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### ECTOPROCT AND ENTOPROCT TYPE MATERIAL:

REEXAMINATION OF SPECIES FROM NEW ENGLAND AND
BERMUDA NAMED BY A. E. VERRILL, J. W. DAWSON
AND E. DESOR

FRANK J. S. MATURO, JR.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF FLORIDA GAINESVILLE, FLORIDA 32601

THOMAS J. M. SCHOPF

Department of Geological Sciences, Lehigh University Bethlehem, Pennsylvania 18015

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### SEP 6 968 ECTOPROCT AND ENTROPROCT TYPE MATERIAL

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A. E. Verrill, J. W. Dawson, and E. Desor named 23 species of North American east coast ectoprocts and entoprocts prior to 1902. Chiefly from lack of illustration, the majority of these have been misunderstood in the literature. We have found material leading to a better understanding of 15 of these species in collections of the Peabody Museum of Natural History, Yale University, the U.S. National Museum, and the American Museum of Natural History. The following ectoproct species are described (original names): Amathia goodei Verrill, Bugula cucullata Verrill, Bugula decorata Verrill, Bugula flexilis Verrill, Bugula (Caulibugula) armata Verrill, Bugulella fragilis Verrill, Cellularia turrita Desor, Discopora nitida Verrill, Escharina porosa Verrill, Gemellaria willisii Dawson, Hippoporina verrilli Maturo and Schopf, Hippothoa expansa Dawson, Lepralia americana Verrill, Lepralia plana Dawson, Porellina stellata Verrill. One entoproct, Barentsia timida Verrill, is described,

The coefficient of variation was determined for standard dimensional features. Data collected support Cheetham's statistical verification that the most useful dimensional features for taxonomic purposes are ovicell length and width, zooid length, and primary orifice length and width. Length of adventitous avicularia and zooid width are the most variable of the traits measured, particularly in encrusting forms which also have extensive secondary calcification.

#### INTRODUCTION

Nineteenth century American marine biologists considered the fauna of the northern part of the east coast continental shelf an extension of the European fauna, and accordingly used chiefly European species names (Packard, 1863; Verrill, 1874). In the summer of 1964, Maturo had the opportunity to study major ectoproct type collections at the British Museum (Natural History), London, and the Naturhistoriska Riksmuseet, Stockholm. He concluded that faunal differences between American and European ectoprocts may be greater than was, or is, generally realized. If this is so, then new species names introduced by early North American workers, several of which have since been placed in

synonymy with European species, become particularly important. However, many early descriptions are less than complete by present standards and type material was not always illustrated (Table 1), thus making uncertain the identity of early-named species.

Prominent among early invertebrate zoologists whose work was of immediate interest to both of us was A. E. Verrill (1839-1926), who named 15 ectoproct and 1 entoproct species. At the kind invitation of the Peabody Museum of Natural History, Yale

TABLE 1. Summary of papers published by nineteenth-century workers having descriptions of new ectoproct and entoproct species collected between the Straits of Florida and the Gulf of St. Lawrence. Species described by de Pourtales (1867) were figured by Smitt (1872-1873).

| PUBLI- |              |         | NO. NEW |   |
|--------|--------------|---------|---------|---|
| CATION |              | NO. NEW | SPECIES |   |
| DATE   | AUTHOR       | SPECIES | FIGURED | GEOGRAPHIC LOCATION OF COLLECTION                   |
| 1848   | Desor        | 3       | 0       | Nantucket shoals, Nantucket, Mass.                  |
| 1853   | Stimpson     | 11      | 7       | Grand Manan Island                                  |
| 1855   | Leidy        | 4       | 4       | Rhode Island; New Jersey                            |
| 1859   | Dawson       | 3       | 0       | Gaspé Peninsula, Quebec                             |
| 1863   | Packard      | 10      | 4       | Caribou Island, Labrador                            |
| 1865   | Dawson       | 1       | 0       | Sable Island, Nova Scotia                           |
| 1867   | Packard      | 2       | 2       | Chateau Bay, Labrador                               |
| 1867   | de-Pourtales | 7       | 7       | Straits of Florida                                  |
| 1872   | Verrill      | 1       | 1       | Long Island Sound; Vineyard Sound;<br>New Jersey    |
| 1872   | Smitt        | 4       | 4       | Florida Straits                                     |
| 1873   | Smitt        | 29      | 29      | Florida Straits                                     |
| 1873   | Verrill      | 2       | 0       | Long Island Sound; Vineyard Sound;<br>New Jersey    |
| 1875a  | Verril1      | 3       | 3       | Long Island Sound; Vineyard Sound;<br>Gulf of Maine |
| 1875b  | Verrill      | 1       | 1       | Martha's Vineyard, Mass.                            |
| 1879b  | Verrill      | ī       | 0       | Gulf of Maine                                       |
| 1879d  | Verrill      | 3       | 0       | Maine; Gulf of Maine                                |
| 1879e  | Verrill      | 2       | 0       | Long Island Sound to Nova Scotia                    |
| 1888   | Hincks       | 5       | 5       | Gulf of St. Lawrence                                |
| 1889   | Hincks       | 1       | 1       | Gulf of St. Lawrence                                |
| 1900   | Verrill      | 2       | 1       | Bermuda   |
| 1901   | Verrill      | 1       | 0       | Bermuda   |
|        |              |         | _       |   |
|        | Totals       | 96      | 69      |   |

University, we spent four days in May, 1966, examining its ectoproct collections in an attempt to locate Verrill's type material. The bulk of the dry specimens in the collection consists of material collected by Verrill. Additional search was made of ectoproct collections of the U.S. National Museum by Maturo and alcohol collections of the Peabody Museum by Dr. Willard D. Hartman, Yale University. George Verrill (1958:74) reported that he gave his father's notes, manuscripts and drawings to the American Museum of Natural History (New York City). Schopf sorted that part of the material that pertained to ectoprocts and found unpublished illustrations of species that Verrill had named. In sum, type lots or unpublished illustrations of type material were located for 10 ectoproct and 1 entoproct species named by Verrill.

Unexpectedly, we also located type lots of three of the four species named by J. W. Dawson (1820-1899) and one of the three species named by E. Desor (1811-1882). This material was found in the dry collections of the Peabody Museum. The purpose of the present paper is to redescribe and illustrate the 15 species for which we have type material or unpublished illustrations (Table 2).

Ours was not the first attempt to locate Verrill's type materials of ectoprocts and entoprocts but has been the most successful. In the archives of the Division of Echinoderms, U. S. National Museum, there is correspondence on this subject by J. E. Benedict and Mary Rathbun, who had been sent by the Smithsonian Institution in 1909 to assist Verrill in the division of that part of his collections which were gathered by government agencies, chiefly the U. S. Fish Commission. This division was according to the terms of an agreement between Verrill and the Smithsonian which provided that all unique specimens and a first share of the type series were to be returned to the Smithsonian. Both Benedict and Rathbun deplored the fact that Verrill had not clearly identified the significant specimens and thus they were only partly successful in retrieving the type collection.

The eight species that were named by Verrill, Dawson or Desor but which we were unable to locate and hence about which we can offer no new information are: Alcyonidium ramosum Verrill, 1872; A. rubrum Verrill, 1879; Cellularia densa Desor, 1848; Hippothoa reversa Verrill, 1875; Lepralia belli Dawson, 1859;

Membranipora tenuis Desor, 1848; Vesicularia armata Verrill, 1873; and V. dichotoma Verrill, 1873.

We have chosen to consider each species under its original designation and in alphabetical order. We believe this will facilitate the practical usage of this study since most workers will likely approach it with an original name from the literature and seek our analysis of the species. Our nomenclatorial decisions are summarized in Table 2. The new name is also given after the synonymy under "Present authors' designation."

Table 2. Listing of original and revised species names as used in the paper. Barentsia timida is an entoproct, the rest are ectoprocts.

| ORIGINAL DESIGNATION                         | PRESENT DESIGNATION                                  |
|--|--|
| Amathia goodei Verrill, 1901                 | Zoobotryon verticillatum<br>(delle Chiaje) 1828      |
| Barentsia timida Verrill, 1900               | No change  |
| Bugula cucullata Verrill, 1879               | Bugula harmsworthi Waters, 1900                      |
| Bugula decorata Verrill, 1879                | Dendrobeania decorata<br>(Verrill) 1879              |
| Bugula flexilis Verrill, 1875                | Kinetoskias smitti Danielssen, 1868                  |
| Bugula (Caulibugula) armata<br>Verrill, 1900 | Caulibugula armata Verrill, 1900                     |
| Bugulella fragilis Verrill, 1879             | No change  |
| Cellularia turrita Desor, 1848               | Bugula turrita (Desor) 1848                          |
| Discopora nitida Verrill, 1875               | Parasmittina nitida (Verrill) 1875                   |
| Escharina porosa Verrill, 1879               | (part) Hippoporina porosa<br>(Verrill) 1879          |
|  | (part) <i>Hippoporina verrilli</i> Maturo and Schopf |
| Gemellaria willisii Dawson, 1865             | Eucratia loricata (Linnaeus) 1758                    |
| Hippothoa expansa Dawson, 1859               | No change  |
| Lepralia americana Verrill, 1875             | Hippoporina americana<br>(Verrill) 1875              |
| Lepralia plana Dawson, 1859                  | Myriozoella plana (Dawson) 1859                      |
| Porellina stellata Verrill, 1879             | No comments  |

#### ORGANIZATION

Remarks on each of the redescribed species are organized under the topics listed below. Hippoporina verrilli is newly described under the topics: synonymy, type, additional material, diagnosis, description, measurements and remarks.

SYNONYMY. Listings of the synonymy include chiefly those papers that describe or illustrate a species. A few additional citations are included when we were able to verify the identification.

### PRESENT AUTHORS' DESIGNATION.

TYPE. Type designation, current museum member and data from original label(s). Abbreviations YPM, USNM, and BM refer to Peabody Museum of Natural History, Yale University, U. S. National Museum, and the British Museum.

ADDITIONAL MATERIAL. Type designation, current museum number and data from original label(s). Paralectotypes, if any, are listed here.

ORIGINAL DESCRIPTION. The quotation of the original description.

SUBSEQUENT DESCRIPTION. The quotation of a more complete description of the species from a subsequent paper by the original author.

ADDITIONAL DESCRIPTION. Our descriptive remarks.

MEASUREMENTS. The following abbreviations are used:

Lz = zooid length. = zooid width 1z

Lo = primary orifice length.

including sinus. = primary orifice width. 10

Lfm = frontal membrance

length.

lfm = frontal membrane

width.

lov = ovicell length.

Lov = ovicell width.

Lav = avicularium length

lay - avicularium width.

Lkz = kenozooid length.

lkz = kenozooid width.

Lp = pedicel length. lp = pedicel width.

Lm = musclium length.

lm = musclium width. Lcx = calvx length.

lcx = calyx width.

Unless otherwise indicated, the measurement is the maximum dimension in question. Zooids that were part of a bifurcation, whether erect or in encrusting forms, were not used. All measurements are in millimeters. Dimensions are reported in the following form (after Cheetham, 1966): abbreviation of item measured; number of specimens measured; mean; standard deviation; observed range. For example, Lz (15) 0.447 (0.028) mm., 0.40—0.51 mm. means that 15 measurements were made of zooid length, that the mean was 0.447, the standard deviation 0.028, the range of measured values from 0.40 to 0.51 millimeters.

REMARKS. Our discussion of items of nomenclatorial or taxonomic interest and other interpretations.

### **OUANTITATIVE DATA**

We have calculated corrected coefficients of variation ( $V_e$ ) for the measurements made on our specimens (Table 3). This statistic has been shown by Cheetham (1966) to be useful in evaluating the constancy of various taxonomic characters. In addition, mean values were used to compare traits in two populations in order to help determine whether the populations in question should be considered separate taxa.

The coefficient of variation is expressed by the formula,  $V = \frac{100s}{\bar{x}}$ , where V = coefficient of variation, s = standard deviation and  $\bar{x} =$  mean. This is corrected for small sample size and is given as,  $V_c = \frac{V(4N+1)}{4N}$ , where  $V_c =$  corrected coefficient of variation, and N = sample size. A  $V_c$  less than 10 indicates a relatively constant character, one in which the standard deviation is less than 10 per cent of the mean value (see Simpson, Roe and Lewontin, 1960).

Mean values can be compared by the following formula to determine the distinctiveness of the variation in two populations. If populations A and B are 90 per cent distinct from each other for the dimension in question, then  $(|\tilde{x}_A - \tilde{x}_B|)$  will be more than 0.128  $(\tilde{x}_A + \tilde{x}_B)$  (see Cheetham, 1966).

Workers comparing populations from other areas with species described herein should be able to make better value judgments

Corrected coefficients of variability of linear dimensions of Ectoprocta and Entoprocta. TABLE 3.

|      |                            | Lz         | lz   | ន    | 10                | Lov     | lov   | Lav  | lav       | Lfm        | Ifm      |
|------|----------------------------|------------|------|------|-------------------|---------|-------|--|-----------|------------|----------|
| -    |                            | 36.3       | 300  |      |                   | 2.70    | 3.86  | (5.69(a)                                   | ĩ         | 1          | ł        |
| -    | Bugula cucullara           | 07.0       | 2.30 | ł    | l                 | 0//0    | 2.00  | (2.74(0)                                   | Î         |            |          |
| ٠i   | Bugula decorata            | 5.89       | 9.44 | ı    | 1                 | 5.82    | 3.78  | 9.81                                       | I         | !          | I        |
| 33   | Bugula flexilis            | 3.83       | 10.2 | 1    | ı                 | 4.87    | 2.08  | 8.90                                       | 12.2      | 1          | 1        |
| 4.   | Bugulella fragilis         | 2.23       | 3.32 | ì    | 1                 | 4.11    | 3.85  | 16.8                                       | 8.73      | 7.41       | 5.40     |
| 5.   | Caulibugula armata         | 6.11       | 6.17 | ١    | 1                 | I       | 1     | 7.32                                       | 1         | I          | 1        |
| 9    | Cellularia turrita(c)      | 6.37       | 7.93 | l    | ı                 | 1       | 1     | 7.04                                       | ı         | I          | I        |
| 7a.  |                            | 14.2       | 10.8 | 3.47 | 8.34              | 1       | I     | 10.7                                       | 1         | ı          | 1        |
| 7b.  | Discopora nitida(e)        | 13.0       | 12.0 | 6.47 | 6.42              | 6.70    | 10.0  | 10.4                                       | 1         | 1          | I        |
| 7c.  | 7c. Discopora nitida(f)    | 11.9       | 17.1 | 6.84 | 6.84              | 4.65    | 4.66  | 9.16(k)<br>7.04(l)                         | 11        | 1          | ١        |
|      |                            |            |      |      |                   |         |       | (8.27(m)                                   |           |            |          |
| οć   | Escharina porosa           | 14.0       | 11.8 | 4.93 | 9.50              | 4.71    | 8.84  | 1  | I         | 1          | I        |
| 9.   | Gemellaria willisii        | 3.60       | 7.34 | l    | ı                 | ı       | I     | I  | I         | 4.12       | 7.34     |
| 10a. | Hippoporina verrilli(g)    | 8.55       | 13.9 | 6.03 | 5.93              | 5.22    | 6.75  | 1  | I         | ١          | ١        |
| 10b. | Hippoporina verrilli(h)    | 4.91       | 17.3 | 7.40 | 5.50              | 3.86    | 4.01  | 7.47                                       | ı         | 1          | I        |
| 11a. | Hippothoa expansa(i)       | 6.34       | 11.1 | 11.3 | 8.61              | I       | 1     | l  | 1         | 1          | ١        |
| 11b. | Hippothoa expansa(j)       | 4.24       | 2.32 | 12.7 | 13.4              | I       | I     | i  | ı         | l          | 1        |
| 12.  | Lepralia americana         | 8.50       | 87.9 | 3.44 | 3.38              | 3.38    | 5.25  | Ī  | 1         | I          | 1        |
| 13.  | Lepralia plana             | 9.25       | 7.96 | 9.63 | 8.88              |         | I     | 16.0                                       | 1         | I          | I        |
|      |                            | $\Gamma$ b | lp   | Гm   | П                 | Ħ.      | Lp:Lm | Lcx  | lcx       |            |          |
| 4.   | Barentsia timida           | 29.4       | 1.56 | 23.9 | 14.0              | 22.9    | 34.5  | 5.58                                       | 50.6      |            |          |
| F00  | FOOTNOTES: (a) Large form. |            |      | (f)  | (f) Morphotype B. | type B. | (k)   | (k) Pointed form, associated with orifice. | rm, assoc | iated with | orifice. |

 Pointed form, associated with ovicell.
 Spatulate form. Holotype. Nonfertile zooids. Fertile zooids. Paratype. 9**333** Holotype. Morphotype A, usually growth form. Morphotype A, nodule. Small form. <u>මෙමෙම</u>

by utilizing these calculations. We have found them helpful in the following two examples.

Two morphologically distinct groups that were considered possibly distinct species are those designated morphotype A and B of Discopora nitida. The difference between the mean values of the orifice width is (0.122-0.111)=0.011, whereas 0.128 (0.122+0.111) is 0.029. Hence the groups are less than 90 per cent distinct in this relatively stable character and inclusion of them in the same species is supported.

Two other morphologically distinct groups that were considered possibly distinct are the larger and smaller forms of *Escharina porosa* of Verrill. The difference in mean values of orifice length for these populations is 0.046 and of orifice width is 0.050. The calculation for 10 per cent overlap in these characters is 0.036 and 0.037, respectively. Hence these groups are more than 90 per cent distinct for the features tested and this supports separation of them as distinct species.

Finally, Cheetham (1966) used  $V_e$ 's to generalize about the reliability of characters for taxonomic purposes; our more limited data (Table 4) mostly support his conclusions. We consider any trait with a  $V_e$  of less than 10 in a given species as reliable for that species (or larger taxon). From comparison of  $V_e$ 's and mode of growth in various species, it is clear that characters that in encrusting forms are subject to great modification by secondary calcification or substrate effects may in erect forms be considerably less modified, have a low  $V_e$ , and be taxonomically quite useful.

TABLE 4. Relative variability of linear dimensions where measured in six or more species.

|    |                                   | NO. SPECIES | NO. SPECIES $V_c < 10.0$ | %    |
|----|-----------------------------------|-------------|--------------------------|------|
| 1. | Length of ovicell                 | 8           | 8                        | 100  |
| 2. | Width of ovicell                  | 8           | 7                        | 87.5 |
| 3. | Length of zooid                   | 13          | 11                       | 84.6 |
| 4. | Height of primary orifice         | 6           | 5                        | 83.4 |
| 5. | Width of primary orifice          | 6           | 5                        | 83.4 |
| 6. | Length of adventitious avicularia | 8           | 5                        | 62.5 |
| 7. | Width of zooid                    | 13          | 8                        | 61.6 |

# Systematic Zoology Amathia goodei Verrill, 1901 Figure 7A.

Hydra verticillata delle Chiaje, 1828:203. Amathia goodei Verrill, 1901:329. not Amathia goodei Verrill: Osburn, 1914:219. Zoobotryon verticillatum (delle Chiaje): Maturo, 1957:25, fig. 13.

PRESENT AUTHORS' DESIGNATION. Zoobotryon verticillatum (delle Chiaje, 1828).

IYPE. Holotype of Amathia goodei Verrill: YPM 2894a-b, "Amathia goodei, Bermuda, 1876, [G. B.] Goode coll[ector], fig[ure]d type." In handwriting of A. E. Verrill. YPM 2894a is the basic lot; YPM 2894b is the figured specimen.

ORIGINAL DESCRIPTION. "This forms large, intricately branched clusters, 4 or 5 inches high and broad, with the branches thick, soft, and flaccid, and more or less anastomosing, often 2 to 3 mm in diameter. The zooids are numerous, arranged in large, dense, elongated clusters, composed of several close rows, which often nearly or quite surround the stem, and extend for some distance below the nodes, but are scarcely at all spiral (coll. of G. Browne Goode)."

ADDITIONAL DESCRIPTION. The colony commonly branches dichotomously or trichotomously. Zooid rows are mostly parallel, two rows on each side of the stolon as in typical *Zoobotryon*.

REMARKS. Osburn (1914, 1940) seems the only author to have discussed *Amathia goodei*. In 1914, he indicated that "several colonies, growing attached to piles, seem to belong to this species." We have examined this material and it is indeed an *Amathia*, but quite distinct from Verrill's "*Amathia*." In 1940, Osburn assigned *A. goodei* to *A. brasiliensis* Busk, 1886, and wrote "... but I must confess that I do not understand Verrill's statement in regard to the zooids 'in large dense, elongated clusters composed of several rows'." It is now clear that this confusion arose from the acceptance of Verrill's generic assignment. In all important respects, the type of *A. goodei* is like the widespread tropical species *Zoobotryon verticillatum* (delle Chiaje, 1828) and is here placed in synonymy with that species.

Although the label on Verrill's specimen (YPM 2894a-b) says "figd. type," to our knowledge no figure was ever published. We were also unable to find a drawing or photograph among the Verrill documents at the American Museum.

### Barentsia timida Verrill, 1900 Figures 1B-E, 7B-C.

Barentsia timida Verrill, 1900:594, pl. 70, fig. 4.

? Barentsia discreta (Busk): Osburn, 1912a:214, pl. 18, figs. 5, 5a.

? Barentsia discreta (Busk): Osburn, 1944:9-10, fig. 2.

PRESENT AUTHORS' DESIGNATION. No change.

TYPE. Holotype (colony) of Barentsia timida Verrill: YPM 2895a-c, "Barentsia timida V[errill]. Bermuda Exped. 1898. Types." In handwriting of A. E. Verrill. YPM 2895a is dried material; YPM 2895b is material restored in detergent; YPM 2895c is the restored, figured material.

ORIGINAL DESCRIPTION. "A large species forming extensive groups, connected by slender round stolons, that usually branch at right angles, from under the base of each zooid.

"Stem not very long, varying in length from three to five times as long as the height of the body, its basal portion, for a length equal to about the height of the body, much enlarged, cylindrical, tapering abruptly to the slender portion, and containing a large deflector muscle; above this the slender stem gradually increases in size distally; one or two annulations at the base of the body; the enlarged basal portion is covered with numerous fine annulations; the slender part appears punctate, owing to small tubular extensions of the lighter yellow inner layer, but these usually do not cause any elevations of the exterior.

"Body cup-shaped or wide campanulate. Tentacles numerous, long,

slender, curled in contraction.

"Height of stems, 4-6 mm; of basal enlargement, 0.75 to 0.90 mm; its diameter, about 0.3 mm; height of body, 1 mm; its diameter, 0.8 to 1 mm. "On under side of stones, on sponges, corallines, ascidians, etc., at low-

tide, common.

"This species is closely allied to *B. discreta* (Busk), Voy. Challenger, xvii, p. 44, pl. x, figs. 6-12. The latter has, however, a shorter and more strongly annulated basal cylinder and also several annulations of the stem below the base of the cup; its tentacles are only 12 in number."

ADDITIONAL DESCRIPTION. Type material consists of approximately three hundred individuals that encrust another organism, possibly a tunicate, and calcareous polychaete tubes.

Our observations of *Barentisa timida* agree well with the original description of Verrill (1900) differing chiefly in that the species does not seem as large as Verrill indicated. He recorded specimens with a length of 4-6 mm for combined pedicel and musclium whereas the same parts in specimens we have observed have a maximum total length of 4.3 mm.

Of 21 specimens examined in detail, one had a joint in the pedicel (Fig. 1D). Ten to 15 per cent more pores or conical

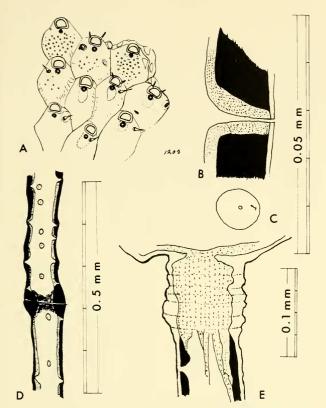


FIGURE 1. A. Porella stellata, sketch by A. E. Verrill. American Museum of Natural History, Department of Living Invertebrates; X26. Sketch bears designation "Porina sp. nov." Number 1203 is Verrill's reference number. B-E. Barentsia timida, YPM 2895c; part of holotype colony. B. Section through pedicel wall at pore. Muscle and other tissues are stippled; inner layer of pedicel is black; outer layer is white. C. Frontal view of pedicel pore. Inner circle is diameter of pore at the surface; outer circle is approximate diameter of pore at the inner pedicel layer. D. Section of wall of pedicel showing area of jointing. Muscle and other tissues are stippled; outer and inner walls of pedicel are black; pores in the pedicel wall indicated in plan view by circles with dots (pore exit point) in central part. Note that the inner layer of the pedicel thins and the outer layer thickens at the joint. E. Section of pedicel at junction with calyx (i.e., the region of the "peduncle"). Muscle and other tissues are stippled. Inner layer of pedicel is black; outer layer is white. Note that inner layer of pedicel disappears below junction with calyx.

depressions occur in the 0.3 mm immediately above the joint than for a comparable distance elsewhere on the pedicel.

The pedicel wall is composed of two layers, the inner one normally being at least three to four times as thick as the outer one (Fig. 1B, E). The inner layer is yellowish and the outer layer is transparent. At the joint, the inner layer is two to three times its thickness in the remainder of the pedicel. At the upper end of the pedicel at the junction with the calyx, the inner pedicel layer disappears (Fig. 1E) and the outer pedicel layer becomes two to four times its normal thickness. The outer layer of the two pedicel layers is apparently the more flexible because when the inner layer is absent the outer layer has a few irregularly developed annulations.

The interior of the area of the pedicel immediately below the junction with the calyx (i.e., the region known as the peduncle), is filled with a muscular tissue that divides into strands a short distance below the bottom of the peduncle. Some muscle strands continue basally parallel to the sides of the pedicel and other strands cross the pedicel cavity.

The calyx bears 17(?) to 19 tentacles (two counts).

Particular attention was given to the presence of conical depressions in the inner walls of the pedicel because of their possible significance in classification (as suggested by Johnston and Angel, 1940), and because their function is not known. Harmer (1915: 30) thought that they may be "vestigial spines" and Marcus (1937) suggested that they may serve a sensory function.

When viewed frontally and laterally at approximately 1500X, the conical depressions can be resolved into true pores. In frontal view, the circular orifice of the pore is readily seen (Fig. 1C-D). In lateral view (Fig. 1B), it was not always certain that the conical depressions continued to the exterior, but in the best optical sections, the small (less than 10 micron) pathway from the easily visible conical depression to the exterior was seen. Busk (1886) was likely correct when he wrote that true pores occur in the pedicel of *Barentsia discreta*.

The pores might function as places for exchange of gases between the pedicel cavity and surrounding sea water. This exchange would help to provide oxygen to muscular tissue in the pedicel, possibly also to the musclium and peduncle. Oka (1895)

mm.

Lp

lcx

found that different cell types line the perforate and imperforate portions of the pedicel of Barentsia misakiensis. If present in B. timida, these could not be seen because of its poor state of preservation. The functional interpretation of the conical depressions and pores needs to be determined from live material.

MEASUREMENTS. Dimensions of the holotype, YPM 2895b, were taken chiefly from larger, presumably mature individuals. The specimens, found in dried condition, were restored by soaking for a few hours in a weak sodium triphosphate solution. Material was then transfered to formalin, then to alcohol, and all dimensions were taken from specimens in 70 per cent alcohol. Measurements of the calyx are uncertain.

(20) 2.56 (0.77) mm., 1.26 - 3.56 mm.

```
(21) 0.065 (0.010) mm., 0.042 — 0.083 mm.
lp
                 (21) 0.76 (0.18) mm., 0.48 — 1.20 mm.
Lm
                 (20)\ 0.29\ (0.040)\ \text{mm.},\ 0.24\ -0.36\ \text{mm.}
lm
Total height of
  pedicel and
  musclium
                 (19) 3.40 (0.77) mm., 2.04 — 4.34 mm.
Ratio pedicel
  height to
  musclium height (19) 3.52 (1.20) mm., 1.8 — 6.8
                                                        mm.
                 (6) 0.56 (0.030) mm., 0.54 — 0.60
Lcx
                                                        mm.
                            (0.065) mm., 0.28 - 0.45
```

(6) 0.33

REMARKS. Unusually high V 's of the commonly measured features of entoprocts are suggested by data presented here for Barentsia timida (Table 3). The pedicel height, musclium height, pedicel to musclium ratio, and total height each had a V<sub>c</sub> of greater than 20 though the specimens measured were part of the same colony. Accordingly one can expect that these dimensions have little taxonomic value. The preservation of the material was not good and this may have introduced a non-biological variation. However, this would be most apparent in soft tissues, such as the calyx, and possibly the musclium width, which nevertheless appeared to be the dimensional features of greatest taxonomic interest.

In the course of determining if Barentsia timida is a valid

species, we have surveyed the 14 species of *Barentsia* in which pores (the conical depressions referred to above) occur in the pedicel. These species are divided into four groups on the basis of whether or not pores occur throughout the length of the pedicel and on the degree to which branching and muscular joints are developed.

- Group A. The species in which pores occur throughout the length of the pedicel and in which branching and muscular joints are well developed includes *B. ramosa* (Robertson, 1900).
- Group B. The species group in which pores, poorly developed, occur only in the lower part of the pedicel and in which muscular joints are common but branches are rare includes *B. geniculata* Harmer, 1915.
- Group C. The species group in which pores occur only in the lower part of the pedicel and in which the lower half of the pedicel is rigid and the upper half membranous includes *B. hozawai* Toriumi, 1949, and *B. subrigida* Osburn, 1953.
- Group D. The species group in which pores occur throughout the length of the pedicel and in which branching and muscular joints are rarely if ever developed includes *B. robusta* Osburn, 1953 (not *B. robusta* O'Donoghue, 1924), *B. fruticosa* (Hincks, 1884), and the eight named species referred to *B. discreta* by various authors, most recently Rogick (1956), (hereafter referred to as the *discreta* complex). The other two species may be distinguished from the *discreta* complex in the following ways:
- (1) B. robusta Osburn has a musclium that is longer than the pedicel whereas other species have a pedicel from two to five times longer than the musclium.
- (2) B. fruticosa (Hincks) has four "more or less regular series of funnel-shaped perforations" that extend the length of the pedicel (Busk, 1886) and has a spine at the upper part of the pedicel at the junction with the calyx. With the possible exception of B. misakiensis (of the discreta complex), other Barentsia species have pores arranged irregularly and, only in rare individuals, such as that figured by Waters (1904: pl. 7, fig. 6f), is there an indication of a spine at the upper part of the pedicel at

the junction with the calyx. Oka (1895) figured *B. misakiensis* with four longitudinal rows of pores but wrote nothing of this striking feature in an otherwise detailed text description. In any event, *B. misakiensis* apparently does not develop a spine and, in this way, is easily distinguished from *B. fruticosa*.

If Rogick (1956) was correct in her assignment of all of the discreta complex populations to the same species, then a corollary is that these populations are capable of interbreeding. Her conception of Barentsia discreta included material from the following places: Arctic, North Atlantic, South Atlantic, Northern Pacific and Indian Oceans, the Malayan archipelago area, and off Antarctica. All except two of these records are from continental shelf localities of less than 100 meters; the exceptions are 300 meters off Enerby Land, Antarctica (Johnston and Angel, 1940) and 183-274 meters depth off Tristan da Cunha (Busk, 1886).

An alternative taxonomic approach to the *discreta* complex derives from skepticism that all of these local populations are, in fact, part of a larger interbreeding population. We wish to examine the idea that the *discreta* complex involves several species.

The discreta complex includes the following named species: Barentsia discreta (Busk, 1886), B. australis (Jullien, 1888), B. macropus (Ehlers, 1890), B. misakiensis (Oka, 1890), B. timida Verrill, 1900, B. robusta O'Donoghue, 1924, B. antarctica Johnston and Angel, 1940, and B. intermedia Johnston and Angel, 1940.

Table 5 summarizes the salient features of entoproct morphology for these named species as derived from (1) original publications, (2) type material (for *B. timida*), and (3) one secondary source (Prenant and Bobin, 1956, in part for *B. macropus*). Similarly, Table 6 summarizes data for specimens referred to *B. discreta* (Busk) that come from secondary sources that describe or illustrate the species.

Many of the measurements and counts presented in Tables 5 and 6 have been made by us from figures of specimens and our results alter the importance of some of the generalizations cited in the literature. For example, *B. antarctica* was said to have a pedicel to musclium ratio of 11-14:1 (Johnston and Angel, 1940), but the figured specimen of that species had a ratio of only 9.4:1. Similarly, *B. intermedia* was said to have a pedicel to

Table 5. Summary of morphological features of named species in the discreta complex. Figures in parentheses indicate a range in values.

| res Source | Jo t     | el Data          | O'Donoghue,<br>1924:21      | Jullien, 1888:113    | This paper<br>Verrill, 1900       | Oka, 1890<br>Oka, 1895 | Busk, 1886:44                            | Ehlers, 1890:9 Prenant and Bobin, 1954:111 | 18 Johnston and Angel,<br>J &A: 1940;225<br>48) | 11 Johnston and Angel,<br>J &A: 1940:226<br>36) |
|------------|----------|------------------|-----------------------------|----------------------|-----------------------------------|------------------------|--|--|---|---|
| No. Pores  | /mm      | Pedic            | ٥.                          | c-                   | 42<br>(40-<br>44)                 | 110                    | 27                                       | c-   | 18<br>J &A:<br>48)                              | 11<br>(J &A:<br>36)                             |
| 4          |          | Locality Pedicel | Natal,<br>S. Africa<br>49 m | Cape<br>Horn<br>40 m | Bermuda                           | Japan<br>5-10 m        | Tristan<br>da Cunha,<br>183, 274m        | Mediter-<br>ranean                         | Antarc-<br>tica<br>27-46m                       | Antarc-<br>tica (                               |
|            | Tentacle | No.              | ic.                         | 12-14                | (17?-19)                          | 20-24                  | 16-20                                    | (16-20)                                    | ~ 20  | $\sim 16$                                       |
| Ratio of   | Pedicel; | Musclium         | (5, 6-7.0) (2,2-3,7:1)      | ć.                   | 3,4:1                             | 3:1                    | .5 (.3056) (.1835) (1.7-4.3) (2.9-6.5:1) | 2, 1:1                                     | (.2630) (2.8-6.5) (4.6-7(9?);1)                 | 4, 95 9, 4:1 (8-11(14°):1)                      |
|            | Total    | Height           | 6, 3<br>(5, 6-7.0)          | ₹3.0                 | (. 48-1.2) (.24-, 36) (2, 6-4, 9) | 3.5                    | 3.8 (1.7-4.3)                            | 1.5  | 4.6<br>(2.8-6.5)                                | 4,95  |
|            | lium     | Width            |                             | c.                   | .29                               | .34                    | .3                                       |  | .30   | . 26  |
|            | Musclium | Ht.              | 1.4 (65.7)                  | ٥.                   | .76                               | 87.                    | .5(.3056)                                | . 35                                       | .8 (.58)  | . 5   |
|            |          | Shape            |                             | Δ                    |                                   |                        |  |  |   |   |
|            | Pedicel  | Width            | c.                          | ć                    | . 06                              | . 07 - 09              | 90 *                                     | 90.  | . 62  | . 33 50   |
|            | Ped      | Ht.              | (3.3-4.8)                   | ć                    | 2.6 (1.3-3.6)                     | 2.1                    | 3.0 (1.1-3.4)                            | .73  | 4.0 (2.3-5.7)                                   | (4.0-5.4)                                       |
|            |          | Width            |                             | ć.                   | .57 2.6 .06 (1.3-3.6) (.408)      | 7.                     | .41                                      | .32 .73<br>(.1550) (.35-1.5)               | . 55<br>(. 3774) (2.3-5.7) (. 5075)             | . 18<br>(. 14-, 22) (4.0-5, 4) (. 33-, 50)      |
|            | Calyx    | Ht.              | .9                          | a.                   | .69                               | . 7                    | (.27-,64) (.25-,62) (1.1-3.4)            | .38  | . 62  | .27   |
|            | Species  |                  | B. robusta                  | B. australis         | B. timida                         | B. misakiensis         | B, discreta                              | B. macropus                                | B. intermedia                                   | B, antarctica                                   |

1. Values for calyx from immature specimens.

musclium ratio of 7-9:1, but the figured specimen of that species has a ratio of only 5.5:1. A second example is the diameter of the pedicel. The published pedicel diameter for *B. discreta* from Antarctica (Johnston and Angel, 1940) is 0.09 mm whereas the figured specimen representing that species has a diameter of 0.06 mm.

All of the estimates of the number of pores per millimeter of pedicel are based on counts from figures of specimens except for *Barentsia timida* which was measured directly. Johnston and Angel (1940) are the only authors previously to record numbers of pores per unit length, and they suggested that this may be a good taxonomic character. There are, however, large discrepencies between their published figures and those that can be derived from the figured specimens (Tables 5, 6). It is possible that pore counts made from figured specimens are underestimated because only pores that are visible in the figured surface might be shown. However, drawings sufficiently detailed to indicate pores also indicate the inner wall of the pedicel thus showing that the drawing is actually an optical section with pores transferred into this section from above and below.

Our resolution of the *discreta* complex is derived in the following manner. There appear to be three groups of species in the *discreta* complex which are distinguished by the way in which the pedicel grows; that is, whether it grows with a decreasing, increasing or constant diameter from musclium to calvx.

- (1) Decreasing diameter of the pedicel. *Barentsia robusta* O'Donoghue, 1924, is the only species to grow with a decreasing diameter of the pedicel. (Note that *B. robusta* Osburn, 1953, is a junior homonym and thus requires a new name).
- (2) Increasing diameter of the pedicel. Three named species, i.e., *Barentsia australis* (Jullien), *B. timida* Verrill, and *B. misakiensis* (Oka), have an increasing diameter to the pedicel. In addition, specimens referred to *B. discreta* by Harmer (1915) from Siboga (and Japanese?) collections, by Toriumi (1949, 1951) and Yamada (1956) from Japanese collections, by Osburn (1912a) from Woods Hole, Massachusetts, and by Osburn (1953) from the west coast of North and South America have an increasing diameter to the pedicel.

Table 6. Summary of morphological features of specimens referred to <u>Barentsia discreta</u> by authors who described or figured material.

| Species     | Calyx               | :                  | Pedi             | cel              |          | Muscli            | ium              |
|-------------|---------------------|--------------------|------------------|------------------|----------|-------------------|------------------|
|             | Ht.                 | Width              | Ht.              | Width            | Shape    | Ht.               | Width            |
| B. discreta | ?                   | ?                  | ?                | ,                | $\nabla$ | ?                 | 9                |
| B. discreta | . 27                | .20                | , 83             | ?                | $\nabla$ | . 4               | .14              |
| B. discreta | ≤ .78               | ≤.60               | 2.0<br><1-2      | ?                | $\nabla$ | .50               | . 18             |
| B. discreta | .51<br>(.4369)      | .42<br>(, 38-, 46) | 1.5 (.8-2.2)     | .045             | $\nabla$ | (, 27-, 43)       | (.14-,16)        |
| B. discreta | .61<br>(.4576)      | .50<br>(.4456)     | 1.9 (1.6-2.2)    | .045             | ?        | .50<br>(.4058)    | .19              |
| B. discreta | . 87                | .65                | 3.5              | ~.1(?)           | $\nabla$ | 1,1               | . 42             |
| B. discreta | . 60                | .60                | 1.8              | ~.07(?)          | $\nabla$ | .75               | . 25             |
| B. discreta | .65<br>(up to 1.3)  | .81<br>(up to 1.3) | 3.7<br>(2.4-5.2) | .7               | $\nabla$ | .75<br>(.78)      | .33<br>(,2938)   |
| B, discreta | . 5                 | . 4                | 1.2              | ?                |          | .35<br>(.34)      | (.0913)          |
| B. discreta | .8<br>(,7584)       | .73<br>(,678)      | 4.8<br>(2.2-5.4) | .06<br>(.06-,09) |          | . 8               | . 4              |
| B. discreta | .74<br>(.5693)      | .64<br>(.5081)     | 4.5<br>(3.1-5.9) | .068             | )        | .86<br>(.56-1.15) | (.2641)          |
| B. discreta | . 48<br>(, 41-, 54) | . 47               | 2,9<br>(,95-3,5) | .048             |          | .76<br>(2495)     | . 22             |
| B. discreta | .67<br>(.5085)      | .49<br>(.4070)     | 2.5<br>(1.9-2.9) | ?                |          | .70<br>(.6577)    | .30<br>(,25-,34) |
| B. discreta | .21                 | 0.18               | ?                | ?                | ?        | ?                 | ?                |
| B. discreta | .57<br>(.4768)      | ?                  | 6.0<br>(4.9-7.2) | .07<br>(.05085)  |          | .64<br>(.6068)    | .28<br>(.2629)   |
|             |                     |                    |                  |                  |          |                   |                  |

Waters (1905:230) stated that *B. australis* (Jullien) is a synonym of *B. discreta* (Busk) but no basis was given for this decision. Jullien (1888) provided no illustration and his description is brief. *B. australis* appears to be separate from *B. discreta* as that species has a pedicel of constant diameter, but the true affinities of *B. australis* cannot be established on present information.

The great distance and separation by land masses between Bermuda (type locality of *Barentsia timida*) and the Far East suggests that populations from these two areas are not part of the same interbreeding population, and thus *B. timida* is considered a separate species. "B. discreta" from Woods Hole (Osburn,

|             |                    | Ratio of                | 1               | No. Pores      |                                 |                               |
|-------------|--------------------|-------------------------|-----------------|----------------|---------------------------------|-------------------------------|
| Species     | Total              | Pedicel:                | Tentacle        | /mm            |                                 | Source                        |
|             | Height             | Musclium                | No              | Pedicel        | Locality                        | of Data                       |
| B. discreta | ?                  | ?                       | ?               | ?              | Woods Hole,<br>Mass.<br>Shallow | Osburn; 1912a;<br>214         |
| B. discreta | 1,5                | 3, 1:1                  | ~18             | ?              | Chesapeake<br>Bay               | Osburn: 1944:9                |
| B. discreta | 1.8 (1-3)          | 2,5:1<br>(2-4:1)        | 14-20?          | ?              | S. Cal. to<br>Peru.<br>Shallow  | Osburn; 1953;766              |
| B. discreta | 2.3<br>(1.6-3.0)   | 4.3:1<br>(3,0-5.1:1)    | ~20-24          | 50<br>(44-56)  | Siboga<br>Dredgings             | Harmer: 1915:29               |
| B. discreta | 2,75<br>(2,5-3,1)  | 3.8:1<br>(3,4-4,8:1)    | ~20-24          | ?              | Japan                           | Harmer: 1915:29               |
| B. discreta | 4,5<br>(?-5,5)     | 3:1                     | ~20             | 28(?)          | Japan                           | Toriumi: 1949;<br>225         |
| B. discreta | 3.15               | 2.4:1                   | ~20             | 33(?)          | Japan                           | Toriumi: 1951:19              |
| B. discreta | 5.1<br>(up to 9.5) | 4,9:1                   | ~ 20            | 80             | Japan                           | Yamada: 1956:241              |
| B. discreta | 1.7<br>(1.5-2.0)   | 3.5:1<br>(3-4:1)        | 16-20           | ?              | Gulf of<br>Naples               | Zirpolo: 1927:<br>413         |
| B. discreta | 5.1<br>(4-6.3)     | 4.2:1<br>(3,4-5:1)      | 24<br>(24-28)   | 43<br>(J&A:96) | Kergulen<br>I. 91m              | Johnston & Angel:<br>1940:223 |
| B. discreta | 5.65<br>(4.5-7.2)  | 5, 3:1<br>(5, 2-5, 5:1) | 17?<br>(17-28?) | 53             | Antarc-<br>tica 65-<br>73 m     | Rogick: 1956;225              |
| B. discreta | 4.1 (1.6-5.0)      | 3.9:1<br>(3-4:1)        | 16              | 63             | Sangama<br>Brazil<br>20 m       | Marcus: 1937:15               |
| B. discreta | 3.8 (3.2-4.4)      | 3,5:1<br>(2,9-3,8:1)    | ?               | ?              | Southern<br>Chile               | Waters: 1904:99               |
| B. discreta | ?                  | ?                       | ?               | ?              | India                           | Annandale: 1912:205           |
| B. discreta | 8.1 (6.7-9.5)      | 9.4:1<br>8.2-11:1       | 20-24           | ?              | Arctic<br>~150°E.               | Kluge: 1946a:150,<br>156      |

1912a) and from Chesapeake Bay (Osburn, 1944) are tentatively placed in synonymy with it because of their geographic proximity and the lack of any positive characters to distinguish them.

"Barentsia discreta" from the west coast of North and South America (Osburn, 1953) has been recorded from several tropical and subtropical localities from Peru to southern California. The western coast of the Americas has not been connected with the Gulf of Mexico for approximately 8 to 12 million years, late Miocene (Olsson, 1932, cited by Durham and Allison, 1960), or Pliocene (Lloyd, 1963). Thus present Bermuda and west coast populations are not likely part of the same interbreeding population although both modern populations are probably descended

from common ancesters. The Bermuda population (*B. timida* Verrill) is considered a sibling species separate from west coast populations.

We are uncertain whether west coast specimens could form part of an interbreeding population with Far East specimens. Representatives from these two areas, however, do not seem distinguishable on morphological grounds. In the absence of breeding experiments, they are tentatively referred to the same species, *Barentsia misakiensis* (Oka) (see below).

Remaining specimens with an increasing diameter of the pedicel are all from the Far East and may represent a single species, the oldest available name for which is *Barentsia misakiensis* (Oka). However, as Rogick (1956) pointed out, Oka (1895, pl. 12, fig. 2) illustrated a specimen with linearly arranged pores on the pedicel. This striking feature was not shown on his earlier figures of the species (1890), nor was it mentioned in his detailed description (1895). If this is a characteristic of the type material, then it may be sufficient reason to separate *B. misakiensis* from other Far East *Barentsia*'s. This would seem to be a particularly reasonable course of action because this character has previously been used to help distinguish another species of *Barentsia*, namely *B. fruticosa*.

(3) Constant diameter of the pedicel. Remaining elements of the discreta complex have an essentially constant diameter of the pedicel. This includes Barentsia discreta (Busk), B. macropus (Ehlers), B. intermedia and B. antarctica of Johnston and Angel.

On the basis of the close examination given to *Barentsia* macropus by Prenant and Bobin (1956), we agree that it can be maintained as a species distinct from *B. discreta*, opposite to the opinion of Marcus (1939:212) and Rogick (1956). *B. macropus* (1) lacks a flexible and muscular region at the junction of the pedicel and calyx. This muscular region occurs in most specimens of *B. discreta*. [Waters (1918) mentioned specimens assigned to *B. discreta* from the Cape Verde Island that often lack the annulations at the base of the calyx. These, however, are not figured nor described, and it appears possible that he was actually referring to *B. macropus*.] *B. macropus* (2) is said to lack muscular regions in the pedicel. Such regions occur rarely in specimens assigned to

B. discreta and B. timida. B. macropus (3) is generally a small species whose total height is about 1.5 mm and whose pedicel to musclium ratio is about 2:1; B. discreta is commonly 3 to 4 mm high and has a pedicel to musclium ratio of 3-5:1. (We realize that these statistical data may be misleading and over this distinction only because of the exceedingly large differences involved.) Prenant and Bobin (1956) suggested that B. macropus (4) has a calyx that is more strongly gibbous on the dorsal side than occurs in B. discreta, but well preserved material is necessary in order to show this. Greatest weight is given to criterion (1). According to the concept of B. macropus expressed above, this species has only definitely been found in the Mediterranean.

Johnston and Angel (1940) erected two new *Barentsia* species from the Antarctic, and distinguished them from each other and from *B. discreta*, which they also report in their collection, by (1) the ratio of pedicel to musclium, (2) the number of pores per millimeter in the pedicel and (3) the diameter of the pedicel. As indicated above, the range of values suggested for each species does not agree with measurements from their illustrated specimens. In addition, criteria (1) and (3) may have a V<sub>c</sub> either so high or so low (as in *B. timida*) as to be taxonomically very unreliable.

In the light of our new measurements and of comparison of variability in other reports, it appears to us that Johnston and Angel's B. antarctica, B. intermedia, and B. discreta, and Rogick's (1956) B. discreta cannot be kept apart. All of these forms are here referred to B. discreta (Busk) although the Antarctic colder water forms are larger than Busk's type material. We consider that B. discreta is correctly reported to occur in the Antarctic (Johnston and Angel, 1940; Rogick, 1956), in the south Atlantic (Busk, 1886), in the central Atlantic (Marcus, 1937), and off the southern end of South America (Waters, 1904).

Remaining specimens that have been illustrated or described and referred to *Barentsia discreta* were reported by Annandale (1912) and Kluge (1946a). Annandale's account is of an Indian specimen from an estuary of about 2.55% salinity (Annandale, 1915). The description is quite short. If the calyx measurements of 0.21 mm high and 0.18 mm wide apply to adult individuals as he believed,

then their very small size suggests either separation as a distinct species or striking reduction in surface area in regions of lowered salinity. Nothing has been published on the characteristics of the musclium or pedicel in this form.

Kluge (1946a) described some enormous *Barentsia* specimens from the Arctic. Their pedicel to musclium ratio is about 9:1 and their total height approximately 8.0 mm. These specimens commonly have muscular enlargements of the pedicel (which are responsible for the large size of individuals). Although joints have been rarely found in the pedicel of *B. discreta* by Waters (1904) and Rogick (1956), and of *B. timida* (this paper), the common occurrence of this important morphological feature as well as the arctic locality suggest that Kluge's specimens cannot be referred to *B. discreta*. Kluge's specimens have the muscular joints but not the branches of *B. ramosa* Robertson (1900) from the west coast of North America. Kluge's form appears to represent a species separate and distinct from those previously named.

Authors who simply record specimens of the discreta complex are Annandale (1915), Hutchins (1945), Kirkpatrick (1890), Marcus (1921, 1953), Mawatari (1948, 1952), Okada and Mawatari (1938), Osburn (1914, 1947), Robertson (1900), Sumner, Osburn, Cole, and Davis (1912), Thornely (1905, 1924), and Waters (1918). Not enough information was provided to verify their identifications.

The suggested synonymy for species of the discreta complex is summarized in Table 7. Species that are considered recognizable are (1) B. discreta (Busk), (2) B. macropus (Ehlers), (3) B. misakiensis (Oka), (4) B. timida Verrill, (5) B. robusta O'Donoghue, and (6) "B. discreta" of Kluge (1946a) which requires a new name. In addition, (7) B. australis (Jullien) and (8) "B. discreta" of Annandale (1912) may be distinct, but not enough has been published on their anatomy for them to be reasonably understood. The characters that we have used to distinguish species in the discreta complex are chiefly biogeographic. Certainly, more compelling reasons than we have been able to derive are desirable for species discrimination in these entoprocts.

TABLE 7. Synonymy for species of the discreta complex.

| Species Name                   | Literature synonyms                          | Geographic Location | Remarks                          |
|--------------------------------|--|---------------------|----------------------------------|
| 1. B. discreta (Busk. 1886)    |  | South Atlantic      |                                  |
|                                | B. discreta (Busk); Waters, 1904             | South Pacific       |                                  |
|                                | B. discreta (Busk); Marcus, 1937             | Central Atlantic    |                                  |
|                                | B. antarctica Johnston & Angel;              | Antarctica          |                                  |
|                                | Johnston & Angel, 1940                       |                     |                                  |
|                                | B. intermedia Johnston & Angel;              | Antarctica          |                                  |
|                                | Johnston & Angel, 1940                       |                     |                                  |
|                                | B. discreta (Busk); Johnston &               | Antarctica          |                                  |
|                                | Angel, 1940 B. discreta (Busk); Rogick, 1956 | Antarctica          |                                  |
| 2. B. macropus (Ehlers, 1890)  |  | Mediterranean       |                                  |
|                                | B. discreta (Busk); Zirpolo, 1927            | Mediterranean       |                                  |
|                                | B. macropus (Ehlers); Prenant &              | Mediterranean       |                                  |
|                                | Bobin, 1954                                  |                     |                                  |
|                                | ? B. discreta (Busk); Waters, 1918           | Cape Verde Islands  |                                  |
| 3. B. misakiensis (Oka, 1895)  |  | Japan               |                                  |
|                                | B. discreta (Busk); Harmer, 1915             | Siboga Collections  |                                  |
|                                | B. discreta (Busk); Harmer, 1915             | Japan               |                                  |
|                                | B. discreta (Busk); Toriumi, 1949            | Japan               |                                  |
|                                | B. discreta (Busk); Toriumi, 1951            | Japan               |                                  |
|                                | ? B. discreta (Busk); Osburn, 1953           | American west coast |                                  |
|                                | B. discreta (Busk); Yamada, 1956             | Japan               |                                  |
| 4. B. timida Verrill, 1900     |  | Bermuda             |                                  |
|                                | B. discreta (Busk); Osburn, 1912             | Woods Hole, Mass.   |                                  |
|                                | B. discreta (Busk); Osburn, 1944             | Chesapeake Bay      |                                  |
| . B. robusta O'Donoghue, 1924  |  | Natal, S. Africa    |                                  |
| - 1                            | B. discreta (Busk); Kluge, 1946              | Arctic (150°E)      | Needs new name                   |
| . B. australis (Jullien, 1888) |  | Cape Horn           | Questionable<br>distinct species |
|                                | B. discreta (Busk); Annandale, 1912          | India               | Questionable<br>distinct species |

### Bugula cucullata Verrill, 1879 Figures 2D, 4D, 10D.

not Bugula cucullata Busk, 1867:241.

Bugula cucullata Verrill, 1879d:52.

Bugula cucullata Verrill: Verrill, 1879e:188.

Bugula harmsworthi Waters, 1900:54, pl. 7, fig. 13; pl. 8, fig. 1.

Bugula harmsworthi Waters: Nordgaard, 1906a:8, figs. 1-5. Bugula harmsworthi Waters: Nordgaard, 1912:16, figs. 7-8.

Bugula cucullifera Osburn, 1912a:225, figs. 24-24c.

Bugula cucullifera Osburn: Osburn, 1912b:277 (specimen seen).

Bugula harmsworthi Waters: Kluge, 1962:340, fig. 213.

Bugula harmsworthi Waters: Hansen, 1962:24.

PRESENT AUTHORS' DESIGNATION. Bugula harmsworthi Waters, 1900.

TYPE. Holotype of Bugula cucullata Verrill: USNM 4150a-c, "Bugula avicularia var. fastigiata, Jeffrey's Ledge [off Agamenticus Mountain, Maine], [Sta.] 46 [Bache], 51 f[athoms], Fish Com[mission], [Sept. 4], 1874." In handwriting of A. E. Verrill. USNM 4150a is the basic lot; USNM 4150b is the figured specimen; USNM 4150c is a slide of avicularia.

ORIGINAL DESCRIPTION. "Off Maine. Remarkable for the small, hood-like, upturned ooecia, widely open in front. Zooecia in two rows; usually two spines on each angle; avicularia lateral."

SUBSEQUENT DESCRIPTION. "Zoarium much branched, branches slender, dichotomously divided, the branchlets diverging but little. Zooecia in two alternating rows, rather large, elongated, narrow, with the long, narrow, frontal area occupying most of the length. At the distal angles there are usually two rather long slender spines on each side, but often three on the outer angle. The spines are unequal, divergent, more or less curved and directed upward; the one farthest in front is usually longest, curved forward and upward at base. Avicularia large, elongated, the length greater than the width of the zooecia, situated rather in advance of the middle of the outer margin of the frontal area, the beak reaching beyond the distal end of the zooecia; the head is compressed, broad-oval, and tapers below at the posterior end into the pedicel, which is thick at first, but narrows to a slender base; the beak is long, concave above, but strongly incurved or hooked at the tip. Ooecia short, but wide, nearly hemispherical, the front edge turned upward, showing a large opening in a front view, and giving them a hood-like appearance; surface more or less areolated, glistening.

"Jeffrey's Ledge, off Maine, 51 fathoms, taken by Dr. A. S. Packard and Mr. C. Cooke, while dredging on the "Bache," in 1874, for the Fish Commission. A second specimen of this fine species was dredged this season, off Cape Cod, in 75 fathoms, mud. When placed in alcohol, it quickly became bright rose-red; but the alcohol soon disolved the color, becoming light pink, while the specimen became white." (Verrill, 1879e)

ADDITIONAL DESCRIPTION. The colony is small, being only 1.3 cm high. Branches are spread out in a single whorl that results in a

cup-shaped form. The bifurcation plan (Fig. 2D) corresponds to type 3 of Harmer (1923). The more proximal bifurcations have a chitinous joint passing transversely just above the proximal fork of the zooids. Frontal membrane is two-thirds to three-fourths the length of the zooid.

There are two sizes of avicularia. The larger form (Fig. 4D) is attached halfway down the outer frontal margin (Fig. 10D) and its beak reaches the distal end of the zooid. There is a tendency for this form to become longer toward the distal end of branches. The smaller avicularia were found detached in the sample, their position in the colony being unknown.

Long radicles issue from the lower sides of zooids and prevented an examination of the ancestrula and all zooids below the first bifurcation.

MEASUREMENTS. Dimensions are of the holotype, USNM 4150.

Lz (10) 0.837 (0.043) mm., 0.78 — 0.93 mm.

lz (10) 0.212 (0.007) mm., 0.20 — 0.22 mm.

Lov (11) 0.194 (0.007) mm., 0.18 — 0.20 mm.

lov (11) 0.239 (0.009) mm., 0.23 — 0.26 mm.

Lav (10) 0.306 (0.017) mm., 0.28 — 0.34 mm. (large size)

Lav (10) 0.231 (0.022) mm., 0.22 — 0.25 mm. (small size)

REMARKS. The colony at hand clearly agrees with Verrill's description of *Bugula cucullata* and label data corresponds precisely with that given in his expanded description (Verrill, 1879e). We conclude that the original description (Verrill, 1879d) was based on the single specimen from Jeffrey's Ledge collected in 1874 because the last paragraph of the expanded 1879 discussion describes a "second specimen...dredged this season [1879]." The name on the label of the first specimen (*Bugula avicularia* var. *fastigiata*, in Verrill's handwriting) is an early, preliminary identification, possibly of 1874, and Verrill evidently failed to put a new label on the specimen following his erection of *B. cucullata* in 1879. USNM 4150 is thus the holotype.

Osburn (1912a) noted that Verrill's name was preoccupied by *Bugula cucullata* Busk, 1867, and proposed a new name for the species, *Bugula cucullifera*. Hansen (1962) called attention to the similarity between *B. cucullifera* and *B. harmsworthi* Waters, 1900, from Franz-Josef Land, and provisionally grouped them

together, pending description of the bifurcation type of *B. cucullifera*. The bifurcation type of *B. cucullifera* (type 3) is the same as that reported for *B. harmsworthi*, thus confirming Hansen's suggestion. Therefore *B. harmsworthi* Waters, 1900, is the oldest available synonym of *B. cucullata* Verrill, 1879, and becomes the valid replacement name.

### Bugula decorata Verrill, 1879 Figure 8C-D.

Bugula murrayana var. quadridentata Smitt, 1868a:292, 351 (in part), pl. 18, figs. 25-26.

Bugula decorata Verrill, 1879d:52.

Bugula decorata Verrill: Verrill, 1879e:188.

Bugula elongata Nordgaard, 1906b:80, pl. 1, figs. 1-6.

Bugula elongata Nordgaard: Norman, 1905:358, text-figs. 1-3.

Bugula elongata Nordgaard: Kluge, 1962:345, fig. 218. Dendrobeania elongata (Nordgaard): Hansen, 1962:25.

PRESENT AUTHORS' DESIGNATION. Dendrobeania decorata (Verrill, 1879).

TYPE. Lectotype of *Bugula decorata* Verrill, chosen here: USNM 4974; "*Bugula avicularia* var. *fastigiata* (L.), off NW border of St. Georges B[an]k. Sta. 89-91 B[ache], 110 fms., U. S. F[ish] C[ommission]. 1872." In part in handwriting of A. E. Verrill.

### ADDITIONAL MATERIAL, Paralectotypes.

(1) YPM 2896; "Bugula avicularis var. fastigiata Sm[itt], [locality] (o) [NW of E end of St. Georges Bank, 42° 5′ N, 67° 49′ W], 110 f[athoms] Fish Com[mission], 1872." In part in handwriting of A. E. Verrill. (2) USNM 11917; "Bugula elongata; ovicells, avic[ularia], Eastport [Maine], 1872; A. E. V[errill]." In handwriting of and identified by L. W. Hutchins. Two slides.

ORIGINAL DESCRIPTION. "Zoarium rather large with thick, much branched stems, producing densely branched, somewhat plumose tufts, two inches or more high. Branches unequally dichotomous, often somewhat spirally arranged. Zooecia in two alternating rows, large, broad, prolonged proximally. Frontal area, large, elongated, sunken and wrinkled in the dry state. The distal angles are prolonged into a single stout, often short spine on each side, frequently absent on the inner angle. Avicularia on the middle of the front side of the zooecia, toward the base; they have a short, broad, swollen head, with a short strongly curved beak; the pedicels are short and thick, rapidly enlarged from the base upward. Ooecia large, globose, brilliantly iridescent, elegantly sculptured, with a series of raised curved lines passing up over each side and converging to the middle of front side, while their concave interspaces are covered with microscopic

transverse lines. Dredged at Eastport, Me., by the writer, and also in the Gulf of Maine, 110 fathoms, near George's Bank, by Dr. A. S. Packard and Mr. C. Cooke, in 1872 (U. S. Fish Com.)."

ADDITIONAL DESCRIPTION. Only a few observations need to be added to Verrill's good description. Some zooids in the present material are uniserial which, however, may be an artifact because alternate members of biserial branches are only loosely adherent to one another; commonly they are connected only in the area of the lateral communication pore chamber. The frontal membrane is one-third to one-half the total zooid length (Fig. 8C-D). The development of distal angles into spinous projections is quite variable. Very rarely, a true spine may be present on the lateral margin of the frontal membrane, its position varying from median-proximal to disto-lateral.

MEASUREMENTS. Dimensions are of the lectotype, USNM 4974.

Lz (8) 1.000 (0.028) mm., 0.95 — 1.09 mm.

lz (8) 0.251 (0.023) mm., 0.20 — 0.27 mm.

Lov (10) 0.299 (0.017) mm., 0.27 — 0.32 mm.

lov (10) 0.354 (0.020) mm., 0.32 — 0.39 mm. Lav (6) 0.138 (0.013) mm., 0.12 — 0.15 mm.

REMARKS. The description of *Bugula decorata* fits precisely the Verrill material cited above. The data on labels of the material are identical to the collection data given by Verrill in the original description. It is thus probable that this material represents the syntypes of *Bugula decorata* even though the labels of YPM 2896 and USNM 4974 bear a name in Verrill's handwriting that he used in pre-1879 reports, namely *B. avicularia* var. *fastigiata*. The best and most complete material is in USNM 4974.

Verrill's specimens agree perfectly with Nordgaard's (1906b) and Norman's (1905) descriptions of *Bugula elongata* from the northwestern coast of Norway, and East Finmark and the west coast of Norway, respectively. Hansen (1962) refers *B. elongata* to *Dendrobeania* Levensen, 1909, a conclusion which we support. Therefore, Verrill's species is designated *Dendrobeania decorata* (Verrill). The chief concept of *Bugula murrayana* var. *quadridentata* as used by Smitt (1868a) is closely tied with that of *Dendrobeania fruticosa* var. *quadridentata* (see Kluge, 1962:333) and not with *D. decorata* (Verrill).

### Bugula flexilis Verrill, 1875 Figures 2A, 3, 4A-B, 8A-B.

Kinetoskias smithi [sic] Danielssen, 1868:24. [See Harmer, 1923:312].

Bugula flexilis Verrill, 1875a:415, pl. 7, figs. 1-2.

Bugula flexilis Verrill: Verrill, 1879d:52.

Bugula flexilis Verrill: Verrill, 1879e:189.

Kinetoskias smittii Danielssen: Koren and Danielssen, 1877:104, pl. 3, figs. 12-14; pl. 12, figs. 4-8.

Kinetoskias smittii Danielssen: Verrill, 1879a:259.

Kinekoskias [sic] smitti Danielssen: Norman, 1893:448, pl. 19, figs. 2-5.

Kinetoskias smitti Danielssen: Silen, 1938:326, text-fig. 67.

Kinetoskias smitti Danielssen: Marcus, 1940:194, figs. 101A-C.

? Kinetoskias smitti Danielssen: Kluge, 1946b:195, pl. 2, fig. 2.

? Kinetoskias smitti Danielssen: Kluge, 1962:350, fig. 221.

PRESENT AUTHORS' DESIGNATION, Kinetoskias smitti Danielssen, 1868.

TYPE. Lectotype of Bugula flexilis, chosen here: USNM 4365, "Bugula flexilis, 110 f[athoms], loc[ation] 54. Fish Com[mission], 1874, A. S. P[ackard]. Kin[etoskias] Smittii." In handwriting of A. E. Verrill.

### ADDITIONAL MATERIAL. Paralectotypes.

- (1) YPM 2893 (USNM 4365), "Off G[eorges] Bank, Fish Com[mission], 110 f[athoms], 1874." In handwriting of A. E. Verrill. This specimen was identified as *Bugula flexilis* Verrill by R. C. Osburn and L. W. Hutchins in 1942 (auxilliary label data) and called a "cotype." It is damaged beyond recognition by dessication and fungus, except for a few avicularian mandibles.
- (2) USNM 11878, "Bugula flexilis Verrill, part of cotype Y-4368." The material on this slide (Y-4368) from the USNM Hutchins collection appears to be part of the Yale specimen YPM 2893 (USNM 4365) in spite of the difference in last digit of the number. [Hutchins received his doctorate from Yale in 1941 on Long Island Sound ectoprocts and in 1941-1942, he and R. C. Osburn undertook a comprehensive study of all American Atlantic Coast ectoprocts (not published). During these studies, Hutchins subsampled several of Verrill's lots, and this is probably the origin of the slide.]

ORIGINAL DESCRIPTION. "Several rather long, slender, flexible, dichotomously divided branches radiate from close to the point of attachment, making a stellate cluster. Zooccia in two alternating rows, smooth, oblong, slightly swollen in the middle, with a short tooth or spine on the outer angle; aperture terminal, oblique, rounded or oval. Avicularia, on the front of the zooccia, remarkably large, nearly as broad as the zooccia and more than half their length, compressed, fusiform, tapering gradually to the point of attachment. East of St. George's Bank, 430 fathoms, 1872; off Casco Bay, 95 fathoms, 1873; Gulf of Maine, 110 fathoms, 1874 [3-3/4 miles NW Cashes Ledge]."

ADDITIONAL DESCRIPTION. Figure 2A is a previously unpublished habit drawing made by Verrill, taken from the Verrill material at the American Museum of Natural History. The branches (Fig. 8A-B) are held far above the substrate by a prominent stalk, not mentioned by Verrill. Globular ovicells are attached to the inner angle of the distal end of zooids. Embryos are present in several of them. Avicularia are attached to the outer side of zooids at one-third to one-half the distance from the base of zooids; they vary considerably in size (Figs. 3, 4A-B). Soft conical processes formed by the radicles (rootlets), as described by Koren and Danielssen (1877), are rare and poorly developed.

MEASUREMENTS. Dimensions are of the lectotype, USNM 4365.

Lz (10) 0.694 (0.026) mm., 0.67 — 0.74 mm.

lz (10) 0.261 (0.026) mm., 0.22 — 0.30 mm.

Lov (5) 0.302 (0.014) mm., 0.29 — 0.32 mm.

lov (5) 0.353 (0.007) mm., 0.34 — 0.36 mm.

Lav (100) 0.522 (0.046) mm., 0.36 — 0.24 mm.

lav (100) 0.182 (0.022) mm., 0.13 — 0.24 mm.

Stem length prior to first zooid: 65 mm.

Stem diameter at base: 1.6 mm.

Stem diameter 0.5 mm below first zooid: 1.0 mm.

Length of anchoring rootlets: 13 mm.

Length of branches: 20 mm.

REMARKS. Upon reviewing the description of *Kinetoskias smitti* given by Koren and Danielssen (1877), Verrill (1879a) concluded that *K. smitti* Danielssen, 1868, and *Bugula flexilis* Verrill, 1875, represented the same species, and we concur. However, types of *B. flexilis* differ from the extensive description of *K. smitti* (as given in Koren and Danielssen, 1877) in three probably insignificant ways. Koren and Danielssen state that the ovicells are attached to the outer zooid margin, but their illustration is not definitive. Material at hand has ovicells attached to the inner distal angle as also occurs in material figured by Marcus (1940). It appears that Koren and Danielssen were wrong in their statement of ovicell position. Secondly, Koren and Danielssen describe transverse striations on the lower part of the dorsal zooid surface. One can occasionally see transverse wrinkles in Verrill's material

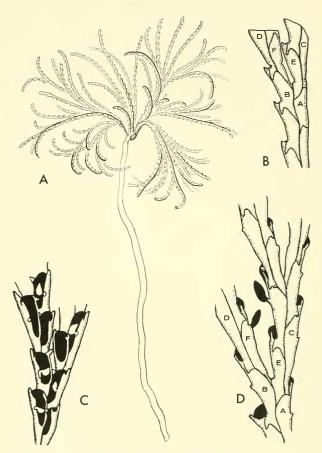


FIGURE 2. A. Bugula flexilis, sketch by A. E. Verrill of USNM 4365, lectotype. American Museum of Natural History, Department of Living Invertebrates; X 1.15. Number 1184 is Verrill's reference number. B-C. Cellularia turrita, YPM 2897c; part of syntype; X 29.4 B. Dorsal view showing type 3 bifurcation. C. Frontal view with area of frontal membrane in black. D. Bugula cucullata, USNM 4150b; part of holotype. Dorsal view showing type 3 bifurcation; avicularia and ovicells in black.

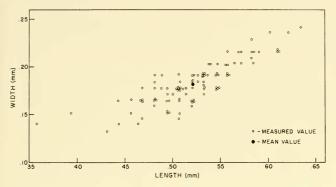


FIGURE 3. Distribution of 100 measurements of length and width of avicularia of *Bugula flexilis*, USNM 4365; lectotype. Note that sizes are gradational from small to large forms.

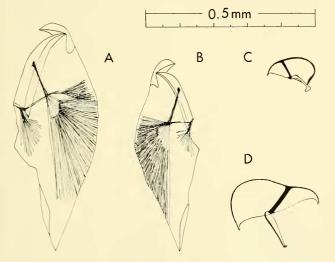


FIGURE 4. A - B. Bugula flexilis, USNM 4365; from lectotype. A. Very large avicularium. B. Medium-sized avicularium. C. Cellularia turrita, YPM 2897d (slide); from syntype. Avicularium. D. Bugula cucullata, USNM 4150 (slide); from holotype. Avicularium. Scale is approximate.

by using low angle incident light and these may be the striations referred to. Norman (1893) also failed to see these striations. Thirdly, the soft conical processes formed by the radicles (rootlets) (see description of Koren and Danielssen) are rare and poorly developed in Verrill's material.

Specimens assigned to *Bugula flexilis* by Kluge (1946b, 1962) possess two apparently different sizes of avicularia. For comparison, the size distribution of avicularia in Verrill's material was plotted (Fig. 3). The wide spread in size indicates that the forms illustrated by Kluge could probably fall within the range of *B. flexilis* avicularia. Other differences between Kluge's material and that of Verrill, however, suggest that they might have been dealing with different species. Kluge's figures show two basic types of avicularia — a smaller elongate form and a larger ovoid type with a mandible almost as long as the avicularium itself. All avicularia in Verrill's material are of the same basic type. In addition, Kluge's figures show the avicularia just reaching the distal ends of zooids to which they are attached, instead of projecting well beyond the distal end as in *B. flexilis*.

### Bugula (Caulibugula) armata Verrill, 1900 Figure 9A-B.

Bugula (Caulibugula) armata Verrill, 1900:593.
 Bugula caraibica Levinsen, 1909:104, pl. 3, figs. 2a-2n.
 Caulibugula armata Verrill: Maturo, 1966:575.
 not Caulibugula armata of authors [Caulibugula dendrograpta (Waters, 1913].

PRESENT AUTHORS' DESIGNATION. Caulibugula armata Verrill, 1900.

TYPE. Holotype of Bugula (Caulibugula) armata Verrill: YPM 2891a-c, "Types. Caulibugula armata. Bermudas Exped. 1898. Ver[rill], Photog [raphed]." In handwriting of A. E. Verrill. 2891a-b is dry material; 2891c is slide with avicularia.

ORIGINAL DESCRIPTION. "A much more delicate, white *Bugula* consists of divergent fan-shaped branches attached to the alternate sides and to the tip of slender jointed stems, sometimes having alternately a long joint and a very short joint, but more frequently the short joint is lacking and the ends of the long joints are swollen, as in *Stirparia*.

"There are usually 2 or 3 annulations at the base of each main branch, and these arise just below the internodes. Many of the cells have a slender distal vibraculum [actually, a spine], or sometimes two.

"It should, doubtless, form the type of a new genus or subgenus

(Caulibugula), intermediate between Bugula and Bicellaria, on account of its articulated spines or vibracula, and related to Stirparia by its jointed stem. It may be named Bugula (Caulibugula) armata. Its zooecia are oblong and biserial, alternate; the pedicellariae [avicularia] are on short pedicles large, lateral, not numerous."

ADDITIONAL DESCRIPTION. Colony fragments consist of jointed stems composed of elongate kenozooids, from which flabellate branches of autozooids arise in an alternate pattern (Fig. 9A). Stalk kenozooids are cylindrical to quadrangular, with one to three proximal annulations and are supported internally by two longitudinal thickenings. Branches of autozooids or new stalks arise from just below the distal end of segments. Bifurcations are of type 5 of Harmer (1923).

The primary zooid of a branch is abortive; and it possesses three proximal annulations, a V-shaped frontal membrane, and no spines (Fig. 9B). Other zooids are biserial, alternate, tapering slightly toward the base, and have a constriction just above the forked proximal end. The frontal membrane is buguloid and occupies about three-fourths of the frontal surface. Zooids are turned strongly toward the median axis of the branch. The orificial area is directed distally.

Spines on the distal margin of zooids are rare in proximal portions of branches. Higher up, a single, long, basally jointed spine is commonly present; it arises somewhat dorsally in the middle of the distal margin. Still higher up a branch, from one to three spines may occur on a zooid. One is on the outer angle of the distal margin and the other one or two are equally spaced around the distal margin.

Avicularia occur on most zooids. They are located about twothirds of the way down on the lateral margin of the zooid. The beak is moderately elongated and abruptly hooked.

Ovicells are absent in this material. Additional description and good figures were given by Levinsen (1909).

MEASUREMENTS. Dimensions are of the holotype, YPM 2891a-b.

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Lz (11) 0.520 (0.031) mm., 0.46 — .57 mm.
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REMARKS. Figure 9A is evidently the photograph referred to by Verrill in his label data. The nomenclatorial changes and relationship to other species attributed to *Caulibugula armata* were reviewed by Maturo (1966). In brief, *C. armata* of authors is *C. dendrograpta* (Waters). *Caulibugula* has been accepted as a well established genus rather than a subgenus; therefore, the species discussed here is correctly cited as *Caulibugula armata* Verrill.

### Bugulella fragilis Verrill, 1879 Figures 5A-E, 10A-C.

Bugulella fragilis Verrill, 1879b:472.

Bugulella fragilis Verrill: Verrill, 1879e:189.

Brettia pellucida Dyster, 1858, var. gracilis Nichols, 1911:7, pl. 1, figs, 1-3.

PRESENT AUTHORS' DESIGNATION. No change.

TYPE. Holotype of Bugulella fragilis Verrill: YPM 2892, "Eucratia sp., Sch[ooner] Alice G. Wonson, Arnol[d] Carlsen [Captain], 220 f[athoms], E[ast] of George's Bank, on Acanella, A. E. V[errill]." In handwriting of A. E. Verrill. Auxilliary label data: "Bugulella fragilis Verrill. Undoubtedly the holotype (and genotype?), Osburn and Hutchins, 1942." Additional label data: Gloucester Fisheries Lot 51; Gully between Brown's and George's Bank.

Six slides prepared from the holotype are recorded under USNM 11915a-f. (The material in the type lot consists of many separate branches so that it is not possible to determine if more than one colony was originally present. With no evidence to the contrary, we consider that all the material belonged to a single colony).

ORIGINAL GENERIC DESCRIPTION. "Stems slender, dichotomously branched, consisting of single series of cells (zooccia), which are connected by short tubular joints that arise medially, from the back and near the distal end of the preceding cell, either singly or two together. Zooccia elongated, expanded distally, with a large sunken, elliptical frontal area on the front side, close to the end; gradually tapered to the proximal end, which is united, by an articulation, with the tubular process of the preceding cell, representing the stem. New branches arise laterally from these small joints. Frontal area surrounded by spines. Ooccia subglobular, attached to the distal end of the zooccia. Avicularia median, at the distal end of the zooccia, shaped as in Bugula. Allied to Bicellaria and perhaps to Breetlia."

ORIGINAL SPECIES DESCRIPTION. "Zoarium translucent, shining, delicate, filiform, much branched; forming intricate divaricate clusters, sometimes an inch or more in height. Apertures broad oval or elliptical, oblique, with a distinct rim, and with five spines on each side; of these the two nearest the distal end are much shorter than the other three, which are as long as the

breadth of the aperture, and arch over it. Sometimes a median spine is also present at the proximal edge. Ovicells globose, prominent, nearly as wide as the zooecial apertures, smooth, shining, sometimes sculptured with raised lines, or with rounded sunken areas on the sides. A small oval disk on the lateral surfaces of the zooecia. Avicularia small, with a rather short, thick, swollen head, the pedicel shorter than the vertical diameter of the head, attached to the distal end of the zooecia.

"East of George's Bank, 220 fathoms, on Acanella Normani. Presented to the U. S. Fish Commission by the captain and crew of the schooner

'Alice G. Wunson' [sic]."

ADDITIONAL DESCRIPTION. The mode of branching is very distinctive. In uniserial growth, two zooids are connected by a short segment that arises dorso-medially from the distal end of the parent zooid (Figs. 5B-C, 10B-C). This segment is the proximal segment of the daughter zooid and it is separated from the remainder of the daughter zooid by a chitinous joint. The proximal segment is not part of the parent zooid, as Verrill thought.

Two zooids arising distally from the same parent zooid differ from one another (Figs. 5A, D-E, 10A). One zooid has a typical single proximal segment; the other zooid usually has two proximal segments both of which are less robust than normal. In addition, the latter zooid is connected to its mate by a short tubular bridge; the lumen of the bridge connects through a pore with the interior of the other zooid. At least part of the bridge is chitinous and flexible.

Verrill's statement that new branches arise from the proximal joints rather than from parent zooids seems unlikely, but it cannot be proved or disproved on the basis of present material, which lacks terminal growth portions.

On each side of the proximal end of the frontal membrane, there is usually a pore chamber ("oval disk" of Verrill) from which new branches may originate (Figs. 5B, D-E, 10B). The proximal portion of the first zooid of this type of branch often resembles a long chitinous rhizoid or radicle, but it terminates in the usual zooid form. Additional pores, consisting of a large, elongate, ovoid pore and three small circular ones are arranged in a row down each side of the zooid at the level of the frontal membrane, and can be seen in cleared preparations (not illustrated here). They appear as perforations in the calcareous skeleton and are not associated with new branches.

In one instance, branching from the distal end of a zooid con-

sists of four zooids rather than the usual two (USNM 11915f). These are arranged in pairs, one behind the other. Although the left member of the front pair is broken off just above the joint of its proximal segment, it evidently was connected by a bridge to its

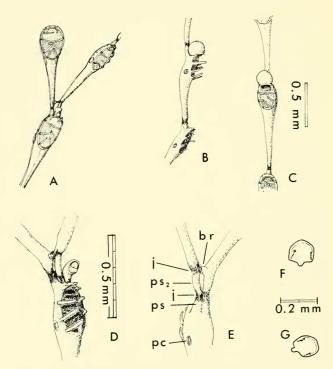


FIGURE 5. A-B. Bugulella fragilis, USNM 1915a-f; part of holotype. A. Free-hand sketch showing frontal view of bifurcation. B. Camera lucida sketch of lateral view of zooid with ovicell. C. Camera lucida sketch of frontal view of zooid with ovicell. Scale applies to B and C. D. Detail of bifurcation and avicularium. Scale applies to D and E. E. Detail of bifurcation, dorsal view. br=bridge, j=joint, pc=pore chamber (i.e., "oval disk" of Verrill), ps=proximal segment, ps=second proximal segment. F-G. Lepralia plana, YPM 2907; from holotype. Opercula. Scale applies to F and G.

mate because the remaining member is single-jointed and possesses an exposed pore for the bridge connection. The back pair has the reverse orientation; i.e., the left member is single-jointed and bears the bridge connection pore and the right member has two proximal joints. Another unusual feature of the zooid series is that the zooid which arises from the distal end of the front right-hand zooid failed to develop normally and is instead a kenozooid (radicle-like) connected to a lateral pore chamber of the posterior right-hand zooid. This phenomenon of potentially normal zooids of one branch fusing with the lateral pore chambers (or outgrowths thereof?) of a zooid in another branch and aborting to kenozooids has been observed several times in the material of this species. (Two examples of this were mounted on slide USNM 11915f).

Other features not mentioned by Verrill follow. The markings on the ovicell appear to be on the inner wall, the outer wall being smooth. A few ovicells contain embryos. The avicularian mandible is semicircular.

MEASUREMENTS. Dimensions are of the holotype, YPM 2892. Zooid length is from just above the proximal joint.

Lz (11) 0.935 (0.024) mm., 0.79 — 1.0 mm.

lz (11) 0.185 (0.006) mm., 0.18 — 0.20 mm.

Lfm (10) 0.249 (0.018) mm., 0.23 — 0.27 mm.

lfm (10) 0.249 (0.018) mm., 0.23 — 0.27 mm.

Lov (10) 0.152 (0.008) mm., 0.14 — 0.16 mm.

lov (10) 0.160 (0.006) mm., 0.15 — 0.17 mm.

Lav (13) 0.109 (0.018) mm., 0.085 — 0.14 mm. lav (7) 0.095 (0.008) mm., 0.085 — 0.12 mm.

REMARKS. Three species have been assigned to the genus Bugulella: B. fragilis Verrill, 1879; B. gracilis Verrill, 1879; and B. clavata Hincks, 1887. B. fragilis is an easily distinguished, well-defined species. B. gracilis is a nomen nudum that appeared in Verrill's preliminary checklist of marine invertebrates of the Atlantic coast (Verrill, 1879c). It may have been a manuscript name for B. fragilis. B. clavata, from the Mergui Archipelago, has an extensive frontal membrane and a different form of branching from B. fragilis and bears more resemblance to a form like Beania intermedia

Brettia pelucida var. gracilis was named by Nichols (1911) from material dredged from approximately 1300 meters southwest of Ireland. The characteristics of the ovicells, frontal, communication pores and branching are essentially the same as those in material at hand.

Bugulella is a well-defined genus. It is distinct from Brettia which lacks both ovicells and avicularia (Osburn, 1952) and has a different mode of branching. Bugulella may be a senior synonym for Corynoporella Hincks, 1888, as suggested by Harmer (1926:197).

## Cellularia turrita Desor, 1848 Figures 2B-C, 4C.

Cellularia turrita Desor, 1848:66. Bugula turrita of authors.

PRESENT AUTHORS' DESIGNATION. Bugula turrita (Desor, 1848).

TYPE. Syntypes of Cellularia turrita Desor: YPM 2897a-d, "Type of Desor, Cellularia turrita Des[or], Nantucket, Coll[ector] E. Desor, Donor Bost[on] Soc[iety] Nat[ural] Hist[ory], No. 519." In handwriting of A. E. Verrill. YPM 2897a is dry material, as found; YPM 2897b is material in alcohol, after wetting in trisodium phosphate; YPM 2897c is figured material; YPM 2897d is a slide of avicularia.

ORIGINAL DESCRIPTION. "Polypidom dense, like a bush; stem orange colored, divided into a great number of branches, so that each stem looks like a small tower or pyramid. Found in depths varying from three to fifteen fathoms. Thrown in great quantity on the beaches of the islands of Nantucket and Martha's Vineyard."

ADDITIONAL DESCRIPTION. Branches, which have bifurcations of Harmer's type 3 (Fig. 2B), are spirally arranged. The ancestrula is not present but it and perhaps one or two other zooids are the only ones missing from the lower part of one of the syntypes. Several rootlets occur. Zooids are biserial, narrowed proximally, and with an opesia approximately three-quarters the length of the frontal. A single true spine occurs on the inner distal angle. The outer distal edge curves frontally. A large true spine occurs on the outer distal angle and a smaller true spine occurs in front of it where the distal edge stops curving frontally.

An avicularium (Fig. 4C) is attached about half-way down the outer margin of the opesia (Fig. 2C). It is a little shorter than the zooid is wide. No ovicells occur in type material.

MEASUREMENTS. Dimensions are of a syntype, YPM 2897b, which is a young colony.

Lz (15) 0.447 (0.028) mm., 0.40 — 0.51 mm. lz (10) 0.168 (0.013) mm., 0.15 — 0.19 mm.

Lav (10) 0.131 (0.009) mm., 0.12 — 0.14 mm.

REMARKS. Type material consists of portions of four colonies, intimately mixed and partly fragmented (YPM 2897a). Parts of this small collection were used for wet examination (YPM 2897b), for figuring (YPM 2897c) and for avicularia examination (YPM 2897d). These specimens appear to be the syntypes because (1) they bear the notation "type of Desor," and (2) they were received by Verrill from the Boston Society of Natural History, in whose proceedings the species was described with the notation that "Mr. Desor offered for the acceptance of the Society, the original specimens of the above-described species." Bugula turrita of authors (e.g., Osburn, 1912a; Ryland, 1960; Maturo, 1966) represents the same species as that described by Desor.

## Discopora nitida Verrill, 1875 Figures 12D, 13A-B.

Discopora nitida Verrill, 1875a:415, pl. 7, fig. 3. Discopora nitida Verrill: Verrill, 1875b:42.

Mucronella nitida (Verrill): Verrill, 1879e:195. not Smittia nitida (Verrill): Hincks, 1881:159, pl. 9, figs. 5, 5a [=Smittina

egyptiaca (Waters); see Harmer, 1957:937]. Smittina trispinosa (Johnston): Osburn, 1912a:246 (part), pl. 27, fig. 65a. Smittina trispinosa var. nitida (Verrill): Osburn, 1912a:246, pl. 27, figs.

66-66e, 88.

Smittina trispinosa (Johnston): Canu and Bassler, 1923:143, pl. 22, figs. 7-14.

Smittina maleposita Canu and Bassler, 1923:144 (part), pl. 31, fig. 11. not Smittina trispinosa (Johnston): Osburn, 1933:45, pl. 10, fig. 6. [= Parasmittina jeffreysi (Norman)].

Smittina trispinosa var. nitida (Verrill): Marcus, 1937:104, pl. 21, fig. 56.

Smittina trispinosa var. nitida (Verrill): Osburn, 1940:437.
 Smittina trispinosa (Johnston): Rogick and Croasdale, 1949:67, pl. 10, figs. 68-71.

Smittina nitida (Verrill): Harmer, 1957:916.

Parasmittina trispinosa (Johnston): Maturo, 1957:55 (part), fig. 62.

Parasmittina trispinosa (Johnston): Schier, 1964:638 (part).

PRESENT AUTHORS' DESIGNATION. Parasmittina nitida (Verrill, 1875).

TYPE. Lectotype of *Discopora nitida* Verrill, chosen here: USNM 4340, "Snititia nitida (Verrill), Vineyard Sound, Sta[tion] 19(419), 40 f[atho]ms, July 17, 1874." One shell bearing colonies with numbers 37, 38, 38\* (asterisk our mark). Colony 38\* is the lectotype (morphotype A).

#### ADDITIONAL MATERIAL. Paralectotypes.

- (1) USNM 4340, "Smittia nitida (Verrill), Vineyard Sound, Sta[tion] 19(419), 40 f[atho]ms, July 17, 1874." One shell bearing colonies with numbers 37, 38, 38\* (asterisk our mark). Colony 38 is paralectotype (morphotype B).
- (2) YPM 2898(4791), "38, D[iscopora] sp. nov. with avicularia. Long I[sland] Sound, Fish Com[mission], 1874." In handwriting of A. E. Verrill. Morphotype A.
- (3) YPM 2899, "Discopora sp. nov., Thimble 1[sland] pools, [18] 74, A. E. V[errill]." In handwriting of A. E. Verrill. Morphotype B.
- (4) USNM 4333, "Discopora sp. nov. Long Island Sound, Fish Commission, 1874." In handwriting of A. E. Verrill. Morphotype B.

ORIGINAL DESCRIPTION. "Discopora nitida, sp. nov. Plate VII, figure 3. From Vineyard Sound and Long Island Sound.

"Easily distinguished by the very small apertures with elongated processes projecting inward from the sides; and by the acute lateral avicularia."

SUBSEQUENT DESCRIPTION. "This Journal, ix, p. 415, pl. VII, fig. 3, June, 1875. Thimble Islands, on algae in pool at low-water; Fisher's I. Sound, 3 to 12 fathoms; Vineyard Sound, 5 to 10 fathoms, common on shells." (Verrill, 1875b).

ADDITIONAL DESCRIPTION. Colonies are incrusting, forming thin circular patches when young and thick, irregular, nodular multilaminate crusts on rocks and shells when old. Some colonies develop into large, subglobular masses several inches in diameter with a mammillate surface. The color of specimens dried with the chitinous surfaces intact is either bright greenish yellow or brownish.

Zooids are small to moderate in size, quadrate to hexagonal, arranged in a regular radiating pattern in primary layers but generally lacking orientation in superimposed layers. Zooid boundaries are distinct and separated by a raised line. The frontal is perforated by a marginal row of rather large areolar pores and a few additional frontal pores in very young zooids. The surface is convex with numerous low tubercles in younger zooids. In older zooids with advancing calcification, the frontal becomes somewhat flattened, the areolar pores become funnel-shaped and separated

by prominent costate processes, and the tubercles sometimes coalesce to form low, rounded knobs.

Primary orifices are round to squarish, with a lyrule and a pair of condyles with decurved tips. Secondary orifices are open, wide proximally and lack a sinus. Orificial collars (peristomes) may be produced as a pair of lateral lappets between which proximal finger-like projections may develop. Two or three spines occur on the distal border of the orifice.

Ovicells are globose, have a perforated frontal area surrounded laterally and distally by an imperforate, thickened rim which becomes progressively roughened and tuberculate during secondary calcification. Avicularia are variable in size and position (see below). Mandibles are acute or oval and may widen distally. The number and size of interzooidal pores is variable in both lateral and distal walls.

MEASUREMENTS. Three series of measurements were made. The first series is of the lectotype (USNM 4340, morphotype A), the second is of two nodules from Lambert Cove, near Woods Hole, Mass. (YPM 2900, 2901, morphotype A) and the third is of one of the paralectotypes (USNM 4340, morphotype B).

```
(1)
       Lz
              (15) 0.417 (0.058) \text{ mm.}, 0.31 - 0.52 \text{ mm.}
       12
              (15) 0.358 (0.038) \text{ mm.}, 0.26 - 0.40 \text{ mm.}
              (15) 0.117 (0.004) mm., 0.11
       Lo
                                               — 0.13 mm.
       10
              (15) 0.122 (0.010) mm., 0.11
                                               - 0.14 mm.
       Lav
              (15) 0.123 (0.013) mm., 0.11
                                               -0.15 mm.
              (15) 0.322 (0.041) mm., 0.24
(2)
       Lz
                                               — 0.40 mm.
              (15) 0.280 (0.033) mm., 0.21
       1z
                                               - 0.36 mm.
       Lo
              (15) 0.110 (0.007) mm., 0.09
                                               - 0.12 mm.
              (15) 0.111 (0.007) mm., 0.10 — 0.12 mm.
       10
              (15) 0.117 (0.012) mm., 0.09
                                              - 0.14 mm.
       Lav
       Lov
              (10) 0.199 (0.013) mm., 0.18
                                             — 0.22 mm.
       lov
              (10) 0.255 (0.025) mm., 0.23
                                              - 0.31 mm.
              (15) \ 0.497 \ (0.058) \ \text{mm.}, \ 0.42 \ --- \ 0.60 \ \text{mm.}
(3)
       Lz
              (15) 0.267 (0.045) \text{ mm.}, 0.21 - 0.37 \text{ mm.}
       1z
              (15) 0.104 (0.007) mm., 0.094 — 0.12 mm.
       Lo
              (15) 0.104 (0.007) mm., 0.089 — 0.12 mm.
       lo
              (20) \ 0.196 \ (0.009) \ \text{mm.}, \ 0.18 \ -- \ 0.21 \ \text{mm.}
       Lov
```

lov (20) 0.239 (0.011) mm., 0.22 — 0.26 mm. Lav (14) 0.100 (0.009) mm., 0.085 — 0.11 mm. (orifice associated) Lav (10) 0.102 (0.007) mm., 0.094 — 0.12 mm. (ovicell associated) Lav (15) 0.086 (0.007) mm., 0.068 — 0.096 mm. (spatulate form)

REMARKS. The colony chosen as lectotype, from Vineyard Sound, 1874, was found at the U.S. National Museum with the number "38" on it in Verrill's handwriting. This number matches a label found with specimens in the Peabody Museum Verrill collection with the designation "38, D[iscopora] sp. nov. with avicularia. Long I[sland] Sound, Fish Com[mission], 1874"; both number and species name are in Verrill's handwriting. The U. S. National Museum specimen is the same species (but not the same specimen) as that which Verrill (1875a) illustrated. (The fate of the illustrated specimen is not known). Verrill's original description was based on specimens collected in 1874 "from Vineyard Sound and Long Island Sound"; thus we conclude that the U. S. National Museum and Yale specimens belong to Verrill's syntypes.

All of the syntype material can be sorted very easily into two phenotypic groups. The same groups are found in the abundant material from the southern New England area in the collections of the U. S. National Museum and in our collections from along the Atlantic coast of the United States. This observation seems to be novel although both phenotypes have been illustrated in the literature. Depending upon their characteristics, such sympatric, infraspecific, and morphologically distinct units have been called demes, varieties, forms, morphotypes, clines or subspecies (see Simpson, 1961:176-180). In the examples at hand, the geographic range of each group is sufficiently large that one knows he is not dealing with a deme. In addition, both forms occur together over a wide part of their range so it is unlikely (though not impossible) that this is a cline. We follow current usage in referring these to the least objectionable term for such populations, namely morphotypes. Further consideration of the species in the "Parasmittina trispinosa" complex in studies now being made may lead us to designate morphotype B as a distinct species, separate from P. nitida.

The two morphotypes have the following characteristics:

Morphotype A (Fig. 13A-B) is the form figured by Verrill (1875a:pl. 7, fig. 3) and is the same kind as the lectotype.

- (1) Avicularium acute, single, directed proximally, placed on the frontal to one side of the mid-line, partly to completely *proximal* to the orifice, its chamber originating from one of the lateral areolar pores.
- (2) Orifice squarish; condyles prominent; lyrule low, rectangular, free margin straight, about one-quarter to one-third width of orifice.
- (3) Orificial collar low, rarely produced into lappets or fingerlike projections; proximal border free of projections, gently sloping down to lyrule.
- (4) Frontal area of ovicell evenly perforated by many (usually more than 10) small, round pores; its orificial margin lacking a beak or border formed by the orificial collar; no avicularium associated with ovicell.

Morphotype B is the form emphasized by Osburn (1912a) and the one that has since been accepted as the typical *P. nitida* (Fig. 12D).

- (1) Avicularia most frequently of two types (a) and (b), but a third type (c) is also found. (a) A small, narrow, acute, single form placed *lateral* to the orifice, its rostrum elevated on the side of an orificial lappet, its orientation disto-medial. This type is absent in some colonies and is not illustrated here. Rarely it has a reverse (proximal) orientation, but in this instance, its position relative to the orifice and its narrowness distinguish it from those of morphotype A. (b) An oval avicularium, often widened distally, with variable orientation, is found on the side of the orifice opposite to that of the acute avicularium; additional avicularia of this type may be scattered around the frontal margin of the zooids. The ovoid avicularium type is nearly always present. (c) Giant avicularia of various shapes and with enlarged chambers are present in a few zooids (not illustrated here).
- (2) Orifice rounded; condyles commonly reduced; lyrule narrow, usually one-quarter width of orifice, or less.
- (3) Orificial collar elevated as lateral lappets, frequently with additional projections around the proximal margin.

(4) Ovicell perforated by fewer (up to about 10), larger, and more irregularly shaped pores than those of morphotype A. Orificial collar continued around proximal border of ovicell to form a beak or raised border. An acute avicularium with its rostrum raised on the sides of the ovicell is present in most ovicells.

The following additional differences separate morphotype A from B:

(1) The dimensions of the two morphotypes are similar but differences are present (Fig. 6). Morphotype B, in general, has longer and narrower zooids, shorter and narrower orifices, and shorter avicularia than morphotype A.

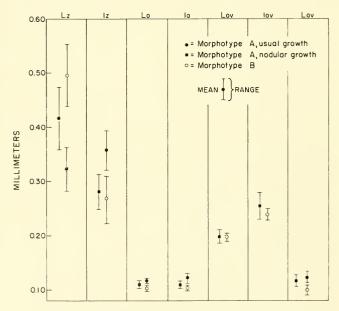


FIGURE 6. Graphic comparison of mean and one standard deviation of linear dimensions from three series of measurements on *Discopora nitida*. Note that morphotype A is not clearly distinguished from morphotype B. The avicularium type plotted for morphotype B is the normal, pointed variety associated with the orifice.

- (2) Only morphotype A appears to form the nodular growths (discussed below), such as the one figured by Osburn (1912a:pl. 30, fig. 88).
- (3) Morphotype A is a bright greenish-yellow in dried condition whereas morphotype B is brownish or brownish yellow.
- (4) Morphotype A presents a remarkably uniform microscopic appearance in bleached specimens whereas morphotype B has a much more variable appearance.

Literature illustrations are assigned, where possible, to the two morphotypes as follows:

Morphotype A
Verrill, 1875a:pl. 7, fig. 3
Osburn, 1912a:pl. 27, figs. 66b, 66e.
Canu and Bassler, 1923:pl. 31, fig. 11.
Rogick and Croasdale, 1949:pl. 10, fig. 71.

Morphotype B
Osburn, 1912a:pl. 27, figs. 65a, 66, 66a, 66c, 66d.
Canu and Bassler, 1923:pl. 22, figs. 7-14.
Marcus, 1937:pl. 21, fig. 56.
Rogick and Croasdale, 1949:pl. 10, figs. 68-70.
Maturo, 1957:fig. 62.

Ectoproct nodules with a diameter commonly of one to six centimeters occur in basins approximately five to ten meters deeper than the remainder of Vineyard Sound, near Woods Hole, Massachusetts. Basins off Lambert Cove and Tarpaulin Cove, Naushon Island, near Woods Hole, Mass., are examples. Two species of ectoprocts, Schizoporella unicornis and Parasmittina nitida (morphotype A) form nodules. The origin of these nodules is postulated as follows: After the larvae settle, colonies expand around a pebble or other small solid substrate and form a spheroidal crust. The pebbles are washed back and forth in the basins by tides which have a velocity of up to 2.6 knots (Sumner, Osburn, Cole and Davis, 1913). Tidal action removes most of the fine material from the basins and the pebbles are unable to come to a stable position. If the pebble were in one place, as is the usual situation over most of Vineyard Sound (and other areas), then

the ectoproct could only grow on the exposed surface. Measurements of *Parasmittina nitida* from a nodule showed smaller average dimensions than those from a stable substrate (the lectotype).

Verrill's *Discopora nitida* belongs in the genus *Parasmittina* Osburn, 1952. Most authors have followed Osburn (1912a) in designating *nitida* as a variety of *P. trispinosa* (Johnston). However, Harmer (1957) considered *P. nitida* to be a distinct species, an opinion with which we agree. The lectotype of *P. trispinosa* (BM 47.9.16.61, chosen by Brown, 1952) differs most noticeably from *P. nitida* in the following ways:

- (1) Its common avicularium type is large, frontally placed, and always oriented disto-medially, the rostrum terminating on the orificial collar.
- (2) The proximal border of the orificial collar is elevated and possesses a conspicuous V-shaped notch or groove which gives the secondary orifice a prominent sinus as calcification proceeds.
- (3) Perforations of the ovicell are limited to about three large pores in the central area.

Cotype material of *Smittina maleposita* Canu and Bassler consists of several specimens from the "Pliocene, DeSoto Co., Florida (USNM 68641)" and from the "Pleistocene (Recent?) of Vero, Florida (USNM 68642)." The Pleistocene (Recent?) specimens are referable to *Parasmittina nitida* and the Pliocene material thus forms the basis for *S. maleposita*.

Genetic and geographic relationships among the species discussed above and others closely related, including *Parasmittina spathulata* and *P. jeffreysi* have yet to be determined. At present, *P. nitida* appears limited to the western Atlantic between New England and Brazil.

## Escharina porosa Verrill, 1879 Figure 12A.

Escharella pertusa? (Esper): Verrill, 1875b:41.

Escharina porosa Verrill, 1879e:193.

Lepralia pertusa (Esper): Osburn, 1912a (part):241, pl. 26, fig. 56, (not fig. 56A).

Hippodiplosia pertusa (Esper): Osburn, 1933:41, pl. 14, fig. 8. ?Hippodiplosia pertusa (Esper): Hastings, 1930:724, pl. 17, fig. 118.

PRESENT AUTHORS' DESIGNATION. (Part) Hippoporina porosa (Verrill, 1879), (part) Hippoporina verrilli Maturo and Schopf.

TYPE. Lectotype of *Escharina porosa* Verrill, chosen here: YPM 2902 (4811), "*Escharella pertusa*?, Long I[sland] S[oun]d, U. S. F[ish] C[ommission], 1874, A. E. V[errill]." In handwriting of A. E. Verrill.

ADDITIONAL MATERIAL. Paralectotypes.

- (1) USNM 4811, from same lot as above.
- (2) YPM 2903A, "Esch[arella] pertusa, Long I[sland] Sound, Fish Com[mission], 1874." On shell marked "Noank." Label and shell marking in handwriting of A. E. Verrill. [Shell No. 2, colony A (our designation)].

ORIGINAL DESCRIPTION. "Zoarium encrusting shells and stones. Zooecia large, oblong, perforated by numerous, rather large, round pores; apertures large, roundish, with a broad, shallow, median sinus, and small, lateral, opercular denticles. Ooecia large, prominent, globose, the surface rough with sharp granules, and perforated by small, inconspicuous pores. Avicularia scarce, often absent, when present lateral, opposite the side of the aperture, broad, obtusely rounded, the point directed toward the zooecial aperture [but see below]. Color, when dry, reddish brown.

"Vineyard Sound and Long Island Sound, 8 to 12 fathoms, common."

ADDITIONAL DESCRIPTION. Lateral walls have communication pores in two rows: usually five in upper row and seven in lower row. Distal wall has approximately 12 communication pores in a row which follows the basal and lateral margins of the wall. Hinge condyles are well developed.

MEASUREMENTS. Dimensions are of the lectotype, YPM 2902. Other specimens which we would assign to *Escharina porosa* may have larger dimensions.

Lz (15) 0.510 (0.070) mm., 0.39 — 0.65 mm.

z (15) 0.328 (0.038) mm., 0.25 — 0.39 mm.

Lo (15) 0.165 (0.008) mm., 0.15 — 0.18 mm.

lo (15) 0.171 (0.016) mm., 0.14 — 0.21 mm.

Lov (15) 0.259 (0.012) mm., 0.24 — 0.29 mm.

lov (15) 0.322 (0.028) mm., 0.24 — 0.34 mm.

REMARKS. Escharina porosa was erected by Verrill in 1879 for the material that he obtained in 1874 and described in 1875 as being possibly representative of Escharella pertusa (Esper). The lectotype and paralectotypes were collected in 1874 and carry the name "Escharella pertusa?" and "Esch. pertusa," respectively, in Verrill's handwriting.

Close examination of Verrill's 1874 material shows that two distinct species were included in the designation "Escharella pertusa?" and apparently in Verrill's description of Escharina porosa. As first revisors, we here designate the lectotype and paralectotype of Escharina porosa to include the usual, larger form. This appears to agree with the concept expressed by Verrill of large zooids, orifices and ovicells. The rarer, smaller form represents a new species of Hippoporina, described on p. 000.

The large form has orifices about 0.17 mm in length and width, and zooids 0.51 mm in length. The small form has orifices approximately 0.14-0.12 mm in length and width and zooids approximately 0.40 mm in length (compare Figs. 12A and 12B). Although no avicularia occur in the Verrill material now available (see Verrill's original description), an examination of specimens in the Osburn collection at the U. S. National Museum and collections of Maturo indicate that the small avicularia, located lateral to the orifice, are limited to the small form.

Following Osburn (1912a), most authors have placed *Escharina* porosa in the synonymy of *Cellepora pertusa* Esper, 1796, the type of the genus *Hippoporina* Neviani, 1895. We agree that *Hippoporina* is the appropriate genus for porosa Verrill. We find, however, that there are at least five concepts of pertusa Esper, none of which encompasses porosa Verrill. These may represent five distinct species and are briefly reviewed here.

- (1) Hincks (1880:305) seems to have been the first author to have given a useful description of what was presumed to be pertusa. In fact, his interpretation was considered by Marcus (1920:83) as the one that systematists must use in lieu of the original. Surprisingly, however, neither of the two figures supplied by Hincks (1880: pl. 43, figs. 4-5) fits his text description as well as do the figures published more recently by Kluge (1962: fig. 340), Silen (1943: fig. 4), and Osburn (1952: pl. 40, figs. 5-8). In particular, the avicularia shown in Hincks's figure 4 bear a strong resemblance to those of Hippoporina reticulato-punctata (Hincks) and the ovicells in Hincks's figure 5 seem to lack the "smooth border around the base" that characterizes the ovicells figured by the more recent authors listed above. This feature of ovicell calcification is not found on Verrill's porosa.
  - (2) Another interpretation of Hippoporina pertusa (Esper) is

that represented by the descriptions and figures of Canu and Bassler (1928:106, text-fig. 19b, pl. 9, fig. 6, not pl. 32, fig. 10), Cheetham and Sandberg (1964:1043, text-fig. 54), and Schier (1964:632) for Gulf of Mexico specimens. Taken together, these figured specimens represent a species that differs from Escharina porosa Verrill in the following ways: (a) They have larger zooids with the frontal more finely perforated. (b) Much more of the primary calcified layer (olocyst) is exposed proximal to the orifice, with the perforated secondary calcified layer (tremocyst) forming a pronounced collar around the orificial area. (c) The orifice is conspicuously wider than long, almost semicircular. (d) The operculum is scarcely produced proximal to the condyles. (e) The ovicell is deeply submerged in the tremocyst of distal zooids so that it is barely noticeable even at the growing edge of the colony. (f) At least seven, frequently 12, lateral communication pores and four to seven distal communication pores are located in a row at the junctions of the vertical wall with the basal wall.

- (3) Cook (1964) reported *Hippoporina pertusa* from off Ghana. The material described by her differs from *porosa* in that it has much larger dimensions, larger and more irregular pores on the ovicell, and the communication pores are fewer and differently arranged.
- (4) Smitt (1873) referred a specimen to *Escharella pertusa* from southwest of Tortugas Island, Florida. It had elongate avicularia which were two-thirds the length of the zooid. This feature is not found in *porosa*.
- (5) Hincks (1892) figured as Lepralia pertusa a specimen from the Gulf of St. Lawrence which differs from porosa by having a much more elongate orifice with greater development of the area proximal to the condyles.

In addition, specimens figured by Waters (1879) from Naples and by Nordgaard (1905) from Norwegian fiords (see Nordgaard, 1918, for his synonymy of *Eschara nordlandica* with *Hippoporina pertusa*) have been referred to *pertusa*. We are uncertain of their correct identity but believe neither represents Verrill's *porosa*.

It is apparent from this diversity of opinion on the correct interpretation of *Cellepora pertusa* Esper that a definitive interpretation needs to be made. This, however, cannot be done until Esper's material is redescribed and types determined because his description and figures are not diagnostic. Thus, although it remains possible if unlikely that *porosa* of Verrill is a junior synonym of *pertusa* Esper, we can say that *porosa* Verrill is distinct from any of the other concepts of *pertusa* mentioned above.

### Gemellaria willisii Dawson, 1865 Figure 15A-B.

Gemellaria willisii Dawson, 1865:3.

Gemellaria loricata var. willisii Dawson: Hincks, 1880:21, pl. 3, fig. 3. Gemellaria willisii Dawson: Cornish, 1907:75.

Gemellaria loricata var. willisii Dawson: Osburn, 1933:74, pl. 4, fig. 6.

PRESENT AUTHORS' DESIGNATION. Eucratia loricata (Linnaeus, 1758).

TYPE. Holotype of Gemellaria willisii Dawson: YPM 2904a-c, "Gemellaria loricata = G[emellaria] Willisii Dawson (type specimen). Sable I[sland], Rec[eive]d from Dr. Dawson, April, 1875." In handwriting of A. E. Verrill. "Gemellaria willisii D[awson]. Sable Is[lan]d." In handwriting of J. W. Dawson (?). YPM 2904a is dry material, the basic lot; YPM 2904b is material restored in detergent for wet examination; YPM 2904c is a slide.

ORIGINAL DESCRIPTION. "General Appearance. — Coenaecium branching in dense tufts from a stout stem (attached to sea-weed). Height of largest specimen, 2½ inches. Fibres flexible, but somewhat brittle; membranous in texture, but effervescing strongly with an acid and leaving a very delicate membranous skeleton. Color brownish white or light-fawn.

"Microscopic Characters. — Pairs of cells seen in profile have at top and bottom a breadth of about one-fifth their length. From the top they increase in width to the base of the aperture, which is a little above the middle of the cells, where the breadth is equal to about one-third of the length, decreasing regularly toward the base. Single cells seen in front are broadest at the top, where the aperture occupies nearly the whole breadth. Aperture oval-ovate, covered with a flat membrane having a semi-circular slit at top. In branching, the highest pair of cells give off from their sides a pair of branches, and usually also one or two stems from their upper ends. This gives to the Coenaecium a densely tufted character.

"The species differs from G. loriculata [Linnaeus] of Britain in its narrower and less inflated cells and longer apertures, and in its more dense habit of growth, arising from the mode of branching above indicated. It differs from G. dumosa [Stimpson, 1853] of the Bay of Fundy, in so far as can be ascertained from the short description of that species, in the form of the aperture."

ADDITIONAL DESCRIPTION. The type colony was found dried and consisting of many separate branches, apparently originally part of a single colony. The ancestrula was not present.

Branches of the colony are slightly twisted along their longitudinal axes (Fig. 15A). Two or three branches may arise from a parent zooid. One branch attaches distally and the other(s) attaches disto-laterally. Frontal surfaces of the daughter zooids initially open in the same plane as that of the parent zooid. In three samples of 100 branchings each, 20, 13, and 13 per cent of the branches were tripartite (Fig. 15B), the remainder bipartite (Fig. 15A).

The orifice is located at the distal end of the frontal membrane and has a semi-circular operculum with a bordering sclerite.

One to three communication pores occur near the proximal end of the basal wall of each zooid. In addition, one communication pore often occurs in the proximal lateral wall at the place where radicals develop.

MEASUREMENTS. Dimensions are of material that had been restored in detergent, YPM 2904b.

Lz (15) 0.620 (0.022) mm., 0.59 — 0.65 mm.

lz (15) 0.180 (0.013) mm., 0.15 — 0.20 mm.

Lo (10) 0.324 (0.013) mm., 0.29 — 0.35 mm.

lo (15) 0.180 (0.013) mm., 0.15 — 0.20 mm.

REMARKS. Specimens referred by Dawson in 1865 to Gemellaria willisi have since been considered by all authors to be identical with, or close to specimens referred to Gemellaria [later Eucratia] loricata Linneaus, 1758. From observations of the type of G. willisi we agree that it belongs to E. loricata although specimens like G. willisi appear to constitute an infraspecific population separate from the "typical" form. Dawson stated that E. willisi differed from E. loricata "in its narrower and less-inflated and longer apertures, and in its more dense habit of growth arising from the mode of branching..." These characters in combination with its tan rather than white color, and stout rather than slender appearance permitted Hincks (1880), Cornish (1907), and Osburn (1933) to recognize E. willisi as a distinct "variety." Osburn (1933:74) thought that this stout variety had also been called americana by Lamouroux (1816) and dumosa by Stimpson (1853).

Besides willisi (and its synonyms), several other "varieties" of Eucratia loricata have been distinguished: arctica of Kluge (1915), aurita of Hasenbank (1932), cornuta of Osburn (1932), and

macrostoma of Ortmann (1890). Consistent differences between "varieties" and "typical" forms have not been considered sufficient for modern authors to regard "varieties" of E. loricata as separate species or subspecies. This may be because the morphology of this group of Eucratia's is exceedingly simple and accordingly any differences that do occur are minor compared to those that distinguish other groups of closely related ectoproct species.

# Hippoporina verrilli Maturo and Schopf, n. sp. Figure 12B-C.

Escharella pertusa? (Esper): Verrill, 1875b:41 (part). Lepralia pertusa (Esper): Osburn, 1912a:241 (part), pl. 26, figs. 56a,b,c. Hippodiplosia americana (Verrill): Maturo, 1957:51, fig. 56. Hippodiplosia americana (Verrill): Lagaaij, 1963:192, pl. 5, fig. 4. Hippodiplosia americana (Verrill): Schier, 1964:631.

TYPE. Holotype of *Hippoporina verrilli*: USNM 11920, "New River Inlet, N[orth] C[arolina], 1-1.5 naut[ical] miles offshore; [depth] 16 f[ee]t; coll[ectors] [W. K.] Brooks, [H.] Eppert; 18 June [19]63; F. J. Maturo, [specimen number] 1542." Figure 12C.

ADDITIONAL MATERIAL. Paratypes.

- (1) YPM 2903B, "Esch[arella] pertusa, Long I[sland] Sound, Fish Com [mission], 1874." [On shell number 1, colonies A and B (our designations)]. Figure 12B.
- (2) USNM 11921, "N[orth] of C[ape] Hatteras, 75° 12′ W, 35° 18′ N; 14 f[atho]ms; B[athy] T[hermograph] [Temperature] 50°F. 4 March [19]63; coll[ector] M. Cerame-Vivas; F. J. Maturo [specimen number] 1044."
- (3) USNM 11922, "Cape Lookout, N[orth] C[arolina]; 76° 37′ W, 34° 25′ N; 12 f[atho]ms; divers [W. K.] Brooks and [H.] Eppert; 17 June 119]63; F. J. Maturo [specimen number] 1554."
- (4) USNM 11923, "New River Inlet, N[orth] C[arolina]; 34° 32′ N, 77° 18′ W, 1-1.5 Naut[ical] miles offshore; 16 f[ee]t; coll[ectors] [W. K.] Brooks and [H.] Eppert; 18 June [19]63; F. J. Maturo [specimen number] 1545."
- (5) USNM 11924, Same locality as paratype USNM 11923. "F. P. Maturo [specimen number] 1544."
- (6) USNM 11925, "Off Sapelo Is[land], G[eorgi]a; Drag No. 3; 5 miles off Sapelo Whistle, bearing 340°; shell bottom; 72 f[ee]t; (slide of opercula made); 6/6/[19]62; F. J. Maturo [specimen number] 450."

DIAGNOSIS. A small species of *Hippoporina* with polymorphic avicularia lateral to the orifice, directed proximo-laterally in most specimens, and with a prominent ovicell.

DESCRIPTION. Colonies are encrusting on shell and rock; color when dry is a reddish-brown. Frontal has approximately a dozen evenly-spaced, moderate-sized pores. Orifice is rounded to somewhat squarish with a slight proximal bow behind delicate cardelles. Orificial collar is best developed below the orifice where a prominent umbo can occur (Fig. 12B). Ovicells are hyperstomial and globular, with approximately 20 small pores evenly distributed over the surface (Fig. 12B-C). Areas between pores appear as small nobs giving the ovicell the general aspect of a roughened crust.

Different colonies appear to have different dominant or exclusive kinds of avicularia, which if present, are located on one or both sides of the orifice and are directed proximo-laterally (at various angles) in most cases. The narrow type (Fig. 12C) is directed proximo-laterally; the ovoid and the broadly acute types may also be oriented this way or, less commonly, proximo-medially, laterally, or according to Verrill (1875b) and Osburn (1912a: fig. 56a), disto-medially. Two rows of communication pores occur in lateral walls: four to five in the upper row, four in the lower row. The distal wall has one row of five to eight communication pores.

MEASUREMENTS. Dimensions are of the holotype, USNM 11920, followed by a paratype, YPM 2903B.

```
Lz (15) 0.414 (0.020)
                       mm., 0.37 — 0.47 mm.
                       mm., 0.33 — 0.44 mm.
Lz (15) 0.392 (0.033)
                       mm., 0.22 — 0.39 mm.
lz (15) 0.324 (0.055)
                       mm., 0.23 — 0.37 mm.
lz (15) 0.299 (0.041)
Lo (11) 0.138 (0.010)
                       mm., 0.12 — 0.15 mm.
                       mm., 0.11 — 0.13 mm.
Lo (10) 0.119 (0.007)
                       mm., 0.12 — 0.15 mm.
10
    (11) 0.130 (0.007)
                       mm., 0.11 — 0.13 mm.
    (10) 0.121 (0.007)
                       mm., 0.20 — 0.23 mm.
Lov (10) 0.212 (0.008)
                       mm., 0.17 — 0.21 mm.
Lov (15) 0.195 (0.010)
                       mm., 0.26 — 0.30 mm.
lov (10) 0.281 (0.011)
                       mm., 0.21 — 0.26 mm.
lov (15) 0.241 (0.016)
Lav (10) 0.122 (0.0089) mm., 0.11 — 0.14 mm.
```

REMARKS. Examination of Verrill's specimens of "Escharella pertusa" revealed that large and small forms had evidently been

grouped together. The large form is Hippoporina porosa (Verrill's Escharina porosa, see discussion under that species), and the small form is our newly described Hippoporina verrilli. On close examination, several features serve to distinguish H. verrilli from H. porosa and other closely related forms. Of the four species especially needing comparison (Table 8), H. porosa is by far the largest and it also lacks avicularia. The other three species have about the same dimensions although H. lacrimosa is slightly bigger than the others. H. verrilli has polymorphic avicularia whereas H. acuta and H. lacrimosa each have but one type — acute and spatulate forms, respectively. The ovicell of H. acuta is less prominent than that of H. lacrimosa or H. verrilli, Communication pores of the distal wall are about one-third of the distance up from the base in H. acuta but are nearly at the junction with the basal wall in H. lacrimosa and H. verrilli, H. verrilli and H. lacrimosa have fewer frontal pores than do H. acuta.

The specimen figured by Osburn (1912a: pl. 26, fig. 56a) shows one of the broader avicularia directed disto-medially. Verrill (1875b) also refers to a broad avicularium directed "toward the zoecial aperture." We have not seen this avicularian orientation in our material. However, specimens do occur that are apparently like those of Osburn's figure 56a in all other respects although the size of individuals, which is of special interest for *Hippoporina verrilli*, is not indicated by him.

The range of *Hippoporina verrilli* is at least from Cape Cod southward to the Gulf of Mexico.

# Hippothoa expansa Dawson, 1859 Figure 16.

Hippothoa expansa Dawson, 1859:256.

not Hippothoa expansa Norman, 1868:216, pl. 6, figs. 1, 2.

not Hippothoa expansa Dawson: Hincks, 1880:291-293, pl. 1, fig. 1.

Hippothoa expansa Dawson: Waters, 1900:69-70, pl. 8, fig. 19.

Hippothoa expansa Dawson: Osburn, 1933:34, pl. 9, fig. 19.

Hippothoa expansa Dawson: Osburn, 1952:279, pl. 30, fig. 9.

Hippothoa expansa Dawson: Mawatari, 1956:123, fig. 6a-6e.

Hippothoa expansa Dawson: Kluge, 1962:515, fig. 359.

PRESENT AUTHORS' DESIGNATION. No change.

TYPE. Syntypes of Hippothoa expansa Dawson; YPM 2905a-b. "Hippothoa expansa Daw[son], Type (f[ide] Dawson), Gaspé. Dawson. = H[ippothoa]

TABLE 8. Comparison of four similar species of Hippoporina. Measurements are in millimeters and represent mean values.

| Character                        | Hippoporina porosa<br>(Verrill, 1875) | Hippoporina verrilli<br>Maturo and Schopf   | Hippoporina acuta<br>Cook, 1964                        | Hippoporina lacrimosa<br>Cook, 1964                               |
|----------------------------------|---------------------------------------|---|--|---|
| Zooid length                     | 0.51                                  | 0.40  | 0.40   | 0.50  |
| Zooid width                      | 0.33                                  | 0.31  | 0.30   | 0.35  |
| Orifice length                   | 0.17                                  | 0.13  | 0.11   | 0.11  |
| Orifice width                    | 0.17                                  | 0.12  | 0.12   | 0.125   |
| Ovicell length                   | 0.26                                  | 0.20  | 0.20   | 0.20  |
| Ovicell width                    | 0.32                                  | 0.26  | 0.32   | 0.27  |
| Condyles                         | robust                                | delicate  | delicate   | delicate  |
| Operculum sclerite               | well-developed                        | poorly-developed  | ę.   | 6   |
| Lateral wall communication pores | 5 upper row<br>12 lower row           | 4-5 upper row<br>4 lower row  | ¢.   | 6.  |
| Distal wall communication pores  | 12                                    | 5 to 8<br>very low on<br>distal wall  | about ½ way up<br>distal wall                          | very low on distal wall   |
| Avicularia                       | absent                                | Polymorphic. Narrow<br>and ovoid forms; can<br>be absent; chiefly di-<br>rected proximo-later-<br>ally but occasionally<br>laterally or even disto-<br>medially | medium width,<br>pointed; directed<br>proximo-medially | broad, spatulate; di-<br>rected proximally (at<br>various angles) |
| Ovicell                          | very prominent                        | very prominent  | somewhat ob-<br>scured by cal-<br>cification           | very prominent  |
| Frontal wall                     | about 40 pores                        | about 15 pores  | ? number pores   | about 25 pores  |
|                                  |                                       |   |  |   |

divaricata var." In handwriting of A. E. Verrill. YPM 2905a is dry material encrusting a pebble; YPM 2905b is a slide with zooids from YPM 2905a.

ORIGINAL DESCRIPTION. "Cells oval, depressed, and expanded at the sides, not contracted at the base, branching dichotomously. When magnified the surface presents indistinct tranverse wrinkles and delicate longitudinal lines. Aperture, small, round, with a slight sinus. Texture hyaline, but less delicate than H[ippothoa] divaricata."

ADDITIONAL DESCRIPTION. In the type colonies, all zooids encrust a small pebble, 1.0 X 0.5 X 0.5 cm. An ancestrula is absent. Zooids are ovate to sub-rectangular, with indistinct lateral borders, and may have a flattened calcareous basal expansion. Fertile zooids are approximately equal in length to nonfertile zooids. Orifices are subterminal. Fertile zooids have a reduced secondary orifice and are of about the same size and shape as autozooids (Fig. 16). The primary orifice of fertile zooids is wider and shorter than that of infertile zooids.

MEASUREMENTS. Dimensions are of the syntypes, YPM 2905a-b. Autozooids

```
Lz (5) 0.479 (0.029) mm., 0.45 - 0.52 mm.
```

lo (5) 0.073 (0.0137) mm., 0.058 — 0.085 mm.

### Fertile zooids

```
Lz (3) 0.471 (0.018) mm., 0.45 — 0.50 mm.
```

REMARKS. Very few of the zooids of the type material are connected to each other at the present time. Our concept of this species is based on all of the available material. We call attention to these facts by designating the type material as syntypes rather than choose a few zooids as the holotype.

Dawson's type material from Nova Scotia and material illustrated by Kluge (1962) from the European Arctic agree in all important respects. Waters (1900) described an operculum of a specimen from Franz Josef Land that is approximately 0.07 mm wide and 0.08 mm long. This is in good agreement with the orifice size of Dawson's type material. Hence specimens figured by Kluge

and Waters are considered to represent Dawson's Hippothoa expansa.

Specimens figured by Norman (1868) and Hincks (1880) are separate from Dawson's species, but similar to each other, in the following ways: (1) Both are pyriform in outline. (2) Both have a terminal orifice. (3) Both have a prominent tubular stolon at the base of most zooids. (4) Both have a very broad calcareous lamina extending laterally from zooids. (5) Both have transverse striae that appear to be very prominent and regularly spaced. In addition, Norman (1868) states that the zooid length is 1/20 inch, or 1.3 mm which is more than twice as long as the species named by Dawson. Norman was unaware of Dawson's work when, in 1868, he named a species Hippothoa expansa thus inadvertently establishing a junior homonym. It appears from the above listings that Norman's and Dawson's specimens represent two different species. Hence Norman's species needs to be renamed.

Other specimens have been referred to Hippothoa expansa by Osburn (1933, 1952) from off New England and the west coast of North America, and by Mawatari (1956) from the Kurile Islands, Each of these differ from the concepts outlined above in one or more possibly fundamental ways. However, we do not know enough about variation within a population to be certain of their placement. Osburn's New England material has a pyriform outline, wide calcereous lamina, terminal orifice and thus appears closer to Norman's British species than to Dawson's Canadian species. Osburn's west coast material has ovicells that are broader than long, a feature not found in either Dawson's or Norman's species. Mawatari's Japanese material apparently lacks a sinus in the primary orifice of fertile zooids. At least in Dawson's species, the primary orifice of the fertile zooid has a distinct sinus although obscured in frontal view.

## Lepralia americana Verrill, 1875 Figure 11A-C.

Lepralia americana Verrill, 1875a (part):415, pl. 7, fig. 4; [fig. 5 = Cryptosula pallasiana (Moll)].

Lepralia americana Verrill: Verrill, 1875b:42 (in part).

Lepralia americana Verrill: Osburn, 1912a:241, pl. 25, figs. 55, 55a.

not Hippodiplosia americana (Verrill): Hastings, 1930:725, pl. 11, fig. 61.

Hippodiplosia americana (Verrill): Osburn, 1933:40, pl. 14, figs. 6, 7. not Hippodiplosia americana (Verrill): Marcus, 1937:101, pl. 20, figs. 54a-b. Hippodiplosia americana (Verrill): Hutchins, 1945:543. not Hippodiplosia americana (Verrill): Osburn, 1952:339, pl. 40, fig. 4. not Hippodiplosia americana (Verrill): Maturo, 1957:51, fig. 56. not Hippodiplosia americana (Verrill): Lagaaij, 1963:192, pl. 5, fig. 4. not Hippodiplosia americana (Verrill): Cook, 1964:6, text-fig. 1B. not Hippodiplosia americana (Verrill): Schier, 1964:631.

PRESENT AUTHORS' DESIGNATION. Hippoporina americana (Verrill, 1875).

TYPE. Lectotype of Lepralia americana Verrill, chosen here: YPM 2906, "Lepralia pallasiana V[errill] (or porosa nov.), off Noank, [Connecticut], 40 f[athoms], [locality] 29, Fish Com[mission], 1874." Second label: "4815, L[epralia] Americana V[errill]." Both labels in handwriting of A. E. Verrill.

ORIGINAL DESCRIPTION. "Plate VII, figures 4, 5. = L. Pallasiana? V., in former papers. Long Island Sound to Beverly, Mass., low water to 30 fathoms."

Subsequent description. "This Journal, vol. ix, p. 415, plate VII, figs. 4, 5, =L. Pallasiana? Verrill, Report on Invert., p. 713, 1873. New Haven Harbor; Noank, on eel-grass, etc.; Vineyard Sound; Beverly, Mass.; Long. 1. Sound, low-water to 40 fathoms (loc. 29), on shells, stones, etc., with ooecia." (Verrill, 1875b)

ADDITIONAL DESCRIPTION. The type colony is encrusting on a shell. Zooids are of moderate size, quadrangular to hexagonal in outline. The frontal wall is perforated by a few evenly-spaced pores (usually fewer than 15) which form a marginal row at the lateral and proximal borders with a few additional pores occurring on the proximal half of the frontal surface. The frontal surface is roughened by a thickening of the calcification between the pores. In some zooids the thickenings become costate and may rise to a prominent, thick, blunt umbonate process proximal to the orifice (Fig. 11C). Viewed from its distal side, the umbo appears as a thick, elevated fold in the frontal calcification which does not reach the proximal edge of the orificial collar (peristome) and thus leaves a thin, triangular, imperforate area subjacent to the orifice.

The orifice is large, rounded or slightly quadrate, somewhat longer than wide, and with a broadly curved proximal portion (behind small condyles) that varies in depth from one-third to one-quarter the length of the orifice (Fig. 11B). The operculum has a narrow, encircling sclerite that is set in slightly from the border. The orificial collar is low proximally and distally, but in many zooids is elevated laterally into lappet-like processes.

Four communication pores occur near the base of each lateral wall and a pair of multiporous rosette plates are present in the lower part of the distal wall. Ovicells are large, subglobular, wider than long, and occasionally partially immersed. The outer wall of the ovicell is perforated by from four to ten rounded to irregularly-shaped pores, approximately two to five of which are very large (Fig. 11A-C).

Avicularia are absent in the lectotype but occur, for example, on a bilaminate specimen in the U.S. National Museum Osburn Collection (USNM 11916) (Fig. 11A). They are medial and suboral on the distal surface of the umbo. The avicularian chamber is in the umbo fold and appears to arise from a lateral pore that connects with the umbo chamber on one side only. The rostrum is elevated and points proximally. The mandible is broadly acute, about as wide as long. The hinge bar is very delicate and absent in many zooids.

MEASUREMENTS. Dimensions are of the lectotype, YPM 2906.

Lz (15) 0.538 (0.045) mm., 0.48 — 0.60 mm.

lz (15) 0.314 (0.021) mm., 0.27 — 0.35 mm.

Lo (15) 0.177 (0.006) mm., 0.17 — 0.19 mm.

lo (15) 0.150 (0.005) mm., 0.14 — 0.16 mm.

Lov (15) 0.210 (0.007) mm., 0.20 — 0.22 mm. lov (15) 0.249 (0.013) mm., 0.23 — 0.27 mm.

REMARKS. In a paper discussing the results of dredgings made in 1874 off the New England coast, published in June of 1875, Verrill erected *Lepralia americana* on the basis of two figures, stated that it equaled the "*L. pallasiana*?" in his former papers, and gave the range in general terms as Long Island Sound to Beverly, Massachusetts. Verrill's Figure 5, believed by him to be *L. americana* without ovicells, is now clearly regarded as *Cryptosula pallasiana* (Moll) and has been cited as such by works from Osburn (1912a) to date. The name *L. americana* thus has been restricted to the species represented by the remaining Figure 4 which illustrates an ovicelled colony.

In July of 1875, a month after the original description, and still considering the results of the 1874 dredgings, Verrill included *L. americana* in a list of species new to the fauna of southern New England, indicating, however, that it was, strictly speaking,

"not new to the fauna" but was listed "in order to confirm the localities..." This was a clarification of the general distribution mentioned in the original description.

One of the new citations is "Long Island Sound, low water to 40 fathoms (loc. 29), on shells, stones, etc., with ooecia." The specimen at hand bears ovicells and has this same label with the addition that it was collected in July, 1874. Thus it appears that this specimen is one of those that Verrill had in hand when he erected *L. americana*.

At least six specimens were sent as a single lot from locality 29 to the U. S. National Museum. The U.S.N.M. entry for this lot (USNM 4815) reads (in part): "1 A.E.V., 5+ NM, on shell fragments," meaning that one of the specimens was held by Verrill and 5+ were held at the U.S.N.M. A search of National Museum collections failed to produce its part of lot 4815. The lectotype is the specimen from the Peabody Museum Verrill collection and presumably is the sole remaining syntype.

The americana of most authors differs from Verrill's species by having: (1) a series of uniporous communication pores, usually four in a row, in the distal wall of the zooids, instead of two multiporous rosette plates; (2) smaller dimensions, particularly of the primary orifice; (3) a more arcuate proximal border of the orifice; (4) more numerous and more closely set frontal and marginal pores; and (5) avicularia that are lateral rather than proximal to the orifice, the mandible variously oriented.

Verrill's *americana* belongs in *Hippoporina* (see Cook, 1964, for discussion of the genus). The range of *H. americana* (Verrill) appears limited to the region from Mt. Desert Island, Maine, to the north side of Cape Hatteras, North Carolina (data of Maturo).

## Lepralia plana Dawson, 1859 Figures 5F-G, 13C, 14.

Lepralia plana Dawson, 1859:256.

?Schizoporella crustacea (Smitt): Waters, 1900:64-65, pl. 8, figs. 11-13.

? Myriozoum crustaceum (Smitt): Robertson, 1908: 295, pl. 21, fig. 54. not Myriozoella plana (Dawson): Osburn, 1952;516-517, pl. 64, figs. 1-2. not Myriozoella planum (Dawson): Mawatari, 1956:135.

PRESENT AUTHORS' DESIGNATION. Myriozoella plana (Dawson, 1859).

TYPE. Holotype of Lepralia plana Dawson: YPM 2907, "Lepralia plana D[awson] (type) f[idc] Daws[on]. Gaspé. J. W. Dawson. = Myriozoum crustaceum." In handwriting of A. E. Verrill.

ORIGINAL DESCRIPTION. "Cells flat, confluent, shallow; walls deeply and irregularly furrowed; mouth rounded above, straight below, often with a narrow sinus in the middle. Young cells hyaline; old cells, opaque and deeply furrowed in a stellate manner. Forms very thin and flat expanding crusts. L. adpressa Busk from Chiloe, resembles it more nearly than any other species known to me."

ADDITIONAL DESCRIPTION. Type colony encrusts shell and consists of approximatey 500 zooids. Transverse furrows cross the colony at 1-2 mm. or four to eight zooid intervals. The outermost of these furrows corresponds with the change from the most recently formed groups of zooids (which have large pores and a hyaline appearance) to the previously formed groups of zooids (which have mostly small pores, often silt-like, and a more opaque appearance) (Fig. 14). Remaining transverse furrows (two or three?) apparently are associated with similar transition zones from previous growth periods. Thus colonies of *Lepralia plana* exhibit a very unusual growth pattern for an ectoproct by increasing in lateral expansion in spurts of approximately four rows of zooids.

The ancestrula is absent in type material and information on it is derived from a figure of Waters (1900) which shows a typical tata with nine spines surrounding the frontal area and with three buds, one anterior and two antero-lateral. However, there is a question if this represents *Lepralia plana* because it hasn't developed sufficiently to show the features of taxonomic usefulness, particularly the ovicells and later calcification.

The frontal of newly formed zooids has fine perforations that very quickly become large pores. These are filled during later stages of calcification and the final appearance is a frontal with several slit-like, comma-shaped openings. Individual zooids lack distinct borders in all stages of growth. Levinsen (1909:297) made the statement the dietellae are present but this could not be confirmed.

The orifice is rounded distally, has straight lateral margins and a straight proximal margin that is interupted medially by a prominent narrow sinus. Muscle scars are prominent on the operculum (Fig. 5F-G). Small, oval avicularia occur lateral or proximo-

lateral to the orifice. They are chiefly directed proximo-laterally. A hinge bar is lacking.

Ovicells are hyperstomial. In ovicelled zooids the orifice slopes strongly towards the basal wall in distinct contrast to normal zooids in which the orifice is in the plane of the frontal. The operculum does not close the ovicell. The upper surface of the ovicell wall is smooth or with minute longitudinal striations. This surface is soon overgrown by an extension of the thick porous calcified crust of neighboring zooids (Fig. 13C). In final calcification, the ovicell is completely overgrown and the only indication of its presence is that the primary orifice slopes steeply toward the basal wall.

MEASUREMENTS. Dimensions are of the holotype, YPM 2907. Precise length and width of zooids were very difficult to determine because zooid boundaries are entirely covered by secondary calcification.

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Lz (5) 0.568 (0.050) mm., 0.51 — 0.64 mm.

lz (7) 0.325 (0.025) mm., 0.29 — 0.37 mm.

Lo (6) 0.119 (0.011) mm., 0.10 — 0.14 mm.

lo (6) 0.129 (0.011) mm., 0.12 — 0.15 mm.

Lav (5) 0.046 (0.007) mm., 0.038 — 0.055 mm.
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REMARKS. Type material of Lepralia plana has not been previously illustrated and the original description was brief. Hence identification of Dawson's species has been problematic since its description in 1859. Norman (1894:127) considered Sars' specific name coarcticum (Sars, 1862; sensu Smitt, 1868:18) as a synonym of Dawson's plana, but later he (Norman, 1903:110) stated that he had seen specimens named by Dawson and that Dawson's plana was definitely Smitt's crustaceum (Smitt, 1868:18). Other writers who have used Dawson's specific name have depended largely on Norman's determination of the synonymy. Writers wishing to make their own identification have used Smitt's crustaceum and stated that Dawson's description was too inadequate to be useful.

Seven authors have figured specimens referred to *plana* or to *crustaceum*. In addition to the four listed in the synonymy, they are Smitt (1868b), Lorenz (1886), and Kluge (1962). Smitt's (1868b) illustrations and description of *crustaceum* differ from *plana* in the following ways: (1) The 'fully calcified' ovicell has

distinct radiating ribs rather than being completely immersed in a crust that has a few small pores. (2) The frontal is reticulate in early and middle stages of calcification rather than being characterized by small round to comma-shaped pores. We conclude that *crustaceum* and *plana* are separate species.

Lorenz (1886) and Kluge (1962) figured colonies in which the frontal surface is reticulate and the ovicells have large drop-shaped pores. In addition, zooid borders are distinct. These specimens appear to be correctly referred to *crustaceum*.

Robertson (1908) figured zooids from the west coast of North America. The ovicells are in an early stage of calcification and have rounded pores and distinct outlines. It is not possible to state if the pores are in the ovicell or in a layer of secondary calcification. The frontal in later stages of calcification is described as "thickly punctate." It is possible though unlikely that Robertson's crustaceum should be referred to plana.

Osburn (1952) also figured zooids from the west coast of North America. Illustrated material is from the margin of a colony and from a more crowded area of secondary growth. These figured zooids differ from plana in the following ways: (1) Later calcification yields a reticulate surface with large pores rather than a smoother surface with small comma-shaped pores. (2) Avicularia are moderate to large rather than small. (3) Avicularia are placed disto-lateral to the orifice rather than proximo-lateral. We conclude that Osburn's plana and Dawson's plana are separate species.

Lastly, Mawatari (1956) described material from the Kurile Islands. These specimens have a frontal that is "perforated rather coarsely" and an ovicell that is marginally distinct and possesses marginal pores. These features are not found in the type of Dawson's plana, and thus Mawatari's plana represents a distinct species. We accept tentatively Myriozoella Levinsen (1909) as the correct genus for the placement of Lepralia plana Dawson. Thus Dawson's species is referred to as Myriozoella plana (Dawson).

## Porellina stellata Verrill, 1879 Figure 1A.

Porellina stellata Verrill, 1879d:53.

Porellina stellata Verrill: Verrill, 1879e:190.

Microporella ciliata var. stellata (Verrill); Osburn, 1912a:234, pl. 24, fig. 45.

TYPE. No type specimens are known to exist.

ORIGINAL DESCRIPTION. "A large, handsome species, forming radiating patches on shells, etc. Zooecia arranged in quincunx, large, broad, moderately convex, white, shining, mostly imperforate and smooth, the marginal ones more or less perforate in front. Apertures nearly semi-circular, the proximal edge straight or nearly so, often with two spines on the distal border, median pore, a short distance from the aperture, large, nearly circular, provided with numerous, slender, convergent spinules, which nearly reach the center, giving the pore a stellate appearance. Avicularia near the lateral margin, about opposite the median pore, varying in size and form: in the same colony some are short triangular, others long triangular, while others with a long and acute, erect tip show the transition toward vibracula. Length of zooecia, .60 to .70 mm; breadth, .50 to .60 mm; breadth of apertures, .12 to .15 mm; of median pore, .05 to .06 mm. The zooecia are about twice as large as those of *P. ciliata*.

"Casco Bay, Maine. (U. S. Fish Comm., 1873).

"In the nearly circular form of the median pore this species approaches the genus *Porina*, as restricted by Smitt, (Florida Bryozoa), but in all other respects, except size, it agrees so closely with *P. ciliata*, made the type of *Porellina* by Smitt, as to forbid a generic separation, although the latter has a crescent-shaped pore. It would belong to *Microporella* Hincks, if that name be adopted."

REMARKS. Verrill did not publish a figure with his original or subsequent (Verrill, 1879e:190) descriptions of *Porellina stellata*. We found a drawing of this species (Fig. 1A) among papers of the Verrill estate given to the American Museum of Natural History by his son, G. E. Verrill (see Verrill, 1958:74). The drawing was evidently prepared by Verrill or under his supervision and bears the designation "*Porina* sp. nov." in Verrill's handwriting.

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FIGURES 7-16

FIGURE 7. A. Amathia goodei, YPM 2894b; part of holotype; X 40. Portion of a branch showing zooids arranged in series on the sides of the nearly transparent stolon. Specimen partially restored by soaking in detergent. B - C. Barentsia timida, YPM 2895c; part of holotype; X 40. Specimens restored by detergent. Note increasing diameter of pedicel from musclium (base) to calyx.

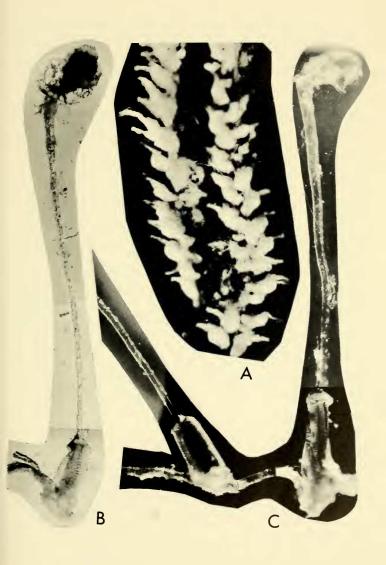


FIGURE 8. A - B. Bugula flexilis, USNM 4365; part of lectotype; X 40. A. Dorsal view showing the bifurcation. B. Dorsal view; note muscles in lower part of zooids. Kenozooid strands occur in the central area between the autozooid branches. C - D. Bugula decorata, YPM 2896; part of lectotype; X 40. C. Frontal-lateral view of zooids, one with ovicell. D. Frontal view of zooids with avicularia.

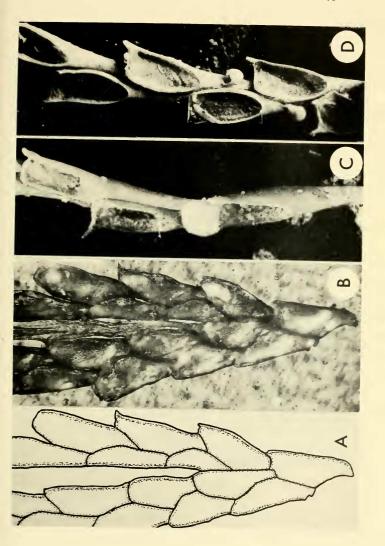
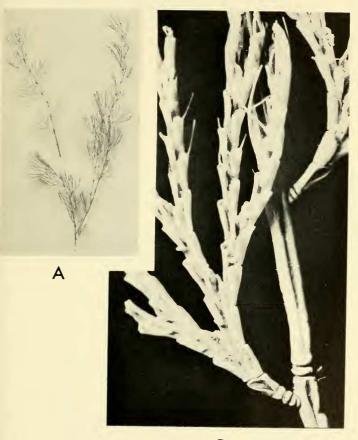


FIGURE 9. A - B. Bugula (Caulibugula) armata. A. YPM 2891a-c; holotype. Photographed by A. E. Verrill; note that the specimen is under water. B. YPM 2891b, part of holotype; X 25. Frontal view showing zooids, branching, avicularia, and spines.



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FIGURE 10. A - C. Bugulella fragilis, part of holotype; X 40. A. USNM 11915d; frontal view of bifurcation. B. YPM 2892; lateral view of zooids with ovicells. C. USNM 11915d; frontal view of zooids with ovicells. D. Bugula cucullata, USNM 4150b; part of holotype; X 40. Frontal view of zooids with ovicells and avicularia.

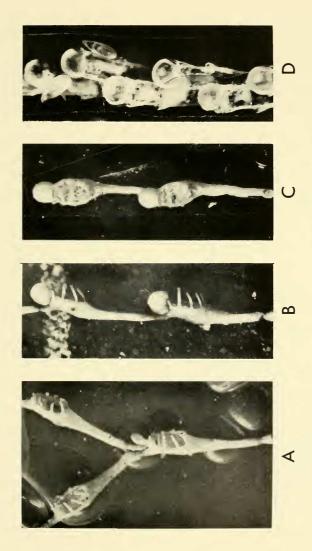
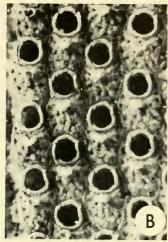


FIGURE 11. A - C. Lepralia americana; X 40. A. USNM 11916; U. S. Fish Commission Station 1577, Bridgeport, Connecticut, October 1, 1890. Note suboral avicularia. B - C. YPM 2906 (4815); lectotype. B. Frontal view of non-ovicelled zooids from near growing edge of colony. C. Frontal view of ovicelled zooids from older portion of colony.





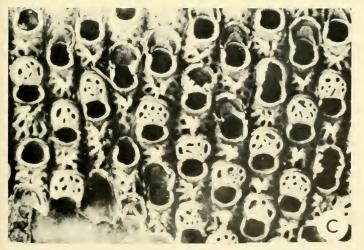


FIGURE 12. A. Escharina porosa, YPM 2902 (4811); lectotype; X 40. Frontal view showing zooids with ovicells. B. Hippoporina verrilli, YPM 2903B, colony A; paratype; X 40. Frontal view showing zooids with ovicells. C. Hippoporina verrilli, USNM 11920; holotype; X 40. Frontal view showing zooids with ovicells and avicularia; note avicularia in "reversed" orientation, i.e., pointing proximally. D. Discopora nitida, USNM 4340; paralectotype; X 40. Frontal view of morphotype B. Note oval avicularia associated with frontal, acute avicularia associated with ovicells, orificial collar, and few large pores of ovicell.

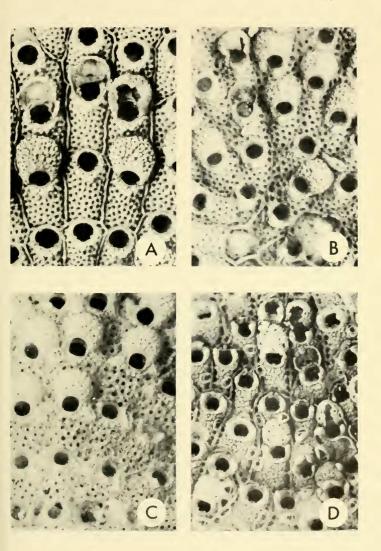


FIGURE 13. A - B. Discopora nitida; X 40. A. USNM 4340; lectotype. Frontal view of morphotype A; note one type of avicularium and lack of orificial collar. B. USNM 4705; Vineyard Sound, U.S. Fish Commission, 1875. Frontal view of morphotype A; note many small pores of ovicell. C. Lepralia plana, YPM 2907; holotype; X 40. Note various stages of calcification of frontal over the ovicells.

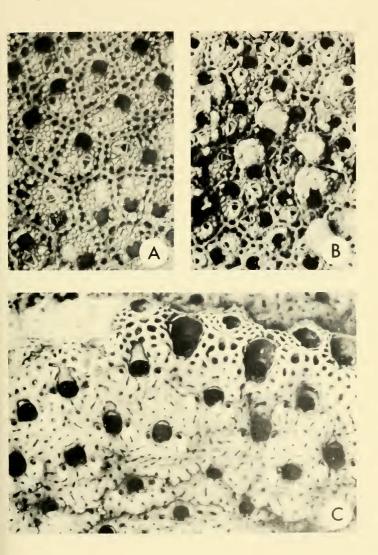


FIGURE 14. Lepralia plana, YPM 2907; holotype; X 25. Approximately upper 40 per cent of photograph is remnant of a former colony. Central band of zooids is the advancing growth edge of a new colony; youngest zooids are in the region with the large frontal pores. Bottom band of zooids represents a period of previous growth.

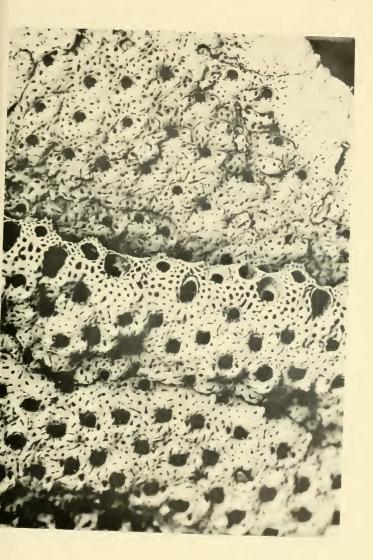


FIGURE 15. A - B. Gemellaria willisii, YPM 2904c; part of holotype; X 40. A. Branch with bifurcation; specimens coated with ammonium chloride sublimate prior to photography. B. Branch with trifurcation; specimen not coated as in A.





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FIGURE 16. Hippothoa expansa, YPM 2905; syntype colony; approximately X 40. Note ovicelled zooids in lower center and in upper left. Note that the orifice of the ovicelled zooid (in upper left) is considerably wider than the orifice of a normal zooid.

