ON SOME LUNULITIFORM BRYOZOA

by EVELINE and ERNST MARCUS

(with 5 plates)

Contents

MATERIAL AND LOCALITIES

The present study comprises: a) *Cupuladria canariensis* (Busk, 1859), b) *Discoporella umbellata* (Defrance, 1823), c) its var. *conica* (Canu & Bassler, 1930), and d) *Mamillopora cupula* Smitt, 1873. Forms a, c, and d are new for the Brazilian coast. We obtained material from seven different localities which follow in the sequence from South to North:

1) Off the coasts of Paraná and São Paulo, Lat. 26° 19' — 25° 45' S, Long. 46° 36' — 46° 58' W, 125 — 150 m; 26. IX. 1955 (a, c).

2) Alcatrazes Island, Lat. 24° 03' S, Long. 45° 40' W, 32 m (principally b, a few c).

3) E of Santos, Lat. 24° 02' S, Long. 46° 07' W, 23 m (b).

3a) Ibid., Lat. 23° 57' S, Long. 46° 09' W, 16 m; 1. VII. 1960 (b).

4) Bay of Flamengo, 14 km W of Ubatuba, Lat. 23° 57' S, Long. 45° 06' W, about 4 m (b).

5) Canal between Anchieta Island (former Porcos Island) and the continent, 14 km W of Ubatuba (see 4), 30 m; 6. V. 1958 (b, c).

6) Near Cabo Frio, Lat. 22° 57' S, Long. 42° 01' W, about 3 m; VII. 1957 (a, c).

7) Off mouths of River Amazon, Lat. 02° 23' N, Long. 48° 26' W, 70 m (a-d).

7a) Ibid., Lat. 02° 58' N, Long. 49° 19' W, 71,5 m (a-d).

The bottom of localities 7 and 7a is silt, that of the others silty sand. The sand grains of our most important locality, no. 4, whence living colonies were examined, generally measure 50-200μ and more, up to 300μ. The sand is especially coarse (grains 0,5-3 mm) at locality 5, whose sand is rich in fragments of shells. The sample of locality 6 consists of fragments of shells, broken and complete Bryozoa.

ACKNOWLEDGMENTS

Dr. Edmundo F. Nonato, Head of the Northern Research Base of the Oceanographic Institute São Paulo, during his ecological survey of the Bay of Flamengo (locality 4) found colonies of *Discoporella umbellata,* collected further specimens together with us, and set up aquaria for observing them alive. Lic. Luiz Roberto Tommasi kindly gave us his samples collected at localities 3, 3a, and 6. From the Oceanographic Institute (Director: Dr. Ingvar Emílsson) we received the material from localities 1, 2, 5, 7, and 7a by courtesy of Drs. Liliana Forneris and Walter Narchi. To our helpful colleagues we express our cordial thanks, and remember our dear friend, the late João de Paiva Carvalho, gratefully, who collected the material of locality 5 together with Dr. Edmundo F. Nonato.

ENVIRONMENT OF LUNULITIFORM BRYOZOA

Mud, silt, and sand are unfavourable for most of the Bryozoa whose larvae generally settle on rocks, stones, shells, algae and other substrata. However species whose larvae undergo metamorphosis after fixation on a sand grain or foraminifer, and whose colonies grow out free beyond this small point of attachment, can thrive on sand or mud. Some of them are anchored to the soft bottom by chitinous or membranous rootlets which may terminate with delicate ramifications (Harmer 1957, p. 649); others, e. g. those of the present study, lie loosely on the bottom. Here competition with arborescent species is insignificant, and that with encrusting ones nearly absent. So the number of free colonies is often abundant in this biotope. At locality 4 a grab whose surface is about 10 × 10 cm hauled 1 litre of sand per sample. As 100 living colonies were obtained with 4 seizings, the density of the population can be computed to 2-3 thousand zoaria per sq. metre. In the eastern Atlantic, near the Cape Verde Islands, and on the coast of Liberia Studer (1887, p. 13, 27) dredged so many lunulitiform Bryozoa that the dead colonies constituted a noticeable component of the bottom.

In the upper littoral where wave action is strongly felt (Stach 1936, p. 63) species with free colonies do not occur. On the other hand, they exceed an upper limit of about 25 m (l. c.) in sheltered localities. This is shown by our localities 4 and 6, and indicated in the literature, e. g. Robertson (1908, p. 315) 7 m near San Pedro, S of Los Angeles, and Osburn (1947, p. 18) 3,7 m in the Gulf of Maracaibo. Samples with all or almost all colonies dead, as those of our localities 7 and 7a, were probably accumulated by currents and do not represent the normal biotope of these species. This possibility should be taken into consideration when isolated findings of numerous lunulitiform Bryozoa are evaluated paleoecologically.

Exceptionally lunulitiform Bryozoa (species a) were caught at the surface of the ocean (Silén 1942a, p. 13; 1947, p. 10). Probably they were lifted by upwelling water. According to Stach (1936, p. 63) the benthic lunulitiform Bryozoa are restricted to places on the bottom where current action is strong. *Species a* found in the pelagial has neither voluminous nor heavily calcified zoaria, so that they may be able to float for a certain time, but we do not believe that they swim actively.

The shape of lunulitiform Bryozoa, resembling a disc with a more or less elevated centre, a bowl, umbrella, or cup, is not natatory. This form is suitable for an aquatic animal that lies on soft bottom. When the colony is cupuliform, sediments drifting down upon the sea floor will not bury the individuals. Moreover vibracula, these cleaners developed especially in anascan Cheilostomata with their membranous frontal wall, occur in the lunulitiform colonies of widely different species. Full conical colonies as those of form c are heavier than the inverted saucer-shaped ones. They remain smaller, so evidently avoiding to be buried in the sand by their weight.

SYSTEMATIC REMARKS

By natural selection the free round colonies of systematically distant species have become similar, and, as in our material, were found together at the same locality (Canu & Bassler 1918, p. 119; 1923, p. 81). "Lunulitiform" and "selenariiform" are descriptive terms used for such colonies, indifferently to which family the species belongs. Convergent shape and high geological age makes the taxonomy of the Bryozoa with lunulitiform colonies rather complex. It is not our intention to exhaust this subject. However for an evaluation of the morphology, in part specific and in part phenotypic, we cannot avoid a summary systematic discussion. Moreover a survey of the geographical distribution of the species studied here requires critical comparison of the previous descriptions and figures.

Three cup- or saucer-shaped Bryozoa of the present material belonging to different taxa of the Cheilostomata occur on the Brazilian coast, in the West Indian region (Osburn 1947, p. 46) and on the American Pacific coast (Hastings 1930, p. 714, 718, 733). These are:

1) *Cupuladria canariensis* (Busk 1859a, p. 66) of the Suborder Anasca (Levinsen 1909, p. 12, 88, 91), Division Malacostega (Levinsen 1902, p. 2), Family Cupuladriidae (Lagaaij 1952, p. 31);

2) *Discoporella umbellata* (Defrance 1823, p. 361) of the Anasca, Division Coilostega (Levinsen 1902, p. 2), Family Calpensiidae (Canu & Bassler 1923, p. 67); and

3) *Mamillopora cupula* Smitt (1873, p. 33) of the Suborder Ascophora (Levinsen 1909, p. 12, 88, 213), Division Ascophora Vera (Harmer 1957, p. 645), Family Mamilloporidae (Canu & Bassler 1927, p. 9, 22).

These species evidence the marine Central America connexion of older Tertiary times (Ekman 1935, p. 57).

CUPULADRIA CANARIENSIS

The name of the genus is justified in the introduction to the following *Discoporella umbellata;* our concept of the species *C. canariensis* is evidenced by the succeeding list of the geographic distribution:

Brazil, off the coasts of Paraná and São Paulo, 125-150 m; near Cabo Frio, about 3 m; off mouths of River Amazon, 70-71,5 m (present material). Caribbean Sea, from N coast of Venezuela (Osburn 1947, p. 10) to Yucatan (Silén 1942a, p. 14); Gulf of Mexico (Canu & Bassler 1928b, p. 16). Lesser Antilles, also from the stomach of a sea-urchin (Silén 1942a); Pôrto Rico (Osburn 1940, p. 354); Florida, incl. Tortugas Keys and Key West (Smitt 1873, p. 10; Osburn 1914, p. 194; Canu & Bassler 1928b; Silén 1942a). Azores, also on the surface of the ocean (Silén 1942a); Madeira (Busk 1859a, p. 66; Norman 1909, p. 289); Canaries (Busk 1859a; Calvet 1907, p. 393). Coast of Liberia (Waters 1888, p. 37); Mauretania, Cape Blanco (Calvet 1907; Canu & Bassler 1928a, p. 16); coast of Morocco (Smitt 1873; Canu & Bassler 1925, p. 13) and Algeria (Waters 1921, p. 412; Dartevelle 1935, p. 560; Gautier 1955, p. 231). American Pacific coast from Cedros Island, Lat. 28° 12' N, Long. 115° 15' W (Osburn 1950, p. 34) and Gulf of California (Canu & Bassler 1929, p. 73; Soule 1959, p. 8-9) along the coasts of Mexico, Costa Rica and Panama to Colombia (Hastings 1930, p. 714), Galapagos and Ecuador (Osburn 1950).

C. canariensis was found in shallow water, about 3 m (present material from Cabo Frio, and Osburn 1947, p. 10) to 259 m (Calvet 1907). According to Osburn's rich material (1950, p. 34) the species is most frequent between 18 and 36 m. Geologically it appears first in the Lower Miocene (Canu & Bassler 1923, p. 29; Lagaaij 1952, p. 34).

The preceding list is based on the exclusion of *Cupuladria guineensis* (Busk 1854, p. 98) and *C. monotrema* (Busk 1884, p. 207). For the inclusion of the material from the coast of Liberia Waters' figure 12 (1921, pl. 30) with numerous basal pores was decisive.

C. canariensis to which our material belongs is characterized by parallel series of chambers which permeate the basal wall of the zoarium. They were first drawn by Busk (1859b, pl. 13, f 2 e) and analyzed by Waters (1921, p. 400). In *C. guineensis* these chambers do not occur; the basal wall contains fine striations, perpendicular to the surface of the colony (Hastings 1930, pl. 8, f. 39). In many cases the zoaria of *guineensis* are thinner than those of *canariensis* (Silén 1942a, p. 9).

Hastings (l. c.) confirms Harmer's statement (1926, p. 267) that *canariensis* has longer and narrower zooecia than the Indowestpacific *guineensis*, narrower cryptocyst, and larger pores on the basal surface. We do not contest these differences when numerous colonies proceeding from the Atlantic and Indic Ocean are compared. However within a given material, as the present one, the measurements of the zooecia vary, and the same holds for the breadth of the cryptocyst. Large and small pores as well as smooth basal surfaces occur in our colonies. The diameter of these pores depends on the stage of growth of the basal chambers (Silén 1942a, p. 9).

According to Hastings (1930, p. 715) also the largest colonies of *C. monotrema,* which are as large as the largest of *canariensis* in the British Museum, have only one layer of kenozooecia on their basal surface. By reason of this character we have classified our material collected N and S of the locality of *monotrema,* off Bahia, as *canariensis*. As young colonies of *canariensis* have one layer too, it was necessary to determine our material from Cabo Frio, rich in young colonies, with help of the relatively few large ones. The "monotrematous" condition of the basal surface of *monotrema* has been emended by Hastings' re-examination of the "Challenger" material. "There are fewer pores on the basal surface of *C. monotrema,* and, though those at the edge are larger than those in *canariensis,* they are soon nearly filled up" (p. 715). We therefore think that the above-mentioned material from Liberia can be placed with *canariensis*. Our material contains small colonies with single pores only, but the larger ones have one pore in some areae and several in others. We cannot judge the operculum of *monotrema*, because our material is *canariensis*. In the latter the operculum can assume the appearance of a basal thickening set off from the frontal membrane, when it becomes somewhat curved by drying. The distal and lateral rims of the opercula in our material are thick; proximally only two lateral sclerites on which the occlusors insert are thickened, the middle passes without limits into the frontal membrane.

The large heterozooecia of *monotrema*, described by Busk as avicularia, and also seen by Kirkpatrick (Waters 1888, p. 37), do not constitute a specific character. They are actually vibracula (Hastings 1930, p. 715) and will be mentioned in the following.

The ancestrula of *C. canariensis* is single (Fig. 1, a), not double (Waters 1926, p. 426). The primary can be recognized by its regular oval form, while the opposite zooecium, which Waters considered as also ancestrular, has somewhat irregular outlines. In Waters' diagram (p. 425), it is true, the contours of this zooecium are as regular as all others, but in his drawing (pl. 18, f. 10) the single primary is the one directed downwards, and the opposite zooecium is not completely ovoid. Young colonies with the zooids d still developing evidence the sequence of the central individuals clearly. Zooecium c, Waters' presumed second primary, occupies the space left between the earlier formed zooids b, and its shape is influenced by their walls. Hence it is often narrower than the primary and the first buds, and its contours are irregular.

The actual centre of young colonies is generally triaxial. The distal-proximal extension of the ancestrula (a) is the first axis; the two first buds (b) form the two other axes and diverge from the primary at angles of 120°. By the development of the third bud (c) between the two first, and of two further individuals (d) between the first buds and the ancestrula, a six-rayed star is brought about as in Waters' figure 11 (1921, pl. 30). Occasionally the first buds stand at right angles to the primary. After development of zooid c, the intervals between c and the two zooecia b allow for budding two further individuals d, and so the centre of the colony appears as an

8-rayed star. The primary and the two first developed zooecia (b) are generally smaller than the later ones, whose growth is sustained by food supplied by more numerous polypides.

Sometimes the larva settles on very small substrata, in other cases on bigger ones, measuring, e. g., 1 × 2 mm. A zoarium on a large sand grain was drawn by Waters (1921, pl. 30, f. 12). Under these conditions the colony grows encrusting for a long time before it incorporates the substratum, or even attains its specific size before it reaches the borders of the stone which remain free. Colonies on big substrata which had grown distorted were found by Osburn (1950, p. 34). He was right to consider *Cupuladria elongata* Sakakura (1935, p. 6) as a distorted *C. guineensis* (Bsk.).

Our material contains many young colonies consisting of the central star only and evidently without any substratum. Some were slowly and partially decalcified in order to preserve a possible minute grain or the vestiges of its incorporation by the basal walls of the first zooecia. It is difficult to explain the inexistency of a substratum satisfactorily. Perhaps the least improbable hypothesis is the settlement of the larva on a substratum to which it did not adhere firmly with its basal wall and fell off immediately after metamorphosis. Another possibility is, if the first hold was a calcareous fragment, its absorption for building the walls of the first zooecia.

Of course the first polypides of the colony normally degenerate first. In our material dead central zooecia are not closed by a more or less porous cryptocyst, as happens in *Cupuladria capriensis* (Waters 1926, p. 432) or in the colony from Anguilla, Lesser Antilles, which Silén (1942a, p. 14) considers as possibly belonging to *canariensis*. As far as our zoaria were caught alive, their central individuals were complete or regenerated (Fig. 2). Regeneration had brought forth an autozooid or a vibraculum (av-dv) bigger than that (v) at the distal end of the autozooecia and with a broader, not longer, seta (si) than the ordinary ones (s). Replacement of an autozooecium by an avicularian heterozooecium was discovered by Levinsen (1907, p. 154) and later described by Buchner (1918, p. 458), Canu & Bassler (1920, p. 67), Silén (1938, p. 329), and Marcus (1938, p. 74). In the present cases of substitution of an autozooid by a vibraculum the original proximal-distal direction is sometimes inverted (Fig. 2, cv), and the old walls are included in the rebuilding. In one of our colonies the six autozooids of the central star and further nine were replaced by large vibracula. This type of total regeneration was first observed by Hastings (1930, p. 714); it is common in *C. canariensis*. In the 8-rayed central star of Smitt's figure 70 (1873, pl. 2) the primary directed to the right and downwards and the adjacent first buds directed to the right and left are evidently regenerated large vibracula with the characteristic oblique chambers. Also in the central region of Hastings' colony from the coast of Colombia (1930, pl. 8, f. 40) and in the ancestrula of a zoarium from the Pliocene (Lagaaij 1953, pl. 1, f. 1 a) substitution of an autozooid by a vibraculum is figured. Several large vibracula are also found in the new central area of colonies originated by regulative budding of a fragment. This zoarial regeneration is described in the following. When the vibracular bristle is lost, as frequently in our material, the rostrum or beak-like opesia (subopercular field) resembles an avicularian opesia. This was certainly the case in Busk's material of *monotrema*.

Autozooecia as well as vibracula produce the above-mentioned basal chambers. They are morphologically kenozoecia (Waters 1921, p. 400; Hastings 1930, p. 715) connected with one another by pores (Waters, pl. 29, f. 2). The one to four series of thick-walled chambers corresponding to one surface zooecium form a common prismatic block whose limits are indicated by stronger brown lines of the basal membrane or epitheca. These limits do not coincide with those of the frontal zooids but with the mid-lines of the latter. Young colonies have thin-walled kenozooecia with spacious central cavities. Their weight is certainly lower than that of older zoaria. In no case, however, is their specific weight so reduced that the 9 colonies fished in the plancton (Silén 1942a, p. 13, no. 7; 1947, p. 10) could float without a sustaining current.

Our material contains fragments along whose breaking-lines numerous zooids produce regenerative buds. Such will be described in *Discoporella umbellata*. Our biggest colony of *C. canariensis* (Fig. 3) has originated from a fragment. This is recognized by the directions of the rows of prisms on the underside. In the centre of this zoarium there is an area with parallel rows of prisms belonging to the fragment. This area is surrounded by radiating rows of the growth after breaking. By comparison of lunulitiform, fossil and recent (*C. canariensis*) species from different localities Dartevelle (1933, p. 69-71; 1935, p. 560) came to the conclusion that agitated water is responsible for the breaking of the colonies (see also Brown 1952, p. 140). Our following observations concerning *Discoporella umbellata* confirm Dartevelle's statement that the regenerative reconstitution of the zoarial form proceeds rapidly. When the zooids near the break produce buds, budding is stopped temporarily on the opposite side. So the colony grows as a coordinated whole, though there is no colonial centre. Silén (1942a, pl. 3, f. 10-12) gave instructive photographs of a regenerated zoarial fragment of *Cupuladria guineensis* (Busk).

DISCOPORELLA UMBELLATA

Smitt (1873, p. 14), Levinsen (1909, p. 155) and Harmer (1926, p. 262-63, 266) recognized that membraniporine as well as microporine species had been united in *Cupularia*. Waters (1921, p. 415) also declared that "a new genus must probably be created for *Cupularia lowei* Busk (1854, p. 99) and *C. umbellata* (Defrance 1823, p. 361, pl. 47, f. 1-1 b)", but did not mention their microporine character.

Canu & Bassler (1919, quoted from 1920, p. 103) introduced the genus *Cupuladria* for a membraniporine species whose original name (Busk 1859a, p. 66; 1859b, p. 87) is *Cupularia canariensis*, not *Membranipora canariensis*, as Canu & Bassler wrote. *Membranipora canariensis*, erroneously given as original name by Jelly (1889, p. 79), is the name used by Smitt (1873, p. 10) in connexion with his above-mentioned distinction between membraniporine and microporine species of *Cupularia*.

The name *Cupularia* was applied by Canu & Bassler (1923, p. 75) to *Lunulites umbellata* Defrance 1823 (see above), a microporine form. Hastings (1930, p. 717-18) did not accept this arbitrary nomenclature. She explained that the first generic name for a microporine "*Cupularia*" is *Discoporella* d'Orbigny (1852, p. 472) and abandoned *Cupularia* whose fossil type-species cannot be defined as membraniporine or microporine. As Bassler (1935, p. 86, 99) formally adopted Hastings' view, the nomenclature of the three genera is now established.

However the confusion as to their contents continues. Canu & Bassler (1923) allocated their genus *Cupularia* to a new family Calpensiidae (p. 67) characterized by the diagnosis "No ovicell. The cryptocyst is perforated by one or two opesiules". Not even the type-species, *C. umbellata* corresponds to this diagnosis, as it has a row of opesiular pores on each side of the cryptocyst. In the description of *C. robertsoniae* (ibid., p. 82) the cryptocyst is described as perforated laterally by seven large opesiules, hence in contrast with the diagnoses of genus and family. Also in the treatise on invertebrate paleontology (1953) Bassler gave a generic diagnosis of *Discoporella*, "zooecia porous with 2 rounded opesiules", discordant with the type-species.

As *Discoporella* d'Orbigny has received a complete and modern definition (Hastings 1930, p. 718), the mentioned incongruities do not affect the state of *D. umbellata* (Defrance 1823). Worse is Canu & Bassler's incorporation of membraniporine species in their microporine genus *Cupularia*. *Lunulites haidingeri* Reuss 1847 (see Lagaaij 1953, p. 35), *Discoflustrella doma* d'Orbigny 1853, frequently called *Cupularia johnsoni* Busk (1859a, p. 67) by neozoologists (Waters 1921, p. 413; Silén 1942a, p. 17), and other malacostegous species come in Canu & Bassler's system under the Coilostega Levinsen 1902, or Coelostega as Harmer (1926, p. 188), Silén (1942b, p. 53 etc.), Brown (1952, p. 122), and Lagaaij (1952, p. 37) prefer to write. Canu & Bassler knew (1929, p. 144) that a microporine cryptocyst with a broken centre is similar to a membraniporine opesia into which calcareous denticles project from the edge of the cryptocyst, and that only microscopic examination reveals the difference of these two types. Nevertheless Bassler (1935) codified the zoological error of 1923 in his widely distributed catalogue (p. 86, 99) alotting all species of *Cupularia* published by Busk, Canu & Bassler, and others to *Discoporella*.

Therefore Silén (1942a, p. 15) following Canu & Bassler (1928; 1929) applied *Cupularia* to *umbellata, lowei,* and *johnstoni,* two coilostegous and one malacostegous form, and Osburn (1940, p. 374), after Bassler's catalogue (1935) called *doma* a *Discoporella,* though he correctly mentions that the spinous processes of its cryptocyst never coalesce. Maturo (1957, p. 41) followed Osburn.

Discoporella umbellata occurs in warm and warm-temperate waters of the Atlantic Ocean, enters the western Mediterranean Sea and reaches the eastern Pacific. Canu & Bassler's opinion (1928b, p. 64) that the species on the American side of the Atlantic is now much less common than in the E Atlantic and in course of extinction is not supported by the following list.

Argentina, Puerto Militar of Bahia Blanca (Canu 1908, p. 275) Post-Pampean, i. e., Recent (p. 327); off La Plata (Silén 1942a, p. 16). Brazil, off coasts of Paraná and São Paulo; São Paulo, between Santos and Ubatuba (present material); off Rio de Janeiro and at Cabo Frio (Silén 1942a); off mouths of Amazon (present material). Caribbean Sea, from the northern coast of Venezuela to Yucatan (Silén 1942a; Osburn 1947, p. 18). Gulf of Mexico (Canu & Bassler 1928b; Silén 1942a). Florida, incl. Tortugas Keys and Key West (Smitt 1873, p. 15; Osburn 1914, p. 194; Silén 1942a). North Carolina, off Cape Fear River and Beaufort (Smitt 1873; Osburn 1914), both localities S of Cape Hatteras. Middle Atlantic (Silén 1942a); Madeira (Busk 1854, p. 99; Norman 1909, p. 290; Soule & Duff 1957, p. 100 mistook this for "Spain"); Canaries (Calvet 1907, p. 393); coast of Algeria (Waters 1905, p. 11; 1921, p. 413; Canu & Bassler 1923, p. 76: explanation of text-fig. 13 A). ?South Africa, Cape St. Blaize, Lat. 34° 11' S, Long. 07° 10' E (O'Donoghue 1924, p. 39). American Pacific coast, from Point Conception (Lat. 34° 25' N, Long. 120° 30' W), the northern Channel Islands (Osburn 1950, p. 114) and San Pedro (Robertson 1908, p. 314), the Gulf of California (Soule 1959, p. 34), along the Central American coast (Hastings 1930, p. 718) to the Galapagos Islands (ead.; Canu & Bassler 1930, p. 11; Silén 1942a) and the continental coast of Colombia (Hastings 1930) and Ecuador, Point of Santa Elena, Lat. 02° 15' S, Long. 80° 55' W (Osburn 1950) and Gulf of Guayaquil (Silén 1942a). Pacific Ocean, between California and Hawaii, Lat. 29° 50' N, Long. 141° 40' W (Canu & Bassler 1929, p. 144).

Discoporella umbellata was found in depths from 4 m (Osburn 1947; present material) and 7 m (Robertson 1908) to 4.979 m (Canu & Bassler 1929). In the regions explored by the Allan Hancock Foundation (Osburn 1947; 1950) it is most abundant between 36 and 73 m. For the first time the species appeared in the Upper Aquitanian of France (Canu 1916, p. 322), that is Lower Miocene (l. c., p. 321).

In the preceding list *Cupularia lowei* Busk (1854, p. 99) is considered as identical with *D. umbellata*. The doubts as to this identity (Hastings 1930, p. 719) disappear in the following study. As Hastings (l. c.) re-examined O'Donoghue's material (1924, p. 39) we also include its locality with a question mark, though O'Donoghue's reference to a malacostegous species, *Cupuladria owenii* (Gray 1828, see Busk 1854, p. 99), indicates that his classification was influenced by a geographic conception. Waters (1905, p. 11), Hastings (1930, p. 719), and Osburn (1950, p. 113) have shown that *Discoporella berardana* d'Orbigny (1853, p. 474), *Cupularia canariensis* Robertson (1908, p. 314; non Busk), and *Cupularia robertsoniae* Canu & Bassler (1923, p. 82) are synonyms of *Discoporella umbellata*. Hincks' *Cupularia umbellata* from the Mergui Archipelago on the coast of Tenasserim (1887, p. 125), already questioned by Waters (1921, p. 414), belongs to *Cupuladria guineensis* (Busk 1854, p. 98), as verified by Hastings (l. c.). In the dredgings of the Travailleur and Talisman (Calvet 1907, p. 393) only the colony from the Canary Islands comes under *D. umbellata,* while the material from 1900 m near the Cape Verde Islands, compared with Busk's *Cupularia denticulata* (1859b, p. 85), seems to be a *Cupuladria* (see Lagaaij 1952, p. 35).

THE COLONY

The colour of living colonies is yellowish red, darker on the upper than on the basal surface. The skeleton begins transparent, so that the black digestive tracts shine through the basal walls, and becomes opaque white with increasing thickness. The polypides and the soft parts of the vibracula are red, storing alimentary amoebocytes dark red. In the vibracular chambers and the opesiular passages the dark red cords of these cells are especially distinct.

The diameter of the colonies is commonly up to 6 mm, and the centre of such zoaria rises 1-1,5 mm above the border. One fragment from locality 2, whose centre and border are wanting, is 7 mm long; the diameter of the complete colony must at least have been 15 mm.

Some thin-walled colonies from locality 5 are rather high, they measure 3 mm in height, 9 mm in diameter.

The origin of a zoarium from a larva, or by the process described as zoarial budding in the following, can be recognized in all colonies, not only by details of the centre, but also by the zoarial shape. Due to the included substratum ancestrular colonies are higher than those that began as buds. To the latter the description "inverted saucer-shaped" is appropriate. Ancestrular colonies begin encrusting, later they incorporate the substratum if possible, and often become distorted. A colony of typical *umbellata* had grown longish, because it had incorporated a 3 mm long stone. Most of our irregular colonies belong to the variety *conica* (Canu & Bassler 1930, p. 12).

Many colonies are quite round. Those whose zoarial buds were detached recently have ragged outlines as that of figure 8 of Norman's *Cupularia lowei* (1909, pl. 37). Zoarial buds and also fragments of colonies broken by mechanical factors generally regulate their orbicular form rapidly (Fig. 22). Under certain conditions the regulation of buds or fragments becomes irregular. This happens when the zoarial bud is already very large at the time of its separation, or when a fragment is nearly as big as the common size of a colony, or perhaps when zoarial budding is delayed by cold or scarce food. Possibly O'Donoghue's zoaria (1924, p. 39; Hastings 1930, p. 719) are irregularly regenerated fragments. Presumably also Busk's colony of *lowei* (1854, pl. 116, f. 1) is a fragment. We have fragments of *D. umbellata* with 5 mm long complete outer border and 6 mm long broken sides which are far from reaching the colonial centre. They must come from colonies about 25 mm in diameter.

THE AUTOZOOECIA

The autozooecia are 0,4-0,5 mm, rarely 0,6 mm long, and 0,3-0,4 mm broad. Their limits are brown chitinous lines. The opercula are broader than high and have thickened rims, also proximally. Their proportions vary; in one and the same colony the height of one operculum was 43,5% of the breadth, that of another 83%. The frontal membrane is thickened around the operculum; this smooth rim ends proximally with two "curves" level with the base of the operculum (Waters 1921, p. 413, pl. 30, f. 1; Hastings 1930, p. 719).

Fig. 4 shows the formation of the frontal cryptocyst by coalescing processes. Sometimes irregular perforations remain in the middle beside the specific 5-10 peripheral opesiules. The latter are all penetrated by parietal muscles which depress the frontal membrane. There are 13-16 tentacles.

The zooids are separated by thick calcareous walls (Fig. 5, ca) and connected with one another by epidermal tubes (Figs. 7, 21, u, w) containing mesenchymal cords. Generally there are two, but also one or three oblique lateral tubes in each quadrant of a zooecium, and one (Fig. 5, me) to each of the vibracula. Exceptionally two tubes are connected with one another. Each tube begins with a chamber (Fig. 6, k) which develops as an outward fold of the body-wall. The fold forms two narrow diaphragms, one at its zooecial origin, and another where it communicates with the tube. The cellular layer of the chamber, the epidermis accompanied by the peritoneum is scarcely distinguishable from the loose mesenchymal cords. The exoskeleton of the chamber is chitinous, not calcified.

Under normal budding conditions the chambers belong to the proximal zooecium, whose tubes form the distal individuals. Here the tubes pass into the body-wall without folds. Where chambers occur in the proximal tubes of a distal zooecium, these have contributed to the regeneration of a proximal zooecium. The frequent destruction of the frontal membrane and cryptocyst with the consequent entrance of water and sand into the body-cavity of a zooecium evidently exercises a stimulus upon the adjacent zooids. Of these also the distal ones react (Fig. 7). These, originally receivers of proximal tubes become producers and develop a chamber at their former entrances, now outlets, of the proximal tubes. The sand grains which fill the broken zooecium are not removed by the budding tissue which produces a new cuticular basal wall over them.

The basal zooecial endocyst (Fig. 5, ez) that is inwards peritoneum and outwards epidermis lies over and produces a thick calcareous base. The external surface of the base is also covered by two layers of cells and an external cuticle. The zooecial and zoarial strata and the basal cuticle are connected by rows of tubules (l). Seen from the basal surface these have the aspect of pores, especially where they end in pits. These pits were described as pores (Waters 1921, p. 400, pl. 30, f. 4), and are retouched in a photograph of Canu & Bassler (1918, pl. 53, f. 4). The series of tubules generally go out from the the mid-line of the zooecia or from a more lateral plane. Waters (1921, p. 412) called the tubules muscles, but they are neither topographically nor histologically myofibrils. They are principally cuticular, and their cellular layers are not visible in the part of the tubules that runs within the calcareous mass. The shallow furrows on the underside (Smitt 1873, pl. 3, f. 76, 80) branching dichotomously from the zoarial centre outwards correspond to the rows of tubules. The calcareous base of the colony secreted by the tubules as well as by the individual basal walls does not show zooecial limits. Only in the centre of young colonies such are recognizable (Fig. 19). In older zoaria calcareous tubercles develop. They are well figured on Canu & Bassler's photograph 16 (1923, pl. 2), rather uniformly distributed, or in about two rows on the bulge between the above-mentioned furrows. By further calcification these tubercles coalesce into a general granular crust. This can later be covered by a new calcareous layer which develops from the margins towards the centre of the basal surface; such a covering can be formed repeatedly. Canu & Bassler (1929, pl. 15, f. 9) figured an under surface whose superposed layers grow from the centre towards the margin.

The polypides are evidently short-lived. The number of such in degeneration and regeneration frequently exceeds that of the functioning ones by far. In a small colony originated by budding which consisted of 5 rows with a total of 27 autozooids only 5 polypides functioned. These were situated in the two outer circles, the outermost individuals were in development, and those of the three inner circles were all in de- and regeneration. The rests of the brown bodies are not accumulated in the zooecial cavity but eliminated by the regenerated polypide, whose digestive tract grows rapidly around them. An optical section of budding or regenerating, hence short polypides, or possibly also completely retracted ones, brings about the aspect of Waters' figure 2 (1921, pl. 30). Such phases did evidently not occur in Hastings' material (1930, p. 719). The present explanation of Waters' figure 2 deprives *Cupularia lowei* Busk (1854, p. 99) of the last distinguishing character from *Discoporella umbellata*.

In none of our well preserved colonies belonging to the budding population did we find any traces of germ cells.

THE VIBRACULA

The vibraculum lies distal to the autozooecium. Its frontal side is generally 0,15 mm, exceptionally 0,2 mm long. The seta is almost colourless, grey to light yellow, smooth, and slightly curved at the tip. Setae of central vibracula are 0,4-0,5 mm long, those of marginal ones 1-1,5 mm. Budding and regenerating vibracula evidence that the area of the frontal membrane (opesia, subopercular field, aperture) is the distal, short part of the chamber, and the proximal long one is the area of the orifice (oral shelf, opercular field). Over the latter rests the developing bristle enclosed in a bag of formative cells, so that it appears broad and beak-like (Fig. 7, sr). The narrowed opercular part of the chamber is asymmetrical, directed to the right or to the left side of the autozooecium. A rule for the distribution to right or left was not recognized in large colonies, but in 65 primaries the distal vibraculum pointed 64 times to the left, only once to the right. The vibracula of the two first buds are symmetrical to one another, both pointing inwards.

A narrow cryptocyst is developed in the opercular and the subopercular area. The cuticle of the gymnocyst is thickened and contiguous with that of the adjacent opercular region of the autozooecium. On the opposite side the thickening is stronger. Also the cystidial projection or hinge-tooth (Fig. 8, h) on this side is bigger than the other. The bigger tooth is more distal than the smaller one. This oblique position of the hinge-teeth contributes to amplify the mobility of the seta.

A concave thickening (Fig. 9, 10, x) of the frontal membrane which corresponds to the frontal plate of certain avicularia (Marcus 1939, figs. 47-48, 50, s) is connected with the base of the bristle (s). At this plate numerous smooth abductor fibres (au) insert, each with its own tendon as in the cited avicularia. The nuclei of the epidermal cells that become tendinous fibres lie all at the same level, in the middle of the tendons. The antagonistic cross-striated adductor fibres (ac) have a long common tendon which inserts on the basal arch of the bristle. Two further bundles of smooth muscle fibres, also with collective tendons, insert at the right and left basal knobs of the seta and act as gyrators (j). The knobs are fastened to the hinge-teeth with tendinous fibres.

The vibracular polypide, though rudimentary, allows to discern tentacle sheath (p) sensory organ (q) with tuft of cilia (ci), ganglion (g), and a tiny gland (r) attached to the tentacle sheath. The two small glands of Waters' figure 15 (1921, pl. 29) are not developed in our material. The nerve going out from the ganglion enters the proximal autozooecium.

The biological significance of the vibracula can be deduced from their substitution in the centre and in other regions of the colony, where the surrounding autozooecia are closed by secondary calcification. Maybe their most important function is the protection of frontal membranes and polypides when the colonies fall upside down. When they are thrown into the aquarium, this position occurs frequently, and the stiff bristles prevent the active surface of many autozoids from touching the sand. On the other hand the setae do not hold the zoaria completely clean from other organisms. The heterotrichous ciliate *Folliculina* is frequent on the basal surface; Foraminifera settle on living colonies; sometimes stolons of thecate hydrozoans grow from the underside on to the upper surface, and one or other incipient encrusting colony of Bryozoa was also seen, oddly enough not *Beania cupulariensis* Osburn (1914, p. 190) which occurs in the littoral of Brazil (Marcus 1944, p. 1). Some boring Ctenostomata had attacked the basal surface of living *Discoporella umbellata* var. *conica*.

LIVING COLONIES

In living colonies the vibracular setae are abduced. This is their resting position. The abduced bristles of the marginal zone project far beyond the border increasing the diameter of the colony, e. g., from 5 to 7,5 mm, and prevent it from sinking into the soft bottom. A mechanical stimulus applied to the frontal membrane of an auto- or heterozooecium is answered by rapid adduction of the neighbouring bristles. According to the intensity of the stimulation a larger or smaller area of vibracula responds. This proves the existence of colonial nervous connexions in addition to that observed between vibraculum and proximal autozooecium.

Adduction is followed by slow abduction after about 4 seconds at 28° C. The bristles react to a single stimulus by several adductions and abductions. The rapid adductions and relatively slow abductions correspond to the striated and smooth fibres of the effecting muscles. The bristle moves downwards in a plane vertical to the surface of the colony; upwards the seta sweeps in a curve. The inclination of the vibracula to the right and the left brings forth a crossing of the opening bristles. They act like tweezers grasping particles and removing them from the surface. However they always act over the same spot and do not attain the areae between their radii of action. The threshold of the stimulus is rather high, at least when the polypides are retracted. Under these conditions a small nematode or mite moving about on the frontal membrane of a vigorous colony did not provoke any reaction of the setae.

The reaction of a colony lying upside down was surprising. A mechanical stimulus applied to the basal surface was evidently strong enough to press the vibracula against the sand. Thereupon the entire colony wavered, set in motion by repeated adductions and abductions of the setae. Locomotion was not brought forth by this general wavering, but may perhaps happen if a localized basal stimulus is responded only by the bristles of the corresponding sector of the upper surface. Such a displacement cannot be called a progressive movement. The vibracula of *Discoporella umbellata* are not locomotive. This function was considered as possible for the vibracula of lunulitiform cheilostomes and even indicated in the older literature (Busk 1854, p. 97, 106; Hincks 1878, p. 9; Tenison-Woods 1880, p. 3), but never confirmed (Harmer 1926, p. 263; 1931, p. 151 ff.; 1957, p. 649).

Upset colonies cannot return to their normal position by themselves. When they lie like saucers on the bottom, they are more exposed to movements of the water than in normal position. This exposure together with the wavering may favour their turning upwards.

ZOARIAL GROWTH

The centre of the colony agrees with that of *Cupuladria canariensis*. The ancestrula is single, and together with it the first zooids form a 6-rayed star (Fig. 11). Sometimes the ancestrula has its first two buds developed laterally, not latero-proximally as is more frequent. In these cases the ancestrula ,the first lateral buds, and the zooid opposite to the ancestrula constitute a cross, and the following 4 zooids transform it into a 8-rayed star (Fig. 12). This type of centre is known of several lunulitiform zoaria (Stach 1938, p. 412). Ancestrular colonies of *Discoporella umbellata* are photographed, e. g., by Canu & Bassler (1928b, pl. 7, f. 1) and by Lagaaij (1953, pl. 1, f. 3a); the former has a 6-rayed, the latter an 8-rayed centre. In one of our zoaria two larvae had settled one beside the other on a stone. One perfectly round colony developed with only slight irregularities in the zone of coalescence.

As in other lunulitiform colonies the frontal wall of old autozooecia in the centre of the zoarium is closed by secondary calcification (Fig. 11). Some opesiulae may continue pervious, but the polypides can no longer function. The endocyst and the funicular cords persist and conduct material for the vibracula which continue active after the central and later on also more peripheral autozooecia are calcified. The outermost zooecia of a colony are vibracula. Between and beyond these heterozooecia the autozooecia produce a thin, not yet individualized budding zone which comprises the frontal as well as the basal side. On the latter the above-mentioned secondary calcification begins early. This is especially distinct in sectors of the zoarial periphery where a further outward growth is hindered by juxtaposed zoarial buds. The young budding zone needs careful examination of colonies preserved in neutral liquids; it collapses in dry zoaria, and if the liquid of preservation is even only a little acid, its thin lime is dissolved. In the following phase calcification and individualization of auto- and heterozooids proceed rapidly. The longest lasting process is the formation of the polypide and the seta.

We have only fragments of colonies of *D. umbellata* without budding zone or without zoarial buds on their margin. These are the above-mentioned parts of colonies with a diameter of about 25 mm.

Their border has ceased to grow and has assumed the characters described later on of *D. umbellata* var. *conica* that frequently has definitive borders in our material.

ZOARIAL BUDDING

The most interesting feature observed in our *D. umbellata* is the vegetative reproduction by colonial buds. Many colonies from the localities 3, 3a and 4 were budding; few were seen from locality 2 (32 m), and some from 5 (30 m) had probably shed their buds. The deep-water samples from 70-150 m did not contain any zoarial buds. We have numerous ancestrular colonies from depths of 30 to 150 m, none at all in 3 and 4 m. Perhaps the settlement of the larva is difficult in irregularly agitated shallow waters. However by budding the species succeeds to populate this biotope. As we have material collected in summer (December, January), autumn (March and April), and winter (June to August), with colonial buds, this propagation seems to be independent of the season. Buds are sometimes already produced by zoaria of 4 mm diameter. As far as can be judged from the small number of colonies that are just beginning to bud, the first two buds arise on opposite sides. The largest colony with buds measured 9 × 7 mm. Up to 15 buds were counted on the periphery of one colony (Figs. 13, 14), but as their connection with the mother--zoarium is fragile, they fall of easily during manipulation, and so still more may occur. In some old colonies encrusted with covering black sediments and with opaque white basal surface the only active zooids were the marginal vibracula. Their buds however continue with transparent calcareous walls and red functioning zooidal organs.

The first step to colonial budding consists in a slight advancement of an autozoid and its vibraculum. Simultaneously the buds beside this zooecium do not develop. On the frontal surface the primordial zooid of the zoarial bud exhibits the same aspect as the adjacent proximal invididuals, but on the basal side it is set off from these by a deep furrow. Sections (Fig. 15) show that the basal membrane of this zooecium is considerably thickened (uc). This cuticular area is less strongly calcified than the further basal surface of the zoarial bud, and constitutes a preformed zone through which the bud readily breaks off. As first individual of a new group this zooid (f) may be called a pseudoancestrula (Canu & Bassler 1923, p. 20; Marcus 1938, p. 70). Its shape differs as little as that of the ancestrula from common autozooids. Canu & Bassler's "membraniporoid ancestrula" (1923, pl. 2, f. 19) is a common autozooecium with broken cryptocyst. The pseudoancestrula is nourished by the two neighbouring proximal autozooecia whose distal connective tubes communicate with it. Exceptionally also material from the undifferentiated budding zone contributes to the formation of the pseudoancestrula. The complete pseudoancestrula emits two distal tubes on either side, thus giving origin to two latero-distal individuals. If such a zoarial bud composed of three autozooids and one heterozooid breaks off, it can already live independently, but generally 10-30 autozoids with their vibracula develop, before the young zoarium detaches. Of course, budded colonies have no central sandgrain or other substratum.

When numerous buds are produced at the same time, the daughter-colonies grow narrow (Fig. 17) and are brimmed with an inhibited and undifferentiated budding zone along their sides. With a smaller number of buds these assume a broad, flabellate shape (Fig. 16) whose budding zone is individualized all round. The detachment of the bud generally takes place by the pseudoancestrula breaking in two (Fig. 17, f). Rarely its proximal end loses the contact with the mother-zoarium. Subsequently the pseudoancestrula, or, in most cases, its distal half, produces a proximal zooecium or a new half (Figs. 16, 18). This regenerated half is a distal one with operculum and a vibraculum .Also the complete zooecium and vibraculum developed in exceptional cases lie opposite to the pseudoancestrula. Therewith the polarity is seen to be inverted in the regeneration or the regulative budding which proceeds from the pseudoancestrula. The direction of the new vibraculum to the right or to the left is not correlated with that of the pseudoancestrular vibraculum. This heterozooid continues active while the original operculum of the pseudoancestrula is closed by calcification. The first polypide of the pseudoancestrula degenerates and a new one appears which is orientated towards the new orifice. The inversion of the polarity of the pseudoancestrula is accompanied by generalized budding of zooids in the sector hitherto facing the mother-colony. So the fan-shaped daughter-colony closes to a circle.

When a large zoarial bud is freed, e. g., one with 40 autozooids, the zooecia on the two sides budding towards one another do not coalesce (Fig. 21, cu). Sometimes this gap remains visible only on the basal surface.

ZOARIAL FRAGMENTS

Of the fragments we treat first those containing parts of the original budding zone. The broken or complete zooecia along the breaking-line produce new opercula and vibracula opposite to the old ones. As in total regeneration (Fig. 7) and regulation of liberated buds (Fig. 18, 19) the reparation of fragments begins with the development of connective tubes. The polarity of the tubes and buds may be inverted, but otherwise the mentioned processes agree with the outward budding in the normal zone of growth of the colony. The production of proximal buds in the fragment stops for a while the development of distal ones in the original budding zone. Thus the fragment approaches circular form and attains it rapidly. By the great number of new zooids in the fragment a somewhat irregular growth of the different sectors takes place, contrary to the colonial bud whose regulation goes out from a single autozooid. We interpret Norman's irregular colonies (1909, pl. 37, f. 7, 9) of *Cupularia lowei* as regulating fragments, and his figure 8 as a zoarium that has recently shed its buds. What Canu & Bassler (1923, p. 81) called an "ancestrula replaced by a special region in which the zooecia are arranged in contrary order" evidently refers to regulating fragments (pl. 2, f. 17-18), whose explanations "ancestrular region" are not correct.

Frequently fragments broken in several directions have defective borders all round and have no original budding zone left (Fig. 22). Their regulation to circular form begins with buds directed proximally and proximo-laterally, while growth in the normal, distal, direction pauses. In our opinion this phenomenon explains the first processes in fragments broken off and in zoarial buds separated from the mother-colony. In all these cases, even when a colonial bud becomes free with an unbroken pseudoancestrula, the proximal continuity is interrupted. Evidently this interruption of the proximal continuity produces an inverted proximal budding and a standstill of the distal budding. It is not known whether this effect is brought about by nervous conduction between the zooecia or by an inverted transport of food in the mesenchymal cords or by both.

DISCOPORELLA UMBELLATA var. CONICA

The colonies of this form are smaller than typical *umbellata,* solid, and their zooecia smaller. The preserved or dry zoaria caught alive are ivory, the bristles of the vibracula golden-yellow. Three millimetres in diameter and 1,6-2 mm in height are common measurements. There are also bigger colonies, 4,7 × 2,8 mm, but these are worn and cannot be determined with certainty. The same holds for flat (5 × 1,5 mm) and hollow (5 × 3 mm) zoaria which might be typical *umbellata,* though the zooecia are smaller.

The autozooecia are 0,2-0,3 mm long, rarely up to 0,4 mm. Their breadth is 0,15-0,25 mm. The periancestrular vibracula have 0,5 mm long bristles, the marginal ones up to 1,1 mm long setae.

Old zoaria are approximately hemispherical or a little broader; some are irregularly longish, due to the shape of the enclosed substratum. Many colonies are middle-sized or young. They begin encrusting on generally small, but sometimes also up to 5 mm big substrata. Old worn colonies expose their substratum under the apex. The colonies are neither lobed nor do they produce zoarial buds. Typical basal surfaces are plane and smooth with or without slight traces of radiate striation (Fig. 23, 24). As solid and hollow zoaria occur in *Cupuladria johnsoni* (Busk 1859a, p. 67) (see Silén 1942a, p. 7), the hollow colonies with small zooecia whose basal surface is radiate, or rough without radial structure, are difficult to be referred to typical *umbellata* or to var. *conica*. Probably they belong to the latter, because the zooecia are small. These hollow colonies have the same structure of the edge as typical *umbellata*. A single row of vibracula, whose chambers appear as long cylinders on the basal surface, projects over the periphery. All young colonies have this aspect and can be recognized as var. *conica* only when their basal side is filled.

Colonies of *D. umbellata* var. *conica* attain their definitive size much earlier than those of typical *umbellata*. The configuration of the zoarial border which ceases to grow is the same in the typical form and the variety. This definitive border (Fig. 25) is smooth, because kenozooecia (z) are formed between the marginal vibracula. Also the autozooids proximal to these vibracula are closed by a granular cryptocyst which sometimes leaves several opesiules open. There are stages of transition between these closed autozooecia and the functioning autozooids farther inwards, viz. small zooecia with low operculum, evidently restricted by the growing cryptocyst. Smooth and shining chitinous bulges (ei) overlie the closed autozooecia of the marginal zone as distal caps; they correspond to the chitinous thickenings which surround the opercular region of typical autozooecia in *umbellata* and var. *conica*. The margin of *umbellata* and its var. *conica* is similar to the basal surface ("face supérieure" in Duvergier's terminology, 1924, p. 19) of *Discoporella peyroti* (Duvergier 1921, p. 2; description: 1924, l. c.), where vibracula between porous cryptocysts are developed. As the definitive edge also the older regions of the colonies agree in *umbellata* and in var. *conica*. The ancestrula and the periancestrular autozooids are closed by secondary calcification, but the vibracula of the centre have their setae and are evidently still functioning.

MAMILLOPORA CUPULA

Geographic distribution: Northern coast of Brazil, off mouths of River Amazon (localities 7 and 7a of the present material). Caribbean Sea, Margarita, Tortuga, Aruba Islands, Gulf of Maracaibo, and Cape de la Vela, eastern Colombia (Osburn 1947, p. 46). Gulf of Mexico, W off Florida, Straits of Florida (Canu & Bassler 1928b, p. 155), Florida (Smitt 1873, p. 33). American Pacific coasts: Gulf of California, Angel de la Guarda Island (about Lat. 29° N); W coast of Lower California, Mexico, Costa Rica, and Panama (Osburn 1952, p. 518); Gorgona Island, Colombia (Hastings 1930, p. 733); Galapagos Islands (Canu & Bassler 1930, p. 45; Osburn 1952), to Lat. 1° 17' S, Long. 90° 30' W.

In depths from 18 to 130 m; first fossil findings in the Lower Miocene. As Osburn (l. c.) informed that the species is abundant in the Gulf of California and about the Galapagos, Canu & Bassler's opinion (1930, p. 46) that it has degenerated in the Pacific since the formation of the Isthmus of Panama cannot be maintained.

Our material, 6 dead colonies, up to 1 mm in height, and 2 mm in diameter, does not allow for additions to the good descriptions of Smitt (1873, p. 33) and Hastings (1930, p. 733). But the literature concerning *M. cupula* requires some comments. The occurrence of avicularia on the basal surface seems to have caused Osburn's idea (1947, p. 66) that "the colony may have some small capacity for movement by means of the avicularia or vibracularia". There are no vibracula, and that the short, semicircular avicularian mandibles of the basal side should produce a locomotory effect by opening and closing is not easy to conceive. Still less probable is that living colonies float with the top of the cone touching the surface and "at their pleasure rise or descend" (Canu & Bassler 1928b, p. 153, 155). The experience with a dry colony plunged into water is not convincing. "The larva is not fixed then, but it is transformed into a swimming larva (misprint for colony)". Canu & Bassler continue calling this transformation "a very curious phenomenon", but we must state that it is a mere supposition and moreover a quite improbable one.

Canu & Bassler (1928b, p. 155) did not find substrata in their sections, and such are absent also in the typical material (Silén 1947, p 6). Evidently the ancestrula is only loosely fixed to the substratum (ibid., p. 29) and detaches from it when the colony grows. The zoaria of *Mamillopora cupula* lie on the bottom as do those of *Cupuladria canariensis and Discoporella umbellata*.

The Suborder Hexapogona Canu & Bassler (1927, p. 9, 22) criticized by Harmer (1931, p. 159-162) is now abandoned (Harmer 1957, p. 854, 887), also in North American papers (Osburn 1952, p. 517; Bassler 1953, p. 327). The Mamilloporidae are a Family of the Ascophora Vera (Harmer 1957, p. 645).

RESUMO

Há Briozoos de várias famílias dos Cheilostomata cujas larvas se fixam em grãos de areia, Foraminíferos ou outros substratos pequenos. As colônias assim originadas crescem em forma de disco, cone ou cúpula ao redor do ponto de fixação, e deitam-se sôbre fundo arenoso ou lodoso. Quatro espécies com tais colônias, chamadas de lunulitiformes, foram obtidas do litoral brasileiro entre 26° 19' S e 2° 58' N, em profundidades de 3-150 m. Estudamos, principalmente, *Discoporella umbellata* (Defr.) da Enseada do Flamengo, 14 km. oeste de Ubatuba. A cêrca de 4 m. de profundidade, em certa região de areia fina e lodosa desta baía, ocorrem 2-3.000 colônias de *D. umbellata* por m². Durante o ano inteiro reproduzem-se vegetativamente, por brotamento colonial. Colônias originadas da larva metamorfoseada encontramos sòmente em material de maiores profundidades.

A agitação irregular do mar raso parece ser desfavorável à fixação das larvas de *D. umbellata*. No brotamento, até 15 botões ligados cada um à colônia-mãe por um único zoécio projetam-se no bordo da colônia (Fig. 13). Separam-se com tamanho muito diferente, sendo 10-30 autozoécios e outras tantas vibráculas o número comum de botões individualizados. Os autozoécios são ligados entre si por tubos com câmaras especiais na sua base (Fig. 6). Cada autozoécio forma 2 tubos látero-distais direitos e 2 esquerdos para os zoécios correspondentes, e um distal para a vibrácula.

As vibráculas têm músculos abdutores e giradores lisos, adutores transversalmente estriados, órgão sensorial com cílios e gânglio cujo nervo passa ao autozoécio proximal. As cerdas das vibráculas encontram-se, normalmente, abduzidas. Nesta posição as cerdas marginais, projetadas sôbre o bordo (Figs. 13, 14) sustentam a colônia. Estímulos mecânicos provocam adução rápida da cerda cuja volta à posição abduzida se processa lentamente. Na colônia caída, com a superfície frontal para baixo, as cerdas abduzidas das vibráculas encontram-se interpostas entre a areia e a membrana frontal dos indivíduos.

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EXPLANATION OF LETTERS

a — ancestrula.
ac — adductor.
ar — rectum.
au — abductor.
av — vibraculum substituting ancestrula.
b — first buds of ancestrula.
bv — vibraculum substituing one of first buds.
c — second bud of ancestrula.
ca — calcareous wall.
ci — cilia of vibracular polypide.
cu — kenozooecial structure.
cv — vibraculum substituting second bud.
d — third buds of ancestrula.
dv — vibraculum substituting one of third buds.
e — stomach.
ei — chitinous thickening of closed zooecia.
en — tentacles.
ez — endocyst.
f — pseudoancestrula.
g — ganglion.
h — hinge-tooth.
i — cryptocyst.
is — hypostegia.

j — gyrators.
k — chamber of connecting tube.

l — cuticular tubes.
m — frontal membrane.
me — connecting tube.
n — basal membrane.
nc — amebocytes.

o — operculum.
oe — opesiule.

q — tentacle sheath of vibraculum.
r — vibracular gland.

re — retractor of polypide.
s — vibracular seta.

si — seta of substitutive vibraculum.
sr — vibracular seta in regeneration.
t — budding polypide.
u — distal connecting tube.
uc — basal cuticle of pseudoancestrula.
v — vibraculum.
ve — vestibulum.
w — proximal connecting tube.
x — frontal plate.
y — destroyed autozooecium.
z — kenozooecium.

PLATES

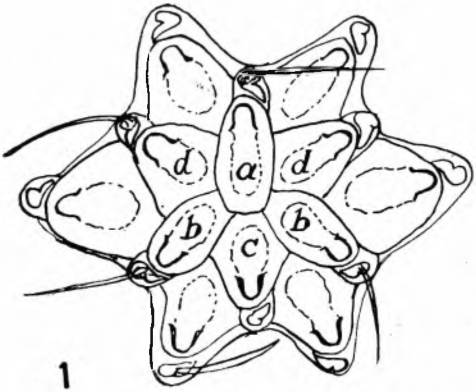
PLATE 1

Fig. 1 — Young colony of *Cupuladria canariensis*.

Fig. 2 — Centre of older colony of *Cupuladria canariensis* with substitution of autozooecia by vibracula.

Fig. 3 — Basal surface of big colony of *Cupuladria canariensis* regenerated from a fragment.

Fig. 4 — Formation of cryptocyst in *Discoporella umbellata*, calcined.



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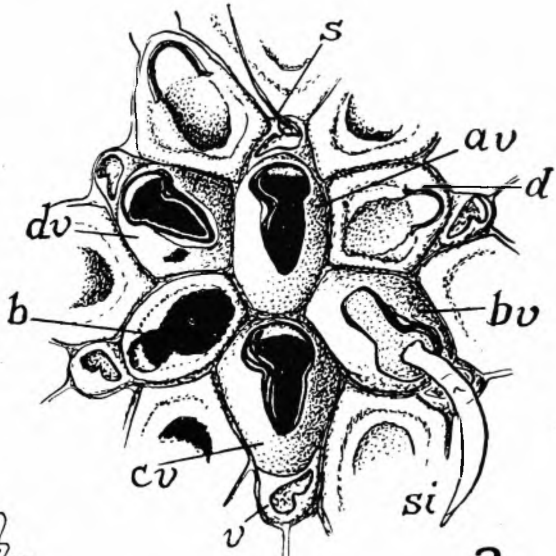

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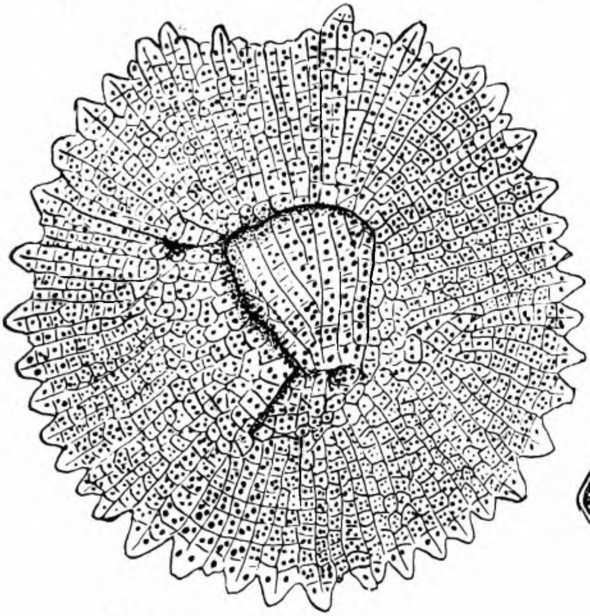

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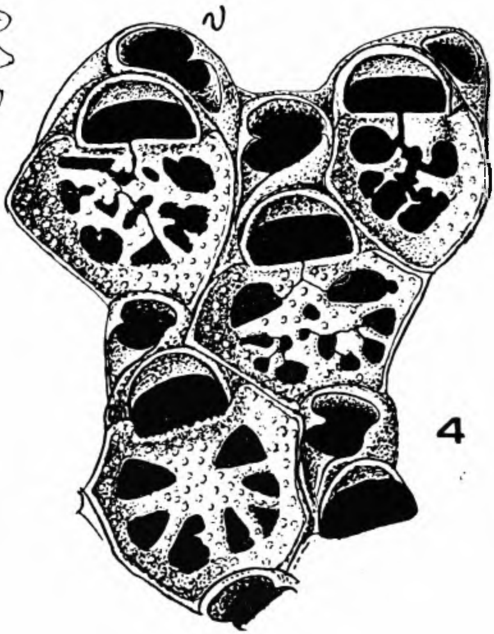

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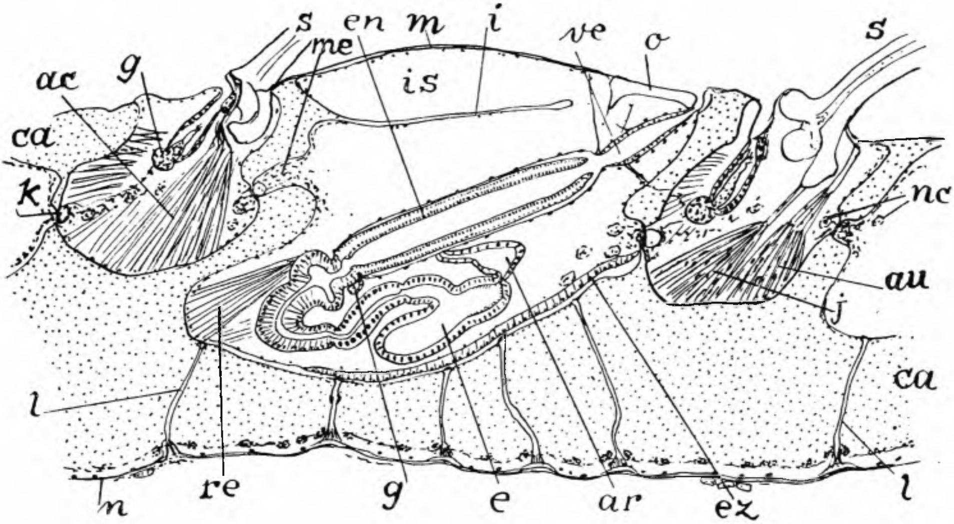
PLATE 2

Fig. 5 — *Discoporella umbellata,* combined sagittal section of autozooecium and two vibracula.

Fig. 6 — Connective tube with chamber of *D. umbellata.*

Fig. 7 — Total regeneration in *D. umbellata.*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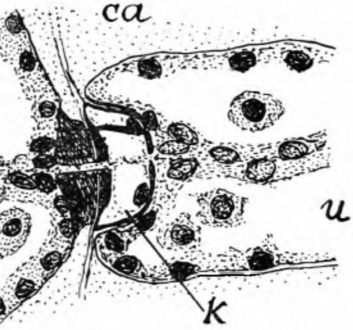
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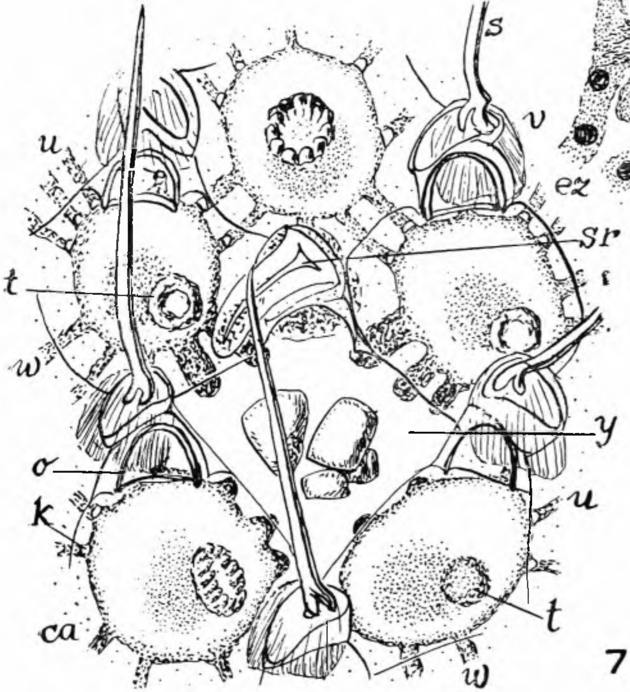
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PLATE 3

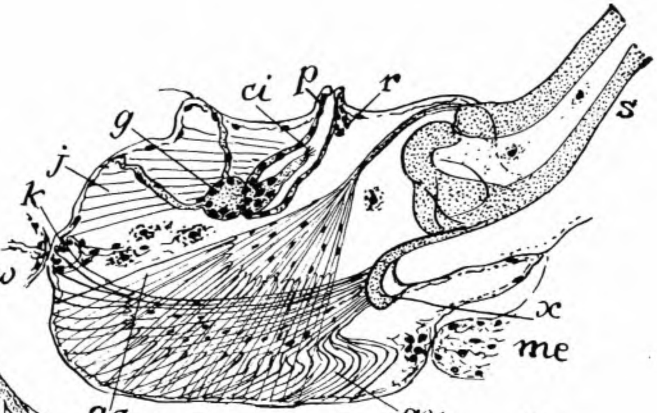
Fig. 8 — Vibraculum of *Discoporella umbellata,* decalcified and clarified; abductor omitted.

Fig. 9 — Combined sagittal section of open vibraculum of *D. umbellata*.

Fig. 10 — Same of closed vibraculum.

Fig. 11 — Six-rayed centre of colony of *D. umbellata* with closed autozooecia.

Fig. 12 — Eight-rayed centre of colony of *D. umbellata* var. *conica.*



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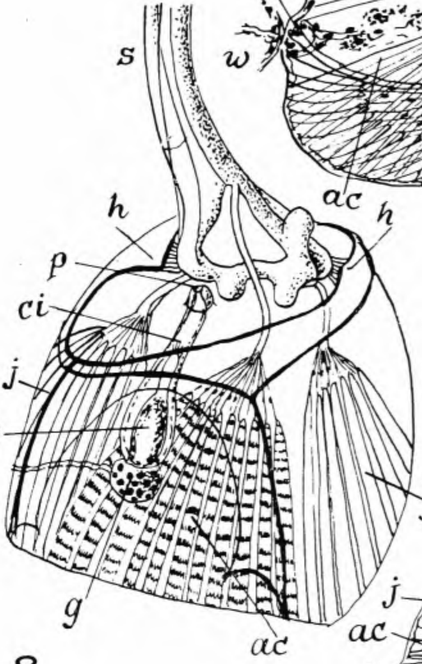

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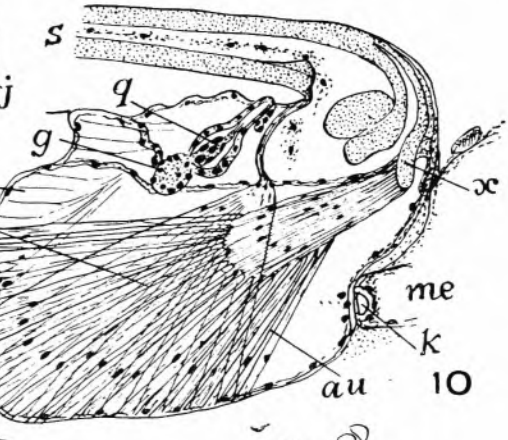

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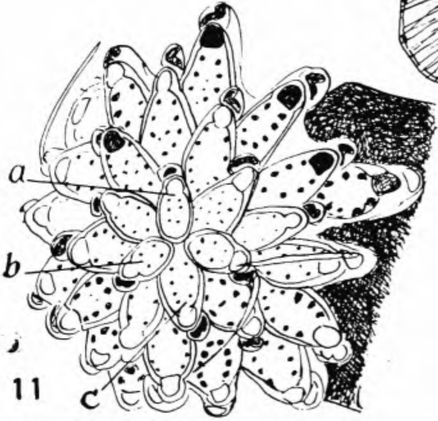

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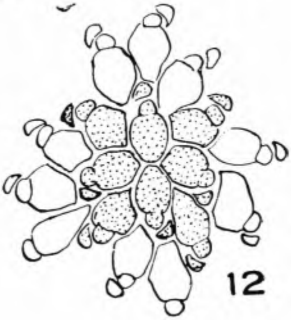

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PLATE 4

Fig. 13 — Budding colony of *Discoporella umbellata,* frontal view; buds stippled.

Fig. 14 — Basal view of same; buds not stippled.

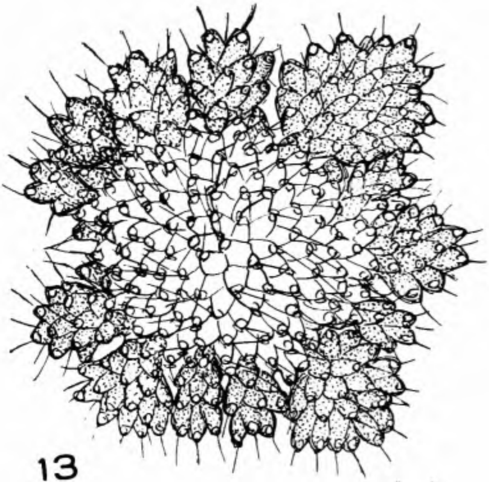
Fig. 15 — Combined sagittal section of incipient zoarial bud of *D. umbellata*.

Fig. 16 — Flabellate colony of *D. umbellata* arisen from bud.

Fig. 17 — Narrow colony of *D. umbellata* shed recently; pseudo-ancestrula (f) not regulated yet.

Fig. 18 — Budded colony of *D. umbellata,* regulated.

Fig. 19 — Basal surface of young budded colony of *D. umbellata.*



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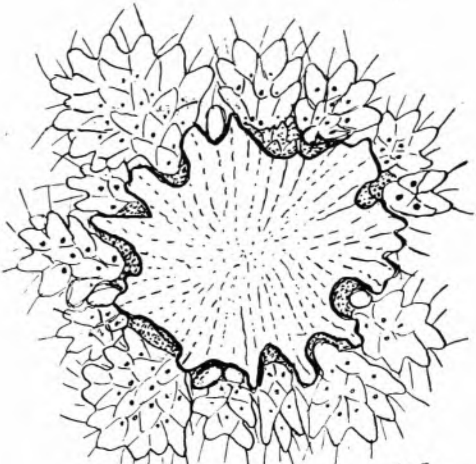

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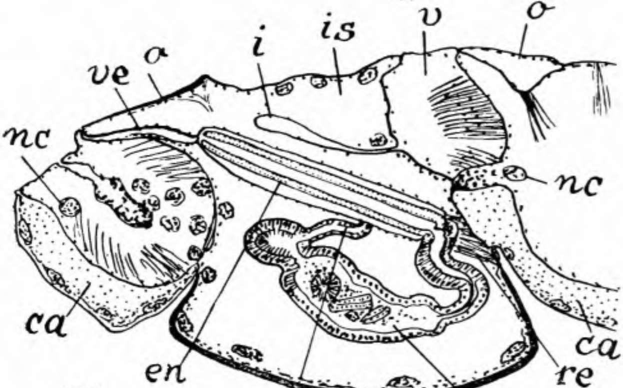

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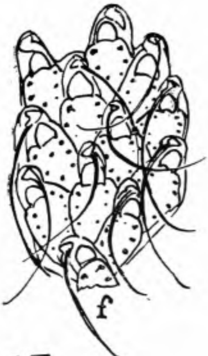

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PLATE 5

Fig. 20 — Budded colony of *Discoporella umbellata* not completely regulated and producing buds. Stippled part magnified in Fig. 21.

Fig. 21 — Gap of Fig. 20, bordered by kenozooecial structure (cu).

Fig. 22 — Fragment of *D. umbellata* with proximal and latero-proximal regulative zooidal buds; the dashed line indicates the break.

Fig. 23 — Concave basal surface of *D. umbellata* var. *conica*.

Fig. 24 — Plane basal surface of *D. umbellata* var. *conica*.

Fig. 25 — Definitive border of old colony of *D. umbellata* var. *conica*.

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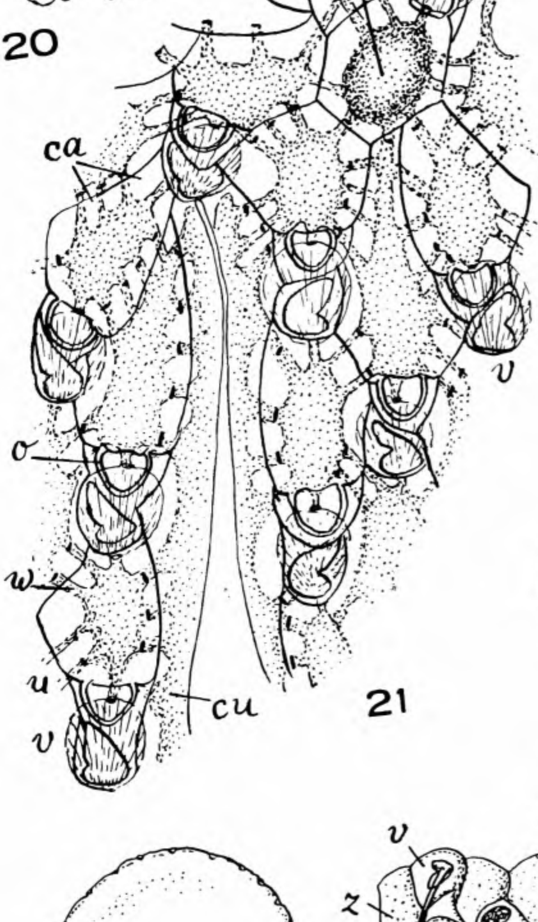

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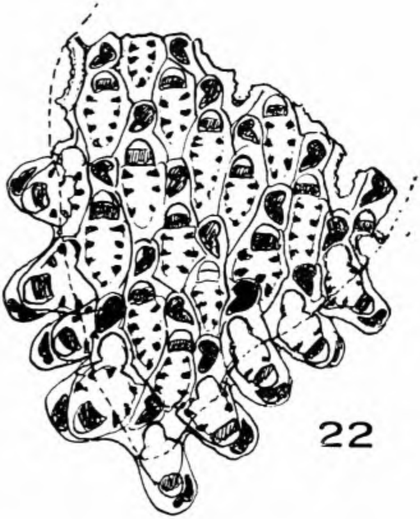

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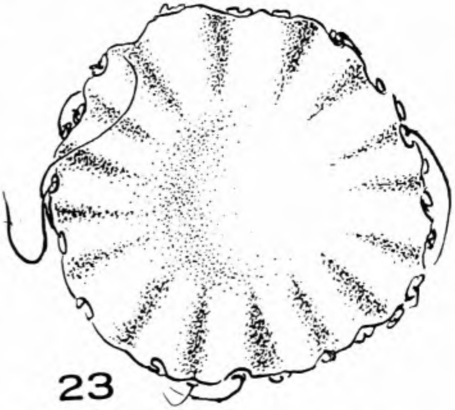

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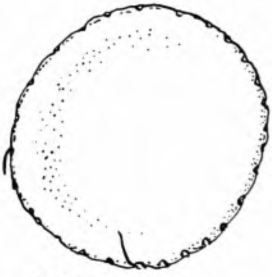

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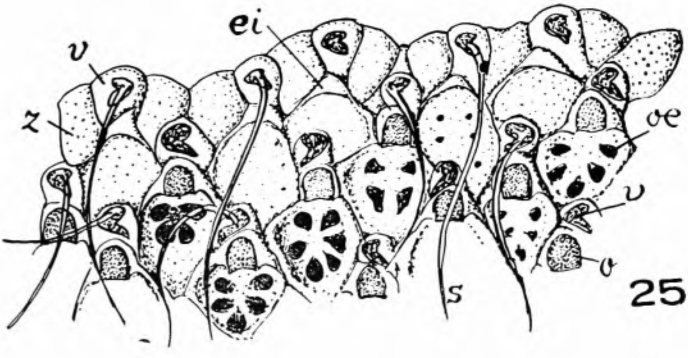

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