

A GENERIC REVISION OF THE STYLASTERINA (COELENTERATA: HYDROZOA).

PART I. DESCRIPTION OF THE GENERA

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ABSTRACT

Prior to a phylogenetic analysis of the Stylasterina, the 23 genera and one subgenus in the order are redescribed with special emphasis on scanning electron microscopy of the skeleton, histology of soft parts, and variation within each genus. Two new genera are described. The type-species of each genus is also redescribed and figured by scanning electron micrographs. Tissue of 21 of the 23 Recent genera and subgenera was examined by histological serial sections; 18 of these 21 were type-species of genera. The first three-dimensional (SEM) photographs of stylasterine nematocysts are provided. Much of the terminology used to describe stylasterines is reviewed and some new terms introduced.

A critical checklist of all stylasterine taxa is given, which includes 23 genera, 1 subgenus, 184 valid species, 7 subspecies, 11 formae or facies, and 42 synonyms. Numerous new synonyms and new combinations are made in this checklist, many of the latter caused by the synonymy of *Allopora* with *Stylaster*.

This is the first of a two-part study to redefine and phylogenetically analyze the genera of Stylasterina. Here, the 23 genera and 1 subgenus are redescribed based on the traditionally used gross skeletal characteristics and augmented with scanning electron microscopy of the skeleton and histological examination of the soft parts. The type-species of each genus is given special attention in describing the genera; however, as many species as possible were examined in an attempt to place each species in the correct genus and to better define the variation within each genus. The order of the subfamilies and the genera within each subfamily was determined by their degree of morphological complexity: the simplest, least modified genera first; the complex, most highly modified genera last. Character state series used to rank the genera are briefly discussed by Cairns (in press); however, a thorough analysis of the character states, their polarity, and a phylogenetic analysis of the genera will form the basis of the second paper of this study.

MATERIAL AND METHODS

Material.—Of the 244 nominal taxa of Stylasterina (Table 1: species, subspecies, formae, synonyms but not nomina nuda), the type-specimens of 54 were examined from the United States National Museum (USNM) and an additional 67 were examined on loan from other museums, for a total of 121, or 50% of all taxa. Additional nontype specimens were examined from the USNM, and of the 202 valid taxa (not including synonyms and nomina nuda), I have examined 146 (type and/or nontype), representing 72% of all taxa of Stylasterina. Specimens were borrowed from: British Museum (Natural History), London (BM); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Museum of Comparative Zoology, Harvard, Cambridge (MCZ); Zoologisch Museum, Amsterdam (ZMA); Zoologisk Museum, Copenhagen; Geologisk Museum, Copenhagen; Zoologisches Museum, Berlin; and Naturhistoriska Riksmuseet, Stockholm.

Methods.—Scanning electron microscopy (SEM) is a particularly good technique for the study and illustration of small stylasterine structures, such as gastro- and dactylostyles and coenosteal texture. Ordinarily a natural or induced fracture revealed these structures, but if material was scarce and the styles delicate or well protected (longitudinally instead of radially disposed), I used an ultra-high-speed precision air grinder (Dentsply 300 KS, #55001, 55006) with a 1-mm-diameter burr for removal of excess calcium carbonate to reveal the structure. Most of the SEM photomicrographs were made with

Table 1. Checklist of the nominal species of Stylasterina. The arrangement of genera within subfamilies was determined by increasing morphological complexity, following, in general, the character state series proposed by Cairns (In press). The order of species within genera is geographic, those from the Indian Ocean first, proceeding eastward, and concluding with the Antarctic. The type-species of each genus is indicated by an asterisk (*); fossil species are indicated by crosses (+); junior synonyms are indented and preceded with an equals sign; and species of uncertain generic placement are preceded with a question mark. Currently there are 23 genera, 1 subgenus, 184 valid species, 7 subspecies, 11 formae or facies, 4 nomina nuda, 4 unnamed "species," and 42 junior synonyms of Stylasterina

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|---|--|
| Subfamily Errininae Hickson, 1912 | 1879) n. comb. |
| * <u>Lepidopora glabra</u> (Pourtalès, 1867) | * <u>Errinopsis reticulum</u> Broch, 1951 |
| <u>L. decipiens</u> Boschma, 1964 | <u>E. fenestrata</u> Cairns, 1983 |
| <u>L. carinata</u> (Pourtalès, 1867) | <u>Errina novaezealandiae</u> Hickson, 1912 |
| <u>L. hicksoni</u> Boschma, 1963 | facies <u>ramosa</u> Hickson, 1912 |
| <u>L. diffusa</u> Boschma, 1963 | facies <u>benhami</u> Hickson, 1912 |
| <u>L. sarmentosa</u> Boschma, 1968 | facies <u>dendeyi</u> Hickson, 1912 |
| <u>L. granulosa</u> (Cairns, 1983) | facies <u>cooki</u> Hickson, 1912 |
| <u>L. acrolophos</u> Cairns, 1983 | <u>E. rubra</u> Broch, 1942 |
| <u>Sporadopora mortenseni</u> Broch, 1942 | <u>E. cruenta</u> Boschma, 1968 |
| + <u>S. marginata</u> Tenison-Woods, 1880 | <u>E. macrogastra</u> Marenzeller, 1904 |
| ?+ <u>S. faxensis</u> Nielsen, 1919 | <u>E. cochleata</u> Portalès, 1867 |
| * <u>S. dichotoma</u> (Moseley, 1877) | <u>E. dabneyi</u> Portalès, 1871 |
| <u>Pliobothrus spinosa</u> (Hickson & England, 1905) | = <u>E. amoena</u> Boschma, 1956 |
| * <u>P. symmetricus</u> Portalès, 1868 | * <u>E. aspera</u> (Linnaeus, 1767) |
| <u>P. tubulatus</u> (Portalès, 1867) | <u>E. a. mascarina</u> Boschma, 1965 |
| ?+ <u>P. dispergens</u> Nielsen, 1919 | <u>E. atlantica</u> Hickson, 1912 |
| ?+ <u>P. laevis</u> Nielsen, 1919 | + <u>E. irregularis</u> (Nielsen, 1919) |
| * <u>Cheiloporidion pulvinatum</u> Cairns, 1983 | <u>E. capensis</u> Hickson, 1912 |
| <u>Lepidotheca tenuistylus</u> (Broch, 1942) n. comb. | <u>E. antarctica</u> (Gray, 1872) |
| <u>L. cervicornis</u> (Broch, 1942) n. comb. | = <u>E. moseleyi</u> Ridley, 1881 |
| <u>L. horrida</u> (Hickson & England, 1905) n. comb. | = <u>E. spongiosa</u> Broch, 1942 |
| <u>L. ramosa</u> (Hickson & England, 1905) n. comb. | <u>E. fissurata</u> Gray, 1872 |
| <u>L. hachijoensis</u> (Eguchi, 1968) n. comb. | <u>E. gracilis</u> Marenzeller, 1903 |
| <u>L. japonica</u> (Eguchi, 1968) n. comb. | <u>E. kerguelensis</u> Broch, 1942 |
| * <u>L. fascicularis</u> (Cairns, 1983) n. comb. | <u>E. laterorifā</u> Eguchi, 1964 |
| * <u>Phalangopora regularis</u> Kirkpatrick, 1887 | = <u>E. carneā</u> Boschma, 1964 ^{†S} |
| = <u>Pliobothrus seriatus</u> Broch, 1942 | <u>E. boschmai</u> Cairns, 1983 |
| * <u>Inferiolabiata labiata</u> (Moseley, 1879) | <u>E. cheilopora</u> Cairns, 1983 |
| <u>I. lowei</u> Cairns, 1983 | <u>Errinopora styliifera</u> (Broch, 1935) |
| * <u>Paraerrina decipiens</u> Broch, 1942 | = <u>E. intervacans</u> Naumov, 1960 |
| ? <u>P. spp.</u> Squires, 1962 | ? <u>E. porifera</u> (Naumov, 1960) |
| * <u>Stellapora echinata</u> (Moseley, 1879) n. comb. | <u>E. latifundata</u> Naumov, 1960 |
| | <u>E. nanneca</u> Fisher, 1938 |
| | <u>E. zarhyncha</u> Fisher, 1938 |
| | * <u>E. pourtalesii</u> (Dall, 1884) |
| | ?+ <u>E. lobata</u> (Nielsen, 1919) |
| | <u>E. cestoporina</u> Cairns, 1983 |
| | ? <u>E. cyclopora</u> (Cairns, 1983) |
| | * <u>Gyropora africana</u> Boschma, 1960 |
| | Subfamily Adeloporinae Cairns, 1982 |
| | * <u>Adelopora pseudothyron</u> Cairns, 1982 |
| | Subfamily Distichoporinae Stechow, 1921 |

Table 1. Continued

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| <u>Distichopora</u> (D.) <u>profunda</u> Hickson & England, 1909 | <u>S. solidus</u> Broch, 1935 |
| <u>D. providentiae</u> (Hickson & England, 1909) | <u>S. boreopacificus</u> Broch, 1932 |
| * <u>D. violacea</u> (Pallas, 1766) | <u>S. incassatus</u> (Eguchi, 1941) |
| = <u>D. cinnabarina</u> Nardo, 1844 | <u>S. brochi</u> (Fisher, 1938) n. comb. |
| ?= <u>D. fulvacea</u> Michelin, 1862 | <u>S. moseleyanus</u> (Fisher, 1938) n. comb. |
| ?= <u>D. rosea</u> Kent, 1871 | <u>S. m. forma leptostylus</u> (Fisher, 1938) n. comb. |
| = <u>D. fisheri</u> Broch, 1942 | <u>S. stejnegeri</u> (Fisher, 1938) n. comb. |
| <u>D. irregularis</u> Moseley, 1881 | <u>S. purpuratus</u> (Naumov, 1960) n. comb. |
| <u>D. serpens</u> Broch, 1942 | <u>S. boschmai</u> (Eguchi, 1965) n. comb. |
| <u>D. livida</u> Tenison-Woods, 1879 | <u>S. hattorii</u> (Eguchi, 1968) n. comb. |
| <u>D. gracilis</u> Dana, 1848 | <u>S. californicus</u> (Verrill, 1866) n. comb. |
| = <u>D. conferta</u> Quelch, 1885 | <u>S. venustus</u> (Verrill, 1870) n. comb. |
| = <u>D. fragilis</u> Quelch, 1885 | + <u>S. milleri</u> Durham, 1942 |
| = <u>D. granulosa</u> Quelch, 1885 | <u>S. miniatus</u> (Pourtalès, 1868) n. comb. |
| = <u>D. milesii</u> Quelch, 1885 | <u>S. norvegicus</u> (Gunnerus, 1768) |
| <u>D. nitida</u> Verrill, 1864 | <u>S. rosaceus</u> (Greef, 1886) n. comb. |
| = <u>D. alnutti</u> Wright, 1882 | <u>S. blatteus</u> (Boschma, 1961) n. comb. |
| = <u>D. brasseyae</u> Wright, 1882 | + <u>S. compressus</u> (Römer, 1863) |
| = <u>D. breviserialis</u> Quelch, 1884 | = <u>Dendracis pygmaea</u> Römer, 1863 |
| = <u>D. ochracea</u> Quelch, 1884 | = <u>Dendracis multipora</u> Römer, 1863 |
| <u>D. coccinea</u> Gray, 1860 | = <u>Dendracis tuberculosa</u> Römer, 1863 |
| = <u>D. purpurea</u> Schmeltz, 1875 (nom. nud.) | = <u>Cryptaxis allopoides</u> Reuss, 1865 |
| = <u>Lithodendrum saccharatum</u> von Martens, 1902 | <u>S. subviolaceus</u> (Kent, 1871) |
| = <u>D. violacea</u> forma <u>cornuta</u> Broch, 1942 | <u>S. nobilis</u> (Kent, 1871) |
| + <u>D. spp.</u> Squires, 1962 | = <u>S. explanatus</u> (Kent, 1871) |
| <u>D. borealis</u> Fisher, 1938 | = <u>S. ochraceus</u> (Quelch, 1884) |
| <u>D. b. japonica</u> Broch, 1942 | <u>S. bithalamus</u> Broch, 1936 |
| + <u>D. parairregularis</u> Eguchi, 1968 (nom. nud.) | <u>S. eguchii</u> (Boschma, 1966) n. comb. |
| <u>D. sulcata</u> Pourtalès, 1867 | <u>S. robustus</u> (Cairns, 1983) n. comb. |
| <u>D. foliacea</u> Pourtalès, 1868 | |
| <u>D. cervina</u> Pourtalès, 1871 | <u>Stylaster</u> (Group B) |
| <u>D. barbadensis</u> Pourtalès, 1874 | <u>S. bocki</u> Broch, 1936 |
| <u>D. contorta</u> Pourtalès, 1878 | <u>S. granulatus</u> Milne Edwards & Haime, 1850 |
| + <u>D. antiqua</u> Defrance, 1826 | <u>S. bellus</u> (Dana, 1848) |
| <u>D. (Haplomerismos) anceps</u> Cairns, 1978 | <u>S. sanguineus</u> Milne Edwards & Haime, 1850 |
| | = <u>S. tenuis</u> Verrill, 1864 |
| Subfamily Stylasterinae Gray, 1847 | |
| <u>Stylaster</u> (Group A) | |
| <u>S. stellulatus</u> Steward, 1878 | |
| <u>S. verrillii</u> (Dall, 1884) | |
| = <u>S. moseleyi</u> (Dall, 1884) | |
| ?= <u>S. norvegicus pacificus</u> Broch, 1936 | |
| <u>S. scabiosus</u> Broch, 1935 | |
| = <u>S. s. infundibuliporus</u> (Eguchi, 1968) n. comb. | |

Table 1. Continued

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| = <u>S. elegans</u> Verrill, 1864 | <u>S. e. facies irregularis</u> Hickson & England, 1905 |
| <u>S. campylecus</u> (Fisher, 1938) | <u>S. e. facies minor</u> Hickson & England, 1905 |
| <u>S. c. parageus</u> (Fisher, 1938) | <u>S. microstriatus</u> Broch, 1936 |
| <u>S. c. tylotus</u> (Fisher, 1938) | <u>S. cancellatus</u> Fisher, 1938 |
| <u>S. c. trachystomus</u> (Fisher, 1938) | <u>S. elassotomus</u> Fisher, 1938 |
| <u>S. carinatus</u> Broch, 1936 | <u>S. alaskanus</u> Fisher, 1938 |
| <u>S. polyorchis</u> (Fisher, 1938) n. comb. | + <u>S. chibaensis</u> Eguchi, 1954 |
| ?= <u>S. abei</u> (Eguchi, 1968) n. comb. | <u>S. duchassaingii</u> Pourtalès, 1867 |
| <u>S. dentatus</u> Broch, 1936 (junior homonym of <u>S. eximius facies dentatus</u> Hickson & England, 1905, if facies raised to species) | = <u>S. elegans</u> Duchassaing & Michelotti, 1864 |
| <u>S. profundiporus</u> Broch, 1936 | = <u>S. eximius</u> Kent, 1871 |
| <u>S. p. crassicaulis</u> Broch, 1936 | = <u>S. eximius forma atlantica</u> ^{USA} Broch, 1936 |
| <u>S. pulcher</u> Quelch, 1884 | <u>S. filogranus</u> Pourtalès, 1871 |
| <u>S. divergens</u> Marenzeller, 1904 | <u>S. punctatus</u> Pourtalès, 1871 |
| * <u>S. roseus</u> (Pallas, 1776) | <u>S. echinatus</u> Broch, 1936 |
| <u>S. gemmascens</u> (Esper, 1794) | <u>S. antillarum</u> Zibrowius & Cairns, 1982 |
| + <u>S. priscus</u> Reuss, 1872 | <u>S. erubescens</u> Pourtalès, 1868 |
| <u>S. profundus</u> (Moseley, 1879) | + <u>S. antiquus</u> Sismonda, 1871 |
| <u>S. polymorphus</u> Broch, 1936 | <u>S. densicaulis</u> Moseley, 1879 |
| <u>Stylaster</u> (Group C) | <u>Stylaster</u> (Incertae Sedis) |
| + <u>S. sp.</u> Tornquist, 1905 | <u>S. rossoamericanus</u> Brandt, 1872 nom. nud. |
| <u>S. amphelioides</u> Kent, 1871 | + <u>S. nagaoui</u> (Eguchi, 1968) nom. nud. |
| <u>S. crassior</u> Broch, 1936 | * <u>Stylanthea porphyra</u> Fisher, 1931 |
| <u>S. lonchitis</u> Broch, 1947 | <u>S. petrograpta</u> (Fisher, 1938) n. comb. |
| <u>S. ramosus</u> Broch, 1936 47 | <u>S. papillosa</u> (Dall, 1884) n. comb. |
| <u>S. bilobatus</u> Hickson & England, 1905 | * <u>Calyptopora reticulata</u> Boschma, 1968 |
| <u>S. b. facies alba</u> Hickson & England, 1905 | <u>C. complanata</u> (Portalès, 1867) n. comb. |
| <u>S. multiplex</u> Hickson & England, 1905 | = <u>Crypthelia virginis</u> Lindström, 1876 |
| <u>S. flabelliformis</u> (Lamarck, 1816) | <u>C. pachypoma</u> (Hickson & England, 1905) |
| <u>S. gracilis</u> Milne Edwards & Haime, 1850 | <u>Stenohelia minima</u> (Hickson & England, 1905) |
| <u>S. brunneus</u> Boschma, 1970 | <u>S. tiliata</u> (Hickson & England, 1905) |
| <u>S. papuensis</u> Zibrowius, 1981 | <u>S. umbonata</u> (Hickson & England, 1905) |
| + <u>S. mooraboolensis</u> (Hall, 1893) | <u>S. conferta</u> Boschma, 1968 |
| + <u>S. sp.</u> Wells, 1977 | <u>S. echinata</u> Eguchi, 1968 |
| <u>S. asper</u> Kent, 1871 | <u>S. yabei</u> (Eguchi, 1941) |
| <u>S. incompletus</u> (Tenison-Woods, 1883) | <u>S. y. forma minor</u> (Eguchi, 1941) |
| <u>S. "eximius"</u> | |
| <u>S. e. facies altus</u> Hickson & England, 1905 | |
| <u>S. e. facies dentatus</u> Hickson & England, 1905 | |

Table 1. Continued

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| <u>S. robusta</u> Boschma, 1964 | <u>C. stenopoma</u> Hickson & England, 1905 |
| <u>S. concinna</u> Boschma, 1964 | <u>C. japonica</u> (Milne Edwards & Haime, 1849) |
| <u>S. profunda</u> Moseley, 1879 | <u>C. cryptotrema</u> Zibrowius, 1981 |
| = <u>S. challengerii</u> Boschma, 1951 | + <u>C. vetusta</u> Wells, 1977 |
| * <u>S. maderensis</u> (Johnson, 1862) | <u>C. trophostega</u> Fisher, 1938 |
| <u>Conopora</u> (Group A) | <u>C. gigantea</u> Fisher, 1938 |
| <u>C. major</u> Hickson & England, 1905 | <u>C. peircei</u> Pourtalès, 1867 |
| <u>C. verrucosa</u> (Studer, 1878) | <u>C. affinis</u> Moseley, 1879 |
| = <u>C. pauciseptata</u> Broch, 1951 | = <u>C. moseleyi</u> Hickson & England, 1905 |
| <u>C. laevis</u> (Studer, 1878) | <u>C. formosa</u> Cairns, 1983 |
| *= <u>C. tenuis</u> Moseley, 1879 | <u>C. fragilis</u> Cairns, 1983 |
| = <u>C. obliquus</u> (Studer, 1878) | |
| <u>Conopora</u> (Group B) | * <u>Astyia subviridis</u> (Moseley, 1879) |
| <u>C. dura</u> Hickson & England, 1909 | + <u>A. nielsenii</u> Wells, 1977 |
| +? <u>C. arborescens</u> Nielsen, 1919 | Incertae Sedis |
| <u>Crypthelia clausa</u> Broch, 1947 | +* <u>Congregopora nasiformis</u> Nielsen, 1919 |
| * <u>C. pudica</u> Milne Edwards & Haime, 1849 | + <u>"Astya" crassa</u> (Nielsen, 1919) |
| <u>C. ramosa</u> Hickson & England, 1905 | + <u>"Stenohelia" boschmai</u> Wells, 1977 |
| <u>C. balia</u> Hickson & England, 1905 | <u>"Errina" porifera</u> Naumov, 1960 |
| <u>C. platypoma</u> Hickson & England, 1905 | (also listed under <u>Errinopora</u>) |

a Cambridge Stereoscan 4-10 microscope; stereo pairs were taken with an 8° tilt of the specimen. The magnifications of all SEM photomicrographs, and therefore most measurements of small skeletal structures, have a $\pm 5\%$ margin of error. All figured specimens are deposited at the USNM unless otherwise noted.

Specimens used for histological examination were first decalcified with a commercial bone decalcification solution (Scientific Products, Decal D 1210) diluted 1:4 with ethanol. This required 1–2 days for small pieces. Decalcified tissue was embedded in paraffin, serial-sectioned at 6 μm thickness, and stained with hematoxylin and eosin. Most of the specimens used were originally fixed and preserved in ethanol; however, fixation in formalin gives better results. In addition, the gastro- and dactylozooids were dissected from decalcified tissue of each genus, processed in a critical point drying apparatus (Denton Vacuum, Inc., DCP-1), and photographed by SEM.

Definitions of terms used to describe stylasterines are found in Fisher (1938), Boschma (1956), and Cairns (in press); however, it is necessary to introduce and resurrect several terms here. The coenosteal texture of most stylasterines is either a *reticulate* maze or a series of straight, parallel, longitudinal bands (*linear*) of calcium carbonate. These bands, termed *coenosteal strips*, are usually between 50–100 μm wide and bordered by thin (5–10 μm) discontinuous grooves or *slits* along and through which coenosteal canals pass. The strips are often sparsely covered by low, rounded, or irregularly shaped granules 7–10 μm in diameter. Some genera are characterized by having linear strips which are not granular but bear rows of imbricated scales, called *platelets*. These two coenosteal textures, referred to as *reticulate-granular* (e.g., pl. 11, fig. B) and *linear-imbricate* (e.g., pl. 14, figs. C–D; pl. 21, figs. D, F, G), respectively, are the most common among the Stylasterina and are, in general, consistent at the generic level. The other two combinations, *reticulate-imbricate* (e.g., pl. 7, figs. B–C) and *linear-granular*, do occur, but are very rare.

Dactylopores often occur as apically perforate mounds or slit spines. If the slit (groove) is on the proximal side of the spine it is termed *adcauline*; if on the distal side of the spine, *abcauline*. Sometimes slit dactylo pore spines are *clustered* in groups of 2–5, often resulting in a disordered orientation of the slits. When a spine is enlarged and bears several slits, it is termed *composite*.

The dimensions of a gastrostyle are indicated by a height to width ratio (*H:W*), the width measured at the widest level, exclusive of spines. An H:W of 2–4 is considered medium height; less than 2,

squat; over 4, elongate. Gastrostyles are always ornamented with spines, which are tall and *simple*, or *fused* (three or more together, usually aligned on the crest of a ridge). In some species there is a ring of tiny, blunt spines projecting from the wall of the gastropore tube at the level of the gastrostyle lip (e.g., pl. 20, fig. C). This ring, called the *cheval-de-frise* by Fisher (1938) is herein renamed the *ring palisade*. It constricts the gastropore tube into a lower *gastrostyle chamber* and an upper funnel-shaped part leading to the branch surface. In some genera lacking gastrostyles (i.e., *Conopora*, *Astyra*, *Crypthelia*), the ring palisade, or its analog, forms a solid ring constricting the gastropore tube into a small flat *lower chamber*, which contains the bulk of the gastrozoid, and a larger, spacious *upper chamber*, into which the dactylozooids enter.

Some genera have fixed *lids* which overhang their cyclostyles; one genus, *Adelopora*, has hinged *opercula*, one concealing each gastropore. Ampullae are usually present as *superficial* hemispheres; less commonly they are completely submerged in the coenosteum (*internal*). Gonophores release their sexual products via *efferent ducts* which are usually seen as small irregular pores on or near the ampulla or, in the case of some female ampullae, as a truncated lateral tube issuing from the side of the ampulla. Dactylozooids are attached to the coenosteal canal network either basally (*simple* dactylozooids) or by a broad "adhesive" base, called *adnate* dactylozooids. In the latter case, a short, free tentacle originates from about the midpoint of the attached base. *Nematopores* are small, shallow pores in the coenosteum which house the *nematophores*. dense concentrations of long, slender nematocysts oriented perpendicular to the branch surface. Nematopores are most common around cyclostyles, especially on pseudosepta and lids, if present.

Species synonymies include only pertinent references, i.e., distributional records or comments of systematic or biologic importance. Exhaustive, but uncritical, synonymies are given by Boschma (1957).

Order STYLASTERINA
Family STYLASTERIDAE Gray, 1847
Subfamily Errininae Hickson, 1912

Diagnosis.—Gastro- and dactylopores not arranged in distinct cyclostyles, usually scattered irregularly over coenosteum. If dactylopores are organized into short lines or irregular circles around gastropores (i.e., pseudocyclostyles), the space between the two types of pores is wide and usually additional, randomly placed dactylopores are present.

Lepidopora Pourtalès, 1871

Errina: Pourtalès, 1867: 117 (part).

Pliobothrus: Pourtalès, 1868: 141 (part).

Lepidopora Pourtalès, 1871: 40.—Cairns, in press.

Errina (*Inferiolabiata*): Boschma, 1956: F102 (part).

Errina (*Lepidopora*): Boschma, 1963a: 336.

Diagnosis.—Colonies usually uniplanar but sometimes bushy; branches not coalescent, with pointed, blunt, or clavate branch tips. Coenosteal texture quite variable, including: ornamented by tufts of calcium carbonate along longitudinal ridges; reticulate with tall, slender spines; reticulate with irregular granules; reticulate with rounded granules; linear with granules; and linear-imbricate. Gastro- and dactylopores usually randomly arranged over coenosteum, but sometimes gastropores aligned on anterior branch face and dactylopores aligned on lateral branch edges. Both gastro- and dactylopores tubes long, forming a cluster along each branch axis. Gastropore tube may or may not have a ring palisade. Gastro-pores sometimes have a lower lip. Gastrostyles cylindrical, without ridges; usually long and slender, with tall, simple spines; H:W usually over 4 and up to 20. Dactylopores usually elevated on small mounds which are apically perforate; pores sometimes linked by ridges; no dactylostyles. Ampullae superficial, large, and hemispherical, sometimes with an efferent tube leading from side. Soft parts unknown.

Discussion.—*Lepidopora* is an extremely variable genus, varying in characters such as: coordination of gastro- and dactylopores, gastrostyle shape, dactylopores shape, colony and branch shape, and especially coenosteal texture. These characters, ordinarily conservative at the generic level, are variable in *Lepidopora*, which leads to the conclusion that it is either an artificially composed, polyphyletic group or perhaps the primitive ancestral stock.

Lepidopora is distinguished from all other genera by its apically perforate dactylopores, nonridged, slender gastrostyles, and large superficial ampullae. No one character distinguishes *Lepidopora* (three other genera have apically perforate dactylopores, three have nonridged styles, and many have superficial ampullae), but these characters taken together are found in all eight species of the genus, and this combination of characters is significantly different from that of any other genus. Boschma (1964a: 61) indicated that *Lepidopora* and *Sporadopora* were very similar, differentiated primarily by the relative height of their dactylopores. They are similar, but, on closer examination, many differences can be found, e.g., the coenosteal texture of *Sporadopora* is different, its gastrostyles are ridged and bear fused spines, it has tabulae, and it has internal ampullae.

Lepidopora, therefore, is considered to be a distinct genus, but an extremely variable one, which, in its range of variation, has characters similar to many other genera in the Errininae, Adeloporinae, and Stylasterinae, especially with regard to coenosteal texture. Because many of its characters are morphologically simple and because it is so variable in otherwise conservative generic characters, it is considered to resemble the primitive genus from which the other stylasterines may have evolved. A discussion of primitive and derived characters and the phylogenetic position of *Lepidopora* will be made in the second paper of this series.

Occurrence.—?Paleocene: Denmark; Recent: North Atlantic, Scotia Ridge, off South Africa, South Pacific, off Antarctica. 84–1,874 m.

Type Species.—*Errina glabra* Pourtalès, 1867, by subsequent designation (Boschma, 1963a: 336).

Lepidopora glabra (Portalès, 1867)
Figure 1A–I

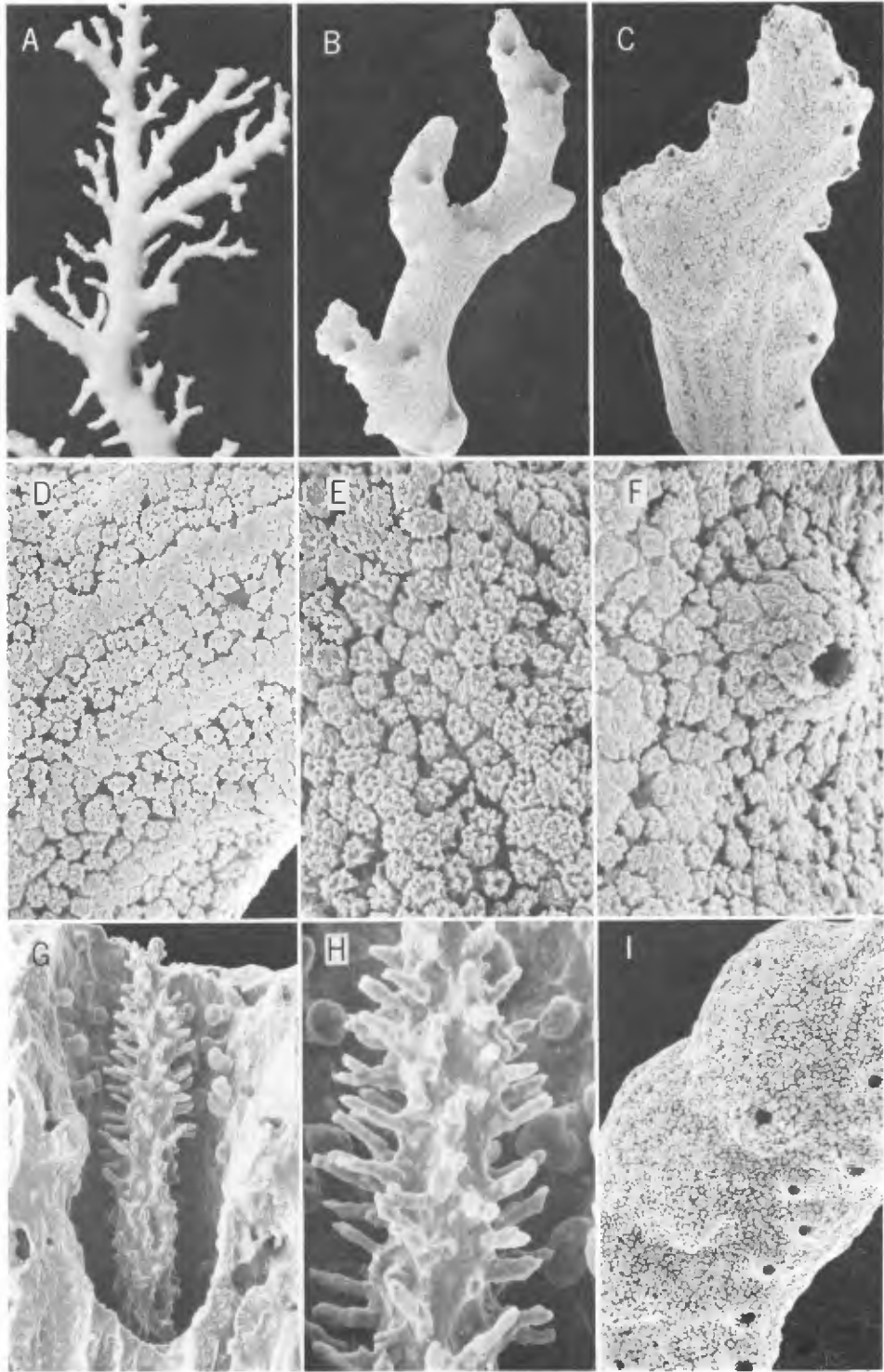
Errina glabra Portalès, 1867: 117.—Boschma, 1957: 54.

Lepidopora glabra: Portalès, 1871: 40, pl. 7, figs. 8–9; 1878: 211.

Errina (Inferiolabiata) glabra: Boschma, 1963a: F102, fig. 84, 1a.

Errina (Lepidopora) glabra: Boschma, 1963a: 336, 338; 1963b: 395; 1964a: 60; 1968b: 205.

Diagnosis.—Colonies up to 5.5 cm tall; distal branches slender, pointed, and compressed, about 0.5 mm in diameter; basal branches up to 7 mm in diameter, elliptical in cross section. Coenosteum composed of closely adjacent, irregularly shaped, crystalline (nongranular) tufts of calcium carbonate, each measuring between 21–25 μm in diameter. Adjacent tufts fuse into slightly elevated longitudinal ridges, which run the length of the branches. Fused ridges about 44 μm wide and separated by about 0.12 mm of individualized tufts. Gastropores, about 0.2 mm in diameter, occur only on the anterior side of the colony, always bordered by a broad, triangular, abcauline lip. Gastrostyles long and cylindrical (illustrated style 0.42 mm tall, H:W = 9.1), bearing sparse cylindrical spines measuring up to 30 μm long and 6.5 μm in diameter. The gastropore tube bears a diffuse ring palisade, the spines measuring up to 30 μm tall and 25 μm in diameter. Dactylopores occur



in rows on the lateral branch edges, their centers about 0.2 mm apart. Dactylopore mounds about 110 μm wide, 60–80 μm tall, perforated apically by a pore 30–38 μm in diameter. Ampullae 0.82–0.90 mm in diameter, some with efferent tubules of 0.15 mm diameter.

Discussion.—*Lepidopora*, usually considered a subgenus of *Errina*, was elevated to generic rank by Cairns (in press). The eight species attributed to this genus are listed in Table 1. Representatives of all of these species have been examined by the author.

In his last revision of the subgenus *Lepidopora*, Boschma (1968b) listed four more species than are included in Table 1; however, closer examination has revealed that *E. ramosa* Hickson and England, 1905, and *E. horrida* Hickson and England, 1905, have abcauline slit dactylopore spines and thus belong to *Inferiolabiata*. The description of *L. porifera* (Naumov, 1960) also indicates a placement in *Inferiolabiata* or *Errinopora*. *L. cochleata* (Pourtalès, 1867) has adcauline slit dactylopore spines and is therefore placed in *Errina* s.s.

The type-specimens of *L. carinata* (Pourtalès, 1867) are among the very few Poutalès coral types that cannot be located at the MCZ. Poutalès' original and subsequent descriptions (1871) clearly pertain to a species of *Lepidopora*; however, the specimens he identified as *E. carinata* in 1878 belong to *Inferiolabiata*. In view of this confusion, a neotype is designated for *L. carinata* which corresponds very closely to the description of Poutalès (1871) and was collected near the type-locality: Albatross 2319–2350, 23°10'–11'N, 82°17'–20'W, 60–420 m, USNM 15991 (Fig. 4H–I).

Three species described by Nielsen (1919) from the Paleocene of Denmark (*Sporadopora faxensis*, *Pliobothrus laevis*, and *P. dispergens*) are not confidently identifiable to genus and may all be referable to *Lepidopora*.

New Records.—ALBATROSS-2152, off Havana, 708 m, USNM 7167; ALBATROSS-2153, 23°10'19"N, 82°23'54"W, 518 m, USNM 15986; ALBATROSS-2161, 23°10'36"N, 82°20'28"W, 267 m, USNM 15987; ALBATROSS-2167, 23°10'40"N, 82°20'30"W, 368 m, USNM 15996; ALBATROSS-2332, 23°10'38"N, 82°20'06"W, 285 m, USNM 16035; ALBATROSS-2333, 23°10'36"N, 82°19'12"W, 309 m, USNM 60511; ALBATROSS-2336, 23°10'48"N, 82°18'52"W, 287 m, USNM 15988; EASTWARD-26537, 27°14.2'N, 79°15.5'W, 520 m, USNM 60353; EASTWARD-26538, 27°12.6'N, 79°13.7'W, 420 m, USNM 60354; EASTWARD-26549, 27°17.5'N, 79°12.5'W, 370 m, USNM 60355.

Distribution.—From the Blake Plateau off Georgia through the Straits of Florida off Havana. 183–1,097 m.

Types.—The syntypes of *L. glabra* are deposited at the MCZ. The largest and best-preserved colony bears the number 3926; five other branches or fragments are present, one of which is numbered 5530. Types examined by the author.

Sporadopora Moseley, 1879

Polypora Moseley, 1876b: 94.

Sporadopora Moseley, 1879a: 429 (nom. nov.); 1881: 93–94.—Broch, 1942: 27–28.—Boschma, 1956: F104.

Figure 1. *Lepidopora glabra* (A, syntype from off Havana, 494 m, MCZ 3926; B–D, F, Eastward-26538: 27°12.6'N, 79°13.7'W, 420 m, 29 Mar. 1975; E, G–I, Albatross-2152: 4 km off Havana, 708 m, 30 Apr. 1884): A, part of syntype colony, $\times 1.5$; B–C, branches showing arrangement of gastro- and dactylopores, $\times 13$, $\times 40$, respectively; D–E, coenosteal texture, $\times 135$, $\times 200$, respectively; F, dactylopore, $\times 185$; G–H, gastrostyle and ring palisade, $\times 135$, $\times 330$, respectively; I, ampullae with efferent tubules, $\times 43$.

Diagnosis.—Colonies uniplanar with occasional anastomosis of branches; branches stout, bluntly tipped, and round in cross section; branch axils U-shaped. Coenosteum irregularly porous to reticulate; if reticulate, coenosteal strips short, discontinuous, and not granular. Gastro- and dactylopores scattered randomly over coenosteum, both usually flush with the surface. Both gastro- and dactylopores tubes long, forming clusters along the branch axis. Long gastropore tubes have multiple, thin, complete tabulae or very fine bridges, which support the gastrostyle. Gastrostyles very long and slender (H:W up to 21) and prominently ridged; dactylostyles absent. Ampullae internal, opening to branch surface by small efferent ducts.

Discussion.—The resemblance of *Sporadopora* and *Lepidopora* noted by Boschma (1964a: 61) has previously been discussed; however, *Sporadopora* is probably most similar to *Distichopora*, particularly the aberrant species *D. providentiae* (Hickson and England, 1909). Originally described as a *Sporadopora*, *D. providentiae* was transferred to *Distichopora* by Broch (1942: 27), this transfer being confirmed by Boschma (1959: 163), the latter author indicating that it was intermediate between the two genera. *D. providentiae* resembles *Sporadopora* by its flabellate corallum and blunt-tipped branches; long, slender (H:W > 10) ridged gastrostyle (a character found only in these two genera); and its low to flush gastro- and dactylopores. Differences include coenosteal texture, shape of dactylopores, and a tendency for the gastropores of *D. providentiae* to be concentrated on the branch edges, flanked by irregular rows of elongate dactylopores. It is the latter character that allies it most closely to *Distichopora*. *D. providentiae* will be discussed again under *Distichopora*.

Occurrence.—?Paleocene: Denmark; ?Miocene: Chatham Island and Victoria, Australia; Recent: Subantarctic South America, New Zealand. 122–1,498 m.

Type Species.—*Polypora dichotoma* Moseley, 1876, by monotypy.

Sporadopora dichotoma (Moseley, 1876)

Figures 2A–H, 24F, 25H, 27A, 28C

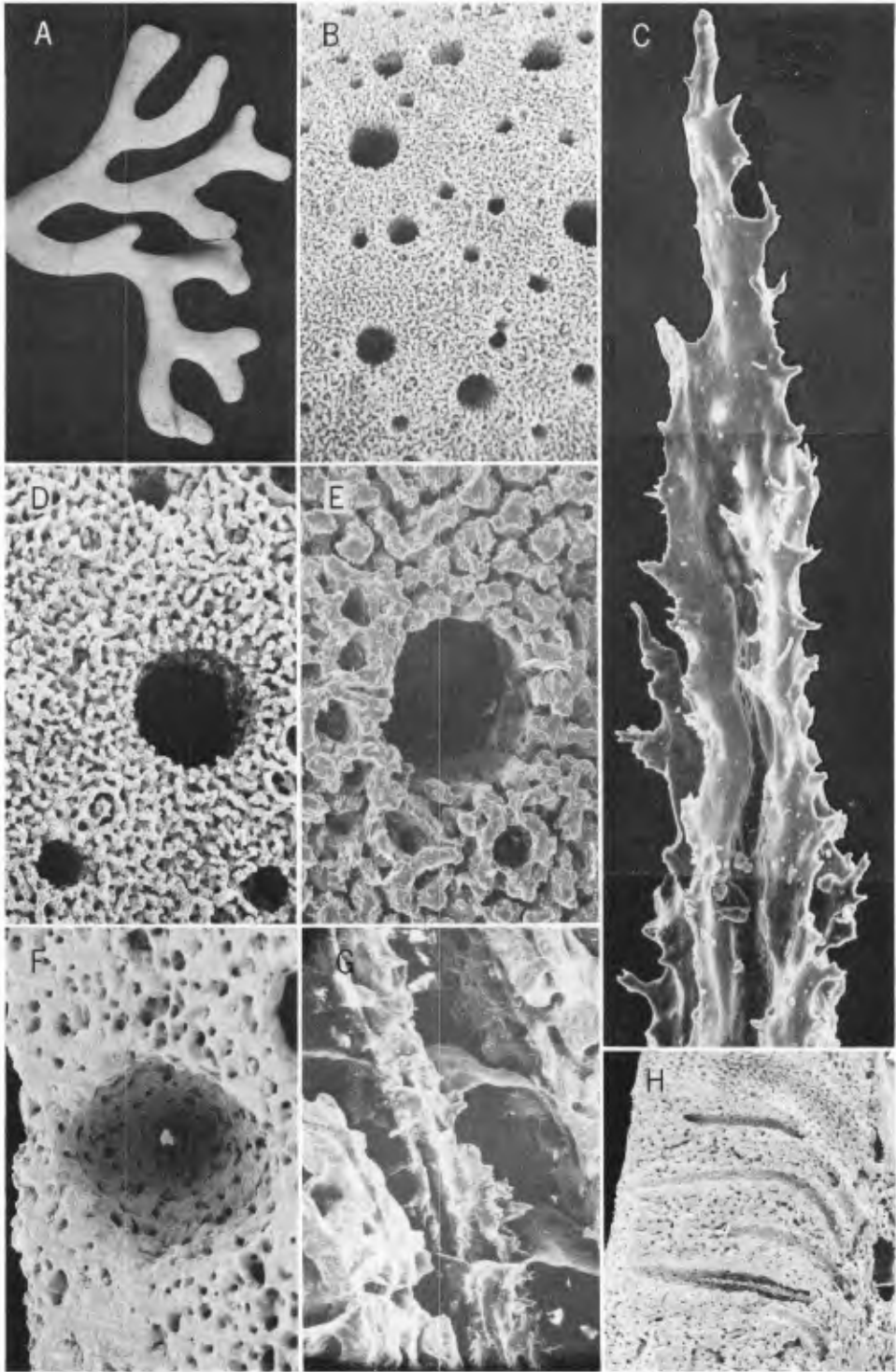
Polypora dichotoma Moseley, 1876b: 94–95.

Sporadopora dichotoma: Moseley, 1879: 429–440, pl. 34, figs. 1–2, pl. 35, figs. 1–2, 9, pl. 36, pl. 43, figs. 1–9, 12, pl. 44, figs. 13–14; 1881: 36–47, 83, pl. 1, figs. 1–2, pl. 2, figs. 1–2, 9, pl. 3, pl. 10, figs. 1–9, 12, pl. 11, figs. 13–14.—Weill, 1934: 484, fig. 315a–b.—Boschma, 1956: F104, figs. 85, 3a–b; 1957: 60–61.—Boschma and Lowe, 1969: 15, pl. 5, map 5.—Cairns, in press: figs. 1A–B, 2A–I, 3A–B.

?*Sporadopora dichotoma* Hall, 1898: 177–178.

Diagnosis.—Colonies up to 14 cm tall; distal branches 4–20 mm in diameter, basal branches up to 4.45 cm in diameter. Coenosteum of distal branches homogeneously porous; that of older basal branches composed of short, discontinuous strips in a reticulate pattern. Coenosteum not granulated. Gastropores 0.20–

Figure 2. *Sporadopora dichotoma* (A, Vema 17–65: 50°18'S, 54°11'W, 1,498–1,501 m, 14 May 1961; B, D, Eltanin-970: 54°59'S, 64°53'W, 586–641 m, 11 Feb. 1964; C, Eltanin-1593: 54°43'S, 56°37'W, 339–357 m, 14 Mar. 1966; E–F, Islas Orcadas 575-34: 54°42'S, 34°51'W, 563–598 m, 19 May 1975; G–H, Hero 715–895: 55°00'S, 64°50'W, 438–548 m, 3 Nov. 1971): A, colony, ×0.56; B, D, arrangement of gastro- and dactylopores, ×15, ×33, respectively; C, tip of gastrostyle, ×167; E, gastropore encircled by ring of shallow pits, ×83; F, cross section of internal ampulla, efferent duct visible in center, ×40; G, gastrostyle supported by tabulae, ×67; H, longitudinal section of branch showing gastrostyle in place, ×12.



0.62 mm in diameter, sometimes surrounded by a ring of 10–15 shallow pits, each about 40–70 μm in diameter. Gastrostyles up to 3.9 mm long, but rarely over 0.20 mm in diameter (H:W to 21); style held in place by thin, complete tabulae. Dactylopores about 0.12 mm in diameter.

Contracted gastrozoid about 0.4 mm in diameter and 1.1 mm long, enveloped by a thin bottle-shaped sheath or sac, which opens to the branch surface. Radiating coenosteal canals extend from the gastrozoid sac for about 1 mm (Fig. 24F). Gastrozoids have 4–7 short tentacles. Dactylozoids dimorphic: larger ones adnate, smaller ones simple. Nematocysts of three sizes: (1) 29.6–32.7 \times 6.2–8.6 μm , and (2) 20–23 \times 4.7–6.2 μm , both types common in gastrovascular cavity of gastrozoids, coenosteal canals, and surface nematophores, and (3) 7.8–9.0 \times 3.5–4.0 μm , common in dactylozoids and coenosteal canals.

Discussion.—The skeleton of *S. dichotoma* has been described and illustrated in greater detail by Cairns (in press), and Moseley (1879, 1881) has beautifully illustrated and described the soft parts. I can only add that Moseley reported two size classes of nematocysts (40–42 \times 6.6–7.7 μm and 15.7–16.2 \times 6.6 μm), both of which are larger than the nematocysts reported here. Also, the number of gastrozoid tentacles, reported as four by Moseley, ranges to seven per gastrozoid.

Three other species are assigned to *Sporadopora*, only one of them being Recent, *S. mortenseni* Broch, 1942. Known only from the New Zealand region at 122–282 m, it is distinguished from *S. dichotoma* by its more delicate colony form, more solid coenosteum, incomplete tabulae, and smaller gastropores (Cairns, in press). The two fossil species are *S. marginata* Tenison-Woods, 1880, known only from the Miocene of Chatham Island, and *S. faxensis* Nielsen, 1919, known only from the Danian of Fakse, Denmark (Lower Paleocene). A figured syntype of *S. faxensis* was examined (deposited at the Copenhagen Geologisk Museum, MMH 1750). It differed from Recent *Sporadopora* by having superficial ampullae and a smooth coenosteal texture. The preservation was not adequate to determine the presence or absence of gastrostyles, and dactylopores were not noted. In view of its differences from Recent *Sporadopora* and its poor preservation, it is possible that this species could belong to *Sporadopora*, *Lepidopora*, or *Pliobothrus*.

According to Boschma (1957), the types of *S. marginata* are no longer in existence; from the original description, Boschma (1964a) doubted its placement in *Sporadopora* but was unable to place it in any genus with certainty.

Two other species have been incorrectly assigned to *Sporadopora*. *S. providentiae* Hickson and England, 1909 was transferred to *Distichopora* by Broch (1942) (also see Boschma, 1959), and *S. cleithridium* Squires, 1958 was transferred by Squires (1962) to the milleporine genus *Axoporella*. *Axoporella* has subsequently been synonymized with *Axopora* and placed in a separate order, the Axoporina (Boschma, 1963c).

Distribution.—Off Uruguay; Falkland Rise; Scotia Ridge from Tierra del Fuego to South Georgia; South Shetland Islands. 250–1,498 m.

Types.—Syntypes of *S. dichotoma* are deposited at the BM (1880.11.25.166–168, 1957.2.28.42). Specimens examined by the author.

Pliobothrus Pourtalès, 1868

Pliobothrus Pourtalès, 1868: 141.—Moseley, 1881: 94.—Broch, 1942: 32–33 (part).—Boschma, 1956: F104.

Steganopora Hickson and England, 1905: 26.

Diagnosis.—Branching uniplanar and nonanastomosing; branches round in cross section or flattened in flabellar plane. Coenosteum composed of longitudinal strips

covered by imbricated platelets of variable width. Strips bordered by large, elongate coenosteal pores. Dactylopores coenosteum may be coarsely granulate. Gastro- and dactylopores irregularly scattered; however, usually slightly more abundant on anterior side. Gastropores round to slightly elliptical, flush with surface, opening in to a larger, roughly hemispherical chamber below (Fig. 31). Rudimentary, perforate tabulae sometimes occur in the gastropore tube. Dactylopores apically located on tall tubes or low mounds; dactylopores tubes extend along center of branch axis for a considerable distance. No gastro- or dactylostyles. Ampullae usually internal and hemispherical, opening to surface by a small efferent pore. No sexual dimorphism in size was noted.

Discussion.—*Pliobothrus* and *Phalangopora* are the only two genera in the Erriniinae that lack gastrostyles. They also have linear-imbricate coenosteal texture, but otherwise differ in many characters: i.e., *Pliobothrus* has large coenosteal pores, rudimentary gastropore tabulae, apically perforate dactylopores, randomly placed gastro- and dactylopores, internal ampullae, clustered axial dactylopores tubes, and a less uniform imbrication of coenosteal platelets. Most of these character states are considered as more simple than those of *Phalangopora* and therefore *Pliobothrus* is provisionally grouped with *Sporadopora* and *Lepidopora* as among the most primitive of the stylasterine genera.

Occurrence.—?Paleocene: Denmark; Recent: North Atlantic, Indonesia. 80–1,097 m.

Type Species.—*Pliobothrus symmetricus* Pourtalès, 1868, by subsequent designation (Kühn, 1928).

Pliobothrus symmetricus Pourtalès, 1868
Figures 3A–H, 24G, 25G, 27B

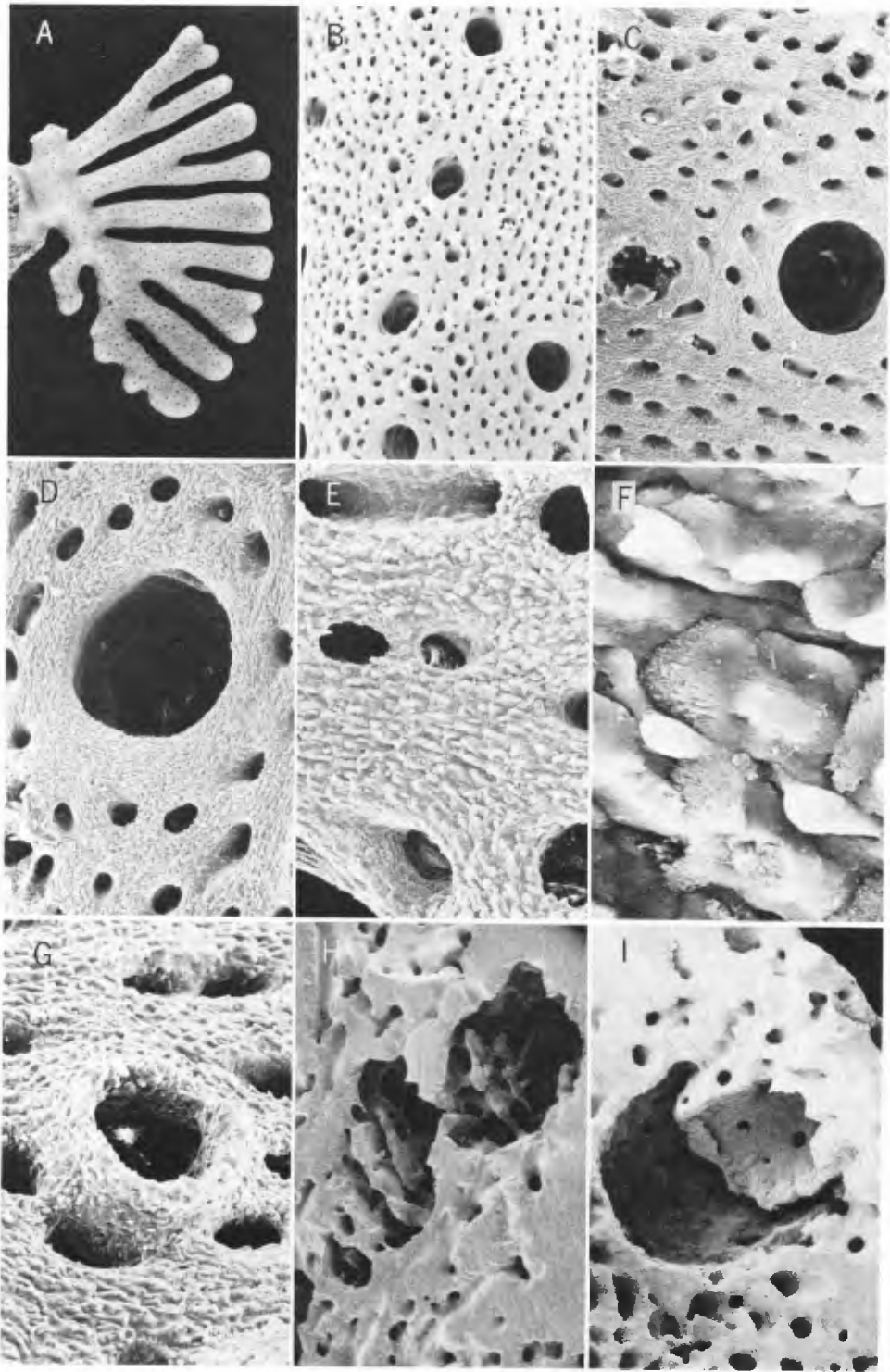
Pliobothrus symmetricus Pourtalès, 1868: 141.—Duncan 1870: 297.—Portalès, 1871: 57, pl. 4, figs. 7–8.—Duncan, 1873: 336, pl. 49, fig. 7.—Portalès, 1878: 211.—Moseley, 1881: 47–50, 84, pl. 8, figs. 2–3.—Agassiz, 1888: 138–139, fig. 444.—Nutting, 1895: 177.—Hickson, 1912b: 465–466.—Broch, 1914: 3–7, pl. 1, figs. 1–3, pl. 3, figs. 19–20, 28–29, pl. 4, figs. 34, 40–42.—Dons, 1939: 196–197, figs. 1–2.—Boschma, 1956: F104, figs. 85, 1a–b; 1957: 59–60.—Squires, 1965: 24, pl. 2, figs. 7–8.—Boschma, 1967: 333–335, pl. 1, figs. 5–6.

Pliobothrus n. sp. Moseley, 1876a: 548.

Diagnosis.—Colonies up to 5 cm tall and 8 cm broad; branch tips blunt, sometimes clavate, up to 6 mm in greater diameter. Coenosteal strips 80–90 μ m wide, platelets 4–11 μ m wide. Coenosteal pores about 45 μ m wide and up to 170 μ m long. Gastropores 0.35–0.41 mm in diameter. Dactylopores 90–110 μ m in diameter, raised on mounds up to 0.1 mm tall. Ampullae 0.80–0.90 mm in diameter.

Gastrozooids with at least five small tentacles; mouth cruciform. Dactylozooids simple, with central lumen. Nematocysts of two kinds: larger nematocysts (39.3–43.8 \times 7.8–12.5 μ m) are common in coenosteal canals and epithelium; smaller (8.0–9.5 \times 3.0–3.2 μ m) are very rare in ectoderm of gastrozooid. Each male ampulla contains one compound gonophore, i.e., a compartmentalized mass containing “pseudofollicles” (Broch, 1914), each of which contains sperm of varying degrees of development. Male spadix bifurcate.

Discussion.—Because of the detailed studies of Moseley (1881) and Broch (1914), *P. symmetricus* is one of the morphologically best known stylasterine corals. However, both authors failed to detect the tiny gastrozooid tentacles, at least five of which occur on each polyp, as Moseley (1881: 48) indicated for the closely related *P. tubulatus*. Otherwise, little can be added to the histological analyses of these two workers.



Four other species are assigned to the genus *Pliobothrus*. *P. tubulatus* (Pourtalès, 1867), known only from the Greater Antilles at 493–704 m, differs from *P. symmetricus* in having much taller, granulated, dactylopore tubes (up to 0.65 mm tall) and more slender, pointed branches. *P. spinosa* (Hickson and England, 1905), known only from the type-locality off Halmahera, Indonesia at 1,089 m, was originally described as the basis of the new genus *Steganopora*. Broch (1914) synonymized it with *Pliobothrus*, but Boschma (1956; 1957) treated it as a monotypic genus. Unfortunately the type, and only known specimen, of *P. spinosa* is lost (personal communication, van Soest, 1981); however, its description is remarkably similar to *P. tubulatus*, differing primarily in its even longer dactylopore tubes and superficial ampullae. Two other species, *P. dispergens* and *P. laevis* are known only from their type-locality of the Danian of Fakse, Denmark (Lower Paleocene). A figured type and a topotypic specimen of *P. laevis* were examined (Copenhagen Geologisk Museum, MMH 1757); both were shown to have large hemispherical ampullae, smooth coenosteum, apically perforate dactylopore mounds, and low, elliptical gastropores. Types of *P. dispergens* (Copenhagen Geologisk Museum, MMH 1756) have reticulate coenosteum, apically perforate dactylopore mounds, low gastropores, and no ampullae. In both cases the preservation was not adequate to distinguish gastrostyles, if present at all, and for this reason both species are not identifiable as to genus and may well belong to *Lepidopora*, instead. Other species referred to *Pliobothrus* included *P. grantmackieii* Squires, 1965, which is herein assigned to the bryozoan genus *Porina* (personal communication, A. Cheetham, 1981), and *P. seriatus* Broch, 1942, a junior synonym of *Phalangopora regularis* Kirkpatrick, 1887.

New Records.—ALBATROSS-2660, 28°40'N, 78°46'W, 921 m, USNM 60361; SILVER BAY-2418, 24°15'N, 81°24'W, 265–293 m, USNM 60359; OREGON-1348, 24°29'N, 81°50'W, 274 m, USNM 60357; GERDA-702, 26°29'N, 78°39'W, 73–220 m, USNM 60358; Johnson-Smithsonian Deep-Sea Expedition-43, 18°02'N, 67°51'W, 439–549 m, USNM 60360, SABP, BLM-3F, 31°46'N, 79°05'W, 540 m, USNM 49141; SABP, BLM-2H, 32°20'N, 78°10'W, 411 m, USNM 49130, 49131; off Sombrero Light, Pourtalès Plateau, 73–210 m, USNM 60356.

Distribution.—North Atlantic: Sombrero, D.W.I.; Mona Island; Straits of Florida; Bahamas; Blake Plateau to South Carolina; Iceland; off Norway; Faeroe Channel; Azores. 80–1,097 m.

Types.—Two syntypes are deposited at the MCZ. The larger colony from Bibb-64 (illustrated by Pourtalès, 1871: pl. 4, fig. 7) is designated lectotype (MCZ 5529), the other specimen as paralectotype (MCZ 5550). Both were examined by the author.

Cheiloporidion Cairns, in press

Cheiloporidion Cairns, in press.

Diagnosis.—Colonies uniplanar with a strong tendency toward branch anastomosis, producing a network of irregularly shaped fenestrae. Branches elliptical to

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Figure 3. *Pliobothrus symmetricus* (A, lectotype from Bibb-64: 24°17'N, 81°43'W, 262 m, 11 May 1868, MCZ 5529; B–G, off Marathon, Florida, USNM 49692; H, Oregon-1348: 24°29'N, 81°50'W, 273 m, 18 July 1955): A, colony, ×0.9; B, arrangement of gastro- and dactylopores, ×19; C, gastropore on right and opening of efferent duct on left, ×43; D, gastropore surrounded by coenosteal pores, ×67; E–F, coenosteal texture, ×167, ×1,530, respectively; G, dactylopore, ×175; H, longitudinal section of a gastropore containing several porous tabulae, ×33. *Pliobothrus tubulatus*: I, Albatross-2152: 4 km off Havana, 708 m, 30 Apr. 1884, longitudinal section of a gastropore tube, ×50.

rectangular in cross section, the greater axis perpendicular to the plane of branching. Branches ridged on both anterior and posterior faces. Coenosteum reticulate, composed of short discontinuous strips, which are smooth (not granulate) and have rounded edges. Dactylopores occur randomly on anterior and lateral branch surfaces; gastropores loosely aligned along lateral edges. Gastro- and dactylopore tubes short, branches compact. Gastropores flush with branch surface; gastrostyles ridged, bearing fused spines. Dactylopores rimmed by two to four vertical platelets, which form a discontinuous collar around the pore; no dactylostyles. Ampullae superficial. Soft parts unknown.

Discussion.—*Cheiloporidion* has several characters not shared with any other genera, i.e., low, rimmed dactylopores composed of platelets; a nongranulate (smooth), reticulate coenosteal texture; and a very short gastrostyle, which is supported by a very broad base. Its resemblance to *Errinopsis* in colonial form is probably convergent. It is placed near the more primitive genera because of its lack of coordination of gastro- and dactylopores and its relatively simple dactylopore structure.

Occurrence.—Recent: Argentina to Tierra del Fuego. 642–1,137 m.

Type Species.—*C. pulvinatum* Cairns, in press, by original designation.

Cheiloporidion pulvinatum Cairns, in press
Figure 4A–G

N. gen., n. sp. Boschma and Lowe, 1969: 15, pl. 5, map 4.

Cheiloporidion pulvinatum Cairns, in press: figs. 11A, 12A–F.

Diagnosis.—Holotypic colony a fragment 5.7 cm broad and 3.5 cm tall. Ratio of length to width of branch cross section up to 2; intermediate-sized branch measures 6.2×3.4 mm in diameter. Posterior sides of distal branches carinate; anterior sides also bear discontinuous and coarser ridges. Coenosteal strips 50–65 μ m wide; coenosteum light pink. Gastropore 0.17–0.40 mm in diameter. Gastropore tube consists of a spherical gastrostyle chamber which leads, via a slight constriction (but no ring palisade), to a funnel-shaped upper tube that opens to the surface. Gastrostyle massive and squat, composed of a wide, cylindrical basal main shaft, which abruptly tapers to a lesser diameter at the constriction, and finally to a point at the branch surface. The illustrated gastrostyle is 0.49 mm tall and 0.35 mm broad, basally (H:W = 1.4). Dactylopores 47–80 μ m in diameter; surrounding collar up to 65 μ m tall. Internal diameter of ampullae 0.42–0.70 mm.

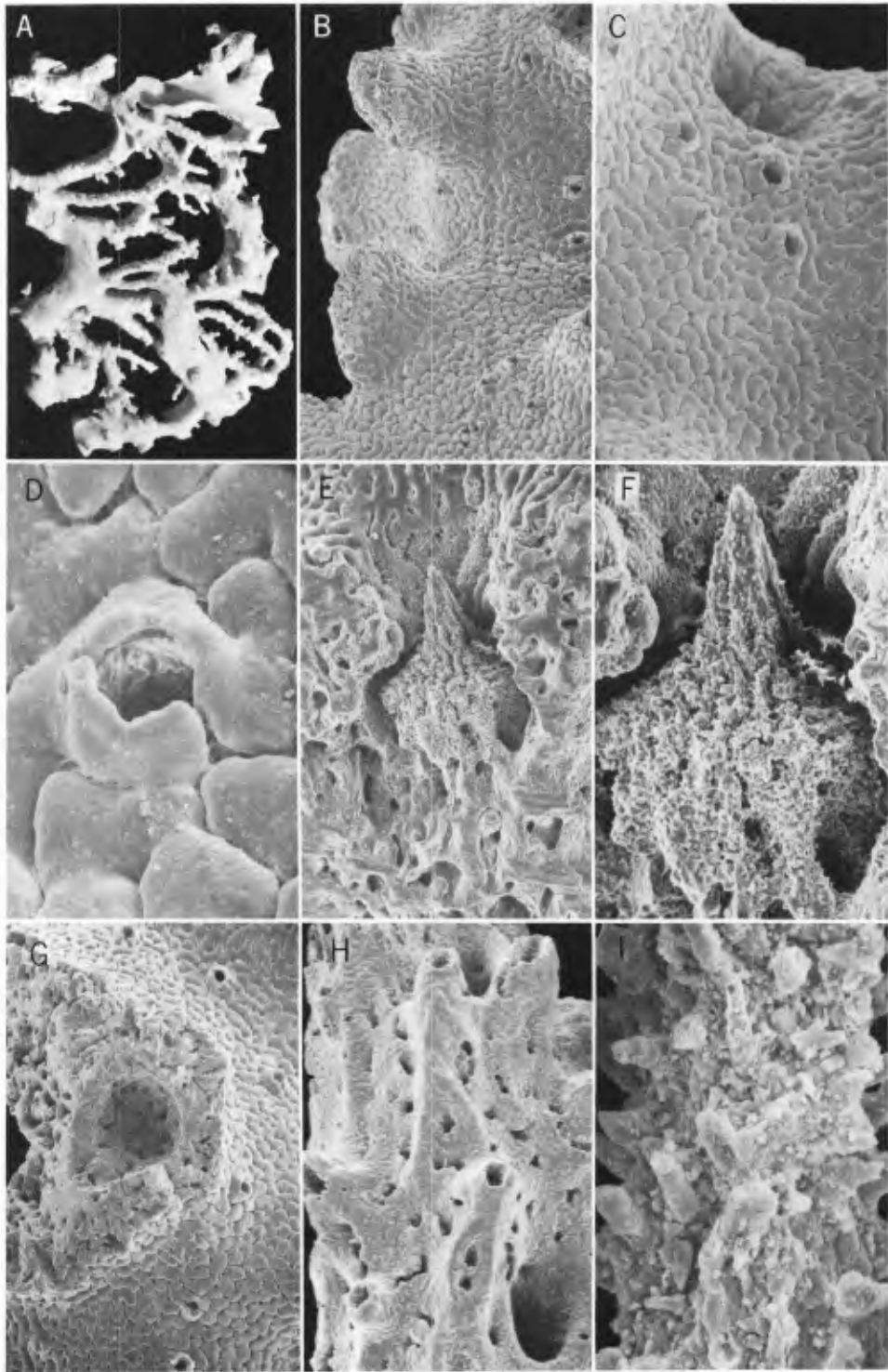
Discussion.—*Cheiloporidion* is a monotypic genus. It is more fully described and illustrated by Cairns (in press).

Distribution.—Off Argentina; off Cape Horn, Tierra del Fuego. 642–1,137 m.

Types.—Holo- and paratypes deposited at the USNM.

→

Figure 4. *Cheiloporidion pulvinatum* (A–G, holotype from Vema 17-RD14: 38°58'S, 55°17'W, 595–642 m, 19 June 1961): A, colony, $\times 1$; B, discontinuous branch carina, $\times 29$; C, reticulate coenosteal texture and dactylopores, $\times 50$; D, dactylopore, $\times 230$; E–F, gastropore containing gastrostyle, $\times 60$, $\times 125$, respectively; G, cross section of internal ampulla, $\times 33$. *Lepidopora carinata* (neotype from Albatross 2319–2350: 23°10'31"N, 82°17'45"W, 60–421 m, 17–20 Jan. 1885): H, gastro- and dactylopores, $\times 120$; I, gastrostyle, $\times 500$.



Lepidotheca new genus

Errina: Hickson and England, 1905: 18–19 (part).—Boschma, 1957: 49 (part).—Eguchi, 1968: 47.

Errina (Errina): Hickson, 1912a: 880 (part).

Errina (Labiata): Broch, 1942: 39, 57 (part).

Errina (Inferiolabiata): Boschma, 1956: F102 (part); 1963a: 337–338 (part); 1964e: 294 (part).

Errina (Lepidopora): Boschma, 1963a: 338 (part).

Diagnosis.—Colonies flabellate and usually delicate; branches do not anastomose. Coenosteal texture linear-imbricate. Gastro- and dactylopores randomly distributed, but predominantly on the anterior side, or with gastropores located at or near branching axils. Gastropores round to elliptical, sometimes bordered by an abcauline lip. Gastrostyles long and slender ($H:W = 4-9$) and usually not ridged, resembling those of *Lepidopora*; however, the styles of several species are slightly ridged. Ring palisade usually present. Dactylopore spines low, horseshoe-shaped structures usually strongly inclined toward the distal branch tip. Walls of dactylopore spines thin, the slit usually occupying over half the width of the spine. Slits of spines abcauline, always facing the top of the colony. Spines well separated from one another, never clustered or composite, and never ridged. Dactylostyles usually absent; only *L. tenuistylus* has dactylostyles, similar to those of *Inferiolabiata*. Ampullae large superficial hemispheres.

Discussion.—Most of the seven species referred to *Lepidotheca* were previously assigned to *Errina (Inferiolabiata)*, a catchall genus for all *Errina* with distally directed (abcauline) dactylopore spine slits. As stated in my discussion of *Inferiolabiata*, these seven species constitute a discrete genus having its closest affinities with *Inferiolabiata*. To reiterate, *Lepidotheca* differs from *Inferiolabiata* by its linear-imbricate coenosteal texture (vs. reticulate-imbricate); consistently flabellate colony form (vs. tendency towards bushy); lack of dactylostyles (except for *L. tenuistylus*); and short, nonridged, horseshoe-shaped dactylopore spines, which are always well separated (vs. tall, ridged, spout-like spines, which are often clustered or fused together).

Etymology.—The generic name refers to the scale-like coenosteal texture produced by the imbricate platelets. Gender: feminine.

Occurrence.—Recent: off Mauritius, Indonesia, Japan, New Zealand, Subantarctic, Greater Antilles. 85–2,010 m.

Type Species.—*Errina (I.) fascicularis* Cairns, in press, here designated.

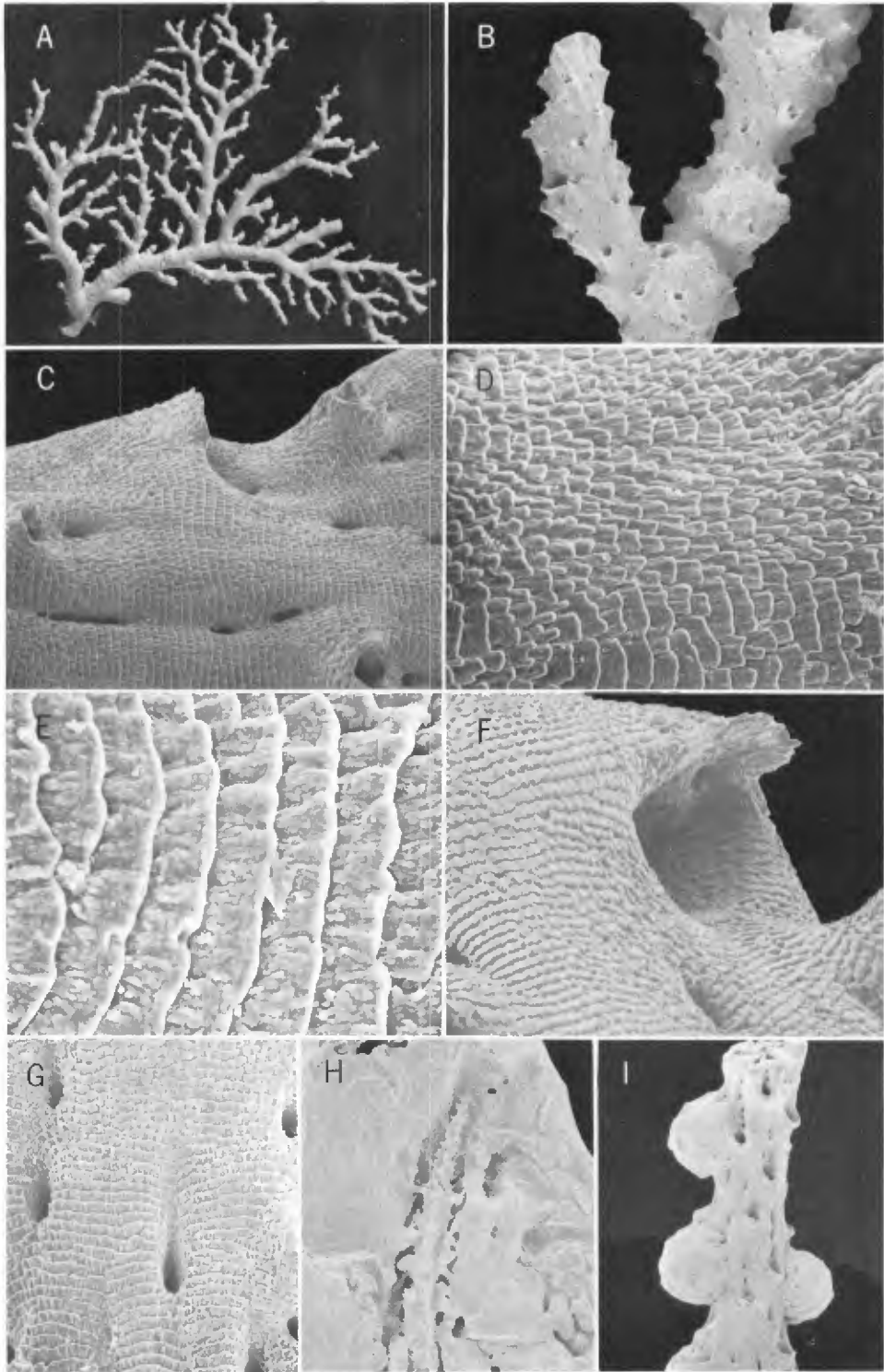
Lepidotheca fascicularis (Cairns, in press)

Figures 5A–I, 24E, 25E

Errina (Inferiolabiata) fascicularis Cairns, in press; figs. 22H, 29A–K, 30A–E.

Diagnosis.—Colonies extremely delicate, up to 6 cm tall with a basal branch diameter of 9.2 mm. Longitudinal coenosteal strips slightly convex and broad

Figure 5. *Lepidotheca fascicularis* (A–C, F, H, Eltanin-1423: 56°21'S, 158°28'E, 1,574–1,693 m, 12 Feb. 1965; D, Gazelle 66/44: 35°21'S, 175°40'E, 1,092 m, 12 Nov. 1875, Museum für Naturkunde, Berlin; E, G, I, Eltanin-684: 54°55'S, 38°05'W, 595–677 m, 25 Aug. 1963): A, holotype colony, $\times 1$; B, branch tip bearing ampullae, $\times 12$; C, gastropore lip and several dactylopores, $\times 51$; D–E, imbricate coenosteal texture, $\times 133$, $\times 333$, respectively; F, gastropore lip, $\times 67$; G, coenosteal texture and coenosteal pores, $\times 67$; H, gastrostyle, $\times 33$; I, branch with ampullae, $\times 12$.



(0.25–0.38 mm wide), becoming less apparent toward branch tips. Width of platelets variable: some very broad, extending from slit to slit across a strip, others quite slender (13 μm wide); approximately 40–45 leading edges of platelets occur per mm. Gastropores invariably occur at branch axils, and occasionally on lateral branch surfaces. Those occurring at axils are often flanked by two lips; those on the sides are bordered by an abcauline lip. Gastrostyle composed of a slender, spinose, distal section and a much longer and wider, non spinose basal part, which are separated by a tabula. The distal section is 0.25–0.43 mm long and 0.07–0.08 mm in diameter (H:W = 3.3–6.1), sparsely ornamented with blunt, often fused, spines up to 25 μm tall, which are vertically aligned. The entire style measures up to 1.31 mm long and 0.12 mm in diameter (H:W = 11). No ring palisades. Dactylopore spines 0.15–0.20 mm tall and 0.18–0.25 mm wide, usually located along coenosteal slits or on ampullae. Female ampullae 0.98–1.10 mm in diameter; male, 0.77–0.82 mm in diameter.

Gastrozooids cylindrical with an almost square, concave (when preserved) hypostome, one tentacle corresponding to each corner of the square. Dactylozooids simple. Neamtocysts measuring 6.0–7.0 \times 2.5–3.5 μm are very common in gastro- and dactylozooids tentacle tips.

Discussion.—The other six species of *Lepidotheca* are briefly diagnosed. *L. cervicornis* (Broch, 1942): branches coarse; gastro- and dactylopores randomly dispersed; however, gastropores always bordered proximally by a dactylopore spine; gastrostyle slightly ridged (H:W about 5); off New Zealand (101 m). *L. tenuistylus* (Broch, 1942): branches delicate; gastro- and dactylopores randomly distributed; no gastropore lips; rudimentary dactylostyles present; gastrostyle not ridged (H:W about 6); Mauritius (238–274 m). *L. ramosa* (Hickson and England, 1905): branches delicate, gastropores below axils on anterior side bordered by a large abcauline lip; Suva Sea, Indonesia (520 m). *L. horrida* (Hickson and England, 1905): very similar to *L. fascicularis* but with smaller, carinate dactylopore spines; Djilolo Passage, Indonesia (1,089 m). *L. japonica* (Eguchi, 1968): branches coarse; gastro- and dactylopores randomly distributed; no gastropore lip; H:W of gastrostyle about 6.9; Sagami Bay, Japan (85 m). *L. hachijoensis* (Eguchi, 1968): branches delicate; gastro- and dactylopores randomly distributed; no gastropore lip; H:W of gastrostyle about 6; dactylopore spines very low (flush on basal branches); Sagami Bay (200 m). The types of all but the last two species have been examined by the author.

Distribution.—Subantarctic. 540–2,010 m.

Types.—Holotype and most paratypes deposited at USNM. One paratype at BM.

Phalangopora Kirkpatrick, 1887

Phalangopora Kirkpatrick, 1887: 212.—Boschma, 1956: F104.

Pliobothrus: Broch, 1942: 33–36.

Diagnosis.—Branching uniplanar and nonanastomosing; branches round in cross section and blunt tipped. Coenosteum composed of longitudinal strips covered by narrow, imbricate platelets of relatively uniform width. Strips delimited by narrow, elongate pores. Gastropores linearly arranged on both flabellar faces, each bordered by a broad abcauline lip. Elongate dactylopores linearly arranged on branch edges, and more highly raised on abcauline side. Branch core dense, permeated by narrow diameter coenosteal canals. Gastropore tubes short; dactylopore tubes long and slender, but do not form clusters of tubes in branch axis; no tabulae

present. No gastro- or dactylostyles. Female ampullae large, superficial. Male colonies unknown.

Discussion.—Broch (1942: 33) indicated that *Phalangopora* was morphologically intermediate between *Pliobothrus* and *Inferiolabiata*; he finally placed the type-species of *Phalangopora* in *Pliobothrus* and *P. seriatus*. I basically agree with Broch's interpretation: *Phalangopora* has characters in common with both *Pliobothrus* and *Inferiolabiata* (my *Lepidotheca*) but is also sufficiently different from both to be treated as a separate genus. I previously compared it to *Pliobothrus* in the discussion of that genus. *Phalangopora* is similar to *Lepidotheca* in coenosteal texture, presence of a lower gastropore lip and superficial ampullae, and shape of dactylopore. It differs primarily in its lack of a gastrostyle and its linear arrangement of gastro- and dactylopores.

Occurrence.—Recent: Mauritius. 238–274 m.

Type Species.—*P. regularis* Kirkpatrick, 1887, by monotypy.

Phalangopora regularis Kirkpatrick, 1887
Figures 6A–H, 25D, J

Phalangopora regularis Kirkpatrick, 1887: 212–214, pl. 8, figs. 1–5.—Broch, 1951b: 126.—Boschma, 1956: F104, figs. 85, 2a–c; 1957: 59.

Pliobothrus seriatus Broch, 1942: 33–36, pl. 3, fig. 10, text-fig. 9.

Diagnosis.—Colonies up to 6 cm tall and 7 cm broad; branches bluntly tipped, about 1 mm in diameter distally, increasing up to 3.5 mm in diameter at the basal attachment. Branch axils often U-shaped; occasionally distal branches strongly recurved. Coenosteal strips 85–120 μm wide; platelets about 12 μm wide, such that 5–10 adjacent platelets comprise the width of a strip at any point. Coenosteal pores elongate, about 16 μm wide. Gastropores, measuring about 0.2 mm across, occur approximately every 1 mm; dactylopores occur about every 0.33 mm. Isolated or short rows of dactylopores sometimes occur on the flabellar faces. Dactylopores are elongate in the direction of the branch, about 0.15 mm long, 0.06 mm wide, and elevated about 0.11 mm at the proximal edge. Female ampullae prominent, up to 1.5 mm in diameter, occurring singly and in clusters. The majority of ampullae (68/81 of the holotype's) occur on the posterior side. A small, round depression, about 0.2 mm in diameter, occurs on some ampullae (? incipient efferent duct).

Gastrozooids with 0–6 tentacles. Dactylozooids dimorphic: isolated individuals, large and simple; those in series, smaller and adnate. Nematocysts of only one size (7.0–8.5 μm \times 4.0–4.5 μm) common in coenosteal canals and dactylozooids.

Discussion.—*Phalangopora* is a monotypic genus. There is no doubt that *Pliobothrus seriatus* Broch, 1942 is a junior synonym.

Distribution.—Known only from three localities off Mauritius, 238–274 m.

Types.—The holotype of *P. regularis* is deposited at the BM (1891.12.12.1). The types of *P. seriatus* are deposited at the Zoologisk Museum, Copenhagen. Both types examined by the author.

Inferiolabiata Broch, 1951

Errina: Moseley, 1879: 443–447 (part).

Errina (*Errina*): Hickson, 1912a: 880 (part).

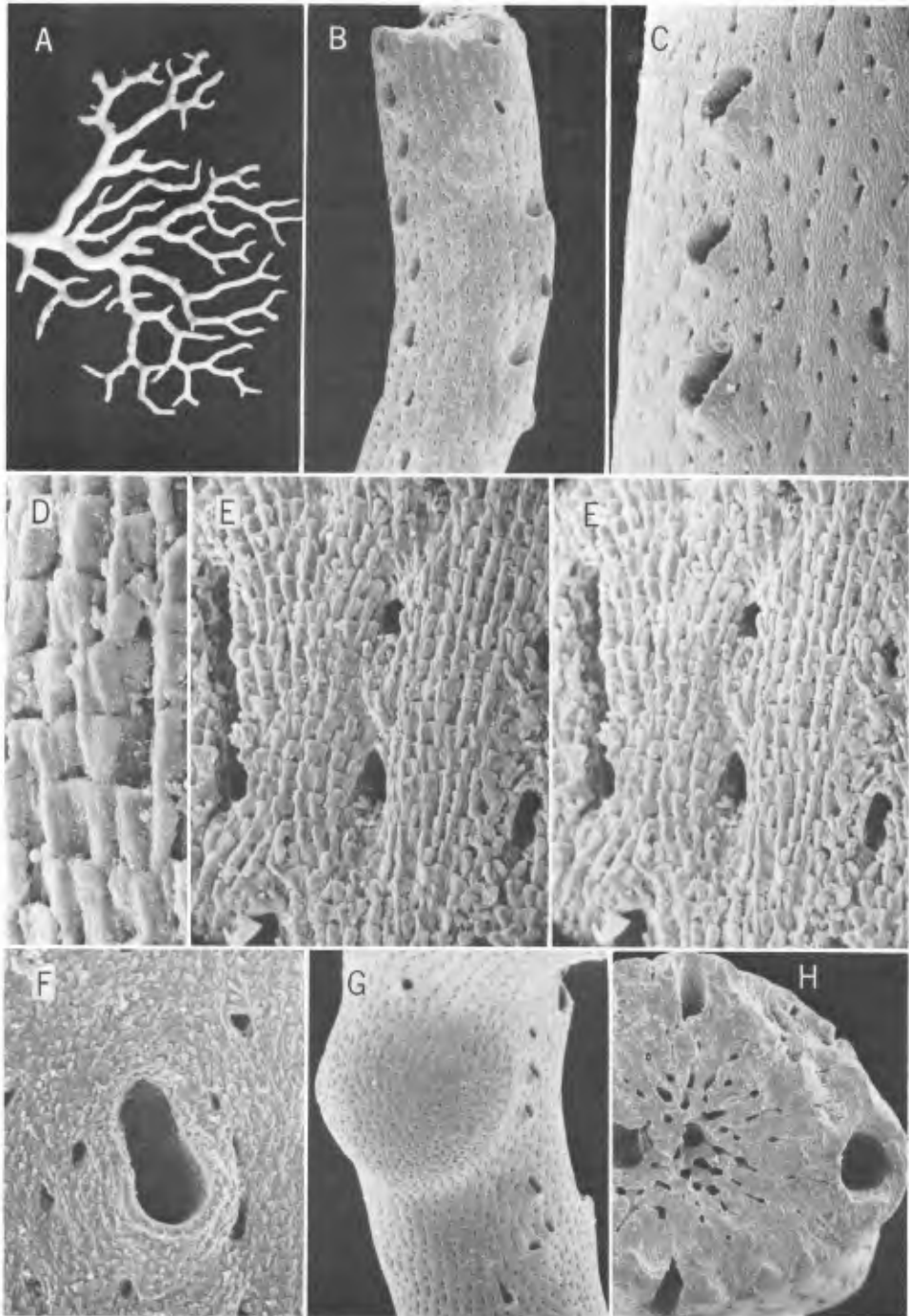


Figure 6. *Phalangopora regularis* (A-H, holotype from off Mauritius, BM 1891.12.12.1): A, holotype colony, $\times 0.75$; B, branch showing arrangement of gastro- and dactylopores, $\times 20$; C, row of dactylopores, $\times 50$; D-E, coenosteal texture, $\times 670$, $\times 200$, respectively, E is a stereo pair; F, dactylopore, $\times 133$; G, branch with ampullae, $\times 19$; H, cross section of branch, $\times 47$.

Errina (Labiata) Broch, 1942: 39 (part).

Errina (Inferiolabiata) Broch, 1951b: 125 (pro *Labiata*).—Boschma, 1956: F102 (part); 1963a: 337 (part); 1965b: 21 (part).

Diagnosis.—Colonies flabellate to bushy; branches round in cross section and blunt tipped, sometimes anastomosing in response to a polychaete worm symbiosis. Coenosteal texture reticulate-imbricate, the reticulation sometimes obscure away from base; no granules. Gastro- and dactylopores randomly distributed; gastropores round and not lipped. Gastrostyles cylindrical, gradually attenuate, and not ridged (H:W = 3–10). Styles bear large individual spines and may be held in place by tabulae. Dactylopore spines tall (up to 0.7 mm) and spout-like, with an abruptly truncated tip. Dactylopore spines grooved along the side facing top of colony (abcauline); lower side of spine longitudinally ridged. Adjacent spines often joined at their edges, forming a tier of 2–5 fused spines encircling part of the branch. Dactylopores bear 1–4 rudimentary dactylostyles. Ampullae large superficial hemispheres.

Discussion.—*Inferiolabiata* has, in the past, been treated as a subgenus including those 12 species of *Errina* s.l. which have abcauline slit dactylopore spines. However, when examined more closely, this artificial assemblage of species can be divided into three groups, each of which is considered a distinct genus. The type-species, *I. labiata*, limits the genus to only two species, it and *I. lowei* Cairns, in press. *I. echinata* (Moseley, 1879) defines a second, monotypic genus, *Stellapora*, and seven species are placed in the new genus, *Lepidotheca*. The remaining two species, *Spinipora irregularis* and *Labiopora lobata*, both described by Nielsen (1919) and placed in *Inferiolabiata* by Boschma (1964e), are reattributed to *Errina* s.s. and *Errinopora*, respectively. The only characters that all three genera have in common are the presence of abcauline grooved dactylopore spines and large superficial ampullae. *Inferiolabiata* differs from *Lepidotheca* by its reticulate-imbricate coenosteum (vs. linear-imbricate), 1–4 dactylostyles per dactylopore (vs. none), and very tall, ridged, spout-like dactylopore spines which are often fused together (vs. short, smooth, horseshoe-shaped dactylopore spines which are always separate). It differs from *Stellapora* in coenosteal texture and in the shapes of its gastropore, gastrostyle, and dactylopore spines. The only other genus in the Errininae to have both gastro- and dactylostyles is *Errinopora*; however, the resemblance appears to be superficial as the two genera differ in many other characters.

Occurrence.—Recent: Antarctic and Subantarctic. 87–2,100 m.

Type Species.—*Errina labiata* Moseley, 1879, by original designation (Broch, 1951b).

Inferiolabiata labiata (Moseley, 1879)

Figures 7A–H, 25B, 28I

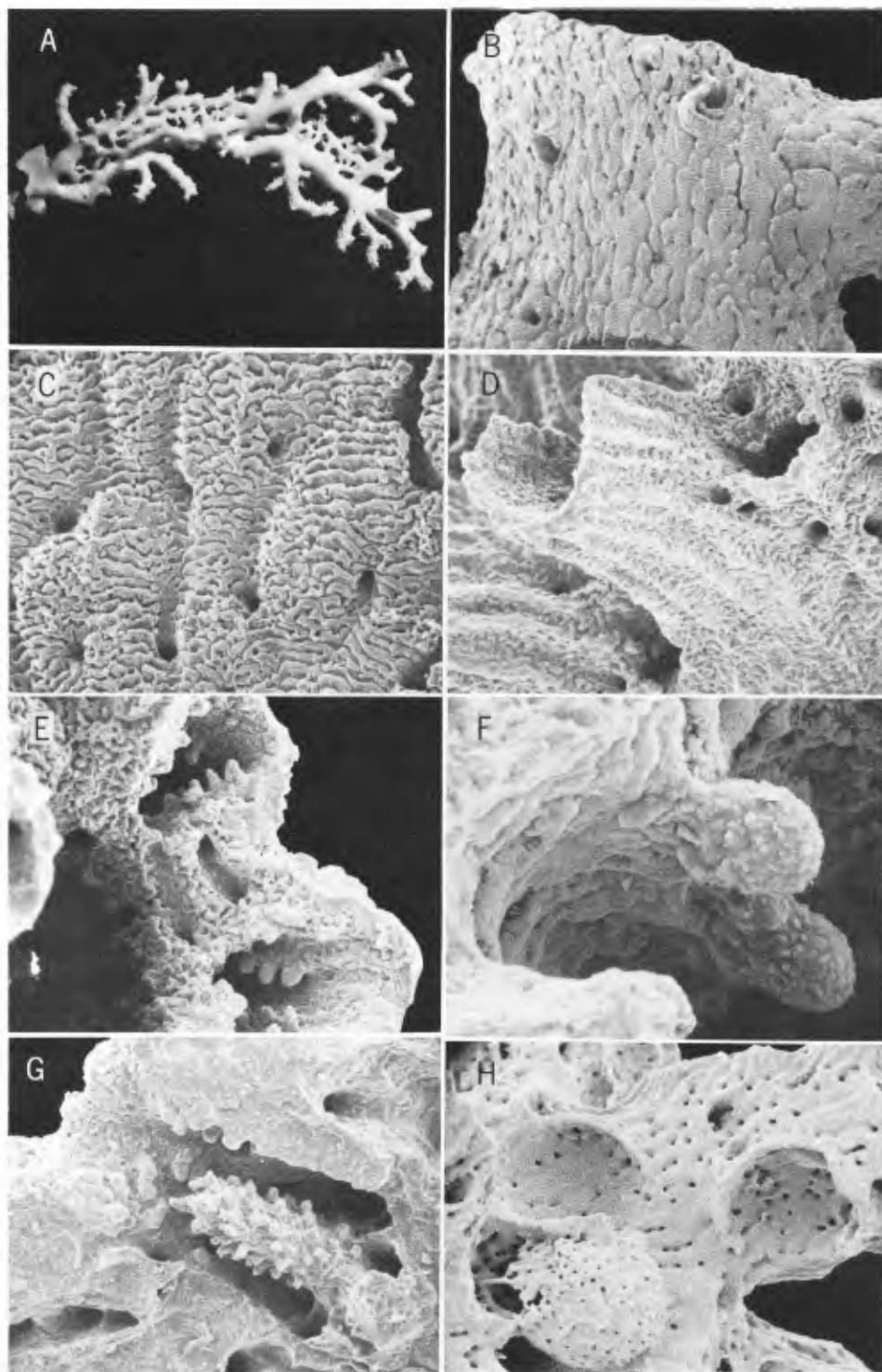
Errina labiata Moseley, 1879: 443–447, pl. 34, fig. 7, pl. 37, pl. 44, figs. 9–11; 1881: 50–55, 80, pl. 1, fig. 7, pl. 4, pl. 11, figs. 9–11 (part: not *Challenger* sta. 135).—Boschma, 1957: 55; 1964e: 287–299, pl. 1; 1966: 109, 117.—Boschma and Lowe, 1969: 15, pl. 5, map 2 (part).

Errina (Errina) labiata: Hickson, 1912a: 880.

Errina (Labiata) labiata: Broch, 1942: 39.

Errina (Inferiolabiata) labiata: Broch, 1951b: 125.—Boschma, 1963a: 337–338.—Cairns, in press: figs. 22D–E, 26A–I, 27A–C.

Diagnosis.—Colony flabellate to bushy; branches highly anastomotic, caused primarily by a symbiotic polychaete worm. Coenosteal reticulation distinct over



entire colony, becoming longitudinal at branch tips. Overall texture at low magnification is porous. Gastropores 0.28–0.33 mm in diameter; gastrostyle up to 1 mm tall, having an H:W of 2.7–6.6. Spines on gastrostyle up to 35 μm tall and 15 μm in diameter. Diffuse ring palisade present. Dactylopore spines up to 0.70 mm tall and 0.23 mm wide, usually laterally fused into tiers of 2–6 spines which encircle part of the branch. Each dactylopore with 1–4 rudimentary dactylostyles, each style composed of 5–10 discrete, cylindrical, blunt pillars up to 50 μm tall and 20 μm in diameter. Ampullae 1.02–1.30 mm in diameter.

Gastrozooids short, squat cylinders with four clavate tentacles. Dactylozooids long and slender, extending far above coenosteal surface. According to Moseley (1881), large nematocysts measuring about $37 \times 15 \mu\text{m}$ occur in nematophores and surface epithelium. Smaller nematocysts measuring $6\text{--}7 \times 3.3\text{--}3.9 \mu\text{m}$ occur abundantly in the dactylozooids. The tube of an exploded nematocyst is about 0.55 μm in diameter and bears a triple spiral of cylindrical spines, each measuring about 0.50 μm long and 0.25 μm in diameter. The spines are directed toward the capsule (Fig. 28I).

Discussion.—This species has been more fully described, discussed, and illustrated by Cairns (in press), and its histology has been well illustrated and discussed by Moseley (1881). Moseley reported two size classes of nematocysts, the larger measuring about $37 \times 15 \mu\text{m}$, the smaller, $16 \times 11 \mu\text{m}$ (from Moseley, 1881: pl. 11, fig. 10). I was unable to find the larger nematocysts in my sections and the smaller nematocysts in many specimens were considerably smaller than Moseley's.

Only one other species is placed in this genus, *I. lowei* Cairns, in press. A comparison of the two species is made in the original description.

Distribution.—Widely distributed in Antarctic and Subantarctic. 87–2,100 m.

Types.—All syntypes deposited at the BM; examined by the author.

Paraerrina Broch, 1942

Paraerrina Broch, 1942: 60–61.—Boschma, 1956: F104.

Diagnosis.—Colonies flabellate; branches round in cross section and blunt tipped; branch anastomosis rare. Coenosteal texture reticulate, covered by small, sharp granules. Gastro- and dactylopores randomly arranged. Gastropores round and flush with surface or very slightly rimmed. Gastrostyles of medium height, not ridged, and bear extremely long, robust, branching spines. Horizontal and vertical tabulae stabilize proximal end of gastrostyle. Dactylopores flush with surface except near branch tips where they are bordered by low dactylopore spines with abcauline slits. Rudimentary dactylostyles present. Ampullae superficial hemispheres, female twice the diameter of male.

Discussion.—At first glance, *Paraerrina* closely resembles *Inferiolabiata* (as previously redefined); in fact, Broch (1942: 61) suggested that the genera may be synonymous. Characters shared by them include: abcauline slit dactylopore spines,

Figure 7. *Inferiolabiata labiata* (A, Burton Island 592-3: 72°08'S, 172°10'E, 433 m, 13 Jan. 1958; B–C, Eltanin-2021: 73°49'S, 178°13'W, 495–503 m, 15 Jan. 1968; D–H, Eltanin-2092: 76°00'S, 168°49'W, 526 m, 3 Feb. 1968): A, colony with elongate, porous worm tube, $\times 0.62$; B–C, imbricate coenosteal texture, $\times 16$, $\times 80$, respectively; D, ridged dactylopore spines, $\times 70$; E, two dactylopore spines with multiple dactylostyles, $\times 87$; F, dactylostyle elements, $\times 600$; G, gastrostyle and diffuse ring palisade, $\times 87$; H, ruptured and intact ampullae, $\times 17$.

reticulate coenosteal texture, nonridged gastrostyles, rudimentary dactylostyles, and large superficial ampullae. However, *Paraerrina* differs in several significant characters: (1) it has slit dactylopore spines only on distal branch tips, (2) it has only one very rudimentary dactylostyle per dactylopore, (3) its dactylopore spines are well spaced, never clustered, (4) its coenosteal microarchitecture is granular, not imbricate, and (5) its gastrostyle is quite distinctive, with large, branching spines. *Paraerrina* is therefore considered a distinct genus.

Occurrence.—?Oligocene: New Zealand; Recent: known only from off Mauritius, 238–274 m.

Type Species.—*Paraerrina decipiens* Broch, 1942, by monotypy.

Paraerrina decipiens Broch, 1942

Figures 8A–G, 26B

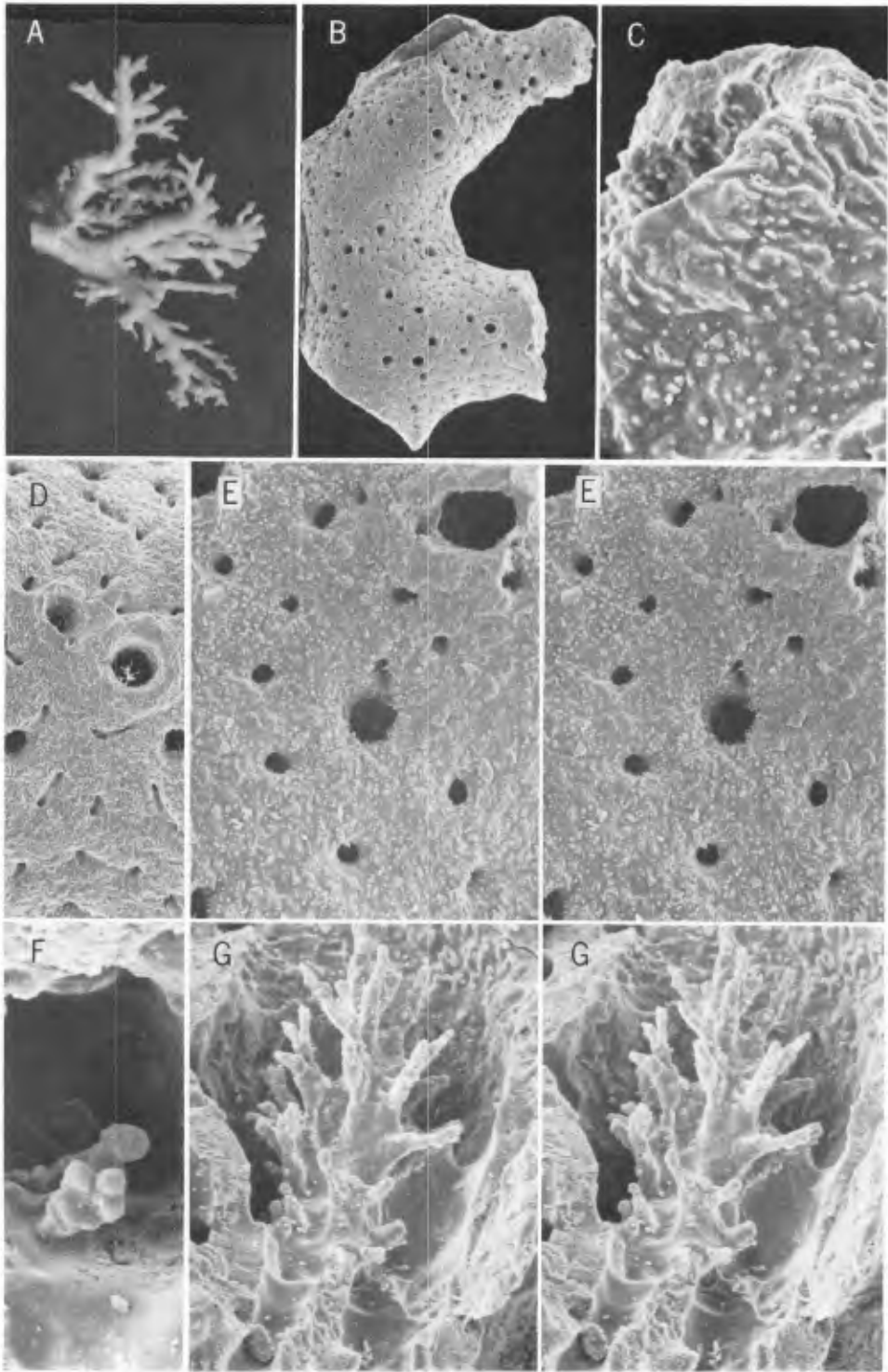
Paraerrina decipiens Broch, 1942: 61–63, 82–83, pl. 5, fig. 19, text-figs. 19, 29.—Boschma, 1956: F104, fig. 84, 2a–b; 1957: 58.

Diagnosis.—Colonies up to 5.5 cm tall and 10 cm broad, with a basal branch diameter up to 9.0 mm. Coenosteal strips 0.13–0.17 mm wide bordered by short, discontinuous grooves about 20 μm wide and equally deep. These grooves, which are paths of superficial coenosteal canals, terminate in deep pores through which the surface canals communicate with the interior canals. Coenosteum covered by irregularly shaped, pointed granules up to 7.5 μm tall and 2.5–4.5 μm in diameter. On the sides of dactylopore spines the granules are elongate, and fuse into vertical ridges up to 40 μm long. Gastropores 0.12–0.14 mm in diameter. Illustrated gastrostyle 0.25 mm tall, 0.064 mm wide (H:W = 3.9), and bears cylindrical spines up to 75 μm long and 11 μm in diameter. Style stabilized by four thick, vertical tabulae and several horizontal tabulae. Dactylopores of same size as gastropores, those on branch tips with a lower lip raised up to 0.12 mm high. Dactylostyle elements up to 26 μm tall and 9 μm in diameter. Female ampullae up to 2.0 mm in diameter; male, 0.57–0.69 mm.

Gastrozooids with 0–4 rudimentary tentacles apiece; dactylozooids adnate. One kind of nematocyst, measuring 5.5–6.5 \times 2.2–3.0 μm , occurs in the coenosteal canals and dactylozooids.

Discussion.—*Paraerrina* is a monotypic genus. It has been reported only twice: the type-specimens of *P. decipiens*, and one fossil fragment from the middle Oligocene of New Zealand identified as *Paraerrina* sp. by Squires (1962). This latter specimen, examined by the author, is similar to *P. decipiens* in branch shape and size, reticulate coenosteal texture, unridged gastrostyle, gastropore tabulae, and superficial ampullae. It differs in having slightly raised, apically perforate gastro- and dactylopores, the latter sometimes linked by low ridges, a condition found in some *Lepidopora*. No grooved dactylopore spines or dactylostyles were present, but this may be the result of the preservation. I share Squires's hesitation in identifying this specimen as belonging to *Paraerrina*, but agree that *Paraerrina* is the most likely choice.

Figure 8. *Paraerrina decipiens* (A–G, figured syntype from Mauritius, Copenhagen Zoologisk Museum); A, colony, $\times 0.67$; B, branch fragment with gastropores, $\times 11$; C, dactylopore spines on branch tip, $\times 350$; D–E, coenosteal texture and gastropores, $\times 47$, $\times 100$, respectively, E is a stereo pair; F, dactylostyle element, $\times 550$; G, gastrostyle, $\times 215$, stereo pair.



Distribution.—Known only from off Mauritius. 238–274 m.

Types.—The types are deposited at the Zoologisk Museum, Copenhagen. The figured syntype was examined by the author. The type-specimens are heavily infested by boring barnacles (*Lithoglyptes* fide Broch, 1942), which produce large slits about 1.5 mm long and 0.5 mm wide along the lateral branch edges.

Stellapora new genus

Acanthopora Moseley, 1876b: 94 (name preoccupied by Orbigny, 1849).

Spinipora Moseley, 1879: 447, 476; 1881: 55 (name preoccupied by Agassiz, 1846).

Errina (*Spinipora*): Hickson, 1912a: 881.—Broch, 1942: 39.

Errina (*Inferiolabiata*): Boschma, 1956: F102 (part); 1963a: 338 (part); 1964e: 294 (part).

Errina: Boschma, 1957: 53 (part).

Diagnosis.—Colonies robust, flabellate to slightly bushy; branches thick, anastomotic, and bluntly tipped. Coenosteal texture reticulate, covered by irregularly shaped granules. Gastro- and dactylopores randomly distributed over coenosteum. Gastropores large, round, or stellate in shape. Gastrostyle slender with longitudinal ridges and a pointed tip; fused spines ornament the ridges. No ring palisades. Dactylopore spines are dimorphic: the larger spines are very tall, thin-walled, and spout-like with an abruptly truncated tip. They are grooved along the side facing the top of the colony (abcauline) and are not ridged on their lower sides. They often cluster together and some appear to be composite. The smaller dactylopore spines are small, raised, elliptical slits or apically perforated mounds. No dactylostyles. Ampullae superficial, hemispherical.

Discussion.—The single species referred to *Stellapora*, *S. echinata* (Moseley, 1879), was placed by Moseley in a separate genus, *Spinipora*, which he considered to be "closely allied to *Errina*." Hickson (1912a) maintained *Spinipora* as a discrete, monotypic taxon but as a subgenus of *Errina*, and Boschma (1956; 1963a) finally merged it with the subgenus *Inferiolabiata*, which arbitrarily combined all *Errina* that have abcauline grooved dactylopore spines. In my opinion, Moseley was correct in placing *S. echinata* in a separate genus because of its significant morphological differences from *Inferiolabiata*, i.e., reticulate-granular coenosteal texture (vs. reticulate-imbricate), stellate gastropores (vs. round), ridged gastrostyles with fused spines (vs. cylindrical gastrostyles with individual spines), and dimorphic, nonridged dactylopore spines without dactylostyles (vs. monomorphic, ridged dactylopore spines with 1–4 dactylostyles apiece). *Stellapora* differs from *Lepidotheca* in the same characters as well as being much more robust and having much better developed dactylopore spines. The character of stellate gastropores is unique to *Stellapora*.

Both of Moseley's generic names are preoccupied and the type-species of *Inferiolabiata* is *I. labiata*, a separate genus, making it necessary to establish a new generic name for *S. echinata*.

Etymology.—The generic name refers to the stellate appearance of some of the gastropores of *S. echinata*. Gender: feminine.

Occurrence.—Recent: Southwest Atlantic. 357–1,647 m.

Type Species.—*Spinipora echinata* Moseley, 1879.

Stellapora echinata (Moseley, 1879)

Figures 9A–I, 25I

Spinipora echinata Moseley, 1879: 447–449, pl. 34, fig. 3, pl. 35, fig. 4, pl. 38; 1881: 55–57, pl. 1, fig. 3, pl. 2, fig. 4, pl. 5.

Errina (*Spinipora*) *echinata*: Hickson 1912a: 881, pl. 95, fig. 8.

Not *Spinipora echinata*: Hickson and England, 1909: 352, pl. 44, fig. 8.

Errina echinata: Boschma, 1957: 53.—Boschma and Lowe, 1969: 15, pl. 5, map 2.

Errina (*Inferiolabiata*) *echinata*: Boschma, 1963a: 338; 1964e: 293–294, 298.—Cairns, in press: figs. 22B–C, 24A–H, 25A–B.

Diagnosis.—Colonies up to 23 cm tall with a basal branch diameter of 2.5 cm; distal branches round in cross section, 2.5–5.0 mm in diameter. Coenosteal strips 0.16–0.22 mm wide, covered by irregularly shaped granules 5–10 μ m in diameter. Gastropores abundant and large (0.41–0.68 mm in diameter); each stellate pore has 1–7 grooves along its inner edge, which produce a stellate pattern at the surface not unlike a cyclo-system. Gastrostyles up to 0.9 mm tall with an H:W around 4–5. Large dactylopore spines are up to 2.5 mm tall and 0.55 mm wide; smaller spines with pore diameters of 0.12–0.20 mm. Ampullae 1.1–1.3 mm in diameter, often ruptured.

Gastrozooids long and cylindrical, each with six long tentacles. Larger dactylozooids adnate, composed of an elongate base which lies along the dactylopore spine and a short, free part near the end of the base (see Moseley, 1881: pl. 5). Smaller dactylozooids simple, basally attached. Nematocysts common in dactylozooids and coenosteal canals, measuring 11.0–11.5 \times 4.5–5.0 μ m.

Discussion.—*Stellapora* is a monotypic genus. It has been more fully described and discussed by Cairns (in press) as *E. (I.) echinata*.

Distribution.—Known only from off Uruguay and off Burdwood Bank. 357–1,647 m.

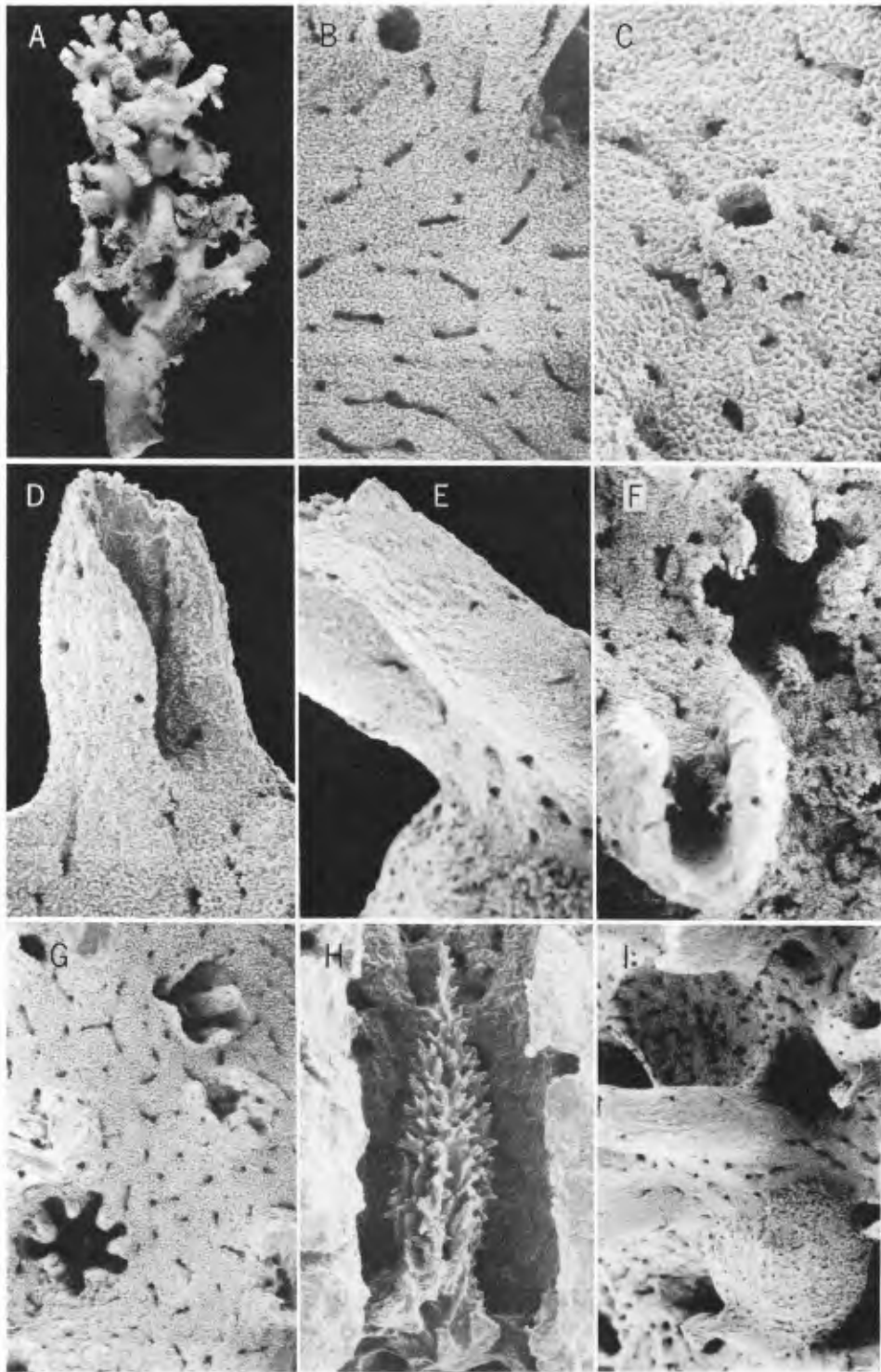
Types.—The holotype is deposited at the BM (1880.J1.25.174, 196); examined by the author.

Errinopsis Broch, 1951

Errinopsis Broch, 1951a: 40.—Boschma, 1956: F104, fig. 85, 4.

Diagnosis.—Colonies uniplanar, sometimes with accessory flabella projecting perpendicular to main flabellum. Colony secondarily attached to substrate by numerous, relatively slender branches. Branching highly anastomotic, producing fenestrate flabella. Branches elliptical to rectangular in cross section, the greater axis of the branch oriented perpendicular to the flabellum; ratio of branch edges as high as 1:4. Coenosteal texture reticulate to slightly linear, covered by low, rounded granules; however, some dactylopore spines are coarsely imbricate. Gastro- and dactylopores occur on all branch surfaces but tend to concentrate on anterior and anterolateral edges. Gastrostyles lanceolate, attaining their greatest width at their midpoints; H:W ratio medium. Styles ridged, the ridges bearing fused spines; no ring palisades or tabulae. Dactylopore spines of two kinds: (1) low, apically perforate mounds, and (2) tall, thick, adcauline-grooved tubercles. The tall dactylopore spines sometimes add one or more extensions apically which serve as the forerunner of branch anastomosis. They may also have additional dactylopores producing large, usually bifurcate, composite spines. No dactylostyles. Ampullae superficial and irregular in shape, sometimes with a lateral tubular efferent duct.

Discussion.—*Errinopsis* appears to be morphologically intermediate between the more primitive genera with apically perforate dactylopores, such as *Lepidopora*, and the more advanced errinine genera that have coordinated, thick-walled, grooved dactylopore spines, such as *Errina*, *Errinopora*, and *Gyropora*. It is similar to *Lepidopora* in having randomly arranged gastro- and dactylopores and apically



perforate dactylopores, but more advanced in having ridged gastrostyles and thick-walled, adcauline-grooved dactylopore spines. It differs from the other group of errinine genera (*Paraerrina*, *Inferiolabiata*, *Lepidotheca*, *Stellapora*, and *Phalangopora*) in having differently shaped and oriented dactylopore spines and a different coenosteal texture (reticulate-granular vs. predominantly imbricate).

Occurrence.—Recent: Off southern tip of South America. 250–771 m.

Type Species.—*E. reticulum* Broch, 1951, by original designation.

Errinopsis reticulum Broch, 1951
Figures 10A–H, 27C

Errinopsis reticulum Broch, 1951a: 37–41, pl. 2, fig. 2, pl. 3, figs. 1–2, text-figs. 3–7.—Boschma, 1956: F104, fig. 85, 4; 1957: 59; 1966: 117.—Boschma and Lowe, 1969: 15, pl. 5, map 4.—Cairns, in press: figs. 1G–H, 9A–H.

Diagnosis.—Colonies up to 25 cm tall and 35 cm broad; fenestrae rarely larger than 2–3 square mm. Coenosteal strips about 50 μ m wide covered by rounded granules 6–8 μ m in diameter; coenosteum orange to pink. Gastropores round, 0.15–0.30 mm in diameter, and flush with the surface. Styles up to 0.60 mm tall; H:W ranges from 3.3–3.9. Small, apically perforate dactylopores 45–70 μ m in diameter, about 25 μ m tall. The less numerous, grooved dactylopore spines are between 0.20–0.30 mm in diameter and up to 1.7 mm tall (including apical extensions), having grooves 40–60 μ m wide. Ampullae 0.65–0.77 mm in diameter.

Gastrozooids have 4–6 short tentacles. Dactylozooids both simple and adnate. Rod-shaped nematocysts measuring 8.6–11.1 \times 2.3–3.1 μ m and more spherical ones measuring 10.5–12.0 \times 4.0–4.5 μ m occur in coenosteal canals, dactylozooids, and in the ectoderm, oriented perpendicular to the surface. Male ampullae may contain 2–4 gonophores, female ampullae usually have but one.

Discussion.—Broch (1951a: 40) stated that *E. reticulum* has only one kind of dactylopore spine, hypothesizing that the large, grooved spines grew from the low, apically perforate ones. Although he stated that he was able to find many intermediate forms bridging the differences between the simple and spiniferous pores, I do not find these intermediate forms by examination of either the skeleton or the dactylozooids. At least two kinds of dactylozooids (and dactylopore spines) occur, of which the medium-sized, grooved spines (Fig. 10G) are very similar to those of *Errina*. Broch also stated that only simple dactylozooids are present, but adnate dactylozooids occur in the tall dactylopore spines.

Only one other species is known in this genus, *E. fenestrata* Cairns, in press; comparisons to *E. reticulum* are made by Cairns (in press).

Distribution.—Known only from area bounded by Tierra del Fuego, Burdwood Bank, and Falkland Islands. 250–771 m.

Types.—Broch (1951a) designated two allotypic syntypes from the four colonies he examined. Their deposition is unknown.

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Figure 9. *Stellapora echinata* (A–I, Eltanin-1593: 54°43'S, 56°37'W, 339–357 m, 14 Mar. 1966): A, colony, \times 0.27; B, coenosteal texture, \times 40; C, dactylopore, \times 75; D–E, dactylopore spines, \times 47, \times 40, respectively; F, dactylopore spine from above and stellate gastropore, \times 40; G, stellate gastropores, \times 27; H, gastrostyle, \times 60; I, dactylopore spines and an ampulla, \times 20.

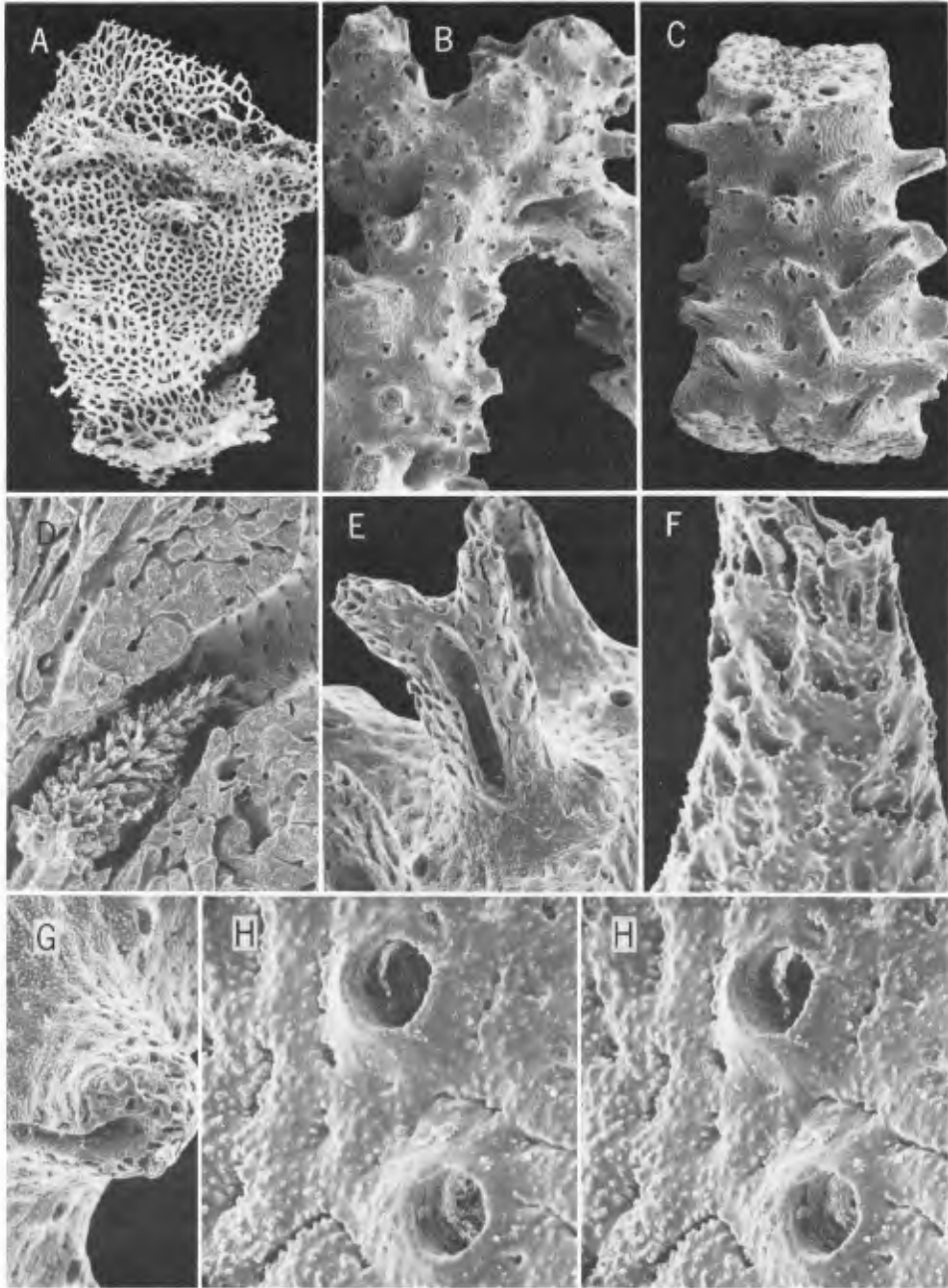


Figure 10. *Errinopsis reticulum* (A, Walther Herwig 19/76: 54°49'S, 57°52'W, 230–250 m, 27 Nov. 1975; B, D, Hero 715–895: 55°00'S, 64°50'W, 438–548 m, 3 Nov. 1971; C, E–H, Hero 715–879: 54°50'S, 63°50'W, 342–353 m, 28 Oct. 1971): A, large colony, $\times 0.27$; B, branch fragment with gastropores, both types of dactylopores, and ampullae, $\times 15$; C, branch fragment with gastropore and both types of dactylopores, $\times 14$; D, gastrostyle, $\times 57$; E–G, dactylopores spines, $\times 53$, $\times 150$, $\times 77$, respectively; H, two conical, apically perforate dactylopores, $\times 175$, stereo pair.

Errina Gray, 1835

Millepora: Linnaeus, 1767: 1282 (part).

Madrepora: Müller, 1775: 715 (part).

Errina Gray, 1835: 85.—Cairns, in press.

Porella: Gray, 1872: 482.

Labiopora Moseley, 1879: 476.

Errina (*Labiopora*): Hickson, 1912a: 879, 881.

Errina (*Eu-Errina*) Broch, 1942: 38.

Errina (*Errina*): Boschma, 1956: F102, figs. 83, 1a–b; 1963a: 337; 1964d: 284; 1965b: 21.

Diagnosis.—Colonies usually flabellate but may be slightly bushy; branches robust to delicate, usually round in cross section, may or may not anastomose. Coenosteal texture usually reticulate with irregularly shaped granules, but may be linear and have low, rounded granules; the sides of dactylopore spines are sometimes imbricate. Coenosteum white, orange, or pink. Gastro- and dactylopores usually randomly arranged on branch; however, gastropores often more abundant on anterior side, and sometimes seem to be aligned along the anterior or lateral branch edges. Gastropores may or may not bear an abcauline lip. Gastrostyles usually of medium H:W; however, they range from 1.6–26, the longer styles held in place by transverse tabulae. Styles lanceolate, usually vertically ridged, the ridges bearing simple and fused spines; a ring palisade is present in some species. Dactylopore spines shaped as grooved tubercles, the grooves predominantly directed away from the branch tip (adcauline). Walls of the dactylopore spines usually thick, such that the groove constitutes only one-third the width of the spine. Spines vary greatly in size from rudimentary to over 1 mm tall; small dactylopores also occur as slits, flush with the branch surface. Spines are often clustered and sometimes composite. No dactylostyles. Ampullae vary from internal to slightly submerged to fully superficial hemispheres.

Discussion.—*Errina* is similar to *Errinopsis*, differing primarily in having either grooved dactylopore spines or dactylopores flush with the surface, not apically perforate conical or composite dactylopores. *Errina* also has more openly branched colonies and cylindrical branches (vs. rectangular in cross section).

Occurrence.—Paleocene: Denmark; Recent: North Atlantic, off South Africa, ? off Mauritius, New Zealand Region, Subantarctic and Antarctic. 6–1,772 m.

Errina has been reported from Mauritius as *E. aspera mascarina* by Boschma (1965a); however, Zibrowius strongly doubts this distributional record, implying that this specimen probably was collected in the Mediterranean (personal communication, 1981).

Type Species.—*Millepora aspera* Linnaeus, 1767, by monotypy.

Errina aspera (Linnaeus, 1767)

Figure 11A–G

Millepora aspera Linnaeus, 1767: 1282–1283.

Madrepora aspera: Müller, 1775: 715.

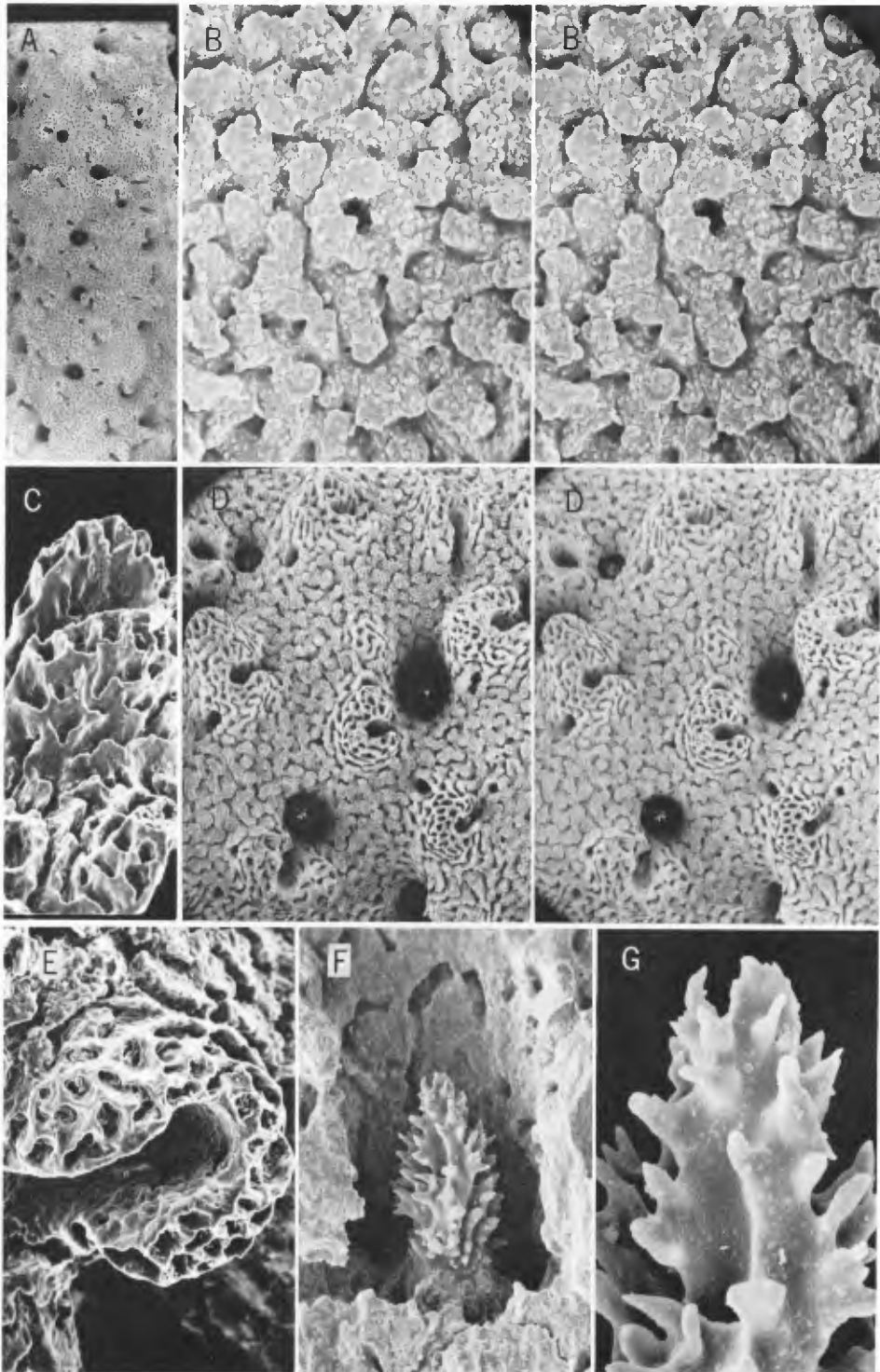
Errina aspera: Gray, 1835: 85.—Not Verrill, 1864: 46 (= *E. dabneyi*).—Not Pourtalès, 1867: 116 (= *E. dabneyi*).—Boschma, 1953a: 301–310, figs. 1–5; 1953b: 311–314; 1953c: 32–34; 1954: 143–149, pls. 1–3, text-fig. 1; 1957: 50–51; 1965a: 1–6, pl. 1, figs. 5–7, text-fig. 2.—Not Boschma and Lowe, 1969: 15 (= *E. gracilis*).

Errina (*Labiopora*) *aspera*: Hickson, 1912a: 888–889, pl. 95, fig. 6; ?1912b: 462.

?*Errina dabneyi*: Hickson, 1912b: 463–464, pl. 8, lower fig.

Errina (*Eu-Errina*) *aspera*: Broch, 1942: 38 (not pp. 40–42).

Errina (*Errina*) *aspera*: Boschma, 1956: F100; 1963a: 337.



Diagnosis.—Colonies predominantly flabellate with only a few branches out of the plane of the fan. Branches of moderate diameter; no branch anastomosis. Coenosteal texture reticulate: strips about 45 μm wide, bordered by broad, shallow grooves. Strips covered by irregularly shaped granules, the texture changing to fused imbricated platelets on the sides of dactylopore spines. Coenosteum white. Gastropores round, 0.15–0.20 mm in diameter, without lower lip. Gastrostyles lanceolate, 0.19–0.27 mm tall with an H:W = 1.5–3.1. Style ridged, the ridges bearing simple and fused spines. No supporting tabulae or ring palisades. Dactylopore spines up to 0.50 mm tall and 0.25 mm wide; adcauline groove about 50–60 μm wide or one-fourth to one-third the width of the spine. Dactylopore spines sometimes clustered. Some dactylopores are flush with the surface and measure about 160 \times 60 μm . Ampullae partially submerged in branch, 0.35–0.70 mm in diameter. Soft parts unknown.

Discussion.—Soft parts of *E. aspera* were not available for study, but tissue of the closely related species *E. antarctica* was studied by Broch (1942; 1951a). He observed that the gastrozooids have 3–6 tentacles, usually 4. The dactylozooids are dimorphic: the smaller ones corresponding to flush dactylopores are simple, whereas those corresponding to grooved dactylopore spines are adnate (Fig. 25C). Three to six male gonophores and one female gonophore occur per ampulla (Fig. 26G). The spadix is highly branched. To this I can add that rod-shaped nematocysts, measuring 12.0–13.5 \times 3.0–3.3 μm , are common in the coenosteal canals, dactylozooids, and ectoderm.

Sixteen species are attributed to *Errina* (Table 1). Representative specimens—usually the types—have been examined of all but two of these species. Additional species are likely to be described from the New Zealand region by the elevation of some of the four “facies” of *E. novaezealandiae*, and the description of new species by Zibrowius (personal communication, 1981).

The fossil species *E. irregularis* Nielsen, 1919 is herein transferred from *Errina* (*Inferiolabiata*) to *Errina* s.s., as Boschma (1964e: 294) thought might be the case. Examination of the types reveals typical clustered *Errina*-type dactylopore spines with adcauline grooves and a reticulate coenosteal texture.

Another species, *E. macrogastrea* Marenzeller, 1904, from the Galapagos, has, in the past, been tentatively assigned to *Errina* s.s. Both Hickson (1912a) and Broch (1942) recognized that this species has the dactylopore spines of *Errina* s.s. but the coenosteum of *Inferiolabiata* (*Lepidotheca* in this paper). Boschma (1964d: 285), giving less importance to coenosteal texture, assigned it to *Errina* s.s. In my opinion, *E. macrogastrea* remains an enigma, having linear-imbricate coenosteal texture (like all *Lepidotheca*, not like *Errina* s.s.) but adcauline grooved dactylopore spines (like all *Errina*, not like *Lepidotheca*). As Broch (1942: 39) stated, it holds a perplexing intermediate position between the two genera.

New Records.—CALYPSO, 6°00'W, 33°54'N, 110 m, 30 Aug. 1958, USNM 59931 and SME 1282.

Distribution.—Mediterranean Sea, off Morocco, ? off Cape Verde Islands. ?–110 m—? *E. aspera* is the only stylasterine known from the Mediterranean (Boschma, 1965a).

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Figure 11. *Errina aspera* (A–G, Calypso-“1282”; 33°54'N, 6°00'W, 110 m, 30 Aug. 1958): A, branch segment showing gastro- and dactylopores, $\times 10$; B, reticulate coenosteal texture, $\times 133$, stereo pair; C, E, dactylopore spines, $\times 113$, $\times 133$, respectively; D, gastropores and dactylopore spines, $\times 36$, stereo pair; F–G, gastrostyle, $\times 133$, $\times 465$, respectively.

Types.—Deposition unknown; probably lost.

Errinopora Fisher, 1931

Errina: Dall, 1884: 470 (part).

Errinopora Fisher, 1931: 397; 1938: 536.—Boschma, 1956: F102.

Protoerrina Broch, 1935: 59; 1936: 99–100.

Diagnosis.—Colonies uniplanar to slightly bushy, sometimes attached by a broad encrusting base. Branches round, elliptical, or platelike in cross section; usually robust with blunt or clavate tips; branch anastomosis sometimes occurs. Coenosteal texture reticulate to spongy, covered by round to irregularly shaped granules; coenosteum orange, yellow, pink, or white. Gastropores arranged in irregular vertical rows, short horizontal terraces, or randomly; no gastropore lips. Gastrostyles of medium H:W, bearing vertical or oblique ridges. Ridges bear tall, cylindrical, clavate spines, some of which are bifurcate. Gastropores do not have tabulae or ring palisades. Dactylopore spines robust, like those of *Errina* s.s., often fused laterally, forming chains flanking one or both sides of a line of gastropores, their grooves directed toward the pores. Often, towards the base of a colony, several dactylopores are positioned around an isolated gastropore, so as to closely resemble a cyclo-system. Sometimes there is no coordination of gastro- and dactylopores, the dactylopore spine grooves being uniformly abcauline. Dactylostyles well developed, expressed as a spiny ridge extending most of the length of the dactylopore spine. Ampullae superficial, sometimes clustered, and usually quite large; hemispherical or conical.

Discussion.—*Errinopora* represents an advance over *Errina* in two major features: the presence of a well-developed dactylostyle and a higher degree of gastro- and dactylopore coordination. A progression of this increased coordination is seen within the genus: the dactylopore spines of *E. nanneca* are primarily abcauline, slightly terraced but usually individualized, with little coordination with the gastropore; the dactylopore spines of *E. zarhyncha* are often fused and terraced but only on one side of a gastropore row; the dactylopore spines of *E. cestoporina* and *E. lobata* are terraced beneath rows of gastropores and have some reduced, adcauline dactylopore spines distal to the gastropores; finally, the dactylopore spines of *E. pourtalesii*, *E. stylifera*, and *E. latifundata* form fused terraces on both sides of gastropore rows and, on basal branches, rings of dactylopore spines encircle isolated gastropores, forming pseudocyclo-systems. It is this last character that led Broch (1936) to place *Protoerrina* (= *Errinopora*) in the Stylasterinae. Because of the similarities of *Protoerrina* with *Errina* and *Distichopora*, Broch (1936) went on to suggest that it was a primitive genus, and that the Stylasterinae was the most primitive of the subfamilies. However, I agree with Boschma (1960: 432–433) that the pseudocyclo-systems of *Errinopora* are not primitive but a result of ontogenetic reduction, the typical condition revealed at the branch tips, i.e., meandering rows of gastro- and dactylopores. I would therefore place *Errinopora* as the most advanced genus of Errininae (with the possible exception of *Gyropora*), with close affinities to *Stylaster* (Group A), forming a transition between these two subfamilies.

Occurrence.—? Paleocene: Denmark; Recent: North Pacific, off Tierra del Fuego. 49–518 m.

Type Species.—*Errina pourtalesii* Dall, 1884, by original designation.

Errinopora pourtalesii (Dall, 1884)

Figures 12A-I, 24I, 25K, 28D

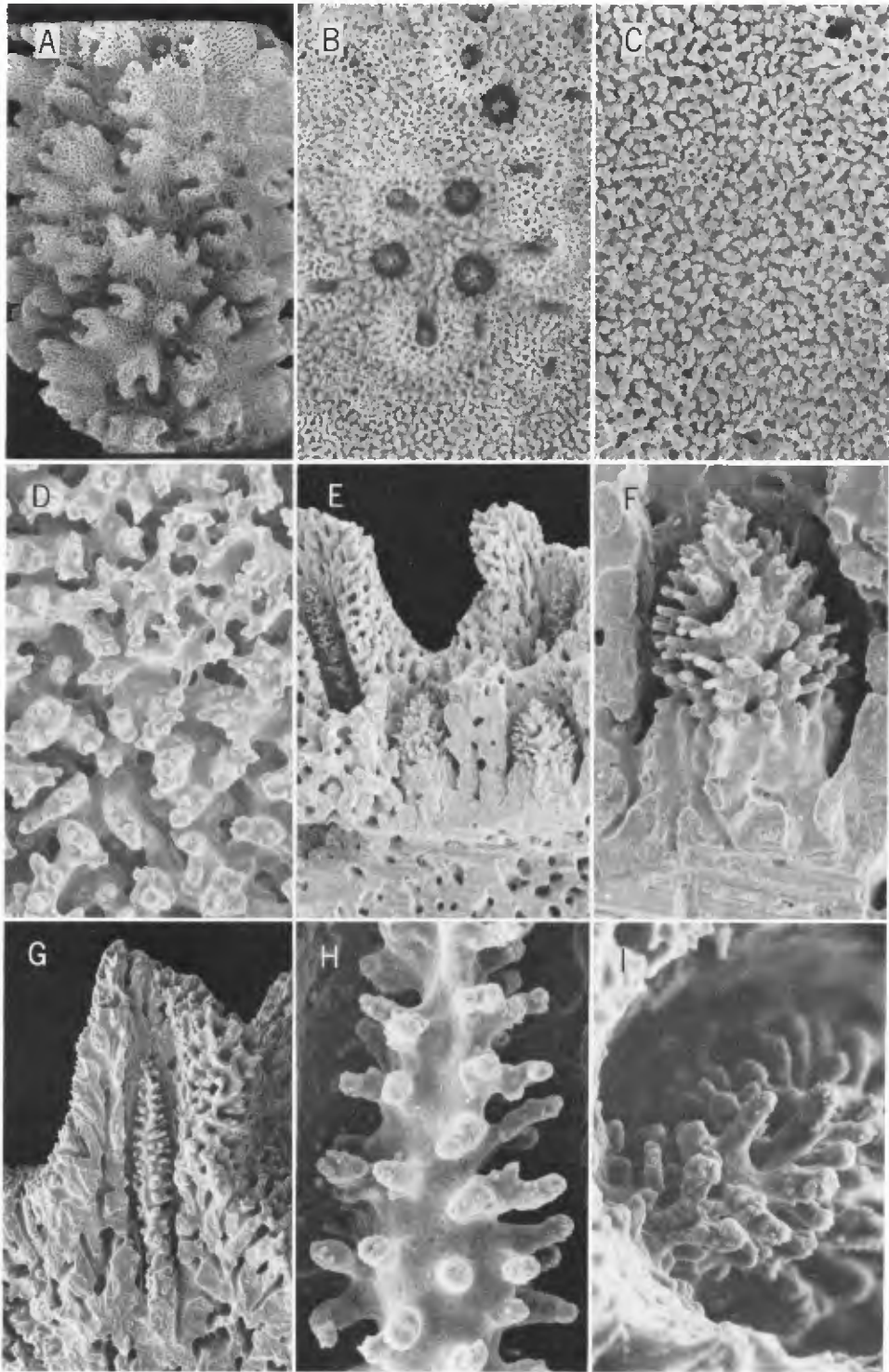
Errina pourtalesii Dall, 1884: 114-115.*Errinopora pourtalesii*: Fisher, 1931: 397-398, pl. 16, fig. 4, pl. 17, fig. 7; 1938: 541-542, pl. 65, fig. 2, pl. 66, fig. 2, pl. 70, fig. 1.—Boschma, 1956: F104; 1957: 58; 1960: 428-430.—Lowenstam, 1964: 382-383.

Diagnosis.—Colonies flabellate to slightly bushy, up to 18 cm tall and 26.5 cm broad, firmly attached by a broad encrusting base. Branches robust and round in cross section with blunt or slightly clavate branch tips; anastomosis rare. Distal branches 4-6 mm in diameter, basal branch diameters up to 1.5 cm. Coenosteum very similar to that of *Sporadopora dichotoma*: reticulate-granular, but very porous, with very short strips bordered by broad, deep channels. Coenosteum pinkish orange, except at branch tips and leading edges of basal encrustation, which are white. Gastropores round, 0.20-0.35 mm in diameter, flush with the surface. Gastropores arranged in irregular vertical to oblique rows of 5-20 pores near branch tips, becoming isolated into shorter rows or single pores toward the base. Illustrated gastrostyle 0.32 mm tall, 0.15 mm broad (H:W = 2.1) with broad, diagonal ridges. Spines on gastrostyle up to 39 μ m tall and 9-10 μ m in diameter, each terminating in a crown of several dozen small tufts, each tuft about 1.6 μ m in diameter. Dactylopore spines often fused laterally, their grooves invariably pointing toward the closest gastropore, resulting in long chains of dactylopore spines flanking a row of gastropores or, toward the base, 4-5 spines surrounding one or two gastropores: a pseudocyclosystem. Dactylopore spines up to 1.2 mm tall and 0.37-0.46 mm broad, the groove about 0.14 mm wide. Exterior of spines vertically ridged, the ridges about 20 μ m wide and separated by broad, shallow grooves also about 20 μ m wide. Inside each dactylopore spine there is another ridge opposite the slit, the dactylostyle, measuring about 60 μ m tall and 60 μ m broad, up to 0.67 mm long, bearing spines similar to those of the gastrostyle: 30 μ m tall, 10 μ m in diameter, with a tufted, clavate tip. Ampullae very spongy, about 0.50 mm in diameter.

Gastrozooids tentacles very small. Dactylozooids adnate, the free part overhanging an adjacent gastrozooid. Large nematocysts, 12.5-14.0 \times 4.1-5.0 μ m, are common in the ectoderm, especially the tissue of the dactylopore spines and around each gastropore. The dactylo- and gastrozooid tentacles bear smaller nematocysts measuring 7.0 \times 3.0-3.5 μ m. Another type, 10.0 \times 2.7 μ m, is rare in coenosteal canals. Gonophores not examined.

Discussion.—Six species are assigned to the genus *Errinopora* (Table 1) and another two, *Labiopora lobata* Nielsen, 1919 and *Errina porifera* Naumov, 1960, are tentatively assigned to the genus. *L. lobata* has a reticulate coenosteum and dactylopore spines arranged similar to those of *E. cestoporina*; unfortunately, few other characters are adequately preserved (e.g., the dactylostyle), making a confident generic placement unlikely. Specimens of *Errina porifera* were not examined; however, Naumov's description also indicates a dactylopore spine arrangement similar to that of *E. cestoporina*. But, without examining the type, it is impossible to rule out a placement in *Inferiolabiata* or even *Lepidopora* for *E. porifera*.

Errinopora intervacans Naumov, 1960, is herein synonymized with *E. styliifera*. The character used by Naumov to distinguish *E. intervacans* from other species—its hollow branches—is the result of a clonid sponge excavation (personal communication, K. Ruetzler, 1982). It is otherwise similar to *E. styliifera*.



The specimen described by Naumov (1960: 555) as *Errina antarctica* is an *Errinopora*, also very similar to *E. stylifera*.

Finally, the taxonomic position of "*Errina*" *cyclopora* Cairns, in press, is problematic. It has the gastro-dactylopore coordination and coenosteal texture of *Errinopora cestoporina* but differs primarily in lacking dactylostyles. *E. cyclopora* probably represents either an offshoot from *Errinopora*, involving the loss of dactylostyles, or occupies a transitional position between *Errina* and *Errinopora* before dactylostyles had developed.

Remarks.—*E. pourtalesii* is often infested with a spionid polychaete, which forms a U-shaped tube, each arm of which is closely adjacent and measures about 1 mm in diameter. Boring bivalves and barnacles also live within the coenosteum of this hydrocoral, both producing prominent galls.

New Records.—ALBATROSS-3160, 37°48'35"N, 123°12'40"W, 71 m, USNM 52254.

Distribution.—Known only from off central California. 49–183 m.

Types.—A small fragment (syntype) bearing the number 6853 is deposited at the USNM. Presumably the larger colony is at the MCZ. The former was examined. Representatives, usually types, of all of the species mentioned in the discussion, except *E. porifera*, have been examined by the author.

Gyropora Boschma, 1960

Gyropora Boschma, 1960: 423.

Diagnosis.—Colonies flabellate and sparsely branched; small colonies columnar. Branches thick, round to elliptical in cross section, and blunt. Coenosteum reticulate-granular and pale reddish purple. Gastropores linearly arranged in sunken, meandering, and bifurcating valleys up to 30–40 pores long; shorter valleys and isolated pores also occur. Gastrostyles longitudinally ridged and prominently spinose, of medium H:W. Dactylopore spines similar to those of *Errina* s.s. and *Errinopora* in construction; however, the spines are fused laterally, often having common walls between them. Grooves of spines always directed toward gastropores, forming a low, continuous perimeter on each side of a gastropore valley. A ring of dactylopore spines encircles isolated gastropores, producing pseudocyclostystems. No dactylostyles. Ampullae not observed.

Discussion.—*Gyropora* is considerably more advanced than *Errina* in regard to its gastro-dactylopore coordination. It is similar to *Errinopora* in its gastrostyle structure and dactylopore spine orientation, but is more specialized in having sunken rows of gastropores, reduced dactylopore spines, and, in most cases, common dactylopore spine walls; *Gyropora* also differs in lacking dactylostyles. I agree with Boschma's (1960) placement of *Gyropora* in the Errininae. In my opinion, it is the most specialized genus in the subfamily (because of its highly coordinated gastro- and dactylopores) but probably represents an evolutionary cul-de-sac; the closely related *Errinopora* seems to be the transition between the Errininae and Stylasterinae.

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Figure 12. *Errinopora pourtalesii* (A, E–I, Albatross-3160: 37°49'N, 123°13'W, 71 m, 22 Mar. 1890; B–D, Albatross-3159: 37°47'N, 123°10'W, 49 m, 22 Mar. 1890): A, branch segment, ×12; B, a short pore row near base of colony, ×23; C–D, coenosteal texture, ×33, ×133, respectively; E, branch cross section revealing gastro- and dactylostyles, ×40; F, gastrostyle, ×133; G–I, dactylostyle, ×50, ×350, ×430, respectively.

Occurrence.—Known only from off Cape Agulhas, South Africa. 22 m.

Type Species.—*Gyropora africana* Boschma, 1960, by original designation.

Gyropora africana Boschma, 1960
Figures 13A–H, 24J, 25L

Gyropora africana Boschma, 1960: 423–433, pl. 1, figs. 1–9, text-fig. 1a–d. — Vervoort and Zibrowius, 1981: 26–27.

Diagnosis.—Colonies up to 2.9 cm tall and 2.7 cm broad; terminal branches 5.5–6.5 × 4.0–4.5 mm in diameter, basal branch up to 13.5 mm in greater diameter. Coenosteal strips 0.10–0.11 mm wide, flat to slightly convex, and separated by deep slits about 15–20 μm wide. Gastropores round, 0.20–0.41 mm in diameter, linearly arranged in meandering valleys sunken about 0.7 mm below the coenosteal surface. Toward the branch tips the valleys sometimes anastomose, forming irregularly shaped “islands” of coenosteum. Toward the base of colonies the space between valleys is much broader and the valleys shorter, with less branching. Gastrostyles lanceolate with a blunt tip; the H:W ranges from 1.46–4.2; height of style rarely more than 0.45 mm. Gastrostyle spines up to 70 μm long and 15 μm in diameter, terminating in a clavate tip of crystalline tufts, each about 2.8–3.0 μm in diameter. Dactylopore spines raised only slightly (0.1–0.2 mm) above the coenosteum; however, their grooves (“dactylotomes”) extend to the bottom of the gastropore valley, or about 0.7–0.8 mm in total length. Width of groove about 0.15 mm; width of dactylopore spine wall between grooves as much as 0.50 mm when the walls are individualized, as little as 0.15 mm when the wall is common.

Dactylozooids adnate, as in *Errinopora* and *Errina*. Large nematocysts, measuring 19.0–21.0 × 7.0–8.0 μm, are common in coenosteal ectoderm and coenosteal canals; smaller nematocysts, 7.0–7.3 × 3.0–3.5 μm, occur in high density in gastro- and dactylozooid tentacles.

Discussion.—*Gyropora* is a monotypic genus.

New Records.—Off Cape of Good Hope, South Africa, depth unknown (found in J. S. Gardiner's coral collection identified as *Distichopora irregularis* (personal communication, H. Zibrowius, 1981)), BM 1977.8.5.1.

Distribution.—Off Cape of Good Hope. 22 m.

Types.—The lectotype (as chosen ^{by} Vervoort and Zibrowius, 1981) is deposited at the RMNH (Coel. 13749) and has been examined by the author. The location of the paralectotype is unknown and may be lost.

Subfamily Adeloporinae Cairns, 1982

Diagnosis.—Gastro- and dactylopores not arranged in cyclo systems. Gastropores occur at branch tips and axils, each gastropore covered by a hinged operculum.

Adelopora Cairns, 1982

Adelopora Cairns, 1982a: 71.

Figure 13. *Gyropora africana* (A–H, off Cape of Good Hope, BM 1977.8.5.1): A, colony, ×1.25; B–C, top and side of a distal branch, ×13, ×15, respectively; D–E, pore rows, ×27, ×33, respectively; F, reticulate coenosteal texture, ×33; G, gastrostyle spines, ×520; H, gastrostyle, ×83, stereo pair.