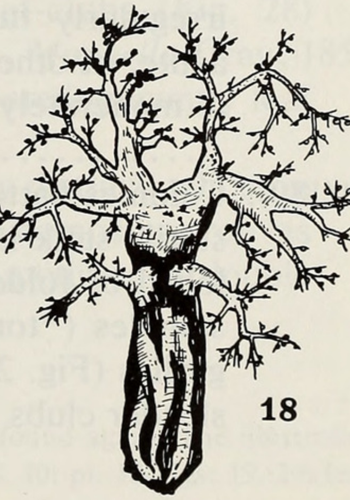

14


16


17


19


15


18

166(167). Colonies divaricate (Fig. 18) .... *Roxasia* Tixier-Durivault & Prevorsek, 1957
167(166). Colonies glomerate (Fig. 19)......... *Spongodes* Lesson, 1831
168(161). Polyps not in lappets but scattered on branchlets of sparsely divided colonies.
169(170). Canal walls in interior of stem with few sclerites .... *Stereonephthya* Kükenthal, 1905
170(169). Canal walls in interior of stem with numerous sclerites forming irregular false axis[5]........ *Neospongodes* Kükenthal, 1903
171(106). Polyps generally distributed over surface of spreading or massive colonies with upper surface more or less folded or lobed.
172(179). Polyps monomorphic.
173(174). Colonies thin, membranous, spreading .... *Parerythropodium* Kükenthal, 1916
174(173). Colonies lobate or massive, not membranous.
175(176). Colonies upright, lobate, not massive; sclerites are thorny spindles and capstans (Fig. 20) ..... *Alcyonium* Linnaeus, 1758
176(175). Colonies thick, massive, upper surface plicate or lobate.
177(178). Predominant sclerites are stout, thorny or spinose double stars (Fig. 21); lobes of upper surface of colonies usually short and rounded...................... *Cladiella* Gray, 1869
178(177). Predominant sclerites are large, tuberculate spindles covered by superficial layer of small clubs (Fig. 22); upper surface of colonies with low, complex plication, or digitate processes, sometimes long and more or less branched .... *Sinularia* May, 1898
179(172). Polyps dimorphic.
180(181). Colonies with distinct sterile stalk and rounded, often marginally folded capitulum; inner coenenchymal sclerites are irregularly tuberculated spindles, in some species rather acute, in others stout and blunt; outermost sclerites weakly to moderately developed slender clubs (Fig. 23) .... *Sarcophyton* Lesson, 1834[6]
181(180). Colonies flattened, thick and spreading, sometimes with low sterile stalk not sharply delimited from capitulum, which is lobed or folded; sclerites of inner coenenchyme are stubby spindles ("tonnelets") with tubercles usually in transverse girdles (Fig. 24), sometimes more irregular; outer layer with slender clubs .... *Lobophytum* Marenzeller, 1886

---

[5] Highly questionable.

[6] The distinction between *Sarcophyton* and *Lobophytum* is minimal.

182(25). Colonies with a consolidated axial support composed of sclerites firmly united by horny material and/or $CaCO_3$ but without a chambered central core, (except in nodes if present).

183(186). Axial skeleton continuous, composed of inseparably fused sclerites.

184(185). Sclerites of cortex are capstans often modified as double clubs and "opera glasses" .... *Corallium* Cuvier, 1798

185(184). Sclerites of cortex are irregular plates and spindles .... *Pleurocoralloides* Moroff, 1902[7]

186(183). Axial skeleton jointed, consisting of internodes composed of inseparably fused sclerites, alternating with nodes composed of sclerites bound together by flexible horny sheaths.

187(188). Branches arise from rigid calcareous internodes; ends of internodes nearly flat and radially grooved; sclerites are profusely tuberculated, rounded plates, medullar sclerites with tuberculate sculpture; color white (Parisididae) .... *Parisis* Verrill, 1864

188(187). Branches arise from flexible nodes; ends of internodes more or less conical and smooth, not radially grooved; sclerites of cortex of variable form, of medulla, smooth rods; color red, orange, yellow, rarely white (Melithaeidae).

189(190). Predominant sclerites are large, thorny spindles often unilaterally developed (Fig. 10), sometimes terminally more or less enlarged to form coarse thorn-clubs ..... *Acabaria* Gray, 1859

190(189). Spindles may be present but other forms occur in abundance.

191(192). Coenenchyme covered by a pavement layer of large, globular or pebblelike bodies externally ridged (Fig. 27) .... *Wrightella* Gray, 1870[8]

192(191). No pavementlike layer of spheroidal bodies.

193(194). Cortical sclerites include numerous leaf-clubs (Fig. 28) .... *Mopsella* Gray, 1857[8]

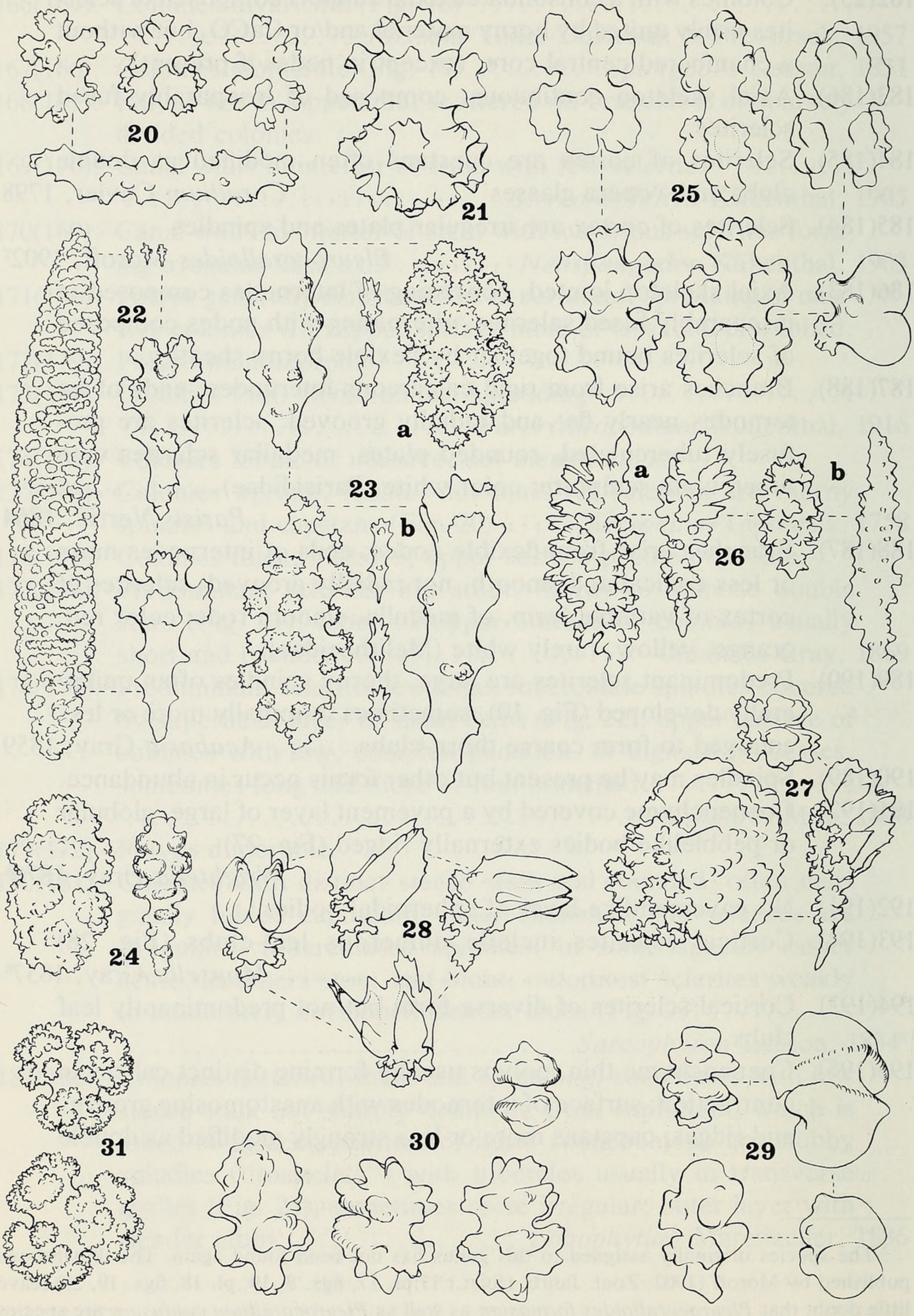
194(192). Cortical sclerites of diverse form but not predominantly leaf clubs.

195(196). Coenenchyme thin, polyps usually forming distinct calices in contraction; surface of internodes with anastomosing grooves and ridges; capstans more or less strongly modified as double

---

[7] The species originally assigned to this genus has not been found again. The illustrations published by Moroff (1902, Zool. Jahrb. (Syst.) 17:pl. 17, figs. 8, 10; pl. 18, figs. 19, 20) leave little doubt that *Pleurocoralloides formosum* as well as *Pleurocorallium confusum* are species of Melithaeidae.

[8] These nominal genera probably do not merit even subgeneric status.


20
21
25
22
a
23
b
a
26
b
27
24
28
31
30
29

wheels ("birotulates") (Fig. 29) ....
.... *Melithaea* Milne Edwards & Haime, 1857[8,9]

196(195). Coenenchyme thicker, polyps fully retractile and not forming calices; surface of internodes marked by parallel grooves interrupted by pits; sclerites are spindles, clubs and small leafy spheroids (Fig. 30) .... *Clathraria* Gray, 1859[8]

197(24). In addition to sclerites (which may be absent), colonies have a proteinous axial support more or less extensively permeated by calcium carbonate.

198(325). Axial support has a hollow, cross-chambered central core.

199(204). Chambered core surrounded by terete, smooth sclerites cemented together by conspicuous horny sheaths.

200(201). Polyps retractile into a thick common coenenchyme, not forming prominent calices; branches thick; sclerites are compact triradiates (Fig. 31); color red ... *Ideogorgia*, nom. nov.[10]

201(200). Polyps not retractile, forming prominent calices; branches thin; sclerites spindles or plates.

202(203). Calices bluntly conical or hemispherical, little or no taller than wide, margins not forming conspicuous lobes or teeth; sclerites are stout, tuberculate, blunt spindles, rods, or thick plates, tentacles with crutch-shaped sclerites. Red or white
.... *Keroeides* Studer, 1887

203(202). Calices cylindrical, taller than wide, margins with 8 distinct lobes filled with converging sclerites; sclerites slender, acute, prickly spindles; tentacles with small, curved spindles, no crutch-shaped bodies. White .... *Lignella* Gray, 1870

204(199). Chambered core of axis surrounded by concentric layers of

[9] Synonyms: *Melitella* Gray, 1859, and *Birotulata* Nutting, 1911.

[10] Pro *Dendrogorgia* Simpson, 1910 (type-species, *Juncella elongata capensis* Hickson, 1904), not Duchassaing, 1870.

←

Figs. 20–31. 20, *Alcyonium digitatum* Linnaeus, sclerites, ×225; 21, *Cladiella krempfi* (Hickson), sclerite, ×225; 22, *Sinularia* sp., large spindle and 3 clubs at same scale, ×30, and 2 clubs ×275; 23, *Sarcophyton* spp.: a, *S. trocheliophorum* Marenzeller, spindle and 2 clubs at same scale, ×70, and club, ×275; b, *S.* sp. cf. *spongiosum* Thomson & Dean, spindle and 3 clubs at same scale, ×70, and club ×275; 24, *Lobophytum crassum* Marenzeller, sclerites ×140; 25, *Corallium* spp., sclerites ×275; 26, *Acabaria* spp.: a, *A. crosslandi* Stiasny, sclerites ×140; b, *A. erythraea* (Ehrenberg), sclerites, ×140; 27, *Wrightella coccinea* (Ellis & Solander), sclerites, ×140; 28, *Mopsella* spp., leaf-clubs ×140; 29, *Melithaea ocracea* (Linnaeus), club and 3 birotulates, ×275; 30, *Clathraria rubrinodis* Gray, "leafy spheroids," i.e., capstans modified toward birotulate type, ×275. 31, *Ideogorgia capensis* (Hickson), sclerites, ×275.

hornlike scleroprotein that may contain calcareous deposits but not formed as sclerites.

205(218). Polyps not functionally differentiated into anthocodia and anthostele, contractile but not retractile within common coenenchyme, tentacles folding over oral disk in contraction.

206(207). Sclerites are small spindles and capstans, sometimes weakly developed as clubs, not individually conspicuous and not regularly arranged on calices .... *Calcigorgia* Broch, 1935

207(206). Sclerites are large spindles, very conspicuous on calices, where commonly arranged *en chevron* in 8 longitudinal double rows.

208(209). Distal ends of sclerites surrounding tentacle bases differentiated as sharp projecting spines forming a conspicuous thorny crown around infolded tentacles .... *Acanthogorgia* Gray, 1857

209(208). Distal ends of sclerites around tentacle bases not specially differentiated as spines, though the tips may project somewhat around calicular apex.

210(211). Calicular and coenenchymal sclerites with tubercles of outer side developed as foliate or spinous processes; calicular sclerites transversely arranged, separated from subtentacular sclerites by inconspicuous suture (where body wall may lack sclerites), but distal part of polyps not retractile within calices .... *Cyclomuricea* Nutting, 1908

211(210). Coenenchymal sclerites with tubercles of inner and outer sides similarly developed; polyps without suture separating calicular from subtentacular sclerites.

212(213). Calices short, cylindrical, margin with several projecting spindles; sclerites of tentacles abruptly smaller in size than those of calicular walls; no radiates in coenenchyme .... *Versluysia* Nutting, 1910

213(212). Calices short and verruciform to tall and cylindrical, sclerites arranged more or less distinctly *en chevron* in 8 double rows, the distal ones projecting little or not at all; sclerites of calices gradually merging with those of tentacle bases, which are not abruptly smaller; inner layer of coenenchyme with more or less abundant radiates.

214(215). Calices low, verruciform .... *Muricella* Verrill, 1869

215(214). Calices prominent, tall, cylindrical.

216(217). Calices clavate; sclerites of calicular walls only indistinctly *en chevron* .... *Anthogorgia* Verrill, 1868

217(216). Calices not clavate; sclerites of calicular walls *en chevron* in 8 longitudinal double rows ..... *Acalycigorgia* Kükenthal, 1908

218(205). Polyps functionally differentiated into anthocodia and anthostele, or fully retractile into common coenenchyme; spiculation of tentacular part of polyp not continuous with that of proximal part but separated by neck zone with few or no sclerites, permitting retraction of anthocodia into anthostele or directly into common coenenchyme.

219(250). Sclerites in the form of spindles with tubercular sculpture arranged in whorls, of moderate size (up to 0.3 mm, commonly less); when present, anthocodial sclerites are tapered, flat rodlets with scalloped or lobed edges, not usually forming a crown and points; core of axis narrow, cortex dense, with little or no loculation (Gorgoniidae).

220(221). The proteinous axis is flat and lamellar .... *Phycogorgia* Milne Edwards & Haime, 1850

221(220). The proteinous axis is nearly or quite cylindrical, or somewhat flattened in the basal part of colony.

222(227). Branches of axis anastomose to form a network.

223(224). Meshes of axial network filled in by coenenchyme, forming flat, more or less dissected, leaflike fronds .... *Phyllogorgia* Milne Edwards & Haime, 1850

224(223). Meshes of axial network not filled in by coenenchyme, forming net-like, reticulate fans.

225(226). Scaphoids present as well as spindles and capstans (Fig. 32) .... *Gorgonia* Linnaeus, 1758

226(225). Spindles and capstans only, no scaphoids (Fig. 33) .... *Pacifigorgia* Bayer, 1951

227(222). Branches of axis not anastomosing to form a meshwork.

228(229). Coenenchyme contains only spindles and capstans with symmetrically developed tuberculation .... *Lophogorgia* Milne Edwards & Haime, 1857

229(228). Many spindles and capstans modified in form or asymmetrically sculptured.

230(233). Numerous double wheels (i.e., capstans with tubercles fused into disks) present as well as spindles (Figs. 35, 36).

231(232). Double wheels large, lengths to 0.15 mm, spindles to 0.2 mm, some developed as leaf clubs (Fig. 35); anthocodiae weakly to moderately armed with flat rods 0.15–0.3 mm long .... *Adelogorgia* Bayer, 1958

232(231). Double wheels smaller, lengths to 0.05 mm, spindles 0.12–0.18 mm, not developed as clubs (Fig. 36); anthocodiae unarmed .... *Eugorgia* Verrill, 1868

233(230). No double wheels present.

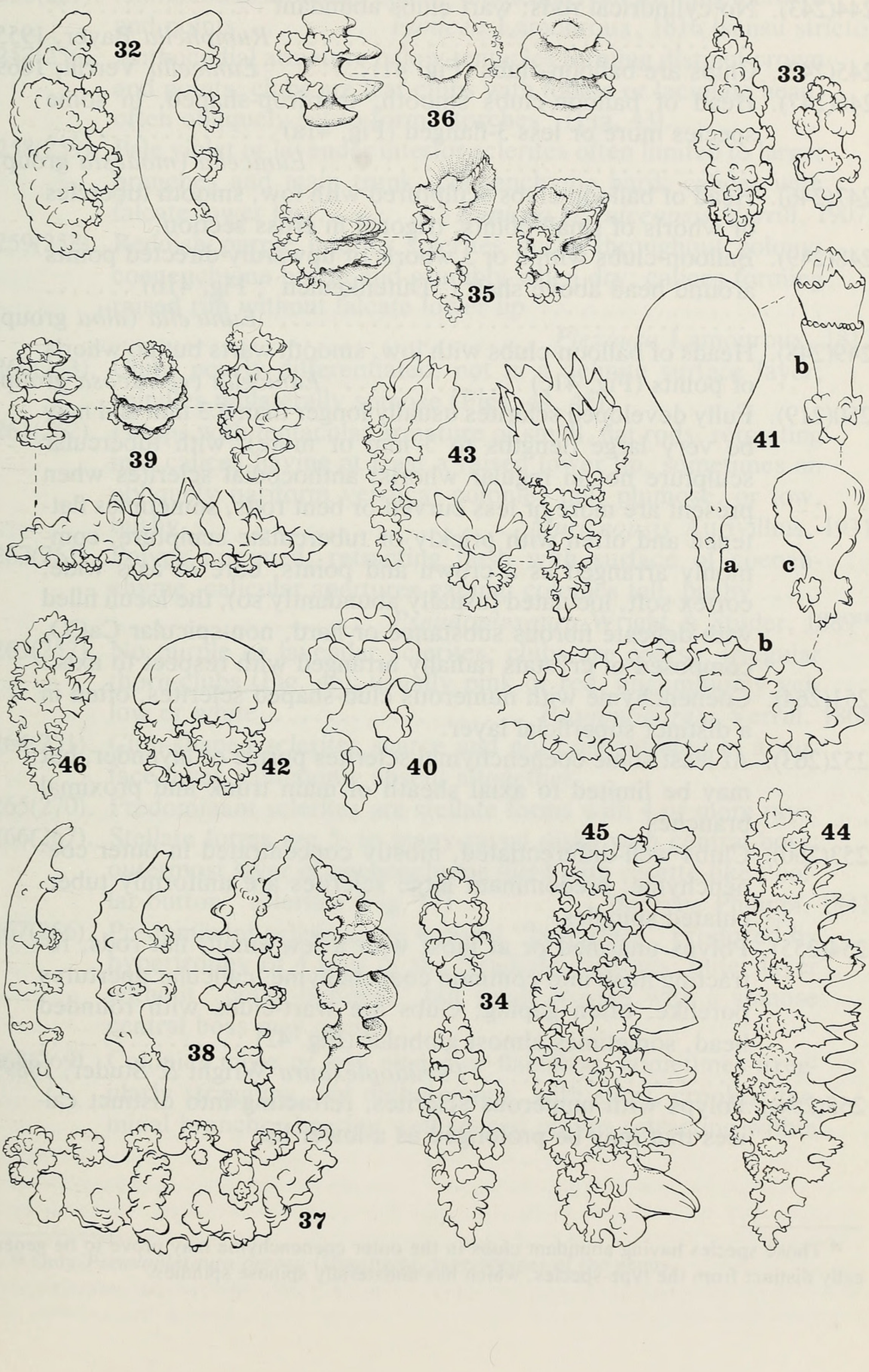
234(239). Scaphoids present as well as spindles and capstans.

235(236). Polyps retractile into distinct verruciform calices; colonies small, loosely pinnate.................. *Olindagorgia,* n. gen.[11]
236(235). Polyps retract flush with coenenchymal surface, not forming calices.
237(238). Colonies dichotomously branched, bushy; polyps retracting into edges of flat or triangular branches .... *Pterogorgia* Ehrenberg, 1834
238(237). Colonies pinnately branched, plumose; polyps in biserial tracts, rarely all around cylindrical or weakly flattened branches, retracting flush with coenenchymal surface .... *Pseudopterogorgia* Kükenthal, 1919
239(234). No scaphoids present.
240(241). Unilaterally spinose spindles present as well as symmetrical spindles and capstans, some capstans weakly modified as disk-spindles (Fig. 39) .... *Leptogorgia* Milne Edwards & Haime, 1857
241(240). No unilaterally spinose spindles present; sclerites predominantly symmetrical spindles or capstans and small clubs.
242(245). Clubs are wart-clubs; tubercles of head prominent and set in a regular transverse whorl (Fig. 40).
243(244). Blunt, cylindrical rods scantily distributed among tuberculate spindles and wart-clubs .... *Hicksonella* Nutting, 1910

[11] *Olindagorgia,* n. gen. Small, loosely pinnate colonies under 10 cm in height; polyps biserial, usually alternate, retractile within prominent hemispherical calices, anthocodiae armed with small flat rods with more or less distinctly spatulate ends; coenenchymal sclerites consisting of acute spindles with compound tubercles in whorls, and scaphoids with surface of convex side weakly undulated. Type-species, *Pseudopterogorgia marcgravii* Bayer, 1961 [1962], Stud. Fauna Curacao 12:255, fig. 82. Holotype, USNM 50228, off Parahyba do Norte, Brazil, 6°59′30″S, 34°47′60″W, 20 fms (36.6 m), *Albatross* sta. 2758, 16 Dec. 1887.

→

Figs. 32–46. 32, Scaphoids of *Gorgonia* spp., ×275; 33, spindle and capstan of *Pacifigorgia irene* Bayer, ×275; 34, Spindle and capstan of *Lophogorgia hebes* (Verrill), ×275; 35, Double wheel, leaf-club and intermediate form, *Adelogorgia phyllosclera* Bayer, ×140; 36, Double wheels of *Eugorgia ampla* Verrill, ×275; 37, Scaphoid of *Pterogorgia anceps* (Pallas) ×275; 38, Scaphoids of *Pseudopterogorgia* spp., ×275; 39, Asymmetrical spindle, capstan and double wheels of *Leptogorgia virgulata* (Lamarck), ×275; 40, Wart-club of *Rumphella* sp., ×275; 41, Spindle and balloon-clubs of *Eunicella* spp.: a, *E. modesta* Verrill; b, *E. papillosa* (Esper); c, *E. verrucosa* (Pallas), all ×275; 42, Globular wart-club of *Pseudoplexaura wagenaari* (Stiasny), ×140; 43, Foliate club and torches of *Eunicea* spp., ×140; 44, Unilaterally spinose spindle of *Muriceopsis flavida* (Lamarck), ×140; 45, Unilaterally spinose spindle of *Pseudoplexaura porosa* (Houttuyn), ×140; 46, Irregularly spinose club of *Psammogorgia arbuscula* (Verrill), ×140.


32
33
36
35
41
b
39
43
a
c
b
46
42
40
45
44
34
38
37

244(243). No cylindrical rods; wart clubs abundant .... *Rumphella* Bayer, 1955

245(242). Clubs are balloon-clubs (Fig. 41) .... *Eunicella* Verrill, 1869

246(247). Head of balloon-clubs smooth, teardrop-shaped, in some species more or less 3-flanged (Fig. 41a) .... *Eunicella* (*modesta* group)

247(246). Head of balloon-clubs sculptured with low, smooth tubercles or whorls of small points, trigonal in cross section.

248(249). Balloon-clubs with 2 or 3 whorls of upwardly directed points around head above shaft (''Dütenkeulen''; Fig. 41b) .... *Eunicella* (*alba* group)

249(248). Heads of balloon-clubs with low, smooth warts but no whorls of points (Fig. 41c) .... *Eunicella* (*verrucosa* group)

250(219). Fully developed sclerites usually longer than 0.3 mm and may be very large (lengths to 5 mm or more), with tubercular sculpture not in regular whorls; anthocodial sclerites when present are more or less curved or bent rods, sometimes flattened and often with prickly or tuberculate sculpture, commonly arranged as a crown and points; core of axis wide, cortex soft, loculated (usually abundantly so), the loculi filled with delicate fibrous substance or hard, non-spicular $CaCO_3$ composed of crystals radially arranged with respect to axis.

251(264). Coenenchyme with numerous club-shaped sclerites, often in a distinct superficial layer.

252(263). At least some coenenchymal sclerites purple or lavender, but may be limited to axial sheath of main trunk and proximal branches.

253(260). Clubs well-differentiated, mostly concentrated in outer coenenchyme; predominant large sclerites are uniformly tuberculated spindles.

254(255). Polyps unarmed or at most with a few small, flat rods, retracting flush into common coenenchyme, calicular apertures porelike, often gaping; clubs are wart-clubs with rounded head, sometimes almost globular (Fig. 42) .... *Pseudoplexaura* Wright & Studer, 1889[12]

255(254). Polyps with numerous sclerites, retracting into distinct calices that may be prolonged as a lower lip.

[12] Those species having abundant clubs in the outer coenenchyme may prove to be generically distinct from the type-species, which has unilaterally spinose spindles.

256(257). Anthocodial armature chiefly tentacular, not forming a crown and points .... *Eunicea* Lamouroux, 1816 (sensu stricto)
257(256). Anthocodial armature below tentacles forming distinct crown and points; clubs are leaf-clubs with foliate or laciniate head, often obliquely set to form "torches" (Fig. 43).
258(259). Pale violet or lavender interior sclerites often limited to larger branches and main trunk; coenenchyme hard; calices with falcate lower lip .... *Eunicea* (*Euniceopsis* Verrill, 1907)
259(258). Reddish purple interior sclerites occur throughout colony; coenenchyme brittle and crumbly when dry; calices forming raised rim without falcate lower lip .... *Plexaura* Lamouroux, 1812
260(253). Clubs poorly differentiated, not in a definite surface layer; spindles unilaterally spinose (Figs. 44, 45).
261(262). Polyps with tentacular armature of small, flat rods, retracting into calices having at least a raised lower lip, sometimes an obliquely nariform verruca; colonies tall, plumose, or low, bushy .... *Muriceopsis* Aurivillius, 1931
262(261). Polyps unarmed, retracting flush with surface of coenenchyme, calicular apertures gaping; colonies tall, bushy .... *Pseudoplexaura* Wright & Studer, 1889[13]
263(252). No purple or lavendar sclerites; clubs are coarse, irregular thorn-clubs (Fig. 46); usually pink or red, uncommonly yellow or white .... *Psammogorgia* Verrill, 1868
264(251). Club-shaped sclerites scarce and not concentrated in a surface layer, commonly absent altogether.
265(270). Predominant sclerites are stellate forms with 4 or more rays.
266(267). Stellate forms are 5- to many-rayed disks with central boss; outermost layer of coenenchyme filled with rosette-like "collar-button" sclerites (Fig. 47) .... *Bebryce* Philippi, 1841
267(266). Predominant sclerites are 4-rayed "butterflies" produced by hypertrophy of 4 rays of the 6-radiate capstans; outer layer without "collar-buttons," but small crosses with a spinose central boss may occur.
268(269). Colonies more or less planar or flabellate, sometimes irregularly straggling, not dichotomous, with short, crooked terminal branches bearing well-spaced polyps retracting within

[13] Only *Pseudoplexaura porosa* (Houttuyn), type-species of the genus.

low, conical or hemispherical calices; rays of 4-radiate sclerites about equal in length (Fig. 48) .... *Nicaule,* n. gen.[14]

269(268). Colonies robustly bushy, dichotomous, with cylindrical branches usually long and straight or nearly so, bearing crowded polyps retracting into slitlike (occasionally porelike) apertures often with a raised, bilabiate rim (or, rarely, prominent bilabiate calices); 2 rays of 4-radiate sclerites usually stronger than the others (Fig. 49) .... *Plexaurella* Valenciennes, 1855

270(265). Stellate forms not predominant.

271(276). Coenenchyme with an outer layer of large, thick plates or flattened spindles, tightly fitted as in mosaic or with smaller spindles in interstices.

272(273). Branches long and ascending (rarely unbranched); calices with 8 marginal lobes formed by converging sclerites; outer surface of coenenchymal plates with undulated or "washboard" appearance .... *Thesea* Duchassaing & Michelotti, 1860

273(272). Branches short, crooked; calices without marginal lobes.

274(275). Polyps biserial; anthocodial armature with numerous sclerites converging in each section of the points; coenenchymal sclerites without spines .... *Scleracis* Kükenthal, 1919

275(274). Polyps on all sides, or absent from only one side of branches; anthocodial armature with only a few (1 or 2 pairs) large sclerites in each sector of the points; coenenchymal sclerites sometimes spiny .... *Paracis* Kükenthal, 1919

276(271). Coenenchymal sclerites may be large but not forming a pavementlike layer of thick plates.

---

[14] *Nicaule crucifera,* n. gen., n. sp. Colony irregularly branched in one plane, about 30 cm tall, branches crooked, terminal branchlets up to 60 mm but mostly 30–40 mm long, diameter about 3 mm. Polyps on all sides, about 1.5–3.0 mm apart, retractile into low calices with 8 marginal lobes; anthocodiae occasionally preserved exsert, armature consisting of 8 points each composed of 2 bent, tuberculated rods about 0.4 mm long, above a transverse neck ring (collaret) 2–3 sclerites wide, composed of curved spindles (Fig. 48a); smaller, straight rodlets longitudinally placed extend upward from the points along the proximal part of the tentacles. Coenenchyme filled with elaborately tuberculated 6-radiate capstans (Fig. 48b) many of which develop into 4-rayed "butterflies" about 0.25 mm wide (Fig. 48c), similar to those of *Plexaurella,* by the suppression of 2 rays and elongation of the outer 4; a few may be 3-rayed and some approach the stellate forms of *Bebryce* by the development of 5 or 6 rays. Sclerites colorless. Axis with spacious central core and thin loculated cortex, soft, collapsing upon drying. Surface of coenenchyme overgrown by attached epizoa supporting a diverse community of small crustaceans. Color in life dull orange, polyps orange except for oral disk and oral surface of tentacles, which are white. Holotype, USNM 59482, Palau Islands, south point of Augulpelu Reef, 10 m, coll. Douglas Faulkner, 27 October 1971, by diving.

277(300). Calicular sclerites are thorn-scales or thorn-spindles.
278(283). Thorn-scales wider than high, consisting of two broad, diverging basal processes and a distal projection either foliate or spinose, usually strong but in some species inconspicuous; coenenchyme with 4-radiates having a central projection (Fig. 50) .... (*Villogorgia* s.l.).
279(280). Outer process an inconspicuous point, more or less flattened in a plane normal to that of base (Fig. 50a) .... *Villogorgia* (''Brandella'' type)
280(279). Outer process conspicuously projecting.
281(282). Outer process digitate or spinelike (Fig. 50b) .... *Villogorgia* (''Perisceles'' type)
282(281). Outer process foliate .... *Villogorgia* s.s. (''Acamptogorgia'' type)
283(278). Thorn-scales as high as, or higher than, wide, consisting of several diverging basal processes (sometimes only 2, but then not broad and flat); no 4-radiates in coenenchyme.
284(293). Anthocodia with few, large sclerites in crown points.
285(286). Calicular thorn-scales with rather short, blunt, serrated projection arising obliquely from a single, elongated root set longitudinally in calicular wall (Fig. 51) .... *Dentomuricea* Grasshoff, 1977
286(285). Calicular thorn-scales with spinelike outer projection arising marginally from complex, spreading base.
287(288). Coenenchymal sclerites elongate, without projecting spines .... *Paramuricea* Kölliker, 1865
288(287). Coenenchymal sclerites with projecting spines.
289(290). Coenenchymal sclerites not conspicuously large, projecting spines of only infrequent occurrence .... *Placogorgia* Studer, 1887
290(289). Coenenchymal sclerites large, platelike or scalelike, many or all with one or more spinelike projections.
291(292). Coenenchymal sclerites thick, coarse spindles or plates with one to several strong, projecting spines .... *Pseudothesea* Kükenthal, 1919[15]
292(291). Coenenchymal sclerites scalelike, with complicated margins

---

[15] Although I have previously synonymized this genus with *Placogorgia* (Bayer, 1959, J. Wash. Acad. Sci. 49:54), it seems to be generically distinct, at least from the type-species of that genus. It may, however, be impossible to distinguish it from *Paracis,* from which it was distinguished by Kükenthal (1924, Tierreich 47:140–141, in key) on the basis of having sclerites of very diverse form, including strongly spinose, unilateral thorn-scales, but these occur in both *Pseudothesea* and *Paracis*.

and short but stout conical spike at or near middle of outer surface; scales at calicular margin with spine obliquely directed at distal edge (Fig. 52) .... *Lepidomuricea* Kükenthal, 1919

293(284). Anthocodiae with numerous, smaller sclerites, sometimes completely unarmed.

294(295). Base of calicular thorn-scales is a single elongated root set longitudinally in calicular wall, from the distal end of which a single stout, serrated process arises obliquely; coenenchyme with thorn-spindles (Fig. 53) .... *Muriceides* Studer, 1887

295(294). Base of calicular thorn-scales consists of diverging or branching root-processes.

296(297). Distal projection of calicular thorn-scales is a single strong spike; coenenchyme with thorn-spindles (Fig. 55) .... *Echinomuricea* Verrill, 1869

297(296). Distal projection of calicular thorn-scales is foliate or broadly lobate (Figs. 54, 56).

298(299). Projection of thorn-scales is a broad blade, thick or thin, often lobed marginally; coenenchyme with irregular spindles (Fig. 54) .... *Menella* Gray, 1870[16]

299(298). Projection of thorn-scales consists of several thick, usually pointed lobes; coenenchyme with coarse, irregular bodies with serrated outer surface, sometimes unilaterally spined spindles (Fig. 56) .... *Echinogorgia* Kölliker, 1865

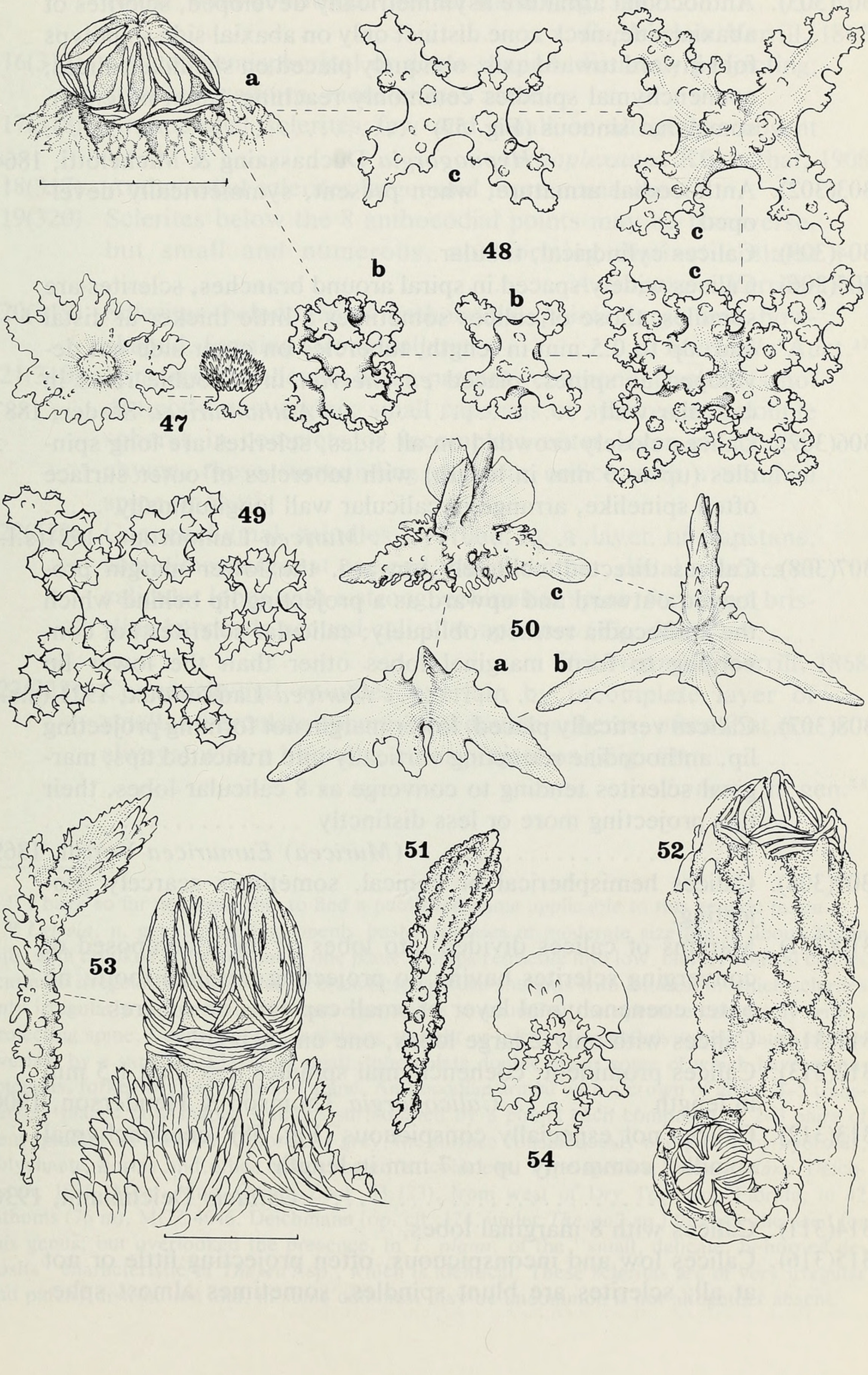
300(277). Calicular sclerites are not thorn-scales or thorn-spindles, although marginal sclerites may have projecting edge.

301(324). Sclerites of coenenchyme include spindles, sometimes short and blunt; capstans, if present, not developed as disk spindles.

[16] Synonym: *Plexauroides* Wright & Studer, 1889.

→

Figs. 47–54. 47, Stellate and rosette sclerites of *Bebryce cinerea* Deichmann, ×140; 48, *Nicaule crucifera* Bayer, n. sp.: a, Calyx with partly exsert anthocodia, ×25, scale = 1 mm; b, 6-radiate capstans, ×140; c, 4-rayed "butterflies," ×140; 49, Capstan and 4-rayed "butterfly" of *Plexaurella nutans* (Duch. & Mich.), ×140; 50, Calicular thorn-scales of *Villogorgia* spp.: a, "Brandella" type; b, "Perisceles" type; c, "Acamptogorgia" type, all ×105; 51, Calicular thorn-scale of *Dentomuricea meteor* Grasshoff, ×70, drawn from SEM, Grasshoff, 1977; 52, *Lepidomuricea ramosa* (Thomson & Henderson), calyx from type colony, British Museum (Nat. Hist.), ×10; 53, *Muriceides hirta* (Pourtalès), calicular thorn-scale ×70, and calyx with partly exsert anthocodia ×17; 54, Calicular thorn-scale of *Menella* sp., ×105.


a
c
c
48
b
b
c
c
47
49
c
50
a
b
51
52
53
c
54

302(303). Anthocodial armature asymmetrically developed, sclerites of abaxial side, neck zone distinct only on abaxial side so polyps fold inward toward axis, obliquely placed on shelflike calices; coenenchymal spindles commonly reaching 4 mm in length, somewhat sinuous (Fig. 57) .... *Hypnogorgia* Duchassaing & Michelotti, 1864

303(302). Anthocodial armature, when present, symmetrically developed.

304(309). Calices cylindrical, tubular.

305(306). Calices widely spaced in spiral around branches, sclerites are spindles, those of calices sometimes a little thicker at distal end, up to 0.5 mm in length, tubercles on outer side not developed as spines, placed *en chevron* in 8 double rows in calicular wall .... *Anthomuricea* Studer, 1887

306(307). Calices closely crowded on all sides; sclerites are long spindles (up to 3 mm in length) with tubercles of outer surface often spinelike, arrange in calicular wall longitudinally .... *Muricea* Lamouroux, 1921(s.l.)

307(308). Calices directed obliquely upward, the lower margin prolonged outward and upward as a projecting lip behind which the anthocodia retracts obliquely; calicular sclerites not converging to form marginal lobes other than the lower lip .... *Muricea* Lamouroux, 1921 (s.s.)

308(307). Calices vertically placed, lower margin not forming projecting lip, anthocodiae retracting vertically into truncated tips; marginal sclerites tending to converge as 8 calicular lobes, their tips projecting more or less distinctly .... (*Muricea*) *Eumuricea* Verrill, 1869

309(304). Calices hemispherical or conical, sometimes scarcely projecting.

310(321). Margins of calices divided into lobes or teeth composed of converging sclerites having no projecting terminal tooth; no outer coenenchymal layer of small capstans or spheres.

311(314). Calices with only 2 large lobes, one on each side.

312(313). Calices prominent; coenenchymal spindles less than 1.5 mm in length .... *Calicogorgia* Thomson & Henderson, 1906

313(312). Calices not especially conspicuous (Fig. 58); coenenchymal spindles commonly up to 7 mm in length .... *Caliacis* Deichmann, 1936

314(311). Calices with 8 marginal lobes.

315(316). Calices low and inconspicuous, often projecting little or not at all; sclerites are blunt spindles, sometimes almost spheroidal, with or without median waist (Fig. 59) .... *Euplexaura* Verrill, 1865

316(315). Calices hemispherical or dome-shaped, distinctly projecting; sclerites fusiform, more or less acute.

317(318). Anthocodial sclerites few and small or altogether absent .... *Anthoplexaura* Kükenthal, 1908

318(317). Anthocodial sclerites larger and more numerous.

319(320). Sclerites below the 8 anthocodial points may be transverse, but small and numerous, not forming distinct collaret .... *Astrogorgia* Verrill, 1868

320(319). Sclerites below the 8 anthocodial points large and bow-shaped, forming strong collaret .... *Muricella* Auct.[17]

321(310). If marginal calicular lobes present, component sclerites not distinctly converging; small capstans or spheres and double spheres in complete or incomplete outer layer of coenenchyme, those surrounding calicular orifice with a terminal spine or tooth.

322(323). Coenenchymal spindles overlain by a layer of capstans, sometimes larger at one end than the other; distal sclerites of calicular lobes with a strong, echinulate spine, forming a bristling barricade around calicular aperture (Fig. 60) .... *Heterogorgia* Verrill, 1868

323(322). Coenenchymal spindles overlain by incomplete layer of small, tuberculate spheres and double spheres, often (but not always) with a bifurcate outer projection (Fig. 61) .... *Lytreia,* n. gen.[18]

---

[17] I have so far not been able to find a published name applicable to this generic taxon.

[18] *Lytreia,* n. gen. Sprawling, openly bushy colonies of moderate size (up to about 20 cm tall), with crooked branches not in one plane. Polyps retractile into low, bluntly conical calices scattered irregularly on all sides of branches; calicular margins with 8 lobes, in which sclerites only irregularly and indistinctly converge, those surrounding the aperture commonly with a projecting spine. Coenenchyme containing straight or curved, irregularly tuberculate spindles overlain by a superficial layer of small, tuberculate double heads some of which have a conspicuous, forked or doubly forked spine. Anthocodiae armed with a crown of about 4–5 transversely placed bow-shaped spindles surmounted by 8 points each composed of 2–3 pairs of bent spindles *en chevron.* Color dirty grey, the surface conspicuously overgrown by hydroids, polychaete worms and other epizoa; sclerites colorless. Type-species, *Thesea plana* Deichmann, 1936 (Mem. Mus. Comp. Zool. 53:123), from west of Dry Tortugas, Florida, in 42 fathoms (76 m), MCZ 4646. Deichmann (op. cit.:124, under *Thesea*? sp.) foresaw the need for this genus, but overlooked the presence, in *T. plana,* of the "small, delicate, bi-horned deposits" characteristic of *Thesea*? sp., which is identical. These sclerites are of very irregular and patchy distribution and, in some colonies, may be uncommon if not altogether absent.

324(301). In addition to spindles, sclerites of coenenchyme include capstans with warts more or less conspicuously modified as disks; calices prominent, conical or cylindrical, well separated, usually biserial; calicular margins and bases of tentacles often with stout, barlike rods; anthocodiae often preserved exsert .... *Swiftia* Duchassaing & Michelotti, 1864

325(198). Axial support does not have a chambered central core but is solid, unless the axis is jointed, in which case the calcareous internodes may be hollow, but not chambered.

326(408). Axis continuous.

327(340). Sclerites are tuberculate double heads or double clubs (Figs. 62–65) sometimes larger at one end (Ellisellidae).

328(329). Cortical sclerites are clubs with distinctly enlarged head and smaller handle surrounded by a whorl of tubercles (Fig. 62) .... *Junceella* Valenciennes, 1855

329(328). Cortical sclerites are double clubs with both ends roughly equal in size (Figs. 63–65).

330(331). Branching of colony lyrate, in one plane .... *Ctenocella* Valenciennes, 1855

331(330). Colonies not lyrate.

332(333). Colonies profusely branched, pinnate, ultimate branchlets each terminating in a single polyp shaped like a clay pipe .... *Riisea* Duchassaing & Michelotti, 1860

333(332). Colonies dichotomous or irregular, not pinnate, commonly unbranched.

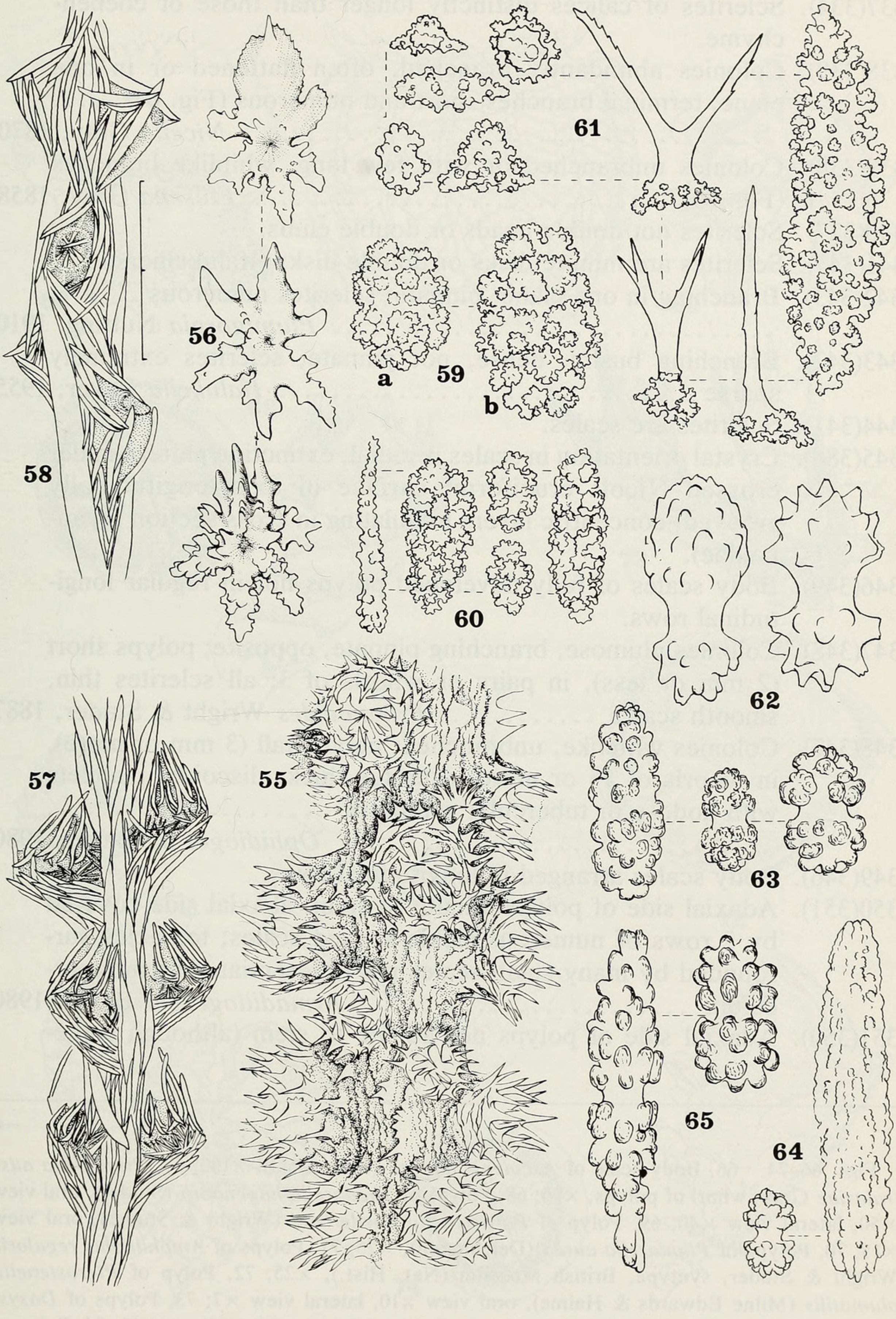
334(337). Sclerites of calices and coenenchyme of about equal size (Fig. 63).

335(336). Colonies abundantly branched in one plane, terminal branches rather short and numerous .... *Verrucella* Milne Edwards & Haime, 1857

336(335). Colonies unbranched or with few long, whiplike branches .... *Toeplitzella* Deichmann, 1936

→

Figs. 55–65. 55, *Echinomuricea coccinea* (Stimson), part of type-colony, Peabody Museum, Yale, ×17; 56, Calicular thorn-scales of *Echinogorgia* spp., upper ×70, lower two ×105; 57, *Hypnogorgia pendula* Duch. & Mich., part of branch, ×10; 58, *Caliacis nutans* (Duch. & Mich.), part of branch, ×10, scale = 2 mm; 59, Sclerites of *Euplexaura* spp.: a, *E. erecta* Kükenthal, ×140; b, *E. capensis* Verrill, type, Museum of Comparative Zoology, Harvard, ×140; 60, Sclerites of *Heterogorgia verrucosa* Verrill, ×105; 61, Sclerites of *Lytreia plana* (Deichmann), ×105; 62, Sclerites of *Junceella juncea* (Pallas), ×275; 63, Sclerites of *Verrucella sanguinolenta* (Gray), ×275; 64, Sclerites of *Nicella dichotoma* (Gray), type, British Museum (Nat. Hit.), ×275; 65, Sclerites of *Ellisella atlantica* (Toeplitz), ×275.



61
56
a
59
b
58
60
62
57
55
63
65
64

337(334). Sclerites of calices distinctly longer than those of coenenchyme.

338(339). Colonies abundantly branched, often flattened or in one plane, terminal branches short and numerous (Fig. 64) .... *Nicella* Gray, 1870

339(338). Colonies unbranched or with few long, whiplike branches (Fig. 65) .... *Ellisella* Gray, 1858

340(327). Sclerites not double heads or double clubs.

341(344). Sclerites are minute disks or double disks (Ifalukellidae).

342(343). Branching in one plane, pinnate; sclerites numerous .... *Plumigorgia* Nutting, 1910

343(342). Branching bushy, dense, not pinnate; sclerites extremely sparse .... *Ifalukella* Bayer, 1955

344(341). Sclerites are scales.

345(386). Crystal orientation in scales is radial, extinction pattern under crossed Nicols cruciform; surface of axis longitudinally grooved, concentric layers undulating in cross section (Primnoidae).

346(349). Body scales of fully developed polyps not in regular longitudinal rows.

347(348). Colonies plumose, branching pinnate, opposite; polyps short (2 mm or less), in pairs or whorls of 3; all sclerites thin, smooth scales .... *Primnoeides* Wright & Studer, 1887

348(347). Colonies whiplike, unbranched; polyps tall (3 mm or more), in whorls of 15 or more; sclerites thick, discoidal platelets with nodose or tubercular sculpture .... *Ophidiogorgia* Bayer, 1980

349(346). Body scales arranged in longitudinal rows.

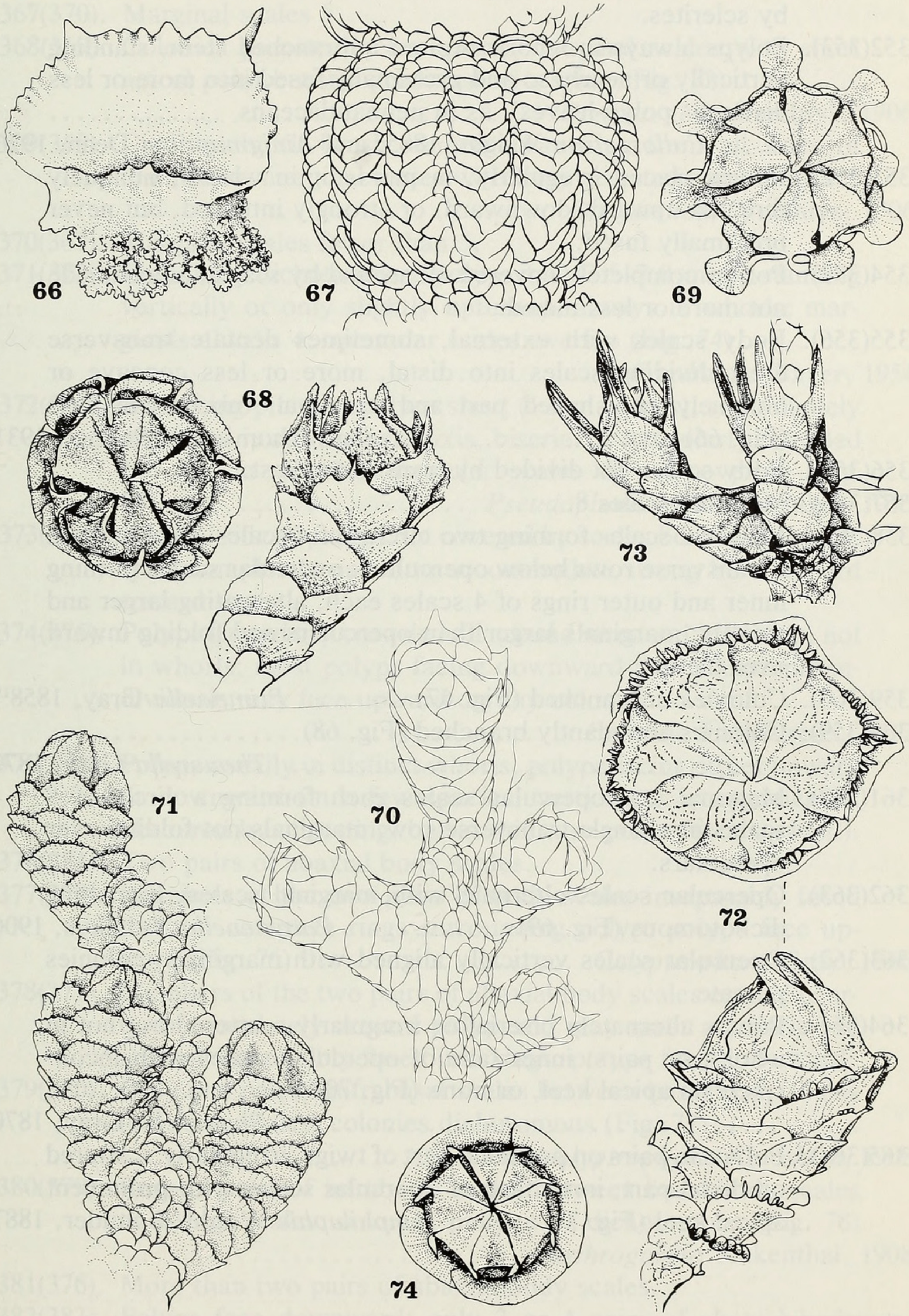
350(351). Adaxial side of polyps adnate to stem, abaxial side covered by 2 rows of numerous sickle-shaped scales; tentacles surrounded by many small scales not differentiated as an operculum .... *Armadillogorgia* Bayer, 1980

351(350). Adaxial side of polyps not adnate to stem (although some-

---

→

Figs. 66–74. 66, Body scale of *Ascolepis nodosa* (Kükenthal), ×100; 67, *Primnoella australasiae* Gray, whorl of polyps, ×20; 68, Polyps of *Thouarella hilgendorfi* (Studer), oral view ×50, lateral view ×40; 69, Polyp of *Parastenella doederleini* (Wright & Studer), oral view ×15; 70, Polyps of *Plumarella aurea* (Deichmann), ×25; 71, Polyps of *Amphilaphis regularis* Wright & Studer, syntype, British Museum (Nat. Hist.), ×25; 72, Polyp of *Pterostenella plumatilis* (Milne Edwards & Haime), oral view ×10, lateral view ×7; 73, Polyps of *Dasystenella acanthina* (Wright & Studer), syntype, British Museum (Nat. Hist.), ×12; 74, Polyp of *Candidella johnsoni* (Wright & Studer), oral view ×15.


66
67
69
68
73
70
71
72
74

times appressed), naked or more or less completely covered by sclerites.

352(353). Polyps always in whorls around unbranched stem, standing vertically or nearly so and proximally fused into more or less distinct "polyp-leaves" as in pennatulaceans .... *Callozostron* Wright, 1885, and *Ainigmaptilon* Dean, 1926

353(352). Polyps placed irregularly, in pairs, or in whorls, obliquely directed upward, downward, or strongly inturned, but never proximally fused.

354(373). Polyps completely covered all around by scales, adaxial side not more or less naked.

355(356). Body scales with external, sometimes dentate transverse crest dividing scales into distal, more or less concave or obliquely cup-shaped part and proximal, tuberculate base (Fig. 66) .... *Ascolepis* Thomson & Rennet, 1931

356(355). Body scales not divided by transverse crest.

357(366). Marginal scales 8.

358(361). Marginal scales forming two circles of 4 scales alternating in 2 transverse rows below operculum; opercular scales forming inner and outer rings of 4 scales each, alternating larger and smaller; marginals larger than operculars and folding inward over them.

359(360). Colonies unbranched (Fig. 67) .... *Primnoella* Gray, 1858[19]

360(359). Colonies abundantly branched (Fig. 68) .... *Thouarella* Gray, 1870

361(358). Marginal and opercular scales each forming a circle of 8 scales in a single transverse row; marginals not folding over operculars.

362(363). Opercular scales alternate with marginal scales; branching dichotomous (Fig. 69) .... *Parastenella* Versluys, 1906

363(362). Opercular scales vertically aligned with marginals; colonies pinnate.

364(365). Polyps alternately biserial or irregularly scattered but not in whorls or pairs; inner face of opercular scales with inconspicuous apical keel, or none (Fig. 70) .... *Plumarella* Gray, 1870

365(364). Polyps in pairs on proximal part of twigs, irregularly scattered on distal part; inner face of opercular scales with prominent apical keel (Fig. 71) ...... *Amphilaphis* Wright & Studer, 1887

---

[19] This genus appears twice in the key.

366(357). Marginal scales fewer than 8.
367(370). Marginal scales 5.
368(369). Colonies pinnate, in one plane; marginal scales with short apical point but not produced as a spine (Fig. 72) .... *Pterostenella* Versluys, 1906
369(368). Colonies bottle-brush shaped, branching from all sides of main stem; marginal scales with long, serrated spine (Fig. 73) .... *Dasystenella* Versluys, 1906
370(367). Marginal scales fewer than 5.
371(372). Branching dichotomous; polyps tall (2.5–7.0 mm), standing vertically or only slightly upturned, always in whorls; marginals always 4; opercular scales overlap (Fig. 74) .... *Candidella* Bayer, 1954
372(371). Branching pinnate; polyps short (1 mm or less), set obliquely or turned inward toward axis, biserial or irregularly crowded but not in whorls; opercular scales do not overlap (Fig. 75) .... *Pseudoplumarella* Kükenthal, 1915
373(354). Adaxial side of polyps not covered by scales but remains partly or completely naked to accommodate strong bend inward toward stem.
374(375). Polyps irregularly crowded all around stem and branches, not in whorls; most polyps facing downward (but occasional individuals may face upward on any colony) .... *Primnoa* Lamouroux, 1812
375(374). Polyps usually in distinct whorls, polyps facing either upward or downward (in a few species, verticillate arrangement is obscured by crowding, but in this case polyps face upward).
376(381). Two pairs of abaxial body scales.
377(378). Members of the two pairs of body scales inseparably fused to form complete rings surrounding polyp; polyps face upward (Fig. 76) .... *Calyptrophora* Gray, 1866
378(377). Members of the two pairs of abaxial body scales extend nearly or completely around polyp and may meet adaxially but are not inseparably fused into rings; polyps face downward.
379(380). Only one pair of infrabasal scales between basal body scales and stem scales; colonies dichotomous (Fig. 77) .... *Paracalyptrophora* Kinoshita, 1908
380(379). Several pairs of infrabasal scales between basal body scales and stem scales; colonies pinnate or dichotomous (Fig. 78) .... *Arthrogorgia* Kükenthal, 1908
381(376). More than two pairs of abaxial body scales.
382(383). Polyps face downward; only 3 or 4 pairs of abaxial body scales (Fig. 79) .... *Narella* Gray, 1870

383(382). Polyps face upward; more than 4 pairs of abaxial body scales.

384(385). Polyps strongly curved inward toward axis; opercular scales distinctly differentiated from body scales, not overreached by marginals which do not bend inward over them; colonies usually pinnate, rarely dichotomous (Fig. 80) .... *Callogorgia* Gray, 1858

385(384). Polyps strongly appressed (but not adnate) to axis; opercular scales poorly differentiated from body scales and more or less conspicuously overreached by marginals, which can fold over them; colonies usually unbranched, in some species dichotomous with long, whiplike branches .... *Primnoella* Gray, 1858

386(345). Crystal orientation in scales is predominantly longitudinal, extinction nearly complete under crossed Nicols; surface of axis smooth or nearly so, concentric layers not undulating (Chrysogorgiidae).

387(393). Colonies unbranched, often spirally twisted.

388(389). Polyps placed uniserially along stem .. *Radicipes* Stearns, 1883

389(392). Polyps placed biserially along stem.

390(391). Distal body scales of polyps forming a distinctly differentiated operculum consisting of 8 triangular scales; abaxial body scales transverse .... *Chalcogorgia* Bayer, 1949

391(390). Distal body scales of polyps not forming an operculum; abaxial body scales longitudinal .... *Distichogorgia* Bayer, 1979

392(389). Polyps closely multiserial along stem, crowded but leaving naked longitudinal tract free of polyps .... *Helicogorgia* nom. nov.[20]

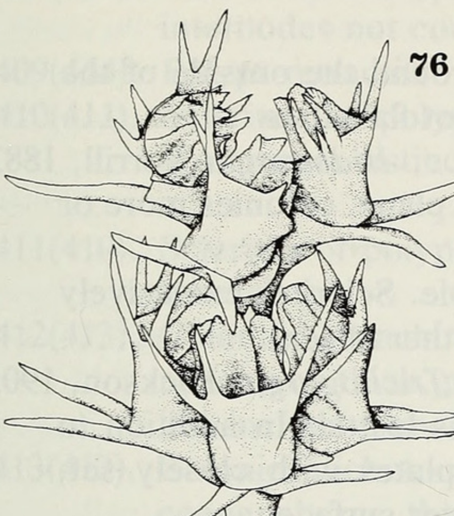
393(387). Colonies branched.

394(399). Colonies with terminal branches long, slender and whiplike,

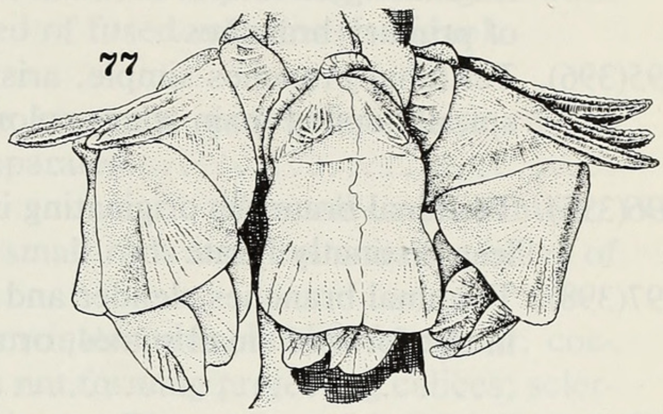
[20] Pro *Hicksonella* J. J. Simpson, 21 Dec. 1910, J. Roy. Microscop. Soc., part 6: 682 (type-species, *Juncella spiralis* Hickson, 1904, here designated); non Nutting, May 1910, Siboga-Exped. Monogr. 13*b*[1]:14 (type-species, *Hicksonella princeps* Nutting, 1910, by original designation and monotypy).

→

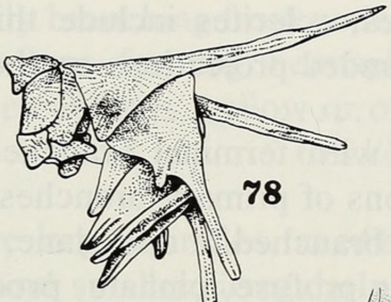
Figs. 75–80. 75, *Pseudoplumarella corruscans* (Thomson & Mackinnon), polyp of syntype, British Museum (Nat. Hist.), ×37; 76, *Calyptrophora clarki* Bayer, 2 whorls of polyps, ×10; 77, *Paracalyptrophora josephinae* (Lindstrom), whorl of polyps, ×15; 78, *Arthrogorgia ijimai* (Kinoshita), polyp, ×12; 79, Polyps of *Narella* spp.: a, *N. leilae* Bayer, ×10; b, *N. bowersi* (Nutting), ×10; 80, *Callogorgia gilberti* Nutting, whorl of polyps, ×30.



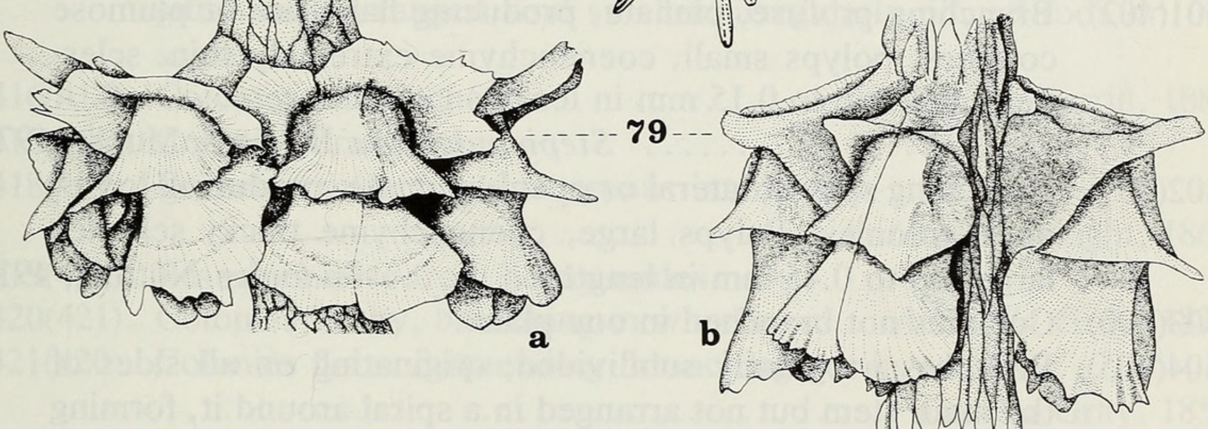
76



77



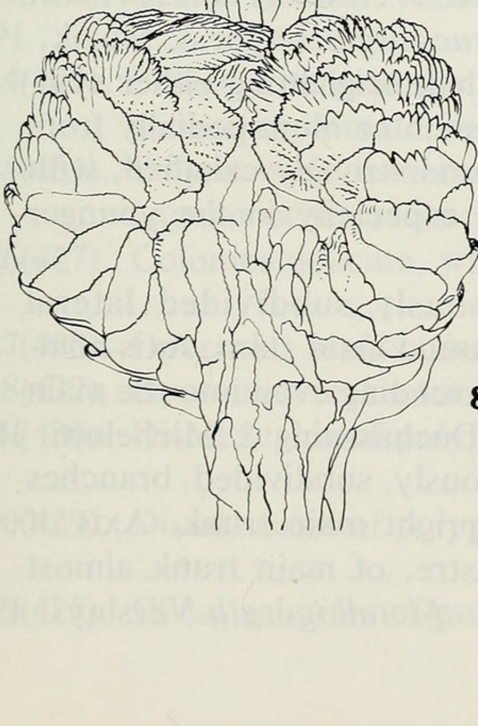
78



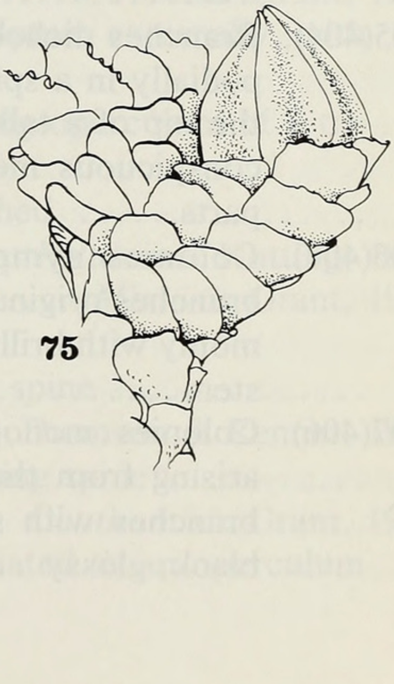
79

a

b



80



75

originating directly from main stem or after a few bifurcations of primary branches.

395(396). Terminal branches simple, arising around the outside of the spirally coiled main stem; colonies not flabellate .... *Iridogorgia* Verrill, 1883

396(395). Terminal branches originating in one plane, colonies more or less distinctly lyrate.

397(398). Terminal branches slender and flexible. Sclerites exclusively in the form of small scales, or altogether absent .... *Trichogorgia* Hickson, 1905

398(397). Terminal branches stiff, more of less brittle. In addition to thin scales, sclerites include thick plates with closely set, stout, rounded projections on the outer surface .... *Pleurogorgia* Versluys, 1902

399(394). Colonies with terminal branches short, the last of several bifurcations of primary branches.

400(403). Colonies branched in one plane.

401(402). Branching profuse, pinnate, producing flabellate or plumose colonies, polyps small, coenenchyme extremely thin, sclerites small (up to 0.15 mm in length) .... *Stephanogorgia* Bayer & Muzik, 1976

402(401). Branching sparse, lateral or openly pinnate, producing loose, open colonies. Polyps large, coenenchyme thick, sclerites large (up to 0.45 mm in length) .... *Isidoides* Nutting, 1910

403(400). Colonies not branched in one plane.

404(405). Branches irregularly subdivided, originating on all sides of the main stem but not arranged in a spiral around it, forming colonies of dense bottle-brush shape. Axis very weakly calcified, without metallic iridescence .... *Xenogorgia* Bayer & Muzik, 1976

405(404). Branches dichotomously subdivided, originating either sympodially in a spiral around main stem or monopodially from the top of a tall, upright trunk. Axis strongly calcified, with conspicuous metallic iridescence especially in the younger parts.

406(407). Colonies sympodial, dichotomously subdivided lateral branches originating in a spiral around main stem. Axis commonly with brilliant iridescence extending even into the main stem .... *Chrysogorgia* Duchassaing & Michelotti, 1864

407(406). Colonies monopodial, dichotomously subdivided branches arising from the top of a tall, upright main trunk. Axis of branches with strong metallic lustre, of main trunk almost black, glossy .... *Metallogorgia* Versluys, 1902

408(326). Axis consists of proteinous nodes alternating with calcareous internodes not composed of fused sclerites (Isididae).
409(414). Polyps retractile.
410(411). Sclerites of polyps are strongly spinose spindles; calices prominent, distinctly separated .... *Muricellisis* Kükenthal, 1915
411(410). Sclerites of polyps are small rods with transverse girdles of tubercles.
412(413). Colonies branching from internodes, bushy or planar, coenenchyme thick, polyps not forming projecting calices; sclerites include clubs, colorless .... *Isis* Linnaeus, 1758
413(412). Colonies dichotomously branching from nodes, in one plane, coenenchyme thin, polyps forming hemispherical calices; sclerites chiefly radiate capstans, yellow or orange .... *Chelidonisis* Studer, 1890
414(409). Polyps not retractile.
415(422). Sclerites of polyps are large spindles, needles or rods, longitudinally arranged, and smaller, irregularly placed rods or scales.
416(417). Colonies unbranched .... *Lepidisis* Verrill, 1883
417(416). Colonies branched.
418(419). Branches arise from calcareous internodes .... *Keratoisis* Wright, 1869
419(418). Branches arise from horny nodes.
420(421). Colonies bushy, branching in whorls ..... *Acanella* Gray, 1870
421(420). Colonies flat and spreading, branching not in whorls .... *Isidella* Gray, 1857
422(415). Sclerites of polyps are scales or plates transversely arranged.
423(424). Scales smooth, with free margins smooth .... *Circinisis* Grant, 1976
424(423). Scales with granular or tubercular sculpture externally, with serrate or dentate free margin.
425(431). Polyps with distalmost sclerites forming operculum of 8 triangular or triradiate scales.
426(427). Colonies delicate, whiplike, not branched .... *Peltastisis* Nutting, 1910
427(428). Opercular scales triangular .... *Minuisis* Grant, 1976
428(427). Opercular scales triradiate.
429(430). Distal scales of polyps with projecting spine .... *Echinisis* Thomson & Rennet, 1928
430(429). Distal scales of polyps without projecting spine .... *Chathamisis* Grant, 1976
431(425). Distal sclerites of polyps not differentiated as an operculum

of 8 scales, bases of tentacles covered by several transverse scales protecting oral disk during contraction.

432(433). Branching on all sides of main stem, colonies bottle-brush shaped .... *Primnoisis* Studer, 1887

433(432). Branching in one plane, pinnate or dichotomous .... *Mopsea* Lamouroux, 1816

434(23). Polyps colonial, polymorphic (always an oozooid with autozooids and sometimes also mesozooids), anchored in soft substrate by a fleshy, muscular, contractile peduncle (PENNATULACEA). For keys to genera see Kükenthal, 1915, Das Tierreich, Lief. 43.

Index to Key

Classification

Detailed comparative investigation of abundant specimens of many species of octocoral genera and families has eliminated more and more of the discontinuities between taxa that were the basis for classification of the subclass devised by Hickson, Kükenthal, and other students of Octocorallia, which became quite complex by the first quarter of the 20th Century. Even in the past decade, this classification was further subdivided by the addition of a new order, Gastraxonacea, by Utinomi and Harada (1973), and I, too, contributed to complexity by reviving the order Protoalcyonaria (Bayer and Muzik, 1976) proposed by Hickson (1894) but later abandoned by him. Although I must say in self defense that I still consider the introduction of vegetative reproduction to be a major step in the evolution of octocorals, I have to admit that in other coelenterate groups, such as Scleractinia, solitary forms are accepted along with colonial ones even in the same family and genus. As the solitary octocorals (other than *Taiaroa*) heretofore reported will in all likelihood prove to be founder individuals of colonial forms, as in the case of *Hartea* suggested by Mr. R. L. Manuel (pers. comm.), the Protoalcyonaria probably does not merit ordinal recognition although it may be a nominal taxon of convenience at subordinal level.

Something similar might be said for the order Xeniacea proposed for members of the family Xeniidae by Bock (1938) and accepted by Madsen (1944). The chief distinguishing character of this order recognized by Madsen is the exclusive occurrence of small, discoidal or biscuit-shaped sclerites, but Kükenthal (1902, 1906) and Hickson (1931) emphasized the presence of only one pair of septal filaments in fully developed autozooids. As minute, discoidal sclerites occur (in addition to larger spindles) in *Clavularia* and *Tubipora,* and as *Ceratocaulon* combines the presence of small discoidal sclerites with a full complement of 8 septal filaments, and the autozooids of *Xenia* have 8 filaments in their early developmental stages, no basis remains for recognition of Xeniacea at ordinal level.

Certain species of *Telestula* that originally were assigned to *Clavularia* bridge the gap between the order Stolonifera and Telestacea, *Pseudogorgia godeffroyi* that between Telestacea and Alcyonacea, and *Protodendron repens* and *Maasella radicans* that between Stolonifera and Alcyonacea. The separation of Alcyonacea from Gorgonacea is challenged by the families Paragorgiidae and Briareidae as was shown by Verseveldt (1940) when he proposed to remove both from the Gorgonacea (Scleraxonia), where they traditionally had been assigned, to the Alcyonacea. The scleroproteinous axis of the gorgonacean suborder Holaxonia would seem to be an unequivocal character, but even it is compromised by the species of *Keroeides, Lignella,* and *Ideogorgia* (nom. nov. for *Dendrogorgia* Simpson), which combine the characteristic cross-chambered proteinous medulla of the Holaxonia with the axial cortex composed of sclerites bound together by gorgonin typical of the Scleraxonia. Moreover, the calcium-filled loculi of the axial cortex of *Plexaurella* are but a short step removed from the axial sclerites of the Keroeididae. Indeed, only the families Ellisellidae, Ifalukellidae, Chrysogorgiidae and Primnoidae are unequivocally separated from the remaining Gorgonacea-Alcyonacea complex by their total lack of a chambered axial medulla, and each is characterized by morphological features that are conclusive and unmistakable.

On the basis of colonial organization and skeletal structure, the only clearly discontinuous major taxa (i.e., orders) are the Pennatulacea (which are not included in the key), the Helioporacea, and the restricted "Holaxonia." The Stolonifera, Telestacea, Gastraxonacea, Alcyonacea, Scleraxonia, and medullate Holaxonia are linked by intermediate forms that preclude concise definitions of orders. These groups are comprised of an uninterrupted series from *Clavularia* to complex holaxonians such as *Paramuricea.* The traditional subdivisions might be retained as a convenience at a quasi-subordinal level, but it must be recognized that no hard and fast boundaries can be drawn between them. In view of these considerations, a realistic classification is as follows.

Order Helioporacea (=Coenothecalia)
  Lithotelestidae: *Epiphaxum* (=*Lithotelesto*)
  Helioporidae: *Heliopora*
Order Alcyonacea
  [Suborder Protoalcyonaria][21]
    Taiaroidae: *Taiaroa*
  [Suborder Stolonifera]
    Cornulariidae: *Cornularia*
    Clavulariidae
      Clavulariinae: *Clavularia* (=*Hicksonia*), *Bathytelesto, Rhodelinda, Scyphopodium*
      Sarcodictyiinae: *Sarcodictyon, Cyathopodium, Scleranthelia, Tesseranthelia, Trachythela*
      Telestinae: *Telesto, Carijoa, Paratelesto, Telestula*
      Pseudocladochoninae: *Pseudocladochonus*
    Tubiporidae: *Tubipora, Pachyclavularia*
    Coelogorgiidae: *Coelogorgia*
    Pseudogorgiidae: *Pseudogorgia*
  [Suborder Alcyoniina]
    Paralcyoniidae (=Fasciculariidae, =Viguieriotidae); *Maasella* (=*Fascicularia*, =*Viguieriotes*), *Carotalcyon, Paralcyonium, Studeriotes*
    Alcyoniidae: *Alcyonium, Acrophytum, Anthomastus, Bathyalcyon, Bellonella, Cladiella* (=*Lobularia*, =*Microspicularia*, =*Sphaerella*), *Lobophytum, Metalcyonium, Minabea, Malacacanthus, Nidaliopsis, Parerythropodium, Sarcophyton, Sinularia*
    Asterospiculariidae: *Asterospicularia*
    Nephtheidae: *Nephthea, Capnella* (=*Eunephthya*, =*Paranephthya*), *Coronephthya, Daniela, Drifa, Duva, Gersemia, Lemnalia, Litophyton* (=*Ammothea*), *Morchellana, Neospongodes, Paralemnalia, Pseudodrifa, Roxasia, Scleronephthya, Spongodes, Stereonephthya, Umbellulifera*
    Nidaliidae
      Nidaliinae: *Nidalia* (=*Cactogorgia*), *Agaricoides*
      Siphonogorgiinae: *Siphonogorgia* (=*Chironephthya*)
    Xeniidae: *Xenia, Anthelia, Ceratocaulon*?, *Cespitularia, Efflatounaria, Fungulus, Heteroxenia, Sympodium*

---

[21] Taxa enclosed in square brackets are not considered to have taxonomic significance, but are included for convenience.

[Suborder Scleraxonia]
Briareidae: *Briareum* (=*Solenopodium*)
Anthothelidae
Anthothelinae: *Anthothela*
Semperininae: *Semperina* (=*Suberia*), *Iciligorgia, Solenocaulon*
Spongiodermatinae: *Homophyton* (=*Spongioderma*), *Alertigorgia, Callipodium* (=*Anthopodium*?), *Diodogorgia, Erythropodium, Titanideum, Tripalea*
Subergorgiidae: *Subergorgia*
Paragorgiidae: *Paragorgia, Sibogagorgia*
Coralliidae: *Corallium* (=*Hemicorallium*, =*Pleurocorallium*), *Pleurocoralloides*?
Melithaeidae: *Melithaea* (=*Melitella*, =*Melitodes*, =*Birotulata*), *Acabaria, Clathraria, Mopsella, Wrightella*
Parisididae: *Parisis* (=*Trinella*)
[Suborder Holaxonia]
Keroeididae: *Keroeides, Ideogorgia* (=*Dendrogorgia*), *Lignella*
Acanthogorgiidae: *Acanthogorgia* (=*Boarella*), *Acalycigorgia, Anthogorgia, Calcigorgia, Cyclomuricea, Muricella, Versluysia*
Plexauridae (including Muriceidae, Paramuriceidae)
[Plexaurinae]: *Plexaura, Anthoplexaura, Eunicea, Euplexaura, Muriceopsis, Plexaurella, Psammogorgia, Pseudoplexaura*
[Stenogorgiinae (=Paramuriceinae)]: *Swiftia* (=*Allogorgia*, =*Callistephanus*, =*Platycaulos*, =*Stenogorgia*), *Acanthacis, Astrogorgia, Bebryce, Calicogorgia, Dentomuricea, Echinogorgia* (=*Bovella*, =*Paraplexaura*, =*Trimuricea*?), *Echinomuricea, Heterogorgia, Hypnogorgia, Lepidomuricea, Lytreia, Menella* (=*Plexauroides*), *Muriceides* (=*Clematissa*, =*Trachymuricea*), *Nicaule, Paracis* (=*Discomuricea*), *Paramuricea, Placogorgia, Pseudothesea, Scleracis, Thesea* (=*Discogorgia*, =*Evacis*, =*Filigella*), *Villogorgia* (=*Acamptogorgia*, =*Brandella*, =*Perisceles*)
Gorgoniidae: *Gorgonia* (=*Rhipidogorgia*), *Adelogorgia, Eugorgia, Eunicella, Hicksonella* (=*Rhabdoplexaura*), *Leptogorgia* (=*Filigorgia*), *Lophogorgia, Olindagorgia, Pacifigorgia, Phycogorgia, Phyllogorgia* (=*Hymenogorgia*), *Pseudopterogorgia* (=*Antillogorgia*), *Pterogorgia* (=*Xiphigorgia*), *Rumphella*
Ellisellidae: *Ellisella* (=*Scirpearia*, =*Viminella*), *Ctenocella* (=*Dichotella*), *Junceella, Nicella, Riisea* (=*Herophile*), *Toeplitzella, Verrucella* (=*Phenilia*)
Ifalukellidae: *Ifalukella, Plumigorgia*
Chrysogorgiidae: *Chrysogorgia* (=*Dasygorgia*), *Chalcogorgia, Distichogorgia, Helicogorgia, Iridogorgia, Isidoides, Metallogorgia, Pleurogorgia, Radicipes* (=*Lepidogorgia*, =*Strophogorgia*), *Stephanogorgia, Trichogorgia* (=*Malacogorgia*), *Xenogorgia*

Primnoidae: *Primnoa, Ainigmaptilon (=Lycurus), Amphilaphis, Armadillogorgia, Arthrogorgia, Ascolepis, Callogorgia, Callozostron, Calyptrophora, Candidella (=Stenella), Dasystenella, Narella (=Stachyodes), Ophidiogorgia, Paracalyptrophora, Parastenella, Plumarella, Primnoella, Pseudoplumarella, Pterostenella*

Isididae

Isidinae: *Isis, Chelidonisis*

Muricellisidinae: *Muricellisis*

Keratoisidinae: *Keratoisis, Acanella, Isidella, Lepidisis*

Mopseinae: *Mopsea, Chathamisis, Circinisis, Echinisis, Minuisis, Peltastisis, Primnoisis*

Acknowledgments

This paper results from research initiated at the Rosenstiel School of Marine and Atmospheric Science, University of Miami, and supported by grant DEB 75-07193 from the National Science Foundation to that institution, F. M. Bayer, Principal Investigator.[22]

I am grateful to Dr. P. F. S. Cornelius of the British Museum (Nat. Hist.) for the privilege of examining type-material in his care, and to Dr. L. B. Holthuis of the Rijksmuseum van Natuurlijke Historie, Leiden, and Dr. Katherine Muzik, Museum of Comparative Zoology, Harvard University as well as many other colleagues, for stimulating discussions regarding the concept and realization of this paper. It is a special pleasure to acknowledge the helpful suggestions and criticisms of Mr. P. N. Alderslade of the Roche Research Institute of Marine Pharmacology, Dee Why, N.S.W., which have rendered the key more accurate, more complete, and more workable than it otherwise would have been. I also owe a considerable debt of gratitude to the Queen Elizabeth Fellowship Program of Australia for the opportunity to work in that country in 1980, and particularly to Drs. J. T. Baker and John Pollard.

Literature Cited

Bayer, Frederick M., and Katherine Margaret Muzik. 1976. A new solitary octocoral, Taiaroa tauhou gen. et sp. nov. (Coelenterata: Protoalcyonaria) from New Zealand.—Journal of the Royal Society of New Zealand 6(4):499–515, figs. 1–10.

Bock, Sixten. 1938. The alcyonarian genus Bathyalcyon.—Kungliga Svenska Vetenskapsakademiens Handlingar (3)16(5):1–54, pls. 1–2.

Hickson, Sydney J. 1894. A revision of the genera of the Alcyonaria Stolonifera, with a description of one new genus and several new species.—Transactions of the Zoological Society of London 13(9):325–347, text figs. 1–4, pls. 45–50.

---

[22] This is a contribution from the Rosenstiel School of Marine and Atmospheric Science, University of Miami.

———. 1931. The alcyonarian family Xeniidae, with a revision of the genera and species.—Great Barrier Reef Expedition 1928–29, Scientific Reports 4(5):137–179, pls. 1–2.

Kükenthal, Willy. 1902. Versuch einer Revision der Alcyonarien. 1. Die Familie der Xeniiden.—Zoologische Jahrbücher (Abtheilung für Systematik, Geographie und Biologie der Thiere) 15:635–662.

———. 1906. Alcyonacea.—Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899 13(1) Lieferung 1:1–111, pls. 1–12.

———. 1915. Pennatularia.—Das Tierreich 43:i–xv + 1–132.

———. 1924. Gorgonaria.—Das Tierreich 47:i–xxviii + 1–478.

Madsen, Fritz Jensenius. 1944. Octocorallia.—The Danish Ingolf-Expedition 5(13):1–65, pl. 1.

Nutting, Charles Cleveland. 1910. The Gorgonacea of the Siboga Expedition. III, The Muriceidae.—Siboga-Expeditie Monographie 13*b*:1–108, pls. 1–22.

Utinomi, Huzio, and Eiji Harada. 1973. Rediscovery of an enigmatic octocoral, *Pseudogorgia godeffroyi* Kölliker, from southern Australia and a discussion of its systematic position.—Publications of the Seto Marine Biological Laboratory 20:111–132, figs. 1–6.

Verseveldt, Jakob. 1940. Studies on Octocorallia of the families Briareidae, Paragorgiidae and Anthothelidae.—Temminckia 5:1–142, figs. 1–52.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.